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DAILY GROWTH INCREMENTS IN OTOLITHS FROM LARVAL AND ADULT FISHES

EDWARD B. BROTHERS,[1] CHRISTOPHER P. MATHEWS,[2] AND REUBEN LASKER[3]

ABSTRACT

Daily growth increments have been found in otoliths of fish larvae. The daily nature of these layers was verified by examining larval fish of known age reared in the laboratory. A simple technique for observing these marks is described and can be used on otoliths from larvae and adults. This provides a convenient method for determining early growth in fishes and is particularly useful for fishes which do not lay down annual or seasonal rings.

The use of otoliths in age determination (by means of annual marks) is well known. The techniques used have been described by Williams and Bedford (1974) and Blacker (1974). Recently Pannella (1971) has suggested that daily marks may be formed in the sagittae (the otoliths used almost universally in age determinations) of some temperate species, while in 1974 Pannella claimed to have detected them in a number of tropical species. He also studied the temperate species—silver hake, *Merluccius bilinearis*; red hake, *Urophycis chuss*; Atlantic cod, *Gadus morhua*; and winter flounder, *Pseudopleuronectes americanus*—in greater detail in this latter paper. For some of these temperate species, particularly for the first, Pannella was able to show that there were fortnightly, monthly, and annual patterns. The annual marks detected in the conventional way were shown to contain about 365 daily units. Pannella used acetate replicas of ground otoliths which had been previously etched with HCl. Pannella's work appears to justify the following conclusions:

1. Daily increments[4] occur in certain temperate fish, e.g., *M. bilinearis*.
2. Periodic variations in increment thickness occur with fortnightly, monthly, and annual frequencies in this species.
3. Structural units that are similar to those shown to be daily in their occurrence in temperate species are also found in some tropical species.

Pannella (1974) was careful to explain that the marks present in otoliths of tropical fish that appeared to be annual on the basis of conventional criteria could be deceptive. He suggested that by analogy with temperate species, certain structures found in otoliths of tropical fish were also daily in occurrence. Although he found spawning marks, he did not find any seasonal or winter growth checks in the otoliths of tropical fish. In view of Pannella's expressed skepticism about the formation of annual marks and his tentative conclusions, further evidence is needed that daily increments occur in tropical fish. Furthermore, no one appears so far to have attempted to apply this method of age determination to larval fish, yet it is in this last area that the most accurate and useful results might be expected. Pannella (1974) commented on the great regularity of the presumably daily marks near the center of the otoliths of both tropical and temperate fish. In these portions of the otoliths, no superposition of more complex patterns (e.g., 14 day, 28 day) were found.

It is the object of this paper to show that 1) true daily increments are found in the otoliths of the larvae of several species, and that daily marks may be used to determine the ages of larval fish with great accuracy and precision, at least for approximately the first 100 days of life; and 2) in adults of fish from a variety of habitats, including tropical waters, daily increments may be proven to exist, and so to confirm Pannella's work.

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[4]The smallest visible concentric layers seen in an otolith.

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METHODS

Some material was examined with a Stereoscan[5] S4 scanning electron microscope (Cambridge Scientific Instruments Ltd.). These otoliths were prepared for viewing by embedding them in polyester resin, grinding and polishing them to the vertical mid-sagittal plane with a graded series of silicon carbide or aluminum oxide compounds (400, 600, and 900 grit), and finishing with 1-μm diamond paste. The polished surface was then etched with 0.1 N HCl before being rotary coated in a vacuum evaporator with 150 Å of gold-palladium alloy.

Both this technique and that of Pannella (1974) involve the use of equipment and materials that may be inaccessible in many countries. This is particularly true for those countries in which daily growth increments might prove to be especially helpful in stock assessment of commercial fish, so that an alternative practical method with minimal equipment was also used here and found to be successful.

Otoliths of adult fish were ground by hand on a glass plate covered with a water-silicon carbide powder mixture (400-600 grit). The final polish may be administered with diamond paste, but this step is not essential. The ground otolith was then examined in immersion oil. The grinding was done in the same plane as described by Pannella (1974). It is possible that storage in oil over a long period of time may reduce the resolution obtained when an otolith is examined. This appears to be particularly true for larval otoliths. The above technique is simple and requires only a good compound microscope. Magnifications used in this work ranged to 1,800×; at least 600× is required for general viewing.

Otoliths from larvae were removed by teasing them from fresh specimens. Oven-dried material needed only to be moistened with a drop of water before otolith removal. The otoliths were manipulated and transferred to clean slides by picking them up on the end of a fine dissecting needle wetted with immersion oil. No additional preparation was necessary, and the otoliths were examined in immersion oil or after being permanently mounted under a cover slip in a quick-drying, neutral mounting medium. Ground sections from juveniles and adults may be similarly mounted with no apparent loss in clarity. Larval otoliths are thin enough that only optical sectioning (i.e., carefully focusing to the plane of maximum clarity) is necessary to make total increment counts.

Material from a variety of species was examined and larval material of known age was obtained by rearing eggs that had been fertilized in the laboratory (Lasker et al. 1970; Leong 1971). The chronological age from these fish was known and could be compared with the number of growth increments observed in their otoliths. Larvae of northern anchovy, *Engraulis mordax*, were kindly made available to us by John R. Hunter of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, at La Jolla, Calif.

RESULTS

Otoliths of 15 *E. mordax*, aged 6 days, were examined. The mean total length of the fish was 4.5 mm. The yolk-sac had been absorbed by the fifth day after hatching. Figure 1a shows the appearance of the otolith of one of these fish.

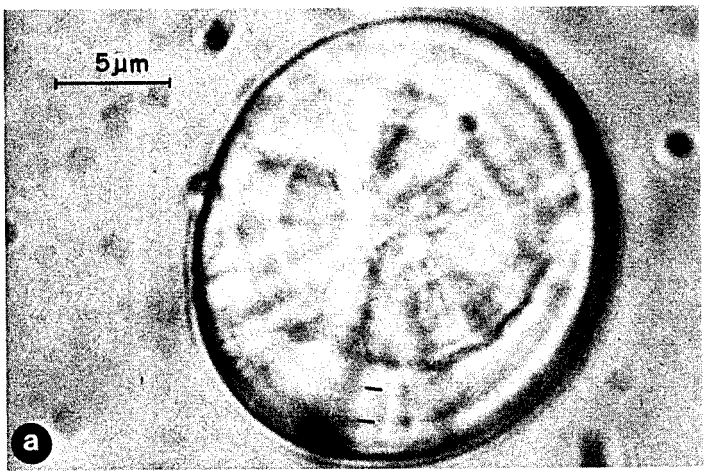
Only one or two daily increments were present, suggesting that daily growth increments appeared in the otoliths of *E. mordax* only after completion of yolk-sac absorption. In the laboratory, anchovy larvae were maintained in 14 h of light when feeding took place and 10 h of darkness when no feeding occurred (Lasker et al. 1970).

Table 1 shows the relation between chronological age and number of apparently daily increments for larvae of *E. mordax* aged 6 to 100 days. It is clear that there is an extremely close correspondence between the chronological age in days and the number of increments. Figure 1b is a micrograph showing the daily increments in an anchovy otolith from a larva 18 days old.

Additional data presently being collected on laboratory and wild-caught larvae indicates that there is some interaction between the rate of larval growth and the rate of increment formation which may complicate the interpretation of otolith age estimates.

Figure 2 shows the structure of adult anchovy otoliths with successively greater magnification of the scanning electron microscope. The darker areas in the photographs represent areas of the otolith that were more heavily etched because they contained a higher proportion of $CaCO_3$, while the lighter areas have relatively more organic material, probably otolin (see Degens et al. 1969). It is seen from Figure 2 that the smallest

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.



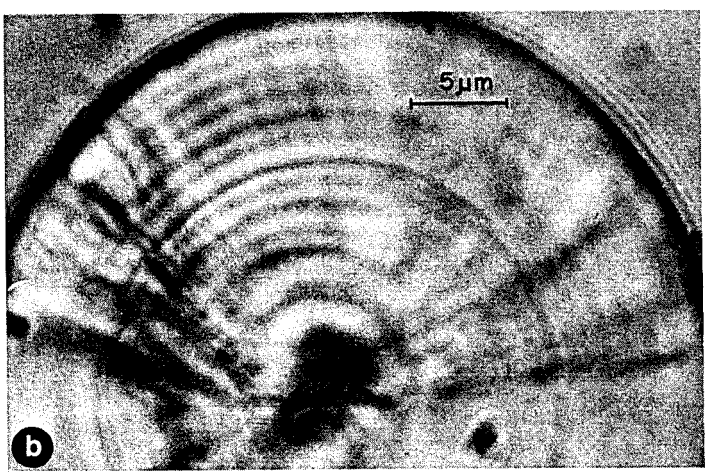


FIGURE 1.—Light microscope photographs of otoliths from laboratory-reared northern anchovy: a) 8-day-old larval otolith showing two daily growth rings; b) 18-day-old larval otolith showing 12 daily growth rings.

TABLE 1.—Chronological age (days from hatching) and numbers of growth increments in otoliths of northern anchovy.

Number of fish	Chronological age in days	Chronological age less 5 days	Mean number of increments	Range
15	6	1	1	0- 2
10	8	3	3	2- 4
10	12	7	7	4- 8
10	15	10	10	8- 11
7	16	11	10	9- 11
5	18	13	13	12- 15
7	20	15	15	14- 16
8	24	19	18	16- 19
9	25	20	20	18- 21
3	26	21	21	18- 23
4	94	89	97	95-100

cyclical units are 1 to 2 μm thick in this part of the anchovy otolith and that they do not appear to contain any smaller units. It is these units that are counted and appear in the data in Table 1. The daily increment would therefore appear to be the smallest unit of growth that is formed at the supra-molecular level and, as such, is in principle the most natural unit to use for age estimation.

Fertilized eggs of the California grunion, *Leuresthes tenuis*, were obtained and reared in the laboratory. The larvae were maintained in a natural light cycle at 17° to 20°C with food (*Artemia* nauplii) continuously available. Larvae were sacrificed at intervals and their otoliths were examined. Table 2 shows the results obtained and Figure 3 shows a photograph of a grunion otolith.

Table 2 shows that there is a close relation between the number of growth increments and the chronological age of the larvae. Although the agreement between age and daily increments is not as good as it is for the anchovy, the results are still very good. Table 2 also shows that in *L. tenuis*, daily increments appear at hatching, rather than at yolk absorption. Prehatching marks also occur, although they were not tallied in Table 2. Clearly the exact timing of the initiation of daily increment formation varies from

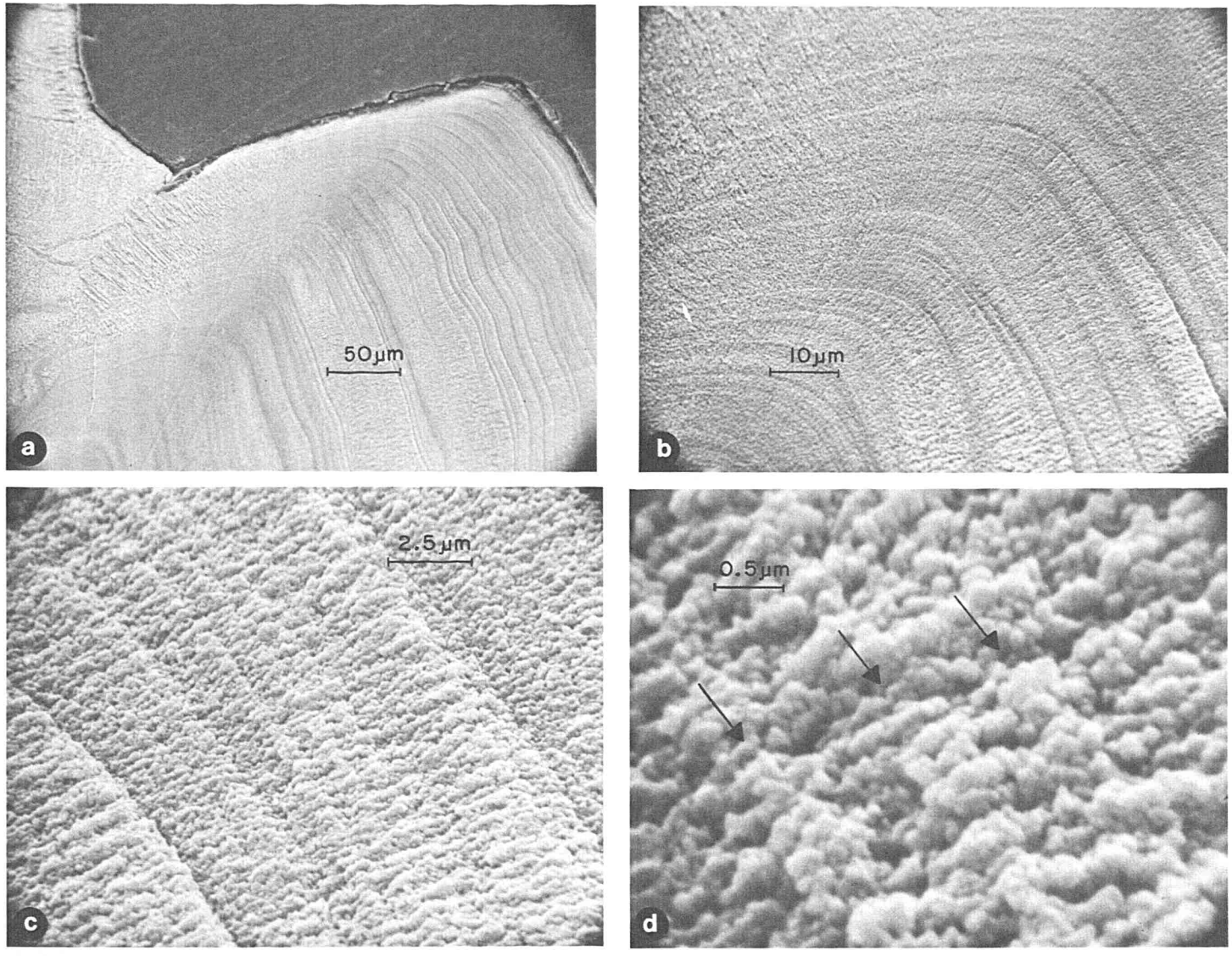


FIGURE 2.—Scanning electron microscope photographs of an otolith from a 2-yr-old northern anchovy. Successively higher magnifications are shown in a through d. At highest magnification, the distance between daily marks (indicated by arrows) is shown to be between 1 and 2 μm.

TABLE 2.—Chronological age and number of growth increments in the otoliths of the California grunion.

Number of fish	Chronological age in days	Mean number of increments	Range
2	0	2	1- 2
3	7	9	8-10
2	16	11	10-12
3	18	17	16-18
5	26	24	20-26

species to species and must be independently determined for each one.

Young striped bass, *Morone saxatilis*, were collected on 2 July 1974 in the Sacramento River delta (Tracy Pumping Station), Calif. These five fish measured 29 to 37 mm SL (standard length) and their otoliths had 62 to 120 observable increments; i.e., a sample of striped bass which should have been 2 to 4 mo old according to their known spawning season (Scofield 1931) were 2 to 4 mo old according to the presence of growth layers found in their otoliths. The spread in the age calculated from daily increments probably corresponds to a considerable spread in the dates when the fish examined were hatched.

Otoliths from two striped bass 135 and 142 mm SL were also examined. Published information on the growth rate of this species (Scofield 1931) indicates that striped bass of this size taken in July should be 14 to 16 mo old. The ages obtained by counting the presumed daily growth marks were 419 and 445 days respectively, i.e., 14 to 15 mo old.

Figure 4 shows the daily marks in an otolith of striped bass. Daily increments were fairly thick near the center, thinner in an intermediate area corresponding to the hyaline zone, and wider again near the edge. In one specimen the central

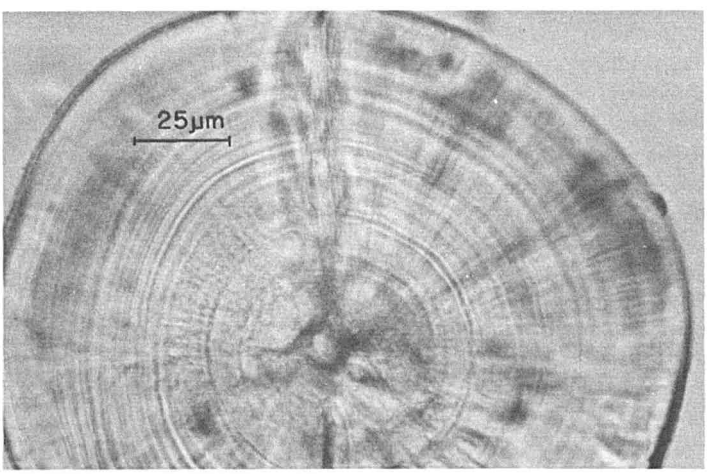


FIGURE 3.—Daily growth rings in an otolith of a California grunion larva. The larva was approximately 26 days old.

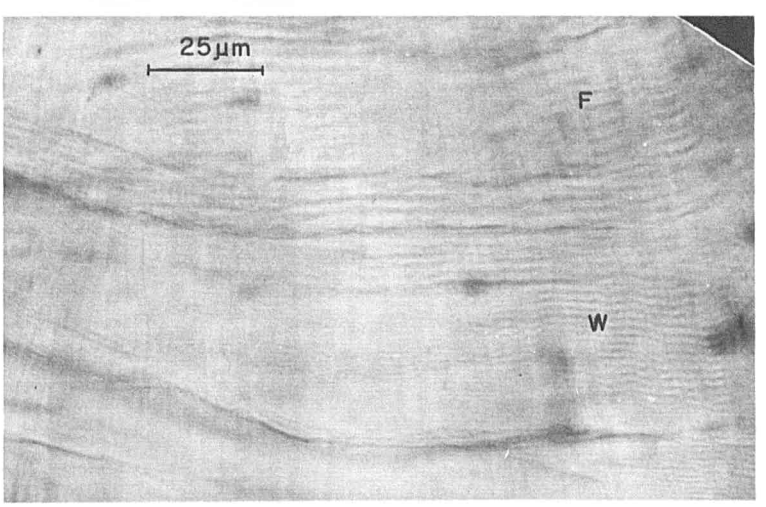
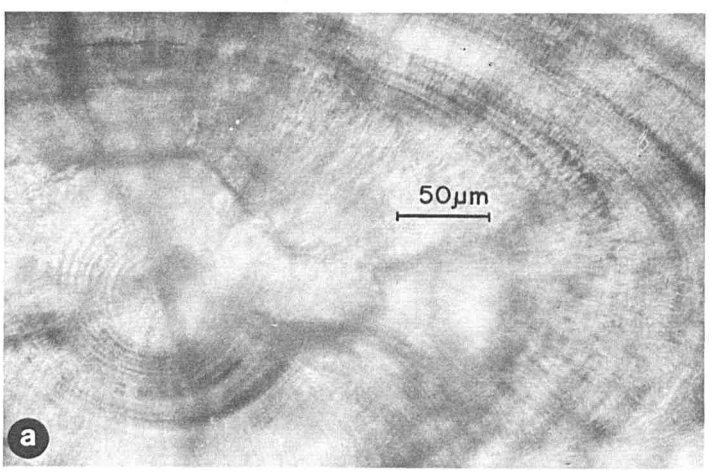


FIGURE 4.—Daily growth rings in a striped bass otolith. This fish was approximately 15 mo old. Differential growth can be seen in rings grown in adjacent seasons. F = fall; W = winter.

area contained 231 daily increments, the marginal area contained 120, and there were 94 thinner marks in the middle zone. Working backwards from the 2 July collection date, this indicated the slow growth zone occurred in December, January, and February. These figures correspond well with the known life cycle (Scofield 1931) which suggests a fast growth period in spring, summer, and fall (230 days, ≈ 8 mo), a short winter of slow growth (≈ 3 mo), and a spring and early summer (≈ 4 mo) of faster growth prior to capture.

Otoliths of postlarvae of the gobies *Clevelandia ios, Ilypnus gilberti*, and *Quietula y-cauda* were also examined. The fish were collected in Mission Bay, San Diego. The 2-mo larval period indicated in the otoliths agree with several independent estimates of the length of time between hatching and settlement (Brothers 1975).

Otoliths of two species of hake obtained from the Gulf of California were studied. Mathews (1975) has shown that annual marks (annuli) may be detected by means of the usual discrimination of hyaline and opaque zones in *Merluccius angustimanus* while in *Merluccius* sp. (Mathews in press) the same techniques have also been applied successfully. The ages of hake determined by means of annuli may be compared with age determined from counting the number of daily increments; these are identified by analogy with the structures shown to be daily in their incidence in anchovy, grunion, striped bass, and other fish and which appear to be the same as those shown by Pannella (1971) to be daily in *M. bilinearis* (Figures 5, 6). In most cases, direct total counts were not possible because increments were not equally visible over a complete nucleus to margin radius. For these otoliths measurements of incre-



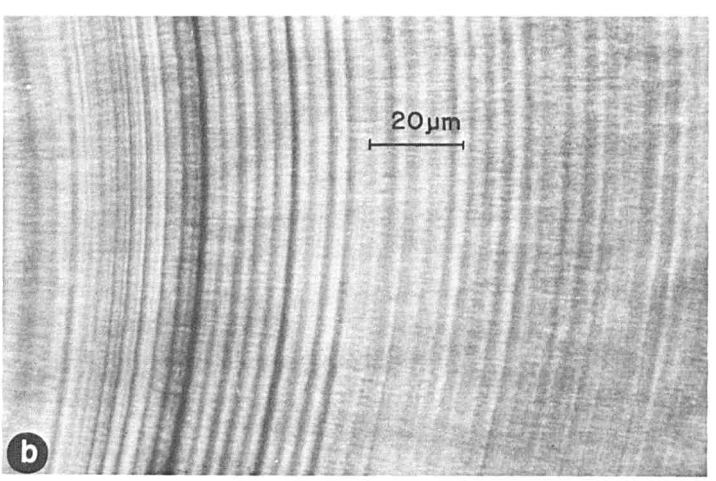


FIGURE 5.— a) Nucleus of an otolith from a *Merluccius* sp., 7 yr old; b) daily growth increments shown from near the center of the otolith.

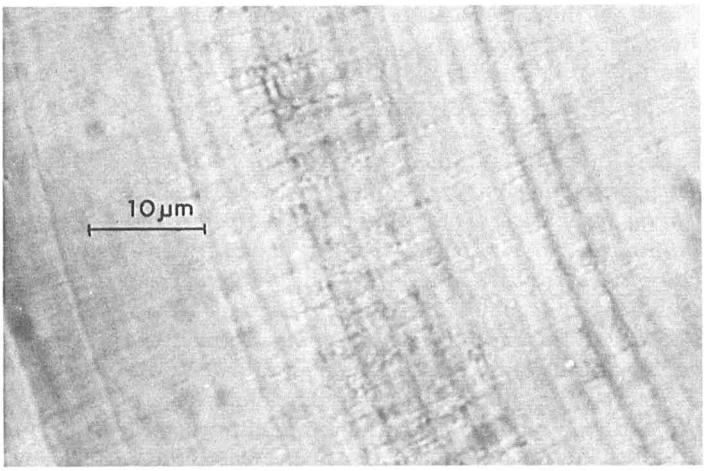


FIGURE 6.—Daily growth increments from the otolith of *Merluccius angustimanus*. Note radial fibers crossing the growth layers.

ment width were made at five or more locations along a radius and then total counts were calculated by extrapolation. No larval or very young hake were available for examination.

For *Merluccius* sp., data were available for 22 specimens aged 1 to 7 yr from the annuli present in their otoliths. Figure 7 shows the graph of age by annuli against age by daily increments for this species. The correlation coefficient was 0.91 (20 df, $P >> 0.001$). The slope of the regression line was 1.14 (99% confidence limits [C.L.], 0.81-1.46). This is not significantly different from the value of 1.00 expected if age by years and by days were to yield identical values.

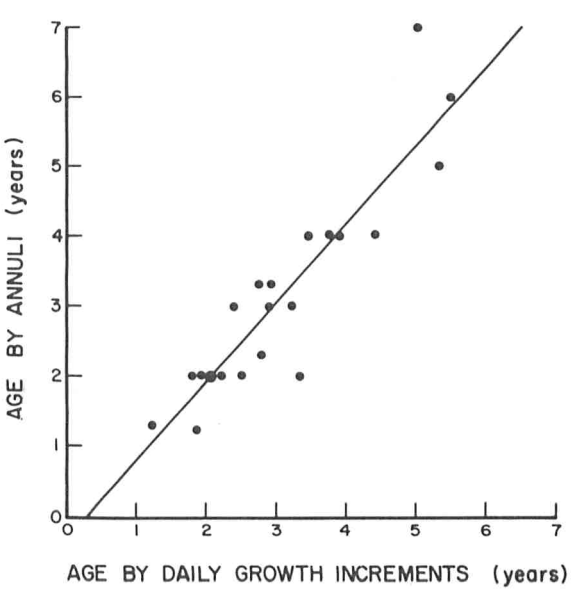


FIGURE 7.—Graph of age-by-annuli against age-by-daily-growth-rings in the otoliths of *Merluccius* sp. The encircled point represents two points at the same position.

Data from seven specimens of *M. angustimanus* were available and they varied in age from only 1 to 2 yr. Given the much narrower ranges and the smaller sample, the results obtained were acceptable: $r = 0.74$ ($0.05 > P > 0.01$) and the slope of the line was 1.25 (99% C.L., 0.24-2.25); i.e., the slope was significantly different from zero, but not from 1.0.

The precision of estimates of age obtained for *M. angustimanus* was not very good, with deviations of up to 0.5 yr being obtained; however, for *Merluccius* sp. a somewhat narrower range was usual, with some values differing by 0.1 yr or less. Extreme variations occurred with fish aged 7 to 13 yr, where errors of up to 2 to 3 yr could be obtained where daily counts were made.

The average widths of the daily bands found in the hake otoliths were 3 to 4 μm, with wider and narrower bands appearing sometimes in apparently weekly, fortnightly, and monthly units. The incidence of these units has not been examined in detail and requires further study, but preliminary work suggests that the basic unit used in age estimates should be the daily unit; the higher order units may be of great ecological interest, but should probably not be used in aging these hake: Only daily increments occur with the necessary consistency and regularity.

In addition to the species mentioned above, apparently daily marks have been found in a wide variety of other fish, e.g., in *Tilapia zilli, T. nilotica*, and *Clarias mossambicus* from Lake Victoria (examined by E. B. B. and C. P. M.; specimens kindly collected by John Rinne and Dr.

Peretti of the East African Freshwater Fisheries Research Organization, Jinja, East Africa), and the following species examined by one of the authors (E.B.B.): in the deep living Pacific rattail *Coryphaenoides acrolepis* (58 cm SL; 10 to 11 yr); in the myctophids *Stenobrachius leucopsarus, Tarletonbeania crenularis,* and *Triphoturus mexicanus*; in the freshwater fish *Cottus asper* and *Salmo gairdneri*; in the tropical marine fish *Chromis atrilobata* and *Apogon retrosella*; in adults of the gobies *Clevelandia ios* and *Gillichthys mirabilis*, where clear growth checks also occur, so that daily marks alone would lead to distinct underestimates of age; and in four species of rapidly growing tropical and temperate tunas. Statoliths from the squid *Loligo opalescens* (both wild caught adults and laboratory-reared juveniles) also show what appear to be growth layers analogous to those in fish otoliths. The appearance of growth interruptions in a number of species, e.g., the rockfish (genus *Sebastes*), either as winter checks, spawning checks, or apparently dispersed more evenly throughout the year, may impose a severe limitation upon the use of daily marks to age these fish. The technique seems best suited to larvae, juveniles, fast-growing species, and tropical species.

It is clear from our work that some difficulties must be overcome before age estimation by means of daily rings can become a standard tool in fisheries biology. However, it is also clear that

1. Daily rings may be used to estimate the ages of larvae of some species up to 100 days old with very great precision and that they probably can be used for fish up to 1 yr of age, perhaps with a smaller degree of precision. Struhsaker and Uchiyama (1976) show similar results with the tropical engraulid *Stolephorus purpureus*.

2. Daily marks may be used as a means of accurate age determination for at least some species of fish up to 6 yr old.

3. Daily marks may be used for age determination of at least some tropical fish. Pannella's (1974) suggestion that daily increments might be used in tropical fish as a means of age estimation is almost certainly true, and should be applicable to most species.

LITERATURE CITED

BLACKER, R. W.
1974. Recent advances in otolith studies. *In* F. R. Harden Jones (editor), Sea fisheries research, p. 67-90. John Wiley and Sons, N.Y.

BROTHERS, E. B.
1975. Comparative ecology and behavior of three sympatric California gobies. Ph.D. Thesis, Univ. California, San Diego, 370 p.

DEGENS, E. T., W. G. DEUSER, AND R. L. HAEDRICH.
1969. Molecular structure and composition of fish otoliths. Mar. Biol. (Berl.) 2:105-113.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MATHEWS, C. P.
1975. Some observations on the ecology and the population dynamics of *Merluccius angustimanus* in the south Gulf of California. J. Fish. Biol. 7:83-94.
In press. The biology, ecology and population dynamics of the large Gulf of California hake. Symposium in Fisheries Biology, Ensenada, B.C., Mexico. Ciencas Marinas, Spec. Suppl.

PANNELLA, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.
1974. Otolith growth patterns: An aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (editor), The ageing of fish, p. 28-39. Unwin Brothers, Ltd., Surrey.

SCOFIELD, E. C.
1931. The striped bass of California (Roccus lineatus). Calif. Dep. Fish Game, Fish Bull. 29, 84 p.

STRUHSAKER, P., AND J. H. UCHIYAMA.
1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

WILLIAMS, T., AND B. C. BEDFORD.
1974. The use of otoliths for age determination. *In* T. B. Bagenal (editor), The ageing of fish, p. 114-123. Unwin Brothers, Ltd., Surrey.

AGE AND GROWTH OF THE NEHU, *STOLEPHORUS PURPUREUS* (PISCES: ENGRAULIDAE), FROM THE HAWAIIAN ISLANDS AS INDICATED BY DAILY GROWTH INCREMENTS OF SAGITTAE

PAUL STRUHSAKER AND JAMES H. UCHIYAMA[1]

ABSTRACT

Direct evidence is presented that the sagittae of nehu, *Stolephorus purpureus*, grow by discernible daily increments. Aging by daily growth increments provides the means to establish a general growth curve for the first 6 mo of life for this species. Adult nehu exhibit nearly linear growth between 30 and 60 mm standard length. Preliminary evidence is presented that the nehu population of Pearl Harbor may grow more rapidly than that of Kaneohe Bay.

Attempts to age tropical fishes by conventional methods have generally been thwarted by the absence of well-defined annuli in calcarious structures and protracted spawning periods which make length-frequency mode progression analyses difficult. Recognizing that exceptions to the above statement exist, Pannella's work (1971) providing indirect evidence of the presence of daily growth layers and periodical deposition patterns in the sagittae (otoliths) of three species of boreal fishes from the western North Atlantic suggested a means for conducting age and growth studies of tropical species. He concluded in that report: "Preliminary observation of growth patterns in sagittae of other species, living at various depths and different climates, appears to support the idea that daily growth may be a universal feature of fish otoliths." Pannella's (1974) later work in Puerto Rico provided circumstantial evidence of daily growth layers in sagittae of several species of tropical fishes.

To gain direct evidence that daily growth increments exist in tropical fishes we studied the nehu, *Stolephorus purpureus* Fowler, a small engraulid endemic to the Hawaiian Islands. The nehu is the basis of a live-bait fishery producing about 4,000 metric tons annually of skipjack tuna, *Katsuwonus pelamis* (Linnaeus), from the vicinity of the Hawaiian Islands. *Stolephorus purpureus* is a short-lived species (less than 1 yr) and has been the subject of relatively numerous studies: Nakamura (1970) has summarized the biological knowledge of this species available through 1965. Our work provides evidence of the presence of daily growth increments in the sagittae of nehu and permits the assembly of a growth curve for the first 6 mo of life for this species.

Brothers et al. (1976) have recently demonstrated the presence of daily growth increments in larval *Engraulis mordax* Girard and *Leuresthes tenuis* (Ayres) and presented evidence that the phenomenon occurs in several other species of California fishes.

METHODS AND MATERIALS

The nehu samples were taken with three types of gear in Pearl Harbor and the southeastern end of Kaneohe Bay, Oahu, Hawaiian Islands. Adults and juveniles (> about 30 mm standard length (SL)) were sampled with commercial bait seines (square mesh measuring 3.2 mm to a bar) in Pearl Harbor. Postlarvae (about ≥ 20 mm SL), juveniles, and adults were obtained in Kaneohe Bay by a similar seine having a bar mesh measurement of 1.6 mm. Larvae (< 20 mm SL) were obtained near Coconut Island by personnel of the Hawaii Institute of Marine Biology with 0.5-m ring nets with mesh sizes of 550 μm.

Three separate holding experiments were conducted to test the hypothesis that the sagittae of nehu grow by discernible daily increments. All animals for these experiments were collected in Pearl Harbor and held in tanks of 38-kl capacity at the National Marine Fisheries Service (NMFS) Kewalo Basin Facility. The tanks were supplied with well seawater of 23°-24°C and 33-35‰ salinity at a rate of about 300 liters/min. The nehu

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were fed with frozen and live brine shrimp, *Artemia* sp., under variable regimes as described below. Each experimental population of nehu was sampled during placement in holding tanks, and then subsampled at various time intervals as described for each experiment. Otoliths were extracted from most specimens within a few hours of sampling. The remaining samples were frozen in seawater or preserved in 75% solution of isopropanol until extraction of otoliths (removal of tissue from otoliths of alcohol preserved specimens is difficult).

The first holding experiment was begun 5 April 1972. A 16-day sample (21 April) and a 34-day sample (9 May) were obtained from this population. The animals were fed once a day with frozen and/or live brine shrimp. The second holding experiment was begun 15 December 1972. This population was initially fed once a day. A high mortality was observed during the first 2 wk, after which food was provided twice daily. Samples were collected weekly after 1 mo of captivity. We examined sagittae from animals collected on 19 January and 26 January 1973. The third holding experiment was begun 4 May 1973. This population was fed two or three times daily with frozen brine shrimp. Samples were obtained weekly between 4 May and 6 July. We examined sagittae from animals collected 25 May and 8 June 1973.

Wild populations of larval, juvenile, and adult nehu were sampled 13 times in Kaneohe Bay between 19 March 1972 and 13 July 1973 to obtain estimates of growth rates at various seasons. Although a second species of *Stolephorus* (*S. buccaneeri* Strasburg) occurs in Hawaii, larvae of this species have not yet been collected in the southeastern end of Kaneohe Bay (Watson and Leis 1974; W. Watson pers. commun.).

After extraction, the sagittae were cleaned and etched for up to 3 min in a 1% solution of HCl, then washed and mounted whole on glass slides with the mounting medium Euparal[2] and covered with glass cover slips. Short lengths of monofilament line were used to prevent the contact of the specimen by the cover slide. Although the smallest growth increments are microscopically discernible immediately after extraction their detection was enhanced after about 30 days of clearing in the mounting medium. Sagittae used in the first holding experiment and those collected from Kaneohe Bay and Pearl Harbor during spring 1972 were placed in glycerine on slides and covered. Some erosion of the sagittae edges was noted after about 5 mo, and this practice was discontinued after the first experiment. Slides were either labeled with date of collection and length of fish or assigned a five digit random number for identification.

Our initial counts were taken from thin sections of sagittae taken on the frontal plane. After mounting the sagittae in epoxy resin, the initial plane of polishing was made with rough sandpaper. As the surface approached the desired section, fine wet silicon carbide sandpaper (400 grit) was used. Final polishing of the surface was done with suspensions of aluminum oxide particles having diameters of 15, 5, and 0.3 μm. The section was thinned on the opposite side to a practical thickness and etched in a 1% solution of HCl for variable periods up to 3 min. A few attempts to make acetate peels of the small nehu sagittae sections as described by Pannella (1971) and Pannella and MacClintock (1968) were unsuccessful. We eventually abandoned the sectioning of sagittae because of the time required and the difficulty in obtaining a precise section from the nucleus to the posterior edge of the sagitta.

Sagittae were obtained from larvae less than about 20 mm SL by placing the specimen on a slide and gently teasing the otoliths from the head region. The sagittae were then mounted in Euparal and read immediately. These otoliths tended to clear completely within a few hours, and photographs are the only permanent record of these specimens.

The smallest growth increments of the mounted sagittae were counted with a compound microscope at magnifications of 400-800×. The smallest growth increment in all fish otoliths consists of both an organic and an inorganic layer (Degens et al. 1969). These two layers in the nehu otolith together measure about 1-4 μm thick. A zoom feature of the microscope was found to be extremely useful. Counts were maintained on a hand tally.

Enumeration of the smallest growth increment layers in whole sagittae is tedious, and reliable counts can be obtained only after a moderate amount of experience has been acquired. Enumeration is, obviously, much easier in sagittae from smaller fishes (Figure 1). Usually, readings cannot be made in a direct line from the nucleus to the selected point on the edge of the sagitta;

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

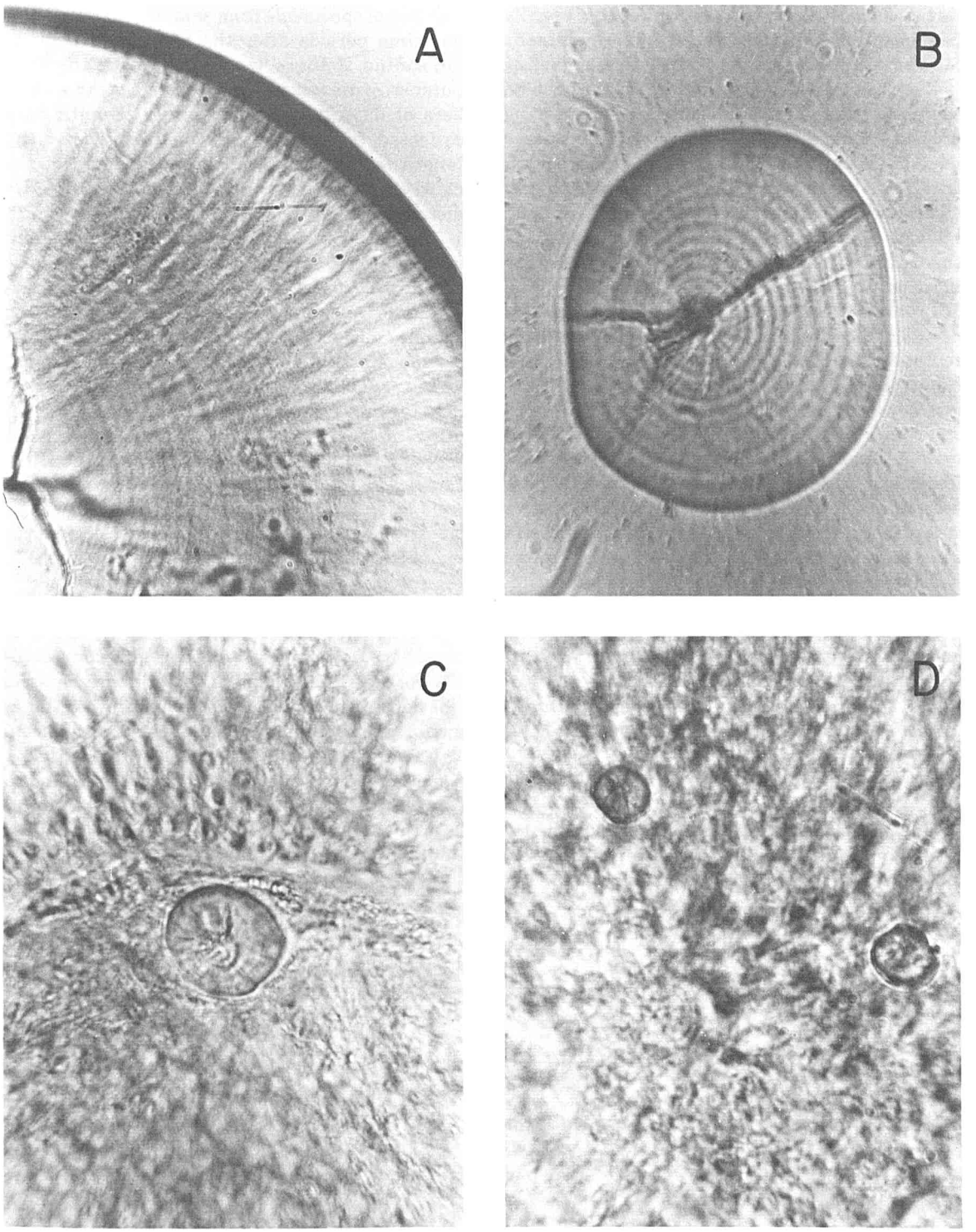

FIGURE 1.—Sagittae of larval *Stolephorus purpureus*. A: Portion of sagitta from a 28.8-mm SL individual with about 65 growth increments. B: 12.6 mm SL, 14 increments. C: 7.3 mm SL, 7 increments. D: 3.9 mm SL, 1 increment.

rather, a somewhat circuitous route must usually be taken from one area of the sagitta to another by following a prominent growth increment.

Each sagitta was counted several times in succession, the number of counts (up to 10) being proportional to the size of the sagitta. Counts were made from the nucleus to the antirostrum, rostrum, and postrostrum (terminology of Messieh 1972). A consistent count for the number of lamellae was then obtained. Verification counts were then made by the same reader at a later time. Verification counts were made by a second reader on 167 otoliths from the second and third holding experiments, as well as randomly selected sagittae representing the wild populations: 26.3% of these counts agreed with the original count; 48.5% differed by less than 1%; 72.5% differed by less than 2%; 86.9% differed by less than 3%; 92.9% differed by less than 4%; and 95.9% differed by less than 5%. Errors of less than 5% were considered acceptable, and the median values of the two readers were then utilized in the analyses. In cases where the results differed by more than 5%, the sagittae were reexamined and either a consensus of opinion reached or the data discarded.

Standard lengths were taken to the nearest 0.01 mm with dial calipers. Sagittae were measured with a micrometer eyepiece.

RESULTS

Holding Experiments

The holding experiments were undertaken as one means to determine if the smallest growth increments observable in the sagittae of nehu represent daily growth increments. We examined sagittae of specimens from samples taken at various time periods after the initial collection to determine if there was an increase in mean number of increments approximating the numbers of days between sampling. (Length data collected from all samples indicate that the length-frequency distributions of most of the captive populations studied were normally distributed.)

The data obtained for each holding experiment were subjected to analysis of covariance and the results are summarized in Table 1 and Figures 2-4. There was homogeneous variance within the samples for each of the three experiments as indicated by Bartlett's test of homogeneity (chi-square values = 0.56, 3.59, and 0.59, respectively).

In the first experiment there were no significant differences between the means of the independent variable (standard length) for each of the three samples at the $P<0.05$ level. There were significant differences between the regression coefficients and the elevation of the regression curves for each sample at the $P<0.01$ level (Table 1, Figure 2).

The significant differences between regression coefficients seems best explained by the effects of captivity. Hypothetically, the regression coefficient of the initial sample of 5 April represents the relationship between number of growth increments and standard length in the wild population. The smaller regression coefficient value of the 21 April sample indicates a slower growth rate of the captive population during the 16-day interval between sampling. This is probably due to less than optimal food supply and/or other effects of captivity. The intermediate regression coefficient value of the 9 May sample indicates that the

TABLE 1.—Summary of analysis of covariance for three holding experiments.

Sampling date	Dependent variable (increments) Unadjusted $\bar{y}$	Adjusted $\bar{y}$	r^2	n	s^2	F ratios: Independent variable (standard length)	Regression coefficient	Elevation
5 Apr. 1972	84.9	86.7	0.77	30	38.2			
21 Apr. 1972	101.1	100.6	0.76	24	10.8			
9 May 1972	118.1	116.4	0.74	24	20.6			
First experiment						1.2	5.4**	206***
19 Jan. 1973	114.8	114.0	0.95	25	14.7			
26 Jan. 1973	120.8	121.6	0.85	24	31.1			
Second experiment						0.1	1.3	31***
25 May 1973	124.9	132.1	0.97	23	13.8			
8 June 1973	140.0	133.4	0.95	24	6.1			
Third experiment						34***	1.1	1.1

**$P \leq 0.01$.
***$P \leq 0.001$.

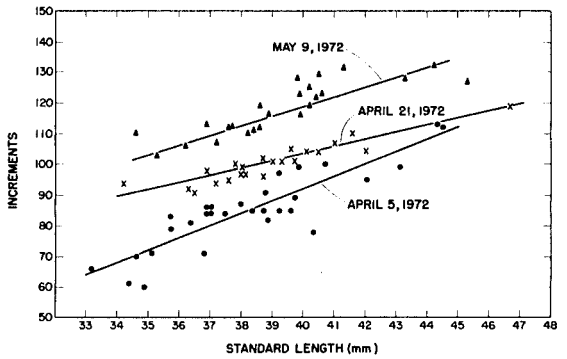

FIGURE 2.—*Stolephorus purpureus*: First holding experiment.

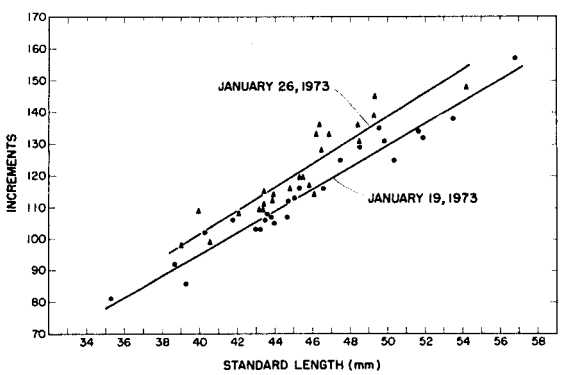

FIGURE 3.—*Stolephorus purpureus*: Second holding experiment.

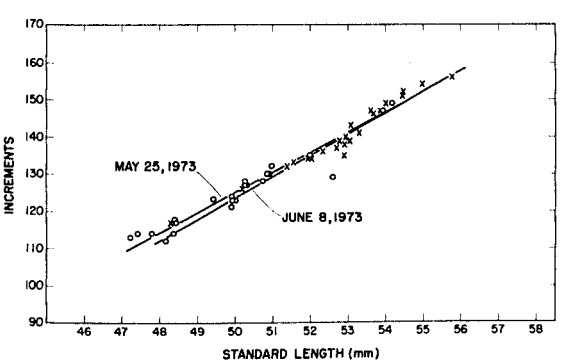

FIGURE 4.—*Stolephorus purpureus*: Third holding experiment.

growth rate has increased in the captive population after 34 days in captivity, but has not reached the value of the wild population from which it was taken.

In the first holding experiment, the second and third samples were collected 16 and 34 days, respectively, after the initial sample. For unadjusted $\bar{y}$ values, these samples differed from the initial sample by 16.2 and 33.2 increments, whereas for the adjusted $\bar{y}$ values, they differed from the initial sample by 13.9 and 29.7 increments (Table 1).

The results of the two samples (collected after more than 30 days in captivity) collected 19 and 26 January 1973, and compared in the second holding experiment, are summarized in Table 1 and Figure 3. There were no significant differences between the means of the independent variables or the regression coefficients at the $P \leq 0.05$ level. The elevations of the two regression curves are significantly different at the $P \leq 0.001$ level. The differences in number of increments between unadjusted $\bar{y}$ values (6.0) and adjusted $\bar{y}$ values (7.6) again closely approximate the expected difference of 7 days between samples.

The results of the samples of 25 May and 8 June 1973 compared from the third holding experiment are given in Table 1 and Figure 4. In this experiment there was a significant difference between the means of the independent variable ($P < 0.001$), but no differences between the regression coefficients and elevations of the two regression curves at the $P \leq 0.05$ level. The significant difference in mean length between the two samples is probably attributable to the increased amount of food provided to the captive population and the resulting high growth rate exhibited throughout the duration of the experiment. Because the treatment significantly affected the independent variable, further examination of the regression statistics is unwarranted. However, if the two samples are subjected to a two-group comparison, there is a significant difference between the mean number of increments for each sample ($P < 0.05$). The difference between the means for each sample (25 May, $\bar{y}$ = 124.9; 8 June, $\bar{y}$ = 140.0) closely approximates the expected difference of 14 days between samples.

We conclude from the relatively good agreement between the increase in mean number of growth increments and the number of days between collection of samples, that these data from the holding experiments provide direct evidence of the presence of daily growth increments in the sagittae of nehu.

Growth of Sagittae

The total lengths of sagittae from the 5 April and 9 May 1972 nehu samples (the initial sample from the wild population and the 34-day sample)

of the first holding experiment were taken in order to examine the effects of captivity on sagittal growth. Four measurements for the 5 April sample were arbitrarily deleted because their values were well below the distribution of the majority of the sample. All 24 measurements from the 9 May sample were utilized. There are significant relationships between sagitta length and fish length for the two samples ($P < 0.001$, r^2 values: 5 April, 0.82; 9 May, 0.70) (Figure 5). The first experiment demonstrated that there was a significant increase in the mean number of increments between the two samples. Analysis of covariance of sagittae lengths indicated that there were no significant differences between the means of the independent variables, regression coefficients, or elevations of the regression curves for the two samples (respective F ratios: 2.5, 1.0, 1.2) presumably because of intrinsic variation, limited precision of measurements, and the relatively short time period between samples. Although there were no statistically significant differences found in the comparison of the two curves, the two regression coefficients exhibit perhaps expectable trends. The lesser regression coefficient and r^2 value for the 9 May sample may be indicative of a decreased growth rate and more variable responses of individuals in the population to the highly variable, and probably less than optimal, conditions of the holding facility. In addition, the differences between the unadjusted and adjusted means of sagittal lengths between the 5 April (1.094 mm; 1.070 mm, respectively) and 9 May (1.176 mm; 1.201 mm, respectively) samples of 0.082 mm and 0.131 mm are to be expected with daily growth increments of about 3-4 μm.

We have noted one apparent example of provisioning rates affecting the growth rates of sagittae of captive nehu. Sagittae from the 19 January sample of the second holding experiment usually exhibited 23-24 distinctive, more widely spaced increments on the edge of the otolith. The numbers of distinctive increments approximately correspond to the number of days during which the daily amount of food provided the sample population was double the initial ration. As might be expected otoliths collected 7 days later in the 26 January sample exhibited 30-31 distinctive increments. Indeed, the wider increments observed after provisioning rates were doubled were much more effective in "labeling" the sagitta than our attempts to accomplish the same objective with Tetracyclene. Possibly, controlled experiments with rapidly growing fish species incorporating this treatment would be a much more expeditious test of the daily growth increment hypothesis.

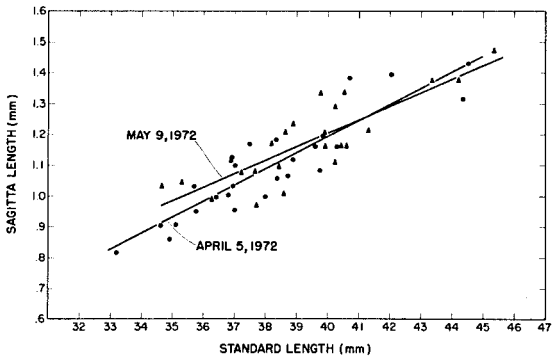

FIGURE 5.—*Stolephorus purpureus*: Growth of sagittae during first holding experiment.

Age and Growth in Wild Populations

We examined larval, juvenile, and adult nehu collected in Kaneohe Bay to obtain an estimate of age and growth of a wild population based on the assumption that the smallest observable growth layers in the sagittae represent daily growth increments. We examined 213 specimens from 13 collections made during most seasons between spring 1972 and summer 1973 (no collections were made in the months November through January). The growth curves obtained from the individual collections are given in Figure 6. Because all individuals in a sample have been exposed to the vagaries of the environment during their observed lifespan, a composite growth curve for all collections is presented in Figure 6F. Although some variation between samples is apparent, the composite scattergram serves as a first estimate of the growth pattern of nehu in Kaneohe Bay.

There are two well-defined segments to the composite growth curve (Figure 6F). Young larvae exhibit exponential growth to a length of about 15-17 mm. At about 20 mm the population enters an almost linear growth phase to about 60 mm. The composite scattergram obscures another, lesser inflection at about 20-30 mm exhibited by the spring 1972 collections (Figure 6A). Yamashita (1951) has demonstrated that nehu have completed larval metamorphosis at about 30 mm. The major inflection at a length of about 17 mm appears to reflect the fact that nehu begin to exhibit exponential growth in body depth at this

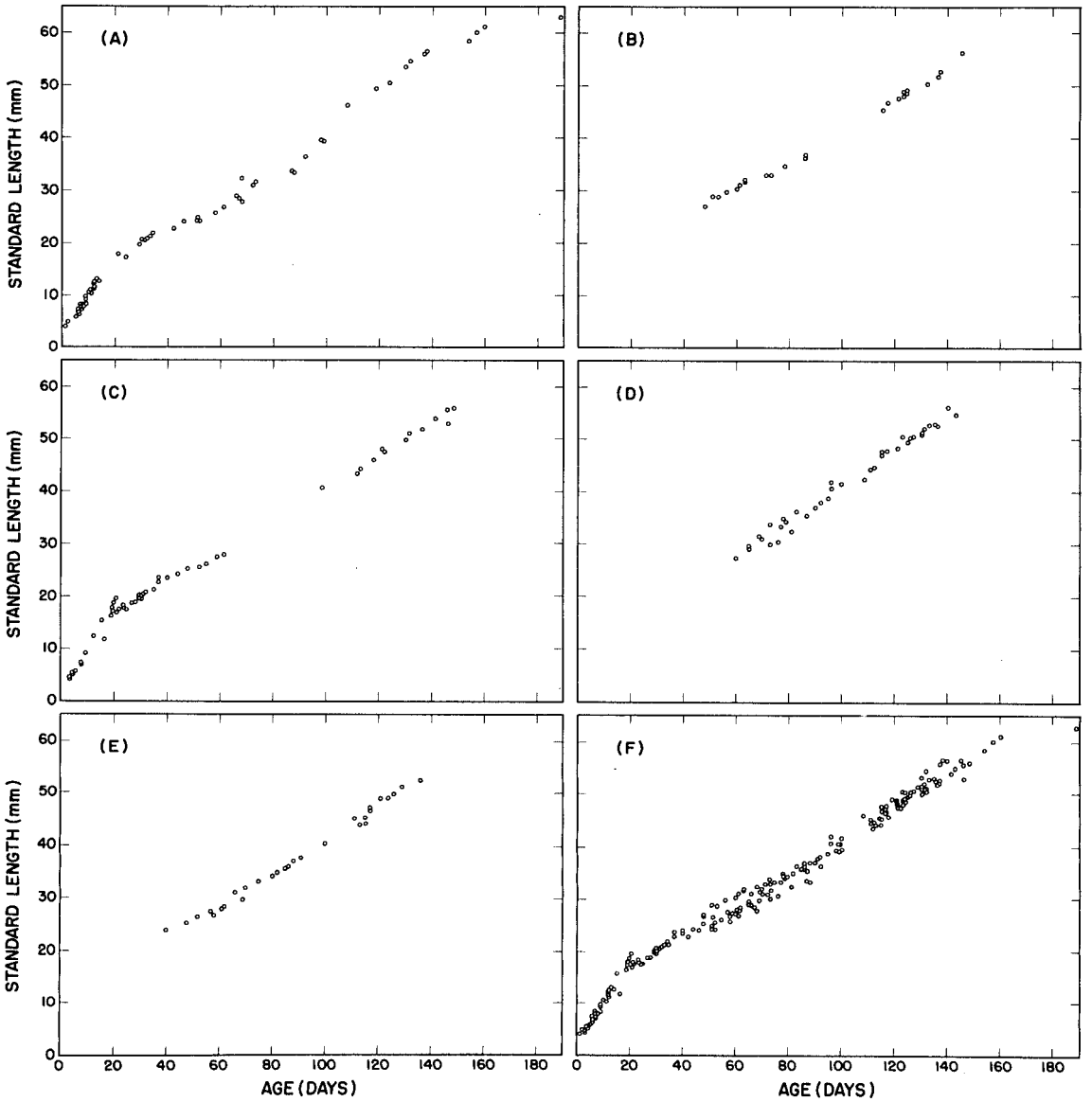

FIGURE 6.—*Stolephorus purpureus:* Age-length relations of 213 individuals from 13 collections in Kaneohe Bay. A: 19 March 1972 (21 individuals, 66-189 days); April 1972 (13, 1-24); 1 May 1972 (11, 6-12); 26 May 1972 (16, 21-68). B: 26 August 1972 (all specimens). C: 7 October 1972 (8, 16-23); 14 October 1972 (23, 19-62); 19 October 1972 (13, 99-148); 25 October 1972 (9,3-9). D: 12 February 1973 (12, 60-87), (11, 115-140); 19 March 1973 (15, 78-125). E: 5 May 1973 (8, 40-69); 13 July 1973 (27, 66-136). F: Composite scattergram of all observations.

size (cf., Nakamura 1970, fig. 4). Thus, much growth of individual nehu is directed to allometric growth of body depth, rather than body length. The growth rate of young nehu (<17 mm) indicated by the composite scattergram is consistent with the estimates of larval growth rates presented by Tester (1951) and Yamashita (1951).

The possibility that the inflection at 15-17 mm is related to a change in diet was examined. Burdick (1969) investigated the feeding habits of larval nehu from hatching to a length of 25 mm in Kaneohe Bay. He found that young nehu less than 5 mm long fed almost exclusively on copepod nauplii. At lengths of 5-7 mm, the diet shifted to a

preponderance of small, adult copepods representing two genera. Larvae less than 20 mm fed exclusively during day, at 20 mm they began occasional feeding at night, and when they attained a length of 25 mm they fed regularly at night. None of these changes in feeding habits seem related to the 15-17 mm inflection.

Only one fish, estimated to be 189 days old at a length of about 63 mm, indicated that the Kaneohe Bay population of nehu may enter an asymptotic growth phase at about 60 mm. Obviously, additional collections of older fishes are required to elucidate this portion of the growth curve.

The absence of large adults might be explained by the heavy exploitation of this stock by commercial fishermen. Another possible explanation relates to the observations of Muller[3] on *Stolephorus heterolobus* Rüppell in the Palau Islands of the western Pacific. He found that large spawning adults occur in open lagoon waters 2-4 km offshore over depths of 30-40 m during night. The daytime distribution of these individuals is unknown, but it is thought that they occur near bottom in the open lagoon. In the case of nehu, however, the explanation of an absence of adults in the asymptotic growth phase by invoking an offshore spawning movement is argued against by a recent study demonstrating that this species is capable of spawning at a length of 35-40 mm (Leary et al. in press).

These readings of whole-mounted sagittae from Kaneohe Bay nehu did not reveal any periodic deposition patterns of increments or spawning checks as reported by Pannella (1971).

Geographical Comparison of Growth Rates

One of the more exciting aspects of being able to accurately determine growth rates of young fishes is the tool that it provides to examine the effects of various environmental conditions. As an exercise, we compared the linear segments of the growth curves of two samples (n = 15) of nehu collected during March and April 1972 in Pearl Harbor and Kaneohe Bay (Figure 7). Unfortunately, the differences in size ranges of the two samples and the small sample sizes resulted in significant heterogeneity of variance (P <0.05). The analysis of covariance did indicate, however, that there may be

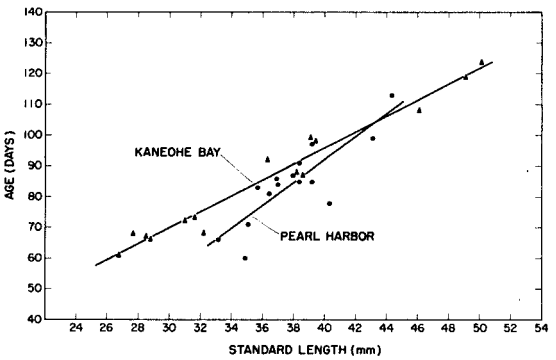

FIGURE 7.—Comparison of *Stolephorus purpureus* growth rates in Pearl Harbor and Kaneohe Bay, spring 1972.

significant differences between the regression coefficients (P <0.05) and elevations (P <0.01) of the two population curves, the Pearl Harbor sample exhibiting a faster growth rate to a length of about 44 mm. Similar, but more intensive, studies should provide a wealth of insight into a variety of aquatic situations.

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LITERATURE CITED

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

BURDICK, J. E.
1969. The feeding habits of nehu (Hawaiian anchovy) larvae. M.S. Thesis, Univ. Hawaii, Honolulu, 54 p.

DEGENS, E. T., W. G. DEUSER, AND R. L. HAEDRICH.
1969. Molecular structure and composition of fish otoliths. Mar. Biol. (Berl.) 2:105-113.

LEARY, D. F., G. I. MURPHY, AND M. MILLER.
In press. Fecundity and length at first spawning of the Hawaiian anchovy, or nehu (*Stolephorus purpureus* Fowler) in Kaneohe Bay, Oahu. Pac. Sci.

MESSIEH, S. N.
1972. Use of otoliths in identifying herring stocks in the southern Gulf of St. Lawrence and adjacent waters. J. Fish. Res. Board Can. 29:1113-1118.

NAKAMURA, E. L.
1970. Synopsis of biological data on Hawaiian species of *Stolephorus*. *In* J. C. Marr (editor), The Kuroshio: A sym-

[3]Muller, R. G. Population biology of *Stolephorus heterolobus* Rüppell in Palau. Ph.D. Dissertation in preparation. University of Hawaii, Honolulu, HI 96822.

posium on the Japan Current, p. 425-446. East-West Center Press, Honolulu.

PANNELLA, G.
1971. Fish otoliths: Daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.
1974. Otolith growth patterns: An aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (editor), The ageing of fish. Proc. International Symposium on the Ageing of Fish, Univ. Reading, Engl., p. 28-39. Unwin Brothers, Ltd., Engl.

PANNELLA, G., AND C. MACCLINTOCK.
1968. Biological and environmental rhythms reflected in molluscan shell growth. Paleontol. Soc. Mem. 2:64-80. (J. Paleontol. 42 (Suppl. to No. 5)).

TESTER, A. L.
1951. The distribution of eggs and larvae of the anchovy, *Stolephorus purpureus* Fowler, in Kaneohe Bay, Oahu, with a consideration of the sampling problem. Pac. Sci. 5:321-346.

WATSON, W., AND J. M. LEIS.
1974. Ichthyoplankton of Kaneohe Bay, Hawaii. A one-year study of fish eggs and larvae. Sea Grant Tech. Rep., UNIHI-SEAGRANT-TR-75-01, 178 p.

YAMASHITA, D. T.
1951. The embryological and larval development of the nehu, an engraulid baitfish of the Hawaiian Islands. M.S. Thesis, Univ. Hawaii, Honolulu, 64 p.

ASPECTS OF THE REPRODUCTIVE BIOLOGY OF THE WEAKFISH, *CYNOSCION REGALIS* (SCIAENIDAE), IN NORTH CAROLINA[1,2]

JOHN V. MERRINER[3]

ABSTRACT

The weakfish, *Cynoscion regalis*, has an extended spawning season in North Carolina's inshore waters (males are ripe March to August, and females are ripe April to August). Peak spawning activity occurs from late April through June. The extended spawning season throughout the range is a major factor in variability of size within a year class.

Published accounts cite attainment of sexual maturity at age II for males and age III for females. I conclude that weakfish of both sexes reach sexual maturity as yearling fish, although some smaller members of a year class do not mature until their second year.

Weight and length of weakfish are better indicators of fecundity than is age (higher correlation coefficients). A female weakfish of 500 mm standard length produces slightly over two million eggs.

The weakfish, *Cynoscion regalis*, is a littoral species of commercial and sport importance in the middle Atlantic states from North Carolina to New York (Bigelow and Schroeder 1953). Welsh and Breder (1923), Higgins and Pearson (1928), Hildebrand and Schroeder (1927), Hildebrand and Cable (1934), Pearson (1941), Roelofs (1951), and Harmic (1958) described portions of the reproductive biology of weakfish. The most recent data concerning reproductive biology of this species in North Carolina were in Hildebrand and Cable (1934).

The decline in commercial catch of weakfish between 1945 and the mid-1960's and speculation as to its cause(s) (Roelofs 1951; Perlmutter 1959; Fahy 1965a, b; Brown and McCoy 1969; Joseph 1972) indicated the need for a biological study of the weakfish along the Atlantic coast (Nesbit 1954; Perlmutter et al. 1956; Massmann et al. 1958). I undertook a study of the weakfish in North Carolina (1967-70) to provide biological data from which recommendations for management could be formulated. This paper presents data on reproduction of weakfish pertaining to: 1) spawning season, 2) age and size at which sexual maturity is attained, 3) fecundity relationships, and 4) possible role of reproductive biology in the observed population decline along the eastern seaboard.

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MATERIALS AND METHODS

A total of 3,635 weakfish were obtained for biological examination from the area bounded by Cape Hatteras and Cape Fear, N.C. Landings of pound nets, haul seines, gill nets, and shrimp trawls in the vicinity of Cape Hatteras, between June 1967 and November 1969, contributed 1,606 specimens (Figure 1). An additional 2,029 weakfish were obtained between June 1967 and January 1970 from trawler landings in Morehead City and Beaufort, and from haul seines landing in Atlantic and Sea Level (Figure 1).

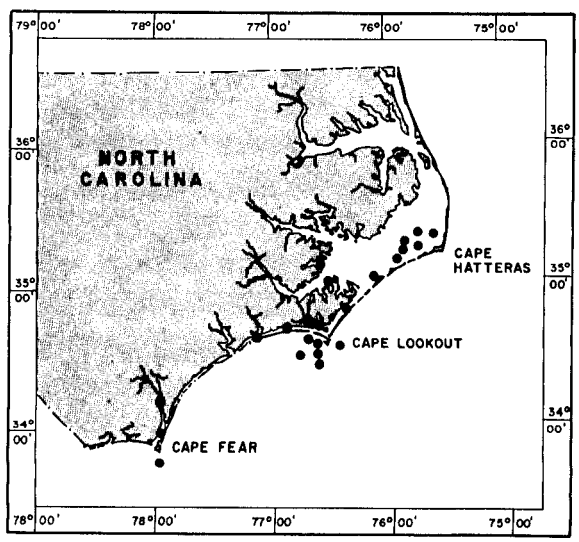

FIGURE 1.—Location of sampling sites included in 1967 to 1970 collections of weakfish from North Carolina waters.

Scale samples were taken from under the tip of the pectoral fin below the lateral line of 2,159 weakfish for age determination. Age-group or age-class cited herein refers to the number of annuli on scales. Weight in grams and length (total, fork, and standard) in millimeters were recorded from all specimens.

Sex and maturation stage of gonads were assigned after macroscopic examination of the gonads using a modification of the classification of Kesteven (1960). Histological sections of representative gonads in each stage provided verification of maturation class assignment (Table 1).

Gonad index indicated duration and peak of spawning season as well as the age and size at which weakfish attain sexual maturity. Gonads from 571 females and 117 males from the Hatteras and Morehead City areas were preserved in 10% Formalin[4] and used for analysis of gonad condition. The index value equals the weight of the preserved gonad, to the nearest 0.01 g, divided by the body weight of the fish, to the nearest 1.0 g, times 100. It represents the percent contribution of gonads to total fish weight.

Twenty-two female weakfish with well-developed oocytes (mature ovaries) provided the basis for fecundity relationships. Age-groups I through IV are represented by 20 fish collected between 25 May and 13 June 1969, from Pamlico Sound. Age-group 0 is represented by two females collected near Morehead City on 4 June 1968. The preserved ovaries were blotted dry and weighed to the nearest 0.01 g. One ovary from each pair was randomly selected for sampling. A thin slice (1-2 mm) was cut from the anterior, middle, and posterior regions of the ovary. These slices were weighed to the nearest 0.0001 g and placed in Gilson's solution for 8 to 12 h to facilitate egg separation from connective tissue (Bagenal 1967). Then the sections were rinsed with tap water and teased apart with dissecting needles. The separated egg samples were placed in a petri dish which was areally divided as a 6 × 6 grid and stirred until equally distributed within the dish before counting. Specific grid sectors were randomly selected. The portion of the sample counted ranged from one-ninth in larger ovaries to a total count in small ovaries. Counts were made using a dissecting microscope and included all eggs having yolk deposition equal to or greater than the diameter of the oil globule.

Treatment of fecundity data included analysis of variance for age-groups 0 through IV (Steel and Torrie 1960) and linear regression. Fecundity was related to total length (TL) and standard length (SL) of the fish in millimeters using the equation,

$$F = aL^b$$

where F = fecundity,
L = total or standard length of the fish,
a, b = constants for the equation.

Fecundity was related to fish weight in grams using the equation,

$$F = a + bW$$

where F = fecundity,
W = fish weight,
a, b = constants for the equation.

RESULTS

Monthly summaries of testes maturation classes revealed an extended spawning season and an early summer peak in spawning for male weakfish. Over one-fourth of the males sampled from March through August were ripe running (Table 2) and over one-half were ripe running from April through July. During September and October,

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Gonad stage designations and macroscopic condition of the male drumming muscle used in describing weakfish maturity.

Female		Male		
Gonad stage[1]		Gonad stage[1]		Condition of drumming muscle
Immature	(I)	Immature	(I)	White, undeveloped
Mature	(II, III, and IV)	Mature	(II and III)	Pink, beginning to thicken
Ripe	(V)	Ripe	(IV)	Red, thickened
Ripe running	(VI)	Ripe running	(V and VI)	Deep red, very thick
Ripe spent	(VII)	Ripe spent	(VII)	Red to deep red, thinner
Spent	(VIII)	Spent	(VIII)	Mottled red to pale red, thinner
Spent resorbing	(VIII and II)	Spent resorbing	(VIII and II)	Pink, thin
Resorbing	(I for larger fish)	Resorbing	(I for larger fish)	Pink to white, thin

[1]Roman numerals indicate the corresponding stage for the Kesteven scheme (1960).

TABLE 2.—Gonad condition for male weakfish from North Carolina as a percent of the monthly sample.

Month	Number	Immature	Mature	Ripe	Ripe running	Spent	Ripe spent	Spent resorbing	Resorbing
January	13	30.8	38.4	23.1	7.7				
March	201	3.5	30.3	39.8	26.4				
April	4				100.0				
May	32				100.0				
June	121	6.6		3.3	90.1				
July	137	13.1		3.7	80.3	2.9			
August	173	34.7	1.2	5.3	46.8	12.1			
September	189	20.1	0.5		4.2	47.6	13.8	13.8	
October	76	26.3			2.6	46.1	7.9	14.5	2.6
November	11	27.3						72.7	
December	11		27.3	72.7					
Total	968								

45% of the males were in the spent condition while only 4.2% and 2.6% respectively were ripe running. Male weakfish examined during November and December were not in the ripe running stage. Testes of fish collected in December were developing, and the drumming muscle was enlarging for the next spawning season (Table 1).

The gradual progression of ovarian maturation state from mature (dominant in March) to resorbing (dominant in December) suggests an extended spawning season for female weakfish. Females were in the ripe or ripe running stage from March through September (Table 3). From April through July, over one-fourth of the females were in the ripe category. Female weakfish completed spawning by October. Over 30% of the ovaries were in the spent resorbing condition during September and October.

Evidence of multiple spawning during a given season by individual fish in age-groups I and older was found during analysis of ovarian condition. Ovaries contained mature follicles during April and May with clusters of immature follicles interspersed among translucent oocytes. These ovaries were staged as ripe or ripe running depending upon the extrusibility of oocytes. During June, 26.6% of the ovaries were classified as ripe spent (Table 3). These ovaries still possessed mature follicles, but were flaccid relative to those of April and May, showed hemorrhage, and the clusters of immature follicles were maturing (enlarging). Ovaries staged as ripe or ripe running in July and August were rather flaccid relative to ovaries collected in the spring and did not have a hemorrhagic appearance. In late August and September, the ovaries possessed spent characteristics including atresia of remaining follicles. In the fall, ovaries exhibited further resorption of follicles and flaccid condition. The ovaries gradually resumed firmness after resorption.

The distribution of gonad index for male and female weakfish of all age-classes was unimodal with the greatest contribution of gonad to total body weight occurring in the early summer. Testicular indices peaked in May at 2.6% and declined to 0.5% in July (Figure 2). After July no change in gonad index occurred until the next spawning season. Ovarian indices reached maximum values in May (8.3%) and declined to an autumn low of less than 0.1% in September (Figure 2). Both male and female indices from April through June were considerably greater than those of either March or July. Mean monthly gonad indices reveal the major spawning period to be April through June. However, some males

TABLE 3.—Gonad condition of female weakfish from North Carolina as a percent of the monthly sample.

Month	Number	Immature	Mature	Ripe	Ripe running	Spent	Ripe spent	Spent resorbing	Resorbing
January	7	57.1	42.9						
March	148	13.5	79.7	6.8					
April	9		33.3	66.7					
May	57	1.8	38.6	56.1	3.5				
June	173	26.6	4.6	31.8	4.0	5.8	26.6	0.6	
July	186	24.2	9.1	27.4	5.9	13.4	17.2	2.2	0.5
August	221	35.7	1.4	15.4	0.9	31.7	11.7	3.2	
September	128	14.0		0.8	1.6	40.6		41.4	1.6
October	62	33.9				12.9		32.2	21.0
December	9		22.2						77.8
Total	1,000								

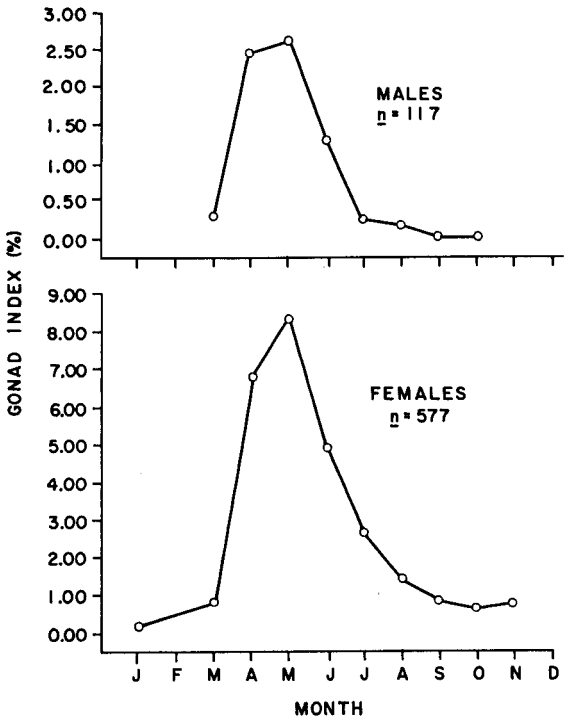

FIGURE 2.—Mean monthly gonad index for male and female weakfish of all age-classes expressed as percent body weight.

and females were in spawning condition from March through September.

Age 0 weakfish (no scale annulus) exhibited a seasonal gonad index pattern similar to that of older fish. The peak index values for age 0 females occurred in June, a month later than age I females (Figure 3). Gonads of age 0 females accounted for only 4% of the total body weight whereas they represented over 8% of body weight in age I females.

Over one-half of the age 0 weakfish collected were classified as mature (Table 4). Of the 201 age 0 females, 105 or 52% were mature. Of the

TABLE 4.—Number of immature and mature age-group 0 weakfish from North Carolina by month.

Month	Female		Male	
	Immature	Mature	Immature	Mature
January	4	2	4	3
March	30	68	8	115
May	1	0	0	4
June	14	9	1	17
July	1	0	3	0
August	6	0	24	5
September	18	4	38	6
October	20	13	19	11
November	2	8	3	2
December	0	1	—	—
Total	96	105	100	163

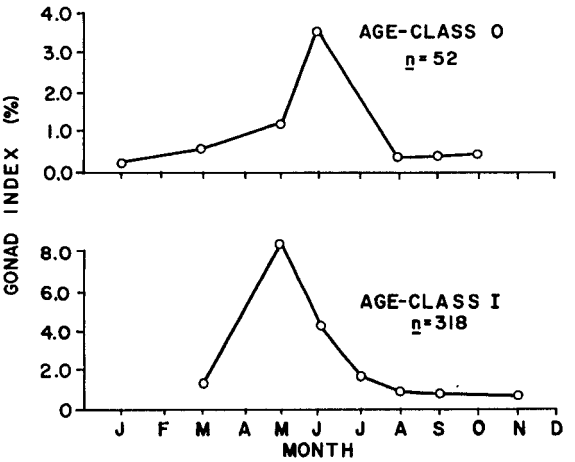

FIGURE 3.—Mean monthly gonad index for female weakfish of age-class 0 and I expressed as percent body weight.

263 age 0 males, 163 or 62% were mature. Deletion of obvious young of the year fish collected after 3 to 4 mo growth elevated the percent mature to 91 for males and 68 for females in age-group 0.

Male weakfish attain sexual maturity at a smaller size than do female weakfish and both sexes attain sexual maturity at smaller size in the vicinity of Morehead City than in Pamlico Sound (Table 5). The standard length range in which 50% of the weakfish were classified as mature, ripe, or ripe running was considered the size at which sexual maturity is attained. Weakfish less than 100 mm SL were not sexually mature in either area. Males from the Morehead City area reached the 50% criterion at about 130 mm SL (n = 1). Male weakfish from Pamlico Sound fulfill the criterion for population maturity at about 150 mm SL (n = 13, 61% mature). Female weakfish from the Morehead City area attain maturity at about 145 mm SL (n = 11, 54% mature), while female weakfish from the Pamlico Sound area attain sexual maturity at about 190 mm SL (n = 28, 57% mature).

Size of the individual fish rather than age is the dominant factor affecting the attainment of sexual maturity by weakfish. In the vicinity of Morehead City, male weakfish of age-group I but less than 170 mm SL were mature (n = 12, 1 immature) (Table 6). All age II male weakfish examined from that area were mature (n = 26). Females of 175 mm SL or larger from the same area with no annulus on their scales were mature. There was only one immature fish among

TABLE 5.—Relationship of standard length and percent mature for weakfish from North Carolina by sex and area (1967-69).

Standard length[1] (mm)	Female				Male			
	Pamlico Sound		Morehead City		Pamlico Sound		Morehead City	
	Number	% mature	Number	% mature	Number	% mature	Number	% mature
≤100			1	0			42	0
105					1	100		
110							2	0
115							7	14
120							2	0
125	4	0	1	0	5	20	2	0
130	4	0			4	0	1	100
135	3	0			9	33	5	60
140	5	20	4	25	12	33	3	67
145	15	7	11	24	9	11	9	56
150	18	22	6	33	13	61	9	67
155	15	7	21	67	15	47	15	80
160	12	42	29	76	18	56	25	96
165	20	15	31	87	24	83	32	100
170	26	23	20	90	19	58	40	95
175	24	21	23	100	15	87	33	97
180	19	26	26	85	31	77	24	100
185	27	48	24	100	20	85	28	100
190	28	57	24	96	34	77	22	100
195	45	69	29	90	36	94	40	100
200	16	81	23	96	25	100	28	100
205	27	93	27	96	32	97	35	100
210	18	78	16	100	14	100	19	100
215	20	85	17	100	13	100	21	100
220	10	80	11	100	15	100	10	100
225	10	100	12	100	7	100	4	100
230	6	100	8	100	6	100	7	100
235	9	100	3	100	4	100	4	100
240	5	100			5	100	3	100
>240	83	99	16	100	25	100	1	100
Total	469		383		411		473	

[1]Midpoint of length interval (102.6 to 107.5 = 105, etc.).

TABLE 6.—Relationship of age-group and standard length to percent sexually mature by sex for weakfish from the vicinity of Morehead City, N.C. (1968-69).

Standard length[1] (mm)	Age-group 0				Age-group I				Age-group II			
	Male		Female		Male		Female		Male		Female	
	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature
≤100	42	0	1	0								
110	2	0										
115	7	14										
120	2	0										
125	2	0	1	0								
130	1	100										
135	4	50			1	100						
140	2	50	4	25	1	100						
145	7	43	9	44	2	100	2	100				
150	7	71	5	40	2	50	1	0				
155	13	77	19	63	2	100	2	100				
160	22	96	29	76	3	100						
165	31	100	26	85	1	100	5	100				
170	35	97	9	78	5	80	11	100				
175	14	100	13	100	19	98	10	100				
180	7	100	5	100	16	100	21	81	1	100		
185	4	100	1	100	24	100	22	100			1	100
190					22	100	23	96			1	100
195	1	100			38	100	29	90	1	100		
200					26	100	22	96	2	100	1	100
>200					82	100	81	99	22	100	29	100
Total	203		122		244		229		26		32	
Mean		67		73		99		95		100		100

[1]Midpoint of length interval.

the female weakfish of age-group I less than 175 mm SL (n = 21). All females in age-group II were mature (n = 32). Males of age-group 0 from Pamlico Sound were sexually mature at 150 mm SL while males in age-group I reached maturity at 135 mm SL (Table 7). All age-group II males examined from this area were sexually mature (n = 89). Females of age-group 0 in the Pamlico Sound area reached sexual maturity at 175 mm SL (n = 3, 1 immature) while age-group I females

TABLE 7.—Relationship of age-group and standard length to percent sexually mature by sex for weakfish from Pamlico Sound, N.C. (1967-69).

Standard length[1] (mm)	Age-group 0				Age-group I				Age-group II			
	Male		Female		Male		Female		Male		Female	
	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature
105	1	100										
125	4	25	3	0	1	0	1	0				
130	2	0	3	0	2	0	1	0				
135	6	17	3	0	3	67						
140	9	22	3	0	3	67	2	50				
145	5	0	12	0	4	25	3	33				
150	12	58	10	10	1	100	8	38				
155	7	43	9	11	8	50	6	0				
160	4	50	5	40	14	57	7	43				
165	4	100	5	20	20	80	14	7			1	100
170	1	100	6	17	18	55	20	25				
175	2	100	3	67	13	85	21	14				
180			3	100	31	77	16	12				
185					19	84	27	48	1	100		
190			1	0	33	76	25	52	1	100		
195	1	100	1	100	31	94	44	68	4	100		
200	1	100			17	100	13	85	7	100	3	67
205					19	95	25	92	12	100	2	100
210					7	100	15	73	7	100	3	100
215					4	100	14	93	9	100	6	67
220					5	100	5	60	10	100	5	100
>220					9	100	33	100	38	100	80	99
Total	59		67		262		300		89		100	
Mean		44		18		80		56		100		96

[1]Midpoint of length interval.

were mature at a length of 190 mm (n = 25, 52% mature) (Table 7).

Average estimated fecundity increased with age from 45,000 eggs for age 0 females to 1,726,000 eggs for age IV females. The increases in fecundity with age were significant (F = 15.64, df = 17.4; $P < 0.01$; Table 8). Variation within individual age groups was great with the standard deviation approaching one-third of the mean estimated fecundity. Relative fecundity, the number of eggs per gram of ovary, decreased from 37,650 at age 0 to 14,867 at age IV.

Regression analysis indicated significant relationships between fecundity and fish length and weight. The equations describing the relationships and coefficients of determination are:

$$F = 0.116\ SL^{2.7755},\ r^2 = 0.85;$$
$$F = 0.152\ TL^{2.6418},\ r^2 = 0.86 \text{ (Figure 4)};$$
$$F = 21{,}198 + 1{,}279\ W,\ r^2 = 0.88.$$

DISCUSSION

Weakfish spawn in or near the various inlets along the coast of North Carolina (Welsh and Breder 1923; Higgins and Pearson 1928; Hildebrand and Cable 1934) and also in Pamlico Sound. Earlier authors did not include sounds and bays as probable spawning sites since no female weakfish in spawning condition had been taken from inshore waters of North Carolina (Roelofs 1951). Higgins and Pearson (1928) reported a few weakfish with "free running ripe eggs" in Pamlico Sound. Twenty-four female weakfish in the ripe running condition were obtained from Pamlico Sound, and this indicates weakfish may also spawn in sounds and bays. These areas may be at the edge of the spawning zone, however.

Spawning activity in coastal waters north of North Carolina is cited by Hildebrand and

TABLE 8.—Fecundity estimates and relative fecundity for 22 weakfish from North Carolina and analysis of variance results for age versus fecundity.

Age-group	Number examined	Mean fecundity estimates	Standard deviation	Mean no. of eggs per gram of ovary	Standard length range (mm)	Anova				
						Source	df	Sum of squares	Mean square	F
0	2	44,880	10,693	37,650	145-160	Age	4	5.219×10^{12}	1.305×10^{12}	15.64**
I	8	285,740	105,600	21,225	190-268	Error	17	1.418×10^{12}	8.341×10^{10}	
II	7	579,660	302,700	19,400	245-308	Total	21	6.637×10^{12}		
III	2	491,700	186,900	15,150	292-335					
IV	3	1,725,920	614,300	14,867	395-480					
Total	22									

**Probability less than 0.01.

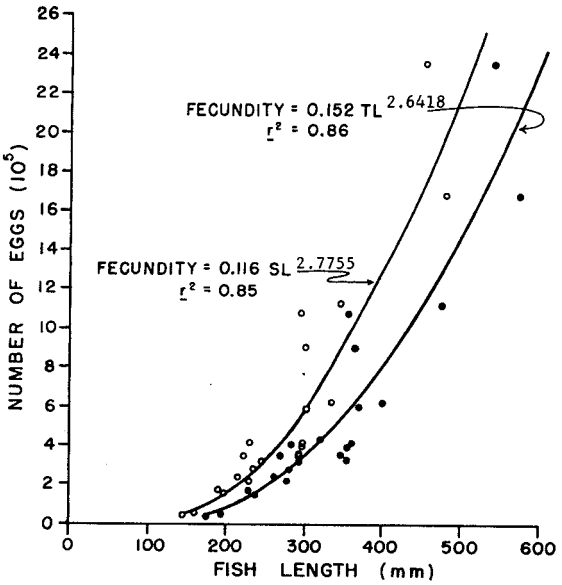

FIGURE 4.—Relationship of weakfish fecundity to fish length based upon data from 22 females.

Schroeder (1927), Pearson (1941), and Massman (1963) for Chesapeake Bay; by Parr (1933), Daiber (1954), Harmic (1958), and Thomas (1971) for Delaware Bay; by Nesbit (1954) and Perlmutter et al. (1956) for New York and New Jersey waters; and by Bigelow and Schroeder (1953) for the Gulf of Maine. However, the magnitude of spawning in northern areas is unknown. Progeny from spawning activity north of Chesapeake Bay are considered insufficient to maintain the northern stock (Harmic 1958), and young from the Carolinas and Chesapeake Bay are thought to be recruited to the northern population as age III or older fish (Pearson 1941; Nesbit 1954; Perlmutter et al. 1956; Harmic 1958). The validity of this supposition remains to be documented.

Mature weakfish enter the inshore waters, sounds, and bays of North Carolina in early spring (Hildebrand and Schroeder 1927; Hildebrand and Cable 1934; Roelofs 1951). Fertilized eggs have been taken in Delaware Bay when water temperatures ranged from 17° to 26.5°C and at salinities from 12.1 to 31.3‰ (Harmic 1958).

Weakfish apparently have an extended spawning season in North Carolina waters as reported by Welsh and Breder (1923), Higgins and Pearson (1928), Hildebrand and Cable (1934), and Pearson (1941). Distributional data for weakfish eggs and larvae are lacking in North Carolina waters. Peak spawning activity occurs from late April through June as indicated by gonad condition and gonadal index. Females appear to spawn the major portion of their eggs in May or June with a second spawn of smaller magnitude possibly occurring in late July or August. Thus, weakfish of a given year class may vary considerably in size due to their extended spawning season and multiple spawning by females.

Weakfish males and females probably attain sexual maturity as 1-yr-old fish throughout their geographic range, though some of the smaller members of a year class may not mature until their second year of life. Weakfish in North Carolina waters were previously reported to reach sexual maturity at age II for males and age III for females (Taylor 1916; Welsh and Breder 1923; Higgins and Pearson 1928), and subsequent papers have reiterated these ages without verification. Higgins and Pearson (1928) reported no mature females less than 200 mm fork length (approximately 170 mm SL) and that a fork length of 230 mm was attained before 50% of the female weakfish mature in Pamlico Sound. This size group was allocated to age-group III without examining scales for annuli. I consider their allocation of age-classes to be in error on the basis of data presented here and in Merriner (1973). I found 21 mature female weakfish 170 mm SL in samples from Pamlico Sound and 90 mature female weakfish of the same size from the vicinity of Morehead City. Over one-half of the female weakfish were mature at 190 mm SL in samples from Pamlico Sound, and male weakfish become sexually mature at a smaller size than females. Weakfish spawned in May or June would be mature the following May or June. Those fish spawned in late July or August probably would not be sexually mature until late summer of the year following their hatch or the following spring. Scrap samples from pound nets in Chesapeake Bay contained mature female weakfish measuring 170 to 250 mm TL during late spring and summer months (McHugh 1960). Maturation at a small size is also likely for fish from more northerly areas (Daiber 1954; Thomas 1971).

No evidence of alternate year spawning was found even in the oldest specimens examined. All of the females of age III or older were either in spawning condition or mature during early summer. However, some of the older weakfish in the population may not migrate inshore during spring and summer.

Weakfish are characterized by high fecundity.

In Delaware Bay a female weakfish, 190 mm SL, contained a total of 267,500 eggs and would release approximately 52,000 eggs at one spawning (Daiber 1954). My estimates of fecundity for females of a similar size are equivalent to the total egg production figure for Delaware Bay. Fecundity increases by approximately 106,000 eggs for each 100 g of body weight for weakfish in Delaware Bay, while my data indicate an increase of 127,900 eggs per 100 g of body weight.

The variation in fecundity per age-group is best explained by the size range present in the samples of each age-group. Regression analysis showed a significant relationship between fecundity and fish length (coefficient of determination $= r^2 = 0.85$) and between fecundity and fish weight ($r^2 = 0.88$). The average range of standard length for all females in age-groups 0 to IV was 57 mm. High variability in fecundity estimates for age-groups is expected due to the range in fish size and variation in gonad size among fish of the same size (Bagenal 1967).

It is highly unlikely that weakfish experienced a synchronous failure or severe depression of embryonic or larval survival in all spawning areas. Harmic (1958) analyzed the early life history of weakfish in Delaware Bay. Fertilized eggs are pelagic and measure from 0.87 to 0.99 mm in diameter. Weakfish larvae emerge after about 40 h at water temperatures of 68° to 70°F and average 1.8 mm SL. Soon after hatching, the demersal larvae disperse into the nursery areas. Throughout the coastal waters from North Carolina to at least New York, anomalous water conditions (such as rapid changes in salinity, temperature, or dissolved oxygen) may occur in small areas due to local weather phenomena or industrial-domestic development. Hurricanes, however, may affect the entire eastern seaboard (tropical storm Agnes—1972) or portions of it (Hurricane Camille—1969) with the greatest impact occurring in the estuarine areas (i.e., weakfish nursery). The extended spawning season of weakfish would tend to minimize any effect of a short-term calamity upon a local population.

Tolerance of weakfish eggs and larvae to temperature, salinity, dissolved oxygen, etc., remains poorly known. According to data compiled by Harmic (1958), natural fluctuations in the estuary approach the ranges that are detrimental to weakfish survival. For Delaware Bay and presumably throughout its range, the variation in water parameters due to natural phenomena alone may largely explain fluctuations in the weakfish population abundance and year class strength.

LITERATURE CITED

BAGENAL, T. B.
1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. John Wiley and Sons Inc., N.Y.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BROWN, J., AND E. MCCOY.
1969. A review of the North Carolina scrap fishery. N.C. Dep. Conserv. Dev., Div., Commer. Sport Fish., Mimeo. Rep., 13 p.

DAIBER, F. C.
1954. Fisheries research program. Mar. Lab. Dep. Biol. Sci., Univ. Del. Biennial Rep. 1953 and 1954. Publ. 2:50-64.

FAHY, W. E.
1965a. Report of trash-fish study in North Carolina in 1962. Div. Commer. Fish., N.C. Dep. Conserv. Dev., Spec. Sci. Rep. 5, Mimeo., 20 p.
1965b. Report of trash-fish study in North Carolina in 1964. Div. Commer. Fish., N.C. Dep. Conserv. Dev., Spec. Sci. Rep. 7, Mimeo., 13 p.

HARMIC, J. L.
1958. Some aspects of the development and ecology of the pelagic phase of the gray squeteague, *Cynoscion regalis* (Bloch and Schneider), in the Delaware estuary. Thesis, Univ. Delaware, Newark, 84 p.

HIGGINS, E., AND J. C. PEARSON.
1928. Examination of the summer fisheries of Pamlico and Core sounds, N.C., with special reference to the destruction of undersized fish and the protection of the gray trout Cynoscion regalis (Bloch and Schneider). Rep. U.S. Comm. Fish., 1927 append. 2:29-65.

HILDEBRAND, S. F., AND L. E. CABLE.
1934. Reproduction and development of whitings or kingfishes, drums, spot, croaker, and weakfishes or seatrouts, family Sciaenidae, of the Atlantic Coast of the United States. U.S. Bur. Fish., Bull. 48:41-117.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1927. Fishes of Chesapeake Bay. U.S. Bur. Fish., Bull. 43:1-366.

JOSEPH, E. B.
1972. The status of the sciaenid stocks of the middle Atlantic Coast. Chesapeake Sci. 13:87-100.

KESTEVEN, G. L. (editor).
1960. Manual of field methods in fisheries biology. FAO Man. Fish. Sci. 1, 152 p.

MCHUGH, J. L.
1960. The pound-net fishery in Virginia. Part 2 – Species composition of landings reported as menhaden. Commer. Fish. Rev. 22(2):1-16.

MASSMANN, W. H.
1963. Age and size composition of weakfish, *Cynoscion regalis*, from pound nets in Chesapeake Bay, Virginia 1954-1958. Chesapeake Sci. 4:43-51.

MASSMANN, W. H., J. P. WHITCOMB, AND A. L. PACHECO.
1958. Distribution and abundance of gray weakfish in the

York River system, Virginia. Trans. 22nd North Am. Wildl. Conf., p. 361-369.

MERRINER, J. V.
1973. Assessment of the weakfish resource, a suggested management plan, and aspects of life history in North Carolina. Ph.D. Thesis, North Carolina State Univ., Raleigh, 201 p.

NESBIT, R. A.
1954. Weakfish migration in relation to its conservation. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 115, 81 p.

PARR, A. E.
1933. A geographical-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic Coast of the United States. Bull. Bingham Oceanogr. Collect. Yale Univ. 4(3):1-90.

PEARSON, J. C.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout, *Cynoscion regalis* (Bloch). U.S. Bur. Fish., Bull. 50:79-102.

PERLMUTTER, A.
1959. Changes in the populations of fishes and in their fisheries in the Middle Atlantic and Chesapeake regions, 1930 to 1955. Trans. N.Y. Acad. Sci., Ser. II, 21:484-496.

PERLMUTTER, A., W. S. MILLER, AND J. C. POOLE.
1956. The weakfish (*Cynoscion regalis*) in New York waters. N.Y. Fish Game J. 3:1-43.

ROELOFS, E. W.
1951. The edible finfishes of North Carolina. *In* H. F. Taylor (editor), Survey of marine fisheries of North Carolina, p. 109-139. Univ. N.C. Press, Chapel Hill.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to the Biological Sciences. McGraw-Hill Book Co., N.Y., 481 p.

TAYLOR, H. F.
1916. The structure and growth of the scales of the squeteague and the pigfish as indicative of life history. U.S. Bur. Fish., Bull. 34:285-330.

THOMAS, D. L.
1971. The early life history and ecology of six species of drum (Sciaenidae) in the lower Delaware River, a brackish tidal estuary. Ichthyol. Assoc. Bull. 3. An ecological study of the Delaware River in the vicinity of artificial island. Delaware Progress Report for the period January-December 1970. Part III, 247 p.

WELSH, W. W., AND C. M. BREDER, JR.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. U.S. Bur. Fish., Bull. 39:141-201.

DDT AND ITS METABOLITES IN THE SEDIMENTS OFF SOUTHERN CALIFORNIA

JOHN S. MACGREGOR[1]

ABSTRACT

To assess the degree of DDT contamination in the marine sediments off Los Angeles, 103 stations in the Pacific Ocean off southern California were sampled in July and August 1971 for DDT and its metabolites, DDD and DDE. Heavy contamination of bottom sediments in this area was expected because of large amounts of DDT that have entered the ocean through the Los Angeles County sewer system as waste from a DDT manufacturing plant.

From the data acquired, it was estimated that there were about 200 metric tons of DDT, DDD, and DDE in the sediments in an area of 14 square nautical miles near the sewer outfalls and 300 metric tons in the entire 911 square nautical mile area sampled. The heaviest concentrations of total DDT were distributed in the relatively shallow-water area on the Palos Verdes shelf to the northwest of the sewer outfalls in the general direction of the current flow.

Metabolism of DDT was inhibited in deepwater sediments. Ratios of DDE to DDT were low, and DDT was more abundant than DDE at some stations. In sediments from shallow-water stations, DDE exceeded DDT by more than 10 times.

The bottom of the ocean off Los Angeles, Calif., has been very heavily contaminated with the pesticide DDT owing to the discharge of wastes from a DDT manufacturing plant into the Los Angeles County sewer system over a period of about 20 yr ending in 1970 (MacGregor 1974).

The amount of DDT which entered the ocean through the Los Angeles County sewer system was estimated at 250 kg/day. Following the cessation of DDT discharges by the manufacturer, the amount entering the ocean dropped to 45 kg/day in December 1970 and to 11 kg/day in October 1971. Most of these later discharges resulted from sewer cleaning operations which stirred up old deposits of DDT in the sewer lines. The discharges resulting from the cleaning operations were primarily DDD and DDE, metabolites of DDT, while the earlier discharges were primarily DDT.

Because there has been a great deal of speculation about the fate of DDT and other toxic chemicals released into the environment by man (Woodwell et. al. 1971; National Academy of Sciences 1971), this investigation was undertaken to determine the areal distribution and fate of these chemicals in the bottom sediments in the ocean off Los Angeles.

MATERIALS AND METHODS

The bottom sediments were sampled from a grid of 103 stations between lat. 33°30′ and 33°58′N and long. 118°00′ and 118°44′W (Figure 1). The stations were designated by four-digit numbers, the first two indicating minutes north

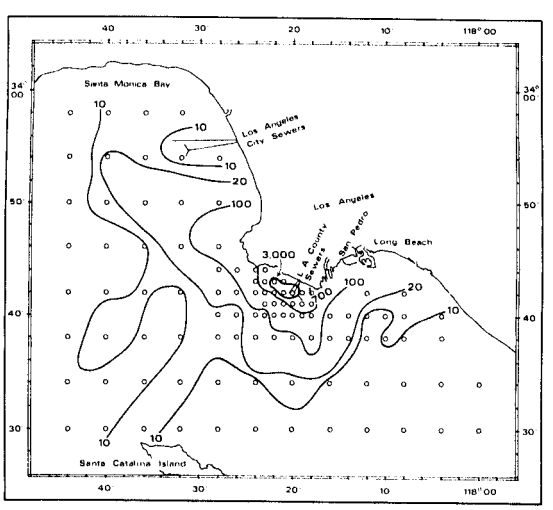

FIGURE 1.—Distribution of total DDT in milligrams per square meter of bottom in the sediments of southern California. Total DDT ranged from 6,600 mg/m² of bottom at station 43-22 to 0.12 mg/m² at station 30-08.

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of lat. 33°N and the second two indicating minutes west of long. 118°W.

The samples were taken aboard the National Marine Fisheries Service RV *David Starr Jordan* between 26 July and 3 August 1971. The Shipek bottom sampler was used to obtain the samples of sediment. This device obtains a block of material equal to 400 cm^2 of bottom sediment to a depth of about 10 cm, or slightly more, in soft mud or to a depth of half as much or less in coarse sand.

Two samples were taken at each station in order to obtain an estimate of sampling error. The vessel was allowed to drift while the samples were being taken, so the sample pairs were taken in only approximately the same location. However, agreement in the various parameters between samples from the same station was good.

The samples were placed in aluminum foil-lined containers of approximately the same size as the sampling bucket and were quick-frozen. They were stored in a freezer until removed for analysis.

In most samples, DDT was confined to the top 2 or 3 cm of the sediment. At most of the stations where the sampler sampled to 10 cm, and at all of the stations where it sampled to a lesser depth, it appeared that all of the DDT under the 400 cm^2 had been sampled. In this study, therefore, DDT concentrations are given as the weight of DDT per unit area of bottom to a depth of 10 cm. In a few areas of rapid sedimentation, where the sampler sampled to about 10 cm depth, there were still significant amounts of DDT below 10 cm. Estimates for the amounts of DDT below 10 cm are based on core samples taken by other investigators in this area.

The bottom sediment samples were thawed and blended in a 1-gallon Waring[2] commercial blender. Before blending, small stones were removed from the few samples that contained them. Some samples contained a few small molluscs or brittle stars, but these were not removed. Measured amounts of distilled water were added to some of the drier (sandy) samples to facilitate blending.

A sample of 15 to 20 g of blended sediment was weighed onto a watch glass, dried to constant weight, and reweighed to obtain percent water in the sediment. This gave an index of bottom type ranging from 30 to 40% water for coarse sand to 60 to 70% water for fine silt.

A second sample weighing about 30 g was weighed into a 1-pint Mason jar for DDT determination. About four or five times as much Na_2SO_4 was weighed into the jar as a drying agent. The sediment and Na_2SO_4 were mixed using a stainless steel spatula, and the mixture was frozen. A cutting assembly was fitted to the jar, and the frozen mixture was thoroughly blended to a powder using an Osterizer blender.

About 5 g of the powder was weighed into a tared, large disposable pipet (Matheson super pipet) plugged with glass wool. The powder was extracted into a 15-ml graduated centrifuge tube with 5 ml of hexane and 5 ml of acetone. The extract was evaporated to dryness and redissolved in 1 ml of hexane. This sample was eluted through a super pipet filled with activated alumina (McClure 1972) using enough hexane to obtain a 6-ml sample.

This sample was reduced or increased in volume as required and injected into a model 402 Hewlett Packard gas chromatograph (GLC) with a Ni^{63} electron capture detector. The 6-foot glass column contained 4% SE-30/6% QF-1 on 100/120 mesh Supelcoport.

There was evidence of a polychlorinated biphenyl, Aroclor 1254, in all samples, but the DDT peaks were so dominant in the chromatograms that they generally obliterated any traces of other chlorinated hydrocarbons within their range. Only the six peaks representing the ortho-para and para-para forms of DDE, DDD, and DDT were quantified. "Total DDT" is used to designate the sum of these six analogs.

RESULTS AND DISCUSSION

Fifty-five correlations were obtained for 11 parameters to determine various DDT relationships. The 55 correlations were obtained for all 103 stations (Table 1, values above 1.000 correlation diagonal) and for 76 stations leaving out those 27 stations having total DDT readings greater than 100 mg/m^2 (Table 1, values below 1.000 correlation diagonal). For 100 observations a correlation coefficient of 0.254 indicates a probability of 0.01. Logarithms were used for total DDT and distance from outfall, arithmetic values for the other nine measurements.

There is a very high negative correlation between log total DDT and log distance from the

[2]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Correlation coefficients for 11 parameters relating to DDT and its metabolites in bottom sediments off southern California. Values above 1.000 correlation diagonal are for 103 stations. Values below diagonal are for 76 stations leaving out those 27 stations having total DDT readings greater than 100 mg/m². For 100 observations, a correlation coefficient of 0.254 indicates a probability of 0.01.

Parameter	Log total DDT	Log distance from outfall	Depth	Sample weight	% H_2O in sample	p,p'DDD / p,p'DDT	p,p'DDE / p,p'DDT	p,p'DDE / p,p'DDD	o,p'DDE / p,p'DDE	o,p'DDD / p,p'DDD	o,p'DDT / p,p'DDT
Log total DDT	1.000	−0.871	−0.253	0.221	0.157	0.142	0.144	0.281	−0.040	−0.272	−0.334
Log distance from outfall	−0.604	1.000	0.228	−0.095	−0.147	−0.032	−0.043	−0.238	0.016	0.332	0.334
Depth	0.078	−0.036	1.000	0.643	0.771	−0.443	−0.512	−0.572	0.315	0.168	0.095
Sample weight	0.245	0.041	0.761	1.000	0.743	−0.265	−0.341	−0.332	0.190	0.036	−0.151
% H_2O in sample	0.095	0.002	0.921	0.756	1.000	−0.315	−0.390	−0.396	0.228	0.019	−0.013
p,p'DDD/p,p'DDT	0.123	0.066	−0.418	−0.268	−0.325	1.000	0.909	0.297	−0.168	−0.194	0.556
p,p'DDE/p,p'DDT	0.100	0.040	−0.492	−0.366	−0.416	0.907	1.000	0.446	−0.208	−0.171	0.463
p,p'DDE/p,p'DDD	0.060	−0.075	−0.535	−0.418	−0.487	0.268	0.408	1.000	−0.289	−0.043	−0.011
o,p'DDE/p,p'DDE	0.190	−0.234	0.296	0.225	0.248	−0.151	−0.196	−0.273	1.000	0.021	0.113
o,p'DDD/p,p'DDD	−0.129	0.275	0.106	0.090	0.059	−0.177	−0.151	0.023	−0.024	1.000	0.130
o,p'DDT/p,p'DDT	−0.154	0.167	0.006	−0.127	0.025	0.630	0.537	0.084	0.068	0.060	1.000

Los Angeles County sewer outfalls ($r = -0.871$). Values ranged from 6,600 mg of total DDT/m² of bottom near the sewer outfalls to about 1 mg/m² at more distant stations.

The distribution of DDT was modified somewhat by currents which tended to deposit the DDT along the coast and to the northwest more than to the east (Figure 1). The apparent relation between total DDT and depth results from the fact that the sewers discharge into relatively shallow coastal waters and the sludge tends to remain there. The deeper waters are merely farther from the sewer outfalls and the areas along the coast favored by the currents.

McDermott et. al. (1974) took sediment samples from the Palos Verdes shallow-water shelf area in the vicinity of the sewer outfalls only. Their tables A-1 and A-4 give total DDT in parts per million dry weight from gravity core samples taken in 1972. I have contoured their data (Figure 2B) for the top 10 cm of sediment to compare with the 1971 data (Figure 2A) which has been converted to parts per million dry weight. Their 1973 data in their table A-5 represents parts per million dry weight of total DDT in the top 5 cm of Shipek samples taken in the same area (Figure 2C). In each of the 3 yr the patch of sediment representing more than 100 ppm. total DDT tends to retain its integrity fairly well as an oblong area stretching to the northwest of the sewer outfalls. The contours representing 10 to 100 ppm. seem to be expanding somewhat to the northwest and in 1973 to the southeast also.

At the Los Angeles County sewage disposal plant, most of the solids are removed by centrifuging, but the supernatant is pumped into the ocean along with the water from the settling tanks. This reduces the amount of particulate matter being discharged into the ocean. Nevertheless, quantities of relatively DDT-free particulate matter have been deposited on the Palos Verdes shelf since dumping of DDT into the sewer system was stopped. In time this could cause a change in the DDT profile of the sediments.

On the other hand, most of the shallow inshore areas along this section of coast tend to have sandy bottoms, and the silt bottoms in the vicinity of the sewer outfalls would appear to be unstable artifacts. Storms, tides, and currents could remove or deposit layers of bottom silts in this shallow-water area and further change the DDT profiles.

Based on the paired samples taken in 1971, the variation within a sampling area for one sample would be roughly plus 100% minus 50% at a one standard deviation level. For an average for two samples it would be plus 70% minus 40%. This could account for the differences in the distribuion of total DDT for the 3 yr. However, the similarities are much more striking than the differences.

High sample weight and high water content both indicate samples containing more silt, while lower weights and lower water content indicate samples containing more sand. Both of these measurements are related to depth, with the bottom in deep basins tending to be fine silt while shallow areas tend to be sandy. This tendency is masked in shallow-water areas where there are sewer outfalls which deposit large quantities of fine material in the shallower waters. This is indicated by the improvement of the correlation coefficients from 0.643 to 0.761 for sample weight and from 0.771 to 0.921 for percent water with

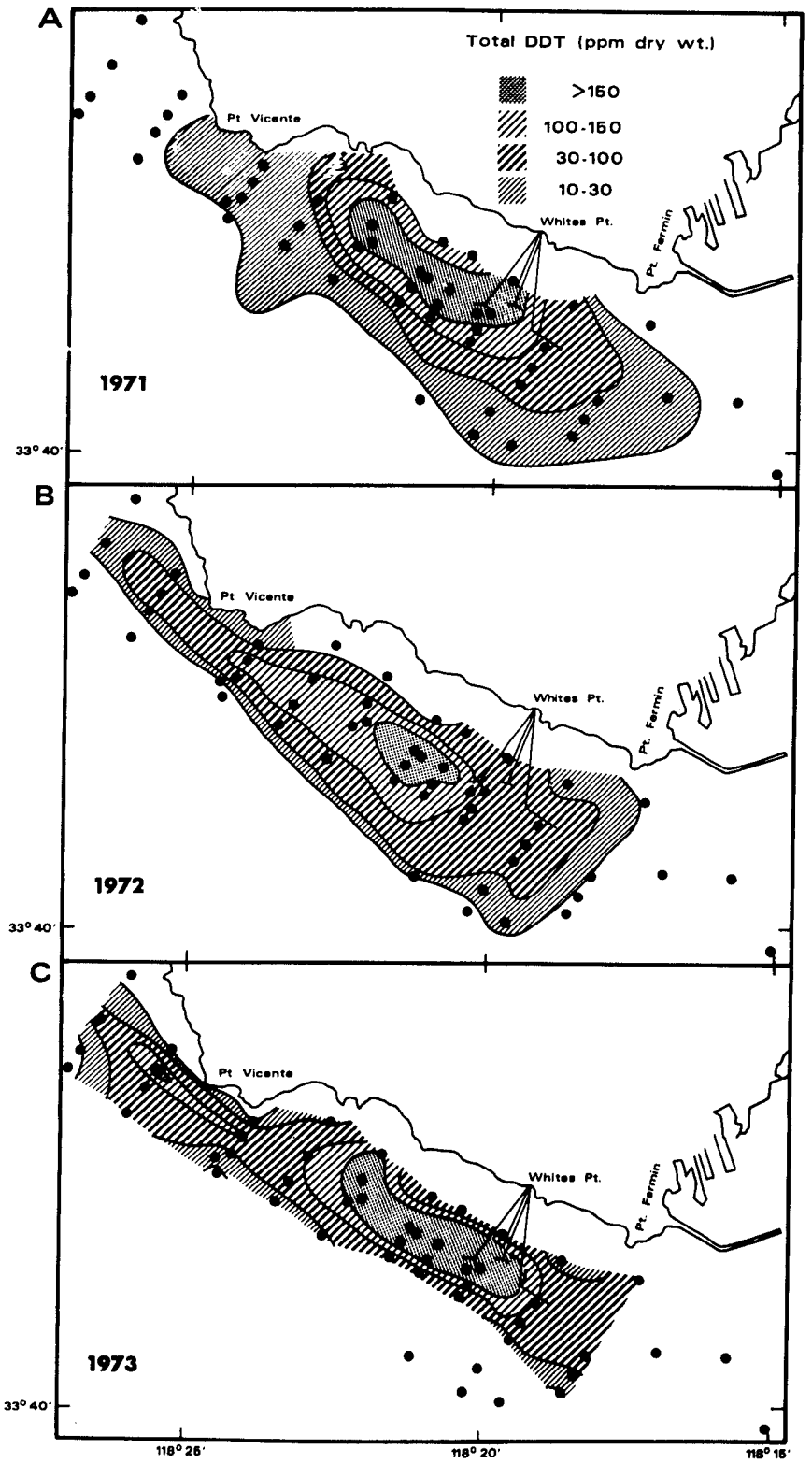

FIGURE 2.—Total DDT (parts per million dry weight) in the bottom sediments off Palos Verdes in the vicinity of the Los Angeles County sewer outfalls. A. Shipek samples (present paper); B. top 10 cm of gravity cores (McDermott et al. 1974); C. top 5 cm of Shipek samples (McDermott et al. 1974).

depth when the 27 stations of heavy sewer deposition in shallower waters are omitted.

The very high correlation coefficient (0.909) between *p,p'*DDD/*p,p'*DDT and *p,p'*DDE/*p,p'*DDT shows that when metabolism of DDT to DDD is high, metabolism of DDT to DDE is high also. These high rates of metabolism are negatively correlated with depth. Actually, they are more probably associated with some of the conditions prevailing at depth in the ocean off Los Angeles. The deep areas sampled tend to be anaerobic, and it is probably the lack of oxygen and colder water that determines the low rate of metabolism. The high correlations of the ratios with sample weight and percent water are secondary effects of the correlations of these two factors with depth.

The high negative correlation between *p,p'*DDE/*p,p'*DDD and depth indicates that metabolism of DDT to DDE is favored over metabolism to DDD in shallower waters. However, the positive correlation of *p,p'*DDE/*p,p'*DDD with *p,p'*DDD/*p,p'*DDT (0.297) as well as with *p,p'*DDE/*p,p'*DDT (0.446) supports the conclusion that metabolism to both metabolites is much greater in shallow aerobic waters than in deep anaerobic waters. Actually, much more DDT is probably metabolized to DDD than to DDE under all circumstances prevailing in the study area, but the DDE is much more persistent than the DDD and accumulates to a greater degree while DDD is further metabolized to DDMU and other metabolites.

There was at least 10 times as much DDE as DDT in the bottom sediments from stations along the coast of the study area, while 10 stations in deeper waters north of Santa Catalina Island had less DDE than DDT in the bottom samples (Figures 3, 4). DDD tended to follow somewhat the same pattern (Figure 5).

At the 10 stations the average total DDT was 19.9 mg/m^2, of which 60% was DDT, 19% DDD, and 21% DDE. Mean depth was 341 fathoms (623 m) and the total area represented by the 10 stations was 111 sq nautical miles containing an estimated 5.74 metric tons of total DDT.

It appears that most of the pesticide discharged from the Los Angeles County sewer outfalls has been DDT with the exception of the period of sewer cleaning operations in 1970-71 when DDD and DDE predominated (MacGregor 1974). Most of the DDT settles on the bottom close to the outfalls in shallow waters. Once the DDT becomes part of the bottom sediment it tends to stay there and metabolize in place, rapidly in shallower waters and more slowly in deeper waters.

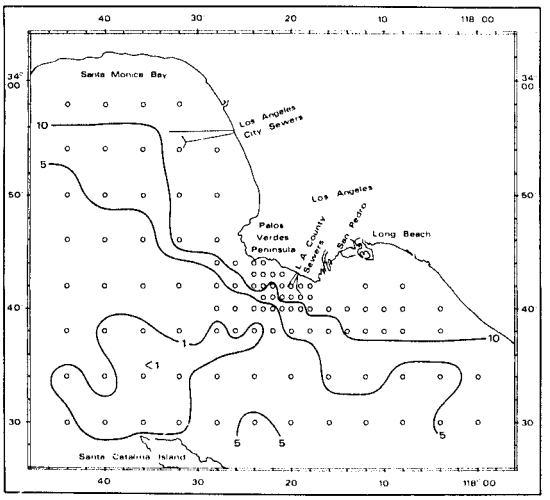

FIGURE 3.—Distribution of ratios of *p,p'*DDE to *p,p'*DDT. In the shallow waters near shore the ratios exceed 10:1, while in the deeper waters north of Santa Catalina Island the ratios are less than 1:1.

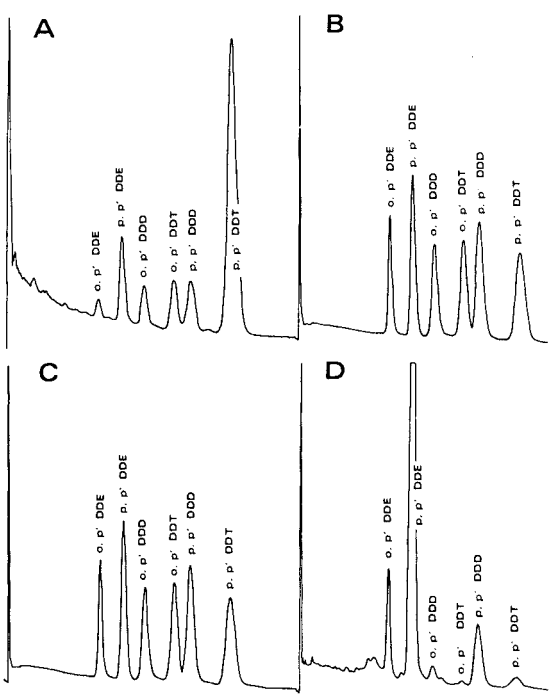

FIGURE 4.—Chromatograms of: A—a deepwater sample (274 m), station 30-40, showing high *p,p'*DDT peak, and D—a shallow-water sample (36.5 m), station 40-16, showing a high DDE peak. B and C are standards of the DDT analogs.

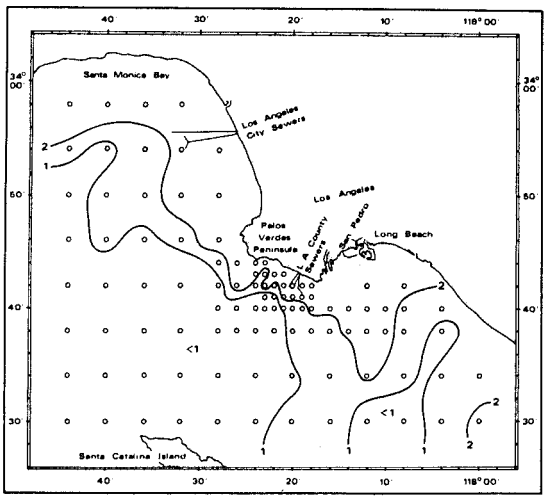

FIGURE 5.—Distribution of ratios of *p,p'*DDD to *p,p'*DDT. In the shallow nearshore areas the ratios exceed 2:1, while in the deeper waters the ratios are less than 1:1. The higher ratios were probably enhanced by sewer cleaning operations in 1970-71.

The DDT deposits in the deeper waters must have been transported there directly from the sewer outlets before much metabolism could take place. If they had originated from bottom sediments closer to the sewer outfalls and in shallower waters, the DDE content would be much higher. DDE averages about 85% of total DDT in biological material in this area; therefore, most of the total DDT in bottom sediments in the deeper water could not have originated from this source.

For the time series for total DDT accumulation in myctophid fish (MacGregor 1974), DDE was less than DDT from 1949 to 1956, but in the subsequent years DDE became much higher. If the deep water with relatively low DDE had resulted from biological fallout as represented by the myctophids for 22 yr (1949-70), and if there had been no metabolism at depth, the DDE would have been twice as high as the DDT rather than one-third as high.

There is either very little metabolism in deep-water sediments, or there is no metabolism, and the small amounts of DDD and DDE found there are the result of fallout from material metabolized in the better-oxygenated surface and intermediate depths.

In commercial DDT, the ratio of *p,p'*DDT to *o,p'*DDT is about 4:1 (i.e., *o,p'*DDT is about 25% of *p,p'*DDT). The distribution of these latter values for the sediment samples indicate that *o,p'*DDT is about what might be expected, while *o,p'*DDD is higher and *o,p'*DDE is lower (Table 2).

In the case of DDT this may mean that *o,p'*DDT metabolizes as readily as *p,p'*DDT. The two high positive correlations with the parameters indicating high metabolism, *p,p'*DDD/*p,p'*DDT and *p,p'*DDE/*p,p'*DDT, may indicate that *o,p'*DDT metabolizes more readily than *p,p'*DDT under conditions of low metabolism of DDT to DDD and DDE. Both the ratios of *o,p'*DDT to *p,p'*DDT and *o,p'*DDD to *p,p'*DDD tend to be high in the bottom sediments north of Santa Catalina Island and in Santa Monica Bay, while ratios tend to be low just south of Palos Verdes Peninsula and in the sandy shallower waters to the east of this area (Figures 6, 7). The association of greater distance from the sewer outfalls and lower total DDT values with high ratios is undoubtedly fortuitous, although the few very high ratios are associated with very low DDT values and probably result from poorer resulting measurements and interfering substances that are no longer completely dominated by DDT at these very low values.

The ratios of *o,p'*DDE to *p,p'*DDE are greater than 1.00:1.00 for 19 stations. Unlike the other two ratios these high ratios are associated with depth. They also tend to be concentrated in the deeper waters just off the Palos Verdes shelf where the sewer outfalls are located (Figure 8). These apparent high relative values of *o,p'*DDE are probably caused by interfering substances, probably DDMU, a metabolite of DDD, which is not being further metabolized under the conditions prevailing at these stations.

TABLE 2.—Frequency distributions of ortho-para isomer as a percent of para-para isomer of DDT, DDD, and DDE in bottom sediments.

Percent	DDT	DDD	DDE
0.0- 5.0	4	0	1
5.1- 10.0	5	0	2
10.1- 15.0	15	0	11
15.1- 20.0	13	7	20
20.1- 25.0	10	8	19
25.1- 30.0	12	16	10
30.1- 35.0	11	24	6
35.1- 40.0	7	16	3
40.1- 45.0	6	9	3
45.1- 50.0	6	9	3
50.1- 55.0	1	1	3
55.1- 60.0	4	4	0
60.1- 65.0	1	1	1
65.1- 70.0	1	0	0
70.1- 75.0	1	1	0
75.1- 80.0	2	0	0
80.1- 85.0	2	0	0
85.1- 90.0	0	0	1
90.1- 95.0	1	1	1
95.1-100.0	0	2	0
>100	1	4	19

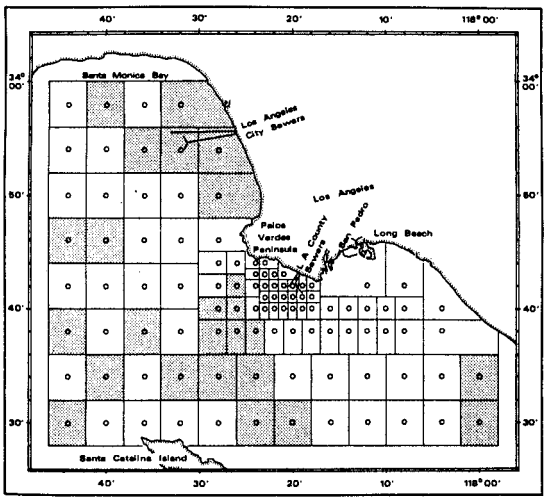

FIGURE 6.—Stations at which the ratio of *o,p'*DDT to *p,p'*DDT was greater than 0.40:1.00.

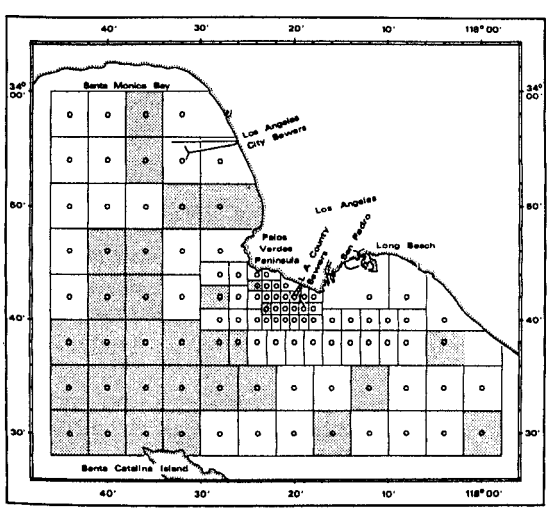

FIGURE 7.—Stations at which the ratio of *o,p'*DDD to *p,p'*DDD was greater than 0.40:1.00.

To estimate the amount of DDT stored in the bottom sediments in the approximately 911 sq nautical miles between long. 117°58′ and 118°46′W and lat. 33°18′N and the California coast, represented by the 103 stations, we must assume that each station is representative of its surrounding area. Each pair of samples from each station showed a high correlation for all pairs of parameters. The correlation coefficient for the logarithms of total DDT for paired samples from 94 stations from which two samples were obtained was 0.964 and the standard error of estimate ±0.321.

The Shipek sampler took bottom silts only to a depth of about 10 cm and sandy bottoms or shallow sediment deposits to a lesser depth. At all stations except those where bottom deposition was very rapid, as near sewer outfalls, all DDT in the sediments was sampled. Near the sewer outfalls the sample represents only DDT deposits in the top 10 cm of sediment. The total amount of DDT determined for the 911 sq nautical mile sampling area was 217 metric tons in the top 10 cm of bottom sediment. Of this total, 179 metric tons (82%) was DDE, 22 metric tons (10%) was DDD, and 16 metric tons (8%) was DDT. McDermott and Heesen (1974) found that the total DDT in the top 5 cm of sediment consisted of 86% DDE, 11% DDD, and 3% DDT in the area of the Palos Verdes shelf. These somewhat different percentages may have resulted from further metabolism of DDT without replenishment. In addition, the DDE percentages tend to be higher in this area, and the DDD was increased in 1970-71 because of sewer cleaning operations.

The total DDT ranged from an estimated 0.42 kg per sq nautical mile at station 30-08 representing 13.3 sq nautical miles to 28.6 metric tons per sq nautical mile at station 43-22 representing 1.25 sq nautical miles.

Five stations representing 6.24 sq nautical miles or 0.7% of the 911 sq nautical mile area represented by the 103 stations contained 47.3%

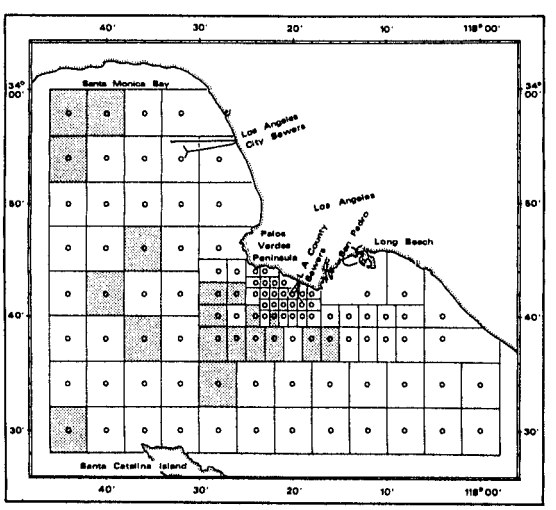

FIGURE 8.—Stations at which the ratio of *o,p'*DDE to *p,p'*DDE was greater than 1.00:1.00. The high apparent *o,p'*DDE values probably were caused by DDMU which has the same retention time as *o,p'*DDE on the column used.

of the total DDT (102.7 metric tons). Sixteen stations representing 18.1 sq nautical miles (2.0% of total area) contained 64.0% (193 metric tons) of the total DDT.

Subsamples taken from the tops and bottoms of the blocks of sediment obtained with the Shipek sampler indicated that most of the pesticide was concentrated in the top strata of the samples except for samples taken in the vicinity of the sewer outfalls where deposition was very rapid. Cores were taken from one sample taken near the sewer outfalls and from a second taken at a greater distance from the outfalls to determine more about vertical distribution of DDT in the sediments (Table 3).

At station 42-36 only *p,p'*DDE was measured because DDT and DDD were not readily measurable in the deeper sediment sections. Half of the DDE was found in the top 2 cm, 81% in the top 4 cm, and 95% in the top 6 cm. At station 42-20, close to the sewer outfall where sewer sediment deposition was heavy, there was very little change in the chlorinated hydrocarbon concentrations at all five depths.

Vance McClure (pers. commun.) has provided me with a plot of the depth distribution of DDT, DDE, DDD, and DDMU found in a box core sample taken about 1 nautical mile west-northwest of the sewer outfall. Subsamples were taken from the core at 3-cm intervals from 0 to 12 cm and at 6-cm intervals from 12 to 36 cm. The pesticide values remained high through 12 cm depth and dropped off rapidly between 12 and 18 cm. DDMU had a deeper distribution than the other three components and increased to a maximum at 9 cm and was still present at 36 cm. DDE was last measured at 24 cm, and DDD and DDT at 18 cm. Excluding DDMU, 72% of the pesticide was found in the column corresponding to the top 10 cm and 28% below that depth. Including DDMU, 67% was in the top 10 cm and 33% below.

If the box core sample is typical of the stations near the sewer undergoing rapid sedimentation, about 30% of the pesticide was missed by sampling only to a depth of 10 cm at these stations. Because these stations near the sewer outfalls contain most of the pesticide, the 217 metric tons of pesticide estimated for the entire area in the top 10 cm could be increased to roughly 300 metric tons as a maximum estimate of total DDT in the area.

In the area of the Palos Verdes shelf only, McDermott and Heesen (1974) estimated that

TABLE 3.—Vertical distribution of DDT in the sediments as determined from core samples taken at stations 42-20 and 42-36.

	Stn. 42-20					Stn. 42-36
Core depth (cm)	*o,p'*DDE (ppm.)	*p,p'*DDE (ppm.)	*o,p'*DDD / *p,p'*DDD (ppm.)	*o,p'*DDT / *p,p'*DDT (ppm.)	Aroclor 1254 (ppm.)	*p,p'*DDE (ppm.)
0-2	14.6	67.4	10.1	3.1	6.2	0.0233
2-4	19.4	90.7	11.4	3.5	6.0	0.0149
4-6	16.2	84.2	10.1	2.9	4.8	0.0063
6-8	34.8	64.4	13.2	3.5	6.2	0.00180
8-10	34.0	79.1	8.2	2.8	4.8	0.00065

there were 218 tons of total DDT under 62 km² of bottom. They calculated that 85% of the total DDT was in the top 12 cm of sediment. If the pesticide is fairly equally distributed in the top 12 cm, about 14% would be in the 10- to 12-cm layer, and the Shipek sampler would sample about 71% of the total DDT.

Sixteen contiguous stations on the Palos Verdes shelf sampled by us in 1971 represented an area of 18.1 sq nautical miles (62.0 km²) and a total DDT load of 139 metric tons. If this was only 71% of the total DDT in the area (the load of the top 10 cm only), then the corrected estimate including DDT below 10 cm would be 196 metric tons.

McDermott et al. (1974) using a reduced sampling area of 48 km² determined that there were 156 tons of total DDT in their revised sampling area. In this present study the area can be adjusted to 48 km² by omitting the effect of 2½ peripheral stations. Estimated total DDT then would be 132 metric tons. However, McDermott et al. (1974, table 5) give estimates of total DDT in the area in 2-cm increments down to a depth of 30 cm of sediments. This table indicates that only about 59% of the total DDT is in the top 10 cm in this area. This would increase my estimate of total DDT to 224 metric tons for the 48 km² area.

The available data indicate that there is considerable variation in the depth distribution of total DDT in the sediments on the Palos Verdes shelf. However, the general conclusion that can be drawn from the samples is that there are about 200 metric tons of total DDT in the bottom sediments in the 14 sq nautical mile area (48 km²) in the vicinity of the sewer outfalls and another 100 metric tons in the remaining 897 sq nautical miles of the 1971 survey area.

On 27-28 June 1972, 11 mo after the first samples were taken, additional samples were obtained from seven of the original stations. Four of these stations were in deeper water, between 600

and 890 m deep, and 5 to 11 nautical miles from the sewer outfalls. Total DDT remained low in these stations averaging about 30 mg/m² of bottom, and the composition was essentially unchanged.

The remaining three stations, in areas of much higher pollution within 1.3 nautical miles of the sewer outfalls and in shallower water, showed some apparent changes in grams per square meter of bottom (Table 4).

TABLE 4.—Changes in composition (in grams per square meter of bottom) at stations 42-21, 43-21, and 42-19 in 11 mo.

Station year	Depth (m)	*o,p'*DDE DDMU	*p,p'*DDE	*o,p'*DDD / *p,p'*DDD	*o,p'*DDT / *p,p'*DDT	Total DDT
42-21						
1971	119	0.54	3.45	0.53	0.19	4.71
1972		2.09	3.36	0.61	0.23	6.29
43-21						
1971	33	0.46	1.80	0.33	0.14	2.73
1972		0.99	0.80	0.11	0.05	1.95
42-19						
1971	37	0.38	1.78	0.32	0.14	2.62
1972		0.82	0.71	0.16	0.13	1.82
Totals						
1971		1.38	7.03	1.18	0.47	10.06
1972		3.90	4.87	0.88	0.41	10.06

At station 42-21, DDT, DDD, and *p,p'*DDE remained relatively unchanged with a total of 4.2 g/m² of bottom in both years, while the *o,p'*DDE-DDMU peak increased by almost four times. At the two shallower stations, 43-21 and 42-19, DDT, DDD, and *p,p'*DDE decreased in 1972 to less than half its value in 1971, while the *o,p'*DDE-DDMU peak more than doubled. These changes could be caused by metabolism, by the addition of sewage deposits that were relatively free of DDT combined with metabolism, or even by the removal of a few centimeters of the deposits in the shallow-water areas without metabolism.

CONCLUSIONS

Total DDT in the bottom sediments in the ocean off southern California in an area of 911 sq nautical miles was estimated to be between 200 and 300 metric tons. Most of the total DDT was concentrated in a relatively small area within a few miles of the Los Angeles County sewer outfalls.

Total DDT in the top 10 cm of sediment ranged from 6,600 mg/m² of bottom near the sewer outfalls to about 1 mg/m² of bottom at the more distant stations.

Eighty-two percent of the total DDT was DDE; 10%, DDD; and 8%, DDT. Metabolism of DDT to DDD and DDE was more rapid in shallow waters and apparently very slow or lacking in deep, cold waters that were low in oxygen. Seven samples taken 11 mo later tended to confirm these findings.

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LITERATURE CITED

MACGREGOR, J. S.
1974. Changes in the amount and proportions of DDT and its metabolites, DDE and DDD, in the marine environment off southern California, 1949-72. Fish. Bull., U.S. 72:275-293.

MCCLURE, V. E.
1972. Precisely deactivated adsorbents applied to the separation of chlorinated hydrocarbons. J. Chromatogr. 70:168-170.

MCDERMOTT, D. J., AND T. C. HEESEN.
1974. Inventory of DDT in sediments. Annual report for the year ended 30 June 1974. Southern California Coastal Water Research Project, p. 123-127.

MCDERMOTT, D. J., T. C. HEESEN, AND D. R. YOUNG.
1974. DDT in bottom sediments around five southern California outfall systems. TM 217. Southern California Coastal Water Research Project, 54 p.

NATIONAL ACADEMY OF SCIENCES.
1971. Chlorinated hydrocarbons in the marine environment. Wash., D.C., 42 p.

WOODWELL, G. M., P. P. CRAIG, AND H. A. JOHNSON.
1971. DDT in the biosphere: Where does it go? Science (Wash., D.C.) 174:1101-1107.

AN ENERGETICS MODEL FOR THE EXPLOITED YELLOWFIN TUNA, *THUNNUS ALBACARES*, POPULATION IN THE EASTERN PACIFIC OCEAN

GARY D. SHARP AND ROBERT C. FRANCIS[1]

ABSTRACT

An energetics model (ENSIM) for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean is developed. Hydrodynamic properties and respiration-swimming work theory are combined to describe the energy expenditure due to swimming as a function of length for tunas. Growth and maintenance energetics are estimated and incorporated into a simplistic three process model. This model is interfaced with a population simulator (TUNPØP) and minimal energy requirements for the exploited yellowfin tuna population are derived for the simulated fishing years 1964-72. A theoretical unexploited population simulation is made, and the energy requirements by this population are compared with primary productivity rates and minimum micronekton (forage) standing stock availability. No obvious food limitation is indicated for yellowfin tunas greater than 40 cm, particularly since the exploited population is at a level of, at most, 50% of the unexploited biomass estimates. Population limitation processes are examined and indications that the recruitment rates are independent of exploited biomass are discussed.

The intent of studies of the population dynamics of exploited populations is the determination of the numbers, biomass, age structure, and potential yield from a population in order that rational management decisions can be made about the manner and rate of exploitation in order to insure efficient utilization of the resource. The validity of the resulting estimates of numbers, biomass, and potential yield is of concern to all those involved with the resource. Underestimations generally result in conservative efforts which are "safe" but not necessarily efficient. Overestimations can result in reduced profit margins or, in the extreme case, decimation of the resource.

Since the implementation of the program for conservation of yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific in 1966, a series of complex changes in the fishery have occurred which make production model results less and less comparable between years (Inter-American Tropical Tuna Commission Annual Reports). Attempts to account for multiple changes in the effort variables and corresponding but independent changes in the exploited population have resulted in serious interpretation problems as to the relative status of the exploited stock.

The economic and temporal problems inherent in the collection and analysis of biological data and the difficulties in representation of the biological processes in a useful mathematical manner has served to hinder utilization in the management procedures of what sparse physiological and ecological information is available.

In this report, an energy budget model is developed for the exploited yellowfin tuna population in the eastern Pacific Ocean within the Inter-American Tropical Tuna Commission's Yellowfin Regulatory Area (CYRA). The model will be used to assess the energy flow through the exploited yellowfin tuna population and also to compare the estimated utilization of energy by yellowfin tuna with the estimated primary productivity in the CYRA. Comparisons will be made using simulations of the population under both exploited and unexploited conditions.

The energy budget estimates are interfaced with an age dependent population simulation model (TUNPØP) (Francis 1974) resulting in a model of the energy utilization by semiannual recruitment cohorts. This model is referred to as ENSIM. The model incorporates the population parameter estimates and variables of TUNPØP and the empirical and estimated size dependent relationships for the major energy consuming processes, resulting in estimates of energy utilization rates. The development of the empirical

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relationships and the resulting formulations are presented so as to encourage research in the area so that improvements on this crude model can be made in the future.

THE MODEL

Population Dynamics

In an attempt to produce a new, more detailed method for evaluating the population or stock status it was decided that the development of TUNPØP, a biologically oriented population simulator, would be appropriate. The only available population data which are collected on a routine basis from within the fishery are length-frequency information from commercial catches. These data are collected according to criteria which require that the several time-area strata be sampled regularly and multiply, whenever possible (Hennemuth 1961). Data from the period 1963-72 have been analyzed and processed in the following manner.

The 12 existing sampling areas in the CYRA were reassembled into three major areas: N—North of lat. 10°N except east of long. 95°W; 5—North of lat. 5°N to the boundary of area N; S—all the CYRA south of the boundary of area 5 (see Figure 1). The areas N and S tend to have separable length-frequency distributions during any given time interval. Area 5 tends to have unique components as compared to N and S, but also contributions from both the other areas can be observed in the data from area 5. (This phenomenon is typically nonseasonal or noncyclic with respect to the fishing year and is probably related to population and environmental pressures within the separate areas.) In all three areas, recruitment components of a semestral nature are evidenced. The apparent relative abundance of these components within the areas changes seasonally and also between years (Table 1). Analysis of this phenomenon has made the separation of the semestral cohorts seem the first logical step when the available genetic, morphometric, and length-frequency data are considered.

The catch data associated with each length-frequency sample were obtained. The individual sample sets were then given relative values proportional to the contributions of the catches (in weight) from which they were drawn. From this basic processing of all the length-frequency data,

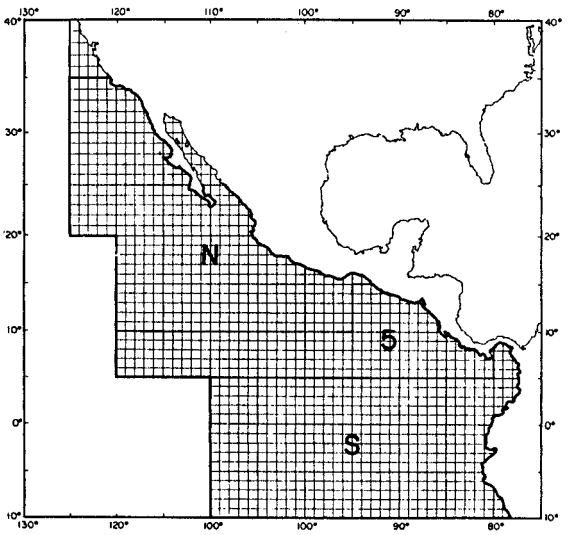


FIGURE 1.—The study area CYRA (Commission Yellowfin Regulatory Area) used in the simulations is enclosed in the dark outline. Three subareas were used in the preliminary population dynamics work in estimating cohort strength from the length-frequency and catch and effort data appropriate to these areas. N = North of lat. 10°N except inside of long. 95°W; 5 = North of lat. 5°N to boundary of N; S = all CYRA South of boundary of subarea 5.

estimates of the catch composition with respect to size-age for each fishing area were made and a growth curve was determined for each of two semestral cohorts. The two curves were essentially identical and warrant no further discussion here other than to say that from 40 to 145 cm fork length it is possible to give relative monthly ages to all individuals, given a length and corresponding date of capture. The labeling problem was handled such that any fish that was 40 cm from 1 January to 30 June is labeled S_A and correspondingly 40-cm recruits from 1 July to 31 December are labeled S_B. The cohorts are identified in relation to their recruitment year when they are 40 cm, not their spawned year. For example, a 40-cm fish caught in February 1969 is attributed to the cohort labeled S_A, 1969; and a 40-cm fish caught in October 1968 is attributed to the semester cohort labeled S_B, 1968. The two semestral groups can be treated as independent units in the population and provide a biological basis in assessment of population size with respect to size-age classes within the fishing year. The annual growth increment in the most often encountered cohort classes (40-140 cm) in the fishery appears to be about 32 cm/yr; therefore,

TABLE 1.—For the years 1964-71 the data are presented for the catch in short tons by semestral cohort in the three areas (N, 5, S) within the CYRA. Also given are the percent of the total catch (S_A + S_B + Big) by cohort within the areas. The category, Big, represents the fish of length $\bar{l}$ greater than 145 cm which we feel are not ageable under the present system. The percent of the individual semestral cohorts (S_A or S_B) caught in the three areas is also given. Note the erratic shifting of the cohort dominance (S_A or S_B) in the catch as well as the distribution of the cohorts between areas.

Year	North A	5 A	South A	Total A	North B	5 B	South B	Total B	Total A + B	Big
1964	27,452	9,401	5,209	42,062	33,561	5,881	17,515	56,957	99,019	2,921
% total A + B	26.9	9.2	5.1	41.2	32.9	5.8	17.2	55.9		2.9
% total A or B	65.3	22.4	12.4		58.9	10.3	30.8			
1965	18,967	13,512	6,406	38,885	24,064	14,164	8,386	46,614	85,499	4,543
	21.1	15.0	7.1	43.2	26.7	15.7	9.3	51.8		5.0
	48.8	34.7	16.5		51.6	30.4	18.0			
1966	7,769	23,128	20,176	51,073	10,292	11,394	14,771	36,457	87,530	3,626
	8.5	25.4	22.1	56.0	11.3	12.5	16.2	40.0		4.0
	15.2	45.3	39.5		28.2	31.3	40.5			
1967	20,699	9,564	7,664	37,927	29,482	8,572	11,867	49,921	87,848	1,802
	23.1	10.7	8.5	42.3	32.9	9.6	13.2	55.7		2.0
	54.6	25.2	20.2		59.1	17.2	23.8			
1968	16,361	23,921	13,552	53,834	33,917	22,132	3,128	59,177	113,011	1,602
	14.3	20.9	11.8	47.0	29.6	19.3	2.7	51.6		1.4
	30.4	44.4	25.2		57.3	37.4	5.3			
1969	22,437	20,034	9,030	51,501	34,887	29,587	5,648	70,122	121,623	4,888
	17.7	15.8	7.1	40.7	27.6	23.4	4.5	55.4		3.9
	43.6	38.9	17.5		49.8	42.2	8.1			
1970	39,197	15,942	10,529	65,668	43,476	13,257	11,125	67,858	133,526	9,176
	27.5	11.2	7.3	46.0	30.5	9.3	7.8	47.6		6.4
	59.7	24.3	16.0		64.1	19.5	16.4			
1971	12,372	18,719	14,453	45,544	17,357	25,283	15,712	58,352	103,896	9,277
	10.9	16.5	12.8	40.2	15.3	22.3	13.9	51.6		8.2
	27.2	41.1	31.7		29.7	43.3	26.9			

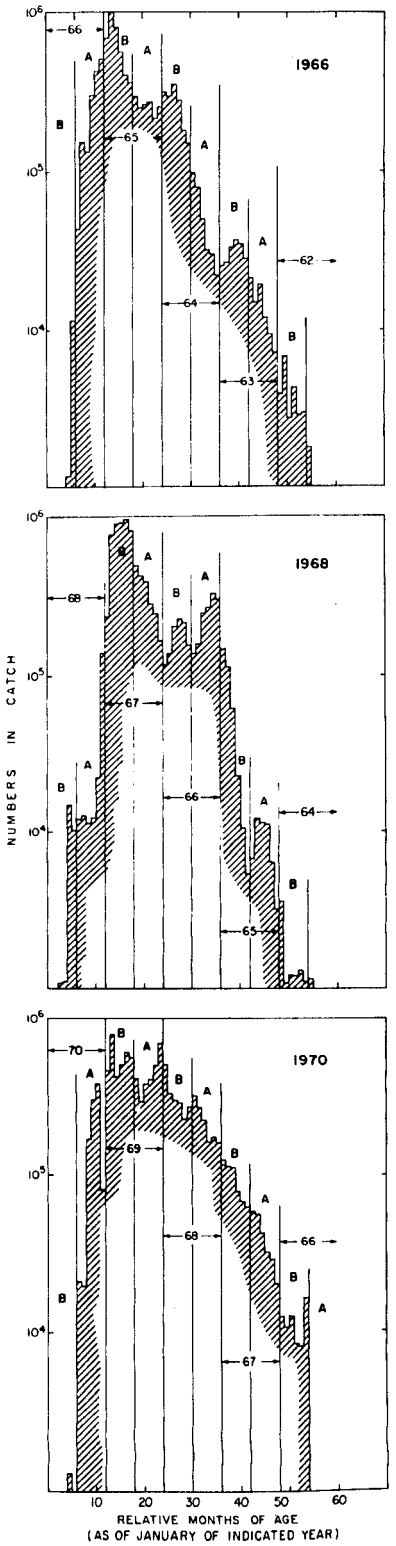
the mean lengths and modes of the two semesteral cohorts are separated by approximately 16 cm (Tomlinson and Sharp work in progress). A significant number of animals may shift from the leading edge of one labeled distribution into the trailing edge of the other, but we are assuming that countershifts are equally as probable and both are irreversible. An effect of shortening the sampling "season," since the implementation of regulations, has been to distort the apparent abundance of the two groups and merge the modal distributions into a single amorphous distribution (Figure 2).

The cohorts are treated independently by the model. Each cohort is considered to have a unique effect in the analysis of the net biomass and numbers estimates for a given fishing year. Differential exploitation of these cohorts can be determined from the catch-effort length-frequency data and as such warrants this disintegration technique as opposed to treating the year class as a single unit. We have, however, decided not to present in this report the area breakdown results in the simulations. When the cohorts are separated, it is possible to construct a catch table for each from the length-frequency sample data from the fishery. With this catch table and the catch data (yield) it is possible to determine the relative mortality (F) attributable to fishing, by assuming a constant natural mortality (M), a necessary, but perhaps poor assumption in the case of tunas due to the inherent rapid changes in ecological status as they grow. The Murphy cohort analysis procedure (Murphy 1965; Tomlinson 1970) was used for estimation of recruitment at first availability to the fishery (N_{40}). Using this approach we have generated the underlying population structure for the historical series we wish to represent.

Energetics

The energetics parameters for free-swimming predatory species such as the tunas must be size-related functions due to the broad range of sizes commonly encountered in the fishery; 1.3 kg to greater than 62 kg, or 40 cm to greater than 145 cm. In no case for fish has anyone measured physiological parameters from such a range of sizes.

Magnuson (1973) discussed the effect of gas bladders and lift surfaces on the velocity of obligatory swimmers such as the tunas. He determined the relationships between size and minimum velocity for maintenance of hydrostatic equilibrium for several scombrid species, including skipjack tuna, *Katsuwonus pelamis*, and *Thunnus albacares*. This work has provided a



basis for determining some of the relative energy expenditures in the population simulation study.

The energy utilization which is simulated in ENSIM is that attributable to 1) maintenance of metabolic stasis, 2) growth, and 3) swimming. Each is calculated independently and summed with the others to give an estimate of the total minimum energy utilized on a daily basis. No attempt has been made to evaluate energy expenditures due to gonad maturation or migratory behavior beyond the daily forage or flight behavior levels because of the inherent void in our knowledge of these processes in tunas.

Metabolic maintenance of stasis energy requirements (E_m) are difficult to assess under optimum conditions and are typically derived from extrapolation of O_2 consumption versus activity relationships to a zero activity level. The magnitude varies greatly between species and in general is a tenuous function of size and physiological state. It is essentially impossible to directly measure the stasis energy requirements of tunas due to their continuous swimming behavior. Estimates of E_m should not include the energy expenditures due to even minimum swimming activity if it is to be useful in the determination of energy expenditures due solely to swimming work.

The respiration rate attributable to tissue stasis can be estimated from the metabolic weight (W_{met}) of fish of length $\bar{l}$ from the equation:

$$E_m = 24\ k\ W_{\text{met}} \text{ (modified from Winberg 1960)}$$

where $W_{\text{met}} = (M_f)^{0.8}$,

and

$$M_f = 1.858 \times 10^{-2}\ (\bar{l})^{3.021} \text{ (grams) (Chatwin 1959)}$$

and where k is estimated to equal 1 cal/g h from data and estimates for other highly active fishes (Fry 1957; Winberg 1960). Therefore

$$E_m = 4.46 \times 10^{-1}\ (\bar{l})^{3.021} \text{ cal/day.}$$

FIGURE 2.—The numbers of fish caught in the fishing years 1966, 1968, 1970, as a function of their recruitment month, and age, relative to the fish of the year are graphically represented. Semestral (A, B) and annual cohort labeling is as indicated. Note the central tendency of the peaks within the semestral limits in the years 1966 and 1968. In these years the fishing "season" was quite long (>6 mo) as compared to 1970 (<3 mo), which combined with cyclic migratory behavior and subsequent availability of cohorts probably results in the drastic change from multimodality to the amorphous distribution seen in the 1970 data.

When estimates of the true stasis energy relations are finally available, they can be easily incorporated into the model.

Probably the most difficult process to define, estimate, and measure is that of growth. The energy requisite to growth (E_g) can be estimated minimally as the biomass gain per time period as converted to calories. This is a highly unsatisfactory method because of the many energy requiring steps between ingestion of a food organism and the consequential deposition of the materials assimilated into the living biomass of the growing organism (Phillips 1969).

One slight change in the accepted methodology of bioenergetic accounting which we will make is in our definition of specific dynamic action (SDA). If one is willing to accept that the SDA contributed little other than heat to the feeding organism, then it can be defined as the loss of energy due to the inefficiency of the digestive processes, including cost of transport, deamination, biosynthesis, and related processes. The rate of inefficiency (percent of SDA energy with respect to total ingested energy) is variable in most animals studied as a function of feeding level (Warren and Davis 1967) and environmental conditions (Warren 1971). In our definition of SDA we do not include the unavailable portion of foodstuffs.

For our purposes we will assume that growth of yellowfin tuna in the CYRA is relatively continuous with respect to season or environmental state. There are several assumptions involved in this basic tenet which require some discussion. Tunas are highly endothermic animals, and Carey and Teal (1966) have shown the presence of a relatively high efficiency heat exchange (conservation) mechanism in tunas. This suggests that tunas are likely to be somewhat independent of ambient temperatures in that the temperature variability encountered within the core of these fishes is likely less than the ambient variability. Their large mass (>1 kg) would contribute to thermal stability over a wide ambient change (Neill and Stevens 1974).

Observations of temperature dependent activity indicate a lower activity as temperature decreases in small yellowfin tuna (<50 cm, <2.5 kg) at a Q_{10} of near 2 (Neill, pers. commun.). This size of yellowfin tuna is rarely encountered in the CYRA at temperatures below 23°C and is found aggregated on the warm side of the north-south surface temperature cline including this temperature, indicating some preference for temperatures near 23°C. Preliminary studies of effects of the environmental characteristics on the abundance and availability of 40- to 70-cm yellowfin tuna in the CYRA indicate a direct relationship between the 23°C isotherm depth of the average number of fish per school, and the overall availability of these fish to surface fishing gear (Inter-American Tropical Tuna Commission 1975).

All this is emphasized to indicate the limited range of temperatures likely to be affecting the metabolic rates of yellowfin tuna as compared to that affecting smaller species without the complex stabilization mechanisms (heat exchangers, etc.) as is the typical situation in fishes.

The relative activity, mobility, and distribution with respect to temperature of yellowfin tuna can be used as supportive background for assuming a relatively stable growth energy availability as they developed, bringing us to the conclusion that a first approximation of the SDA can be made with respect to the energy equivalent to the biomass change on a daily basis. From studies discussed by Paloheimo and Dickie (1966) and Warren and Davis (1967) on several species and estimates by Kitchel et al.[2] for *K. pelamis*, it appears that SDA probably accounts for 30-40% of the total consumed calories which could be part of the growth process. We have, therefore, assumed that E_g is going to equal the equivalent caloric value of the tissues plus the SDA which will be given by the relation

$$\text{SDA} = \frac{\text{(Biomass change in grams per day)}}{2}$$

where, if 1 g is calorically equivalent to 1.46 kcal (Kitchell et al. see footnote 2) then

$$E_g = \frac{3}{2}\,\text{Biomass change (grams)}(1.46\ \text{kcal/g})$$
$$= 2{,}190\ \text{kcal/kg growth.}$$

Smit (1965) has provided the mathematical basis for our determinations of energy output and caloric requirements due to swimming. He shows that:

$$\text{Power} = \frac{(M_e\, g\, S)\ (143 \times 10^3)}{3{,}600}\ \frac{\text{g cm}^2}{\text{s}^3} \qquad (1)$$

[2]Kitchell, J. F., W. H. Neill, and J. J. Magnuson. Bioenergetics of skipjack tuna, *Katsuwonus pelamis*. Manuscr.

where M_e is the efficiency of the muscle tissue when converting chemical energy to mechanical work; S is the respiration due to activity in mg O_2/h; and g is the acceleration due to gravity (981 cm s^{-2}). The propulsion efficiency is assumed to be 0.90 (Lighthill 1970) and is included in the resulting muscle efficiency figure.

For our purposes we assume M_e to be 0.18. Therefore from Equation (1)

$$S = \frac{(\text{Power})\ (3{,}600\ \text{s/h})}{(0.18)\ (143 \times 10^3\ \text{g cm})\ (981\ \text{cm/s}^2)}\ \text{mg O}_2\text{/h}. \tag{1A}$$

From the hydrodynamics theory (Streeter 1962)

$$\text{Power} = \frac{\rho}{2} A\ V^3\ C_d\ \frac{\text{g cm}^2}{\text{s}^3}$$

where ρ = the density of seawater (1.025 g/cm^3)
$A = 0.4(\bar{l})^2$ from Bainbridge (1961) (cm^2)
V = is derived from Magnuson's empirical relationships between $\bar{l}$ and species velocity $\bar{V}$ (cm/s)
C_d = the coefficient of total drag of the fish, which is derived from an empirical relation including the results of studies by Pyatetskiy (1971).

We can therefore rewrite the equation so that respiration due to swimming is equal to

$$S_s = \frac{\rho\ A\ \bar{V}^3\ C_d}{2\ (7{,}017.66)}$$

$$= 2.59 \times 10^{-5}\ (\bar{l})^2\ (\bar{V})^3\ C_d\ \text{mg O}_2\text{/h}. \tag{2}$$

We now have an Equation (2) of three elements for which we have solutions for two ($\bar{V}$ and C_d) as functions of the third ($\bar{l}$) given below.

$\bar{V}$ Determination

From Magnuson (1970), the relation for the minimum velocity (V_{100}) for sustained hydrostatic equilibrium by tunas is given as

$$V_{100} = \left[\frac{L_t}{\frac{\rho}{2}(C_{L_f} A_{f_t} + C_{L_k} A_k)}\right]^{1/2} \tag{3}$$

where C_{L_f} = the coefficient of lift for the pectoral fins
A_{f_t} = the total lifting area of the pectoral fins (cm^2), $\log A_{f_t} = -1.2154 + 1.87 \log \bar{l}$
C_{L_k} = the coefficient of lift of the keel
A_k = the lifting area of the keel (cm^2), $\log A_k = -2.7033 + 2.26 \log \bar{l}$ (cm^2)
L_t = the total weight of the fish in seawater (dynes). (L_t values are obtained by multiplying M_f values by appropriate constants as provided by Magnuson (1973) by species and weight class.)
M_f = mass of the fish = 1.858×10^{-2} $(\bar{l})^{3.021}$ (grams).

Determination of the Coefficient of Total Drag C_d

The relation between the total drag coefficient (C_d) and the Reynolds number (Re) for Atlantic bonito, *Sarda sarda*, reported by Pyatetskiy (1971) is taken to be representative *in form* for scombriform fishes. $Re = \frac{\bar{l}\ \bar{V}}{v}$, where v is the kinematic viscosity of seawater or 0.01 cm^2/s; $\bar{l}$ is the fish fork length in centimeters; and $\bar{V}$ is the fish velocity in centimeters per second.

An analytical expression was derived for estimating the C_d values in the following manner: R. Gooding (Gooding et al. 1973) of the National Marine Fisheries Service Honolulu Laboratory, Honolulu, Hawaii reported respiration rates for unfed *K. pelamis* from 32 to 36 cm fork length, swimming at or near minimum velocities (V_{100}). From these data it was possible to calculate C_d given the observed respiration rate (S_{total}) was 431.5 mg O_2/kg h and $\bar{l}$ = 35 cm. The minimum velocity (V_{100}) = 59.1 cm/s and $Re = 2.07 \times 10^5$ at this velocity.

For skipjack tuna of $\bar{l}$ = 35 cm, W_{met} = 200.5 g, so that

$$S_m = 60.0\ \text{mg O}_2\text{/h}$$

$$S_{\text{total}} - S_m = S_s = 371.5\ \text{mg O}_2\text{/h}.$$

From Equation (2) it is now possible to determine that

$$C_d = \frac{371.5}{2.59 \times 10^{-5}\ (35)^2\ (59.1)^3} = 0.057.$$

This value of C_d was related to the values graphically displayed by Pyatetskiy (1971) and what was assumed to be a good approximation

of the total drag on the test animals was derived relative to his graphed observations as a function of Re. From Re, one can determine the approximate coefficient of total drag (C_d) from the relation:

$$C_d = 0.262\, e^{-4.805 \times 10^{-6} Re}. \quad (4)$$

Gooding also reported respiration data for skipjack, ranging from 45 to 53 cm, swimming at or near $\overline{V}_{100}$ where S_{total} = 1,403 mg O_2/h. These test animals had also been deprived of food for 24 h. Assuming $\bar{l} \cong 50$ cm:

$$W_{\text{met}} = 523.5 \text{ g}; V_{100} = 70.5 \text{ cm/s};$$
$$Re = 3.525 \times 10^5;$$
$$S_m = 156 \text{ mg } O_2\text{/h};$$
$$C_d = 0.262\, e^{-4.805 \times 10^{-6} (3.525 \times 10^5)} = 0.048.$$
$$\therefore S_s = 2.59 \times 10^{-5} (50)^2 (70.5)^3 (0.048)$$
$$= 1{,}233 \text{ mg } O_2\text{/h}.$$
$$S_s + S_m = S_{\text{total}} = \{1{,}233 + 156\} \text{ mg } O_2$$
$$= 1{,}389 \text{ mg } O_2\text{/h, (expected)}$$
$$\text{where } S_{\text{total}} = 1{,}403 \text{ mg } O_2\text{/h, (observed)}$$
$$\text{leaving} \quad 14 \text{ mg } O_2\text{/h, (difference).}$$

The Relation (4) we have used for C_d as a function of Re appears to be adequate for our purposes.

Within the factors M_e and C_d there are an inseparable pair of modifying effects which must be accounted for, but which are essentially indeterminate at the present state of the art. One is the mechanical propulsion efficiency, and the other is the effect of the short-term flux of the rates of acceleration due to caudal fin position and velocity within a single tail beat cycle on the "average" calculations of M_e and C_d. The M_e and C_d values are continuous variables within the tail beat cycle and are inextricably bound together. Where in the integration and estimation of these two values the trade off is made is inconsequential due to the equal and direct effect of the estimate of one on the other value. Until either value is measured and fixed, the other coefficient is relative and therefore not necessarily realistic.

The effect of velocity on propulsion efficiency is probably great in tunas (and other large organisms) due to several processes, including local heating phenomena and subsequent contraction rate increases of the muscle fibers (Walters 1962; Sharp and Vlymen[3]). The graded increase in utilization of white muscle fibers as velocity is increased should result in generalized heating and increased overall efficiency of the energy conversion processes in the muscles. This and other effects may indeed account for the considerable efficiency changes in work done as compared to respiration rate when extended periods of white muscle utilization are monitored (Kutty 1968).

The higher scombrids (*Auxis, Euthynnus, Katsuwonus,* and *Thunnus*) have incorporated, in various designs, a subcutaneous vascular system which is the distribution mechanism for transport of arterial and venous blood to and from the warm swimming musculature (Kishinouye 1923). The direct transport of "warm" venous blood to the fish's surface probably affects the hydrodynamics of the fish and contributes to the dynamic flux of the C_d value. Since no data are available for these phenomena, they have to be ignored in this treatment of the swimming energetics, but future laboratory studies should not ignore or delete these potential effectors.

Considering the range of possible error in estimating both muscle efficiency and/or the coefficient of total drag, the close agreement between observed and expected respiration rates indicates that we have useful estimates of energy requirements.

The only available respiration-activity data from tunas is for *K. pelamis*. Assuming that Magnuson's (1973) empirical relations and density multipliers are representative of the relative hydrodynamic status of the several species, these relations should give a similarly good approximation of energy consuming processes in *T. albacares* as they appear to give for *K. pelamis*.

The three continuous energy consuming processes are, therefore, roughly accountable using the previously described relations. The conversion of oxygen consumption to caloric utilization is made on the basis that 3.359 cal are available from 1 mg O_2. Apparently the major energy consumption process is swimming, including feeding and flight behavior. The energy expended is a function of the velocity $\overline{V}_{\text{typ}}$ which is

[3]Sharp, G. D., and W. J. Vlymen III. The relation between heat generation, conservation and the swimming energetics of tunas. Manuscr.

in turn a function of the length of the individuals (see Figure 3). In Magnuson's (1973) relationships the variables necessary for a solution for the minimum velocity are $\bar{l}$ and the density of the fish. Magnuson (1973) provided data for fish density (in the form of empirically derived multipliers) by weight class for several species including yellowfin tuna. We have extrapolated his data to fit our size distribution with an asymptotic lower limit of fish density at 1.06 g/cm^3 reached by 120-cm fish.

We are assuming that the animals have their pectoral fins 75% extended all of the time that they are in nonfeeding-flight behavior, hence $C_{L_f} = 0.75$, and that the keel surface is 85% effective so that $C_{L_k} = 0.85$. This results in a fish that is swimming somewhat faster on the average than its V_{100} or minimum velocity. These values are "best guess" estimates and as such, represent only minor changes in the appropriate direction as opposed to using absolute minimum energy utilization in the population simulation. Magnuson's V_{100} for a 50-cm yellowfin tuna is 50.91 cm/s. Solving for the "typical" velocity under our "best guess" conditions results in a $\overline{V}_{typ}$ of 58.29 cm/s.

We have set a "typical" feeding-flight speed at 3 m/s. This is an integrated average that includes all velocities above $\overline{V}_{typ}$ and includes the burst speed forays. Since the energy required for different speeds is proportional to a cubic function of the velocities, it should be noted that the most probable velocity is less than 2 m/s, since the energy requirements for a few short bursts of up to 10 body lengths/s rapidly increase the overall energy utilization. With this in mind,

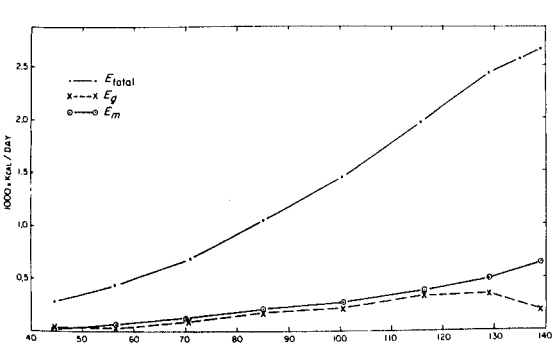


FIGURE 3.—The energy utilization (in kcal/day) for growth (E_g), maintenance (E_m), and the total ($E_g + E_m + E_s = E_{total}$) energy utilization are portrayed as functions of length $\bar{l}$.

we have attributed 95% of the day or 22.8 h of the day to $\overline{V}_{typ}$ requirements and 5% or 1.2 h to $\overline{V}_{feed}$ behavior. This is not to say that the fish are limited to 1.2 h/day of feeding but that on the average the increased velocity due to external stimuli are exhibited for this period. One suspects that the feeding of large and small tuna is entirely different in nature, but for simplicity and since no data are available, it is not unreasonable to assume that the relative effectiveness of feeding is somewhat similar over the life history of the animals. Based on these estimates we hope to have contrived a "reasonable" fiction for use in our model. The need for better estimates is obvious.

MODELING RESULTS

The model ENSIM computes the caloric requirement of each semestral cohort in the exploited population, by quarter of the fishing year. Summary data are listed after each quarterly output which differentiate the semester A cohort caloric expenditure from that of the semester B cohort, and a composite total expenditure is listed (see Table 2). An annual summary for 1972 is also generated and an example is presented in Table 3.

Initial biomass and numbers, yield in weight and numbers, gross growth, and average biomass are tabulated for each quarter, and summary tables are generated for the individual semestral cohorts as well as composite values. The biomass of food ingested per day is generated for each cohort, assuming 1.00 kcal (Paloheimo and Dickie 1966) are available per gram food ingested. The minimum percent biomass ingested per day with respect to the cohort biomass is also calculated for each cohort (see Figure 4). The caloric requirements for maintenance, swimming (at $\overline{V}_{typ}$, $\overline{V}_{feed}$), and growth are tabulated by size of the average animal in each cohort in the simulation by quarter (see Table 4).

We have simulated the fishing years 1964-72 and included the best available estimates for cohort strength, fishing effort, and availability parameters. We have also simulated a nonexploited population which was recruited at the average level for the data from the last 5 yr which includes all the population indicated or expected from inside our study area (see Figure 5). From Figure 5, the plot of the average annual biomass estimate, one can readily see the effect of fishery

TABLE 2.—ENSIM output for quarter three of the 1972 simulation is presented. The calculated kilocalories expended by each cohort (age-class) in the exploited population is given. The appropriate averages ($N\bar{l}$, weight (kg) and $\bar{l}$) are also listed for each cohort. Summary data are given by cohort and for both cohorts summed together.

Age	Maintenance	Swimming V_{typ}	Swimming V_{feed}	E_g	E_{total}	$N\bar{l}$	Weight (kg)	$\bar{l}$
1	.634079E+11	.640848E+11	.280680E+12	.377884E+11	.445961E+12	.186707E+08	.176060E+01	.444182E+02
2	0.	0.	0.	0.	0.	0.	0.	0.
3	.889373E+11	.776321E+11	.354145E+12	.431443E+11	.563858E+12	.141776E+08	.379126E+01	.572565E+02
4	0.	0.	0.	0.	0.	0.	0.	0.
5	.501222E+11	.307991E+11	.185411E+12	.264195E+11	.292751E+12	.521301E+07	.646561E+01	.683217E+02
6	0.	0.	0.	0.	0.	0.	0.	0.
7	.463850E+11	.196178E+11	.157393E+12	.237458E+11	.247142E+12	.292458E+07	.120872E+02	.840421E+02
8	0.	0.	0.	0.	0.	0.	0.	0.
9	.352487E+11	.120881E+11	.111902E+12	.138239E+11	.173063E+12	.151084E+07	.195812E+02	.985929E+02
10	0.	0.	0.	0.	0.	0.	0.	0.
11	.176499E+11	.514907E+10	.528273E+11	.601945E+10	.816457E+11	.537688E+06	.300053E+02	.113553E+03
12	0.	0.	0.	0.	0.	0.	0.	0.
13	.928307E+10	.302828E+10	.263712E+11	.297797E+10	.416605E+11	.208937E+06	.438055E+02	.128704E+03
14	0.	0.	0.	0.	0.	0.	0.	0.
15	.465814E+09	.166772E+09	.128095E+10	.796327E+08	.199317E+10	.868343E+04	.554414E+02	.139141E+03
16	0.	0.	0.	0.	0.	0.	0.	0.
17	.695863E+09	.256764E+09	.189348E+10	.249005E+08	.287100E+10	.122020E+05	.598477E+02	.142709E+03
18	0.	0.	0.	0.	0.	0.	0.	0.
Total A	.153438E+12	.102566E+12	.565646E+12	.729892E+11	.894639E+12			
Total B	.158758E+12	.110257E+12	.606257E+12	.810347E+11	.956307E+12			
Total	.312196E+12	.212823E+12	.117190E+13	.154024E+12	.185095E+13			

TABLE 3.—The 1972 annual summary data are listed which give the yield in number and weight for each of the semestral cohorts as well as the kilocalories utilized in the year by the cohorts and the combined sum.

	Yield numbers	Yield weight (metric ton)	Kilocalories utilized
Total S_A	0.491282 E + 7	0.653748 E + 5	3.85 E + 12
Total S_B	0.534418 E + 7	0.640257 E + 5	2.28 E + 12
Total $S_A + S_B$	0.102570 E + 8	0.129427 E + 6	7.13 E + 12

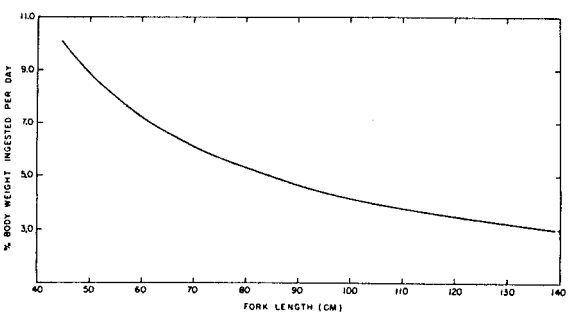


FIGURE 4.—The amount of food required per day is given in percent body weight of the individual yellowfin tuna of length $\bar{l}$.

TABLE 4.—The estimates of the daily energy utilization (in kcal/day) for maintenance, swimming at V_{typ} and V_{feed}, growth, and the total daily energy utilized due to all these activities is provided for the average individual of length $\bar{L}$ and weight W for each cohort in the population during each quarterly time period. The average number of individuals present in each cohort is given in the column headed N. The semestral cohorts are separated (Total A or Total B) and the energy utilization estimates summed and listed for each. The composite estimates ($S_A + S_B$) are also listed (Total).

Age	Maintenance	Swimming V_{typ}	Swimming V_{feed}	E_g	E_{total}	N	W	L
1	.377346E+02	.381374E+02	.167035E+03	.224882E+02	.265395E+03	.192145E+08	.176060E+01	.444182E+02
2	0.	0.	0.	0.	0.	0.	0.	0.
3	.667851E+02	.604781E+02	.267903E+03	.225852E+02	.417752E+03	.125166E+08	.359406E+01	.562530E+02
4	0.	0.	0.	0.	0.	0.	0.	0.
5	.116280E+03	.663364E+02	.423896E+03	.451705E+02	.651683E+03	.863385E+07	.718813E+01	.707599E+02
6	0.	0.	0.	0.	0.	0.	0.	0.
7	.181619E+03	.751903E+02	.613072E+03	.902863E+02	.960167E+03	.562388E+07	.125513E+02	.850967E+02
8	0.	0.	0.	0.	0.	0.	0.	0.
9	.271052E+03	.911480E+02	.853897E+03	.112988E+03	.132909E+04	.387916E+07	.207038E+02	.100429E+03
10	0.	0.	0.	0.	0.	0.	0.	0.
11	.381489E+03	.112386E+03	.113300E+04	.169496E+03	.179638E+04	.252689E+07	.317387E+02	.115684E+03
12	0.	0.	0.	0.	0.	0.	0.	0.
13	.497444E+03	.162886E+03	.141127E+04	.180946E+03	.225255E+04	.174290E+07	.442248E+02	.129111E+03
14	0.	0.	0.	0.	0.	0.	0.	0.
15	.596227E+03	.213496E+03	.163949E+04	.101935E+03	.255115E+04	.113565E+07	.554626E+02	.139159E+03
16	0.	0.	0.	0.	0.	0.	0.	0.
17	.639329E+03	.236943E+03	.173697E+04	.340073E+02	.264725E+04	.783083E+06	.605190E+02	.143236E+03
18	0.	0.	0.	0.	0.	0.	0.	0.
Total A	.156184E+04	.595451E+03	.459307E+04	.395600E+03	.714596E+04			
Total B	.122612E+04	.461550E+03	.365347E+04	.384302E+03	.572544E+04			
Total	.278796E+04	.105700E+04	.824654E+04	.779903E+03	.128714E+05			

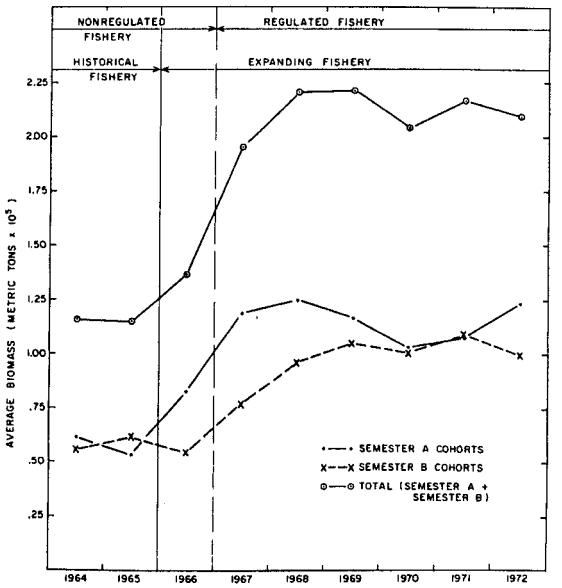


FIGURE 5.—The average biomass estimate of the exploited yellowfin tuna population in the CYRA is shown. The historical fishery label indicates the coastal fishery which operated prior to 1965; the expanded fishery indicates the process of seaward areal expansion which dramatically changed the estimates of exploited biomass from 1966 until approximately 1968. Fishery regulation was implemented in September 1966. The simulation of the unexploited populations yielded estimates of the average biomass for the two cohorts to be S_A = 282,400 metric tons; S_B = 272,700 metric tons; $S_A + S_B$ = 555,100 metric tons. Recruitment was assumed to be consistent with recent levels.

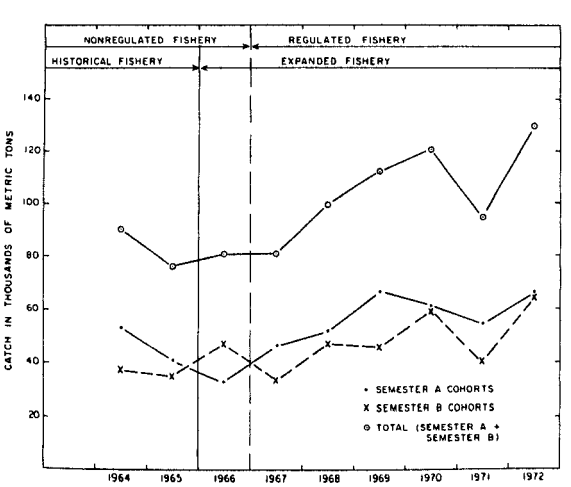


FIGURE 6.—The catch in metric tons of yellowfin tuna from the CYRA is shown for the study period. The cohorts and total catch are indicated by symbols as in Figure 5.

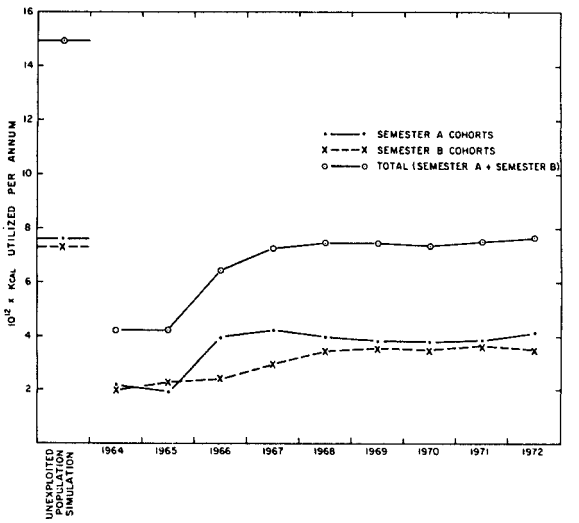


FIGURE 7.—Estimates from ENSIM of the kilocalories used per year by yellowfin tuna in the exploited CYRA population for the 1964-72 period.

growth (areal expansion) on population size estimates. From Figures 6 and 7 it is obvious that the catch has great fluctuations (e.g., 1971) but the energy flow seems to have stabilized in the exploited population estimates. This may be artifactual but we think it may be significant to attempt interpretation.

The ratio of yield in weight to gross growth is another interesting indicator (Figure 8). Note the differential rate of exploitation of the semestral cohorts through time prior to 1967. The S_A and S_B cohorts became approximately equally exploited in this respect about 1967 or at about the end of the changes in fishery strategy and when

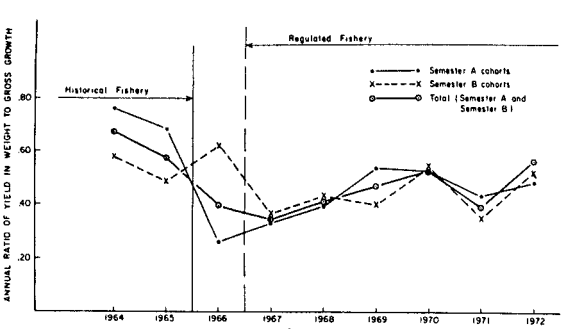


FIGURE 8.—The ratio of the yield in weight (catch) to gross growth for the years 1964-72. Note the relative similarity of the levels of the cohorts respective ratios in the regulated years as compared to the preregulated years.

regulation occurred. The indication is that since approximately 1969, the biomass and exploitation levels on the semestral cohorts have somehow paralleled a somewhat uniform energy utilization by the two cohorts, whereas from 1966 until 1969 a larger semester A biomass was under exploitation compared to the semester B cohort. The large discrepancies in biomass caught as compared to gross growth in the early data (1964-65) compared to the recent data (1969-72) may be an indicator of the relative health of the stocks under exploitation in recent years in contrast to the preregulatory years.

SPECULATIONS

The utility of simulation studies lies in the process of linking together observations, using generalized principles where possible, to generate testable hypotheses which ultimately lead to resolution of cause and effect relationships. As examples, from the results of the simulation model ENSIM, hypotheses were conceived concerning the relative importance of forage organisms, primary productivity and the size of the animals with respect to recruitment limitations.

Food as a Population Regulator

The availability of food is classically attributed the role of limiting population size. We do not intend to assail this premise, but intend only to show that the most probable source of limitations is at very early ages in tunas (<40 cm), and not on the late juvenile or adult population.

Forage for tunas is generally considered to be in the micronekton size range (1-10 cm). It probably extends upwards to 30 cm or more in length for larger sizes of tunas (Magnuson and Heitz 1971; Perrin et al. 1973). Tunas eat largely crustaceans, fishes, and cephalopods in most regions (Alverson 1963; Magnuson and Heitz 1971; Perrin et al. 1973). These organisms are poorly sampled by micronekton sampling devices.

The EASTROPAC cruises sampled from our study area over the year 1967 and early 1968. Productivity, micronekton, and most physical and chemical properties which are linked to biological productivity were sampled. EASTROPAC data (Blackburn et al. 1970) indicate that the average minimum micronekton night haul contained 5 ml of micronekton per 10^3 m^3 of water sampled. The samples represent a 200-m water column.

The surface area of the CYRA is estimated to be 5,012,643 sq nautical miles or 1.696×10^{13} m^2. The minimum available forage is therefore

$$(1.696 \times 10^{13}\ m^2)\ (200\ m)\ \left(\frac{5\ ml\ forage}{10^3\ m^3}\right)$$
$$= 1.696 \times 10^{13}\ cc.$$

If 1 cm^2 forage has approximately 1 g or 1.25 kcal caloric equivalency, then one should expect that there is a minimum forage availability of 1.25 kcal/m^2 or assuming 80% utilization efficiency of these calories by predators (Winberg 1960), 1.0 kcal/m^2 are present for metabolic utilization.

Owen and Zeitzschell (1970) in their analysis of EASTROPAC data also show that the primary productivity averages 169 mg carbon m^{-2} day^{-1} over long. 119°-112°W, 219 mg carbon m^{-2} day^{-1} at long. 105°W, and 282 mg carbon m^{-2} day^{-1} along long. 98°W. They also indicate coastal effects as being the probable cause of the eastward increase in productivity. The average productivity over the entire study area was 205 mg carbon m^{-2} day^{-1}.

The energetic equivalent value for 1 mg carbon fixation is 11.4 cal (Platt and Erwin 1973), so that the average caloric productivity is 2,340 cal/m^2 day (or 2.34 kcal/m^2 day).

We have seen that the minimum estimate of the micronekton standing stocks caloric value is 1,250 cal/m^2, indicating that the probable daily turnover rate is less than 125 cal/m^2 so that maintenance of this stock is not unreasonable if the primary production is 2,340 cal/m^2 day.

The yellowfin tuna population simulation procedure based on average Murphy recruitment estimates of the 1966-71 S_A and S_B cohorts indicates that an unfished population (exhibiting a stable age structure) would have the biomass of 600,000 metric tons (6.0×10^{11} g). Assuming that the yellowfin tuna (YF) are distributed proportionally over the forage:

$$\frac{6.0 \times 10^{11}\ g\ YF}{1.696 \times 10^{13}\ m^2} = 3.54 \times 10^{-2}\ g\ YF/m^2$$
$$= 35.4\ mg\ YF/m^2;$$

$$35.4\ mg\ YF/m^2 \times 1.2\ cal/mg\ YF = 42.5\ cal/m^2.$$

Assuming the average caloric consumption by the yellowfin tuna population per day to be 10% of its caloric biomass, a somewhat higher than realistic estimate, daily utilization in calories would be 4.25 cal/m^2 day. The results of the ENSIM estimates of the total calories utilized per year for the unexploited population was 14.96 × 10^{15} cal/annum, so that the resulting utilization per square meter day is given by:

$$\frac{14.96 \times 10^{15} \text{ cal/annum}}{(365 \text{ day/annum})\,(1.696 \times 10^{13} \text{ m}^2)} = \frac{2.5 \text{ cal}}{\text{m}^2 \text{ day}}.$$

The results of the simulations of the exploited fishery for the years 1964-72 yield estimates of less than 50% of this figure as the energy utilization by the yellowfin tuna population. One would expect the true values of caloric utilization to lie somewhere in the range from approximately 1.5 cal/m^2 day to the upper value of 4.25 cal/m^2 day.

With the primary productivity estimated to be at an average level of 2.34 kcal/m^2 day and forage standing stock utilizable caloric values averaging at a minimum of 1.00 kcal/m^2, it seems hardly likely that yellowfin tuna are food limited from the 40-cm recruitment size.

This brings up the problem of how the eastern tropical Pacific yellowfin tuna population is limited. This, of course, is best taken in perspective. Population limitation examples are typically taken from terrestrial populations and extrapolations made to ecosimilar strategies in closed systems such as lakes and estuaries where primary productivity is greatly affected by season, and indeed can be determined to be the limiting factor in population numbers and biomass.

In those marine animals where density dependent growth functions are evidenced there is generally a two-dimensional limitation imposed such that crowding is likely to affect each individual. For filter-feeding organisms, such as herring and menhaden, the density dependent function is easily conceptualized.

One needs only to examine the relative abundance of food available to highly mobile predatory species which feed opportunistically on organisms ranging in size from 1 to 30 cm, which are available on a relatively continuous basis in a tropical system, to see that dogma general to terrestrial, estuarine, limnetic, two-dimensional substrate tied, or filter-feeding animal ecology does not generally apply to the 40- to 140-cm yellowfin tuna.

There are, however, several possibilities concerning the survival of yellowfin tuna from larvae to 40 cm which would certainly fit into the schemes which typically limit species. Since they are probably particulate feeders (e.g., do not undergo ecometamorphoses at early ages from filter feeders to predators), it can easily be seen that they are victims of the availability of concentrations of food at smaller sizes because of their relative lack of mobility. If a 40-cm tuna requires 10-20% of its body weight per day to maintain, as compared to 3-5% in large yellowfin tuna, then one can hypothesize that the smaller predators must consume even greater amounts due to the pressures of very rapid growth, feeding activity, and competition with peers, indicating that they are more likely severely affected by density of both conspecifics and food than are the larger sized fish.

Another consideration is the size distribution of the forage organisms. It is obvious that there are considerably larger amounts of the smaller food organisms than the bigger sizes, which would perhaps indicate that the real density competition pressures are on the intermediate sizes (vis. 10-40 cm) as compared to the postlarval sizes. This brings us to the next important process, larval survival.

Spawning Survival Versus Population Biomass

For our hypothesized unexploited population of 600,000 metric tons of individuals from 40 to 140 cm fork length, we can calculate the requisite number of postlarval survivors which must be generated each year to maintain this stock at equilibrium. Assuming 40-cm yellowfin tuna are approximately 7 mo of age and that the survival rate is constant for all ages after postlarval transformation and is approximately equal to $e^{-0.8}$ on an annual basis (Hennemuth 1961), the number of postlarval survivors each year is given by the relation

$$N_s = N_{40} e^{0.8\left(\frac{7}{12}\right)}.$$

If N_{40} is approximately 2.12 × 10^7 individuals per year in cohort S_A, and 2.06 × 10^7 in cohort S_B, then there are approximately 6.67 × 10^7 survivors/yr. If we assume that they are aggregated

spatially but not temporally (there are two cohorts of 3.33×10^7 postlarvae spread approximately evenly over the year), approximately 9.13×10^4 postlarvae enter the system daily. (This is the equivalent of nearly 1% reproductive success of either one 155-cm female or five 87-cm females.)

The relative fecundity of yellowfin tuna is given by Joseph (1963) to the following:

$$\text{Number of eggs} = 8.955 \times 10^{-3}\, l^{2.791}$$

where l is the fork length of the fish in mm.

If we assume the average spawning female to weigh 25 kg and we estimate the presence of 175,000 metric tons of females of reproductive age in our unexploited population, then the equivalent number of reproductive females is approximately equal to 7×10^6. These females would be an average of 107 cm in length and therefore:

$$(8.955 \times 10^{-3}((1{,}070^{2.791}) (7 \times 10^6 \text{ females}) = 1.79 \times 10^{13} \text{ eggs produced.}$$

So if 6.67×10^{-7} postlarvae start the process we need invoke only 3.72 postlarval survivors per million eggs spawned. This estimate is conservative due to the assumption that females only spawn once per year, whereas they could spawn more often. (No evidence for or against multiple spawnings is in existence for yellowfin tuna.) It does, however, seem likely that spawning success (survival to postlarvae) is greater than 3.72 individuals per million eggs produced (Sette 1943; Farris 1961). It is also important to mention that all attempts at relating spawning biomass to recruitment estimates for yellowfin tuna in the CYRA have been futile. This could be due to error in either, or both, estimates of spawning biomass and recruitment and/or the possibility that environmental conditions indeed override any obvious relationships.

These comments are presented to point up the likelihood that the density dependent factors for limiting yellowfin tuna abundance are probably more effective on the egg to larvae to juvenile stages than at 40 cm or more. The larvae to 40-cm fish are likely very narrowly distributed in the water column (approximating a two-dimensional distribution) due to thermal and energetic requirements. The recruitment at 40 cm in the highly productive regions such as the periphery of the Costa Rica Dome and the Panama Bight-Ecuador coastal regions can perhaps be best explained by the high productivity levels in these regions which ranges from 500 to 700 mg carbon m^{-2} day^{-1} as compared to the 205 mg carbon m^{-2} day^{-1} average CYRA carbon fixation rate, in conjunction with the relatively shallow oxygen minimum and thermal optima which probably act to compress the available habitat toward the surface. If one could invoke the ability of yellowfin tuna to climb a food gradient, a simple volume change in the preferred thermal-oxygen regime combined with a negatively correlated food gradient could result in the observed coastal "emergence" of recruits, which "grow out" of their previous thermal-oxygen limitations as they develop, and exploit a significantly wider niche than they could as relatively poikilothermal entities at sizes below 40 cm.

To summarize, larval tunas are relatively immobile and for survival are probably dependent on aggregations of food resources. The ability of tunas, particularly postlarval sizes, to detect food gradients is unknown, but may indeed account for the easterly trend in abundance of recruits. The wider distributions of larger fish (postrecruits) probably is a response to competitive feeding problems and changing physiological capabilities. These larger fish are increasing their daily demands but are gaining in adaptive physiological and morphological characteristics which widen their niche as compared to smaller sizes. Their mass and mobility insure their ability to move rapidly from low to high availabilities of food resources, in response to seasonal and areal fluctuations in productivity, perhaps accounting for the cyclic migratory behavior observed in their first few years in the fishery. The relative offshore surface distribution of the larger fish (>40 cm) may be roughly correlated with the depth distribution of the 22°-23°C isotherms, a relationship which we are now starting to study. As the larger fish grow in mass, they can afford deeper and longer forays into colder than optimal zones with low O_2 availability to obtain larger and more calorific food sources; and by thus increasing the maximum excursion depth, competition is likely to be less severe. The disaggregation of larger sized fish into smaller schools (number of individuals) may be accounted for by these effects. The large yellowfin tuna in the offshore areas are certainly concentrated at the surface

over highly productive regions where their main sources of competition are probably porpoise and bigeye tuna, *Thunnus obesus*. The porpoise-tuna composite likely indicates the optimum availability of fish and squid in the eastern tropical Pacific. It is obvious from the Perrin et al. (1973) studies that the two *Stenella* species and tunas coexist but tend to feed differentially. The tuna diet shares most of the organisms found in both species indicating that they are less selective and/or feed throughout the water column.

No data support the concept of food limitation for population size in yellowfin tuna in post-recruit sizes and in most cases the arguments tend toward the opposite conclusion. Since no stable relationship can be found to exist between recruitment and spawning biomass, it is unlikely that reproductive success is affected by spawning biomass at the population levels we are experiencing. More probable is that the environmental parameters are more important in regulating the absolute numbers of surviving larval or juvenile yellowfin tuna which are recruited to the fishery.

In the future, we plan to incorporate the available productivity and environmental data (temperature, oxygen, etc.) with a more complete version of this model. We hope to determine the environmental correlates with the fluctuations in the catch, effort, and length-frequency data generated from the fishery on yellowfin tuna. Preliminary studies have been encouraging (Inter-American Tropical Tuna Commission 1975) and point up the need for data on the thermal preferences (perhaps indicating energetic optima) and the levels of environmental variability which can be sensed and therefore compensated for by the several tuna species at the various developmental stages in their life cycles. Also obvious is the need to work with smaller areas and corresponding population segments rather than assuming "average" conditions in environmental and population parameters. The ultimate goal of these studies is the development of predictive tools for use in assessing likely catch conditions as well as the basic distributional properties of the tunas. The use of unsupported guesses based on overviews which integrate vast areas with significant oceanographic and population structure differences may do little more than obscure the existing relationships which are important to this goal. The application of the crude model we have described in this study will depend upon the development of better estimates of the physiological parameters and appropriate use of the areal breakdown in the population simulator. Studies of trophic dynamics and competition interactions would help complete the picture necessary to "efficiently" manage a dynamic resource. We hope to generalize, where possible, the relationships which arise from these analyses in order to provide a useful descriptive tool as well as a hypothesis testing device for studying the occurrence, abundance, and availability of tunas in the world ocean.

LITERATURE CITED

ALVERSON, F. G.
1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 7:293-396.

BAINBRIDGE, R.
1961. Problems of fish locomotion. Symp. Zool. Soc. Lond. 5:13-32.

BLACKBURN, M., R. M. LAURS, R. W. OWEN, AND B. ZEITZSCHEL.
1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. (Berl.) 7:14-31.

CAREY, F. G., AND J. M. TEAL.
1966. Heat conservation in tuna fish muscle. Zoology 56:1464-1469.

CHATWIN, B. M.
1959. The relationships between length and weight of yellowfin tuna (*Neothunnus macropterus*) and skipjack tuna (*Katsuwonus pelamis*) from the Eastern Tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 3:305-352.

FARRIS, D. A.
1961. Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (*Trachurus symmetricus*). U.S. Fish Wildl. Serv., Fish. Bull. 61:247-279.

FRANCIS, R. C.
1974. TUNPØP, a computer simulation model of the yellowfin tuna population and the surface tuna fishery of the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 16:235-279.

FRY, F. E. J.
1957. The aquatic respiration of fish. *In* M. E. Brown (editor), The physiology of fishes, Vol. 1, p. 1-63. Academic Press Inc., N.Y.

GOODING, R., E. POE, AND C. NAGAMINE.
1973. Tuna newsletter No. 9 July 1973. Natl. Mar. Fish. Serv., Southwest Fisheries Center, La Jolla, Calif.

HENNEMUTH, R. C.
1961. Size and year class composition of catch, age and growth of yellowfin tuna in the eastern tropical Pacific Ocean for the years 1954-1958. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 5:1-112.

INTER-AMERICAN TROPICAL TUNA COMMISSION.
1975. Annual Report of the Inter-American Tropical Tuna Commission, 1974. [In Engl. and Span.] 169 p.

JOSEPH, J.
1963. Fecundity of yellowfin tuna (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) from the Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 7:257-292.

KISHINOUYE, K.
1923. Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric., Imp. Univ. Tokyo 8:293-475.

KUTTY, M. N.
1968. Respiratory quotients in goldfish and rainbow trout. J. Fish. Res. Board Can. 25:1689-1728.

LIGHTHILL, M. J.
1970. Aquatic animal propulsion of high hydromechanical efficiency. J. Fluid Mech. 44:265-301.

MAGNUSON, J. J.
1966. Continuous locomotion in scombroid fishes. (Abstr.) Am. Zool. 6:503-504.
1970. Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. Copeia 1970:56-85.
1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull., U.S. 71:337-356.

MAGNUSON, J. J., AND J. G. HEITZ.
1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. Fish. Bull., U.S. 69:361-370.

MURPHY, G. I.
1965. A solution of the catch equation. J. Fish. Res. Board Can. 22:191-202.

NEILL, W. H., AND E. D. STEVENS.
1974. Thermal inertia versus thermoregulation in "Warm" turtles and tunas. Science (Wash., D.C.) 184:1008-1010.

OWEN, R. W., AND B. ZEITZSCHELL.
1970. Phytoplankton production: Seasonal change in the oceanic eastern tropical Pacific. Mar. Biol. (Berl.) 7:32-36.

PALOHEIMO, J. E., AND L. M. DICKIE.
1966. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Board Can. 23:869-908.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

PHILLIPS, A. M., JR.
1969. Nutrition, digestion, and energy utilization. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 1, p. 391-432. Academic Press, N.Y.

PLATT, T., AND B. ERWIN.
1973. Caloric content of phytoplankton. Limnol. Oceanogr. 18:306-310.

PYATETSKIY, V. YE.
1971. Hydrodynamic swimming characteristics of some fast marine fish, from translation of monograph; Kiev, Bionika, Russian, No. 4; 1970, p. 3-120. Hydrodynamic Problems of Bionics. JPRS 52605, p. 24-31.

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including the growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv., Fish. Bull. 50:149-237.

SMIT, H.
1965. Some experiments on the oxygen consumption of goldfish (*Carassius auratus L.*) in relation to swimming speed. Can. J. Zool. 43:623-633.

STREETER, V. L.
1962. Fluid mechanics. 3rd ed. McGraw Hill Book Co., N.Y., 555 p.

TOMLINSON, P. K.
1970. A generalization of the Murphy catch equation. J. Fish. Res. Board Can. 27:821-825.

WALTERS, V.
1962. Body form and swimming performance in the scombroid fishes. Am. Zool. 2:143-149.
1966. The "problematic" hydrodynamic performance of Gero's great barracuda. Nature (Lond.) 212:215-216.

WARREN, C. E.
1971. Biology and water pollution control. W. B. Saunders Co., Philadelphia, 434 p.

WARREN, C. E., AND G. E. DAVIS.
1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. *In* S. D. Gerking (editor), The biological basis for freshwater fish production, p. 175-214. John Wiley & Sons Inc., N.Y.

WINBERG, G. G.
1956. [Rate of metabolism and food requirements of fishes.] Nauchnye Tr. Belorussk. Gos. Univ. Minsk, 253 p. (Transl. 1960. Fish. Res. Board Can., Transl. Ser. 194.)

APPENDIX.—GLOSSARY OF TERMS

A = wetted surface area of the fish.

A_{f_t} = the total lifting area of the pectoral fins.

A_k = the total lifting area of the keel.

C_{L_f} = the coefficient of lift of the pectoral fins.

C_{L_k} = the coefficient of lift of the keel.

C_d = coefficient of total drag of fish of length $\bar{l}$ which includes an inseparable efficiency term involving acceleration processes during continuous swimming.

E_g = the daily caloric expenditure of fish of length $\bar{l}$ attributable to growth in the form of positive changes in mass.

E_m = the daily caloric expenditure of fish of length $\bar{l}$ to maintain metabolic stasis.

E_s = the daily caloric energy expenditure of fish of length $\bar{l}$ utilized by swimming work, a function of swimming velocity ($\bar{V}_{\text{real}}$).

F = the instantaneous mortality rate due to fishing.

g = acceleration due to the force of gravity.

k = the rate of oxygen consumption due to metabolic stasis of 1 g of respiring tissue, not doing external work.

l = the length of a fish from snout to fork of tail in millimeters.

$\bar{l}$ = the fork length of a fish in centimeters.

L_t = the total weight of a fish in seawater of density ρ, in dynes.

M = the instantaneous natural mortality rate.

M_e = the efficiency of muscle when converting chemical energy to mechanical work.

M_f = mass of the fish in grams where for yellowfin tuna: $M_f = 1.858 \times 10^{-2} (\bar{l})^{3.021}$ (Chatwin 1959).

$N_{\bar{l}}$ = the estimated number of individuals of length $\bar{l}$.

N_s = the number of postlarval survivors from a spawning.

N_{40} = the number of recruits at 40 cm.

Re = the Reynolds number.

ρ = the density of seawater, in this work ρ = 1.025 g/cm^2.

S = the rate of oxygen consumption due to swimming activity, from the power equation of Smit (1965).

S_A = recruitment cohort label for all individuals that attain 40 cm fork length from 1 January to 30 June of each year.

S_B = recruitment cohort label for all individuals that attain 40 cm fork length from 1 July to 31 December of each year.

S_m = the oxygen consumption rate of fish of length $\bar{l}$ attributable to metabolic stasis.

S_s = the oxygen consumption rate of a fish of length $\bar{l}$ attributable to swimming energy expenditures.

$S_{\text{total}} = \dfrac{S_m + S_s}{M_f \times 10^{-3}}$ = respiration rate attributable to swimming and metabolic stasis energy expenditures.

υ = the kinematic viscosity of seawater.

V = the constant velocity of a fish, in centimeters per second.

$\bar{V}$ = the estimated integrated velocity of a fish of length $\bar{l}$ used in determining Re and C_d, and in the estimation of S.

V_{100} = the minimum swimming speed of a fish of given species and $\bar{l}$ for maintenance of hydrostatic equilibrium (Magnuson 1973).

$\bar{V}_{\text{typ}}$ = the velocity which is "typical" of the swimming speed of a fish of length $\bar{l}$.

$\bar{V}_{\text{feed}}$ = the velocity which is meant to integrate all energy expenditures due to fish swimming faster than $\bar{V}_{\text{typ}}$, including short bursts in feeding or flight behavior (assumed to be 3 m/s).

$\bar{V}_{\text{real}}$ = the average daily velocity of a fish of length $\bar{l}$, = $0.95\,\bar{V}_{\text{typ}} + 0.5\,\bar{V}_{\text{feed}}$.

W_{met} = the metabolic weight of a fish, in grams (Winberg 1960).

EFFECTS OF TEMPERATURE AND SALINITY ON THE SURVIVAL OF WINTER FLOUNDER EMBRYOS

CAROLYN A. ROGERS[1]

ABSTRACT

A series of experiments was performed to determine the optimum temperature and salinity for incubating winter flounder, *Pseudopleuronectes americanus*, embryos. Eggs in lots of 50 were subjected to a 0.5 to 45‰ salinity range and a 3° to 14°C temperature range in a total of 67 salinity-temperature combinations. Highest proportion of viable hatches occurred at 3°C over a salinity range of 15 to 35‰. At temperatures above 3°C, the optimal range was 15 to 25‰. Viable hatch decreased with increasing temperature.

The winter flounder, *Pseudopleuronectes americanus* (Walbaum), an important species in local New England commercial and sport fishing industries, occurs from Chesapeake Bay to the northern shore of the Gulf of St. Lawrence (Bigelow and Schroeder 1953). The adults disperse into cooler offshore waters as temperatures rise, but move back into embayments and estuaries in the fall. Spawning occurs in shoal waters of these areas from February to mid-May with the maximum in Rhode Island waters occurring in March (Perlmutter 1947; Bigelow and Schroeder 1953; Pearcy 1962). Winter flounder spawn demersal eggs, which range from 0.74 to 0.85 mm in diameter when fertilized. Hatching occurs in 15 to 18 days at 3° to 4°C, the temperature normally encountered in the natural environment (Bigelow and Schroeder 1953).

This paper reports the optimum temperature and salinity ranges for the development and survival of winter flounder embryos and larvae and discusses the relationship between the two factors as it affects embryo development. An earlier study (Scott 1929) indicated some of the effects of temperature and salinity as separate factors on the hatching of winter flounder eggs but presented no data on possible interaction of the two. Forrester and Alderdice (1966) and Alderdice and Forrester (1968, 1971a, b) working on the effects of temperature and salinity on the embryonic development of the English sole, *Parophrys vetulus*; petrale sole, *Eopsetta jordani*; and Pacific cod, *Gadus macrocephalus*, respectively, indicated a relationship between the two factors, which influenced early development, hatching time, and viable hatch.

METHODS AND MATERIALS

Ripening adult winter flounder were captured by trawl on 29 October 1970 at a depth of 23 to 30 m in Block Island Sound. Surface waters were 15°C, and a bottom temperature of 12°C was estimated for that area (Colton and Stoddard 1973). The live fish were transported to the laboratory where they were held in running water aquaria until they were ripe in early February when ambient water temperature was 3°C. The fish were fed clam worms, earthworms, and cut up clam during the holding period. Eggs were stripped into polyethylene dishpans, fertilized, and coated with diatomaceous earth to prevent clumping, according to the technique of Smigielski and Arnold (1972). Fertilized eggs were transferred to incubation baskets and held at 3°C in running seawater (32‰ salinity) for 24 h when normal development could be distinguished. Day 1 embryos were in the early blastoderm stage when the experiments were started. Three separate experiments were run at salinities ranging from 0.5 to 45‰ and at temperatures of 3° to 14°C. Each experiment was run in duplicate.

To avoid bias, all salinities were prepared by adding Instant Ocean[2] salts to normal seawater (32‰) to bring the salinity up to 50‰. Experimental salinities were then made by diluting the stock salinity with distilled water. Each salinity

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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was checked with a refractometer to within ±0.15‰ of the test salinity. The test salinities were cooled to the ambient seawater temperature (3°C) at which the eggs were incubated for the first 24 h.

Eggs in lots of 50 were counted into 100-ml polyethylene beakers filled with the test salinities. The beakers were covered with fitted 50-mm plastic disposable culture dish bottoms to eliminate evaporation and placed in thermostatically controlled water baths at the experimental temperatures. Dead eggs or larvae were removed daily and examined for stage of development.

Daily observations were made on the development of embryos. The time of hatching and the duration of the hatching interval were noted so that mean hatching time (time from fertilization to 50% hatch) could be calculated. Abnormal larvae (those with curvature of the spine, abnormal yolk sacs, or enlarged fin folds) were noted and counted as nonviable since their chance of continued survival was considered to be small. Prematurely hatched or aborted larvae were also considered nonviable in calculations. Such larvae were easily recognized since they were short, thickened, often curled, and in no way resembled a normal healthy larva.

Each experiment was terminated when all eggs had either hatched or died, and when the larvae could be judged normal or abnormal. From this information, total percentage hatch (percentages of eggs producing live larvae) as well as percentage viable hatch (percentage producing viable or normal larvae) was calculated. Salinities were checked at the end of each experiment.

The experiment was set up as a factorial design. However, replications at different factor combinations were unequal and there were missing data at 3°C due to equipment malfunction. In view of this, a mean value of the replicates was computed for each factor combination and values for the missing data at 3°C were predicted from the hyperbolic equation describing the actual data at 3°C. The resultant design was a 2 factor, 6 × 12 (6 levels of temperature and 12 levels of salinity) factorial design with no replicates. Duncan's multiple range test (Steel and Torrie 1960) was used to compare the mean survivals for each temperature and salinity condition.

RESULTS

The results of these experiments indicate that winter flounder embryos are euryhaline, with best survival occurring between 10 and 30‰ but with some survival from 5 to 40‰. Hatching occurred at all temperatures tested, but the lower temperatures produced the highest survival. Incubation time and hatching interval were decreased by increased temperatures and higher salinities. Abnormal development occurred particularly at extremes of salinity but was also influenced by temperature.

Effects of Salinity and Temperature on Viable Hatch

Results of the temperature-salinity experiments (Table 1) indicated an optimal salinity range between 15 and 25‰ for temperatures above 3°C and between 15 and 35‰ for 3°C (Figure 1, Table 2). Viable hatch was highest at 3°C and lowest at 14°C with similar survival rates at 5, 7, and 12°C for all salinities. Percentage survival at 10°C follows a similar curve at salinities of 25‰ and above, but was between 15 and 30% lower than that of other temperatures at 20‰ and below. At 3°C, high survival (>78%) occurred from 15 to 35‰, but survival decreased sharply at all other temperatures for salinities above 25‰.

TABLE 1.—Number of winter flounder eggs at each of 67 temperature-salinity combinations. Number of replicates shown in parentheses.

Salinity (‰)	Temperature (°C) 3	5	7	10	12	14
0.5	100 (2)	100 (2)	100 (2)	100 (2)	100 (2)	100 (2)
5.0	100 (2)	300 (6)	400 (8)	300 (6)	300 (6)	300 (6)
7.5		100 (2)	100 (2)	100 (2)	50 (1)	100 (2)
10.0	100 (2)	300 (6)	400 (8)	300 (6)	300 (6)	300 (6)
15.0		300 (6)	400 (8)	200 (4)	300 (6)	300 (6)
20.0	100 (2)	300 (6)	400 (8)	300 (6)	300 (6)	300 (6)
25.0		200 (4)	300 (6)	300 (6)	300 (6)	200 (4)
30.0	100 (2)	300 (6)	400 (8)	300 (6)	300 (6)	300 (6)
35.0	100 (2)	300 (6)	400 (8)	300 (6)	300 (6)	300 (6)
37.5		100 (2)	100 (2)	100 (2)	100 (2)	100 (2)
40.0		200 (4)	300 (6)	200 (4)	200 (4)	200 (4)
45.0	100 (2)	100 (2)	100 (2)	100 (2)	100 (2)	100 (2)

Influence of Temperature and Salinity on Total and Viable Hatch

The influence of temperature and salinity is shown in the percentages of mean total hatch and mean viable hatch (Table 3). There is a sharp decrease in mean total hatch and mean viable hatch at temperatures over 3°C, while these means approximate a normal distribution at the salinities tested. The mean percentage of abnormal larvae calculated from total and viable hatch data shows

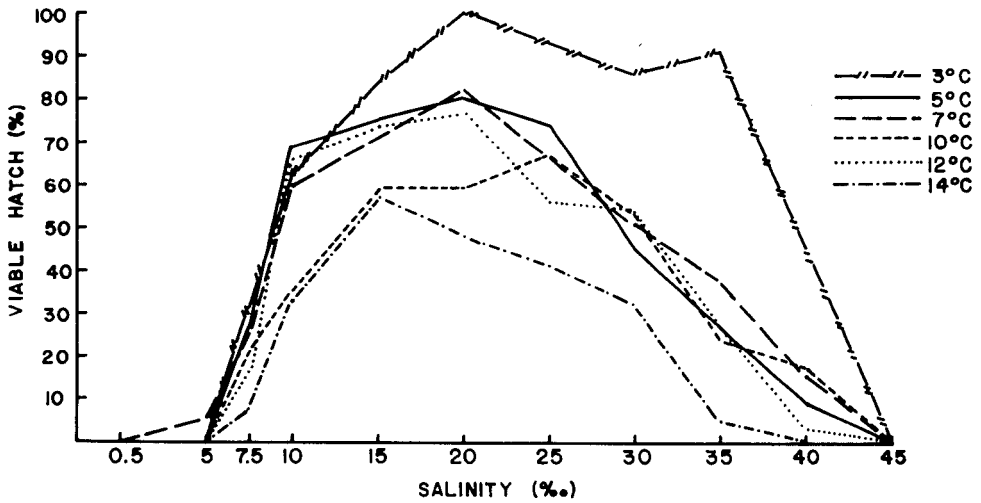

FIGURE 1.—The effects of temperature and salinity on the percent viable hatch of winter flounder embryos.

TABLE 2.—Mean percent total and viable ( ) hatch at the various temperature-salinity combinations.

Salinity (‰)	Temperature (°C) 3	5	7	10	12	14
0.5	0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
5.0	26 (0)	6.3 (0)	14.5 (6.5)	23.0 (0)	0.0 (0)	0.0 (0)
7.5	—	58.0 (26.0)	48.0 (26.0)	49.0 (21.0)	46.0 (17.0)	23.0 (7.0)
10.0	88 (61)	79.7 (65.7)	71.5 (57.8)	59.0 (32.0)	82.7 (65.3)	55.3 (32.7)
15.0	92 (84)	79.3 (75.7)	76.5 (71.0)	71.0 (57.0)	77.0 (69.0)	69.3 (57.3)
20.0	100 (99)	82.3 (79.3)	83.8 (82.0)	70.3 (61.0)	78.3 (68.0)	61.3 (48.7)
25.0	—	75.5 (74.0)	69.3 (66.7)	74.0 (66.5)	62.0 (56.5)	57.5 (42.0)
30.0	74 (64)	54.7 (45.7)	59.8 (51.3)	50.0 (43.7)	63.0 (54.7)	48.7 (32.3)
35.0	84 (67)	31.3 (27.3)	42.8 (37.5)	31.0 (24.0)	47.0 (34.5)	21.0 (7.7)
37.5	—	40.0 (37.0)	86.0 (78.0)	57.0 (52.0)	38.0 (16.0)	5.0 (0)
40.0	—	19.0 (9.5)	63.0 (15.7)	34.0 (17.0)	26.0 (3.5)	0.0 (0)
45.0	0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)

TABLE 3.—Means and ranges for percent total and viable hatches and mean abnormal hatches for each salinity at all temperatures, and each temperature at all salinities.

Item	Mean % total hatch (Range)	Mean % viable hatch (Range)	Mean abnormal hatch[1] (%)
0.5‰	No hatch	No hatch	
5.0‰	12.8(2.3-26.0)	1.6(0-6.5)	11.2
7.5‰	44.8(23.0-58.0)	19.4(7.0-26.0)	25.4
10.0‰	72.7(55.3-88.0)	52.4(32.0-65.7)	20.3
15.0‰	77.5(69.3-92.0)	72.3(57.0-84.0)	5.2
20.0‰	79.3(61.3-100)	73.0(48.7-99.0)	6.3
25.0‰	67.7(57.5-74.0)	61.1(42.0-74.0)	6.6
30.0‰	58.4(48.7-74.0)	48.6(32.3-64.0)	9.8
35.0‰	42.9(21.0-84.0)	33.0(7.7-67.0)	9.9
37.5‰	45.2(5.0-86.0)	36.6(0-78.0)	8.6
40.0‰	15.1(9.5-21.0)	11.4(3.5-17.0)	3.7
45.0‰	No hatch	No hatch	
3°C	77.3(26.0-100)	62.5(0-99.0)	14.8
5°C	51.7(6.3-82.3)	44.0(9.5-79.3)	7.7
7°C	57.3(14.5-86.0)	49.3(6.5-82.0)	8.0
10°C	48.1(2.3-74.0)	37.4(0-66.5)	10.7
12°C	56.3(13.0-82.7)	42.7(3.5-69.0)	13.6
14°C	42.6(5.0-69.3)	28.5(0-57.3)	14.1

[1]Mean abnormal hatch = mean percent total hatches − mean percent viable hatches.

no trend with temperature, but a high percentage of abnormal larvae for salinities of 10‰ and below. Lowest percentages for abnormal larvae were for salinities between 15 and 35‰. The low percentage for 40.0‰ reflects low hatching rates and mortality during embryonic stages and does not reflect values which can be compared with salinities of 37.5‰ and below.

Analysis of variance performed on the survival data indicate that salinity and temperature are both significant factors (Table 4). Because of missing data (Table 1), it was not possible to test for interaction between the two factors; however, by examining the data, especially as it is expressed in Figure 1, it is reasonable to conclude that an interaction does occur. The multiple comparison of means indicates significant differences between hatch means at various temperatures and

TABLE 4.—Analysis of variance for the effects of temperature and salinity on the survival and hatching of winter flounder embryos.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	71	69,248.75		
Salinity	11	51,935.36	4,721.39	31.5**
Temperature	5	9,078.78	1,815.76	12.2**
Residual	55	8,234.61	149.72	

**significant at $P = 0.005$.

TABLE 5.—Duncan's multiple comparison of means for temperature-salinity studies of winter flounder embryos. (Means with similar symbols denote similar mean survival percentages.)[1]

Temperature (°C)	Mean survival (%)	Salinities (‰)	Mean survival (%)
3	56.1√	0.5	0.0√
5	36.2*	5.0	1.1√
7	41.1*√	7.5	21.6*
10	31.4*∞	10.0	53.7°
12	32.4*∞	15.0	69.9†
14	18.9∞	20.0	74.3†
		25.0	67.4†
		30.0	52.6°
		35.0	35.6∞
		37.5	40.3∞
		40.0	15.3*
		45.0	0.0√

[1]$P = 0.05$.

salinities and allows a grouping of each in order of its significance (Table 5). The grouping of the hatch means for variations in both temperature and salinity coincides closely with viable hatch curves illustrated in Figure 1.

Incubation Time and Duration of Hatching Interval

The time to 50% hatch and the total range of hatching time for each temperature and salinity combination are recorded in Table 6. Figure 2 illustrates the time to 50% hatch and the mean incubation time for each temperature and salinity respectively. The mean hatching interval

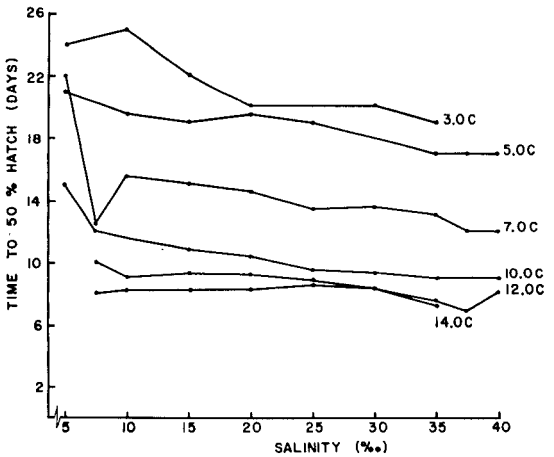

FIGURE 2.—The effects of salinity on the time to 50% hatch of winter flounder embryos.

ranges from 25 days at 3°C (10‰) to 7 days at 12° and 14°C (37.5 and 35‰ respectively). Individual eggs hatched in as few as 5 days in most salinities at 12° and 14°C, but took as long as 31 days at 3°C (10‰). An inverse relationship for temperature with respect to the duration of hatching time is evident.

There is also a trend toward the same inverse relationship with respect to salinity as can be seen in Figure 2 where the time to mean 50% hatch at all temperatures decreased slightly with increasing salinities. This phenomenon of greater hatching time at low salinities was noted in Pacific cod eggs by Forrester and Alderdice (1966). When salinity means versus incubation time is considered by least squares regression, there is a low correlation coefficient and a regression relationship is not applicable (Figure 3). However, temperature means have a high correlation coefficient and there is a strong regression relationship present.

TABLE 6.—Time in days to 50% hatch. Range of hatching interval in days shown in parentheses. NH denotes no hatch.

Temperature (°C)	Salinity (‰) 5.0	7.5	10.0	15.0	20.0	25.0	30.0	35.0	37.5	40.0
3	24		25 (19-31)	22 (19-27)	20 (19-25)		20 (17-25)	19 (16-25)		
5	21	20 (16-20)	20 (17-29)	19 (17-25)	19 (17-29)	19 (22-24)	18 (13-25)	17 (11-25)	16 (14-16)	16 (14-16)
7	22	13 (10-16)	15 (12-23)	15 (12-23)	15 (12-25)	13 (8-17)	14 (8-21)	13 (11-19)	12 (12-14)	12 (8-14)
10	15	12 (10-14)	12 (7-15)	11 (9-14)	10 (7-16)	9 (7-17)	9 (5-13)	9 (8-10)	9 (7-10)	9 (7-10)
12	NH	10 (7-12)	9 (5-10)	9 (7-12)	9 (7-10)	9 (5-10)	8 (5-10)	8 (5-10)	7 (5-10)	8 (5-10)
14	NH	8 (5-10)	8 (5-10)	8 (6-10)	8 (5-10)	8 (5-10)	8 (5-10)	7 (5-10)	NH	NH

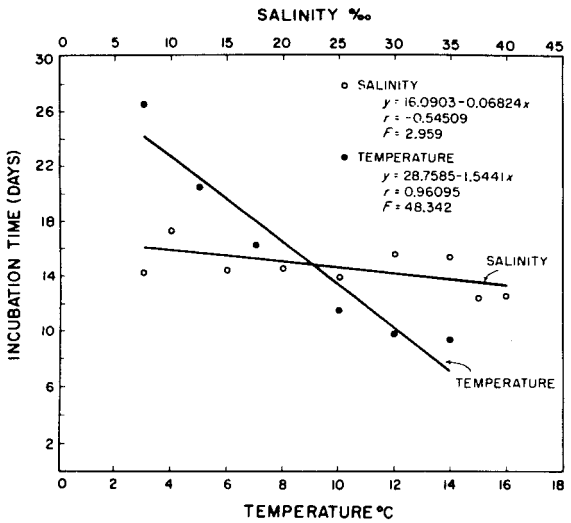

FIGURE 3.—The mean hatching time of winter flounder embryos for each temperature and salinity.

Effects of Temperature and Salinity on Embryonic Development

In each of the three experiments, general observations were made on the eggs, embryos, and larvae (Figure 4). No development occurred in a salinity of 0.5‰; however, the eggs swelled approximately 20% before death occurred. A diameter increase of 8 to 10% was also observed in eggs held at 5‰. Below 10°C, embryos held in 5‰ appeared to develop normally, then died just prior to hatching. At 10°C and above, most of the embryos died during gastrulation. Embryos held in a salinity of 10‰ had the highest mortalities just prior to hatching and at hatching; many larvae were observed dead partly emerged from the chorion. Mortality occurred throughout development at 12° and 14°C.

In salinities between 15 and 30‰, most mortalities occurred just prior to hatching, although

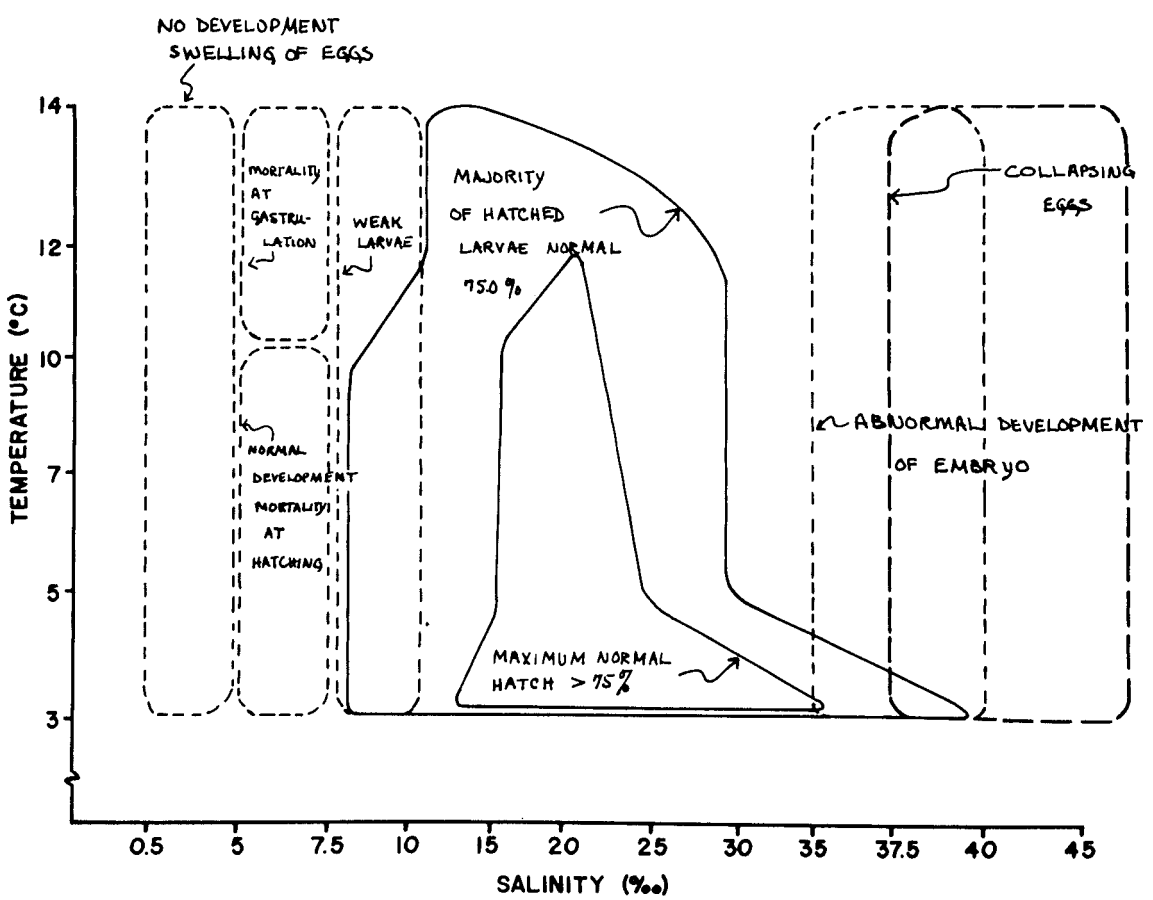

FIGURE 4.—The qualitative effects of temperature and salinity on the development and hatching of winter flounder embryos.

at temperatures of 10°C and above some mortalities usually occurred during gastrulation. At salinities of 35 to 40‰, abnormal development of the embryos was observed. The embryos were shorter and thicker than normal and died just prior to hatching. Collapsing eggs were noted at 37.5‰ and above. Embryos incubated at 40‰ died during gastrulation and throughout development at all temperatures while all embryos held at 45‰ died during gastrulation. At both 40 and 45‰ embryos exhibited shrinkage and often collapsed.

DISCUSSION

The results indicate that although temperature and salinity are both significant, the major effect of increased temperature is to decrease the incubation period, whereas salinity is the factor which has more effect on the successful hatching and survival of winter flounder embryos and larvae (Figure 4, Table 4). It is apparent however, that an interaction between the two does occur since, at the optimum experimental temperature (3°C), the salinity range over which high percentages of viable hatches occurred was extended by 10‰ (Figure 1). At higher than optimal experimental temperatures, the survival curves appear to be dictated primarily by salinity; however, survival occurs over a broad enough range that the embryos and larvae can be described as euryhaline with regard to the natural environment in which they are normally spawned. At all temperatures tested, there was a decrease in incubation time at higher salinities, a phenomenon which was also reported in studies done on *Clupea harengus* (Holliday and Blaxter 1960) and Pacific cod (Forrester and Alderdice 1966). Those authors speculated that the relationships of temperature and salinity with hatching are dependent on conditions that minimize the energy required of the embryos in maintaining osmotic equilibrium with their environment. Salinity also appears to influence the time of embryo mortality. Observations on eggs indicated that mortality usually occurred either at gastrulation, in salinities of 40 and 45‰ at all temperatures, or just prior to hatching in the lower salinities. Battle (1930) noted increased mortality of the four bearded rockling, *Enchelyopus cimbrius*, at hatching in low salinities and she attributed this to poorly developed tail musculature. McMynn and Hoar (1953), working with embryos of the Pacific herring, *Clupea harengus pallasi*, observed that with the closing of the blastopore at the end of grastrulation, embryos had a greater ability to tolerate low salinities. However, many embryos died just prior to hatching or when partly emerged. Holliday (1965, 1969) observed a similar occurrence in cod, *Gadus callarius*, and plaice, *Pleuronectes platessa*. He felt that the low specific gravity of such salinities made it difficult for larvae to free themselves from the chorion so that they died partly emerged. He also maintained that chorions did not rupture as easily at low salinities. This phenomenon is also clearly demonstrated for winter flounder in Table 3. The highest percentages of abnormalities which were aborted or partially hatched occurred at salinities below 15‰.

Results of these laboratory experiments indicate that successful incubation of embryos occurred over a temperature range which exceeded normal spawning season temperatures by as much as 10°C, but coincide quite closely with natural observations for salinity, although there is a shift in survival toward slightly higher salinities than would have been expected. It is possible that the adults, while being held in the laboratory, were conditioned to slightly higher salinities than would have been encountered in a spawning migration into estuaries. This might explain the differences between natural populations and results of laboratory experiments.

Most winter flounder populations move to inshore and estuarine waters to spawn (Perlmutter 1947; Bigelow and Schroeder 1953; Saila 1961), but there are also spawning populations that remain in offshore shoals (Bigelow and Schroeder 1953; Marak et al. 1962). Field observations in two estuaries of Narragansett Bay and in the Bay itself indicate that spawning occurs at salinities ranging from 11 to 32‰. Plankton tows taken in upper Chesapeake Bay produced one egg in 20‰ with maximum numbers of larvae occurring between 6 and 14‰ (Dovel 1971). Salinities in suspected offshore shoal spawning areas range from 32 to 35.5‰ at the bottom (Bumpus 1973), so an overall spawning range from 5 or 6 to 35.5‰ is indicated for natural populations. The normal temperature range for spawning is 0° to 3.3°C with maximum temperatures for any appreciable egg production and spawning being 4.2° to 5.6°C (Bigelow and Schroeder 1953). Since the eggs are demersal and adhesive, they are not subject to transport into areas of unsuitable temperatures; being estuarine, they are subjected instead to

changes in salinity. However, the euryhaline properties of the eggs insure successful incubation and larval development in a constantly varying salinity environment.

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LITERATURE CITED

ALDERDICE, D. F., AND C. R. FORRESTER.
1968. Some effects of salinity and temperature on early development and survival of the English sole (*Parophrys vetulus*). J. Fish. Res. Board Can. 25:495-521.
1971a. Effects of salinity and temperature on embryonic development of the petrale sole *Eopsetta jordani*. J. Fish. Res. Board Can. 28:727-744.
1971b. Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. 28:883-902.

BATTLE, H. I.
1930. Effects of extreme temperatures and salinities on the development of *Enchelyopus cimbrius* (L.). Contrib. Can. Biol. Fish., New Ser., 5:107-192.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BUMPUS, D. F.
1973. Continental Shelf, arms of the sea. *In* Coastal and offshore environmental inventory, Cape Hatteras to Nantucket Shoals. Saul B. Saila, co-ordinator. Univ. R.I., Mar. Publ. Ser. 2, p. 1-1 - 1-46.

COLTON, J. B., JR., AND R. R. STODDARD.
1973. Bottom-water temperatures on the Continental Shelf, Nova Scotia to New Jersey. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC-376, 55 p.

DOVEL, W. L.
1971. Fish eggs and larvae of the upper Chesapeake Bay. Univ. Md. Nat. Res. Inst., Spec. Rep. 4, 71 p.

FORRESTER, C. R., AND D. F. ALDERDICE.
1966. Effects of salinity and temperature on embryonic development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. 23:319-340.

HOLLIDAY, F. G. T.
1965. Osmoregulation in marine teleost eggs and larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 10:89-95.
1969. The effects of salinity on the eggs and larvae of teleosts. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 1, p. 293-311. Academic Press, N.Y.

HOLLIDAY, F. G. T., AND J. H. S. BLAXTER.
1960. The effects of salinity on the developing eggs and larvae of the herring. Mar. Biol. Assoc. U.K. 39:591-603.

MARAK, R. R., J. B. COLTON, JR., AND D. B. FOSTER.
1962. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1955. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 411, 66 p.

MCMYNN, R. G., AND W. H. HOAR.
1953. Effects of salinity on the development of the Pacific herring. Can. J. Zool. 31:417-432.

PEARCY, W. G.
1962. Ecology of an estuarine population of winter flounder *Pseudopleuronectes americanus* (Walbaum). Bull. Bingham Oceanogr. Collect., Yale Univ. 18(1):5-78.

PERLMUTTER, A.
1947. The blackback flounder and its fishery in New England and New York. Bull. Bingham Oceanogr. Collect., Yale Univ. 11(2):1-92.

SAILA, S. B.
1961. The contribution of estuaries to the offshore winter flounder fishery in Rhode Island. Proc. Gulf Caribb. Inst., 14th Annu. Sess., p. 95-109.

SCOTT, W. C. M.
1929. A note on the effect of temperature and salinity on the hatching of eggs of the winter flounder (*Pseudopleuronectes americanus*, Walbaum). Contrib. Can. Biol. 4(11):137-141.

SMIGIELSKI, A. S., AND C. R. ARNOLD.
1972. Separating and incubating winter flounder eggs. Prog. Fish-Cult. 34:113.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill Co., N.Y., 481 p.

REEVALUATION OF FISHING EFFORT AND APPARENT ABUNDANCE IN THE HAWAIIAN FISHERY FOR SKIPJACK TUNA, *KATSUWONUS PELAMIS*, 1948-70

RICHARD N. UCHIDA[1]

ABSTRACT

Catch per effective trip, used in 1948-64 as an index of apparent abundance of skipjack tuna, *Katsuwonus pelamis*, in Hawaiian waters, is biased because effective trip, defined as one on which fish were caught, underestimates effort. Catch per day fished, calculated from data collected in 1965-70, is a refined index because effort includes days with or without catches. This paper describes the existence of a linear relationship between catch per effective trip and catch per day fished in 1965-70, and a method of estimating the latter from the former in 1948-64 based on this relationship. Fishing intensity, which was measured by standard effective trips in past studies, is calculated in standard days fished. Changes in catch per standard day fished are not associated with changes in relative fishing intensity. Skipjack tuna abundance in Hawaiian waters, therefore, is fishery independent and is probably influenced by availability and strength of year classes.

In the study of the dynamics of any exploited fish population, data on commercial catch and fishing effort can be interpreted in a number of ways, giving various estimates of apparent abundance. The ultimate objective, however, is to obtain the best possible estimate of apparent abundance.

Prior to 1965, studies on catch and effort statistics in the Hawaiian pole-and-line fishery for skipjack tuna, *Katsuwonus pelamis*, defined fishing effort as a "productive" or "effective" trip, that is, one in which skipjack tuna were caught (Yamashita 1958; Shippen 1961; Uchida 1966, 1967). Effective trip underestimated the actual amount of fishing pressure, but it was used because catch report forms used by the fishermen in 1948-65 provided no spaces for recording zero-catch trips.

Zero-catch trips should be considered as effort expended to catch fish because they include time spent searching for schools of fish. But the relative importance of search and fishing time depends on type of gear used. Gulland (1969) used whaling as an example of a fishery where the important measure was time spent searching, the gear being operational only for a few minutes. The other extreme was bottom trawling, where the important measure was time spent catching fish with the gear on the bottom and searching was minimal. Beverton and Parrish (1956) suggested that where searching time is important, the gear may have to be regarded as being engaged in searching for fish but giving no catch until a school is encountered. For pole-and-line fishing, where much time is devoted to searching for schools of fish, Shimada and Schaefer (1956) used the day spent on the grounds as the basic unit of fishing time.

Catch reports of 1965-70 were used to obtain two indices of skipjack tuna apparent abundance: catch per effective trip (*C/ET*), calculated from data on trips with catches, and catch per day fished (*C/DF*), calculated from total days fished including zero-catch fishing days. The purpose of this study is to determine whether a relationship exists between *C/ET* and *C/DF*. The importance of the relationship is that it affords a means of converting *C/ET* to *C/DF* for 1948-64, those years for which no data on *C/DF* exist but for which good *C/ET* information is available. A corrected measure of apparent abundance, derived from standard days fished instead of standard effective trip, is used to estimate the relative fishing intensity in 1948-70.

COLLECTION OF DATA

Data on skipjack tuna catch and fishing effort were obtained from the Hawaii State Division of Fish and Game, which collects fish catch statistics in the Hawaiian Islands. In addition, catch

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and effort data were also collected routinely at the cannery by personnel of the Honolulu Laboratory, National Marine Fisheries Service. The cannery records, however, were deficient in that they did not provide information on vessels not returning to Kewalo Basin, where the cannery is located, on vessels based on neighboring islands, or on the area of operation.

Catch Reports of 1948-64

The forms for reporting skipjack tuna catch have been revised several times over the years. Essentially, all the different versions used in 1948-64 had spaces for recording the date of landings, the amount of skipjack tuna landed, and the area fished. The date of landing represented an effective trip that may have lasted from one to several days. Because Hawaiian vessels have limited cruising range, a trip usually lasts 1 day. Studies of interview data collected in 1960 showed that of 329 effective trips, 315 or 96% lasted 1 day (Uchida 1967).

Catch Reports of 1965-70

The catch report forms of 1965-70 provided spaces for recording not only the amount of skipjack tuna caught and the area fished, but also the date of each day spent on the fishing ground, a zero catch when no fish was caught, and the number of men aboard per trip. Each entry represented 1 day's fishing. In using data for these years, therefore, days with catches were assumed to be equivalent to effective trips. The sum of days with and without catches was taken as the total number of days fished.

Reporting of Zero-Catch Trips

Review of catch reports and cannery records for 1965-70 showed that some vessels occasionally failed to report zero-catch fishing days. When the number of zero-catch trips recorded in the cannery records exceeded that reported in the catch reports, the difference was assumed to be the number of unreported zero catches. Most vessels reported more zero catches in the catch reports than were recorded in the cannery records; presumably, trips were not recorded at the cannery when a vessel did not return to home port. These catch reports were assumed to be accurate.

Not all unreported zero-catch days were accounted for. In a few cases, vessels failed to indicate a zero catch in the catch report after an unsuccessful day of fishing and also failed to return to Kewalo Basin, site of the cannery and home port of the Honolulu-based fleet. Then, neither the catch report nor the cannery record showed the effort expended.

For Honolulu-based vessels, unreported zero-catch days in 1965-70 varied between 0.5 and 3.8% of the estimated annual number of days fished (Table 1). Differences between reported and estimated number of days fished were not significant ($t = 1.020$; df = 5; $P = 0.36$); therefore the few zero-catch days that went unreported should not seriously affect the data in this study.

TABLE 1.—Total days fished as reported, estimated number and percentage of zero-catch days not reported, and estimated total days fished by Honolulu-based Hawaiian skipjack tuna fishing vessels, 1965-70.

Year	Total days fished as reported (Number)	Estimated zero-catch days not reported		Estimated total days fished (Number)
		Number	Percent	
1965	1,938	10	0.5	1,948
1966	1,773	39	2.2	1,812
1967	1,678	67	3.8	1,745
1968	1,923	42	2.1	1,965
1969	1,469	54	3.5	1,523
1970	1,605	51	3.1	1,656

SOURCES OF VARIABILITY IN FISHING POWER AMONG VESSELS

Fishing power is usually calculated on the basis of a physical feature of the vessel such as gross tonnage or engine horsepower. Differences in fishing power, however, are certainly more complicated than a comparison of these physical attributes. Rothschild (1972) stated that "A considerable portion of the variability in fishing power among fishing units can be attributed to variability in skill of the fishing skipper." Fishing skill cannot be measured easily, but its influence on the fishing power of the vessels should be understood.

Variability in crew size from trip to trip also complicates the comparison of fishing power among the vessels. For example, catch reports showed that crew size in 1970 varied between 5 and 11 men per trip. Frequently, small vessels were fully crewed while large vessels operated shorthanded. The result was that some of the small vessels were outperforming the larger ones in some years.

ANALYTICAL PROCEDURES

In the sections that follow, the procedures used in grouping vessels and fishing areas and in treating the data are discussed.

Classes of Vessels

The difficulties that arise from differences in fishing power among the vessels may be reduced by separating them into relatively homogeneous classes, using physical features such as gross tonnage. It is convenient, therefore, to determine which of the physical features of the vessels is, on the average, proportional to fishing power, and to use it to group the vessels into classes.

In a study covering the period 1952-62, the vessels were grouped into two size classes according to their bait-carrying capacities. Class 1 vessels had capacities up to 3,000 liters per baitwell whereas class 2 vessels had capacities greater than that (Uchida 1967). But the ability of class 2 vessels to catch more fish than class 1 vessels is not necessarily a permanent characteristic. Although baitwell capacity was a good measure of fishing power in the 1952-62 study, it did not reflect fishing power of the vessels satisfactorily after 1962. In 1963-70, some vessels with small bait capacities had catch rates as high as or higher than those with larger capacities. Reevaluation of the data showed that gross tonnage provided a better approximation of vessel performance. *C/ET* and bait capacity were correlated significantly in 8 out of 11 yr in 1952-62, but only in 2 out of 8 yr in 1963-70 (Table 2). Correlation between *C/ET* and gross tonnage, on the other hand, was significant not only in 8 yr in 1952-62, but also in 6 yr in 1963-70. For this study, therefore, vessels of 27 to 44 gross tons were called class 1 and those of 45 to 77 gross tons were called class 2. The selection of the division point between class 1 and class 2 vessels was based on the tendency of *C/ET*, when plotted against gross tonnage, to be closely grouped among class 1 vessels for almost all the years examined. In contrast, *C/ET* of class 2 vessels varied widely in most years.

The relationship of fishing power to vessel age and to bait usage cannot be overlooked. Among 8 class 1 vessels fishing in 1963-70, only 1 was built after World War II whereas 9 out of 12 class 2 vessels fishing in 1963-70 were built after the war. The relative comfort and reliability of most class 2 vessels undoubtedly accentuated the relation between fishing power and tonnage by attracting better captains and fishermen. Also, the difference between vessel classes in the amount of bait used was pronounced. Whereas class 1 vessels used an average of 8.3 buckets of bait per day fished, class 2 vessels averaged 12.3 buckets.

TABLE 2.—Correlation coefficients of *C/ET* on baitwell capacity and on gross tonnage of Hawaiian skipjack tuna fishing vessels, 1952-70. A single asterisk denotes probabilities between 0.05 and 0.01; two asterisks denote probabilities equal to or less than 0.01.

Year	df	Correlation coefficient of *C/ET* on baitwell capacity	Correlation coefficient of *C/ET* on gross tonnage
1952	23	0.326	0.387
1953	23	0.306	0.275
1954	24	0.602**	0.463*
1955	26	0.498**	0.490*
1956	24	0.390*	0.318
1957	23	0.461*	0.457*
1958	21	0.625**	0.678**
1959	18	0.721**	0.669**
1960	19	0.477*	0.464*
1961	19	0.462*	0.499*
1962	17	0.356	0.528*
1963	18	0.703**	0.757**
1964	18	0.403	0.596**
1965	17	0.368	0.327
1966	15	0.400	0.531*
1967	15	0.593*	0.521*
1968	14	0.434	0.529*
1969	13	0.382	0.516*
1970	13	0.510	0.447

Each year in the Hawaiian fishery the same few vessel captains vie for the distinction of being captain of the "top boat." Variability in skill among captains, therefore, complicated the comparison of fishing power among vessels. Furthermore, captains and crew frequently shifted from one vessel to another, taking their fishing skills with them. In 1965-70, for example, a minimum of nine vessels changed captains and the transfer of a highly regarded captain usually involved the transfer of part of his former crew. The shifting of personnel caused some high-producing vessels to become low- or marginal-producers.

Fishing Areas

After the establishment of the vessel classes, the data within each size class were then grouped into inshore and offshore fishing areas. In the Hawaiian fishery, the deployment of fishing effort and the resulting catches are recorded according to a statistical area system that was established for Hawaiian waters by the Hawaii State Division of Fish and Game in 1947 (Uchida 1970). Basically, three general areas are recognized. The

first extends from the coastline to just outside the reef, a distance of about 4 km, and the second extends from 4 to 37 km. Combined and called inshore for this study, these two areas are made up of relatively small statistical areas of unequal sizes. It has been estimated that about 80% of the effort and 75% of the skipjack tuna catch are concentrated within these areas (Uchida 1967). Beyond 37 km is the third area, called offshore here; the statistical divisions within it are large and nearly equal in size.

The inshore fishing ground, restricted to waters within 37 km of the coastline, covered roughly 69,000 km². The offshore ground, on the other hand, was restricted only by the range of the vessels, and varied from year to year. In 1948-65, the vessels covered 111,000 km² in their offshore fishing, but many distant offshore areas were visited in only 1 or 2 yr over this period. The offshore areas visited most frequently totaled roughly 69,600 km².

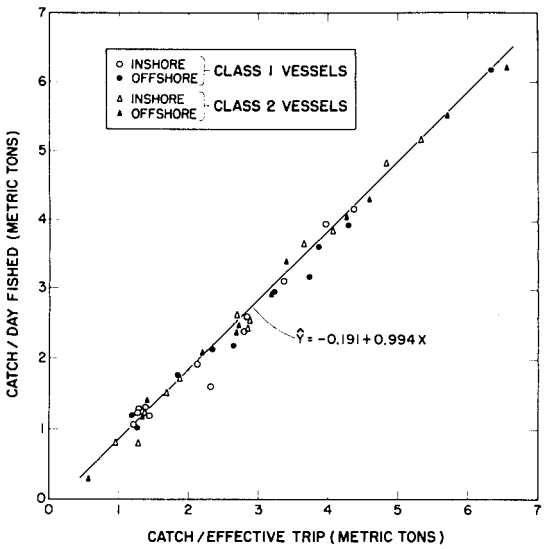

FIGURE 1.—Relationship between catch per effective trip and catch per day fished of Hawaiian skipjack tuna vessels, by areas fished, January-December 1965.

Comparison of Catch Per Effective Trip and Catch Per Day Fished

The monthly catches of skipjack tuna in 1965-70, separated into inshore and offshore areas within each vessel size class, were divided by two different units of effort. One was the number of days with catches, which was assumed to be equivalent to effective trips; and the index derived was *C/ET*. The other was the total number of days fished, which included days of fishing with and without catches; and the index was *C/DF*. The assumption that days with catches was equivalent to effective trips appears justified; Uchida (1967) showed that 96% of the effective trips lasted 1 day.

Figure 1 illustrates the relationship of the monthly *C/DF* (*Y*) against *C/ET* (*X*) calculated for class 1 and class 2 vessels fishing the inshore and offshore areas in 1965. The least squares regression of *Y* on *X* resulted in a close linear fit with the regression line having an angle of 45°.

A good fit between *C/ET* and *C/DF* can be expected because both indexes are small when fishing is poor and large when fishing is good. In Hawaiian waters, periods of high tuna apparent abundance are characterized by the presence of larger schools and more frequent encounters between vessels and fish schools (Uchida and Sumida 1971).

Homogeneity of Data

At the outset of the study, it was decided that one regression equation should be calculated for each area within the size classes. The resulting equations could then be used to estimate *C/DF* from *C/ET* for 1948-64. The decision to calculate one equation for each area by pooling the data for 1965-70 is appropriate, because the data included those years for which skipjack tuna catches from Hawaiian waters were the lowest (1969) and highest (1965) on record. Including data from these 2 yr should provide sufficient low and high values to determine accurately the slope and level of each regression line.

Pooling is appropriate when the samples are homogeneous; therefore, it was necessary to test the hypothesis of homogeneity. Statistical testing of the data, discussed in the following sections, was confined to only one index, *C/ET*, because of the close association between *C/ET* and *C/DF*.

The tests for homogeneity showed that yearly variances of inshore *C/ET* among class 2 vessels differed significantly ($\chi^2 = 11.92$; df = 5; $P<0.05$). A plot of the yearly means and standard deviations, shown in Figure 2A, indicated that they were significantly correlated ($r = 0.883$; df = 22; $P<0.01$). Furthermore, the distribution of *C/ET* was skewed because of many low and few high

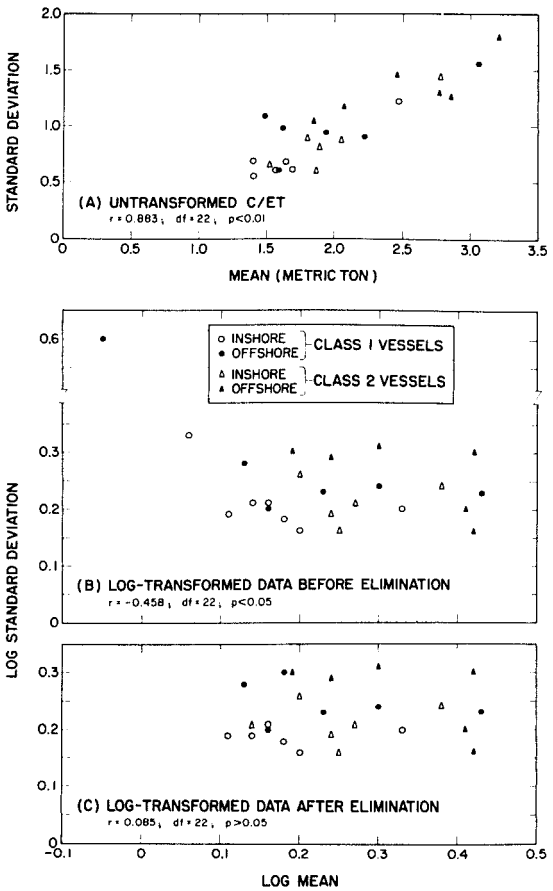

FIGURE 2.—Relationship between mean and standard deviation of catch per effective trip, before and after logarithmic transformation and elimination, by vessel size classes and areas, 1965-70.

values. Because the application of routine statistical procedures requires a normal distribution and independence of the mean and standard deviation, a transformation of the data was required. A logarithmic transformation was selected because the standard deviations tended to be proportional to their means (Figure 2A).

Transformation of the Data

A logarithmic transformation has several theoretical advantages in analyzing catch data (Murphy and Elliott 1954; Gulland 1956). Usually the transformation tends to stabilize the variances and make them independent of the mean. Furthermore, the random components tend to be independently and normally distributed about zero mean and with a common variance.

After the transformation, the means and standard deviations continued to be significantly but negatively correlated ($r = -0.458$; df = 22; $P<0.05$). Examination of the transformed data revealed that there were two points (Figure 2B) that were aberrant and diverged from the cluster of other points. These points represented data for class 1 vessels fishing offshore in 1969 and inshore in 1970. The original monthly catch data showed that the catch rates were affected by very low C/ET, all of which were 0.15 MT (metric ton) or less. These catch rates fell close to or beyond $\mu \pm 3\sigma$ and their elimination from subsequent analysis reduced the correlation between the means and standard deviation (Figure 2C) and stabilized the variances ($r = 0.058$; df = 22; $P>0.05$). Tests for homogeneity of variances also indicated that the transformed data for all years could now be grouped by areas within size classes.

Figure 3 shows the frequency distribution and fitted normal curve of the deviations from the mean of log C/ET for each area within the size classes. None of the histograms departed significantly from normality when chi-square tests were applied. Therefore, the fit of the normal curve is as good as can be expected (χ^2 ranged from 2.18 to 7.59; $P<0.05$).

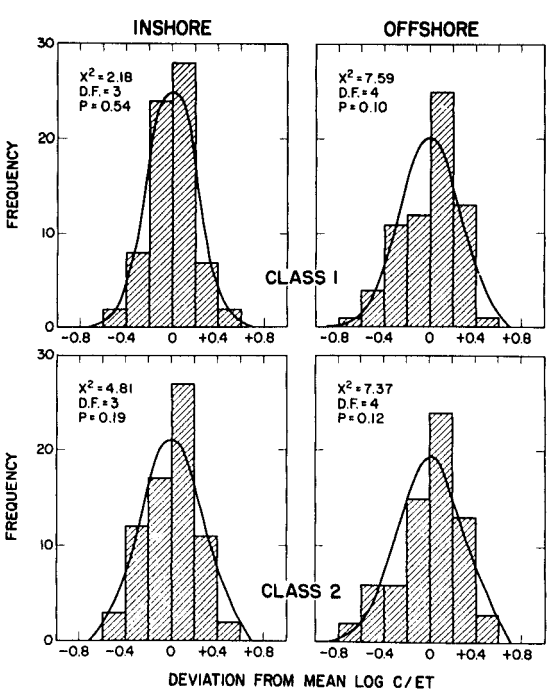

FIGURE 3.—Frequency distribution and fitted normal curve of the deviations from the mean of log C/ET.

Differences in Log Catch Per Effective Trip Between Vessel Classes, Between Areas, and Among Years

A factorial analysis of variance in a randomized complete-block design was used to test whether significant differences occurred in log *C/ET* between vessel classes (blocks), and between areas and among years (main treatment effects). The analysis showed that log *C/ET* with respect to the two vessel classes differed significantly (F = 12.34; df = 1 and 265; $P<0.01$). Significant differences in log *C/ET* also occurred with respect to inshore and offshore areas fished (F = 9.38; df = 1 and 5; $P<0.05$). Furthermore, the results showed significant differences occurred among years fished (F = 9.45; df = 5 and 5; $P<0.05$). A Duncan multiple-range test (Steel and Torrie 1960), with Kramer's (1956) extension of the test, determined that a significant difference in the means occurred primarily between 1965 and 1969, years in which there were considerable differences in fishing conditions.

Relation Between Log Catch Per Day Fished and Log Catch Per Effective Trip

Log *C/DF* increased linearly with log *C/ET* in each of the areas within the size classes. Regression lines, fitted to the data pooled for 1965-70, showed that the scatter about the regression lines was relatively narrow; there were, however, a few observations in each set of data that appeared to have large residuals. To assess the validity or appropriateness of the least-squares fitting of log *C/DF* on log *C/ET*, these residuals were analyzed.

Figure 4 shows the scatter diagrams in which the residuals were plotted against log *C/ET* for the four sets of data. With the exception of a few outliers which can be seen as isolated points with extreme negative ordinates, there were no noticeable peculiarities in the distribution of the residuals. The outliers were rejected at a multiple of the standard deviation using a premium of 2.5% (see Anscombe and Tukey 1963). The overall distribution of the residuals after the rejection procedure appeared in the form of a horizontal band, which indicated that the least-squares analysis of the log transformed data was satisfactory.

After the rejection of large residuals, regression lines were fitted to the data as shown in Figure 5. The dashed lines on either side of the regression lines indicate the 95% confidence limits for the estimates of log *C/DF*. The values of the regression equation and correlation coefficient of log *C/DF* on log *C/ET* are given in Table 3.

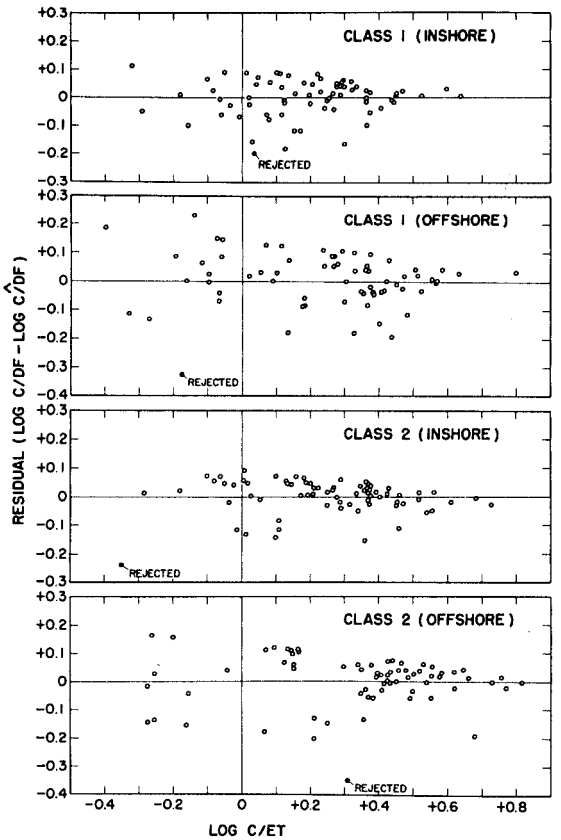

FIGURE 4.—Plots of residuals (log C/DF − log $\hat{C}$/DF) against log C/ET for class 1 and class 2 vessels fishing inshore and offshore in 1965-70.

Substitution of values of log a and b into the logarithmic equation $\log_{10} C/DF = \log_{10} a + b \log_{10} C/ET$ and solution of the equation provided estimates of *C/DF* from *C/ET*, by month, for

TABLE 3.—Data on the regression and correlation of $\log_{10} C/DF$ on $\log_{10} C/ET$ in the Hawaiian skipjack tuna fishery, by vessel size classes and areas, 1965-70. Two asterisks denote probabilities equal to or less than 0.01.

Vessel size class	Area	Log $_{10}a$	b	r	df
1	Inshore	−0.11566	1.13915	0.963**	68
	Offshore	−0.12549	1.08370	0.954**	64
2	Inshore	−0.10342	1.13340	0.976**	69
	Offshore	−0.12268	1.13120	0.968**	66

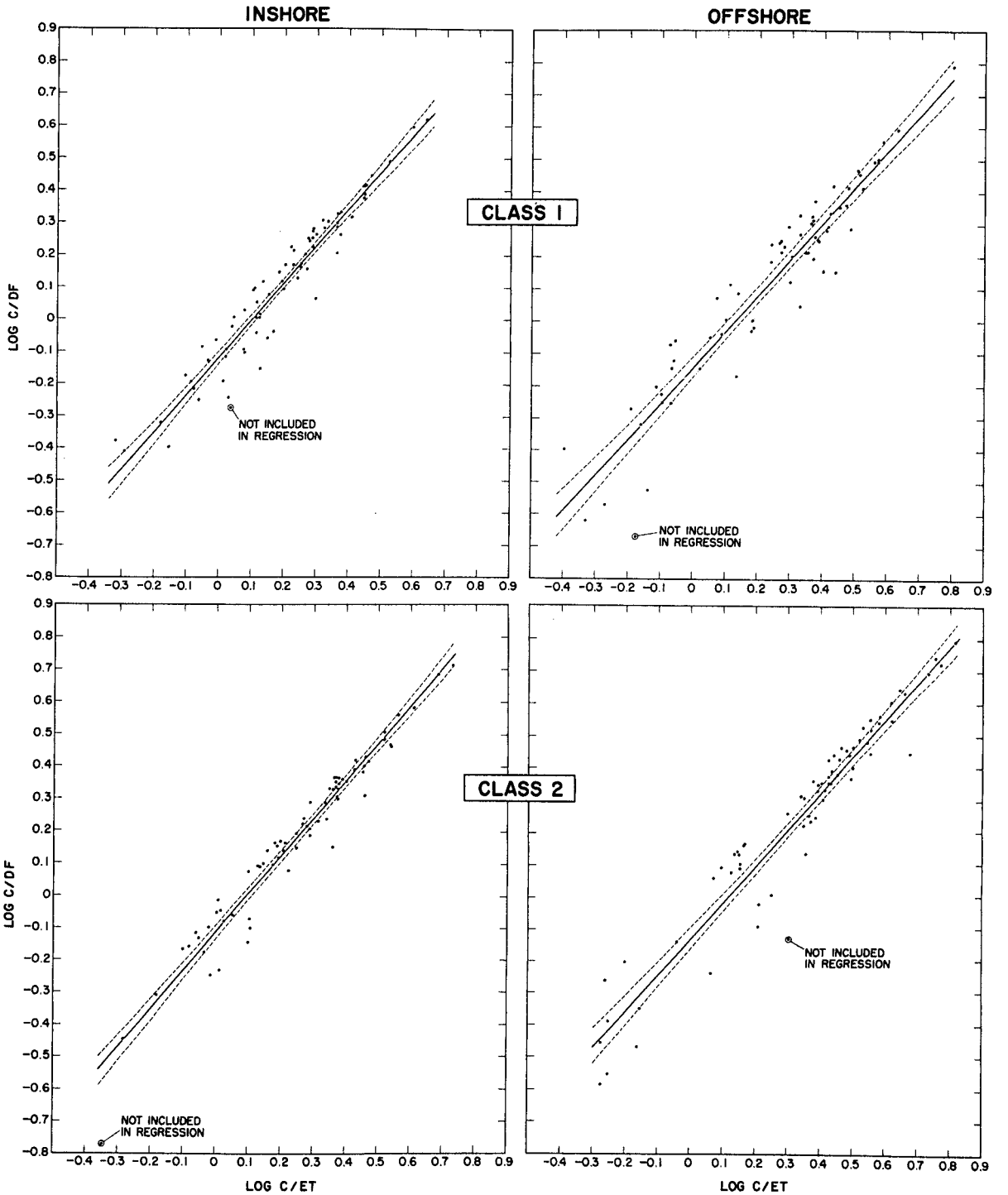

FIGURE 5.—Regression of log C/DF on log C/ET for class 1 and class 2 vessels fishing inshore and offshore in 1965-70.

TABLE 4.—Estimating the number of days fished among class 1 vessels fishing in the inshore area, January-December 1948.

Month	Catch (MT)	Effective trips (No.)	*C/ET* (MT)	$\text{Log}_{10}C/ET$	$\text{Log}_{10}C/DF$	Calculated *C/DF* (MT)	Estimated days fished (No.)
January	205.48	77	2.66857	0.42627	0.36993	2.34388	88
February	108.87	73	1.49137	0.17358	0.08207	1.20803	90
March	59.33	72	0.82403	−0.08405	−0.21141	0.61458	96
April	76.91	99	0.77687	−0.10965	−0.24057	0.57468	134
May	133.94	119	1.12555	0.05136	−0.05714	0.87669	153
June	285.80	154	1.85584	0.26854	0.19024	1.54970	184
July	352.30	147	2.39660	0.37959	0.31675	2.07374	170
August	239.72	120	1.99767	0.30052	0.22668	1.68531	142
September	191.07	104	1.83721	0.26415	0.18525	1.53199	125
October	101.31	81	1.25074	0.09716	−0.00497	0.98861	102
November	49.59	44	1.12704	0.05194	−0.05649	0.87802	56
December	19.26	25	0.77040	−0.11328	−0.24470	0.56923	34
Total	1,823.58	1,115					1,374

1948-64. For example, Table 4 shows the data used in the computations and the results obtained among class 1 vessels fishing the inshore area in 1948. *C/ET* was derived from the equation,

$$C/ET \text{ (col. 3)} = \frac{\text{Monthly catch (col. 1)}}{\text{Number of effective trips (col. 2)}}$$

and converted to logarithms (col. 4). Log *C/DF* (col. 5) was derived from the equation,

$$\log C/DF = \log a + b \log C/ET$$

and converted to *C/DF* (col. 6). Days fished were estimated from the equation,

$$\text{Days fished (col. 7)} = \frac{\text{Monthly catch (col. 1)}}{C/DF \text{ (col. 6)}} .$$

Standardization of Catch Per Day Fished

A method of standardizing effort of different size classes of vessel has been discussed by Shimada and Schaefer (1956) for the eastern Pacific yellowfin and skipjack tuna fishery. I used a similar method to estimate relative fishing power of class 1 vessels in the Hawaiian fishery so that their unit of effort was comparable to that of class 2 vessels, which were selected as the standard size class (Uchida 1966, 1967). Briefly, the method involves the use of correction or efficiency factors that are calculated from *C/DF* of the vessel size classes. Efficiency factors adjust the fishing effort of one size class to that of a standard class. For example, under conditions of equal abundance, the class 1 vessels can be expected to produce a smaller catch than the class 2 vessels. From the catches of the two classes, the fishing power of class 1 vessels can be determined relative to class 2, the standard class, for a given fishing area.

To illustrate the calculation of efficiency factors and the standard unit of effort, the annual *C/DF* given in Table 5 by vessel size classes and areas were used. In 1948, the efficiency factor for class 1 vessels fishing inshore was 1.33/1.78 = 0.747 and for offshore was 2.07/3.46 = 0.598. The efficiency factors for class 2 vessels were fixed at 1.000 for all years. The mean efficiency factor, 0.668, is the geometric mean of the inshore and offshore values. The geometric mean is appropriate for averaging ratios.

Varying from 0.59 to 0.82 (rounded) and averaging 0.71 in 1948-70, the efficiency factors demonstrated not only the greater capability of class 2 vessels, but also the wide variability of the factors from year to year. There was no evidence that the efficiency of class 1 vessels increased or decreased relative to class 2 vessels. Therefore, neither the efficiency of the standard class nor that of class 1 vessels has been altered by the loss of the less efficient or marginal vessels.

MEASURES OF APPARENT ABUNDANCE AND FISHING INTENSITY

Estimate of the apparent abundance of skipjack tuna on the fishing grounds, expressed as catch per standard day fished (*C/SDF*), can be calculated from efficiency factors and the total number of days fished for each of the two classes of vessels. For example, in 1948 there were an estimated 1,444 fishing days among class 1 vessels and 829 days among class 2 vessels. The standard days fished is the sum of the products of the mean efficiency factor and the total number of fishing days of the size classes. *C/SDF* is found by,

TABLE 5.—Catch per day fished inshore and offshore among class 1 and class 2 vessels, class 1 efficiency factors, and their geometric mean, 1948-70.

	Inshore			Offshore			
Year	Class 1	Class 2	Efficiency factors	Class 1	Class 2	Efficiency factors	Geometric mean
1948	1.33	1.78	0.747	2.07	3.46	0.598	0.668
1949	1.56	2.24	0.696	2.54	4.12	0.616	0.655
1950	1.34	1.74	0.770	2.10	3.38	0.621	0.692
1951	1.64	2.59	0.633	2.60	3.58	0.726	0.678
1952	1.31	1.66	0.789	1.31	2.19	0.598	0.687
1953	1.53	1.98	0.773	2.37	2.69	0.881	0.825
1954	1.36	2.54	0.535	2.89	3.80	0.760	0.638
1955	1.39	1.99	0.698	2.08	2.32	0.896	0.791
1956	1.90	2.36	0.805	2.30	3.27	0.703	0.752
1957	1.18	1.63	0.724	1.28	1.61	0.795	0.759
1958	1.17	1.87	0.626	1.79	2.36	0.758	0.689
1959	1.97	3.03	0.650	2.37	2.91	0.814	0.728
1960	1.32	2.02	0.653	1.94	2.40	0.803	0.727
1961	1.82	2.37	0.768	2.42	4.05	0.598	0.677
1962	1.49	2.45	0.608	2.22	3.43	0.647	0.627
1963	1.17	1.77	0.661	1.87	3.55	0.527	0.590
1964	1.40	1.69	0.828	2.07	2.90	0.714	0.769
1965	2.39	2.90	0.824	3.32	4.01	0.828	0.826
1966	1.54	1.82	0.846	1.93	2.91	0.663	0.749
1967	1.47	1.84	0.799	1.65	2.31	0.714	0.755
1968	1.57	1.68	0.934	2.04	2.93	0.696	0.807
1969	1.12	1.43	0.783	1.58	2.26	0.699	0.740
1970	1.32	1.74	0.759	1.30	2.36	0.551	0.646

$$C/SDF = \frac{TC_1 + TC_2}{(EF)\,(DF_1) + DF_2}$$

where TC_1 = total catch of class 1 vessels,
TC_2 = total catch of class 2 vessels,
EF = efficiency factor,
DF_1 = days fished among class 1 vessels, and
DF_2 = days fished among class 2 vessels.

In 1948-70, *C/SDF* of skipjack tuna in Hawaiian waters ranged from a low of 1.61 MT in 1957 to a high of 3.29 MT in 1965, but no trend with time was discernible (Table 6; Figure 6).

Relative fishing intensity is estimated from *C/SDF* and the total state catch, which includes catches of part-time as well as full-time vessels:

$$\text{Relative fishing intensity} = \frac{TC_s}{C/SDF}$$

where TC_s = total state catch.

When examined over the 23-yr period, fishing intensity did not decrease appreciably despite a gradual decrease in the number of vessels fishing from a maximum of 28 in 1951 to 15 in 1970. With a reduction in the fleet, which occurred primarily among the older class 1 vessels, fishing intensity would be expected to decline, but it did not. The reason was that the average days fished per vessel per year increased. Class 1 vessels fished an average of 86.1 days per vessel in 1948-58 when their numbers declined from 15 to 10 vessels and 121.2 days in 1959-70 when their numbers further decreased from 8 to 4 vessels (Figure 7). Class 2 vessels have not decreased in number drastically, declining from 14 in 1955 to 11 in 1970. Averaging 86.9 days fished prior to 1964, class 2 vessels subsequently averaged 119.8 days per year.

INTERRELATION OF TOTAL CATCH, FISHING INTENSITY, AND APPARENT ABUNDANCE

The total catch of skipjack tuna, given in Table 6 and shown in Figure 6, fluctuated with *C/SDF* in a similar fashion in 1948-70 (r = 0.902; df = 21; $P<0.01$). For the years studied, then, total catch may be satisfactory as a gross index of changing apparent abundance but may not be suitable in future years because it is obviously sensitive to changes in demand or fishing effort, competition from other fisheries, and economic constraints upon the fishery.

Changes in *C/SDF* are not associated with changes in fishing intensity (r = 0.302; df = 21; $P>0.05$); therefore, the apparent abundance of skipjack tuna in Hawaiian waters is not influenced by changes in the amount of fishing effort expended, but by fishery-independent factors such as variations in availability, which in turn is related to changes in the fishes' habits or

TABLE 6.—Total landings in metric tons (MT) of skipjack tuna in Hawaii, catch per standard day fished, relative fishing intensity, catch per standard effective trip, and relative effective fishing intensity, 1948-70.

Year	Total catch (MT)	Catch per standard day fished (MT)	Relative fishing intensity (Class 2 days)	Catch per standard effective trip (MT)	Relative effective fishing intensity (Class 2 trips)
1948	3,802.96	2.01	1,891	2.30	1,653
1949	4,488.23	2.53	1,773	2.85	1,575
1950	4,314.38	1.99	2,161	2.31	1,868
1951	5,863.37	2.93	2,001	3.28	1,788
1952	3,307.58	1.83	1,806	2.15	1,538
1953	5,470.15	2.14	2,552	2.46	2,224
1954	6,360.13	2.81	2,256	3.16	2,013
1955	4,397.43	1.95	2,248	2.26	1,946
1956	5,049.58	2.59	1,946	2.91	1,735
1957	2,780.66	1.61	1,726	1.90	1,464
1958	3,100.15	1.87	1,652	2.18	1,422
1959	5,630.65	2.93	1,919	3.26	1,727
1960	3,338.46	1.99	1,673	2.30	1,452
1961	4,941.66	2.69	1,835	3.01	1,642
1962	4,270.81	2.56	1,665	2.88	1,483
1963	3,673.86	2.15	1,712	2.48	1,481
1964	4,093.10	1.98	2,065	2.29	1,787
1965	7,328.96	3.29	2,221	3.54	2,070
1966	4,256.82	2.24	1,896	2.52	1,689
1967	3,646.80	1.99	1,832	2.30	1,586
1968	4,227.41	2.04	2,067	2.32	1,822
1969	2,704.94	1.63	1,658	2.02	1,339
1970	3,334.46	1.89	1,760	2.19	1,523

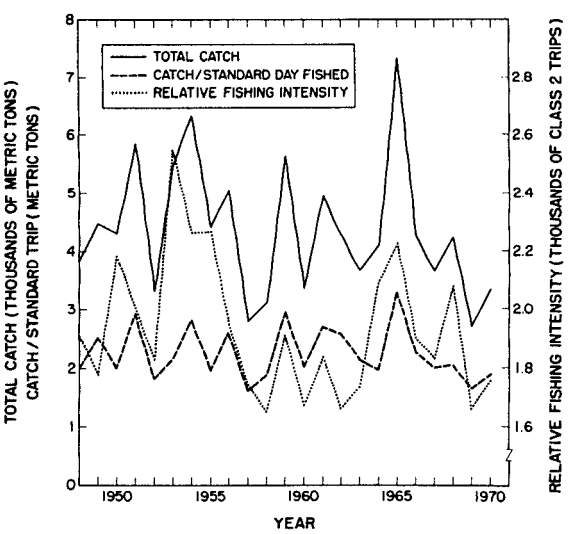

FIGURE 6.—Total catch, catch per standard day fished, and the relative fishing intensity for skipjack tuna in Hawaii, 1948-70.

in the environment, and to the strength of the year classes.

Catch per standard effective trip (*C/SET*) and relative effective fishing intensity, the two indices used in previous studies (Uchida 1966, 1967, 1970), are also given in Table 6. As expected, both *C/SDF* and *C/SET* fluctuated similarly in 1948-70 (r = 0.998; df = 21; $P<0.01$). Likewise the correlation between relative fishing intensity and relative effective fishing intensity was significant, indicating that changes in one paralleled changes in the other (r = 0.982; df = 21; $P<0.01$). It can be concluded that although the use of effective trips in previous studies produced biased results, which deviated from more precise estimates calculated from days fished, its use did

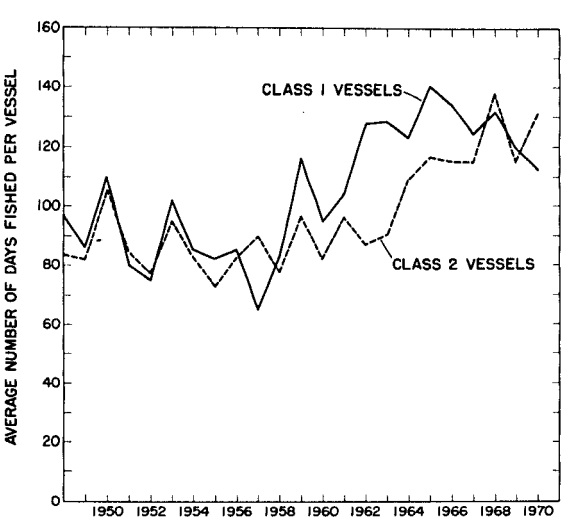

FIGURE 7.—Average number of days fished per vessel per year among class 1 and class 2 Hawaiian skipjack tuna vessels, 1948-70.

not lead to faulty conclusions about the status of the Hawaiian skipjack tuna fishery. The only serious bias appears to be that fluctuations in the *C/SET* were slightly exaggerated and those in effective fishing intensity were dampened.

SUMMARY

The existence of a linear relationship between catch per effective trip and catch per day fished in 1965-70 was described. Based on this relationship, catch per day fished was estimated from catch per effective trip for 1948-64.

Efficiency factors were used to standardize fishing effort of class 1 vessels to that of class 2. The data showed that in 1948-70, efficiency factors for class 1 vessels remained constant relative to class 2 vessels. Fishing intensity, calculated in standard days fished, did not decline over the 23-yr period despite the gradual decrease in the number of vessels fishing. Data from the catch reports showed that in the face of this decline in fleet size, the remaining vessels increased effort by fishing more frequently.

Total catch correlated significantly with *C/SDF*; therefore, it was a good gross indicator of skipjack tuna apparent abundance. Evidence supported the conclusion that in Hawaiian waters, skipjack tuna apparent abundance was not influenced by changes in the amount of fishing effort expended but by fishery-independent factors. And although effective trips as a measure of fishing pressure in previous studies underestimated effort and, therefore, provided a biased estimate of skipjack tuna apparent abundance in the Hawaiian fishery, its use did not lead to faulty conclusions.

ACKNOWLEDGMENTS

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LITERATURE CITED

ANSCOMBE, F. J., AND J. W. TUKEY.
1963. The examination and analysis of residuals. Technometrics 5:141-160.

BEVERTON, R. J. H., AND B. B. PARRISH.
1956. Commercial statistics in fish population studies. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 140 (Part I): 58-66.

GULLAND, J. A.
1956. On the fishing effort in English demersal fisheries. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 20(5), 41 p.
1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO (Food Agric. Organ. U.N.) Man. Fish. Sci. 4, 154 p.

KRAMER, C. Y.
1956. Extension of multiple range tests to group means with unequal numbers of replications. Biometrics 12:307-310.

MURPHY, G. I., AND K. C. ELLIOTT.
1954. Variability of longline catches of yellowfin tuna. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 119, 30 p.

ROTHSCHILD, B. J.
1972. An exposition on the definition of fishing effort. Fish. Bull., U.S. 70:671-679.

SHIMADA, B. M., AND M. B. SCHAEFER.
1956. A study of changes in fishing effort, abundance, and yield for yellowfin and skipjack tuna in the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 1:351-469.

SHIPPEN, H. H.
1961. Distribution and abundance of skipjack in the Hawaiian fishery, 1952-53. U.S. Fish Wildl. Serv., Fish. Bull. 61:281-300.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics: With special reference to the biological sciences. McGraw-Hill, N.Y., 481 p.

UCHIDA, R. N.
1966. The skipjack tuna fishery in Hawaii. *In* T. A. Manar (editor), Proceedings, Governor's Conference on Central Pacific Fishery Resources, State of Hawaii, p. 147-159.
1967. Catch and estimates of fishing effort and apparent abundance in the fishery for skipjack tuna (*Katsuwonus pelamis*) in Hawaiian waters, 1952-62. U.S. Fish Wildl. Serv., Fish. Bull. 66:181-194.
1970. Distribution of fishing effort and catches of skipjack tuna, *Katsuwonus pelamis*, in Hawaiian waters, by quarters of the year, 1948-65. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 615, 37 p.

UCHIDA, R. N., AND R. F. SUMIDA.
1971. Analysis of the operations of seven Hawaiian skipjack tuna fishing vessels, June-August 1967. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 629, 25 p.

YAMASHITA, D. T.
1958. Analysis of catch statistics of the Hawaiian skipjack fishery. U.S. Fish Wildl. Serv., Fish. Bull. 58:253-278.

SEASONAL AND INSHORE-OFFSHORE VARIATIONS IN THE STANDING STOCKS OF MICRONEKTON AND MACROZOOPLANKTON OFF OREGON

WILLIAM G. PEARCY[1]

ABSTRACT

Dry weights of pelagic animals captured along an inshore-offshore station line with Isaacs-Kidd mid-water trawls and 1-m diameter plankton nets during a 5-yr period provided evidence for seasonal changes in the standing stocks of carnivores. Micronekton catches (fishes, shrimps, and squids) were largest inshore (28 and 46 km offshore) in the winter (November-April), and offshore (84 and 120 km) during the summer (May-October), the season of coastal upwelling. No seasonal difference was detected in the biomass of herbivores, or in its primary components, the copepods and euphausiids. Increased biomass of medusae during the summer resulted in significant seasonal differences in the planktonic carnivores at the inshore stations.

The average biomass (grams per square meter) of small nektonic and planktonic carnivores, averaged over the year, peaked at the 84-km station. The biomass of fishes was greater than shrimps and the biomass of shrimps was greater than that of squids at all stations, except 46 km where shrimps predominated. Herbivore biomass was maximal at 46 km, over the inner continental slope, largely because of the high catches of euphausiids at this station. The occurrence of largest average catches at intermediate distances from shore, and inshore-offshore shifts in peak biomass with seasons, may result from seasonal changes in upwelling and downwelling and exclusion of vertical migrants from shoal waters on the shelf.

Herbivore:carnivore biomass ratios differed significantly between inshore and offshore stations. Standing stocks of herbivores were several times larger than those of carnivores in nearshore waters, but the ratio was about 1.0 in offshore waters. Coefficients of variation $(s/\bar{x})$ of herbivore and planktonic carnivore stocks for the entire sampling period were highest inshore, indicating high variability, and decreased markedly in offshore waters. These trends suggest that, compared to offshore or oceanic communities, the pelagic inshore-upwelling ecosystem may be less predictable and have a lower ecological efficiency.

This research was designed to answer two ecological questions about intermediate consumers in the pelagic food chain off Oregon:

(1) Are seasonal variations obvious in the standing stocks of small nekton and macrozooplankton off Oregon, perhaps in response to upwelling along the coast during the summer?

(2) Are there trends in the standing stocks of these animals from oceanic waters into neritic waters and, if so, do they reflect basic ecological differences in these pelagic communities?

Pelagic animals such as fishes, squids, shrimps, and euphausiids are ubiquitous in the open oceans and are important intermediates in the food chain between small plankton and large pelagic carnivores. Yet little is known about their seasonal variations, inshore-offshore distributions, or general ecology. The life span and generation time of many of these intermediate consumers are 1 yr or greater, limiting short-term changes in population sizes. Moreover, many of these animals reside below the depth of seasonal temperature change much of the time. They may undertake diel vertical migrations, and some species may migrate through the thermocline at night. In any event, seasonal changes in physical environment are expected to be less pronounced than those experienced by inhabitants of surface waters. Thus, seasonal variations in population size of these animals are expected to be less than those of small planktonic organisms.

Movements of water may also affect seasonal changes in the abundance of animals at one locality, or spatial distributions within a general region. In areas where water masses and associated pelagic fauna overlap and mix, species structure may be complicated, primarily a result

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of advective processes rather than biological interactions (McGowan 1971). In the headwater region of the California Current off Oregon, however, the water type is predominantly Subarctic and common species of some taxonomic groups of pelagic animals are the same within and among years (Pearcy 1972).

In addition to in situ population changes and changes affected by advection, small nektonic animals may be able to swim or to migrate horizontally. Though migrations of large nektonic animals such as tuna, salmon, hake, etc., are known to result in large seasonal changes in the abundance of these animals off Oregon, little evidence exists for horizontal movements of micronekton, even on a reduced scale. This is another reason to expect temporal stability of their populations.

Basic differences in the structure and energy pathways of neritic and oceanic ecosystems in the northeastern Pacific have been inferred by differences in the seasonal production cycle, seasonal variations in chlorophyll *a* concentrations, and the size of individual phytoplankton and microzooplankton (McAllister et al. 1960; Anderson 1965; Parsons and LeBrasseur 1970; LeBrasseur and Kennedy 1972). Inshore-offshore differences in the standing stocks of pelagic herbivores and carnivores, which have not been studied, are therefore to be expected.

METHODS

Micronekton and macrozooplankton were collected at night with 1.8-m Isaacs-Kidd mid-water trawls (IKMT) and with 1-m diameter plankton nets (MN) along stations west of Newport, Oreg. (lat. 44°39.1′N). The stations were located 28, 46, 84, 120, and >120 km, respectively, offshore (Figure 1). Collections, made about every month, totalled 243 IKMT tows between August 1962 and July 1967, and 179 MN collections between June 1963 and July 1967.

The IKMT had a 5-mm (bar measure) nylon liner throughout. Oblique tows were made to a depth of approximately 200 m, except at inshore stations where about one-half the depth of the water column was sampled (40 m and 130 m at the 28- and 46-km stations, respectively). Tow speed was 6 knots. The trawl was lowered at 50 m wire/min until a 4:1 scope was attained. The trawl was then retrieved at 30 m wire/min to the surface. Volume of water filtered and depth of

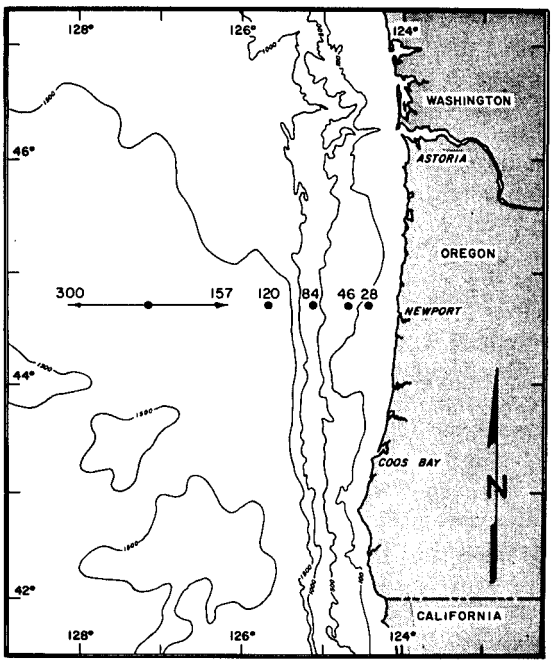

FIGURE 1.—Location of the sampling stations off Newport, Oreg. Stations are designed in kilometers from the coast. Depth contours are in fathoms (100 fathoms = 183 m, 500 fathoms = 914 m, 1,000 fathoms = 1,829 m, 1,500 fathoms = 2,743 m).

trawling was estimated from TSK[2] depth-distance recorders and flowmeters.

The meter nets, which were made of 0.571-mm Nitex, were towed immediately before or after each IKMT tow. From June to November 1963 oblique tows were made to approximately the same depths as the IKMT tows, but because of difficulties resulting from preferential sampling of near-surface waters, oblique tows were abandoned in favor of vertical tows in December 1963. Vertical tows were from 200 m to the surface, or from 60 or 150 m to the surface at the two inshore stations. After a vertical wire angle was obtained, they were retrieved at 50 m wire/min. Flowmeters mounted in the mouth of MN's provided estimates of volumes filtered. In a few instances flowmeters malfunctioned. Volumes were then estimated from the distance towed and 85% IKMT filtration efficiency (Pearcy and Laurs 1966) or from the average volume of other MN tows to the same depth.

[2]Tsurumi-Seiki Kosakusho Co. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Samples were preserved with Formalin at sea and sorted into taxonomic groups ashore. Wet (drained) weights were obtained for micronekton (fishes, shrimps, and squids). Micronekton from 32 different IKMT collections were dried to a constant weight in a drying oven at 65°C. The mean dry weight: wet weight ratios were then used to convert wet weights of other collections to dry weights. The means and standard deviations of the dry:wet weight ratios were 0.23 ± 0.06 for fishes, 0.15 ± 0.02 for shrimps, and 0.11 ± 0.04 for squids.

Dry weights were obtained for all major taxa sorted from MN samples: euphausiids, copepods, chaetognaths, medusae, amphipods, salps-doliolids, and shrimps. These taxa generally comprised over 95% of the total collection weights. The remainder usually consisted of annelids, pteropods, and heteropods. Ctenophores usually disintegrated in the samples, but when fragments were identifiable they were weighed with the medusae. In this paper, dry weights are used as a measure of standing stock, which is considered to be synonymous with biomass.

Sampling Variability

Several series of IKMT's at a single station during a single night were taken to assess sampling variability. The variability of total micronektonic dry weight per 1,000 m³ (Table 1) indicates that the variance for these series was appreciably less than the mean. These data on total biomass of micronekton, which are not in disagreement with the high variability encountered for individual species of micronekton captured in repeated tows at one station (e.g., Pearcy 1964; Ebeling et al. 1970), suggest that most of the temporal fluctuations of biomass illustrated in Figure 2 are independent of short-term sampling variability.

TABLE 1.—Sampling variability of total biomass of micronekton and macroplankton (grams dry weight per 1,000 m³) collected during repeated tows during separate nights.

Gear	Date	Distance offshore (km)	No. tows	Average ($\bar{x}$)	Variance (s^2)
Mid-water trawl	Dec. 1964	84	5	2.7	0.6
	Nov. 1966	120	3	4.7	0.9
	Feb. 1967	120	5	1.8	0.2
	Feb. 1967	120	3	1.5	0.02
	June 1967	306	6	1.9	0.01
	June 1967	120	6	2.2	0.4
Meter net	June 1964	93	6	5.0	3.1
	June 1966	93	5	20.3	99.0
	Nov. 1966	111	7	9.6	2.4
	Feb. 1967	46	3	4.6	1.1
	Mar. 1967	787	6	10.0	101.8

Variances of macrozooplankton biomass from repeated MN tows, on the other hand, were much larger than those for the IKMT (Table 1). In two out of the five series, variance surpassed the mean. Hence, a larger portion of the temporal variability of zooplankton can be ascribed to sampling variability.

RESULTS

Micronekton

Variations of the dry weights of micronekton (fishes, shrimps, and squids) captured per 1,000 m³ are shown in Figure 2 for four stations, 1962-67. Several trends are apparent. Seasonal peaks in the biomass occur inshore at the 28- and 46-km stations during the winter months, with very low values during intervening months. A reversed trend, though less pronounced, is found offshore at the 84- and 120-km stations where maximum catches generally were made during the summer or fall months. Average biomass values appear to be lowest inshore, highest at 84 km, and lower again at 120 km where total variability is the lowest.

The spatial peak of micronekton biomass at 84 km is more obvious in Figure 3, where dry weight is plotted per square meter instead of per cubic meter (to compensate for different depths of sampling at inshore stations). The standing stocks of fishes were greater than shrimps, and shrimp stocks were greater than squids at all stations except at 46 km where shrimps predominated. The neritic, benthopelagic shrimp, *Pandalus jordani*, occasionally made up the bulk of the biomass of collections at both 28 and 46 km (Pearcy 1970). However, mesopelagic animals comprised most of the nighttime IKMT catches: mainly the fishes *Stenobrachius leucopsarus, Diaphus theta, Tarletonbeania crenularis*, and *Tactostoma macropus* (Pearcy 1964, 1972; Pearcy and Laurs 1966; Pearcy and Mesecar 1971); the shrimp *Sergestes similis* (Pearcy and Forss 1966, 1969); and the squids *Gonatus* spp. and *Abraliopsis felis* (Pearcy 1965, 1972).

Seasonal variations in the total biomass (grams/10 m²) of micronekton are illustrated in Figure 4 for two general seasons: May-October, which includes the upwelling season; and November-April, when surface currents are usu-

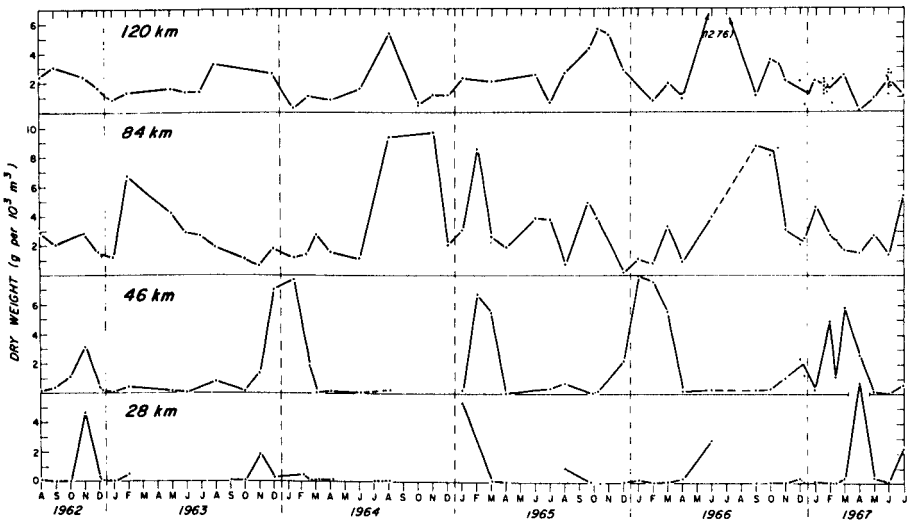

FIGURE 2.—Biomass of micronekton captured in Isaacks-Kidd mid-water trawl collections at four stations, 1962-1967. Each point represents one collection. Average depth of tows was 40 m for 28-km station, 130 m for 46-km station, and 200 m for 84- and 120-km stations.

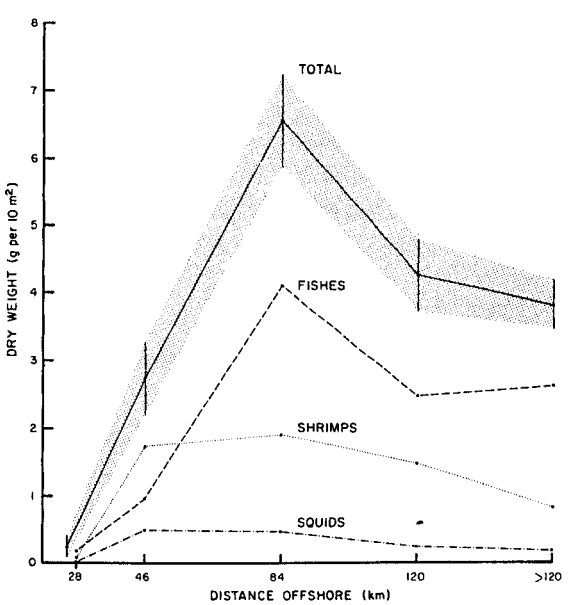

FIGURE 3.—Inshore-offshore variations in the average total micronekton biomass (grams per 10 m² ± 1 SE) and in its component fishes, shrimps, and squids.

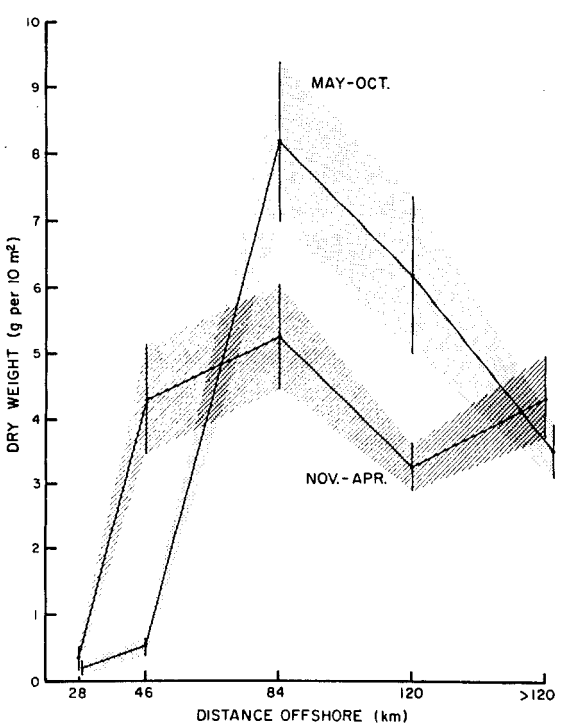

FIGURE 4.—Inshore-offshore variations in the biomass of micronekton during two seasons, May-October and November-April. Shaded areas included means ± 1 SE.

ally reversed, downwelling occurs, and the Davidson Current is often present along the coast (Wyatt et al. 1972; Bakun 1973). The means and medians of the biomass of total micronekton per 10 m², and of its constituents—fishes, shrimps, and squids—are given in Table 2 for these two seasons, along with the probabilities that the two seasonal values are the same. Seasonal differences of total biomass are significant ($P<0.05$) at 46

TABLE 2.—The mean and median biomass (grams dry weight per 10 m²) for micronekton and macroplankton during summer (S = May-October) and winter (W = November-April) at five stations (28, 46, 84, 120 and >120 km) off the Oregon Coast. Probabilities resulting from Mann-Whitney *U* and *t* tests of seasonal differences are given.

	Stn. 28 km		Stn. 46 km		Stn. 84 km		Stn. 120 km		Stn. >120 km	
Item	S	W	S	W	S	W	S	W	S	W
Total micronekton										
Mean	0.19	0.32	0.51	4.30	8.20	5.24	6.20	3.26	3.50	4.30
Median	0.004	0.03	0.38	2.75	7.84	4.04	5.04	2.76	3.28	3.18
Probabilities										
U	NS		S<W** $P<0.01$		S>W $P=0.08$		S>W* $P=0.04$		NS	
t	NS		S<W** $P<0.01$		S>W* $P<0.05$		S>W** $P<0.01$		NS	
Probabilities										
U test										
Fishes	†		S<W** $P<0.01$		S>W** $P=0.01$		S>W* $P=0.02$		NS	
Shrimps	†		S<W* $P=0.03$		NS		NS		NS	
Squids	†		NS		S>W** $P<0.01$		NS		NS	
Total macroplankton										
Mean	24.9	19.3	31.3	38.7	37.0	15.6	27.4	26.6	11.8	15.7
Median	12.6	12.1	9.4	8.1	12.2	6.5	8.0	8.6	4.9	5.0
Probabilities										
U	NS		NS		S>W* $P<0.04$		NS		NS	
t	NS		NS		S>W** $P<0.01$		NS		NS	
Probabilities										
U test										
Copepods	NS		NS		NS		NS		NS	
Euphausiids	NS		NS		NS		NS		NS	
Salps	†		†		†		†		NS	
Medusae	S>W** $P<0.01$		S>W** $P<0.01$		S>W $P=0.06$		NS		NS	
Chaetognaths	NS		NS		NS		NS		NS	
Amphipods	NS		NS		NS		NS		NS	
Shrimps	†		†		S>W* $P<0.05$		NS		NS	

NS - not significant.
† - too many zeros for valid tests.

and 120 km using the non-parametric Mann-Whitney *U* test (Tate and Clelland 1957) and at 46, 84, and 120 km using the parametric *t* test. Mann-Whitney *U* tests for the three taxa of micronekton indicated significant seasonal differences for standing stocks of fishes at 46, 84, and 120 km, for shrimps at 46 km and for squids at 84 km.

Macrozooplankton

Values for the biomass of macrozooplankton collected at four stations during 1963-67 are shown in Figure 5 and Table 3. Inshore-offshore and seasonal trends are less apparent than for micronekton. The total MN biomass per 10 m² is lowest at the 28-km stations, greater at the 120-km stations, and highest at the 46-, 84-, and 120-km stations (Table 3).

Of the taxonomic groups composing the MN samples, copepods were most important on an average dry weight basis at all stations except at 46 km where euphausiids were very abundant (Table 3). The standing stock of medusae ranked second after copepods at all stations except at 46 km where it ranked third after copepods. Even though the maximum biomass of all groups occurred at 46, 84, or 120 km on a square meter basis, the maximum weights of copepods and medusae on a cubic meter basis were found at 28 km, nearest the coast.

TABLE 3.—Biomass of zooplankton per 10 m² collected with 1-m diameter nets at the stations off Newport, Oreg.

Item		Stn. 28 km	Stn. 46 km	Stn. 84 km	Stn. 120 km	Stn. >120 km
Total biomass						
Mean		21	36	26	27	14
Median		8.0	15	16	15	10
SD		34	58	27	33	10
No. collections		36	40	41	37	25
Ave. sampling depth		60	152	200	200	200
Copepods	Mean	11.9	12.2	7.9	11.7	4.3
	Median	2.4	2.0	2.1	2.5	1.5
Euphausiids	Mean	2.6	20.0	6.2	2.4	2.5
	Median	0.6	3.7	2.2	1.5	1.1
Salps	Mean	0.04	0.03	3.2	4.1	1.4
	Median	0	0	0.002	0.002	0
Medusae	Mean	5.8	2.3	6.8	6.4	3.8
	Median	1.2	1.1	3.2	2.5	2.0
Chaetognaths	Mean	0.5	0.9	1.6	1.7	0.9
	Median	0.07	0.6	1.0	1.1	0.7
Amphipods	Mean	0.07	0.1	0.2	0.3	0.3
	Median	0.02	0.06	0.2	0.2	0.2
Shrimps	Mean	0.02	0.6	0.5	0.6	0.8
	Median	0	0	0.2	0.2	0.1

Differences in the biomass of macrozooplankton between the two seasons were only significant at one station, 84 km offshore (Table 2), although distinct peaks occurred during the summers of 2 yr at 120 km (Figure 5). Surprisingly, most of the taxonomic groups of zooplankton, including copepods and euphausiids, evidenced no seasonal changes at any stations. The only significant

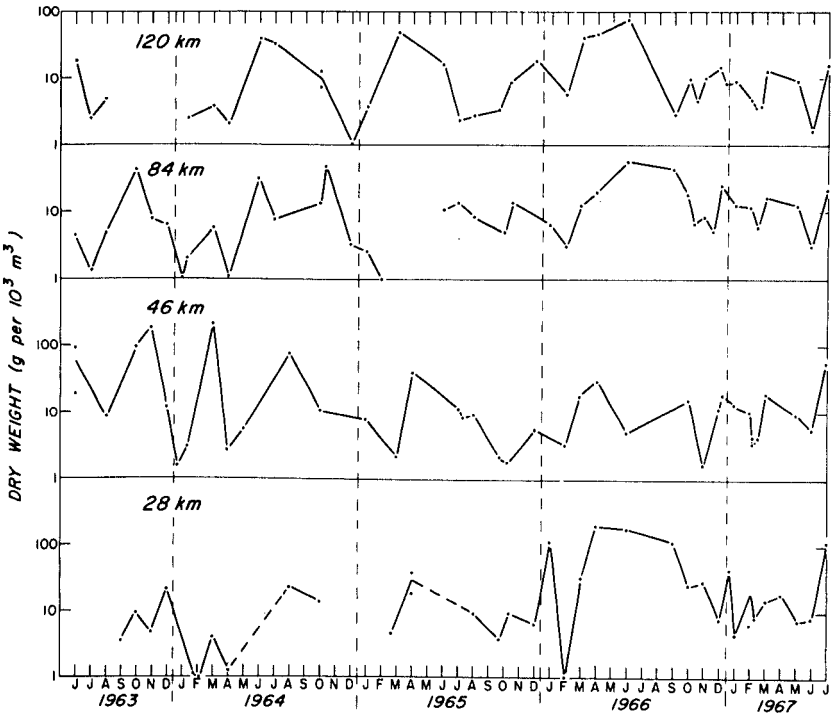

FIGURE 5.—Biomass of macrozooplankton captured in 1-m diameter plankton nets at four stations, 1963-1967. Each point represents one collection.

differences were for medusae, whose standing stocks in the summer exceeded those in the winter at 28 and 46 km (Mann-Whitney U, $P<0.01$) and perhaps at 84 km ($P = 0.06$), and for shrimps at 84 km, where again biomass was larger during summer than winter (Table 2).

Trophic Groups

To estimate seasonal and inshore-offshore variations in the standing stocks of the lower trophic levels of oceanic consumers, the dry weights of the various taxa were combined. Herbivores were assumed to include copepods, euphausiids, and salps-doliolids. Planktonic carnivores included chaetognaths, medusae, amphipods, and shrimps. Nektonic carnivores included fishes, squids, and shrimps. Although it is recognized that some euphausiids and copepods may be carnivorous, the main species captured off Oregon, *Euphausia pacifica*, *Thysanoessa spinifera*, and *Calanus* spp., are considered to be largely herbivorous.

Inshore-offshore variations in standing stocks are illustrated in Figure 6. On the average, the biomass of herbivores was greater than planktonic carnivores, and the biomass of these organisms was greater than that of micronektonic carni-

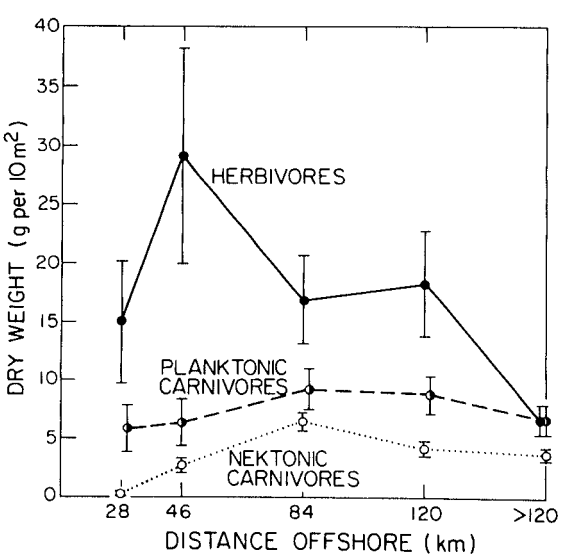

FIGURE 6.—Inshore-offshore variations in the average biomass (± 1 SE) of herbivores, planktonic carnivores, and nektonic carnivores at five stations.

vores at all stations. The high catches of herbivores at 46 km were due to abundant concentrations of euphausiids. Both groups of carnivores, on the other hand, had lowest biomass at the inshore stations and attained maxima farther offshore.

Seasonal variations in the standing stocks of herbivores and planktonic carnivores are illustrated in Figure 7. Mann-Whitney U tests of differences between the two seasons were not significant (all $P>0.1$) for any station, providing no evidence for seasonal changes in the biomass of herbivores. The biomass of planktonic carnivores increased with distance offshore during the winter and tended to decrease during summer. The biomass at 28 km was higher in summer than winter ($P<0.01$), largely due to high catches of medusae during the summer. At 84 km, planktonic carnivores also appeared to be more abundant during the summer ($P = 0.08$), again because of higher catches of medusae. No seasonal differences were apparent at other stations ($P>0.1$).

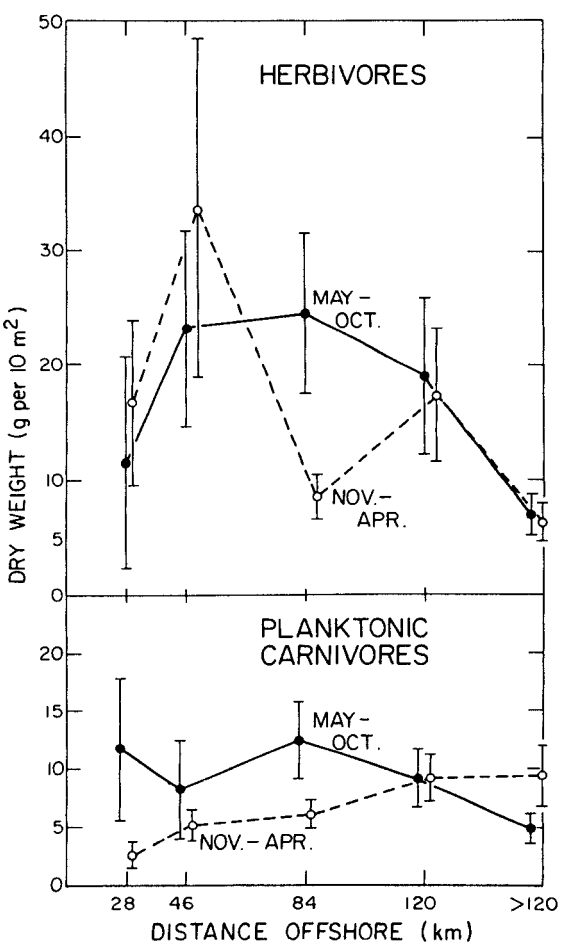

FIGURE 7.—Seasonal variations in the average biomass (± 1 SE) of herbivores (upper) and planktonic carnivores (lower).

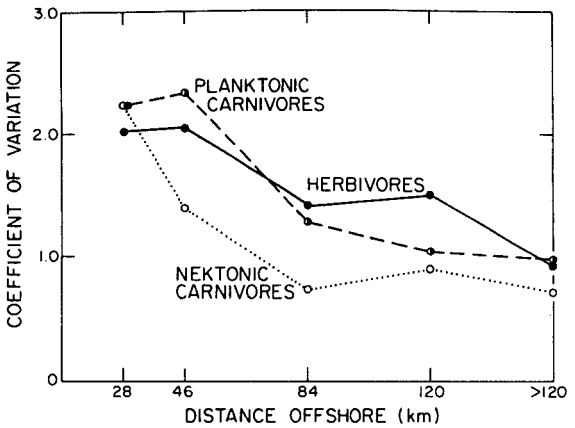

FIGURE 8.—Variability in the catches of herbivore, planktonic carnivores, and nektonic carnivores vs. distance offshore. Variability is expressed as coefficients of variation based on dry weights per 1,000 m³.

The ratio of herbivore:carnivore biomass, as expected from the data shown in Figure 6, averages about 2.0 at 28 km and 4.0 at 46 km, but only about 1.0 at the oceanic stations 84, 120, and >120 km. These ratios were ranked among stations for individual cruises. The sum of the ranks for stations were significantly different ($P<0.01$, Friedman two-way ANOVA by ranks, Tate and Clelland 1957). Thus herbivores predominated over carnivores in inshore waters, whereas the standing stocks of herbivores and carnivores were about equal in oceanic waters 84 km offshore and beyond. No seasonal differences in herbivore:carnivore ratios were found ($P>0.05$, Mann-Whitney U tests).

As a measure of variability of the standing stocks of trophic groups over the sampling period, coefficients of variation ($s/\bar{x}$) of the catches are plotted for each station in Figure 8. A marked decline in the variability of both herbivores and carnivores takes place from inshore into offshore waters.

DISCUSSION

Regional Comparisons of Zooplankton Standing Stocks

Values for the standing stocks of zooplankton in

the upper 140 to 300 m are summarized by Cushing (1971) for upwelling regions of the world. The average biomass of zooplankton collected within 120 km of the Oregon coast (Table 4) is within the range of values given by Cushing, after conversion to displacement volume per 1,000 m^3 and to grams carbon per square meter.

Zooplankton standing stocks off Oregon can also be compared with those reported by the California Cooperative Oceanic Fisheries Investigations (CALCOFI) which used 0.25-0.55-mm mesh in nets towed obliquely from 140 m to the surface. Zooplankton displacement volumes near the Oregon coast accord with values of Reid et al. (1958) and Reid (1962) greater than 400 cm^3/1,000 m^3 for July and August 1955 from Point Conception, Calif., to northern Washington, and with Thrailkill's (1956) values of 100-900 cm^3/1,000 m^3 for 1949 and 1950 off Oregon and northern California. Smith's (1971) median displacement volumes for pooled areas within 100 miles of shore between Point Conception and San Francisco Bay, Calif., are 200-400 cm^3/1,000 m^3 during April-July 1951-60, with decreased volumes south of Point Conception. Median displacement volumes for Oregon (either on an annual or a summer basis, Tables 2 and 4) are appreciably lower than Smith's values for northern California. This difference may be ascribed to differences between vertical and oblique tows, mesh size, or annual differences in standing stocks. Or, a real trend may exist for the nearshore zooplankton standing stocks to increase in the California Current system between Oregon and northern California, a trend that may be attributed to the more intense upwelling—and hence higher productivity—that occurs off northern California (Bakun 1973).

Zooplankton volumes within 120 km of Oregon are several times those given by McAllister (1961) and LeBrasseur (1965) for oceanic areas of the Gulf of Alaska (0-150 m vertical tows with a 0.45-cm diameter net, 0.35-mesh), even after their catches are adjusted for the relatively low catching power of their net (McAllister 1969; LeBrasseur and Kennedy 1972). Average volumes at weather station "P" (lat. 50°N, long. 145°W) were more similar to those at the station >120 km off the Oregon coast. Increased productivity associated with coastal upwelling along Oregon, therefore, enhances the average zooplankton standing stocks out to about 120 km from shore several times above the stocks farther offshore or upstream in the North Pacific Drift (see also Reid 1962). The width of this zone of high zooplankton standing stocks appears to be considerably less than the 200-500 km reported by Cushing (1971) for the region off northern California.

TABLE 4.—Dry weight of Oregon zooplankton converted to displacement volumes and grams carbon.

Item	Stn. 28 km	Stn. 46 km	Stn. 84 km	Stn. 120 km	Stn. >120 km
Mean cm^3/1,000 m^3*	552	450	228	274	85
Median cm^3/1,000 m^3	160	157	140	121	83
Mean gC/m^2†	1.1	1.8	1.3	1.3	0.7
Mean gC/m^2‡	2.3	3.9	2.8	2.9	1.5

*Conversion based on data of Ahlstrom and Thrailkill (1963, Table 7): wet weight plus interstitial water (≅displacement volume) × 0.06 = dry weight.

†C was estimated to be 50% of the dry weight (see Omori 1969, Table 5).

‡Calculated using Cushing's (1971) conversion of 0.065 × displacement volume = gC. This conversion assumes that displacement volumes do not include interstitial water, but according to the data of Ahlstrom and Thrailkill (1963, Table 7) an average of 42% of the wet weight of mixed zooplankton is interstitial water.

Seasonality of Standing Stocks

Seasonality in the biomass of zooplankton, with maxima in the summer and minima in the winter, has been reported in the California Current system off central California (Lasker 1970; Smith 1971) and in waters off the Oregon-Washington coast (Peterson 1972). Yet there was limited evidence for differences in macrozooplankton standing stocks between the two seasons in Oregon waters. Thus seasonality of standing stocks appeared to be more pronounced for micronekton than macrozooplankton, or for carnivores than herbivores. This may be because the high variability of macrozooplankton catches (Figure 8) makes important seasonal changes difficult to detect. Also the months selected for the two seasons may not match the periodicity of natural cycles. Another possible explanation is that the seasonality in catches of common animals such as *Euphausia pacifica* and *Calanus* spp. may be less than that in small herbivores with shorter life spans and generation times. Small copepods such as *Pseudocalanus, Oithona*, and *Acartia*, which were not sampled adequately with my nets, are known to be abundant in Oregon-Washington waters in the summer, especially in upwelled waters along the coast (Frolander 1962; Cross 1964; Peterson 1972; Peterson and Miller 1975).

Inshore-Offshore Variations

Largest standing stocks of macrozooplankton and micronekton (grams per square meter but not

grams/1,000 m^3, Tables 3 and 4, Figure 6) were found intermediate distances off the Oregon coast, namely over the continental slope at stations 46 and 84 km offshore. A trend for maxima at intermediate distances offshore has been reported for other regions. Standing stocks of zooplankton were highest at the edge of the shelf or over the inner slope off New York (Grice and Hart 1962), intermediate distances from shore off California (Smith 1971), and near mid-shelf in the Florida Current off Cape Hatteras, N.C. (St. John 1958). Macrozooplankton and micronekton collected with a 0.9-m IKMT off Vancouver Island, Canada and Washington were maximal over the outer edge of the shelf (Day 1971). The reduced feeding activity of pink, chum, and sockeye salmon as they approach the coast is purportedly explained by the low macroplankton concentrations in neritic waters and higher concentrations in offshore waters of the northwestern Pacific off Kamchatka (Andrievskaya 1957; Mednikov 1958). All of these studies indicate that small intermediate consumers may achieve maximum importance in the pelagic food chain in deep waters beyond the inner shelf (see also Williams et al. 1968).

The reason why catches of micronekton and macrozooplankton were higher offshore than nearshore may be related to their vertical migrations. Most of the species of micronekton and euphausiids caught in upper waters at night undertake diel vertical migrations (Pearcy and Laurs 1966; Pearcy and Forss 1966; Brinton 1967; Pearcy and Mesecar 1971); hence they may be most abundant in waters deep enough to permit vertical movements but where productivity is enhanced near land (Pearcy 1964). If they drift over the shelf, they may be eaten by large benthic or pelagic predators (Isaacs and Schwartzlose 1965; Pereyra et al. 1969).

The inshore-offshore changes in standing stocks of micronekton for the two seasons (Figure 4) suggest that these distributions are interrelated. Movement of animals may be correlated with seasonal oceanographic changes. During the summer, when the biomass increases greatly from 46 km to a peak at 84 km, large inshore-offshore gradients also occur in physical properties because of upwelling, and there is an offshore component of nearshore surface waters (Pillsbury 1972). During the winter, when biomass from 46 to >120 km is relatively uniform, inshore-offshore gradients are weak, surface currents are onshore, and downwelling occurs (Hebard 1966; Laurs 1967). The significant increase in biomass at 46 km in the winter may be caused by inshore advection of surface water and animals and the concentrating effect of shallow water near the edge of the shelf on vertical migrants. The peak at 84 km in the summer, though far from the coast, may be related to upwelling. Sometimes Laurs (1967) found maximum biomass of carnivores at 65-84 km and maxima of lower trophic levels closer inshore off Brookings, Oreg., during the summer, suggesting a succession of trophic level maxima such as reported by Sette (1955), King (1958), and Vinogradov and Voronina (1962) in areas of oceanic upwelling in equatorial waters.

Herbivore:Carnivore Ratios

Others have also found that the herbivore: carnivore biomass ratios decrease from shallow, eutrophic waters to oceanic waters. Grice and Hart (1962) reported that well over one-half of the zooplankton by volume in shelf waters off New York herbivorous, while in the Sargasso Sea only about one-half belonged to this trophic level. The percentage of herbivores in the zooplankton catches decreased from inshore waters that were affected by upwelling into offshore waters of the California Current off Baja California (Longhurst 1967). Greze (1970) reported that the biomass and production of herbivores and carnivores was a larger percentage of that of primary producers in the Equatorial Atlantic or Ionian Sea than the shallow waters of the Black Sea or Sevastopol Bay. These trends suggest that (a) a smaller fraction of the herbivorous biomass is captured in oceanic than neritic waters because of escapement through coarse mesh or avoidance, (b) production per unit biomass of herbivores is higher relative to that of carnivores in offshore waters, or (c) that ecological efficiences (food consumed by tropic level $n + 1$ to food consumed by trophic level n) are higher in oceanic than neritic waters.

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LITERATURE CITED

AHLSTROM, E. H., AND J. R. THRAILKILL.
1963. Plankton volume loss with time of preservation. Calif. Coop. Oceanic Fish. Invest. Rep. 9:57-73.

ANDERSON, G. C.
1965. Fractionation of phytoplankton communities off the Washington and Oregon coasts. Limnol. Oceanogr. 10:477-480.

ANDRIEVSKAYA, L. D.
1957. The food of Pacific salmon in the northwestern Pacific Ocean. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO), Mosc., p. 64-75. (Fish. Res. Board Can., Transl. Ser. 182, 12 p., 1958).

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BRINTON, E.
1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

CROSS, F. A.
1964. Seasonal and geographic distribution of pelagic copepods in Oregon waters. M.S. Thesis, Oregon State Univ., Corvallis, 71 p.

CUSHING, D. H.
1971. Upwelling and the production of fish. Adv. Mar. Biol. 9:255-334.

DAY, D. S.
1971. Macrozooplankton and small nekton in the coastal waters off Vancouver Island (Canada) and Washington, spring and fall of 1963. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 619, 94 p.

EBELING, A. W., R. M. IBARA, R. J. LAVENBURG, AND F. J. ROHLF.
1970. Ecological groups of deep-sea animals off Southern California. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 6, 43 p.

FROLANDER, H. F.
1962. Quantitative estimations of temporal variations of zooplankton off the coast of Washington and British Columbia. J. Fish. Res. Board Can. 19:657-675.

GREZE, V. N.
1970. The biomass and production of different trophic levels in the pelagic communities of south seas. *In* J. H. Steele (editor), Marine food chains, p. 458-467. Univ. Calif. Press, Berkley and Los Ang.

GRICE, G. D., AND A. D. HART.
1962. The abundance, seasonal occurrence and distribution of epizooplankton between New York and Bermuda. Ecol. Monogr. 32:287-309.

HEBARD, J. F.
1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanographic conditions. Ph.D. Thesis, Oregon State Univ., Corvallis, 85 p.

ISAACS, J. D., AND R. A. SCHWARTZLOSE.
1965. Migrant sound scatterers: Interaction with the sea floor. Science (Wash., D.C.) 150:1810-1813.

KING, J. E.
1958. Variation in abundance of zooplankton and forage organisms in the central Pacific in respect to the equatorial upwelling. Proc. Ninth Pac. Sci. Congr. 16:98-107.

LASKER, R.
1970. Utilization of zooplankton energy by a Pacific sardine population in the California current. *In* J. H. Steele (editor), Marine food chains, p. 265-284. Univ. Calif. Press, Berkley and Los Ang.

LAURS, R. M.
1967. Coastal upwelling and the ecology of lower trophic levels. Ph.D. Thesis, Oregon State Univ., Corvallis, 103 p.

LEBRASSEUR, R. J.
1965. Seasonal and annual variations of net zooplankton at Ocean Station P. 1956-1964. Fish. Res. Board Can., Manuscr. Rep. Ser. 202, 33 p.

LEBRASSEUR, R. J., AND O. D. KENNEDY.
1972. Microzooplankton in coastal and oceanic areas on the Pacific Subarctic Water mass: A preliminary report. *In* A. Y. Takenouti (editor), Biological oceanography of the northern North Pacific Ocean, p. 355-365. Idemitsu Shoten, Tokyo.

LONGHURST, A. R.
1967. Diversity and trophic structure of zooplankton communities in the California Current. Deep-Sea Res. 14:393-408.

MCALLISTER, C. D.
1961. Zooplankton studies at ocean weather station "P" in the northeast Pacific Ocean. J. Fish. Res. Board Can. 18:1-29.
1969. Aspects of estimating zooplankton production from phytoplankton production. J. Fish. Res. Board Can. 26:199-220.

MCALLISTER, C. D., T. R. PARSONS, AND J. D. H. STRICKLAND.
1960. Primary productivity and fertility at station "P" in the Northeast Pacific Ocean. J. Cons. 25:240-259.

MCGOWAN, J. A.
1971. Oceanic biogeography of the Pacific. *In* B. M. Funnell and W. R. Riedel (editors), The micropaleontology of oceans, p. 3-74. Cambridge Univ. Press, Camb.

MEDNIKOV, B. M.
1958. On the plankton of the northwestern part of the Pacific Ocean. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO), Mosc., p. 76-86. (Fish. Res. Board Can., Transl. Ser. 183, 7 p., 1958).

OMORI, M.
1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Mar. Biol. (Berl.) 3:4-10.

PARSONS, T. R., AND R. J. LEBRASSEUR.
1970. The availability of food to different trophic levels in the marine food chain. *In* J. H. Steele (editor), Marine food chains, p. 325-343. Univ. Calif. Press, Berkley and Los Ang.

PEARCY, W. G.
1964. Some distributional features of mesopelagic fishes off Oregon. J. Mar. Res. 22:83-102.
1965. Species composition and distribution of pelagic cephalopods from the Pacific Ocean off Oregon. Pac. Sci. 19:261-266.
1970. Vertical migration of the ocean shrimp, *Pandalus jordani:* A feeding and dispersal mechanism. Calif. Fish Game 56:125-129.

1972. Distribution and ecology of oceanic animals off Oregon. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 351-377. Univ. Wash. Press, Seattle.

PEARCY, W. G., AND C. A. FORSS.
1966. Depth distribution of oceanic shrimps (Decapoda: Natantia) off Oregon. J. Fish. Res. Board Can. 23: 1135-1143.
1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. Limnol. Oceanogr. 14:755-765.

PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

PEARCY, W. G., AND R. S. MESECAR.
1971. Scattering layers and vertical distribution of oceanic animals off Oregon. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 381-394. Maury Cent. Ocean Sci., Wash., D.C.

PEREYRA, W. T., W. G. PEARCY, AND F. E. CARVEY, JR.
1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. 26:2211-2215.

PETERSON, W. K.
1972. Distribution of pelagic Copepoda off the coasts of Washington and Oregon during 1961 and 1962. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 313-343. Univ. Wash. Press, Seattle.

PETERSON, W. T., AND C. B. MILLER.
1975. Year-to-year variations in the planktology of the Oregon upwelling zone. Fish. Bull., U.S. 73:642-653.

PILLSBURY, R. D.
1972. A description of hydrography, winds, and currents during the upwelling season near Newport, Oregon. Ph.D. Thesis, Oregon State Univ., Corvallis, 163 p.

REID, J. L., JR.
1962. On circulation, phosphate-phosphorous content, and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7:287-306.

REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest. Progr. Rep. 1 July 1956 to 1 January 1958, p. 25-57.

SETTE, O. E.
1955. Consideration of midocean fish production as related to oceanic circulatory systems. J. Mar. Res. 14:398-414.

SMITH, P. E.
1971. Distributional atlas of zooplankton volume in the California Current region, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest. Atlas 13, 144 p.

ST. JOHN, P. A.
1958. A volumetric study of zooplankton distribution in the Cape Hatteras area. Limnol. Oceanogr. 3:387-397.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

THRAILKILL, J. R.
1956. Relative areal zooplankton abundance off the Pacific Coast. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 188, 85 p.

VINOGRADOV, M., AND N. VORONINA.
1962. The distribution of different groups of plankton in accordance with their trophic level in the Indian Equatorial Current area. Rapp. P.-V. Réun., Cons. Perm. Int. Explor. Mer 153:200-204.

WILLIAMS, R. B., M. B. MURDOCH, AND L. K. THOMAS.
1968. Standing crop and importance of zooplankton in a system of shallow estuaries. Chesapeake Sci. 9:42-51.

WYATT, B., W. V. BURT, AND J. G. PATTULLO.
1972. Surface currents off Oregon as determined from drift bottle returns. J. Phys. Oceanogr. 2:286-293.

CULTURE AND GROWTH OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE

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ABSTRACT

Culture techniques used to rear larval anchovy through metamorphosis using laboratory cultured foods are described. Anchovy larvae fed dinoflagellates *Gymnodinium splendens*, rotifers *Brachionus plicatilis*, harpacticoid copepods *Tisbe furcata*, and brine shrimp nauplii *Artemia salina*, completed metamorphosis (35 mm) in 74 days at 16°C with a minimum survival of 12.5%. Growth in length and weight were recorded over this interval and an excellent fit to the Laird-Gompertz growth equation was obtained. Growth was comparable to that on a wild plankton diet. In a starvation experiment, most of the fish that completed metamorphosis withstood a starvation period of 12-15 days, whereas those that had not completed metamorphosis did not.

Knowledge of the growth rate of northern anchovy, *Engraulis mordax* Girard, is essential for estimating year class success or larval survival. Another important element in estimating survival is the time fish or larvae can withstand starvation. In this report I describe the growth rate of larval anchovy to metamorphosis and present data on the ability of newly metamorphosed juveniles to withstand starvation. Special attention is also given to culture techniques because this is the first time northern anchovy have been reared through metamorphosis entirely on cultured foods.

Kramer and Zweifel (1970) recorded the growth of anchovy larvae at 17° and 22°C for periods of up to 34 days. In their experiments larvae attained an average length of 17 mm but did not reach metamorphosis, which is complete at about 35 mm standard length. Their larvae were fed wild plankton supplemented by *Artemia salina* nauplii. In the ensuing years, rearing techniques using cultured foods have gradually been developed: *Gymnodinium splendens* for 3- to 5-day-old larvae (Lasker et al. 1970), and *Brachionus plicatilis* for 5- to 20-day-old larvae (Theilacker and McMaster 1971). This paper describes the use of the harpacticoid copepod *Tisbe furcata* which are the proper size food for larvae older than 20 days (10 mm). All previous attempts to rear anchovy larvae beyond 35 days on cultured foods have failed. In all attempts *Artemia* nauplii were used after 20 days.

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METHODS

Five rearing experiments were done, four at 16°C and one at 17° to 18°C (Table 1). Eggs for all experiments were obtained from a captive population of anchovy which were maintained in breeding condition continuously at the Southwest Fisheries Center La Jolla Laboratory (Leong 1971).

Rearing tanks were cylindrical, black fiberglass, 122 cm diameter, 36 cm deep, covered with a transparent acrylic plastic top, and immersed in a water bath regulated by a refrigeration unit. Temperature was maintained near 16°C in all but one experiment, and the salinity was 35‰. Fluorescent lamps suspended directly over each tank provided about 2,000 lx at the water surface. The volume of water in the tanks gradually increased from an initial volume of 200 liters of filtered seawater to 400 liters by about 20 days because of additions of seawater containing algae and food organisms. Thereafter, the volume was maintained at about 400 liters by siphoning water from the bottom from time to time which also cleaned the tank.

Records were kept of the quantity of food or algae added to tanks and on alternate days 16, 0.20-ml aliquots were taken to measure the density of *Brachionus plicatilis*, *Gymnodinium splendens*, and *Artemia salina* nauplii in the tanks. Concentrations of *Tisbe furcata* in the tanks were not recorded because they were concentrated on or near the walls and bottom of the tank, but records were kept of the numbers added to the tank. Details regarding the feeding of

TABLE 1.—Characteristics of five larval anchovy rearing experiments.

Experiment	1				2				3				4				5			
Number of eggs	3,000				6,000				3,000				6,000				3,000			
Temperature (±2 SE)	15.7 ± 0.21				17.7 ± 0.52				15.8 ± 0.53				15.7 ± 0.71				16.2 ± 0.33			
Percent survival[1] (age in days)	7.0 (34)				0.1 (46)				6.0 (42)				0.1 (38)				12.5 (74)			
Type additions[2]	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml
Millions of *Brachionus*	5-20	0.8	30	4-20	1.7	21	5-20	2.9	27	4-20	2.0	27	5-20	1.9	118
	21-34	0.5	19	21-46	0.3	8	21-42	2.3	30	21-38	0.1	19	21-74	4.0	15
Millions of *Nannochloris*	5-20	11.7	—	4-20	28.6	—	5-20	36.4	—	4-20	26.0	—	5-20	36.4	—
	21-34	14.3	—	—	—	—	21-42	7.8	—	21-38	20.8	—	21-74	11.7	—
Millions of *Artemia* nauplii	24-34	0.3	1	19-46	0.7	10	—	—	—	—	—	—	48-74	1.6	2
Thousands of *Tisbe*	—	—	—	—	—	—	—	—	—	12-20	180.0	—	6-20	260.0	—
	—	—	—	—	—	—	—	—	—	21-38	200.0	—	21-48	300.0	—
Thousands of *Artemia* adults	—	—	—	—	—	—	—	—	—	—	—	—	66-74	12.0	—

[1]Mortality includes 15 larvae removed on alternate days for length measurements.
[2]Forty liters of *Gymnodinium*, 1,700 cells/ml, were added at hatching in all groups.

anchovy larvae on *Tisbe* will be given in a separate section.

To obtain growth rates, 15 or more larvae were removed every other day from each tank, then measured, rinsed in distilled water, dried, and weighed in groups of 15.

CULTURE

Not until the fifth experiment was the procedure developed sufficiently to rear anchovy through metamorphosis. The first four experiments ended when it became obvious that it would be impossible to rear them to metamorphosis because of slow growth and high mortality. Data are included from the first four experiments to provide the background information for the final successful rearing procedure.

In all experiments, a single inoculation of 40 liters of *Gymnodinium splendens* (1,500-2,000 cells/ml) was given at age 0 days. This was sufficient to provide a final density in the tank in excess of 100 cells/ml for about 12 days. *Gymnodinium* was cultured using techniques described by Thomas et al. (1973). If fed only *Gymnodinium*, survival of anchovy larvae remains high for at least 12 days (about 45% at 12 days) but growth is depressed (Hunter in prep.).

In all experiments *Brachionus* was added on the 4th or 5th day in numbers calculated to yield a density of 30 to 50/ml in the tank (Table 1). Subsequent additions were made daily or on alternate days until day 20 in all experiments.

Nannochloris sp. was used to culture the rotifer *Brachionus* (Theilacker and McMaster 1971), and as a consequence *Nannochloris* was added to larval rearing tanks in all experiments to maintain a food supply for the rotifers. Four liters (about 13,000 cells/ml) were added on days 4 and 5, and further additions were made on the basis of water color. If water in the rearing tank was faintly green none was added as I wished to avoid creating a bloom in the tank because it is difficult to see the larvae in a dense bloom. To avoid a bloom usually required a reduction in the quantity added after 20 days. *Nannochloris* sp. is too small (about 7 μm) to be directly fed upon by larval anchovy although larvae might ingest cells accidently.

In experiments 1 and 2 *Artemia* was added at about 20 days and the level of *Brachionus* was allowed to slowly decline thereafter. In experiment 3, *Brachionus* was maintained at a high

level to the end and no *Artemia* was used. Although high mortalities on the order of 30 to 300 larvae/day occurred in all three experiments between ages 20 to 30 days, the larvae in experiment 3, those fed only *Brachionus*, grew faster (Figure 1) and had a higher survival than in the two groups fed *Artemia*. From these three experiments I concluded that *Artemia* was an inadequate food for 20-day-old anchovy larvae and that growth and survival could be increased by continuing to add large quantities of *Brachionus* after 20 days. Clearly, an adequate food larger than *Brachionus* was needed for 20-day-old larvae.

The food selected was the harpacticoid copepod *Tisbe furcata*. *Tisbe* is a common contaminant in the seawater system of the Southwest Fisheries Center and can be easily reared on dried foods (Johnson and Olson 1948) or algae (DeVauchelle and Girin 1974). Copepods collected from cultures ranged from 50-μm nauplii to 1,000-μm adult females but the typical size was about 650 μm and comparable in size to *Artemia* nauplii. The first attempt to rear anchovy using *Tisbe* (experiment 4) began as the other experiments except that I began adding *Tisbe* at age 12 days at the average rate of 180,000/day. At age 20 days the rate was increased to 240,000/day and the *Brachionus* was allowed to decline. The larvae fed on *Tisbe* but growth was slow and survival low. The low survival was attributed to an insufficient number of *Tisbe* in the tank, failure to maintain *Brachionus* at a high level after 20 days, as I had

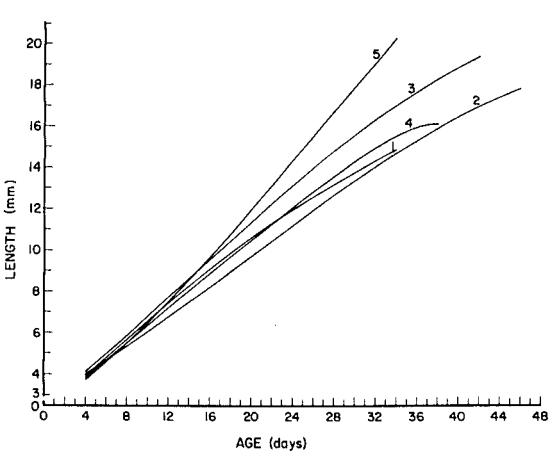

FIGURE 1.—Laird-Gompertz growth curves for lengths of anchovy larvae in five rearing experiments. Growth equation given in text; parameters for equation in Table 2. (Foods used in experiments 1-5 in Table 1.)

in experiment 3, and too high an egg stocking density (6,000 eggs).

The first four experiments established the guidelines needed for experiment 5, the final and successful rearing experiment. Over the first 20 days *Brachionus*, *Nannochloris*, and *Gymnodinium* additions were managed in the same way as in experiment 3. After 20 days, additions of *Brachionus* were increased above that used in experiment 3 and maintained at a high level until the end of the experiment on day 74. *Tisbe* additions were begun at age 6 days at an average rate of 260,000/day and increased to 306,000/day after 20 days. These additions were begun before most larvae were capable of feeding upon them in order to bring the copepod density in the tank to a high level at the time feeding on *Tisbe* became common (about age 12 days, anchovy length, 7-8 mm). This procedure is practical because survival of *Tisbe* in the tank is high and consequently, uneaten animals accumulate. *Tisbe* additions ended at age 48 days (26 mm) because the quantities needed exceeded the capacity of my cultures. Although younger larvae did not survive on a diet of *Artemia* nauplii it seemed possible that larvae 26 mm long might survive because they have a differentiated digestive tract, not simply a straight tube as do younger larvae, and they have a larger gut capacity (C. O'Connell, Southwest Fisheries Center La Jolla Laboratory, pers. commun.) Rosenthal (1969) showed that *Artemia* nauplii in the guts of herring larvae were only partially digested whereas digestion of copepods was nearly complete. From this he concluded that poor survival of herring fed *Artemia* could be attributed to digestive inefficiency. Past experience in maintaining adult anchovy at the Southwest Fisheries Center showed that they survived on *Artemia*; thus, it seemed reasonable that this might first occur when the digestive tract became differentiated. For these reasons I decided to change from a diet of *Tisbe* and *Brachionus* to one of *Artemia* nauplii and *Brachionus* at age 48 days. The change from copepods to *Artemia* nauplii did not cause a noticeable mortality nor a change in growth rate. Adult *Artemia* were added at age 69 days as some of the fish had metamorphosed and readily ingested adult *Artemia*.

In this description of culture I have stressed additions rather than density of food in the tank because I felt they provided a more reliable outline of culture procedures. Density in the tank

was measured before food was added and served as a guide for the quantity of food to be added. Where losses from ingestion or other sources of mortality were high, the density measurements tended to be lower than the level we attempted to maintain. In experiment 5 we attempted to maintain the density of *Brachionus* between 50 and 100/ml and that of *Artemia* nauplii at 2 to 3/ml.

In all experiments, 15 or more larvae were removed on alternate days and consequently, survival estimates include the effect of this sampling. In experiments 1 to 4 no daily counts of dead larvae were made until heavy mortalities occurred after age 20 days. In experiment 5, daily records of dead larvae were begun at age 54 and continued to the end of the experiment (age 74 days). At age 54 days 20% of the larvae were alive and at age 74 days, 374 larvae or 12.5% were alive. If the tank had not been sampled survival would probably have been greater because between 54 and 74 days the number of larvae sampled, 151, exceeded the number that died in the tank, 70. A total of 387 larvae were removed during the experiment. A method exists for estimating mortality in rearing work independent of the effect of sampling (Laurence 1974) but the programming effort required seems unwarranted for the objective of this paper. Collision with the walls of the container was a frequent cause of mortality over the last 3 weeks.

A survival of 12.5% at 74 days contrasts sharply with the other four experiments where nearly all larvae died by 30 to 40 days. Prior to the study described here, marked mortalities were common after 20 days and in all of the attempts *Artemia* was used as food. The pattern had become so typical at this laboratory that we have called it the "*Artemia* syndrome" for some years. The results of the current study suggest that the cause of the *Artemia* syndrome may simply be an inability of young clupeoid larvae with straight tube digestive tracts to digest *Artemia* nauplii but that *Artemia* may be used once the gut becomes differentiated.

It is important to call attention to the fact that 6% of the anchovy larvae in experiment 3 were able to survive for 42 days on a diet of only *Brachionus*. Plaice, *Pleuronectes platessa*, larvae have been reared through metamorphosis on only *Brachionus* although growth was slower than that on *Artemia* nauplii (Howell 1973). Howell found that plaice larvae, immediately prior to metamorphosis (12.7 mm), consumed 1,400 rotifers per day. In experiment 3, at age 42 days, the mean length of the anchovy larvae was 21.6 mm and dry weight was 5.5 mg. Assuming a digestive efficiency of 100%, larvae of this weight would have to ingest about 3,800 rotifers per day to meet metabolic requirements (calculation based on caloric value of *Brachionus* and anchovy respiration data given by Hunter 1972). These results illustrate the value of maintaining a high density of rotifers in culture containers long after a larger food has been added. They also suggest that some fish larvae have the ability to ingest large quantities of small prey and this could be of considerable benefit under natural conditions.

TISBE FURCATA AS A FOOD FOR LARVAL FISH

The evidence for the use of *Tisbe* as a food for rearing larval anchovy to metamorphosis is a single rearing experiment. It would be preferable to have additional experiments but none are planned at present because current work is concerned with only young stages and other species. Two groups of Pacific mackerel, *Scomber japonicus*, have been reared to metamorphosis using *Brachionus* and *Tisbe* as foods and this supports the contention that *Tisbe* is a satisfactory food for pelagic marine fish larvae. The work on *Scomber* will be reported at a later date.

That larval anchovy ate *Tisbe* is supported by records of stomach contents of larvae examined during the course of the rearing work. Seventy-four percent of the stomachs examined in experiment 5 contained only *Tisbe* or *Tisbe* and *Brachionus* and 26% contained only *Brachionus* (N = 69, larval length = 8.6-18.8 mm). The number of *Tisbe* in stomachs of larvae increased from 2.8 per larva (5.6-8.5 mm) to 18 per larva (17.6-20.5 mm). (Data from experiments 4 and 5 combined—Table 2.) The average length of the

TABLE 2.—Number and mean length of *Tisbe furcata* in the stomachs of anchovy larvae in experiments 4 and 5.

Larval anchovy		*Tisbe* in stomachs		
Length class (mm)	Number	Total	Number per larva[1]	Mean length μm ± 2 SE
5.6- 8.5	12	34	2.8	506 ± 57
8.6-11.5	25	90	3.6	681 ± 28
11.6-14.5	16	102	6.4	714 ± 28
14.6-17.5	9	98	10.9	758 ± 32
17.6-20.5	3	54	18.0	734 ± 43

[1]Includes only larvae that had either *Tisbe* and *Brachionus* or only *Tisbe* in stomachs.

copepods ingested by larvae also increased with larval length as expected (Arthur 1956).

Tisbe occurred throughout the rearing tank but the greatest concentrations occurred on or near the walls and on the bottom. Free swimming copepods were plentiful near the walls of the tank because *Tisbe* frequently leave the wall for short periods. Anchovy larvae captured *Tisbe* that were on the walls as well as free-swimming individuals. A pelagic copepod would be preferable to one that prefers surfaces such as *Tisbe furcata* but I have not been able to culture pelagic species in sufficient quantities for rearing work.[2]

GROWTH

The length data from each of the five experiments were fitted to the Laird-Gompertz growth equation (Laird et al. 1965) using Marquardt's Algorithm for fitting nonlinear models (Conway et al. 1970). The equation for length was:

$$L = L_0 e^{K_L(1 - e^{-\alpha t})}$$

where L = standard length in millimeters
L_0 = initial length at time 0
$K_L = A_0/\alpha$
A_0 = rate growth at time 0
α = rate of decay of growth.

A fit of the weight data from experiment 5 was also made to the Laird-Gompertz equation:

$$W = W_0 e^{K_W(1 - e^{-\beta t})}$$

where W = dry weight in milligrams
W_0 = initial weight at time 0
$K_W = B_0/\beta$
B_0 = rate growth at time 0
β = rate of decay of growth.

[2]At present our copepod culture system is composed of 10, 90-liter, glass, rectangular tanks maintained at 17° to 19°C. The *Tisbe* are given green algae, either *Tetraselmis* or *Nannochloris*, which is grown using commercial plant fertilizer (fish emulsion). An inoculation of 50,000 to 100,000 copepodid-adult stages yields on the average 500,000 copepods in these stages in 2 weeks. A tank is drained, harvested, and reestablished 5 days a week producing about 2.5×10^6 copepodid-adult stages per week, which is sufficient to rear one group of anchovy in the manner described. Occasional harvests of over a million in 2 weeks have been obtained suggesting that major improvements in the technique are possible. Contamination by *Brachionus* has been a problem because it increases the amount of algae that must be added to the culture. A more detailed description of this culture system would be premature but a description of a similar method of mass culture exists (DeVauchelle and Girin 1974).

The length-weight relationship for larvae in experiment 5 was derived from the above two equations by James Zweifel (Southwest Fisheries Center) and had the form

$$\ln W = \ln W_0 + K_W \left[1 - \left(\frac{K_L - \ln (L/L_0)}{K_L}\right)^{\beta/\alpha}\right]$$

The Laird-Gompertz equation gave an excellent fit to the growth in length and in weight and to the length-weight relationship (Figures 2-4, Table 3). The curvilinear nature of the length-weight data evident in the log-log plot (Figure 4) clearly indicates that a linear fit to log of length and weight would lead to inaccurate estimates.

The growth of anchovy larvae in experiment 5 was about the same as that recorded by Kramer and Zweifel (1970) for anchovy fed wild plankton at 17°C. At age 34 days, the last day of their experiment, the mean length of larvae was 17.4 ± 1.8 mm and that in experiment 5 at age 34 days was 19.7 ± 1.0 mm. Thus, over at least the first 34 days, growth on the cultured food diets was about the same as that on wild plankton.

SURVIVAL AT METAMORPHOSIS

The object of this experiment was to determine how long newly metamorphosed anchovy larvae can survive without food. Most adult fishes and presumably the anchovy can withstand prolonged periods of starvation of weeks or months. On the

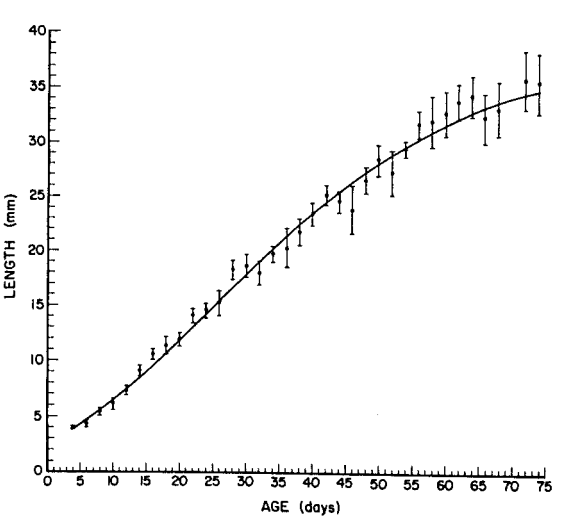

FIGURE 2.—Laird-Gompertz growth curve for length of anchovy larvae in experiment 5 and mean length ± 2 SE. Parameters for equation given in Table 2.

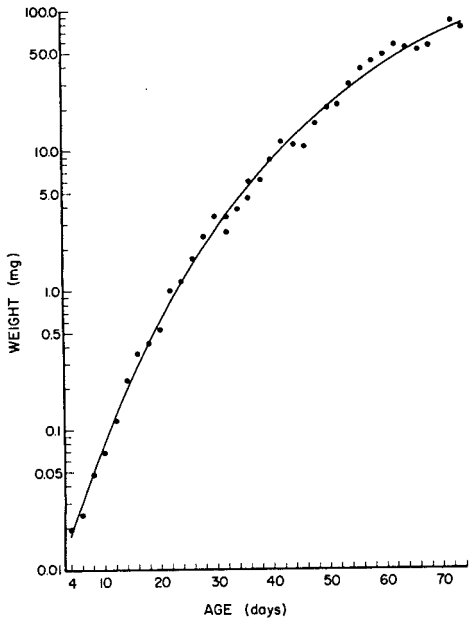

FIGURE 3.—Laird-Gompertz growth curve for dry weight of anchovy larvae in experiment 5. Points are average weight of larvae weighed in groups of 15-26 larvae each. Equation for curve given in text; parameters for equation in Table 2.

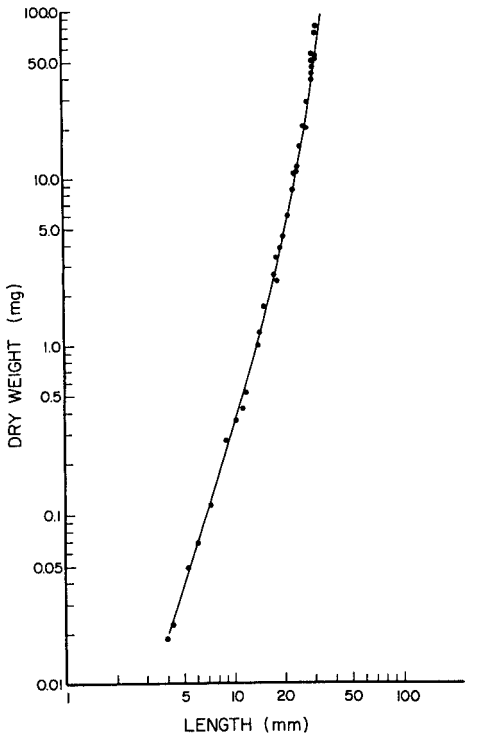

FIGURE 4.—Length-weight relationship of anchovy larvae reared in experiment 5. Equation for curve given in text; parameters for equation in Table 2.

other hand, larval anchovy, after they absorb their yolk, survive only 1 to 2 days without food (Lasker et al. 1970). The point at which this extreme vulnerability to starvation ends is essential information for any model of anchovy ecology and survival.

In this experiment fish reared to metamorphosis in experiment 5 were used. At age 74 days a group of 53 fish (group 1) and one of 73 (group 2) were placed into tanks containing only filtered seawater and a sample of 29 fish was taken for length and weight measurements. The tanks were the same as those described for the rearing experiments and temperature was maintained at 16°C. *Artemia* nauplii were offered to group 1 after 12 days of starvation and to group 2 after 15 days; the experiment ended after 20 days. Daily records were kept of water temperature and lengths of dead fish; after 20 days all surviving fish were measured. Total lipid content was also monitored through the course of the experiment.

TABLE 3.—Parameters and 95% support plane[1] for Laird-Gompertz growth equation for length, experiments 1-5, and weight for experiment 5. Symbols and equations are given in text.

	L_0			A_0			α			
		Support plane			Support plane			Support plane		
Experiment	Parameter	Lower	Upper	Parameter	Lower	Upper	Parameter	Lower	Upper	Number of observations
Length										
1	2.4378	2.0856	2.7901	0.1349	0.1040	0.1658	0.06939	0.05366	0.08512	289
2	3.0600	2.5512	3.5688	0.0835	0.0614	0.1056	0.03936	0.02700	0.05171	358
3	2.8361	2.3894	3.2829	0.1088	0.0835	0.1342	0.04951	0.03696	0.06206	345
4	2.6711	2.1648	3.1774	0.1098	0.0792	0.1404	0.05185	0.03591	0.06779	345
5	2.4928	2.2219	2.7636	0.1167	0.1042	0.1292	0.04264	0.03865	0.04663	553
	W_0			B_0			β			
Weight										
5	0.005758	0.003046	0.008470	0.2997	0.2552	0.3442	0.02725	0.02243	0.03206	35

[1]An approximation of the 95% confidence limits (Conway et al. 1970).

Fat was removed by Soxhlet extraction with chloroform-methanol (Krvarić and Mužinić 1950) from batches of 5 to 9 fish each. One such sample was taken at the beginning of the experiment, one from each group just before food was added, and one from each group when the experiment ended after 5 to 8 days of feeding.

A marked initial mortality occurred on the day following the transfer of the two groups (Figure 5) which was probably caused by handling. For this reason the first day's mortality is excluded from the analysis presented below, but the survival is given for all days in the figure.

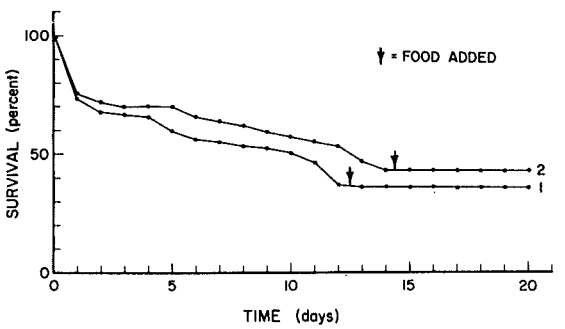

FIGURE 5.—Percent survival of metamorphosed larvae reared in experiment 5 during starvation periods of 12 and 15 days. Arrow indicates end of starvation period.

After 12 days of starvation, 50% of the fish were alive in group 1 (excluding the first day mortality) and 58% were alive in group 2 after 15 days of starvation. One fish in group 1 died the day after the first feeding. This was the only fish to die after feeding began. Thus for fish averaging 35 mm in length, about 50% mortality is reached after about 15 days of starvation and nearly all surviving fish are able to recover from a starvation period of that duration. Mortality during starvation appeared to be dependent on size or state of maturity, however. Metamorphosis is completed in the northern anchovy when they reach 35 mm standard length (E. H. Ahlstrom, Southwest Fisheries Center La Jolla Laboratory, pers. commun.). Eighty-three percent of the fish that died were less than 35 mm whereas only 17% of those longer than 35 mm died (Table 4). About 45% of the fish were less than 35 mm long at the beginning of the experiment. These results are similar to those obtained for herring larvae, *Clupea harengus*. The number of days to irreversible starvation for herring larvae increased from 6 days at the end of the yolk-sac stage to 15 days at age 88 days (Blaxter and Ehrlich 1974).

TABLE 4.—Lengths of fish in starvation groups and lengths of fish that died during starvation.

Group	Number of fish: Length <35 mm	Length ≥35 mm	Total[1]	Percent <35 mm	Mean length mm ± 2 SE
Sample before starvation	13	16	29	45	35.4 ± 1.8
All fish[2]:					
1	29	25	54	54	34.4 ± 1.5
2	16	24	40	40	36.0 ± 1.7
1 + 2	45	49	94	48	35.1 ± 1.1
Dead fish:					
1	21	4	25	84	30.9 ± 1.4
2	14	3	17	82	31.8 ± 1.6
1 + 2	35	7	42	83	31.2 ± 1.1

[1]Fish that died on first day of starvation in groups 1 and 2 not included.
[2]Surviving fish measured at end of experiment after 5- to 8-day feeding period.

Lipid content of fish declined during the starvation period from about 30% of dry weight to about 12% (Table 5). Recovery for the surviving fish was rapid, as they returned to the 30% level after 5 to 8 days of feeding. Water content was inversely related to fat as expected (Iles and Wood 1965). Fat content of muscle of adult anchovy is about 30 to 40% of dry weight during late summer and fall when gonadal fat is low (Lasker, Southwest Fisheries Center La Jolla Laboratory, unpubl. data). Thus, fat levels of these newly metamorphosed larvae appeared to be about the same as that of adult fish.

TABLE 5.—Total lipid and water content of anchovy at metamorphosis before, during, and after starvation.

Treatment	Elapsed time (days)	Water (%)	Total lipid dry wt (%)	Dry wt (mg)	Mean length (mm)	*N*
Before starvation	0	78.1	30.6	74.6	35.0	7
End starvation:						
Group 1	12	83.2	10.5	33.3	32.8	7
Group 2	15	82.9	13.4	54.2	36.9	5
End feeding:						
Group 1	20	79.5	32.3	90.3	39.6	9
Group 2	20	79.2	32.3	83.7	39.8	6

Extreme vulnerability to starvation appears to be characteristic of only the larval phase of the northern anchovy and it is over by the time the fish completes metamorphosis. There is a danger in interpreting these data beyond these general conclusions because reared fish may have more fat than wild ones and this could alter the results (Balbontin et al. 1973).

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James Zweifel (Southwest Fisheries Center La Jolla Laboratory) fit the Laird-Gompertz growth equation to the data and derived the length-weight relationship from the growth equations. Carol Sanchez (Southwest Fisheries Center La Jolla Laboratory) assisted in all phases of this work. Reuben Lasker and Gary Stauffer (Southwest Fisheries Center La Jolla Laboratory) reviewed the manuscript.

LITERATURE CITED

ARTHUR, D. K.
1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Ph.D. Thesis., Univ. California, Scripps Inst. Oceanogr., 231 p.

BALBONTIN, F., S. S. DE SILVA, AND K. F. EHRLICH.
1973. A comparative study of anatomical and chemical characteristics of reared and wild herring. Aquaculture 2:217-240.

BLAXTER, J. H. S., AND K. F. EHRLICH.
1974. Changes in behaviour during starvation of herring and plaice larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 575-588. Springer-Verlag, Berl.

CONWAY, G. R., N. R. GLASS, AND J. C. WILCOX.
1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

DEVAUCHELLE, B., AND M. GIRIN.
1974. Production du rotifere "*Brachionus plicatilis* O. F. Muller" en elevage mixte avec le copepode "*Tisbe furcata*" (Baird). Cent. Nat. Exploit. Oceans, Colloq. Aquaculture, Ser.: Actes Colloq. 1:87-100.

HOWELL, B. R.
1973. Marine fish culture in Britain VIII. A marine rotifer, *Brachionus plicatilis* Muller, and the larvae of the mussel, *Mytilus edulis* L., as foods for larval flatfish. J. Cons. 35:1-6.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

ILES, T. D., AND R. J. WOOD.
1965. The fat/water relationship in North Sea herring (*Clupea harengus*), and its possible significance. J. Mar. Biol. Assoc. U.K. 45:353-366.

JOHNSON, M. W., AND J. B. OLSON.
1948. The life history and biology of a marine harpacticoid copepod, *Tisbe furcata* (Baird). Biol. Bull. (Woods Hole) 95:320-332.

KRAMER, D. AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

KRVARIĆ, M., AND R. MUŽINIĆ.
1950. Investigation into the fat content in the sardine tissues (*Clupea pilchardus* Walb.). Acta Adriat. 4:289-314.

LAIRD, A. K., S. A. TYLER, AND A. D. BARTON.
1965. Dynamics of normal growth. Growth 29:233-248.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LAURENCE, G. C.
1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. J. Fish. Res. Board Can. 31:1415-1419.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

ROSENTHAL, H.
1969. Verdauungsgeschwindigkeit, Nahrungswahl und Nahrungsbedarf bei den Larven des Herings, *Clupea harengus* L. Ber. Dtsch. Wiss. Komm. Meeresforsch. 20:60-69.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

THOMAS, W. H., A. N. DODSON, AND C. A. LINDEN.
1973. Optimum light and temperature requirements for *Gymnodinium splendens*, a larval fish food organism. Fish. Bull., U.S. 71:599-601.

EFFECTS OF COOKING IN AIR OR IN NITROGEN ON THE DEVELOPMENT OF FISHY FLAVOR IN THE BREAST MEAT OF TURKEYS FED TUNA OIL WITH AND WITHOUT α-TOCOPHEROL SUPPLEMENT OR INJECTION

L. CRAWFORD AND M. J. KRETSCH[1]

ABSTRACT

The breast meat of turkeys which had been fed fish oil with and without α-tocopherol supplement or injection were cooked in air or under nitrogen with a slight vacuum. Cooking under nitrogen prevented the development of fishy flavor nearly as well as dietary α-tocopherol acetate supplementation. Some evidence is given which shows that fishy flavor develops postmortem (during cooking) and not in vivo.

Crawford et al. (1974) explored the effects of feeding fish oil with and without α-tocopherol acetate on the flavor of turkeys. This paper and other work by Crawford et al. (1975) showed that dietary α-tocopherol can be very effective in preventing the development of fishy flavor. Similarly, α-tocopherol acetate had a profound effect on the "elimination" of fishy flavor when it and beef fat were substituted for fish oil in the rations of turkeys that had been fed diets containing fish oil for several weeks. Injection of α-tocopherol (a few days before slaughter) into the thighs of turkeys fed diets containing fish oil showed a positive effect on the reduction of fishy flavor.

Consideration of these results and the finding that poultry carcass stability is related to the degree of lipid unsaturation and the tocopherol content (Mecchi, Pool, Behman, Hamachi, and Klose 1956; Mecchi, Pool, Nonaka, Klose, Marsden, and Lillie 1956; Webb, Brunson, and Yates 1972, 1973; Webb, Marion, and Hayse 1972) led us to the reasoning that fishy flavor in poultry may result from in vivo and/or postmortem oxidation of lipids containing long chain ω-3 fatty acids. Crawford et al. (1975) entertained the possibility that such oxidation and subsequent fishy flavor development occur mostly in vivo. At first glance, the effects of dietary α-tocopherol acetate on prevention of fishy flavor seem to support this hypothesis. However, the effectiveness of injecting α-tocopherol only a few days before slaughter casts some doubt on this reasoning since in vivo oxidation prior to injection should have had ample time to occur. Whereas this doubt does not call for total apostasy, it does suggest that postmortem oxidation and subsequent development of fishy flavor is indeed a possibility and deserves consideration.

The exact nature and origin of fishy flavor in turkeys is not known, but it is known that the development of such flavor requires the uptake of ω-3 fatty acids from dietary oils rich in these fatty acids. Most fish oils are rich sources of long chained ω-3 fatty acids which are readily taken up into the carcass of turkeys when included in their diet. Linseed oil contains more than 50% linolenic acid and when incorporated into turkey diets, the linolenic acid is taken up and elongated to the longer chained homologues thereby causing fishy flavor to develop (Klose et al. 1951; Miller et al. 1967a, b; Crawford et al. 1974).

If postmortem oxidation plays a major role in the development of fishy flavor, it is likely that the development would occur largely during cooking. Pippen and Nonaka (1963) found that the amount of volatiles from raw chicken was small and the aroma rather insipid when compared to the relatively large amount of highly odoriferous volatiles from cooked chicken. They also reported that chicken boiled in air yielded a more complex and larger volatile fraction than chicken boiled in nitrogen. Crawford (1972) reported that replacement of air in the headspace with nitrogen gave some protection against scorch during the retorting of 4-pound cans of tuna. This suggests that less carbonyls (volatiles) were formed under nitrogen since volatile carbonyls, sugars, and

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amino compounds (Fujimoto et al. 1968) have been implicated in such nonenzymatic browning (Tarr 1954; Jones 1962).

It is clear that the development of the normal aroma of poultry is time-temperature dependent and that air or nitrogen cooking atmospheres have profound effects on the development of this aroma. Therefore, it is likely that control of the cooking atmosphere may affect the development of fishy flavor in poultry meat if this flavor requires air and/or heat for its development.

This paper explores the effects of cooking in different atmospheres on the flavor of breast meat from turkeys fed diets containing tuna oil with and without dietary α-tocopherol acetate or α-tocopherol injection. Diced breast meat was cooked in air as well as under nitrogen with a slight vacuum.

EXPERIMENTAL

Turkey Diets and Feeding

The turkeys used in this experiment were taken from groups of turkeys raised experimentally for other work. Their diets and feeding are described in some detail by Crawford et al. (1975). Briefly, there were 50 White Broad Breast poults in experiment C that were divided into five groups of 10 each and they were fed as follows: chick starter (6.75% fish meal) was fed to 3 wk of age, then a 50:50 mixture of chick starter and a 50% soybean meal basal diet for a few days, followed by the 50% soybean meal diet supplemented with 2% soybean oil and 2% beef fat to 8 wk of age. At 8 wk of age, the following fat and oil supplements replaced the previous ones and they were fed from 8 to 14 wk of age:

Group	*Oil Supplement to Basal Diet*[1]
1 C	4% BF
2 C	2% BF + 2% TO
3 C	2% BF + 2% TO
4 C	2% BF + 2% TO
5 C	2% BF + 2% TO

[1]BF = Beef fat; TO = Tuna fish oil.

At 14 wk of age, the above groups of turkeys were fed a 30% soymeal basal diet plus the following oil supplement to 16 wk of age:

Group	*Oil Supplement to Basal Diet*[1]
1 C	Keep on 4% BF
2 C	Change to 4% BF
3 C	Change to 4% BF + 100 mg Vit. E/kg
4 C	Change to 4% BF + 200 mg Vit E/kg
5 C	Keep on 2% BF + 2% TO

[1]BF = Beef fat; Vit. E = *dl* α-tocopherol acetate; TO = Tuna fish oil

In experiment B, 50 poults were obtained and handled as above. On day 3, they were fed a basal diet plus 4% beef fat to 14 wk of age. From 14 to 16 wk of age, they were fed as follows:

Group	*Oil Supplement to Basal Diet*
1 B	4% BF
2 B	2% BF + 2% TO
3 B	2% BF + 2% TO (+ injection of 170 mg α-tocopherol into thigh at 72, 48, 24 h before sacrifice)
4 B	2% BF + 2% TO + 100 mg Vit. E/kg
5 B	2% BF + 2% TO + 500 mg Vit. E/kg

Sampling, Canning, and Analysis

All turkeys were sacrificed at 16 wk of age then handled and stored at -30°C as described by Crawford et al. (1974). Two turkeys from each group were randomly selected and thawed overnight in a 2°C cold room. The breasts were excised and diced in the cold after the skin had been removed. Breast meat from turkeys of the same group were mixed together and appropriately identified. The diced breast meat was canned immediately as follows: breast meat from each group was hand packed into 307 × 113 cans (eight cans per group) leaving a headspace of about ½ inch. All cans from each group were alternately evacuated and flushed with nitrogen several times. On the final nitrogen flush, the lids were sealed when the vacuum dropped to 5 inches. Four of the cans from each group were frozen at -30°C until used and the other four cans were cooked immediately at 116°C (15 psi) for 80 min to an internal temperature of ca. 112°-115°C, cooled, and stored at 2°C until used. The four uncooked cans from each group were removed from -30°C storage, thawed to about 2°C, opened, and the contents cooked in aluminum trays (with loose covers) at about 117°C for 30 min (internal temperature ca. 70°C) before serving. Those cans that were cooked at 116°C were warmed in boiling water for 10 min before opening and serving. Organoleptic analysis was performed by a panel of eight judges using a balanced incomplete block design ($t = 5, r = 4$). Only one panel per day was

convened and the air and nitrogen packs were randomly offered from day to day. Duncan's multiple range test (α = 0.05) was used to compare the adjusted mean of the taste panel scores. The scoring was: 1 = no fishy flavor, 5 = very fishy flavor.

RESULTS AND DISCUSSION

The results reported in Table 2 are to be interpreted with some caution because of the low level of fishiness in the meat from turkeys fed 2% fish oil for only 2 wk. Therefore, only trends are indicated for the results in Table 2 where statistical significance could not be achieved.

Tables 1 and 2 report Duncan's multiple range test of the mean taste panel scores of breast meat cooked in air or nitrogen from turkeys fed various diets containing tuna oil and/or beef fat with and without dietary α-tocopherol acetate or α-tocopherol injection. All meats that contained α-tocopherol gave taste panel scores that were comparable to the scores for the control for all methods of cooking. When breast meat is cooked under nitrogen with a slight vacuum no appreciable difference in flavor is caused by any of the diets. However, the breast meat from turkeys fed diets containing 2% tuna oil (treatments 5C and 2B) did have slightly higher scores, although not statistically different from the control (treatments 1C or 1B, 4% beef fat). The breast meat cooked in air from turkeys fed diets containing 2% tuna oil (treatments 5C and 2B) showed more off flavor than those cooked in nitrogen when each is compared to its control (treatments 1C or 1B, 4% beef fat). Furthermore, the order and rank of the scores for the air-cooked meat were very similar to those of breast meat from whole roasted turkeys previously reported by Crawford et al. (1975). These turkeys were randomly selected from the same groups of turkeys used in this experiment and were roasted at 177°C to center breast temperature of about 70°C.

From the results of this experiment, it may be concluded that cooking breast meat of potentially fishy flavored turkeys under nitrogen is nearly as effective in preventing fishy flavor development as feeding α-tocopherol acetate (in the diets with the tuna oil) and roasting in the normal manner. This implies that fishy flavor develops postmortem and requires air for its development. Alternately, it could be concluded that cooking under nitrogen per se had practically no effect in preventing this development but that fishy flavor had already developed in vivo and the heat of cooking at 116°C for 80 min destroyed the components which cause this flavor. Some observations and recent work (Crawford unpubl. data) tend to support the first conclusion.

We have observed that the odor of fresh raw turkey was insipid regardless of the type of dietary oil. However, after comminuting and storing in the refrigerator overnight, the flesh from turkeys fed tuna oil smelled fishy while the odor of beef fat-fed turkeys remained rather insipid.

TABLE 1.—Duncan's multiple range test of mean[1] taste panel scores[2] for breast meat cooked in air or nitrogen from turkeys fed various diets containing tuna oil and/or beef with and without α-tocopherol acetate.

Cooked in nitrogen		Cooked in air		Roasted normally[4]	
Treatment[3]	Scores	Treatment[3]	Scores	Treatment[3]	Scores
5C 2% TO	2.05	5C 2% TO	3.23	5C 2% TO	3.14
4C 4% BF + 200 E	1.80	3C 4% BF + 100 E	1.66	2C 4% BF	2.43
3C 4% BF + 100 E	1.77	2C 4% BF_1	1.63	3C 4% BF + 100 E	1.31
2C 4% BF_1	1.71	1C 4% BF	1.24	1C 4% BF	1.29
1C 4% BF	1.65	4C 4% BF + 200 E	1.08	4C 4% BF + 200 E	0.99

[1]Mean taste panel scores connected by a common line are not significantly different at the 0.05 probability level.
[2]Taste panel scoring: 1 = no fishy flavor, 5 = very fishy flavor. Abbreviations: TO = tuna oil; E = mg *dl* α-tocopherol acetate per kilogram of diet; BF = beef fat; BF_1 = beef fat substituted for 2% TO + 2% BF.
[3]All groups (except group 1C, the control which was maintained on diet with 4% BF for all 16 wk) were fed a basal diet with 2% TO plus 2% BF from 8 to 14 wk of age and from 14 to 16 wk of age, they were fed a basal diet with: group 1C = 4% BF, group 2C = change to 4% BF, group 3C = change to 4% BF + 100 mg/kg α-tocopherol acetate, group 4C = change to 4% BF + 200 mg α-tocopherol acetate, group 5C = kept on 2% TO + 2% BF.
[4]These results for the breast meat of normally roasted whole turkeys were previously reported by Crawford et al. (1975).

TABLE 2.—Duncan's multiple range test of mean[1] taste panel scores[2] for breast meat cooked in air or nitrogen from turkeys fed various diets containing tuna oil and/or beef fat with and without α-tocopherol acetate supplement or injection.

Cooked in nitrogen		Cooked in air		Roasted normally[4]	
Treatment[3]	Scores	Treatment[3]	Scores	Treatment[3]	Scores
2B 2% TO	1.82	2B 2% TO	2.16	2B 2% TO	2.23
4B 2% TO + 100 E	1.71	5B 2% TO + 500 E	1.74	5B 2% TO + 500 E	2.18
5B 2% TO + 500 E	1.61	4B 2% TO + 100 E	1.41	4B 2% TO + 100 E	1.86
3B 2% TO + In	1.59	3B 2% TO + In	1.35	3B 2% TO + In	1.32
1B 4% BF	1.43	1B 4% BF	1.22	1B 4% BF	1.19

[1]Mean taste panel scores connected by a common line are not significantly different at the 0.05 probability level.
[2]Taste panel scoring: 1 = no fishy flavor, 5 = very fishy flavor. Abbreviations: TO = tuna oil; E = milligrams *dl* α-tocopherol acetate per kilogram of diet; In = inject α-tocopherol; BF = beef fat.
[3]All groups were fed a basal diet + 4% BF to 14 wk of age and from 14 to 16 wk of age, they were fed a basal diet with: group 1B = 4% BF, group 2B = 2% BF + 2% TO, group 3B = 2% BF + 2% TO (+ inject 170 mg of α-tocopherol into thigh 72, 48, and 24 h before sacrifice), group 4B = 2% BF + 2% TO + 100 mg α-tocopherol acetate per kilogram, group 5B = 2% BF + 2% TO + 500 mg α-tocopherol acetate per kilogram.
[4]These results for the breast meat of normally roasted whole turkeys were previously reported by Crawford et al. (1975).

Fresh tuna fish also has very little odor but will develop a characteristic odor during refrigerated storage or cooking. These observations tend to support the supposition that fishy flavor develops during postmortem oxidation.

Additionally, volatiles were steam distilled from the same tuna oil that was fed to the turkeys in this experiment. These volatiles appeared to have the same fishy aroma as turkeys judged to have fishy flavor by the taste panel. The volatiles were added to water (ca. 2 μl/125 ml) in cans with a nitrogen or air headspace plus a slight vacuum and cooked at 116°C in the same fashion as the breast meat. An odor panel revealed little, if any, loss in character or intensity for the odor of the volatiles cooked under nitrogen or in air. Although this experiment with the volatiles offers only deductive reasoning, it nonetheless lends support to the argument that a heat-stable fishy flavor develops during cooking in air and that cooking under nitrogen prevents the development of this flavor.

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LITERATURE CITED

CRAWFORD, L.
1972. The effect of premortem stress, holding temperatures, and freezing on the biochemistry and quality of skipjack tuna. NOAA Tech. Rep. NMFS SSRF-651, 23 p.

CRAWFORD, L., D. W. PETERSON, M. J. KRETSCH, A. L. LILYBLADE, AND H. S. OLCOTT.
1974. The effects of dietary α-tocopherol and tuna, safflower, and linseed oils on the flavor of turkey. Fish. Bull., U.S. 72:1032-1038.

CRAWFORD, L., M. J. KRETSCH, D. W. PETERSON, AND A. L. LILYBLADE.
1975. The remedial and preventative effect of dietary α-tocopherol on the development of fishy flavor in turkey meat. J. Food Sci. 40:751-755.

FUJIMOTO, K., M. MARUYAMA, AND T. KANEDA.
1968. Studies on the brown discoloration of fish products—I. Factors affecting the discoloration. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 34:519-523.

JONES, N. R.
1962. Browning reactions in dried fish products. *In* J. Hawthorn and J. M. Leitch (editors), Recent advances in food science, 2:74:80. Butterworths, Lond.

KLOSE, A. A., E. P. MECCHI, H. L. HANSON, AND H. LINEWEAVER.
1951. The role of dietary fat in the quality of fresh and frozen storage turkeys. J. Am. Oil Chem. Soc. 28:162-164.

MECCHI, E. P., M. F. POOL, G. A. BEHMAN, M. HAMACHI, AND A. A. KLOSE.
1956. The role of tocopherol content in the comparative stability of chicken and turkey fat. Poult. Sci. 35:1238-1246.

MECCHI, E. P., M. F. POOL, M. NONAKA, A. A. KLOSE, S. J. MARSDEN, AND R. S. LILLIE.
1956. Further studies on tocopherol content and stability of carcass fat of chickens and turkeys. Poult. Sci. 35:1246-1251.

MILLER, D., E. H. GRUGER, JR., K. C. LEONG, AND G. M. KNOBL, JR.
1967a. Effect of refined menhaden oils on the flavor and fatty acid composition of broiler flesh. J. Food Sci. 32:342-345.
1967b. Dietary effect of menhaden oil ethyl esters on the fatty acid pattern of broiler muscle lipids. Poult. Sci. 46:438-444.

PIPPEN, E. L., AND M. NONAKA.
1963. Gas chromatography of chicken and turkey volatiles: The effect of temperature, oxygen, and type of tissue on composition of the volatile fraction. J. Food Sci. 28: 334-341.

TARR, H. L. A.
1954. The Maillard reaction in flesh foods. Food Technol. 8:15-19.

WEBB, J. E., C. C. BRUNSON, AND J. D. YATES.
1972. Effects of feeding antioxidants on rancidity development in pre-cooked, frozen broiler parts. Poult. Sci. 51:1601-1605.
1973. Effects of feeding fish meal and tocopherol on the flavor of precooked, frozen turkey meat. Poult. Sci. 52:1029-1034.

WEBB, R. W., W. W. MARION, AND P. L. HAYSE.
1972. Tocopherol supplementation and lipid stability in the turkey. J. Food Sci. 37:496.

BIOLOGY OF FIVE SPECIES OF SEAROBINS (PISCES, TRIGLIDAE) FROM THE NORTHEASTERN GULF OF MEXICO

THOMAS C. LEWIS AND RALPH W. YERGER[1]

ABSTRACT

Geographically, Gulf populations of *Prionotus alatus* appear to be restricted almost exclusively to the eastern portion of the Gulf of Mexico, while *Bellator militaris, P. martis, P. roseus*, and *P. stearnsi* occur over the entire Gulf. Bathymetrically, *P. martis* is a shallow shelf species; *B. militaris* and *P. roseus*, middle shelf species; *P. alatus*, middle to deep shelf species; *P. stearnsi*, deep shelf species. The size (standard length) of *B. militaris, P. alatus, P. martis*, and *P. roseus* showed a significant positive correlation with increasing depth of capture. *Bellator militaris* showed a significant "preference" for fine sandy silt, clay, or mud bottoms. *Prionotus stearnsi* was captured in significantly greater numbers during daytime trawling and is postulated to swim actively in the water column at night. It appears to spawn from late summer to fall or early winter, while the remaining species spawn from fall to spring or early summer. Adult *P. stearnsi* differed in food habits by consistently consuming relatively large fishes, while juveniles of this species and all the age groups of the other four species fed consistently on crustaceans.

Searobins of the family Triglidae are commonly taken in shrimp trawls along the coast of the Gulf of Mexico where they comprise an important element of the benthic shelf ichthyofauna (Miles 1951; Hildebrand 1954; Springer and Bullis 1956; Bullis and Thompson 1965; Roithmayr 1965; Franks et al. 1972). They are not commercially important in the Gulf of Mexico, but at least some species are included among the bottomfishes that are canned for pet food and reduced for fish meal by commercial Gulf fisheries (Roithmayr 1965). Triglids also present a rich source of food for the larger, commercially important fishes from the Gulf. *Prionotus ophryas, P. roseus*, and *P. stearnsi* have been found in the stomachs of red snapper, *Lutjanus campechanus*, taken off Pensacola, Fla. (Jordan and Swain 1885; Jordan and Evermann 1887). *Prionotus roseus* was reported from the stomachs of red grouper, *Epinephelus morio*, off Tampa, Fla. (Jordan and Evermann 1887). Hildebrand (1954) regarded *P. stearnsi* as one of the most important forage fishes in the western Gulf where it was noted in the stomachs of rock sea bass, *Centropristis philadelphica*; red snapper; sand seatrout, *Cynoscion arenarius*; and inshore lizardfish, *Synodus foetens*.

Despite their importance as forage fishes, few or no data are available on the biology of the Gulf species, particularly on those found in deeper water. What little is known appears widely scattered in the literature, usually in faunal lists. The only in-depth studies on the biology of western North Atlantic triglids (Marshall 1946; McEachran and Davis 1970) are on the two species *(Prionotus carolinus* and *P. evolans)* that do not occur in the Gulf.

Our study was undertaken to analyze the species composition of the northeastern Gulf triglid fauna on the continental shelf between 20 and 190 m, to determine the distribution and abundance of this fauna, and to investigate aspects of their biology. Thirteen species *(Bellator brachychir, B. egretta, B. militaris, Prionotus alatus, P. martis, P. ophryas, P. paralatus, P. roseus, P. rubio, P. salmonicolor, P. scitulus, P. stearnsi, P. tribulus)* were collected, but only five species *(B. militaris, P. alatus, P. martis, P. roseus, P. stearnsi)* were taken in sufficient numbers to report on their biology.

MATERIALS AND METHODS

Specimens were collected from July 1969 to October 1971 aboard the RV *Tursiops* and the USNS *Lynch*. Most cruises were conducted aboard the *Tursiops* from October 1970 to October 1971 as part of the "Gulf Shelf Project" conducted by the Edward Ball Marine Laboratory, Department of Oceanography, Florida State University. Fishes were captured in a 16-foot (4.9-m) try-net otter trawl with a ¾-inch (1.9-cm)

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square mesh body and a ⅛-inch (0.3-cm) square mesh cod end liner.

The study area extended along the northeastern Gulf of Mexico from east of the Mississippi River Passes, La., to the western edge of Apalachee Bay, Fla., over a depth range of 20 to 190 m (Figure 1). The easternmost stations (between long. 84°37′W and 85°30′W) were visited, with few exceptions, in October and December 1970, and January, April, May, July, August, and September 1971. The remaining stations were visited only once during cruises conducted in one of the following months: July, October, and December 1969; October and November 1970; January, February, April, July, and October 1971. Station locations were determined through loran. Station depth was recorded from fathometer readings. Depths for a few stations were extrapolated from soundings recorded for that location on "1100 Series" U.S. Coast and Geodetic Survey maps. (For complete station data and specimens examined see Lewis 1973.) The principal investigators of the Gulf Shelf Project determined the sampling regime for each station. One trawl sample was taken at each station. Trawling time on the bottom ranged from 10 to 60 min. The time duration for the majority of trawls at shallow stations (i.e. less than 90 m) was 10 min; for the deeper stations, 20 min. In order to standardize these trawling efforts, catches were recorded as number of fish collected per 10 min trawling (catch per unit effort), and transformed [$Y = \log (X + 1)$] for analysis of the variance. Data for all stations (when available) were used for analysis regardless of whether or not the particular species was present.

Bottom temperature was recorded for most stations by bathythermograph and on a few occasions either by expendable bathythermograph or reversing thermometers. Bottom type was determined by examination of samples taken in a bucket dredge dragged over the trawl area. Bottom type was divided into two major classes; coarse sand overlain with shell hash (type I), and fine sandy silt, clay, or mud (type II). Data for bottom type were not collected at some stations and consequently fishes taken at these stations were not used in analysis of bottom type. Night was considered to be that interval of time between 1 h after sunset and 1 h before sunrise at that time of the year, while day was considered to be between 1 h after sunrise and 1 h before sunset. Fish collected at dawn or dusk were not used in the analysis of time of capture data.

The standard length (SL) of each fish was measured to the nearest millimeter. Identifications were made following Ginsburg (1950), Miller (1965), and Miller and Kent (1971). Specimens were preserved in 10% Formalin[2] origi-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

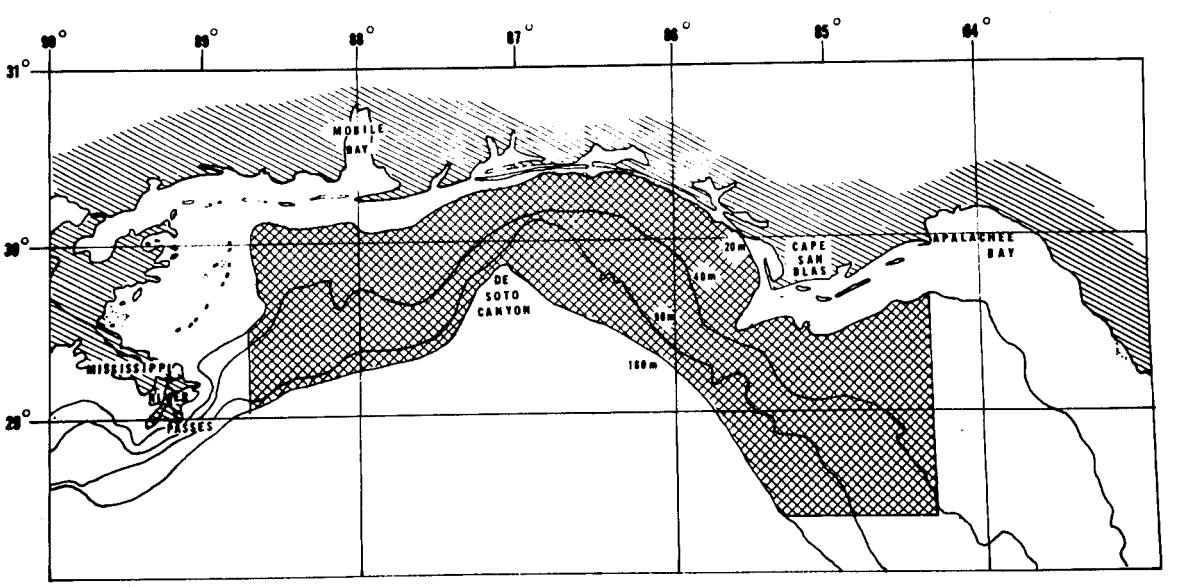

FIGURE 1.—Map of the study area sampled by the RV *Tursiops* and USNS *Lynch* between July 1969 and October 1971.

nally, transferred to 40% isopropyl alcohol and deposited in the Florida State University collection.

Gonads were examined from specimens taken in October, November, and December 1970, and January, February, April, May, July, August, September, and October 1971. Size at sexual maturity was determined by the first appearance of ripe or developing ova in females and enlarged testes in males. Females with numerous ripe ova were judged to be ready to spawn at or very near the date of capture. A ripe egg was determined to be one that was transparent and filled with numerous oil globules. Its size was measured to the nearest 0.1 mm with an ocular micrometer.

Stomachs (including the posterior esophagus) were removed and the contents analyzed for identifiable remains. Food items were identified at least to class, and where possible to order and suborder. The importance of food taxa was judged by their numerical abundance.

RESULTS

Bellator militaris (Goode and Bean) Horned Searobin

Bellator militaris was collected widely at depths of approximately 20 to 100 m (Figure 2a) and temperatures of 15° to 28°C. Specimens ranged in size from 24 to 111 mm SL. This species showed the greatest density of all the species

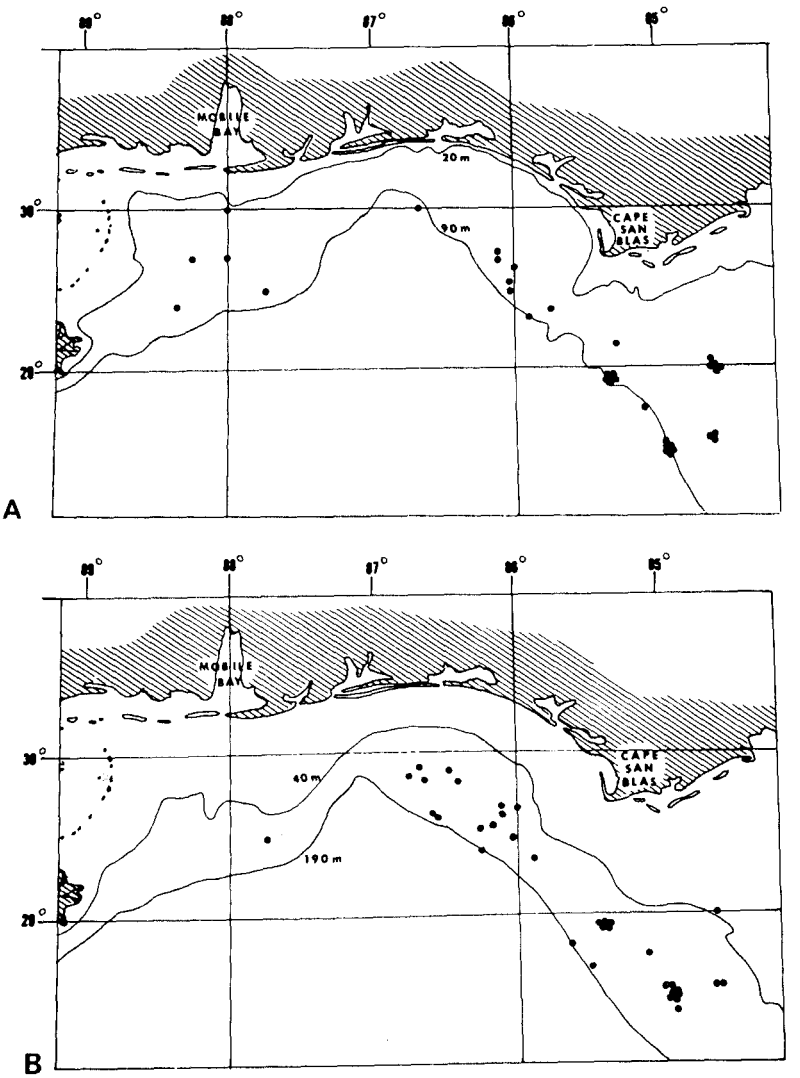

FIGURE 2.—Distribution within the study area of: A, *Bellator militaris* and B, *Prionotus alatus*.

caught, yielding 1.8 specimens per 10 min trawling within its depth range (Table 1).

This species was most abundant between 80 and 90 m (Figure 3a). There was a gradual increase in abundance to this depth range followed by a sharp decrease. There was a significant ($P<0.001$) positive relationship between increasing size and increasing depth of capture.

A statistically greater ($P<0.025$) number of *B. militaris* were taken over a fine sandy mud, silt, or clay bottom (Table 2). There was no statistical difference in catch for day versus night trawling (Table 3).

Bellator militaris appeared to reach sexual maturity at about 65 mm SL in both sexes. The spawning season was protracted as indicated by the presence of females with numerous ripe ova (0.7 to 0.9 mm in diameter) from November 1970 to July 1971.

Bellator militaris fed primarily on crustaceans (90 to 95% of the total stomach contents). Juveniles (Table 4) appeared to feed primarily on amphipods and natantian decapods; adults (Table 5), on natantian decapods, amphipods, and mysids. Adults also fed to a lesser extent on very small fishes (usually less than 15 mm SL), polychaetes, bivalves, and gastropods.

TABLE 1.—Number of specimens of five species of triglids collected and the mean number of fish per 10 min trawling.

Species	No. of specimens	Mean no. per 10 min trawling[1]
Bellator militaris	277	1.8
Prionotus alatus	162	1.0
P. martis	109	1.2
P. roseus	162	1.2
P. stearnsi	113	0.7

[1]For trawls within the depth and geographic range of the species.

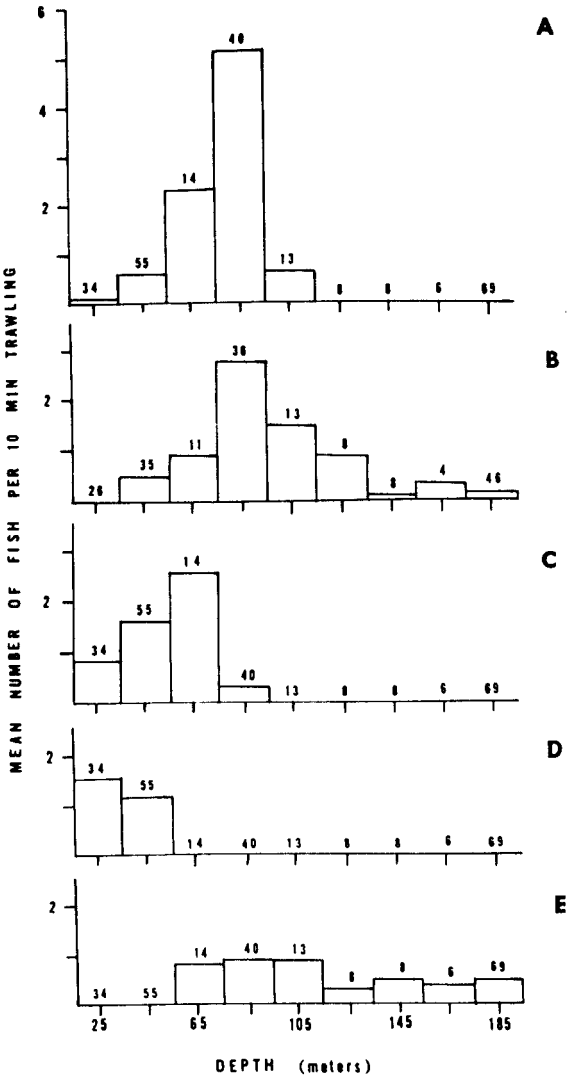

FIGURE 3.—Relationship of depth of capture versus catch per unit effort. A. *Bellator militaris*, B. *Prionotus alatus*, C. *Prionotus roseus*, D. *Prionotus martis*, and E. *Prionotus stearnsi*. Number above each bar refers to the number of 10-min trawling intervals at that particular depth.

Prionatus alatus Goode and Bean Spiny Searobin

With one exception, all specimens of *P. alatus* were collected east of the De Soto Canyon (Figure 2b). For this reason all analyses of this species were based only on data from stations east of the Canyon. Sizes ranged from 24 to 140 mm SL; collection depth, from 40 to 190 m; temperature, from 14° to 28°C. *Prionotus alatus* ranked fourth in density over its depth and geographic ranges (Table 1).

Prionotus alatus appeared to be most abundant around the 80- to 90-m interval of its depth range (Figure 3b). There was a rapid increase in catch to this point followed by a gradual decline. As in *B. militaris*, there was a significant ($P<0.001$) positive relationship between increasing size and increasing depth of capture.

There were no statistical differences in catch per unit efforts between bottom types (Table 2) and between day and night (Table 3).

Prionotus alatus appeared to reach sexual maturity at about 100 mm SL for both sexes. Females with numerous ripe ova (0.8 to 1.0 mm in diam-

TABLE 2.—The relationship of bottom type to density for five species of triglids.

Species	Type I[1] Mean no. per 10 min trawling	Type I[1] Variance	Type I[1] ^2N	Type II[1] Mean no. per 10 min trawling	Type II[1] Variance	Type II[1] ^2N	^3F
Bellator militaris	0.8	4.7	75	3.1	37.7	42	6.3*
Prionotus alatus	0.8	2.2	53	0.7	2.3	85	0.6
P. martis	1.7	27.5	38	0.6	1.3	14	0.3
P. roseus	1.4	8.8	71	1.3	11.4	38	0.0
P. stearnsi	1.1	9.5	30	0.8	2.5	80	0.2

[1]Type I = coarse sand bottom overlain with shell hash. Type II = fine sandy mud, silt or clay bottom.
[2]N = the number of 10-min trawling intervals within the depth and geographic range of the species.
[3]For one factor analysis of the variance for data transformed to $Y = \log(X + 1)$.
*Significant at $P<0.025$.

TABLE 3.—Comparison of day versus night trawling for five species of triglids.

Species	Night Mean no. per 10 min trawling	Night Variance	Night ^1N	Day Mean no. per 10 min trawling	Day Variance	Day ^1N	^2F
Bellator militaris	1.9	30.5	67	2.1	24.3	61	0.1
Prionotus alatus	1.4	14.9	76	0.8	3.4	65	0.3
P. martis	2.0	27.0	33	1.1	4.7	29	1.8
P. roseus	1.0	5.6	64	0.9	9.4	56	0.4
P. stearnsi	0.2	1.7	55	1.6	7.9	59	16.5*

[1]N = the number of 10-min trawling intervals within the species' depth and geographic range.
[2]For one factor analysis of the variance for data transformed to $Y = \log(X + 1)$.
*Significant at $P<0.001$.

TABLE 4.—Percent of total stomach contents for the juveniles of five species of searobins (n = the number of stomachs that contained identifiable remains).

Taxa	*Bellator militaris* n = 15	*Prionotus alatus* n = 24	*P. martis* n = 5	*P. roseus* n = 14	*P. stearnsi* n = 10
Crustacea:					
Ostracoda	1.1	3.0	—	—	—
Copepoda	7.9	—	—	—	2.2
Stomatopoda	—	10.4	—	—	—
Amphipoda	41.6	16.4	38.4	10.2	86.8
Isopoda	—	3.0	7.7	—	2.2
Mysidacea	4.5	13.4	—	13.3	—
Decapoda:					
Natantia	25.8	31.3	7.7	71.6	2.2
Reptantia	7.9	9.0	23.1	1.8	—
Megalops	1.1	4.5	—	—	4.4
Zoea	—	—	—	—	—
Annelida:					
Polychaeta	6.7	1.5	23.1	1.3	—
Mollusca:					
Bivalvia	3.4	1.5	—	1.8	—
Chordata:					
Vertebrata					
Osteichthyes	—	6.0	—	—	2.2

eter) were collected from November 1970 to April 1971. No females were collected in May or June and those collected in July 1971 were not ripe, indicating that spawning ceased somewhere during this interval.

Prionotus alatus fed primarily on crustaceans (91 to 97% of total stomach contents). Juveniles (Table 4) fed on decapods, amphipods, mysids, and stomatopods; adults (Table 5), chiefly on decapods. Small fishes (usually less than 15 mm SL) made up the only substantive non-crustacean food item in both adults and juveniles.

TABLE 5.—Percent of total stomach contents for the adults of five species of searobins (n = the number of stomachs examined that contained identifiable remains).

Taxa	*Bellator militaris* n = 59	*Prionotus alatus* n = 30	*P. martis* n = 25	*P. roseus* n = 54	*P. stearnsi* n = 14
Crustacea:					
Ostracoda	1.2	0.3	—	0.1	—
Copepoda	3.9	—	—	—	—
Stomatopoda	2.4	4.3	—	1.5	—
Amphipoda	30.1	2.5	21.1	3.0	4.5
Isopoda	1.7	1.8	—	0.5	—
Mysidacea	18.6	5.0	6.4	4.7	—
Decapoda:					
Natantia	30.9	71.3	39.8	82.4	9.1
Reptantia	5.2	11.0	10.5	4.5	9.1
Megalops	0.9	1.0	1.2	—	9.1
Zoea	0.5	—	—	—	—
Annelida:					
Polychaeta	0.8	—	4.6	2.0	—
Mollusca:					
Bivalvia	1.5	0.3	0.6	0.2	—
Gastropoda	0.3	—	—	0.1	—
Cephalopoda	—	—	—	—	4.5
Echinodermata:					
Ophiuroidea	—	—	1.2	0.2	—
Chordata:					
Cephalochordata	—	—	11.7	—	—
Vertebrata:					
Osteichthyes	2.0	2.5	2.9	0.8	63.7

Prionotus roseus Jordan and Evermann Bluespotted Searobin

Specimens of *P. roseus* ranging in size from 240 to 170 mm SL were collected throughout the study area at depths of 20 to 90 m (Figure 4a) and bottom temperatures of 16° to 28°C. It ranked, with *P. martis*, second in density within its depth range (Table 1).

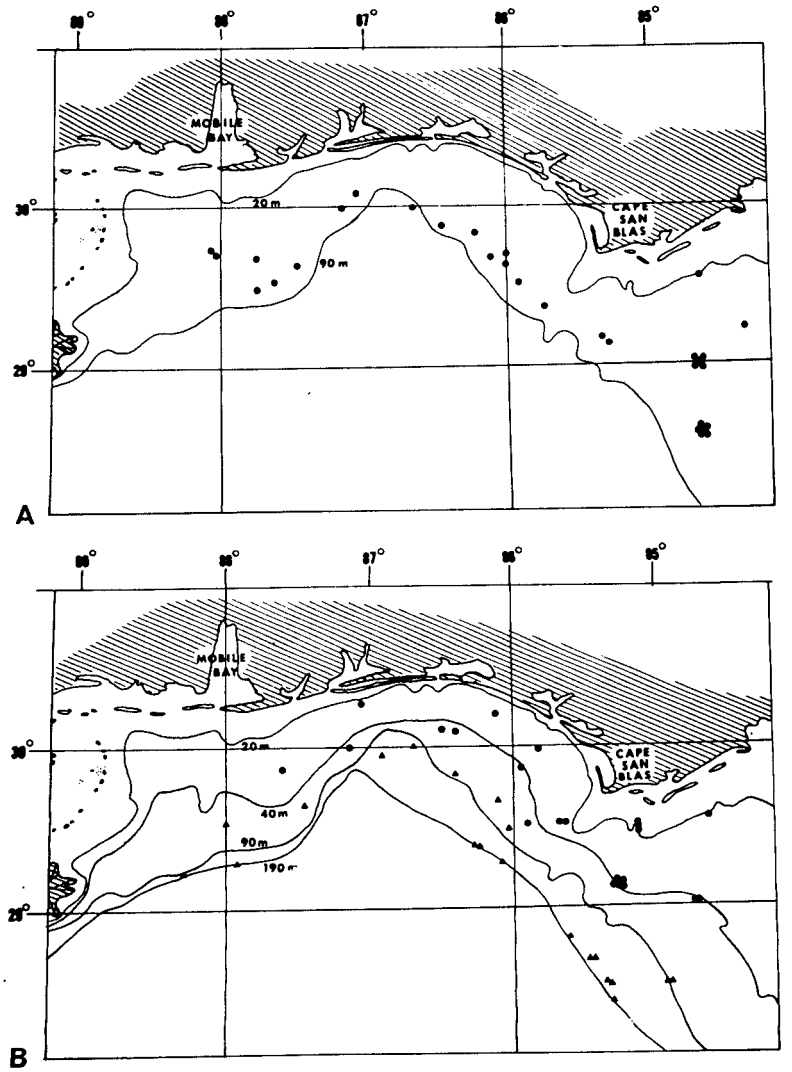

FIGURE 4.—Distribution within the study area of: A, *Prionotus roseus* and B, *Prionotus martis* (●) and *Prionotus stearnsi* (▲).

This species was most abundant between 60 and 70 m. As with the previous two species, *P. roseus* showed a significant ($P<0.001$) positive relationship between increasing size and increasing depth of capture.

There were no statistical differences in catches between bottom types (Table 2) or between night and day collections (Table 3).

Prionotus roseus appeared to reach sexual maturity at 100 mm SL for both sexes. Spawning period was protracted. Females with numerous ripe ova (0.7 to 0.8 mm in diameter) were collected from December to May 1971.

Prionotus roseus also fed primarily on crustaceans (97% of the total stomach contents). Juveniles (Table 4) fed chiefly on decapod shrimp, mysids, and amphipods; adults (Table 5) even more exclusively on decapods.

Prionotus martis Ginsburg Barred Searobin

Prionotus martis was collected widely except at the western edge of the study area at depths of approximately 20 to 45 m (Figure 4b). Sizes of specimens ranged from 51 to 159 mm SL and bottom temperature from 17° to 28°C. *Prionotus martis* ranked, with *P. roseus*, second for density within its depth range (Table 1).

Prionotus martis was most abundant at the 20- to 30-m interval of its depth range (Figure 3d). As was the case for *B. militaris*, *P. alatus*, and

P. roseus, this species showed a significant ($P<0.001$) positive relationship between increasing size and increasing depth.

No statistical differences in catch per unit effort between bottom types (Table 2) or night and day collections (Table 3) were observed.

Determination of size at sexual maturity in *P. martis* was inexact due to a paucity of specimens less than 100 mm SL. Individuals of both sexes at 100 mm SL were mature, while nine specimens below this size were immature. Consequently 100 mm SL was tentatively given as the size at sexual maturity for both sexes. Likewise, the exact spawning season for this species was difficult to determine. Females with numerous ripe ova (0.6 mm in diameter) were collected from October to December 1970. A large sample of females in January 1971 contained no ripe individuals, while a sample from April 1971 contained one ripe female.

Prionotus martis fed primarily on crustaceans but not as extensively as the previous three species (around 80% of the total stomach contents). Juveniles (Table 4) appeared to feed heavily on amphipods, polychaetes, and decapod crabs; adults (Table 5) on decapod crabs and shrimp, amphipods, and cephalochordates. The only other important food items for adults were polychaetes and very small fishes (usually less than 15 mm SL).

Prionotus stearnsi Jordan and Swain Shortwing Searobin

Prionotus stearnsi was collected widely at depths of approximately 60 to 185 m (Figure 4b) and temperatures from 14° to 21°C. Specimens ranged in size from 11 to 117 mm SL. It ranked fifth in density within its depth range.

Prionotus stearnsi was fairly evenly distributed within its depth range, but was slightly more abundant at shallower depths (Figure 3e). Unlike the previous four species, there was no significant relationship between increasing size and increasing depth of capture.

There was no significant difference in catch between bottom types (Table 2). There was, however, a significantly ($P<0.001$) greater catch during daytime trawling (Table 3).

Prionotus stearnsi appeared to reach sexual maturity at about 60 mm SL in both sexes. No ripe females were collected during the 1970-71 season and only one female in October and two in December of 1969 contained numerous ripe ova (0.6 mm in diameter).

This species appeared to have different feeding habits between adults and juveniles. The latter (Table 4) fed primarily on small crustaceans (98% of the number of food organisms), the former (Table 5) chiefly on relatively large fishes (usually larger than 25 mm SL; 64% of the number of food organisms). The only other important food among adults was decapod crustaceans.

DISCUSSION

Geographic Distribution

Four of the five species (*B. militaris, P. martis, P. roseus, P. stearnsi*) have been previously recorded over the entire northern Gulf of Mexico (Ginsburg 1950; Springer and Bullis 1956; Bullis and Thompson 1965; Burns 1970; Franks et al. 1972). *Prionotus alatus* has been reported almost exclusively from east of the De Soto Canyon, but Ginsburg (1950), Burns (1970), Miller and Kent (1971), and Franks et al. (1972, based on the same two specimens examined by Burns) reported small numbers west of the Canyon. Our study confirms this distribution and we conclude that *P. alatus* is quite rare in the western portion of the northeastern Gulf, where it is replaced by *P. paralatus*.

Depth Distribution

The triglids collected in this study fit into four bathymetric categories: 1) shallow shelf and inshore species, 2) shallow shelf to midshelf species, 3) shallow to deep shelf species, and 4) midshelf to deep shelf species.

Prionotus martis is a shallow shelf and inshore species. Springer and Bullis (1956) reported it from 200 fathoms (366 m) but we feel that this record is based on either a misidentification or incorrect station data. All other specimens in their paper came from 25 fathoms (46 m) or less. The maximum depth for our study, 44 m (24 fathoms), is probably the maximum depth reached by this species. It also enters shallow water, being reported from 6 fathoms or less by Reid (1954), Bullis and Thompson (1965), Richmond (1968), and Hastings (1972).

Bellator militaris and *P. roseus* fall into the second category; the maximum depth for both species was about 90 to 100 m. However, *B.*

militaris appears to reach 100 fathoms (183 m) off southwestern Florida (Longley and Hildebrand 1941; Springer and Bullis 1956; Moe and Martin 1965) as does *P. roseus* (Springer and Bullis 1956). *Bellator militaris* has been recorded by Bullis and Struhsaker (1970) from the 100- to 150-fathom (180- to 270-m) interval in their Caribbean study, and at 100 and 1,175 fathoms (180 and 2,150 m) in the northern Gulf by Springer and Bullis (1956). The latter figure is likely wrong. Since neither species was collected at 100 fathoms (183 m) in the present study despite intensive collecting at this depth, we conclude they rarely if ever reach this depth in the northeastern Gulf. Both are seldom recorded from less than 20 m. Moe and Martin (1965) recorded *B. militaris* in less than 3 fathoms (5.5 m) and *P. roseus* from approximately 6 fathoms (11 m) off Tampa, Fla.

Miller and Kent (1971) gave the depth range for *P. alatus* as 30 to 250 fathoms (55 to 457 m) which would place it in the shallow to deep shelf category. Our study reveals that this species occasionally enters water shallower than 30 fathoms (55 m); two specimens were collected in 44 m of water.

Our study indicates that *P. stearnsi* is a mid-shelf to deep shelf species. Like that of *P. alatus*, its depth range extends to deeper waters than those found in our study area. Excluding the armored searobins (which are often placed in Triglidae), it is one of the deepest dwelling western North Atlantic triglids. Ginsburg (1950) examined specimens from 169 fathoms (309 m). Bullis and Struhsaker (1970) reported it from the 150- to 200-fathom (274- to 366-m) interval. Springer and Bullis (1956) reported *P. stearnsi* from as deep as 250 fathoms (457 m, excluding the same erroneous 1,175-fathom station reported for *B. militaris*). *Prionotus stearnsi* has also been recorded from shallower waters. Ginsburg (1950) listed specimens from 13 fathoms (24 m), Hildebrand (1954) from 12 fathoms (22 m), and Springer and Bullis (1956) from 5.5 fathoms (10 m), though this last figure is based on a field identification and is subject to error. We never collected *P. stearnsi* at depths less than 60 m despite intensive collecting and conclude that it rarely enters shallower waters in the northeastern Gulf.

Size-Depth Relationship

In their study in Gulf waters off Pinellas County, Fla., Moe and Martin (1965) reported that larger specimens of various fishes consistently occurred at deeper depths. They pointed out that this phenomenon had been noted before and was correlated with increasing salinity (e.g. Gunter 1945). However, they were unable to draw such a correlation, since salinity changed so little over their study area. Topp and Hoff (1972) showed statistically significant increases in the mean size of *Syacium papillosum* (a bothid) collected between 18 and 37 m and between 37 and 55 m off southwestern Florida. Our results point to similar conclusions. We found a highly significant ($P<0.001$) positive relationship between increasing size and increasing depth of capture for all species except *P. stearnsi*. We concur with Moe and Martin (1965) that this is not correlated with salinity changes (which are small in our study area).

Temperature

The four species in the first three bathymetric categories occurred over a wide range of temperatures. The only species that could in any way be restricted by the temperature of its environment is *P. stearnsi*, the deep shelf species, which was taken over a limited range from 14° to 21°C.

Bottom Type

Bellator militaris was the only species which showed any significant bottom type preference; it was found in greater abundance over fine sandy mud, silt, or clay bottoms. We conclude that bottom type, at least as categorized in this study, does not play a very important part in the distribution of four of the five species studied.

Time of Capture

Only one species, *P. stearnsi*, showed a significant difference in the catch per unit effort between day and night trawls; it was more abundant in daytime trawls. *Bellator militaris* and *P. roseus* were equally abundant in both day and night trawls, while *P. alatus* and *P. martis* tended, though not conclusively so, to be caught in greater numbers at night. Hoese et al. (1968) noted that *P. tribulus crassiceps* as well as other unidentified triglids tended to be caught more frequently at night, though not significantly so.

The occurrence of *P. stearnsi* in such greater numbers during the day is difficult to explain. Two opposing hypotheses can be postulated. First, *P. stearnsi* may be a diurnal species, active over the bottom during the day, and perhaps burrowing during the night and thus eluding capture. Or second, *P. stearnsi* may be nocturnal; during the day it may rest on the bottom exposed to daytime trawls, while at night it may ascend into the water column to feed beyond the reach of the trawl. We favor the second possibility because of the general physiognomy of this species. Food habits, as will be discussed, also suggest a more actively swimming existence compared with other triglids.

Reproduction

Sexual Maturity

Bellator militaris and *P. stearnsi* are rather small triglids maturing at 65 and 60 mm SL and reaching a maximum size around 120 and 135 mm, respectively (Ginsburg 1950). *Prionotus alatus, P. martis,* and *P. roseus* mature at about 100 mm SL and attain at least 189 mm (Ginsburg 1950), 166 mm (Reid 1954), and 225 mm (Ginsburg 1950), respectively. Marshall (1946) found that *P. carolinus* and *P. evolans* mature at about 140 and 180 mm SL, respectively, and attain a much larger size than any Gulf species. It appears that the size at sexual maturity is largely a function of the size attained by the particular species.

Spawning Season

Spawning seasons for the triglids collected in this study can be separated into two ill-defined categories: 1) Late summer to fall or early winter and 2) late fall to spring or summer (see Figure 5).

Prionotus stearnsi appears to fit into the first category. In our study ripe females were collected only in October and December. Longley and Hildebrand (1941) reported collecting a ripe female in August off the Tortugas. These limited data and a large number of very small specimens in collections from October, December, and January indicate that *P. stearnsi* probably spawns from late summer to late fall or early winter. The paucity of ripe females suggests that this species may spawn at greater depths than those sampled in this study.

Three of the remaining four species (*B. militaris, P. alatus, P. roseus*) had obviously protracted spawning seasons from fall to late spring or summer. The presence of a number of small individuals collected throughout the year further corroborated the length of the reproductive period.

Prionotus martis was in spawning condition in October, December, and April. The presence of only a few juveniles in this study leads us to

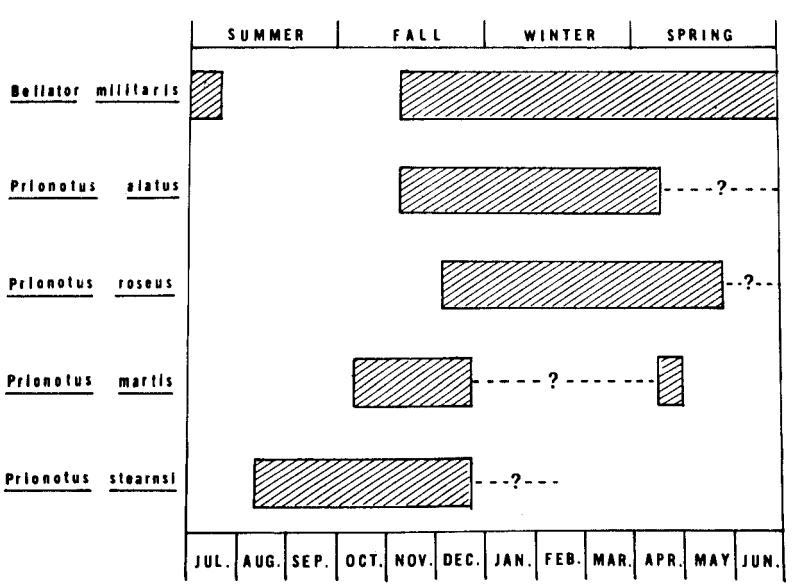

FIGURE 5.—Spawning seasons for five species of searobins.

believe that the young develop in shallower water. The bulk of spawning appears to take place from late fall to late winter or early spring since all specimens less than 45 mm SL that we have examined came from March and April collections from water less than 20 m deep. Also, Hastings (1972) collected small specimens of *P. martis* during February to April only (greatest abundance in April) during his seasonal studies of the jetty fauna at Destin and Panama City, Fla.

Food Habits

Rapid retrieval of the trawl from the bottom often resulted in eversion of stomachs, especially in the deeper water species. Hence, analysis of food habits was impeded by small sample sizes. Also, the use of numerical abundance of taxa to determine dietary preferences presents an obvious bias. Large numbers of small individuals would appear dominant when, in fact, they might make only a small percentage of the volume of food consumed. This was the case in the dominance of amphipods in the stomachs of juvenile *P. stearnsi*. In general, however, individuals of the numerically dominant taxa tended to be dominant in size also.

On the basis of these limited data, four of the five species (*B. militaris, P. alatus, P. martis, P. roseus*) and the juveniles of the fifth (*P. stearnsi*) appear to feed primarily on benthic crustaceans and other benthic organisms. Reid (1954) and Springer and Woodburn (1960) examined *P. scitulus latifrons* and *P. tribulus crassiceps* from the northeastern Gulf and also found that both species fed primarily on crustaceans. Likewise, Marshall (1946) found the same to be true for *P. carolinus* and *P. evolans* from the Atlantic coast.

In contrast, the adults of *P. stearnsi* appear to consume primarily other fishes. The food habits of the adults of this species are different from all other western North Atlantic triglids examined. Its piscivorous habit lends support to our earlier contention that this species is more mobile than its congeners. This type of diet would imply an active pursuit of their prey.

The fusiform shape of this species also implies an active mode of existence. The head of *P. stearnsi* with its terminal mouth does not appear to be adapted for bottom feeding. The free rays of the pectoral fins are more slender and less developed; they likely are not used extensively as tools for searching along the bottom as in other triglids.

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LITERATURE CITED

BULLIS, H. R., JR, AND P. J. STRUHSAKER.
1970. Fish fauna of the western Caribbean upper slope. Q. J. Fla. Acad. Sci. 33:43-76.

BULLIS, H. R., JR., AND J. R. THOMPSON.
1965. Collections by the exploratory fishing vessels *Oregon, Silver Bay, Combat,* and *Pelican* made during 1956 to 1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510, 130 p.

BURNS, C.
1970. Fishes rarely caught in shrimp trawl. Gulf Res. Rep. 3:110-130.

FRANKS, J. S., J. Y. CHRISTMAS, W. L. SILER, R. COMBS, R. WALLER, AND C. BURNS.
1972. A study of nektonic and benthic fauna of the shallow Gulf of Mexico off the State of Mississippi as related to some physical, chemical, and geological factor. Gulf Res. Rep. 4, 148 p.

GINSBURG, I.
1950. Review of the western Atlantic Triglidae (fishes). Tex. J. Sci. 2:489-527.

GUNTER, G.
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1, 190 p.

HASTINGS, R. W.
1972. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Ph.D. Thesis, Florida State Univ., Tallahassee, 555 p.

HILDEBRAND, H. H.
1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci., Univ. Tex. 3:233-366.

HOESE, H. D., B. J. COPELAND, F. N. MOSELEY, AND E. D. LANE.
1968. Fauna of the Aransas Pass Inlet, Texas. III. Diel and seasonal variations in trawlable organisms of the adjacent area. Tex. J. Sci. 20:33-60.

JORDAN, D. S., AND B. W. EVERMANN.
1887. Description of six new species of fishes from the Gulf of Mexico, with notes on other species. Proc. U.S. Natl. Mus. 9:466-476.

JORDAN, D. S., AND J. SWAIN.
1885. Description of three new species of fishes (Prionotus stearnsi, Prionotus ophryas and Anthias vivans) collected at Pensacola, Florida, by Mr. Silas Stearns. Proc. U.S. Natl. Mus. 7:541-545.

LEWIS, T. C.
1973. Biology of searobins (Pisces: Triglidae) from the northern Gulf of Mexico. M.S. Thesis, Florida State Univ., Tallahassee, 84 p.

LONGLEY, W. H., AND S. F. HILDEBRAND.
1941. Systematic catalogue of the fishes of Tortugas, with observations on color, habits, and local distribution. Carnegie Inst. Wash. Publ. 535:1-331. (Tortugas Lab. Pap. 34.)

MARSHALL, N.
1946. Observations of the comparative ecology and life history of two sea robins, *Prionotus carolinus* and *Prionotus evolans strigatus*. Copeia 1946:118-144.

MCEACHRAN, J. D., AND J. DAVIS.
1970. Age and growth of the striped searobin. Trans Am. Fish. Soc. 99:343-352.

MILES, R. M.
1951. An analysis of the "trash fish" of shrimp trawlers operating in Apalachicola Bay and the adjacent Gulf of Mexico. M.S. Thesis, Florida State Univ., Tallahassee, 46 p.

MILLER, G. C.
1965. A new species of searobin (Triglidae). Q. J. Fla. Acad. Sci. 19:259-266.

MILLER, G. C., AND D. M. KENT.
1971. A redescription of *Prionotus beani* (Pisces, Triglidae). Q. J. Fla. Acad. Sci. 34:223-242.

MOE, M. A., JR. AND G. T. MARTIN.
1965. Fishes taken in monthly trawl samples offshore of Pinellas County, Florida, with new additions to the fish fauna of the Tampa Bay area. Tulane Stud. Zool. 12:129-151.

REID, G. K., JR.
1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4, 94 p.

RICHMOND, E. A.
1968. A supplement to the fauna and flora of Horn Island, Mississippi. Gulf Res. Rep. 2:213-254.

ROITHMAYR, C. M.
1965. Industrial bottomfish fishery of the northern Gulf of Mexico, 1959-63. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 518, 23 p.

SPRINGER, S., AND H. R. BULLIS, JR.
1956. Collections by the *Oregon* in the Gulf of Mexico. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 196, 134 p.

SPRINGER, V. G., AND K. D. WOODBURN.
1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv., Mar. Lab., Prof. Pap. 1, 104 p.

TOPP, R. W., AND F. H. HOFF, JR.
1972. Flatfishes (Pleuronectiformes). Memoirs of the Hourglass Cruises. Vol. IV. Part II. Fla. Dep. Nat. Resour., Mar. Res. Lab., 135 p.

AN ACOUSTIC METHOD FOR THE HIGH-SEAS ASSESSMENT OF MIGRATING SALMON[1]

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ABSTRACT

A system of free-floating acoustic buoys with upward-looking transducers has been developed for use in assessing high-seas salmon stocks. The transducers, operating at 120 kHz, are suspended 46 m below the surface. The fish counts and the range to each fish are obtained in digital form, and the data are radioed from each buoy to the tending vessel where the data are decoded and recorded on magnetic tape. The present system consists of four buoys although the receiver-decoder system can accommodate up to 10 buoys operating synchronously.

The assessment of fish stocks is of obvious importance to all segments of the fishing industry in planning their respective operations. A problem of particular interest to the United States Section of the International North Pacific Fisheries Commission has been the assessment of immature sockeye salmon, *Oncorhynchus nerka*, which occur in abundance each summer south of the central Aleutian Islands in the North Pacific Ocean. It has been found (Hartt 1962, 1966) that immature sockeye salmon, mainly of Bristol Bay origin, migrate westward through this area in summer and that their relative abundance is related to the number of mature fish returning to Bristol Bay the following year (Fisheries Research Institute Staff 1960; Rogers 1972, 1973, 1974). This information has been used since 1960 as a means of forecasting the Bristol Bay run. Because the size of the run may vary by a factor of 10, an accurate forecast with a lead time of nearly a year is of obvious importance to the fishing and canning segments of the industry. Mathews (1966) has shown, by means of a comprehensive model simulating the cannery portion of the fishery, the relative value of run forecasts of varying precision. Run forecasts are also of value to the fishery management agencies in setting preliminary escapement goals and in planning their early season strategies to meet these anticipated goals.

The assessment of immature fish at Adak Island has been done by the Fisheries Research Institute using a fine-mesh purse seine 400 fathoms (730 m) long at a series of stations from 5 to 50 nautical miles off the southern shore of Adak Island. From 1956 through 1967, no station pattern was followed—purse seine sets were made randomly, mainly in an area within 20 nautical miles of shore. Since 1968, the fishing has been conducted uniformly at five stations spaced at approximately 10 nautical mile intervals between 5 and 50 nautical miles offshore.

Although the purse seine is a useful tool for providing information on abundance, species composition, and age composition of the stocks present, it suffers from several disadvantages as a research tool. Its use is limited to periods of moderate sea conditions resulting in significant gaps in the time-space coverage in this particularly stormy region. A maximum of five sets can be made in a day under ideal conditions which yields only 2½ h of actual fishing. Also, seines give no direct information on depth stratification or schooling of the fish, and in areas where the direction of migration of the fish is not uniform, multiple sets are required to sample all of the stocks present. Variability in direction of migration is not a serious problem in the area south of the central Aleutian Islands because the direction of migration of immature salmon is uniformly westward (Hartt in press). In an effort to overcome the sampling limitations of the purse seine, the Fisheries Research Institute and the Applied Physics Laboratory jointly developed an

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acoustic assessment system that can be used alone or in conjunction with the purse seine. Some of the anticipated advantages of such a system were that it could obtain abundance estimates and swimming depths with around-the-clock operation in a wide range of weather conditions.

PRELIMINARY CONSIDERATIONS

The final configuration of the system was determined, to a large extent, by consideration of problems related to obtaining adequate numbers of representative samples. The preliminary indications were that most of the fish of interest were concentrated near the surface at a depth of 10 m or less. This conclusion was based on the results of experiments in which longline and gill net gear were fished at various depths (Manzer 1964; Machidori 1966; French et al. 1967) and also by direct visual observation of salmon in the purse seines. This concentration of fish near the surface precluded the use of a hull-mounted device since such a system would necessarily exclude the top 3 or 4 m of the water column. This led to consideration of a transducer suspended in some manner below the main body of fish.

A transducer mounted on a towed platform with a coaxial cable to the towing vessel was considered initially but was abandoned because of the anticipated difficulty of developing a platform that could maintain depth and attitude stability while maintaining position to the side of the vessel. Since the extreme water depths precluded an anchored system the approach eventually adopted was to suspend the transducers from free-floating surface buoys with self-contained electronics. Consideration of the anticipated sampling statistics indicated the need for a multibuoy system which in turn suggested radio telemetry of the data from the buoys to a central shipboard receiver and recorder. This is the type of system that was eventually constructed.

The sampling statistics of particular relevance to the design and operation of the buoy system concerned: a) the level of effort required to obtain a specified precision in the estimation of the density of the fish and b) the purse seine effort required to obtain comparable precision in the estimation of the species composition of the population.

Extensive purse seining over a period of several years indicated that the salmon were relatively sparse and probably did not school or otherwise interact to a significant degree. Under these conditions the echo counts may be assumed to have a Poisson distribution with a parameter, μ, that is proportional to the number density[5] of the fish. Thus we have,

$$\mu = \rho_0 V_s \tag{1}$$

where V_s is the sampling volume of a single counter and ρ_0 is the average fish density defined so that μ is the expected number of echoes per acoustic pulse. If we assume large sample theory, the minimum number of acoustic pulses required to be $100\alpha\%$ confident that the relative error of the estimate of ρ_0 does not exceed ϵ is given by,

$$M_{\min} = \frac{d_\alpha^{\,2}}{\epsilon^2 \rho_0 V_s} \tag{2}$$

where d_α is the $100\alpha\%$ point (two-sided) of $N(0,1)$. The crucial feature of Equation (2) is that the sampling effort must be increased as either ρ_0 or V_s decrease. Preliminary estimates of ρ_0 based on purse seine data, while quite crude, indicated that V_s should be as large as possible subject only to the tradeoffs necessary to obtain an adequate signal to noise ratio. Also, the need for multiple buoys sampling mutually disjoint volumes was indicated.

The high-seas salmon population generally consists of a mixture of species so that it is necessary to determine species composition by some means. In the area south of the central Aleutians significant numbers of chum salmon, *O. keta*, occur mixed with immature sockeye salmon during the sampling period, and occasionally pink, *O. gorbuscha*; coho, *O. kisutch*; and chinook salmon, *O. tshawytscha*, are present in small numbers. The only nonsalmonid species generally found in this area, at the depths being sampled, is the Atka mackerel, *Pleurogrammus monopterygius*. This species generally occurs in small numbers relative to the salmon so that, if counted, it will not seriously affect the estimates of the density of the salmon. Further, this species does not have a swim bladder so that by the proper choice of the detection threshold level these fish will not be detected by the sonar.

[5]For echo counting the number density is the quantity of interest. If acoustic echo integration is utilized, the density on a mass basis is appropriate.

Species and age discrimination by acoustic means is not currently possible so that it is necessary to obtain samples by purse seine in order to determine the species and age composition of the population.

Since sockeye salmon is the only species of interest, we may treat the purse seine samples as binomial events in which the parameter of interest is the proportion, p, of sockeye salmon present in the population. If asymptotic normality is again assumed, it is found that the sample size required to be $100\alpha\%$ confident that the relative error of the estimate of p will not exceed δ is given by,

$$n = \frac{(1 - p)\, d_\alpha{}^2}{p\, \delta} \tag{3}$$

where d_α is that defined for Equation (2).

Equations (2) and (3), as indicated, provide information on the sampling necessary to achieve prescribed levels of precision in the population estimates. A direct but somewhat crude comparison of the purse seine and the acoustic buoys may be made on an area basis. The purse seine has a nominal length of 400 fathoms or about 732 m. The area swept out in a round haul[6] is about 42,600 m². For a transducer having a beam width of 28° to the 3 dB points and suspended 46 m below the surface, the area ensonified is approximately 390 m². Thus the purse seine sweeps out an area about 110 times as great as the area ensonified by a single acoustic pulse. The pulse interval is approximately 10 s. However, it has been found that the individual fish remain in the pattern for longer periods of time, typically about 30 s, although a precise estimate is not available at this time. Thus, a single buoy would have to operate for at least 1 h to obtain coverage equivalent to a single round haul. The additional coverage obtained using 30-min tow hauls is not known precisely but the limited data available indicate a factor of two or three over the round hauls. Thus, to provide coverage comparable to that of the purse seine a single buoy would have to operate for a minimum of 3 h. A comparable sampling time is obtained using Equation (2) with $\rho_0 V_s$ estimated using a typical seine haul of 150 fish. The seine hauls may vary from zero to well over 1,000 fish from which it follows that the time required for adequate acoustic samples may vary, inversely, by corresponding amounts. The sampling considerations just outlined played a significant part in the choice of the hardware configuration and the decision to utilize multiple buoys.

SYSTEM DESIGN AND CHARACTERISTICS

Figure 1 is a schematic illustration of the high-seas assessment system showing only a single buoy. In operation up to 10 buoys can be deployed, each sending information to the shipboard decoding and recording system. A four-buoy system has been used at Adak to help assess the migrating salmon population. A simplified block diagram of the buoy system is given in Figure 2, and a photograph of the buoy is shown in Figure 3. The buoy and shipboard system are discussed below.

The buoy contains an acoustic system which gathers fish count and depth distribution data, a logic system which processes and provides temporary storage for these data, and a telemetry system which sends data to the monitoring ship. The acoustic system operates at 120 kHz and samples the population every 10 s. Sample rates can be changed to 5-s or 2.5-s intervals if desired. The system transmits a 200-μs pulse (24 cycles at 120 kHz) at a source level of + 106 dB. Target returns must be greater than a preset threshold (approximately 2 V) for at least 100 μs before they are validated. This technique, and an adequate source level to give a worst case[7] signal-to-noise ratio of 10 dB, minimizes false target counts.

Pulse elongation and amplitude testing techniques are used to automatically adjust "end-of-sample" so that surface returns and near surface bubbles are not counted.

Measurements at the University of Washington and at Adak during summer operation have shown that the "average" target size of the migrating salmon is about −30 dB within the aspect angles encountered in the sample volume.

A typical plot of signal return versus aspect angle from a single fish is shown in Figure 4. This polar diagram shows target strength from the

[6]Purse seining is normally done in a standard manner using tow hauls in which the seine is held open in a semicircle for 30 min before closing and pursing. In a round haul the seine is set in a circle and pursed immediately after closing the circle.

[7]The worst-case condition exists for minimum target strength (−45 dB) at maximum range (46 m) at the −3 dB point in the transducer beam pattern.

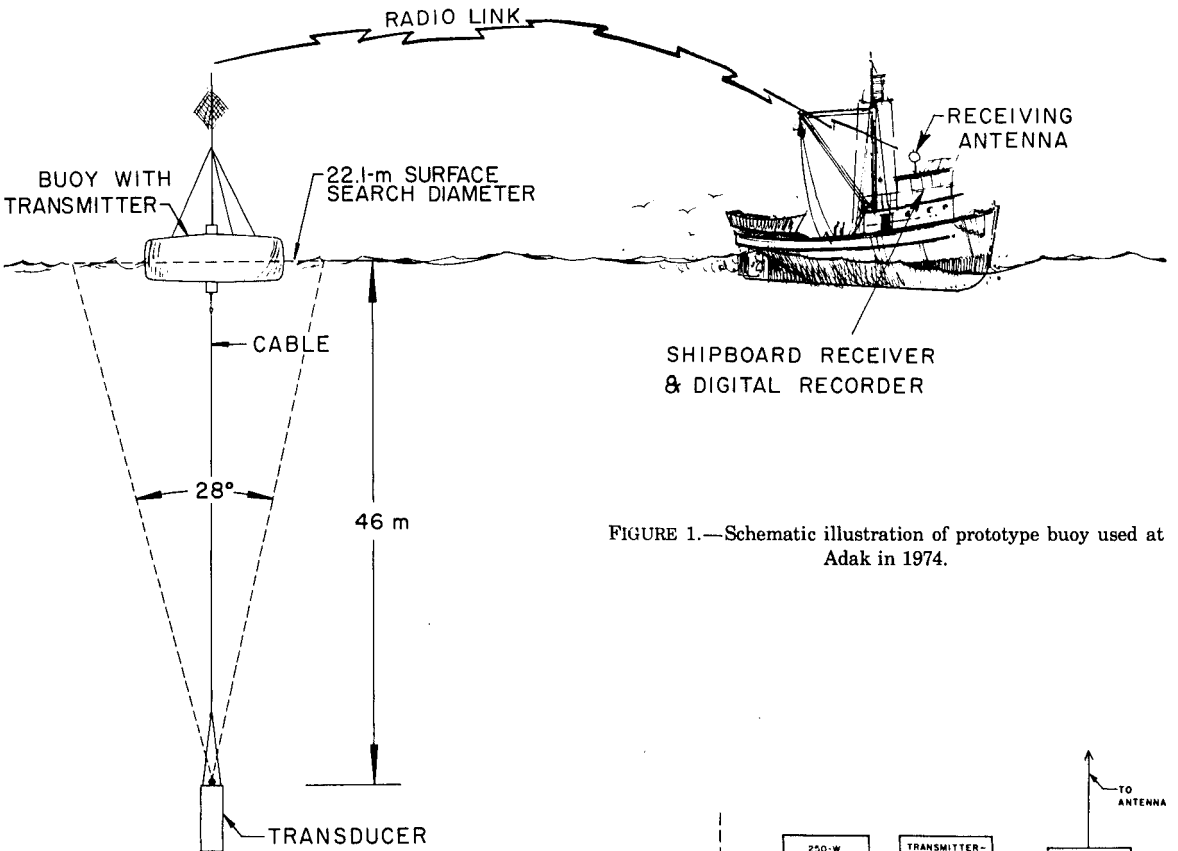

FIGURE 1.—Schematic illustration of prototype buoy used at Adak in 1974.

ventral, head, dorsal, and tail aspects. Inspection of this figure shows that the target strength decreases rapidly for head or tail views but is fairly constant at −30 dB over ±30° when viewed from the dorsal or ventral aspect. This severe dependence of target strength on aspect angle was the limiting factor in the choice of transducer beam width. For the high-seas system, a 28° conical beam is used. This gives an adequate sample volume and minimizes target-size fluctuations to a manageable level. A time-variable-gain (TVG) receiver, adjusted so that its output for a particular target is independent of target range, is used to limit signal dynamic range at the detector. This technique, and proper adjustment of absolute sensitivity, keeps the search volume relatively constant over a fairly wide range of target strength (±15 dB).

Estimates of the fish density in the Adak area indicate that the average count per sample will be less than one fish. Schooling habits of these salmon also reveal that only rarely will more than a few salmon be included in any one sample.

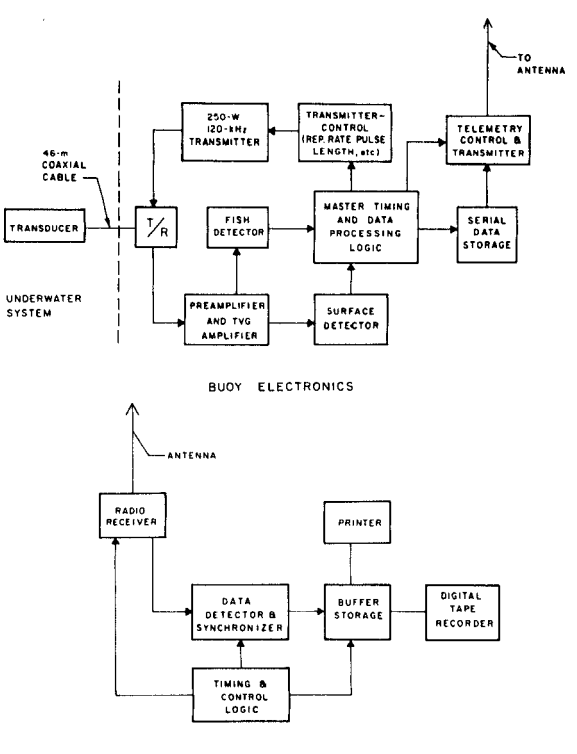

FIGURE 2.—Simplified block diagram of the prototype high-seas system.

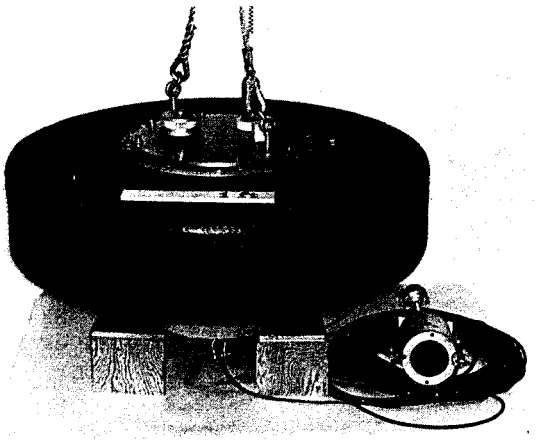

FIGURE 3.—Buoy deployed with detection and recovery gear.

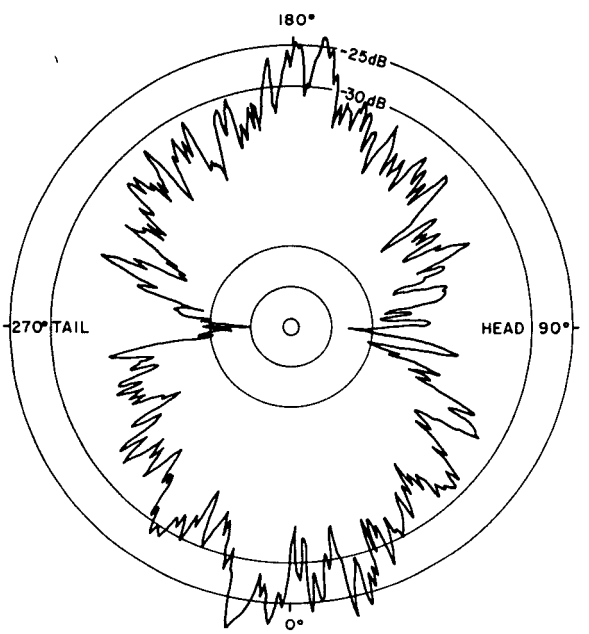

FIGURE 4.—Typical signal level as function of aspect angle for a single fish.

Storage was therefore limited to include data from a maximum of seven fish. The number of fish counted per sample and depth of each fish (to the nearest meter) are stored in a serial shift register memory, as are data on buoy identification and a data synchronization code. These data are stored in a format which makes telemetry noise and false counts easily recognizable and therefore easy to eliminate.

After all data from one acoustic pulse are gathered and stored they are automatically shifted through the telemetry system for transmission to the monitoring ship. Frequency-shift-keying (FSK) through the audio inputs of commercially available transceivers is currently used. The frequency response of the audio channels limits the bit rate to 100 Hz. A reliable telemetry range of 15 km in fairly rough seas has been achieved using this technique. A 6-MHz telemetry system has been developed which will increase the useful range to 100 km and will allow the use of radio direction finding equipment found aboard most seagoing vessels for buoy recovery.

In the current configuration, the buoys will operate continuously for 5 days before battery recharging is necessary. The acoustic and logic systems were carefully designed to minimize average power drain. COSMOS elements were used in logic design, and transmitter and receiver standby current is very low. Battery life is therefore limited by the telemetry system. The relatively low data rate requires that the transmitter be on for 0.6 s/sample. However, the redesigned telemetry system can increase data rate by an order of magnitude which will increase buoy life between charges to more than 6 wk.

The shipboard system consists of a telemetry receiver, a data synchronizer with buffer storage, a printer, and a digital tape recorder. Data from up to 10 buoys can be received and processed at the monitoring ship. Real time readout is provided by the printer. The digital tape recorder provides data storage for later computer analysis.

FIELD OPERATIONS AND RESULTS

The acoustic buoy system has been operated in the Adak area during the summers of 1972, 1973, and 1974. The 1972 operation suggested significant design changes in the electroacoustic portion of the system. These modifications were accomplished during the winter of 1972-73. The results of the 1973 operation indicated that special attention had to be given to system sensitivity and field calibration which was done prior to the start of the 1974 field season. The present configuration represents an essentially final design with only minor modifications to be made in the future.

Whenever feasible, the acoustic buoys have been operated at the same station and at the same time as the purse seine in order to obtain comparable data. This was not always possible,

however, since it was more convenient to operate the buoys continuously for several hours whereas the seine vessel required only 2 h for a set after which it proceeded to the next station. Occasionally the buoys were operated at a station which had been fished by the seine on the same day but not at the same time. Also, even at the same station, it was not feasible to set the seine directly around the buoys so it cannot be said that the two gears sampled precisely the same water. This is of some significance in any gear comparison since there was considerable set-to-set variation in purse seine hauls made at the same station.

Buoy launch and recovery presented no difficulty in any weather conditions in which buoy operation was attempted. Buoy operation is usually limited by the presence of heavy breaking seas with whitecaps in which case the entrained air causes ambiguous echo counts. In the Adak area the limiting weather conditions for operation of either the purse seine or the acoustic buoys depend strongly on the wind direction. Generally the purse seine can be operated in winds up to a maximum of about 20 knots. The acoustic buoys have been operated in higher winds with no serious difficulty in launch or recovery. However, the aforementioned problem of entrained air usually limits buoy operation to winds of less than 25 knots. The buoys, however, can be operated continuously for longer periods of time since, once deployed, no further human activity is required except to monitor the digital printout.

The buoys operate synchronously so that the data for each acoustic pulse may be radioed to the tending vessel as soon as it is obtained. The echo count data are in digital form in which all of the data from each acoustic pulse is coded into a single 60-bit word for telemetry to the shipboard receiver. Each of these 60-bit words contains: a) buoy identification number, b) the number of echo counts up to a maximum of seven, and c) the range from the transducer to each of the targets. The data system requires that the indicated number of targets agrees with the number of ranges actually recorded and that the target ranges must form a nondecreasing sequence. This redundancy permits the detection and rejection of spurious or noise contaminated data. The binary coded 60-bit words are formatted to be compatible with the CDC-6400 computer[8] used for the data reduction. The tape reading and data processing can be accomplished using only FORTRAN and certain FORTRAN callable subroutines thus avoiding the necessity of machine language programming.

The range discrimination of the acoustic system is 25 cm, i.e., two fish separated in range from the transducer by 25 cm or more will be detected as individual fish. Six binary bits are allowed for each of the seven possible ranges. This presently corresponds to a range resolution of 1 m, i.e., more than one fish may be detected and recorded in a single 1-m range increment if they are physically separated in range by at least 25 cm. Target coincidence is a possibility, particularly if the fish are dense or tend to school. This has not been a problem in high-seas use since the average number of echoes per pulse has been of the order of one.

Figure 5 shows typical depth distribution histograms corrected for the effect of a conical sampling volume. The most striking feature is the shallow depth at which most of the fish are found, usually 5 m or less. This had been anticipated and illustrates the need for an upward-looking device.

There is the possibility of ambiguity in the interpretation of echoes originating very near the surface. Indeed this usually proves to be the limiting condition in the operation of the buoys. This situation manifests itself by the consistent presence of targets in two or more successive range increments below the surface. More detail

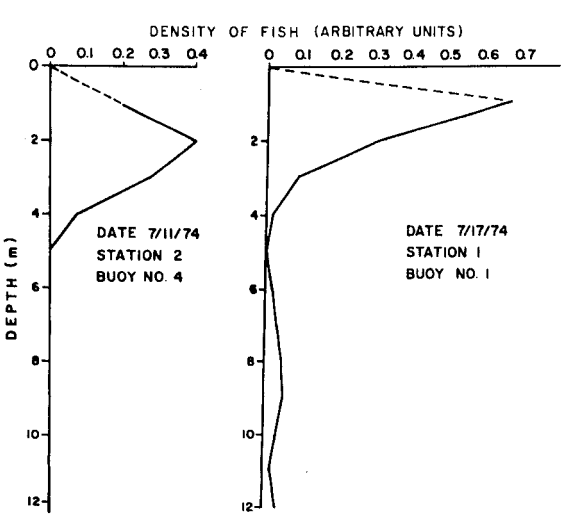

FIGURE 5.—Typical depth distribution histogram.

[8]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

near the surface can be obtained by increasing the depth resolution to 0.5 m from the present 1 m. This increased depth resolution would necessitate the elimination of the first 14 m of the 46-m water column above the transducer since only six bits are available for each range word. This is a desirable tradeoff, however, in view of the concentration of the fish near the surface.

Figure 6 is a series of plots of the computed areal densities of the salmon obtained by integrating the depth distribution histograms over the depth. Also plotted are the purse seine catches which were obtained in reasonable time and space proximity to the buoys. The data are reasonably consistent although significant departures occasionally occur. There are several possible sources for the observed discrepancies: a) set-to-set variations in seine hauls, b) similar variations in the sonar counts, c) the inability of the purse seine and the acoustic buoys to sample precisely the same volumes of water, and d) possible attraction or avoidance of the acoustic gear by the fish. The variations within gear types can be explained by the "patchiness" of the salmon. The digital printouts tend to show small groups of fish, rarely giving more than three echo counts, occurring with widely varying interarrival times. This observation indicates the existence of relatively large areas that are nearly devoid of fish thus explaining the occasional twofold variations in successive seine hauls made at the same station.

Sonar gear avoidance or attraction by the fish is a potentially serious problem, the magnitude of which is not yet known. Occasional sea lions have been observed around the buoys but they usually departed after several minutes. Also, there is little evidence to indicate that the fish are attracted to the sonar gear since none of the observed targets remains in the ensonified region for more than a few pulses. Sonar gear avoidance is a more likely prospect. The Stellar sea lion is common in the area being sampled and it is a known predator of salmon. The sonar buoy is similar in size to that of a sea lion so that avoidance is a distinct possibility. Secchi disc readings of 15 m are typical so that the buoy or cable may be detected at significant distances by the fish. Day versus night data differ slightly but as yet there are too few data on which to base a conclusion concerning gear avoidance.

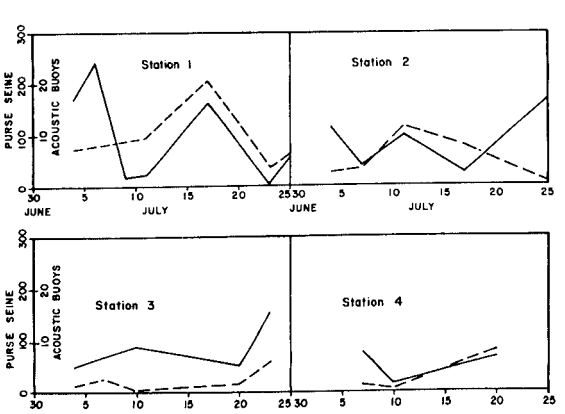

FIGURE 6.—Plots of computed relative areal densities (-----) and purse seine catches (—) by date and station for 1974.

All of the acoustic data from which Figure 6 was obtained were pooled and the sample correlation coefficient for the buoy-purse seine was computed. A value of 0.547 was obtained which, under the assumption of normality, is significant at approximately the 0.5% level (t distributed with $n - 2 = 19$ df). The results indicate that the acoustic buoys can obtain statistically significant population information as well as such ancillary information as depth distribution and density during both day and night. Additionally, indirect information on schooling is available by observing the interarrival times of the fish although this has not been investigated in detail.

The design of the acoustic buoy system is essentially fixed although modifications for use in other situations are possible. For example, a bottom anchored version for use in water depths of about 100 m has been designed but fabrication has not begun. Another possible design change is in the radio telemetry system. The present system, while reliable, is inefficient. An improved system has been designed and will be fabricated upon allocation of a suitable frequency by the Federal Communications Commission.

The current approximate unit cost per buoy, including the radio transmitter, is $6,000. The shipboard receiver-decoder cost is approximately $2,000. The tape recorder currently used is a Kennedy Model 1400 digital incremental which records at 556 bits/inch on ½-inch magnetic tape on 10-inch reels. It is "off the shelf" but is interfaced to the receiver-decoder. The interfacing cost is approximately $1,000 which should remain constant for interfacing to any digital incremental recorder.

LITERATURE CITED

FISHERIES RESEARCH INSTITUTE STAFF.
1960. Collected material on forecast of Bristol Bay red salmon run in 1960. Univ. Wash., Fish. Res. Inst. Circ. 122. [21 p.]

FRENCH, R. R., D. R. CRADDOCK, AND J. R. DUNN.
1967. Distribution and abundance of salmon. Int. North Pac. Fish. Comm. Annu. Rep. 1965, p. 82-94.

HARTT, A. C.
1962. Movement of salmon in the North Pacific Ocean and Bering Sea as determined by tagging, 1956-1958. Int. North Pac. Fish. Comm. Bull. 6, 157 p.
1966. Migrations of salmon in the North Pacific Ocean and Bering Sea as determined by seining and tagging, 1959-1960. Int. North Pac. Fish. Comm. Bull. 19, 141 p.
In press. Problems in sampling Pacific salmon at sea. *In* Symposium on the evaluation of methods of estimating the abundance and biological attributes of salmon on the high seas, p. 128-197. Int. North Pac. Fish. Comm. Bull. 32.

MACHIDORI, S.
1966. Vertical distribution of salmon (Genus *Oncorhynchus*) in the North-western Pacific. I. [In Jap., Engl. Summ.] Hokkaido Reg. Fish. Res. Lab. Bull. 31:11-17.

MANZER, J. I.
1964. Preliminary observations on the vertical distribution of Pacific salmon (genus *Oncorhynchus*) in the Gulf of Alaska. J. Fish. Res. Board Can. 21:891-903.

MATHEWS, S. B.
1966. The economic consequences of forecasting sockeye salmon (*Oncorhynchus nerka* Walbaum) runs to Bristol Bay, Alaska: A computer simulation study of the potential benefits to a salmon canning industry from accurate forecasts of the runs. Ph.D. Thesis, Univ. Washington, Seattle, 238 p.

ROGERS, D. E.
1972. Forecast of the sockeye salmon run to Bristol Bay in 1972, based on purse seine catches of immature sockeye salmon south of Adak. Univ. Wash., Fish. Res. Inst. Circ. 72-3, 32 p.
1973. Forecast of the sockeye salmon run to Bristol Bay in 1973. Univ. Wash., Fish. Res. Inst. Circ. 73-1, 33 p.
1974. Forecast of the sockeye salmon run to Bristol Bay in 1974. Univ. Wash., Fish. Res. Inst. Circ. 74-1, 30 p.

ANALYSIS OF RETURNS OF TAGGED GULF MENHADEN

PAUL J. PRISTAS,[1] ELDON J. LEVI,[2] AND ROBERT L. DRYFOOS[3]

ABSTRACT

From 1969 to 1971 nearly 76,000 adult Gulf menhaden, *Brevoortia patronus*, were tagged in the northern Gulf of Mexico with internal metallic tags. From an estimated 28,000 recaptures it was concluded that there is little east-west movement of adult Gulf menhaden during the fishing season from April to October, and that there is little mixing of menhaden from different areas when fish move offshore during the winter. Total mortality appears to be high, but could not be estimated from the returns. Few Gulf menhaden survive more than 3 yr.

Menhaden are industrial fish that are processed into meal, oil, and solubles. From 1964 to 1973, the annual purse seine catch of Gulf menhaden, *Brevoortia patronus*, which support the largest fishery in the United States, ranged from 316,000 to 728,000 metric tons. Scientists at the Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, N.C. have been studying the fishery since 1964.

A scientifically interesting question, as well as one of practical importance from the standpoint of resource management, is whether Gulf menhaden make extensive coastal movements during or between fishing seasons. To determine their movements in the area 75,673 adults were tagged from 1969 to 1971. In this paper we analyze recoveries from these fish through the 1973 fishing season.

FISHING AREAS

Although Gulf menhaden range from southern Florida to Veracruz, Mexico (Reintjes 1969), the purse seine fishery extends only from western Florida to extreme eastern Texas, with most fishing effort being expended in inshore waters from Mississippi to western Louisiana. The fishing season lasts from about early April until early October, but some plants may begin operations in late March while others may not begin until nearly May. For this study, we arbitrarily divided the fishery into three areas (Figure 1).

1. Western: waters and plants west of long. 92°W.
2. Central: waters and plants west of the mouth of the Mississippi River to long. 92°W.
3. Eastern: waters and plants east of the mouth of the Mississippi River to long. 86°W.

Plants were located at Moss Point, Miss. (three plants); in Louisiana—Empire (two plants), Dulac (two plants), Morgan City (one plant), Intracoastal City (one plant), and Cameron (three plants); and Sabine Pass, Tex. (one plant). The plants at Empire were considered to be in the central area.

Because refrigerated carrier vessels may remain at sea up to 6 days and fish over a wide area, we could not tell where their tagged fish were caught but only where they were processed. Two exceptions are one plant whose vessels fished exclusively in the eastern area and another plant whose vessels fished exclusively in the western area. For tags recovered at these plants, the area of capture was known. Although vessels are far ranging and often travel long distances to reported concentrations of fish, they tend to fish most of the time within a restricted radius of their plant. Most tagged fish, therefore, probably were caught in the vicinity of the plant where the tags were recovered.

METHODS OF TAGGING

Gulf menhaden, which spawn from about No-

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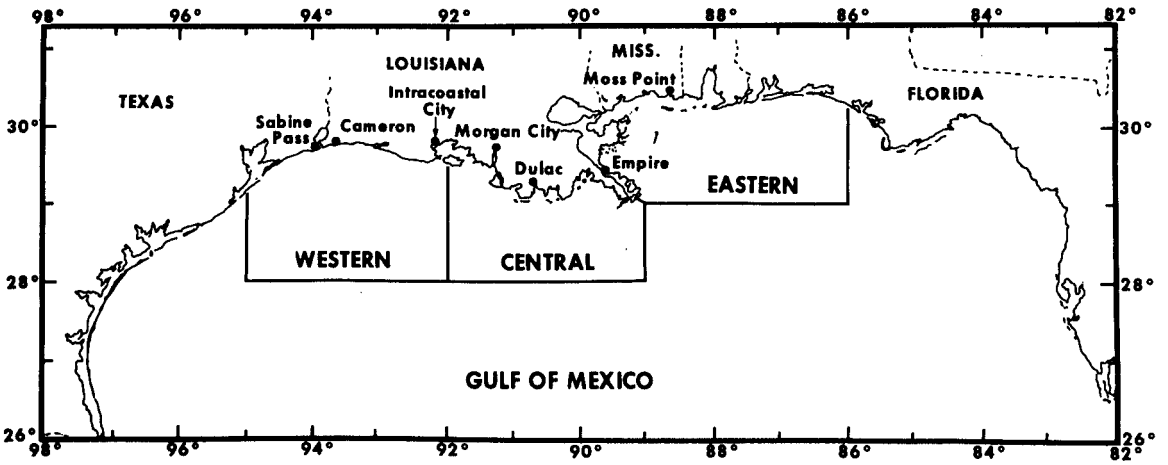

FIGURE 1.—Three areas in which adult Gulf menhaden, *Brevoortia patronus*, were tagged, 1969-71.

vember to March, may arbitrarily be divided into two broad age-classes, juveniles and adults. Juveniles are less than a year old, inhabit the estuaries and rivers during the summer, and move into the open waters of the Gulf in autumn when they are about 65 to 130 mm in fork length. Except in late summer and autumn when some of the larger fish become available, they are not vulnerable to the purse seine fishery. Adults are more than a year old (age 1 or older), inhabit the larger sounds and inshore areas of the Gulf, and are vulnerable to the purse seine fishery.

Techniques for tagging adult Gulf menhaden followed those developed for tagging adult Atlantic menhaden (Pristas and Willis 1973). A numbered internal ferromagnetic tag (14.0 × 3.0 × 0.5 mm) was injected into the body cavity with a tagging gun developed by Bergen-Nautik,[4] a Norwegian firm. Fish were obtained from commercial purse seine catches and were tagged aboard the carrier vessels.

Five percent of the fish tagged in 1969 and 10% of the fish tagged in 1970 were measured. Because measuring fish reduced the number that could be tagged, it was not done in 1971. Mean lengths of fish released in the spring of 1969 ranged from 118 to 130 mm; means of those released in the spring of 1970 ranged from 157 to 171 mm; and means of those released in autumn 1969 ranged from 148 to 164 mm.

Individual fish were not aged. On the basis of length frequencies, nearly all the fish tagged were judged to be either age 1 or age 2. Most of those tagged in spring 1969, probably were age 1. Since the mean lengths were greater in 1970 than in 1969, a greater proportion in 1970 probably were age 2. Nearly all of those tagged in autumn 1969 were age 1.

METHODS OF RECOVERING TAGS

Magnets, installed in reduction plants to recover tags moving along the conveyer system with the fish scrap and meal (Parker 1973), are classified as either primary or secondary, depending on their location. They were cleaned about once a week to remove tags and other scrap metal. Primary magnets are located between the fish scrap dryers and the storage areas. Since newly processed fish scrap moves across the primary magnets, the date tagged fish were caught can be estimated. Tags recovered on these magnets are referred to as primary recoveries. Secondary magnets are usually located in the storage, transfer, or loading areas for scrap and meal. Since fish scrap or meal that moves across the secondary magnets may have been in storage for several months or may have been moved from one plant to another, the date tagged fish were caught cannot be estimated, and the plant at which the tags were recovered cannot always be determined. Tags recovered on these magnets are referred to as secondary recoveries. In this paper we combine both types, since we are interested only in the fishing season a tag was recovered.

[4]Mention of commercial firm does not imply endorsement of product by National Marine Fisheries Service, NOAA.

Because many tags that entered a plant became lodged in machinery or passed over magnets without being captured, the total number of tags that entered a plant could only be estimated. The estimates were based on the actual number of tags recovered and the collective efficiency of the magnets that recovered them. The efficiency for each plant was estimated by adding 100 tagged fish to catches at regular intervals and then determining the number of these test tags that were recovered during the fishing season on both primary and secondary magnets. The efficiency for each plant, expressed as a percentage, was the ratio of the number of test tags recovered each fishing season to the number applied.

The number of tests varied from year to year and plant to plant. In 1969 the number at each plant ranged from 1 to 8 (100-800 tags); in 1970, 2 to 20 (200-2,000 tags); in 1971, 2 to 16 (200-1,600 tags); in 1972, 3 to 17 (300-1,700 tags); in 1973, 3 to 16 (300-1,600 tags).

The percentage of tags recovered from each series of 100 test tags varied from 10 to 90%. The mean seasonal efficiency varied from 13% for the least efficient plant to 73% for the most efficient. It also varied from year to year for each plant.

For this study, the estimated total number of field tags entering a plant was based on the actual number of field tags recovered on both primary and secondary magnets. The total number of field tags entering a plant each month was estimated by dividing the actual number of tags recovered by the mean annual plant efficiency. Tags recovered in spring before fishing began were added to recoveries from the previous year.

Tags remaining in various parts of a plant for up to 2 yr before being recovered caused errors in the recovery data. Nearly 1% of the test tags were recovered in the second or third year (Table 1), but the percentages varied from plant to plant. Test tags introduced late in the season were recovered in subsequent years in greater numbers than tags introduced early in the season. When a field tag that actually had entered a plant in a previous season was recovered, it would in effect be counted twice and expanded by the efficiency factor two or more times. For example, if 100 tags entered a plant whose efficiency was 0.50, the number recovered would be 50. If 1 of the 50 unrecovered tags were to be recovered the following year and the recovery efficiency of the plant had dropped to 0.25, the estimated number recovered would be 4 (1/0.25 = 4). The estimated number of tags recovered would be 104 instead of 100, an error of about 4%, and 4 tags would be assigned to the wrong year.

TABLE 1.—Number and percentage of test tags recovered during the year applied and after 1 and 2 yr.

Test year	No. of test tags	Years applied		After 1 yr		After 2 yr	
		No.	%	No.	%	No.	%
1969	5,600	1,964	35.1	28	0.50	7	0.13
1970	14,000	7,510	53.6	93	0.66	15	0.11
1971	11,900	5,317	44.7	65	0.55	9	0.76

SPRING RELEASES AND RECOVERIES

We tagged 26,995 fish in 1969, 17,775 in 1970, and 22,800 in 1971. Of the number of fish tagged, the estimated percentages recovered through 1973 were 30.2, 51.5, and 32.5%, for 1969, 1970, and 1971, respectively. Of the total number of tags recovered, the largest percentages were in the first year: 70.9% (1969); 84.3% (1970); 84.6% (1971). Returns in the second or following year, accounted for most of the remainder; 26.7% (1969); 15.0% (1970); 14.3% (1971). Returns after the second year ranged from 0.7 to 2.4% (Tables 2-4).

The actual numbers of field tags recovered after the second year probably were much smaller than the numbers reported. The percent-

TABLE 2.—Numbers of adult Gulf menhaden tagged in the spring of 1969 and the estimated number recaptured in subsequent fishing seasons, by area.

Release area	No. of fish tagged	Year of recapture	Area of recovery			Total
			Western	Central	Eastern	
Western	10,298	1969	1,839	273	52	2,164
		1970	316	249	20	585
		1971	14	48	1	63
		1972	0	2	0	2
		1973	0	3	0	3
		Total	2,169	575	73	2,817
Central	3,699	1969	114	1,238	62	1,414
		1970	70	172	13	255
		1971	3	20	1	24
		1972	0	0	0	0
		1973	0	0	0	0
		Total	187	1,430	76	1,693
Eastern	12,998	1969	0	7	2,188	2,195
		1970	39	519	775	1,333
		1971	2	32	47	81
		1972	2	3	14	19
		1973	0	4	2	6
		Total	43	565	3,026	3,634
Combined	26,995	1969	1,953	1,518	2,302	5,773
		1970	425	940	808	2,173
		1971	19	100	49	168
		1972	2	5	14	21
		1973	0	7	2	9
		Total	2,399	2,570	3,175	8,144

TABLE 3.—Numbers of adult Gulf menhaden tagged in the spring of 1970 and the estimated number recaptured in subsequent fishing seasons, by area.

Release area	No. of fish tagged	Year of recapture	Area of recovery			Total
			Western	Central	Eastern	
Western	9,100	1970	2,507	1,268	101	3,876
		1971	286	479	49	814
		1972	4	7	1	12
		1973	0	0	0	0
		Total	2,797	1,754	151	4,702
Central	5,100	1970	969	1,339	142	2,450
		1971	83	273	11	367
		1972	4	8	1	13
		1973	0	0	0	0
		Total	1,056	1,620	154	2,830
Eastern	3,575	1970	0	48	1,348	1,396
		1971	0	32	160	192
		1972	0	12	17	29
		1973	0	3	6	9
		Total	0	95	1,531	1,626
Combined	17,775	1970	3,476	2,655	1,591	7,722
		1971	369	784	220	1,373
		1972	8	27	19	54
		1973	0	3	6	9
		Total	3,853	3,469	1,836	9,158

TABLE 4.—Numbers of adult Gulf menhaden tagged in the spring of 1971 and the estimated number recaptured in subsequent fishing seasons, by area.

Release area	No. of fish tagged	Year of recapture	Area of recovery			Total
			Western	Central	Eastern	
Western	7,400	1971	1,711	843	48	2,602
		1972	80	143	2	225
		1973	3	5	0	8
		Total	1,794	991	50	2,835
Central	5,200	1971	642	904	57	1,603
		1972	27	56	2	85
		1973	0	6	0	6
		Total	669	966	59	1,694
Eastern	10,200	1971	0	58	2,008	2,066
		1972	3	157	589	749
		1973	1	36	33	70
		Total	4	251	2,630	2,885
Combined	22,800	1971	2,353	1,805	2,113	6,271
		1972	110	356	593	1,059
		1973	4	47	33	84
		Total	2,467	2,208	2,739	7,414

ages of test tags recovered after 1 yr (0.5%) and 2 yr (0.1%) probably underestimated the percentage of field tags that remained in a plant and were recovered after 1 or 2 yr, since a greater number of test tags were applied early rather than late in the season and therefore had a greater chance of being recovered in the year they were applied. The tendency of field tags that had been out more than 2 yr to be recovered early, rather than late, in the fishing season suggests that some, at least, had remained in plants over the winter. At plants where recovery efficiencies were relatively low, mainly plants in the eastern and central areas, a greater percentage of field tags were returned after 2 yr than at plants where efficiencies were relatively high. Field tag recoveries after 2 yr were highest at those plants where test tag recoveries after 1 yr were highest. The plant for which no field tag recoveries were reported after 2 yr had the lowest percentage of test tag recoveries after 1 yr—less than 0.1%.

Eastern Releases

Nearly all first year recoveries (tags recovered the same year they were applied) were at plants in the eastern area (99.7% in 1969; 96.5% in 1970; and 97.2% in 1971), and no tags were recovered in the western area. The only tags recovered in the central area were at plants whose vessels also fished in the eastern area. Second year recoveries (tags recovered the year after they were applied) followed the same pattern as first year recoveries, although a greater proportion of tags were recovered in the central area. For 1969 releases, no tags were recovered the second year at the plant in the western area whose vessels fished only in that area. For 1970 releases, no tags were recovered the second year in the western area. For 1971 releases, only three tags were recovered in the western area, all at a plant whose vessels fished in all areas.

Central Releases

Although tags were recovered the first year at plants in all areas, the highest percentages were from plants in the central area (87.6% in 1969; 54.7% in 1970; 56.4% in 1971). The lowest percentages were at plants in the eastern area, as might be expected, since the western and central areas are continuous with each other but are separated from the eastern area by the Mississippi Delta. In 1969 and 1970 no tags were recovered at the plant in the eastern area whose vessels fished only in that area. Some tags were recovered in the western area at the plant whose vessels fished only in that area. The majority of second year recoveries also was at plants in the central area (71% for all release years combined); the fewest were at plants in the eastern area (4% for all release years combined).

Western Releases

Most of the first year recoveries were at plants in the western area (85.0% in 1969; 64.7% in 1970; 65.7% in 1971), and the fewest were at plants in the eastern area (2% in 1969 and 1971;

3% in 1970). No tags were recovered at the plant in the eastern area whose vessels fished only in that area. Fewest second year recoveries were at plants in the eastern area (3% in 1969; 6% in 1970; 1% in 1971). Most second year recoveries were at plants in the western area for fish tagged in 1969 and in the central area for fish tagged in 1970 and 1971.

AUTUMN RELEASES AND RECOVERIES

Fish were tagged in autumn (September) only in 1969, when 900 were tagged in the western area, 2,100 in the central area, and 5,103 in the eastern area (Table 5). By the end of the fishing season in October, 6% had been recaptured. In the following year 33% were recovered. For all years combined 42% were recovered.

As with tags of fish released in spring, tags of fish released in autumn were recovered mainly at plants in the area of release in both the first and second year. Few fish tagged in the western area were recovered in the eastern area and few fish tagged in the eastern area were recovered in the western area. No fish tagged in the western area were recaptured at the plant in the eastern area whose vessels fished only in that area. Approximately 90% of the tags of fish released in the eastern area and recovered in the central area were at plants whose vessels fished up to 25% of the time in the eastern area.

TABLE 5.—Numbers of adult Gulf menhaden tagged in autumn of 1969 and the estimated numbers recaptured in subsequent fishing seasons, by area.

Release area	No. of fish tagged	Year of recapture	Area of recovery			Total
			Western	Central	Eastern	
Western	900	1969	29	3	0	32
		1970	73	66	2	141
		1971	4	20	0	24
		1972	0	0	0	0
		1973	0	0	0	0
		Total	106	89	2	197
Central	2,100	1969	166	10	1	177
		1970	277	305	33	615
		1971	17	42	3	62
		1972	0	0	0	0
		1973	0	0	0	0
		Total	460	357	37	854
Eastern	5,103	1969	0	0	251	251
		1970	21	617	1,300	1,938
		1971	0	44	65	109
		1972	0	18	12	30
		1973	0	3	0	3
		Total	21	682	1,628	2,331
Combined	8,103	1969	195	13	252	460
		1970	371	988	1,335	2,694
		1971	21	106	68	195
		1972	0	18	12	30
		1973	0	3	0	3
		Total	587	1,128	1,667	3,382

CONCLUSIONS

The pattern of first year tag recoveries shows clearly that adult Gulf menhaden make no extensive east-west movement along the coast during the fishing season from April to November. Nearly all tags were recovered at plants located in the same area in which the fish were tagged. Some fish that were released in one area but whose tags were recovered at a plant in another probably were caught in the release area, since vessels at most plants, though fishing mostly within their own area, also were far-ranging. No fish tagged in the eastern area were recovered at plants in the western area; few fish tagged in the western area were recovered at plants in the eastern area. At plants whose vessels fished exclusively in either the eastern or western area, no tags were recovered except those from fish released in the same or adjacent area.

Second year recoveries also point to little or no mixing of fish from different areas during the winter. Gulf menhaden apparently move offshore during autumn and return again in spring to the same general area they previously occupied. Since the boundary between the western and central areas is arbitrary and since we do not exactly know where fish were recovered, the greater number of second year returns in the central, rather than western area of fish tagged in the western area for 1970 and 1971 does not necessarily indicate any significant shift of fish from the western to the central area.

Because there were no estimates of tag losses due to shedding or deaths caused by tagging, and because the variability in recovery efficiencies was large and some tags tended to remain in plants for long periods, calculation of fishing and total mortality rates would be no more than a mathematical exercise. We can estimate from the data, however, whether fishing mortality and exploitation rates are high or low.

Both fishing mortality and exploitation rates appear to be high. First year recoveries of spring releases ranged from 21 to 43% of the number of fish tagged. The total number of tags recovered ranged from 30 to 51% for spring releases and was 42% for the autumn releases. High tagging mortality may account for the relatively low returns for the 1969 and 1971 spring releases (30%

and 32%), since tagging mortality tends to be greater for small Atlantic menhaden than for large ones (Kroger and Dryfoos 1972), and the fish tagged in 1969 were generally smaller than those tagged in spring of 1970 or autumn of 1969.

It is unlikely that more than a small percentage of any year class survive more than 3 yr. Less than 2% of the estimated returns of fish tagged in spring, and 7% of the returns of fish tagged in autumn were recovered after the second year. Because of the tendency of tags to hang up in plants, the majority of tags recovered after the second year probably had come from fish caught in the first or second season after being tagged. If tags that hung up for 1 yr averaged 1.5% and for 2 yr or more 0.2%, and if recovery efficiencies averaged 50%, hung up tags could account for nearly all tags reportedly recovered after 2 yr. Since the majority of fish tagged were in the size class of age-1 fish, the percentage of returns after 2 yr should have been higher than it was if any significant number survived more than 3 yr.

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Only a project report based on returns through July 1971 had been prepared before the authors transferred to other laboratories and work on the manuscript was temporarily suspended. Revision had just begun when Robert L. Dryfoos died suddenly in January 1974. William R. Nicholson and Robert M. Lewis, Atlantic Estuarine Fisheries Center, Beaufort, N.C., prepared the 1971-73 returns for the computer programs, incorporated them into the previous data, and assisted in revising and editing the final manuscript.

LITERATURE CITED

KROGER, R. L., AND R. L. DRYFOOS.
1972. Tagging and tag-recovery experiments with Atlantic menhaden, *Brevoortia tyrannus*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-664, 11 p.

PARKER, R. O., JR.
1973. Menhaden tagging and recovery: Part II—Recovery of internal ferromagnetic tags used to mark menhaden, genus *Brevoortia*. Mar. Fish Rev. 35 (5-6):36-39.

PRISTAS, P. J., AND T. D. WILLIS.
1973. Menhaden tagging and recovery: Part I—Field methods for tagging menhaden, genus *Brevoortia*. Mar. Fish Rev. 35(5-6):31-35.

REINTJES, J. W.
1969. The Gulf menhaden and our changing estuaries. Proc. Gulf Caribb. Fish. Inst., 22nd Annu. Sess., p. 87-90.

DEVELOPMENT AND EXAMPLE APPLICATION OF A SIMULATION MODEL OF THE NORTHERN ANCHOVY FISHERY

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ABSTRACT

A computer simulation model of the reduction fishery for northern anchovy, *Engraulis mordax*, is described. The biological subroutine of this model is an age-structured paradigm which is modified to account for age-dependent exploitation and variable recruitment. To demonstrate the model's utility, two example applications are presented which provide insight into the problems of evaluating alternative regulations while lacking perfect knowledge of economic or biological behavior. The model's current value lies in its use as a tool to identify research needs.

Based upon the systems analyses of Tillman (1972) and Stadelman (1974), it appears that the northern anchovy, *Engraulis mordax* Girard, constitutes one of the largest latent fishery resources available to American flag vessels. Relative to its estimated biomass, only a minute fraction of this species is harvested when compared, for example, to catches taken by the fishery for Peruvian anchoveta, *E. ringens*. The present northern anchovy fleet consists of only a small number of relatively old vessels, and the processing capacity of the fish meal plants servicing this fleet is quite inadequate. Thus, unlike many major fisheries of the United States which are marked by overexpansion and overcapitalization, the northern anchovy fishery is still underdeveloped.

According to the above authors, this lack of development can be attributed to a variety of natural and artificial barriers. The natural barriers comprise those constraints over which man has little or no control, including lack of predictive ability concerning the short-term behavior of the market for fish meal. Moreover, there presently is lacking definitive biological knowledge concerning the inherent variation in size and availability of the northern anchovy population, its dynamic stock-recruit feedback mechanisms, and its natural mortality processes. These gaps provide the context of a dynamic and variable environment within which this fishery system operates and with which its managers must contend.

The artificial barriers, on the other hand, are institutional constraints which man has imposed upon the system. While the intent of these rules or regulations may be to govern the activities of fishery participants, their overall effect, in the opinion of Tillman (1972) and Stadelman (1974), has been to thwart economic development of the fishery. For example, small quotas for reduction purposes are intended to prevent overcapitalization of the fishery but have also acted to hinder the much needed replacement and renovation of antiquated reduction equipment. Other artificial barriers and their apparent effects, as perceived by the foregoing authors, include the following: areal and temporal closures to protect stocks, but which act instead to reduce harvest efficiency; union rules to maintain employment levels, but which in fact work to prevent use of technological innovations that would reduce harvesting costs or increase efficiency; landing taxes of $2 per ton to pay for research and management, but which in fact act to reduce substantially the returns obtained by private interests.

If an appropriate goal for decision makers is to foster economic development of the northern anchovy fishery, then the above institutional barriers would seem to present opportunities for achieving that goal. Consequently, a computer simulation model has been developed which provides the means for evaluating the biological and economic consequences of changing various regulations governing this fishery. The purpose of this study is to briefly describe this simulation model and to present two examples of its application which demonstrate some of its utility. These applications focus on the evaluation of alternative regulations when given imperfect knowledge of biological or economic behavior. Finally, the

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value of modelling this system is discussed, taking into account some of the present model's limitations and shortcomings.

DEVELOPMENT OF THE SIMULATION MODEL

General Description

The basic model of the northern anchovy fishery is formulated in terms of GAMES, the general-purpose simulator of resource use systems developed by Gales (1972). This Fortran IV program has been designed to simulate the activities of major sectors involved in the harvesting and marketing of renewable resources. The sectors modelled by GAMES include locations, stocks, harvesters, processors, regulators, products, and markets.

A specific system such as the anchovy fishery (Figure 1) is modelled by indicating, through appropriate inputs, the number of entities in each sector and their logical linkages. The user must also provide the values of parameters which define system processes and structures and the initial values of variables which describe systems behavior. Tillman (1972) provides a detailed listing of the values required for the northern anchovy model. Through appropriate control values, the user also specifies that certain built-in decision routines be used or else provides algorithms of his own design by adding subroutines to GAMES or by modifying existing ones. The user must also provide an appropriate biological model of the stocks being exploited by the harvester-processor sectors.

The main GAMES program resembles the partial listing given in Figure 2. The "Labelled COMMON Blocks" reserves sections of memory for storage of the values of parameters and variables used in common by the 11 subroutines. Subroutine TAPEIN is called first and reads in the initial values of these parameters and variables, including the starting and ending years of simu-

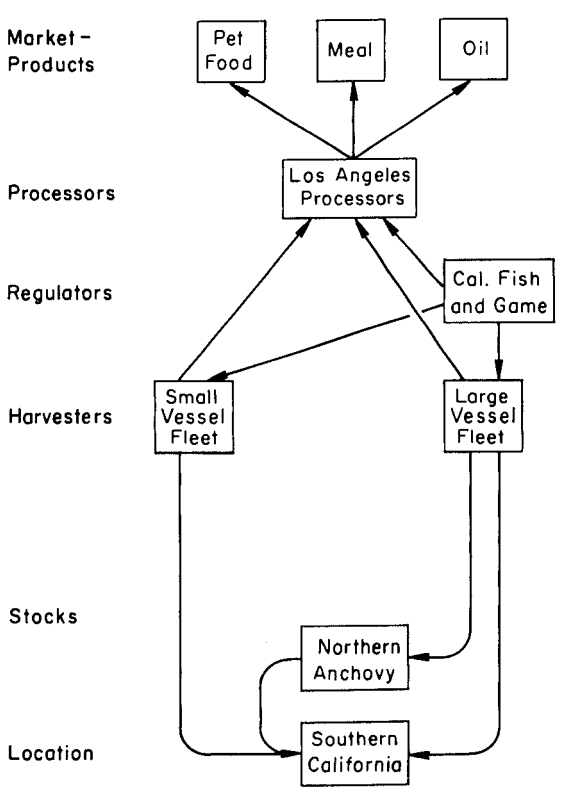

FIGURE 1.—Graphic representation of logical relations between sectors of the present northern anchovy fishery. From Tillman (1972).

```
      PROGRAM MAIN
      [Labelled COMMON Blocks]
      CALL TAPEIN
      DO 110 YEAR=NYEAR1, NYEAR2
      DO 100 MONTH = 1,12
      CALL    PROCS
      CALL    HARVS
      CALL    REGLS
      CALL    STOCKS
      CALL    HRVST
      CALL    RMARKT
      CALL    PRCES
      CALL    CMARKT
      CALL    STATS
      CALL    SMSTAT
  100 CONTINUE
  110 CONTINUE
      [Coding for Subroutines]
```

FIGURE 2.—Partial listing of the main GAMES program.

lation. The succeeding 10 subroutine call statements are imbedded within a double "do-loop" which is indexed by month and year. This double loop is the principal timing mechanism of the program. Hence, each of these 10 subroutines is executed once a month in the order indicated and either simulates a component of the system, their interactions, or else produces output.

Subroutines PROCS, HARVS, and REGLS make programmed monthly decisions for the system's respective processors, harvesters, and regulators. PROCS and HARVS simulate monthly decisions concerning the processing capacity committed, the number of days spent harvesting, the number of harvesting units committed, and the gear efficiency per unit. Moreover, since processors have only limited storage capacity for raw materials, HARVS adjusts allowable vessel capacities as if processors were establishing boat quotas (a situation presently occurring in the reduction fishery); this prevents overfishing and the consequent dumping of excess catches. REGLS compares these decisions to standards (regulations) supplied by the user or determined by the subroutine. If regulations are "broken," the subroutine makes appropriate adjustments to the values of those parameters associated with improper decisions.

STOCKS is a user supplied subroutine which simulates the biomass dynamics of the exploited resource on a monthly basis. The northern anchovy subroutine is an age-structured model which accounts for the processes of growth, mortality, graduation, and reproduction for each of the seven age-groups (ages 0-6) comprising the population. The basic mathematical theory for age-structured models is treated by Ricker (1958) and Beverton and Holt (1957). This basic theory has been modified to account for age-dependent exploitation and variable recruitment processes in the northern anchovy population. Similar age-structured models have been developed in recent years for other species by Tillman (1968), Walters (1969), Fox (1973), and Francis (1974).

Described further in an ensuing section, STOCKS feeds catch values to HRVST, the subroutine which then simulates the monthly harvesting process. HRVST determines the catch of each stock by a harvester, his harvest proportional costs, and the cumulative catch taken from each stock.

RMARKT then simulates the sale of the harvesters' catches to the processors, and PRCES transforms these newly purchased raw materials into finished goods which are added to the processors' inventories. Subroutine CMARKT then simulates the sale of these products on the open market to final consumers. The quantities demanded are determined from a user supplied demand curve and a sales price set by the processor.

STATS then computes and outputs financial statements for the processors and harvesters. It also provides physical reports describing through key variables the activities of the harvester, processor, stock, and market sectors. Subroutine SMSTAT then provides user desired cumulative physical reports. Although all reports may be provided at monthly intervals, printout typically is suppressed until the year's end.

The Biological Sector

Some Important Assumptions

Development of the biological model for northern anchovy depends critically upon two assumptions. One concerns the stock structure of this population and the other, its stock-recruit behavior. The following discussion briefly examines how reasonable these assumptions are and hopefully provides some justification for their application.

Mais (1974) and Tillman (1975) review the evidence which generally supports the hypothesis that three distinct stocks exist within the northern anchovy's total geographic range. The simplifying assumption has been made that the reduction fleet fishes exclusively upon that stock which resides in the southern California-northern Baja California region of the California Current system. Results of tagging studies indicate that some mixing of adult members of adjacent stocks might conceivably occur due to seasonal north-south migrations (Haugen et al. 1969). However, Mais (1974) cites evidence from comparisons of length-frequency and age-length distributions which, in his opinion, indicates that very little, if any, mixing occurs. Moreover, he concludes that anchovies in this region should be treated as a single biological unit for management (and therefore modelling) purposes.

Several studies (Cushing 1971; Tillman and Paulik 1971; Murphy 1973) suggest that recruitment in clupeid and engraulid populations is a density-dependent process. Moreover, these authors imply that the asymptotic stock-recruit

relationship of Beverton and Holt (1957) is generally applicable to populations which have an extended spawning season, whose adults are cannibalistic upon their own young, and whose annual recruitment variations are relatively small. Results from surveys for pelagic eggs and larvae conducted off California indicate that the northern anchovy spawns over virtually the entire year (Ahlstrom 1966). Baxter (1967) stated that this species is a filtering and biting feeder which consumes its own eggs and larvae. Moreover, Murphy (1966) noted that this species has never had spectacularly good nor spectacularly bad year classes and that this may have been a factor in the relatively slow replacement of the Pacific sardine, *Sardinops sagax*, by anchovies following the collapse of the sardine fishery. Consequently, since the northern anchovy apparently fits the required life-style, an asymptotic stock-recruit model does not seem too unreasonable an assumption, although it is an admittedly circumstantial and speculative one at this time.

General Description of STOCKS

STOCKS' main job is to solve the catch equation and pass the result to subroutine HRVST. The following description briefly summarizes the sequence of operations which occur each month and some of the parameter values required to determine the catch in weight for each age group. The details of parameter estimation are given by Tillman (1972).

Following the combined adjustments of PROCS, HARVS, and REGLS, STOCKS first receives the allowed values of the following variables: level of fishing effort (number of vessels), vessel capacity (metric tons (MT)/boat·day), fraction of the month fished, and fishing power of a vessel (Table 1 gives values of relative fishing power for various-sized vessels for which economic performance data are available). These four variables are used to calculate equivalent standard effort, in terms of boats fishing the entire month instead of a fraction of it, and the total harvesting capacity of the reduction fleet.

Next the age structure is updated by accounting for the process of graduation. Since the great bulk of spawning activity occurs during January-May, most anchovies have their birth dates during these 5 mo. Table 2 gives the proportion of each age-group that is expected to graduate at the start of the months indicated. Recruits due to enter in the current month are added to the first age-group, and fish leaving the last age-group disappear. Within each age-group, size of the individual is computed as a weighted average of the sizes of newly entered and residual fish. From these adjusted weights and numbers at age, the biomass of the population is computed.

Contribution to spawning then is calculated for the current month. The number of females eligible to spawn is determined by the proportion of females in the population (Table 3), by a maturity at age schedule (Table 4), and by a schedule of the incidence of monthly spawning activity (Table 5). The egg production of these spawning females is computed by a fecundity at age schedule (Table 6). The results of this procedure are additions to the number of eggs deposited on the stock's spawning ground.

Instantaneous total mortality rates then are

TABLE 1.—Efficiencies and relative fishing powers of hypothetical vessels operating on northern anchovy. From Tillman (1972).

Vessel capacity		Calculated efficiency	Relative efficiency[1]
Tons	MT		
66	60	0.536	0.681
110	100	0.787	1.000
155	140	1.038	1.319
210	191	1.358	1.726
265	240	1.518	1.929

[1]100-MT (metric ton) vessel is standard.

TABLE 2.—Probabilities of graduating from one age group into the next for northern anchovy. From Tillman (1972).

Birth date	Proportion graduating	Cumulative proportion
January	0.17	0.17
February	0.18	0.35
March	0.25	0.60
April	0.25	0.85
May	0.15	1.00

TABLE 3.—Estimates of fraction of females by number in the total northern anchovy population.

Source	Estimate	Source	Estimate
Clark and Phillips (1952)	0.57	Collins (1969)	0.60
Miller et al. (1955)	0.56	Collins (1971)	0.58
Miller and Wolf (1958)	0.52	Average	0.56
MacGregor (1968)	0.56		

TABLE 4.—Maturity at age schedule of northern anchovy. From Tillman (1972).

Age-group	Fraction mature	Age-group	Fraction mature
0	0.10	4	1.00
1	0.40	5	1.00
2	0.80	6	1.00
3	0.95		

TABLE 5.—Incidence of monthly spawning activity by northern anchovy as determined from larval counts. From Tillman (1972).

Month	Fractional occurrence	Adjusted occurrence[1]
1 June	0.10	0.20
2 July	0.05	0.10
3 August	0.03	0.06
4 September	0.01	0.02
5 October	0.02	0.04
6 November	0.03	0.06
7 December	0.03	0.06
8 January	0.11	0.22
9 February	0.20	0.40
10 March	0.17	0.34
11 April	0.17	0.34
12 May	0.08	0.16

[1]Adjusted to insure two spawnings per year.

TABLE 6.—Fecundity at age of northern anchovy, assuming 574 eggs/g body weight. From Tillman (1972).

Age-group	Average weight[1] (g)	Fecundity (eggs/spawning)
0	9.1	5,200
1	14.9	8,600
2	20.4	11,700
3	25.1	14,400
4	28.9	16,600
5	31.9	18,300
6	34.2	19,600

[1]Average weight in month 10, March, the midpoint of the major spawning period.

computed for each age group, which may be subjected to a different total mortality, $Z(A,M)$, depending on natural mortality rate, catchability coefficient, seasonal availability factor, and the total units of standard effort operating upon the stock during the month:

$$Z(A,M) = NM + F(A,M)$$

where NM = constant natural mortality rate
$F(A,M)$ = age specific fishing mortality rate
$= Q(A) \cdot AV(M) \cdot FF(M)$
where $Q(A)$ = age specific catchability coefficient
$AV(M)$ = monthly availability of the stock
$FF(M)$ = standardized level of effort.

According to Schaefer (1967), $NM = 1.10$ and is a constant parameter. Table 7 shows how catchability decreases for ages which are not fully recruited. Figure 3 indicates how availability varies throughout the year, based upon extrapolations of Messersmith's (1969) catch-per-unit-effort (tons/hour) data for two seasons; this seasonal pattern likely is associated with the spawning behavior of adults (Tillman 1972).

Given these mortality rates, the catch of anchovy is then computed for the month subject to the constraint that it may not exceed the reduction fleet's total or assigned harvesting capacity. The fleet and natural mortality at first compete exponentially to determine the number of fish each would take if harvesting capacity were unlimited. The temporary catch in numbers is calculated as:

TABLE 7.—Age specific catchability coefficients for northern anchovy given different areal restrictions and assuming full recruitment occurs at age 2. From Tillman (1972).

Age	Coefficient when inshore closed (10^{-3})	Coefficient when inshore open (10^{-3})
0	0.24	0.38
1	2.78	4.10
2-6	9.04	9.04

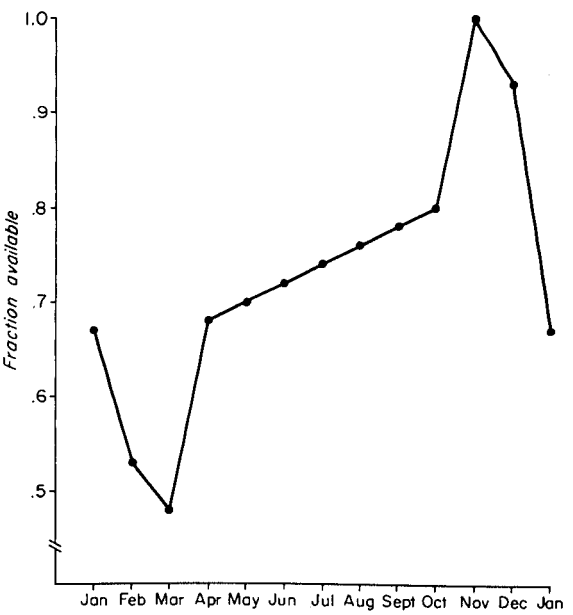

FIGURE 3.—Average monthly availability of northern anchovy in the southern California area. From Tillman (1972).

$$CN(A) = \frac{F(A,M)}{Z(A,M)} \cdot N(A) \cdot EXP$$

where $EXP = 1 - e^{-Z(A,M) \cdot (DT/NCYCL)}$
$N(A)$ = size in numbers of age group
DT = 1 mo

and $F(A,M)$ and $Z(A,M)$ are defined as above. $NCYCL$ is a parameter which determines the accuracy of the solution and typically is set at 4, yielding an effective DT of 1 wk.

The fleet's catch in weight then is temporarily computed as the sum

$$CW(M) = \sum_A CN(A) \cdot WT(A,M)$$

where $WT(A,M)$ is current weight at age. If $CW(M)$ exceeds the allowed harvesting capacity of the fleet, $CAPAC(M)$, the catch in weight is adjusted downward:

$$RC = CAPAC(M)/CW(M)$$
$$CW(M)' = \sum_A RC \cdot CN(A) \cdot WT(A,M).$$

Also, the fleet is rendered inactive for the remainder of the week.

Fish credited to the harvester in excess of capacity are subjected to natural mortality and then returned to the population. Once the catch cycle has been completed, the number of fish remaining in an age-group is determined by subtracting the numbers caught and the numbers taken by natural mortality.

Growth in length which occurred during the month then is computed utilizing a von Bertalanffy equation (Beverton and Holt 1957). Figure 4 shows the growth in length curve for the following parameter values: $L_\infty = 15.91$ cm, $K = 0.32$, $t_0 = -2.08$. New individual weights at age are then computed from a cubic weight-length relation.

Finally, future recruitment is calculated from the number of eggs deposited on the stock's spawning ground and an egg to recruit survival rate:

$$RECRT(M) = EGGS(M) \cdot SER \cdot SMULT(RATIO)$$

where SER is the equilibrium egg to recruit survival rate and $SMULT(RATIO)$ is a multiplier which adjusts SER in a density-dependent manner. Given Vrooman and Smith's (1971) estimate of equilibrium spawning stock size ($SEQ = 4.55 \times 10^6$ MT), Tillman (1972) estimated equilibrium recruitment ($REQ = 420 \times 10^9$ fish) and equilibrium numbers of eggs ($EEQ = 2 \times 10^{15}$ eggs) to obtain $SER = 0.00021$. The number of new recruits created during the current month will subsequently enter the fishable stock after a prerecruit period of 6 mo.

The appropriate value of $SMULT(RATIO)$ is determined from

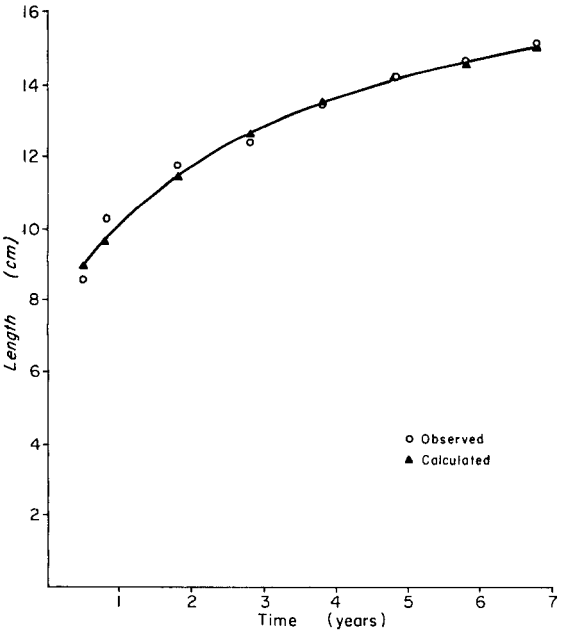

FIGURE 4.—Asymptotic growth in length of northern anchovy. From Tillman (1972).

$$SMULT(RATIO) = \frac{1}{A + B \cdot RATIO}$$

where $RATIO$ provides a measure of the current spawning stock size, $SP(M)$, relative to its equilibrium level, SEQ:

$$RATIO = SP(M)/SEQ.$$

This formulation insures that the stock-recruit process behaves in an asymptotic manner, as has been assumed.

Although data are lacking to estimate specific values for stock-recruit parameters A and B, sets of arbitrary values can be determined by defining a family of curves which pass through the same equilibrium point (SEQ, REQ). Following Tillman (1972), a unique curve in this family is distinguished by its asymptotic level of recruitment, $RMAX$, which can be defined as some multiple of the equilibrium level of recruitment:

$$RMAX = MULT \cdot REQ.$$

A particular set of stock-recruit parameters can then be determined as

$$B = 1/MULT \qquad A = 1 - B.$$

Vrooman and Smith's (1971) larval data provide a rough measure of variation in recruitment during 1962-66, a recent period of population stability. Comparison of their largest index of larval abundance (63×10^{12}) with the mean value during this period (48×10^{12}) indicates that values of *MULT* apparently should not exceed 1.30. Table 8 lists some representative values of *SMULT(RATIO)*, given *MULT* values in the range 1.05-1.20.

TABLE 8.—Egg to recruit survival multipliers *(SMULT)* for a family of three stock-recruit curves passing through the same equilibrium point. A unique curve depends on the value of *MULT* which defines parameters *A* and *B*. Each multiplier corresponds to given ratio between present and equilibrium biomass of the spawning stock.

	Curve	1	2	3
	MULT	1.05	1.10	1.20
	A	0.04762	0.09091	0.16667
RATIO	*B*	0.95238	0.90909	0.83333
0.10		7.00	5.50	4.00
0.20		4.20	3.67	3.00
0.30		3.00	2.75	2.40
0.50		1.91	1.83	1.71
0.75		1.31	1.29	1.26
1.00		1.00	1.00	1.00
2.00		0.51	0.52	0.55
3.00		0.34	0.35	0.38

Some Economic Content

Costs and prices used in this study (Table 9) have been adopted from among those estimated by Stadelman (1974). While these values are dated, particularly with respect to the price increase experienced in 1974, they still serve to illustrate our example applications. Following his suggestion, it is assumed that landing taxes have been removed, that the union has allowed fishermen to receive a guaranteed wage (rather than a share), and that it also has permitted crew size to be reduced on vessels equipped with power drums. Such changes conceivably would permit the fishery to take advantage of new technology that would provide the impetus for its immediate economic expansion. Moreover, it is assumed that quotas have been removed. In their stead, decision makers allow the fishery to expand to its economically optimal level, insuring however that only that fleet size is used and that catch is taken which supplies the optimal level of processing capacity in the system.

These assumptions, particularly the ones pertaining to crew wages and to quotas, may not be very realistic, but they do provide the basis for some interesting modelling applications. Their use infers that the harvesting-processing configurations of this study fulfill three criteria: 1) they maximize net economic yields; 2) they allow for payment of opportunity wages to crew members and of opportunity returns[3] to capital invested in the system; 3) they utilize state of the art technology. Opportunity wages are set at a guaranteed salary of $12,000/man. Also, a 15% rate of return is used to compensate an investor for his loss of alternative uses of capital, for his risk, and for his managerial skill.

TABLE 9.—Costs and prices for the northern anchovy model as adapted from Stadelman (1974).

Item	Without power drum	With power drum
Harvesting costs:		
Annual fixed cost/vessel (Depreciation, moorage, property taxes, office and shore expenses, insurance)	$30,126	$30,126
Return on investment (15%)	24,779	24,779
Guaranteed wages (Crew and captain)	132,000 (11)	84,000 (7)
Drum cost (Depreciation and return on investment)	—	6,900
Fixed cost/year	186,905.00	145,805.00
Fixed cost/day fished (Fuel and maintenance)	77.75	77.75
Cost/MT anchovy caught (Net repair)	2.20	2.20
Processing costs:		
Annual fixed cost/plant (Overhead, 15% return on investment)	$150,000.00	
Purchase price of anchovy/MT	25.00	
Processing cost of anchovy/MT	5.50	
Market prices:		
Fish meal/MT	250.00	
Fish oil/MT	110.00	

State of the art technology implies the use of new plants and new vessels. According to the above study, a new plant has only limited storage capacity for raw materials, a processing capacity of 20 tons/h, and conversion factors of 0.20 for meal and of 0.01 for oil. By working 20 h/day, 252 days/yr, such a plant could process 92,000 MT of anchovy annually. The above study also found that a 210-ton (191-MT) purse seiner was the most economically efficient harvesting unit. A new vessel of this size could be equipped with a power drum, which would lead to a reduction in crew size (from 10 to 6 men) but not necessarily to an increase in harvesting efficiency.

Stadelman (1974) indicated that prices of fish

[3]One who invests labor or capital in a particular economic opportunity should at least earn that amount which might be returned by his next best investment alternative. The amounts that could have been earned from this second choice are termed opportunity returns; i.e., opportunity wages should be earned by labor and opportunity returns by capital.

meal and oil in the United States are established primarily by the world market for these products. Consequently we have assumed that northern anchovy processors can only accept the prices offered for their meal and oil, rather than being able to affect the world market through their own efforts. In this case, demand curves for their products are nonexistent, and the fixed prices given in Table 9 hold throughout a given simulation experiment.

APPLICATIONS OF THE MODEL

Analytical Technique

Nature of Results

Due to the rough nature of many of the estimates utilized by the model, little credence has been attached to the absolute values of economic return, catch in weight, or population size obtained in the following simulation experiments. These results are at best only informed extrapolations, and, even though their values are of the proper orders of magnitude, it is not the intent of the following applications to accurately predict future returns, yields, or sizes. Of greater importance are the relations between values obtained in different experiments. Consequently, the results have been analyzed on a comparative rather than an absolute basis.

Criteria for Comparisons

The primary results obtained from each experiment include the net economic return (before income tax) generated annually by the entire system, the number of days fished each season, the annual catch in weight, and population size in terms of annual average biomass. In most experiments, these four variables satisfactorily measure the economic and biological performance achieved during an experiment. In preliminary long run equilibrium experiments, values of these variables stabilized within a 10-yr period. Thus, 10 yr has been chosen as the length of all experiments.

Differences between various experiments are measured primarily in terms of the differences between respective net economic returns. Net economic return is obtained by subtracting amalgamated harvester-processor costs from amalgamated gross revenues at the end of each year of simulation. Amalgamated costs include the annual opportunity costs of labor and capital.

Alternative Regulations and Stock-Recruit Sensitivity

Recalling the spectacular decline of the sardine fishery during the 1950's and fearing a similar debacle over another forage species, sportsmen and bait fishermen have become allied in sponsoring state legislation to limit commercial development of the northern anchovy. As a consequence of their efforts, the reduction fishery has been plagued by low quotas and currently cannot fish during the summer (15 May-15 September) nor within 3 miles (4.8 km) of shore. These two specific exclusions define areas wherein tradeoffs might be made to gain concessions from the sport and bait fisheries. Decision makers might retain the summer or inshore closures intact to placate the nonindustrial groups and receive in trade the concession of larger quotas for industrial use of anchovy. Some idea of what is lost by such trades might be obtained by contrasting these closures to others wherein more lenient measures were enforced.

Some evidence exists which indicates that considerable gains in harvesting efficiency might be achieved by lengthening the season to a year or by opening the inshore area. In Figure 3, the pattern of availability extrapolated for May-September indicates that an improving trend is expected during the summer. Also, Tillman's (1972) analysis of age-specific catchability revealed that age-groups 0 and 1 tend to be more available in the inshore area than in the offshore commercial fishery area; he subsequently calculated catchability coefficients reflecting this apparent areal difference (results given in our Table 7).

Using these catchability coefficients implicitly assumes that older anchovies (ages 2-6) are equally available in the inshore and offshore areas. As indicated in Figure 3 we have, of course, attempted to account for the seasonal availability of older anchovies as related to their spawning behavior, but the net result of spawning movements might also tend to distribute older fish farther offshore than younger ones. This circumstance would effectively reduce the inshore catchability coefficient for older fish.

Unfortunately, data on the areal distribution of age-groups, such as the age compositions of

catches taken at varying distances from shore, were not available to examine this possibility in detail. However, Messersmith et al. (1969) reported that, during summer and fall echo-sounder surveys, all sizes of anchovies were found concentrated close inshore. Since all sizes were encountered, we speculated that, if fishing were allowed inside of 3 miles (4.8 km), the catchability coefficient for older fish would become reduced only if effort concentrated on or very near nursery grounds, which occur on shallows and flats inside of 50 fathoms. Although lower fuel costs might dictate such a concentration, we further speculated that enforcement of the current minimum size limit of 10.8 cm would make fishing this far inshore unattractive and thus curtail it.

Given these speculations, simulation experiments were conducted in our first application to examine the biological and economic consequences of opening the inshore area to commercial fishing and of allowing a 12-mo fishing season. These were contrasted to a "present" situation consisting of a closed inshore area and an 8-mo season (15 September-15 May). Moreover, sensitivity of the model to changes in the stock-recruit relationship was examined given alternative areal-seasonal restrictions. Stock-recruit curve 2 (Table 8) was arbitrarily chosen as the standard for comparison in these experiments. Each experiment thus determined how an optimal harvesting-processing configuration (numbers of vessels and plants) defined for curve 2 performed when stock-recruit curve 1 or 3 were in effect. Essentially, then, each experiment simulated the decision-making problem wherein a manager assumes that a given biological situation is "true" and plans to meet it but then encounters a completely different situation.

The results of this first group of sensitivity experiments are indicated in Table 10. The main criteria for comparing performances under different stock-recruit curves are the absolute and percentage differences in net economic returns indicated in the last two columns of this table. In all cases, relative to curve 2, harvesting-processing systems performed better under curve 1 and worse under curve 3. As seen from the larger returns, catches, and biomasses generated and from the fewer days of fishing required, curve 1 defined a more productive biological regime relative to curve 2. Likewise, from the smaller returns, catches, and biomasses and from the generally greater number of days of fishing required, curve 3 defined a less productive biological regime.

The economic consequences of imposing different regulatory schemes can also be determined from Table 10. Opening the inshore area would generate about a 30% improvement in net return. Given our assumptions, such an increase is likely due to the increased availability of 0's and 1's which in turn leads to greater catches for the same level of effort. On the other hand, a change in season length would generate an improvement in returns of 120-130%. Quite obviously, from an economic viewpoint, the model indicates that the preferable management scheme would be a change to the 12-mo season. Barring that, the next best scheme would be to open the inshore area.

However, these economic findings should be tempered somewhat by sensitivity considerations. Comparison of areas within seasons (Table 10) reveals that an open inshore area is less sensitive to changes in stock-recruit relations than is a closed inshore area. That is, the percentage change in net returns is less for both curves 1 and

TABLE 10.—Sensitivity of optimal configurations to changes in stock-recruit curves and areal restrictions, given M = 1.10 and deterministic availability.

Length of season	Area	Stock-recruit curve	Fishing time	Average biomass (10^6 MT)	Catch (10^3 MT)	Net return (10^6 dollars)	Difference Absolute	Difference %
8 mo	Inshore closed	[1]2	144	3.92	491.4	6.010	—	—
		1	144	4.00	501.6	6.456	0.446	7.42
		3	144	3.81	477.5	5.408	−0.602	−10.02
	Inshore open	[1]2	141	3.87	537.1	8.014	—	—
		1	140	3.96	547.1	8.454	0.440	5.49
		3	142	3.75	523.9	7.432	−0.582	− 7.26
12 mo	Inshore closed	[1]2	216	3.47	831.9	13.660	—	—
		1	215	3.57	870.5	15.341	1.681	12.31
		3	216	3.32	796.9	12.136	−1.524	−11.16
	Inshore open	[1]2	212	3.43	920.6	17.545	—	—
		1	209	3.63	941.2	18.466	0.921	5.25
		3	214	3.26	886.1	16.024	−1.521	− 8.67

[1]Situations used as standards for comparative purposes.

3 when the inshore area is open, greater when it is closed. Also, in three of four comparisons of seasons within areas, an 8-mo season is less sensitive to changes in stock-recruit relations than is the 12-mo season.

The greater sensitivity of the 12-mo season is probably due to the greater level of effort exerted (e.g., compare days fished) which would tend to drive stock size down into more critical regions of the stock-recruit curve and give rise to density-dependent responses greater than those observed under the 8-mo season. From a sensitivity viewpoint then, harvesting-processing operations planned for the 12-mo season or closed inshore area would tend to suffer most from the present lack of knowledge about stock-recruit behavior; the 8-mo season or open inshore area would tend to suffer least.

Considering our premise that trade offs might be made between quotas and areal-seasonal restrictions, the above model results imply that giving up (trading off) an increased season length represents a considerable loss of potential economic benefit. Such a trade off would therefore seem to require substantial compensation in the form of increased quotas. Trading off a change in areal restrictions, on the other hand, would seem to provide considerably less bargaining power. Moreover, opening the inshore area appears to offer distinct advantages, not only in terms of moderately increased net returns, but also in the form of somewhat decreased operating risk given a lack of biological knowledge. Consequently, the model indicates that trading off a change in season length appears to be the most advantageous tactic for plant and fleet managers if they seek increased quotas.

Technological Change and Employment

In their study of the San Pedro wetfish[4] fleet, Perrin and Noetzel (1970) estimated that the number of jobs on vessels had decreased from 381 in 1963 to 238 in 1968. The figures reflected a reduction not only in the size of the fleet but also in the size of crew as well. In 1963 the average crew size was 10.29 compared to the 1968 average of 9.52. With such a decline in employment, it is not surprising that the union opposes the introduction of technology which would replace more men (Stadelman 1974).

According to Hester et al. (1972), the application of a power drum to purse seining by the wetfish fishery would significantly reduce the size of the crew. Based upon the foregoing author's experiment with a 100-ton (91-MT) capacity vessel, Stadelman (1974) estimated that for a 210-ton (191-MT) purse seiner the introduction of a power drum would reduce the crew from 10 to 6. This would result in significantly reduced vessel operating costs (Table 9) which might allow fleet expansion and a subsequent increase in the overall level of employment. Simulation experiments were therefore conducted to see if a favorable outcome resulted which might dissuade the union from opposing such technological innovation.

Table 11 lists the results obtained for a 12-mo season for both the normal and the power drum methods of purse seining. Use of the drum increased net yield by 80% and the optimal level of fishing effort by 38%. However, the optimal total labor force was reduced from 544 required to man the fleet to an estimated 459. Consequently, the added vessels did not make up for the reduction in crew size.

However, it should be noted that even with the use of the power drum the level of employment would exceed its 1968 level of 238 men. It is also apparent that the additional net yield associated with the power drum, some $2.6 million, might be negotiated into a wage above $12,000. On the assumption that 459 men would be employed, each could receive an additional $5,664/yr and the fishery would still yield the same annual net return as before the innovation. Alternatively, the increased net yield could supply income to employ 215 workers in other activities at the $12,000 wage, whereas prohibition of the power drum would save only 85 jobs in the fishery. This is the type of trade off that must be weighed in determining policy to increase the level of employment.

TABLE 11.—Effect of power drum on employment for a year-long season.

Power drum	Net yield (millions)	Level of effort (standard vessels)	Labor force	Total gross wages paid (millions)
Without	$2.9	49	544	$6.5
With	5.5	68	459	5.5

[4]Wetfish are defined by Perrin and Noetzel (1970) to include northern anchovy for reduction; and Pacific sardine, jack mackerel, *Trachurus symmetricus*, chub mackerel, *Scomber japonicus*, and Pacific bonito, *Sarda chiliensis*, for canning and the fresh-fish market.

The foregoing results assume that the physical efficiency of harvesting is not increased by the power drum. The study by Hester et al. (1972) revealed that the use of a power drum and fish pumps to unload the nets often enabled the experimental vessel to get in an extra set during the brief time fish were available before dawn. This circumstance depended on the size of catches being made since use of the equipment actually increased the set time for very small catches. No data were presented, however, as to the average number of sets or the frequency of catch size for evaluation of efficiencies.

The above analysis points up the importance of union work rules permitting the use of new technology. The application of the power drum to vessels apparently would improve the economic viability of the fishery, permitting its operation even with old hulls or at fish meal prices below $250/MT. Although use of the drum reduces crew size on an individual vessel, its general adoption apparently would provide considerable economic incentive for fleet expansion, leading to an increase in overall employment beyond its 1968 level.

To make this inference, however, we have assumed away the real problem, which is not the adoption of new technology but the alteration of traditional union share agreements which pay the crew a percentage of net revenues. Unless new technology resulted in increased gross revenue as well as a reduction in crew size, the same share of the net revenue would simply be divided among fewer crewmen, and the investor would gain nothing to compensate him for the additional costs of the technological change. Consequently, the present system does not allow the investor a sufficient return, and the fishery suffers in terms of employment levels as well as with respect to economic efficiency.

DISCUSSION

In discussing his model of the ecological bioenergetics of isopods, Hubbell (1971) indicates that there is a twofold utility in modelling a given system. First, the model can be regarded as a tool to guide and orient future research on that system. Second, once the model exhibits satisfactory performance, it can be put to predictive use, answering hypothetical questions about the consequences of different input conditions upon system behavior. As demonstrated by the preceding applications, we feel that the northern anchovy model definitely has the potential for fulfilling both of these purposes.

However, in its current state of development the model is admittedly speculative in some of its content. Several of its shortcomings have already been discussed, but perhaps its greatest failing is that its behavior has not yet been adequately validated. To do so would currently require the circular logic of testing the model against the very data from which its assumptions and estimates derive. Consequently we have been forced to rely upon our own subjective view of what constitutes well-behavedness in the model and have applied this criterion in evaluating its performance.

According to Patten (1972), we probably could do little more to validate the model since there currently exists no theoretical base for approaching this fundamental modelling problem. In any regard, the predictive use of this model should therefore be treated in only the most general of terms, i.e., with the aim of gaining insight into the structure and behavior of the anchovy fishery. In this sense, it presently is a conceptual rather than an analytical model.

This leaves its use as a tool for guiding and planning research as the model's primary reason for being. To that end it has proven quite useful, providing a systematic means by which extant data might be organized and pinpointing areas characterized by a glaring lack of data. For example, our approach to modelling stock-recruit behavior was necessitated by a lack of appropriate indices measuring recent stock and recruitment sizes.

Additionally, we feel that the model provides the capability for identifying and ranking critical research areas. Management decisions must be timely and as correct as possible, yet the cost of collecting and analyzing relevant data is very high both in money and time. Given budgetary constraints, all research needs cannot possibly be satisfied. Therefore, decision makers should be asking themselves whether the cost of better information will be justified by a better choice of management policy.

The model could play an important role here by allowing the decision maker to test the sensitivity of his information upon policy alternatives. Some policy sets will not be affected by slight changes in estimates resulting from fuller information: a somewhat higher growth rate than initially believed, for example, may not occasion any

revision in policy. The degree of sensitivity thus determines which information is trivial and which is critical. Parameters of the model which prove to have little or no effect on the decision then need not be refined by further research.

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LITERATURE CITED

AHLSTROM, E. H.
1966. Distribution and abundance of sardine and anchovy larvae in the California Current Region off California and Baja California, 1951-64: A summary. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 534, 71 p.

BAXTER, J. L.
1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest., Rep. 11:110-116.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest., Minist. Agric., Fish. Food (G.B.), Ser. 2, 19, 533 p.

CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax mordax*) in the California fishery. Calif. Fish Game 38:189-207.

COLLINS, R. A.
1969. Size and age composition of northern anchovies (*Engraulis mordax*) in the California anchovy reduction fishery for the 1965-66, 1966-67, and 1967-68 seasons. Calif. Dep. Fish Game, Fish. Bull. 147:56-74.
1971. Size and age composition of northern anchovies (*Engraulis mordax*) in the California reduction and canning fisheries, 1968-69 season. Calif. Fish Game 57:283-289.

CUSHING, D. H.
1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. 33:340-362.

FOX, W. W.
1973. A general life history exploited simulator with pandalid shrimp as an example. Fish. Bull., U.S. 71:1019-1028.

FRANCIS, R. C.
1974. TUNPØP, a computer simulation model of the yellowfin tuna population and the surface tuna fishery of the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 16:235-279.

GALES, L. E.
1972. NEW GAMES: A multi-purpose interactive resource management program. Univ. Wash., Quant. Sci. Pap. 32, 40 p.

HAUGEN, C. W., J. D. MESSERSMITH, AND R. H. WICKWIRE.
1969. Progress report on anchovy tagging off California and Baja California, March 1966 through May 1969. *In* The northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 75-89. Calif. Dep. Fish Game, Fish. Bull. 147.

HESTER, F. J., D. A. AASTED, AND R. E. GREEN.
1972. Experimental drum seining for wetfish in California. Commer. Fish. Rev. 34(1-2):23-32.

HUBBELL, S. P.
1971. Of sowbugs and systems: The ecological bioenergetics of a terrestrial isopod. *In* B. C. Patten, Systems analysis and simulation in ecology, Vol. 1, p. 269-324. Academic Press, N.Y.

MACGREGOR, J. S.
1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Fish Game 54:281-288.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game, Fish Bull. 162, 79 p.

MESSERSMITH, J. D.
1969. A review of the California anchovy fishery and results of the 1965-66 and 1966-67 reduction seasons. Calif. Dep. Fish Game, Fish Bull. 147:6-32.

MESSERSMITH, J. D., J. L. BAXTER, AND P. M. ROEDEL.
1969. The anchovy resources of the California Current region off California and Baja California. Calif. Coop. Oceanic Fish. Invest., Rep. 13:32-38.

MILLER, D. J., A. E. DAUGHERTY, F. E. FELIN, AND J. MACGREGOR.
1955. Age and length composition of the northern anchovy catch off the coast of California in 1952-53 and 1953-54. Calif. Dep. Fish Game, Fish Bull. 101:36-66.

MILLER, D. J., AND R. S. WOLF.
1958. Age and length composition of the northern anchovy catch off the coast of California in 1954-55, 1955-56, and 1956-57. Calif. Dep. Fish Game, Fish Bull. 106:27-72.

MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sandinops caerulea*). Proc. Calif. Acad. Sci., Ser. 4, 34:1-84.
1973. Clupeoid fishes under exploitation with special reference to the Peruvian anchovy. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 30, 73 p.

PATTEN, B. C.
1972. Systems analysis and simulation in ecology, Vol. II. Preface, p. XI-XIV. Academic Press, Inc., N.Y.

PERRIN, W. F., AND B. G. NOETZEL.
1970. Economic study of the San Pedro wetfish boats. U.S. Fish Wildl. Serv., Fish. Ind. Res. 6:105-138.

RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.

SCHAEFER, M. B.
1967. Dynamics of the fishery for the anchoveta *Engraulis ringens*, off Peru. [In Span. and Engl.] Inst. Mar Peru, (Callao) Bol. 1:191-303.

STADELMAN, D.
1974. Optimal policy and sensitivity analysis of the northern anchovy fishery: A simulation study. Ph.D. Thesis, Univ. Washington, Seattle, 101 p.

TILLMAN, M. F.
1968. Tentative recommendations for management of the coastal fishery for Pacific hake, *Merluccius productus* (Ayres), based on a simulation study of the effects of fishing upon a virgin population. M.S. Thesis, Univ. Washington, Seattle, 197 p.

1972. The economic consequences of alternative systems; a simulation study of the fishery for northern anchovy, *Engraulis mordax* Girard. Ph.D. Thesis, Univ. Washington, Seattle, 227 p.

1975. Additional evidence substantiating existence of northern subpopulation of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 73:212-215.

TILLMAN, M. F., AND G. J. PAULIK.
1971. Biological analysis of the northern anchovy fishery system. Univ. Wash., Quant. Sci. Pap. 28, 65 p.

VROOMAN, A. M., AND P. E. SMITH.
1971. Biomass of the subpopulations of northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest., Rep. 15:49-51.

WALTERS, C. J.
1969. A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98:505-512.

POPULATIONS OF SYMPATRIC SCULPINS, *COTTUS ALEUTICUS* AND *COTTUS ASPER*, IN FOUR ADJACENT SALMON-PRODUCING COASTAL STREAMS ON VANCOUVER ISLAND, B.C.

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ABSTRACT

General life history, distribution and abundance, age structure, and growth and survival are documented for sympatric populations of two cottid fishes. Stream obstructions may largely determine the distributional limits for both cottids with *Cottus aleuticus* penetrating farthest upstream. Biomass density and size of individual fish increased with distance upstream, largest individuals living at the upstream borders of their species ranges. Both sculpins were numerically most abundant in their lower ranges, reflecting the common estuarine origin of benthic young. From 69 to 74% of their combined biomass in the upper estuaries were *C. asper* while 75-100% was *C. aleuticus* in the upper stream zone. *Cottus asper* grew more rapidly and mortality rates were similar, but the oldest *C. aleuticus* was age 8 and 145 mm in length, compared with age 6 and 144 mm for *C. asper*. The length-weight relation was similar for both species. The community role of these sculpins is explored with primary focus on possible competition with the stream-dwelling salmonids, and recommendations are made which might lead to increased production of salmonid smolts to the sea.

As part of a general study of the fish community of Lymn Creek, populations of the sympatric sculpins, *Cottus aleuticus* and *C. asper*, were examined during 1968 with regard to population structure, annual growth and mortality, and general distribution and abundance in the system. In addition, three adjacent streams (Cabin, Chef, and Waterloo) were sampled in the fall of 1968 to provide a comparative basis for interpreting the findings at Lymn Creek. The present communication deals primarily with population characteristics of sculpins in relation to life history. Their role in the community, including possible competition with salmonids, is examined with a view of enhancing salmonid production.

THE STUDY AREA

The four streams studied are neighboring systems emptying into the Strait of Georgia on the east coast of Vancouver Island. They are small streams (drainage area <20 km^2, minimum summer flow <7 m^3/min, Table 1), having similar gradients and streambed materials, but Cabin Creek is considerably smaller than the others. Their watersheds are forested at a similar stage of second-growth conifers, primarily Douglas fir. Lymn and Waterloo creeks closely resemble each other, although the latter stream has fewer major obstructions (logjams) hindering the upstream migration of salmon. Lymn Creek differs from the other three streams in having a swampy sloughlike area resulting from beaver activities near the estuary. Both Lymn and Chef creeks course through some 200 m of intertidal meadow, but Cabin and Waterloo creeks empty directly onto the open beach. Extensive intertidal zones in all four streams result at low tide when nearly the entire zone is exposed to freshwater flow.

Unlike the other systems, Chef Creek is subject to flow extremes, rapid runoff during freshets and, during the late summer and early fall, intermittent flow and isolated pools in the lower reaches.

Cutthroat trout, *Salmo clarki*; coho salmon, *Oncorhynchus kisutch*; three-spined stickleback, *Gasterosteus aculeatus*; coastrange sculpin, *C. aleuticus*; and prickly sculpin, *C. asper*, reside in

TABLE 1.—Some physical characteristics of the four study streams.

Stream	Drainage area (km^2)	Average width[1] (m)	Average gradient (%)	Minimum summer discharge (m^3/min)
Cabin	2.3	1.5	1.2	0.5
Lymn	9.3	2.5	1.0	3.4
Waterloo	10.5	2.5	1.2	2.6
Chef	18.3	7.5	0.9	6.8

[1]Within the sculpin zone.

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all four streams. Chef and Waterloo creeks also contain steelhead trout, *S. gairdneri*, and chum salmon, *O. keta*. Chum salmon occasionally spawn intertidally in Lymn Creek.

METHODS AND MATERIALS

Sampling the Populations

In Lymn Creek, sculpins were collected incidentally to salmonids from April to July 1968. A sampling schedule for cottids was initiated in August and terminated in December 1968. Chef, Cabin, and Waterloo creeks were sampled during September and October.

Fish were collected in the estuaries by seine at low tide. In the streams proper, collections were made with a 440-V DC fish shocker (Smith-Roote Laboratories, Mark V[3]). In both environments, discrete sections of stream, usually 15- to 30-m sections, were sampled and all fish captured were removed.

Specimens were preserved in 5% Formalin. In the laboratory, total length was measured to the nearest millimeter and body weight to the nearest 10 mg. Otoliths were removed for age determination.

No attempts were made to quantify the relative or absolute efficiencies of the two sampling methods. The habitat seined lent itself to efficient seining, and it is considered that any increased capture efficiency or size-related sampling bias usually associated with electrical fishing devices was, at least in part, cancelled by the increased complexity of habitat typical of the stream proper and the concentration of the two youngest age-groups in the lower stream, including the estuaries. Increased stream flow and turbid water following the first significant rains in the late fall probably reduced the efficiency of both collecting methods to a considerable but unknown extent. Therefore, growth and survivorship estimates were based on data collected prior to the onset of the rainy season.

In the laboratory, breeding activity was followed by keeping adults allopatrically in 150-liter fiber glass tanks at ambient freshwater temperature with flow-through conditions, a rubble substrate, and normal photoperiod. Embryological development and larval responses to salinity, illumination, current, and food were investigated. Egg masses of known age and their resulting larvae were kept in 3-liter glass jars filled with aerated fresh water or seawater; and mortality and feeding responses of larvae to microzooplankton were observed. The responses of larvae of known age and salinity history to overhead illumination and water currents were investigated in a Perspex test chamber.

Drift nets were set at several stations in Lymn Creek during the hatching period in the spring to document the timing and extent of the hatching period, upper limits of the spawning ground and characteristics of the fry moving seaward.

Population Estimates

Estimates of population size in Lymn, Cabin, and Waterloo creeks were attempted in the fall for both species of sculpin. Population estimates for Chef Creek were precluded by the large size of the stream, which prevented representative sampling across the stream at most stations. In the other three streams, catches from individual stations were assumed to be representative of that stream section, and population was calculated as follows:

$$N = \Sigma CD$$

where C = station catch (fish/meter of stream) where each station is representative of a larger stream section D
D = stream section (in meters).

The estimated populations were distributed among the various age-classes so as to reflect the age-class composition of the station catches. Admittedly, these estimates are rather crudely derived yet they yielded fairly consistent trends in annual mortality, particularly for the Lymn Creek populations (see Results, Annual Growth, Mortality, and Length-Weight Relations). Attempts to apply mark and recapture techniques to the problem of population estimation proved fruitless due to extensive behavior changes in marked fish following their release. These changes (movement downstream or into the streambed) seriously affected their vulnerability to recapture and led to large scale overestimates of actual population size.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Age Determination

Following dissection, otoliths were dried for several days and then immersed in a 50% solution of glycerin and water. Otolith structure was not clear when examination immediately followed removal of the otolith from the specimen. Otoliths of specimens preserved for more than 1 mo were partly decomposed by the preservative.

Whole otoliths were examined under a dissecting microscope by reflected light against a black background. In both species, the otolith had an opaque nucleus around which were arranged concentric, alternating hyaline and opaque bands extending to the margin. The opaque band reflected rapid summer growth and the hyaline band constituted the annulus. The first hyaline band around the nucleus was not considered an annulus but is assumed to reflect initial postlarval growth, perhaps prior to the onset of a benthic existence. The newly forming annulus was readily discernible in specimens collected in October and December.

Length-frequency histograms were found useful to identify the young of the year (age 0) and yearlings (age I).

RESULTS

General Life History

Both species of sculpins in these short coastal streams are "coastal" forms (McAllister and Lindsey 1960) which spawn during April and May. The prickly sculpin undergoes a downstream spawning migration in the early spring (Mason 1974a) and spawns in the estuary as reported previously by Krejsa (1967). The coastrange sculpin has been reported to make downstream migrations coincident with *C. asper* (Shapovalov and Taft 1954; Hunter 1959) but no such migration was recorded in Lymn Creek where *C. aleuticus* spawned in situ throughout its range in the stream as found in Alaskan streams by McLarney (1968).

The breeding males are territorial and court one or more females which deposit clusters of adhesive eggs on the underside of large rocks or debris forming the nest site. Following spawning, the females depart and the males guard the eggs until hatching. The newly hatched and transparent larvae begin swimming upon hatching and assume a pelagic life for some 30 days, growing from 5 mm at hatching to 12 mm in length before assuming a benthic existence.

In the laboratory at 10°-12°C, the eggs of both species were eyed at 9-10 days; the larvae were active at 15 days; and hatching occurred 19-20 days following fertilization. Hatching commenced in Lymn Creek on or before 11 May when water temperature reached 10°C. On this date, larvae began appearing in the driftnet catches and were taken for some 5 wk until 19 June.

From drift net catches of the larvae in Lymn Creek, coupled with laboratory studies on the reproduction of both species, we concluded that the eggs and larvae are euryhaline but survival and growth of cultured larvae are better in seawater. Feeding on microplankton commenced some 6-10 days following hatching of cultured larvae when the yolk was noticeably depleted and when most stream larvae were either in the estuary or, in the case of coastrange sculpin larvae, in the lower stream near the estuary. Since the average size of the latter larvae in drift samples from four stations located along 1,150 m of stream above the estuary equalled that of 6-day-old larvae in culture at similar temperatures, these larvae probably spend several days in the nest vicinity and in downstream transport following hatching.

Within several hours of hatching, larvae of both species swam to the water surface and maintained themselves vertically immediately beneath the surface film by steady swimming movements. This behavior was sustained through the 25 days of culture in both fresh water and seawater. Tests on 5-day-old and older larvae showed that they were positively rheotactic at velocities greater than 1 cm/s and swam actively against the current in short bouts of rapid swimming.

Post-spawned *C. asper* remained in the estuary of Lymn Creek throughout the summer and early fall. Their return to upstream areas may coincide with the spawning runs of salmon that commence in October (Mason 1974a). The offspring of both species remain in the estuarine zone until the early summer of the following year when they proceed to invade upstream areas.

Distribution and Relative Abundance

Both sculpin populations were limited to the lower reaches and estuaries of all four streams, with coastrange sculpins distributed farthest up-

stream. The prickly sculpin was not found more than about 1 km upstream from high tide mark where the stream gradient did not exceed 1.5%, whereas the coastrange sculpin penetrated upstream some 1.6-2.7 km from high tide mark in a range of stream gradients not exceeding 6%. In Cabin Creek, the smallest stream, the same general difference between the two species in longitudinal distribution prevailed, but the distances involved were reduced by a factor of 10. The upstream distributional limits of both species in all four streams are indicated in Figure 1.

Habitat segregation was evident in cohabitated stream areas, large *C. asper* occupying the deepest locations in pools, under log jams and undercut banks. Intermediate-sized *C. asper* and large *C. aleuticus* were also found at these sites but at shallower depths. Riffle and glide areas were mainly occupied by small and medium-sized *C. aleuticus*.

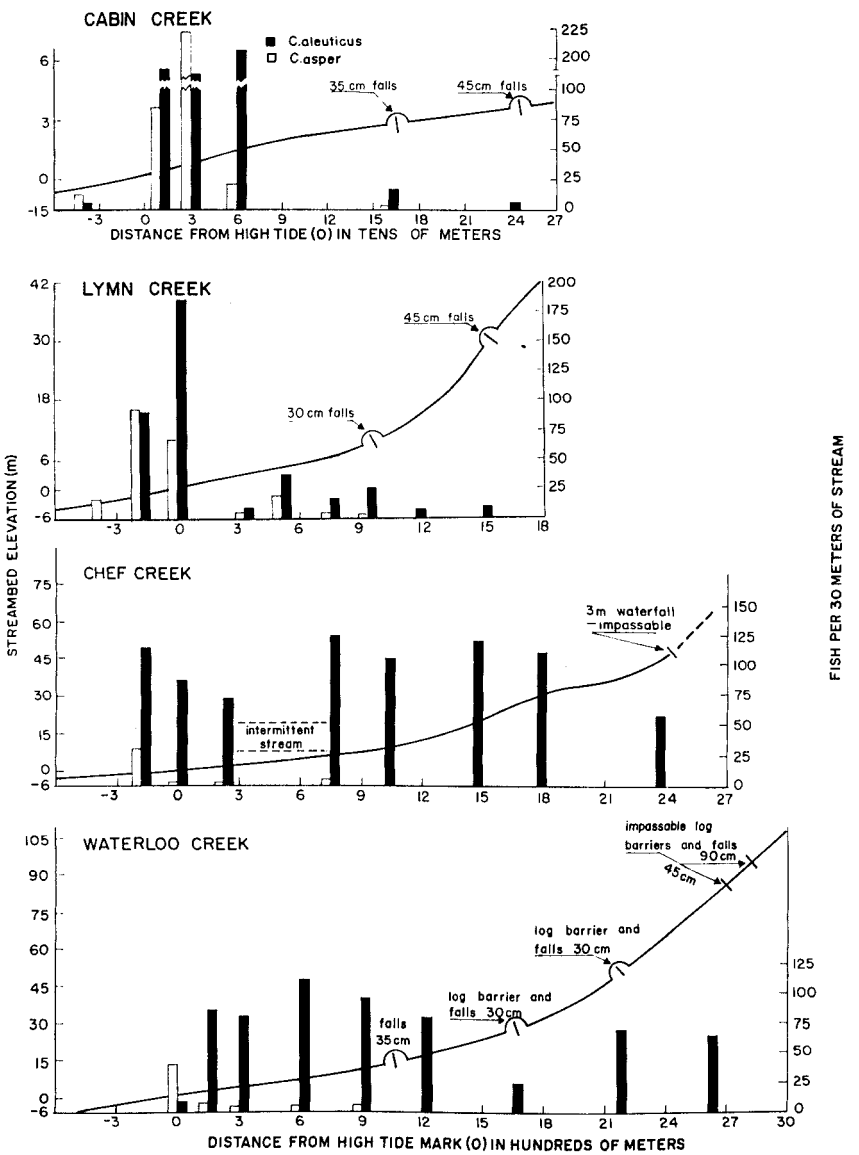

FIGURE 1.—Autumnal distribution and abundance of *Cottus aleuticus* and *C. asper* in relation to stream profile and streambed obstructions. High time mark (0) is a reference benchmark determined by the highest spring tide.

In upstream areas devoid of *C. asper*, the large coastrange sculpins were found in habitats which were usually occupied downstream by large prickly sculpins. Although the subyearlings of both species were found in riffle habitats of the intertidal zone, some habitat segregation was evident since prickly sculpins tended to concentrate in riffle areas where water depth increased and velocity lessened.

The upstream movement of both sculpins is clearly hindered by minor obstructions in the stream, and their respective upstream distributional limits are marked by similar but different obstructions. These obstructions were usually small log jams involving minor waterfalls although in Chef Creek *C. aleuticus* was stopped by a high waterfall (3-4 m) plunging over bedrock. Obstructions resulting in differences in water level greater than 30 cm were impassable for *C. asper* while differences greater than 45 cm were necessary to prevent upstream movement of *C. aleuticus*. The limiting structures in Lymn Creek are shown in Figure 2.

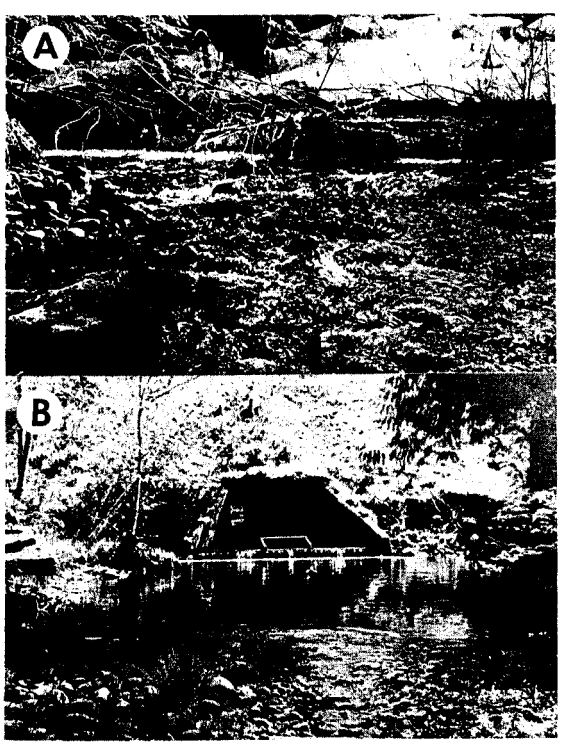

FIGURE 2.—Stream obstructions delimiting the upstream distribution of sculpins in Lymn Creek. A. 45-cm waterfall caused by a large cedar log which blocks the upstream movement of *Cottus aleuticus*. B. 30-cm waterfall at the concrete culvert under Trans-Canada Highway 1, which blocks the upstream movement of *C. asper*.

The upstream limits of both species of sculpin bore a general association with stream gradient, since both stream gradient and frequency of log jams increase with distance upstream, as do streambed disjunctions causing higher falls (Figure 1).

Both species were distributed downstream into the intertidal zone but to dissimilar extent. For *C. aleuticus*, the downstream limit was the upper edge of the barnacle zone (station 0 minus 250 m, Figure 1) while *C. asper* was not collected below the upper edge of the oyster zone (station 0 minus 400 m).

Both sculpins were most abundant in the lower parts of their ranges (Figure 1) although the data for *C. aleuticus* in Chef Creek are inconclusive, possibly due to upstream movement of fish from the region of intermittent flow although such movement was not observed. Skewed distribution is most pronounced in populations of the two smaller streams, Cabin and Lymn creeks, and in large part is due to inequitable distribution of the age-classes. The subyearling sculpins were found to inhabit a narrow zone about the high tide mark, within which the two species showed extensive overlap (Figure 3). The relative contributions of subyearlings to total catches were rather low in Chef and Waterloo creeks, suggesting poor reproductive success or poor recruitment in 1968. This aspect will be dealt with again in a subsequent section.

Neither species of sculpin undertook any obvious seasonal movements in Lymn Creek during the period from August to December (Figure 4), although the large catches of age I+ prickly

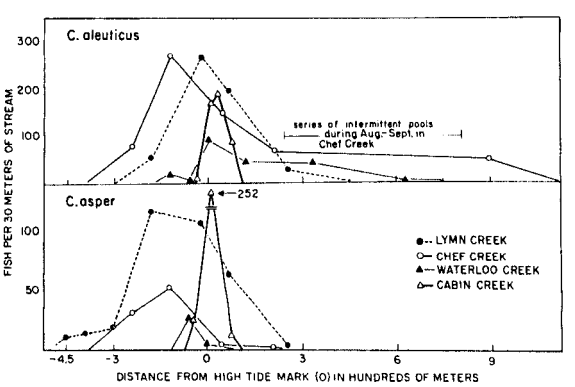

FIGURE 3.—Autumnal distribution and abundance of subyearling sculpins.

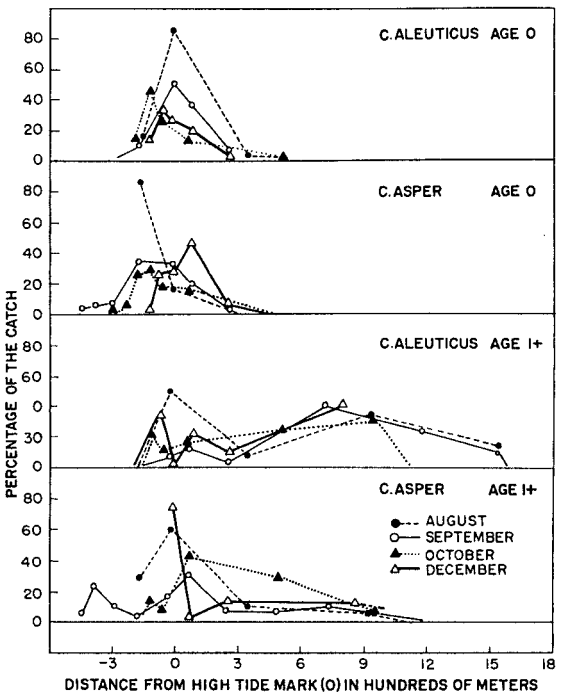

FIGURE 4.—Relative distribution of subyearling and older (I+) sculpins in Lymn Creek during the period August-December.

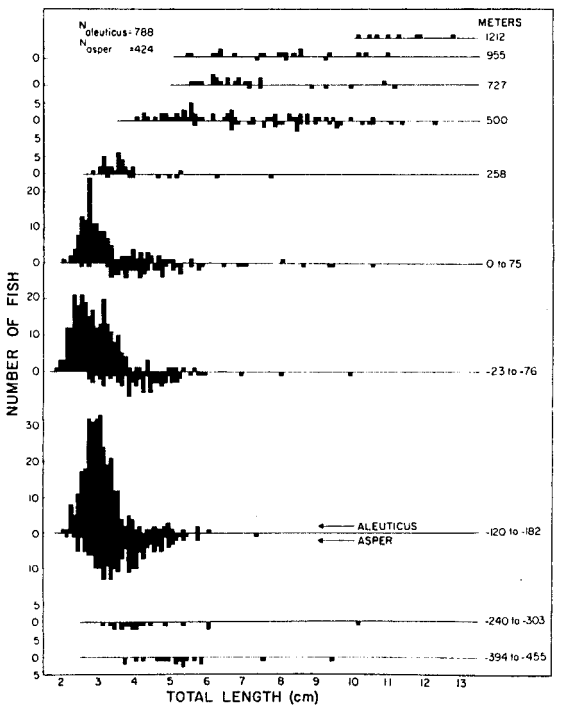

FIGURE 5.—Length-frequency histograms for sculpin populations in Lymn Creek from collections made in September and October. Sampling stations are identified as distances upstream or downstream (−) from high tide mark (0) in meters.

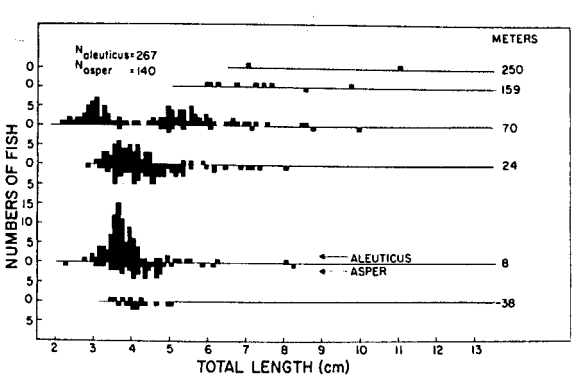

FIGURE 6.—Length-frequency histograms for sculpin populations in Cabin Creek from collections made in September and October. Sampling stations are identified as distances upstream or downstream (−) from high tide mark (0) in meters.

sculpins made at the head of tide in December suggest the return upstream of individuals which made the downstream migration in the previous spring.

In general, size of fish increased with distance upstream, the largest individuals of both species living at the upstream border of their respective ranges (Figures 5-7); however, subyearling and yearling sculpins of both species tended to be larger both upstream and downstream from the head of tide.

Age Structure

Age structure of populations of both species in Lymn, Chef, and Waterloo creeks was determined by reading the otoliths. Only the first two age-classes could be identified from length frequency histograms (Figures 5-7), and these modes agreed with the otolith readings. The Lymn Creek populations were aged from three successive monthly samples (August-October) that indicated similar lengths within age-groups for this time interval (Tables 2, 3). Slight length increases for a given age-group reflected detectable growth.

Both sculpins showed differences in age structure in the three streams (Tables 2, 3). There were eight age-classes of *C. aleuticus* in Lymn Creek but only five in Chef and Waterloo creeks. For *C. asper* there were six age-classes in Lymn and Waterloo creeks but only four in Chef Creek.

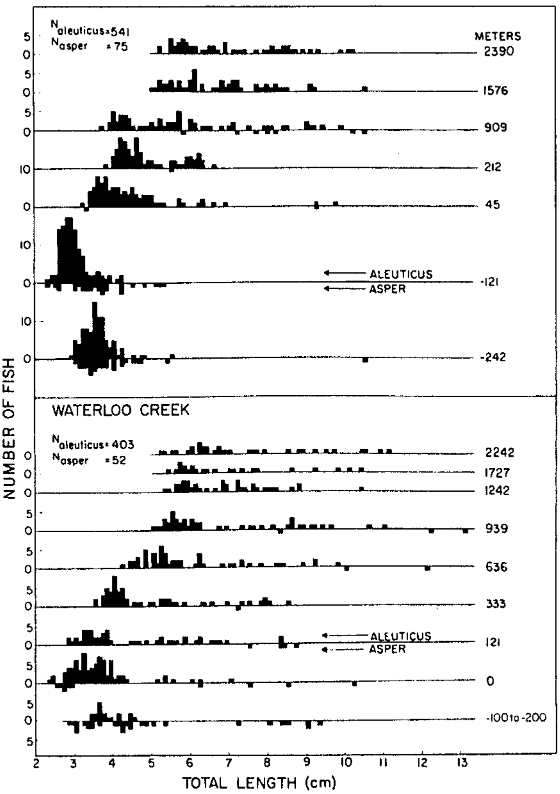

FIGURE 7.—Length-frequency histograms for sculpin populations in Chef and Waterloo creeks from collections made in September and October. Sampling stations are identified as distances upstream or downstream (−) from a high tide mark (0) in meters.

Lymn Creek contained older fish of both species but *C. aleuticus* lived longer than did *C. asper.*

Distribution of Biomass

The autumnal distribution of biomass by stream zone was derived from population estimates and length-weight data for both species of sculpin in Lymn, Waterloo, and Cabin creeks (Table 4). Density of sculpin biomass (grams per square meter) was lowest in the estuaries and increased upstream. *Cottus aleuticus* showed the greatest increase in biomass density with increased distance upstream, particularly when proceeding from the estuary upstream into the lower stream zone. About 69-94% of sculpin biomass in the estuaries was *C. asper*, whereas about 60-100% of sculpin biomass were *C. aleuticus* in the upper zones whose downstream boundaries were marked by the first significant streambed obstruction. Species biomass in the

TABLE 2.—Age distributions of *Cottus aleuticus* in successive 5-mm intervals of total length, sexes combined. Number in parentheses indicates total number of fish when not all fish in the length interval were aged.

Total length (mm)	Lymn Creek																		Chef Creek					Waterloo Creek				
	August								September					October					September-October					October				
	0	I	II	III	IV	V	VI	VII	0	I	II	III	IV	0	I	II	III	IV	0	I	II	III	IV	0	I	II	III	IV
14.5-19.4	(7)								(4)																			
19.5-24.4	12(83)								3(65)					6(24)					(8)					2				
24.5-29.4	5(73)								6(75)					10(154)					3(137)					5				
29.5-34.4	3(50)								10(80)					14(169)					18(132)					13				
34.5-39.4	8(15)								6(40)					3(50)					9(64)	2(13)				17	1			
39.5-44.4	9	8							21	1				9	2				3(6)	22(42)				13	1			
44.5-49.4	3	40							3	2				16	2					39				2	5			
49.5-54.4		37								4				4	9					27					14			
54.5-59.4		25								10					9					13	5				15			
59.5-64.4		6	1							6					12					6	10				15	1		
64.5-69.4			1							2	3				3						9				6	2		
69.5-74.4			8								5				3	3					12	4			3	4		
74.5-79.4			4								1					2					3	3				4	1	
79.5-84.4			6								2					5					1	3				3	1	
84.5-89.4			4	2							1					6						2				3	3	1
89.5-94.4			1	3												3	2					2					3	
94.5-99.4				5													3						1				2	
99.5-104.4				1								3					2										2	
104.5-109.4				4	1							1						1										1
109.5-114.4				1	2								2					1										2
114.5-119.4													1															
119.5-124.4					1								2															
124.5-129.4						1																						
129.5-134.4						1							1															
134.5-139.4						2	1																					
139.5-144.4						1																						
144.5-149.4								1																				
Total fish	240	116	25	16	4	5	1	1	288	25	12	4	6	426	40	19	7	2	347	140	40	14	1	52	60	17	12	4

TABLE 3.—Age distributions of *Cottus asper* in successive 5-mm intervals of total length, sexes combined. Number in parentheses indicates total number of fish when not all fish in the length interval were aged.

Total length (mm)	Lymn Creek															Chef Creek				Waterloo Creek					
	August						September				October					September-October				October					
	0	I	II	III	IV	V	0	I	II	III	0	I	II	III	IV	0	I	II	III	0	I	II	III	IV	V
14.5-19.4	(3)						(4)																		
19.5-24.4	(25)						(16)				1(3)					(2)									
24.5-29.4	3(51)						1(39)				2(19)					1(3)				(8)					
29.5-34.4	6(55)						9(46)				8(30)					8(21)				1(9)					
34.5-39.4	1(41)						18(49)				11(27)					7(17)				(1)					
39.5-44.4	5(33)						33(38)				24					9				7					
44.5-49.4	8(13)	1					26	1			10	1				5				2					
49.5-54.4	1	5					11	4			3	1				4				1	1				
54.5-59.4		8						4				3					1								
59.5-64.4		8						3				4	1								1				
64.5-69.4		11	1					1																	
69.5-74.4		8	7					2				4	4					1			2				
74.5-79.4		2	15					1	5				2					1				2			
79.5-84.4			8	1									5					2				6			
84.5-89.4			2	2									1	1				2				3			
89.5-94.4			5	2					3				4	1					1			2	1		
94.5-99.4			1	1	1				1	1			3	1											
99.5-104.4										2			2						1			1	1		
104.5-109.4				1						1				2					2						
109.5-114.4					2									2											
114.5-119.4										1					1										
119.5-124.4										1													1	1	
124.5-129.4															1										
129.5-134.4					1																			1	
134.5-139.4						1																			
139.5-144.4																									1
Total fish	222	43	39	7	4	1	229	16	9	6	116	13	22	7	2	61	1	6	4	28	4	14	3	2	1

TABLE 4.—The autumnal distribution of sculpin (*Cottus*) biomass in three streams.

Stream	Zone	Sculpin biomass (kg)	Sculpin biomass (g/m²)	*C. aleuticus* (g/m²)	*C. aleuticus* (%)	*C. asper* (g/m²)	*C. asper* (%)
Lymn	Estuary	2.727	0.98	0.31	31.6	0.67	68.8
	Lower	4.345	1.72	0.88	51.2	0.84	48.8
	Upper	4.772	3.38	3.38	100.0	—	—
	Total area	11.844	1.76	1.17	66.3	0.75	39.0
Waterloo	Estuary	0.310	0.69	0.04	5.8	0.65	94.2
	Lower	9.052	3.49	2.95	84.5	0.54	15.5
	Upper	16.454	3.45	3.45	100.0	—	—
	Total area	25.816	3.31	3.09	93.5	0.56	6.5
Cabin	Estuary	0.037	0.33	0.04	12.1	0.29	87.9
	Lower	1.493	4.87	4.42	90.8	0.45	59.2
	Upper	0.508	2.85	1.72	60.4	1.13	39.6
	Total area	2.038	3.41	2.79	81.8	0.62	18.2

TABLE 5.—The autumnal distribution of sculpin (*Cottus*) biomass by age-class in three streams, expressed as a percentage of species biomass.

Stream	0	I	II	III	IV	V	VI	VII
Lymn Creek:								
C. aleuticus	6.7	12.5	10.5	19.6	22.5	17.6	4.4	6.2
C. asper	17.2	14.0	35.2	19.9	10.8	2.7		
Waterloo Creek:								
C. aleuticus	2.9	28.6	20.8	32.3	15.3			
C. asper	4.0	5.4	47.2	24.9	18.5			
Cabin Creek:								
C. aleuticus	14.9	42.5	20.5	17.8	4.2			
C. asper	17.1	15.4	39.6	27.8				

lower stream zone was nearly equal in Lymn Creek but was predominantly *C. aleuticus* (85%) in Cabin and Waterloo creeks.

The two sculpins differed in relative distribution of biomass by age group within their populations (Table 5). Whereas *C. asper* in their third growth season (age II) constituted 35-47% of population biomass, the biomass of *C. aleuticus* populations in Lymn and Waterloo creeks was more evenly distributed in older age groups. The contribution of age I to population biomass of *C. aleuticus* was considerably higher in the two smaller streams than in Lymn Creek and 3-5 times higher than for *C. asper* in these two streams.

Annual Growth, Mortality, and Length-Weight Relations

The annual growth of both sculpins showed a consistent ranking in three streams. Growth was most rapid in Lymn Creek, intermediate in Waterloo Creek, and slowest in Chef Creek (Figure 8) although the growth of *C. asper* in Lymn and Waterloo was not statistically different. Dissimilarities in rate of growth were greatest for *C. aleuticus*, possibly reflecting its greater reliance on the productivity of the freshwater stream than in the case of *C. asper*, which spends considerably more time in the estuary throughout its life history.

C. asper grew more rapidly than did *C. aleuticus*, the age-specific disparity in weight gain increasing with age. Growth of the Lymn Creek

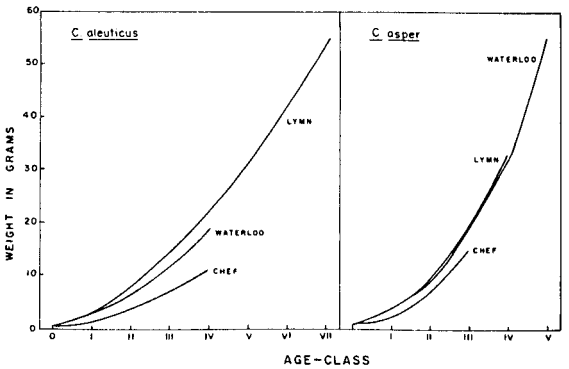

FIGURE 8.—Annual growth rates (weight) of *Cottus aleuticus* and *C. asper* in Lymn, Chef, and Waterloo creeks.

population, which was first sampled in early April, was most rapid during the spring and early summer and nearly completed by mid-August. The largest coastrange sculpin captured was 145 mm in length and 8 yr old while the largest prickly sculpin was 144 mm in length and 6 yr old.

Length-weight linear regressions based on logged data were calculated for both species in the three largest streams (Table 6) and compared by analysis of variance. The length-weight relation was similar for both species in all three streams except for the coastrange sculpin in Chef Creek, which was considerably lighter per unit length than in the other two systems ($F_{2, 2737} = 77.5$). Slow annual growth and a lower slope (b) may reflect poorer feeding conditions or associated population stress during the late summer when the flow in a 500- to 600-m section of this stream becomes intermittent.

Estimates of average annual mortality for both species of sculpins in Lymn, Cabin, and Chef creeks ranged between 58 and 75%, the differences between species and streams depicted in Figure 9 being statistically non-significant. Although similar for both sculpins, mortality in Waterloo Creek was considerably lower than in the other three streams 38-40%. No estimate of annual mortality was attempted for *C. asper* in Chef Creek due to the small population present.

TABLE 6.—Length-weight regression parameters (log $y = a + bx$) for *Cottus aleuticus* and *C. asper* in three streams on Vancouver Island, B.C.

Parameter	*C. aleuticus*			*C. asper*		
	Lymn	Chef	Waterloo	Lymn	Chef	Waterloo
N	1,565	767	397	1,225	73	49
a	−5.312	−5.001	−5.297	−5.268	−5.143	−5.363
b	3.237	3.041	3.224	3.203	3.122	3.259
r	0.993	0.994	0.996	0.992	0.997	0.998
$S_{y \cdot x}$	0.0096	0.0122	0.0136	0.0115	0.0308	0.0268

Despite close agreement to the linear function of the majority of point estimates, some points for young and old age-classes deviated considerably and are taken to indicate poor survival, low recruitment of subyearlings from the estuary in some years, or inadequate sampling. For example, poor survival of age I of *C. asper* is indicated for Lymn, Waterloo, and Cabin creeks (Figure 9). Similarly, age 0 of both species were poorly represented in Waterloo Creek, as were age 0 in Chef Creek, despite intensive sampling in the downstream areas in which they were distributed. In Chef Creek, age IV of *C. aleuticus* was very poorly represented, suggesting either a sudden extensive mortality or inadequate sampling effort in the larger pools upstream where these fish reside.

DISCUSSION

The ecological importance of cottid fishes in the simple fish communities of these coastal streams remains essentially unknown but the present findings appear to be timely in view of the resurging interest in enhancing the natural production of anadromous stream salmonids. Previous

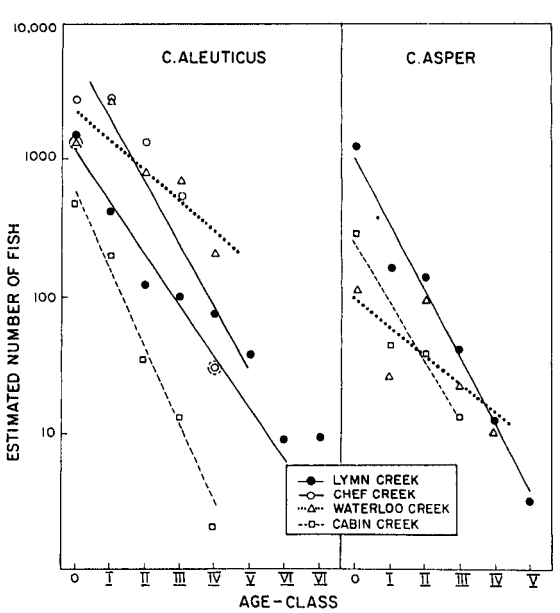

FIGURE 9.—Declining numbers with increasing age within sympatric populations of *Cottus aleuticus* and *C. asper* in four streams. Straight lines describe least-square regressions of best fit.

studies on *C. aleuticus* and *C. asper*, which are widely distributed and commonly abundant in coastal streams from California to Alaska, have emphasized their potentially destructive role as predators on the eggs and fry of salmon and trout (Shapovalov and Taft 1954; Hunter 1959; McLarney 1967). Conversely, it has been generally shown that sculpins in streams of the North Temperate Zone prey incidentally on salmon and trout, but sculpins do share a common source of food—the benthic invertebrate community.

The probable importance of interspecific competition in general, and for food in particular, in such streams where the several species of fishes consume in common a wide variety of food organisms has been readily acknowledged (Hartley 1948; Maitland 1965; Mann and Orr 1969) but continues to defy quantitative analysis. The overlapping summer foods of juvenile coho salmon, cutthroat trout, and coastrange sculpins in Cabin Creek (Table 7) clearly show the possibility of competition for food in the present study streams. Numerically, Ephemeroptera and Diptera were important in all three diets but most important in the coho salmon diet, while Trichoptera were most important in the trout and sculpin diets. The sculpins showed the least varied diet as Ephemeroptera, Diptera, and Trichoptera composed nearly 95% of the food items consumed. Dietary differences can be related to behavioral differences in feeding and habitat response. The sculpins were abundant in all habitats but ate few foods of surface origin, being crepuscular grazers on the benthos. The trout were principally riffle-dwellers and grazed the benthos (both trout and sculpins ate large numbers of Trichoptera larvae) but exploited the invertebrate drift to a lesser extent than did the coho salmon, which preferred the pool and glide habitats of low current velocity. Despite this behavioral diversity, niche differentiation remains poorly developed in the Eltonian sense discussed by Weatherley (1963) who proposed that the niche be defined as "...the nutritional role of the animal in its ecosystem... ."

TABLE 7.—The percentage composition by frequency of occurrence (0) and number (*N*) of the midsummer (June-July) foods eaten by juvenile coho salmon, cutthroat trout, and coastrange sculpins in Cabin Creek. Based on 30 fish of each species collected simultaneously.

	Coho		Trout		Sculpin	
Food category	%0	%*N*	%0	%*N*	%0	%*N*
Oligochaeta	10.0	1.2	—	—	—	—
Diplopoda	—	—	40.0	6.2	—	—
Collembola	23.3	4.1	—	—	—	—
Ephemeroptera	46.7	17.4	30.0	9.2	60.0	30.3
Plecoptera	16.7	4.1	20.0	3.1	3.3	<1
Hemiptera	20.0	3.3	10.0	1.5	—	—
Coleoptera						
Adults	30.0	6.2	30.0	4.6	3.3	<1
Larvae	13.3	1.7	—	—	—	—
Trichoptera	10.0	2.1	40.0	26.2	56.6	44.9
Lepidoptera[1]	3.3	<1	50.0	9.2	6.7	2.8
Diptera						
Adults	70.0	28.5	20.0	7.7	—	—
Larvae	26.7	20.7	43.4	15.4	33.3	18.3
Hymenoptera[1]	10.0	1.2	20.0	3.1	—	—
Araneida	36.7	6.6	10.0	1.5	—	—
Acarina	6.7	1.7	23.3	10.8	3.3	1.8
Gasteropoda	3.3	<1	—	—	—	—

[1]Refers to adult stage, all categories of Insecta are larval stages unless noted otherwise.

Recent experiments have clearly illustrated that populations of juvenile coho salmon in these streams are limited by their food supply during the summer months (Mason 1974b, 1974c). Rates of growth, survival and emigration were amenable to manipulation by varying population density and food availability. Thus, in that young coho salmon share a common food supply with both trout and sculpins, the likelihood of food competition is strongly suspected.

Since direct documentation of competition among stream fishes in natural environments continues to elude us, the inferential definition of competition proposed by Maitland (1965) appears to have greater utility than the modus operandi definition of Larkin (1956), "...the demand, typically at the same time, of more than one organism, for the same resources of the environment in excess of immediate supply." Maitland (1965) suggested that competition occurs " ... when the presence of more than one species causes the average total biomass (standing crop) of one of them to be less than it would be if that species were existing alone—species which are directly parasitic or predatory on one another being excepted."

Fish biomass in small coastal streams of Vancouver Island usually ranges between 7 and 10 g/m^2 in midsummer (unpubl. data). Of this 3-6 g/m^2 (50-80%) consists of sculpins (*C. asper* and *C. aleuticus*) in the first several kilometers above the estuarine zone. Studies by Brocksen et al. (1968) have shown that, within the carrying capacity of laboratory streams producing natural drift foods, production of cutthroat trout was determined by the biomass ratio of trout and sculpin, *C. perplexus*, at time of stocking, whereas sculpin production remained independent of trout biomass. These results were obtained over a

range of species biomass levels commensurate with those encountered in nature and suggest that the availability of drift foods for the trout was determined by the intensity of grazing by sculpins on the stream benthos.

From the present study, the restricted ability of both species of sculpins to surmount obstacles in the streambed, coupled with the life history features of planktonic young and downstream spawning migrations, lend themselves to the potential development of a management strategy for enhancing the production of salmonid smolts to the sea. If the findings of Brocksen et al. (1968) can be corroborated in stream simulator systems more closely approximating the natural environment, studies on the locomotory ability of these sculpins relative to the performance of their communal salmonids could provide the design criteria for physical barriers to be located on test streams at suitable sites above the influence of high tide.

LITERATURE CITED

BROCKSEN, R. W., G. E. DAVIS, AND C. E. WARREN.
1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. J. Wildl. Manage. 32:51-75.

HARTLEY, P. H. T.
1948. Food and feeding relationships in a community of fresh-water fishes. J. Anim. Ecol. 17:1-14.

HUNTER, J. G.
1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835-886.

KREJSA, R. J.
1967. The systematics of the prickly sculpin, *Cottus asper* Richardson, a polytypic species. Part II. Studies on the life history, with especial reference to migration. Pac. Sci. 21:414-422.

LARKIN, P. A.
1956. Interspecific competition and population control in freshwater fish. J. Fish. Res. Board Can. 13:327-342.

MAITLAND, P. S.
1965. The feeding relationships of salmon, trout, minnows, stone loach and three-spined sticklebacks in the River Endrick, Scotland. J. Anim. Ecol. 34:109-133.

MANN, R. H. K., AND D. R. O. ORR.
1969. A preliminary study of the feeding relationships of fish in a hard-water and a soft-water stream in southern England. J. Fish. Biol. 1:31-44.

MASON, J. C.
1974a. Movements of fish populations in Lymn Creek, Vancouver Island: A summary from weir operations during 1971 and 1972, including comments on species life histories. [Can.] Dep. Environ., Fish. Mar. Serv. Tech. Rep. 483, 35 p.
1974b. A first appraisal of the response of juvenile coho salmon (*O. kisutch*) to supplemental feeding in an experimental rearing stream. [Can.] Dep. Environ., Fish. Mar. Serv. Tech. Rep. 469, 21 p.
1974c. A further appraisal of the response to supplemental feeding of juvenile coho (*O. kisutch*) in an experimental stream. [Can.] Dep. Environ., Fish. Mar. Serv. Tech. Rep. 470, 26 p.

MCALLISTER, D. E., AND C. C. LINDSEY.
1960. Systematics of the freshwater sculpins (*Cottus*) of British Columbia. Natl. Mus. Can. Contrib. Zool., Bull. 172:66-89.

MCLARNEY, W. O.
1967. Intra-stream movement and food habits of a population of coastrange sculpins, *Cottus aleuticus*, in relation to a spawning run of the pink salmon, *Oncorhynchus gorbuscha*. Ph.D. Thesis, Univ. Michigan, Ann Arbor, 154 p.
1968. Spawning habits and morphological variation in the coastrange sculpin, *Cottus aleuticus*, and the prickly sculpin, *Cottus asper*. Trans. Am. Fish. Soc. 97:46-48.

SHAPOVALOV, L., AND A. C. TAFT.
1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*). Calif. Dep. Fish Game, Fish Bull. 98:1-375.

WEATHERLEY, A. H.
1963. Notions of niche and competition among animals, with special reference to freshwater fish. Nature (Lond.) 197:14-17.

REVIEW OF THE DEEP-SEA FISH GENUS *SCOPELENGYS* (NEOSCOPELIDAE) WITH A DESCRIPTION OF A NEW SPECIES, *SCOPELENGYS CLARKEI*, FROM THE CENTRAL PACIFIC

JOHN L. BUTLER[1] AND ELBERT H. AHLSTROM[2]

ABSTRACT

Scopelengys has been known previously from a few widely scattered collections. Recent collections by the Scripps Institution of Oceanography in the Pacific, the RV *Walther Herwig* in the Atlantic, and the International Indian Ocean Expedition have made possible a critical study of this genus. No significant differences were found in either morphometric characters or meristic counts between specimens of *S. tristis* Alcock from the eastern North Pacific (lat. 16° to 33°N, long. 117° to 126°W) and those from the eastern South Pacific (lat. 5° to 16°S, long. 77° to 90°W). When Pacific Ocean specimens were compared with those from the Atlantic and Indian oceans, no significant differences were found in morphometric characters, and although differences in average meristic counts were somewhat larger between oceans than among Pacific specimens, such differences exceed one for only one meristic character (gill rakers), and the ranges for all counts from all oceans almost completely overlapped.

Scopelengys clarkei is described from the central North Pacific. It differs from *S. tristis* mainly in pectoral ray count (2.5 average difference), average counts of vertebrae (3.3 average difference), deeper caudal peduncle, narrower maxillary, and in a differently pigmented larva.

In 1890, Alcock described a new genus and species, *Scopelengys tristis*, from a single denuded specimen collected in the Arabian Sea. Although there was no evidence of photophores, Alcock placed his new genus in the family Scopelidae (=Myctophidae) allowing that the "exact position among the Scopelidae cannot be accurately defined at present." Garman (1899) described *S. dispar* from two specimens collected in the Gulf of Panama. Garman distinguished *S. dispar* from *S. tristis* by its lower dorsal- and anal-fin ray counts. *Scopelengys dispar* was considered a junior synonym by Parr (1928), Bolin (1939), and Norman (1939). Until 1963, *Scopelengys* was known only from the Indian and Pacific oceans. Its discovery in the Caribbean Sea by Mead (1963) resulted in the description of a third species, *S. whoi* Mead.

A recent survey of mid-water fishes conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) provided us with specimens which indicated that two species of *Scopelengys* were present in the Pacific Ocean. Additional specimens made available to us by Thomas A. Clarke of the Hawaiian Institute of Marine Biology (see in this regard Clarke 1973), confirmed that the second form was an undescribed species. Study of *Scopelengys* from the Atlantic, Pacific, and Indian oceans indicates that *S. dispar* and *S. whoi* Mead are synonyms of *S. tristis* Alcock.

METHODS AND MATERIALS

Measurements were made following Hubbs and Lagler (1958). Measurements are given in percent of standard length (SL), unless indicated otherwise. Only lath-shaped gill rakers on the first gill arch are included in gill raker counts. Vertebral counts were determined from radiographs; the urostyle was included as one vertebra.

Morphometric and meristic data were obtained from 211 specimens from the Atlantic, Pacific, and Indian oceans. Subsamples equal to the smallest N (32 in the Atlantic) were randomly taken from the Indian Ocean, the eastern North Pacific between lat. 16° and 33°N and long. 117° to 126°W, and the eastern tropical Pacific between lat. 5° and 16°S and long. 77° to 90°W. Morphometric data were compared by analysis of covariance. Meristic data were compared by Tukey's multiple comparison procedure at the 5% level (Rothschild 1963).

Material was examined from the following collections: Scripps Institution of Oceanography

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(SIO); University of Southern California (USC); Institut für Seefischerei, Hamburg (ISH); Museum of Comparative Zoology (MCZ); U.S. National Museum (USNM); International Indian Ocean Expedition (IIOE); and Field Museum of Natural History (FMNH).

GENUS *SCOPELENGYS* ALCOCK 1890

Type-species *Scopelengys tristis* Alcock, by monotypy.

Description.—Head and body laterally compressed, eyes small, mouth large. Premaxillary, dentary, and palatines with bands of villiform teeth. Teeth absent at symphysis of upper and lower jaw. Vomer indented at head with teeth in two patches. Teeth on basihyal and on gill rakers. Anterior gill rakers reduced to toothed knobs. Maxillary extending past eye, expanded posteriorly. Supramaxillary present. Head and body covered with large deciduous, cycloid scales. Pectoral fins lateral, extending beyond bases of pelvic fins. Pelvic fins abdominal. Origin of dorsal fin about over base of pelvic fin. Anal fin completely behind dorsal. Base of adipose fin over posterior half of anal fin. No photophores. No swim bladder in adults.

D 11-13; A 12-14; P 12-17; V 8; Br 8; C principal 19 (1 + 17 + 1); procurrent C 6-9 dorsal and 7-8 ventral, hypurals (including parhypural) 4 + 3; epurals 3; uroneurals 2. Urostyle with two centra. As in all myctophiform fishes retaining two ural centra (personal observation reenforced by Rosen and Patterson 1969), the anterior ural centrum (labelled $PU_1 + U_1$ in Rosen and Patterson) supports both the parhypural and the 2 inferior hypurals, whereas the posterior ural centrum (U_2 in Rosen and Patterson) is associated exclusively with the 4 superior hypurals.

Scopelengys tristis Alcock

Scopelengys tristis Alcock 1890:302.
Scopelengys dispar Garman 1899:254, plate 54, fig. 2-2d.
Scopelengys lugubris Garman 1899:400, (synonym *Scopelengys dispar).*
Scopelengys whoi Mead 1963:255, fig. 1.

Description of Adult

Body moderately slender, maximum body depth at nape, tapering to a narrow caudal peduncle (Figures 1A, 2A); body depth at dorsal origin 11.7-19.8 (15.4); least depth at caudal peduncle 5.6-8.3 (6.8). Dorsal profile of head slightly concave; head length 24.4-33.9 (29.4); head depth 16.7-25.5 (20.2); eye small, orbit 3.1-4.2 (3.5); snout 7.5-10.1 (8.8). Width of maxillary as percentage of its length 29.9-36.7 (32.2). Snout to: dorsal fin origin 36.1-47.0 (41.9); anal fin origin 56.4-72.6 (66.4); ventral fin origin 34.7-48.0 (41.8).

Meristic Data.—D.11-13 (11.5); A 12-14 (13.0); P 14-17 (15.4); vertebrae 29-32 (30.8); total gill rakers 7-11 (8.5).

Larvae

Twenty-five specimens 3.5-10.3 mm were available from the eastern Pacific. Measurements and counts were given for two eastern Pacific (EASTROPAC) specimens (6.2 and 6.4 mm SL) by Okiyama (1974) and the smaller specimen illustrated. The larvae have a small round eye without choroid tissue, a snout as long proportionately as in adults, a gut terminating just forward of the anal fin, and a gas bladder, best seen on late preflection and flexion specimens, becoming obscured by overlying musculature in larger postflexion specimens.

Rays form early in the pectoral fins; a 3.5-mm specimen has large pectorals extending posteriad to the anus; caudal fin forms and notochord flexion occurs between ca. 5 and 7 mm; dorsal and anal fins form during flexion; pelvic buds appear between 6.5 and 7.0 mm; fin formation, including procurrent caudal rays, complete by about 10.0 mm. Pigmentation is scanty; pigment develops on dorsal margin of peritoneal cavity, spreading laterally on preflexion and flexion stage specimens but becoming obscured on postflexion larvae; preflexion larvae have a series of 6 or 7 small, inconspicuous spots along the ventral margin of the tail which are later obscured by the anal fin formation and lacking on late postflexion larvae; head pigment, best developed on postflexion specimens, consists of a striking horizontal bar extending from snout to eye and continuing behind the eye onto the operculum (Figure 3A).

Distribution

Records are from the tropical Atlantic, Pacific, and Indian oceans (Figure 4). The range is expanded poleward in the eastern part of the Pacific

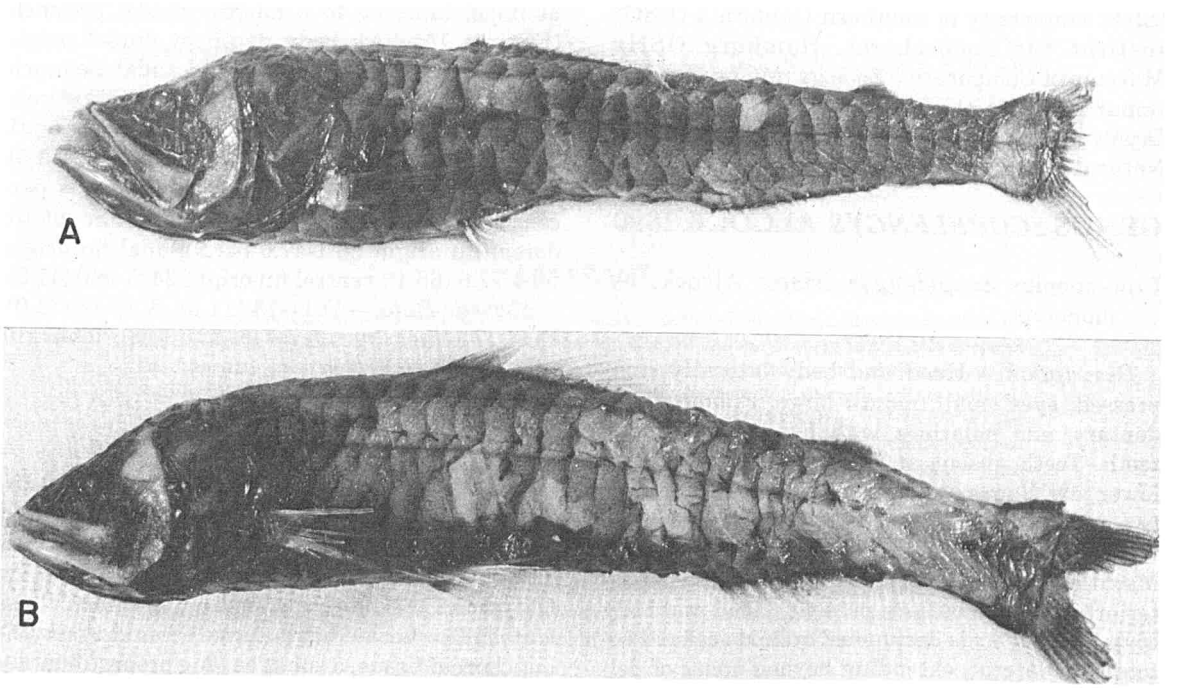

FIGURE 1.—A: *Scopelengys tristis*, 126 mm, *Velero IV*, cruise 1238, stn. 18762/10. B: *S. clarkei*, 176 mm. SIO 73-160, holotype.

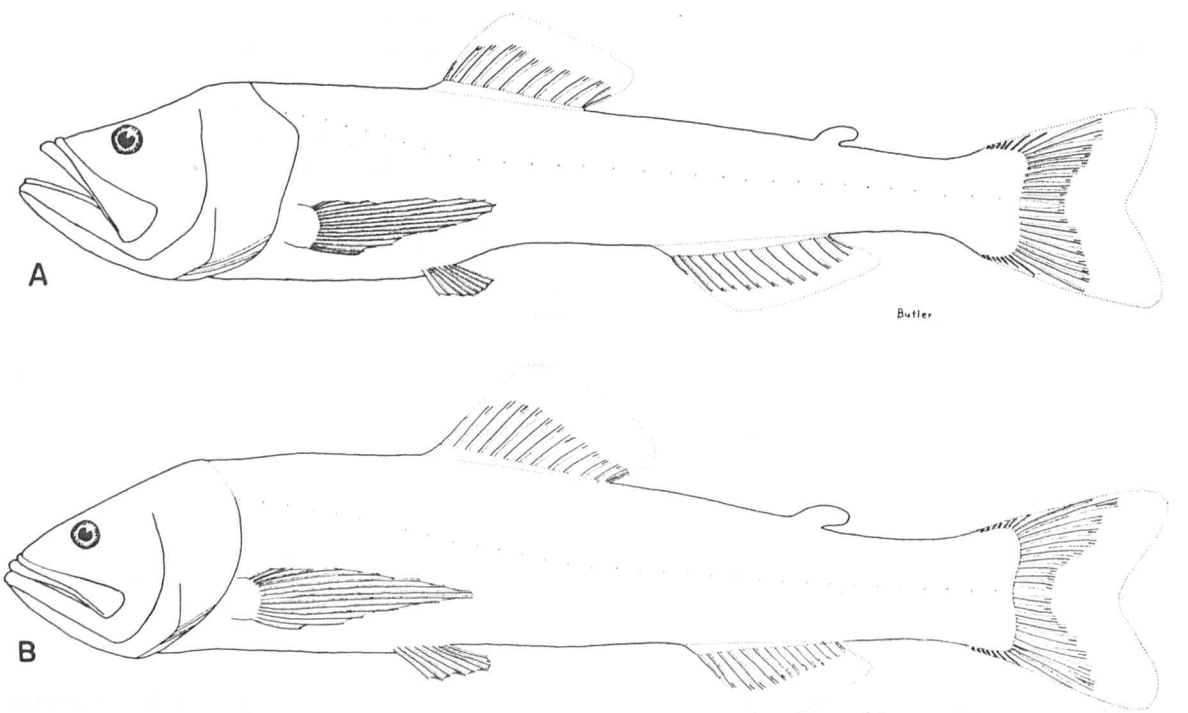

FIGURE 2.—A: *Scopelengys tristis*, 126 mm, *Velero IV*, cruise 1238, stn. 18762/10. B: *S. clarkei*, 176 mm. SIO 73-160, holotype.

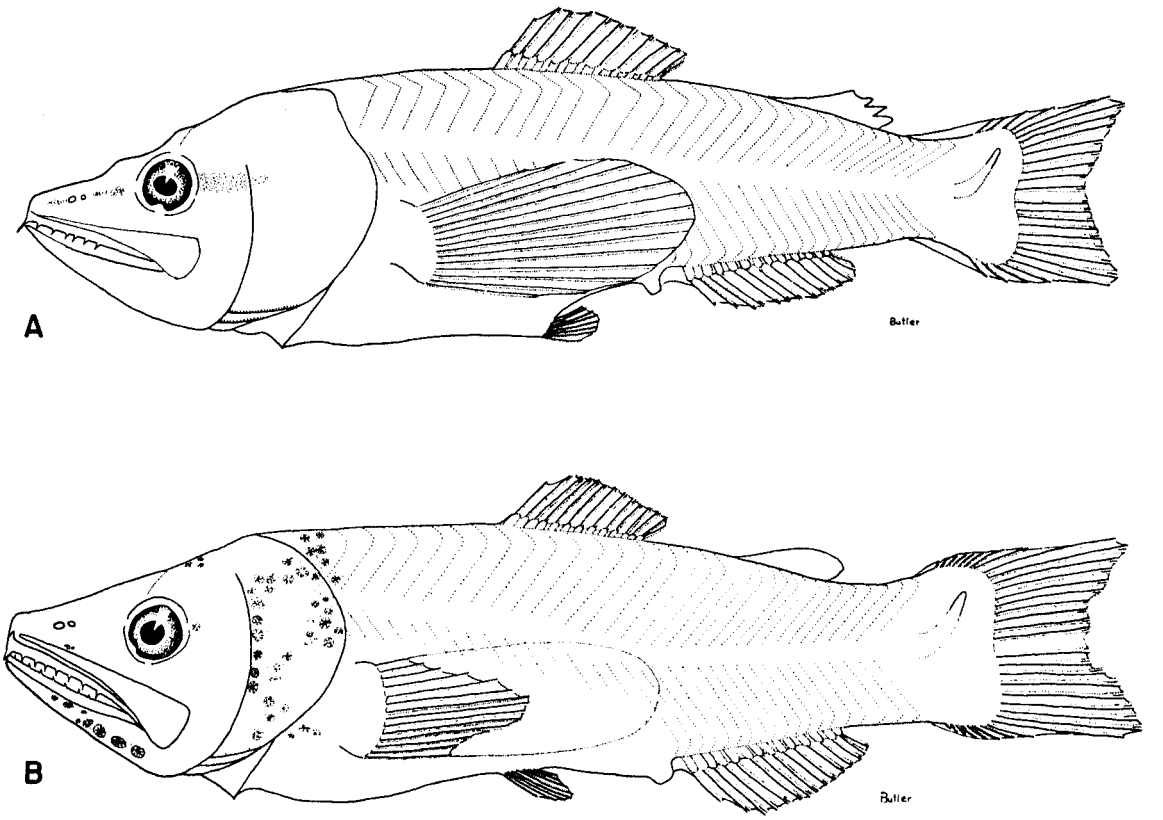

FIGURE 3.—A: *Scopelengys tristis*, 13.9 mm, from the western Indian Ocean. B: *S. clarkei*, 15.4 mm, from off Hawaii.

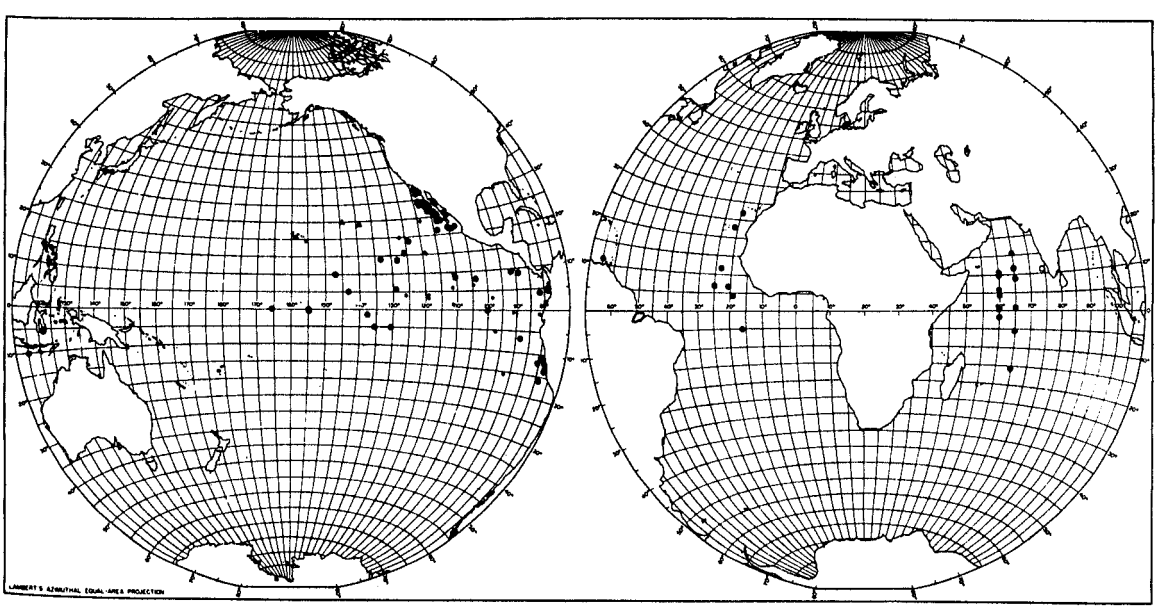

FIGURE 4.—Distribution of *Scopelengys tristis* (circles) and *S. clarkei* (triangles). Small symbols indicate larvae.

and Atlantic oceans and is narrowed along the equator to the west. In the western part of the Pacific and Atlantic, the species appears to be rare. Records of larvae from the Indian Ocean were presented by Nellen (1973).

Geographic Variation

Most of the specimens studied from each area were in poor condition, which added to the variability of body proportions (Table 1). No significant difference was found in any morphometric character between regions. Meristic characters of 32 specimens each from four areas are presented in Table 2. Samples from the two eastern Pacific areas showed no significant differences between means of any meristic character. Indian Ocean specimens differed from Pacific material in mean vertebral counts (30.4 vs. 30.9), pectoral-fin ray counts (15.2 vs. 15.7), and in gill raker counts (9.1 vs. 7.9). Atlantic material differed from Pacific material in dorsal-fin ray counts (12.0 vs. 11.4), in anal-fin ray counts (13.4 vs. 12.8), in gill raker counts (9.2 vs. 7.9), and in pectoral-fin ray counts (15.0 vs. 15.7). Atlantic material differed from Indian Ocean material in dorsal-fin ray counts (12.0 vs. 11.1), anal-fin ray counts (13.4 vs. 12.9), and vertebral counts (31.1 vs. 30.4). Although these differences are small, they are as marked between Indian and Atlantic ocean specimens as be-

TABLE 1.—Comparison of morphometric characters of *Scopelengys tristis* from four geographic areas (N = 32 for each area).

Character	Eastern North Pacific		Eastern tropical Pacific		Indian Ocean		Atlantic Ocean	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Standard length (mm)	124.0	73.8-154.3	130.2	74.5-172.0	104.6	28.8-185.9	133.1	69.5-185.8
Head length	30.9	28.7- 33.9	28.5	28.2- 33.2	30.5	27.8- 33.5	27.6	24.4- 32.2
Head depth	20.2	18.6- 25.5	20.0	16.7- 22.5	20.9	17.2- 24.6	19.6	17.5- 21.7
Snout to origin of dorsal fin	42.7	39.6- 45.5	42.5	39.5- 46.2	41.9	36.1- 47.0	40.6	37.1- 43.6
Snout to origin of pelvic fin	41.7	39.4- 45.3	42.8	39.4- 48.0	41.2	34.7- 46.1	41.6	37.8- 46.9
Snout to origin of anal fin	66.3	63.0- 69.5	67.5	62.5- 72.1	65.2	56.4- 71.2	66.6	61.3- 72.6
Least depth of caudal peduncle	6.8	5.7- 8.1	7.0	6.1- 7.9	6.7	5.6- 8.3	6.9	5.9- 8.0
Body depth at origin of dorsal fin	16.0	13.3- 19.4	15.6	12.6- 19.3	14.5	11.7- 17.2	15.7	12.6- 19.8

TABLE 2.—Meristic data for *Scopelengys tristis* from the eastern North Pacific, eastern tropical Pacific, the Indian Ocean, and the Atlantic Ocean.

Meristic character / Area	Numbers of character and frequency										N	Mean	Overall mean
Dorsal rays	10	11	12	13									
Eastern North Pacific		18	14								32	11.44	
Eastern tropical Pacific		21	11								32	11.34	
Indian Ocean		28	4								32	11.12	
Atlantic Ocean		2	29	1							32	11.97	11.47
Anal rays	11	12	13	14									
Eastern North Pacific		10	20	2							32	12.75	
Eastern tropical Pacific		8	22	2							32	12.81	
Indian Ocean		5	24	3							32	12.94	
Atlantic Ocean			19	13							32	13.41	12.98
Pectoral rays	14	15	16	17									
Eastern North Pacific		33	24	7							64	15.59	
Eastern tropical Pacific		20	32	12							64	15.88	
Indian Ocean	2	48	14								64	15.19	
Atlantic Ocean		62	2								64	15.03	15.42
Vertebrae	29	30	31	32									
Eastern North Pacific		5	28								32	30.88	
Eastern tropical Pacific		3	25	4							32	31.03	
Indian Ocean	1	20	9	2							32	30.38	
Atlantic Ocean	1	3	21	7							32	31.06	30.84
Gill rakers	7	8	9	10	11								
Eastern North Pacific	10	52	1								63	7.86	
Eastern tropical Pacific	17	39	4	3							63	7.89	
Indian Ocean	1	4	49	7	2						63	9.08	
Atlantic Ocean		2	47	12	2						63	9.22	8.51

tween specimens from these areas and from the Pacific. Because there is no clinal pattern in the variation and because of extensive overlap in all counts, no taxonomic importance was placed on the small meristic differences.

Garman distinguished *S. dispar* from *S. tristis* by the lower dorsal and anal-fin ray counts: D 11 vs. 12 and A 12-11 vs. 13 (Garman 1899). The types of *S. dispar* are in poor condition but the anal fins appear to have 12 or 13 rays (Robert Schoknecht pers. commun.). The counts of *S. dispar* are within the range of *S. tristis*. *Scopelengys dispar* has been correctly considered a junior synonym by Parr (1928), Bolin (1939), and Norman (1939). *Scopelengys lugubris* Garman 1899:400, the specific name regarded as a *lapsus calami* by Bolin (1939), is a synonym of *S. dispar*, hence of *S. tristis*. *Scopelengys whoi* was described from the Carribbean Sea (Mead 1963). The diagnosis was based on a shorter head, higher number of anal fin rays (14 vs. 12-13), and the insertion of the pelvic fin in advance of the origin of the dorsal. According to Mead (1963), however, the head length is ". . .a poor measurement because of the condition of the opercular flap." The anal-fin ray count is within the range of *S. tristis* (Table 3). The insertion of the pelvic fin is a variable character in *S. tristis*. In most specimens the fin is inserted below the origin of the dorsal fin but insertion in advance of the dorsal is not uncommon. Based on this study, we conclude that *S. whoi* is a junior synonym of *S. tristis*.

Study Material

PACIFIC OCEAN ADULTS.—SIO 51-186 1 (134); SIO 64-21 6(78-148); SIO 65-243 2(122-134); SIO 64-997 1(122); SIO 65-244 1(75); SIO 55-229 9(31-113); SIO 65-206 1(92); SIO 60-212 4(20-133); SIO 52-309 2(36-56); SIO 73-170 1(49); SIO 73-171 1(30); SIO 55-265 1(54); SIO 65-620 1(139); SIO 65-606 4(92-151); SIO 65-220 5(14-138); SIO 65-611 17(85-176); SIO 51-84 3(74-123); SIO 69-497 6(92-170); SIO 72-186 8(73-179); SIO 65-215 1(121); SIO 54-124 1(147); SIO 52-367 1(145); SIO 60-232 1(168); SIO 65-213 3(88-158); SIO 60-219 2(42-170); SIO 55-246 4(65-140); SIO 68-579 1(140); SIO 53-235 1(154); SIO 51-146 3(127-144); SIO 65-603 17(62-160); SIO 55-244 2(159-167); SIO 72-195 17(88-175); SIO 65-608 14(43-200); SIO 72-193 2(106-169); SIO 72-192 18(10.2-177); SIO 60-216 2(42-76); SIO 60-218 1(48); SIO 66-355 1(135); SIO 69-19 1(24); SIO 72-182 1(90); SIO 66-407 1(42); SIO 64-24 1(116); SIO 60-234 1(69); SIO 64-13 1(113); SIO 52-409 1(65); SIO 59-202 1(83); SIO 52-90 1(113); SIO 64-15 1(85); SIO 63-444 1(103); SIO 60-243 4(18-44); SIO 68-534 1(28); SIO 65-443 1(142); SIO 68-104 1(97); SIO 60-209 1(78); SIO 52-363 2(56-115); SIO 64-28 3(95-144); SIO 57-43 1(126); SIO 65-237 1(128); SIO 61-32 2(105-106); SIO 63-42 1(109); SIO 66-30 1(113); SIO 51-45 1(132); SIO 60-215 7(19-94); SIO 52-32 1(150); SIO 50-270 2(110-115); SIO 51-77 1(110); SIO 51-189 1(120); SIO 54-82 1(107); SIO 54-102 2(116-147); USC *Velero IV*, cruise 1238, stn. 18762/10; MCZ 41695 2(121-141); USNM 135842 1 (X-ray); MCZ 28058 1 (X-ray) (lectotype *S. dispar* Garman).

PACIFIC OCEAN LARVAE[3].—Larvae taken at 17 EASTROPAC stations and 2 CalCOFI stations as follows: EASTROPAC stations 11.282 1(4.8); 13.105 1(5.5); 13.172 2(6.4, 6.8); 20.018 1(5.5); 30.114 2(4.0, 4.5); 45.032 1(8.1); 45.073 1(6.0); 45.078 1(10.3); 45.293 1(6.6); 45.316 1(6.9); 46.034 1(6.2); 46.096 2(6.7, 6.9); 47.001 1(5.2); 47.005 4(3.5-4.3); 47.035 1(7.0); 47.040 1(5.3); 47.065 1(9.2); CalCOFI 7205-20.127 1(5.0); 4907-112 1(9.1).

ATLANTIC OCEAN.—MCZ 41638 1(X-ray)

[3]Station data in EASTROPAC Information Paper 6 and Ahlstrom (1972).

TABLE 3.—Means and differences among means of meristic counts of *Scopelengys tristis* from four areas (eastern North Pacific, ENP; eastern tropical Pacific, ETP; Indian Ocean, IO; and Atlantic Ocean, AO) and *S. clarkei*.

Meristic character	*S. tristis* Range	Overall mean	Mean ENP	Mean ETP	Mean IO	Mean AO	Greatest differences among regions	*S. clarkei* Range	*S. clarkei* Mean	Difference in counts between *S. clarkei* and *S. tristis* Average difference	Least difference
Dorsal rays	11-13	11.47	11.4	11.3	11.1	12.0	0.9	13	13.0	1.5	1.0-AO
Anal rays	12-14	12.98	12.8	12.8	12.9	13.4	0.6	14	14.0	1.0	0.6-AO
Pectoral rays	14-17	15.42	15.6	15.9	15.2	15.0	0.9	12-13	12.9	2.5	2.1-AO
Vertebrae	29-32	30.84	30.9	31.0	30.4	31.1	0.7	34-35	34.1	3.3	3.0-AO
Gill raker	7-11	8.51	7.9	7.9	9.1	9.2	1.3	7-10	8.2	0.3	0.3-EP

(type *S. whoi* Mead); USNM 20678, 5(152-164), eastern tropical Atlantic, lat. 07°32′N, long. 20°54′W, 1813-2125, 12 April 1971, 1,300 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 623/68, 7(73-162), eastern tropical Atlantic, lat. 12°07′N, long. 23°08′W, 30 January 1968, 2,000 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 2095/71, 1(167), eastern tropical Atlantic, lat. 05°30′S, long. 16°28′W, 9 April 1971, 1,950 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 2447/71, 12(86-160), eastern tropical Atlantic, lat. 04°38′N, long. 19°21′W, 13 April 1971, 756 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 3099/71, 5(132-160), eastern tropical Atlantic, lat. 07°32′N, long. 20°54′W, 14 April 1971, 1,300 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 2942/71, 2(134-155), eastern tropical Atlantic, lat. 23°47′N, long. 20°59′W, 19 April 1971, 2,100 m, 1,600-mesh Engels trawl, RV *Walther Herwig.*

INDIAN OCEAN[4].—IIOE 7001 *Anton Bruun* III, 16 (25-94); IIOE 7004 *Anton Bruun* III, 7 (32-120); IIOE 7012 *Anton Bruun* III, 2 (23-25); IIOE 7022 *Anton Bruun* III, 1 (113); IIOE 7027 *Anton Bruun* III, 1 (138); IIOE 7037 *Anton Bruun* III, 2 (40-87); IIOE 7046 *Anton Bruun* III, 3 (66-179); IIOE 7143 *Anton Bruun* VI, 1 (131); IIOE 7147 *Anton Bruun* VI, 28 (28-142); IIOE 7153 *Anton Bruun* VI, 4 (42-161); IIOE 7154 *Anton Bruun* VI, 12 (48-114); IIOE 7163 *Anton Bruun* VI, 12 (28-152); IIOE 7165 *Anton Bruun* VI, 3 (22-27); IIOE 7206 *Anton Bruun* VI, 1 (27); IIOE 7277 *Anton Bruun* VI, 2 (40-87).

Scopelengys clarkei n.sp.

Holotype

SIO 73-160, female (176 mm), central Pacific, lat. 29°56.0′N, long. 144°56.6′W, 0224-0556 h; 14 February 1973, 10-foot IKMT, 0-1,000 m, RV *Alexander Agassiz.*

Paratypes

USNM 210707, male (160 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 1204-1637 h; 15 September 1970, 10-foot IKMT, 0-1,000 m, RV *El Pescadero I*; USNM 210706, male (156 mm), central Pacific, lat. 24°N, long. 139°W, 0049-0149 h; 29 November 1972, 50-foot Universal trawl, 0-494 m, RV *David Starr Jordan;* FMNH 76366, female (154 mm), central Pacific, lat. 22°N, long. 158°W, 1240-1645 h; 13 November 1969, 10-foot IKMT, 0-800 m.

Other Materials Studied

SIO 51-76, female (109 mm), southeast of Guadalupe Island, 17 March 1951, 10-foot IKMT, 0-549 m; FMNH 76367, juvenile (65 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 0421-0600 h; 27 February 1971, ⅔ Cobb trawl, 0-150 m, RV *Townsend Cromwell;* FMNH 76368, juvenile (42 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 2236-0105 h; 16-17 November 1969, 10-foot IKMT, 0-250 m, RV *Teritu*; T. Clarke, 71-3-9, larva (15 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 1252-1645 h; 2 March 1971, 10-foot IKMT, 800-900 m, RV *El Pescadero I,* retained at the Southwest Fisheries Center.

Adult Morphology

Body proportions of the holotype are given first, followed, in parentheses, by range of values for holotype and three paratypes. Body slender; greatest body depth at origin of dorsal fin, 19.0 (18.4-19.0), tapering to a moderately deep caudal peduncle (Figures 1B, 2B), less than three in length of head, 9.4 (9.4-10.2). Head slightly concave in dorsal profile, head length 25.4 (24.5-26.4); head depth 17.6 (16.7-17.9); eye small, orbit 3.0 (2.9-3.6); interorbital width 8.7 (7.6-8.7); snout about one-third of head length, 8.3 (7.7-8.8); length of maxillary 11.3 (11.3-12.6), greatest width of maxillary 3.1 (2.8-3.6). Snout to: dorsal fin origin 43.5 (39.0-43.5); anal fin origin 68.6 (65.1-69.6); pelvic fin origin 40.2 (40.2-43.4). Length of dorsal fin base 17.3 (17.0-19.4); length of anal fin base 16.0 (16.0-17.9). Color dark brown, preserved in alcohol.

Meristic Data

Counts are based on all seven specimens. D 13 (7); A 14 (6), ? (1); P 13/13 (6), 13/12 (1); V 8/8 (7); principal C 10 + 9 (7), procurrent C 7-8/6-9; branchiostegal rays 8/8 (7); vertebrae 15 + 19 = 34 (6), 15 + 20 = 35 (1); gill rakers 1-2 + (6-8) = 7-10 (mean 8.2).

[4]Station data in Nafpaktitis and Nafpaktitis (1969).

Larvae

A single specimen was available, 15.4 mm SL (Figure 3B). Body shape similar to that of adults but with a relatively larger head—length 35.7 and depth 25.0; eye 5.5; snout 12.8; body depth 23.5; least depth of caudal peduncle, 14.6. Fin origins farther back on body than in adults. Snout to: dorsal fin origin 50.0; anal fin origin 72.8; pelvic base 53.6. Pigment confined to head and nape, extensively developed on the operculum and lower jaw; a small pigment patch on upper jaw behind eye; several melanophores on mid-brain; body pigment confined to nape and to a patch anterior to pectoral base.

Name

This species from the central North Pacific is named in honor of Dr. Thomas A. Clarke of the Hawaii Institute of Marine Biology.

COMPARISON OF *SCOPELENGYS CLARKEI* AND *SCOPELENGYS TRISTIS*

Scopelengys clarkei differs from *S. tristis* in meristic counts, in some morphometric characters, and in larval pigmentation.

For differences in meristic characters, refer to Table 3. Most marked differences are in average number of vertebrae—34.1 (*S. clarkei*) vs. 30.8 =3.3; average pectoral-fin ray count—12.9 (*S. clarkei*) vs. 15.4 =2.5; and average dorsal-fin ray count—13.0 vs. 11.5 =1.5. As regards morphometric characters, *S. clarkei* has a deeper caudal peduncle, a narrower maxillary, and a more fusiform body. Several distinctive adult characters also can be recognized in larger larvae of the two species, i.e., differences in meristic characters and depth of caudal peduncle. The most striking differences between larvae of the two species are found in the head pigment which is restricted to an eye-bar in *S. tristis,* as compared with the scattered pigment on the operculum, lower jaw, etc. of *S. clarkei.*

The two species are similar in general body shape, head size, eye size, length of snout, and position of fins on the body. *Scopelengys clarkei* has its greatest body depth at the dorsal origin, whereas *S. tristis* has its greatest body depth at the nape.

When an analysis of covariance was performed on the morphometric characters of 7 *S. clarkei* and 32 *S. tristis* from the eastern North Pacific, eastern tropical Pacific, Indian, and Atlantic oceans, only the least depth of caudal peduncle

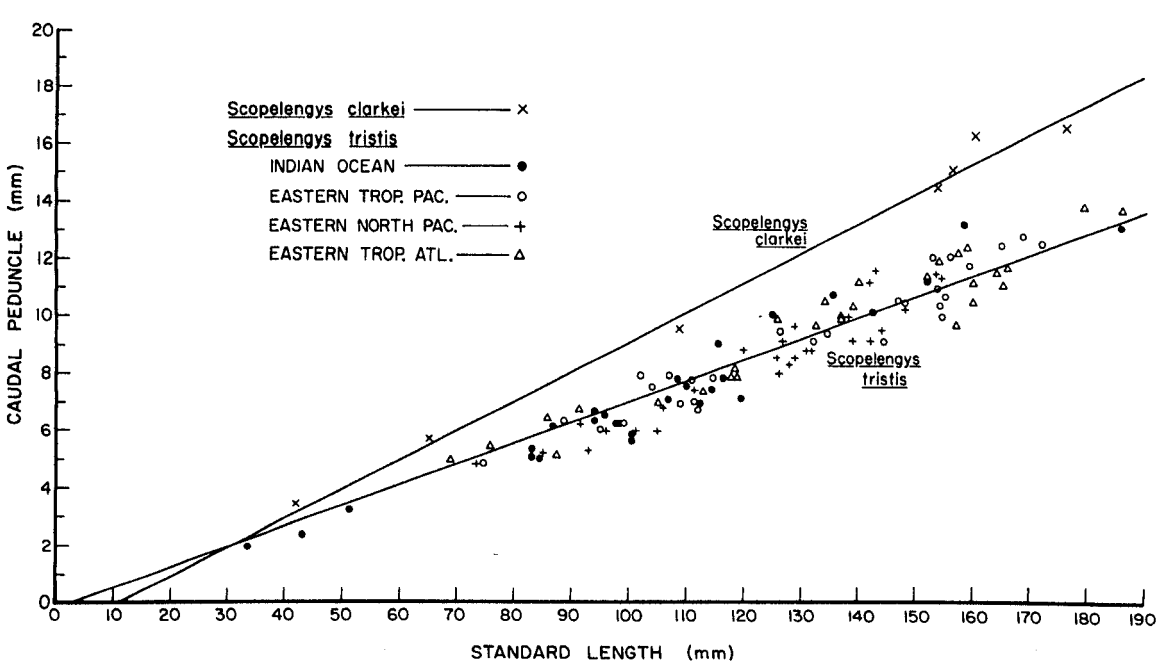

FIGURE 5.—Regression of least depth of caudal peduncle on standard length of *Scopelengys tristis* and *S. clarkei.*

showed a significant difference at the 1% level, $F = 3.72$, between the two species.

The Atlantic specimens of *S. tristis* had counts for four characters that were closer to those of *S. clarkei* than were counts of these characters from other geographic areas. These differences in counts between Atlantic *S. tristis* and *S. clarkei* were as follows: dorsal fin rays 1.0 (12.0 vs. 13.0), anal fin rays 0.6 (13.4 vs. 14.0), pectoral fin rays 2.1 (15.0 vs. 12.9), and vertebrae 3.1 (31.1 vs. 34.2). Differences of two in pectoral-fin ray counts and three for vertebrae are much greater than the regional variability found among specimens of *S. tristis*.

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LITERATURE CITED

AHLSTROM, E. H.
1972. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. Fish. Bull., U.S. 70:1153-1242.

ALCOCK, A.
1890. On the bathybial fishes of the Arabian Sea, obtained during the season 1889-90. Ann. Mag. Nat. Hist., Ser. 6, 6:295-311.

BOLIN, R. L.
1939. A review of the myctophid fishes of the Pacific coast of the United States and of lower California. Stanford Ichthyol. Bull. 1:89-156.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.

GARMAN, S.
1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U. S. N., commanding. XXVI. The fishes. Mem. Mus. Comp. Zool., Harvard Coll. 24:1-431.

HUBBS, C. L., AND K. F. LAGLER.
1958. Fishes of the Great Lakes region. Revised ed. Cranbrook Inst. Sci. Bull. 26, 213 p.

MEAD, G. W.
1963. Observations on fishes caught over the anoxic waters of the Cariaco Trench, Venezuela. Deep-Sea Res. 10:251-257.

NAFPAKTITIS, B. G., AND M. NAFPAKTITIS.
1969. Lanternfishes (family Myctophidae) collected during cruises 3 and 6 of the R/V *Anton Bruun* in the Indian Ocean. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 5, 79 p.

NELLEN, W.
1973. Fischlarven des Indischen Ozeans. "Meteor" Forsh-Ergebnisse, Ser. D, 14:1-66.

NORMAN, J. R.
1939. Fishes. John Murray Exped. 1933-1934, Sci. Rep. 2(1):1-116.

OKIYAMA, M.
1974. The larval taxonomy of the primitive Myctophiform fishes. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 609-621. Proc. Int. Symp. Dunstaffnage Mar. Res. Lab., Scott. Mar. Biol. Assoc., Oban, Scotl. May 17-23, 1973. Springer-Verlag, N.Y.

PARR, A. E.
1928. Deepsea fishes of the order Iniomi from the waters around the Bahama and Bermuda islands. With annotated keys to the Sudidae, Myctophidae, Scopelarchidae, Evermannellidae, Omosudidae, Cetomimidae and Rondeletidae of the world. Bull. Bingham Oceanogr. Collect., Yale Univ. 3(3):1-193.

ROSEN, D. E., AND C. PATTERSON.
1969. The structure and relationships of the Paracanthopterygian fishes. Bull. Am. Mus. Nat. Hist. 141(3):357-474.

ROTHSCHILD, B. J.
1963. Graphic comparisons of meristic data. Copeia 1963:601-603.

WEIGHT LOSS, MORTALITY, FEEDING, AND DURATION OF RESIDENCE OF ADULT AMERICAN SHAD, *ALOSA SAPIDISSIMA*, IN FRESH WATER[1]

MARK E. CHITTENDEN, JR.[2]

ABSTRACT

Linear regression equations are given for each sex for the regressions of total weight, somatic weight, and gonad weight on length prior to spawning, and for total weight on length after prolonged stay in fresh water.

Most shad began to return seaward by late June and probably had spent a maximum of about 2 mo in fresh water. Many fish, however, remained near the spawning grounds well into summer; and many died near the spawning grounds, probably from starvation. Opportunistic feeding occurred on "planktonic" items, but adult shad do not regularly obtain energy sufficient to maintain their weight in fresh water. Weight loss was related to sex and increased with increasing size. Mean length males and females averaged 45 and 57% total weight loss, respectively. Daily somatic weight loss was at least 5.75 g for males of average size and 12.47 g for females.

The anadromous American shad, *Alosa sapidissima,* an important commercial and sport fish, ranges widely on the Atlantic and Pacific coasts of North America. There is much literature on this fish, but little of it pertains to adults in fresh water, except for aspects of their spawning and population dynamics. In the course of other studies on the Delaware River from 1960 to 1968, I made many opportunistic observations on weight loss, mortality, feeding behavior, and duration of residence of adult shad on their spawning grounds in fresh water. This paper summarizes those observations and presents data on total-fork length conversion, regressions of total weight, somatic weight and gonad weight on length prior to spawning, and regressions of total weight on length after spawning.

MATERIALS AND METHODS

Adult shad were collected during their spawning runs at Lambertville, N.J., 22.5 km above tidal water (but far downstream of the present-day spawning grounds) using a 76-mm stretch-mesh, 107 m long and 3.6 m deep haul seine that was paid out from a boat and landed about 400 m downstream. Sampling occurred at 3- or 4-day intervals from 5 April to 19 May 1963, from 20 March to 18 May 1964, from 26 March to 7 May 1965, and from 27 March to 19 May 1966. Data for the period 1959-62 were obtained from rotenone surveys (hereinafter referred to as the Tri-State Surveys) during July and August by the States of New Jersey, New York, and Pennsylvania in cooperation with the U.S. Fish and Wildlife Service.

I examined grossly the stomach contents of many adults captured during the Tri-State Surveys in mid-July 1961, most of the 526 fish collected at Lambertville and many fish captured on the spawning grounds after 1962.

Length and total weight were determined on most fish in 1961 and 1962 and on all fish thereafter. Gonad weight was measured after 1962. Length, always taken in inches, was measured as fork length during 1961 and 1962 and as total length thereafter. To develop conversion factors, both measurements were taken on 490 adults collected at Lambertville during 1963 and 1964 and on 100 young captured in summer 1966. Total weight was measured in pounds (to the closest 0.1 lb) during 1961-63 but in grams thereafter. Gonad weights were always taken in grams (to the closest 0.1 g). All measurements were converted to grams, millimeters, and fork lengths for presentation herein.

Regression analyses and related statistics were calculated using computer program BMD-03R (Dixon 1967). All regressions presented herein were significant at $\alpha = 0.005$. The coefficient of

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determination (Steel and Torrie 1960) was used to estimate the amount of variation in y associated with variation in x. Residuals were used to examine the data for differences due to categories of classification such as year of collection. Size ranges are given within which regressions were linear.

When first referred to, locations are followed in parentheses by their approximate distances in kilometers upstream from Marcus Hook, Pa., which is situated about 90 km downstream from the fall line at Trenton, N.J. and near the transition between brackish and fresh water.

RESULTS AND DISCUSSION

Total and Fork Length Conversion

The relationship between total length (TL) and fork length (FL) for 590 young and adult fish was linear, and 99.96% of the variation in one measurement was explained by variation in the other. Regression equations were FL = 1.28 + 0.88 TL and TL = 1.00 + 1.13 FL. Extreme deviations from regression were about ±7.6 mm for adults and less for young. The slope of the regression of fork length on total length coincides with La Pointe's (1958) factor of 0.894 to convert total length to fork length.

Total Weight-Length Relationships Prior to Spawning

The relationships between total weight (TW) and length determined for fish captured at Lambertville were TW = 1,106.77 + 8.09 (FL - 427.98) for 268 males and TW = 1,737.26 + 11.54 (FL - 476.71) for 244 females. About 81% (males) and 78% (females) of the variation in total weight was associated with variation in length. Valid ranges for linear interpolation were about 330-520 mm for males and 410-550 mm for females.

The observed arithmetic mean weights with 95% confidence limits were 1,107 ± 36 g for males and 1,737 ± 45 g for females. The smallest males were 272 and 680 g and the smallest female was 1,089 g. The heaviest male and female fish were 1,905 and 2,585 g, respectively.

Somatic Weight-Length Relationships Prior to Spawning

The relationships between log somatic weight (SW) and length determined for 85 males and 130 females captured at Lambertville in 1964 and 1965 were $\log_{10}$ SW = 3.0047 + 0.0036 (FL - 428.20) for males and $\log_{10}$ SW = 3.1807 + 0.0029 (FL - 480.73) for females. About 91% (males) and 81% (females) of the variation in log somatic weight was associated with variation in length. Valid ranges for linear interpolation were about 360-500 mm for males and 410-540 mm for females. Mean somatic weights with 95% confidence limits were 1,011 ± 56 g for males and 1,516 ± 38 g for females.

Gonad Weight-Length Relationships Prior to Spawning

The relationships between log total gonad weight (TGW) and length determined for 267 males and 244 females captured at Lambertville were $\log_{10}$ TGW = 1.8633 + 0.0033 (FL - 428.43) for males and $\log_{10}$ TGW = 2.3892 + 0.0024 (FL - 476.93) for females. Valid ranges for linear interpolation were about 330-520 mm for males and 410-550 mm for females. About 45% (males) and 26% (females) of the variation in log total gonad weight was associated with length variation. Much variation in gonad weight, especially for females, is not explained by the regression equations. Much gonad development occurs during the spawning run (Chittenden 1969), and residual plots suggested that gonad weights were heavier in 1963 than in 1964. These factors account for some unexplained variation in gonad weight.

Mean total gonad weights with 95% confidence limits were 73 ± 7 g for males and 245 ± 22 g for females.

Duration of the Freshwater Residence

Most fish begin to return seaward by about late June. I observed hundreds of adults near Hancock, N.Y. (403) until 17 June 1964, but very few were present on 14 July. Most fish had died or migrated seawards during the interim period. Delaware River shad runs begin in early April at Lambertville and the peak occurs about 1 May, depending upon the degree of pollution near Philadelphia (34) (Chittenden 1969). This suggests most fish probably spend a maximum of 2 mo in fresh water before returning seaward, in agreement with Bean's (1892, 1903) observations.

Many fish remain near the spawning grounds well into summer. The Tri-State Surveys cap-

tured many adults during midsummer between Skinners Falls, N.Y. (348) and Minisink Island, N.J. (266): 538 fish were captured at three stations in mid-July 1961; 237 fish were captured at two stations in mid-July 1962; 30 adults were captured near Milford, Pa. (269) on 7 August 1959, and 13 were captured there on 1 August 1961.

Upstream Mortality

There was a large mortality of shad upstream near the spawning grounds about the end of the spawning period. In 1963, I observed many dead fish along the banks or in shallow water on 5 July; and a surface gill net set overnight at Milford, Pa. on 22 June captured 15 fish that appeared to have been dead for several days. In 1964, dead shad first appeared in the East Branch near Hancock about 14 June; on that date, I walked the bank for about 0.8 km and observed 26 dead fish within 10 m of the shoreline. I observed hundreds of dead shad on 8 July 1964 during a 19-km float from Matamoras, Pa. (274) to Dingmans Ferry, Pa. (258). I frequently saw dead fish in shallow water during August.

Shad may die before being completely spent. Some dead fish examined near Hancock had ovaries about a fourth the size of those in fish captured at Lambertville. The ovaries of these dead fish contained many translucent eggs, a criterion (Milner 1874; Brice 1898; Leach 1925) indicating that the fish is ripe.

Feeding Behavior in Fresh Water

Feeding did occur in freshwater, at least near the upstream spawning grounds. The stomachs of most shad captured at Lambertville were empty, but a few contained a slight amount of amorphous material. Stomachs of fish collected upstream from Port Jervis, N.Y. (295) in late May and June frequently contained a few insects. I observed a large mayfly hatch in late May 1964 near Hancock: hundreds of adult shad were rising to the surface, apparently to feed, and the stomachs of many fish (about 50) captured by angling were packed with mayflies. Similar surface feeding behavior was observed on several other occasions, although fish were not collected to confirm feeding. Many adults captured during the Tri-State Surveys contained recently eaten young shad and shield darters, *Percina peltata*. For example, four stomachs contained: 1) 2 darters and 9 young shad, 2) 6 darters and 17 shad, 3) 46 shad, and 4) 15 shad. Young shad were the first fish to react to rotenone, and the adults probably foraged on distressed and dying young.

Weight Loss in Fresh Water

Much weight was lost while the adult shad were in fresh water. Fish captured near Hancock had noticeably lost weight by late May, and they became more emaciated the longer they remained in fresh water. Tri-State Survey data obtained 10-13 July 1961 from Belvidere, N.J. (197) to Hancock, N.Y. and 16-17 July 1962 at Minisink Island and Skinners Falls were used to estimate the changed weight-length relationship for each sex. The relationships between total weight and length of these fish were $TW = 536.34 + 3.24(FL - 407.34)$ for 296 males and $TW = 661.29 + 3.01(FL - 451.18)$ for 19 females. Valid ranges for linear interpolation were about 265-450 mm for males and 340-475 mm for females. About 66% (males) and 63% (females) of the variation in total weight was associated with variation in length. These regressions explain less variation in total weight than the 80% explained for fish taken at Lambertville.

The average percentages of total weight loss in fresh water were estimated by comparing Lambertville and Tri-State Survey regression means at different lengths for each sex (Figure 1). The

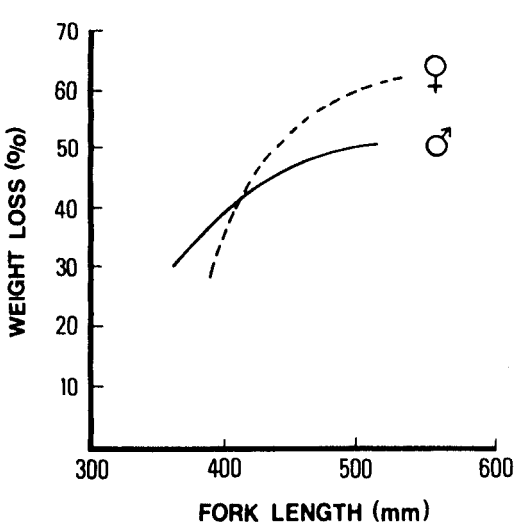

FIGURE 1.—Minimum average total weight loss of American shad in fresh water.

average percent weight loss depended upon length. Large fish lost a greater percentage than small fish. Average total weight loss was from 30 to 50% for 359-493 mm FL males and from 48 to 62% for 421-531 mm FL females, sizes which closely approximate the observed size range of fish in the 1963 and 1964 runs (Chittenden 1969). The observed mean fork lengths of fish captured at Lambertville were 428 mm for males and 477 mm for females, based upon the regression equations, and these sizes averaged 45 and 57% total weight loss, respectively.

Somatic weight loss, a better measure of the toll taken by the spawning migration, was estimated by subtracting the predicted total gonad weight from the predicted total weight at Lambertville before making a comparison with the Tri-State Survey total weight regressions. No correction was made for the gonads of fish captured during the Tri-State Surveys; however, these were a negligible fraction of the total weight. The total testes weights of 15 males collected near Hancock on 14 July 1964 and on 21, 24 June and 1 July 1965 ranged from 3.7 to 27 g and averaged 15.9 g while the total ovary weights of 3 females collected then varied from 18.2 to 35 g and averaged 27.1 g. The average percentage of somatic weight loss in males was 24% at 359 mm, 46% at 493 mm, and 42% for the mean-sized male of 428 mm. For females, somatic weight loss was 38% at 421 mm, 56% at 531 mm, and 50% for the mean-sized female of 477 mm.

Absolute daily weight loss was estimated from the duration of the freshwater residency. Fish captured during the Tri-State Surveys had probably been upstream about 75 days. This approximates their maximum stay in fresh water because the peak of the run at Lambertville is about 1 May (Chittenden 1969), and most fish move seaward from the Hancock area by late June. Therefore, the average daily loss in somatic weight of males was 1.63 g at 359 mm, 9.37 g at 493 mm, and 5.75 g for mean-sized males of 428 mm. For females the average daily loss in somatic weight was 5.75 g at 421 mm, 18.87 g at 531 mm, and 12.47 g for mean-sized females of 477 mm.

Daily weight loss can be used to suggest how long fish of different sizes can remain in freshwater before death. The amount of weight loss which results in death of shad is not known, but death occurs in many animals when weight loss exceeds 40% (Curtis 1949). Assume 50% for simplicity in calculation, this may not be quite correct, but it may be conservative and the size pattern, at least, remains the same if the percentage is a constant. From this, males could remain 154 days at 359 mm, 81 days at 493 mm, and the average sized male (428 mm) could remain 90 days. Females could remain 100 days at 421 mm but only 68 days at 531 mm, and the mean-sized female of 477 mm could remain 75 days. There is apparently little difference in the amount of time an average to maximum-sized fish can spend in fresh water before death, but small fish can survive much longer.

GENERAL DISCUSSION

Weight loss data presented herein agrees reasonably with those of Leggett (1972) who noted that his figures were probably underestimates. The present figures ignore weight loss in the 100-km migration between Marcus Hook and Lambertville and may be based on a longer than average stay in fresh water. Both factors tend to underestimate weight loss which affects related estimates.

Many shad apparently remain upstream near the spawning grounds well into the summer. However, the percentage they comprise of the run is unknown. A few fish remain far upstream until late fall. Bishop (1936) captured emaciated individuals 305-330 mm long near Hancock in November. These fish must have migrated upstream during the previous spring, because low dissolved oxygen water near Philadelphia presents a virtually impassable barrier through summer and fall (Ellis et al. 1947; Sykes and Lehman 1957; Chittenden 1969). Nichols (1959) captured an emaciated male during October in the Connecticut River and estimated it had been in freshwater at least 120 days. I captured an emaciated male (287 mm FL, 194 g) in fresh water in the James River, Va. on 7 October 1969.

The finding of little or no food in adults collected at Lambertville is similar to the reports of Bean (1903), Leim (1924), Leach (1925), Hildebrand and Schroeder (1928), Moss (1946), and Hildebrand (1963) that adults take little or no food while ascending rivers. My observations of instances of intensive feeding while upstream are exceptional, although Atkinson (1951) reported an artificial instance of feeding in freshwater ponds. Adult shad at sea feed largely on planktonic forms such as copepods and mysids (Leim 1924; Hildebrand and Schroeder 1928;

Bigelow and Schroeder 1953; Hildebrand 1963; Leim and Scott 1966), although Holland and Yelverton (1973) reported that they occasionally take large amounts of fish. Atkinson (1951) attributed the general absence of food in the stomachs of adults to their planktonic feeding habit and the absence of suitably large plankton in fresh water. My observations suggest that adult shad would opportunistically feed in fresh water if suitably large "planktonic" forms were readily available.

Although adults feed opportunistically in fresh water, they do not regularly obtain energy sufficient to maintain their weight and must use energy reserves accumulated during their life at sea to support migration in fresh water, final development of the gonads, and spawning. Adults use up their somatic substance at a size and sex dependent rate of at least about 1.6-18.9 g/day. Their physical activity deteriorates greatly as Fowler (1908) and Walburg (1960) noted. Death by starvation may occur when weight loss exceeds 40% (Curtis 1949), and this is probably the main cause of the mortality I observed on the spawning grounds. Further work is needed to quantitatively describe upstream mortality, but its magnitude would appear large as Bean (1892, 1903) and Anonymous (1902) also observed in the Delaware River and Walburg (1960) observed in the St. Johns River, Fla.

Weight loss was related to sex and size in agreement with Leggett (1972). The apparent relationship between weight loss and sex, however, may not be direct. Metabolic rate, in general, increases with temperature within limits. Leggett (1972) noted that females tend to migrate later and at a higher temperature than males and suggested that temperature was responsible for the apparent sex difference in weight loss. The relationship between size and total metabolism in a wide variety of organisms can be expressed as:

$$\log M = \log a + b \log W$$

where M is total metabolism and W is weight (Paloheimo and Dickie 1966; Prosser 1973). The relationship between metabolic rate and size can be expressed (Prosser 1973) as:

$$\log M/W = \log a + (b - 1) \log W.$$

From the latter expression it follows that a b value less than 1.0 implies that the metabolic rate decreases with increasing size, while a b value greater than 1.0 indicates that the metabolic rate increases with size. The value generally found for b is about 0.8 (Paloheimo and Dickie 1966; Prosser 1973), although Fry (1971) cautions that this value should not yet be accepted as dogma. Present findings on the relationship between size and weight loss in shad on their spawning migration are consistent with a b value greater than 1.0. Calculations made herein obviously assume that adult fish of all sizes are in fresh water the same length of time. If b is not greater than 1.0, we must conclude that: 1) small adults enter fresh water later than large fish and thus are in fresh water for a shorter period of time, or 2) small fish make better use of available freshwater food resources.

Estimates of the time that adults can remain in fresh water suggest that only small fish can survive upstream into the fall. The small fish I captured in the James River in October apparently had lost only about 33-39% of its weight in comparison with the Delaware River somatic weight regression at Lambertville and an unusually small fish (285 mm FL, 288 g) captured at Lambertville. It is noteworthy that, except for Nichols' (1959) report of a 430 mm FL male, the adult shad reported in fresh water during the fall have all been males about 305 mm long. Fish this small, however, are rare in the age compositions reported from many Atlantic Coast rivers (Talbot 1954; Fredin 1954; Walburg 1956, 1957, 1960, 1961; Sykes 1956; Sykes and Lehman 1957; Walburg and Sykes 1957; La Pointe 1958; Nichols and Tagatz 1960; Nichols and Massmann 1963; Godwin 1968; Leggett 1969; Chittenden 1975).

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LITERATURE CITED

ANONYMOUS.
1902. Rep. Pa. State Comm. Fish. 1902.

ATKINSON, C. E.
1951. Feeding habits of adult shad (*Alosa sapidissima*) in fresh water. Ecology 32:556-557.

BEAN, T. H.
1892. The fishes of Pennsylvania. Rep. Pa. Comm. Fish. 1889-90-91, p. 1-149.
1903. Catalogue of the fishes of New York. N.Y. State Mus. Bull. 60, 784 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BISHOP, S. C.
1936. Fisheries investigations in the Delaware and Susquehanna Rivers. *In* A biological survey of the Delaware and Susquehanna watersheds, p. 122-139. N.Y. Conserv. Dep. Suppl. 25th Annu. Rep., 1935.

BRICE, J. J.
1898. A manual of fish-culture, based on the methods of the United States Commission of Fish and Fisheries. U.S. Comm. Fish Fish. Part 23, Rep. Comm. 1897, append., p. 1-261.

CHITTENDEN, M. E., JR.
1969. Life history and ecology of the American shad, *Alosa sapidissima*, in the Delaware River. Ph.D. Thesis, Rutgers Univ., New Brunswick, N.J., 458 p.
1975. Dynamics of American shad, *Alosa sapidissima*, runs in the Delaware River. Fish. Bull., U.S. 73:487-494.

CURTIS, B.
1949. The life story of the fish. Scientific Book Club, Lond., 276 p.

DIXON, W. J. (editor).
1967. Biomedical computer programs. 2nd ed. Univ. Calif. Press, Berkeley, 600 p.

ELLIS, M. M., B. A. WESTFALL, D. K. MEYER, AND W. S. PLATNER.
1947. Water quality studies of the Delaware River with reference to shad migration. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 38, 19 p.

FOWLER, H. W.
1908. The king crab fisheries in Delaware Bay, and further note on New Jersey fishes, amphibians and reptiles. Annu. Rep. N.J. State Mus. 1907 Part 3, p. 349-432.

FREDIN, R. A.
1954. Causes of fluctuations in abundance of Connecticut River shad. U.S. Fish Wildl. Serv., Fish. Bull. 54:247-259.

FRY, F. E. J.
1971. The effect of environmental factors on the physiology of fish. *In* W. S. Hoar and D. J. Randall (editors), Fish Physiology, Vol. 6, p. 1-98. Academic Press, N.Y.

GODWIN, W. F.
1968. The shad fishery of the Altamaha River, Georgia. Ga. Game Fish Comm., Mar. Fish. Div., Contrib. Ser., 8, 39 p.

HILDEBRAND, S. F.
1963. *Family* Clupeidae. *In* Fishes of the western North Atlantic, Part 3, p. 257-454. Mem. Sears Found. Mar. Res. Yale Univ. 1.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. U.S. Bur. Fish., Bull. 43, Part 1, 366 p.

HOLLAND, B. F., JR., AND G. F. YELVERTON.
1973. Distribution and biological studies of anadromous fishes offshore North Carolina. N.C. Dep. Nat. Econ. Resour., Div. Commer. Sport Fish., Spec. Sci. Rep. 24, 132 p.

LAPOINTE, D. F.
1958. Age and growth of the American shad, from three Atlantic Coast Rivers. Trans. Am. Fish Soc. 87:139-150.

LEACH, G. C.
1925. Artificial propagation of shad. Rep. U.S. Comm. Fish. 1924, append. 8, p. 459-486. Doc. 981.

LEGGETT, W. C.
1969. A study of the reproductive potential of the American shad (*Alosa sapidissima*) in the Connecticut River, and of the possible effects of natural or man induced changes in the population structure of the species on its reproductive success. Essex Mar. Lab., Essex, Conn., 72 p.
1972. Weight loss in American shad (*Alosa sapidissima*, Wilson) during the freshwater migration. Trans. Am. Fish. Soc. 101:549-552.

LEIM, A. H.
1924. The life history of the shad (*Alosa sapidissima* (Wilson)) with special reference to the factors limiting its abundance. Contrib. Can. Biol., New Ser. 2:163-284.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

MILNER, J. W.
1874. Report on the propagation of the shad (*Alosa sapidissima*) and its introduction into new waters by the U.S. Fish Commissioner in 1873. U.S. Comm. Fish Fish., Part 2, Rep. Comm. 1872-73, p. 419-451.

MOSS, D. D.
1946. Preliminary studies of the shad (*Alosa sapidissima*) catch in the lower Connecticut River, 1944. Trans. North Am. Wildl. Conf. 11:230-239.

NICHOLS, P. R.
1959. Extreme loss in body weight of an American shad (*Alosa sapidissima*). Copeia 1959:343-344.

NICHOLS, P. R., AND W. H. MASSMANN.
1963. Abundance, age, and fecundity of shad, York River, Va., 1953-59. U.S. Fish Wildl. Serv., Fish. Bull. 63:179-187.

NICHOLS, P. R., AND M. E. TAGATZ.
1960. Creel census Connecticut River shad sport fishery, 1957-58, and estimate of catch, 1941-56. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 351, 12 p.

PALOHEIMO, J. E., AND L. M. DICKIE.
1966. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Board Can. 23:869-908.

PROSSER, C. L.
1973. Oxygen: respiration and metabolism. *In* C. L. Prosser (editor), Comparative animal physiology, 3rd ed., p. 165-211. Saunders, Phila.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw Hill, N.Y., 481 p.

SYKES, J. E.
1965. Shad fishery of the Ogeechee River, Georgia, in 1954. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 191, 11 p.

SYKES, J. E., AND B. A. LEHMAN.
1957. Past and present Delaware River shad fishery and considerations for its future. U.S. Fish Wildl. Serv., Res. Rep. 46, 25 p.

TALBOT, G. B.
1954. Factors associated with fluctuations in abundance of Hudson River Shad. U.S. Fish Wildl. Serv., Fish. Bull. 56:373-413.

WALBURG, C. H.
1956. Commercial and sport shad fisheries of the Edisto River South Carolina, 1955. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 187, 9 p.
1957. Neuse River shad investigations, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 206, 13 p.
1960. Abundance and life history of shad, St. Johns River, Florida. U.S. Fish Wildl. Serv., Fish. Bull. 60:487-501.
1961. Natural mortality of American shad. Trans. Am. Fish. Soc. 90:228-230.

WALBURG, C. H., AND J. E. SYKES.
1957. Shad fishery of Chesapeake Bay with special emphasis on the fishery of Virginia. U.S. Fish Wildl. Serv., Res. Rep. 48, 26 p.

DISTRIBUTION, ABUNDANCE, AND SIZE OF PENAEID SHRIMPS IN THE ST. ANDREW BAY SYSTEM, FLORIDA

HAROLD A. BRUSHER AND LARRY H. OGREN[1]

ABSTRACT

Shrimp collections were made every 2 weeks at 12 stations in varying depths (1.5-12.2 m) of the St. Andrew Bay system, Fla., from September 1972 through August 1973. The eight species of penaeid shrimps caught in 312 trawl hauls were, in decreasing order of abundance: pink shrimp, *Penaeus duorarum*; broken-neck shrimp, *Trachypenaeus similis*; rock shrimp, *Sicyonia brevirostris*; rock shrimp, *S. dorsalis*; broken-neck shrimp, *T. constrictus*; brown shrimp, *P. aztecus*; white shrimp, *P. setiferus*; and rock shrimp, *S. typica*. Of the total catch of penaeids, 57.7% were of the genus *Penaeus*, 22.6% of *Sicyonia*, and 19.7% of *Trachypenaeus*. Penaeids were more abundant in the sections of the bay system close to the Gulf of Mexico. Seasonal abundance varied for each species. Shrimps of the genus *Penaeus* were larger in deeper sections of the bay. The hydrological characteristics of the St. Andrew Bay system are much more similar to the waters of the Gulf of Mexico than are those of other estuaries of the northern gulf. This similarity probably accounts for the relatively high abundance of shrimps of the genera *Trachypenaeus* and *Sicyonia* in the bay system. Also, this similarity probably delays the gulfward migration of shrimps of the genus *Penaeus* and accounts for their large sizes in the system.

Personal observations made on exploratory collecting trips and on cruises aboard shrimp trawlers within the St. Andrew Bay system in northwest Florida had led us to believe that some species of marine organisms normally found in offshore waters of the Gulf of Mexico occurred commonly within the system. For example, penaeid shrimps of the genera *Trachypenaeus* and *Sicyonia,* which are rare in bay systems of the northern gulf, were observed frequently. Also, shrimps of the genus *Penaeus* appeared to be much larger within the St. Andrew Bay system than other estuarine areas. It thus appeared to us that the penaeid shrimps of the St. Andrew Bay system were unusual in terms of species composition and size.

Although utilization of estuarine waters by populations of shrimps of the genus *Penaeus* is well known (Lindner and Cook 1970; Cook and Lindner 1970; Costello and Allen 1970), the abundance, distribution, and size are not completely described for all penaeid species within many estuarine waters. This information is especially lacking along the northwest Florida coast. The objectives of our study were to estimate these parameters for penaeid shrimps in the St. Andrew Bay system.

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STUDY AREA

The St. Andrew Bay estuarine system is located on the northwest coast of Florida between lat. 30°00′ and 30°20′N and long. 85°23′ and 85°53′W. The system consists of four bays—North, West, East, and St. Andrew (Figure 1)—with mean depths of 1.8, 2.1, 2.1, and 5.2 m, respectively, and covers an area of 280 km^2 (McNulty et al. 1972). Various aspects of the physical and biological characteristics of the St. Andrew Bay system have been presented by Ichiye and Jones (1961), Waller (1961), Vick (1964), Hopkins (1966), Salsman et al. (1966), Cosper (1972), and McNulty et al. (1972).

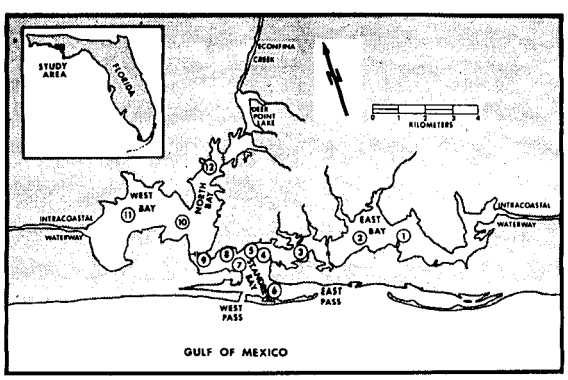

FIGURE 1.—Location of sampling stations in the St. Andrew Bay System, Fla.

Waters in the St. Andrew Bay system are relatively high in transparency. This high transparency results in part from the porosity of the soils of the watershed, the low freshwater inflow, and the proximity of the system to the clear waters of the northeastern Gulf of Mexico. In terms of extinction coefficients, the transparency of gulf waters adjacent to St. Andrew Bay are typical of clear oceanic waters (Tolbert and Austin 1959).

The bottom of the bay system is composed of distinct sediment regimes. The sand regime (>80% sand) is generally restricted to areas near the passes and in depths less than 6 m. The silt-clay regime (>50% clay, <50% silt, and <20% sand) is located in the deeper waters of the system, but not in the passes (Waller 1961).

The bay system also contains areas covered by rooted submerged vegetation. The submerged vegetation includes turtle grass, *Thalassia testudinum*; manatee grass, *Syringodium filiforme*; and shoal grass, *Diplanthera wrightii*. These grasses cover an area of about 3,200 hectares.

METHODS

Sampling was conducted every 2 wk from 6 September 1972 through 21 August 1973 at 12 stations (Figure 1, Table 1). Two consecutive nights were required to sample at all stations with samples taken between sunset and 0200 h. On 23-24 August 1973 additional sampling was conducted between 1000 and 1400 h at the 12 stations to compare day catches with the night catches of 20-21 August 1973.

Biological samples were obtained at each station with an 11.5-m wing trawl with stretched meshes of 7.6 cm in the wings, 3.8 cm in the body, and 2.5 cm in the cod end. The trawl was towed at about 3.5 knots for 10 min. The entire catch at each station was placed on ice and transported to the laboratory and frozen. Catches were thawed and processed usually within 1 wk of collection. Penaeid shrimps from each sample were enumerated by species, and 30 individuals, or all if less than 30, were measured to the nearest 0.5 cm total length (tip of rostrum to tip of telson).

TABLE 1. — Locations and depth ranges of sampling stations in the St. Andrew Bay system, Fla.

Station	Lat.[1]	Long.[1]	Identifying landmark	Depth range (m)
1	30°05.0′N	85°31.0′W	Goose Point	4.6- 6.1
2	30°06.3′N	85°35.0′W	Shoal Point	7.6- 9.1
3	30°07.6′N	85°37.7′W	Palmetto Point	7.6- 9.1
4	30°09.0′N	85°40.8′W	Redfish Point	10.7-12.2
5	30°09.5′N	85°41.6′W	Baker Bayou	6.1- 7.6
6	30°06.2′N	85°41.3′W	Shell Island	6.1- 7.6
7	30°09.4′N	85°42.8′W	Courtney Point	7.6- 9.1
8	30°10.4′N	85°43.0′W	Lake Huntington	6.1- 7.6
9	30°10.5′N	85°44.2′W	Dyers Point	10.7-12.2
10	30°14.1′N	85°44.3′W	Shell Point	6.1- 7.6
11	30°15.7′N	85°46.6′W	Breakfast Point	3.1- 4.6
12	30°15.4′N	85°40.0′W	Haven Point	1.5- 3.1

[1]United States Department of Commerce, Nautical Chart 868-SC.

Environmental data were also obtained at each station. A water sample for determining dissolved oxygen and turbidity was taken 0.5 m above the bottom at each station with a 3-liter water sampler. Salinity and temperature were determined in situ with a Beckman[2] RS5-3 portable salinometer (accuracy ±0.5°C and ±0.3‰) at the above mentioned depth. Turbidity was determined with a Hach turbidimeter (Formazin turbidity units—accuracy ±0.02 FTU), and dissolved oxygen determined by the modified Winkler method (accuracy ±0.05 ml/liter).

For each species, differences in catch per unit effort (average catch per tow), and in size (average length by date) between subareas were tested statistically with Tukey's w-procedure (Steel and Torrie 1960). For length comparisons, data were used for only those dates when shrimps of a species were caught in all subareas. For comparisons of distribution and abundance, the data were grouped into the following subareas: East Bay (stations 1, 2); North Bay (station 12); West Bay (stations 10, 11); St. Andrew Bay (stations 3-5, 7-9); and East Pass (station 6).

Mean catches per tow and mean total lengths were also compared between upper and lower bay areas. The upper area included all stations in East Bay, North Bay, and West Bay, and the lower area included all stations in St. Andrew Bay and East Pass.

ENVIRONMENTAL FACTORS

Mean values of environmental factors near the bottom were determined for subareas. Salinities and dissolved oxygen were higher in St. Andrew Bay and East Pass than in the other subareas (Table 2). Turbidities in North Bay, East Bay, and West Bay were greater than in St. Andrew Bay and East Pass. Bottom temperatures, however, were similar among subareas.

When subarea data were combined into the respective upper and lower areas, the average values were: salinity—29.2, 33.2‰; turbidity—3.0,

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Annual means and ranges of environmental factors measured in 1972-73 in five subareas of the St. Andrew Bay system, Fla.

Environmental factor	North Bay	West Bay	East Bay	East Pass	St. Andrew Bay
Salinity (‰)					
Mean	27.20	29.08	30.34	32.97	33.27
Range	13.1-32.5	20.5-34.1	25.3-33.9	30.3-35.2	30.6-35.6
Turbidity (FTU)[1]					
Mean	2.69	3.40	2.63	1.09	1.75
Range	0.50-13.00	1.53-7.55	1.50-5.20	0.60-2.15	0.87-4.09
Temp (°C)					
Mean	21.74	21.82	21.79	22.13	21.74
Range	13.1-31.1	13.6-30.2	13.8-29.9	13.0-30.2	13.2-30.0
Dissolved O_2 (ml/liter)					
Mean	3.87	3.77	3.27	4.43	4.01
Range	1.33-5.37	2.06-4.70	1.64-5.58	3.47-5.13	3.13-4.80
No. of samples	26	52	52	26	182

[1]Formazin turbidity units.

1.7 FTU; temperature—21.8°, 21.8°C; dissolved oxygen—3.6, 4.1 ml/liter. Generally, salinity and dissolved oxygen values were higher in the lower area, turbidity values were higher in the upper area, and temperatures were similar between areas (Figure 2). The only noteworthy variation

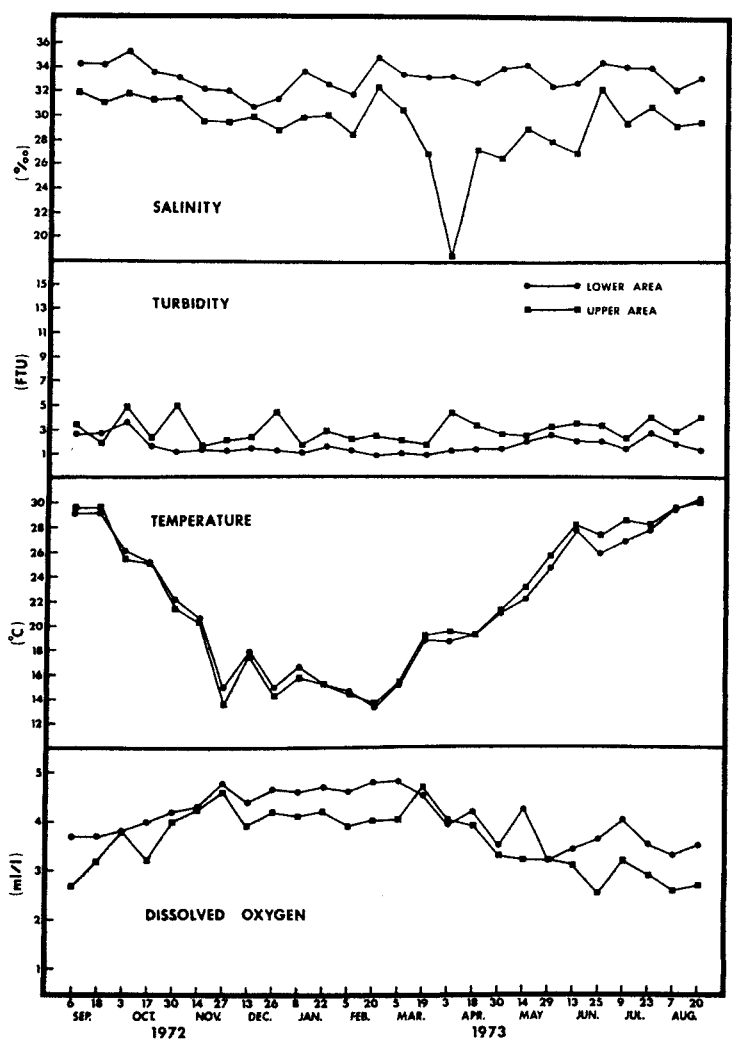

FIGURE 2.—Mean values of salinity, turbidity, temperature, and dissolved oxygen in the upper and lower areas of the St. Andrew Bay system, Fla., 1972-73.

in these values occurred in the salinity of the upper area where heavy spring rains accounted for an exceptional drop in salinity in early April.

Compared to hydrological data from other northern gulf estuaries (Gunter 1950; Swingle 1971; Dunham 1972; Stokes 1974), the values within the St. Andrew Bay system are more oceanic than estuarine (Waller 1961; Hopkins 1966).

CATCHES

Eight species of penaeids were taken during the study: three species of *Penaeus* (*P. duorarum*, *P. aztecus*, and *P. setiferus*), two species of *Trachypenaeus* (*T. similis* and *T. constrictus*), and three species of *Sicyonia* (*S. brevirostris*, *S. dorsalis*, and *S. typica*). Catches of each species at each of the 12 stations are shown in Table 3. The greatest number of individual shrimps (species combined) was taken at station 4 (St. Andrew Bay), the least at station 2 (East Bay). *Penaeus duorarum* was the most abundant species, *S. typica* the least. Since only 25 *S. typica* (ranging in size from 3.5 to 5.5 cm) were caught, this species will not be discussed in the following sections.

Although methods were similar, a striking difference was apparent between our catches and those from other estuarine systems in the northern Gulf of Mexico. In our study, 57.6% of the total penaeid catch consisted of members of the genus *Penaeus*, 22.6% of the genus *Sicyonia*, and 19.7% of *Trachypenaeus*. In contrast, studies in other estuarine systems in Alabama (Swingle 1971), Louisiana (Dunham 1972), and Texas (Gunter 1950; Moffett 1968; Stokes 1974) showed that the genus *Penaeus* represented 99 to 100% of the total trawl catch of penaeids.

DISTRIBUTION AND ABUNDANCE

To determine where shrimp were more abundant in the St. Andrew Bay system, relative abundances were compared by subarea (Table 4). Significant differences were found for four of the seven species: *T. similis*, *S. brevirostris*, *S. dorsalis*, and *T. constrictus*. Either St. Andrew Bay or East Pass or both had significantly greater abundance of these species than the other subareas.

When subarea data were combined for each species and apportioned into upper and lower areas, the relative abundances were greater in the upper area for *P. aztecus* and *P. setiferus* and were greater in the lower area for the other penaeids. Average catches per tow for the upper and lower areas, respectively, were: *P. duorarum*, 110.8, 129.3; *T. similis*, 12.8, 49.4; *S. brevirostris*, 6.0, 51.3; *S. dorsalis*, 2.9, 32.9; *T. constrictus*, 3.1, 14.8; *P. aztecus*, 10.1, 4.6; *P. setiferus*, 2.7, 0.3.

To determine seasonal distribution and abundance, the catches per tow were calculated by area and by date for each species. The results, shown in Figure 3, indicate summer and fall abundances for the three species of *Penaeus*, although not necessarily in both areas. For *Trachypenaeus* and *Sicyonia*, seasonal abundances were evident only in the lower area, with *T. similis* and *S. dorsalis* more abundant during spring and summer, *S. brevirostris* more abundant during winter and early spring, and *T. constrictus* during spring.

TABLE 3. — Total numbers of penaeid shrimps caught in 312 trawl hauls within the St. Andrew Bay system, Fla., from September 1972 through August 1973.

Species	Station 1	2	3	4	5	6	7	8	9	10	11	12	Total
Pink shrimp, *Penaeus duorarum*	3,485	1,613	2,724	1,879	5,097	3,115	3,348	4,767	2,382	3,062	3,371	2,737	37,580
Broken-neck shrimp, *Trachypenaeus similis*	79	1,140	1,553	2,724	101	418	1,095	1,218	1,878	383	7	3	10,599
Rock shrimp, *Sicyonia brevirostris*	12	19	147	984	1,758	3,812	1,552	717	198	17	9	9	9,234
Rock shrimp, *Sicyonia dorsalis*	3	273	632	3,433	66	247	434	226	993	80	0	0	6,387
Broken-neck shrimp, *Trachypenaeus constrictus*	56	53	150	207	704	907	275	248	208	41	93	122	3,064
Brown shrimp, *Penaeus aztecus*	125	81	144	119	19	146	187	165	85	197	342	279	1,889
White shrimp, *Penaeus setiferus*	42	22	18	5	0	0	14	13	21	52	166	71	424
Rock shrimp, *Sicyonia typica*	0	0	0	4	4	12	0	2	3	0	0	0	25
Total	3,802	3,201	5,368	9,355	7,749	8,657	6,905	7,356	5,768	3,832	3,988	3,221	69,202
Rank	10	12	7	1	3	2	5	4	6	9	8	11	

TABLE 4. — Comparisons of mean catch per tow of penaeid shrimps between subareas (Tukey's w-procedure with 125 df) of the St. Andrew Bay system, Fla., from September 1972 through August 1973.

Species	Subarea, mean catch in parentheses and significance lines[1]				
Penaeus duorarum	East Bay (100.4)	North Bay (105.3)	East Pass (119.8)	West Bay (124.4)	St. Andrew Bay (130.9)
Trachypenaeus similis	North Bay (0.1)	West Bay (7.7)	East Pass (15.9)	East Bay (24.3)	St. Andrew Bay (55.0)
Sicyonia brevirostris	North Bay (0.4)	East Bay (0.6)	West Bay (0.7)	St. Andrew Bay (35.4)	East Pass (146.6)
S. dorsalis	North Bay (0.0)	West Bay (1.8)	East Bay (5.5)	East Pass (9.5)	St. Andrew Bay (36.8)
T. constrictus	East Bay (2.2)	West Bay (3.1)	North Bay (4.7)	St. Andrew Bay (11.4)	East Pass (34.9)
P. aztecus	East Bay (4.0)	St. Andrew Bay (4.4)	East Pass (5.6)	West Bay (10.5)	North Bay (10.7)
P. setiferus	East Pass (0.0)	St. Andrew Bay (0.4)	East Bay (1.4)	North Bay (2.6)	West Bay (4.1)

[1]Any two means not underscored by the same line are significantly different at the 5% level.

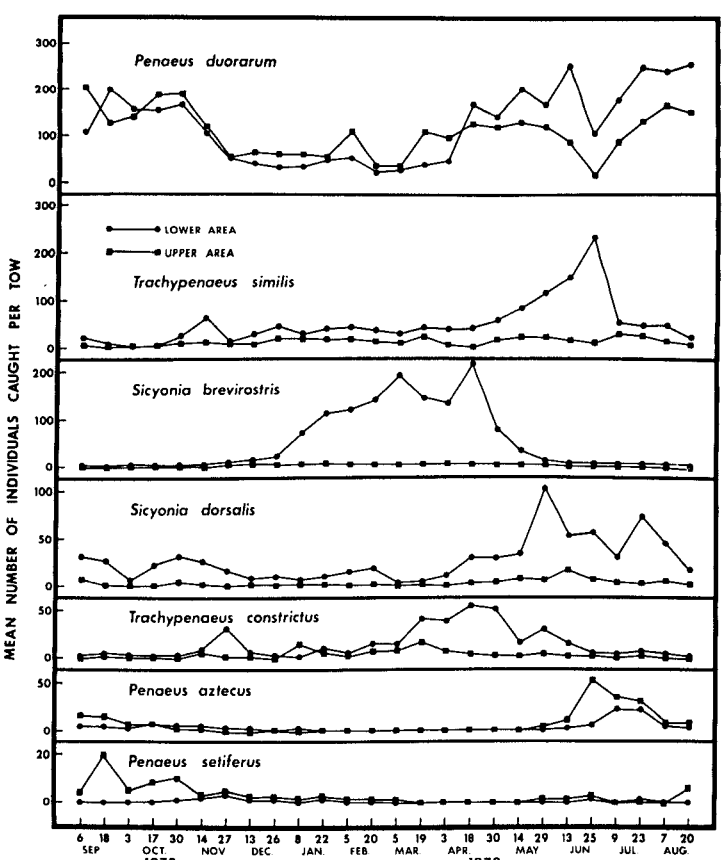

FIGURE 3.—Mean catch per tow of seven penaeid shrimp species in the upper and lower areas of the St. Andrew Bay system, Fla., 1972-73.

Penaeid shrimps taken from the St. Andrew Bay system showed definite habitat preference by genera when abundance was related to depth. As shown in Table 5, the higher mean catches per tow for *Penaeus* occurred in the shallower waters, while those for *Trachypenaeus* and *Sicyonia* occurred in the intermediate and deeper waters of the sampled area. Ninety-two percent of all *Trachypenaeus* and *Sicyonia* were taken from the lower area where the average station depth was 8.6 m.

Day and night comparisons showed mean catch per tow to be greater at night for all seven species (Table 6).

TABLE 5. — Comparisons of mean catch per tow and mean length (cm) of penaeid shrimps in relation to depth and species within the St. Andrew Bay system, Fla., from September 1972 through August 1973.

Species	1.5-4.6 m Stn. 11, 12	4.6-7.6 m 1, 5, 6, 8, 10	7.6-12.2 m 2, 3, 4, 7, 9
Penaeus duorarum	117.5 (9.1)	150.2 (9.5)	91.9 (10.0)
Trachypenaeus similis	0.2 (6.3)	16.9 (6.3)	64.6 (6.8)
Sicyonia brevirostris	0.3 (6.1)	48.6 (6.0)	22.3 (6.2)
S. dorsalis	0.0 (—)	4.8 (5.3)	38.8 (5.5)
T. constrictus	4.2 (4.7)	15.1 (4.8)	6.9 (4.9)
P. aztecus	12.0 (11.1)	5.0 (12.4)	4.7 (12.7)
P. setiferus	4.6 (11.5)	0.8 (12.9)	0.6 (14.1)

TABLE 6. — Comparisons of mean catch per tow and mean total length (cm) between day and night catches of penaeid shrimps taken from the St. Andrews Bay system, Fla., in August 1973.

Species	Day	Night
Penaeus duorarum	34.8 (8.2)	172.4 (8.4)
Trachypenaeus similis	0.3 (6.4)	8.0 (6.2)
Sicyonia brevirostris	0 (—)	1.7 (7.6)
S. dorsalis	1.2 (5.6)	5.2 (5.4)
T. constrictus	0 (—)	0.3 (4.1)
P. aztecus	3.0 (13.1)	9.5 (13.2)
P. setiferus	0.8 (11.1)	1.5 (10.2)
No. of tows	12	12

SIZE

Shrimps of the genus *Penaeus* were larger than shrimps of the other two genera. *Penaeus setiferus* had the largest mean length, while *S. dorsalis* had the smallest. Mean total lengths in centimeters and length ranges in centimeters for each species in the St. Andrew Bay system were: *P. duorarum,* 9.5, 4.0-18.5; *T. similis,*6.6, 3.0-10.0; *S. brevirostris*, 5.7, 2.8-9.5; *S. dorsalis*, 5.5, 2.0-7.8; *T. constrictus,* 4.5, 2.5-8.0; *P. aztecus,* 12.4, 4.5-18.5; and *P. setiferus,* 13.3, 7.0-16.0.

Differences in lengths of shrimps associated with water depth were examined (Table 5); notable differences were discernible only for the genus *Penaeus,* the larger specimens of which generally were found in deeper waters. This relation has also been reported by others (Lindner and Cook 1970; Cook and Lindner 1970; Costello and Allen 1970). Species of *Trachypenaeus* and *Sicyonia* showed little difference in mean lengths with water depths, although the largest mean sizes were found in the deeper zone.

Examination for differences in lengths associated with sampling at night and during the day revealed clearly that hour of sampling had no effect on size of captured shrimps (Table 6).

Comparisons of mean total lengths for the seven species between those subareas from which sufficient data were available showed that the largest shrimps were in either St. Andrew Bay or East Pass (Table 7). However, statistically significant differences were found for only three species: *P. duorarum, T. similis,* and *P. setiferus*.

For five of the seven species, larger specimens were caught in the lower area more often than in the upper area. The situation was reversed for *S. brevirostris,* whereas, for *T. constrictus* the mean sizes for the two areas were the same. Mean lengths in centimeters by species between upper and lower bay areas, respectively, were: *P. duorarum,* 9.1, 9.9; *T. similis,* 6.4, 6.7; *S. brevirostris,* 6.3, 5.7; *S. dorsalis,* 5.4, 5.6; *T. constrictus,* 4.5, 4.5; *P. aztecus,* 11.9, 12.8; and *P. setiferus,* 11.7, 14.7.

Shrimps of the genus *Penaeus* were almost consistently larger in the lower area throughout the year (Figure 4). As shrimps of this genus grow larger, they tend to move into deeper, more saline, and less turbid waters.

When present in both areas at the same time, the two species of *Trachypenaeus* were larger in the lower area more often than in the upper, whereas the reverse was true of the two species of *Sicyonia.*

DISCUSSION AND CONCLUSIONS

In general, water depths and salinities are greater, and turbidities, temperature fluctua-

TABLE 7. — Comparisons of mean total length (cm) of penaeid shrimps between subareas (Tukey's *w*-procedure) of the St. Andrew Bay system, Fla., from September 1972 through August 1973.

Species	Subareas, mean total length in parentheses, and significance lines[1]					df
Penaeus duorarum	North Bay (8.89)	West Bay (9.12)	East Bay (9.19)	East Pass (9.77)	St. Andrew Bay (9.81)	120
Trachypenaeus similis	East Pass (5.86)	West Bay (6.20)	East Bay (6.67)	St. Andrew Bay (6.82)		72
Sicyonia brevirostris	St. Andrew Bay (5.66)	East Pass (5.81)				24
S. dorsalis	East Bay (5.37)	West Bay (5.44)	St. Andrew Bay (5.50)	East Pass (6.30)		36
T. constrictus	East Bay (4.23)	St. Andrew Bay (4.43)	West Bay (4.67)	North Bay (4.77)	East Pass (4.90)	10
P. aztecus	North Bay (11.41)	West Bay (11.53)	East Bay (12.50)	St. Andrew Bay (12.79)	East Pass (12.96)	30
P. setiferus	East Bay (11.03)	West Bay (11.68)	North Bay (12.90)	St. Andrew Bay (14.68)		12

[1]Any two means not underscored by the same line are significantly different at the 5% level.

tions, and river discharges are lower in the St. Andrew Bay system than in other northern gulf estuaries (Apalachicola Bay to the Rio Grande River). The dominant group of spermatophytes in the lower area are the submerged sea grasses, whereas in most other northern gulf estuaries the dominant groups are the emergent grasses in the intertidal zone (Kutkuhn 1966). This unusual estuarine environment in the St. Andrew Bay system may induce shrimps of the genus *Penaeus* to remain within the system for longer periods of time, especially in the lower areas where oceanic conditions often prevail.

Such environmental differences probably account for the differences observed in composition, abundance, and size of penaeid shrimps between the St. Andrew Bay system and other estuarine systems in the northern Gulf of Mexico. For example: 1) large adult (total length ranges of 16.5 to 18.5 cm) *P. duorarum* and *P. aztecus* usually occur only in offshore waters, but we caught many of these large specimens throughout the St. Andrew Bay system; 2) in low salinity waters characteristic of other bay systems subadult *P. setiferus* and *P. aztecus* are more abundant than *P. duorarum*, whereas in the St. Andrew Bay system we found subadult *P. duorarum* more abundant than *P. setiferus* and *P. aztecus*; and 3) previous reports indicated that *T. similis*, *S. brevirostris*, and *S. dorsalis* do not ordinarily enter estuaries (Eldred 1959; Joyce 1965; Kutkuhn 1966; Cobb et al. 1973), but we caught many individuals of these species within the St. Andrew Bay system.

The abundance of shrimps of *Trachypenaeus* and *Sicyonia* in the St. Andrew Bay system contrasts sharply with those reported from other estuarine areas of the Gulf of Mexico. Other investigators have included catches made adjacent to barrier islands or tidal passes and reported abundances of less than 1 shrimp per tow. (Dunham 1972; Gunter 1950; Saloman 1964, 1965; Swingle 1971). In our study, average catch per tow (excluding Station 6, which is adjacent to a barrier island) for each species was: *T. similis*, 36; *T. constrictus*, 8; *S. brevirostris*, 19; *S. dorsalis*, 21.

Periods of greatest abundance of *S. brevirostris* in offshore waters of the northwestern and southeastern gulf occur in summer and early fall (Brusher et al. 1972; Cobb et al. 1973). In the St. Andrew Bay system, this species was almost absent during this period. We believe that this shrimp migrates from inshore to offshore gulf waters during spring months.

Means and ranges of total lengths of species of *Trachypenaeus* or *Sicyonia* taken in other estuarine areas were usually less (Swingle 1971; Dunham 1972) than those taken in offshore areas

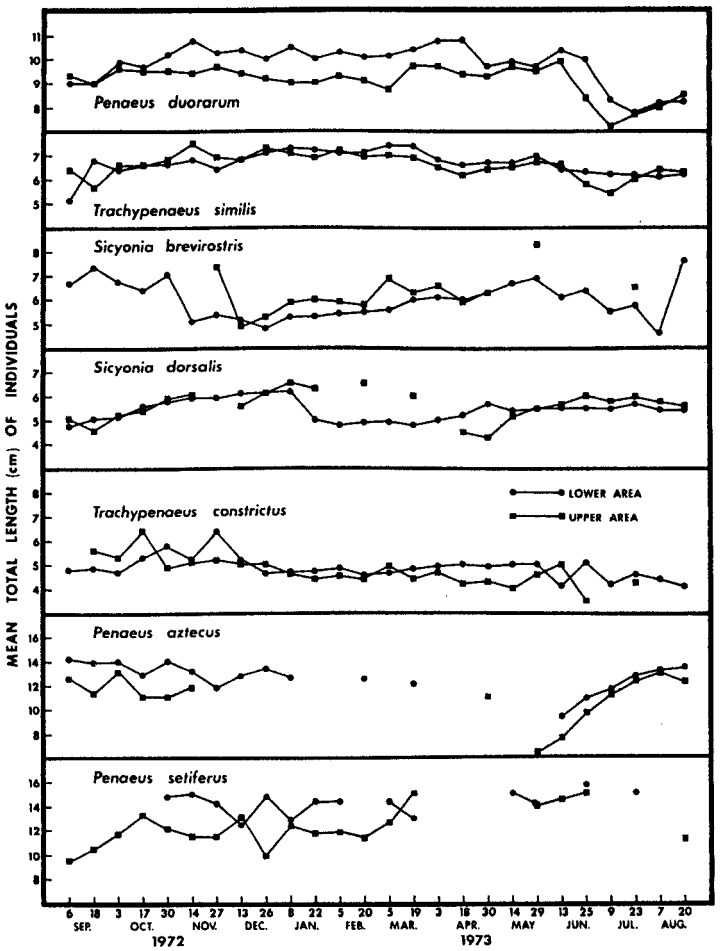

FIGURE 4.—Mean total lengths of seven penaeid shrimp species in the upper and lower areas of the St. Andrew Bay system, Fla., 1972-73.

of the Gulf of Mexico (Brusher et al. 1972). The mean total lengths of the penaeids with the exception of *T. constrictus* (Table 7) were similar to those reported by Brusher et al. (1972) for specimens caught in the Gulf of Mexico. We believe that species of *Trachypenaeus* and *Sicyonia* utilize St. Andrew Bay as a nursery area owing to the similarity of the bay to offshore oceanic habitats.

Of the three species of *Penaeus* caught in this study, *P. duorarum* was the most abundant. High abundance of *P. duorarum* was expected, because the highest concentration of this species in the Gulf of Mexico occurs in the eastern areas (Costello and Allen 1970). Costello and Allen associated *P. duorarum* with grass beds; grass beds are abundant in St. Andrew Bay. Low abundance of *P. aztecus* and *P. setiferus* was expected also, as these are found most abundantly in the northwestern (Texas coast) and north central (Louisiana coast) portions of the Gulf of Mexico, respectively (Cook and Lindner 1970; Lindner and Cook 1970).

Although similar gear and trawling methods were used, mean total lengths and length ranges of *P. aztecus* and *P. duorarum* caught in the St. Andrew Bay system differed greatly from those caught in other gulf estuaries (Saloman 1965; Trent et al. 1969; Dunham 1972). Our catches included many specimens over 13.0 cm total length which, according to Joyce (1965), is well above the size at which shrimps of the genus *Penaeus* are believed to leave estuarine areas. Shrimps of this genus greater than 10 cm total length are usually found in offshore waters (Lindner and Cook 1970; Cook and Lindner 1970; Costello and Allen 1970).

We conclude that the St. Andrew Bay system is unusual among estuaries of the northern Gulf of

Mexico; its environmental qualities which are much more similar to those in the gulf account for the common occurrence in the bay of penaeid shrimps of the genera *Trachypenaeus* and *Sicyonia* normally found in the offshore waters of the open gulf; the unusual environmental factors within the system also delay the migration of penaeid shrimps of the genus *Penaeus* into the open gulf, thereby allowing them to grow larger within the St. Andrew Bay system.

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LITERATURE CITED

BRUSHER, H. A., W. C. RENFRO, AND R. A. NEAL.
1972. Notes on distribution, size, and ovarian development of some penaeid shrimps in the northwestern Gulf of Mexico, 1961-62. Contrib. Mar. Sci. 16:75-87.

COBB, S. P., C. R. FUTCH, AND D. K. CAMP.
1973. The rock shrimp, *Sicyonia brevirostris* Stimpson, 1871 (Decapoda, Penaeidae). Mem. Hourglass Cruises 3(1):1-38.

COOK, H. L., AND M. J. LINDNER.
1970. Synopsis of biological data on the brown shrimp *Penaeus aztecus aztecus* Ives, 1891. FAO (Food Agric. Organ. U.N.) Fish. Rep. 57:1471-1497.

COSPER, T. C.
1972. The identification of tintinnids (Protozoa: Ciliata: Tintinnida) of the St. Andrew Bay system, Florida. Bull. Mar. Sci. 22:391-418.

COSTELLO, T. J., AND D. M. ALLEN.
1970. Synopsis of biological data on the pink shrimp *Penaeus duorarum duorarum* Burkenroad, 1939. FAO (Food Agric. Organ. U.N.) Fish. Rep. 57:1499-1537.

DUNHAM, F.
1972. A study of commercially important estuarine-dependent industrial fishes. La. Wildl. Fish. Comm., Tech. Bull. 4, 63 p.

ELDRED, B.
1959. A report on the shrimps (Penaeidae) collected from the Tortugas controlled area. Fla. State Board Conserv. Mar. Lab., Spec. Sci. Rep. 2, 6 p.

GUNTER, G.
1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):7-51.

HOPKINS, T. L.
1966. The plankton of the St. Andrew Bay system, Florida. Publ. Inst. Mar. Sci., Univ. Tex. 11:12-64.

ICHIYE, T., AND M. L. JONES.
1961. On the hydrography of the St. Andrew Bay system, Florida. Limnol. Oceanogr. 6:302-311.

JOYCE, E. A., JR.
1965. The commercial shrimps of the northeast coast of Florida. Fla. State Board Conserv. Mar. Lab., Prof. Pap. Ser. 6, 224 p.

KUTKUHN, J. H.
1966. The role of estuaries in the development and perpetuation of commercial shrimp resources. Am. Fish. Soc., Spec. Publ. 3:16-36.

LINDNER, M. J., AND H. L. COOK.
1970. Synopsis of biological data on the white shrimp *Penaeus setiferus* (Linnaeus) 1797. FAO (Food Agric. Organ. U.N.) Fish. Rep. 57:1439-1469.

MCNULTY, J. K., W. N. LINDALL, JR., AND J. E. SYKES.
1972. Cooperative Gulf of Mexico estuarine inventory and study, Florida: Phase 1, area description. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC-368, 126 p.

MOFFETT, A.
1968. A study of Texas shrimp populations, 1968. Tex. Parks Wildl. Dep., Coastal Fish. Proj. Rep., p. 67-93.

SALOMAN, C. H.
1964. The shrimp *Trachypeneus similis* in Tampa Bay. Q. J. Fla. Acad. Sci. 27:160-164.
1965. Bait shrimp (*Penaeus duorarum*) in Tampa Bay, Florida—biology, fishery economics, and changing habitat. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 520, 16 p.

SALSMAN, G. G., W. H. TOLBERT, AND R. G. VILLARS.
1966. Sand-ridge migration in St. Andrew Bay, Florida. Mar. Geol. 4:11-19.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill Book Co., N.Y., 481 p.

STOKES, G. M.
1974. The distribution and abundance of penaeid shrimp in the lower Laguna Madre of Texas, with a description of the live bait shrimp fishery. Tex. Parks Wildl. Dep., Tech. Ser. 15, 32 p.

SWINGLE, H. A.
1971. Biology of Alabama estuarine areas—cooperative Gulf of Mexico estuarine inventory. Ala. Mar. Resour. Bull. 5, 123 p.

TOLBERT, W. H., AND G. B. AUSTIN.
1959. On the nearshore marine environment of the Gulf of Mexico at Panama City, Florida. U.S. Navy Mine Def. Lab., Tech. Pap. TP-161, 104 p.

TRENT, W. L., E. J. PULLEN, C. R. MOCK, AND D. MOORE.
1969. Ecology of western Gulf estuaries. *In* Report of the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas, fiscal year 1968, p. 18-24. U.S. Fish Wildl. Serv., Circ. 325.

VICK, N. G.
1964. The marine ichthyofauna of St. Andrew Bay, Florida, and nearshore habitats of the northeastern Gulf of Mexico. Tex. A&M Univ. Dep. Oceanogr. Meteorol., Proj. 286-D, Ref. 64-19T, 77 p.

WALLER, R. A.
1961. Ostracods of the St. Andrew Bay system. M.S. Thesis, Florida State Univ., Tallahassee, 46 p.

SOME FEATURES OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, FRY EMERGING FROM SIMULATED REDDS AND CONCURRENT CHANGES IN PHOTOBEHAVIOR

J. C. MASON[1]

ABSTRACT

The emergence of sibling coho fry from simulated redds lasted 20-23 days during which 97-98% of the fry emerged. Average size of emerging fry increased with time but the largest fry emerged during the peak of emergence. No clear preference was shown for nocturnal or daylight emergence but the latter increased with time. Fry showed a positive current response, 69-82% moving upstream following emergence. Most fry emerged when yolk reserve was reduced to less than 10% of total dry weight. Later-emerging fry did not have lower yolk reserves, but fry moving downstream had slightly more yolk reserve than did fry moving upstream. Fry which were captured shortly after emergence had fed actively but had not yet filled their air bladders. Chironomids composed 70% of their diet.

Photoresponse of sibling fry denied the redd experience was studied in light-dark choice boxes with reference to the timing of emergence of fry from the simulated redds. The pronounced photonegative behavior of the denied fry was suddenly lessened at time of emergence but remained photonegative. Weakening of the negative photoresponse was not the outcome of starvation or recent light experience, and was not modified by repeated testing. Retention of the photonegative response is referred to hiding behavior and use of the gravel bed as a refuge.

The anadromous female Pacific salmon, *Oncorhynchus*, usually buries her eggs in several adjacent pockets in streambed or lakeshore materials and these egg pockets collectively constitute a redd. The eggs hatch after several months and the larvae may spend several weeks or months using up their extensive yolk stores prior to emerging from the redd area into open water.

Mortality during this extended period of subterranean life may be considerable (Royce 1959) and probably routinely exceeds 70% for most species of salmonids in natural habitats. Adaption to suboptimal conditions includes physiologic and behavioral responses in the embryo and larva which were reviewed, especially for sockeye salmon, *O. nerka*, by Bams (1969).

Because destructive influences on the egg and alevin stages are amenable to amelioration through manipulation of substrate structure and flow regime, spawning channels pioneered by Wickett (1952) at Nile Creek have become a major component of salmon enhancement strategy. Despite these advances, we have yet to define optimal redd conditions, biotic and abiotic, which maximize preemergence survival of any salmonid. Furthermore, fry surviving to emergence may face extended ecological consequences of suboptimal conditions in the redd which alter timing of, or size at, emergence (Mason and Chapman 1965; Mason 1969). Neither can we yet define for the emerging fry physiologic and behavioral states which optimize survival in open waters. Thus, premature emergence, implying underdevelopment and reduced ability to respond adaptively is not referrable to a defined state of normality.

Alevins of *Oncorhynchus*, as are those of *Salmo* and *Salvelinus* (White 1915; Stuart 1953; Woodhead 1957), are initially negatively phototactic and respond to light by hiding (Hoar 1958). They become positively phototactic and rheotactic as emerged fry, orientation to current preceding the shift from negative to positive phototaxis (Dill 1969) as in *Salmo* (Grey 1929a; Stuart 1953) but the timing of this photobehavioral change in relation to emergence and remaining yolk reserve remains unknown in *Oncorhynchus* and disagreement has arisen as to its timing in *Salmo* (Woodhead 1957). Histophysiological studies by Ali (1959) showed that only emerged fry and older stages of *Oncorhynchus* are capable of full retinomotor responses; however, partially developed responses have obvious survival value.

In this paper, some features of sibling coho fry

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emerging from simulated stream redds are described. Light and current responses; length, weight, and condition; remaining yolk reserves at emergence; and changes in photoresponse were investigated. The possible effects on photoresponse of repeated testing, previous exposure to light, and feeding experience were also examined.

MATERIALS AND METHODS

Emergence from Simulated Redds

The emergence of coho salmon fry of known parentage (two males × one female) from four simulated redds was investigated in two pairs of wooden channels (Figure 1) located outdoors. Each channel was divided into three equal-sized compartments, and to simulate a redd, each center compartment was filled to a depth of 27 cm with stream pebbles 2-5 cm in diameter. A standpipe terminating at its lower end in a 10 cm × 10 cm platform on 10 cm stilts so as to enclose a chamber of 100 cm^3 volume was buried in each redd at this time. In each redd the gravel surface was entirely underwater, but a shallow median depression served to concentrate the surface flow issuing through the V-notch openings.

The frames of the inner partitions were covered with a double layer of fine plastic screen to allow for circulation through the redds. Water flow through each channel was 12 liters/min, about 30% of which passed through the redds.

Ten days after hatching, 150 alevins from eggs incubated and hatched in standard baskets and previously unexposed to light were introduced into each redd at night via its standpipe and allowed to emerge spontaneously. Each standpipe was cleared of fry 1 h after stocking the redd by inserting a wire rod capped with rubber stoppers at either end and leaving the rod in place. Emerged fry could enter either the upstream or downstream compartments by way of the V-notch openings and were collected there daily at dawn and dusk.

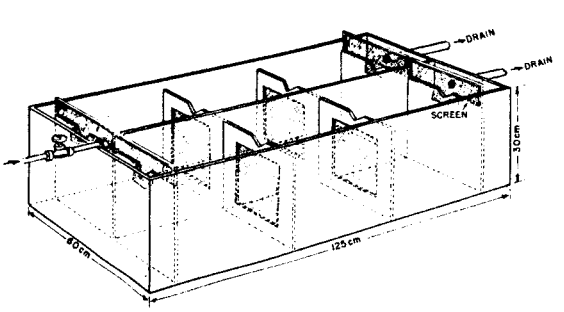

FIGURE 1.—Compartmentalized wooden channels. Center compartments contained the simulated redds. Dotted areas signify screens.

Emerging fry were anesthetized with MS-222,[2] fork length was measured to the nearest 0.1 mm using a dissecting microscope, weight determined to the nearest 0.1 mg on a Mettler Grammamatic balance after blotting, and the fry then preserved in 5% Formalin. For each redd, samples of 20 fry were extracted from each quartile of the emerging population (total of 80 fry per redd) divided between fry moving upstream or downstream following emergence. Yolk reserve at emergence was determined by dissecting out the yolk material, drying both yolk and fry to constant weight at 80°C, and expressing yolk reserve as a percentage of total dry weight.

The resulting data were processed by regression and analysis of variance techniques to expose possible correlations between length, weight, condition (K) and yolk reserve with time, directional movement in current, and emergence during the daylight or darkness.

Photoresponse Tests

Ten days after hatching, sibling alevins from the same experimental stock as those used for the emergence study but denied the redd experience were separated into five groups of 50 fish each and held indoors in wire baskets except during testing. Two groups were held in complete darkness. One of these groups was tested frequently (dark experimental, DE); the other was tested once then not retested until 15 days later (dark control, DC). The three remaining groups were held in baskets partly exposed to daylight of about 200 ft-candles peak intensity from an adjacent window and were given three different treatments. One group was tested frequently (light experimental, LE); one was tested once then not retested until 15 days later (light control, LC). The remaining group was not tested until the 18th day and, in contrast to the other groups, was fed frozen ground beef liver three times daily from day 9 onward (light control plus food).

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Photoresponse tests were conducted in four choice boxes placed in an uncompartmentalized replicate of the emergence channels and located adjacent to them. The choice boxes were constructed of fine plastic screen on a wire framework (Figure 2) and divided equally into two compartments by a vertical partition that allowed a passage height of 1.5 cm beneath it. Both hinged top and the partition were made of black polyethylene sheeting. The wooden channel was covered with the same material, except in the areas taken up by the boxes, so that the compartments not covered by the hinged tops received most of the illumination in the boxes. Each box presented a choice between sharply contrasting light conditions rather than between "light" and "no light," because some light leaked under the partitions. A series of mirrors was mounted 1 m above the water surface, allowing observation from a blind.

Water flow in the channel was 10 liters/min and velocity less than 10 cm/min. Water depth in the choice boxes was 10 cm providing an air space of 3 cm between the water surface and the ceiling of the covered compartment. Average fish density was set so as to allow about twice as much water volume and 2.4 times as much bottom area as in the holding baskets. Temperature of the water supply (stream) ranged from 7.8° to 11.7°C during the experimental period. Light intensities at the exposed water surface ranged from 700 to 4,000 ft-candles during photoresponse tests.

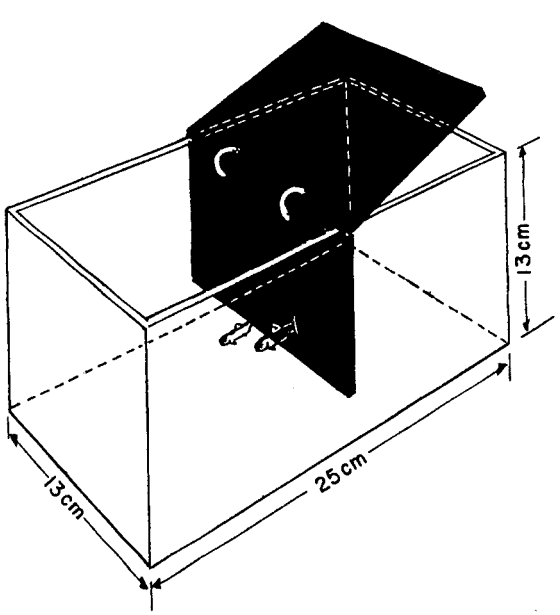

FIGURE 2.—Light-dark choice box showing the reversible opaque lid.

The procedure for a photoresponse test was as follows. The appropriate group of fry was transferred to the test site in a covered pail, 40 fry were netted out and 10 fry put in each of the four choice boxes with the lids in an upright position. The lids were then closed in a common direction, and the remaining fry were returned to their holding basket. In the choice boxes, all fry swam into the dark compartments when the lids were dropped. After 30 min, the number of fry observed in the light compartments were recorded every 10 min for 40 min (5 observations in each of 4 compartments = 20 observations). A fish was considered to be in a light compartment when its head was visible. The lids were then reversed and, after 10 min, five additional observations were made at 10-min intervals. Thus, for each test, 40 counts were recorded on 40 fry, which spent 2 h in the choice boxes per test and about 10 min in the transfer process. The photoresponse tests were initiated 1 day before fry began emerging from the simulated redds and continued until the 22nd day of emergence. Length and weight measurements were taken for all fry groups on the following day. Data were tested for homogeneity using chi-square. There was no significant difference ($P<0.01$) between the first and second runs of five observations each made in individual choice boxes, χ^2 values ranging from 0.0 to 2.8 in 132 pairs of runs. Similarly, the data from individual choice boxes proved homogeneous within each test in 29 of the 33 tests performed ($P<0.01$) χ^2 values ranging from 1.1 to 7.8 with 3 degrees of freedom. The remaining four tests contained heterogeneous data, χ^2 values ranging from 14.7 to 36.5 and were excluded from further analysis. With homogeneity assured within most tests, the data within tests were pooled and processed.

RESULTS

Emergence from the Simulated Redds

Fry began emerging 25 days after hatching and 15 days following introduction to the redds. Emergence proceeded for 20-23 days during which 97-98% of the fry emerged. All four redds showed a similar pattern of emergence, peaking at the same time, 74 to 94% of the fry emerging during the median 10 days (Figure 3).

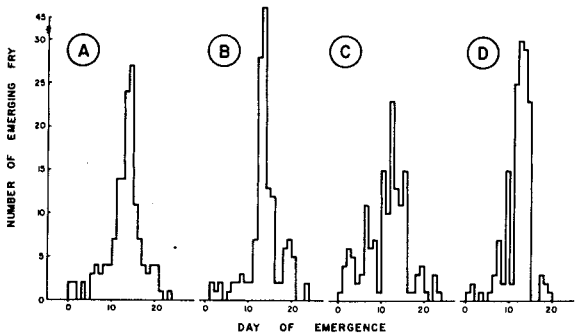

FIGURE 3.—Timing of coho salmon fry emergence from the simulated redds.

The average size of fry increased significantly ($P<0.01$) as emergence proceeded but the largest fry emerged during the peak of emergence from day 10 to day 15 (Figure 4).

More fry emerged at night than during the day in redds 2 and 3 (57% and 60%, respectively), but more fry emerged during the day in redd 1 (Table 1). No preference was shown by fry in redd 4 which emerged in equal numbers. Dividing the data into two time intervals, days 1 through 11, and days 12 through 24, revealed that emergence during the day increased some 30% in all four redds in the latter period.

Emerging fry showed a strong positive current response, the majority (69-82%) moving upstream subsequent to emergence, upstream movement increasing but slightly as emergence proceeded.

There were no significant differences in average length and weight ($P<0.01$) of fry moving upstream or downstream following emergence, but fry emerging during the day were, on the average, larger than those emerging at night (Table 1), significantly so in two redds (redd 3, $P<0.05$;

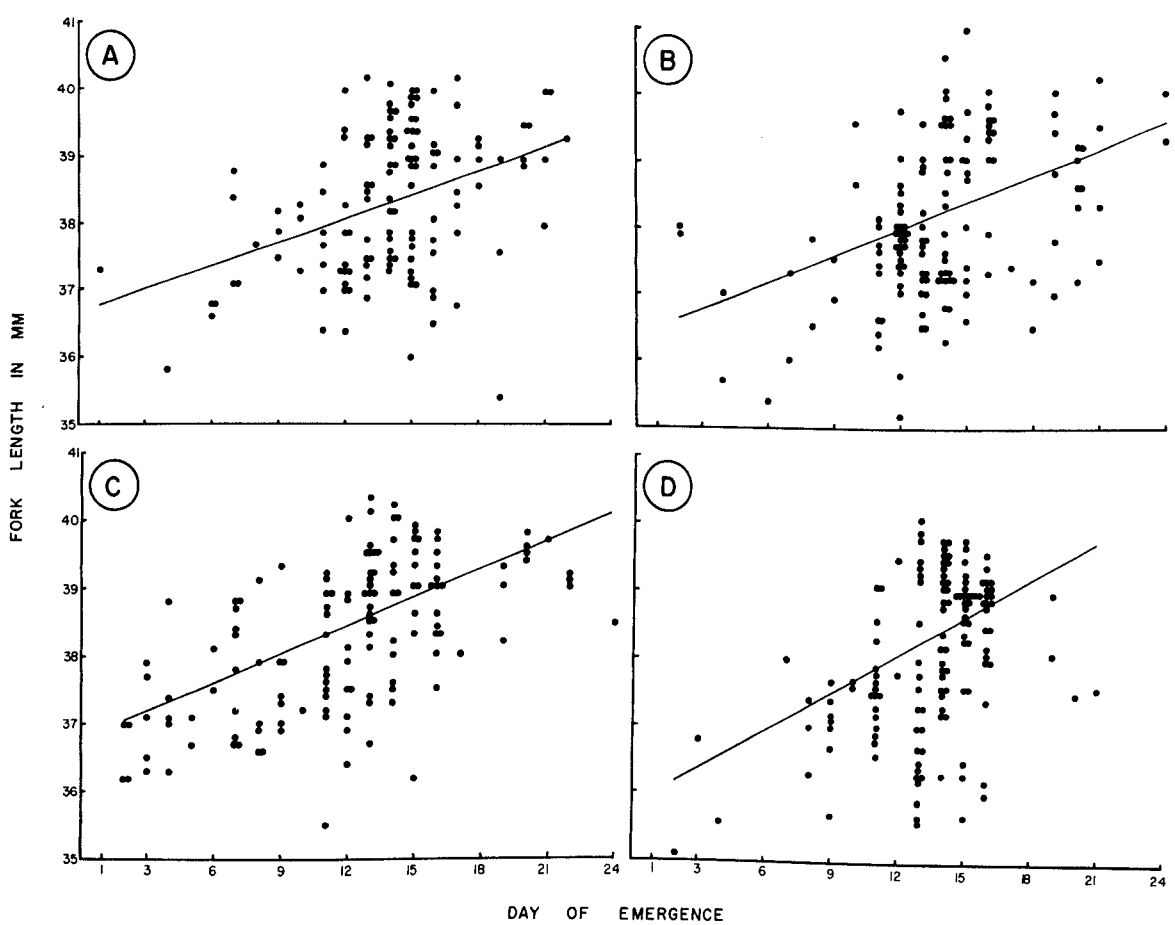

FIGURE 4.—Size of coho salmon fry at emergence including the regression lines.

TABLE 1. — Average lengths of sibling coho fry emerging from four simulated redds, stratified as to night and day timing and direction of movement. Values in parentheses are percentages.

Redd		Upstream movement	Downstream movement	Night emergence	Day emergence
1	Number of fry	94(69.1)	42(30.9)	53(39.0)	83(61.0)
	Mean fork length (mm) ± SE	38.39 ± 0.11	38.12 ± 0.18	38.13 ± 0.18	0.15 ± 0.15
2	Number of fry	115(80.4)	28(19.6)	82(57.3)	61(42.7)
	Mean fork length (mm) ± SE	38.08 ± 0.11	37.91 ± 0.21	38.00 ± 0.12	38.11 ± 0.15
3	Number of fry	113(79.0)	30(21.0)	86(60.1)	57(39.9)
	Mean fork length (mm) ± SE	38.25 ± 0.11	38.48 ± 0.18	38.14 ± 0.11	38.54 ± 0.15
4	Number of fry	116(82.3)	25(17.7)	70(49.6)	71(50.4)
	Mean fork length (mm) ± SE	38.10 ± 0.11	38.00 ± 0.38	37.68 ± 0.15	38.48 ± 0.13
Total emerging fry		438(77.8)	125(22.2)	291(51.7)	272(48.3)
Pooled mean fork length (mm)		38.19	38.14	38.12	38.38

redd 4, $P<0.01$). This is the outcome of the tendencies for both increased emergence during the day and increased size at emergence as time progressed.

Of the 584 fry that emerged from the simulated redds, 14 rather small fry emerged 5 or more days prior to the onset of general emergence. Twelve of these fry emerged at night and went downstream. They, and seven additional fry which also moved downstream and were designated as cripples due to truncated vertebral columns, were deleted from the analyses.

Most fry emerged when their yolk reserve was reduced to less than 10% of total dry weight (Figure 5), average reserve being 5-7% of total dry weight. The three rather high points (days 9-10) for fry moving downstream represent small samples whose means were inflated by premature fry. Yolk reserve in these samples was either less than 8% or ranged between 26 and 60% for individual fry. The large standard errors shown in Figure 5 are all associated with mean values inflated by premature fry. Yolk reserve did not diminish with time, indicating that the majority of fry were in a similar nutritional state at emergence. Although there were no significant differences in length and weight between fry moving up or downstream, fry moving downstream had more yolk reserve (9.2%) than did fry moving upstream (7.4%), this difference being significant at the 1% level. Similarly, in 13 of 16 possible pairs of samples from the four redds, the downstream fry contained more yolk reserve.

To discover if fry were feeding within a short time of emergence, the digestive tracts of 75 fry emerging from redds 1 and 2 were examined. These fry were representative with regard to night or day emergence and upstream or downstream movement following emergence, throughout the period of emergence. No dietary differences were found in the 74 fry that had fed shortly before their capture. As both stomach and intestine contained food particles, fry emerging at night probably fed that night or during the preceding hours of daylight while in the redd. Chironomids constituted nearly 65% of their diet (Table 2), mites and Collembola made up 17%, and together these three items were consumed by 83% of the fry.

At time of capture in the upstream and downstream compartments, no fry had yet reached neutral buoyancy although some had partially filled air bladders.

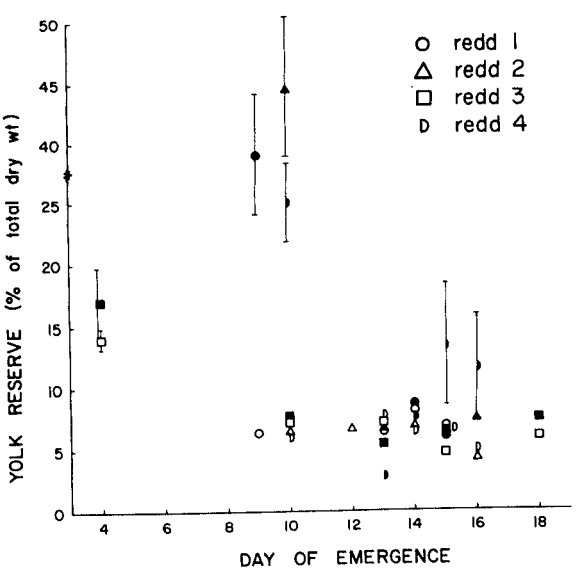

FIGURE 5.—Yolk reserve of coho salmon fry at emergence. Solid symbols indicate downstream movement following emergence; open symbols indicate upstream movement. Vertical bars indicate ±2 SE. For the remaining points, the range in SE was 0.1-1.0, and 90% ranged from 0.1 to 0.6.

TABLE 2. — Diet of 75 coho salmon fry emerging from two of four simulated redds supplied with river water.

Food item	Number of items	% of total items	% incidence
Chironomidae:			
Larvae	43	34.4	32.0
Pupae	20	16.0	21.4
Imagines	16	12.8	14.7
Total	79	63.2	68.1
Hydracarina	17	13.6	2.7
Collembola	13	10.4	12.0
Ephemeroptera nymphs	5	4.0	6.7
Arachnida	4	3.2	5.3
Trichoptera larvae	2	1.6	2.7
Plecoptera nymphs	1	0.8	1.3
Coleoptera imagines	1	0.8	1.3
Hymenoptera	1	0.8	1.3
Plant fragments	2	1.6	2.7

Concurrent Changes in Photoresponse

Photoresponse testing of fry denied the redd experience began on day 1, 1 day before their counterparts in the simulated redds began emerging. Their photoresponse remained essentially negative throughout the time period when, normally, they would have emerged. Until the eighth day of emergence (day 9), less than 3% of the denied fry were seen in the light compartments (Figure 6) and they remained strongly photonegative although nearly 13% of their sibs had emerged from the redds. By day 12, the collective negative photoresponse had weakened considerably, and nearly 15% of the denied fry were recorded then in the light compartments. By the 16th day of emergence, when 90% of their sibs had emerged, the percent of the fry recorded in the light compartments reached a plateau. From day 17 onward, 20-30% of the fry were seen in the light compartments (15 of 19 tests), but the response was more variable during the last day of testing, two of the tests (LC and DC) providing heterogeneous data. Interaction stemming from territorial behavior was the most likely source of variability, the light compartments being sporadically defended by single fry attempting to drive the others away.

Despite a decidedly negative photoresponse during the first 10 tests (Figure 6, Table 3), in 8 of these tests more fry held in darkness between tests were recorded in the light compartments than were those exposed to illumination between tests ($P<0.01$). Because there was no significant difference attributable to light history in subsequent tests, novelty due to limited light experience may have stimulated exploratory behavior during testing in fry held in darkness between tests. When tested on days 15 and 17, the control

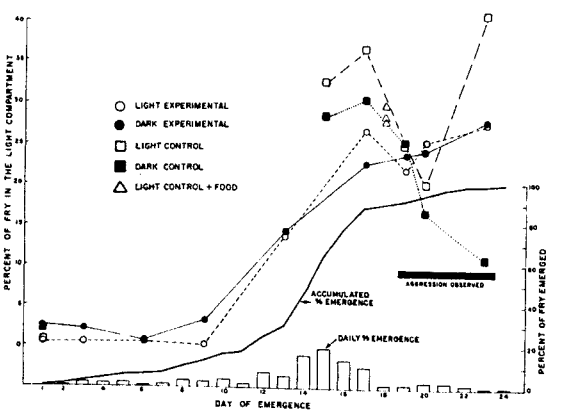

FIGURE 6.—Change in photoresponse of coho salmon fry held in baskets between tests. The histogram depicts the concurrent rate of emergence of 584 sibling fry from the four simulated redds.

TABLE 3. — Fry sightings in the light compartment of each of four choice boxes containing 10 fry during photoresponse tests, expressed as a percentage of possible sightings (400/test). Bracketed values are standard errors.

Day	Light experimental (LE)	Dark experimental (DE)	Light control (LC)	Dark control (DC)	Light control plus food (LC+F)
1	0.3(0.3)	2.5(0.6)	0.5(0.3)	1.8(0.5)	
3	0.3(0.6)	2.0(0.8)			
6	0.3(0.1)	0.5(0.3)			
9	0.0	3.0(0.8)			
13	13.3(1.6)	13.8(1.5)			
15			32.2(2.4)	28.0(2.3)	
17	26.3(1.8)	22.3(1.9)	36.3(2.9)	30.0(2.3)	
18					26.8(2.8)
					[1]29.3(2.9)
					26.5(2.3)
19	21.5(1.8)	23.3(1.9)	24.3(2.0)	24.8(1.4)	
[2]20	25.0(1.6)	23.8(1.9)	19.8(1.6)	[1]16.3(1.9)	
23	27.0(1.8)	27.5(2.3)	[1]41.0(3.6)	[1]10.8(1.3)	

[1]Heterogeneous data.
[2]Fed in previous evening and 1 h prior to testing.

groups LC and DC showed higher counts ($P<0.01$) than did their experimental counterparts LE and DE tested on day 17 (Table 3). Nonsignificant differences in subsequent tests suggested that frequency of testing may have depressed the magnitude of photoresponse change.

Fry receiving supplemental food (LC+F) made scores similar to DC and LE groups ($P<0.01$) when tested on day 18, but lack of homogeneity in the data from one of the three tests performed precluded further evaluation.

Light history and recent feeding did not significantly affect response level when the four previously unfed groups were tested on day 20 (t = 1.3 with 158 df, $P<0.020$).

Differences in average length among the four unfed groups of fry 1 day after the last tests were not significant (Table 4, F = 0.33 with 3, 96 df) but fish in the LE and DE groups weighed significantly more and therefore had higher K values. Their heavier weight is attributed to feeding on natural drift foods available only in the choice boxes. The control group given supplemental food from day 9 onward were significantly longer than the other four groups of fry in average length (F = 11.4 with 4, 122 df, $P<0.01$) and weighed considerably more.

TABLE 4. — Average lengths, weights, and condition factors (K) of samples of 25 coho fry used in the photoresponse experiment, measured 1 day after final testing.

Treatment	Fork length (mm) SE	Live weight (mg)	K[1]
Light experimental	38.38 ± 0.23	442.2	0.783
Dark experimental	38.29 ± 0.21	432.4	0.771
Light control	38.33 ± 0.19	391.6	0.695
Dark control	38.17 ± 0.23	399.6	0.719
Light control with food supplement	39.60 ± 0.24	473.6	0.763

[1] $K = W \times 10^5/L^3$ where W is weight in milligrams and L is length in millimeters.

The average length of fry emerging from the redds (Table 1) did not differ significantly from that of the unfed siblings used in the photoresponse tests (Table 4). However, the emerging fry weighed somewhat less than fry of the experimental groups but more than those of the control groups ($\bar{X}$ = 425.7 mg) and were in similar condition to the experimental groups (K = 0.766).

DISCUSSION

Emergence from these simulated redds involved several differences from that reported by Koski (1966) for natural redds of coho salmon. Fry from individual natural redds took from 10 to 47 days ($\bar{X}$ = 35 days) to complete emergence which peaked 8-10 days after first emergence, and size of fry decreased as emergence proceeded. In the simulated redds, duration of emergence was 20-23 days peaking at 12-13 days and size increased with time although yolk reserve remained nearly constant. The physical structure of the natural redd, particularly the proportion of smaller particle sizes, restricted permeability and impeded emergence. Low permeability reduced size of fry and increased mortality, later-emerging fry and those failing to emerge that were excavated from redds were emaciated, weight loss indicating exhaustion of yolk prior to emergence.

As yolk reserves remained fairly constant throughout emergence from the simulated redds, the larger, later-emerging fry probably developed from larger eggs. Koski (1966) found that large female spawners produced large fry at emergence, but large size of progeny did not alleviate physical hindrance to emergence, typifying the majority of redds, leading to decreasing size of fry as emergence progressed.

The strong upstream response shown by fry emerging from the simulated redds is characteristic of coho fry emerging in natural streams. Apart from counteracting downstream transport, upstream movement provides for the seeding of upstream rearing areas unavailable to, or not used by, spawners. The small but significant difference in yolk reserve between fry moving upstream or downstream may reflect, rather than a minor difference in swimming ability, behavioral differences associated with rising aggression, onset of territoriality, and commencement of feeding on the invertebrate drift.

The lack of preference for nocturnal emergence is in contrast to findings for sockeye salmon; pink salmon, *O. gorbuscha*; and chum salmon, *O. keta*, fry which emerge primarily at night (Neave 1955; Heard 1964). But like these other species, the coho salmon fry retained a photonegative response at emergence of potential survival value, e.g. escape from predators. Stuart (1953) also reported that fry of brown trout, *Salmo trutta*, remained photonegative during their ascent in simulated redds, even upon reaching positions only 1 or 2 inches from the gravel surface. For several days after emerging, fry of coho salmon and cutthroat trout, *S. clarki*, will bolt back into the gravel bed when disturbed (pers. obs.) and

similar observations led Neave (1955) to comment that migrating chum and pink salmon fry, failing to reach the ocean in a single night, hide during the day and resume migration at nightfall. Hiding behavior disappears in coho salmon fry at time of complete yolk absorption but is retained for several days at high light intensities (Hoar 1958); this suggests a threshold intensity for the avoidance response which increases as the alevin stage proceeds.

Concurrence between change in numbers of fry observed in the choice chambers, a collective response, and the accumulated number of emergent sibs could reflect either a sudden shift in photoresponse of individual fry or gradual erosion of the negative response occurring simultaneously in all fry. The sudden shift alternative is best supported by three patterns of behavior noted in the choice chambers. Individual fry were observed to spend considerable time in the light compartment upon entering it, alternately swimming about slowly and remaining locally quiescent. Positions were commonly adopted with the head projecting into the light compartment (Figure 1), or entrance, and departure was rapid, irrespective of the presence or absence there of other fry until the last few days of testing when aggression was observed (Figure 6).

Despite near depletion of vitellus at time of emergence, the shift in photoresponse did not appear to be due to starvation because the response was not altered significantly by feeding. This is of interest as Smith (1952) reported marked metabolic changes in rainbow trout, *S. gairdneri*, alevins a few days prior to emergence, suggesting that these physiological events signified the onset of starvation. The change in photobehavior appears to be an ontogenetic behavioral change normally associated with emergence from the redd rather than one instigated by nutritional deficiency, premature feeding, or light experience. It remains unclear as to whether or under what conditions such stimuli can modify this change significantly; however, under hatchery conditions, Harvey (1966) found that sockeye salmon fry took food 2 wk after hatching but that emergence of fry from a simulated redd coincided with complete yolk absorption some 3 wk later. Heard (1964) noted that most emerging sockeye salmon fry trapped from natural redds in an Alaskan stream contained little or no yolk, remained photonegative, and emerged primarily during hours of darkness.

The timing of the photoresponse change relative to emergence and yolk reserves may vary within common limits for most stream salmonids and differences may reflect species-specific adaptions of value to fishery biologists. As in the fry emerging from the simulated redds, the yolk reserve of coho salmon fry emerging from natural redds averaged 7% (unpubl. data). Stuart (1953) observed a definite change in photoresponse of *S. trutta* when yolk neared depletion, and the photoresponse change was employed by Gray (1929b) to denote the conclusion of incubation when measuring the effect of temperature on alevin size at time of yolk depletion. Woodhead (1957) disagreed with Stuart as to the timing of the photoresponse change in *S. trutta*, and asserted that it occurred coincident with maximum activity of the alevin 15 days after hatching when yolk reserve constituted 70% of the dry weight of the fry. This considerable difference in timing remains unresolved.

Denying the photoresponse fry streambed experience during the last few weeks of the alevin stage had no apparent effect on the final size of the fry, probably due to their advanced stage of development prior to application of treatment differences. Marr (1963, 1965) has shown that developmental efficiency is reduced by exposure to natural light or lack of substrate contour which stimulate locomotor activity at the expense of growth. However, marked effects on locomotor activity were only measurable until development was 75-80% complete. The weight disparity between experimental and control groups of fry (Table 4) which was the outcome of weight loss or reduced weight gain is presumed to be an outcome of reduced feeding opportunity.

In summary, the present results show that coho salmon fry underwent a definite shift (sudden or otherwise) from a strong to a weak negative photoresponse. This shift was accompanied by a positive response to water current leading to preferred movement upstream. The emerging fry was an actively feeding animal yet to fill, or in the process of filling, its air bladder, fed in the gravel prior to emergence, and emerged when average yolk reserves declined to 7% of total dry weight. In contrast to fry emerging from natural redds (Koski 1966), later-emerging fry were larger than those emerging earlier and may have derived from larger eggs. Because first-emerging fry held ecological advantage over later-emerging fry in stream aquaria (Mason and Chapman

1965), the timing of emergence and environmental conditions which modify it and the ecological state of fry at emergence should be fruitful considerations in future research.

ACKNOWLEDGMENTS

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LITERATURE CITED

ALI, M. A.
1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. Can. J. Zool. 37:965-996.

BAMS, R. A.
1969. Adaptations of sockeye salmon associated with incubation in stream gravels. *In* T. G. Northcote (editor), Salmon and trout in streams, p. 71-87. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver, B.C.

DILL, L. M.
1969. The sub-gravel behavior of Pacific salmon larvae. *In* T. G. Northcote (editor), Salmon and trout in streams, p. 89-99. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver, B.C.

GRAY, J.
1929a. The growth of fish. II. The growth-rate of the embryo of *Salmo fario*. J. Exp. Biol. 6:110-124.
1929b. The growth of fish. III. The effect of temperature on the development of the eggs of *Salmo fario*. J. Exp. Biol. 6:125-130.

HARVEY, H. H.
1966. Commencement of feeding in the sockeye salmon (*Oncorhynchus nerka*). Verh. Int. Ver. Theor. Angew. Limnol. 16:1044-1055.

HEARD, W. R.
1964. Phototactic behaviour of emerging sockeye salmon fry. Anim. Behav. 12:382-388.

HOAR, W. S.
1958. The evolution of migratory behaviour among juvenile salmon of the genus *Oncorhynchus*. J. Fish. Res. Board Can. 15:391-428.

KOSKI, K. V.
1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. M.S. Thesis, Oregon State Univ., Corvallis, 84 p.

MARR, D. H. A.
1963. The influence of surface contour on the behaviour of trout alevins *S. trutta* L. Anim. Behav. 11:412.
1965. Factors affecting the growth of salmon alevins and their survival and growth during the fry stage. Assoc. River Auth. Yearb., 1965:1-9.

MASON, J. C.
1969. Hypoxial stress prior to emergence and competition among coho salmon fry. J. Fish. Res. Board Can. 26:63-91.

MASON, J. C., AND D. W. CHAPMAN.
1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Board Can. 22:173-190.

NEAVE, F.
1955. Notes on the seaward migration of pink and chum salmon fry. J. Fish. Res. Board Can. 12:369-374.

ROYCE, W. F.
1959. On the possibilities of improving salmon spawning areas. Trans. North Am. Wildl. Conf. 24:356-366.

SMITH, S.
1952. Studies in the development of the rainbow trout (*Salmo irrideus*). II. The metabolism of carbohydrates and fats. J. Exp. Biol. 29:650-666.

STUART, T. A.
1953. Spawning migration, reproduction and younger stages of loch trout (*Salmo trutta* L.). Freshwater Salmon Fish. Res. 5:1-39.

WHITE, G. M.
1915. The behaviour of brook trout embryos from the time of hatching to the absorption of the yolk sac. J. Anim. Behav. 5:44-60.

WICKETT, W. P.
1952. Production of chum and pink salmon in a controlled stream. Prog. Rep. Pac. Coast Stn., Fish. Res. Board Can. 93:7-9.

WOODHEAD, P. M. J.
1957. Reactions of salmonid larvae to light. J. Exp. Biol. 34:402-416.

FEEDING BEHAVIOR, FOOD CONSUMPTION, GROWTH, AND RESPIRATION OF THE SQUID *LOLIGO OPALESCENS* RAISED IN THE LABORATORY

ANN C. HURLEY[1]

ABSTRACT

The squid *Loligo opalescens* was raised in the laboratory to a maximum age of 100 days on a diet of *Artemia* nauplii and adults. Newly hatched squid (2.7 mm mantle length) readily attacked *Artemia* nauplii (length 0.7 mm), *Artemia* adults (length 5 mm), copepods (length 1 mm), and larval fish (length 4 mm). Feeding rates varied between 35 and 80% of squid body weight per day. Growth rate was highly variable in different individuals, ranging from 0.5 to nearly 4.5 mm mantle length per month. Respiration rates were obtained at 15°C for squid of three different ages and at 10°, 15°, and 20°C for 1-day-old squid.

The squid *Loligo opalescens* Berry is a common pelagic predator off the west coast of North America from British Columbia to Baja California. Because a fishery exists for this species, considerable information is available concerning adults in the spawning schools (Fields 1965), but little is known about the early life stages. In a paper on larval squid abundance off California, Okutani and McGowan (1969) found few *L. opalescens* in their samples; and McGowan (1954) reported that despite considerable effort he could not catch newly hatched *L. opalescens* over the spawning grounds.

To obtain information on the early life history, I reared *L. opalescens* in the laboratory. Several workers have succeeded in rearing decapod cephalopods, but all of the species they used tend to be closely associated with the bottom (Choe 1966, three species of *Sepia*, the squid *Sepioteuthis lessoniana*, the sepiolid *Euprymna berryi*; LaRoe 1971, *S. sepioidea*; Boletzky et al. 1971, four species of *Sepiola* and two species of *Sepietta*; Arnold et al. 1972, the sepiolid *E. scolopes*). Attempts to raise pelagic species such as *Loligo opalescens* have met with little success (Fields 1965; Arnold et al. 1974). Workers have attributed their failure to lack of food and to infections. I describe here a simple technique for rearing early stages of *L. opalescens* and present data on the growth, respiration, and food requirements of *L. opalescens* reared for 100 days in the laboratory.

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MATERIALS AND METHODS

Five groups (referred to as groups 1 through 5) of squid have been reared, three (1 through 3) of which will be described in detail in this report. Eggs were collected from a water depth of 20 m off La Jolla, Calif., and were maintained in circulating seawater at about 13°C. The young squid were transferred to the rearing tanks after they had hatched. Fields (1965) and McGowan (1954) have described the methods of egg deposition and structure of the egg masses in detail.

The rearing tanks were cylindrical (122 cm diameter, 36 cm deep) and made of black fiber glass. Tanks were illuminated by fluorescent lights which had a cycle of 18 h light, 6 h dark. During the dark period, lights in other rooms of the aquarium building provided a source of dim light. The tanks were immersed in water baths which kept the temperature within the tanks between 15° and 17°C. Squid were transferred to the rearing tanks with a beaker. Squid in groups 2 and 3 were counted during transfer. In group 1, the number of squid was estimated after the squid were in the tank. Groups 1 and 2 began with 300 squid; group 3 began with 250. The water in the tanks was noncirculating. Each tank was aerated by a gently bubbling air supply. The squid in group 1 were transferred to a holding tank on day 62 and on day 76, and on each day their tank was drained, cleaned, and refilled. Tanks 2 and 3 were both similarly cleaned on day 49. Dead food was removed from the bottom of all tanks with a siphon, and small amounts of seawater were added to maintain a constant volume.

During the first 4 wk the squid (groups 1 through 3) were fed newly hatched brine shrimp, *Artemia salina*, nauplii which were kept at densities ranging from 1 to 20 nauplii/ml. After this time, small adult brine shrimp were added (average length 5.4 mm; range 2.5 to 8.0 mm) and were the major source of nourishment for the remainder of the rearing period. In groups 4 and 5, small adult *Artemia* as well as nauplii were used as food during the first 4 wk.

Squid were measured using an optical micrometer on a dissecting microscope. Measurements are of dorsal mantle length (measured dorsally from the tip of the tail to the farthest anterior point on the mantle). Mantle length is less variable than a measurement of total length, which depends upon the degree of stretch of the arms and tentacles. To make possible conversions to total length, measurements were made of both dorsal mantle length (ML) and total length (to tips of arms, not tentacles) (TL) on 35 juvenile animals, and the average ratio ML/TL was 0.62 ± 0.014 (±2 SE). Measurements are all on freshly dead unpreserved animals. For weight measurements, squid were rinsed in distilled water and oven dried at 60°C to a constant weight.

Respiration measurements were made using a Warburg constant volume respirometer with respiration vessels kept at constant temperature in a water bath. The respiration vessels contained from 2 to 30 squid and were kept in constant motion by gentle shaking.

Estimates were made of the number of squid surviving at intervals throughout the study. The number of squid alive on any day was the average of three counts taken of live animals in the tank.

Daily observations were made of the feeding behavior of the squid. At various times throughout the day, a squid was selected and observed for about 5 min. The number of feeding attempts and successful captures of prey were recorded.

RESULTS

Survival

Mortality in all of the tanks was initially high (Figure 1). This is similar to what LaRoe (1971) found in rearing *Sepioteuthis sepioidea*. LaRoe speculated that the high initial mortality was due to insufficient quantities of food. This probably was not the case in my studies, as a large amount of food was continually available at this stage. Some of this mortality could have been caused by squid which did not initiate feeding. Fields (1965) found that *L. opalescens* which did not appear to be feeding lived up to 10 days and still had some internal yolk reserves left at the end of this time. From 30 to 60 days mortality was low, but after 60 to 70 days mortality again increased. It is possible that the brine shrimp did not provide an adequate diet for squid older than 60 days.

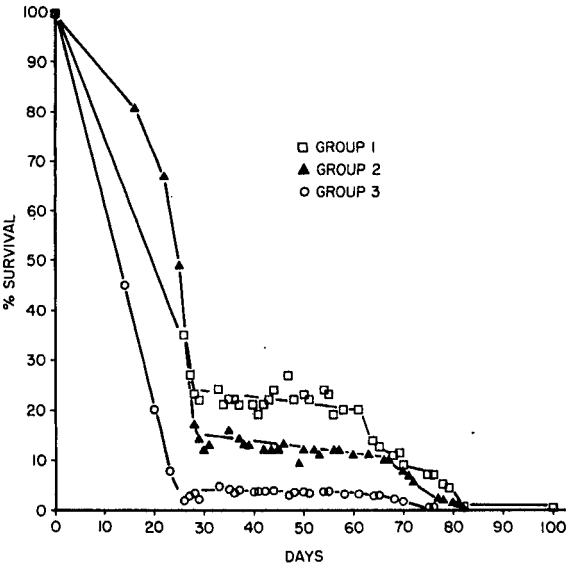

FIGURE 1.—Estimated percent survival of *Loligo opalescens* in the rearing tanks. Group 1 started with 300 squid; group 2, with 300 squid; and group 3, with 250 squid.

Feeding Behavior

Attack

The attack of a young *L. opalescens* is similar to that described for adult *Loligo* (Fields 1965), *Sepioteuthis* (LaRoe 1970), and *Sepia* (Messenger 1968). Messenger divided the *Sepia* attack into three motor patterns: attention, positioning, and seizure. These three patterns may also be used to describe the attack of young *L. opalescens*. During attention, the squid orients toward a particular prey. The arms and tentacles are extended in front of the squid and form a tight cone which is pointed toward the prey. Color changes such as those noted for *Sepioteuthis* (LaRoe 1970) and *Sepia* (Messenger 1968) were not observed.

After the squid oriented toward a particular prey, it approached the prey until it was within attacking distance (positioning). This distance was not constant. At times there was no clear separation between the attention and positioning patterns. LaRoe (1970) suggested that the positioning approach is an example of an aggression-fear conflict. This appears to be the case in *Loligo*. The young squid would sometimes flee rapidly after closely approaching a large prey.

The prey was usually captured with the tentacles (seizure), although occasionally the arms alone were used. The arms were used to maneuver the food toward the mouth. At times a new attack began while the squid was holding other prey in the arms.

LaRoe (1970) reported that for *Sepioteuthis sepioidea* physical fights over food were rare. This was not true for young *L. opalescens*. Fighting between squid was never observed when prey was small (brine shrimp nauplii), but if the prey was large and could not be completely enclosed within the arms, other squid would often chase the one which caught the food and try to take the food away from it. Often several (in one case, four) squid held on to the captured prey and all fed on it. The prey would be tugged about until one squid pulled it away from the others. This behavior occurred even when there was an abundance of prey in the tank. This attack on captured prey at times allowed small squid to eat larger prey organisms than they could normally subdue alone.

Prey Selection

Unlike *Sepioteuthis* (LaRoe 1971), young *L. opalescens* were not extremely selective as to the type and size of prey they would attack. Within a few days after hatching, the young *Loligo* (2.7 mm ML) readily attacked *Artemia* nauplii (0.7 mm long), *Artemia* adults (5 mm long), copepods (1 mm long), and larval fish (4 mm long). Occasionally, squid attacked and ate dead prey (e.g., dead *Artemia* dropped into the tank), but usually the food had to move before it was attacked. An exception to this was that the squid attacked fish larvae which appeared to be motionless in the water.

When the squid were 17 days old, nine squid from group 2 were placed in a small cylindrical container (8 liters of water) to determine whether a food size preference existed in *Loligo*. The food used was *Artemia* nauplii (0.6 to 0.8 mm long) at 10/ml and small adult *Artemia* (2 to 4 mm long) at 0.2/ml. After the squid were added, I recorded the number of attacks until a prey was captured and the type of prey being attacked. If no prey was captured in 20 min, I selected another squid. At this age, the squid attacked both large and small prey. During the 164 min of observation, 23 nauplii were attacked (9 actually captured) and 30 adults were attacked (8 actually captured). These results are different from those given for *Sepioteuthis sepioides* (LaRoe 1971). That squid only attacked food species in a very limited size range. Within several days, *Sepioteuthis* would cease to attack the prey it had previously eaten and would only attack larger prey. This seemed to occur when the squid were 1 to 1½ times as large as their prey. Although *Loligo* captured both large and small prey with about equal frequency, a preference may exist for larger prey as their density in the container was much lower.

An experiment was run with group 1 when the *L. opalescens* were 49 days old. In this case the choice was between two different prey species of approximately the same size. Two thousand 2-day-old chub mackerel, *Scomber japonicus*, larvae were added to one of the rearing tanks where the squid had been feeding on *Artemia* adults. There were approximately 2,000 *Artemia* in the tank. The same method was used to record feeding as in the previous experiment. Observation time in this case was 69 min. The squid showed a high incidence of attacks on fish larvae (52 attacks, 6 captures) even though the success rate was much lower than when attacking *Artemia* (4 attacks, 3 captures). This may indicate a preference for fish larvae, but without further experiments it is impossible to say whether this is true.

Feeding Success

The ability of the squid to successfully complete an attack sequence depended on the size and species of prey and the age and experience of the young squid. Figure 2 is a record of the percent of successful attacks on *Artemia* nauplii as a function of the age of the squid. Each point is an average from the squid observed during that day. The number of squid observed per day ranged from 5 to 11, with the total daily observation time ranging from 25 to 55 min. The attack efficiency increased with the age of the squid, but a number of prey were still being lost even after 3 wk. LaRoe

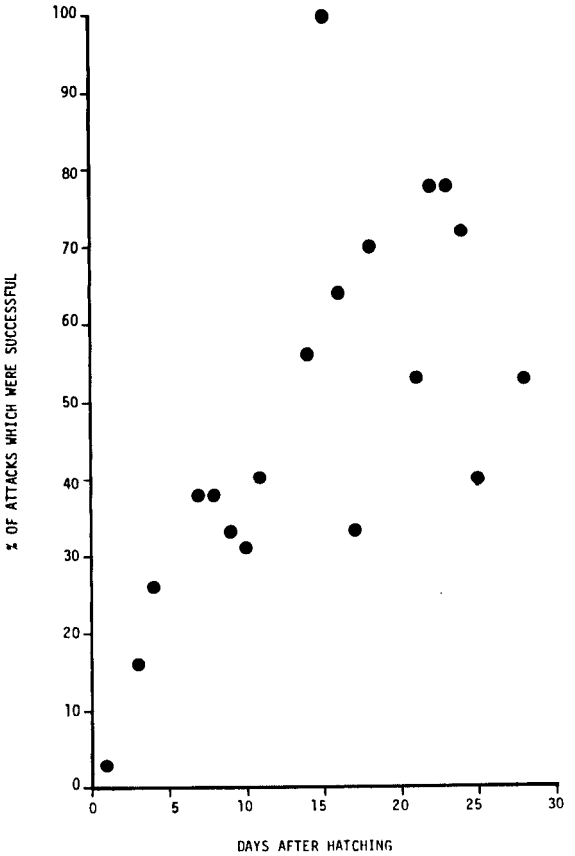

FIGURE 2.—Percent of attacks on *Artemia* nauplii which were successful as a function of the age of the squid.

(1970) found that for *Sepioteuthis*, the majority of the prey were lost because the squid were unable to judge the attack distance. In my experiments, most unsuccessful attacks occurred because the prey managed to escape after being initially struck. Some of the variability in success rates may have been due to different motivational states of the squid.

Feeding Rates

Several methods were used to determine the food ration of the developing squid. When the squid fed on nauplii, feeding rates were determined at irregular intervals by choosing a squid and watching it for 5 min to determine the number of *Artemia* nauplii consumed during this period. All of the observations accumulated during a given week were combined. For each week, I calculated the food eaten over a 24-h and 18-h feeding period. The squid captured prey when the overhead lights were off, but it was not possible to establish how much was eaten. When adult *Artemia* was the primary source of nourishment, record was kept of the approximate number of food organisms introduced to the tank and their average weight. There is some error introduced here because some of the brine shrimp died and were not consumed. The average weight of the squid during each week was obtained from the growth data and length-weight relationships presented in the next section. Average weight of *Artemia* adults was 0.3 mg (obtained from six random samples of 10 to 20 individuals each) and average weight of nauplii was 0.002 mg (John R. Hunter pers. commun.). Food consumption is shown in Table 1.

TABLE 1. — Estimated feeding rates (percent body weight eaten per day) of squid in rearing tanks. Each value is average for all values for a given week. Values through week 4 are based upon observed short-term feeding rates on *Artemia* nauplii and are given for assumed 18- and 24-h feeding periods. Subsequent values are based on counts of *Artemia* adults consumed in tanks 1 and 2.

	Nauplii		Adults	
Week	18 h	24 h	Tank 1	Tank 2
1	46	60	—	—
2	46	61	—	—
3	47	63	—	—
4	37	50	—	—
5	—	—	—	—
6	—	—	36	45
7	—	—	67	80
8	—	—	48	51

One short-term experiment was performed to examine the feeding rate of 36-day-old squid on yolk-sac larval anchovies. Five squid were placed with 100 anchovy larvae in 8 liters of water and were left for 285 min. At the end of this period 58 larvae had been eaten. This gives a feeding rate of 2.4 larvae/squid·hour. Theilacker and Lasker (1974) gave the average weight of a larva of this size as 0.022 mg. Using this information and the average weight of the squid, a feeding rate of 0.028 mg anchovy/mg squid·h is obtained.

Growth

Since the number of squid being reared was small, specimens were not sacrificed for growth measurements alone. Every time a squid died, it was immediately measured. These measurements constitute the majority of the points on the growth curve shown in Figure 3. The points indicated by the ×'s are measurements which were made on squid that had been selected while alive

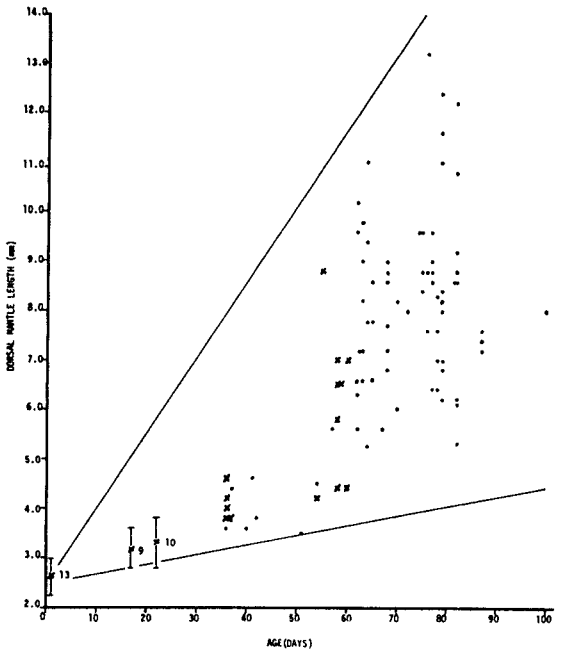

FIGURE 3.—Size data for *Loligo opalescens*. A dot denotes measurement made on squid which had died, and × denotes measurement made on squid that had been selected while alive to give an indication of the size range of individuals in the tanks. For days 1, 17, and 22, the numbers of squid measured, means, and ranges are given. The upper solid line gives a constant growth rate of 4.5 mm/mo. The lower one gives a rate of 0.5 mm/mo.

to give an indication of the full size range of squid in the tank. Since the squid were not randomly sampled during this time, Figure 3 cannot be taken to give an average growth rate for the population, but it does give an indication of the range of growth rates. There was a large difference in the rates of growth of individuals. Maximum growth rates were nearly 4.5 mm/mo (upper line in Figure 3). Minimum growth rates were 0.5 mm/mo (lower line in Figure 3).

The linear regression equation for the log length-log weight relationship for the developing squid is log weight (mg) = −1.22 + 2.37 log length (mm) with little scatter around the regression line.

Respiration

Measurements were taken of the oxygen consumption of young *L. opalescens* using a Warburg respirometer and a constant temperature water bath. Measurements were taken at 15°C for squid of three different ages and at 10°, 15°, and 20°C for 1-day-old squid (Table 2). Average oxygen consumption values are as follows: 1 day, 10°C, 1.5 μl O_2/mg squid·h; 1 day, 15°C, 2.5 μl O_2/mg squid·h; 1 day, 20°C, 3.5 μl O_2/mg squid·h; 3 wk, 15°C, 3.5 μl O_2/mg squid·h; 8 wk, 15°C, 3.7 μl O_2/mg squid·h. These measurements may be artificially high because of the crowding which occurred in the small respiration vessels. It was observed, however, that the oxygen consumption tended to decrease (at a given temperature) with increasing number of animals present in the same vessel. It is possible that these lower rates occurred because some of the animals became moribund in the crowded conditions. But this is not likely, since the respiration rates remained constant over the course of the 2-h experiments.

To compare these measurements to those made by other investigators, conversion factors had to be obtained to transform dry weight to wet weight. The ratio wet/dry was calculated for nine juvenile squid and gave a mean of 5.4 ± 0.21 (±2 SE). Wet weights were calculated by placing the squid on the weighing pan, blotting it with filter paper, weighing it at measured time intervals, and extrapolating the line obtained to zero time.

The previous rates expressed in terms of wet weight are: 0.28, 0.46, 0.65, 0.65, and 0.69 μl O_2/mg squid·h. These values are similar to those obtained by LaRoe (1971) for 2- and 6-day-old *Sepioteuthis sepioidea* (0.64 μl/mg·h at 23°C) and with the figure of 0.60 μl/mg·h for adult *L. pealei*, calculated from data in Redfield and Goodkind (1929).

TABLE 2. — Oxygen consumption rates for *Loligo opalescens*. Respiration vessels had a volume of 18 ml and contained approximately 5 ml seawater. The duration of the experiments was 2 h.

Temp. (°C)	*N*	Age of squid (days)	Number of squid/vessel	Range of oxygen consumption (μl O_2/mg squid (dry wt)·h)
10	3	1	10-30	1.4-1.6
15	3	1	8-25	2.1-3.6
20	3	1	10-21	3.2-3.8
15	1	21	10	3.5
15	2	56	2-3	3.5-3.9

DISCUSSION

It is extremely difficult to assess the role which an animal such as *L. opalescens* plays in the California Current ecosystem. Estimates of population size of adults are very poor because of the difficulties involved in sampling large active

animals. Fisheries statistics are not particularly helpful because the catches come mainly from a few locations. It has been possible to get some field information on the diet of the adult squid (Fields 1965) but these data are completely lacking on such necessary information as feeding rates.

It appears to be equally difficult to obtain information on young *L. opalescens* from field samples. The young squid have well-developed eyes and are very sensitive to vibrations. Therefore, even the young are likely to be able to avoid many nets. Okutani and McGowan (1969) published data on the abundance of young *L. opalescens* (size range 3.5 to 7 mm dorsal ML) taken in net tows during the California Cooperative Oceanic Fisheries Investigations cruises in 1954 to 1957. In their report, however, they emphasized the problems involved in sampling the young squid and stressed that the abundances given probably should only be used to compare relative abundances of different species. They found that *L. opalescens* was the third most abundant species of larval squid present in their samples, but that its abundance was quite low when compared to the most common fish larvae present (e.g., 0.008 times the abundance of northern anchovy, *Engraulis mordax*).

If the role of a young *L. opalescens* as a predator is to be evaluated, it is necessary to know the type of prey which it eats. Fields (1965) has determined the diet of the adult squid from an examination of stomach contents, but to my knowledge no one has done a similar study on the very small squid. From the laboratory results presented in this paper, it appears that young *L. opalescens* must be considered as predators on a wide range of prey types and prey sizes. They are capable of preying on species ranging in size from 0.7 to 7 mm and they readily attack prey species ranging from brine shrimp adults and nauplii to copepods and larval fish. McGowan (pers. commun.) has found that they also successfully attack the mysid *Metamysidopsis elongata*.

It is also possible to use the data presented here to estimate a feeding rate for the young squid. The respiration data can be used to calculate the amount of food a young squid would need to sustain itself. The respiration rate of the squid in the rearing tanks can be taken as 3 μl O_2/mg dry wt·h. An average value for the caloric value of oxygen consumed is 5×10^{-3} cal/μl of O_2. Therefore, a newly hatched squid (2.7 mm ML, weighing 0.625 mg) would use 0.22 cal for respiration alone in 24 h.

It is possible to determine how many prey items of different types of prey would satisfy this requirement. A newly hatched *Artemia* nauplius is the equivalent of 0.0096 cal (John Hunter pers. commun.). Therefore, a newly hatched squid would need 23 *Artemia* nauplii per day. If the squid were instead feeding on newly hatched northern anchovies, it would need a total of 2 anchovy larvae per day (using a value of 5 cal/mg, weight of larva = 0.022 mg; Theilacker and Lasker 1974). Similar calculations can be made for older squid. A squid 7 mm ML (~2 mo old, 6 mg) would consume 225 nauplii or 20 anchovy larvae simply to meet its metabolic needs. The actual amount of food consumed per day was appreciably more than this, averaging about 50% of body weight per day. At this rate, a newly hatched squid would consume 150 nauplii or 14 anchovy larvae per day, while a 7-mm squid would consume 1,500 nauplii or 135 anchovy larvae per day.

Data on feeding rates and abundance could be used to calculate the impact that young squid might have on populations of potential prey items, but before such calculations can be meaningful, more information must be known about the ability of the squid to locate sources of food. *Loligo opalescens* was only one hundredth as abundant as the most common fish larvae (Okutani and McGowan 1969). But with feeding rates of 15 to 135 larvae per day, young squid could potentially have a large impact on such populations if they concentrate on this type of food and if they have effective means of finding such prey. Laboratory observations indicate that larval fish may be a preferred food, and the squid do occur in areas where larval fish are common. Okutani and McGowan found that *L. opalescens* was most common in the upper 40 m, and this is the stratum where the highest abundance of northern anchovy larvae occur (Ahlstrom 1959).

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Wildl. Serv., Fish. Bull. 60:107-146.

ARNOLD, J., W. SUMMERS, D. GILBERT, R. MANALIS, N. DAW, AND R. LASEK.
1974. A guide to laboratory use of the squid *Loligo pealei*. Mar. Biol. Lab., Woods Hole, 74 p.

ARNOLD, J. M., C. T. SINGLEY, AND L. D. WILLIAMS-ARNOLD.
1972. Embryonic development and post-hatching survival of the sepiolid squid *Euprymna scolopes* under laboratory conditions. Veliger 14:361-364.

BOLETZKY, S. VON, M. V. VON BOLETZKY, D. FRÖSCH, AND V. GÁTZI.
1971. Laboratory rearing of Sepiolinae (Mollusca: Cephalopoda). Mar. Biol. (Berl.) 8:82-87.

CHOE, S.
1966. On the eggs, rearing, habits of the fry, and growth of some Cephalopoda. Bull. Mar. Sci. 16:330-348.

FIELDS, W. G.
1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. Dep. Fish Game, Fish. Bull. 131, 108 p.

LAROE, E. T.
1970. The rearing and maintenance of squid in confinement with observations on their behavior in the laboratory. Ph.D. Thesis, Univ. Miami, Coral Gables, Fla., 136 p.
1971. The culture and maintenance of the loliginid squids *Sepioteuthis sepioidea* and *Doryteuthis plei*. Mar. Biol. (Berl.) 9:9-25.

MCGOWAN, J. A.
1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. Calif. Fish Game 40:47-54.

MESSENGER, J. B.
1968. The visual attack of the cuttlefish, *Sepia officinalis*. Anim. Behav. 16:342-357.

OKUTANI, T., AND J. A. MCGOWAN.
1969. Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California current, April, 1954-March, 1957. Bull. Scripps Inst. Oceanogr., Univ. Calif. 14, 90 p.

REDFIELD, A. C., AND R. GOODKIND.
1929. The significance of the Bohr effect in the respiration and asphyxiation of the squid, *Loligo pealei*. J. Exp. Biol. 6:340-349.

THEILACKER, G. H., AND R. LASKER.
1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 287-299. Springer-Verlag, N.Y.

CONTRIBUTION OF THE NET PLANKTON AND NANNOPLANKTON TO THE STANDING STOCKS AND PRIMARY PRODUCTIVITY IN MONTEREY BAY, CALIFORNIA DURING THE UPWELLING SEASON

DAVID L. GARRISON[1]

ABSTRACT

Net plankton and nannoplankton standing stocks and primary production were measured in Monterey Bay, Calif. from January through August 1972. Throughout the period of seasonal upwelling, the phytoplankton stocks were dominated by net plankton. Both fractions showed seasonal changes: the net plankton concentrations increased dramatically during upwelling, while nannoplankton concentrations were decreased. Nannoplankton growth rates exceeded net plankton rates at incubator light levels; however, at higher in situ light levels near the surface, this relationship appeared to be reversed.

Nannoplankton decreases may have been related to their selective removal from the area of upwelling by horizontal advection or selective grazing on the nannoplankton fraction. Net plankton dominance during upwelling has been related to their higher growth rates when populations are retained in shallow nutrient-rich nearshore waters.

Frequently, phytoplankton are divided into two size classes, depending on whether they are retained by fine mesh nets (net plankton) or pass through the mesh (nannoplankton). The inadequacy of net collections for estimating standing stocks or production is clear. The standing stocks of the two fractions and their relative contributions to primary productivity, however, are less well-known. The size distribution, which may be environmentally controlled (Semina 1972; Parsons and Takahashi 1973), is an important feature of the phytoplankton populations because the size of the primary producers may affect the length and efficiency of pelagic food chains (Ryther 1969; Parsons and LeBrasseur 1970). The purpose of this study was to determine the relative importance of the two fractions during the upwelling season in Monterey Bay, a neritic environment of the California Current system.

Most previous studies reported that the nannoplankton fraction usually exceeds the net plankton fraction, often accounting for 80 to 100% of the standing stocks and primary production (e.g., Steeman Nielsen and Jensen 1957; Holmes 1958; Yentsch and Ryther 1959; Kawamura 1961; Holmes and Anderson 1963; Teixeira 1963; Gilmartin 1964; Saijo 1964; Anderson 1965; Saijo and Takesue 1965; Malone 1971a, c; Parsons 1972; McCarthy et al. 1974). Only a few authors reported net plankton dominated communities (Digby 1953; Subrahmanyan and Sarma 1965). It is difficult to compare these studies, however, because mesh sizes of 22 to 110 μm have been variously used to separate the net plankton and nannoplankton fractions.

The nannoplankton fraction may show little seasonal fluctuation, while the net plankton shows pronounced seasonal trends with periods of abundance corresponding to increased water temperatures (Yentsch and Ryther 1959), peak periods of primary production (Subrahmanyan and Sarma 1965), or seasonal upwelling (Malone 1971c). Malone (1971a) reported higher net: nanno ratios for standing stocks and production in neritic environments as compared with oceanic areas and pronounced onshore to offshore lowering of the ratio in the California Current region during upwelling (Malone 1971c). The growth rate (as indicated by the assimilation ratio = mg C mg Chl a^{-1} h^{-1}) of the nannoplankton fraction is greater than that of the net plankton fraction (Yentsch and Ryther 1959; Saijo and Takesue 1965; Malone 1971a, c).

Arguments presented for the predominance of net plankton or nannoplankton in a given environment relate cell area to volume ratios (Malone 1971a, c; Eppley 1972; Parsons and Takahashi 1973). There is a general relationship between

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cell size and the ability to take up nutrients (Dugdale 1967; Eppley et al. 1969; Eppley and Thomas 1969). Large species generally have higher half saturation constants (K_s) and may have higher maximum uptake rates (V_{max}), whereas small species have lower K_s and V_{max} (Dugdale 1967). Maximum net plankton growth rates are favored at higher ambient nutrient concentrations while nannoplankton reach their maximum growth rates at lower ambient nutrient levels. There is also a direct relationship of increasing cell size (or chain length) with increasing sinking rates (Smayda 1970), and larger cells and chain formers tend to be aggregated in areas of upward advection, while motile or positively buoyant cells tend to be concentrated in areas of downward advection (Stommel 1949). Net plankton will have a longer residence time in the euphotic zone and concentrate in areas of upwelling, while the nannoplankton (if the population is primarily motile flagellates) will be concentrated in areas of downwelling.

Parsons and Takahashi (1973) related the growth rate (μ) to physiological characteristics of the cell (maximum growth rate, half saturation constants for nutrients and light, and sinking rates) and environmental conditions (incident radiation, extinction coefficients, mixed layer depth, and upwelling rates) and used the relationship to explain characteristic phytoplankton cell size in a number of environments. Recently, Laws (1975) expanded the Parsons and Takahashi model and showed that under certain light conditions the decreasing respiration rate with increasing cell size may regulate the growth rate of large versus small cells.

The effect of grazing on the net:nanno ratios and, conversely, the size of the primary producers on food chains have not been well documented. Grazing may ultimately control net plankton stocks (Malone 1971c; Ryther et al. 1971) and determine the lower net:nanno standing stock ratios in oceanic as opposed to neritic areas (Malone 1971a). Grazing has been suggested as the primary cause for failure of phytoplankton stocks to develop in otherwise favorable waters (Mc Allister et al. 1960; Strickland et al. 1969). Shorter food chains have been shown for some clupeid fishes which feed directly on the large phytoplankton species (e.g., Bayliff 1963; Rojas de Mendiola 1969; Dhulkhed 1972) and for herbivorous euphausids in the diatom-rich antarctic region (Marr 1962). The general argument for larger phytoplankton cells resulting in shorter, more efficient food chains may not always apply to the smaller grazers, as Parsons and LeBrasseur (1970) have reported on selective feeding related to cell shape.

Previous studies have been made on the hydrographic seasons in Monterey Bay and their relationship to the seasonal phytoplankton blooms (Bolin and Abbott 1963; Abbott and Albee 1967). Malone (1971c) reported the seasonal variability of the net plankton and nannoplankton in the California Current, which included one deep station on the edge of Monterey Bay. The present study was part of a monthly sampling program conducted by Moss Landing Marine Laboratories to provide information on the hydrographic conditions and plankton populations in Monterey Bay, particularly from the extensive shallow areas of the bay. Although it was not possible to carry this study through a complete seasonal cycle, information is presented for the upwelling period, when seasonal blooms of phytoplankton appear in Monterey Bay.

MATERIALS AND METHODS

Measurements of primary productivity and phytoplankton standing stocks were made at stations 3 and 8 for the period January through August 1972 and at station 15 for the period June through August 1972 (Figure 1). The stations were located over the Monterey Submarine Canyon at depths of 110, 240, and 718 m, respectively. Samples were taken monthly during hydrographic and plankton cruises conducted by Moss Landing Marine Laboratories and, occasionally, between these periods on instructional cruises. Sampling times varied between cruises but fell between 0700 and 1100 h.

Samples were collected with 5-liter Niskin water sampling bottles from depths corresponding to 100, 50, 25, 10, and 1% light penetration levels as measured with a submarine photometer or calculated using the relationship: depth of 1% light = 3.5 × Secchi disk (Silver and Hansen 1971a). Hydrographic parameters (salinity, ‰; temperature, °C; O_2) and nutrients (PO_4, NO_3, NO_2, NH_3, SiO_2) were samples at standard depths (Broenkow and Benz 1973).

Primary productivity was measured using the carbon-14 method (Steeman Nielsen 1952). For each depth two light and one dark bottles were innoculated with 5 or 10 μCi of $Na_2{}^{14}CO_3$. The

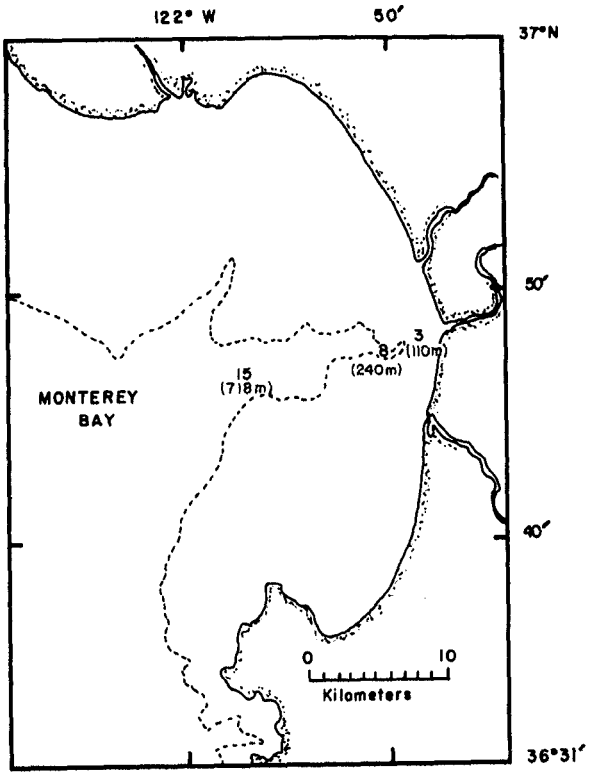

FIGURE 1.—Location of stations in Monterey Bay. Broken lines indicate the position of the 100-fathom (183-m) contour line.

samples were incubated immediately after collection for 3 to 4 h in a shipboard incubator (Doty and Oguri 1958) using Luxor Magnalux fluorescent lamps[2] (approx. 0.06 langley min^{-1}). Neutral density filters of 50, 25, 10, and 1% transmittance were used on subsurface samples.

The net plankton and nannoplankton fractions were separated by passing the samples through a 22-μm Nitex-net filter (net plankton) and then a Gelman, type A glass-fiber filter having 0.3-μm pore size (nannoplankton). Both filters were washed with approximately 20 ml of freshly filtered seawater and placed directly in scintillation fluor for counting at a later time.

All samples were counted for at least 10 min with a Nuclear Chicago (Unilux II) scintillation counter. Carbon uptake was calculated as outlined in Strickland and Parsons (1968). Since Malone (1971b) reported no diurnal periodicity in assimilation ratios in the California Current regions, daily production was estimated by using the sunrise to sunset interval as the day length and multiplying by the hourly production rates that were determined during the first part of the day.

Phytoplankton standing stocks were measured as chlorophyll *a* by using the fluorometric method of Holm-Hansen et al. (1965). The Turner fluorometer (model 111) was calibrated using the spectrophotometric method for chlorophyll *a* as outlined by Strickland and Parsons (1968). The two size fractions were separated by taking two replicate samples from each depth and passing one through a Gelman glass-fiber filter (total chlorophyll) while the other sample was filtered through 22 μm Nitex-net filter and then a glass-fiber filter (nannoplankton). Both filters were immediately frozen, stored in the dark, and analyzed within a month after collection. Net plankton was calculated as the difference between total chlorophyll and nannoplankton chlorophyll.

Productivity and chlorophyll *a* values determined for the discrete samples were integrated to the depth of the 1% light level by trapezoidal approximation. Carbon:chlorophyll *a* ratios vary widely and depend on light and nutrient conditions. For most of the study, nutrient levels were high and a C:Chl *a* ratio of 40 was used to convert chlorophyll *a* to carbon biomass (Lorenzen 1968; Eppley et al. 1970; Eppley et al. 1971). Phytoplankton growth rate and standing stock doubling time were calculated using exponential growth expression.

RESULTS

In January, the weak thermal gradient in the upper 50 m (Figure 2) is indicative of the Davidson Current period, when the subsurface countercurrent extends to the surface and flows northwestward on the inshore side of the California Current (Reid et al. 1958; Bolin and Abbott 1963; Smethie 1973). Rising isotherms and nitrate isopleths from February through May indicate upwelling over the Monterey Submarine Canyon. After May there was a slacking or an end to upwelling, and the isotherms and isopleths are found progressively deeper as denser upwelling waters subside. In July and August, conditions of the oceanic period were evident with low nutrient levels, higher surface temperatures, and lower salinities; however, upward movement of the isotherms and isopleths in August may indicate a developing upwelling pulse.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

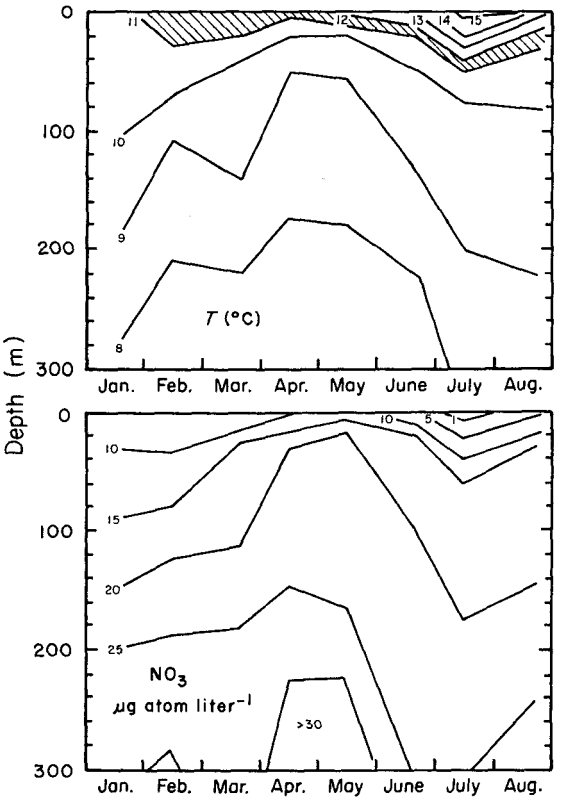

FIGURE 2.—Average depth of isotherms and nitrate isopleths for hydrographic stations samples over Monterey Submarine Canyon, January through August 1972 (data from Broenkow and Benz 1973).

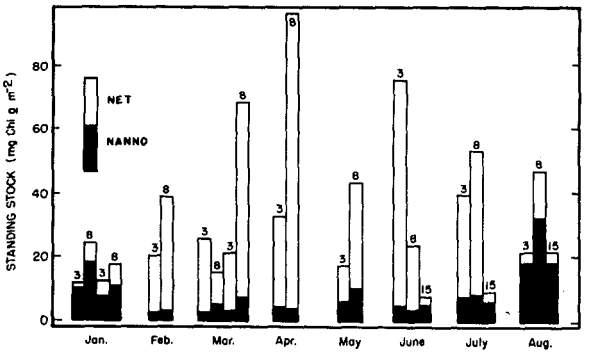

FIGURE 3.—Phytoplankton standing stocks in the euphotic zone, January through August 1972. Numbers over histogram bars refer to stations.

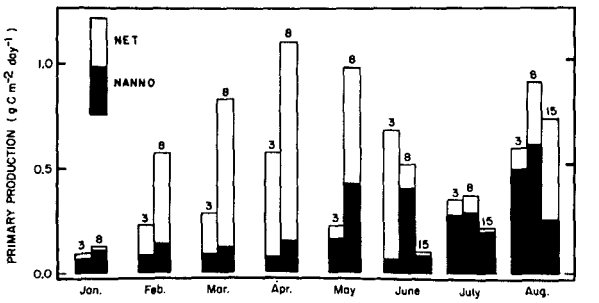

FIGURE 4.—Estimated primary production in the euphotic zone, January through August 1972. Numbers over histogram bars refer to stations.

Standing Stocks and Primary Production

In January, at the end of the Davidson Current period, standing stocks were near their lowest levels and nannoplankton dominated (Table 1, Figure 3). Throughout the period from February through July, however, the net plankton fraction exceeded the nannoplankton. In August, the standing stocks were again predominantly nannoplankton. Estimated primary production followed the general trend shown by the standing stocks (Figure 4), but lower production per unit chlorophyll for the net plankton fraction in January and July is apparent. The highest standing stock was measured in April at the time the isotherms and nutrient isopleths reached their highest positions (see Figure 2). At this peak, the stocks were 97% net plankton, and net plankton concentrations in the euphotic zone ranged from 4.63 to 6.88 mg Chl *a* m^{-3}. Concentrations of net plankton as high as 9.26 mg Chl *a* m^{-3} were recorded in June. During the April peak, the corresponding total productivity was approximately 1.1 g C m^{-2} day^{-1}. It is difficult to equate incubator productivity to in situ productivity; however, these values are similar to productivity estimates calculated from nutrient uptake and oxygen production in the water column (Smethie 1973).

The changes in the ratios of the two fractions were largely a result of changes in the biomass of the net plankton fraction. The net plankton fraction experienced large seasonal changes in concentrations, and occasionally there was significant vertical stratification within the water column; however, nannoplankton fluctuations fell within a much narrower range (Figure 5). There were significant differences in the average concentrations in the euphotic zone of the two fractions in all three hydrographic seasons, and both fractions showed significant differences between seasons (Mann Whitney *U* test; $P = 0.01$). The

TABLE 1. — Standing stock, primary production, and growth rate (μ) of the net plankton and nannoplankton in Monterey Bay for the period January through August 1972.

Date	Station	Euphotic zone depth (m)	Phytoplankton standing stock (mg Chl *a* m^{-2})		Primary production (g C m^{-2} day^{-1})		Growth rate, (doubling day^{-1})	
			Net	Nanno	Net	Nanno	Net	Nanno
20 Jan.	3	20	2.2	10.2				
	8	28	5.8	18.5				
27 Jan.	3	15	4.6	7.8	0.017	0.076	0.1	0.3
	8	35	6.0	12.0	0.012	0.113	0.1	0.3
15 Feb.	3	15	18.2	2.4	0.142	0.084	0.3	0.9
	8	15	36.4	3.0	0.437	0.137	0.4	1.1
1 Mar.	3	12	23.2	2.8				
	8	35	10.0	4.4				
8 Mar.	3	10	17.6	3.2				
	8	40	61.0	7.6				
23 Mar.	3	11			0.262	0.116		
	8	15			0.706	0.126		
18 Apr.	3	23	29.8	3.0	0.491	0.075	0.5	0.7
	8	16	95.4	2.6	0.955	0.153	0.5	1.3
16 May	3	30	11.6	5.8	0.058	0.160	0.2	0.8
	8	30	34.0	9.6	0.558	0.418	0.5	1.1
20 June	3	10	73.0	3.4	0.612	0.067	0.3	0.6
	8	20	20.8	3.4	0.401	0.115	0.6	0.9
	15	30	2.0	5.0	0.011	0.093	0.2	0.5
20 July	3	20	31.6	8.2	0.172	0.276	0.2	0.9
	8	50	45.0	8.6	0.085	0.286	0.1	0.9
	15	65	7.6	9.6	0.010	0.207	>0.1	0.6
29 Aug.	3	30	[1]1.4	20.2	0.094	0.507	1.4	0.7
	8	30	[1]4.6	32.4	0.309	0.612	0.6	0.6
	15	29	[1]3.2	18.7	0.488	0.252	2.3	0.4

[1]Value appears low, corresponding growth rate (μ) may be too high.

seasonal effect during upwelling seems to be a reduction of the average concentration of nannoplankton and an increase in the average concentration of net plankton.

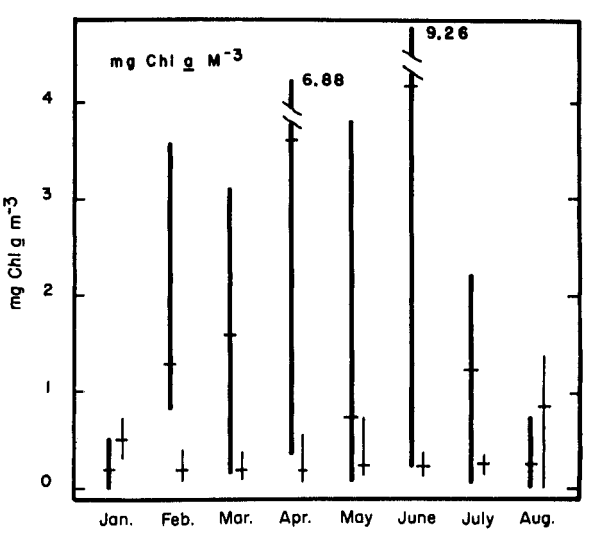

FIGURE 5.—Seasonal changes in the concentration of net plankton chlorophyll (heavy line) and nannoplankton chlorophyll (thin line). (Davidson Current period—January; upwelling period—February through June; oceanic period—July, August.) Average and range of concentrations in the euphotic zone are shown. The number of samples for each month is given in Table 1.

Standing Stock Growth Rate

The growth rate, μ (doublings day^{-1}), and assimilation ratio (mg C mg Chl a^{-1} h^{-1}), of the nannoplankton fraction was greater than the corresponding value for the net plankton during all three seasons, and both fractions showed their highest growth rate during the upwelling period; however, assimilation ratios of the surface samples for both fractions were higher in the oceanic period than during upwelling (Table 2). There is no correlation ($P > 0.10$) between the growth rates of either phytoplankton fraction and average nutrients (NO_3, SiO_2) in the upper 10 m on individual sampling days for the three hydrographic periods.

Net plankton growth rates exceeded nannoplankton growth rates in only two of the samples;

TABLE 2. — Growth rates of the standing stocks in the euphotic zone and assimilation ratios of surface samples.[1]

Hydrographic period	Growth rate, μ (doublings day^{-1})		Assimilation ratio (mg C mg Chl a^{-1} h^{-1})	
	Net	Nanno	Net	Nanno
Davidson Current	0.1 ± 0.0(2)	0.3 ± 0.1(2)	0.4 ± 0.2(2)	2.2 ± 0.5(2)
Upwelling	0.4 ± 0.1(9)	0.9 ± 0.2(9)	2.7 ± 1.5(9)	5.2 ± 2.2(9)
Oceanic	0.2 ± 0.3(4)	0.7 ± 0.2(6)	3.0 ± 1.6(3)	10.3 ± 1.2(4)

[1]Growth rates were calculated from daily productivity and standing stock estimates integrated to the depth of 1% light penetration, while assimilation ratios are for surface samples incubated at 0.06 langley min^{-1}. $\bar{X}$ ± SD(N); questionable data indicated in Table 1 have been excluded.

however, the growth rates were determined at incubator light levels which were not representative of in situ conditions. The regression of light level on the ratio of the growth rates (μ net:μ nanno) is significant ($P < 0.01$) during the upwelling months (Figure 6). Light levels approximately equivalent to full incubator light are found at depths of 8 to 15 m during the upwelling period, and the upper one-fourth to one-third of the euphotic zone receives light which is in excess of incubator light levels.

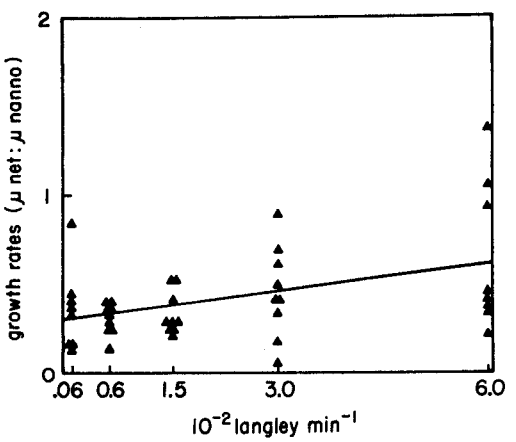

FIGURE 6.—Regression of incubator light levels on the net:nanno growth rates.

Distribution in the Water Column

Since nannoplankton concentrations were relatively homogeneous in the water column, maxima were often not well defined. Net plankton maxima, however, were usually apparent and corresponded to the depth of the seasonal pycnocline. There was no regularly observed depth relationship between nannoplankton and net plankton maxima, and they often were at the same depth. Phaeophytin peaks appeared at the surface and in conjunction with, or just below, the chlorophyll maxima. High NH_3 concentrations in the deeper phaeophytin maxima may be indicative of grazing on the phytoplankton stocks in the chlorophyll maxima (see Figures 7-10).

During the Davidson Current period there is little vertical stability in the water column, and the net plankton stocks are poorly developed (Figure 7). With the onset of upwelling net plankton stocks develop above the strong, shallow pycnocline (Figures 8, 9) and the nannoplankton stocks decline. With strong or persistent upwelling, the pycnocline may intersect the surface and the phytoplankton stocks are concentrated in a relatively shallow layer (Figure 9).

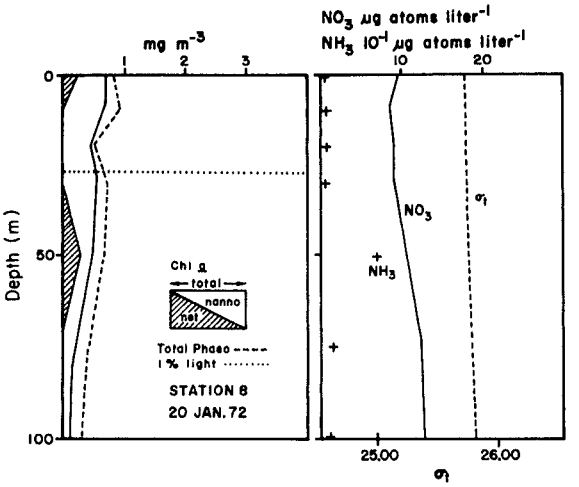

FIGURE 7.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during the Davidson Current period.

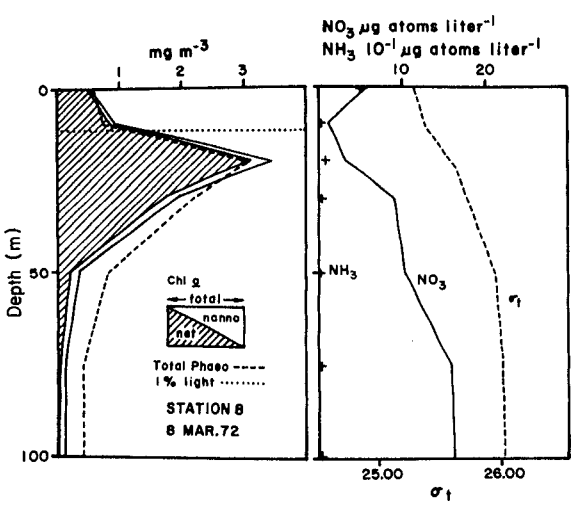

FIGURE 8.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during upwelling period. Station was sampled during a flowing tide.

After a slacking of upwelling the denser waters subside and the pycnocline depths become progressively deeper. The surface layer can be strongly stratified by the onshore movement of warmer, low salinity oceanic water, and nutrient concentrations in the near surface waters are low during the oceanic period. The net plankton

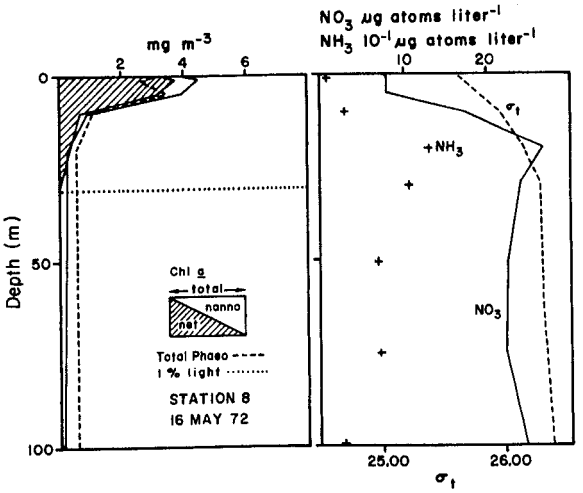

FIGURE 9.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during upwelling period. Station was sampled during an ebbing tide.

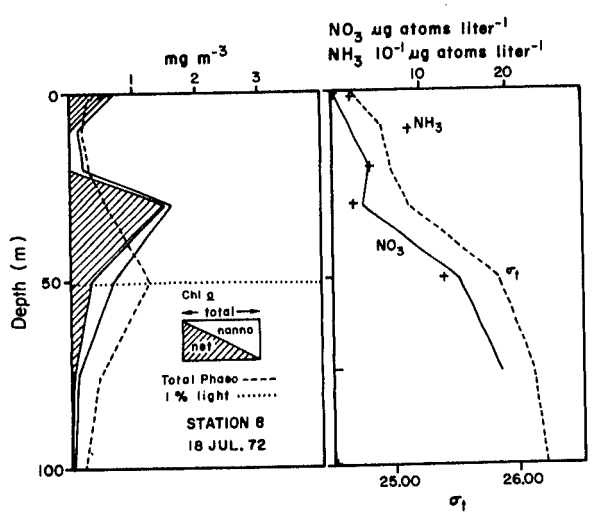

FIGURE 10.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during the oceanic period.

maximum remains associated with the sinking pycnocline and, although nutrients do not reach limiting concentrations in the pycnocline, light levels are below optimal intensity for maximum growth rates (Figure 10).

Broenkow and McKain (1972) demonstrated that tidal effects have a marked influence on the distribution of hydrographic parameters over the canyon: during a flow tide there is a down-canyon current and isotherms and isopleths over the canyon are depressed; conversely, during an ebb tide the flow is up the canyon and isotherms and isopleths are nearer the surface. The source waters for the down-canyon flow are subsurface waters from the shallow areas adjacent to the canyon. These tidal effects can be identified in the distribution of the phytoplankton stocks (Silver and Hansen 1971b), but their importance is unknown. The chlorophyll *a* maximum at station 8 (in Figure 8) appears to be an intrusion of stocks developed in shallower areas and carried to depth by the down canyon flow during the flow tide. Station 3 was sampled earlier during an ebb tide, and the sigma-t surface at 50 m (σt = 26.14) was found deeper than 100 m at station 8 (see Figure 8). At a full ebb tide the pycnocline and the standing stocks may be located very near the surface (Figure 9).

DISCUSSION

The net plankton-dominated blooms that developed during this study were similar to those described by Bolin and Abbott (1963) and Abbott and Albee (1967) in their close association with seasonal upwelling and in their composition (i.e., the net plankton was dominated by colonial diatoms—M. Silver unpubl. data[3]). Malone (1971c) noted an increase in net plankton fraction during the upwelling season; however, he reported net plankton dominated stocks only during strong upwelling pulses. Malone also reported a marked decrease in net plankton chlorophyll and productivity between inshore and offshore stations near the end of the upwelling season. Although these studies cannot be directly compared, they suggest phytoplankton blooms which develop during upwelling are mostly net plankton forms, and higher standing stocks may develop inshore.

There seems to be a fundamental contradiction in the measured growth rates of the two fractions and the observed standing stocks. The growth rates of the nannoplankton were consistently higher than those of the net plankton, whereas the standing stocks of nannoplankton decrease and the stocks of net plankton increase during the upwelling season. The observed development of the stocks could result theoretically from one or a combination of the following conditions: 1)

[3]The unpublished data supplied by M. Silver can be found in a data report filed in 1971-72 at Oceanographic Services, Inc., 135 East Ortega Street, Santa Barbara, CA 93101.

the nannoplankton fraction may be selectively removed from the area by horizontal advection because of their low sinking rates; 2) nannoplankton may be selectively grazed; 3) environmental conditions may favor higher net plankton growth rates.

Malone (1971c) discussed the argument for selective removal of nannoplankton from upwelling areas by horizontal advection. Briefly restated, nannoplankton cells tend to have slower sinking rates than net plankton cells (or they are motile) and in convection cells they will tend to be removed from the areas of upward movement and concentrated in areas of downward movement (Stommel 1949). In upwelling areas then, nannoplankton may be selectively removed by mass transport of surface waters offshore. There is little direct evidence to show that this takes place; however, the advection hypothesis is supported by the observed decrease in nannoplankton stocks between the Davidson Current period and the upwelling period. During the Davidson Current period there is a general onshore movement of surface waters with water sinking along the coast, while during the upwelling period the circulation is reversed and water moved upward along the coast, and the surface waters are transported offshore (Skogsberg 1936; Bolin and Abbott 1963). Malone (1971c) found the level of the nannoplankton stocks remained relatively constant throughout the year; however, he reported that during periods of onshore water movement there was an enhancement which could be attributed to concentrating the nannoplankton in an area of downward water movement.

The decrease in nannoplankton stocks reported in the present study may have been the result of selective grazing by microzooplankton and planktotrophic larvae (Thorsen 1950; Beers and Stewart 1969; Parsons and LeBrasseur 1970). In this area many of the benthic invertebrates have their reproductive season during the spring (M. Houk pers. commun.)[4]; increased grazing pressure by these larvae may have caused the decrease in nannoplankton stocks. However, the extent of grazing on either fraction of the phytoplankton in Monterey Bay is not known. Zooplankton samples were collected as part of the routine sampling program, but gelatinous and colonial phytoplankton could not be separated from the zooplankton for biomass estimates.

Throughout the period of upwelling, nitrate levels in the upper 10 m remained high (> 5 μg atoms liter^{-1}) and the chlorophyll maximum was frequently located near the surface. At these shallow depths light levels were in excess of incubator light levels (0.06 langley min^{-1}). Eppley et al. (1969) have shown that the diatoms *Skeletonema costatum* and *Ditylum brightwellii* grow faster than *Coccolithus huxleyi* at high light levels (0.1 langley min^{-1}) when nitrate levels are in excess of 0.8 μg atoms liter^{-1}, while at lower light levels (0.02 langley min^{-1}), the situation is reversed and *C. huxleyi* will grow faster at any nitrate concentration. In situ nutrient and light conditions near the surface during the upwelling period should favor net plankton growth.

In the present study and in that of Malone (1971c), growth rates of the net plankton were lower than the growth rates of the nannoplankton; however, the two fractions responded differently to increasing light as shown by the ratio of the growth rates (μ net:μ nanno) increasing with higher light levels (Figure 6). The regression predicts that net plankton growth rates would exceed the nannoplankton growth rates at light levels similar to those where Eppley et al. (1969) showed a reversal of growth rate relationships. Estimated light levels in the upper part of the euphotic zone are higher than the incubator light levels which have been used in this study and that of Malone. Since the net plankton growth rates show greater enhancement with increasing light than the nannoplankton, light levels in the upper water column may favor the growth of the net plankton fraction and lead to net plankton domination of the standing stocks.

Laws (1975) suggested that, under certain environmental conditions, large cells may realize a higher net growth rate because of a decreasing respiration rate with increasing cell size. In Laws' model, when surface light levels are low or the product of the attenuation coefficient and mixed layer depth is large, integral productivity efficiency is low and respiration losses become more important. During the present study, however, under low light levels, the net growth rates of the smaller cells (nannoplankton) exceeded larger cells, and the phytoplankton populations were net plankton dominated at a time when the mixed layer was extremely shallow.

Notwithstanding the possible effects of selec-

[4]M. Houk, Department of Natural Science, University of California, Santa Cruz, CA 95064.

tive grazing on the nannoplankton or their selective removal by horizontal advection, the development of the upwelling bloom in Monterey Bay is largely a result of the increase in the net plankton fraction and may be explained in terms of conditions which are favorable for net plankton growth. High nutrient concentrations can be maintained in the euphotic zone by downward mixing from the surface which extends below the pycnocline or by a continual input of nutrients to the surface waters by upwelling. Optimal light levels, however, are found only in the upper part of the euphotic zone. The combination of these conditions that constitute optimal growth conditions for the net plankton fraction occur when the phytoplankton stocks are restricted to a shallow mixed layer above the pycnocline which has been "pushed up" by upwelling water. Optimal growth conditions vary spatially and seasonally and may be primarily responsible for the net plankton and nannoplankton relationship observed in Monterey Bay.

Nutrients do not appear to limit the growth rates of either fraction as correlation coefficients of nutrient levels with growth rates were not significant and, although nutrient levels change seasonally, Malone (1971c) reported little seasonal variation in assimilation rates. Light levels, however, are potentially limiting a short distance from the surface and can influence the ratio of net:nanno growth rates.

An increase in the depth of the mixed layer results in a decrease in the average light exposure for phytoplankton cells in the mixed layer (Parsons and Takahashi 1973). The net plankton fraction will be more strongly influenced than the nannoplankton because their optimal growth rates occur at light levels near the surface, and their vertical distribution is strongly controlled by water movement. Upwelling water movements result in a shallow pycnocline and shallow mixed layer; with a slack in the upwelling rate, the pycnocline sinks and there is a deeper mixed layer. In the present study, net plankton maxima were concentrated above the pycnocline, whereas no particularly strong relationship between the nannoplankton maxima were observed (the nannoplankton maxima were often not well defined). Malone (1971c) showed that the net plankton maxima were located below the nannoplankton maxima during periods when upwelling was slack or that both were located at the surface during periods of upwelling, and he emphasized the role of upward movement in controlling the vertical distribution of the net plankton fraction.

Malone (1971c) showed an onshore to offshore decrease in the ratio of net:nanno standing stocks. Yoshida (1967) showed the potential for a narrow zone of stronger upwelling associated with the edge of the continental shelf where the effects of upwelling are maximal at the edge of the shelf and decrease exponentially shoreward and seaward. A decrease in the upwelling rate away from the continental shelf would result in reduced suspension of sinking cells, a deeper mixed layer, and lower average light levels for phytoplankton cells in the mixed layer and could reduce the net:nanno growth rate ratio. Malone's data showed shallow mixed layers during periods of strong upwelling at inshore stations and a trend for an increasing mixed layer depth offshore. In Monterey Bay during the upwelling season, the mixed layer is frequently shallow or the pycnocline intersects the surface. There are considerable amounts of hydrographic data which show this characteristic distribution (Broenkow and Benz 1973) and corresponding phytoplankton standing stock data which show significant stratification of the phytoplankton standing stocks above the shallow pycnocline (Silver see footnote 3).

The depth of the pycnocline and mixed layer vary seasonally in response to the upward movement of isotherms during upwelling and the sinking of isotherms when upwelling ceases. Upwelling, however, is not a continuous process and may be particularly sporadic near the end of the upwelling season (Bolin and Abbott 1963; Smethie 1973). Malone (1971c) reported net plankton dominated stocks only during periods of strong upwelling, which suggests that in deep water continual upwelling is necessary to maintain optimal growth conditions for the net plankton fraction. During the present study the net plankton fraction dominated the phytoplankton populations in shallow water throughout the upwelling season. This evidence and previous evidence for an offshore decrease in the net:nanno ratios (Malone 1971c) suggest that physical processes in shallow water are sufficient to maintain net plankton populations and mitigate the lack of continual upwelling.

The physical processes in shallow water that could serve to maintain favorable growth conditions for the net plankton fraction or maintain the population between periods of favorable con-

ditions are poorly known. Tidal mixing and increased turbulence in shallow water could facilitate cell suspension of sinking populations or resting spores, and increase nutrient input to the surface waters. Over Monterey Canyon and, to a lesser extent, in the shallow areas of the bay, the vertical distribution of nutrients (Broenkow and McKain 1972; Smethie 1973) and phytoplankton stocks (Silver and Hansen 1971b; Silver see footnote 3) are strongly influenced by tidal effects. Turbulence and mixing in deep water results in a decrease in the average amount of light to which a phytoplankton cell is exposed; however, in shallow water the depth of mixing is limited by the bottom and mixing here may result in resuspension of sinking cells. Many of the neritic diatoms form resting spores which sink to the bottom and may be an important source of innoculum to initiate blooms if they are resuspended by turbulence during favorable growth conditions.

The decline in the net plankton populations during this study corresponded to the influx of oceanic waters in July. The end of net plankton domination of the population appears to have been the result of the low nutrient concentrations in the oceanic surface waters and subsidence of previously upwelled waters and its entrained net plankton populations. During oceanic conditions, nutrient levels in the surface waters favor the growth of nannoplankton and the light levels in the sinking net plankton maxima are not optimal for growth. Malone (1971c) suggested, however, that the net plankton are ultimately limited by grazers as the grazing index (phaeo:Chl *a*) increased and the netplankton concentrations decreased even before the end of the upwelling period. Direct evidence for the extent of grazing in Monterey Bay is not available; however, when upwelling becomes sporadic and periodic influxes of oceanic water occur, the stage is set for a decline in the net plankton fraction without the need for an increase in grazing pressure.

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LITERATURE CITED

ABBOTT, D. P., AND R. ALBEE.
1967. Summary of thermal conditions and phytoplankton volumes measured in Monterey Bay, California 1961-1966. Calif. Coop. Oceanic Fish. Invest. Rep. 11:155-156.

ANDERSON, G. C.
1965. Fractionation of phytoplankton communities off the Washington and Oregon coasts. Limnol. Oceanogr. 10:477-480.

BAYLIFF, W. H.
1963. The food and feeding habits of the anchoveta, *Centengraulis mysticetus*, in the Gulf of Panama. Inter-Am. Trop. Tuna Comm. Bull. 7:399-432.

BEERS, J. R., AND G. L. STEWART.
1969. The vertical distribution of microzooplankton and some ecological observations. J. Cons. 33:30-44.

BOLIN, R. L., AND D. P. ABBOTT.
1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Oceanic Fish. Invest. Rep. 9:23-45.

BROENKOW, W. W., AND S. BENZ.
1973. Oceanographic observations in Monterey Bay, California January 1972 to April 1973. Moss Landing Mar. Lab., TP73-3, 336 p.

BROENKOW, W. W., AND S. J. MCKAIN.
1972. Tidal oscillations at the head of Monterey Submarine Canyon and their relation to oceanographic sampling and circulation of water in Monterey Bay. Moss Landing Mar. Lab., TP72-5, 42 p.

DHULKHED, M. H.
1972. Food of the oil sardine taken by bottom nets and surface gill net in the Mungalore area. Indian J. Fish. 19:163-166.

DIGBY, P. S. B.
1953. Plankton production in Scoresby Sound, East Greenland. J. Anim. Ecol. 22:289-322.

DOTY, M. S., AND M. OGURI.
1958. Selected features of the isotopic carbon primary productivity technique. Rapp. P.-V. Réun., Cons. Perm. Int. Explor. Mer 144:47-55.

DUGDALE. R. C.
1967. Nutrient limitation in the sea: dynamics, identification, and significance. Limnol. Oceanogr. 12:685-695.

EPPLEY, R. W.
1972. Temperature and phytoplankton growth in the sea. Fish. Bull., U.S. 70:1063-1085.

EPPLEY, R. W., A. F. CARLUCCI, O. HOLM-HANSEN, D. KEIFER, J. J. MCCARTHY, E. VENRICK, AND P. M. WILLIAMS.
1971. Phytoplankton growth and composition in shipboard cultures supplied with nitrate, ammonium, or

urea as the nitrogen source. Limnol. Oceanogr. 16:741-751.

EPPLEY, R. W., F. M. H. REID, AND J. D. H. STRICKLAND.
1970. The ecology of the plankton off La Jolla, California, in the period April through September, 1967. Part III. Estimates of phytoplankton crop size, growth rate, and primary production. Bull. Scripps Inst. Oceanogr., Univ. Calif. 17:33-42.

EPPLEY, R. W., J. N. ROGERS, AND J. J. MCCARTHY.
1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnol. Oceanogr. 14:912-920.

EPPLEY, R. W., AND W. H. THOMAS.
1969. Comparison of half-saturation constants for growth and nitrate uptake of marine phytoplankton. J. Phycol. 5:375-379.

GILMARTIN, M.
1964. The primary production of a British Columbia fjord. J. Fish. Res. Board Can. 21:505-538.

HOLMES, R. W.
1958. Size fractionation of photosynthesizing phytoplankton. *In* Physical, chemical, and biological oceanographic observations obtained on expedition SCOPE in the Eastern Tropical Pacific, November - December 1956, p. 69-71. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 279, 117 p.

HOLMES, R. W., AND G. C. ANDERSON.
1963. Size fractionation of C^{14}-labeled natural phytoplankton communities. *In* C. H. Oppenheimer (editor), Symposium on marine microbiology, p. 241-250. Charles C. Thomas Publisher, Springfield, Ill.

HOLM-HANSEN, O., C. J. LORENZEN, R. W. HOLMES, AND J. D. H. STRICKLAND.
1965. Fluorometric determination of chlorophyll. J. Cons. 30:3-15.

KAWAMURA, T.
1961. Data on phytoplankton photosynthetic activity. Data Rec. Oceanogr. Obs. Expl. Fish (Hokkaido) 5:142-165.

LAWS, E. A.
1975. The importance of respiration losses in controlling the size distribution of marine phytoplankton. Ecology 56:419-426.

LORENZEN, C. J.
1968. Carbon/chlorophyll relationships in an upwelling area. Limnol. Oceanogr. 13:202-204.

MALONE, T. C.
1971a. The relative importance of nannoplankton and net plankton as primary producers in tropical oceanic and neritic phytoplankton communities. Limnol. Oceanogr. 16:633-639.
1971b. Diurnal rhythms in net plankton and nannoplankton assimilation ratios. Mar. Biol. (Berl.) 10:285-289.
1791c. The relative importance of nannoplankton and net plankton as primary producers in the California Current system. Fish. Bull., U.S. 69:799-820.

MARR, J.
1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Rep. 32:33-463.

MCALLISTER, C. D., T. R. PARSONS, AND J. D. H. STRICKLAND.
1960. Primary productivity and fertility at station "P" in the north-east Pacific Ocean. J. Cons. 25:240-259.

MCCARTHY, J. J., W. R. TAYLOR, AND M. E. LOFTUS.
1974. Significance of nannoplankton in the Chesapeake Bay estuary and problems associated with the measurement of nannoplankton productivity. Mar. Biol. (Berl.) 24:7-16.

PARSONS, T. R.
1972. Size fractionation of primary producers in the Subarctic Pacific Ocean. *In* A. Y. Takenouti (editor), Biological oceanography of the northern North Pacific Ocean, p. 275-278. Idemitsu Shoten, Tokyo.

PARSONS, T. R., AND R. J. LEBRASSEUR.
1970. The availability of food to different trophic levels in the marine food chain. *In* J. H. Steele (eidtor), Marine food chains, p. 325-343. Oliver & Boyd, Edinb., Scotl.

PARSONS, T. R., AND M. TAKAHASHI.
1973. Environmental control of phytoplankton cell size. Limnol. Oceanogr. 18:511-515.

REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest., Prog. Rep., 1 July 1956 to 1 Jan. 1958, p. 27-56.

ROJAS DE MENDIOLA, B.
1969. The food on the Peruvian anchovy. J. Cons. 32:433-434.

RYTHER, J. H.
1969. Photosynthesis and fish production in the sea. Science (Wash., D.C.) 166:72-76.

RYTHER, J. H., D. W. MENZEL, E. M. HULBURT, C. J. LORENZEN, AND N. CORWIN.
1971. The production and utilization of organic matter in the Peru coastal current. Invest. Pesq. 35:43-59.

SAIJO, Y.
1964. Size distribution of photosynthesizing phytoplankton in the Indian Ocean. J. Oceanogr. Soc. Jap. 19:187-189.

SAIJO, Y., AND K. TAKESUE.
1965. Further studies on the size of photosynthesizing photoplankton in the Indian Ocean. J. Oceanogr. Soc. Jap. 20:264-271.

SEMINA, H. J.
1972. The size of phytoplankton cells in the Pacific Ocean. Int. Rev. Gesamten Hydrobiol. 57:177-205.

SILVER, M., AND J. HANSEN.
1971a. Plankton studies. *In* Environmental studies of Monterey Bay and the central California coastal zone, Annual Report July 1971, p. 116-131. Moss landing Mar. Lab., Moss Landing, Calif.
1971b. Plankton studies in nearshore Monterey Bay. *In* Abstract volume, Second National Coastal and Shallow Water Research Conference. Geog. Programs, Off. Nav. Res.

SKOGSBERG, T.
1936. Hydrography of Monterey Bay, California. Thermal conditions, 1929-1933. Trans. Am. Philos. Soc., New Ser. 29:1-152.

SMAYDA, T. J.
1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol., Annu. Rev. 8:353-414.

SMETHIE, W. M.
1973. Some aspects of the temperature, oxygen and nutrient distributions in Monterey Bay, California. Moss Landing Mar., Lab. TP73-1, 97 p.

STEEMAN NIELSEN, E.
1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. J. Cons. 18:117-140.

STEEMAN NIELSEN, E., AND E. A. JENSEN.
1957. Primary oceanic production. The autotrophic pro-

duction of organic matter in the ocean. Galathea Rep. 1:49-136.

STOMMEL, H.
1949. Trajectories of small bodies sinking slowly through convection cells. J. Mar. Res. 8:24-29.

STRICKLAND, J. D. H., R. W. EPPLEY, AND B. ROJAS DE MENDIOLA.
1969. Phytoplankton populations, nutrients, and photosynthesis in Peruvian coastal waters. Inst. Mar. Perú (Callao), Bol. 2:4-45.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1968. A practical handbook of seawater analysis. Fish. Res. Board Can., Bull. 167, 311 p.

SUBRAHMANYAN, R., AND A. H. VISWANATHA SARMA.
1965. Studies on the phytoplankton of the west coast of India. Part IV. Magnitude of the standing crop for 1955-1962, with observations on nanoplankton and its significance to fisheries. J. Mar. Biol. Assoc. India 7:406-419.

TEIXEIRA, C.
1963. Relative rates of photosynthesis and standing stock of net phytoplankton and nannoplankton. Bol. Inst. Oceanogr. (São Paulo) 13:53-60.

THORSEN, G.
1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. (Camb.) 25:1-45.

YENTSCH, C. S., AND J. H. RYTHER.
1959. Relative significance of the net phytoplankton and nannoplankton in the waters of Vineyard Sound. J. Cons. 24:231:238.

YOSHIDA, K.
1967. Circulation in the eastern tropical oceans with special reference to upwelling and undercurrents. Jap. J. Geophys. 4(2):1-75.

ABUNDANCE OF MACROCRUSTACEANS IN A NATURAL MARSH AND A MARSH ALTERED BY DREDGING, BULKHEADING, AND FILLING[1]

LEE TRENT,[2] EDWARD J. PULLEN,[3] AND RAPHAEL PROCTOR[3]

ABSTRACT

Indices of abundance of macrocrustaceans during March-October 1969 in West Bay, Tex., were determined for day and night and statistically compared between 1) a natural marsh area, 2) upland and bayward canal areas of a housing development, and 3) an open bay area. Significance levels of 5% or 1% were used in the statistical comparisons. Catches of brown shrimp, *Penaeus aztecus*; white shrimp, *P. setiferus*; blue crab, *Callinectes sapidus*; and pink shrimp, *P. duorarum*, were significantly greater at night than during the day at one or more stations in the marsh. More grass shrimp, *Palaemonetes* sp., were caught at night than during the day, but the differences were not statistically significant. Individuals of each species appeared to migrate into the more shallow areas of the marsh at night. At night, brown shrimp and blue crabs were significantly more abundant in the marsh and bayward canal areas than in the upland canal and bay areas, white shrimp were significantly more abundant in the marsh area than in the other three areas, and pink shrimp were significantly more abundant in the marsh than in the upland and bayward canal areas. During the day, brown shrimp were significantly more abundant in the bayward canal area than in the upland canal and bay areas, while pink shrimp were significantly more abundant in the marsh area than in the upland canal area. The generally lower catches of each species in the open bay and upland canal areas when compared with the marsh and bayward canal areas were attributed to: 1) permanent loss of intertidal vegetation in the housing development; 2) low abundance of detrital material and benthic macroinvertebrates in the open bay and upland canal areas; and 3) eutrophic conditions in the upland canal area.

Development of bayshore property into housing sites by dredging, bulkheading, and filling is occurring in many estuaries. When this property is developed, shallow bay and tidal marsh areas are often dredged or filled with spoil, thus changing the environment for marine organisms. Information is available on some of the environmental changes that are critical, but the effects of these changes on the abundance of macrocrustaceans in Gulf coast estuaries are poorly known.

Ecological studies conducted by personnel of the National Marine Fisheries Service in the Jamaica Beach housing development in West Bay, Tex., during 1969 were reported by Trent et al. (1972). That report described the study area and included summary information on phytoplankton production, oyster production, benthic organisms, sediments, hydrology, and the abundance of macrocrustaceans and fishes. Detailed analyses were reported by Corliss and Trent (1971) on phytoplankton production, Moore and Trent (1971) on oyster production, and Gilmore and Trent (1974) on benthic organisms and sediments.

Mock (1966) studied the abundance of brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, in Galveston Bay, Tex., after the bayshore was altered by bulkheading. He stated that catches of brown shrimp were 2.5 times greater, and catches of white shrimp were 14 times greater in a natural habitat than in a bulkhead area.

The objectives of this study in the Jamaica Beach area during 1969 were to evaluate relative abundance of selected macrocrustaceans between: 1) day and night; 2) housing development canals, natural marsh areas, and open bay areas; and 3) areas with different concentrations of dissolved oxygen.

STUDY AREA AND METHODS

The study area, located in West Bay, included a natural marsh area, an open bay area, and a canal area. The canal area was similar to the natural marsh before it was altered by channelization, bulkheading, and filling (Figure 1). The altered area, which included, prior to alteration,

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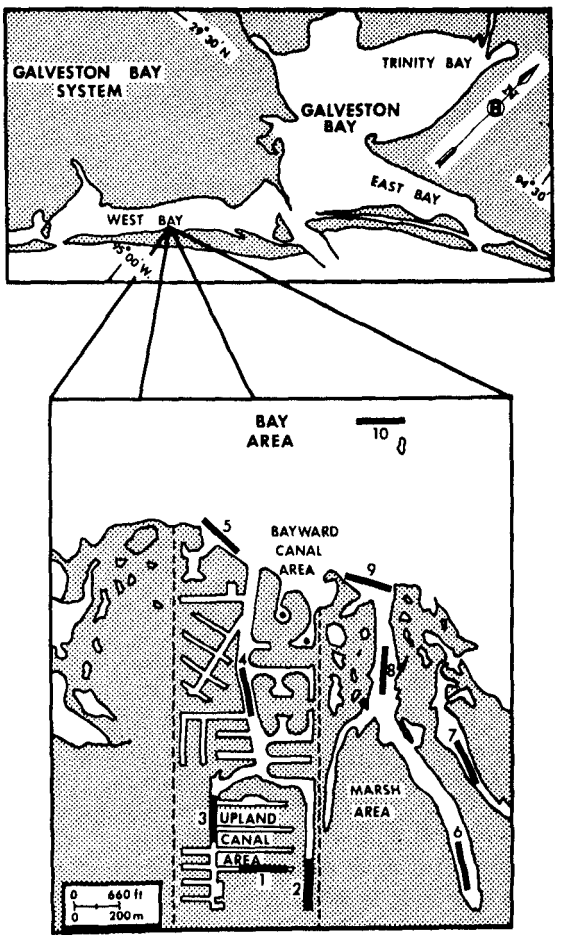

FIGURE 1.—Study area and sampling locations in the Jamaica Beach area of West Bay, Tex.

about 45 hectares of emergent marsh vegetation (predominantly *Spartina alterniflora*), intertidal mud flats, and subtidal water area was reduced to about 32 hectares of subtidal water area by dredging and filling; water volume (mean low tide level) was increased from about 184,000 m^3 to about 394,000 m^3. Ten sampling stations were established in the study area. Average water depths (mean low tide level) at stations 1 through 10 were 1.6, 2.6, 2.2, 1.4, 1.3, 0.5, 0.2, 0.4, 0.5, and 1.0 m, respectively.

Samples of water and crustaceans were collected during the day between 1000 and 1400 h and at night between 2200 and 0200 h at 2-wk intervals from 25 March to 21 October 1969 at each station. Water samples for determining dissolved oxygen were taken 30 cm above the bottom. Oxygen was measured using a modified Winkler method (Carritt and Carpenter 1966). Crustaceans were collected in a trawl that had a mouth opening of 0.6 m by 3.0 m and a stretched mesh of 28.0 mm in the body and 2.5 mm in the cod end. At each station the trawl was towed 200 m at about 2 knots. "Abundance" and "catch" are used synonymously in this report as our index of relative abundance. These terms refer to either the number or average number of animals caught per 200-m tow with the trawl.

Data were treated differently than those reported by Trent et al. (1972) in that stations 1-5 in the altered area were subclassified into upland canal area (stations 1-3) and bayward canal area (stations 4, 5); classification of stations 6-9 in the marsh and station 10 in the bay remained the same.

The data were treated statistically as follows for the five species caught in greatest abundance (Table 1): differences in catches between day and night were tested with a paired-comparison t-test using individual catches at a station as observations; differences between areas were tested with Tukey's w-procedure (Steel and Torrie 1960) using the average catch by area, date, and time of day as observations.

COMPARISONS OF CATCH BETWEEN DAY AND NIGHT

Eight genera and at least 11 species were represented in the catches (Table 1). Four species and members of the genus *Palaemonetes* were

TABLE 1. — Species or genera and total numbers of crustaceans caught by area during the study.

Species	Upland canal	Bayward canal	Marsh	Bay
Brown shrimp, *Penaeus aztecus*	6,112	16,195	27,063	2,505
White shrimp, *P. setiferus*	1,150	2,738	10,961	172
Grass shrimp, *Palaemonetes* sp.	54	23	8,336	21
Blue crab, *Callinectes sapidus*	181	583	1,149	59
Pink shrimp, *Penaeus duorarum*	78	80	636	61
Mantis shrimp, *Squilla* sp.	2	70	7	7
Brokenback shrimp, *Trachypenaeus* sp.	0	8	1	9
Stone crab, *Menippe mercenaria*	0	2	0	0
Mud crab, *Eurypanopeus* sp.	0	0	0	2
Swimming crab, *Callinectes similis*	1	0	0	1
Pistol shrimp, *Alpheus* sp.	0	0	1	0

caught in sufficient numbers for detailed analyses.

Brown shrimp was caught in greater numbers during the day in the canal and bay areas and in greater numbers at night in the marsh area except at station 6 (Table 2). In the canals, day catches were much greater than night catches at the upland canal stations but were only slightly greater than night catches at the bayward canal stations. In the marsh, night catches were significantly greater than day catches at stations 8 and 9, slightly greater than day catches at station 7, and less than day catches at station 6.

White shrimp was caught in greater numbers at night than during the day at all stations except station 5. The differences were statistically significant at stations 7-9.

Grass shrimp, *Palaemonetes* sp., was caught in greater numbers during the day at two of the canal stations and in greater numbers at night at the remaining stations; the differences were not statistically significant, however.

Blue crab, *Callinectes sapidus*, was caught in greater numbers during the day at the upland canal stations (significant at station 3) and in greater numbers during the night at the remaining stations (statistically significant at stations 5-8).

Pink shrimp, *Penaeus duorarum*, was caught in greater numbers at night than during the day at all stations except station 6. Differences were statistically significant at stations 5 and 8.

COMPARISONS OF CATCH BETWEEN AREAS

Statistically significant differences in night catches between areas were observed for four of the five species; day catches were significantly different between areas only for brown and pink shrimps (Table 3). Abundance of brown shrimp during the day was significantly greater in the bayward canal area than in the upland canal and bay areas, whereas at night, brown shrimp were significantly more abundant in the marsh and bayward canal areas than in the other two areas. Catches of white shrimp at night were significantly greater in the marsh area than in the other three areas. Blue crabs were significantly more abundant at night in the marsh and bayward canal than in the bay and upland canal areas. Catches of pink shrimp were significantly greater in the marsh than in the upland canal area during the day and significantly greater in the marsh than in both canal areas at night.

CATCH RELATED TO DISSOLVED OXYGEN

Mean dissolved oxygen values and mean catch of each species by date and area are shown in Figure 2. Mean oxygen values in the bayward canal, marsh, and bay areas were above 3.0 ml/liter throughout the study except on 1 July in the bayward canal and on 23 September in the

TABLE 2. — Comparisons between day and night catches (mean number caught per tow) by species and station (paired comparison *t*-test with 15 df).

Species and time of day	Upland canal stations			Bayward canal stations		Marsh stations				Bay station
	1	2	3	4	5	6	7	8	9	10
Brown shrimp:										
Day	194.4	27.6	77.3	222.9	298.1	210.7	137.1	212.5	93.5	81.4
Night	47.1	14.5	21.1	203.4	287.8	167.6	177.3	481.9	210.8	75.2
t-value	−1.90	−1.02	−1.24	−0.42	−0.18	−1.04	0.98	3.29**	4.43**	−0.20
White shrimp:										
Day	5.8	1.7	12.5	30.1	73.4	76.0	16.1	4.4	8.1	2.9
Night	11.9	3.3	36.7	35.0	32.6	127.6	188.6	178.4	85.8	7.9
t-value	0.79	1.42	1.23	0.75	−0.89	1.18	3.25**	2.93*	2.55*	2.00
Grass shrimp:										
Day	0.1	1.5	0.0	0.4	0.4	31.8	37.7	22.4	2.2	0.4
Night	1.0	0.4	0.4	0.1	0.6	320.4	43.0	61.0	2.5	0.9
t-value	1.45	−0.94	1.60	−1.23	1.00	1.03	0.21	1.40	0.18	1.09
Blue crab:										
Day	3.9	1.5	2.4	6.6	7.6	8.8	2.3	8.0	2.6	1.3
Night	1.6	0.8	1.1	7.4	14.8	18.8	10.7	16.2	4.4	2.4
t-value	−1.61	−1.74	−2.77*	0.46	2.74*	1.93	2.87*	2.85*	1.04	1.28
Pink shrimp:										
Day	0.1	0.1	0.1	0.5	0.2	4.8	2.1	1.1	0.2	1.0
Night	1.6	1.9	1.1	1.2	3.2	0.6	4.2	12.2	14.6	2.8
t-value	1.67	1.24	1.52	0.90	2.35*	−1.79	1.20	2.12*	2.04	1.93

*Significant at 5% level.
**Significant at 1% level.

TABLE 3. — Comparisons of catches between areas (bay; bayward canal, BC; marsh; upland canal, UC) by species and time of day (Tukey's *w*-procedure with 60 df).

Species and time of day	Area, mean catch ( ), and significance lines[1]			
Brown shrimp:				
Day	Bay (81.4)	UC (99.7)	Marsh (163.4)	BC (260.5)
Night	UC (27.6)	Bay (75.2)	BC (245.7)	Marsh (259.4)
White shrimp:				
Day	Bay (2.9)	UC (6.7)	Marsh (26.1)	BC (51.7)
Night	Bay (7.9)	UC (17.3)	BC (33.8)	Marsh (145.1)
Grass shrimp:				
Day	Bay (0.4)	BC (0.4)	UC (0.5)	Marsh (23.5)
Night	BC (0.3)	UC (0.6)	Bay (0.9)	Marsh (106.7)
Blue crabs:				
Day	Bay (1.3)	UC (2.8)	Marsh (5.4)	BC (7.1)
Night	UC (1.2)	Bay (2.4)	BC (11.2)	Marsh (12.5)
Pink shrimp:				
Day	UC (0.1)	BC (0.3)	Bay (1.0)	Marsh (2.0)
Night	UC (1.5)	BC (2.2)	Bay (2.8)	Marsh (7.9)

[1]Any two means not underscored by the same line are significantly different at the 5% level.

marsh. In contrast, mean oxygen values observed in the upland canal area remained below 3.0 ml/liter from 20 May to 12 August and were below 2.0 ml/liter on three occasions. From 20 May to 12 August, about 24% of the individual observations of oxygen values from the upland canal stations were below 1.0 ml/liter, whereas all individual observations from the other three areas were above 1.5 ml/liter.

The normal patterns of seasonal abundance were reflected for brown shrimp, white shrimp, and blue crabs by catches in the bayward canal, marsh, and bay areas (Figure 2). Immigration and emigration in Galveston Bay by brown and white shrimps occur during different seasons (Baxter and Renfro 1966; Trent 1967; Pullen and Trent 1969). Brown shrimp postlarvae immigrate in late winter and early spring and most of the juveniles emigrate in late spring and early summer. White shrimp postlarvae immigrate in the summer, and the juveniles emigrate in the fall or early winter depending on water temperature. Blue crabs are abundant throughout the year in Galveston Bay (Chapman 1965).

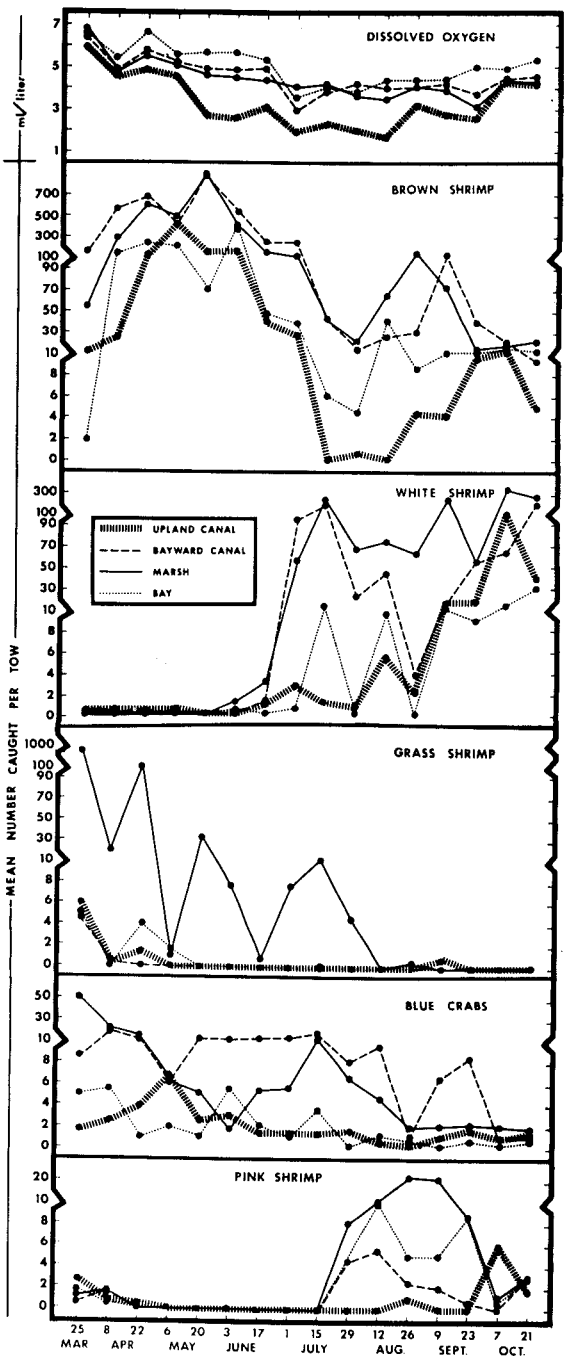

FIGURE 2.—Mean dissolved oxygen values, and mean catch of each species by area and time of year.

Patterns of seasonal abundance for grass and pink shrimps are not documented for the Galveston Bay system. In Redfish Bay, Tex. (about 150 miles southwest of our study area), Hoese and

Jones (1963) caught grass shrimp in greatest numbers during late winter and early spring and pink shrimp in greatest numbers during spring and early fall. Seasonal abundance patterns reflected by catches in this study were similar to those reported in Redfish Bay: for grass shrimp in the marsh area; and for pink shrimp in the bayward canal, marsh and bay areas during late summer and early fall.

Seasonal abundance of brown shrimp, white shrimp, blue crabs, and pink shrimp deviated from what we expected in the upland canal area. These deviations were probably caused by low dissolved oxygen. During the period of low dissolved oxygen (below 3.0 ml/liter; from 20 May to 12 August) in the upland canal area, mean catches of brown shrimp dropped and remained below the mean catches of brown shrimp in the other three areas; mean catches of white shrimp and blue crabs remained below mean catches of white shrimp and blue crabs in the bayward canal and marsh areas after 3 June. The abundance of pink shrimp increased on 29 July in all areas except the upland canal area and remained higher than in the upland canal area until 7 September. Grass shrimp were not caught in large numbers in any area except the marsh and therefore were not used to evaluate the effects of low dissolved oxygen.

DISCUSSION AND SUMMARY

Indices of abundance revealed differences in day-night distribution of brown shrimp, white shrimp, blue crabs, and pink shrimp in the study area. Assuming that our catch per unit effort data provided an index which unbiasedly represented density, migration of individuals of all four species into the more shallow areas of the marsh at night best explains these distributional differences. Inherent in the assumption that catch per unit effort unbiasedly estimates density is the equal vulnerability of the animals to capture during both day and night. Factors which could make this assumption invalid include: 1) burrowing or swimming above the trawl by the animals during one but not the other time period, and 2) avoidance of the trawl during the day or night. Regardless of the correctness of our assumption, the importance of sampling during both day and night to determine differences in abundance between areas was clearly shown.

All five species were more abundant in the marsh than in the upland canal area during both day and night. Brown shrimp, white shrimp, blue crabs, and pink shrimp were more abundant in the bayward canal area than in the upland canal area. The distributional patterns of pink shrimp and blue crabs in this study were similar to those reported by Lindall et al. (1975), who provided data showing that catches of blue crabs and pink shrimp were highest in the bayward portion of an upland canal in a housing development in Tampa Bay, Fla.

Four factors probably account for most of the differences observed in abundance of shrimps between areas. Intertidal vegetation was permanently eliminated by alteration of the natural area for the housing development. Detrital materials and abundance of benthic macroinvertebrates were lowest in the open bay area, low in the upland canal area, and highest in the bayward canal and marsh areas (Gilmore and Trent 1974). Eutrophic conditions observed represent the fourth factor.

Eutrophic conditions, indicated by the observed low values of dissolved oxygen in the upland canals of the housing development during the summer, probably account for the comparatively low catches of brown shrimp, white shrimp, pink shrimp, and blue crabs during that period. Further evidence of eutrophication in this area was provided by studies on: the American oyster, *Crassostrea virginica*, in which setting, survival, and growth rates were less in the upland canal area than in the marsh area (Moore and Trent 1971); phytoplankton in which production was higher in the upland canal area than in the marsh or bay areas (Corliss and Trent 1971); and benthic macroinvertebrates in which the abundance of the organisms declined drastically during the summer months in the upland canal area (Gilmore and Trent 1974). Symptoms of eutrophic conditions in the upland canals of the housing development include inadequate water exchange and high nutrient levels. These factors were discussed in detail by Moore and Trent (1971).

Alteration of estuaries by dredging and filling for housing developments and boat basins results in an environment highly susceptible to recurrent low dissolved oxygen levels. This probelm of low oxygen has been shown also in Forida (Taylor and Saloman 1968; Lindall et al. 1973) and California (Reish 1961). Stresses resulting from low dissolved oxygen reduce the abundance of crustaceans and other animals in the stressed

areas and may produce mass mortalities. Flow dynamics and sedimentation patterns should be carefully evaluated when new developments in estuaries are being considered in order to prevent areas of stagnant water from being created.

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LITERATURE CITED

BAXTER, K. N., AND W. C. RENFRO.
1966. Seasonal occurrence and size distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species identification. U.S. Fish Wildl. Serv., Fish. Bull. 66:149-158.

CARRITT, D. E., AND J. H. CARPENTER.
1966. Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in seawater; a NASCO report. J. Mar. Res. 24:286-318.

CHAPMAN, C. R.
1965. Estuarine program. *In* Biological Laboratory, Galveston, Tex. fishery research for the year ending June 30, 1964, p. 60-75. U.S. Fish Wildl. Serv., Circ. 230.

CORLISS, J., AND L. TRENT.
1971. Comparison of phytoplankton production between natural and altered areas in West Bay, Texas. Fish. Bull., U.S. 69:829-832.

GILMORE, G., AND L. TRENT.
1974. Abundance of benthic macroinvertebrates in natural and altered estuarine areas. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-677, 13 p.

HOESE, H. D., AND R. S. JONES.
1963. Seasonality of larger animals in a Texas turtle grass community. Publ. Inst. Mar. Sci., Univ. Tex. 9:37-47.

LINDALL, W. N., JR., W. A. FABLE, JR., AND L. A. COLLINS.
1975. Additional studies of the fishes, macroinvertebrates, and hydrological conditions of upland canals in Tampa Bay, Florida. Fish Bull., U.S. 73:81-85.

LINDALL, W. N., JR., J. R. HALL, AND C. H. SALOMAN.
1973. Fishes, macroinvertebrates, and hydrological conditions of upland canals in Tampa Bay, Florida. Fish. Bull., U.S. 71:155-163.

MOCK, C. R.
1966. Natural and altered estuarine habitats of penaeid shrimp. Proc. Gulf Caribb. Fish. Inst., 19th Annu. Sess., p. 86-98.

MOORE, D., AND L. TRENT.
1971. Setting, growth, and mortality of *Crassostrea virginica* in a natural marsh and a marsh altered by a housing development. Proc. Natl. Shellfish. Assoc. 61:51-58.

PULLEN, E. J., AND W. L. TRENT.
1969. White shrimp emigration in relation to size, sex, temperature and salinity. FAO Fish. Rep. 57:1001-1014.

REISH, D. J.
1961. A study of benthic fauna in a recently constructed boat harbor in southern California. Ecology 42:84-91.

STEEL, R. G. D., AND J. R. TORRIE.
1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill Book Co., N.Y., 481 p.

TAYLOR, J. L., AND C. H. SALOMAN.
1968. Some effects of hydraulic dredging and coastal development in Boca Ciega Bay, Florida. U.S. Fish Wildl. Serv., Fish. Bull. 67:213-242.

TRENT, W. L.
1967. Size of brown shrimp and time of emigration from the Galveston Bay system, Texas. Proc. Gulf Caribb. Fish. Inst., 19th Annu. Sess., p. 7-16.

TRENT, W. L., E. J. PULLEN, AND D. MOORE.
1972. Waterfront housing developments: Their effect on the ecology of a Texas estuarine area. *In* M. Ruivo (editor), Marine pollution and sea life, p. 411-417. Fishing News (Books) Ltd., West Byfleet, Surrey.

NOTES

MORTALITIES AND EPIBIOTIC FOULING OF EGGS FROM WILD POPULATIONS OF THE DUNGENESS CRAB, *CANCER MAGISTER*[1,2]

Cultured crustaceans have been found to be susceptible to fouling by a variety of epibionts. Nilson et al. (1975) recently described mortalities attributed to epibiotic fouling in the eggs and larvae of the American lobster, *Homarus americanus,* the larvae of the prawn, *Pandalus platyceros,* and larvae of the Dungeness crab, *Cancer magister* Dana. This same type of fouling has also been found on juveniles of Penaeid shrimp, where it causes death in rearing ponds with low oxygen content by inhabiting the gill filaments and suffocating the animal (Johnson et al. 1974; Lightner et al. 1975). The organisms most commonly encountered have been filamentous bacteria and algae.

Work on the larval cultivation of the Dungeness crab at the Bodega Marine Laboratory, Bodega Bay, Calif., revealed heavy fouling on the eggs of oviposited female crabs held in rearing tanks. Further investigation showed that the condition also existed on eggs of crabs obtained from local fishermen. Egg masses with extensive fouling also showed a large number of empty egg cases, although eyespot development on the remaining embryos showed the time until hatching to be distant. Similar fouling of the eggs of wild caught Atlantic blue crabs, *Callinectes sapidus,* has been observed and well documented (Sandoz et al. 1944; Rogers-Talbert 1948). With *Callinectes*, however, the predominant fouling organism appears to be the fungus *Lagenidium callinecti.*

These observations of fouling and mortality in the natural population suggest a possible explanation for the decline in Dungeness crab catches recorded in the San Francisco Bay region since 1960 (Biostatistical Section 1961, 1963, 1964, 1965; Greenhood and Mackett 1965, 1967; Heimann and Frey 1968a,b; Heimann and Carlisle 1970; Pinkas 1970; Bell 1971; Oliphant 1973). In order to investigate this possibility, a distributional study was undertaken, comparing mortalities and epibiotic fouling of crab eggs from various locations along the coast of northern California.

Materials and Methods

Egg samples of *C. magister* were obtained from fishermen along the northern California coast during the period from 27 November 1974 to 30 January 1975. A total of 105 samples of eggs from individual crabs were obtained from six regions which included the following localities (Figure 1): region I — Pacifica (4 samples); region II — Drake's Bay (18 samples); region III—Point Reyes (39 samples); region IV—Bodega Bay, Russian River, and Gualala (10 samples); region V — Fort Bragg (20 samples); region VI — Eureka (14 samples).

In the field, a portion of eggs were removed from the Dungeness crab egg masses and placed in vials

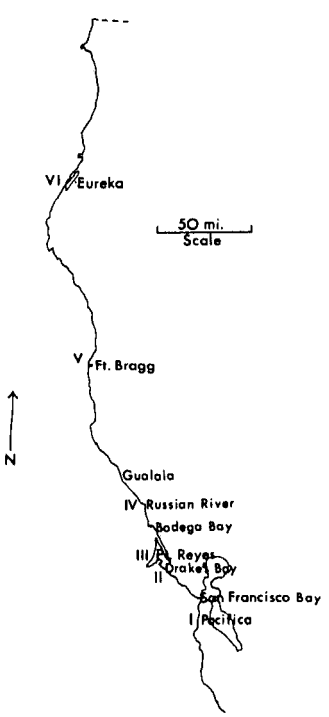


FIGURE 1.—The coast of northern California showing the Dungeness crab collection sites: I - Pacifica; II - Drake's Bay; III - Point Reyes; IV - Bodega Bay, Russian River, and Gualala; V - Fort Bragg; VI - Eureka.

[1]This work was supported by California State Legislature Aquaculture funds.

[2]This work was done at the University of California, Bodega Marine Laboratory at Bodega Bay, CA 94923.

containing 10% Formalin[3] in seawater. The sample size was variable—all exceeded 100 eggs, usually several hundred. The vials were then shipped to the laboratory for examination with the aid of a dissecting microscope. The epibiotic organisms were clearly visible using transmitted light for illumination (Fisher et al. 1975). Closer examination of the egg cases was carried out with a phase microscope to aid in the characterization of the fouling organisms. Portions of the samples were categorized as to the comparative developmental state of the eggs, extent of epibiotic fouling, and egg mortality by the following methods:

1. The following observations of the eyespots which develop as the embryos develop were used to give a comparative estimate of the time the eggs had been carried externally on the female:

D1. No visible eyespot.
D2. Emerging eyespot.
D3. Full eyespot.

Any samples which showed evidence of hatching were not used. Occasionally, there was variation in the degree of development of the eggs from a single sample, in which case the eggs that had developed furthest were used for observation.

2. The extent of epibiotic fouling was determined by the following observations of the external egg membrane:

F1. None—no evidence of epibionts at 100× (Figure 2A).
F2. Light—occasional short filaments.
F3. Moderate—the majority of the surface covered with short filaments and occasional long filaments (Figure 2B).
F4. Heavy—the surface extensively covered with short and long filaments (Figure 2C).
F5. Very heavy—the surface extensively covered with short filaments, long filaments, and detrital material.

3. The number of empty egg cases was used as an estimate of mortality.

M1. <10% mortality.
M2. 10-25% mortality.
M3. 26-50% mortality.
M4. 51-75% mortality.
M5. 76-100% mortality.

Only empty egg cases (Figure 3) were considered mortalities. Other abnormal conditions, such as discolored eggs which might have eventually led to mortalities, were observed but not used in the estimates. All developmental stage D3 samples were checked for emerging embryos to ensure that the empty egg cases were not due to hatching.

In addition to the field samples, seven ovigerous females from the Point Reyes area were examined before being placed into flow-through seawater tanks at the laboratory. After 25 days the eggs were reexamined to determine the progress of the infestation. In addition, one complete egg mass from an ovigerous female was examined to determine the homogeneity of the fouling condition throughout the egg mass.

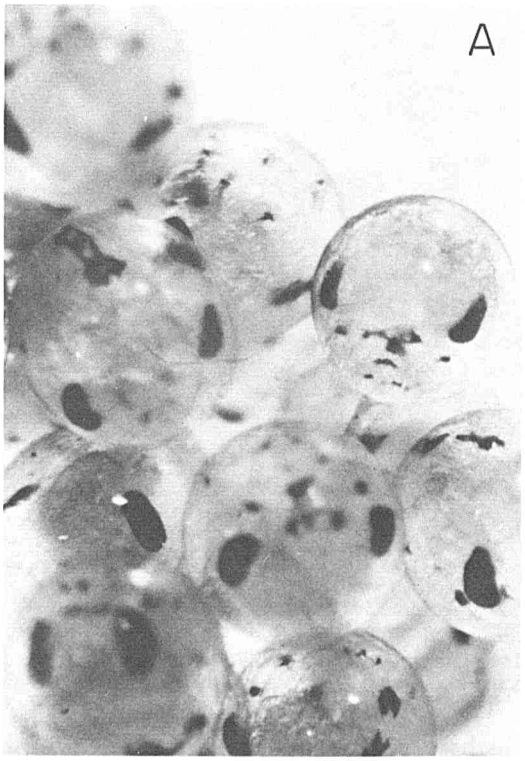
Results

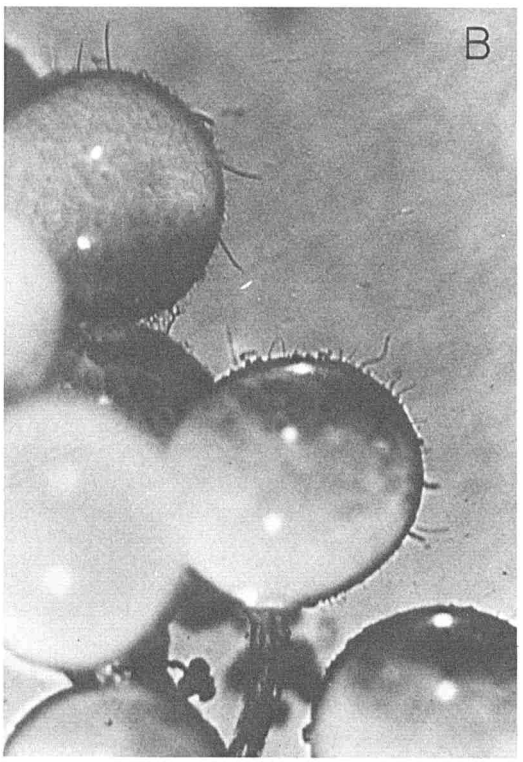
Observation of eyespot development placed 10.5% of the samples into category D1, 35.2% into D2, and 54.3% into D3. Fouling was observed in all developmental categories, but mortalities were generally higher in the more developed eggs. The histograms presented in Figure 4 show the percent of samples from each region placed in each mortality category (M1-M5) and fouling category (F1-F5) after combining the developmental categories.

The eggs of the seven females held in the laboratory for 25 days showed an average increase in their development, fouling and mortality of one level in each category. The greatest observed change was on an egg mass in developmental stage 2 which originally showed light fouling (category 2) and were in mortality category M2. After 25 days it was in developmental stage 3 and showed very heavy fouling (category 5) and had advanced to mortality category, M5. Another showed no increase in fouling as it matured from developmental stages 1 to 3, but the egg mortality category advanced from M1 to M3.

Examination of the entire egg mass of one specimen showed that the extent of the fouling was variable and concentrated mostly on the periphery of the mass and on the inner eggs near the fold of the abdomen. This raises the possibility of sampling error; however, it would probably be insignificant since the field samples came primarily from the exterior of the egg masses.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.





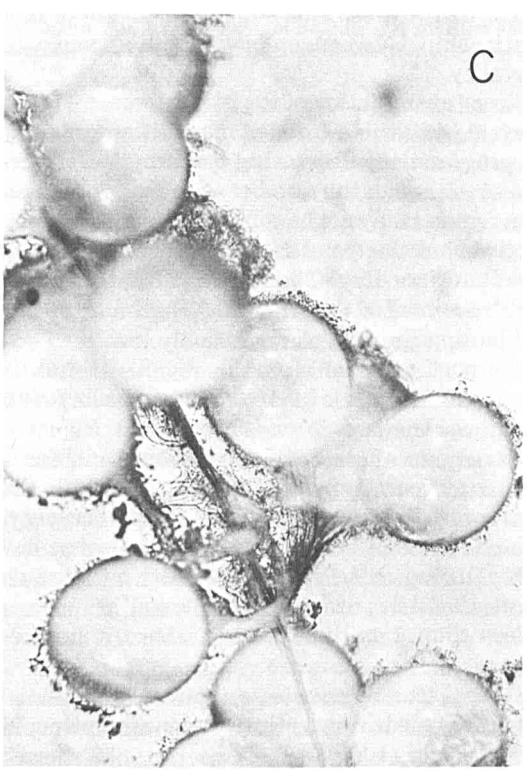


FIGURE 2.—Dungeness crab egg samples showing (A) no epibiotic fouling on the egg membrane (78×), (B) moderate epibiotic fouling on the egg membrane (96×), and (C) very heavy epibiotic fouling on the egg membrane (57×).

The epibiotic fouling organisms found were similar to those noted on other crustaceans by Nilson et al. (1975). Particularly prominent were the long filamentous cyanophytes which resembled *Oscillatoria* and bacterial filaments similar to *Leucothrix*. In heavily fouled samples stalked protozoans (vorticellids) were also observed. These and the filamentous organisms trapped detrital material, which added to the overall contamination of the eggs. Fouling on the egg stalk was often more extensive than fouling on the egg membrane proper. Empty egg cases also showed heavier fouling than those containing embryos. In many cases where fouling was observed, worms were found, and the population of worms was generally larger on egg samples with heavier fouling. The worms were identified as the nemertean egg predator *Carcinonemertes epialti* as described by Kuris (1973).

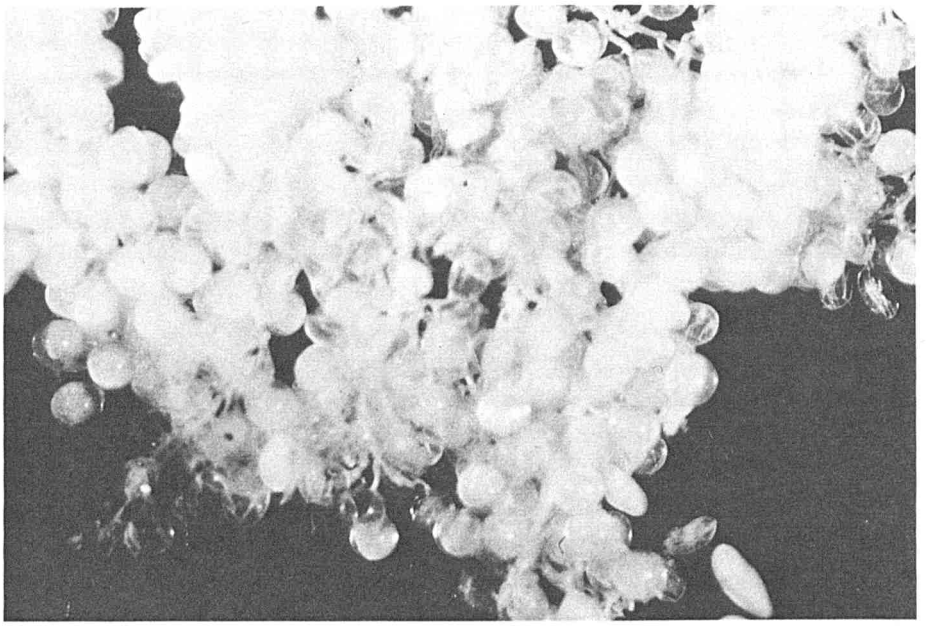


FIGURE 3.—Dungeness crab egg sample showing empty egg cases representing egg mortalities alongside viable eggs from the same egg mass (24.5×).

Discussion

Various workers have attributed mortalities (Johnson et al. 1974; Lightner et al. 1975; Nilson et al. 1975; Fisher et al. 1975) in cultured crustaceans to epibiotic fouling. These reports suggest that death may be caused either by mechanical interference in larval molting or restriction of gaseous exchange across the egg or gill membrane. The fouling organisms may also consume a great deal of the available oxygen from the environment. The dramatic effect of this condition may be seen in Figure 5 where the moderately fouled egg case is entirely intact, yet the embryo is atrophied and nonviable.

Infestation with fouling organisms presumably does not begin until the eggs are oviposited. Although heavy fouling may occur, few mortalities are observed in the early developmental periods. Fouling on the eggs held in rearing tanks progressed as the eggs developed. The progression was an increase in the number or filament length of any one type of the organisms or the addition of other types of organisms. By the second and third developmental categories, mortalities were regularly encountered where fouling occurred.

The samples obtained from regions II and III showed the heaviest epibiotic fouling, as well as the highest levels of mortality. In comparison, region V showed the least extensive fouling and the fewest mortalities. This suggests that there is a relationship between epibiotic fouling and egg mortality.

Closer examination of the histograms in Figure 4 reveals a possible trend of mortalities and fouling progressively decreasing from region II to region V. Although the number of samples obtained from region I may not be conclusive evidence, they suggest that the trend may not continue south of San Francisco Bay. The region VI data show a slight reversal of the trend although mortalities and fouling are still comparatively low.

The mortalities observed in regions II and III are particularly relevant when the coastal crab catch over the last 25 yr is considered. Figure 6 shows a general coast-wide decline in Dungeness crab catch commencing in 1958. In 1965, the northern fishery areas began a strong recovery, whereas the San Francisco area remained at low level. During this decline, the catch of the San Francisco fishery dropped from 8½ million pounds to less than 1 million pounds where it has remained.

Several studies have investigated the potential impact of overfishing on the Dungeness crab population. Poole (1962) and Cordier (1966) showed

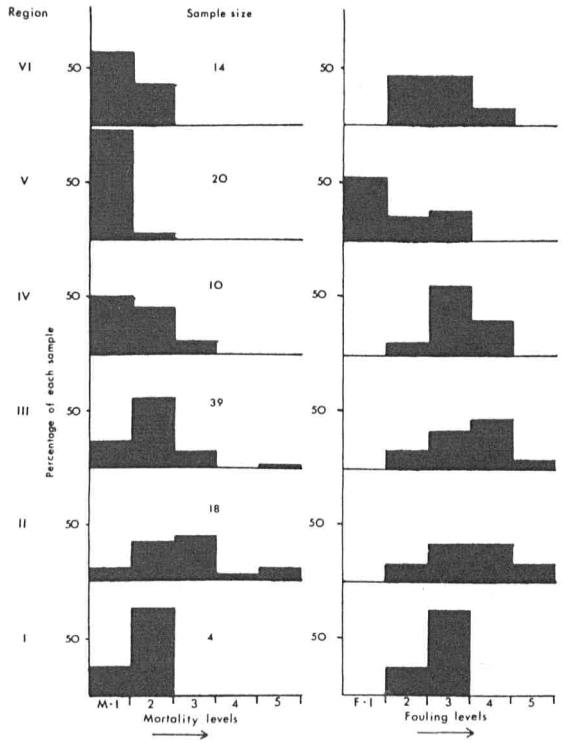


FIGURE 4.—Histograms representing the percent of Dungeness crab samples from each region found in the mortality and fouling categories. The arrows represent increasing mortalities and increasing fouling. Sample sizes from each region are shown.

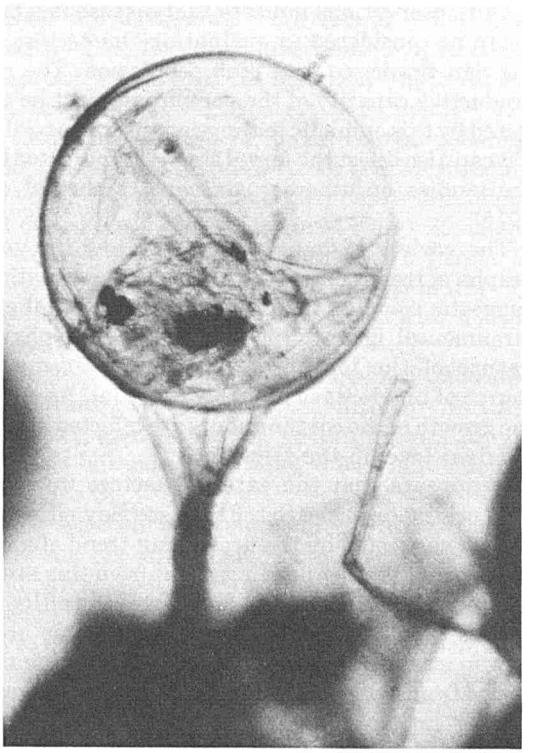


FIGURE 5.—A single Dungeness crab egg showing an intact membrane, an atrophied and nonviable embryo (168×).

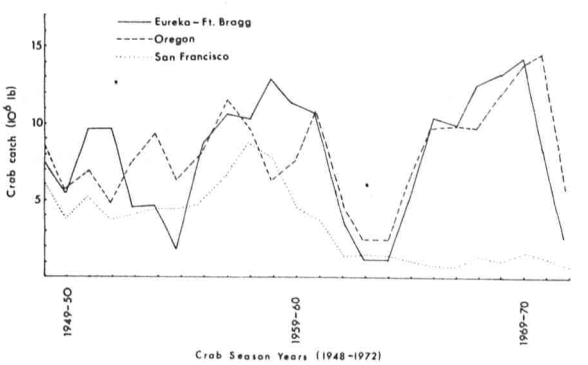


FIGURE 6.—A graph comparing the Dungeness crab catches reported from 1948 to 1972 in three areas. Note that the San Francisco crab catch did not increase from the 1961-62 level.

that 99% and 98%, respectively, of the adult female population had been inseminated, indicating that the fishing industry (which only legally catches males greater than 6¼ inches across the carapace) is not significantly reducing the reproductive capabilities of the crab population. Also, tagging studies have shown that an estimated 90 to 100% of the legal-size males in fishing areas of the California coast have been caught each year since 1929 (Pacific Marine Fisheries Commission 1965). Cleaver (1949) and Peterson (1973) stated that the fishing pressure has been similar in Washington and Oregon. It therefore appears that fisheries along the coast are capable of maintaining production despite the virtually maximum fishing pressures. Poole and Gotshall (1965) concluded that the fishing regulations at that time were sufficient to protect the crab from depletion through overfishing.

Physical factors may be responsible for periodic fluctuations in crab abundance. The Pacific Marine Fisheries Commission (1965) suggested that shifting currents played a role in these fluctuations by disturbing larval settlement. Lough (1974) found a correlation between rainfall during salinity-sensitive larval stages and crab catch 4 yr later when those larvae were to enter the fishery. Peterson (1973) and Botsford and Wickham (1975) have found a positive correlation between upwelling intensity and crab catch.

Our observations indicate that disease is a factor to be considered in evaluating the decline of the San Francisco area crab population. The reproductive capacity of the population must be affected by this epibiotic fouling condition especially if it can also infest the larval stages as indicated by the studies on other crustaceans (Fisher et al. 1975).

The variety of fouling organisms and the geographical trends observed in this disease situation suggest a complex relationship with external environmental factors. In view of the saprophytic nature of the fouling organisms, their major source of nutrients is probably external. As such, the growth of the contaminants are affected by the nutrient level in the seawater.

It appears that the external factors involved may originate in the San Francisco Bay effluent. This is suggested by the decreasing trend of mortalities and fouling heading north from this area, presumably reflecting the dilution of the effluent waters. The normal water currents in this area flow in a southerly direction; however, during the period from November through February, the prevailing inshore flow is the northerly Davidson Current (Reid et al. 1958). During the egg-bearing season, the effluent from San Francisco Bay is carried northward.

The observations of this study were limited by the collection of samples during only the 1974-75 crab season. Because of the potential relationship of these findings to a valuable natural resource, we felt that it was important to communicate the available information. It is clear that further studies during the next season will enhance our understanding of the situation.

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Literature Cited

BELL, R. R.
1971. California marine fish landings 1970. Calif. Fish Game, Fish Bull. 154, 50 p.

BIOSTATISTICAL SECTION, MARINE RESOURCES OPERATIONS.
1961. The marine catch of California for the year 1960. Calif. Fish Game, Fish Bull. 117, 45 p.
1963. The California marine fish catch for 1961. Calif. Fish Game, Fish Bull. 121: 1-47.
1964. The California marine fish catch for 1962. Calif. Fish Game, Fish Bull. 125, 45 p.
1965. The California marine fish catch for 1963. Calif. Fish Game, Fish Bull. 129, 45 p.

BOTSFORD, L. W., AND D. E. WICKHAM.
1975. Correlation of upwelling index and Dungeness crab catch. Fish. Bull., U.S. 73:901-907.

CLEAVER, F. C.
1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Wash. Dep. Fish., Biol. Rep. 49A:47-82.

CORDIER, P.
1966. Cruise report 66-N-9 crab. Calif. Dep. Fish Game, Mar. Resour. Oper.

FISHER, W. S., E. H. NILSON, AND R. A. SHLESER.
1975. Diagnostic procedures for diseases found in egg, larval, and juvenile cultured American lobsters (*Homarus americanus*). Proc. 6th Annu. Workshop World Maricult. Soc., Seattle, Wash., 1975.

GREENHOOD, E. C., AND D. J. MACKETT.
1965. The California marine fish catch for 1964. Calif. Fish Game, Fish Bull. 132, 45 p.
1967. The California marine fish catch for 1965. Calif. Fish Game, Fish Bull. 135:1-42.

HEIMANN, R. F. G., AND H. W. FREY.
1968a. The California marine fish catch for 1966. Calif. Fish Game, Fish Bull. 138:1-48.
1968b. The California marine fish catch for 1967. Calif. Fish Game, Fish Bull. 144, 47 p.

HEIMANN, R. F. G., AND J. G. CARLISLE, JR.
1970. The California marine fish catch for 1968 and historical review 1916-1968. Calif. Fish Game, Fish Bull. 149, 70 p.

JOHNSON, S. K., J. C. PARKER, AND H. HOLCOMB.
1974. Control of *Zoothamnium* sp. on penaeid shrimp. Proc. 4th Annu. Workshop World Maricult. Soc., Monterrey, Mexico, 1973.

KURIS, A.
1973. Population interactions between a shore crab and two symbionts. Ph.D. Thesis, Univ. California, Berkeley.

LIGHTNER, D. V., C. T. FONTAINE, AND K. HANKS.
1975. Some forms of gill disease in penaeid shrimp. Proc. 6th Annu. Workshop World Maricult. Soc., Seattle, Wash., 1975.

LOUGH, R. G.
1975. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Thesis, Oregon State Univ., Corvallis, 229 p.

NILSON, E. H., W. S. FISHER, AND R. A. SHLESER.
1975. Filamentous infestations observed on eggs and larvae of cultured crustaceans. Proc. 6th Annu. Workshop World Maricult. Soc., Seattle, Wash., 1975.

OLIPHANT, M. S.
1973. California marine fish landings for 1971. Calif. Fish Game, Fish Bull. 159, 49 p.

PACIFIC MARINE FISHERIES COMMISSION.
1965. Discussion that followed the report on Dungeness crabs. 16th and 17th Annu. Rep. Pac. Mar. Fish. Comm., p. 38-39.

PETERSON, W. T.
1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull., U.S. 71:902-910.

PINKAS, L.
1970. The California marine fish catch for 1969. Calif. Fish Game, Fish Bull. 153, 47 p.
POOLE, R.
1962. Cruise report 62-N-2g, h, i and l crab. Calif. Dep. Fish Game, Mar. Resour. Oper.
POOLE, R., AND D. GOTSHALL.
1965. Regulations and the market crab fishery. Outdoor Calif. 26(9):7-8.
REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current System. Calif. Coop. Oceanic Fish. Invest. Rep. 1 July 1956 - 1 January 1958, p. 27-56.
ROGERS-TALBERT, R.
1948. The fungus Lagenidium callinectes Couch (1942) on eggs of the blue crab in Chesapeake Bay. Biol. Bull. (Woods Hole) 94:214-228.
SANDOZ, M. D., R. ROGERS, AND C. L. NEWCOMBE.
1944 Fungus infection of eggs of the blue crab Callinectes sapidus Rathbun. Science (Wash., D.C.) 99:124-125.

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SECOND RECORD OF BLACK SKIPJACK, *EUTHYNNUS LINEATUS*, FROM THE HAWAIIAN ISLANDS

Matsumoto and Kang (1967) reported the first capture of the black skipjack, *Euthynnus lineatus* Kishinouye, in the Hawaiian Islands. Recently (14 July 1975), a second black skipjack was taken in these waters by a Hawaiian pole-and-line skipjack tuna fishing vessel, the *Marlin*, skippered by Walter Asari. The fish was noticed by a fish receiver at Hawaiian Tuna Packers, Richard Howell, who contacted Robert T. B. Iversen, Southwest Region Representative stationed at the Southwest Fisheries Center Honolulu Laboratory. Iversen brought the fish to me for identification.

The specimen, 454 mm fork length, and weighing 1.53 kg, was caught from a school of small skipjack tuna, *Katsuwonus pelamis*, at the extreme tip of Penguin Banks, about 40 km south of the eastern end of Oahu. The specimen is deposited in the U.S. National Museum collection (USNM 214683).

Measurements in millimeters taken according to the methods described by Godsil and Byers (1944) are as follows: Fork length - 454; head length - 126; 1st dorsal insertion - 144; 2d dorsal insertion - 271; anal fin insertion - 306; ventral fin insertion - 144; greatest body depth - 112; greatest body width - 73; dorsal-ventral distance - 108; dorsal-anal distance - 188; ventral insertion to vent - 160; length 1st dorsal base - 130; length 2d dorsal base - 29; length anal base - 25; length pectoral - 70; height 1st dorsal - 61; height 2d dorsal - 28; height anal - 28; diameter of iris - 19; maxillary length - 50; snout to posterior margin of eye - 54.

Counts: 1st dorsal spines - 14, plus 1 imbedded; 2d dorsal rays - 12; dorsal finlets - 8; anal rays - 12; anal finlets - 7; pectoral rays - 26; gill rakers - left side 9 + 1 + 24 = 34, right side 9 + 1 + 25 = 35.

The external characters agree with that of the previous capture (Matsumoto and Kang 1967) and with Godsil's (1954) description of the species. Five black unbranched stripes run parallel to the longitudinal axis of the body on the back from the corselet to the caudal fin, and five or six faint unbranched stripes run horizontally on the belly. Two black thoracic spots are located on each side at the indentation of the corselet near the ventral margin of the body.

The vertebral count is 20 + 17 = 37. As in the previous capture, four large protuberances are present on the 31st vertebra, a characteristic of this species (Godsil 1954).

Although this is only the second specimen recorded, an interview with the skipper of the vessel disclosed that fish similar to this are often caught but are not reported. The question posed in 1967 as to whether this is a chance migrant from the eastern Pacific Ocean still stands.

Literature Cited

GODSIL, H. C.
1954. A descriptive study of certain tuna-like fishes. Calif. Dep. Fish Game, Fish Bull. 97, 185 p.
GODSIL, H. C., AND R. D. BYERS.
1944. A systematic study of the Pacific tunas. Calif. Dep. Fish Game, Fish Bull. 60, 131 p.
MATSUMOTO, W. M., AND T. KANG.
1967. The first record of black skipjack, *Euthynnus lineatus*, from the Hawaiian Islands. Copeia 1967:837-838.

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OPTICAL MALFORMATIONS INDUCED BY INSECTICIDES IN EMBRYOS OF THE ATLANTIC SILVERSIDE, *MENIDIA MENIDIA*

Since the banning of DDT from use in the United States, other insecticides such as malathion, parathion, and Sevin[1] (carbaryl) have come into greater use. Though not persistent like DDT, these insecticides, like DDT, find their way into aquatic ecosystems and thus into the spawning grounds of aquatic organisms. Various insecticides have been shown to cause developmental abnormalities. Malathion, for example, has been shown to cause skeletal malformations in birds (McLaughlin et al. 1963; Walker 1967; Greenberg and LaHam 1969), mammals (Tanimura et al. 1967), and reptiles (Mitchell and Yntema 1973).

The experiments described herein were designed to study the effects of DDT, malathion, and Sevin on the development of the Atlantic silverside, *Menidia menidia*. Since previous studies had all indicated that sensitivity decreases with embryonic age, we initiated our treatment early in development.

Materials and Methods

Adult *M. menidia*, from the vicinity of Montauk, N.Y., were collected by a seine during June and July. Eggs and sperm were obtained by stripping the fish, as described by Costello et al. (1957:228-233). The fertilized eggs were separated into small clumps and, after being washed, were placed randomly in glass finger bowls in 100 ml of Millipore-filtered seawater (salinity 30‰) and incubated at 20°C. The insecticides malathion (95% analytical reagent, Supelco Inc., Bellefonte, Pa.), DDT (*p,p'*-DDT, 72% technical grade, Montrose Chemical Co., Torrance, Calif., recrystallized from ethanol to yield 98% *p,p'*-DDT), and Sevin (99.2% carbaryl, Union Carbide Corp., New York, N.Y.) were introduced as acetone solutions into experimental dishes during either early cleavage (2-4 cell stage) or late cleavage (about 100 cells—see Costello et al. 1957, fig. 104), at concentrations of 10 to 500 parts per billion (ppb). Control dishes received an equivalent amount of acetone (10 μl). The solutions were not changed; thus we were studying the effect of a single application of the chemicals (the concentration of which undoubtedly decreased over time due to adsorption). Development was followed with reference to the descriptions of Costello et al. (1957). At appropriate times, eggs were examined to see the percentage which had successfully completed gastrulation and, later, the percentage which had successfully initiated heartbeat. In the first two experiments hatching rates were noted and only the newly hatched fry were examined for malformations. Since they appeared normal, in the subsequent experiments embryos were examined for malformations with considerably more success. Some embryos were preserved in glutaraldehyde, dechorionated, sectioned, and stained with hematoxylin and eosin.

A repeat experiment was performed in the following summer using the same procedures.

Results

In the first experiment, eggs were treated at the late cleavage stage with malathion at 10 and 100 ppb and Sevin at 25 and 100 ppb. There were over 200 eggs in each dish. Percents of successful axis formation and heartbeat initiation were lower than controls in most treated groups (Table 1) but did not always show a dose-related effect. Hatching commenced 14 days after fertilization and continued for 6 days, at which time the experiment was terminated. No difference was noted in hatching times in the various groups and no abnormalities were observed in the fry, although some dead ones were seen in each group.

In the second experiment, eggs at the 2-4 cell stage were exposed to DDT at 25 and 100 ppb and to malathion at 10 and 100 ppb. There were again about 200 eggs in each dish. As in the previous experiment (Table 1) treated groups had lower rates of axis formation and of heartbeat initiation than controls. Hatching commenced 14 days after fertilization and continued for 6 days, at which time the experiment was terminated. No difference was noted in hatching times in the various groups and no abnormalities were noted in the fry, although, as before, some dead ones were noted in each group.

In the third experiment, eggs at the late cleavage stage were exposed to DDT at 10, 25, and 100 ppb, malathion at 10, 100, and 500 ppb, and Sevin at 25, 100, and 500 ppb. There were about 50 eggs in each dish. When checked for axis formation and heartbeat initiation, the treated eggs were again lower than controls. Embryos were care-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1. — Insecticide effects on percentage of axis formation, heartbeat, optic abnormalities, and hatching. Concentrations in parts per billion (ppb).

		DDT (ppb)			Malathion (ppb)						Sevin (ppb)			
Item	Control	10	25	100	10	25	100	500	1,000	2,500	10	25	100	500
Experiment 1 (late cleavage):														
Axis formation	54				23		19					36	48	
Heartbeat	46				22		13					35	48	
Hatch	21				19		6					21	27	
Experiment 2 (2-4 cell stage):														
Axis formation	41		27	9	28		21							
Heartbeat	41		25	5	23		21							
Hatch	28		14	2	11		7							
Experiment 3 (late cleavage):														
Axis formation	17	12	13	10	17		13	15				16	7	13
Heartbeat	17	12	11	6	13		9	13				16	7	9
Optic anomalies	0	50	50	60	40		60	33				40	57	25
Experiment 4 (late cleavage):														
Axis formation	53	45	30	21	37	13	10				30	24		
Heartbeat	53	43	30	20	34	13	6				30	20		
Optic anomalies	1	11	9	15	9	22	30				17	11		
Experiment 5 (late cleavage):														
Axis formation	96	81	82	29					83	65	65	50	50	
Heartbeat	96	70	82	6					83	32	62	50	50	
Optic anomalies	0	1	0	50					4	12	6	12	30	

fully examined for developmental abnormalities, and various optic malformations were discovered in the insecticide-treated embryos. These took the form of unilateral and bilateral microphthalmia (reduced size of eyes), unilateral and bilateral anophthalmia (absence of eyes), and cyclopia (a single median eye) (Figure 1). Severely retarded embryos were also noted. Percentages of those with successful axis formation which showed optical abnormalities were quite high in all treated groups, while none were observed in the control group. Abnormal embryos were fixed prior to hatching. (It was assumed that they would die prior to hatching since no abnormal fry had been found in the previous experiments.) At hatching, which commenced 15 days after fertilization and continued for 7 days, one fish with scoliosis was noted in 10 ppb malathion.

In the fourth experiment, eggs were again exposed at the late cleavage stage to DDT at 10, 25, and 100 ppb, malathion at 10, 25, and 100 ppb, and Sevin at 10 and 25 ppb. There were about 200 eggs in each dish. When checked for axis formation and heartbeat, treated groups were lower

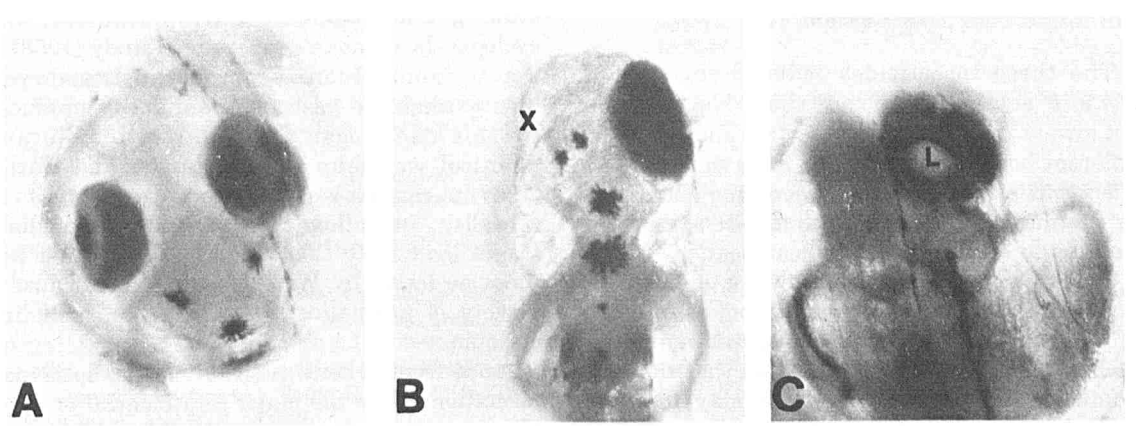

FIGURE 1.—Photomicrographs of whole, fixed, 2-wk-old *Menidia menidia* embryos at approximately 20×. A is a control embryo, while B is a 10 ppb Sevin-treated embryo with unilateral anophthalmia (the site of the undeveloped eye is marked by X), and C is a cyclopic embryo from a 10 ppb malathion-treated batch (transmitted light illuminates the single lens at L).

than controls. At this time, and for several days after, abnormal embryos were noted. These included the severely retarded embryos and the optical abnormalities noted earlier. Only one control embryo showed slight microphthalmia. Hatching commenced after 11 days and continued for 9 days, at which time the experiment was terminated. After hatching, lordotic fry were seen in the 10 ppb malathion, 10 ppb Sevin, and 25 ppb DDT groups. These skeletal abnormalities were quite rare, however.

Eye diameters of hatched fry were measured with an ocular micrometer to see if there were slight reductions in optic size in the apparently normal specimens, but no difference between experimental and control fry was seen.

The fifth experiment was performed the following summer using about 100 eggs per dish. Eggs were exposed at late cleavage to DDT at 10, 25, and 100 ppb, Sevin at 10, 25, and 100 ppb, and malathion at 1 and 2.5 ppm. Treated groups were again lower than controls in rate of axis formation and heartbeat initiation. Abnormal embryos were seen in most treated groups (Table 1) and all embryos which exhibited optic malformations also showed retardation, stunting of growth, sparse body pigment, and abnormal cardiac development in which the heart remained a very thin, feebly beating tube without differentiation of the chambers. There were also embryos with this syndrome in which the eyes appeared normal. Hatching commenced after 12 days, and several fry with scoliosis were seen in the malathion dishes.

Discussion

The three insecticides reduced survival of *Menidia* embryos, although this reduction was not always correlated with the dose and varied in different batches of eggs. The main embryotoxic effect was at early stages, preventing successful axis formation. Of those which formed axes, most went on to establishment of heartbeat.

Notable optic malformations were observed in embryos exposed to DDT, malathion, and Sevin. These three insecticides are quite different from each other chemically, and the fact that they all produced similar malformations may indicate that this species has a propensity toward this type of malformation and various agents can invoke them. This propensity is supported by the presence of one control embryo with slight microphthalmia in one eye. McEwan et al. (1949) likewise concluded that the jewelfish, *Hemichromis bimaculata*, had a tendency to vary abnormally in certain directions and that an abnormal environment accentuated this tendency. The most common optic abnormalities seen in our fish were unilateral anophthalmia and microphthalmia. True cases of cyclopia were rare, though several embryos showed partial convergence of the eye cups, with optic cups directed somewhat ventrally rather than laterally.

Stockard (1907) produced cyclopia in *Fundulus* embryos by treatment with $MgCl_2$. In another study (1910) he produced cyclopean, anophthalmic, and monophthalmic *Fundulus* embryos after treatment with alcohol, results similar to those in the present study.

Histological examination of our material revealed a case in which the optic cup had partly formed, but appeared to be facing inward rather than outward and had lost its connection to the brain. No lens was present in this specimen. Smithberg (1962) found that tolbutamide caused eye malformations in the medaka, *Oryzias latipes*. However, these malformations involved degeneration of the eye cup after the lens had been formed, and lenses were present in all the abnormal embryos. These malformations were accompanied by circulatory defects, which he considered responsible for the eye defects.

Retardation of development was seen by Battle and Hisaoka (1952) in their studies of effects of ethyl carbamate (urethan) on embryos of the zebrafish, *Brachydanio rerio*. Some of their embryos also exhibited optical malformations including anophthalmia, microphthalmia, and cyclopia. In Hisaoka's subsequent study (1958) of 2-acetylaminofluorene on zebrafish embryos, microphthalmia was one abnormality produced by this carcinogen. The antibiotic chloramphenicol was found by Anderson and Battle (1967) to cause a variety of teratogenic effects in zebrafish, including cyclopia and intermediate stages leading to this condition. Colchicine was likewise found by Waterman (1940) to cause a variety of anomalies in the medaka, including cyclopia.

Aside from general retardation, the optic malformations were the major teratological effect of the insecticides on *Menidia* the first year. Skeletal malformations were also noted but they were relatively rare. In the following year, a variety of malformations in addition to the optic ab-

normalities were produced. This difference is perplexing, and is probably due to genetic differences among individuals of this species in susceptibility to the chemicals. This is more understandable when it is realized that relatively few females can supply all the eggs needed for an entire experiment. Such variability in response makes this species a poor one to use in teratological studies.

Effects were seen at dosages as low as 10 ppb. These are levels far lower than those which produced noticeable effects in *Fundulus heteroclitus* embryos (Weis and Weis 1974) in which it was necessary to increase the dosage to parts per million. This may be due to differential permeability of the chorions of the two species and/or to a higher general resistance of *Fundulus* which is generally considered a hardier fish than *Menidia*. The dose levels which affected *Menidia* are levels near those which have been found temporarily, in solution or suspension, in natural areas (Finley et al. 1970; Kennedy and Walsh 1970). Therefore these adverse effects could occur during the development of fish embryos in nature.

Acknowledgments

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Literature Cited

ANDERSON, P. D., AND H. I. BATTLE.
1967. Effects of chloramphenicol on the development of the zebrafish, Brachydanio rerio. Can. J. Zool. 45:191-205.

BATTLE, H. I., AND K. K. HISAOKA.
1952. Effects of ethyl carbamate (urethan) on the early development of the teleost *Brachydanio rerio*. Cancer Res. 12:334-340.

COSTELLO, D. P., M. E. DAVIDSON, A. EGGERS, M. H. FOX, AND C. HENLEY.
1957. Methods for obtaining and handling marine eggs and embryos. Mar. Biol. Lab., Woods Hole, Mass., 247 p.

FINLEY, M. T., D. E. FERGUSON, AND J. L. LUDKE.
1970. Possible selective mechanisms in the development of insecticide-resistant fish. Pestic. Monit. J. 3:212-218.

GREENBERG, J., AND Q. N. LAHAM.
1969. Malathion-induced teratisms in the developing chick. Can. J. Zool. 47:539-542.

HISAOKA, K. K.
1958. The effects of 2-acetylaminofluorene on the embryonic development of the zebrafish. I. Morphological studies. Cancer Res. 18:527-535.

KENNEDY, H. D., AND D. F. WALSH.
1970. Effects of malathion on two warmwater fishes and aquatic invertebrates in ponds. U.S. Bur. Sport Fish. Wildl., Tech. Pap. 55, 13 p.

MCEWAN, R. S., J. B. BRIGGS, AND M. S. GILBERT.
1949. The effects of various abnormal agents applied to early developmental stages of Hemichromis bimaculata, and their theoretical significance. Anat. Rec. 105:491 (abstr.)

MCLAUGHLIN, J., JR., J.-P. MARLIAC, M. J. VERRETT, M. K. MUTCHLER, AND O. G. FITZHUGH.
1963. The injection of chemicals into the yolk sac of fertile eggs prior to incubation as a toxicity test. Toxicol. Appl. Pharmacol. 5:760-771.

MITCHELL, J. T., AND C. L. YNTEMA.
1973. Teratogenic effect of malathion and captan in the embryo of the common snapping turtle, *Chelydra serpentina*. Anat. Rec. 175:390.

SMITHBERG, M.
1962. Teratogenic effects of tolbutamide on the early development of the fish, *Oryzias latipes*. Am. J. Anat. 111:205-213.

STOCKARD, C. R.
1907. The artificial production of a single median cyclopean eye in the fish embryo by means of sea water solutions of magnesium chloride. Arch. Entwicklungsmech. Org. (Wilhelm Roux) 23:249-258.
1910. The influence of alcohol and other anaesthetics on embryonic development. Am. J. Anat. 10:369-392.

TANIMURA, T., T. KATSUYA, AND H. NISHIMURA.
1967. Embryotoxicity of acute exposure to methyl parathion in rats and mice. Arch. Environ. Health 15:609-613.

WALKER, N. E.
1967. Distribution of chemicals injected into fertile eggs and its effect upon apparent toxicity. Toxicol. Appl. Pharmacol. 10:290-299.

WATERMAN, A. J.
1940. Effect of colchicine on the development of the fish embryo, Oryzias latipes. Biol. Bull. (Woods Hole) 78:29-34.

WEIS, P., AND J. S. WEIS.
1974. Cardiac malformations and other effects due to insecticides in embryos of the killifish, *Fundulus heteroclitus*. Teratology 10:263-267.

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GOOSE BARNACLES (CIRRIPEDIA: THORACICA) ON FLOTSAM BEACHED AT LA JOLLA, CALIFORNIA

The macroscopic floating biota of the ocean surface—the pleuston—has been comparatively little studied (see review by Cheng 1975). It comprises a few species of insects, which skim over the surface; a few species of siphonophores equipped with floats; a few species of barnacles; etc. These organisms can be collected by the use of special nets towed at the level of the ocean surface, but the numbers of such tows made on oceanographic expeditions have been comparatively few compared with the much larger numbers of plankton tows made below the sea surface. Under exceptional circumstances, when an onshore wind blows for an extended period, pleustonic organisms are cast ashore in appreciable numbers, presenting unusual opportunities to study numbers of individuals of this little known community. Such mass beachings of the siphonophores *Physalia* and *Velella* have been reported in several parts of the world (Bingham and Albertson 1974; Cheng 1975). This paper presents some data on a mass beaching of pleustonic goose barnacles, mostly attached to floating objects and mostly still living, found washed ashore between 5 and 9 July 1974, in front of the Scripps Institution of Oceanography, La Jolla, Calif.

Methods

A stretch of beach approximately 1 km long and 5 m wide was searched systematically for five successive days, around the time of the low tide in daylight, and every barnacle or piece of flotsam bearing barnacles was collected, taken to the laboratory in plastic bags, and there kept in tanks with running seawater. Some observations were made on the living animals, which remained alive, feeding actively, for several days, and specimens were photographed (Figure 1A-F). They were sorted according to substrate, the species were identified, and the lengths of the capitula were measured from base of scutum to apex of tergum (peduncle lengths being variable).

Observations

In all, some 329 substrate objects were collected and examined; they bore a total of 2,555 individual barnacles. The data, for all collections, are summarized in Tables 1 and 2, and the size distributions of each species on each of the major substrate types are shown in Figure 2A-L. The following generalizations were made on the basis of this material.

TABLE 1. — Numbers and percentages of substrates bearing barnacles: *Lepas (Dosima) fascicularis* and *Lepas (Lepas) pacifica*.

Substrates	Total Number *Dosima* + *Lepas*	*Dosima* No.	*Dosima* %	*Lepas* No.	*Lepas* %	% of total specimens *Dosima*	% of total specimens *Lepas*
Feathers	878	657	75	221	25	34	34
Sea grass leaves:							
Phyllospadix	537						
Zostera	373						
Subtotal	910	835	92	75	8	44	12
Brown algae:							
Macrocystis	202	117	58	85	42	6	13
Colpomenia	18						
Egregia	3						
Halidrys	55						
Sargassum	6						
Scytosiphon	2						
Subtotal	84	83	99	1	1	4	0
Terrestrial debris:							
Wood	69						
Peanut shells	2						
Plastic straws	9						
Cigarette filters	5						
Subtotal	85	47	55	38	45	3	6
Tar lumps	322	113	35	209	65	6	33
None	74	61	82	13	18	3	2
Total	2,555	1,913	75	642	25	100	100

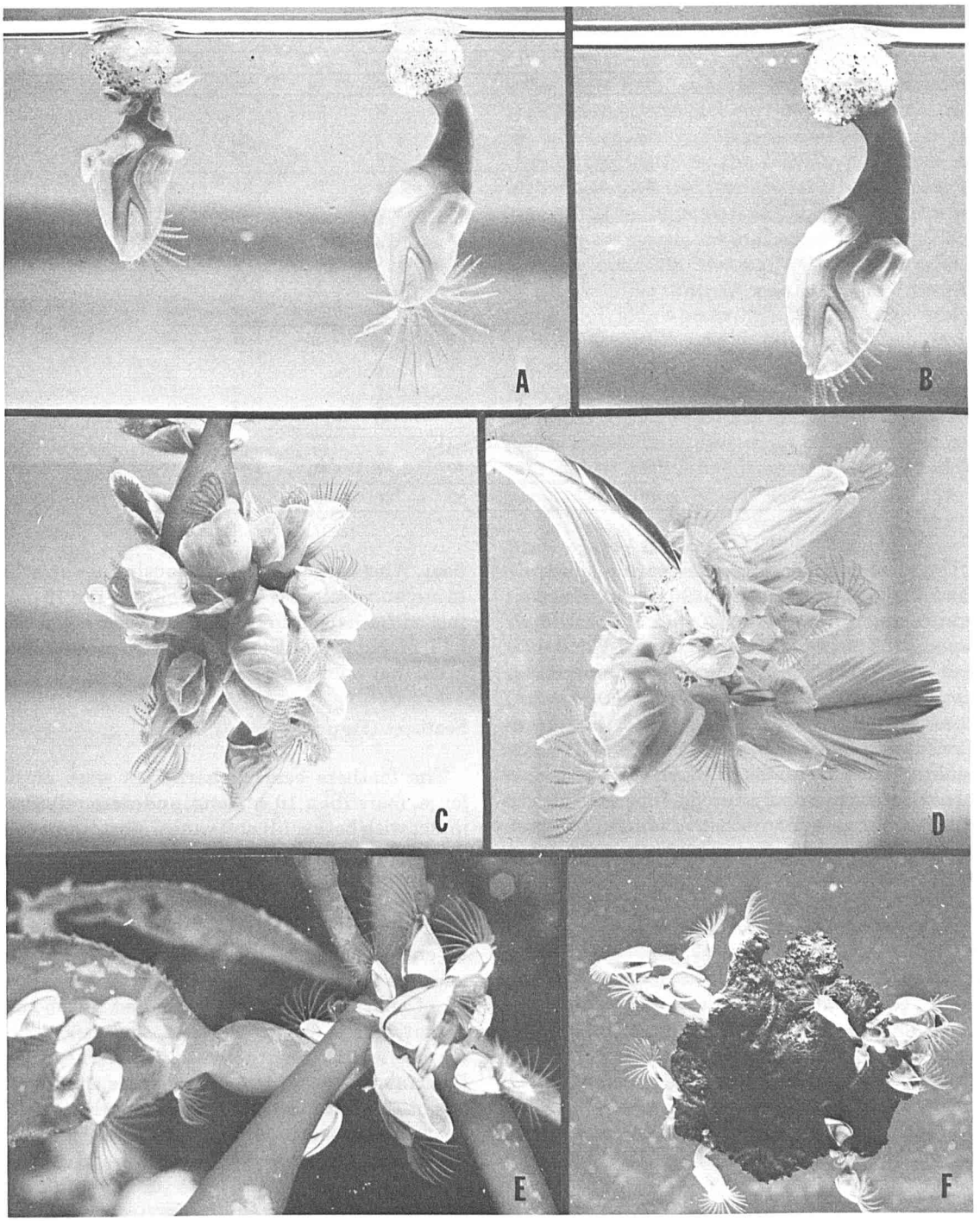

FIGURE 1.—*Lepas (Dosima) fascicularis* and *Lepas (Lepas) pacifica*, living specimens photographed in aquarium. A. Specimens of *Dosima* supported by their own floats at the water surface (note young barnacles attached to specimen on left); B. Right-hand specimen, from Figure 1A, showing cirri withdrawn; C. *Dosima* on detached float of *Macrocystis*; D. *Dosima* on feather; E. Goose barnacles, mostly *Lepas*, on piece of *Macrocystis*; F. Small specimens of *Lepas* on flat lump of tar.

TABLE 2.—Numbers and percentages of barnacles [*Lepas (Dosima) fascicularis* and *Lepas (Lepas) pacifica*] on various substrates.

Substrates	*Dosima* only		*Lepas* only		*Dosima* + *Lepas*		Total of substrates	
	No.	%	No.	%	No.	%	No.	%
Feathers	41	45.5	7	8	42	46.5	90	27
Sea grass leaves:								
Phyllospadix	76		2		8		86	
Zostera	22		1		13		36	
Subtotal	98	80	3	3	21	17	122	37
Brown algae:								
Macrocystis	11	55	0	0	9	45	20	6
Colpomenia	5		0		0		5	
Egregia	1		1		0		2	
Halidrys	9		0		0		9	
Sargassum	1		0		0		1	
Scytosiphon	2		0		0		2	
Subtotal	18	95	1	5	0	0	19	6
Terrestrial debris:								
Wood	8		3		6		17	
Peanut shells	2		0		0		2	
Plastic straws	0		1		0		1	
Cigarette filters	1		0		0		1	
Subtotal	11	52	4	19	6	29	21	7
Tar lumps	14	25	24	42	19	33	57	17
Total	193	59	39	12	97	29	329	100

The most common barnacle-bearing substrate was found to be bird feathers (90 items). The next most common were leaves of the surfgrass *Phyllospadix* (86 pieces) and tar (57 lumps). Other substrates included bits of brown algae *Colpomenia*, *Egregia*, *Halidrys*, *Macrocystis*, *Sargassum*, *Scytosiphon*; leaves of the sea grass *Zostera*; pieces of wood; cigarette filters; peanut shells; and plastic drinking straws. (Pieces of other debris without barnacles, such as polystyrene cups and plastic bottles and caps—many clearly of local origin—were not collected and are not further discussed here.)

Most of the barnacles belonged to two species: *Lepas (Dosima) fascicularis* Ellis and Solander, the soft blue barnacle (about 75% of the individuals); and *Lepas (Lepas) pacifica* Henry, a common Pacific goose barnacle (about 25%). Two other species of barnacle were also found: three specimens of *Tetraclita squamosa* on pieces of *Macrocystis* stipe, and one young specimen of *Lepas (Lepas) anatifera* on a piece of tar. These have not been included in the data of Tables 1 and 2, and will not be considered further.

Unattached (Figure 1A, B)

An appreciable number of the *Dosima* specimens (61) were found unattached to flotsam, either occurring singly, each with its own float, or else with several specimens sharing a communal float. Whether these had previously been attached to any substrate was not determined. The 13 unattached *Lepas* specimens found in our collections had probably become detached from substrates after they were collected.

Feathers (Figures 1D, 2A, B)

The feathers bearing barnacles were mostly large, more than 10 cm long, and were relatively intact with both quill and vanes. Most were white or grey; the species of seabirds from which they originated were not identified. Though a few of the barnacles were attached singly along the shaft, most occurred in clusters, generally near the distal end of the feather. Such clusters comprised as many as 20 individuals of different sizes, many or all of which must have contributed to the communal bubble floats which in some specimens reached a diameter of almost 20 mm. The largest *Dosima* specimen found on a feather was 20 mm long; the largest *Lepas*, only 13 mm. About 50% of the feathers bearing barnacles had only *Dosima* specimens; only seven (7.8%) were found carrying *Lepas* alone, and on all of these the barnacles were rather small and few. On the feathers that carried a mixture of both species, the majority of the animals were *Dosima*; in fact, some 18 of the *Lepas* specimens (all less than 10 mm) were found attached to the larger individuals of *Dosima*. The highest cluster numbers found on single feathers

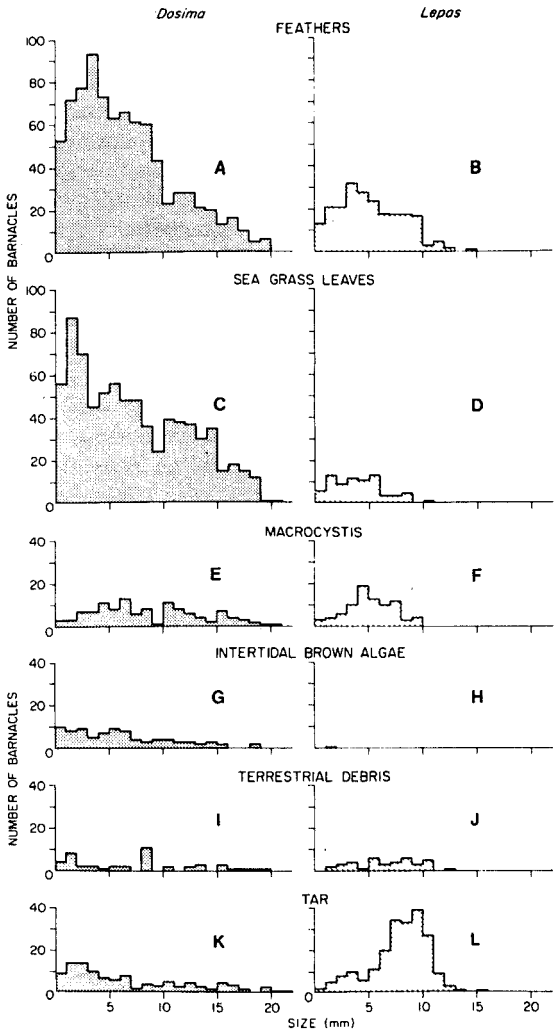

FIGURE 2.—Size-frequency distributions of *Lepas (Dosima) fascicularis* and *Lepas (Lepas) pacifica* on various substrates as indicated.

were 34 for *Dosima* and 15 for *Lepas*. Thirty-six of the *Dosima* clusters consisted of more than 10 individuals, whereas only six of the *Lepas* clumps on feathers comprised more than 10 animals. From these data it appears that on feathers *Dosima* is much commoner than *Lepas* and can occur more densely and in larger clumps, presumably because of its ability to produce its own float.

Sea Grass Leaves (Figure 2C, D)

Many of the *Phyllospadix* and *Zostera* leaves bearing barnacles had been completely bleached; possibly they had become detached from the parent plants and had drifted out to sea before being colonized. The majority of the leaf sections collected were found to carry one or more specimens of *Dosima*. Almost 80% carried only *Dosima*; only 3% bore *Lepas* alone; the rest had both. As in the case of the feathers, the *Dosima* specimens attached to leaves had produced their own floats, as many as 23 individuals being found in one cluster. The largest specimens of *Dosima* found on *Phyllospadix* and *Zostera* were 22 mm and 19 mm long, respectively. In contrast, on these substrates the *Lepas* individuals generally occurred either singly or in pairs, and the majority of these animals did not measure more than 5-6 mm in length, though a few of those which occurred together with *Dosima* exceeded 10 mm. Presumably, larger specimens of *Lepas* cannot be supported by a floating leaf section unless additional buoyancy is supplied by floats of *Dosima*.

Brown Algae (Figures 1C, E, 2E-H)

It is significant that the only algae found bearing barnacles are parts of brown algae (Phaeophyta), which either produce well-differentiated gas-filled floats or, as in the cases of *Colpomenia* and *Scytosiphon*, have hollow thalli usually filled with air. The majority of the barnacles were found on float-bearing segments of *Macrocystis*, and in Tables 1 and 2 the data for this alga, which occurs in offshore waters, are presented separately from those of other brown algae, which are more or less intertidal. Since none of these algae normally carry goose barnacles while growing in their natural habitats, it appears probable that the pieces of thallus were colonized by barnacles after they had been detached. They must have floated for some time, however, since the barnacles had reached appreciable sizes: up to 21 mm in length for *Dosima* and up to 12 mm in length for *Lepas*. With the exception of one piece of *Egregia* bearing a small 2-mm *Lepas*, the littoral brown algae bore only *Dosima* (83 specimens in all), whereas a large proportion of the *Macrocystis* pieces bore mixed populations.

Terrestrial Debris (Figure 2I, J)

The majority of the fragments grouped in this category were pieces of wood, which may be considered a "natural" substrate since fallen branches are a normal component of the flotsam carried

by rivers out to sea. So far, plastics—in pieces sufficiently large and buoyant to support goose barnacles—evidently constitute a substrate of only minor importance for this kind of animal.

Tar (Figures 1F, 2K, L)

The 57 pieces of barnacle-bearing tar, presumably originating from natural seepage or oil bunkers, were mostly flattened 2-3 mm thick, 10-60 mm in diameter. This substrate, unlike those described hitherto, appeared to be preferred by *Lepas*. More than 42% of the lumps collected bore only this species, and many of the pieces had more than 10 animals attached. About 65% of the barnacles found on tar were of this species. Some were more than 15 mm long. They were generally not clumped, but occurred scattered over the surface of the substrate, often on both upper and under surfaces, suggesting that the lump had repeatedly turned over while afloat on the ocean. Comparatively fewer of the tar lumps bore only specimens of *Dosima*, and only 10 of these had more than 10 animals each. Per unit of surface area, the individuals of *Dosima* appeared to be more sparsely distributed on tar than on feathers or grass leaves.

Discussion

Lepas (Dosima) fascicularis is the most specialized pleustonic goose barnacle, with an almost uncalcified shell and a gas-filled bubble float. The larval stages were described on the basis of material collected and reared during the *Challenger* Expedition (Willemöes-Suhm 1876). Since there were several errors and omissions in that paper, all the stages were redescribed by Bainbridge and Roskell (1966).

Boëtius (1952-53) reported that all of the specimens of *Dosima*, which he found on the Danish North Sea coast in September 1952, had floats roughly proportional in diameter to the length of the animal. These barnacles are able to support themselves in the adult stage by their own float, but the cyprid larvae must settle on some substrate before they can metamorphose. The larvae of *Dosima* have been shown to settle preferentially on small floating objects; only later do they produce a bubble float which enables them to stay at the sea surface even when detached from such a support (Boëtius 1952-53; Newman 1974). In our collections, all of the *Dosima* specimens, but none of the *Lepas* specimens, were attached to bubble floats of their own making. Some 27 individuals of *Lepas* (1-10 mm), the smaller of the two species, were found attached to larger specimens of *Dosima*, but, despite their larger absolute numbers, only 8 *Dosima* specimens (1-14 mm) were found on other animals of this species. Evidently floating barnacle colonies do not normally grow by accretion in this way.

The blue pigment of *Dosima* was studied by Fox et al. (1967), who reported that it is a conjugated carotenoid. Although many of the blue barnacles which they studied (washed ashore in the same location) were found attached to the floats of *Velella*, and although we have found large numbers of these siphonophores stranded at various other times in recent years, we found no *Velella* floats among the barnacle substrates in this study. In fact, although hundreds of pleustonic barnacles were stranded on our beach during the period studied, we found no specimen of *Physalia*, *Velella*, or *Ianthina*, which are all common components of the pleuston community in the open ocean. We found only one *Glaucus* (a pelagic nudibranch), a few specimens of *Fiona* (another nudibranch, normally associated with *Macrocystis*), and several polychaete worms. This probably indicates the relatively nearshore rather than oceanic origin of the barnacle colonies. Although, when brought back to a laboratory aquarium and given fresh running seawater, many of the specimens remained alive and apparently healthy for more than 1 wk, such stranded animals are normally unable to return to the sea. When exposed to the sun on the beach they would probably be eaten by gulls or dry up within a few hours.

We have not attempted to study the gut contents of our animals but assume that, like other barnacles in nature, they probably feed mainly on microorganisms and small zooplankton (Howard and Scott 1959; Crisp and Southward 1961). We noted that in the laboratory, when supplied with a suspension of the unicellular alga *Platymonas*, many individuals of *Dosima* extended their cirri, apparently moving them towards the food source, directing it towards the mouth.

Goose barnacles are hermaphrodites. Adults develop both male and female organs at the same time and can cross-fertilize each other. The eggs are brooded in the mantle cavities, and hatch as larvae which live in the plankton before settling. They attach themselves to a solid substrate by an adhesive secreted by the cement glands; the composition of the cement of *Lepas fascicularis* has

been analyzed by Barnes and Blackstock (1974). We do not know how long it takes for them to reach the adult stage after metamorphosis. Horn et al. (1970), who collected 150 specimens of *Lepas pectinata*, 2-8 mm long, attached to four lumps of tar found floating on the sea surface, noted that, in the laboratory, these animals increased in length by about 1 mm per week. The larger specimens in our collections (20 mm for *Dosima*, 15 mm for *Lepas*) contained mature eggs. We have no information on the numbers of generations in the year; our size distribution data (Figure 2) show no evidence for separate generations (which might have been indicated by distinguishable size-class modes). *Lepas* species are known to be widely distributed from tropical to polar seas. Our specimens probably came from populations floating in the eastern Pacific Ocean, which is the most likely area affected by the anomalous meterological conditions occuring during June and July 1974 (J. Namias, pers. commun.).

Summary

A total of 1,913 specimens of *Lepas (Dosima) fascicularis* and 642 specimens of *L. (Lepas) pacifica*, many still alive, were collected on a 1,000-m stretch of beach at La Jolla between 5 and 9 July 1974. They were attached to various substrates which had enabled them to float at the sea surface before being cast ashore. The predominant substrates were feathers (90 pieces, bearing 657 *Dosima*, 221 *Lepas*), sea grass leaves (122 pieces: 835 *Dosima*, 75 Lepas), brown algae (39 pieces: 200 *Dosima*, 86 *Lepas*), and tar (57 pieces: 113 *Dosima*, 209 *Lepas*). *Dosima* is the predominant species on most of the substrates whereas tar lumps appeared to be preferentially settled by *Lepas*. The size distributions (*Dosima*, 1-22 mm; *Lepas*, 1-16 mm) provided no indications of generational discontinuities. The beaching of these normally pleustonic animals should be considered in relation to preceding and prevailing wind conditions.

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Literature Cited

BAINBRIDGE, V., AND J. ROSKELL.
1966. A re-description of the larvae of *Lepas fascicularis* Ellis and Solander with observations on the distribution of *Lepas* nauplii in the north-eastern Atlantic. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 67-81. George Allen & Unwin Ltd., Lond.

BARNES, H., AND J. BLACKSTOCK.
1974. The biochemical composition of the cement of a pedunculate cirripede. J. Exp. Mar. Biol. Ecol. 16:87-91.

BINGHAM, F. O., AND H. D. ALBERTSON.
1974. Observations on beach strandings of the *Physalia* (Portuguese-man-of-war) community. Veliger 17:220-224.

BOËTIUS, J.
1952-53. Some notes on the relation to the substratum of *Lepas anatifera* L. and *Lepas fascicularis* E. et S. Oikos 4:112-117.

CHENG, L.
1975. Marine pleuston—animals at the sea-air interface. Oceanogr. Mar. Biol., Annu. Rev. 13:181-212.

CRISP, D. J., AND A. J. SOUTHWARD.
1961. Different types of cirral activity of barnacles. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 243:271-307.

FOX, D. L., V. E. SMITH, AND A. A. WOLFSON.
1967. Disposition of carotenoids in the blue goose barnacle *Lepas fascicularis*. Experientia 23:965-967.

HORN, M. H., J. M. TEAL, AND R. H. BACKUS.
1970. Petroleum lumps on the surface of the sea. Science (Wash., D.C.) 168:245-246.

HOWARD, G. K., AND H. C. SCOTT.
1959. Predaceous feeding in two common gooseneck barnacles. Science (Wash., D.C.) 129:717-718.

NEWMAN, W. A.
1974. Cirripedia. Encyclopaedia Britannica, 15th ed. 4:641-643.

WILLEMÖES-SUHM, R. VON.
1876. On the development of *Lepas fascicularis* and the Archizoea of Cirripedia. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 166:131-154.

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CALORIC VALUES OF SOME NORTH ATLANTIC CALANOID COPEPODS

Evaluation of the dynamics of energy exchange of a marine ecosystem necessitates a knowledge of the caloric equivalents of its living constituents. This information, in combination with information on growth, metabolism, and assimilation rates can lead to predictions of energy conversion between trophic levels and estimates of production.

Researchers have accumulated a considerable quantity of data concerning the caloric value of marine organisms (Cummins 1967; Thayer et al. 1973; Tyler 1973); however, values recorded for marine, planktonic copepod species have been few (Slobodkin and Richman 1961; Comita et al. 1966; Cummins 1967). My research reports the caloric values for seven species of marine copepods, six of which apparently have not been previously recorded. These studies are part of an overall investigation of the bioenergetics of the early life stages of some North Atlantic fish species.

Materials and Methods

Plankton samples were collected in July and August 1972 off Narragansett Bay, R.I. except for samples of *Pseudocalanus minutus* which were collected in April 1971 off the coast of Delaware. All samples were preserved in 5% Formalin[1] and were prepared and combusted in July and August 1972. Laboratory preparation included rinsing the samples in distilled water for 1 h, sieving through a coarse mesh screen to remove large detritus, and hand sorting adults of the various copepod species under a dissecting microscope. Pure copepod species samples were dried for 24 h at 90°C and desiccated in a silica gel desiccator after which they were made into pellets for combustion. All combustion was done in a Parr 1241 automatic, adiabatic calorimeter adapted for a microbomb. Combustion samples for each copepod species were done in triplicate. Percent ash for each copepod species was determined by ashing uncombusted pellets in triplicate at 500°C for 4 h in a muffle furnace.

Results

Mean values for the caloric determinations of the seven species of copepods (Table 1) were as follows: 5,251.9 cal/g dry weight, 5,626.3 cal/g ash-free dry weight, and 6.70% ash. Statistical analysis of the means of caloric values for each species (Duncan's New Multiple Range Test, Steel and Torrie 1960) indicated that *Calanus finmarchicus* had significantly higher values of both calories per gram dry weight and calories per gram ash-free dry weight than all other species, that *Temora longicornis* had significantly lower values for calories per gram ash-free dry weight than all species except *Centropages hamatus*, and that the differences between *Acartia tonsa*, *Tortanus discaudatus*, *P. minutus*, *Centropages typicus*, and *C. hamatus* were minimal (Table 1).

Temora longicornis had the highest percent ash. *Acartia tonsa* and *P. minutus* also had relatively high ash values in comparison with the other species, while *Calanus finmarchicus* was intermediate and higher than the three remaining species (Table 1).

TABLE 1. — Caloric and ash values for some North Atlantic copepods. Species are recorded in order from largest to smallest mean value under each category. Those species side-scored have similar means (Duncan's New Multiple Range Test, $P = 0.05$).

Species	Mean	Standard deviation
cal/g dry weight		
Calanus finmarchicus	6,425.1	±187.0
Tortanus discaudatus	5,398.3	±14.6
Centropages typicus	5,244.7	±183.3
Acartia tonsa	5,160.0	±78.8
Pseudocalanus minutus	5,070.9	±181.7
Centropages hamatus	4,998.6	±246.3
Temora longicornis	4,466.3	±92.8
cal/g ash-free dry weight		
Calanus finmarchicus	6,835.2	±191.2
Acartia tonsa	5,664.1	±86.6
Tortanus discaudatus	5,642.0	±15.3
Pseudocalanus minutus	5,541.9	±198.6
Centropages typicus	5,503.4	±192.3
Centropages hamatus	5,212.3	±256.9
Temora longicornis	4,984.7	±103.6
% ash		
Temora longicornis	10.40	±0.16
Acartia tonsa	8.90	±0.16
Pseudocalanus minutus	8.50	±0.11
Calanus finmarchicus	6.00	±1.82
Centropages typicus	4.70	±0.28
Tortanus discaudatus	4.32	±0.07
Centropages hamatus	4.10	±0.13

Discussion

Since the species in this study were preserved in Formalin for short periods of time and rinsed in distilled water to remove the Formalin before processing, the estimates of caloric and ash content

[1]Reference to trade names does not imply endorsement by National Marine Fisheries Service, NOAA.

and dry weight may have been slightly affected due to an unknown loss of chemical constituents. Methods of preservation of animals before combusting or determining chemical composition and weights have been a subject of debate. Omori (1970) showed there was considerable variation with no apparent trend of chemical composition and weight of *Calanus cristatus* that were frozen, dried, or preserved in Formalin. Except for dry weight, which was lowest in Formalin-preserved specimens, he found no clear relationship between percent ash, carbon, nitrogen, and hydrogen composition and the methods of preservation. Faustov and Zotin (1965) determined that fixing by drying or in 4% Formalin had no significant effect on the caloric value of fish embryos and, consequently, results obtained with fresh or fixed material could be directly compared. In the present study, samples of fresh and preserved (5% Formalin) *C. finmarchicus* were compared. Calories per gram dry weight and percent ash were less for the preserved sample, however, the differences were minimal (274.8 cal/g dry weight and 3.78% ash which corresponds to 275.0 cal/g ash-free dry weight) and only slightly greater than one standard deviation (Table 1).

In view of the apparent lack of specific effects of preservation method on chemical composition, weights, and caloric values reported in the literature and the results with *C. finmarchicus* in this research, it may be concluded that the values presented in this paper are only slightly underestimated, if at all. Also, since all samples in this study were treated the same way, relative comparisons between them should be valid.

Attempts to explain the differences in caloric values on the basis of phylogeny proved inadequate. All species are calanoid copepods and, although *C. finmarchicus* and *P. minutus* are members of a different, more primitive taxonomic subdivision under the Calanoida than the other species (Sars 1903), the values for *P. minutus* were statistically more similar to the lower values for the other species than to *C. finmarchicus*.

There is a lack of information on the specific chemical composition of the species tested in this research with the exception of *C. finmarchicus*. *Calanus finmarchicus* is known to have a reasonably high fat content. Comita et al. (1966) noted that, upon fixation, globules of fat were extruded from living specimens and that a layer of oil formed on the surface of the fixed sample. They determined the caloric value of the fat of *C. finmarchicus* to be 9,500 cal/g. Fisher (1962) determined the lipid content for a number of marine Crustacea and found the concentrations in *C. finmarchicus* to be consistently among the higher values recorded. Although there are no fat content values for the six other species tested in this research to compare with *C. finmarchicus*, the implication is that the lipid content in *C. finmarchicus* may be the cause of its higher caloric value. The caloric determinations of *C. finmarchicus* recorded in this research (Table 1) compare closely with the results of other workers (Slobodkin 1962; Comita and Schindler 1963; Comita et al. 1966). In fact, the caloric values of *C. finmarchicus* have been some of the highest recorded for copepods.

Temora longicornis had lower caloric values than the other species and the highest percentage of ash (Table 1). This may be the result of its morphology which is somewhat different compared to the other species. It has a proportionately rounder and deeper cephalothorax that may contribute to a higher percentage of inorganic exoskeleton.

The overall means for the caloric values of all the species (5,251.9 cal/g dry weight and 5,626.3 cal/g ash-free dry weight) are similar to composite sample caloric values recorded by other investigators. A calculation based on the data of Ostapenya et al. (1967) using their values of calories per gram dry weight and percent organic matter for Gulf of Mexico plankton samples, which were predominantly copepods including *Acartia* sp., *Centropages* sp., and *Temora* sp. (separate values for each of these genera were not reported), produced a mean value of 5,187 cal/g ash-free dry weight. A similar confirming value of 5,016 cal/g dry weight was obtained using the percent organic matter in the dry material in my research (calculated by subtracting the mean percent ash, 6.70%, from 100) and the regression relationship between that and ash-free dry weight devised by Platt et al. (1969).

Seasonal changes in the caloric value of zooplankton have been verified in several studies (Comita et al. 1966; Conover 1968; Siefken and Armitage 1968). The species in this study undoubtedly undergo seasonal variations also, and this is a subject for future investigation. However, all the species used in this research, with the exception of *P. minutus,* were collected at approximately the same time in the same general area and can be used for a comparison of the potential energy available to predators at a particular time and place.

Examination of data on the abundance of adult and nauplii stages in the Narragansett Bay and Block Island Sound areas (Deevey 1952; Faber 1966) for the time of year samples for this research were collected (July-August) showed that, although all seven species were present, only *A. tonsa*, *T. longicornis*, and *C. hamatus* were available in sufficient quantity to be considered major prey organisms. They represented 24.6, 10.8, and 10.4%, respectively, of the total copepods available, while the other four species were less than 3%. The results of this study in calories per gram ash-free dry weight (Table 1) show that *A. tonsa* had the second highest value while *C. hamatus* and *T. longicornis* had the two lowest values. In fact, the difference between *A. tonsa* and *T. longicornis* is 680 cal/g. This indicates, assuming equivalent assimilation rates, that predators utilizing the copepods like *A. tonsa* with higher caloric values may have an advantage in acquiring energy for growth and metabolic processes. Predators feeding on copepods with lower values, especially *T. longicornis*, would have to consume more prey organisms for an equivalent energy intake and, given the same density of plankton, would spend more energy searching for their prey.

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Literature Cited

COMITA, G. W., AND D. W. SCHINDLER.
1963. Calorific values of microcrustacea. Science (Wash., D.C.) 140:1394-1396.

COMITA, G. W., S. M. MARSHALL, AND A. P. ORR.
1966. On the biology of *Calanus finmarchicus*. XIII. Seasonal change in weight, calorific value and organic matter. J. Mar. Biol. Assoc. U.K. 46:1-17.

CONOVER, R. J.
1968. Zooplankton—Life in a nutritionally dilute environment. Am. Zool. 8:107-118.

CUMMINS, K. W.
1967. Calorific equivalents for studies in ecological energetics. 2nd ed. Univ. Pittsburg, Pittsburg, 52 p.

DEEVY, G. B.
1952. Quantity and composition of the zooplankton of Block Island Sound, 1949. Bull. Bingham Oceanogr. Collect., Yale Univ. 13:120-164.

FABER, D. J.
1966. Seasonal occurrence and abundance of free-swimming copepod nauplii in Narragansett Bay. J. Fish. Res. Board Can. 23:415-422.

FAUSTOV, V. S., AND A. I. ZOTIN.
1965. Changes in the heat of combustion of the eggs of fishes and amphibians during development. Akad. Nauk SSSR (Doklady) Biol. Sci. 162:965-968.

FISHER, L. R.
1962. The total lipid material in some species of marine zooplankton. Rapp. P.-V. Réun., Cons. Perm. Int. Explor. Mer 153:129-136.

OMORI, M.
1970. Variations of length, weight, respiratory rate and chemical composition of *Calanus cristatus* in relation to its food and feeding. *In* J. H. Steele (editor), Marine food chains, p. 113-126. Univ. Calif. Press, Berkeley.

OSTAPENYA, A. P., L. M. SUSHCHENYA, AND N. N. KHMELEVA.
1967. Caloricity of plankton from the tropical zone of the ocean. [In Russ., Engl. abstr.] Okeanol. Keanologiza 6:1100-1107.

PLATT, T., V. M. BRAWN, AND B. IRWIN.
1969. Caloric and carbon equivalents of zooplankton biomass. J. Fish. Res. Board Can. 26:2345-2349.

SARS, G. O.
1903. An account of the crustacea of Norway, Vol. 4, Copepoda Calanoida. Bergen Museum, Christiana, 171 p.

SIEFKEN, M., AND K. B. ARMITAGE.
1968. Seasonal variation in metabolism and organic nutrients in three *Diaptomus* (Crustacea: Copepoda). Comp. Biochem. Physiol. 24:591-609.

SLOBODKIN, L. B.
1962. Energy in animal ecology. Adv. Ecol. Res. 1:69-101.

SLOBODKIN, L. B., AND S. RICHMAN.
1961. Calories/gm in species of animals. Nature (Lond.) 191:299.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., N.Y., 481 p.

THAYER, G. W., W. E. SCHAAF, J. W. ANGELOVIC, AND M. W. LACROIX.
1973. Caloric measurements of some estuarine organisms. Fish. Bull., U.S. 71:289-296.

TYLER, A. V.
1973. Caloric values of some North Atlantic invertebrates. Mar. Biol. (Berl.) 19:258-261.

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METHOD FOR RESTRAINING LIVING PLANKTONIC CRUSTACEANS[1]

Studies of the feeding and swimming mechanisms of small, active planktonic crustaceans require restraining the organisms so that water flow and limb movements can be observed under the microscope. The usual technique is to place the organism in a watch glass or cavity slide (Cannon 1928; Gauld 1966) or to secure the dorsal side of the animal to a drop of stopcock grease in

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some type of water chamber (McMahon and Rigler 1963). For many studies, these methods are undesirable because of the confinement of the animal to a small volume of medium or because of the solid boundaries nearby, both of which affect the flow of water and possibly the movement of limbs or other behavior by the animal (Lowndes 1935). Whenever the animal must be placed within a relatively large volume of water, other methods must be used. In a study of mate-seeking behavior, Katona (1973) tethered female copepods by means of fine stainless steel wires looped about their bodies. While this method allows the subsequent release of the animals unharmed, the restraining wire can interfere with limb movements.

I have found a relatively simple method for restraining small crustaceans in large volumes of water for extended periods of microscopic examination. A short segment (1-2 cm) of nylon monofilament fishing line of small diameter relative to the organism is mounted in a dissecting needle holder or pin vise. The free tip of the monofilament is then cut off square with a razor blade. The animal is placed dorsal side up in a small drop of water on a microscope slide or watch glass. The tip of the monofilament is dipped in a fresh droplet of "instant" drying polymer glue (such as Dixon Duradix)[2] and quickly applied and held to the center line of the dorsal surface of the animal for about 5 s. The organism can then be lifted from the slide and placed in the test vessel, with the dissecting needle holder mounted in a micromanipulator or other type of clamping device. The rapid filming over of the glue and its tendency to spread when placed on the wet animal sometimes makes a neat attachment difficult and several attempts may be needed before a satisfactory mount is achieved.

Organisms restrained in this way appear to carry out swimming movements in a natural manner and live for several days on the mount. Removal of the animal from the monofilament usually results in its death. To make limb movements easier to observe, organisms can be vitally stained with neutral red prior to mounting (Dressel et al. 1972).

I have since found a description of this mounting technique given by Scourfield (1900) in which he regrets that no satisfactory cement could be found. The polymer glues appear to solve the problem.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Literature Cited

CANNON, H. G.
1928. On the feeding mechanism of the copepods, *Calanus finmarchicus* and *Diaptomus gracilis*. Br. J. Exp. Biol. 6:131-144.

DRESSEL, D. M., D. R. HEINLE, AND M. C. GROTE.
1972. Vital staining to sort dead and live copepods. Chesapeake Sci. 13:156-159.

GAULD, D. T.
1966. The swimming and feeding of planktonic copepods. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 313-334. George Allen and Unwin, Ltd., Lond.

KATONA, S. K.
1973. Evidence for sex pheromones in planktonic copepods. Limnol. Oceanogr. 18:574-583.

LOWNDES, A. G.
1935. The swimming and feeding of certain calanoid copepods. Proc. Zool. Soc. Lond. 1935:687-715.

MCMAHON, J. W., AND F. H. RIGLER.
1963. Mechanisms regulating the feeding rate of Daphnia magna Straus. Can. J. Zool. 41:321-332.

SCOURFIELD, D. J.
1900. The swimming peculiarities of *Daphnia* and its allies, with an account of a new method of examining living Entomostraca and similar organisms. J. Quekett Microsc. Club 7:395-404.

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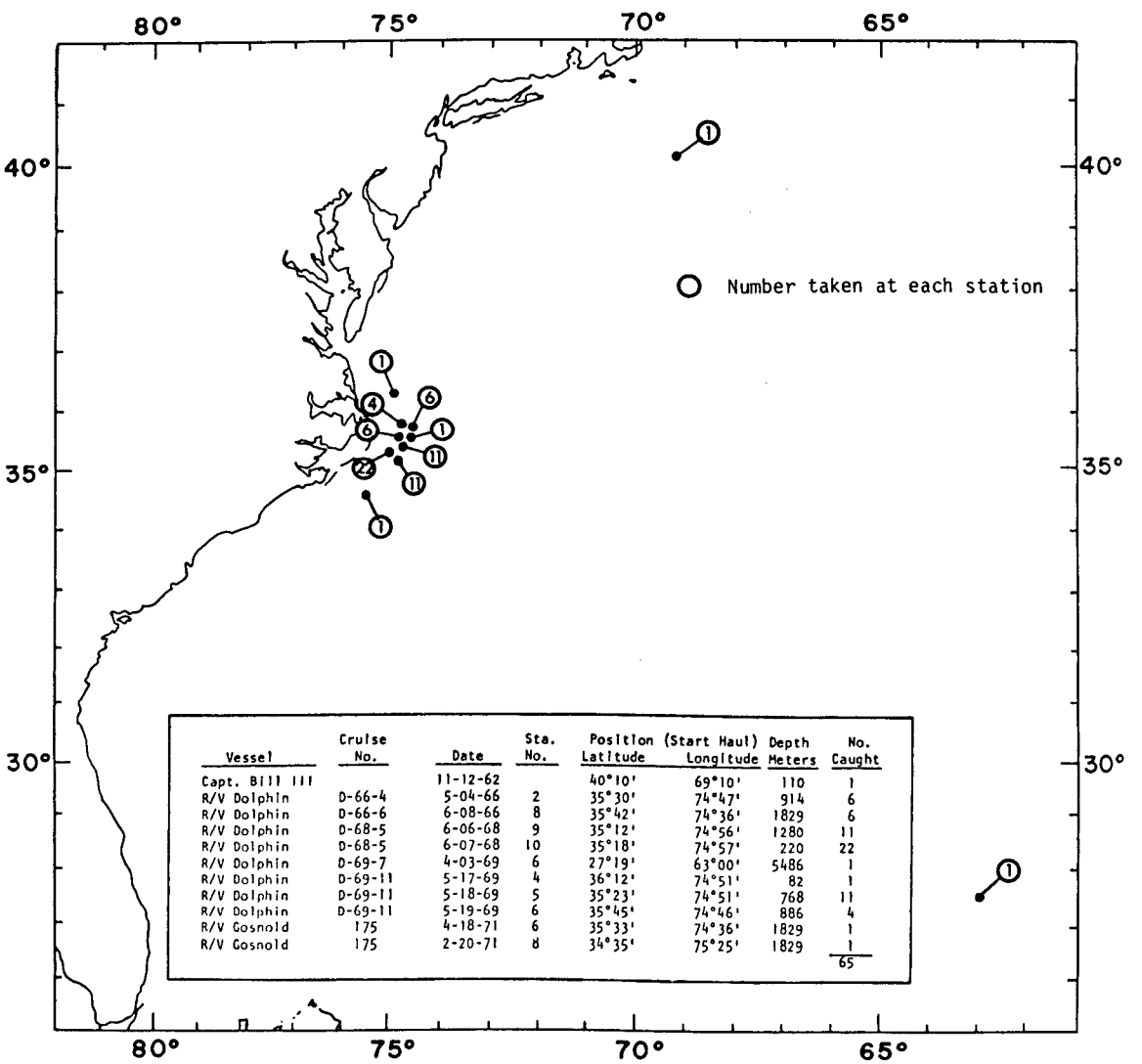
OBSERVATIONS ON THE BIGEYE THRESHER SHARK, *ALOPIAS SUPERCILIOSUS*, IN THE WESTERN NORTH ATLANTIC

Thresher sharks of the genus *Alopias* are distributed throughout the tropical and warm temperate zones of the world's oceans. Of the two species reported from the western North Atlantic, the thresher shark, *A. vulpinus*, is commonly found in coastal waters of the middle Atlantic states (Bigelow and Schroeder 1948). The second member of the genus, the bigeye thresher, *A. superciliosus*, is a little known offshore resident of the continental slope and open sea.

Lowe first described the bigeye thresher in 1840 from a specimen taken off the island of Madeira (Bigelow and Schroeder 1948). The species was not reported again until 1941 when Springer (1943) documented the occurrence of a gravid female taken near Salerno, Fla. Records of other bigeye threshers from the Atlantic include a gravid female, two embryos, a juvenile male, and an 18-foot specimen all taken from the north

coast of Cuba in the late 1940's (Bigelow and Schroeder 1948); an adult female from Nassau in 1962 and an adult male from Cape Hatteras, N.C., in 1963 (Fitch and Craig 1964). Bigelow and Schroeder (1948) reported proportional measurements from two individuals taken off Cuba; Strasburg (1958) and Fitch and Craig (1964) reported similar data from two Pacific specimens.

We report observations of *A. superciliosus* taken on pelagic longlines aboard the commercial fishing vessel *Cap'n Bill III*, in 1962, the RV *Dolphin* of the Sandy Hook Laboratory in 1966-69, and the RV *Gosnold* of the Woods Hole Oceanographic Institution in 1971. All previous evidence suggests *A. superciliosus* is not abundant anywhere in its range. However, our data, together with anecdotal information from experienced commercial longliners, show that concentrations of bigeye threshers occur during April-June off Cape Hatteras. Other sharks and teleosts occurring in the area with *A. superciliosus* included blue shark, *Prionace glauca*; short fin mako shark, *Isurus oxyrinchus*; scalloped hammerhead, *Sphyrna lewini*; bignose shark, *Carcharhinus altimus*; night shark, *Hypoprion signatus*; dusky shark, *C. obscurus*; and silky shark, *C. falciformis*, along with swordfish, *Xiphias gladius*; and yellowfin tuna, *Thunnus albacares*. Additional



Vessel	Cruise No.	Date	Sta. No.	Position (Start Haul) Latitude	Longitude	Depth Meters	No. Caught
Capt. Bill III		11-12-62		40°10'	69°10'	110	1
R/V Dolphin	D-66-4	5-04-66	2	35°30'	74°47'	914	6
R/V Dolphin	D-66-6	6-08-66	8	35°42'	74°36'	1829	6
R/V Dolphin	D-68-5	6-06-68	9	35°12'	74°56'	1280	11
R/V Dolphin	D-68-5	6-07-68	10	35°18'	74°57'	220	22
R/V Dolphin	D-69-7	4-03-69	6	27°19'	63°00'	5486	1
R/V Dolphin	D-69-11	5-17-69	4	36°12'	74°51'	82	1
R/V Dolphin	D-69-11	5-18-69	5	35°23'	74°51'	768	11
R/V Dolphin	D-69-11	5-19-69	6	35°45'	74°46'	886	4
R/V Gosnold	175	4-18-71	6	35°33'	74°36'	1829	1
R/V Gosnold	175	2-20-71	8	34°35'	75°25'	1829	1
							65

FIGURE 1.—Location of *Alopias superciliosus* longline catches in the western North Altantic.

species taken occasionally, included sandbar shark, *C. milberti*; oceanic white tip, *C. longimanus*; and porbeagle, *Lamna nasus*; bluefin tuna, *Thunnus thynnus*; white marlin, *Tetrapturus albidus*; sailfish, *Istiophorus platypterus*; dolphin, *Coryphaena hippurus*; and lancetfish, *Alepisaurus* sp.

All longline sets resulting in catches of bigeye threshers were made between 0000 and 0300 with gear retrieval beginning after 0700. The depth at which the gear was fished ranged from near surface to a maximum of 65 m and was controlled by float lines of varying length. Temperature-depth profiles obtained from bathythermograph casts were routinely used to determine the optimum depth for the gear. The best catches of bigeye threshers were made in areas where the water regime ranged from 16° to 25°C at the surface to a minimum of 14°C at 75 m.

A total of 65 *A. superciliosus* were hooked at 11 longline stations (Figure 1); of these, 7 broke free as they were being held alongside the vessel, 23 were tagged and released, and 35 (15 females and 20 males) were brought aboard for examination. Length measurements and internal examination of stomachs and reproductive organs were made on all sharks brought aboard. Total lengths (TL) for the 15 females ranged from 233 to 399 cm ($\bar{x}$ = 312 cm); the 20 males ranged from 155 to 352 cm ($\bar{x}$ = 307 cm).

Morphometric measurements from eight males and four females, summarized in Table 1 as percents of fork length, were collected following the methods of Bigelow and Schroeder (1948). Fork length (FL) measurements were used as a primary growth parameter in the morphometric relationships in order to discern more accurately any changes occurring in body proportions with increasing size. The same accuracy could not be expected if total lengths were used because of the difficulty in obtaining precise length measurements due to the extreme size and shape of the caudal fin.

Proportional data from Table 1 shows that allometric growth is reflected in several characters. The most obvious change associated with increasing fork length is a proportionately shorter head length resulting in a decrease in the ratios of snout to: eye, nostrils, mouth, first gill, and pectoral fin. The relative size of the eye and mouth also decrease as the body lengthens. Characters that increase allometrically with growth include height of first dorsal, length of claspers in males, and interspaces between fins except in females

TABLE 1. — Proportional dimensions of body parts in percent of fork length for 12 *Alopias superciliosus*.

	Male								Female			
Body part	1	2	3	4	5	6	7	8	1	2	3	4
Total length (cm)	155.0	307.0	315.0	331.0	332.0	342.4	351.7	339.0	257.5	340.0	355.0	399.0
Fork length (cm)	100.0	188.0	192.5	197.0	197.0	207.0	212.5	217.0	167.0	207.0	210.0	221.0
% of total length	64.5	61.2	61.1	59.5	59.3	60.4	60.4	64.0	64.9	60.8	59.1	55.3
Distance from snout to:												
eyes	9.0	6.4	7.4	6.3	6.3	7.5	6.7	7.4	6.7	6.8	6.2	7.2
nostrils	6.5	5.3	6.0	5.6	5.2	6.0	6.0	5.5	5.7	5.5	5.0	5.2
mouth	9.5	7.8	8.2	7.9	7.7	7.9	7.8	8.3	8.0	7.5	7.4	7.9
first gill (base)	25.5	21.2	23.6	23.4	20.6	22.7	22.3	22.6	22.4	22.9	22.1	21.7
pectoral	29.0	24.1	28.2	27.2	24.4	26.1	25.7	24.0	25.6	26.3	24.3	25.8
first dorsal	57.0	55.4	52.5	51.8	55.1	55.5	53.2	53.0	51.2	52.2	51.0	52.3
second dorsal	82.0	82.2	79.2	80.5	81.7	82.1	80.5	80.2	79.9	82.6	79.5	80.5
pelvic	66.0	65.2	66.2	66.0	64.5	66.9	65.2	64.1	65.3	64.4	64.3	66.0
anal	87.0	88.0	87.6	87.3	86.3	87.9	87.8	85.7	83.5	85.0	83.3	86.0
upper caudal pit	90.5	90.8	89.7	89.3	90.4	90.6	89.7		88.8	91.8	90.0	90.5
Interspace between:												
1st & 2nd dorsal	16.8	17.8	16.4	17.0	19.8	16.6	17.2	18.0	18.9	18.4	17.9	18.1
2nd dorsal & caudal	7.2	7.8	8.6	8.8	8.8	8.1	8.3	9.2	7.7	7.9	8.2	
pelvic & anal	9.5	12.2	13.0	12.9	11.3	11.8	13.2	12.9	7.2	8.2	7.4	8.1
anal & caudal	3.2	3.6	3.4	4.3	4.6	3.6	3.3	3.2	6.0	4.8	4.3	5.0
nostrils (proximal)	4.5	2.5	2.7	2.7	2.5	2.9	2.6	2.8	2.4	2.7	2.4	2.5
Height of:												
first dorsal	10.0	11.5	13.0	11.5	11.9	11.7	11.6	12.4	11.8	13.5	12.8	14.0
free tip	1.5	1.6	1.7	2.0	2.0	1.9	1.8		1.8	1.8	1.9	1.3
second dorsal	.8	.9	.8	.8	.8	.8	.8	.7	1.1	1.3	1.0	1.8
free tip	.2	2.1	2.9	2.5	2.5	2.4	2.6	2.8	2.7	3.4	2.5	4.3
Diameter of eye[1]												
horizontal	3.5	2.5	2.6	2.4	2.4	2.9	2.5	3.5	2.8	2.8	2.8	3.2
vertical		4.0	4.2	4.2	4.2	4.5	4.4		4.4	3.8	3.8	
Right clasper	3.0	12.4	13.0	12.9	11.9	12.4	10.8	12.0				
Left clasper	3.1	12.4	11.4	12.9	11.7	12.1	11.6	12.0				
Width of mouth	9.0	6.2	7.3	7.0	7.0	7.7	7.7	8.3	7.6	7.5		8.1
Height of mouth	5.0	4.5	4.7	4.8	4.4	4.3	5.0		3.6	4.7	4.3	4.5
Max length pectoral fin	32.3	31.2	33.6	32.0	32.1	31.6	31.8	31.8	32.3	35.5	32.4	33.5

[1]Orbit.

where the distance between anal and caudal fin decreases.

The length-weight relationship for this species (Figure 2) was derived using data from 5 females and 11 males. To determine the regression line, the equation, $\log Y = 11.1204 + 2.99269 \log X$ was calculated using the nonlinear least squares method of Pienaar and Thomson (1969).

Clark and von Schmidt (1965) noted that adult and juvenile males of several species of sharks can be distinguished by the differences in the relative size and rigidity of the claspers. This characteristic applies to *A. superciliosus*. Of the males examined, the claspers of all but five individuals were large (10.8-13.0% of their FL), heavily calcified, and quite obviously mature. Internal examinations of the larger males revealed the presence of sperm in the epididymis and spermatophores in the lower ductus deferens. The smallest male positively identified as mature was 307 cm TL. A smaller individual however of 289 cm TL had testes in a relatively advanced state of development. Female *A. superciliosus* apparently mature at a larger size than males. Of the 13 females examined (233-355 cm TL) only the largest was mature. Ovaries of immature individuals were 10-13 cm long and 3-5 cm wide and contained thousands of white opaque follicles from less than 1 to 5 mm diameter. The oviducts were firm, ribbonlike tubes 0.5 to 2.5 cm in diameter. The 355-cm female differed in that the ovary was 30 cm long and 10 cm wide and contained yellow ova up to 10 mm in diameter. Also the oviducts in this individual were considerably larger (10 cm in diameter) and more flaccid and similar in appearance to the post gravid condition of other species we have seen. We suggest *A. superciliosus* males may mature at 290-300 cm TL, but females are not mature until they reach 350 cm.

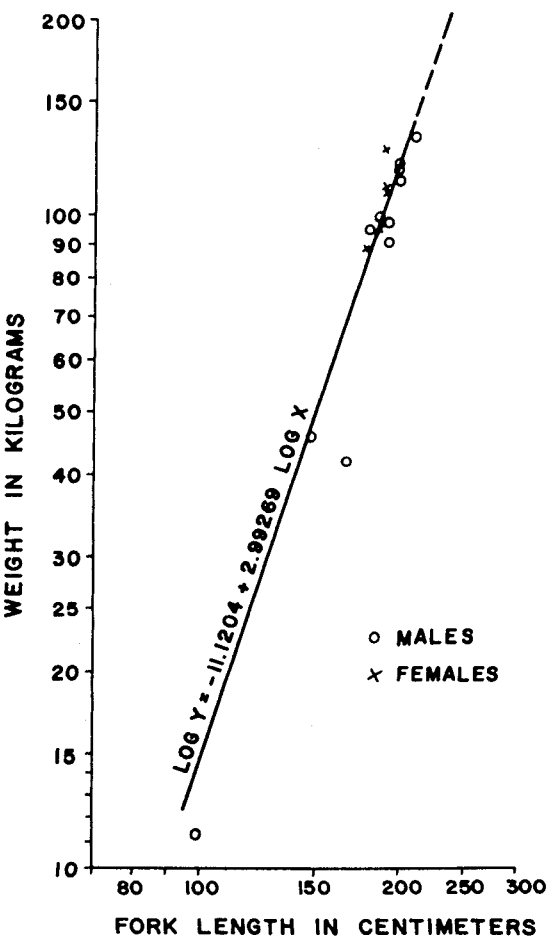


FIGURE 2.—Length-weight relationship for *Alopias superciliosus*.

Examination of the stomachs showed 17 (48.5%) were empty. Of the 18 that contained food the most common items were squid (66%) and scombrid remains (27%). One stomach contained remains of 5 lancetfish; another, 30 small (5-10 cm) herringlike fishes; and a third had parts of a small billfish, tentatively identified as an istiophorid. The occurrence of two or more whole longline baits in stomachs was not uncommon and suggests they had been dislodged from hooks elsewhere on the line. *Alopias superciliosus* may utilize its tail to herd or stun its prey in the manner described for *A. vulpinus* (Bigelow and Schroeder 1948; Strasburg 1958). Several individuals including some of those lost at the rail were foul hooked in the tail.

Acknowledgments

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Literature Cited

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr and Y. H. Olsen (editors), Fishes of the western North Atlantic. Part One, p. 59-546. Sears Found. Mar. Res., Yale Univ., Mem. 1.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf Coast of Florida. Bull. Mar. Sci. 15:13-83.

FITCH, J. E., AND W. L. CRAIG.
1964. First records for the bigeye thresher *(Alopias superciliosus)* and slender tuna *(Allothunnus fallai)* from California, with notes on eastern Pacific scombrid otoliths. Calif. Fish. Game 50:195-206.

PIENAAR, L. V., AND J. A. THOMSON.
1969. Allometric weight-length regression model. J. Fish. Res. Board Can. 26:123-131.

SPRINGER, S.
1943. A second species of thresher shark from Florida. Copeia 1943:54-55.

STRASBURG, D. W.
1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 58:335-361.

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EPIZOITES ASSOCIATED WITH *BATHYNECTES SUPERBUS* (DECAPODA: PORTUNIDAE)[1,2]

The only known documentation of epizoites occurring on *Bathynectes superbus* (Costa 1853) is that of Capart (1951), who noted a stalked barnacle, *Scalpellum* sp., on specimens from the South Atlantic coast of Africa. This note describes epizoites present on *B. superbus* from the western North Atlantic Ocean.

Crabs were obtained from several cruises along the eastern coast of North America (lat. 36°33′N-39°38′N to long. 73°00′W-74°43′W): RV *Columbus Iselin* (cruise 73-10) from 252 to 335 m; RV *Dan Moore* (73-030) from 122 to 232 m; RV *Albatross IV* (74-4) from 236 to 300 m; and RV *Eastward* (E-2-74) from 280 to 350 m. Gills, branchial chambers, and external surfaces of 172 crabs were examined. Crabs often supported more than one epizoite.

Crabs were most heavily fouled (65%) with a *"Perigonimus"*-like hydroid. Quotations are present around the name *"Perigonimus"* because the genus is not valid and is a representative of a poorly known group, the systematics of which need revision (D. R. Calder, pers. commun.). The *"Perigonimus"*-like hydroid was most frequently found associated with setae along the ventral anterolateral border and on the ecdysial suture line. *Trilasmis (Poecilasma) kaempferi inaequilaterale* Pilsbry (Cirripedia: Scalpellidae) was found on 13% of the *B. superbus* examined. It was present on all exposed regions of the carapace, pereopods, and abdomen. An eastern Atlantic specimen in the U.S. National Museum collections (*Geronimo*-2-203) had approximately 100 *T. k. inaequilaterale* on the dorsal carapace, pereopods, eyes, and mouthparts. *Anomia aculeata* (Pelecypoda) was relatively abundant (14%) and frequently occurred in indentations of the dorsal carapace and on the carinae of pereopods. Other organisms on the carapace were calcareous tubes of an unidentified polychaete (<1%) and *Stegopoma plicatile*, a thecate hydroid (<1%). The latter were found along the ventral anterolateral surface of the carapace. No organisms were found within the branchial chamber.

Figure 1 shows the occurrence of epizoites on *B. superbus* according to sex, size group, and molt stage. Size groups of short carapace width (≤35 mm, 36-45 mm, 46-57 mm, ≥58 mm) are based on arbitrarily chosen modes from a size-frequency distribution (Lewis 1975).

Crabs were assigned to molt stages described by Drach and Tchernigovtzeff (1967): anecdysis (C_1-C_4), proecdysis (D_1-D_4), postecdysis (A_1-B_2).

There is apparently no preference of epizoites for male or female crabs, but there is an association with molt stage and size. As expected, crabs in anecdysis are more heavily fouled than those which have recently molted (A_1-B_2). Larger crabs (>46 mm) supported a variety of epizoites while those ≤35 mm were colonized by *Perigonimus* only. This may be attributable to the greater surface available for epizoite set on larger crabs and the lower frequency of molt for these crabs.

The epizoites are inhabitants of the shelf-edge upper slope habitat within the bathymetric range of *Bathynectes*. *Trilasmis (Poecilasma)* has a known range along the western Atlantic from Martha's Vineyard, Mass. to Key West, Fla., having been recorded at depths from 21.6 to 1,733 m, chiefly on the carapace of the brachyurans *Geryon*

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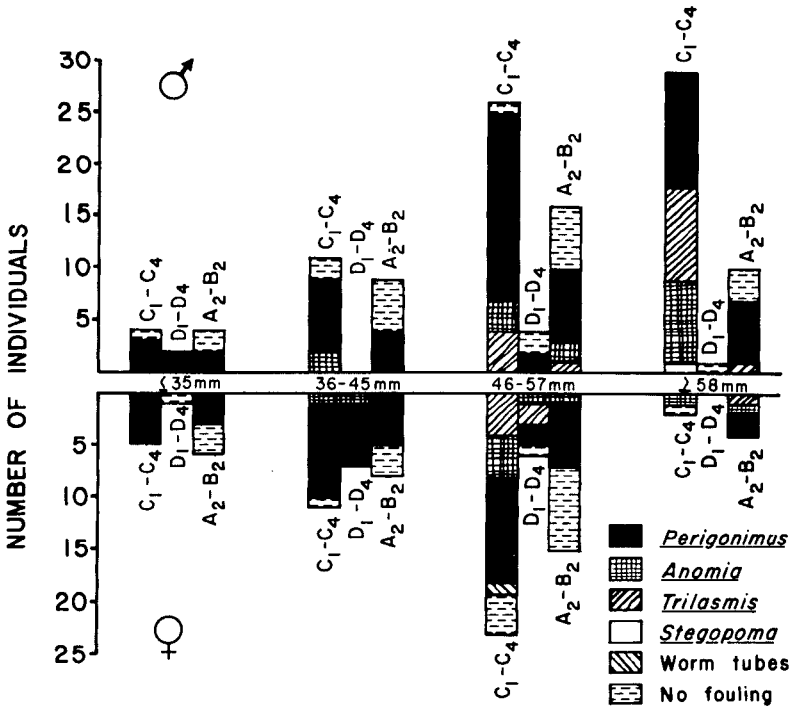

FIGURE 1.—Occurrence of epizoites on male and female *Bathynectes superbus* at anecdysis (C_1-C_4), proecdysis (D_1-D_4), and postecdysis (A_2-B_2) for four modal size (short carapace width) groups (≤35 mm, 36-45 mm, 46-57 mm, ≥58 mm).

quinquedens Smith (Pilsbry 1907) and *Cancer borealis* Stimpson, collected from the same cruises from which *Bathynectes* were obtained. *Trilasmis (Poecilasma)* was also observed on mature lobsters, *Homarus americanus* H. Milne-Edwards. These decapods are bathymetric associates of *B. superbus* (Lewis 1975). *Trilasmis (Poecilasma)* has also been found on *Hyposophrys noar*, a brachyuran from the Straits of Florida (Williams 1974).

Anomia aculeata has been recorded from the Arctic Ocean to Cape Hatteras, N.C. within a bathymetric range of 1.8 to 144 m (Smith 1937). The stations at which this pelecypod occurred on *Bathynectes* were in depths greater than 200 m.

The hydroid, *Stegopoma plicatile*, is common along the east coast of the United States from Hudson Bay to Cape Hatteras with a bathymetric range of 45 to 1,733 m (Fraser 1944).

Acknowledgments

I thank Frank Holland (North Carolina Division of Commercial and Sports Fisheries) for collection of specimens (RV *Dan Moore*) and Charles Wenner (Virginia Institute of Marine Science; RV *Albatross IV*). Ship time on RV *Columbus Iselin* and RV *Eastward* was provided by J. A. Musick through NSF grants GS-37561 and GS-27725, respectively. Dale Calder (South Carolina Marine Resources Research Institute) identified the hydroids found on *B. superbus*, and Mariana Doyle (U.S. National Museum) confirmed identification of *Trilasmis (Poecilasma) kaempferi inaequilaterale*. I also thank George Grant, P. A. Haefner, Jr., Fred Jacobs, and W. A. Van Engel for their criticism of the manuscript.

Literature Cited

CAPART, A.
1951. Crustacés décapodes, Brachyures. Expéd. oceánogr. Belge dans les Eaux côtières afr. Atl. Sud. (1948-1949) 3(1):11-205.

DRACH, P., AND C. TCHERNIGOVTZEFF.
1967. Sur la méthode de détermination des stades d'intermue et son application générale aux crustacés. Vie Milieu 18:595-609.

FRASER, C. M.
1944. Hydroids of the Atlantic coast of North America. Univ. Toronto Press, Toronto, 451 p.

LEWIS, E. G.
1975. Contributions to the biology of *Bathynectes superbus* (Costa) (Decapoda: Portunidae) from the Chesapeake Bight of the western North Atlantic. M.A. Thesis, College of William and Mary, Williamsburg.

PILSBRY, H. A.
1907. The barnacles (Cirripedia) contained in the collections of the U.S. National Museum. Smithson. Bull. 60:1-122.

SMITH, M.
1937. East coast marine shells. Edwards Brothers, Inc., Ann Arbor, 308 p.

WILLIAMS, A. B.
1974. A new species of *Hypsophrys* (Decapoda: Homolidae) from the Straits of Florida, with notes on related crabs. Proc. Biol. Soc. Wash. 87:485-492.

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Seattle, Washington

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Fishery Bulletin

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GROWTH AND REPRODUCTION OF THE SPOTTED PORPOISE, *STENELLA ATTENUATA*, IN THE OFFSHORE EASTERN TROPICAL PACIFIC

WILLIAM F. PERRIN, JAMES M. COE, AND JAMES R. ZWEIFEL[1]

ABSTRACT

This study is based on data from several thousand specimens of spotted porpoise, *Stenella attenuata*, incidentally killed in the purse seine fishery for yellowfin tuna, *Thunnus albacares*. Average length at birth is 82.5 cm. Gestation is 11.5 mo. Average length at 1 yr is 138 cm. Length-weight equations are given for fetuses and postnatal males and females. Age was estimated from dentinal layers in thin sections of teeth. A two-phase Laird-Gompertz growth model was fitted to the layer-length data. Direct calibration of the dentinal layers beyond the first year (two layers) was not possible, and three alternative hypotheses were considered: 1) two layers per year, until pulp cavity occluded, 2) two layers per year in first year, and one per year thereafter, and 3) two layers per year until puberty, and one per year thereafter. The second alternative is most probably the correct one, but reproductive parameters were estimated in terms of layers. Breeding is diffusely seasonal, with prolonged calving seasons in spring and fall and a pronounced low in winter. A third calving season may exist in the summer. Average age at attainment of sexual maturity of males is approximately 12 layers (average length about 195 cm and average weight about 75 kg). Females attain sexual maturity on the average at about 9 layers and 181 cm. Ovarian changes in adult females are described. Apparently postreproductive females were encountered in the samples. It is concluded that corpora albicantia of ovulation and pregnancy persist indefinitely in the ovaries. It was not possible to distinguish between the two types of corpora. Ovulation rate changes with age, from about four per layer in very young adult females, to about one per layer in older females. The average calving interval is 26 mo long and consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus. About 9.6% of lactating females are also pregnant. Pregnancy rate decreases with age, from about 0.6 per year at 8 to 10 layers, to about 0.3 at 16 layers. The overall sample contained 44.9% males and 55.1% females. Sex ratio changes with age, from near parity at birth, indicating higher mortality rates for males. Gross annual production of calves, based on age and sex structures of the sample and the estimated pregnancy rate, is 14.4% of the population per year. No evidence was found of age or sex segregation in schooling. The estimated parameters differ in a consistent way from those estimated for a population of *Stenella attenuata* in the western Pacific, possibly reflecting the exploitation in the eastern Pacific.

Porpoises of the genera *Stenella* and *Delphinus* are killed incidentally in the tuna seine fishery in the eastern tropical Pacific (Perrin 1969, 1970a; National Oceanic and Atmospheric Administration[2]). Since 1968, the National Marine Fisheries Service (NMFS) has conducted a program of research into the population biology of the major porpoise species to assess the impact of this fishing mortality on the porpoise stocks. The purpose of this paper is to describe the life history of the spotted porpoise, *Stenella attenuata* (Gray),[3] the animal most frequently killed in the fishery.

Little information on life history of the spotted porpoise has been available until very recently. Harrison et al. (1972) examined the gonads of 6 specimens from Japan (5 males and 1 female) and 45 specimens of *S. attenuata* from the eastern tropical Pacific (19 males and 26 females), but did not separate their results and conclusions from

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[2]National Oceanic and Atmospheric Administration. 1972. Report of the NOAA Tuna-Porpoise Review Committee, September 8, 1972. Unpubl. rep. U.S. Dep. Commer., Wash., D.C., 63 p.

[3]The taxonomy of the spotted porpoise has long been confused. Recent morphological studies (Perrin in press) have shown that the spotted porpoise in the tuna fishery is conspecific with the spotted porpoise occurring around Hawaii. The name *S. attenuata* (Gray 1846, holotype from unknown locality) applied by True (1903) to the Hawaiian form is used here for the eastern Pacific form, taking priority over *S. graffmani* (Lönnberg 1934). This usage is strictly provisional, pending the completion of current taxonomic studies, when a different name, such as *S. dubia* (G. Cuvier 1812) or *S. frontalis* (G. Cuvier 1829) may take priority.

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those for *S. longirostris*. Preliminary unpublished results of our studies indicate that these two species are probably disparate in such growth parameters as length at birth, length at maturity, and asymptotic length. Harrison et al. (1972) stated that lengths of the fetuses examined indicate that parturition occurs both in the spring and in the autumn. They described in detail the gross and microscopic histological appearances of several pairs of ovaries. A maximum of nine corpora albicantia were encountered. They concluded that if all the corpora albicantia in ovaries of specimens of this species do not represent past pregnancies, either the fertility is very low or the corpora are not permanent.

Nishiwaki et al. (1965) published length-frequency distributions of 34 fetuses (up to 106 cm long) and 194 postnatal animals (104 to 208 cm) from a school driven ashore in Japan. They estimated that gestation lasts 1 yr, length at birth is about 105 cm, juveniles reach 150 cm in 6 mo, and adult size (180 cm for females and 190 cm for males) is reached in 1 yr. They concluded that there are two seasons for mating and parturition, in the spring and in the autumn, and that there are fewer males than females among adults. Ontogenetic changes in coloration, external proportions, organ weights, the skeleton, parasite load, and feeding habits have been described (Perrin 1970b, in press; Perrin and Roberts 1972; Dailey and Perrin 1973; Perrin et al. 1973).

Kasuya et al. (1974) recently published results of a study of several hundred specimens caught in the Japanese fishery for *S. attenuata*. Their results are discussed and compared with ours in the body of this paper.

METHODS AND MATERIALS

Observer Program

Beginning in 1968, NMFS placed observers aboard U.S. tuna seiners to collect information on the incidental take of cetaceans in the eastern tropical Pacific. Observers were placed on 1 cruise in 1968, 5 in 1971, 12 in 1972, and 22 in 1973. Most of the cruises were 30 to 60 days long. In addition, biological data were collected during chartered cruises of commercial seiners: one in 1971, one in 1972, and two in 1973.

The data collecting had to be carried out in such a way as to not interfere with the fishing operation. Hence, the amount of information collected on the animals killed in a net set varied widely, depending on the amount of time that was available before the next set was made. Following is the hierarchy of types of data that were collected (sample sizes were largest for the first and smallest for the last):

Animals killed were:

1. Counted (estimates were made in cases where counts were not possible), usually on the deck or in the net,
2. Identified to species (and race when possible),
3. (*S. attenuata* only) identified to developmental color pattern phase (Perrin 1970b), and sexed,
4. Measured (to nearest centimeter with 2-m calipers), and
5. Dissected to collect information on reproductive condition (for females, mammaries were examined and reproductive tract collected; for males, the right testis was collected) and age (a section of the left lower jaw at midlength was collected). The gonadal material and jaw sections were preserved in 10% Formalin.[4] Small fetuses (≤ 30 cm) were preserved in the uterus. Larger fetuses were removed from the uterus and frozen.

For each specimen that was at least measured (step 4 above), a field serial number was assigned, and a specimen data sheet was filled out. Data for specimens that were not at least measured were collected on a running tally.

The Study Area

One of us has described the distribution of *S. attenuata* in the eastern tropical Pacific (Perrin 1975). The known occurrence of mixed aggregations of cetaceans and tuna is strongly correlated with certain oceanographic conditions peculiar to that region. The porpoise-tuna association is known only in the eastern tropical portion of the Pacific. That area, which has been called the North Pacific Equatorial water mass (Seckel 1972), has an unusual oxygen-salinity-temperature structure. The reason for this is not

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

fully understood but certainly has to do with the latitude of the area, its position relative to the rest of the Pacific and to the American continents, and the shapes of the adjacent land masses. These factors interact with general global oceanic and atmospheric circulation to produce a water mass with relatively high surface temperature, low surface salinity, a strongly developed, shallow thermocline (usually within 100 m of the surface), and a pronounced, thick oxygen minimum layer just below the thermocline. The effect is to create a very extensive but shallow warm habitat with a sharp oxythermal floor. To the west, these conditions tail off along a divergence centered on lat. 10°N (Wyrtki 1964). The conditions must be causally interrelated, but one of the more striking correlations with the occurence of the mixed-species aggregation is in the thickness of the oxygen minimum layer (Figure 1).

The occurrence of the aggregation is not tightly correlated with the geographic distributions of the major prey species of the participating predators. Major shared prey items are the ommastrephid squid *Dosidicus gigas,* an unidentified ommastrephid (probably *Symplectoteuthis* sp.), a scombrid fish *Auxis* sp. (*A. thazard* or *A. rochei*), and the exocoetid fish *Oxyporhamphus micropterus* (Perrin et al. 1973). *Dosidicus gigas* is primarily equatorial but migrates sporadically as far as California and southern Chile, far beyond the limits of the distribution of the mixed-species aggregation (Clarke 1966; Young 1972). Species of *Symplectoteuthis* occur widely in the tropical Pacific and Indian oceans (Clarke 1966). *Auxis thazard* occurs in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans," and *A. rochei* in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans, including the Mediterranean Sea" (Richards and Klawe 1972). The genus *Oxyporhamphus* is also pantropical (Bruun 1935). At least some of the several myctophid fishes in the aggregate apparently are a mainstay of the diet of the spinner porpoise in mixed schools (Perrin et al. 1973) and are not restricted to the tropics but occur also in temperate waters of the eastern Pacific (Moser and Ahlstrom 1970) and elsewhere. These facts, combined with the pantropical distributions of the cetaceans, tunas, and birds, suggest that the multispecies aggregation does not have its roots in the distribution of the component species or their prey but rather in the peculiarities of the physical oceanography of the region.

The Sample

In 1971 and early 1972, when more specimens were decked than could be processed in the time available (the limit per net set was usually about 35 to 40 specimens), adult females were selected for measuring and dissection. The intention was to insure that sample sizes would be large enough to allow estimation of pregnancy rate with adequate precision. The information on age structure of the catch for that period is limited to the coloration phase data. The observer program subsequently expanded, and beginning in October 1972 no selection was practiced in determining which animals were to be dissected; the first 35 to 40 specimens of both sexes and all ages that came to hand were set aside for measuring and dissection and the remainder discarded. The length data for 1968 and for October 1972-December 1973 are presumably cross-sectional with respect to the kill.

The sample of animals at least measured included 3,504 postnatal animals and associated fetuses from known localities and 23 from imprecisely known localities (Figure 2). Coloration phase and sex data were collected for another 6,150 specimens. In addition, some data were available for 45 other specimens collected by other research agencies, museums, and private individuals. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1).

Two races of *S. attenuata* exist in the eastern tropical Pacific — a large coastal form and a small offshore form (Perrin 1975, in press). This paper deals only with the offshore form. The estimates of life history parameters cannot be assumed to apply also to the coastal form.

TABLE 1.—Samples of postnatal spotted porpoise by month for all years.

Month	Males	Females	Total
January	748	443	1,191
February	263	209	472
March	298	147	445
April	216	155	371
May	181	97	278
June	69	58	127
July	1	0	1
August	6	5	11
September	0	0	0
October	222	158	380
November	110	87	197
December	30	24	54
Total	2,144	1,383	3,527

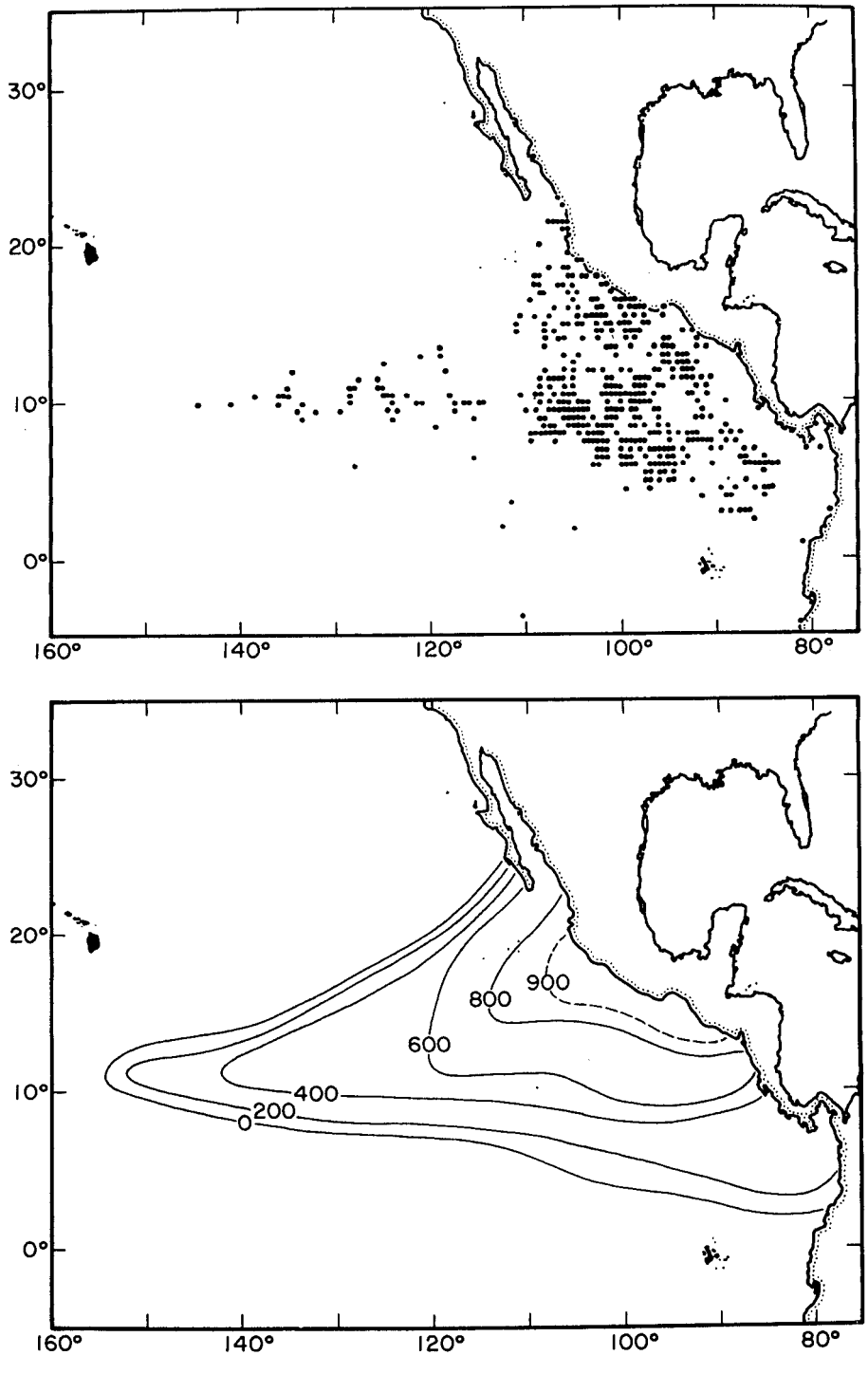

FIGURE 1.—Comparison of the known occurrence of spotted porpoise in the eastern Pacific (above) with average thickness of the subsurface layer of water (contours in meters) in which the dissolved oxygen is less than 0.25 ml/liter (below, after Knauss 1963). The entire layer lies above 1,000 m.

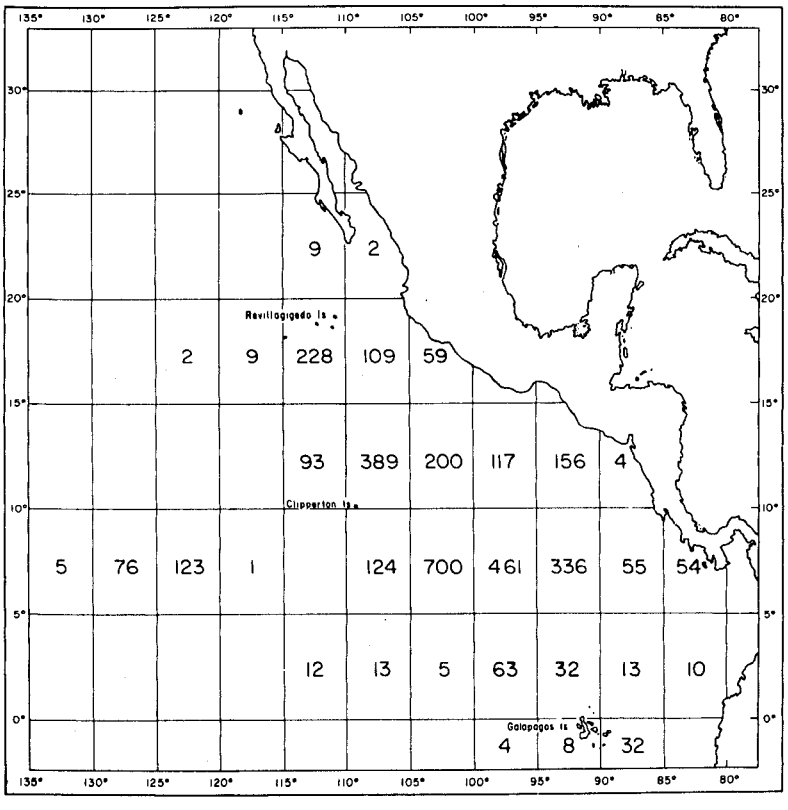

FIGURE 2.—Samples of spotted porpoise used in life history studies by 5° square. Does not include specimens that were not at least measured.

Because the field program is a continuing one, the sample sizes for the various analyses were different and depended on how much material was available at the time each analysis commenced. Restrictions on sample size are set out in the text below.

Laboratory Procedures

Fetuses were measured with dial calipers or with calipers mounted on a 1-m stick. Postnatal animals were weighed to the nearest pound on platform scales. Fetuses were weighed to the nearest gram on a triple beam balance. Testes were weighed to the nearest gram on a platform balance. A 1-cm^3 cube from the center of each testis[5] and a similarly sized sample of the epididymis from midlength of the testis were sectioned and stained with hematoxylin and eosin. The mounted sections were subsequently examined under a compound microscope.

Ovaries were weighed to the nearest 0.1 g on a platform balance. They were then cut into transverse sections approximately 1 mm thick with a scalpel and the sections examined under a dissecting microscope. The corpora albicantia in each ovary were scored to eight categories based on size, color, vascularization, and gross appearance (categories described below). If a corpus luteum was present, it was measured with dial calipers to the nearest millimeter in its three largest dimensions. The diameter of the largest follicle was measured to the nearest 0.1 mm.

Age was estimated for 442 animals by examination of dentinal layers in the teeth. Three or four teeth were extracted from the lower right tooth row at approximately midlength and mounted on wooden blocks in dental wax or plastic resin. A longitudinal section 0.012 inch (0.31 mm) thick was cut from each tooth with a diamond saw. The sections were cleared for several days in a 1:1 mixture of glycerine and 95% ethanol, mounted under cover slips in balsam, and examined with transmitted light under a

[5]Some early samples were taken near the dorsal surface of the testis. Tubule diameter in these was subsequently found not to differ relative to length, weight, and age of the animal from that in those taken at the center of the testis, and the lots were therefore combined for analysis.

compound microscope at approximately 30 diameters. One postnatal layer was considered to consist of an opaque subunit and a translucent subunit (Figure 3). The layers in most of the teeth examined were not as well-defined or as regular in thickness as those illustrated by Kasuya (1972) for *Stenella coeruleoalba* or by Klevezal' and Kleinenberg (1969) for *Delphinus delphis*. Teeth from 39 of the 442 animals were completely unscorable, being heavily worn or showing no discrete layers in the sections examined. All the teeth were scored several times, over a period of several months, without referring to specimen numbers or to values obtained previously, until the scorer felt confident of the results. The values used in the analyses are those obtained in the final round of scoring. The teeth were scored to the nearest postnatal layer when possible, or a range, e.g., "8 to 10 layers," was estimated. Average accuracy is estimated at ±1 layer for teeth with 5 layers or less and ±2 layers for teeth with 5 to 12 layers. Convoluted secondary dentine was present in most of the teeth with more than 12 layers, making counts very difficult and of dubious reliability. We feel that the counts for many of these teeth are probably underestimates. Teeth in which the pulp cavity was entirely closed in all sections examined were scored as "occluded."

The NORMSEP computer program was used to define modes in the length-frequency distributions for fetuses. The program was written by Hasselblad (1966) and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates the mixture of normal length distribution into its components, assuming that the lengths of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained.

GROWTH

Length at Birth

Average length at birth of 82.5 cm was obtained from a linear regression line based on 3-cm groupings of fetuses and neonatals (Figure 4). The largest fetus of the 461 examined was 904 mm long. The smallest neonatal animal was 780 mm long. Eighty-six calves and fetuses between 73 and 94 cm were measured in random samples. Assumptions inherent in the method used to arrive at this estimate are that pregnant females and calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. For example, if neonates were less likely to be included in the samples than were pregnant females, average length at birth would be overestimated. Other potential sources of error are differential rates of prenatal and postnatal natural mortality and premature births caused by stresses imposed by pursuit and by capture in the purse seine.

Gestation Period and Fetal Growth

The most commonly used method for estimating the gestation time of cetaceans is that of Huggett and Widdas (1951). They showed that for a variety of mammals of widely different orders, a plot of the cube root of fetal weight on age is linear except during the first part of pregnancy, when growth is exponential. Their model can be expressed in the general formula $W^{1/3} = a(t - t_0)$, where W = weight, t = age, a = the *"Specific Fetal Growth Velocity,"* and t_0 = "the intercept where the linear part of the plot, if produced backwards, cuts the time axis." Laws (1959) applied the method of Huggett and Widdas to fetal length/time data for three odontocetes (*Physeter catodon*, *Delphinapterus leucas*, and *Phocoena phocoena*) and obtained estimates of gestation periods (15, 14, and 11 mo, respectively). He assumed that weight is proportional to the cube of length and used the form $L = a(t_g - t_0)$, where L = length. This assumption is not entirely correct (see length-weight results below), but is a close enough approximation of the real relationship between length and weight to allow its use in estimating gestation period. Laws' estimates corresponded closely with other estimates obtained by more direct methods. Laws' version of Huggett and Widdas' method is used here.

A gestation period of 11.5 mo was obtained from an analysis based on 281 fetal and postpartum specimens collected in January, February, March, April, May, and October 1972 (Figure 5). The January-May samples comprised all of the fetuses of all of the females examined. The postpartum samples in these months were not random and are therefore not included. The October samples were random over all age-classes in the catch; therefore, all specimens less than 160 cm long, approximately the length at onset of puberty (Harrison et al. 1972), are included in the plot. Obvious modes are present in the length distributions (seasonal-

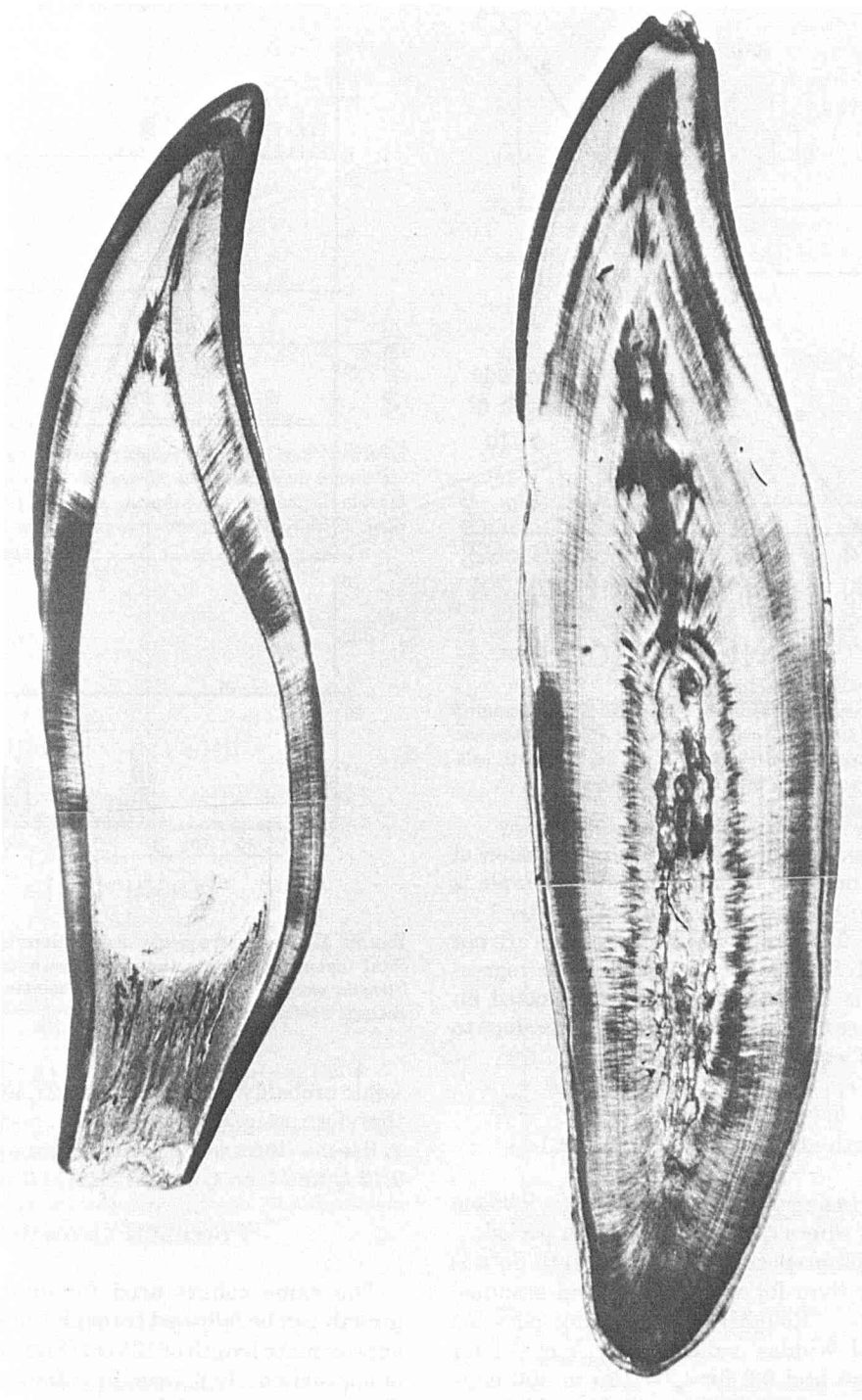

FIGURE 3.—Longitudinal thin sections of teeth from two specimens of *Stenella attenuata* from the offshore eastern tropical Pacific. (Left) field number CV300 male, 144 cm, with two postnatal dentinal layers; (right) number LR55 female, 191 cm, with 13 layers.

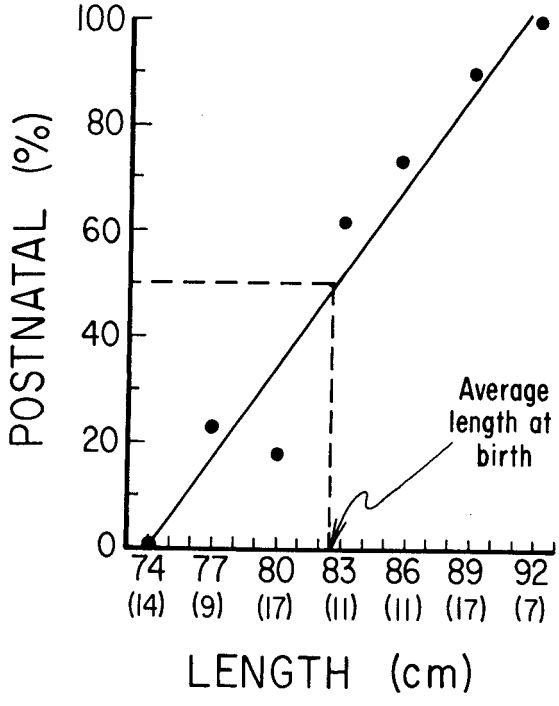

FIGURE 4.—Linear regression analysis of percent postnatality on body length for 86 fetuses and calves of *Stenella attenuata* from the offshore eastern Pacific grouped in 3-cm intervals. Sample size for each 3-cm interval in parentheses.

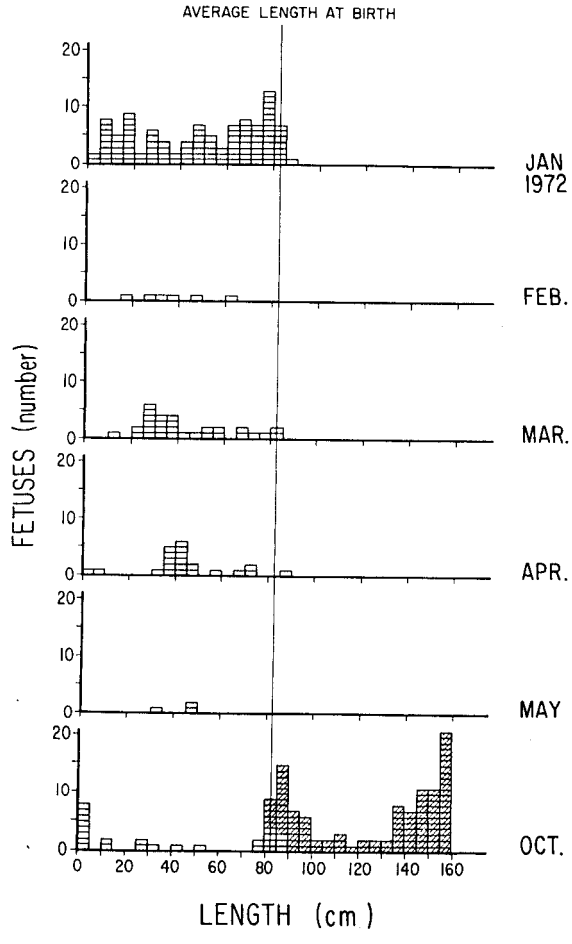

FIGURE 5.—Length-frequency distributions by month for 281 fetal (open) and young (hatched) postnatal specimens of *Stenella attenuata* captured by tuna seiners in the offshore eastern tropical Pacific in 1972.

ity is discussed below). Apparent progression of the smaller mode in the January 1972 sample is consistent with a gestation period of roughly 1 yr. Sample sizes for the other apparent modes are not large enough for similar analysis. Linear regression analysis of the modal lengths plotted on month (Figure 6) yields an estimate of the slope to use in Laws' equation:

$$L = 8.283\ (t - t_0), \text{ or}$$
$$\text{length at birth} = 8.283\ (t_g - t_0)$$

with $(t_g - t_0)$ (using months of 30.4 days) = 9.96 mo or 303 days, where t_g = total gestation period.

Laws (1959) proposed that t_0 for length data is slightly less than for weight data and assumed $t_{0_{Ln}} = 0.9\ t_{0_{wt}}$. Roughly interpolating between Huggett and Widdas' values for $t_{0_{wt}}/t_g$ of 0.1 for $t_g > 400$ days and 0.2 for t_g = 100 to 400 days (using provisional $t_g \cong 330$ days to enter the iteration) (Figure 7) and applying Laws' correction, $t_{0_{Ln}}$ of $\cong 0.135\ t_g$ is obtained. This value yields an estimate of gestation time of 11.5 mo (349 days). The estimate of t_0 (47 days) is crude, but the true value probably lies between $0.12\ t_g$ and $0.15\ t_g$. We therefore estimate the gestation period to be 11.5 ± 0.2 mo (interval between estimates using $t_0 = 0.12\ t_g$ and $0.15\ t_g$), or 11.3 to 11.7 mo.

Postnatal Growth

The same cohort used for analysis of fetal growth can be followed through the samples until approximate length of 125 cm (Figure 8) at the age of approximately 8.5 mo. In order to optimize resolution, 4-cm intervals were used, and the samples for April, May, and June were combined. Modes were estimated with NORMSEP.

A linear regression line through the modal lengths yields the postnatal growth equation

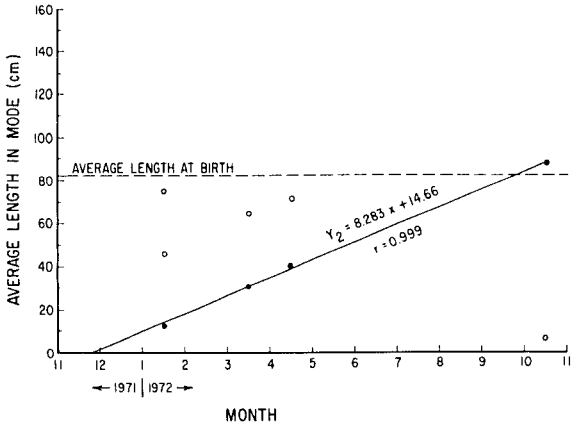

FIGURE 6.—Linear regression analysis of modal lengths of fetal and neonatal specimens of *Stenella attenuata* (from Figure 4). Open circles are modes not included in the analysis. Modal lengths defined with computer program NORMSEP (see Materials and Methods).

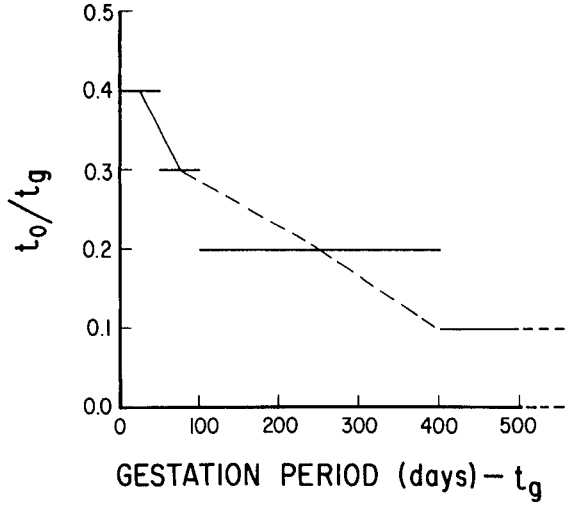

FIGURE 7.—Ratio t_0/t_g interpolated between empirical estimates of Huggett and Widdas (1951)—"...for gestation times up to 50 days $t_0 \triangleq 0.4 \times$ (gestation time), from 50-100 days $t_0 \triangleq 0.3 \times$ (gestation time), from 100-400 days $t_0 \triangleq 0.2 \times$ (gestation time), over 400 days $t_0 \triangleq 0.1 \times$ (gestation time)."

$$L = 82.5 + 5.42\,t,$$

where L = length in centimeters
t = postnatal age in months.

Analysis Based on Analogy with Other Cetaceans

Fetal growth in length of cetaceans, except for an initial slow phase (t_0), is nearly linear. Postnatal growth during at least a period equivalent in length to the gestation period is also nearly linear, but at a lower rate. The difference between the

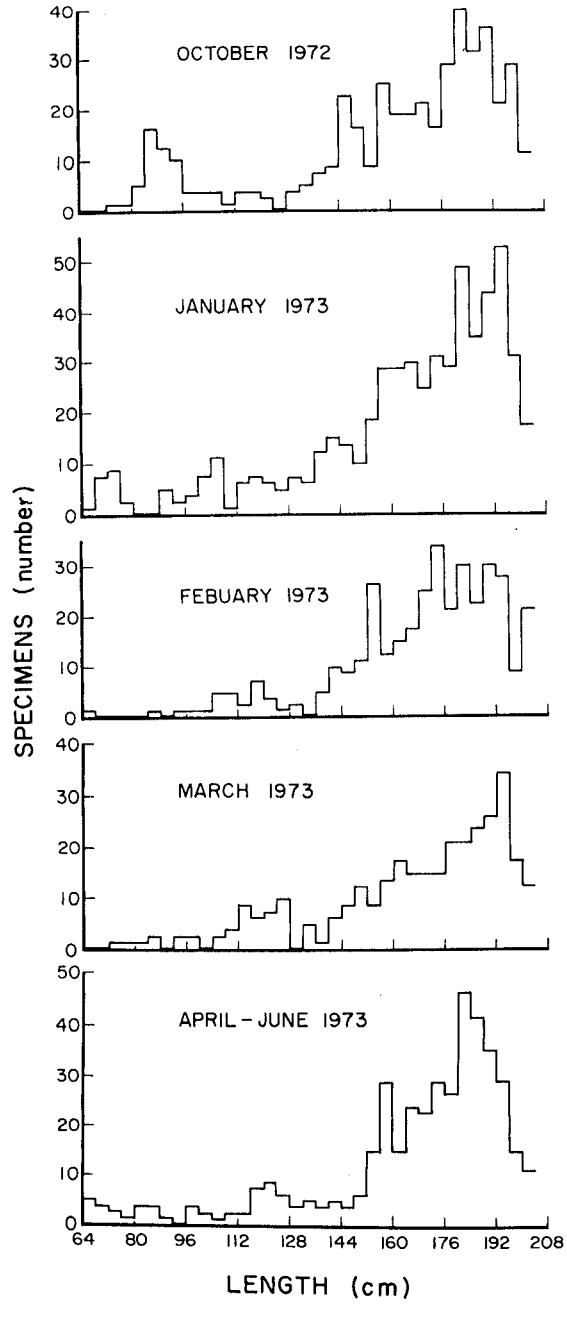

FIGURE 8.—Length frequencies of fetuses and postnatal specimens of *Stenella attenuata* between 64 and 204 cm long, of both sexes, by month.

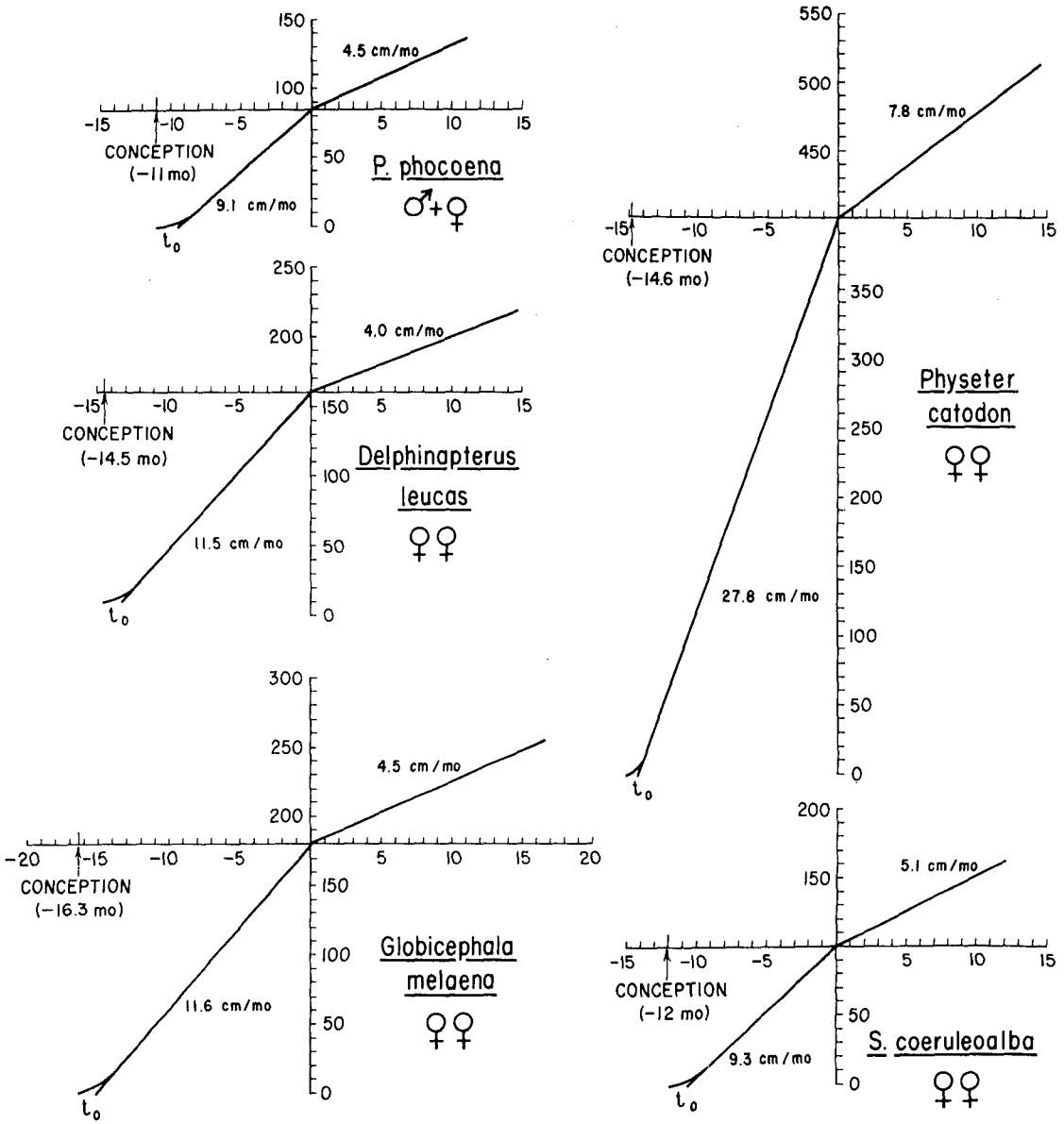

FIGURE 9.—Fetal growth and average postnatal growth during a period equal to the gestation period in five odontocete cetaceans: *Phocoena phocoena* (gestation period and postnatal growth from Møhl-Hansen 1954; t_0 from Laws 1959; length at birth from Fisher and Harrison 1970); *Delphinapterus leucas* (from Brodie 1971); *Globicephala melaena* (from Sergeant 1962); *Physeter catodon* (from Best 1968, 1970); and *Stenella coeruleoalba* (from Kasuya 1972).

fetal rate and the average rate during a postnatal period equal to the gestation period differs among the five odontocete species for which sufficient data exist (Figure 9) and is correlated with length at birth (Figure 10). The least-squares line for log of the difference between fetal and postnatal growth rates (Y) on log of length at birth (X) yields $Y = -1.33 + 0.997X$, from which a predicted Y of 3.75 cm/mo is estimated for *S. attenuata* and an average growth rate in the first year of 4.66 cm/mo is estimated. This average rate is close to those for the other three delphinids (5.1 for *S. coeruleoalba*,

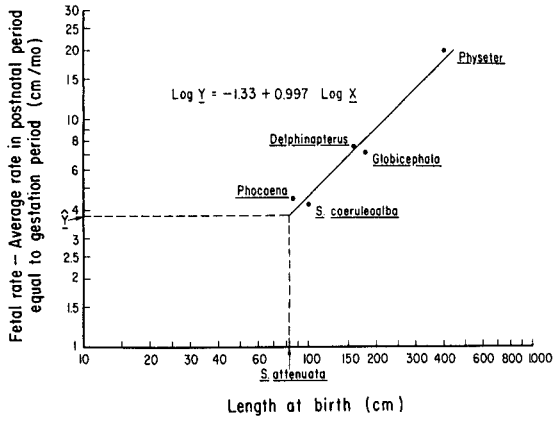

FIGURE 10.—Relationship of difference between fetal growth rate during linear phase and average growth rate during postnatal period equal to gestation period to length at birth in five odontocete cetaceans. Line is linear regression line of log difference on log length. Data from Figure 11. $\hat{Y}$ is predicted difference for *Stenella attenuata* from the offshore eastern tropical Pacific.

4.5 for *Globicephala*, and 4.5 for *P. phocoena*)[6]; and yields a predicted length at 1 yr of 138 cm.

Length Relative to Tooth Layers

Total length was plotted on number of postnatal layers for 115 males and 306 females (Figure 11). The teeth of five males and three females had completely filled pulp cavities. These are included in the plots in a separate category "occluded."

The plots of means for 2-layer intervals (the points in Figure 12; the curves were fitted as explained below) very closely resemble the growth curve obtained by Sergeant (1962) for *Globicephala*. Asymptotic length (L_∞) for females is approximately 190 cm and for males approximately 200 cm. There appears to be a secondary surge in growth at about 6 layers. With the restriction that the curves must pass through birth length of 82.5 cm and asymptotic lengths of 190 and 200 cm, it is not possible to fit any continuous equation to the data satisfactorily. Continuous curves that fit well at the upper and lower ranges of layer count seriously underestimate length at 5 to 7 layers. Kasuya (1972) also encountered difficulty in attempting to fit a continuous model to growth of a delphinid, *S. coeruleoalba*. Good fits can be obtained, however, by assuming a dynamic growth function. A two-phase version of Laird's (1969) growth model was fitted to the 2-cm means for all males and females, using an iterative least-squares method. The occluded specimens were assigned to the 16+ interval.

Laird's model is

$$L(t) = L_0 \exp\left\{\frac{a}{\alpha}\left[1 - \exp(-\alpha t)\right]\right\},$$

where

$L(t)$ = length at time t
L_0 = length at birth (82.5 cm in this case)
t = time (layers in this case)
a = specific rate of exponential growth
α = rate of decay of exponential growth.

This model assumes that an organism's growth pattern is determined at conception. The fitted parameters a and α express the premise that "growth is fundamentally exponential (implied by the normal binary fission of cells), and it also undergoes exponential retardation by some as yet unknown physiological mechanism" (Laird 1969).

In the two-phase approach, separate equations were simultaneously fitted to the upper and lower range of means. The assumptions were made that juvenile growth is the same for males and females (supported by the data) and that the growth discontinuity comes at about the same age for males and females. The only fixed point was 82.5 cm at 0 layers (birth). The convergence point (inflection in the growth curve) was allowed to float to the position that gave the best fit, with males and females considered jointly for lesser ages. The equations converged at 5.59 layers (rounded off to 6 below) at which predicted length is 159.9 cm. The fit is excellent for females (Figures 11, 12). Asymptotic length is 190 cm at predicted age of 18 layers. Average length of adult females (those with ovarian scars) is 187.3 cm, based on a sample of 555 (Perrin 1975). The largest female of 2,138 measured was 220 cm long. The equation for juvenile growth to less than 6 layers is

$$L = 82.5 \exp\left\{\frac{0.4817}{0.7172}\left[1 - \exp(-0.7172t)\right]\right\},$$

where L = length, in centimeters
t = age in layers.

[6]Fisher and Harrison (1970) stated that their data suggest that *Phocoena* in Canadian waters grows approximately 30 cm during the first year of life, or at an average rate of about 2.5 cm/mo, as opposed to the 4.5 cm/mo hypothesized by Møhl-Hansen (1954). However, they also suggested, and their figure 2 showed, an average rate of at least 5 cm/mo during the first 4 mo. It seems unlikely that the rate would drop to an average of ~ 1.25 cm/mo in the remaining 8 mo of the first year.

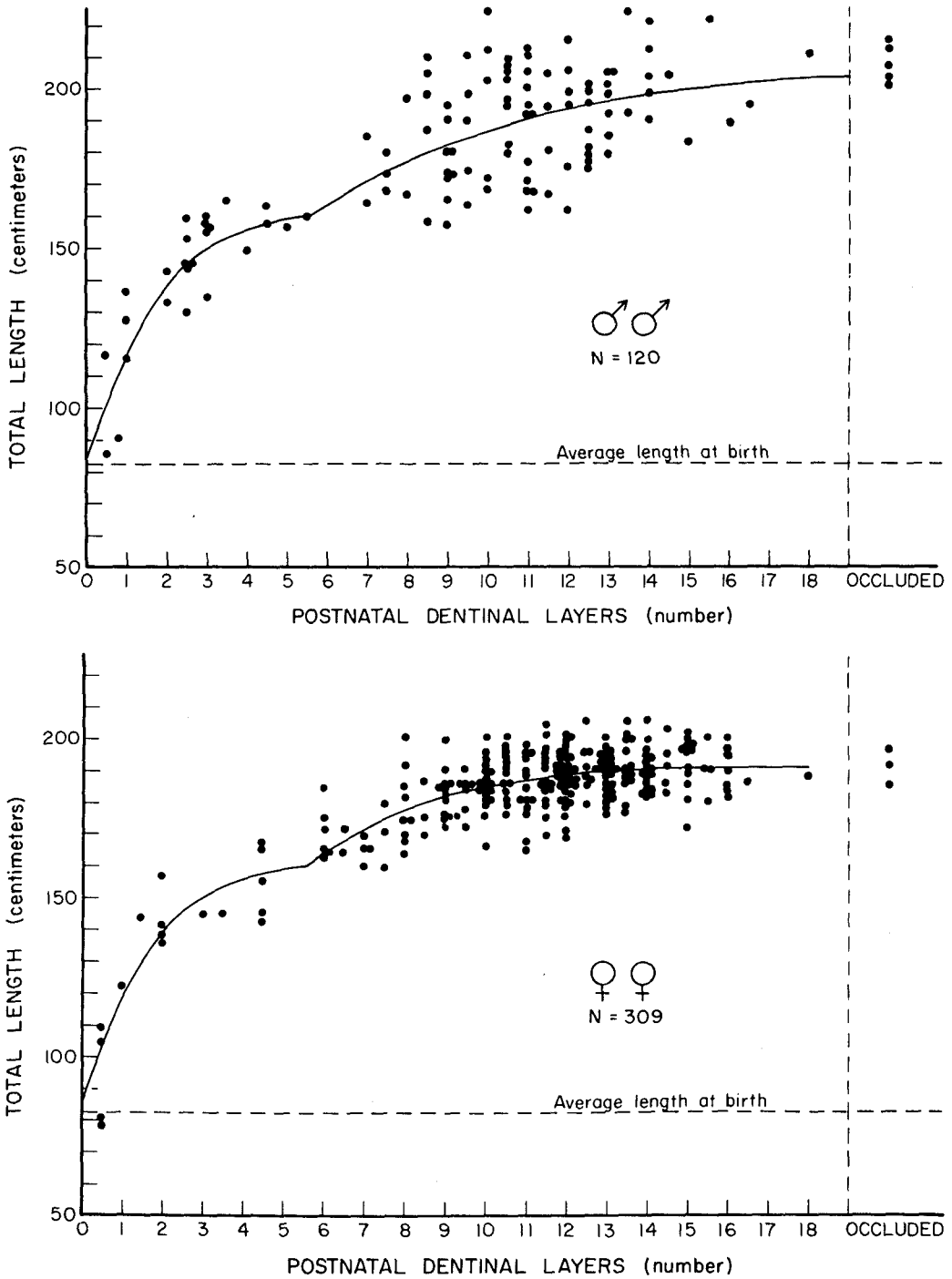

FIGURE 11.—Scatterplots of body length on number of postnatal dentinal layers from males (top) and females (bottom) of *Stenella attenuata* from the offshore eastern Pacific. Lines are fit to the growth model (see text).

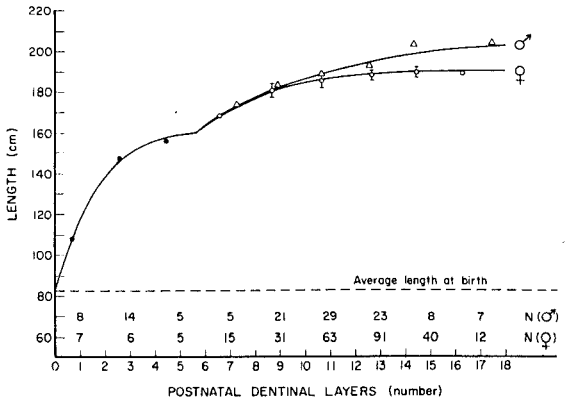

FIGURE 12.—Fit of the double Laird growth model (see text) to 2-cm mean values of body length on number of postnatal dentinal layers for males and females of *Stenella attenuata* from the offshore eastern Pacific. For samples greater than 30, ± standard errors indicated as vertical line.

For females with 6 or more layers, the growth equation is

$$L = 159 \exp \left\{ \frac{0.0657}{0.3707} \left[1 - \exp(-0.3707(t - 5.588))\right] \right\}.$$

In this case, both the growth rate and the rate of decay of growth are sharply lower than for juveniles.

The fit for males is not as good (Figures 11, 12) as it is for females, probably due to greater variability and to inadequate sample sizes for the two oldest strata (the tooth-reading effort was concentrated on females because of their importance in population dynamics). Another possible explanation for the relatively poorer fit for males is that growth (real, or as inferred from tooth layers) in adult males is more complex than in adult females, and a model more complex than the Laird model is called for. Inferred asymptotic length is 206 cm, achieved at predicted age of 26 layers. Average length of adult males (defined as those having testes weighing 200 g or more) is 200.7 cm, based on a sample of 253 (Perrin 1975). The largest male of 1,083 measured was 226 cm long. The growth equation for males with 6 or more layers is

$$L = 159.5 \exp \left\{ \frac{0.0524}{0.2032} \left[1 - \exp(-0.2032(t - 5.588))\right] \right\}.$$

The secondary growth rate (a, 0.0524) is very slightly smaller than for females, but the rate of decay (α, 0.2032) is sharply smaller, reflecting the attainment of greater size in males. The equations rearranged and reduced for estimating age (in terms of layers) from length are

$$t(\text{M and F} < 160 \text{ cm}) = -1.394 \ln (7.531 - 1.48 \ln L)$$

$$t(\text{F} \geq 160 \text{ cm}) = 5.588 - 2.698 \ln (29.606 - 5.64 \ln L)$$

$$t(\text{M} \geq 160 \text{ cm}) = 5.588 - 4.921 \ln (20.669 - 3.878 \ln L).$$

Note: These equations should not be used to estimate age from length except for grouped samples of smaller animals (about 180 cm or less), for which growth rate is still large compared to individual variation in length.

The juvenile growth curve based on tooth layers can be calibrated for the first year by comparison with the growth curve derived from analysis of modal progression (above) and by deduction from what is known about juvenile growth of other odontocetes (the fetal-postnatal growth argument above). Estimated average length at 8 mo based on analysis of modal progression is 125.5 cm. The predicted number of layers at that length (Figure 12) is 1.53. If the average growth rate during the first year is assumed to be the same as the average during the first 8 mo, the predicted number of layers at 1 yr ($1.53 \cdot 12 \div 8$) is 2.3. This extrapolation, however, is a slight overestimate, because while growth during the first year in delphinids is approximately linear, there is some decay of rate. The predicted number of tooth layers (using Figure 12) at 138 cm, the above-predicted length at 1 yr based on camparison with other odontocetes, is 2.0. It seems safe to assume that about 2 layers are laid down during the first year of life.

Calibration of the remainder of the tooth-layer curve is more difficult. Kasuya et al. (1974) examined the innermost layer in teeth of *S. attenuata* and related type and thickness of layer to season of capture. They concluded that one layer (one transparent plus one opaque subunit) represents 1 yr of growth. We found no correlation between thickness of the innermost layer and season of capture. Almost all of the samples for which teeth were sectioned, however, were collected in the first few months of the year. Lacking such direct calibration, several alternative possibilities can be examined. The results, however,

must remain tentative and inconclusive until growth has been monitored directly in one or more captive or free-ranging, tagged individuals.

Some alternatives that can be considered are:

1. Two layers per year until the teeth are occluded.
2. Two layers in the first year and one per year thereafter until the teeth are occluded.
3. Two layers per year until puberty (about nine layers in males and seven in females; see section below on age at puberty), and one per year thereafter.

This list of alternatives can be extended to great length by making assumptions such as that layers are laid down at irregular intervals, males and females lay down layers at different rates, layers disappear with age, etc., but the above are probably the main possibilities that should be considered. All references below to age are in terms of layers, with the above alternative possibilities considered or implied. None of the alternatives can be eliminated with certainty. One tooth layer deposited per year has been inferred for the western Pacific population of *S. attenuata* by Kasuya et al. (1974). One layer per year has also been suggested for other closely related delphinids, including *S. coeruleoalba* (Kasuya 1972) and *Tursiops truncatus* (Sergeant et al. 1973). Two tooth layers per year have been found in *Delphinapterus leucas* (Sergeant 1973), but this form is less closely related to *Stenella*. Thus, there is more support in the literature for the one-layer-per-year model (number 2 above) than for the others.

Length-Weight Relationships

Length-weight relationships were determined for 218 fetuses, 66 postnatal males, and 33 nonpregnant, postnatal females by using linear regressions of log weight on log length.

Fetuses

The fetuses ranged from 20 to 897 mm long and weighed from 2 to 7,588 g. Ten fetuses less than 20 mm long were not included. The regression equation is

$$\log W = 3.5532 + 2.501 \log L,$$

where W = weight in grams
L = length in millimeters.

In exponential form, the relationship is

$$W = 2.79 \times 10^{-4}\ L^{2.501}.$$

Females

The females ranged from 100 to 200 cm and weighed from 12.0 to 69.1 kg. The regression equation is

$$\log W = -4.1576 + 2.6120 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 6.95 \times 10^{-4}\ L^{2.612}$.

Males

The males ranged from 86 to 218 cm and weighed from 6.8 to 90.0 kg. The regression equation is

$$\log W = -4.7135 + 2.873 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 1.93 \times 10^{-5}\ L^{2.873}$.

The slopes of the regression equations are statistically different (t-test at $\alpha = 0.05$) for males and females. Males are lighter for their length at birth, and heavier for their length after about 135 cm has been attained.

Color Pattern

Perrin (1970b) has previously described the development of the color pattern of *S. attenuata* in the offshore eastern Pacific. The animal begins life unspotted, develops dark spots ventrally that later coalesce, as light spots develop dorsally. The ontogenetic continuum can be divided into five stages as defined below and as shown in Figures 13 and 14:

1. *Newborn stage.* Dark purplish-gray dorsal surfaces and lateral blazes, with white ventral surfaces and no spots; about 80 to 160 cm.
2. *Two-tone stage.* General two-tone pattern with dark-gray surfaces above, lighter gray lower surfaces, and a well-defined pattern in varying shades of gray about the head and flippers; no spots; about 95 to 175 cm.

The division between this and the previous category is somewhat subjective and arbitrary.

3. *Speckled stage.* Same as two-tone but with discrete, very dark-gray spots on the ventral surfaces; discrete light-gray spots on the upper, darker surfaces present on some animals but lacking on others; about 140 to 190 cm.

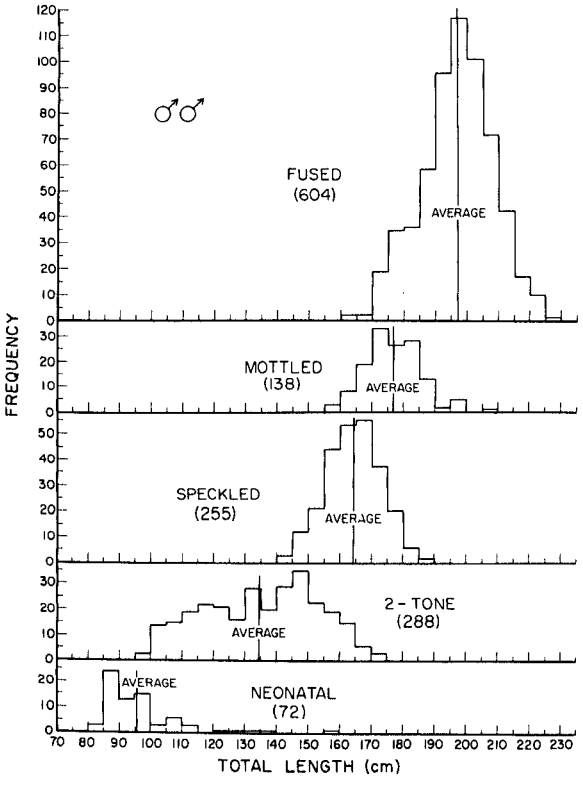

FIGURE 13.—Length-frequency distributions of males of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phase.

4. *Mottled stage.* Ventral spots converging and overlapping in places, but patches of the lighter gray background still visible, yielding a mottled effect; discrete or merging light-gray spots present on the upper surfaces; about 155 to 210 cm.
5. *Fused stage.* Ventral spots completely convergent, to give the effect of a uniform, medium-gray to dark-gray surface; on close inspection, the individual overlapping spots still discernible; about 160 to 230 cm.

REPRODUCTION

Seasonality

Nishiwaki et al. (1965) suggested that *S. attenuata* in Japanese waters breeds in the spring and in the autumn. Harrison et al. (1972) stated that lengths of fetuses indicate that parturition in the eastern tropical Pacific (of *S. graffmani* = *S. attenuata*) also occurs both in the autumn and in the spring. The postnatal length-frequency data for large samples (Figures 15, 16; April 1968 and October 1972, for example) support the thesis of major reproductive seasons in spring and autumn but also suggest that there is a reproductive peak in summer as well. There is year-to-year variation in the timing of reproductive peaks, and there is some reproduction occurring throughout most of the year. It is difficult to define the reproductive seasons with precision because most of the sampling effort was in the early (January-April) and late (October-December) parts of the calendar year. The sampling intersected obvious calving seasons in April 1968, January 1972, October 1972, January 1973, and June 1973 (Figures 15, 16). Calving peaks were probably also present in some of the other sampling months, but the samples were too small to detect them or were biased in some fashion. A summary of predicted birth dates for 373 fetuses more than 15 cm long collected in 1971, 1972, and 1973, however, indicates that there may have been three calving peaks in each of the 3 yr (Figure 17). In each year there was a definite calving low in winter. The synchrony was diffuse, and some peaks were much sharper than others. The statistical evidence for three annual peaks in calving is weak, and when the data for all years are combined, all that can be said with certainty is that the calving season is prolonged, with a low point in winter and a tendency for high points in spring and fall.

The Male

Sexual development of the male was examined under three criteria: 1) weight of testes, 2) average diameter of seminiferous tubules, and 3) amount of sperm in the epididymis. Each of these was examined relative to total length, weight, and age (number of postnatal dentinal layers).

Weight of the testes (Figure 18) increases precipitously at body length of about 175 to 190 cm,

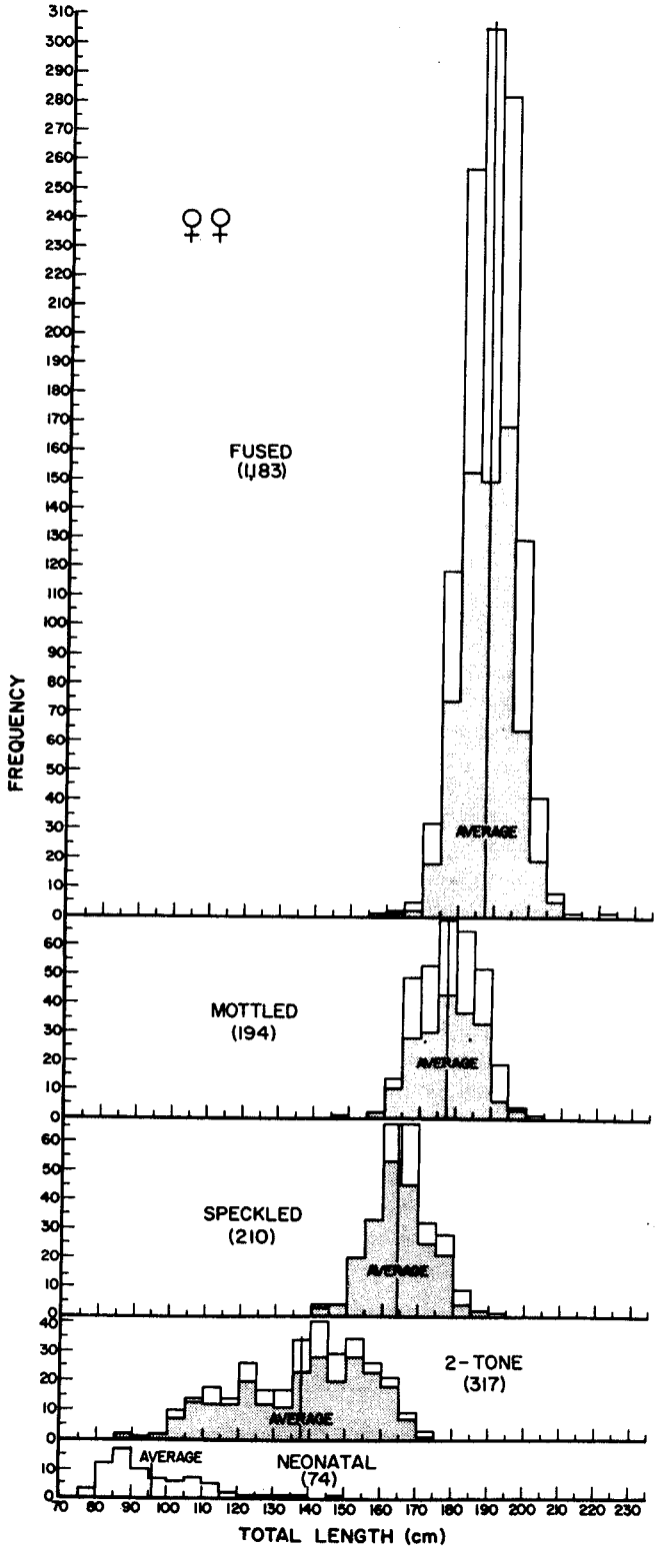

FIGURE 14.—Length-frequency distributions of females of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phases. On cruises between January 1971 and October 1972, adult females (≥160 cm) were selected for measuring and dissection. Earlier and later samples were nonselective. Average lengths for neonatal, two-tone, and fused are based on all the samples (no length bias), and averages for speckled and mottled are based on the nonselective samples (shaded). The analyses of coloration transition are based on all the samples for neonatal-to-two-tone and on the nonselective samples for the remaining three transitions. Size of sample used for calculation of average is given in parentheses.

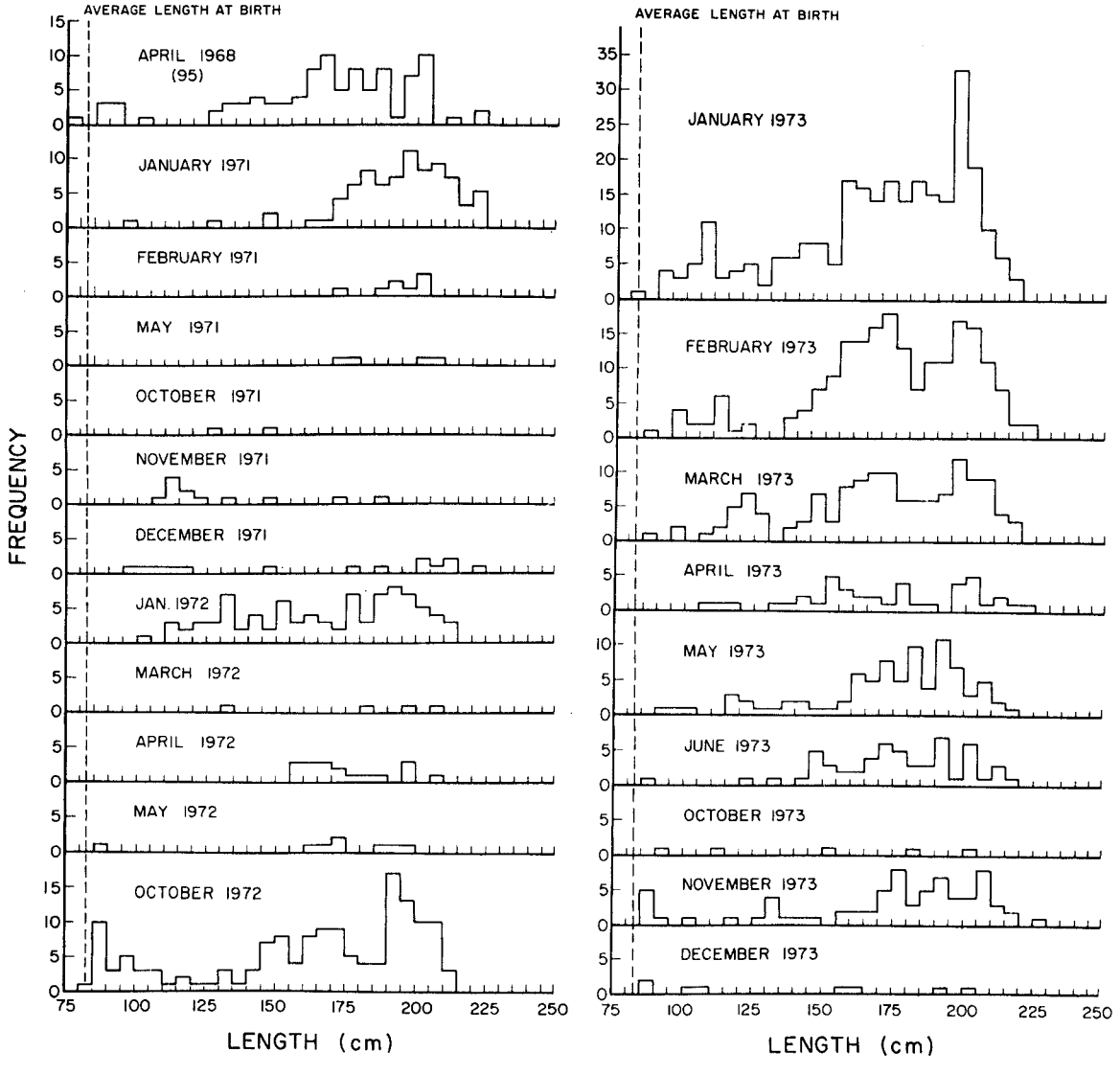

FIGURE 15.—Length-frequency distributions of postnatal male specimens of *Stenella attenuata*, 1968-73, by month.

but in animals larger than about 200 cm, there is little correlation with length. The largest testes encountered weighed 2,400 g and were possessed by a male 196 cm long. However, some males more than 210 cm long had testes weighing less than 300 g. Testes weight begins to increase sharply at 50- to 55-kg body weight and is strongly correlated with weight in larger animals. Males in the sample that weighed more than 70 kg (eight animals) had testes weighing more than a kilogram. The male with the third heaviest testes (2,017 g—heaviest testes for which body weight also available) weighed 80 kg; the heaviest male in the sample weighed 91 kg and had testes weighing 1,348 g. A rapid increase in testes weight (Figure 19) occurs at age 7 to 13 layers, with maximum size increasing until 12 to 16 layers. All animals with more than 14 layers had testes weighing 500 g or more. Again, there is wide variation in testes size relative to age. Part of the variation is ascribable to the considerable error in the estimate of number of dentinal layers (±2 layers for animals with more than 5 to 12 layers, more for older), but it must be concluded that there is probably about a 5-layer period during which the onset of puberty may

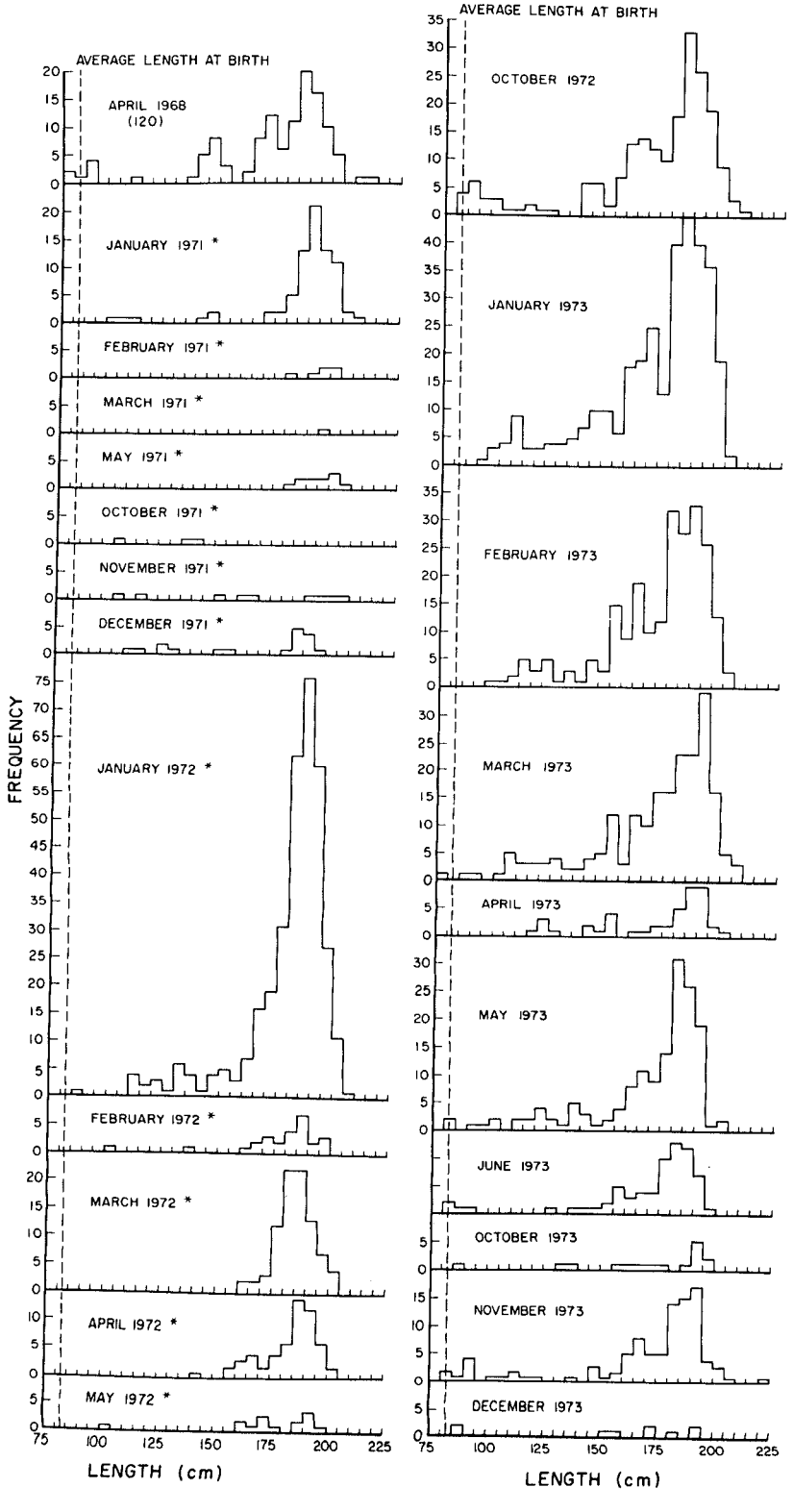

FIGURE 16.—Length-frequency distributions of postnatal female specimens of *Stenella attenuata*, 1968-73, by month.

take place (age about 7 to 12 layers) and that about 2 to 4 layers are required to attain "adult"

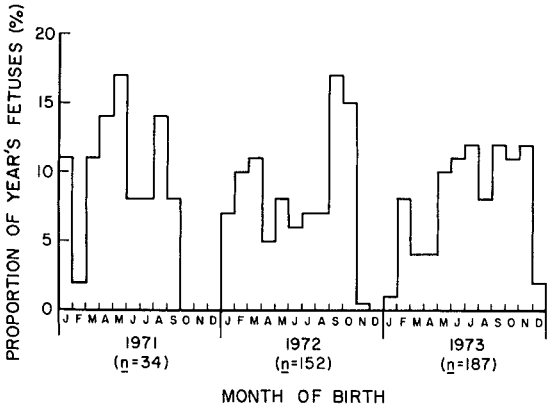

FIGURE 17.—Predicted month of birth for 373 fetuses of *Stenella attenuata*, based on fetal growth curve.

testes size (500 to 2,000 g). The third largest testes were possessed by an animal (202 cm long, 80 kg, discussed above) that had nonreadable teeth that were worn to the gum in all four tooth rows. Such tooth wear may be a correlate of relatively great age.

The diameter of the seminiferous tubules begins to increase rapidly at body length of about 155 to 170 cm (Figure 20), or at lengths about 15 cm shorter than those at which testes weight begins to increase. Tubule diameter is definitely correlated with body length until at least about 200 cm. The heaviest male (91 kg) had the largest tubules. The plot of tubule diameter on layers (Figure 21) indicates that the tubules enter a rapid development stage at 6 to 11 layers, before the onset of a rapid increase in testes weight (Figure 19). Asymptotic diameter is about 170μm and appears to be attained by 10 to 14 layers.

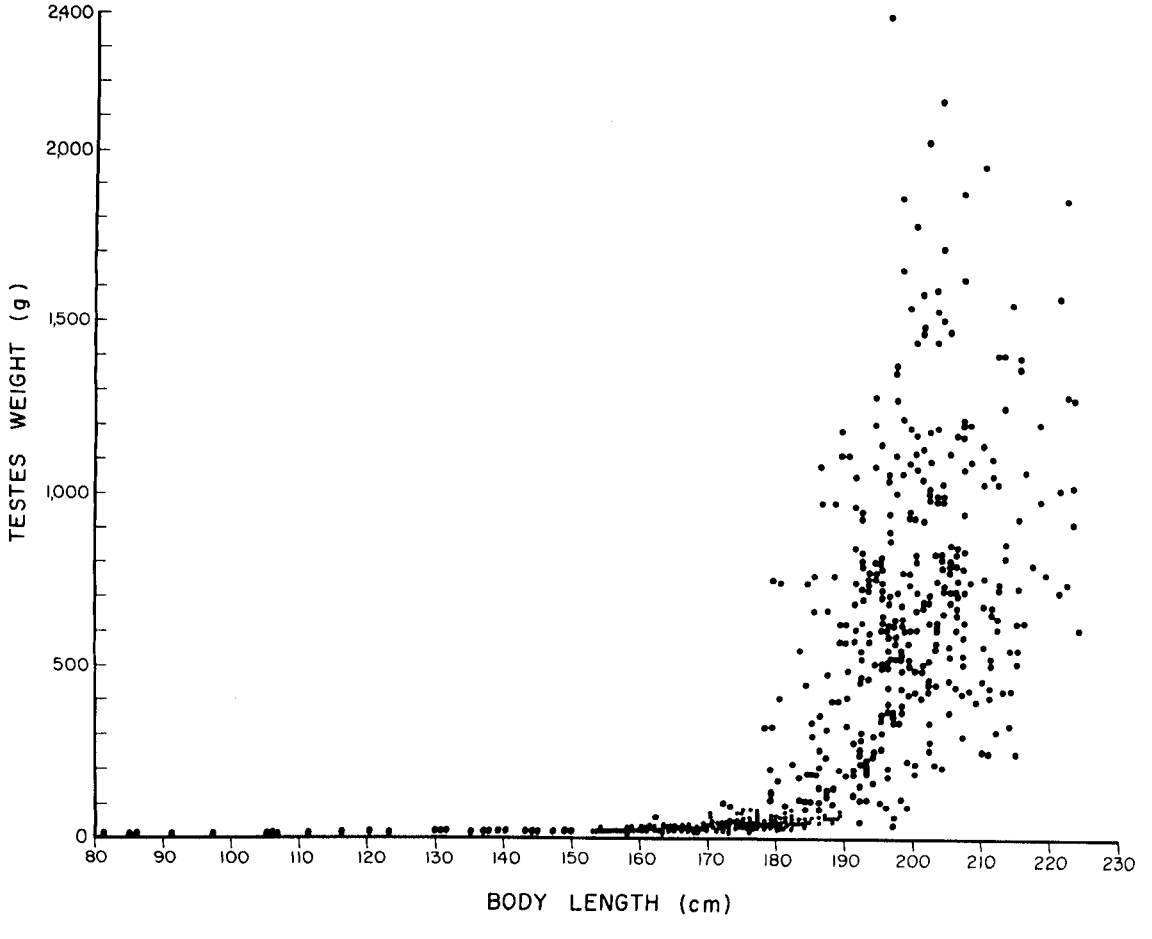

FIGURE 18.—Scatterplot of testes weight on body length in *Stenella attenuata*.

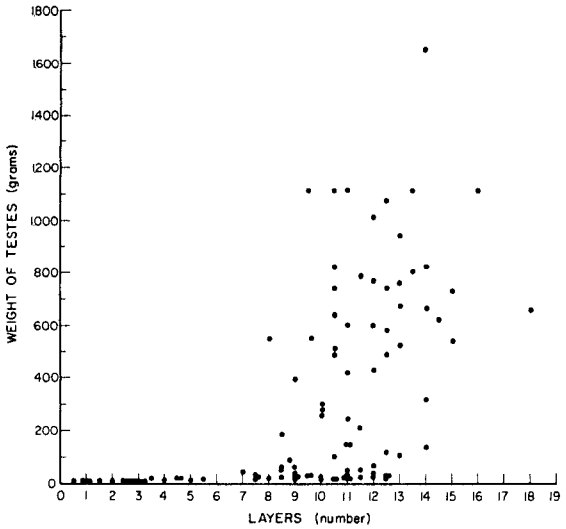

FIGURE 19.—Scatterplot of testes weight on number of postnatal dentinal layers in *Stenella attenuata*.

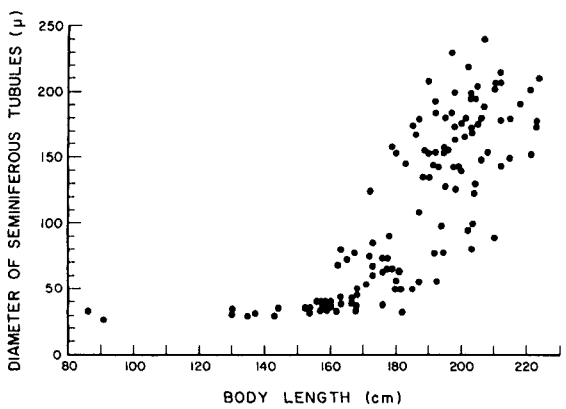

FIGURE 20.—Scatterplot of average diameter of seminiferous tubules on body length in *Stenella attenuata*.

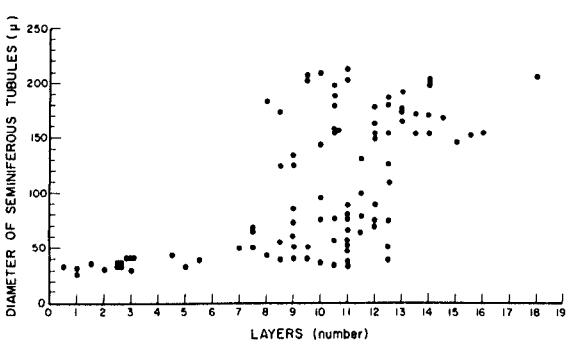

FIGURE 21.—Scatterplot of average diameter of seminiferous tubules on number of postnatal dentinal layers in *Stenella attenuata*.

Sperm in the epididymis were scored as "absent," "present in small numbers," or "copious" (easily seen in the histological sample without searching). The shortest individual with large numbers of sperm in the epididymis was 179 cm long. This animal weighed 62 kg. In animals larger than 180 cm and heavier than 58 kg, presence or absence of sperm in the epididymis bears little relationship to total length. Thirty-six large adults (>200 cm) were equally distributed among the three categories of no sperm, some sperm, and copious sperm.

The smallest testes bearing epididymis with sperm weighed 200 g, and the smallest testes with copious sperm weighed about twice as much. Some animals with testes heavier than 1.5 kg, however, had no sperm in the epididymis. The same pattern of wide variation is apparent in the relationship between epididymis code and layers. The youngest male with sperm in the epididymis had 9 layers. The youngest animal with copious sperm had 10 layers. After about 10 layers, there appears to be no relationship between age and presence or absence of large numbers of sperm.

In summary, the onset of puberty, as indicated by a rapid increase in diameter of seminiferous tubules and increase in testes weight, is at 7 to 12 layers (average ~9 layers; an estimate of ages at puberty) and at lengths of 155 to 170 cm and weights of 40 to 50 kg. Sexual maturity is attained about 2 to 4 layers later, at 10 to 14 layers, ≥180 cm, and ≥58 kg. The midpoint of the range of 10 to 14 layers, or 12 layers, may be taken as an approximation of average age at attainment of sexual maturity. Whether or not males at this point are "socially mature" (sense of Best 1969) can be determined only through behavioral studies. Average length of males 12 layers old is about 195 cm, and average weight is about 75 kg.

The Female

Attainment of Sexual Maturity

Harrison et al. (1972) described and figured the ovaries of *S. attenuata* (as *S. graffmani*). The ovaries weigh less than 0.5 g each at birth. Weight increases gradually to about 1.5 g at about age 6 to 8 layers (average ~7 layers; an estimate of age at puberty), when there is a sudden increase in average ovary size and weight due to presence of corpora of ovulation and/or pregnancy (Figure 22). This change comes at an

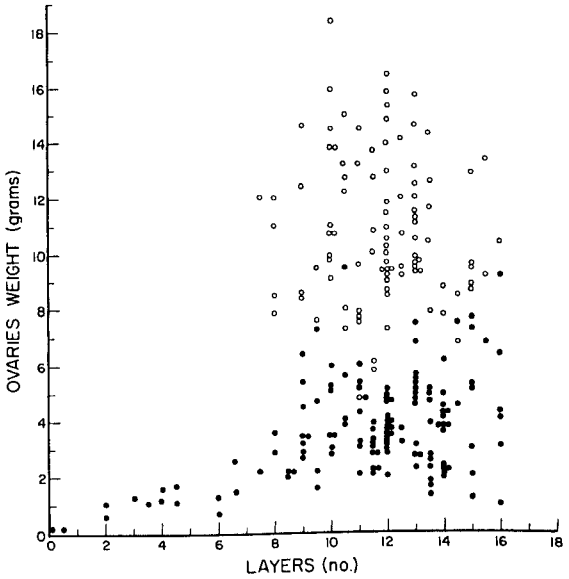

FIGURE 22.—Relationship between weight of ovaries and number of postnatal dentinal layers in *Stenella attenuata*. Open dots are females with a corpus luteum.

average total length of about 170 to 180 cm and weight of 50 to 60 kg (Figure 23).

Analysis of lengths of females with and without ovarian scars yields a more precise estimate of length at attainment of sexual maturity. The smallest of 1,410 specimens (160 cm long or longer) that possessed scars were two that were 167 cm long (one with a corpus luteum only and one with a corpus luteum and four corpora albicantia). The largest female with no scars was 193 cm long. The length-maturity curve is slightly asymmetrical, but a linear regression line through the nearly linear central portion ($M = 5.76L - 960.95$) estimates that average length at which scarring is first evident is 175.4 cm. This analysis probably underestimates length at attainment of maturity, because some of the small adults (170 to 180 cm) with many scars are those that have stopped growing at a shorter-than-average length. In other words, the left-hand portion of the frequency distribution of physically mature adults to an unknown extent artificially elevates the central portion of the length-maturity curve, making it asymmetrical.

An estimate of age and length at attainment of sexual maturity can also be derived directly from the smaller sample of females for which the number of tooth layers was determined. The youngest specimen exhibiting ovarian scarring had 7.5 layers. The oldest with no scarring had 12 layers. The estimated age at which 50% have scars is 9.14 layers ($M = 19.5t - 128.25$). Predicted length at this age is 181.6 cm (based on growth equation above). This estimate is less biased than the others above but based on much smaller samples, especially at the lower end of the layer-maturity curve.

Another estimate of length and age at first ovulation can be made by back extrapolation of a relationship between body length and number of corpora (including corpora lutea) in the ovaries (Figure 24). Length increases with corpora count until at least six to eight corpora have been accumulated, at about 183 to 190 cm. A fit of the data to the Laird growth model (above) yields the equation

$$L = 180.17 \text{ cm } \exp\{0.0541[1 - \exp(-0.2815C)]\},$$

where L = length in centimeters
C = number of corpora.

Back extrapolation of the curve to zero corpora yields an estimate of 180.2 cm. Predicted age from the growth equation is 8.74 layers.

An estimate of length at first conception can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Fifty-four primiparous females averaged 181.7 cm in length (range 167 to 193 cm). Predicted age at that length is 9.17 layers. The average length of their fetuses was 372 mm. This length is attained by about the beginning of the sixth month of gestation. Using the growth equations above to predict growth during 6 mo for the various tooth-layering models and substracting the growth increment from 181.7 cm yields estimates of length at first conception ranging from 177.7 to 180.0 cm (number 4 in Table 2). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because many females ovulate several times, and presumably continue to grow, before becoming pregnant the first time (see Ovarian Changes below).

The various methods of estimating age and length at attainment of sexual maturity yield estimates of varying accuracy (Table 2). The estimates based on tooth layers and length at first

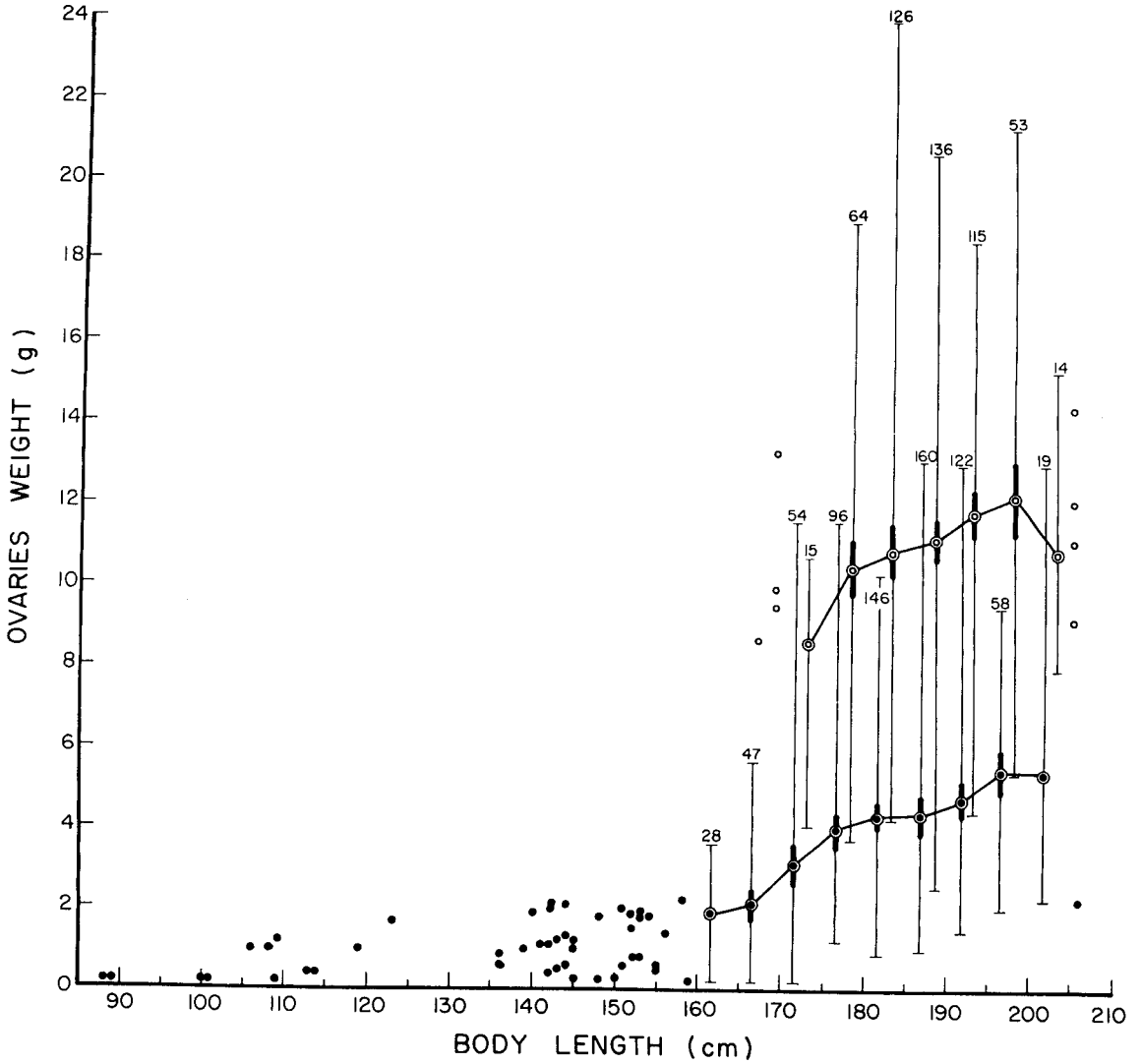

FIGURE 23.—Scatterplot of weight of both ovaries on body length in *Stenella attenuata*. Open dots represent females with a corpus luteum. For animals 160 cm or longer, where sample for 5-cm interval is 10 or more, means (circled symbols) and ranges are graphed and points are not plotted. Where the sample is ≥30, ± two standard errors are indicated by bars.

conception are the best of the four and probably bracket the true values. Under method number 3, age hypotheses numbers II and III are more probably correct than number I. Accordingly, we estimate that sexual maturity is, on the average, attained at 181 ± 1 cm and 9.0 (8.6 to 9.3) layers (5.1 to 8.3 yr, depending on the alternative layering hypothesis used).

An increase in size of Graafian follicles is another criterion of approaching sexual maturity. Diameter of the largest follicle also shows a sharp increase after 160 cm total length (Figure 25), concurrent with the increase in ovary weight (Figure 23). The largest follicle in immature females usually is less than 1 mm in diameter. The largest follicles in most ovaries containing scars are between 1 and 8 mm in diameter, but a few follicles (possibly cystic) as large as 10 to 16 mm in diameter were encountered.

Ovarian Changes in Adults

The analyses of ovarian changes are based on material collected through 1972. The corpus

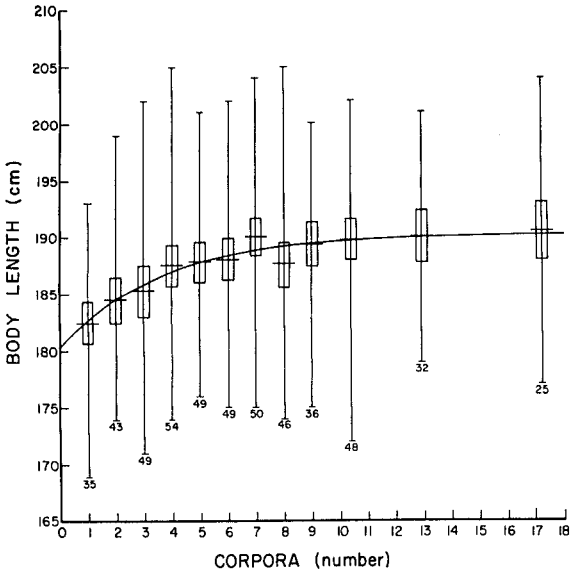

FIGURE 24.—Relationship between body length and number of corpora in *Stenella attenuata*. Average (bar), ± two standard errors (box), range (vertical line), and sample size shown.

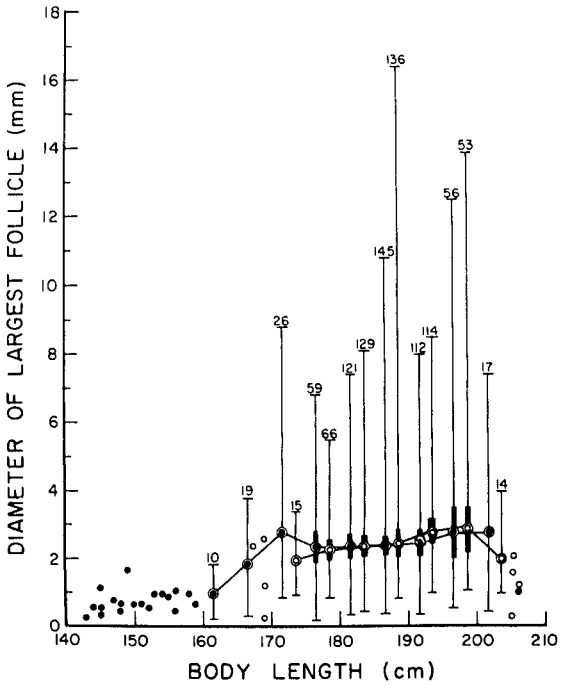

FIGURE 25.—Relationship between body length and diameter of the largest Graafian follicle in *Stenella attenuata*. Open dots represent females with corpus luteum. For length ≥160 and $n \geq 10$, means (circled symbols) and ranges shown. For $n \geq 30$, ± two standard errors are shown. Not included are 27 "senile" specimens with follicles <0.1 mm and five juveniles 88 to 122 cm with 0- to 1-mm follicles.

TABLE 2.—Results of analyses of length and age at attainment of sexual maturity in *Stenella attenuata*, with comments (in parentheses) on pros and cons of the methods. Lengths and layer counts predicted with the growth equations are in parentheses.

Analysis	Length (cm)	Layers (no.)	Age (yr), under hypothesis I	II	III
1. Length at which 50% have corpora (probable underestimate).	175.4	(7.66)	3.8	6.7	4.3
2. Number of tooth layers at which 50% have corpora (interpolation, but small sample sizes).	(181.6)	9.14	4.6	8.1	5.6
3. Back-extrapolation of corpora-length curve (large samples, but extrapolation).	180.2	(8.74)	4.4	7.7	5.2
4. Length at first conception under hypothesis: I	177.7	(8.17)	(4.1)	—	—
II	180.0	(8.57)	—	7.6	—
III	180.0	(8.57)	—	—	5.1
(includes only those that become pregnant at first ovulation; probable underestimate).					

luteum of pregnancy arises from the ruptured follicle and has an important secretory function in maintaining early pregnancy in all mammals and full gestation in most (Amoroso and Finn 1962). The gross and microscopic structures of corpora lutea in various delphinids, including *S. attenuata,* have been described by Harrison et al. (1972).

The corpus luteum decreases in size during gestation (Figure 26). Of 242 females with corpora lutea, 229 were pregnant. Eleven with fetuses less than 20 mm long (range 1 to 20 mm) had corpora with diameters of 23 to 29 mm (average 26.0 mm, SD 2.90). The mean diameter dropped sharply to 23.6 mm (range 21 to 27 mm, SD 2.27) in 17 females with fetuses between 20 and 100 mm (using Student's t, means are significantly different at $\alpha = 0.01$). This amounts to about a 32% decrease in luteal volume. Size of the corpus luteum continues to decrease at a slower rate, to 22.2 mm (range 19 to 28 mm, SD 1.79) in females with fetuses 700 to 825 mm (average length at birth is 825 mm) long, a further decrease in volume of about 15%. Luteal volume in females with near-term fetuses is only about half of that shortly after conception. Mean diameter in 10 females with fetuses longer than average birth length (825 mm) was 24.0 mm (range 20 to 26 mm, SD 2.21, greater than mean for 700 to 825 mm at $\alpha = 0.01$), a volume difference of about 38% more than for fetuses 700 to 825 mm long. Delayed regression (or re-enlargement) of the corpus luteum is apparently correlated with greater-than-average length at birth.

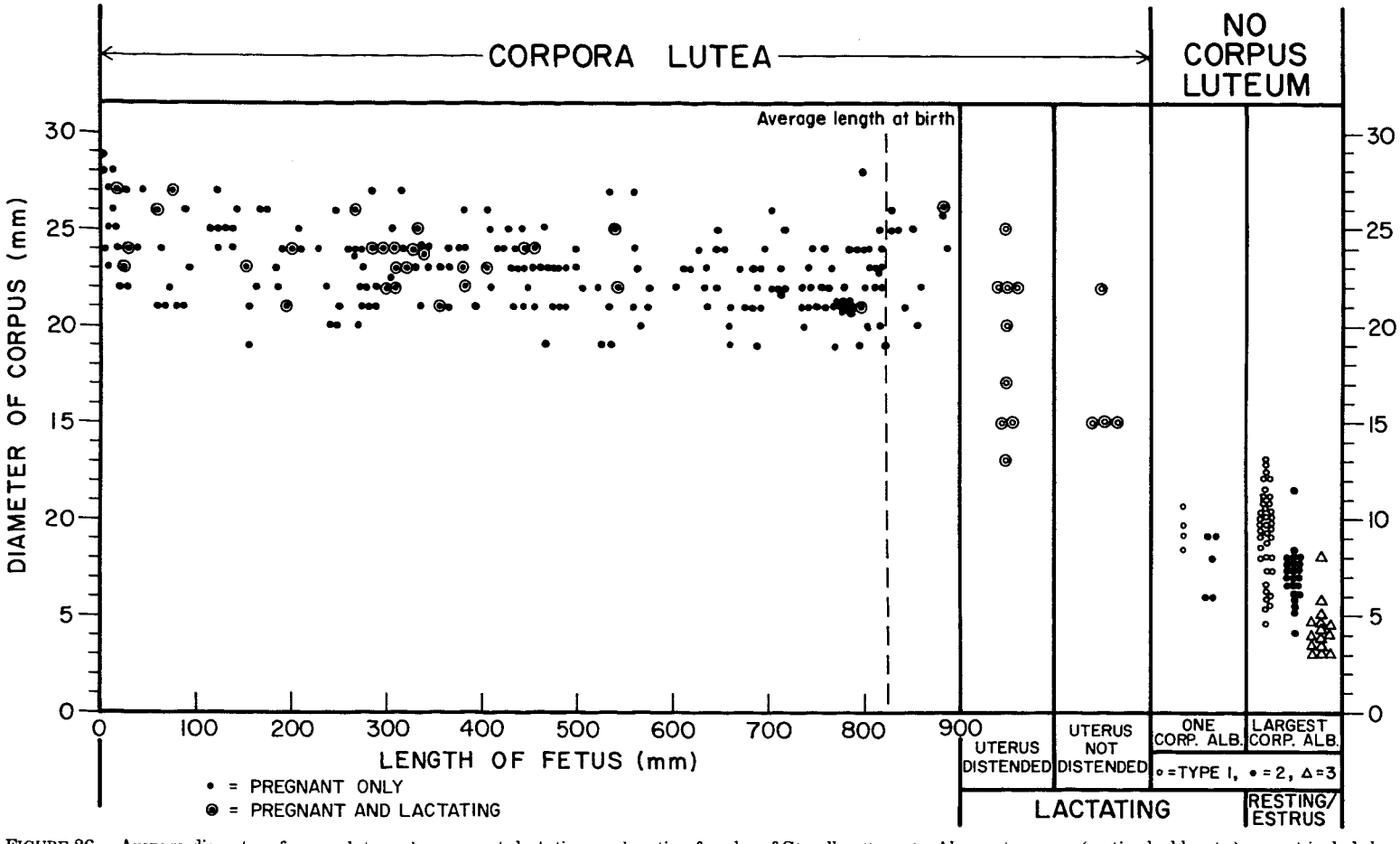

FIGURE 26.—Average diameter of corpus luteum in pregnant, lactating, and resting females of *Stenella attenuata*. Aberrant corpora (cystic, double, etc.) are not included.

Nine obviously postpartum females had corpora lutea 13 to 25 mm in diameter (Figure 26). Four lactating females with uteri not obviously distended had corpora lutea in the same size range. Average luteal volume in these lactating animals was less than half of that in animals at parturition. Some of these 13 cases may represent miscarriages.

The corpus luteum of pregnancy shrinks still further during the suckling period, losing its glandular appearance and becoming a corpus albicans. Nine of 197 lactating females without corpora lutea each had a single corpus albicans, which must represent the regressed corpus luteum of the first pregnancy. These corpora (Figure 26) were approximately spherical and 5.9 to 10.6 mm in diameter (average 8.5 mm). The lower end of this range—about 6 mm—must approximate the limit of regression during the suckling period (about 11.2 mo; see below). The small number of lactating females with corpora lutea (13) compared to the number with only copora albicantia (197) indicates that initial regression following parturition must be very rapid, perhaps occurring in less than 15 days. Still further regression in size and histological structure of the corpus albicans of pregnancy probably occurs. Many adult females have a large corpus albicans (in most cases, one of several) between 3 and 6 mm in diameter (Figure 26) with greatly degenerated structure. Unless these corpora all represent ovarian events not resulting in pregnancy, i.e., the females are all completely barren, the corpus albicans of pregnancy must decrease in diameter during a resting period following a pregnancy, to possibly as little as 3 mm.

Multiple corpora lutea are uncommon in *S. attenuata*. They were encountered in only 2 out of 258 females with corpora lutea. One of these was pregnant with twin fetuses (males, 83 and 86 mm) in the left horn of the uterus. The left ovary contained two corpora lutea of approximately equal size, each possessing a surface scar of ovulation, together with seven corpora albicantia visible on the surface. The right ovary was devoid of scars. Another female with two corpora lutea had a 592-mm fetus (male) in the left horn of the uterus. The left ovary looked very much like that of the specimen with twin fetuses, having two corpora lutea of approximately equal size and eight corpora albicantia on the surface. Neither corpus luteum bore a discernible surface scar. The right ovary was unscarred. There are two possible explanations for the presence of two corpora lutea in this specimen: 1) one of them was an accessory corpus, or 2) one of a pair of twin fetuses was aborted during early pregnancy. In any case, the incidence of multiple corpora lutea is very low in *S. attenuata,* less than 1% in the sample examined. This is in sharp contrast to some other cetaceans, in which rates of presence of accessory corpora range to 15.6% (*Delphinapterus leucas* —Brodie 1972). The contribution of double and accessory corpora lutea to the accumulation of corpora albicantia can be considered to be negligible in *S. attenuata.*

Corpora albicantia in *S. attenuata* represent both regressed corpora lutea of pregnancy and regressed corpora of ovulations that do not result in pregnancy. This conclusion is based on the accumulation rate of corpora albicantia and on the estimate of the mean length of the calving interval (see below). We were not, however, able to differentiate between small regressed corpora lutea and regressed corpora of ovulation. This impasse, also encountered by workers dealing with other cetaceans (Harrison et al. 1972) is caused by the wide and largely discordant variation in size, shape, surface texture, and internal structure and color of the corpora albicantia. If one looks at enough corpora, it is possible to find corpora with these characters in almost any combination of expressions.

Harrison et al. (1972) found no more than six corpora albicantia in the ovaries of any *Stenella* female. In the present sample, however, nearly half (44%) of the females had more than six corpora, including the corpus luteum. Fifty-five females of 1,131 had 15 or more corpora; one had 28 (Figure 27). Three thousand five hundred and two corpora from ovaries of 530 females were scored to six categories. These categories are somewhat arbitrary in view of the continuity of regression and the wide variation discussed above, but, nonetheless, they are useful in analyzing the course of regression. The numbers and proportion of total corpora complement represented by each of these categories varies with the total number of corpora (Table 3, Figure 28). The categories were defined as follows:

Type 1. Surface raised, smooth or slightly wrinkled. Looks externally like a small corpus luteum. Cortex white or yellow, with obvious remnants of vascularization. Center solid or loosely constructed, consisting mainly of white

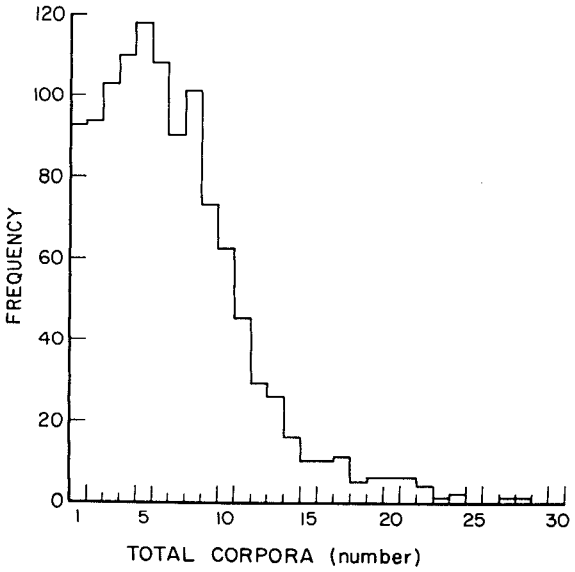

FIGURE 27.—Frequency distribution of corpora count in 1,131 females of *Stenella attenuata*.

connective tissue, 3.5 to 15.5 mm in diameter, average 7 mm. These corpora almost certainly are nearly all regressed corpora lutea. Four hundred fifty-six were encountered (13.2%). Females with two or more corpora have, on the average, about one Type 1 corpus (Figure 28), although as many as five may be present (Table 3).

TABLE 3.—Types of corpora present in ovaries of *S. attenuata* in relation to total corpora. Averages in Figure 28.

Total number of corpora (including corpora lutea)	Sample size (no.)	Range of number of each type of corpus albicans—Type: 1	2	3	4	5	6
1	35	0-1	0-1	0	0	0	0
2	42	0-2	0-2	0-1	0-1	0-1	0
3	48	0-3	0-3	0-2	0-1	0	0
4	53	0-3	0-4	0-3	0-1	0-2	0
5	49	0-5	0-4	0-5	0-2	0-2	0
6	49	0-5	0-4	0-6	0-3	0-1	0
7	50	0-5	0-5	0-6	0-3	0-2	0-1
8	46	0-5	0-6	0-7	0-2	0-4	0
9	36	0-2	0-5	2-9	0-4	0-3	0-1
10-11 (average 10.4)	48	0-4	0-5	3-10	0-2	0-2	0-1
12-14 (average 12.9)	32	0-2	0-5	3-14	0-3	0-4	0-3
15-27 (average 17.2)	25	0-4	0-5	7-19	0-2	0-9	0-1
Total	513	0-5	0-6	0-19	0-4	0-9	0-3

Type 2. Surface raised and wrinkled. Interior white to yellow, often with traces of luteal cortex and vascularization. Center solid or loosely constructed, consisting mainly of white connective tissue. Definitely less integrated in structure than Type 1 (above). Diameter 3.0 to 12.0 mm, average 6 mm. The evidence on accumulation rate (below) suggests that these corpora are probably a mixture of regressed corpora lutea and corpora of ovulation. We found 787 of this type (22.5%). The number of Type 2 corpora is relatively constant in females with three or more corpora, at about one and one-half (Figure 28) with a

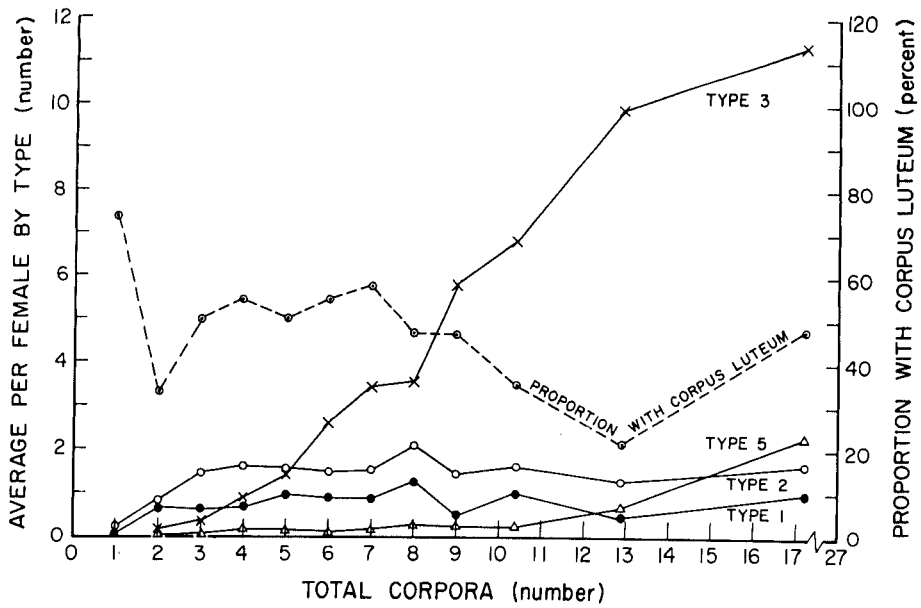

FIGURE 28.—Relationships between numbers of corpora of various types and total number of corpora in ovaries of females of *Stenella attenuata*. Ranges and sample sizes in Table 4.

range of 0 to 6 (Table 3). This number is tightly correlated with the number of Type 1 corpora (Figure 28), indicating that there may be some overlap in the classification criteria for these categories.

Type 3. Surface usually not raised; scar usually smaller than Type 2 and heavily wrinkled. May be pedunculate and flattened. May be flattened against the surface or may run deep into the ovary. Interior consists of white connective tissue. May have yellow "stains" around the white center. When many corpora are present, some of this type may be present but not apparent at the surface. Diameter 2.0 to 8.5 mm, average 3.5 mm. This is a catch-all category for all small compact corpora with surface scars and internal structure. It probably includes both regressed corpora lutea and corpora representing ovulation and other events. We found 1,999 corpora of this type (57.1%). The number increases steadily with total corpora number (Table 3, Figure 28), while the numbers of Types 1 and 2 corpora remain constant, indicating that Types 1 and 2 corpora regress into and accumulate as Type 3 corpora. This is assuming, of course, that total corpora count is related to age (see below).

Type 4. Thin, flattened against the surface of a new corpus luteum. Two to 15 mm in diameter. These are Types 2 and 3 corpora that cannot be allocated to those categories because of distortion caused by the corpus luteum. One hundred were encountered (2.9%).

Type 5. Surface trace very slight or apparently absent. Interior deep yellow or orange, with no concentrated connective tissue or apparent internal structure. Diameter 0.5 to 5.5 mm, average 2 mm. Harrison et al. (1972) have suggested that this type of corpus is the end result of regression of an atretic lutealized follicle. We encountered 149 (4.3%).

Type 6. A small surface scar with no discernible internal structure. Two to 5 mm in diameter. Only 11 corpora of this type were encountered (0.3%). They may represent extremely regressed corpora of other types or may originate from different ovarian events.

Types 1, 2, and 3 comprise a series of increasing regression and/or decreasing complexity of original structure, and it is probable that regressing corpora lutea pass through these types or stages. The shapes of the diameter frequency distributions (Figure 29) suggest that corpora albicantia regress to an average size of about 3 mm in diameter and then persist and accumulate at that size for at least part of the remainder of the life of the female. The skewness of the aggregate distribution (sum Types 1, 2, and 3 in Figure 29) becomes even more significant when one considers that the volume of the corpus decreases as the cube of the diameter. On a volume scale, the left

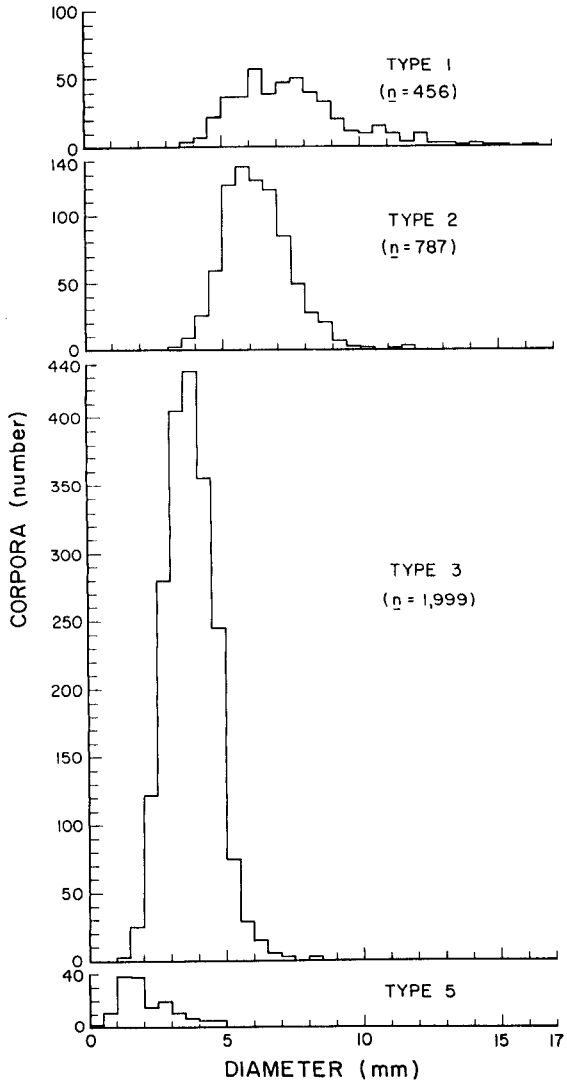

FIGURE 29.—Frequency distribution of diameter of Types 1, 2, 3, and 5 corpora albicantia in *Stenella attenuata*.

side of the curve would be steeper and the right side less steep.

Consideration of the relative rates of deposition of corpora in the left and right ovaries is important to the question of persistence of corpora. The distribution of corpora between left and right ovaries is related to the number of corpora present (Table 4). The first corpus occurs in the left ovary about 94% of the time. Subsequent corpora occur in the same ovary as preceding ones at about the same rate (~95%), causing a gradually increasing percentage of animals with corpora in both ovaries, until about 10 to 11 corpora have been deposited, when emphasis switches sharply to the opposite ovary (left or right). All females with 15 or more corpora (27 specimens) had corpora in both ovaries.

A group of 15 seemingly postreproductive females was encountered. These specimens had very small, obviously regressed ovaries with 10 to 15 Type 3 or smaller corpora albicantia (Figure 30). They had no corpora lutea or Type 1 corpora

TABLE 4.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 488 specimens of *Stenella attenuata*.

Corpora (no.)	Sample size (no.)	Location of corpora: Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	31	93.6	6.4	—
2	40	85.0	7.5	7.5
3	44	86.5	4.5	9.0
4	53	88.7	1.9	9.4
5	47	78.8	2.1	19.1
6	48	75.0	4.2	20.8
7	45	73.4	2.2	24.4
8	41	61.0	2.4	36.6
9	34	70.6	2.9	26.5
10-11	47	46.8	2.1	51.1
12-14	31	6.5	0.0	93.5
15-27	27	0.0	0.0	100.0
Total	488			

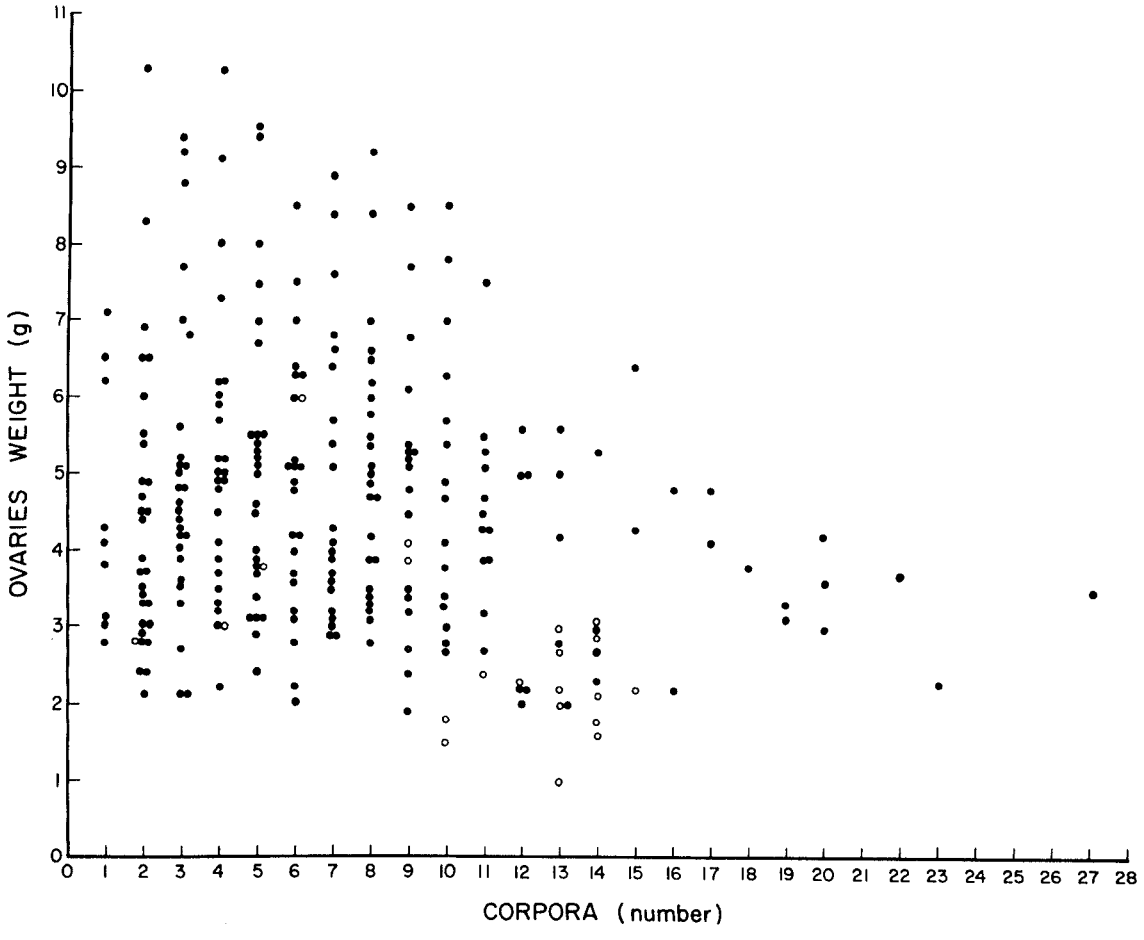

FIGURE 30.—Scatterplot of ovaries weight on number of corpora in *Stenella attenuata*. Females with corpus luteum not included. Open dots are females with no Type 1 or 2 corpora albicantia.

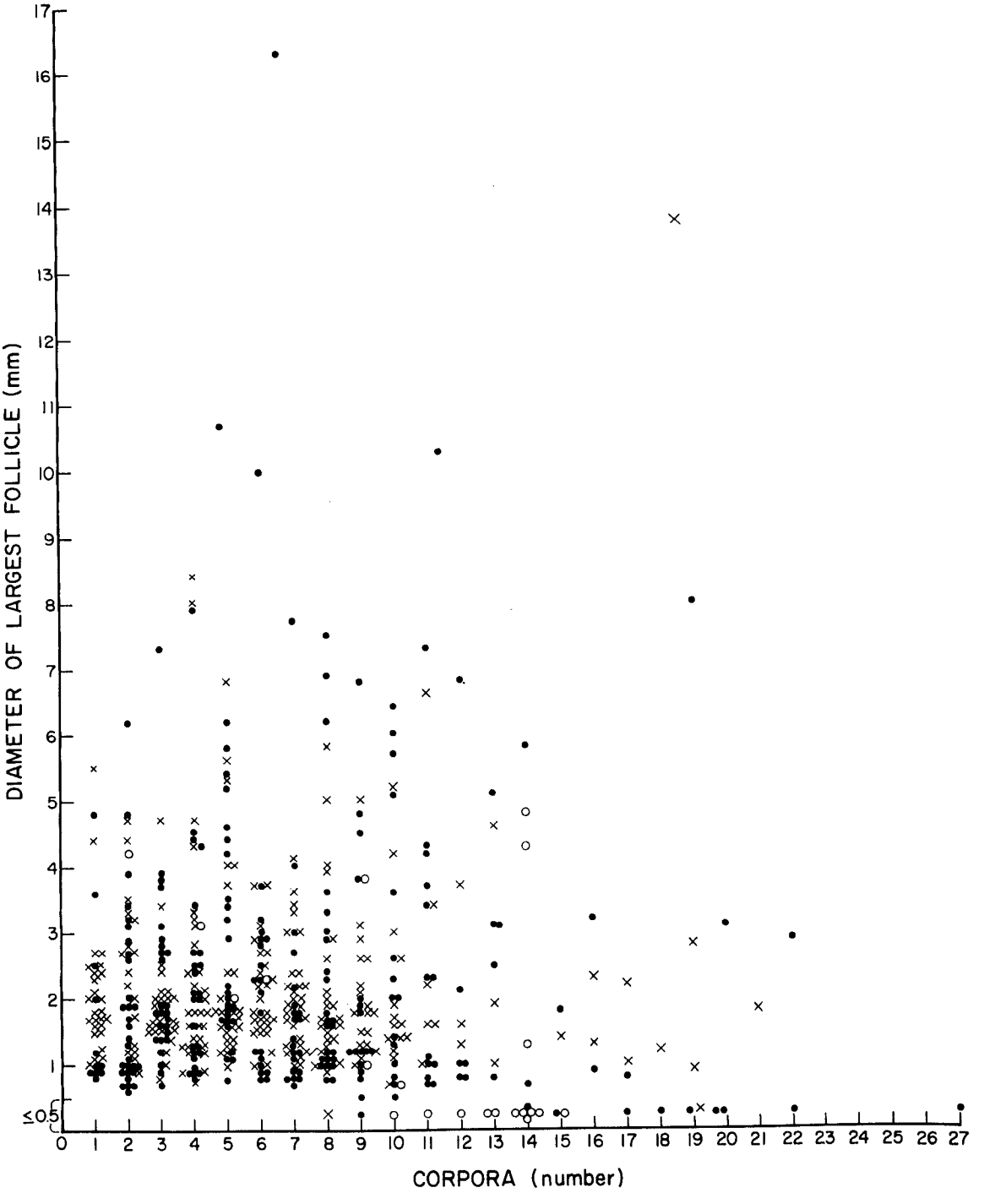

FIGURE 31.—Scatterplot of diameter of largest follicle on number of corpora in *Stenella attenuata*. Females with corpus luteum indicated with ×. Open dots are females with nor corpus luteum or Type 1 or 2 corpora albicantia.

albicantia. They also typically had very small Graafian follicles (Figure 31). A consideration of these females bears on the question of persistence of corpora albicantia. Sergeant (1962) encountered similar females in *Globicephala*. They comprised about 5% of adult females. He called them "senile" and concluded that the ovarian scars in these animals represent some residual subset of the maximum complement of corpora of pregnancy, ovulation, and other events. He implied that they probably are the corpora of pregnancy, since those corpora are larger at the outset and presumably less likely to regress to the point of macroscopic disappearance. The ovarian data for *S. attenuata* do not support this hypothesis of disappearance of some corpora in regressed ovaries. The regressed ovaries have 10 to 15 corpora (Figures 30 and 31). The ovaries of other, still reproductive females are larger and have 16 to 27 corpora, although follicles are typically smaller than in reproductive females with fewer corpora (Figure 31). Three alternative hypotheses explain this apparent dichotomy in females with 10 or more corpora:

1. The usual maximum number of corpora is about 21, and some corpora disappear in postreproductive females, i.e., the "senile" group in Figure 30 properly belongs at the far right side of the plot at the end of a downward trend in ovary weight (the hypothesis of Sergeant 1962).
2. Corpora are laid down at about the same rate in all individuals, but some become postreproductive at about 10 to 15 corpora while others continue to accumulate corpora (16 to 27) until a greater age, i.e., the corpora scale in Figure 30 is effectively an age scale. Under this hypothesis, corpora do not disappear.
3. Corpora are accumulated at rates varying widely among individuals, but the typical maximum complement is 10 to 15 corpora, i.e., the reproductive females with more than 15 corpora in Figure 30 properly belong in the body of the distribution in the left two-thirds of the plot. A possible explanation for widely varying rates of accumulation is that some females are more fecund and the senile period is reached with some maximum number of pregnancies, so that the varying ratios of corpora of pregnancy to corpora of ovulation may produce the apparent dichotomy. Sergeant (1973) found greatly varying individual rates of ovulation in the white whale, *Delphinapterus leucas*.

In order to examine these alternative hypotheses, the females in Figure 30 and 31 with 10 or more corpora were examined in three groups—A, B, and C:

A. 10 to 15 corpora, reproductively active (corpus luteum and/or Types 1 and 2 corpora albicantia).
B. 16 or more corpora, reproductively active.
C. 10 to 15 corpora, postreproductive (ovaries regressed, no corpus luteum or Types 1 or 2 corpora albicantia).

The three groups were compared in terms of corpora count, weight of ovaries, size of largest follicle, number of dentinal layers, total length, and relative corpora counts in left and right ovaries (Table 5). Only nonpregnant females were included in the sample for ovary weight. Follicle size was examined separately for pregnant and nonpregnant animals.

Ovary weight and follicle size for nonpregnant animals decline progressively from A to C. This is

TABLE 5.—Characteristics of females of *Stenella attenuata* in groups A, B, and C (see text).

Item	A	B	C
Corpora (no.)			
Sample size	67	24	15
Average	11.2	18.9	12.9
Range	10-15	16-27	10-15
SD	1.41	2.56	—
Ovary weight (g) (nonpregnant)			
Sample size	44	13	15
Average	4.4	3.6	2.2
Range	2.0-8.5	2.2-4.8	1.0-3.1
SD	1.61	0.81	0.59
Largest follicle (mm) (nonpregnant)			
Sample size	27	13	<14
Average	2.9	1.5	<0.5
Range	<0.5-10.3	<0.5-8.0	0.5-4.3
SD	2.53	2.35	—
Layers (no.)			
Sample size	30	18	7
Average	13.1	13.1	13.2
Range	10.0-16.0	11.0-15.0	11.5-16.0
SD	1.39	1.31	1.52
Length (cm)			
Sample size	67	24	15
Average	190.1	190.3	187.0
Range	172-202	177-204	179-192
SD	6.43	6.78	3.54
Left/right ovary			
Sample size	65	23	15
Average in right (%)	24	33	29
Left/right (no./no.)	548/178	291/144	—

a requirement of hypothesis 1, above, but does not eliminate hypotheses 2 and 3.

The three groups do not differ in average estimated number of tooth layers. This may, in part, be due to the difficulty of accurately counting the innermost layers in teeth with more than 12 layers (the number of layers is probably underestimated by as much as one-third in teeth with large amounts of convoluted secondary dentine), but careful comparison of the teeth of the three groups in terms of other features presumably correlated with age, such as tip wear, degree of closure of the pulp cavity, and amount of secondary dentine does not indicate that any group is older than any other. This evidence is against hypothesis 1, which requires that group C be older than A, and hypothesis 2, which requires that B be older than A and C.

Groups A and B have reached asymptotic length (~190 cm). The animals in group C averaged about 3 cm less. A statistical comparison of A with B using Student's t indicates that the difference is significant at $\alpha = 0.05$. These results do not eliminate or support directly any of the hypotheses. Since A, B, and C are about the same age, the length data indicate that asymptotic length may be less for females that become senile with 10 to 15 corpora. This indirectly supports the idea of considerable individual variation in life history.

The most convincing evidence against hypothesis 1 has to do with number of corpora in right versus left ovaries. If the emphasis in corpus deposition shifts from left to right at about 10 corpora, and if group C regresses from group B (animals with about 20 corpora) losing about 6 corpora in the process, then group C should have about equal numbers of corpora in the right and left ovaries. If most corpora of ovulation come in early reproductive life (as data analyzed below indicate) and, as suggested by Sergeant (1962), are more likely to disappear than corpora of pregnancy because of smaller initial size, then the regressed group C should have, on the average, more corpora on the right than on the left, because most of the corpora of pregnancy would be in the right ovary. Forty-one percent of the corpora in 14 individuals having 18 to 22 corpora (average 19) were on the right. Only 29% of the corpora in group C were on the right. The difference between C and A (29 and 24%) can be accounted for simply by the difference in average total corpora count (12.9 and 11.2). These results eliminate the hypothesis (number 1 above) of loss of corpora with regression of ovaries.

The various lines of evidence largely speak against hypotheses 1 and 2 and support hypothesis 3, that of great individual variation in life history and of persistence of corpora albicantia. This is in line with findings by some other workers in small cetaceans (Sergeant 1962, 1973; Brodie 1971).

The data on the relationship of percent occurrence of corpora lutea to number of corpora (Figure 28) also support the hypothesis of widely varying rate of accumulation of corpora albicantia. After stabilization at about 50% at 3 to 4 corpora, the rate declines after 8 to 9 corpora to 20% at 13 corpora; but the rate for females with 17 to 27 corpora is again 50%. Assuming that fecundity is inversely related to age, this pattern suggests that the females in the 17 to 27 group are about the same age as those in the 3 to 9 group.

Ovulation Rate

Even assuming that corpora albicantia persist and represent various ovarian events, estimating average rates of accumulation is difficult because of 1) the above-mentioned unreliability of age estimates based on more than 12 tooth layers, 2) the evident individual variation in accumulation rate, and 3) change in ovulation rate during the reproductive span. All of these factors must contribute to the scatter in a plot of corpora number (including corpus luteum) on estimated age (Figure 32). Several workers have pointed out that cetacean ovaries often contain two or more corpora of the same size and same stage of regression. It has been suggested that these are the result of multiple infertile ovulations or lutealization of atretic follicles in newly mature animals (Harrison et al. 1972). Many in the present series of ovaries had two or more corpora (of Type 1 or 2) that were very similar in size and structure and must have resulted from nearly contemporaneous events. One probable multiple ovulation is apparent in Figure 32. This female, field number CWOR8, possessed 7 or 8 well-defined layers in its teeth. In spite of its extreme youth, it had a small corpus luteum, three Type 1 corpora, two Type 2 corpora, one Type 3 corpus, and one Type 4 corpus. The uterus was empty, and there was no milk in the mammaries. The animal could not have been reproductively active for more than about a year, but had already experienced eight

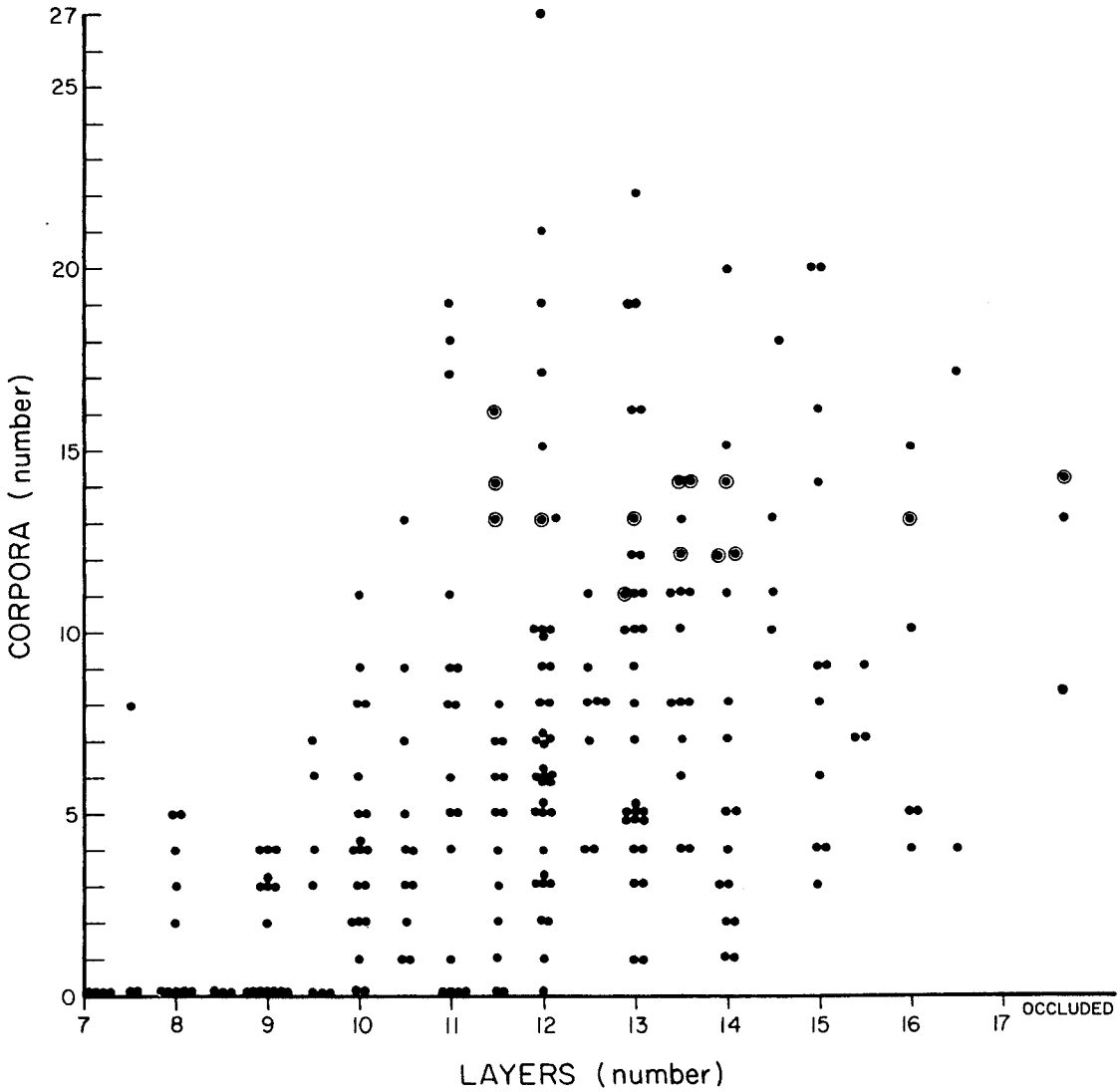

FIGURE 32.—Scatterplot of number of corpora on number of postnatal dentinal layers in *Stenella attenuata*. Circled symbols are senile females [shriveled ovaries with no corpus luteum or Type 1 or 2 corpora albicantia].

apparently nonreproductive ovarian events that resulted in corpora belonging to all of the types through which a corpus luteum must pass during regression to a small corpus albicans.

Calculation of average ovulation rates from the data in Figure 32 must take into account individual variation in age at first ovulation. The females in Figure 32 were grouped into 10 one-layer intervals beginning with 7.5 layers (Table 6). The average reproductive age in interval p was calculated as

$$\bar{A} = \left(\sum_{i=1}^{p} a_i b_i \right) \div c,$$

where a_i = % maturing in ith interval (% mature in i minus % mature in i - 1)

b_i = average reproductive age in interval p of females mature in i

c = % mature in interval p.

Average reproductive age in the ith interval of

TABLE 6.—Average reproductive ages and corpora counts of females of *Stenella attenuata* used in estimating ovulation rate based on corpora and tooth layers.

Layers (no.)	Sample (no.)	Proportion mature (%)	Average reproductive age of mature (layers)		Average corpora (no.)	
7.5- 8	13	46.2	0.50		4.50	
8.5- 9	18	44.4	1.56	1.43	3.25	4.21
9.5-10	24	79.2	1.67		4.53	
10.5-11	25	84.0	2.56		6.42	
11.5-12	52	94.2	3.25		8.35	
12.5-13	36	100.0	4.05		8.92	
13.5-14	31	100.0	5.06		8.71	
14.5-15	15	100.0	6.07		10.87	
15.5-16	7	100.0	7.08	6.60	9.86	10.45
>16	3	100.0	8.09		9.75	
Total	224					

Note: Teeth of all available females with more than 12 corpora were sectioned, while only a nonselective subsample of females with fewer corpora were included. The effect on estimate of average reproductive age is negligible, since nearly all had 11 or more layers.

females maturing in i was set at 0.50 layers. Because of small sample sizes, the first three intervals and the last three were pooled. The results show an increase in average corpora count (number of ovulations) with reproductive age (Figure 33). A curvilinear fit to the interval means, using a power model forced through the origin, fits well and indicates that ovulation rate is higher in animals of reproductive age 0-2 layers than in older animals. The breaking point seems to come at about 12 layers, when about 6 corpora have been accumulated and rate appears to become nearly constant. Average ovulation rates estimated from the curve are about four during the first layer, two during the second, and about one per layer thereafter.

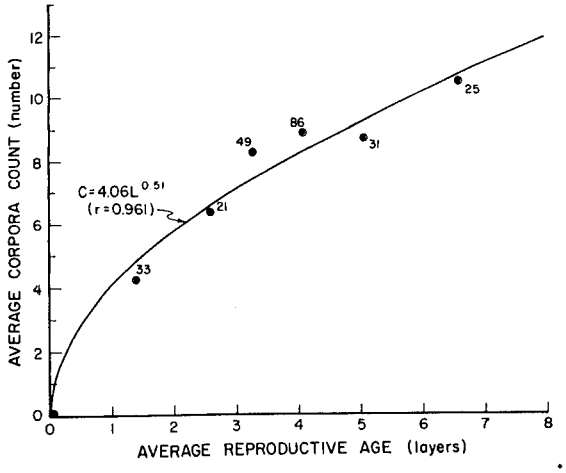

FIGURE 33.—Relationship between average number of corpora and average reproductive age (in layers) in *Stenella attenuata*.

Calving Interval

The pattern of reproduction definable with the methods used here consists of three phases: pregnancy, lactation, and a period of inactivity and/or estrus called here "resting/estrus." The length of pregnancy was estimated above as 11.5 ± 0.2 mo. We estimated length of lactation in three ways, based on 1) stomach contents of calves, 2) numbers of lactating females and calves, and 3) ratio between numbers of lactating and pregnant females.

The forestomachs of 45 calves less than 150 cm long were opened and examined by eye for presence of milk. Twenty-one were empty. The stomachs of four calves 120 to 130 cm long contained both milk and solid food (fish and/or squid). Stomachs of 8 smaller calves (80 to 115 cm) contained only milk, and 12 of the larger calves (130 to 150 cm) apparently contained only solid food. About 130 cm appears to be the length at which effective weaning occurs. The estimated time required to grow to 130 cm is 9.4 mo (based on growth curve above). This estimate is not very reliable for two reasons: the sample is small, and small amounts of milk could be present and undetectable by eye, i.e., suckling could continue at a low level after the effective shift to solid food. The estimate can, however, be considered to be a probable lower bound on length of lactation.

A second estimate is based on the assumptions that 1) a suckling calf exists for each lactating female and 2) the samples of specimens are unbiased with respect to suckling calves and lactating females. Given these assumptions, the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length at weaning. This length in eight variously sized, 1-mo "random" samples of calves and females ranged from 125 to 145 cm (Table 7). The aggregate estimate for the eight samples pooled (320 lactating females) is 137 cm. Average age at 137 cm is estimated at 1.94 tooth layers, or (assuming two layers accumulated during first year) 11.6 mo. If calves were overrepresented in the samples, this would be an underestimate. If they were underrepresented, it would be an overestimate. It would be an overestimate if the assumption that the number of lactating females equals the number of nursing calves were not valid. The assumption is not valid if the mortality of nursing calves is

TABLE 7.—Length at which cumulative frequency of calves equals the number of lactating females in eight 1-mo samples of *Stenella attenuata*.

Sample (mo)	Lactating females (no.)	Length (cm) at which cumulative frequency of calves = no lactating females
Oct. 1972	51	132
Jan. 1973	65	125
Feb. 1973	50	144
Mar. 1973	48	136
Apr. 1973	13	142
May 1973	32	142
June 1973	18	145
Nov. 1973 (Oct. 28-Dec. 11)	43	142
Total	320	137

higher than that of lactating females and lactation continues after death of a nursing calf.

A third estimate of length of lactation was derived from the ratio of lactating to pregnant females. This analysis included all the material from 1971 and 1972, when only adult females were sampled, as well as the material included in the calf-lactating female analysis above. Females both lactating and pregnant were included in both categories. The assumption is made that samples were unbiased with respect to relative representativeness for lactating and pregnant females. The ratio was 0.95 in the 1971 sample (86 adult females), 1.00 in 1972 (455), 0.96 in 1973 (573), and 0.97 for the pooled samples (n = 1,114; Table 8). The ratio of lactating to pregnant should equal the ratio of the lactation period to the gestation period. Gestation is 11.5 mo, therefore lactation is by this method estimated at 0.97 times 11.5 mo, or 11.2 mo. Estimated length at this age is 135.5 cm.

The three estimates of 9.6, 11.6, and 11.2 mo are based on largely independent assumptions and are close enough to each other to indicate that length of lactation is almost certainly between 9 and 12 mo. Of the three, the central estimate, 11.2 mo, is best in terms of sample size and probable validity of assumptions and is used below in estimating length of the calving interval.

The basic data used for estimating average length of calving interval were the relative frequencies of adult females in several reproductive conditions (Table 8). Adult females were defined as those with at least one corpus luteum or corpus albicans. Senile females were those with 10 or more corpora albicantia, no corpus luteum or Type 1 or 2 corpora albicantia and ovaries weighing less than 3.5 g. Resting/estrus females were those nonsenile adults that were neither pregnant nor lactating. Many of these (16 to 31%) had a corpus luteum. The corpus luteum may have represented an undetected very early pregnancy, a very recently aborted pregnancy, loss of a calf shortly after birth (resulting in cessation of lactation), or may have been a corpus luteum of ovulation. All of these alternatives may be represented in the samples.

In calculating the proportions of females in the three phases of pregnant, lactating, and resting (Table 9), senile females were excluded. One-half of the animals simultaneously pregnant and lactating were assigned to the pregnant category and one-half to the lactating category.

The average length of calving interval was estimated by two methods — 1) using the estimates of gestation and lactation periods and 2) using the percentage of females pregnant. The data for the 3 yr are comparable (Table 9), with the exception of possible existence of a trend in proportion resting; therefore, length of calving interval was estimated from the pooled data. Eighty-four and one-half percent of reproductive females were pregnant or lactating. Pregnancy (11.5 mo) plus lactation (11.2 mo) total 22.7 mo. If the proportion in a phase is equal to the proportion of the total

TABLE 8.—Reproductive condition of 1,114 adult female specimens of *Stenella attenuata*, collected 1973.[1]

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant only (P)	31	36.0	180	39.7	233	40.7	444	39.6
Lactating only (L)	29	33.7	180	39.7	223	38.9	432	38.8
Pregnant and lactating (PL)	13	15.1	16	3.5	17	3.0	46	4.1
Resting/estrus (R) $\left(\frac{A}{B}\right)$	11 $\left(\frac{3}{8}\right)$	12.8	64 $\left(\frac{10}{54}\right)$	14.1	94 $\left(\frac{29}{65}\right)$	16.4	169 $\left(\frac{42}{127}\right)$	15.2
Senile[2]	2	2.3	15	3.3	6	1.0	23	2.1
Total	86	100	455	100	573	100	1,114	100

[1]In the resting/estrus category, subcategories A and B (in parentheses) are specimens with and without a corpus luteum, respectively.
[2]≥10 corpora, no Type 1 or 2 corpora, and ovaries ≤3.5 g.

TABLE 9.—Proportions of 1,091 adult reproductive females of *Stenella attenuata* in pregnant, lactating, and resting/estrus phases.

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant (P + ½PL in Table 8)	37.5	44.6	188	42.8	241.5	42.6	467	42.8
Lactating (L + ½PL)	35.5	42.3	188	42.8	231.5	40.8	455	41.7
"Resting" (R)	11	13.1	64	14.4	94	16.6	169	15.5
Total reproductive females	84	100	440	100	567	100	1,091	100

calving interval spent in that phase, then total length of the interval cycle is 22.7 mo divided by 0.845, or 26.9 mo.

A second estimate was obtained directly from the proportion of females pregnant. In calculating this proportion, all pregnant animals were included (P + PL in Table 8): 490 of 1,091 reproductive females were pregnant, or 44.9%. Division by length of pregnancy, 0.958 yr (11.5 mo), yields an estimate of annual pregnancy rate, 0.469. The reciprocal of pregnancy rate, 2.133 yr, or 25.6 mo, is an estimate of average length of calving interval.

Both estimates of length of calving interval, 26.9 and 25.6 mo, are overestimates to the extent that the "resting" females with corpora lutea represented uncounted pregnancies, but the effect can be at most very minor. For example, if all these females represented undetected pregnancies or pregnancies aborted during capture, the unlikely extreme case, the estimates would be 25.7 and 24.7 mo respectively, an average difference of about 1 mo. Since the "resting" females with corpora lutea probably represent a mixture of causes and conditions, including nonfertile ovulations, the probable effect on the estimates is less than 1 mo. Considering this factor and the closeness of the two estimates to each other, it seems certain that the true length of the interval is between 24 and 27 mo. The lower of the two estimates, which is based on fewer assumptions and calculations, was rounded off to 26 mo and is used below in further analysis of life history. The average pattern of events then, consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus.

Overlapping Lactation and Pregnancy

About 9.6% of lactating females were also pregnant (Table 8). Most had fetuses less than 35 to 40 cm long (Figure 26), about halfway through the gestation period. This suggests that overlap when it occurs is usually about 5 to 6 mo long, i.e., conception occurs about halfway through the lactation period of about 11 mo, making the calving interval about 20 mo long instead of 26. The very few lactating females with near-term fetuses may have conceived during postpartum estrus or may have begun to lactate shortly before parturition.

The data on Graafian follicles are consistent with the theory that postpartum estrus occurs during lactation (Figure 34). The largest follicle in the ovaries of resting/estrus females (including those presumably about to ovulate) is on the average 3 to 4 mm in diameter. After ovulation and conception, the remaining large follicles regress rapidly to about 2 mm (or become lutealized or atretic). There is a further net decline during gestation to about 1.5 mm, and during lactation the main modal diameter is about 1.0 mm. During both pregnancy and lactation, however, about 10% of the females (excluding senile individuals, as defined above) have follicles that are within the size range (≥3.0 mm) of the presumably ripe follicles present during the resting/estrus phase. This is most clear-cut during lactation. Most of the larger follicles during pregnancy occur in females having fetuses 400 to 500 mm long, or about halfway through the gestation period (Figure 34).

Decrease in Reproductive Rate with Age

Reproductive rate decreases with age. Age-specific estimates of pregnancy rates and lactation rate were calculated from a random sample of the data for specimens for which teeth were sectioned (stratified to insure representation of corpora-number strata in about the proportions as in the entire sample). The analysis shows decline of pregnancy rate from about 0.6 at 8 to 9 layers to about 0.3 at 16 to 17 layers (Figure 35). The weighted rate for the pooled sample of 138 used in the calculation was 0.51, comparable to the rate of 0.47 obtained for 1,091 animals (above). The specimens for which teeth were sectioned were about one-third from 1971 and two-thirds from 1972, with a few specimens from earlier years. Lactation rate

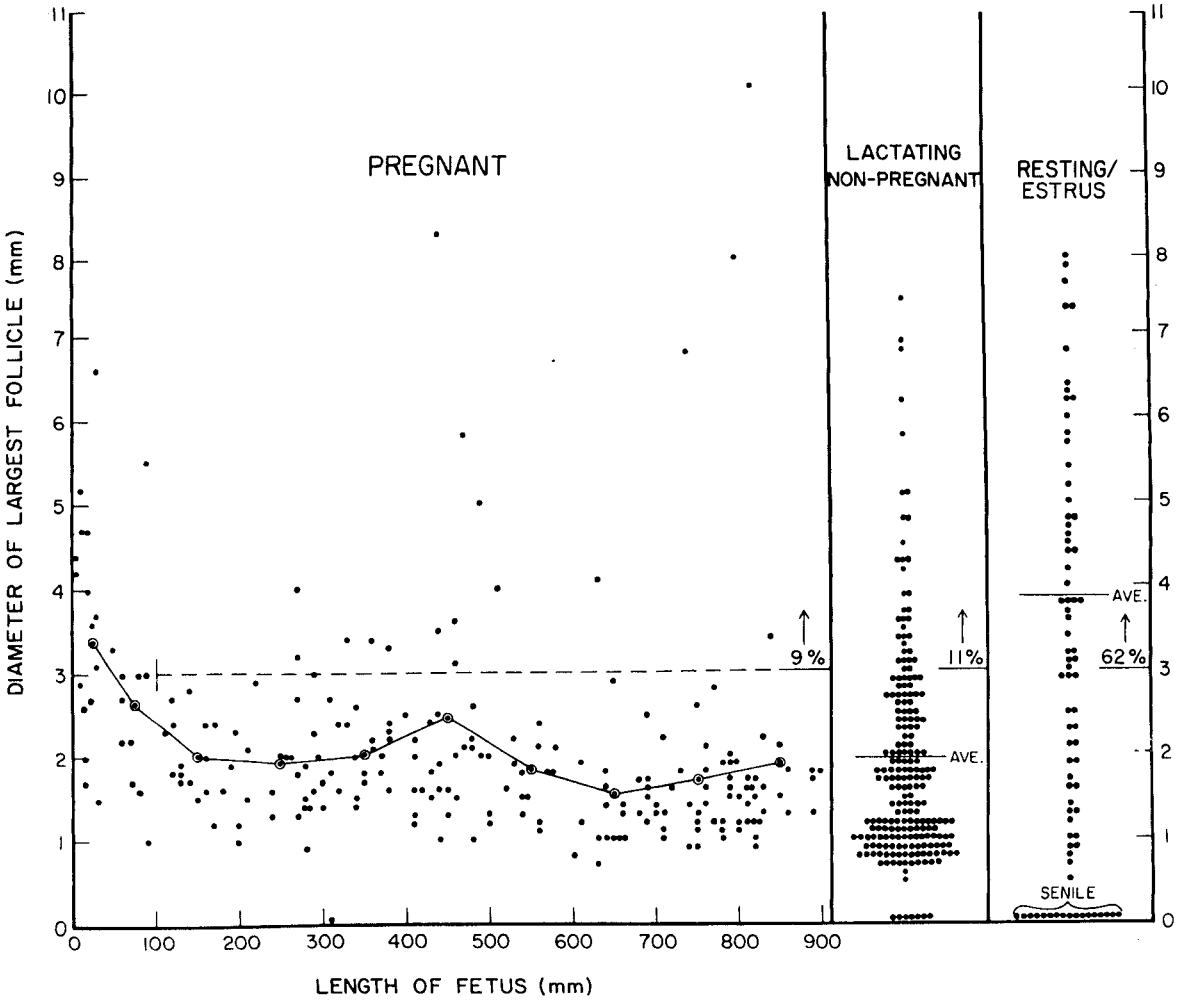

FIGURE 34.—Diameter of largest follicle in pregnant, lactating, and resting females of *Stenella attenuata*.

(Figure 35) increases from about 0.1 at 8 layers to about 0.6 at 12 layers and then again decreases to about 0.5.

The initial very low lactation rate compared to pregnancy rate, of course, reflects the fact that a very high percentage of the young females are pregnant for the first time and thus cannot be lactating. The lactation rate climbs rapidly to a level about equal to the pregnancy rate (at about 12 layers) and behaves like the pregnancy rate thereafter. The apparent decline of reproductive rates in older females may be related to the physiological or social mechanisms that cause the appearance of postreproductive females in this age group (see above; not included here).

Sex Ratios

The overall sex ratio was 44.9% males and 55.1% females (Figure 36). Many large samples examined were predominantly female. Fourteen of 32 single-school samples of 50 or more specimens were more than 60% female, whereas none was more than 60% male. The largest single-school sample examined (342) was almost half and half males and females.

Sex ratio changes with age (Table 10). This is, of course, making the assumption that the samples examined were representative of the population. Neonates and two-tone animals were almost equally divided between the sexes, but only about

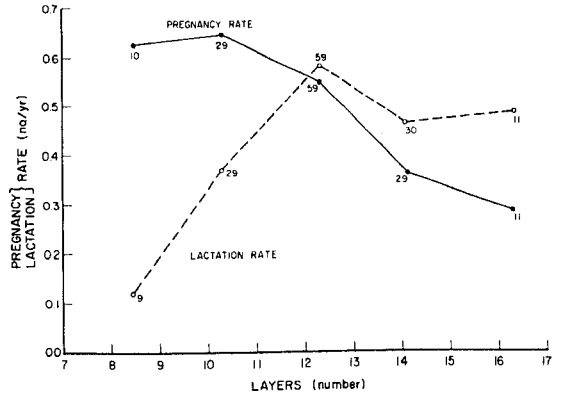

FIGURE 35.—Age-related changes in pregnancy (solid line) and lactation rates (dashed line) in *Stenella attenuata*, based on tooth layer data. Postreproductive females not included.

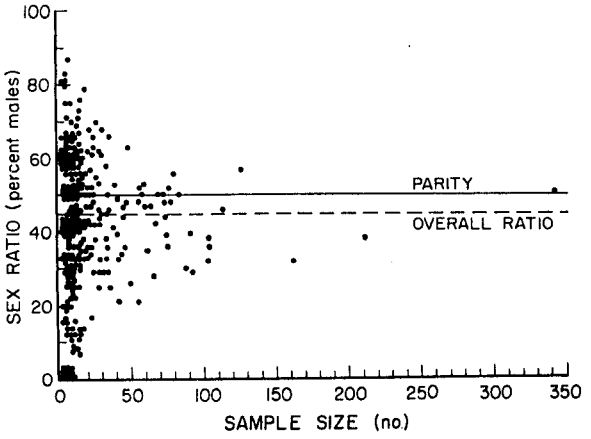

FIGURE 36.—Scatterplot of sex ratio (percent males) on sample size in single-school samples of five or more specimens of *Stenella attenuata*. Overall ratio (dashed line) from Table 12.

TABLE 10.—Sex ratio, by color pattern stage, in 9,371 specimens of *Stenella attenuata*, 1971-73.

Color pattern stage	Males		Females		Total
	No.	%	No.	%	
Neonate	205	49.8	207	50.2	412
Two-tone	666	48.7	701	51.3	1,367
Speckled	609	47.8	666	52.2	1,275
Mottled	569	43.8	729	56.2	1,298
Fused	2,154	42.9	2,865	57.1	5,019
Total	4,203	44.9	5,168	55.1	9,371

43% of the adults examined were males. The greatest change in ratio, from 48.0 to 43.5% male, comes about during the transition to mottled coloration between 7 and 8 layers of age. Assuming random sampling of the population, male and female mortality rates must diverge sharply at this point.

Gross Annual Production

An estimate of average gross annual production of calves for 1971 to 1973 was calculated based on the estimate of annual pregnancy rate, the color pattern phase data, and the proportions of mottled and fused females found to be sexually mature (Table 11).

Seven hundred and twenty-nine of 9,371 animals were mottled females (7.8%) and 2,865 were fused females (30.6%). Of 127 mottled and 1,141 fused females, 47.4 and 88.4% were sexually mature, respectively (Table 11). Average pregnancy rate was 0.469. Production = $[(0.078 \times 0.474) + (0.306 \times 0.884)]\,0.469 = 0.144$ of the population per year.

TABLE 11.—Sexual maturity (presence of ovarian corpora) in mottled and fused females of *Stenella attenuata*, 1971-73.

Year	Mottled			Fused		
	N	Mature No.	Mature %	*N*	Mature No.	Mature %
1971	6	5	(—)	99	82	(82.8)
1972	92	37	(40.2)	473	417	(88.2)
1973	170	85	(50.0)	569	510	(89.6)
Total	268	127	(47.4)	1,141	1,009	(88.4)

Schooling in Relation to Reproduction

Kasuya (1972) reported changes in structure and size of schools of *S. coeruleoalba* correlated with breeding condition and breeding activities. Kasuya et al. (1974) proposed a complex hypothetical system of school formation and breakdown determined by reproductive activities in the Japanese population of *S. attenuata*. They suggested that juveniles of *S. attenuata* in Japanese waters leave breeding schools and school separately, rejoining the breeding schools at puberty. There is nothing to indicate that this happens in the eastern Pacific. We examined the coloration structure (= age structure) of single-school samples. Of 324 single-school samples of seven or more animals, only 1 (of 17 animals) contained no adults (or neonatal calves, which would indicate presence of adult lactating females in the school). This sample (8 two-tone, 2 speckled, and 7 mottled) was from a school of about 600 spotted porpoise, *S. attenuata*, congregated with about 600 spinner porpoise, *S. longirostris*. Given that about half the animals examined were adults, the probability of

a single-school sample of seven containing no "fused" individuals is about 0.01 (= 0.5^7). If schools consisting only of juveniles were common, many more all-juvenile samples would have been encountered. Conversely, juveniles (two-tone, speckled, and/or mottled) occurred in all but 3 of the 324 samples. It must be concluded that juveniles probably do not school separately in the eastern Pacific. Another possibility, albeit unlikely, is that all-juvenile schools exist but are not captured by tuna seiners.

COMPARISON WITH THE JAPANESE POPULATION

Many of the estimates of life history parameters presented here differ from those published by Kasuya et al. (1974) for the relatively unexploited population of *S. attenuata* in Japanese waters (Table 12). The differences could be caused by 1) differential procedures or analytical methods, 2) intrinsic racial differences between the populations, or 3) differential population status, e.g., exploited versus unexploited. The comparisons below of similarly calculated average estimates, of course, rest on the assumption that the overall samples in both cases were not biased with respect to age or sex. The major sampling differences between the two studies is that the Japanese sample consisted mostly of large samples from a few schools, whereas our sample consisted mainly of aggregated, small samples from many schools. Both studies assume no sampling bias. Comparison of large, single-month samples in the present study with large, single-school samples in the Japanese study (e.g., the October 1972 sample in Figures 15 and 16 with sample number 2 in Figure 2 of Kasuya et al. 1974) indicate very similar length-frequency distributions and support the idea that the aggregated samples are probably not biased, or, if biased, are biased in the same way. This inference is, of course, based on the assumption that the underlying population structures are about the same in the two populations.

The estimate of Kasuya et al. (1974) of length at birth was based on only 5 full-term fetuses and newborn calves versus 86 in the present study. Our estimate can, therefore, be considered more reliable, although the possibility does exist that length at birth is greater in the Japanese population. The difference between the estimated lengths at 1 yr for the two populations is about the same as the difference between the estimates of length at birth. Estimated length at attainment of sexual maturity and maximum length (for males) are also greater for the Japanese samples. The estimate of length at maturity of males is greater in spite of the fact that Kasuya et al. used a lower testis-weight criterion than we did (68 versus 100 g). The average lengths of both adult males and

TABLE 12.—Comparison of estimates of average life history parameters of *Stenella attenuata* by Kasuya et al. (1974) and in present paper.

Parameter (average)	Kasuya et al.	Perrin et al.
1. Length at birth	89 cm	82.5 cm
2. Growth rate in 1st year	4.5 cm per mo	4.6 cm per mo
3. Length at 1 yr	143 cm	138 cm
4. Length at onset of sexual maturity:		
Males	197 cm	~195 cm
Females	187 cm	181 ± 1 cm
5. Age at onset of sexual maturity:		
Males	10.3 layers (10.3 yr)	12 layers (6-11 yr)
Females	8.2 layers (8.2 yr)	9 layers (4.5-8 yr)
6. Average length of sexually mature adults:		
Males	204-207 cm	200.7 cm
Females	192-195 cm	187.3 cm
7. Maximum length:		
Males	234 cm	226 cm
Females	220 cm	220 cm
8. Maximum number of consistently readable tooth layers	~13	12-13
9. Average ovulation rate (based on layers)	0.8 per layer (0.8 per yr)	~1 per layer (1 or 2 per yr) in fully mature, more in younger
10. Pregnancy rate (overall)	0.27 per yr	0.47 per yr
11. Breeding seasons	3 per yr	multiple
12. Gestation	11.2 mo	11.5 ± 0.2 mo
13. Lactation	29.3 mo	11.2 mo
14. Resting	9.8 mo	3.3 mo
15. Length of calving interval	4.19 yr	2.17 yr
16. Sex ratio:		
Overall	0.76 male:1 female	0.81 male:1 female
At birth	1.3-1.5:1	1.00:1
Adults	0.58:1	0.75:1

females are also greater in the Japanese population, and in this case, all four of the estimates are based on large and certainly adequate samples. These differences all suggest that the Japanese form is about 6 to 8 cm larger than the eastern Pacific form.

The estimates of Kasuya et al. (1974) of age at attainment of sexual maturity are based on their conclusion that one tooth layer corresponds to 1 yr of growth. It appears from comparisons of their first-year growth curve with ours (note rate in first year and length at 1 yr) that our first two layers correspond to their first layer. Kasuya (1972) in his paper on growth of *S. coeruleoalba* mentioned observing "one or two faint translucent layers in the thick opaque layer accumulated just after the birth" that were "not used for age determination because it was not expected to show the annual accumulation cycle," and Kasuya et al. (1974) stated that the "dentinal growth layers of this species [*S. attenuata*] does not differ so much from that of *S. coeruleoalba*." After the first year, our hypothesis 2 corresponds to the assumption of Kasuya et al. of one layer per year, e.g., nine layers of Perrin et al. (1973) = eight layers of Kasuya et al. = 8 yr.

The average length of calving interval in both studies was estimated by several methods that converged on the respective central estimates. One minor difference between the two analyses is that Kasuya et al. (1974) did not exclude postreproductive females from the "resting/estrus" group. Thus, their estimate of the average resting/estrus period of 9.8 mo may be a slight overestimate. The probable effect of this on the estimate of length of total calving interval is very small, however, and it therefore seems that the estimates are analytically comparable and that the difference between them is real. Kasuya et al. estimated that individual intervals in the Japanese population vary from 23 to 60 mo, with modes at 28 to 30, 36 to 38, and 54 to 56 mo. The potential thus probably exists for a shift in average length from 50 mo (4.17 yr) to 26 mo (2.17 yr) under exploitation.

Kasuya et al. (1974) used the same methods used here to estimate length of the lactation period and arrived at a "best" estimate of 29.3 mo, some 18 mo longer than our estimate of 11.2 mo. They found that the major shift from milk to solid food occurs at body length of about 133 cm, about the same as in our sample, but that some suckling and lactation of the mother continues for an average additional 20 mo. The prolonged suckling is probably nutritionally a largely nonfunctional aspect of general prolonged parental care. It has been suggested on the basis of comparison of the life histories and behavior of mysticetes and odontocetes that this period in odontocetes may allow for "sophisticated" communicational-navigational training (Brodie 1969). Thus the apparent shorter lactation period in the eastern Pacific, and the concomitant shorter calving interval and higher pregnancy rate, does not necessarily mean earlier effective weaning, but may reflect a truncated parental care period.

The apparent overall sex ratios are almost the same for the two populations, but the proportion of males was higher at birth and lower at maturity in the Japanese samples than in the eastern Pacific samples. A lower proportion of males at birth could be a response to exploitation. Kasuya et al. (1974) suggested that the very low proportions of males in mature age-classes in the Japanese catches could be partially caused by segregation of adult males or by differential catchability but are largely due to differential mortality rates. If the decrease in proportion of males with age is caused by differential mortality, the apparent faster decrease in the Japanese population must mean that the disparity in mortality rates between the sexes is greater there than in the eastern Pacific.

In summary, the two sets of estimates differ in a consistent way, and the differences are real. It seems possible that the differences in some way reflect exploitation in the eastern Pacific.

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LITERATURE CITED

AMOROSO, E. C., AND C. A. FINN.
1962. Ovarian activity during gestation, ovum transport and implantation. *In* S. Zuckerman (editor), The ovary. Vol. 1, p. 451-537. Academic Press, N.Y.

BEST, P. B.
1968. The sperm whale (*Physeter catodon*) off the west coast of South Africa. 2. Reproduction in the female. S. Afr. Div. Sea Fish., Invest. Rep. 66, 32 p.
1969. The sperm whale (*Physeter catodon*) off the west coast of South Africa. 3. Reproduction in the male. S. Afr. Div. Sea Fish., Invest. Rep. 72, 20 p.
1970. The sperm whale (*Physeter catodon*) off the west coast of South Africa. 5. Age, growth and mortality. S. Afr. Div. Sea Fish., Invest. Rep. 79, 27 p.

BRODIE, P. F.
1969. Duration of lactation in Cetacea: An indicator of required learning? Am. Midl. Nat. 82:312-314.
1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. J. Fish. Res. Board Can. 28:1309-1318.
1972. Significance of accessory corpora lutea in odontocetes with reference to *Delphinapterus leucas*. J. Mammal. 53:614-616.

BRUNN, A.
1935. Flying-fishes (*Exocoetidae*) of the Atlantic. Systematic and biological studies. Dana Rep. 2(6), 106 p.

CLARKE, M. R.
1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. 4:91-300.

DAILEY, M. D., AND W. F. PERRIN.
1973. Helminth parasites of porpoises of the genus *Stenella* in the eastern tropical Pacific, with descriptions of two new species: *Mastigonema stenellae* gen. et sp. n. (Nematoda: Spiruroidea) and *Zalophotrema pacificum* sp. n. (Trematoda: Digenea). Fish. Bull., U.S. 71:455-471.

FISHER, H. D., AND R. J. HARRISON.
1970. Reproduction in the common porpose (*Phocoena phocoena*) of the North Atlantic. J. Zool. (Lond.) 161:471-486.

HARRISON, R. J., R. L. BROWNELL, JR., AND R. C. BOICE.
1972. Reproduction and gonadal appearances in some odontocetes. *In* R. J. Harrison (editor), Functional anatomy of marine mammals. Vol. 1, p. 361-429. Academic Press, N.Y.

HASSELBLAD, V.
1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.

HUGGETT, A. ST. G., AND W. F. WIDDAS.
1951. The relationship between mammalian foetal weight and conception age. J. Physiol. 114:306-317.

KASUYA, T.
1972. Growth and reproduction of *Stennella caeruleoalba* based on the age determination by means of dentinal growth layers. Sci. Rep. Whales Res. Inst. (Tokyo) 24:57-79.

KASUYA, T., N. MIYAZAKI, AND W. H. DAWBIN.
1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. (Tokyo) 26:157-226.

KLEVEZAL', G. A., AND S. E. KLEINENBERG.
1969. Age determination of mammals from annual layers in teeth and bones. Izdatel'stvo "Nauka," Mosc., 1967. (Translated by Israel Program Sci. Transl., Jerus., 128 p.)

KNAUSS, J. A.
1963. Equatorial current systems. *In* M. N. Hill (editor), The sea. Vol. 2, p. 235-252. Interscience Publ., N.Y.

LAIRD, A. K.
1969. The dynamics of growth. Res./Dev. 20(8):28-31.

LAWS, R. M.
1959. The foetal growth rates of whales with special reference to the fin whale, *Balaenoptera physalus* Linn. Discovery Rep. 29:281-307.

MØHL-HANSEN, U.
1954. Investigations on reproduction and growth of the porpoise (*Phocaena phocaena* (L.)) from the Baltic. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 116:369-396.

MOSER, H. G., AND E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.

NISHIWAKI, M., M. NAKAJIMA, AND T. KAMIYA.
1965. A rare species of dolphin (*Stenella attenuata*) from Arari, Japan. Sci. Rep. Whales Res. Inst. (Tokyo) 19:53-64.

PERRIN, W. F.
1969. Using porpoise to catch tuna. World Fishing 18(6): 42-45.
1970a. The problem of porpoise mortality in the U.S. tropical tuna fishery. Proc. 6th Annu. Conf. Biol. Sonar Diving Mammals, Stanford Res. Inst., Menlo Park, Calif., p. 45-48.
1970b. Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* Lönnberg (Cetacea, Delphinidae). Zoologica (N.Y.) 54:135-149.
1975. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. J. Fish. Res. Board Can. 32:1059-1067.
In press. Variation of spotted and spinner porpoises (genus *Stenella*) of the eastern tropical Pacific and Hawaii. Bull. Scripps Inst. Oceanogr., Univ. Calif.

PERRIN, W. F., AND E. L. ROBERTS.
1972. Organ weights of non-captive porpoise (*Stenella* spp.). Bull. South. Calif. Acad. Sci. 71:19-32.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares,* in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

RICHARDS, W. J., AND W. L. KLAWE.
1972. Indexed bibliography of the eggs and young of tunas and other scombrids (Pisces, Scombridae), 1880-1970. U.S. Dep. Commer., NOAA Tech. Rep., NMFS SSRF-652, 107 p.

SECKEL, G. R.
1972. Hawaiian-caught skipjack tuna and their physical environment. Fish. Bull., U.S. 70:763-787.

SERGEANT, D. E.
1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Fish. Res. Board Can. Bull. 132, 84 p.
1973. Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. J. Fish. Res. Board Can. 30:1065-1090.

SERGEANT, D. E., D. K. CALDWELL, AND M. C. CALDWELL.
1973. Age, growth, and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. J. Fish. Res. Board Can. 30:1009-1011.

TRUE, F. W.
1906. Notes on a porpoise of the genus *Prodelphinus* from the Hawaiian Islands. Bull. U.S. Fish Comm. 23:811-815.

WYRTKI, K.
1964. The thermal structure of the eastern Pacific Ocean. Ergänzungsh. Dtsch. Hydrogr. Z. Reihe A 8(6), 84 p.

YOUNG, R. E.
1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithson. Contrib. Zool. 97, 159 p.

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GROWTH OF LABORATORY-REARED NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, FROM SOUTHERN CALIFORNIA

GARY T. SAKAGAWA AND MAKOTO KIMURA[1]

ABSTRACT

The northern anchovy, *Engraulis mordax*, was experimentally reared in the laboratory at the Southwest Fisheries Center, La Jolla, Calif. Data from three experiments were used to empirically fit a two-phase Gompertz growth model. The model describes growth from hatching to about 20 mo of age. It was estimated that the average length of laboratory-reared anchovies is 102 mm at 1 yr old and 119 mm at 2 yr old. Growth of laboratory-reared anchovies was comparable to that of anchovies in the wild.

Attempts to rear the northern anchovy, *Engraulis mordax*, at the Southwest Fisheries Center (SWFC), La Jolla, Calif., were begun in 1966 when G. O. Schumann collected anchovy larvae in the ocean off La Jolla and successfully reared them using wild plankton as food in the laboratory (Bardach 1968). Schumann's success was followed by other laboratory experiments in which anchovies were reared from eggs, larvae, and juveniles that were caught in the ocean (Table 1). In 1970, Leong (1971) developed a method for artificially inducing anchovies to spawn by controlling the photoperiod and injecting hormones. This technique is currently used at the SWFC to produce eggs and to rear anchovies for experimental purposes.

One of the purposes of the rearing experiments at the SWFC has been to obtain physiological and biochemical information needed for describing the energy budget of the northern anchovy, and to relate the results to the feeding dynamics of the anchovy population in the California Current, which consists of primarily young fish less than 3 yr old. Growth data are needed for analysis of the budget, and various attempts have been made to measure growth in the laboratory. Kramer and Zweifel (1970) and Lasker et al. (1970) reported growth rates of anchovy larvae. In this report we extend their analyses to include growth from hatching to about 20 mo old. We also present a mathematical model that describes this growth and compare our results with those of other investigators.

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SOURCES OF DATA

Data primarily from experiments of G. O. Schumann (Schumann-I; Schumann-II), G. O. Schumann and A. Saraspe (Schumann-III), and R. Leong (pers. commun., SWFC) were used in our study (Table 1).

Schumann-II successfully reared larval anchovies for 22 days at about 22°C water temperature, which is higher than the temperature (15° to 16°C) at which anchovy larvae are frequently found in large numbers in the California Current (pers. commun., P. Smith, SWFC). The larvae were fed wild plankton and samples were taken for length measurement approximately daily.

Schumann-III reared anchovies from the egg stage through the juvenile stage in aquaria for 83 days on a diet of wild plankton, *Artemia salina*, and commercial trout food. The experiment was conducted from March to June and the water temperatures in the aquaria were not recorded. However, during March to June the average water temperature in rearing aquaria at the SWFC is generally about 18° to 22°C.

Leong (pers. commun.) obtained juvenile anchovies from a live-bait dealer and reared the fish to maturity in a 4.6-m diameter pool (13.2 kl) with circulating seawater. The water temperature in the pool was a few degrees higher than the prevailing water temperature off Scripps Pier, La Jolla, site of the water intake for the experimental pool (Lasker and Vlymen 1969). Leong fed the fish a diet of *Artemia salina*, ground squid and anchovies, and commercial trout food. Once a month about 25 fish were sacrificed for length and weight measurements.

TABLE 1. — Laboratory experiments of rearing the northern anchovy at the Southwest Fisheries Center, La Jolla, Calif.

Source	Life stage at start	Start of rearing	Rearing duration (days)	Average length (mm)		Food
				Start	Finish	
Hunter (1976)	Eggs	April	74	4.0	35.0	*Gymnodinium splendens, Brachionus plicatilis, Tisbe furcata,* and *Artemia salina*
Kramer and Zweifel (1970)	Eggs	August and September	35	3.2	17.4	Wild plankton and *A. salina*
Lasker et al. (1970)	Eggs	February	50	3.4	21.0	*Bulla gouldiana, G. splendens,* and *A. salina*
Leong (unpubl. data)[1]	Juveniles	April	474	88.3	117.7	Squid, anchovy, *A. salina,* and trout food
Paloma (see text footnote 3)	Juveniles	November	624	75.0	106.2	*Artemia salina* and trout food
Schumann-I (G. O. Schumann unpubl. data)[2]	Larvae	March	97	18.0	81.9	Wild plankton
Schumann-II (Kramer and Zweifel 1970)	Eggs	March	22	2.9	16.2	Wild plankton
Schumann-III (G. O. Schumann and A. Saraspe unpubl. data)[2]	Eggs	March	83	3.5	67.1	Wild plankton, *A. salina,* and trout food
Theilacker and McMaster (1971)	Eggs	—	19	—	12.0	*Gymnodinium splendens, B. plicatilis,* and *A. salina*

[1]Pers. commun., Southwest Fisheries Center, La Jolla, Calif.
[2]Data are on file at the Southwest Fisheries Center, La Jolla, Calif.

In all of these experiments the fish were from the southern California stock (Vrooman and Smith 1971), reared at laboratory ambient water temperature, and not subjected to experimental treatment or excessive handling. All fish sampled for measurements were sacrificed. The length measurement is standard length.

TREATMENT OF DATA

The age of anchovies reared by Schumann-II and Schumann-III were known because the anchovies were hatched from eggs at the start of the rearing experiments. In Leong's (pers. commun.) experiment, the exact age of his fish was not known because juvenile fish of average length of 88.3 mm were used at the start of the experiment. We estimated the age of Leong's fish from data from Schumann-I in which anchovies were reared for 97 days from an average length of 18.0 to 81.9 mm (Table 1), and data from Schumann-III which indicated that an 18.0 mm fish, raised from eggs, was about 30 days old. Our age estimate is 4 mo.

Several mathematical models describing growth of organisms are available (e.g., Parker and Larkin 1959; Richards 1959; Laird 1969). The commonly used models in fisheries are the exponential, the von Bertalanffy, and the Gompertz models (Beverton and Holt 1957; Silliman 1969). The Gompertz model was selected for our study because it was shown by Kramer and Zweifel (1970) to be better than the exponential model for describing growth of laboratory-reared anchovy larvae and because it generally describes the growth of fishes fairly well. Also, preliminary analysis of our data indicated that the von Bertalanffy model poorly described the growth of young fish.

The Laird version of the Gompertz growth model (Laird 1969) describes an asymmetric sigmoid curve of the form.

$$L_t = L_0 \exp \{C \left[1 - \exp (-at)\right]\}$$

where L_0 = length at zero age or hatching
C = a constant
a = rate of decay of exponential growth
t = age in months.

This model was fitted to our data using an iterative least squares procedure (Conway et al. 1970). Our goal was to describe growth on a coarse time scale, i.e., monthly rather than on a fine time scale, i.e., daily.

GROWTH FROM HATCHING TO JUVENILE STAGE

The Gompertz growth model and an exponential growth model were applied to data of Schumann-II by Kramer and Zweifel (1970). Both models described the data from Schumann-II reasonably well, although the Gompertz model de-

scribed the data better. In the Kramer-Zweifel analysis the length at zero age, L_0, was fixed at 2.5 mm, the average size at hatching. We also applied the Gompertz growth model to data of Schumann-II. Kramer and Zweifel (1970) used data only for 17 days of growth. We used all of the data of Schumann-II, which included sampling through 22 days of growth, and fitted the model first with L_0 fixed at 2.5 mm and again without this constraint, i.e., L_0 was estimated. The results (Figure 1) indicate that there is not much difference in the curves with L_0 fixed or estimated within the range of the data. Outside the range of the data, the curves diverge considerably and there is a substantial difference; the curve with L_0 estimated has a lower asymptotic length (61 mm) than the curve with L_0 fixed at 2.5 mm (asymptotic length of about 696 mm).

Zweifel and Lasker[2] showed that a two-phase Gompertz curve described the data from Schumann-II better than a single-phase Gompertz curve. The separation of the phases occurred at about 6 days of age, the onset of feeding in anchovy larvae.

Schumann-III reared anchovies for a longer period than Schumann-II. Fish reared by Schumann-II, however, were larger than those reared by Schumann-III at similar ages. For example, at 0.5 mo of age fish reared by Schumann-II averaged 12.1 mm long and fish reared by Schumann-III, 8.2 mm long. Although the sample size is small, this difference is statistically significant at the 1% probability level. Differences in rearing procedures, i.e., diet and temperature of water, probably produced the difference in growth (Kramer and Zweifel 1970; Lasker et al. 1970).

The Gompertz growth model was applied to data from Schumann-III first with L_0 fixed at 2.5 mm and then with L_0 estimated (Figure 2). As in the case with data from Schumann-II, this model describes the growth data reasonably well, and the curve with L_0 estimated has a lower asymptotic length (81 mm) than the curve with L_0 fixed (asymptotic length of about 93 mm).

GROWTH DURING JUVENILE TO ADULT STAGE

Anchovies reared by Leong (pers. commun.) were juveniles at the start of the experiment and grew to an average size of 117.7 mm in 474 days (Table 2). Growth was in steplike stages characterized by rapid growth followed by a leveling off. The first stage was between 4 and 12 mo of age and the second was between 12 and about 20 mo of age.

[2]Zweifel, J. R. and R. Lasker. 1974. Prenatal and postnatal growth of fishes — a general model. Unpubl. manuscr. Southwest Fisheries Center, La Jolla, CA 92038.

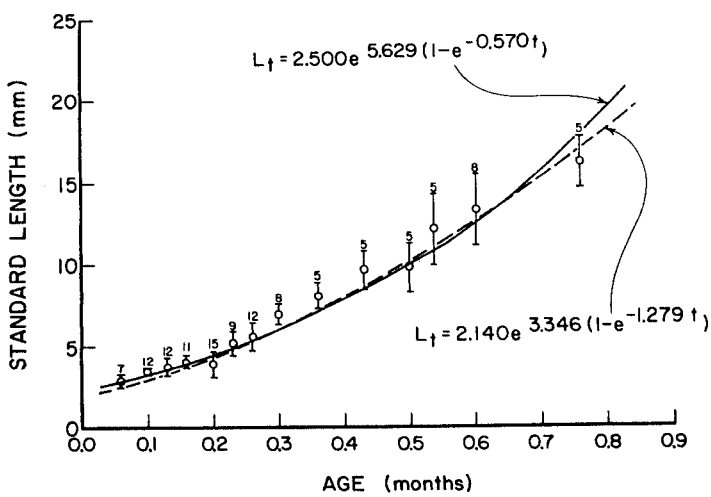

FIGURE 1.—Growth of anchovy larvae reared in the laboratory. The Gompertz growth model of the form, $L_t = L_0 \exp\{C[1 - \exp(-at)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm and broken line is based on L_0 estimated, 2.140 mm. Data from Schumann-II (Kramer and Zweifel 1970). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

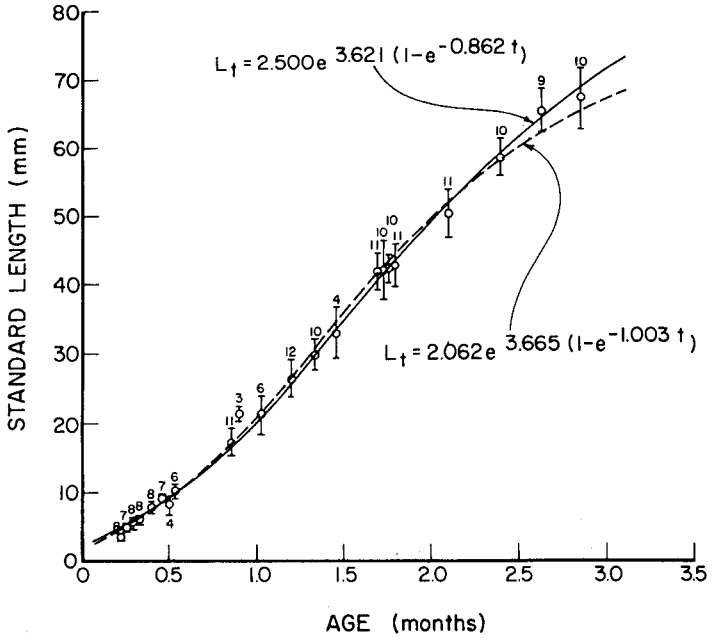

FIGURE 2.—Growth of anchovy reared in the laboratory. The Gompertz growth model of the form $L_t = L_0 \exp\{C[1 - \exp(-at)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm, and broken line is based on L_0 estimated, 2.062 mm. Data from Schumann-III (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

TABLE 2.—Estimated age and average standard length of northern anchovies reared in the laboratory by R. Leong (pers. commun., Southwest Fisheries Center, La Jolla, Calif.)

Age		Number of fish	Average length (mm)	Standard deviation
Days	Months			
120	4.00	10	88.30	6.34
153	5.10	23	92.35	4.90
189	6.30	24	94.63	5.85
231	7.70	25	97.68	6.40
270	9.00	25	96.48	6.19
301	10.03	23	99.30	5.14
351	11.70	25	101.52	4.59
385	12.83	25	105.72	5.26
413	13.77	25	109.16	5.75
444	14.80	26	109.23	6.07
471	15.70	26	110.58	6.82
503	16.77	25	114.56	6.57
533	17.77	24	117.38	6.11
562	18,73	25	116.32	7.07
594	19.80	25	117.68	6.69

The Gompertz growth model was applied, but did not adequately fit the data. This is characteristic of asymptotic models like the Gompertz model when all the data points are for a segment of the growth curve where growth is relatively slow and the plot of the data exhibits little curvature.

GROWTH FROM HATCHING TO ADULT STAGE

Growth Curve

As indicated earlier, anchovies reared by Shumann-III grew slightly faster than those of Schumann-II, probably due to slight differences in the rearing environment and procedures. Because our goal was to construct a general growth curve and the differences in the data were relatively slight, we elected to disregard the difference and pooled the data from the three experiments (Schumann-II, Schumann-III, and Leong). The Gompertz growth model was applied to the pooled data. The results (Figure 3) indicate that the model does not adequately describe the data. For example, the model overestimates the sizes of fish at about 4 to 12 mo old and underestimates the sizes of fish older than about 13 mo. These biases are caused by the steplike growth pattern which produces plateaus at about 6 mo and 19 mo of age.

To account for this steplike growth pattern, a

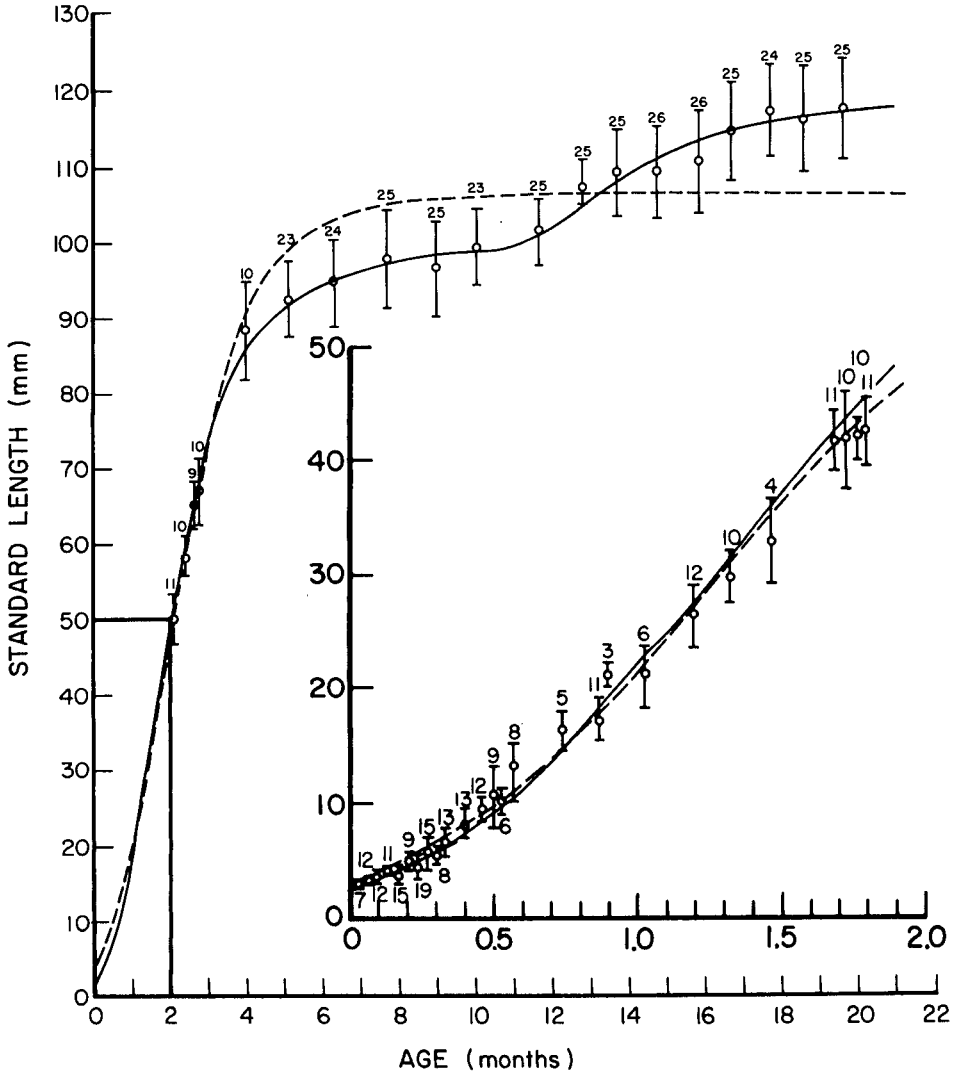

FIGURE 3.—Growth of northern anchovy reared in the laboratory. One-phase (broken line) and two-phase (solid line) Gompertz growth models are used to describe the data. Data from Schumann-II (Kramer and Zweifel 1970), Schumann-III, and Leong (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown. Broken line is described by $L_t = 2.825 \exp\{3.623[1 - \exp(-2.877t)]\}$ and solid line by $L_t = 2.745 \exp\{3.563[1 - \exp(-0.848t)]\}$ for $t \leq 11$ mo, and $L_{(t-11)} = 96.782 \exp\{0.213[1 - \exp(-0.258\{t - 11\})]\}$ for $t > 11$ mo.

two-phase Gompertz model (Zweifel and Lasker see footnote 2) was fitted to the data. The two-phase model is essentially two separate Gompertz equations that describe different segments of the growth curve. The equations were fitted simultaneously and the convergence point of the equations was determined on the basis of least squares analysis. Our best fit of the data was with the equation, $L_t = 2.745 \exp\{3.563[1 - \exp(-0.848t)]\}$ for growth from hatching to 11 mo of age and the equation, $L_{(t-11)} = 96.782 \exp\{0.213[1 - \exp(-0.258\{t - 11\})]\}$ for growth from 11 to 20 mo of age (Figure 3). From the equations, the estimated average length of anchovies after 1 yr of life is 101.6 mm and after 2 yr of life, 118.9 mm (Table 3).

TABLE 3.—Estimated growth for the first 24 mo of life of the northern anchovy reared in the laboratory. Estimates are based on a two-phase Gompertz growth curve (see text).

Age (mo)	Standard length (mm)	Age (mo)	Standard length (mm)
hatching	2.7	13	105.5
1	21.0	14	108.6
2	50.4	15	111.0
3	73.2	16	112.9
4	85.9	17	114.5
5	92.0	18	115.6
6	94.7	19	116.6
7	95.9	20	117.3
8	96.4	21	117.8
9	96.6	22	118.3
10	96.7	23	118.6
11	96.8	24	118.9
12	101.6		

General Remarks

The steplike growth pattern is commonly found in fishes. Gerking (1967) reviewed the literature on this subject and noted that many temperate species have seasonal, sigmoid growth curves. Lockwood (1974) recognized this feature in the growth of plaice and brown trout and applied a multiphase von Bertalanffy growth model to describe the data mathematically. His results were satisfactory but because the von Bertalanffy growth equation does not describe a sigmoid curve, his analysis was confined to growth for part of the season only.

In this study we used the Gompertz growth equation to describe the sigmoid curve. The two-phase model satisfactorily described our data for laboratory-reared anchovy, and a cycle that occurs at 12-mo intervals is evident in our results. This is quite similar to the seasonal growth patterns described by Gerking (1967), Mann (1971), Kroger et al. (1974), and others. The cycle indicates that for the northern anchovy, about 95% of the first year's growth is completed by the 8th month of life and about 91% of the second year's growth is completed by the 20th month of life.

If this cyclic pattern in growth also occurs in anchovies in the wild, then it may have a considerable impact on yield models, such as yield-per-recruit models, and on management decisions. It might be that the best harvesting strategy in terms of maximum yield-per-recruit is during the period of the cycle when growth is relatively slow, i.e., period of plateau. It seems important, therefore, that a multiphase growth function be considered for use in yield models for northern anchovy.

We point out the possibility that the cyclic pattern could have been artificially created because our data were from three cohorts that were reared under different laboratory conditions during different periods of the year and the ages of fish reared by Leong (pers. commun.) were estimated. However, we discount that possibility because the cyclic pattern persists even if our age estimates of Leong's fish were off by 1 or 2 mo. Rearing conditions, on the other hand, could have produced the cyclic pattern if the pattern is influenced primarily by environmental factors, e.g., temperature, length of day, and food density and quality.

WEIGHT-LENGTH RELATION

Weight-length relations for the northern anchovy were reported by several investigators (Table 4). Only Lasker et al. (1970), however, reported on estimates for laboratory-reared anchovies, and their estimates were for anchovy larvae.

Length and weight data were collected by Leong (pers. commun.) and Paloma[3] from fish reared in their experiments. We used their data from 757 fish to estimate the weight-length relation of laboratory-reared anchovies of 70 to 131 mm long. Data from Paloma were only from fish in their first year of life, in which growth was somewhat similar to that of fish reared by Leong. Separate estimates were made for males and females (Table 4), and the results subjected to covariance analysis (with log transformed data) to test whether the relation could be represented by a single line. The analysis indicated that the separate lines were parallel and not significantly different from a common line. The data were, therefore, pooled and a weight-length relation estimated for the combined (all sexes) data (Table 4).

Our estimates are compared with those of Collins (1969) for anchovies from southern California (Figure 4). Collins based his estimates on data from anchovies caught in the reduction fishery off southern California. For a given length, fish examined by Collins were lighter than the laboratory-reared fish. This phenomenon appears common for fishes (Kramer 1969; Kimura and Sakagawa 1972). Kimura and Sakagawa (1972) mentioned that for Pacific sardines, differences in diet and reduced amount of exercise because of confinement were some possible causes for

[3]Paloma, P. 1971. Annulus formation in the scale of marked anchovy *Engraulis mordax* Girard. Unpubl. manuscr. Southwest Fisheries Center, La Jolla, CA 92038.

TABLE 4.—Coefficients of the weight-length relation for the northern anchovy as reported by various investigators. The coefficients are for the equation, weight = $a \times$ length^b.

Origin of sample	Source	Rearing environment: Ocean	Rearing environment: Laboratory	Sex	Number of fish	b	a	Unit of measure: Length	Unit of measure: Weight	Range of length (mm)
Southern California	Clark and Phillips (1952)	X		Combined sexes	(1)	3.453	2.7×10^{-4}	mm	ounce	56-134
	Collins (1969)	X		Male	926	3.049	8.1×10^{-6}	mm	gram	97-161
	Collins (1969)	X		Female	1,513	2.984	1.1×10^{-5}	mm	gram	
	Lasker et al. (1970)		X	Combined sexes	63	3.324	1.5×10^{-4}	mm	mg	3- 25
	Present study[2]		X	Male	257	3.521	1.0×10^{-6}	mm	gram	73-126
	Present study		X	Female	500	3.433	1.5×10^{-6}	mm	gram	70-131
	Present study		X	Combined sexes	757	3.461	1.4×10^{-6}	mm	gram	70-131
Central California	Clark and Phillips (1952)	X		Combined sexes	(1)	3.252	7.2×10^{-6}	mm	ounce	114-160
	Collins (1969)	X		Male	270	2.805	2.7×10^{-5}	mm	gram	80-171
	Collins (1969)	X		Female	407	2.743	3.6×10^{-5}	mm	gram	

[1]Clark and Phillips (1952) used data from 17 samples from southern California and 77 samples from central California but they did not specify the number of fish in each sample.

[2]Unpublished data from R. Leong and P. Paloma (pers. commun.), Southwest Fisheries Center, La Jolla, Calif. The coefficients with the more appropriate functional regression (Ricker 1973) are: 1) male, $a = 7.0 \times 10^{-7}$, $b = 3.608$; 2) female, $a = 1.0 \times 10^{-6}$, $b = 3.518$; 3) combined sexes, $a = 9.2 \times 10^{-7}$, $b = 3.547$.

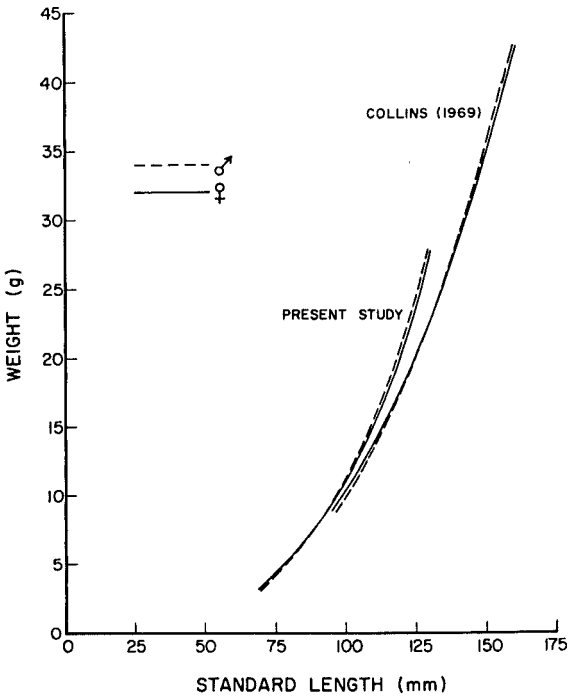

FIGURE 4.—Weight-length relation for northern anchovy from southern California. Laboratory-reared fish were used in present study, and fish caught in the California reduction fishery were used by Collins (1969).

laboratory-reared fish being heavier than fish in the wild. Zweifel and Lasker (see footnote 2) mentioned the possibility that the differences arise when the curves are based on fish in different phases of their growth cycle.

COMPARISONS OF GROWTH

Growth of anchovies reared in the laboratory was studied by Kramer and Zweifel (1970), Lasker et al. (1970), Theilacker and McMaster (1971), Hunter (1976), and Paloma (see footnote 3). Kramer and Zweifel and Lasker et al. studied the effects of diet and water temperature on growth of anchovy larvae. They concluded that larval growth was best at 22°C with wild plankton as a food source. The growth curve of Figure 3 for the larval stage is for fish reared on wild plankton and *Artemia salina* at about 22°C. It is the best so far attained in the laboratory.

Theilacker and McMaster (1971) and Hunter (1976) reared anchovy larvae on cultured foods. Results of their studies show that growth of anchovies on cultured food diets is about the same as that on wild plankton.

Paloma (see footnote 3) obtained juvenile anchovies from a live-bait dealer and reared the fish in the laboratory for 624 days (Table 1). He injected oxytetracycline hydrochloride into the fish at various times to label the body structures for ageing. At 2-wk intervals, scales and data on body measurements were collected. Fish reared by Paloma started at a smaller average size (75 mm long) than fish reared by Leong (pers. commun.) (88 mm long) and grew at a much slower rate (21 mm in about 470 days versus 30 mm in about 470 days for Leong's fish) without a noticeable steplike pattern. Perhaps the frequent handling, injection of tetracycline, and small size of the rearing pool (2.74-m diameter) contributed to the slow growth and eliminated the steplike pattern.

Clark and Phillips (1952), Miller et al. (1955), Collins (1969), and Collins and Spratt (1969), studied growth of anchovies caught in the California fisheries. They used scales and otoliths for ageing fish to the nearest whole year. Clark and Phillips reported their results for the combined

southern and central California fisheries. Miller et al., Collins, and Collins and Spratt, on the other hand, reported their results separately for each fishery.

To compare growth of anchovies in the wild with that of laboratory-reared anchovies, we limited the comparison to fish from southern California to eliminate possible regional biases in growth. We also adjusted Miller et al.'s (1955) data upward by 1 yr to make them comparable to those of Collins (1969) and Collins and Spratt (1969) (Figure 5). This was necessary because Miller et al. did not correct their age readings for date of capture (August to March) and growth on the margin of the scale relative to the birthdate (April 1); hence, they underestimated the age of their fish by approximately 1 yr.

The growth curves in Figure 5 indicate that anchovies in the wild are 95 to 115 mm long at about 1 yr old and 115 to 125 mm long at about 2 yr old and possibly growth was slower in the 1960's than in the 1950's owing to the dramatic increase in the northern anchovy population (Spratt 1975). Our growth estimates for laboratory-reared anchovies are 102 mm for 1 yr olds and 119 mm for 2 yr olds; hence, growth of laboratory-reared fish seems to be similar to that of anchovies in the wild. However, we note that this direct comparison is not entirely valid because inherent biases exist in the growth curves in Figure 5. The biases exist because: 1) larger fish are generally more available to the reduction fishery than the live-bait fishery (Messersmith 1969) and thus are overrepresented in the data for the reduction fishery; 2) live-bait fishermen "consciously avoid taking large anchovies, since they are less desirable for bait than smaller anchovies" (MacCall 1973:5-6) and thus large fish are underrepresented in the data for the live-bait fishery; 3) the true birthdate of anchovies aged by otolith or scale readings is not known although it is known that the birth date varies (Kramer and Smith 1971; Smith 1972), the ages, therefore, are not exact ages; and 4) growth of several year classes are averaged and consequently, variability in growth is reduced.

Spratt (1975), who also studied growth of the northern anchovy from otoliths, accounted for some of these biases by using back-calculated lengths and fish from the reduction fishery, live-bait fishery, and catches of a research vessel. He estimated that the mean standard length of anchovies in the wild is 92 and 112 mm at the end of the first and second year of life, respectively. These

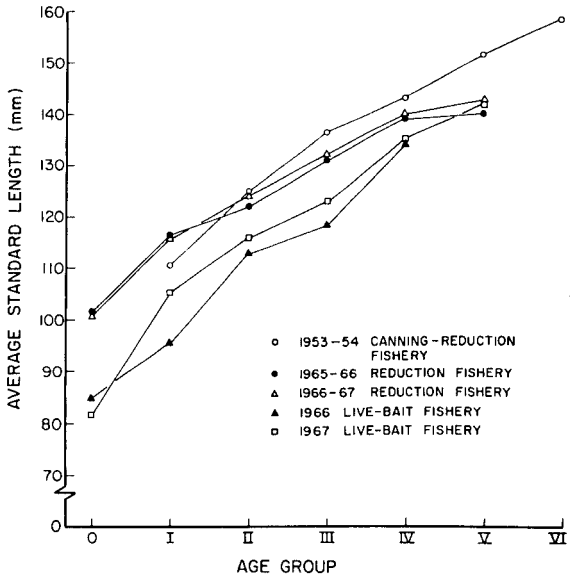

FIGURE 5.—Growth curves for northern anchovy caught off southern California in the fisheries for reduction (Collins 1969), live-bait (Collins and Spratt 1969), and canning-reduction (Miller et al. 1955).

estimates are somewhat less than ours for laboratory-reared fish but they are close.

It appears that growth of anchovies in the wild is similar to that estimated, on an annual basis, from our growth curve. We have not demonstrated, however, whether there is a cyclic pattern in growth of anchovies in the wild similar to that revealed in our results for laboratory-reared fish. On the other hand, studies on growth of other temperate fishes have shown that a seasonal cycle is common, which leads us to believe that a seasonal cycle exists for anchovies in the wild. The use of our growth curve for describing the feeding dynamics of northern anchovies of at least 2 yr of age in the California Current is therefore practical until a seasonal growth curve is described for anchovies in the wild.

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Zweifel read the manuscript and offered valuable comments and suggestions. Robson Collins and members of his staff at the California Department of Fish and Game read the manuscript and brought to our attention related studies that were in press.

LITERATURE CITED

BARDACH, J. E.
1968. Fish culture. *In* The status and potential of aquaculture, particularly fish culture, Part III, Vol. 2, p. 1-193. American Institute of Biological Sciences. Available Clgh. Fed. Sci. Tech. Inf., Springfield, VA 22151 as PB 177 768.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 19, 533 p.

CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax mordax*) in the California fishery. Calif. Fish Game 38:189-207.

COLLINS, R. A.
1969. Size and age composition of northern anchovies (*Engraulis mordax*) in the California anchovy reduction fishery for the 1965-66, 1966-67, and 1967-68, seasons. *In* The northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 56-74. Calif. Div. Fish Game, Fish Bull. 147.

COLLINS, R. A., AND J. D. SPRATT.
1969. Age determination of northern anchovies, *Engraulis mordax*, from otoliths. *In* The northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 39-55. Calif. Div. Fish Game, Fish Bull. 147.

CONWAY, G. R., N. R. GLASS, AND J. C. WILCOX
1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

GERKING, S. D.
1967. Annual growth cycle, growth potential, and growth compensation in the bluegill sunfish in northern Indiana lakes. J. Fish. Res. Board Can. 23:1923-1956.

HUNTER, J. R.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74: 81-88.

KIMURA, M., AND G. T. SAKAGAWA
1972. Observations on scale patterns and growth of the Pacific sardine reared in the laboratory. Fish. Bull., U.S. 70:1043-1052.

KRAMER, D.
1969. Synopsis of the biological data on the Pacific mackerel, *Scomber japonicus* Houttuyn (Northeast Pacific). U.S. Fish Wildl. Serv., Circ. 302, 18 p.

KRAMER, D., AND P. E. SMITH.
1971. Seasonal and geographic characteristics of fishery resources, California Current region—V. Northern anchovy. Commer. Fish. Rev. 33(3):33-38.

KRAMER, D., AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

KROGER, R. L., J. F. GUTHRIE, AND M. H. JUDY.
1974. Growth and first annulus formation of tagged and untagged Atlantic menhaden. Trans. Am. Fish. Soc. 103:292-296.

LAIRD, A. K.
1969. The dynamics of growth. Res./Dev. 20(8):28-31.

LASKER, R., AND L. L. VLYMEN.
1969. Experimental sea-water aquarium, Bureau of Commercial Fisheries Fishery-Oceanography Center, La Jolla, California. U.S. Fish Wildl. Serv., Circ. 334, 14 p.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

LOCKWOOD, S. J.
1974. The use of the von Bertalanffy growth equation to describe the seasonal growth of fish. J. Cons. 35:175-179.

MACCALL, A. D.
1973. The mortality rate of *Engraulis mordax* in southern California. Calif. Fish Game, Mar. Res. Tech. Rep. 4, 23 p.

MANN, R. H. K.
1971. The populations, growth and production of fish in four small streams in southern England. J. Anim. Ecol. 40:155-190.

MESSERSMITH, J. D.
1969. A review of the California anchovy fishery and results of the 1965-66 and 1966-67 reduction seasons. *In* The northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 6-32. Calif. Div. Fish Game, Fish Bull. 147.

MILLER, D. J., A. E. DAUGHERTY, F. E. FELIN, AND J. MACGREGOR.
1955. Age and length composition of the northern anchovy catch off the coast of California in 1952-53 and 1953-54. *In* Age determination of the northern anchovy, *Engraulis mordax*, p. 36-66. Calif. Div. Fish Game, Fish Bull. 101.

PARKER, R. R., AND P. A. LARKIN.
1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16:721-745.

RICHARDS, F. J.
1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

SILLIMAN, R. P.
1969. Comparison between Gompertz and von Bertalanffy curves for expressing growth in weight of fishes. J. Fish. Res. Board Can. 26:161-165.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

SPRATT, J. D.
1975. Growth rate of the northern anchovy, *Engraulis mordax*, in southern California waters, calculated from otoliths. Calif. Fish Game 61:116-126.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

VROOMAN, A. M., AND P. E. SMITH.
1971. Biomass of the subpopulations of northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 15:49-51.

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DEVELOPMENT AND USE OF SONAR MAPPING FOR PELAGIC STOCK ASSESSMENT IN THE CALIFORNIA CURRENT AREA[1]

ROGER P. HEWITT, PAUL E. SMITH, AND JOHN C. BROWN[2]

ABSTRACT

A method for pelagic fish stock assessment is presented which utilizes a fixed sonar beam for mapping fish schools. Samples of the two major acoustic properties of fish schools are presented, i.e., acoustically derived horizontal dimensions (representative of school volume) and target strengths (which may be representative of school compaction). Sampling biases and sources of sampling variability in the measurement of these properties are discussed. The results of two experiments, conducted to determine the weight of a fish school as a function of its acoustic characteristics, are presented. In the first experiment, an acoustically transparent trap was used to recreate an aggregation of fish and in the second, commercial fishing boats were chartered to capture whole schools. An automated sonar data acquisition and processing system is described and test results presented. The results of paired automated surveys of the Los Angeles (southern California) Bight are presented and discussed. The paper reports development of the sonar-fish school mapping method first documented by P. E. Smith in 1970.

Field investigations, conducted in cooperation with the Navy and the California Department of Fish and Game, indicate a median school size of 30 m diameter, a mean fish density of 15 kg of fish biomass per square meter of horizontal school area, and a biomass estimate of 1.23 to 2.30 × 10^6 metric tons for pelagic schooled targets in the Los Angeles Bight.

Fishermen have used hydroacoustic apparatus for locating concentrations of fish for almost as long as practical echo sounding devices have been available, although quantification of the information they provide has been attempted only in recent years. Horizontal echo ranging (sonar) to locate fish schools was first used off the coast of California in 1946 (Smith 1947; Smith and Ahlstrom 1948). The 1950 progress report of the California Cooperative Sardine Research program notes the use of sonar and echo sounders on the RV *Yellowfin* for locating fish schools, and cites the "considerable experimental value" of the acoustic apparatus. A research sonar on the RV *David Starr Jordan* has been used to count fish schools in the eastern tropical Pacific (McClendon 1968) and in the California Current area (Smith 1970). For recent reviews of the use of echo sounders and sonars for fishery research, consult Forbes and Nakken (1972) and Cushing (1973).

The work presented here is a method for quantifying sonar records and further using these records for estimating the size of pelagic fish stocks. The paper is divided into four sections:

1. The section entitled "Sources of sampling variability" describes the scale and variance of measured acoustic parameters of fish schools, i.e., horizontal fish school dimensions and peak target strength or echo intensity. It further discusses major biases affecting the measurement of these values.
2. The estimation of fish biomass in an aggregation involves the determination of a conversion factor by which the detected horizontal area of a fish school may be multiplied. Experiments to determine the weight of the fish under a square meter of school area are described in a section entitled "Horizontal school area to biomass conversion factors."
3. An automated data acquisition system is described in the third section.
4. The results of a paired sonar survey of the Los Angeles Bight, utilizing the automated system and a biomass factor determined during the cruise, are presented and discussed in the fourth section.

This report is the second in a series describing

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progress on a number of objectives established in early 1968. In order to develop "sonar mapping" as a stock assessment tool, it was decided that such a system should be able to: 1) count the number of schools per unit area in the upper mixed layer from a ship proceeding at 12 knots, 2) measure the horizontal size of each fish school, 3) calculate the biomass of each school, 4) estimate the size of individual fish within a school, and 5) distinguish the northern anchovy from all other schooling species.

Smith (1970) developed a technique for "mapping" fish schools in the area where the northern anchovy, *Engraulis mordax*, is abundant off the coast of southern California. Sonar mapping differs from echo sounding; with sonar, estimates can be made of the number of fish schools per unit area, of their horizontal dimensions, and of the degree of aggregation of fish schools. We do not routinely estimate depth of the school in the water column, nor thickness of the school in the vertical plane. Hull-mounted echo sounders provide estimates of the number of schools per line transect deeper than 4 m, measures of chords across the horizontal dimension of the school in the plane of ship travel, depth in the water column, and thickness or vertical height of the fish school. Experience indicates that the process of "sonar mapping" encounters one or two orders of magnitude more fish-school targets per unit of ship time as compared to echo sounding from the same vessel. It is important to emphasize that this technique was developed because fish schools are frequently found in the upper mixed layer of the ocean where echo sounders are relatively ineffectual at counting or measuring them.

In the first report on this project, Smith (1970) described a series of experiments designed to determine the feasibility of the use of sonar to count and measure the size of pelagic fish aggregations (objectives 1 and 2). Optimum instrument settings were determined for source level, receiver gain, pulse length, transducer bearing, transducer directivity, and range. Methods were developed for correcting target width (dimension measured on axis parallel to ship's track) for the effect of the beam angle and for correcting target count "edge biases." Since no target was counted unless it lay entirely within a specified range, the latter adjustment was made to compensate for the narrowing possible interval of detection for larger targets.

Holliday (1972, 1974) investigated the frequency domain processing of fish school echoes using experimental equipment brought aboard the *David Starr Jordan*. By detecting and measuring Doppler spread, Holliday was able to calculate tail beat amplitudes of schooled fish and, indirectly, their length (objective 4).

Holliday also examined the resonance structure of pulse returns from fish schools and was able to detect the presence or absence of a swim bladder in the school constituents. This information, when supplemented by observations on school behavior and free vehicle camera drops, may be used to distinguish anchovy from other pelagic schooling organisms in a sample taken randomly from targets encountered during a survey (objective 5). The statistical base thus obtained would be applied to the entire survey.

The California Department of Fish and Game (CF&G) has been engaged in sea surveys using sonar methods since 1967 (Mais 1974). Its approach has been the collection of large amounts of data and its interpretation, while the work at the Southwest Fisheries Center (SWFC) has been in the isolation of sampling errors and the development of an automated hydroacoustic data acquisition and processing system. As such, the two groups complement each other with field experience and technological development.

SOURCES OF SAMPLING VARIABILITY

We have made the assumption that quantitative errors associated with system instrumentation are small in comparison to errors generated by sampling an adult schooling population whose behavior is little understood. For this reason, we monitored our sonar system response when it was operated in a variety of circumstances and changed that system in answer to practical rather than theoretical considerations. Using operating techniques developed in 1968, school size frequency distributions were generated and a lower detectable size threshold defined; school target strengths were calculated and compared with similar work conducted by the Navy and the CF&G; the relationship between the detected occurrence of pelagic fish schools and bottom topography was investigated; and the variable range of detection of schools due to internal waves was studied (Smith[3]).

[3]Smith, P. E. 1973. The effects of internal waves on fish school

Based on Smith's (1970) work, sonar mapping cruises aboard the *David Starr Jordan* were conducted with a 30-kHz sonar unit directed 90° to starboard and 3° down. The sampled range band was 200 to 450 m from the transducer. The receivers were rebuilt using solid state circuitry with the remaining system as described by Smith (SIMRAD 580-10 Scientific Sonar and Sounder).[4]

Target Size

Frequency distributions of fish school sizes were generated from data taken on several cruises (April-May, November, December 1973; and March-April 1974) using the maximum difference between the leading and trailing edge of the echo envelope, corrected for pulse length, on an axis perpendicular to the ship's track. The calculation of target widths (measured on an axis parallel to the ship's track) was discontinued due to uncertainties in choosing the effective beam width (see Smith 1970), fluctuations in the ship's speed, and the inability to quantify other factors which may affect apparent target width (i.e., target strength).

School size distributions (based on range differences) remained nearly constant during several sampling periods and agreed well with a much larger sample collected by the CF&G. A total of 4,355 sonar targets were counted and assigned to size classes on three cruises approximately 6 mo apart. Ten-meter class intervals were used and frequencies were corrected for recording edge bias employing the method described by Smith (1970). This bias is encountered when one excludes targets which do not entirely occur within the observation band. Thus, frequencies of targets other than point sources, are underestimated by virtue of the fact that their physical size limits the probability of their detection. To determine unbiased relative proportions of target sizes, one must correct observed target count (those targets which lie entirely within the observation band) to a count of targets whose centers lie within the observation band.[5]

In developing a correction for recording edge bias, a diagram may be useful. In Figure 1 a school of diameter d is shown at the maximum and minimum ranges of detection for an observer on a ship sampling an observation band of k units. The difference between the maximum and minimum range of detection is $k - d$ units.

Let A represent the event that a school of d diameter has its center within an observation band of k units. Let B represent the event that a school of d diameter is not intersected by either edge of the observation band. Then the probability of event B occurring given that event A has occurred may be expressed:

$$P[B/A] = \frac{k - d}{k}.$$

Further, let N_d represent the count of targets of diameter d who lie entirely within the observation band. Let N'_d represent the count of targets of diameter d whose centers lie within the observation band. Since N'_d represents both edge intersected and non-edge intersected targets of diameter d, the portion of non-edge intersected targets may be estimated by:

$$N_d = N'_d P[B/A] = N'_d\left(\frac{k - d}{k}\right).$$

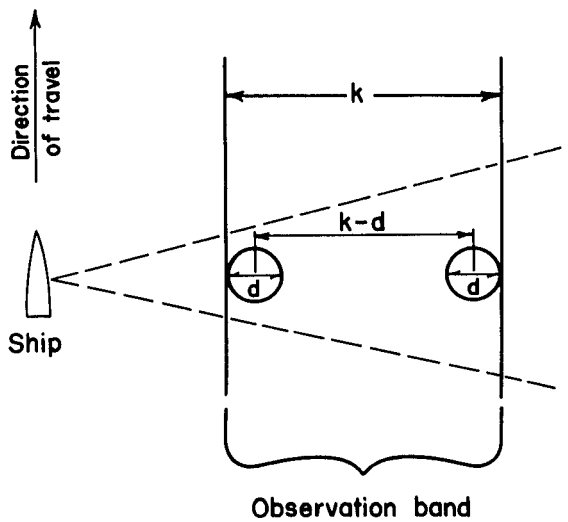

FIGURE 1.—Plan view of sonar mapping technique showing maximum and minimum ranges of detection for a target of diameter d within an observation band of k units.

mapping. Presented at the ICES-ICNAF-FAO Symposium on the Acoustic Methods in Fisheries Research, Bergen, Norway, Contrib. No. 8, 13 p.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]It is assumed that range-dependent, size-specific target losses are a minimum for the observation band sampled (Smith 1970). A similar study expanded to include the effects of target strength on detection ranges would be of value.

In actual practice N_d is tabulated. N'_d is then estimated by rearranging the above expression:

$$N'_d = N_d\left(\frac{k}{k-d}\right)$$

where N_d = observed class frequency
N'_d = edge corrected class frequency
k = extent of the observation window in meters (usually 250 m)
d = mean class diameter in meters.

As an example, when using a 250-m observation band, a 50-m target may be entirely detected over 200 m of that band, whereas a 100-m target must occur within a band of only 150 m to be detected. If one counts 10 50-m targets and 3 100-m targets, the counts, when corrected for edge bias, will be 10(250)/(250 − 50) = 12.5 and 3(250)/(250 − 100) = 5, respectively.

Horizontal school area is calculated by multiplying N' by the area of a circle whose diameter is equal to the class mark. The calculation is based on the assumption that with an increasing sample size the school dimension perpendicular to the ship's track will approximate the diameter of a circle whose area is equal to the area of a given school, however irregularly shaped. This assumption contains the condition that the orientation of a sample of schools is random and in no way related to that of the survey ship.

The resulting cumulative frequency diagram (Figure 2) would indicate that over 50% of the schools are less than 30 m in diameter while 90% of the horizontal school area is contributed by schools larger than 30 m in diameter. Mais' (1974) experience with over 23,000 schools (corrected for edge bias) in the same survey area indicated a similar distribution with a mode at 30 to 40 m (Figures 2, 3).

Smaller schools (<20 m in diameter) were likely to be undersampled by both the National Marine Fisheries Service (NMFS) and CF&G as the probability of their detection decreases faster with range than larger schools. Even if an exponential model of target size obtains in nature, schools smaller than 20 m would contribute little in amounts of horizontal school area.

The significance of a negative bias in the lower end of the observed school size distribution may be evaluated by fitting a power curve to that portion of the distribution between 15 and 165 m.

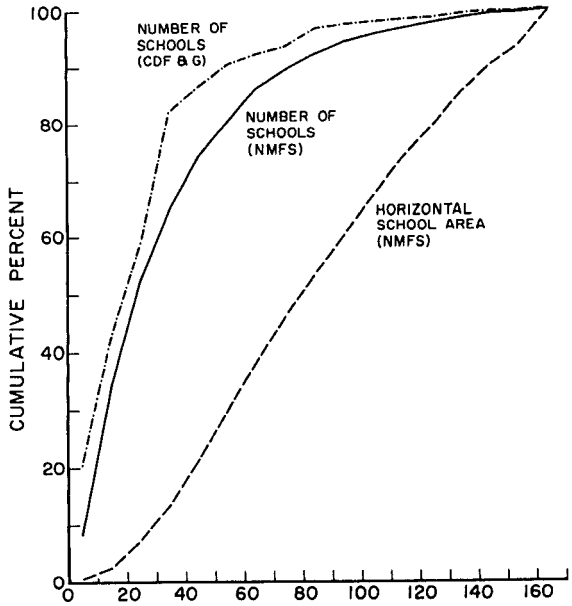

FIGURE 2.—Cumulative frequencies of sonar-detected fish schools by size and their contributing horizontal area (NMFS data only). The two modes in the CF&G data curve, drawn from a much larger sample (5×), might suggest either a systematic sampling error or optimum fish school sizes.

The equation, derived by a least squares fit, assumes the following form:

$$y = ax^b.$$

Using the NMFS sample of 4,355 targets:

$$N'_i = 428{,}864\ (D_m)_i^{-1.874}$$

where N'_i = edge-bias corrected target frequency within class i
$(D_m)_i$ = mean diameter of class i in meters.

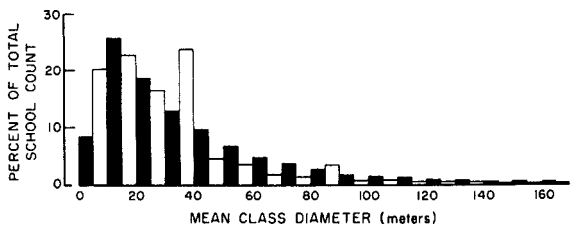

FIGURE 3.—Percent of total school count by size class. NMFS data are represented by the shaded bars; the open bars are calculated from CF&G data.

The correlation coefficient (r) = −0.969. Table 1 summarizes horizontal school area contributions by size class for observed frequencies corrected for edge bias and for frequencies derived from the exponential model. In both cases more than 90% of the area was contributed by schools larger than 20 m. The importance of horizontal school area is that it is probably proportional to the tonnage of fish in schools and, in this sense, decreases the significance of any bias in the counts of small schools.

TABLE 1.—Cumulative percent of total horizontal school area contributed by size class for observed frequencies (corrected for edge bias) and for frequencies derived from an exponential model.

Mean class diameter	N	N'	Model	Cumulative % A Observed	Cumulative % A Model
5	420	429	21018	0.09	4.24
15	1,247	1,347	2682	2.48	9.12
25	843	937	1030	7.17	14.32
35	556	647	548	13.52	19.73
45	403	491	342	21.50	25.32
55	277	355	235	30.11	31.05
65	182	246	172	38.44	36.91
75	124	177	131	46.33	42.88
85	86	130	104	53.98	48.98
95	57	92	84	60.63	55.09
105	47	81	70	67.79	61.39
115	32	59	59	74.07	67.72
125	22	44	50	79.58	74.03
135	19	41	44	85.61	80.42
145	11	26	38	90.02	86.89
155	7	18	34	93.57	93.53
165	10	29	30	99.99	99.99
>165	12				
	4,355				

Diurnal and Seasonal Effects

Time specific frequency distributions were drawn for data collected on cruises in April-May and in November 1973 for the purpose of discerning variations in sizes and detection of schools during various times of the day. While variations were noticed, their pattern was neither pronounced nor consistent from cruise to cruise. This is not to say that daily changes in schooling behavior do not exist, but that our data base is insufficient, at present, to delineate them. In the evening, discrete, well-formed schools of anchovy have been observed to disperse into a thin scattered layer but no program of study on this problem has been undertaken.

The data base is insufficient to detail seasonal changes in school size distributions, although, from communication with Mais and several commercial fishermen, we have reason to expect somewhat larger schools in the fall and smaller, scattered schools in the spring. Mid-spring is considered to be the main spawning season of the northern anchovy.

Target Strength

Acoustic target strength is proportional to the ability of an object or group of objects to reflect sound waves. Acoustic reflections from schools of fish are not presently well enough understood for rigorous characterization of the biomass of a fish school by the use of sonar. Nevertheless, we have measured apparent fish school target strengths with the objective of providing data which may lead to the quantification of fish schools in terms of total biomass.

Peak echo amplitudes were collected and corrected for propagation and absorption losses by employing the active sonar equation:

$$EL = SL - 2TL + TS$$

where EL = echo level in decibels (dB)
SL = source level in decibels, reference 1 μbar at 1 m
TL = transmission loss in decibels
TS = target strength in decibels.

Solving for target strength and using signal voltage level as a measure of echo level:

$$TS = 20 \log V - k + 40 \log R + 2 \propto R$$

where V = peak echo signal amplitude in volts
k = calibration coefficient which is the algebraic sum of source level, receiver sensitivity, and system gain expressed in decibels
$40 \log R + 2 \propto R$ = range dependent transmission loss (assuming spherical losses as in a homogeneous fluid) where R = midrange of target (as an approximation of the (location of peak echo amplitude), and $\propto$ = absorption coefficient expressed in decibels per meter.

Figure 4 illustrates five samples of peak target strengths computed from data taken by the

NMFS, U.S. Navy, and CF&G. Two of the distributions are "absolute" target strength in decibels and three are relative measurements, i.e., the calibration coefficient was not included in the calculations. The range of peak target strengths observed in any one sample varies from 28 to 34 dB. The two distributions of absolute target strength were obtained with the same sonar unit aboard the *David Starr Jordan*. The value of the calibration coefficient was recomputed after hydrophone calibration between cruises and remained constant. As such, the favorable comparison between the samples may be deceptive. The CF&G data were obtained and processed in a similar fashion using a 38-kHz sounder.

The theoretical target strength of a fish school has been discussed by Weston (1967) and Uretsky (1963). Modeling a fish school as a two dimensional array of bubbles in a liquid, both Weston and Uretsky predicted a sharp drop in response

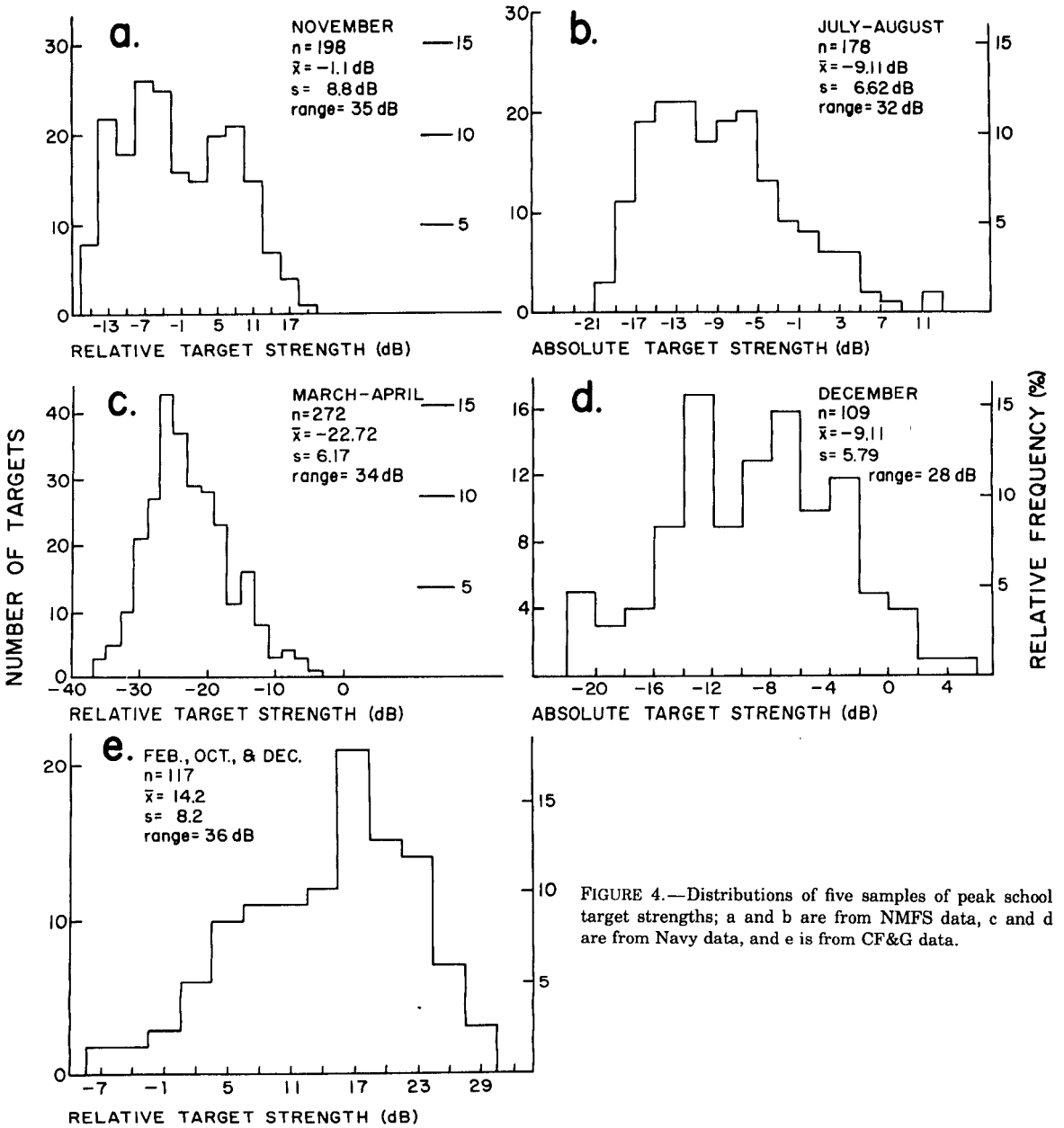

FIGURE 4.—Distributions of five samples of peak school target strengths; a and b are from NMFS data, c and d are from Navy data, and e is from CF&G data.

with increasing frequency above resonance. Using this approach, the energy scattered by the boundary of a fish school ensonified (irradiated acoustically) with 30 kHz sound becomes negligible.

Weston (1967) further suggested that an incoherent addition of reflected energy from individual fish may be expected as sound is transmitted across the boundary of a fish school. At 30 kHz, this component of target response becomes dominant and is reduced (or enhanced) by multiple scattering and absorption within the school.

The target response due to sound scattering by individual fish, assuming a mean wave phase interference of zero, may be calculated by summing the scattering cross sections of the fish comprising the target. Expressed in target strength, TS:

$$TS = TS_i + 10 \log n \text{ (decibels)}$$

where TS_i = the average target strength of the individual scatterer
n = the number of scatterers contributing to the total echo.

The number of scatterers contributing to the measured echo, n, may be estimated by applying observed and theoretical school densities (fish per cubic meter) to the ensonified volume. The ensonified volume may be estimated from:

$$V = \frac{c\tau}{2}(d)(D) \text{ (cubic meters)} \qquad (1)$$

where $\frac{c\tau}{2}$ = the range extent of the volume sampled by a sound pulse τ seconds long and moving at a speed of c meters per second
D = the vertical dimension of the school in meters
d = the horizontal dimension of the school.

School dimensions, D and d, are further limited by beam geometry, i.e., a school may not be fully ensonified if its dimensions exceed the effective beam width at the range of detection. The effective horizontal beam width may be estimated as that between the half-power points or:

$$2R \tan \beta$$

where R = range of detection
$\beta = 5°$ for the 30-kHz transducer used in this study.

Thus, d is the smaller of the measured horizontal dimensions or $0.175R$. Vertical dimensions of fish schools are not readily measured with sonar. However, in studying echograms of thousands of schools, Mais (1974) noted less variation in the vertical school dimension than the horizontal dimension and reported a mean school thickness of 12 m. The vertical effective beam width is estimated to be 12° or 42 m at 200-m range. If D is then assumed to be 12 m for all schools, there is no limitation imposed by the vertical beam width except that caused by vertical positioning of the school.

Using a 10 ms pulse length and estimating the speed of sound in a seawater medium at 1,500 m/s, Equation (1) becomes:

$$V = 90\, d$$

where d is the smaller of the measured horizontal dimensions or $0.175\, R$.

Mais (1974) reported visual observations of anchovy schools and estimated average packing density at 50 to 75 fish/m^3. Graves[6] analyzed in situ photographs of three anchovy schools and reported a mean density of 115 fish/m^3 at a mean spacing of 1.2 body lengths. Hewitt[7] used an idealized model of anchovy school compaction and calculated school densities of 0.5, 1.4, 6.6, 217, and 4,219 fish/m^3 at interfish distances of 10, 7, 4, 1, and 0.2 body lengths, respectively.

The target strength of an individual scatterer, TS_i may be estimated from considerations of acoustic theory and extensions of empirical measurements. Weston (1967) had shown the acoustic response of an ideal gas bubble to be essentially independent of frequency above resonance and proportional to the surface area of the bubble. When predicting the response of a fish swim bladder, Weston suggested an enhancement of

[6]Graves, J. 1974. A method for measuring the spacing and density of pelagic fish schools at sea. SWFC Administrative Report No. LJ-74-44. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

[7]Hewitt, R. 1975. Sonar mapping in the California Current area: A review of recent developments. Unpubl. manuscr. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038. The compaction model cited here used an anchovy of 12 cm standard length and computed the space required for the fish and a surrounding volume expressed in body lengths. The inverse of the resulting volume yields compaction in fish per cubic meter for a school of fish uniformly distributed in space.

75% due to shape distortion. Expressed in target strength:

$$TS_i = 20 \log L - 25 \text{ (decibels)} \quad (2)$$

where L is the fish length in meters. Swim bladder volume is assumed to be 4.1% of total fish volume and the radius of a sphere of equal volume equal to 0.043 L (after Haslett 1965).

Using a standard length of 12 cm as typical of anchovy school constituents detected by sonar (Mais 1974), Equation (2) yields a TS_i of −43.4 dB. It should be noted that Equation (2) makes no provision for reflection, interference, or attenuation of sound waves by fish tissue.[8]

McCartney and Stubbs (1970) measured maximum dorsal aspect target strengths of six fish species at varying frequencies and lengths. They fit Equation (3) to their data and further showed that the swim bladder can account for practically all of the scattering over a wide band of frequencies:

$$TS_i = 24.5 \log L - 4.5 \log \lambda - 26.4 \quad (3)$$

where λ = the wavelength of incident sound defined as $c(f)^{-1}$, where c is the speed of sound in a saltwater medium $\approx$ 1,500 m/s^{-1} and f is the frequency. For a 12 cm anchovy ensonified with 30 kHz sound, Equation (3) gives a TS_i of −43.1 dB.

Love (1971) reviewed maximum dorsal and side aspect target strength measurements made by several investigators. The data were obtained using fish from eight different generic orders, varying 100-fold in length, some with swim bladders and some without, and ensonified over a frequency range of 8 to 1,480 kHz. For dorsal aspect, Love related maximum target strength, fish length, and frequency by:

$$TS_i = 19.4 \log L + 0.6 \log \lambda - 24.9. \quad (4)$$

For the anchovy described above, Equation (4) predicts a TS_i of −43.5 dB at dorsal aspect.

Love described the side aspect data with the following equation:

$$TS_i = 22.8 \log L - 2.8 \log \lambda - 22.9 \quad (5)$$

or −40.2 dB for the anchovy described at side aspect.

A similar regression on target strength measurements taken from dead fish in dorsal aspect by six investigators and collated by Haslett (1965) would describe a TS_i of −49.8 dB for a 12-cm fish ensonified at 30 kHz (McCartney and Stubbs 1970). An application of the equations that Shibata (1970) used to describe his results yielded values of −42.8 dB for maximum dorsal aspect target strength and −40.0 dB for maximum side aspect target strength.

Several authors have noted that acoustic equipment commonly used by the biologist operates at frequencies (10 to 200 kHz) which generate sound at wavelengths comparable with the size of fish under study. Interferences will occur among the scattering components of a fish (swim bladder, flesh, skeleton, and organs) and may be expected to be a function of species and aspect. Further, our measurements are of peak school target strength taken from several transmissions along one tangential to the school and may not be the maximum value which would be obtained from interrogation at several angles.

Let us return now to the original calculations, i.e., the incoherent summation of echoes from an aggregation of fish which may now be expressed as:

$$TS = TS_i + 10 \log \left[q\,(90\,d)\right] \quad (6)$$

where TS_i may vary from −50 to −40 dB, q is the school density in fish per cubic meter and may vary from 0.5 to 4,219, and d may vary from 5 m (mean diameter of the minimum class size) to 79 m (0.175 R at R = 450 m, the maximum range within the observation band). The expected range of peak school target strengths (assuming incoherent addition and no interference or absorption within the school) are listed below for four assumptions of fish target strength, TS_i:

TS_i	*Minimum* TS where q = 0.5 fish/m^3 and d = 5m	*Maximum* TS where q = 4,219 fish/m^3 and d = 79 m
−40 dB	−16 dB	+35 dB
−43 dB	−19 dB	+32 dB
−45 dB	−21 dB	+30 dB
−50 dB	−26 dB	+25 dB

where τ = 10 ms, β = 5°, and D = 12 m.

Based on a framework of several assumptions, we may expect a range of peak school target strengths of about 50 dB whose position on the decibel scale is determined from the value one assumes to be the average target strength of the individual scatterers comprising the school.

[8]Holliday (1972) reported an average swim bladder volume of 2.8% of the total fish volume for a sample of 239 anchovy. The use of this value predicts an anchovy swim bladder response of −44.3 dB.

From the data presented so far (Figures 3, 4) we may assume the most probable target strength for all schools to be −9 dB. Further, assuming that the "typical" school has a vertical dimension of 12 m and that the measured target strength is the summation of scattering strength of the individual fish ensonified with no effects from multiple scattering or attenuation, we may use Equation (6) to estimate q:

TS_i	q	*Spacing*
−40 dB	0.93 fish/m³	8.1 body lengths
−43 dB	1.86	6.5
−45 dB	2.95	5.5
−50 dB	9.33	3.4

Bottom Topography

Fixed transect surveys require that the distribution of schools be independent of fixed geographic locales whose scale is smaller than transect spacing.

A cruise in March-April 1974, was designed to test a postulated relationship between the occurrence of pelagic fish schools and bottom topography. The area chosen was the Los Angeles Bight and for the purposes of the experiment was defined as that body of water bounded by the southern California coast from Pt. Arguello to the U.S.-Mexican border and seaward by a line extending south from Pt. Arguello to a point west of San Miguel Island, thence southeast along an extension of the Santa Rosa-Cortez Ridge to a point north of the east end of Cortez Bank, thence east to the intersection of the shoreline and the U.S.-Mexican border. The survey area, excluding island masses, contains approximately 11.5×10^3 square nautical miles of sea surface area.

The "Bight" was further divided into four classes of bottom topography and transects designed to distribute survey effort within these zones as described below. The method used was to delineate and compute the combined areas of the first three categories and then assign the remaining area to the fourth general zone.

Bottom topography	*Total area (nautical miles²)*	*% of survey area*	*% of sampling effort*
Banks and seamounts	547	4.8	14.4
Basins and troughs	2,946	25.9	27.4
Escarpments and canyons	467	4.1	24.1
Slopes	7,510	65.2	34.1

Combined seas and swells in excess of 7 feet prohibited sonar operations on 1 day out of 12 and somewhat altered the distribution of survey effort. A detailed breakdown of zones and actual survey effort is listed in Appendix Table 1.

Daylight sonar tracking was accomplished during two time periods separated by 2 wk: 25-29 March, 1 April, and 15-19 April 1974. No difference in schooling behavior was detected between the two periods and results are presented for the total cruise time in Appendix Table 2. If an area was surveyed and no targets were detected, a "0" under "No. targets obs." so indicates; if an area was not surveyed during one or both time periods then no numbers are recorded in the appropriate columns. "Linear nautical miles surveyed" is the distance traversed while sonar tracking over the designated area. The observation window (250 m wide beginning at 200 m from the ship, and 90° to starboard from the ship's track) is multiplied by the linear distance traversed and divided into the number of targets observed to obtain target density, expressed in units of targets per square nautical mile.

The geographic names of various topographic features are commonly accepted and can be located on National Ocean Survey bathymetric maps (numbers 1205N-15, 1206N-16, 1306N-19, and 1306N-20) with the exception of the following features informally named for the sake of convenience: Coronado Bank (lying immediately to the east of Coronado Escarpment), San Diego Escarpment (along the west side of the San Diego trough), Cortez Escarpment (east-northeast of Cortez Bank), San Clemente Bank (a relatively deep bank northeast of San Clemente Island), Santa Rosa North and South Bank, San Nicolas Escarpment (southeast of San Nicholas Island), Santa Cruz Bank (south-southeast of Santa Rosa Island), Santa Barbara Escarpment (west of Santa Barbara Island at the southeast end of Santa Cruz Basin), Santa Barbara Bank (north of Santa Barbara Island), and Santa Monica Escarpment (along the southwest side of Santa Monica Basin).

The data fail to support the notion that the occurrence of pelagic fish schools can be related to bottom topography over which they are detected. Mean target densities (number of targets observed per square nautical mile) were calculated for the four classes of bottom topography and although these densities range from 2.98 (banks and seamounts) to 8.23 (escarpments and can-

TABLE 2.—A comparison of the variance in detected target densities within the classes of bottom topography (zone) and between the zones. Probability <0.5 that there is an other than random relationship between the four classes of bottom topography and detected school occurrence rates (target densities).

Zone	Targets observed (no.) 25 Mar.-1 Apr.	15-19 Apr.	Total	Target density (targets/nmi²) 25 Mar.-1 Apr.	15-19 Apr.	Total
Banks and seamounts	36	2	38	3.57	0.75	2.98
Basins and troughs	117	244	361	4.42	12.08	7.74
Escarpments and canyons	29	229	258	2.11	12.81	8.23
Slopes	194	69	263	8.55	3.25	5.98

	Sum of squares	Degrees of freedom	Means of squares	F
Within zone	72.9765	29	2.5164	
Between zones	2.9932	3	0.9977	0.40

yons), an analysis of the variance would suggest that there is no variance between the zones that could not be explained by the existing variability within the zones (Table 2).

HORIZONTAL SCHOOL AREA TO BIOMASS CONVERSION FACTORS

Fish Trap Experiment

The first effort toward determining a horizontal school area to biomass conversion factor was conducted in 1970 and briefly described in the discussion following the presentation of Smith's (1970) paper and transcribed in the publication of that paper.

An acoustically transparent trap (Figure 5) was constructed and live northern anchovy enclosed. Two groups of fish were ensonified and their horizontal area measured. A 354-kg group yielded a target strength within the range frequently encountered while a 2,017-kg group's target strength was well above that observed in nature for schooling fish.

Ensonification of additional weight groups was not possible due to the presence of predators and attempts at visual observation of the fish aggregation using a manned submersible eventually destroyed the trap. A value of 31 kg of fish biomass/m² was derived from the 354-kg group and judged to be our best estimate (Table 3). Mais (pers. commun.) reports from his experience

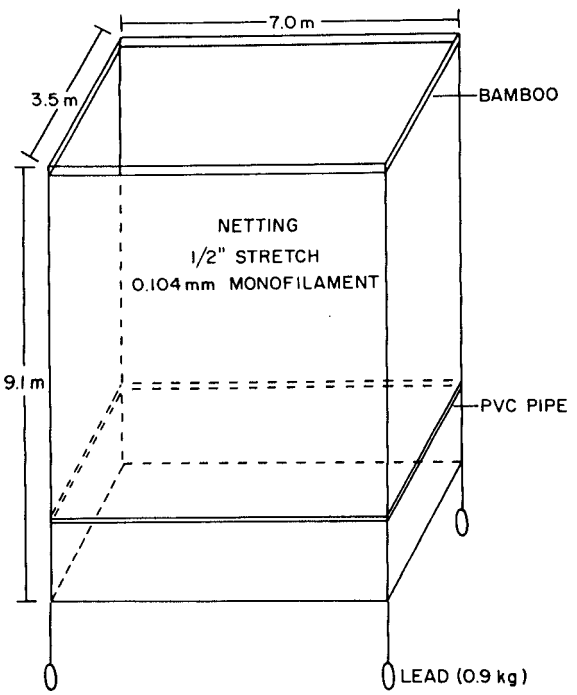

FIGURE 5.—Diagram of an acoustically transparent trap for ensonifying a group of fish of known size and weight.

TABLE 3.—Computation of a horizontal school area to biomass conversion factor from data gathered during the fish trap experiment (February 1970).

Weight class (g)	50-fish sample No. of fish	% of sample weight	354-kg group No. of fish	Total weight (g)	2,017-kg group No. of fish	Total weight (g)
10	24	33.8	11,925	119,652	68,175	681,746
15	15	31.7	7,481	112,218	42,626	639,389
20	9	25.4	4,496	89,916	25,616	512,318
25	1	3.5	496	12,390	2,824	70,595
30	0	0	0	0	0	0
35	0	0	0	0	0	0
40	1	5.6	496	19,824	2,824	112,952
Total	50	100.0	24,894	354,000	142,065	2,017,000

Surface area[1]	354-kg group [2]Mt/m²	No./m²	2,017-kg group Mt/m²	No./m²
11.39	0.031	2,190	0.177	12,473

[1]The fish are schooled in an ellipse with a major radius of 2.90 m and a minor radius of 1.25 m (surface area 11.39 m²).
[2]Metric tons per square meter.

a representative anchovy school compaction around 50 fish/m^3 or a distance of two body lengths between fish. Using a single fish weight of 18 g and an average school thickness of 12 m (Mais 1974), one obtains a horizontal school area to biomass conversion factor of 8.4 kg/m^2.

Charter Boat Experiment

A second experiment was designed and executed in late summer 1974, to relate measured school size, calculated target strength, and school compaction. Purse seine boats were chartered to make directed sets on fish schools first ensonified by the acoustic system aboard the *David Starr Jordan*.[9] Target strength and school size were calculated from the observation. The fishing boat supplied information on the tonnage caught and the portion of the school taken. Using these data, a biomass conversion factor was calculated for each school by dividing the total estimated school tonnage by a circular area based on the difference between its near and far ranges.

Fifty-two sets were judged to be the minimum sample size necessary to distinguish between two estimates of the portion of detectable pelagic aggregations that are schools of northern anchovy. Squire (1972), using data from 6 yr of observations from several commercial air spotters, reported that at least 50% of the surface schools off southern California can be expected to be anchovy. Mais (pers. commun.) estimates that 90% of the schools sampled by mid-water trawl are anchovy.

Seventy-six sets were made landing 1,901 short tons of anchovy; 63 were directed by the *David Starr Jordan* and 13 directed by the State of California's RV *Alaska*. Forty-nine positive data points were tabulated from the *David Starr Jordan*'s work and eight from the *Alaska*.

Average target size was 119 m (as measured by the difference between the near and far ranges on a line perpendicular to the ship's head) with a range from 31 to 305 m. Average peak target strength was +5.18 dB (as calculated from peak amplitude and range dependent losses) with a range from −9 to +18 dB and a SD of 5.63 dB.

Practical considerations forced us to expend a larger portion of effort on schools of larger than average size and target strength. This circumstance accounts for the fourfold increase in median target size and a 15-dB increase in mean target strength over a sonar-generated data base reported earlier. In addition, this sample was chosen from a detected school population whose acoustic dimensions were, in general, larger than that experienced on previous cruises.

To facilitate the direction of sets, the observation window was increased from 250 to 500 m wide and moved 100 m closer to the vessel. A time-varied gain increase was also accomplished in the receiver previous to signal display on an oscilloscope. Either or both of these changes to the sonar system configuration could produce circumstances under which similar data distributions would appear to be different. Point scatters encountered when plotting target size versus target strength, target strength versus horizontal school area to biomass conversion factor, and target size versus horizontal school area to biomass conversion factor are too wide to detect a relationship between these school parameters.

A distribution of horizontal school area to biomass conversion factors is presented in Figure 6. The distribution is skewed right with an arithmetic mean of 15.16 kg/m^2. While no relationship is as yet demonstrated between individual target strengths and horizontal school area to biomass conversion factors, the data have contributed to a refinement of a general conver-

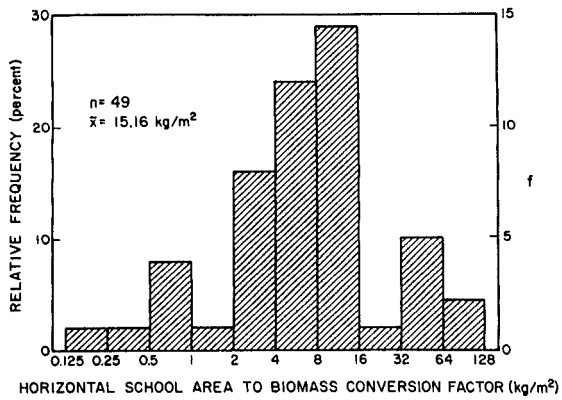

FIGURE 6.—Distribution of horizontal school area to biomass conversion factors obtained from the charter boat experiment.

[9]Contracts were let for a total of 104 sets assuming 50% success rate for positive sets and a permit was secured from CF&G to land 2,500 tons of anchovy during the experiment. A charter agreement was written establishing criteria for the successful bidders as minimum tonnage bid with the proceeds from any excess tonnage, not to exceed the permit, to be given to the State. In addition, each boat was guaranteed a fixed fee over and above the proceeds from the landed fish.

sion factor based previously on only one data point.

Eight horizontal school area to biomass conversion factors calculated from sets directed by the *Alaska* have a range from 10.14 to 30.22 kg/m^2 with a mean value of 18.42 kg/m^2. The *Alaska* participated in the experiment during the last 2 wk when only large schools were available in shallow water.

AUTOMATED HYDROACOUSTIC DATA ACQUISITION AND PROCESSING SYSTEM

In an effort to reduce observer subjectivity in the collection of large amounts of sonar data necessary for the isolation of sampling errors and biases, a decision was made to develop the capability to automatically count and measure the horizontal dimensions of sonar targets. Peak echo amplitude was also to be measured with the intention of eventually relating it to school compaction and depth.

A digital PDP8/I computer with an additional 16k memory, an analog-to-digital converter and a teletype terminal were acquired on loan from the Naval Undersea Center at San Diego. Using this gear, a project was undertaken which would allow us to do automatically what we were doing manually but with the additional benefits of real-time target strength calculation and rapid raw data processing.

The raw data used for hand target collection is in the form of a paper record containing a field of parallel lines, each line being an incremental distance along the survey track. If the amplitude of the signal is sampled during the recording of one of these lines, at a sample rate of 750 samples/s (velocity of sound/two-way path length), the result is a record of the instantaneous echo amplitude at 1-m increments along a line perpendicular to the survey track.

When several of these lines have been recorded, the result is a data field which is a numerical counterpart of the paper record. Once the word "target" is defined numerically, the number of targets in this field can be counted.

The numerical definitions used for this purpose are:

Threshold (THS) = some signal amplitude greater than the average reverberation or noise level.

Target line = at least five consecutive samples greater than THS, preceded and followed by five samples below THS.

Target block = two target lines which have at least five coincident and consecutive samples greater than THS.

Target = a target block + N additional coincident target lines, bounded by noise (signal less than THS).

The threshold, for the initial program was a predetermined constant. The five sample target line is selected on the assumption that a 5-m target may be the smallest significant unit. The two line target block is selected since random or asynchronous noise greater than THS can cause a target line, but will rarely cause at least five coincident samples on consecutive lines. Three consecutive lines of data are stored in the memory of the PDP8/I computer. As each new line of data is stored it is tested for the presence of target lines. When a target line is found, the amplitude of the samples is compared and the value of the peak amplitude is stored in the first data point location.

The newest data line is then compared with the previous one and any occurrence of a target block is recorded in the block register. The previous data line is compared with the oldest data line and, with the information in the target block register, the following decisions are made:

1. Is the target block the beginning of a new target? If so, assign it a number and record its initial range, final range, and peak amplitude in the temporary target storage register.
2. Is the target block the entire target? If so, store its information in the final target storage field with the current time and the ship's speed.
3. Is the target block part of a previous target? If so, update the temporary storage information.
4. Is the target block the end of a previous target? If so, update the temporary information and store in final storage.

Additional logic decisions are required if two or more previously recorded individual targets later merge to form a single target, or if the inverse should occur.

There are four analog data input lines to the

system which are multiplexed and sampled at appropriate times by the analog-to-digital converter. These are:

The start pulse—the trigger pulse for the sonar transmitter.
The sonar signal—the 1,000 cycle band width detected video from the sonar receiver.
The ship's speed—a DC voltage from the ship's log proportional to speed.
The hour mark—a pulse from the ship's precision simplex clock system occurring at the end of each hour.

The start pulse initiates the program, which then counts 200 sample times before recording data. Two hundred fifty samples are then taken between 200 and 450 m, to be operated on by the program as previously described. A running count of the number of start pulses occurring after the beginning of each new hour is kept and used as a time base for all events recorded during that hour. During data reduction, this count is divided into 60 min and used to provide absolute time data.

The ship's speed is recorded with each target, and may be used to calculate the area surveyed. It is used in the data collection program to determine when a hydrographic and/or biological station has been reached and to suspend data recording while on station; start pulses continue to be counted, however, thus the time at the beginning and end of the station is recorded.

In shipboard operation, the system requires no attendance. Prior to leaving the dock, the computer is started, and the hour counter is preset to the current time. The sonar system is then started and may be left in operation 24 h a day or turned off at night. In either case, the data collection program will begin sampling automatically at 0800 each morning and continue until 1600 each afternoon, except while on station. There are six memory storage fields in the PDP8/I of 4,096 words each. One field is used for programming and temporary data storage. The other five fields provide final storage for 3,300 targets, at six data words per target. At the end of the day (1600 h) the data collection program in field zero is replaced by a general computational program used in the PDP8/I called FOCAL. This program change is accomplished automatically from a prerecorded magnetic tape cartridge. With FOCAL programming, the stored target data is now reduced, summarized, and dumped onto peripheral mass storage capable of holding the entire cruise.

When the output is finished, the collection program is reread into field zero, and the computer waits for 0800 h the following morning to again begin data recording.

Field testing of this system was conducted in July 1974, by comparing computer listings of events with the corresponding wet paper records. The system proved to have a greater resolution than was felt necessary and the criteria for a target block changed to two coincident and consecutive samples above threshold. Ten samples below threshold rather than five were judged adequate to terminate a target on any given line. A variable threshold based on an integrated value of volume reverberation is being developed.

The system was field tested under a wide variety of conditions and judged satisfactory for our requirements. Figure 7 describes a cumulative frequency diagram for school count and horizontal school area. A median school size of 30 m agrees with data from previous cruises.

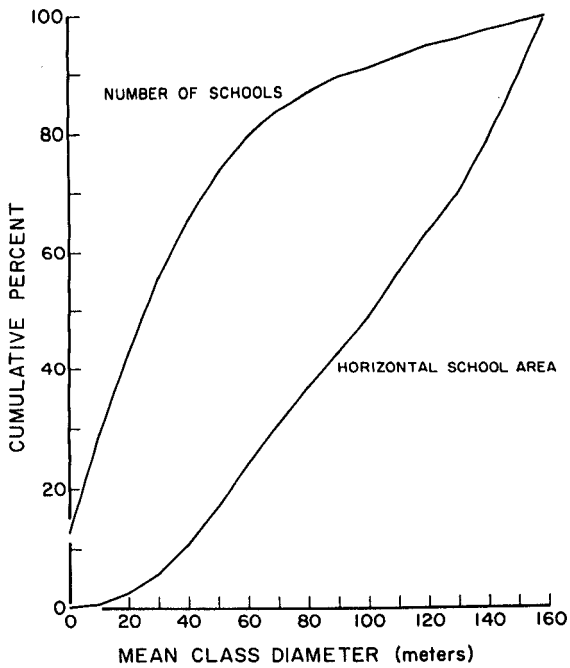

FIGURE 7.—Cumulative frequency diagram of school count and horizontal school area from a sample taken during the field test of an automated sonar system in July 1974.

AUTOMATED SONAR SURVEY

An automated sonar survey of the Los Angeles Bight was accomplished during the last 2 wk of the charter boat cruise. A 721-nautical-mile track (Figure 8) was transected two times providing a 3.4% areal sample of the 11,500-mile^2 Bight. Each track (1.7% sample) was processed as a separate survey.

Appendix Table 3 lists target counts on tracks 1 and 2 by target size and mid-range. Target size refers to the maximum dimension normal to the ship's track and is calculated from the difference between the leading and trailing edges of the echo envelope corrected for the pulse length (15 m at 10 ms pulse length). The first mode, common to both tracks at a target diameter of 30 m, is consistent with earlier data collected by NMFS (approximately 4,500 targets) and CF&G (approximately 23,000 targets). A second mode occurring at a school diameter of 250 m is also common to both tracks. This mode has not been seen before or during any season in any year since sonar activities were initiated off southern California. An explanation for the mode, other than the reflection of an optimum school size, is that it may be a bottom reverberation mode particular to the observation window used on the survey.

Bottom reverberation, as logged by the system, was collected for 2 h over water depths of approximately 100 m during the cruise. Distributions of target size, midrange, and target strength are shown in Appendix Table 4. Notable are two size modes at 50 and 225 m, an optimum midrange of 450 m, and an average target strength of +5 dB.

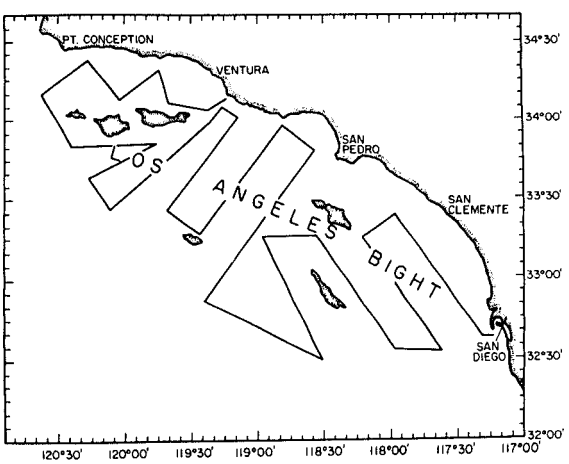

FIGURE 8.—Los Angeles Bight including a 721-mile sonar survey track transected twice, 17-26 September 1974.

Targets contributing to the 250-m size class mode have a midrange mode of approximately 450 m for both tracks 1 and 2. Average target strength was +7 dB for the subsample. This information reinforces the theory that the 250-m size class mode is caused by false targets caused in turn by bottom reverberation. Changes in the sonar system operating parameters (i.e., the enlargement of the observation window and the addition of a time gain circuit) are assumed to be responsible for the variation in system response. These changes were made to facilitate the fish biomass work and will not be in effect during the sonar surveys to be conducted on a series of California Cooperative Oceanic Fisheries Investigations cruises beginning in November 1974. Operating procedures will be the same as used for the initial field of testing of the automated hydroacoustic data acquisition and processing system.

Since those targets which begin or end beyond the observation band are not counted, an edge bias exists which is a function of the target size and the extent of the observation window. Frequencies within target size class intervals were corrected for edge bias by the following formula:

$$N'_d = N_d \frac{500}{500 - d}$$

where N_d = frequency of observation within a given size class
N'_d = frequency corrected for edge bias
d = mean class diameter.

The largest school size corrected for edge bias was 160 m (target size distributions from previous cruises, CF&G and NMFS, indicate that 160 m includes the 99th percentile). Table 4 lists observed frequencies, edge corrected frequencies, and horizontal school area contributions for size classes up to a maximum mean class diameter of 160 m.

The total detected school area was 2.6×10^6 m^2 for track 1 and 1.4×10^6 m^2 for track 2. Integrating over the entire survey area by simple proportion, assuming no stratification, and using a conversion factor of 15.16 kg/m^2, biomass estimates of pelagic schooling fish in the Los Angeles Bight were calculated at 2.30×10^6 metric tons and 1.23×10^6 metric tons for tracks 1 and 2, respec-

TABLE 4.—Observed frequencies, edge corrected frequencies, and horizontal school area contributions for size classes (metric tons, mt) up to a maximum of 160 m school diameter.

Class limits (mt)		Mark	N (f)	N'	$\%\Sigma N'$	Cum. $\%N'$	$N'A$ (mt)^2	$\%\Sigma N'A$	Cum. $\%N'A$
Track 1									
−5	5	0	35	35.000	5.171	5.171	0.000	0.000	0.000
5	15	10	74	75.510	11.156	16.327	5,930.557	0.229	0.229
15	25	20	86	89.583	13.236	29.563	28,143.434	1.091	1.321
25	35	30	89	94.680	13.989	43.553	66,925.949	2.594	3.916
35	45	40	68	73.913	10.920	54.473	92,881.869	3.601	7.517
45	55	50	47	52.222	7.715	62.189	102,538.093	3.975	11.493
55	65	60	36	40.909	6.044	68.234	115,667.729	4.484	15.978
65	75	70	30	34.883	5.154	73.388	134,248.290	5.205	21.183
75	85	80	21	25.000	3.693	77.081	125,663.706	4.872	26.056
85	95	90	21	25.609	3.783	80.865	162,922.228	6.317	32.373
95	105	100	18	22.500	3.324	84.190	176,714.586	6.851	39.225
105	115	110	12	15.384	2.273	86.463	146,204.888	5.668	44.894
115	125	120	15	19.736	2.916	89.379	223,218.425	8.655	53.549
125	135	130	13	17.567	2.595	91.975	233,178.346	9.041	62.590
135	145	140	12	16.666	2.462	94.437	256,563.400	9.947	72.538
145	155	150	14	20.000	2.955	97.392	353,429.173	13.703	86.242
155	165	160	12	17.647	2.607	99.999	354,815.170	13.757	99.999
Total			603	676.815			2,579,045.851		
Track 2									
−5	5	0	33	33.000	7.902	7.902	0.000	0.000	0.000
5	15	10	46	46.938	11.240	19.143	3,686.562	0.267	0.267
15	25	20	57	59.375	14.218	33.362	18,653.206	1.353	1.621
25	35	30	50	53.191	12.738	46.100	37,598.848	2.729	4.350
35	45	40	39	42.391	10.151	56.252	53,270.484	3.866	8.217
45	55	50	39	43.333	10.377	66.629	85,084.801	6.175	14.393
55	65	60	24	27.272	6.531	73.160	77,111.819	5.597	19.990
65	75	70	24	27.906	6.683	79.843	107,398.632	7.795	27.786
75	85	80	8	9.523	2.280	82.124	47,871.888	3.474	31.261
85	95	90	8	9.756	2.336	84.461	62,065.610	4.505	35.766
95	105	100	8	10.000	2.394	86.855	78,539.816	5.700	41.467
105	115	110	8	10.256	2.456	89.312	97,469.925	7.074	48.542
115	125	120	6	7.894	1.890	91.202	89,287.370	6.481	55.023
125	135	130	5	6.756	1.618	92.820	89,683.979	6.509	61.533
135	145	140	9	12.500	2.993	95.814	192,422.550	13.967	75.500
145	155	150	4	5.714	1.368	97.182	100,979.763	7.329	82.830
155	165	160	8	11.764	2.817	99.999	236,543.446	17.169	99.999
Total			376	417.576			1,377,668.706		

tively. Identification of the fish is not yet possible on a routine basis. However, it is assumed that the majority of schooling fish in the Los Angeles Bight are northern anchovy (Smith 1972; Squire 1972; Mais 1974).

DISCUSSION

It is our impression that the ultimate value of sonar mapping is its potential to reconstruct geographic patterns of school distributions at a moderate cost of time both in data collection and data reduction. However, before this potential can be fully realized, several problems must be recognized, investigated, and placed in proper perspective.

With regard to counting and sizing targets:

1. An edge bias has been described which will be present with any sonar system designed to count and size schools. The determination of effective detection ranges establishes a finite observation band. Larger schools tend to be undersampled relative to smaller schools; in terms of school area the bias may be significant.
2. Increasing the observation band would tend to reduce the effect of edge bias. However, the effects of target size and target strength on maximum ranges of detection should be investigated before defining the observation band. Undersampling small schools may be acceptable when considering their area contribution.
3. Effective detection ranges may also be limited by inhomogeneities in the medium caused by short-period internal waves. Smith (see footnote 3) investigated this phenomenon and suggested the only practical solution is a statistical approach

whereby the number of sound velocity profiles taken in an area-time stratum would be limited to the number of samples necessary to reduce the standard error to a uniform value for all strata. A probability of detection diagram could then be constructed from the ray trace analyses and target counts corrected by range. We have not so far considered these effects in our area of operation, however, the implication of undersampling should be investigated when designing a serious stock assessment survey using sonar.

4. Diurnal and seasonal variations in school sizes can be expected. In order to properly evaluate their affect on a stock assessment scheme the period and amplitude of these variations must be measured. The collection of a data base sufficient in size to detail these changes, as well as geographic distribution patterns by season, was the primary motivation in designing an automated data collection system.
5. While it appears that influences of bottom topography on school distribution may be neglected, there is no reason to expect areal distributions to be uniform. In fact, there is evidence from aerial reconnaissance, sonar transects obtained at long ranges (2,500 m), and fishermen that fish schools may be distributed in a highly contagious fashion similar to the distributions of fish eggs and larvae. In our opinion, this is a most important consideration in arriving at an optimum survey design. Smith[10] and MacCall[11] have approached the problem by direct measurement and simulation modeling and suggest a transect spacing of 15 miles as adequate to reconstruct groups of anchovy schools off southern California.
6. Holliday (1972, 1974) demonstrated the feasibility of sizing individual fish within schools and provided information which would aid in species identification. A development of these techniques as practical additions to a sonar survey system would reduce a presently loosely quantified factor, i.e., the percent of detected schools which can be expected to be the target species of a survey.

With regard to school target strength:

1. The target strength of an individual fish is an essential element in interpreting the measured target strength of a school. At the frequencies commonly used for sonar mapping we can expect interference of energy reflected from the various scattering parts of a fish. This makes the target strength of a fish strongly aspect dependent. Unfortunately there is presently no method of acoustically determining the aspect of individuals in a school and hence their effective target strength. As such, the maximum dorsal or side aspect target strength is generally an overestimate and the use of these values in interpreting school target strengths results in an underestimate of the number of individual scatterers.
2. We may also expect multiple scattering, shadowing, and attenuation within a school. These effects may tend to reduce or enhance the target strength of a school and cannot be evaluated until we know the effective contribution of the fish taken as individual scatterers. Love (1971) stated that the quantification of a fish school using its target strength is possible because the target strength of a school depends on the average size, number, distribution, and aspect of the individuals in the school. If the effects of the distribution of fish in space and their aspect can be removed, we may assume an average size and estimate their numbers.
3. We have assumed spherical spreading losses which may only be expected in a three-dimensional homogeneous fluid. In fact, the upper mixed layer, in which we operate our sonar, is characteristically bounded by density discontinuities which reflect and refract sound waves. The actual path of transmitted and target-reflected sound waves may not be direct as implied in the use of spherical transmission losses.

[10]Smith, P. E. 1975. Precision of sonar mapping for pelagic fish assessment in the California Current area. SWFC Administrative Report No. LJ-75-60. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

[11]MacCall, A. 1975. Anchovy population survey simulation. Contribution No. 4, CalCOFI Anchovy Workshop, July 1975. Document on hand at the Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

Continuing development of acoustic stock assessment techniques rests on the comparison of measurements and the best available theoretical models for target strength and fish school biomass. Improved instrumentation, particularly data logging and processing equipment will make the comparison more timely and useful. The existing system will be used seasonally over the entire California Current survey area (about 200,000 nautical miles^2) in 1975. It is intended that the data base thus furnished will allow a balanced approach to such biological problems as migration and patchiness of fish schools in the context of better theory and instrumentation.

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LITERATURE CITED

CUSHING, D. H.
1973. The detection of fish. Pergamon Press Ltd., Oxford, 200 p.

FORBES, S. T., AND O. NAKKEN.
1972. Manual of methods for fisheries resource survey and appraisal, Part 2: The use of acoustic instruments for fish detection and abundance estimation. FAO Manuals in Fisheries Science, 138 p.

HASLETT, R. W. G.
1965. Acoustic backscattering cross sections of fish at three frequencies and their representation on a universal graph. Br. J. Appl. Phys. 16:1143-1150.

HOLLIDAY, D. V.
1972. Resonance structure in echoes from schooled pelagic fish. J. Acoust. Soc. Am. 51:1322-1332.
1974. Doppler structure in echoes from schools of pelagic fish. J. Acoust. Soc. Am. 55:1313-1322.

LOVE, R. H.
1971. Measurements of fish target strength: A review. Fish. Bull., U.S. 69:703-715.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Fish Game, Fish Bull. 162, 79 p.

MCCARTNEY, B. S., AND A. R. STUBBS.
1970. Measurements of the target strength of fish in dorsal aspect, including swimbladder resonance. *In* G. B. Farquhar (editor), Proc. International Symposium on Biological Sound Scattering in the Ocean, p. 180-211. Maury Center for Ocean Science, Dep. Navy, Washington, D.C.

MCCLENDON, R. I.
1968. Detection of fish schools by sonar (eastern tropical Pacific, July-November 1967). Commer. Fish. Rev. 30(4):26-29.

SHIBATA, K.
1970. Study on details of ultrasonic reflection from individual fish. Bull. Fac. Fish. Nagasaki Univ. 29:1-82.

SMITH, O. R.
1947. The location of sardine schools by super-sonic echo-ranging. Commer. Fish. Rev. 9(1):1-6.

SMITH, O. R., AND E. H. AHLSTROM.
1948. Echo-ranging for fish schools and observations on temperature and plankton in waters off central California in the spring of 1946. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 44, 43 p.

SMITH, P. E.
1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar. *In* G. B. Farquhar (editor), Proc. International Symposium on Biological Sound Scattering in the Ocean, p. 563-591. Maury Center for Ocean Science, Dep. Navy, Washington, D.C.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

SQUIRE, J. L., JR.
1972. Apparent abundance of some pelagic marine fishes off the southern and central California coast as surveyed by an airborne monitoring program. Fish. Bull., U.S. 70:1005-1019.

URETSKY, J. L.
1963. The acoustical properties of compacted schools of fish. SIO Ref. 63-21, Scripps Inst. Oceanogr., Univ. Calif., 3 p.

WESTON, D. E.
1967. Sound propagation in the presence of bladder fish. *In* V. M. Albers (editor), Underwater acoustics, Vol. 2, p. 55-88. Plenum Press, N.Y.

APPENDIX TABLE 1.—Topographic breakdown of Los Angeles Bight by four classes of bottom configuration (zone) and distribution of design and actual sampling effort.

Zone and name	Area (nautical mile²)	Total area (%)	Sampling effort	
			Design (%)	Actual (%)
Banks:				
Thirtymile Bank	44.8			
Fortymile Bank	39.6			
Tanner Bank	50.2			
Osborn Bank	13.4			
San Clemente Bank	37.3			
San Nicolas Bank	125.4			
Santa Rosa N. Bank	17.7			
Santa Rosa S. Bank	34.0			
Coronado Bank	19.1			
Santa Barbara Bank	72.7			
Santa Cruz Bank	79.3			
Lasuen Seamount	13.2			
Total	546.7	4.8	14.4	9.4
Basins:				
San Clemente Basin	91.7			
Catalina Basin	540.8			
San Nicolas Basin	497.3			
San Diego Trough	264.2			
San Pedro Basin	145.6			
Santa Monica Basin	490.3			
Santa Cruz Basin	213.2			
Santa Barbara Basin	733.2			
Total	2,976.3	25.9	27.4	34.4
Escarpments and canyons:				
Coronado Escarpment and Canyon	37.3			
Catalina Escarpment	99.5			
San Clemente Escarpment	97.4			
San Diego Escarpment	38.9			
San Pedro Escarpment and Redondo Canyon	33.4			
San Nicolas Escarpment	34.2			
Santa Cruz Escarpment and Canyon	75.4			
Santa Monica Escarpment	15.5			
Santa Barbara Escarpment	23.3			
Cortez Escarpment	12.4			
Total	467.3	4.1	24.1	23.7
Slopes		65.2	34.1	32.5

APPENDIX TABLE 2.—Detected targets and target densities for four classes of bottom topography (zone) in the Los Angeles Bight.

Zone and name	No. targets obs.	Linear nautical miles surveyed	Target density (targets/nmi²)
Banks and seamounts:			
Thirtymile Bank	3	12.40	1.79
Fortymile Bank	18	16.99	7.85
Tanner Bank			
Osborn Bank	1	6.19	1.20
San Clemente Bank			
San Nicolas Bank			
Santa Rosa Bank			
Santa Rosa S. Bank			0
Coronado Bank	0	8.0	0.75
Santa Barbara Bank	2	19.8	0
Santa Cruz Bank	0	21.59	0
Lasuen Seamount	14	9.59	10.81
$\overline{\ln x}$ excluding zero values			0.9835
$S_{\ln x}$			1.1758
Basins and troughs:			
San Clemente Basin	43	22.60	14.09
Catalina Basin	84	83.99	7.41
San Nicolas Basin	135	44.19	22.63
San Diego Trough	94	58.19	11.84
San Pedro Basin	4	21.40	1.38
Santa Monica Basin	1	31.59	0.14
Santa Cruz Basin	0	23.4	0
Santa Barbara Basin	0	37.4	0
$\overline{\ln x}$ excluding zero values			1.4325
$S_{\ln x}$			1.9237
Escarpments and canyons:			
Coronado Escarpment and Canyon	1	19.40	0.38
Catalina Escarpment	15	28.19	3.94
San Clemente Escarpment	3	40.39	0.55
San Diego Escarpment	172	51.53	24.73
San Pedro Escarpment and Redondo Canyon	25	19.80	9.35
San Nicolas Escarpment	38	14.99	18.78
Santa Cruz Escarpment and Canyon	4	33.18	0.89
Santa Monica Escarpment	0	11.00	0
Santa Barbara Escarpment	0	12.4	0
Cortez Escarpment	6	6.79	6.55
$\overline{\ln x}$ excluding zero values			1.2431
$S_{\ln x}$			1.6145
Slopes	0	9.40	0
	21	20.19	7.71
	0	6.00	0
	0	6.80	0
	0	5.00	0
	0	7.99	0
	5	22.80	1.62
	0	7.80	0
	4	7.20	4.16
	9	12.39	5.38
	65	30.69	15.69
	46	16.59	20.54
	23	9.00	18.93
	21	6.20	25.09
	7	15.20	3.41
	20	4.00	37.04
	0	3.60	0
	0	3.20	0
	1	55.00	0.13
	0	5.40	0
	22	11.20	14.55
	0	27.20	0
	2	17.20	0.86
	17	15.51	8.12
$\overline{\ln x}$ excluding zero values			1.7850
$S_{\ln x}$			1.5365

APPENDIX TABLE 3.—Target counts by size and midrange detected on an automated survey of the Los Angeles Bight (tracks 1 and 2) during September 1974.

Size (m)	100-150	150-200	200-250	250-300	300-350	350-400	400-450	450-500	500-550	550-600	Total
<5	3	3	6	11	17	6	3	5	7	6	67
6- 15	4	5	7	16	26	18	7	13	14	10	120
16- 25	1	8	11	23	24	16	15	11	17	17	143
26- 35	4	3	4	15	29	21	15	11	22	15	139
36- 45		2	4	9	24	14	11	13	19	11	107
46- 55		1	3	7	8	10	10	10	21	16	86
56- 65		3	2	4	11	2	9	6	16	7	60
66- 75			1	2	7	2	7	8	27		54
76- 85		1		1	1	4	6	5	11		29
86- 95			1	3	3	2	3	2	15		29
96-105					2	2	3	4	15		26
106-115				1	1	3	3	4	8		20
116-125				3	1	2	4	4	7		21
126-135						4	1	5	8		18
136-145				1	2	3		8	7		21
146-155				1		5	5	3	4		18
156-165			1		4	3	2	5	5		20
177-175			1		1		3	6			11
176-185						2	9	11			22
186-195					1	1	11	7			20
196-205				4	1	3	12	8			28
206-215					2	2	11	10			25
216-225					1	5	14	23			43
226-235					2	3	27	25			57
236-245						3	26	22			51
246-255					1	3	31	27			62
256-265						3	34	14			51
266-275						1	21				22
276-285						2	24				26
286-295						1	23				24
296-305				1	1	2	22				26
306-315						3	16				19
316-325				1	1	1	8				11
326-335						3	4				7
336-345						1	1				2
346-355						3					3
356-365						2	1				3
366-375						3					3
376-385						4					4
386-395						1					1
Total	12	26	41	103	171	169	402	270	223	82	1,499

APPENDIX TABLE 4.—Bottom reverberation by detected size, midrange, and target strength from data collected during 2 h in 100 fathoms on 7 September 1974.

Item	Mark	f	Relative %	Item	Mark	f	Relative %
Size	25 m	9	5.4	Midrange	480	15	8.9
	50	24	14.3		500	7	4.1
	75	11	6.5		520	7	4.1
	100	9	5.4		540	1	0.6
	125	8	4.8		560	1	0.6
	150	10	6.0	Target strength	−2dB	1	0.6
	175	18	10.7		−1	1	0.6
	200	26	15.5		0	4	2.4
	225	24	14.3		1	11	6.5
	250	23	13.7		2	18	10.7
	275	6	3.6		3	21	12.4
	300	0	0		4	25	14.8
Midrange	340 m	5	3.0		5	28	16.6
	360	7	4.1		6	25	14.8
	380	6	3.6		7	6	3.6
	400	9	5.3		8	9	5.3
	420	25	14.8		9	7	4.1
	440	44	26.0		10	8	4.7
	460	42	24.9		11	5	3.0

ECONOMIC AND FINANCIAL ANALYSIS OF INCREASING COSTS IN THE GULF SHRIMP FLEET[1,2]

WADE L. GRIFFIN, NEWTON J. WARDLAW, AND JOHN P. NICHOLS[3]

ABSTRACT

The 115 Gulf of Mexico shrimp vessels used in this study were grouped into classes I (larger vessels) through V (smaller vessels) based on their type of construction, length of keel, and index of effort. In 1973, class II vessels were the only vessels able to register a positive return to owner's labor and management, $560; the other four classes registered negative returns. The payback period occurred during the eighth year due to the sale of the vessels in classes II, III, and V, whereas payback did not occur for classes I and IV. A positive rate of return on investment was experienced by the vessels in classes II, III, and V in the amount of 13.21, 2.65, and 2.63%, respectively. The internal rate of return on investment was negative for vessels in classes I and IV.

Input prices increased some 20% from 1973 to 1974 whereas production remained approximately constant and ex-vessel shrimp prices were lower. Thus none of the classes of vessels would have experienced a break-even cash flow for 1974. Increasing input cost another 10% above the 1974 level, and assuming normal production, the average vessel in class II seems to be operating at a better than a break-even level in 1975 assuming ex-vessel shrimp prices remaining constant at 1973 levels. Classes I, III, IV, and V experienced less than break-even cash flows under the same conditions in 1975.

The U.S. economy has faced some strong buffeting in recent years. In spite of temporary wage and price controls and other efforts by the administration, inflation has continued to be a major problem for most sectors. The percentage increases in the wholesale price index (including all commodities) were 4.2% from 1971 to 1972, 13.1% from 1972 to 1973, and approximately 20% from 1973 to 1974 (Board of Governors of the Federal Reserve System 1974). Since inflation can occur at different rates for different products, profit and loss positions in almost every sector or industry in the economy have been affected. Of particular interest to shrimp vessel owners are changes in the price for basic inputs used in the shrimp industry: the price index for fuel, which accounted for approximately 25%of variable costs of shrimp production in 1971 (excluding crew shares) (Hayenga et al. 1974) increased 76% from December 1971 to December 1973; and the price index for lumber, metals, and machinery and equipment (inputs used in the construction of shrimp vessels) jumped 46.5, 19.2, and 7.9%, respectively, during the same period (Board of Governors of the Federal Reserve System 1973).

With regard to prices and production in the Gulf States, in 1973 ex-vessel shrimp prices increased 33% from the 1972 figures, but landings were off from the 1972 levels by 21% (United States Department of Commerce 1974).

Due in part to the economic climate, vessel owners, managers, financial institutions, and marine resource researchers have come to rely heavily upon cost and return data in analyzing investment, financing, and profitability alternatives within the Gulf shrimp industry. But a classification problem exists because of the wide range of combinations of vessel size, construction, power, and fishing capability within the Gulf shrimp fleet and the wide range of variable costs, fixed costs, investment requirements, and profitability associated with the various vessel configurations. It is the purpose of this paper to investigate, for different vessel classes, the profitability of investing in and operating a vessel in the Gulf shrimp fleet based on data collected for the 1973 calendar year, and then with the data adjusted to estimated 1974 and 1975 levels.

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METHODOLOGY

Standard techniques of cost and return, cash flow, and break-even analysis were used in this study. A budget-generating computer program was established to assimilate and report the data according to each of the desired vessel configurations, in the form of total costs and returns budgets, unit costs and returns budgets, and projected cash-flow budgets.

The vessels were classified in terms of their average costs per pound of shrimp landed. An average cost equation was estimated using regression analysis with construction, keel length (U.S. Coast Guard registry), and effort index[4] as dummy variables. Vessels included in the sample were constructed of either wood or steel. Grouping of vessels according to keel length and effort index for use as dummy variables in the regression analysis was based on a natural frequency distribution of the vessels in the sample.

It must be stressed here that this method of classification is simply a means to group the vessels for the purpose of analysis and is not necessarily a criterion for evaluation of the performance of the different classes. Performance or profit depends not only upon unit cost but also upon unit price. Even though one class of vessels may have a higher average cost curve for a given level and type of shrimp produced, it may not necessarily produce less profit. Therefore, while the product produced may be homogeneous with respect to cost of production, it may be heterogeneous with respect to price.

DATA DESCRIPTION

Data Collection and Vessel Description

The cost and return and financial data used in this study were gathered by personal interview with shrimp vessel owners and/or managers operating from ports in Florida, Mississippi, and Texas. Additional financial information was obtained from officials of various lending institutions which engage in shrimp vessel financing. All data were for the period covering the calendar year 1973.

The original sample for this study consisted of 126 vessels. However, due to incomplete data, only 115 vessels were used in the analysis. Vessels in the sample were constructed of wood and steel, with keel lengths of from 45 to 78 feet, and from 104 to 777 horsepower. The ages of the vessels ranged from 1 to 36 yr.

Costs and Returns and Cash Flow Data

Variable cost items were separated into variable costs not directly proportional to catch: ice; fuel; nets, supplies, and groceries; repair and maintenance; and variable costs directly proportional to catch: crew shares, payroll taxes, and packing charges. Actual variable cost data reported by the vessel owners were used except for crew shares, payroll taxes, and packing charges, which were determined on the basis of reported pounds landed and gross revenues. Vessel owners paid their captains and/or crew on the basis of a percentage of pounds landed. This percentage ranged from 30% in the eastern Gulf to 40% in the western Gulf. Thirty-five percent was the average share paid and is used in the analysis.

Fixed cost items were separated into: insurance, depreciation, overhead, interest, and opportunity cost (required return to equity capital). Fixed charges for insurance and overhead are reported data. Charges relating directly to investment—depreciation, interest, required return on equity capital for costs and returns, and principal and interest for cash flow budgets—were standardized in terms of 1973 dollars in order to make valid comparisons. Since most of the vessels included in the sample were purchased new, vessel owners (some of which were shipbuilders) were asked to estimate the replacement value of their

[4]The effort index is defined as the amount of fishing power that a vessel can exert in a day fished relative to that of a standard vessel. The value for the effort index for each vessel was calculated using the formula:

$$EI_i = \frac{(HP)_i^{0.1385} \quad (LFR)_i^{0.4064}}{(38)^{0.1385} \quad (14.6)^{0.4064}}$$

where EI_i = effort index for vessel i, $(HP)_i$ = horsepower for vessel i, $(LFR)_i$ = sum of the lengths of the footropes measured in yards for vessel i, (38) = average horsepower of the smallest class of vessels operating in the Gulf from 1962 to 1971, and 14.6 = average net size measured in yards of footrope used by the smallest class of vessels for the same period [Griffin, W. L., M. L. Cross, R. D. Lacewell, and J. P. Nichols. 1973. Effort index for vessels in the Gulf of Mexico shrimp fleet. (Unpubl. rep. to NMFS, contract no. 03-3-042-19 with the Tex. Agric. Exp. Stn., Tex. A&M Univ.].

vessels in 1973 prices. Depreciation charges were calculated using the straight-line method, based on the estimated 1973 replacement value for each vessel, and using an 8-yr depreciable life with 35% book salvage value. For the amortization schedule, the same 1973 equivalent new vessel costs were used, with 67% of the cost financed at a 9% interest rate, for 8 yr, and with 12 equally amortized payments per year. These terms were found to be representative for 1973 through interviews with officers of financial institutions which engage in shrimp vessel financing. The specific amount of interest reported in each costs and returns budget is for the fifth year of the amortization schedule since the majority of the vessels in the sample taken were from 3 to 6 yr old.

Required return to equity capital is economic rather than financial in concept and is an attempt to place a value on the opportunity cost of the equity capital committed to an investment. At the time an owner invests in a shrimp vessel he has several alternative investments available with various rates of return associated with each. Theoretically these different rates of return are representative of the relative risks associated with each—that is, risk and return vary directly. Because the alternative investment opportunities are different for each owner, in the interests of standardization the rate of interest charged by financial institutions for shrimp vessel financing (9%) was assumed to be the highest alternative rate available to the owners for an investment of equivalent risk and can be adjusted by an individual owner to reflect his own investment alternatives.

A note of explanation is necessary concerning the cash flow budgets and cash flow analysis. Terminal vessel value (sale value) and holding period were established by asking each vessel owner to estimate, in 1973 dollars, what that same vessel would be worth as a used vessel if he had held it for the number of years that he customarily fishes a new vessel. Respondents indicated they fished a new vessel from 3 to 15 yr, with 8 yr being the most frequent response, and that even in periods of relative price stability an 8-yr-old shrimp vessel is worth approximately 65% of its original cost. Furthermore, that difference between the 35% book value for depreciation purposes and the 65% terminal value is evidenced by the frequency of income taxes levied on vessel owners for depreciation recapture at the time of replacement. For those reasons, an 8-yr holding period and a 65% terminal value were used in the cash flow budgets.

RESULTS

Classification of Vessels

Vessels were grouped according to construction, keel length, and effort index (Table 1). All vessels in the sample were either wood or steel. Vessels were divided into three keel length intervals: 45-62 feet, 63-69 feet, and 78-80 feet. The range of effort indices was divided into three intervals: 1.64-1.89 units, 1.90-2.19 units, and 2.20-2.51 units. Using these groupings for classification, 12 combinations were possible and the vessels in the sample fell into 9 of those possible combinations (See Appendix).

Predicted average cost values for the 115 vessels were plotted and vessels were classed into five general categories as shown in Table 1, where class I is the highest cost curve and class V is the lowest. Classes I and II, the two highest cost curves, consist entirely of steel vessels whereas classes III, IV, and V consist entirely of wooden vessels. The position of the average cost curves seem to be related to vessel length for each type construction except for class IV which includes two length intervals.

These results are not surprising. Previous research by Nichols and Griffin (1974) indicated that smaller, less powerful wooden vessels can produce a given quantity of shrimp at a lower cost than can a larger, more powerful steel vessel. As a matter of fact, their research showed that a 50% reduction in total effort exerted by the shrimp fleet would only reduce total catch by about 10%.

For the 4-yr period, 1962-65, the average vessel exerted about 1.16 units of effort in a day fished

TABLE 1.—Classification of Gulf of Mexico shrimp vessels, based on construction, keel length, and effort index from a sample of 115 vessels, 1973.

Vessel class	Construction	Keel length (feet)	Effort index (units)
I	Steel	70-78	1.90-2.19
			2.20-2.51
II	Steel	63-69	1.90-2.19
			2.20-2.51
III	Wood	63-69	1.90-2.19
			2.20-2.51
IV	Wood	45-62	1.90-2.19
		63-69	1.64-1.89
V	Wood	45-62	1.64-1.89

and the annual landings per vessel were 31,700 pounds of shrimp (heads-off). However, in the 4-yr period, 1970-73, the average vessel exerted about 1.68 units of effort in a day fished and the annual landings were only 28,900 pounds (heads-off). The average length of the vessel operating in the Gulf also increased over time (Nichols and Griffin 1975). Thus, as additional effort has been added to the Gulf of Mexico shrimp fishery—by increasing the number of vessels and/or the average size of the vessel—the total pounds landed have been divided between more and more units of effort.

From these figures it is apparent that the average Gulf of Mexico shrimp vessel has been increasing in size and relative fishing power and the annual landings per vessel have declined. Due to the lower investment levels and lower operating costs of smaller, less powerful vessels it follows that those smaller vessels could produce a pound of shrimp at a lower unit cost than could a larger, more powerful vessel if both were fishing the same or equally abundant fishing grounds. However, two distinctions and/or disadvantages of the smaller vessels compared to larger vessels must be noted here. First, as discussed earlier, shrimp is not a homogeneous product, and larger shrimp command higher ex-vessel prices than do smaller shrimp. Because the larger shrimp are usually associated with deeper waters, farther out in the Gulf, a smaller vessel with less capacity both for deepwater trawling and for holding fuel and shrimp is at a disadvantage compared with a larger vessel because of that depth and distance from shore.

The second distinction, and associated with the first, is the fact that larger vessels are better able to operate in and cope with rougher seas and the frequent storms in the Gulf than are smaller vessels. Therefore, the smaller vessels would either be forced to trawl closer to shore for smaller, less valuable shrimp, or for a given period of time in the deeper fishing grounds with typical weather conditions, the smaller vessels would not be able to realize as many actual fishing hours as a larger vessel operating in the same waters during the same period of time.

Comparison of Classes

Table 2 shows a summary of the costs and returns, equity requirements, payback period, and internal rate of return for the five classes of shrimp vessels operating in the Gulf of Mexico in 1973 (a more detailed break down of cost is available from the authors). Class I vessels received the highest price per pound, $2.03, for the shrimp landed but produced 5,500 pounds less shrimp than the smaller class II vessels. Class I vessels also had the highest levels of variable costs not proportional to catch, $45,152, the highest fixed costs, $31,906, and the highest total costs, $108,291, of any of the general classes. These cost relationships were to be expected since the larger steel vessels should have the highest initial investment requirements and operating costs. Due to low production and high cost, these vessels averaged the greatest loss for the year, $20,704, and payback did not occur. The internal rate of return on investment was negative.

TABLE 2.—Summary of costs and returns information, net present value analysis, and pay back period for five classes of shrimp vessels operating in the Gulf of Mexico in 1973.

Item	Vessel class				
	I	II	III	IV	V
Number of vessels	14	28	48	15	10
Catch (pounds)	43,146	48,602	39,170	30,716	30,950
Gross revenue:					
Per pound ($)	2.03	1.89	1.93	1.65	1.55
Total ($)	87,587	91,802	75,764	50,770	48,044
Cost:					
Variable					
Not proportional to catch ($)	42,152	31,694	28,134	22,835	16,784
Total ($)	77,195	68,600	58,543	43,444	36,385
Fixed ($)	31,096	22,642	22,231	18,550	15,296
Total ($)	108,291	91,242	80,774	61,994	51,681
Returns above variable cost ($)	10,392	23,202	17,221	7,326	11,659
Net revenue ($)	-20,704	560	--5,010	-11,224	-3,637
Equity requirement ($)	47,407	38,921	30,630	24,200	22,176
Payback period (yr)	(1)	(2)	(2)	(1)	(2)
Internal rate of return (%)	(3)	13.21	2.65	(3)	2.63

[1]Does not occur.
[2]Does not occur through operations—payback in the eighth year is due to sale of the vessel.
[3]Less than 0%.

Class II vessels had the highest landings, 48,602 pounds, of the five classes of vessels. They also had the highest gross revenues even though the average price per pound received was $0.14 less than class I vessels. They did experience relatively high total costs, yet the variable costs not proportional to catch, the "manageable" variable costs, were $10,500 less than class I. Class II vessels were able to register a positive return to owner's labor and management of $560—the only one of the classes to achieve that. Payback occurred only with the sale of the vessel in the eighth year. The internal rate of return on investment was 13.21%, which was the highest of the five classes.

Class III was the most populous class. Gross revenue was approximately $15,000 below and total costs were about $10,500 below those of class II vessels. The difference in the total costs was due to costs directly proportional to catch—a reflection of the fact that class III vessels caught roughly 9,000 pounds less shrimp than did the class II vessels. Class III vessels had a negative net return of $5,010. The internal rate of return on investment was 2.65% and payback occurred during the eighth year only with the sale of the vessel.

Class IV vessel production was about 9,000 pounds less than class III vessels and the price per pound was about $0.30 less, so that gross revenue was $25,000 lower for the class IV vessels. Variable costs not directly proportional to catch were roughly $5,000 lower, and total cost was $19,000 less for class IV vessels than for class III vessels. Because of the low level of production and gross revenues, class IV vessels had the second greatest net loss, $11,224, of any of the five classes, and payback did not occur. The internal rate of return on investment was negative.

Class V vessels reached roughly the same level of production as did class IV vessels, but at $6,000 lower variable costs not directly proportional to catch. Comparison of the returns above variable costs shows class V vessels contributed over $4,000 more towards fixed costs than did class IV, while receiving some $2,000 less in gross revenues. Net revenue was a negative $3,637, but was still the second highest with respect to the other four classes. Payback occurred in year 8 only with the sale of the vessel and the internal rate of return on investment was 2.63%.

Financial Analysis with Cost Adjusted to 1974 and 1975

Fishing for shrimp in the Gulf of Mexico in 1973 was definitely not an enterprise in which profits could be achieved across the board. Figure 1 shows the break-even undiscounted cash flow analysis for each of the five vessel classes, based on 1973 costs and for costs updated to 1974 and 1975. Costs for 1974 were calculated by increasing all cost items (fixed and variable) by 20%[5] except fuel and new vessel cost. Because fuel represents such a large portion of a vessel's operating costs, it was treated separately and increased from 18 to 32 cents per gallon. New vessel cost was held constant at 1973 levels since there has not been a significant number of vessels entering the industry since 1973. Inflation is expected to continue to increase at a rate between 5 and 15%; therefore, 1975 costs were increased by 10% over 1974 levels with the exception of new vessel prices. For comparison purposes the vertical dashed lines, labeled 1973, indicate the 1973 average landings and the horizontal dashed lines indicate the 1973 average ex-vessel price received for each vessel class.

1974 Analysis

Input prices continued their upward trends in 1974. At the same time landings showed approximately a 2% improvement over the 1973 levels, but shrimp prices fell by approximately 20%; the combined effect was a 15% drop in the value of shrimp produced in the Gulf of Mexico in 1974.[6] Figure 1 explains graphically the ramifications of such conditions on the undiscounted break-even cash flows for each of the five vessel classes. As the graphs show, none of the classes would have experienced a break-even cash flow for 1974 given the 20% decrease in shrimp prices and minimal increase in landings over the 1973 levels. This of course means that none would

[5]Based on the July 1974 wholesale price index including all commodities (Board of Governors of the Federal Reserve System 1974).

[6]Total Gulf of Mexico shrimp landings (heads-off) in 1973 were 114.8 million pounds, average ex-vessel price per pound received was $1.50 and the value was $171.7 million (United States Department of Commerce 1974). Landings for the same period in 1974 were 116.9 million pounds, the average ex-vessel price per pound was $1.18, and the value of the landings was $137.4 million (United States Department of Commerce 1974-75).

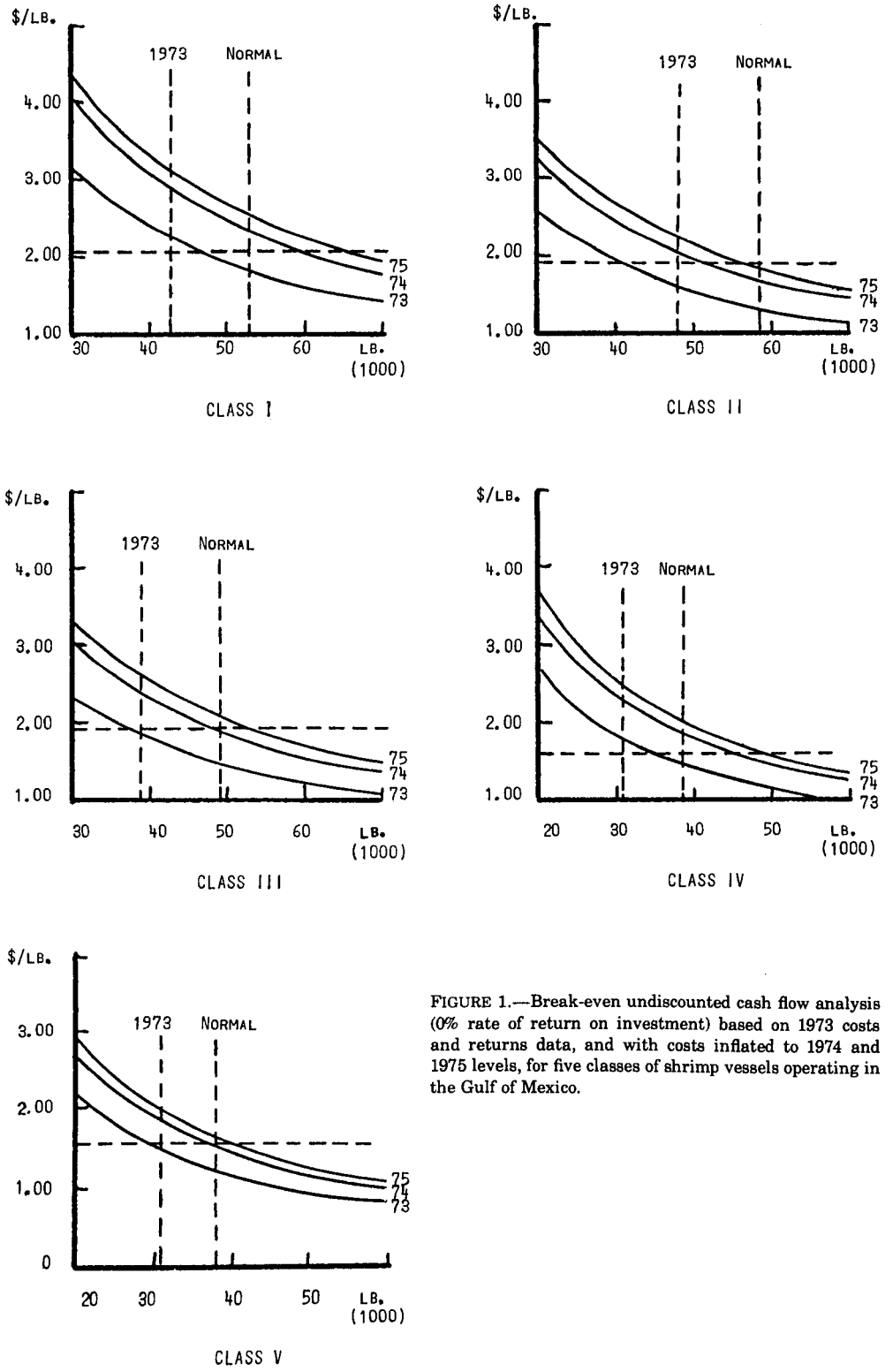

FIGURE 1.—Break-even undiscounted cash flow analysis (0% rate of return on investment) based on 1973 costs and returns data, and with costs inflated to 1974 and 1975 levels, for five classes of shrimp vessels operating in the Gulf of Mexico.

have registered a positive return on investment. As a matter of fact, the class II vessels, which had the highest rate of return in 1973, would have had to receive approximately $2.20 per pound of shrimp landed to achieve a break-even investment (0% internal return on investment) if annual production of shrimp is held constant at the 1973 level of 48,602 pounds. Since they only received $1.89 per pound in 1973 and prices declined in 1974, investment in a class II vessel in 1974 would have yielded a negative rate of return on investment.

1975 Analysis

If inflation continues at a 10% rate in 1975, and production remains at approximately the 1973 level, Figure 1 indicates that ex-vessel prices would have to increase to approximately $3.10, $2.25, $2.65, $2.50, and $2.00 per pound of shrimp landed for vessel classes I, II, III, IV, and V, respectively, to achieve even a zero internal rate of return on investment. Or, on the other hand, with prices remaining constant at the 1973 level, production would have to increase to approximately 66,000, 57,000, 52,000, 49,000, and 40,000 pounds of shrimp landed per vessel, respectively.

However, based on production functions estimated by Nichols and Griffin (1974) for the Gulf of Mexico shrimp fleet where catch is a function of effort, 1973 production of shrimp from the Gulf was below normal. Average annual landings for the vessels in the sample were estimated in a normal year to be approximately 53,000, 59,000, 49,000, 37,000, and 38,000 pounds of shrimp landed per vessel for classes I, II, III, IV, and V, in that order. The vertical dashed lines in Figure 1 labeled "normal" indicate the average landings for each class of vessel for the normal production year.

The average vessel in class II seems to be operating at better than a break-even level in 1975 assuming normal production and 1973 ex-vessel prices for shrimp. That is, given normal production, class II vessels would have to receive $1.85 per pound for shrimp landed in 1975 while the 1973 average price for the class was $1.89 per pound. But, a new vessel cost of $130,000 would be just enough to set this cash flow at the break-even level and the replacement of a class II type vessel is estimated to be in excess of $150,000 in 1975.

From the graphs in Figure 1 it is obvious that none of the other classes (I, III, IV, V) are operating at the break-even level assuming a normal production year and 1973 average shrimp prices and new vessel costs. In order to bring the cash outflows down to the levels necessary to achieve break even, class III-type vessel owners could only invest approximately $30,000 in a new vessel in 1975, and class V owners could invest no more than $40,000. To reiterate, these break-even levels represent a zero internal rate of return on investment. Significantly, class I and class IV-type vessel owners could not achieve the breakeven level even with a zero investment requirement.

DISCUSSION AND IMPLICATIONS

The resolution of problems facing the Gulf shrimp industry may come about as a result of changing economic conditions and/or changes in specific policies which may or may not be initiated or suggested by the industry. A number of possible changes have been suggested which bear consideration.

One suggestion has been a fuel subsidy for the fishing industry. This would be a direct saving to vessel owners on the largest single input cost item. Assuming a normal production year, it would take a subsidy of 35, 13, 48, and 15 cents per gallon for classes I, III, IV, and V, respectively, to break even with a zero return on investment assuming prices stayed constant at the 1973 level. Chances of obtaining any relief in this area are very slim. At best, the extent of such relief would likely be limited to future increases related to oil import taxes. Current fuel expenses would probably not be reduced.

Efforts to improve the efficiency of fishing operations are also a priority consideration. The operation of fishing vessels during periods of marginal profitability required improved management and closer consideration of the effects of the day-to-day decisions in running the vessel.

Import quotas and tariffs are one suggested alternative to the current cost-price squeeze in the industry. By controlling imports it is anticipated that supplies on the market can be reduced thus preventing prices from being depressed below the domestic producer's costs. The goals of free trade and stabilized or lower consumer prices may make approval of the necessary controls through the political process difficult to realize.

Market expansion and development programs have also been suggested as a means of shifting demand and increasing prices. Market development is a long term process and the industry should commit itself to such a program. This suggests a greater continuity of programs than the occasional reaction to crisis situations which are evident in the recent history of the industry.

A much larger question has been introduced in this discussion of economic efficiency. Industry sources have indicated a concern that the industry has become overcapitalized in shrimp trawling vessels. One classic solution to this is a total fisheries management scheme which includes a limited entry concept. Other conditions assumed equal, this would increase catch per unit of effort and would result in lower costs per unit of shrimp landed. This is not a short-run solution, however. It is only now being experimented with in U.S. fisheries. A great deal of planning and information would be needed to design and implement such a program.

Long-run problems of limited entry include the possibility of creating a stagnant, protected industry which loses touch with both the consumer market and the market for resources. In the long-run this may be more detrimental than going through periodic readjustments such as that which the industry currently faces.

If it can be assumed that the relative positions of the unit cost and revenue curves remain constant in the future and assume normal production years, then based on the sample size of each vessel class, the percentage reduction in vessels needed for break even can be calculated. Using class I as an example, in a normal year, the 14 vessels in class I would have landed a total of 742,000 pounds of shrimp. To experience a break-even rate of return, each vessel would have to land 66,000 pounds of shrimp. Dividing 66,000 pounds per vessel into 742,000 pounds implies that class I's total production of 742,000 pounds could only support approximately 11 vessels or 79% of the vessels sampled.[7]

CONCLUSIONS

The major conclusion from the analysis presented here is that investment in a shrimp trawler is unprofitable assuming the environment existing in 1973 when these data were collected and for which the average relationships were estimated. The analysis permits tracing the effects of altered assumptions regarding average prices and vessel landings on profitability. Only class II vessels showed profits under the 1973 conditions.

The shrimp industry is undergoing considerable economic stress. The underlying causes relate to factors in the general economy beyond industry control and the rapid expansion in potential fishing effort which occurred during the period since the late 1960's. Means of coping with this stress include both improved management to reduce costs and various forms of government programs will be necessary to permit the implementation of some of these ideas.

Perhaps some would prefer to allow a period of significant readjustment forcing the marginal firms to leave the industry. The costs of this readjustment, both economic and social, must be considered by those who propose this solution. Several things could happen which would prevent a significant readjustment: landings could increase dramatically, the economy could recover quickly thus improving demand and prices, or input costs could decline. However, these things may not happen soon enough to avoid the difficult readjustment problems.

[7]It is obvious that if the total Gulf shrimp fleet were reduced to 79% of its current size, total production would also decrease. That is, the estimated reduction in the fleet should be adjusted with respect to the production function. However, calculations using the production function made less than a 1% difference.

LITERATURE CITED

BOARD OF GOVERNORS OF THE FEDERAL RESERVE SYSTEM.
1973. Federal Reserve Bulletin. Div. Admin. Serv., Board Gov. Fed. Res. Syst., Wash., D.C. 59:837-A119.
1974. Federal Reserve Bulletin. Div. Admin. Serv., Board Gov. Fed. Res. Syst., Wash., D.C. 60:683-A88.

HAYENGA, W. A., R. D. LACEWELL, AND W. L. GRIFFIN.
1974. An economic and financial analysis of Gulf of Mexico shrimp vessels. Tex. Agric. Exp. Stn., Misc. Publ. 1138, 14 p.

NICHOLS, J. P., AND W. L. GRIFFIN.
1974. Recent trends in catch and fishing effort in the Gulf of Mexico shrimp industry and economic implications. Dep. Agric. Econ. Inf. Rep. 74-5 SP-1. Texas A&M Univ., College Station.
1975. Trends in catch-effort relationships with economic implications : Gulf of Mexico shrimp fishery. Mar. Fish. Rev. 37(2):1-4.

UNITED STATES DEPARTMENT OF COMMERCE.
1974. Fisheries of the United States, 1973. Curr. Fish. Stat. 6400, 106 p.
1974-75. Gulf coast shrimp data. Curr. Fish. Stat. 6442, 6462, 6503, 6523, 6544, 6564, 6593, 6613, 6633, 6652, 6671.

WARDLAW, N. J., III, AND W. L. GRIFFIN.
1974. Economic analysis of costs and returns for Gulf of Mexico shrimp vessels: 1973. Dep. Agric. Econ. Tech. Rep. 74-3, Tex. Agric. Exp. Stn., Tex. A&M Univ., College Station.

APPENDIX

Average cost equations were estimated using ordinary least squares regression analysis for each of the nine groups of vessels by the use of linear, quadratic, and log linear functions. In general, considering all nine equations, the log linear model gave the best statistical results whereas the quadratic gave the worse. This implies that the average cost curves were ever decreasing over the range of the data available. Predicted values from the log linear model for the nine equations were plotted by the computer on one graph and compared. Because all nine plots were relatively parallel, economies of scale did not exist over the range of the sampled data.

Since the plotted predicted values were relatively parallel, one average cost equation was estimated using construction, length, and effort as dummy variables. All three were statistically significant variables at least at the 95% level of confidence in explaining the average costs of producing shrimp. For a more detailed discussion see Wardlaw and Griffin (1974).

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LONG-TERM FLUCTUATIONS OF EPIBENTHIC FISH AND INVERTEBRATE POPULATIONS IN APALACHICOLA BAY, FLORIDA

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ABSTRACT

A 3-yr study was made concerning seasonal changes in the biota of Apalachicola Bay. The Apalachicola River causes a temporal progression of changes of various environmental parameters in the bay such as salinity, turbidity, nutrients, and detritus levels. Fishes were more widespread in their distribution throughout the bay than invertebrates. This was thought to be related to trophic response and habitat preference. High levels of relative dominance prevailed for both groups with the top three species of each group accounting for more than 80% of the total number of individuals taken.

Peak levels of monthly abundance of various dominant fish species tended not to overlap through a given 12-mo period. Invertebrate species abundance usually reached peak levels during summer and fall periods. The seasonal appearance and distribution of organisms in the Apalachicola Bay system was comparable to that found in other estuaries in the northern Gulf of Mexico. The temporal and spatial distribution of estuarine fishes and invertebrates was associated with species-specific reproductive cycles, trophic relationships, and habitat preferences. The Apalachicola estuary was viewed as a seasonally stable system, with regular temporal fluctuations of the biota through each annual cycle.

There is a rapidly growing literature concerning fluctuations of populations of epibenthic estuarine organisms (Dahlberg and Odum 1970; Bechtel and Copeland 1970; Copeland and Bechtel 1971; McErlean et al. 1973; Oviatt and Nixon 1973; Copeland and Bechtel 1974; Gallaway and Strawn 1974; Livingston 1975). Haedrich and Haedrich (1974) noted that seasonal changes of fish populations in a Massachusetts estuary allow more species to utilize the estuary than if there were constant direct competition. Staggered reproductive cycles were postulated as a partial explanation for this "dynamic situation." Trophic variability was also considered a mechanism for reduced competition. Copeland and Bechtel (1974) identified key environmental requirements for six Gulf coast species, and considered such limits as potential criteria for estuarine management programs. Oviatt and Nixon (1973) noted that although fish biomass remained constant throughout the year, individual species abundance varied seasonally. They found that biomass and numbers of individuals could not be accounted for on the basis of physical parameters alone, and it was considered that biological functions such as competition and predation could be more important determinants of species distribution in estuarine systems.

The present study is part of a comprehensive field program in Apalachicola Bay, Fla. (Livingston et al. 1974). This is a relatively unpolluted, shallow coastal estuary bounded by barrier islands. The bay is physically dominated by the Apalachicola River (Estabrook 1973; Livingston et al. 1974). This paper is concerned with long-term, seasonal fluctuations of epibenthic fish and invertebrate populations, and the possible interrelationships of the physicochemical and biological elements of the Apalachicola Bay system.

MATERIALS AND METHODS

Field Operations

A detailed description of the sampling methodology is already available (Estabrook 1973; Livingston et al. 1974). Physicochemical and biological samples were taken monthly from March 1972 to February 1975 at a series of stations in East Bay and Apalachicola Bay (Figure 1). Water samples were taken at the surface and

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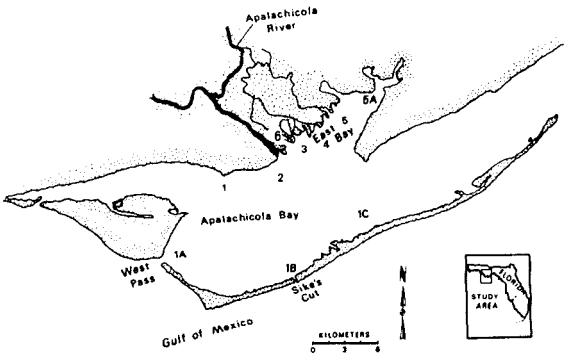

FIGURE 1.—The Apalachicola Bay system with permanent sampling stations for long-term studies concerning fluctuations of populations of epibenthic fishes and invertebrates.

bottom with a 1-liter Kemmerer bottle. Temperature was measured with a stick thermometer and/or a YSI[2] dissolved oxygen meter. Salinity was determined with a temperature-compensated refractometer periodically calibrated with standard seawater. Color was measured with a (Hach) American Public Health Association platinum-cobalt standard test while turbidity was determined with a Hach model 2100A turbidimeter. Light penetration readings were taken with a standard Secchi disk. River flow data were provided by the U.S. Army Corps of Engineers (Mobile, Ala.) while local climatological information was provided by the Environmental Data Service, NOAA, U.S. Department of Commerce.

Biological collections were made with 5-m (16-foot) otter trawls (¾-inch mesh wing and body; ¼-inch mesh liner). Repetitive, 2-min trawl tows were taken at each station at speeds of 2-3 knots. Seven subsamples were taken at stations 1, 2, 4, 5, and 6 while two samples were taken at stations 1A, 1B, 1C, 3, and 5A. All organisms were preserved in 10% Formalin, sorted and identified to species, measured and/or counted (standard length for fishes; total length for shrimps; carapace width for blue crab, *Callinectes sapidus*). Stations 1 and 4 were also sampled at night, approximately 1-2 h after sunset for the first 2 yr of the study.

All statistical analysis was carried out using an interactive computer program designed for the study of extensive data collections. The extent of interstation community similarity was tested using the C_λ index of overlap (Morisita 1959; Horn 1966). This index determines the probability that two randomly drawn samples from populations X and Y will be the same species relative to the probability that two individuals of the same species will be drawn from population X or Y alone.

$$\lambda_x = \frac{\sum_{i=1}^{S} x_i^2}{X^2} \qquad \lambda_y = \frac{\sum_{i=1}^{S} y_i^2}{Y^2}$$

$$C_\lambda = \frac{2\sum_{i=1}^{S} x_i y_i}{(\lambda_x + \lambda_y)\,XY}$$

where S = number of species
x_i and y_i = number of individuals of the ith species in populations X and Y
X and Y = total number of individuals in the two communities
λ_x and λ_y = measures of diversity (Simpson 1949) as modified for sampling with replacement (Horn 1966).

Values for this index range from 0 (no species in common) to 1. A hierarchical (stepwise) multiple regression analysis was carried out using monthly population size as the dependent variable. Various physicochemical and biological parameters (temperature, salinity, chlorophyll *a*, turbidity, color, Secchi disk depth, total depth, local rainfall, wind speed and direction, tidal stage, river flow, and dissolved oxygen) were used as the independent variables. All such functions were tested in the same month of collection and with a 1-mo lag in the physicochemical parameters. Due to the relatively high number of independent variables, the stepwise regression was used whereby one variable at a time was systematically introduced into the equation, and, at each step, the variable added was the one giving the greatest increase in the multiple correlation coefficient. While not necessarily giving the "best" equation, this method is computationally feasible, and frequently gives results comparable to methods that would determine all possible regressions. Since the salinity, color, and turbidity

[2]Yellow Springs Instrument Co. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

data had skewed distributions, logarithmic transformations were used for such variables to approximate normality.

RESULTS

Physicochemical Parameters

Depths of the various stations ranged from 1 to 2.5 m. With the exception of shallow areas, such as station 6, which are characterized by periodically moderate concentrations of widgeon grass, *Ruppia maritima*, East Bay has a silty-sand bottom with little benthic macrophyte development. Stations proximal to river drainage (stations 2-4) are marked by strong currents and seasonally high deposits of allochthonous detritus (leaf litter, branches, etc.). Except for shallow fringing areas, Apalachiocola Bay (stations 1, 1A-1C) has little benthic macrophyte development; it is dominated by silty-sand bottom with interspersed oyster bars.

The Apalachicola River is a major determinant of the physical environment of the bay system. There is a seasonal fluctuation in flow with peak levels occurring during winter and spring months. Local rainfall, with peaks during late summer and early fall, is out of phase with this pattern. During the present period of study, river flow determined salinity throughout the bay. Mean salinity in East Bay was lower than that in Apalachicola Bay; oligohaline areas (stations 5A, 6) were without measureable salinity from midwinter to early summer. Outer bay stations had higher salinities; at station 1B, the salinity did not go below 15‰ during the 3-yr study. During periods of increased salinity, the shallow bay system was vertically stratified (Estabrook 1973; Livingston et al. 1974). However, there was little horizontal or vertical variability in water temperature at any given time. Low temperatures occurred during the winter months. Turbidity levels were relatively high throughout the bay, and were directly related to river flow rates. Color levels reflected both river flow and proximity to land runoff, with elevated levels in East Bay areas during the summer. Although there were various complex physical changes in different areas of the bay due to basin physiography, local runoff, tidal currents, depth, etc., the major habitat features of the Apalachicola Bay system were determined by river conditions.

Distribution of Fishes and Invertebrates

Similarity coefficients (cumulative, by station) are shown in Table 1. Species such as bay anchovy, *Anchoa mitchilli*; Atlantic croaker, *Micropogon undulatus*; and sand seatrout, *Cynoscion arenarius*, were dominant throughout the sampling area. Others such as scaled sardine, *Harengula pensacolae*, and Gulf menhaden, *Brevoortia patronus*, were taken primarily in East Bay. High interstation similarity of species assemblages of fishes was noted, although grass bed areas such as station 6 were characterized by higher numbers of species than other (mud-flat) stations. There was increased spatial variability among the invertebrate assemblages. Species such as the blue crab and the penaeid shrimps (*Penaeus setiferus*, *P. duorarum*) were more evenly distributed throughout the system than others. Grass shrimps (*Palaemonetes pugio, P. vulgaris, P. intermedius*) were more frequently taken in the grass beds of East Bay while the brief squid, *Lolliguncula brevis*, was a dominant species in Apalachicola Bay. High levels of species similar-

TABLE 1.—C_λ values (by station) for invertebrates and fishes taken in the Apalachicola Bay system (March 1972-February 1975).

Station		Station 1 Day	Station 1 Night	1A	1B	1C	2	3	4 Day	4 Night	5	5A	6
							Fishes						
1 day			0.96	0.94	0.79	0.95	0.97	0.80	0.92	0.99	0.94	0.95	0.93
night		0.63		0.76	0.52	0.95	0.87	0.58	0.77	0.95	0.79	0.83	0.85
1A		0.85	0.54		0.93	0.84	0.95	0.93	0.96	0.69	0.96	0.97	0.80
1B		0.36	0.29	0.22		0.65	0.84	0.94	0.88	0.73	0.98	0.87	0.91
1C		0.57	0.46	0.86	0.91		0.94	0.67	0.84	0.95	0.89	0.90	0.78
2		0.82	0.34	0.58	0.22	0.23		0.85	0.94	0.96	0.95	0.97	0.94
3		0.68	0.53	0.50	0.15	0.31	0.49		0.95	0.78	0.95	0.91	0.84
4 day	Invertebrates	0.96	0.54	0.73	0.20	0.38	0.92	0.68		0.91	0.99	0.98	0.92
night		0.87	0.90	0.69	0.24	0.69	0.62	0.69	0.82		0.93	0.94	0.93
5		0.74	0.25	0.53	0.10	0.19	0.98	0.41	0.85	0.50		0.98	0.92
5A		0.84	0.36	0.58	0.09	0.58	0.97	0.54	0.94	0.64	0.97		0.96
6		0.23	0.20	0.16	0.06	0.09	0.16	0.79	0.28	0.25	0.17	0.21	

ity were noted among river-dominated and East Bay stations (1, 2, 4, 5, 5A); outer bay stations (1A, 1B, 1C) also were somewhat alike according to the C_λ similarity analysis. Station 6, as a grass-bed area, differed from most of the other collections. Station 1B, with consistently higher salinity than the other stations, differed in terms of invertebrate species composition. These data indicate that fishes are more widespread in their distribution throughout the bay system than the invertebrates, which were more habitat-specific with respect to substrate, salinity, etc.

Seasonal Fluctuations of Dominant Species

Comparative dominance figures for the 10 most numerous fish and invertebrate species are given in Table 2. Relative dominance is high in both groups with the top three species of fishes and invertebrates constituting 77.0 and 80.7% of the respective combined totals. Some species such as *H. pensacolae, B. patronus,* and Atlantic threadfin, *Polydactylus octonemus*, were found during limited periods (April 1973, April 1974, and May-August 1973, respectively). Seasonal variations in the six dominant species are shown in Figure 2. The most conspicuous species was *A. mitchilli*, which was particularly abundant during the first year of study. Peaks of numbers usually occurred during fall or early winter (October-January). With *M. undulatus*, peak levels usually were noted during late winter or early spring (February-March) whereas *C. arenarius* reached abundance during late spring and summer months (usually around August). The sea catfish, *Arius felis*, usually peaked by midsummer (July) while Atlantic bumper, *Chloroscombrus chrysurus*, and southern kingfish, *Menticirrhus americanus*, were prevalent during late summer or early fall (August-October). The spot, *Leiostomus xanthurus*, usually peaked during winter and spring months; silver perch, *Bairdiella chrysura*, had a variable abundance curve. Overall, there was considerable regularity in the appearance of the dominant bay fishes even though there was often a marked within-species variation in total numbers from year to year.

TABLE 2.—The 10 dominant species of fishes and invertebrates taken in the Apalachicola Bay system from March 1972 to February 1975. Figures are expressed in percentages of total numbers of individuals.

Fish	%	Invertebrate	%
Anchoa mitchilli	42.3	*Penaeus setiferus*	40.1
Micropogon undulatus	26.0	*Palaemonetes pugio*	20.4
Cynoscion arenarius	8.7	*Callinectes sapidus*	20.2
Leiostomus xanthurus	5.4	*Penaeus duorarum*	5.3
Harengula pensacolae	2.6	*Lolliguncula brevis*	4.3
Bairdiella chrysura	1.6	*Penaeus aztecus*	2.6
Chloroscombrus chrysurus	1.5	*Neritina reclivata*	1.5
Polydactylus octonemus	1.4	*Portunus gibbesii*	1.1
Arius felis	1.3	*Palaemonetes vulgaris*	0.8
Brevoortia patronus	1.2	*Rhithropanopeus harrisii*	0.5

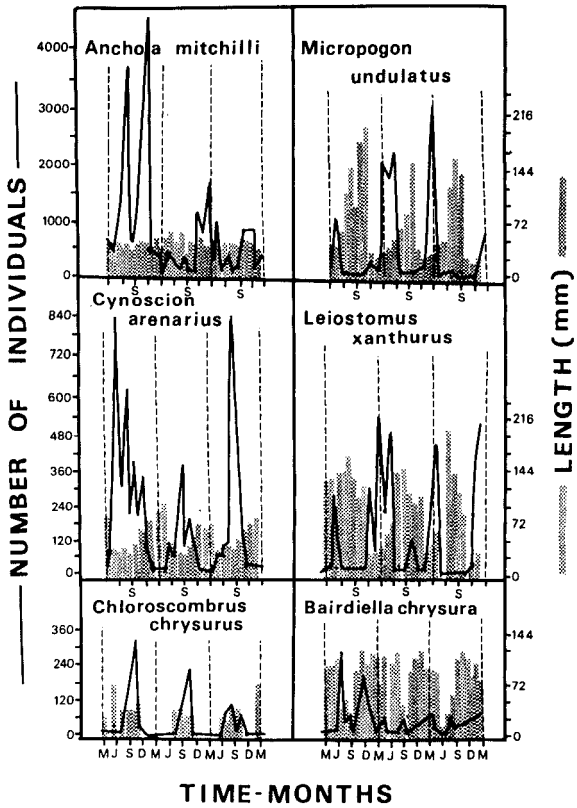

FIGURE 2.—Seasonal changes of numbers of individuals and mean size of six dominant species of fishes taken in the Apalachicola Bay system from March 1972 to February 1975.

Annual fluctuations of the dominant invertebrate species are shown in Figure 3. The white shrimp, *Penaeus setiferus*, was prevalent from August to November with autumn peaks of abundance; the other penaeids usually reached high numbers in the late spring (*P. aztecus*) or late summer (*P. duorarum*). *Palaemonetes pugio* was usually found in the bay during spring months (March-May) while *P. vulgaris* reached high numbers in November. The blue crab peaked during summer and winter periods. Early summer and fall peaks were noted for *Lolliguncula*

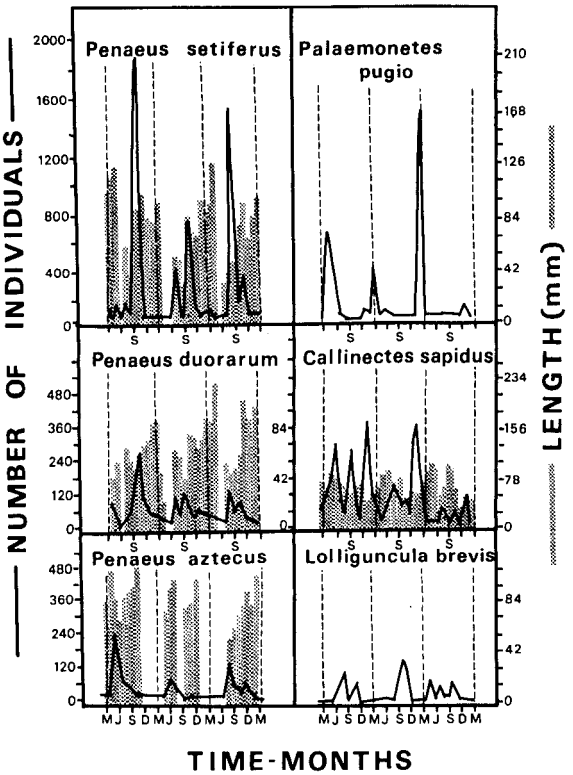

FIGURE 3.—Seasonal changes of numbers of individuals and mean size of six dominant species of invertebrates taken in the Apalachicola Bay system from March 1972 to February 1975 (*Palaemonetes pugio* and *Lolliguncula brevis* were not measured).

brevis. Unlike the fishes which usually reached peak levels during different months of the year, the invertebrates tended to increase in numbers during spring and fall periods.

Annual peaks of abundance often coincided with influxes of juvenile fishes and invertebrates. A more detailed analysis of this is shown for two representative species of fishes (Figure 4) and invertebrates (Figure 5). The young stages of *Micropogon undulatus* entered the bay during the winter at which time there was a continuous recruitment for several months. Decreased numbers coincided with gradual increases in size during spring and summer months. With *Cynoscion arenarius*, recruitment of young occurred during spring and summer, with subsequent increases in size during fall and winter months. The blue crab had peaks of young individuals during summer and winter periods although an almost continuous succession of young crabs entered the bay during the year. Young stages of *Penaeus setiferus* were found during the summer with growth occurring through fall and winter. The other penaeid shrimps had similar growth patterns with recruitment of the young during summer and fall periods. The data indicate that various patterns of recruitment and growth occur among the different estuarine species, although the inverse relationship of numbers and size appears to hold for most of the dominants.

Results of the regression analysis are shown in Table 3. Factors such as chlorophyll *a*, Secchi disk readings, and color repeatedly accounted for some of the variability associated with fluctuations of estuarine populations. Often such associations were made with a 1-mo lag in the independent variable. In most cases, the given independent variables accounted for less than 50% of the variability of the population data. There was a distinct correlation with factors related to trophic phenomena such as chlorophyll *a* and Secchi disk readings; this would indicate that biological functions such as feeding behavior and reproduction could play an important role in the determination of population shifts in the Apalachicola Bay system. These data indicate that no single set of forcing functions can account for the population changes of various estuarine species. Species abundance is dependent on complexes of interactions and possibly can be accounted for more adequately by relating such processes to dynamic changes in physical variables as well as important biological parameters. It is obvious that regression analysis cannot account for changes in

TABLE 3.—Results of the stepwise regression analysis of various independent parameters and species (population) occurrence in the Apalachicola Bay system from March 1972 to February 1975. Independent variables are listed by order of importance with R^2 expressed as a cumulative function of the given parameters.

Species	Independent variables	R^2
Anchoa mitchilli	Chlorophyll *a*, Secchi	0.38
Micropogon undulatus	River flow (lag), Secchi (lag)	0.46
Cynoscion arenarius	Chlorophyll *a*, wind, Secchi (lag), temp	0.83
Polydactylus octonemus	Chlorophyll *a* (lag), salinity, Secchi	0.58
Arius felis	Temp, wind	0.30
Leiostomus xanthurus	Turbidity (lag), Secchi, salinity, temp	0.85
Chloroscombrus chrysurus	Temp (lag), temp, salinity	0.44
Menticirrhus americanus	Temp (lag)	0.19
Symphurus plagiusa	Color (lag), color, Secchi	0.63
Bairdiella chrysura	Wind, temp, color	0.40
Penaeus setiferus	Wind, chlorophyll *a*, incoming tide, color	0.48
Palaemonetes pugio	Turbidity	0.36
Callinectes sapidus	Secchi, incoming tide	0.49
Penaeus duorarum	Chlorophyll *a*, Secchi	0.41
Lolliguncula brevis	Chlorophyll *a* (lag), temp	0.43
Portunus gibbesii	Chlorophyll *a* (lag), Secchi	0.39
Palaemonetes vulgaris	Turbidity	0.32
Rhithropanopeus harrisii	Wind	0.18
Callinectes similis	Chlorophyll *a*, temp	0.34

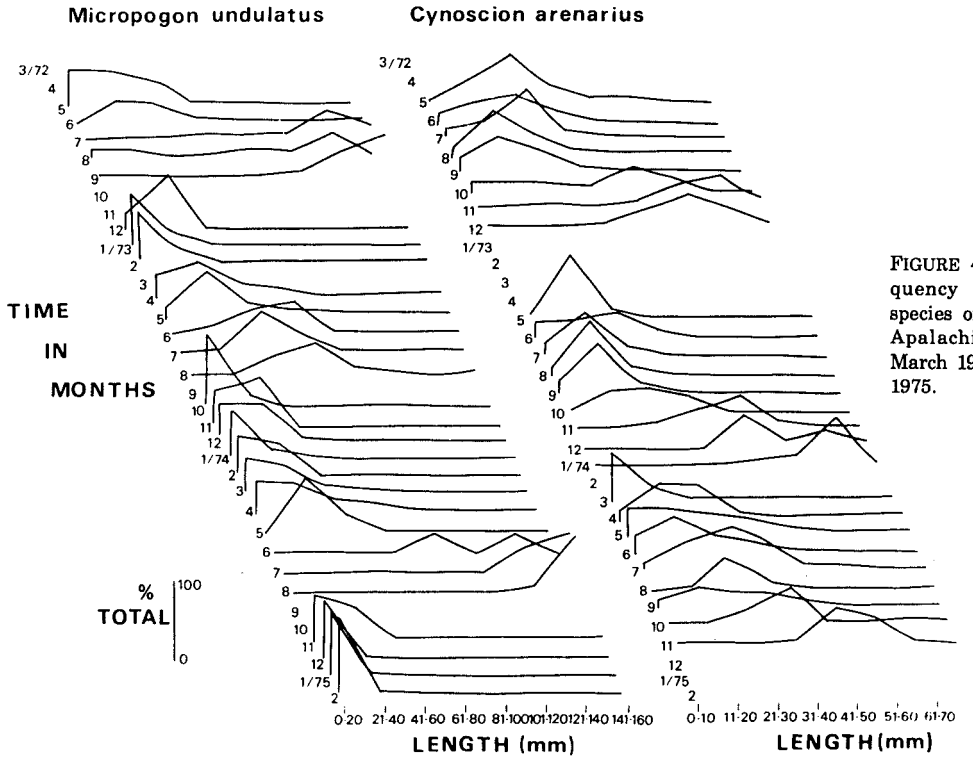

FIGURE 4.—Monthly size-frequency distribution of two species of fishes taken in the Apalachicola estuary from March 1972 through February 1975.

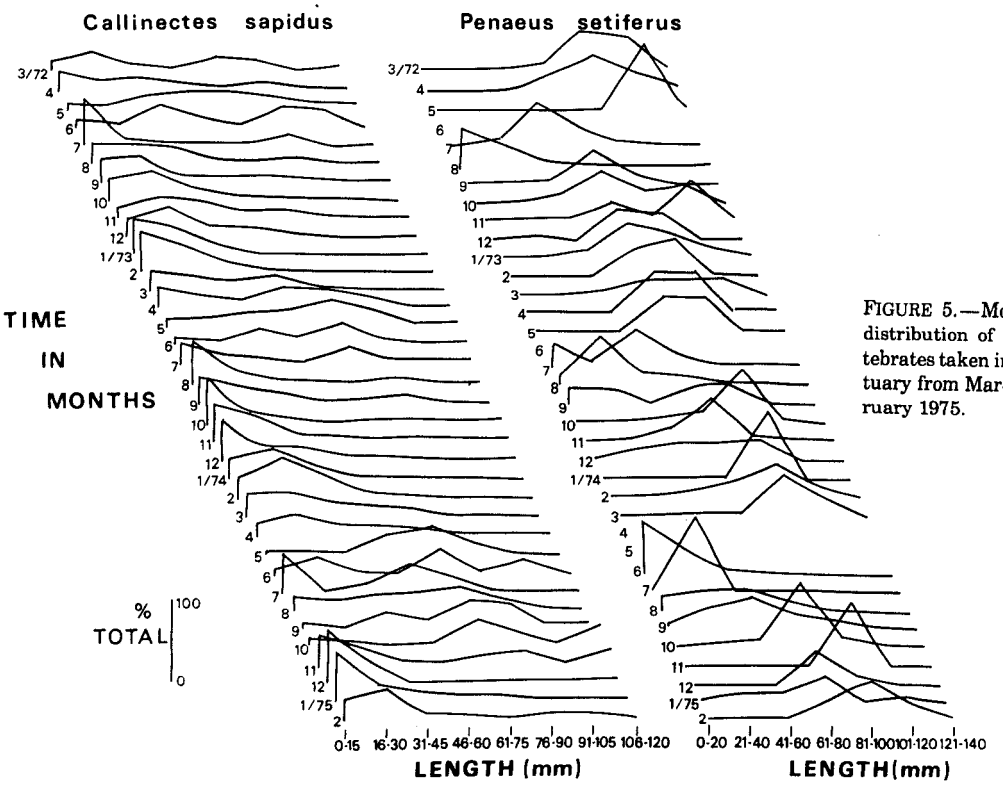

FIGURE 5.—Monthly size-frequency distribution of two species of invertebrates taken in the Apalachicola estuary from March 1972 through February 1975.

the adaptive response of populations to the extremely complex environment of the estuary. The data indicate that, in this case, temperature and salinity might not be as critical in the determination of seasonal fluctuations of estuarine populations as biological functions such as trophic response and possibly reproduction.

DISCUSSION

A review of the literature (Gunter 1945, 1950; Daugherty 1952; Reid 1955; Van Engel 1958; Gunter and Hall 1965; Williams 1965; Tagatz 1968; More 1969; Pérez Farfante 1969; King 1971; Lyons et al. 1971; Swingle 1971; Perret and Caillouet 1974; Stokes 1974; Swingle and Bland 1974) confirms that although minor variations were evident (notably among the fishes), there was a generally high level of conformity concerning the time of appearance of various dominants in the Apalachicola estuary with previously recorded data from other northern Gulf areas. Although such timing was essentially stable from year to year, there was considerable within-species variability in annual abundance. For example, the bay anchovy was particularly dominant during the summer and fall of 1972, while fewer individuals were taken during the succeeding 2 yr. The Atlantic bumper, although not considered a common Gulf species (Perret and Caillouet 1974), was relatively common in the Apalachicola estuary, especially during the first year of collection. Some species reflected particular habitat preferences: *Palaemonetes pugio* was located primarily in grass-bed areas of East Bay during periods of low salinity while *L. brevis* was found in outer bay areas during summer and fall periods of increased salinity. Although generalized temperature and salinity preferences have been shown for various estuarine species (Copeland and Bechtel 1974), as a whole these organisms show a wide tolerance for short-term changes in these parameters. This could help to explain the general lack of importance of temperature and salinity as critical variables in the multiple regression analysis; quite obviously, other functions such as acclimatization would tend to complicate such a direct approach to determination of causative agents. The multiple regression technique was limited in its application to causal relationships since various biological functions are probably involved in the determination of a given population curve.

It is possible that trophic relationships and reproductive cycles are of critical importance in the spatial and temporal distribution of estuarine populations. As in other Gulf estuaries, the Apalachicola Bay system is dominated by juvenile stages of a small number of species. The bay anchovy, abundant in a size range of 35-50 mm, is considered to be a generalized zooplanktivore at this stage, feeding in the water column on copepods, amphipods, mysids, larval and juvenile shrimps and fishes, etc. (Darnell 1958; Odum and Heald 1972; Carr and Adams 1973). Various studies (Roelofs 1954; Darnell 1958; Fontenot and Rogillio 1970) indicate that *M. undulatus* (juveniles, 10-50 mm) feeds primarily on zooplankton (copepods and amphipods) while *C. arenarius* (juveniles, 40-99 mm) consumes larger zooplanktors such as mysids, shrimp, and larval or juvenile fishes (Darnell 1958; Springer and Woodburn 1960). Juvenile (up to 40 mm) spot also feed on zooplankton; more mature fish of this species (40-200 mm) become benthic omnivores (Roelofs 1954; Darnell 1958; Springer and Woodburn 1960). Juvenile *B. chrysura* (16-160 mm) feed on copepods, mysids, shrimp, and small fishes (Darnell 1958; Carr and Adams 1973). Thus, the dominant fishes in the Apalachicola Bay system are primarily planktivorous although possible differences could exist in vertical feeding distribution and the size and species composition of the prey organisms. Previous work has shown that *Anchoa mitchilli* feeds on small crustaceans and *C. arenarius* eats the larger, more motile crustaceans. Both *Leiostomus xanthurus* and *B. chrysura* feed on small mid-water planktors (mainly copepods) as early juveniles, with later stages becoming benthic omnivores feeding largely on mysids and shrimp. Increased concentrations of zooplankton occur in Apalachicola Bay during the spring and summer while palaemonetid shrimp are abundant during winter and early spring (H. L. Edmiston pers. commun.). Thus, diversity in feeding behavior would contribute to the observed vertical partitioning of prey organisms among various planktivorous species; such data are consistent with the observed distribution of fishes in Apalachicola Bay at any given period of time.

Of the six most prevalent invertebrates in the Apalachicola estuary, five are benthic omnivores and one is a probable planktivore. Juvenile blue crabs consume detritus while larger individuals (20-200 mm) are omnivorous, feeding on detritus

and plant material, mollusks, polychaetes, crustaceans, and fishes (Darnell 1959; Tagatz 1968; Odum and Heald 1972). Penaeid shrimp are also omnivores, feeding on similar forms (Williams 1965; Darnell 1958; Eldred et al. 1961; Odum and Heald 1972). *Palaemonetes pugio* feeds primarily on detritus (Adams and Angelovic 1970; Oviatt and Nixon 1973; Welch 1975). Qualitative observations indicate that *Lolliguncula brevis* is a planktivore (Dragovitch and Kelly 1967). Thus, most of the epibenthic invertebrates utilize detritus and are more closely associated with sediment type, benthic macrophyte distribution, and placement of allochthonous forms of detritus than the planktivorous fishes; this, together with certain (species-specific) temperature and salinity tolerances, could provide a partial explanation for the observed differences in the spatial distribution of the fishes and invertebrates.

Another important evolutionary mechanism for the partitioning of the energy resources of an estuary is the temporal succession of species over an annual cycle. Abundance interrelationships expressed as percentage of total catch are shown in Figure 6. There was a certain regularity of percent representation of dominant species of fishes and invertebrates in the Apalachicola system. For example, relative occurrence of *P. pugio* was high during spring months while *Penaeus setiferus* was dominant during late summer and fall. The blue crab was abundant during winter periods. Among the fishes, *C. arenarius* was dominant during the spring and summer while *A. mitchilli* (after the first year of sampling) predominated in the fall and *M. undulatus* prevailed during the late winter and spring. When a comparison was made among the 10 most dominant species of fishes for peaks of abundance, such increases were evenly distributed over a 12-mo period. However, of the top 10 species of invertebrates, most peaks of abundance occurred during fall periods (September-November) with secondary concentrations of peaks during early summer (May-June). Livingston (in press), describing patterns of species richness and diversity in Apalachicola Bay, noted that there was an annual double peak in fish and invertebrate diversity although there was far more seasonal variability in N (numbers of individuals) and S (numbers of species) among fishes than invertebrates. These data would tend to corroborate and elucidate such findings. Thus, although the top dominants in both groups showed distinct temporal sequences in relative peak abundance, there was a tendency for increased numbers of invertebrate species during summer and fall periods whereas peaks of N and S for fishes were more continuously distributed throughout the year. Major dominants for both fishes and invertebrates thus showed temporal partitioning through an annual cycle. The noted differences in temporal distributional patterns of fishes and invertebrates could be related to trophic response, with the planktivorous fishes competing for a more limited resource than the omnivorous (detritovore and omnivore) invertebrate species.

Several conclusions can be made with regard to the biotic component in the Apalachicola estuary. Various independent ecological factors operate to determine the spatial and temporal distributions of such organisms. Biological functions, as adaptive responses to the physical and trophic environment, determine such distributional patterns, allowing a somewhat orderly temporal succession of dominant forms within certain broad trophic spectra. Patterns of reproduction of various dominant estuarine species have evolved in such a way as to permit such long-term partitioning of the estuarine environment. Superimposed on this are certain in situ mechanisms whereby further resource division occurs due to vertical and horizontal distribution of the component species. This is largely determined by various microhabitat phenomena such as salinity, bottom type, currents, availability of detritus, etc. In addition, biological determinants such as intraspecific competition and predation further modify the individual component populations. Thus, no single parameter prevails in the determination of the community structure of an estuary which undergoes predictable seasonal changes even though it is a physically forced system. Although there is considerable short-term fluctuation in the numbers of individuals of various populations, the system maintains a certain temporal constancy which, according to a traditional view of such phenomena, could be termed stability. This does not mean that such a system is not in a constantly transient state; on the contrary, through various natural and unnatural mechanisms such as habitat alteration and destruction, hurricanes, etc., the various population equilibria can be shifted so that the system is no longer characterized by a stable temporal succession of energy utilization. Each population fluctuates around a certain point of equilibrium; such fluctuations are

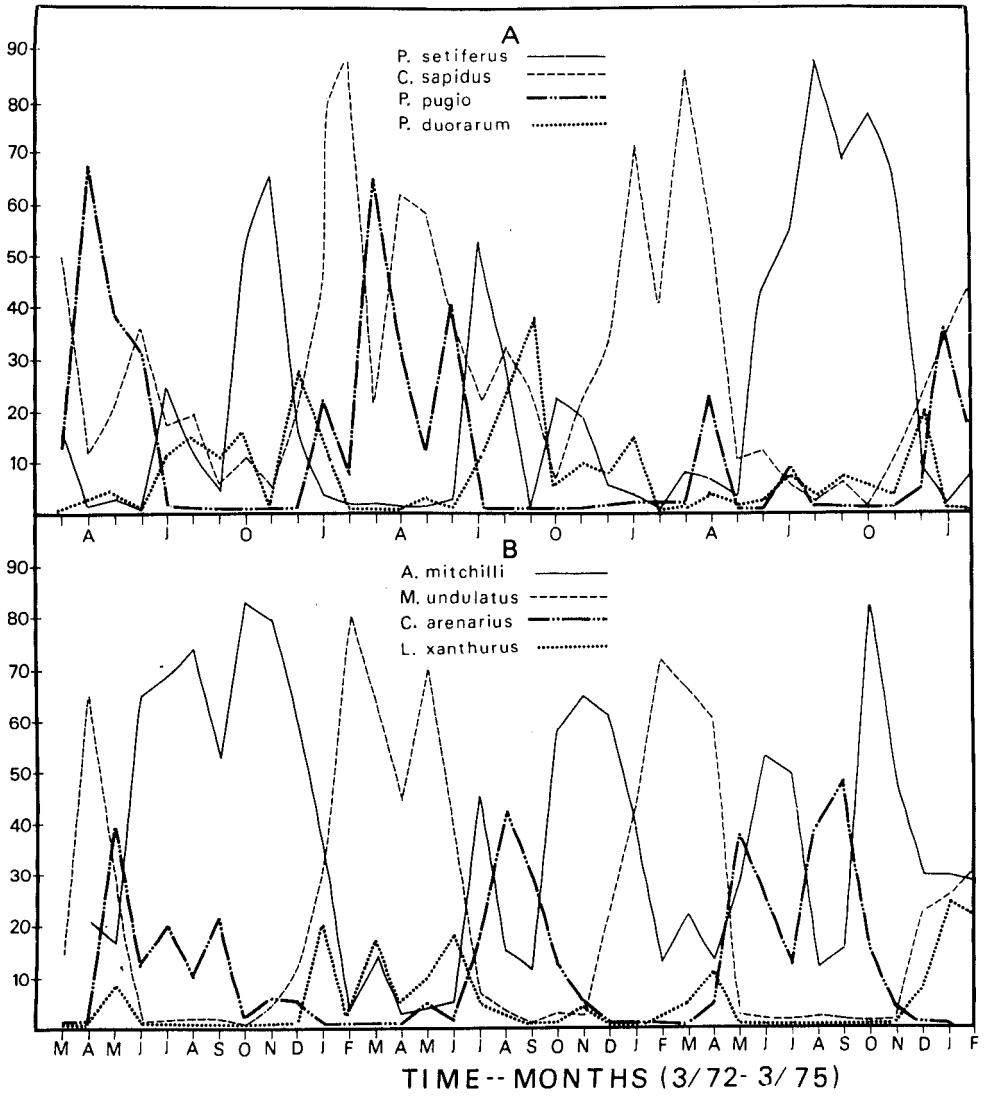

FIGURE 6.—Relative importance (% of total) of four dominant species of invertebrates and fishes taken in the Apalachicola Bay system from March 1972 through February 1975. Such species represent 82.4 and 86.0% of the respective 3-yr totals.

determined by various natural and man-induced phenomena such as overfishing and pollution. The stability of the system depends on the maintenance of various populations within certain limits of fluctuation. This has serious implications for any estuarine management program. Holling (1973) pointed out that instability (in the sense of large fluctuations) of individual populations may actually introduce a capacity for persistence or resilience. Such resilience can be attributed not only to component populations but to the system as a whole. Stability thus is seen as the "ability of a system to return to an equilibrium state after a temporary disturbance," (Holling 1973). Resilience, however, is a measure of the ability of a given system to absorb changes of primary forcing functions and still persist. By this measure, an estuarine system such as Apalachicola Bay comprises various populations which undergo considerable annual fluctuations but nevertheless are maintained within a relatively stable temporal succession.

ACKNOWLEDGMENTS

We thank Duwayne A. Meeter and Richard Gurnee for their advice concerning the statistical applications in this study. Thanks are also due to Robert C. Harriss and his staff at the Edward Ball Marine Laboratory (Florida State University) for the use of various support facilities. The authors also acknowledge Glenn C. Woodsum and J. Elton Jernigan for their help with the computer programs used in this study. Many students have also helped in the field, and are acknowledged for their interest in this project. Much of the field collections was funded by grants from NOAA Office of Sea Grant, U.S. Department of Commerce (Grant Number 04-3-158-43), and the Board of County Commissioners of Franklin County, Fla. Data analysis was supported by EPA Program Element #1 BA025 under Grant Number R-803339.

LITERATURE CITED

ADAMS, S. M., AND J. W. ANGELOVIC.
1970. Assimilation of detritus and its associated bacteria by three species of estuarine animals. Chesapeake Sci. 11:249-254.

BECHTEL, T. J., AND B. J. COPELAND.
1970. Fish species diversity indices as indicators of pollution in Galveston Bay, Texas. Contrib. Mar. Sci. 15:103-132.

CARR, W. E. S., AND C. A. ADAMS.
1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans. Am. Fish. Soc. 102:511-540.

COPELAND, B. J., AND T. J. BECHTEL.
1971. Species diversity and water quality in Galveston Bay, Texas. Water Air Soil Pollut. 1:89-105.
1974. Some environmental limits of six Gulf coast estuarine organisms. Contrib. Mar. Sci. 18:169-204.

DAHLBERG, M. D., AND E. P. ODUM.
1970. Annual cycles of species occurrence, abundance, and diversity in Georgia estuarine fish populations. Am. Midl. Nat. 83:382-392.

DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Ponchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci., Univ. Tex. 5:353-416.
1959. Studies of the life history of the blue crab (Callinectes sapidus Rathbun) in Louisiana waters. Trans. Am. Fish. Soc. 88:294-304.

DAUGHERTY, F. M., JR.
1952. The blue crab investigation, 1949-50. Tex. J. Sci. 4:77-84.

DRAGOVICH, A., AND J. A. KELLY, JR.
1967. Occurrence of the squid, *Lolliguncula brevis*, in some coastal waters of western Florida. Bull. Mar. Sci. 17:840-844.

ELDRED, R. M. INGLE, K. D. WOODBURN, R. F. HUTTON, AND H. JONES.
1961. Biological observations on the commercial shrimp, *Penaeus duorarum* Burkenroad, in Florida waters. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 3, 139 p.

ESTABROOK, R. H.
1973. Phytoplankton ecology and hydrography of Apalachicola Bay. M.S. Thesis, Florida State Univ., Tallahassee.

FONTENOT, B. J., JR., AND H. E. ROGILLIO.
1970. A study of estuarine sport fishes in the Biloxi marsh complex, Louisiana. F-8 Completion Rep., La. Wild Life Fish. Comm., 172 p.

GALLAWAY, B. J., AND K. STRAWN.
1974. Seasonal abundance and distribution of marine fishes at a hot-water discharge in Galveston Bay, Texas. Contrib. Mar. Sci. 18:71-137.

GUNTER, G.
1945. Studies on the marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1:1-190.
1950. Distributions and abundance of fishes on the Aransas National Wildlife Refuge, with life history notes. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):89-101.

GUNTER, G., AND G. E. HALL.
1965. A biological investigation of the Caloosahatchee estuary of Florida. Gulf Res. Rep. 2, 71 p.

HAEDRICH, R. L., AND S. O. HAEDRICH.
1974. A seasonal survey of the fishes in the Mystic River, a polluted estuary in downtown Boston, Massachusetts. Estuarine Coastal Mar. Sci. 2:59-73.

HOLLING, C. S.
1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4:1-23.

HORN, H. S.
1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.

KING, B. D., III.
1971. Study of migratory patterns of fish and shellfish through a natural pass. Tex. Parks Wildl. Dep., Tech. Ser. 9, 54 p.

LIVINGSTON, R. J.
1975. Impact of kraft pulp-mill effluents on estuarine and coastal fishes in Apalachee Bay, Florida, USA. Mar. Biol. (Berl.) 32:19-48.
In press. Diurnal and seasonal fluctuations of estuarine organisms in a north Florida estuary. Estuarine Coastal Mar. Sci.

LIVINGSTON, R. J., R. L. IVERSON, R. H. ESTABROOK, V. E. KEYS, AND J. TAYLOR, JR.
1974. Major features of the Apalachiocola Bay system: Physiography, biota, and resource management. Fla. Sci. 37:245-271.

LYONS, W. G., S. P. COBB, D. K. CAMP, J. A. MOUNTAIN, T. SAVAGE, L. LYONS, AND E. A. JOYCE, JR.
1971. Preliminary inventory of marine invertebrates collected near the electrical generating plant, Crystal River, Florida, in 1969. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 14, 45 p.

MCERLEAN, A. J., S. G. O'CONNOR, J. A. MIHURSKY, AND C. I. GIBSON.
1973. Abundance, diversity, and seasonal patterns of estuarine fish populations. Estuarine Coastal Mar. Sci. 1:19-36.

MORE, W. R.
1969. A contribution to the biology of the blue crab (*Callinectes sapidus* Rathbun) in Texas, with a description of the fishery. Tex. Parks Wildl. Dep., Tech. Ser. 1, 31 p.

MORISITA, M.
1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ., Ser. E, Biol. 3:65-80.

ODUM, W. E., AND E. J. HEALD.
1972. Trophic analyses of an estuarine mangrove community. Bull. Mar. Sci. 22:671-738.

OVIATT, C. A., AND S. W. NIXON.
1973. The demersal fish of Narragansett Bay: An analysis of community structure, distribution and abundance. Estuarine Coastal Mar. Sci. 1:361-378.

PERRET, W. S., AND C. W. CAILLOUET, JR.
1974. Abundance and size of fishes taken by trawling in Vermilion Bay, Louisiana. Bull. Mar. Sci. 24:52-75.

PÉREZ FARFANTE, I.
1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.

REID, G. K., JR.
1955. A summer study of the biology and ecology of East Bay, Texas. Part I. Introduction, description of area, methods, some aspects of the fish community, the invertebrate fauna. Tex. J. Sci. 7:316-343.

ROELOFS, E. W.
1954. Food studies of young sciaenid fishes, *Micropogon* and *Leiostomus*, from North Carolina. Copeia 1954: 151-153.

SIMPSON, E. H.
1949. Measurement of diversity. Nature (Lond.) 163:688.

SPRINGER, V. G., AND K. D. WOODBURN.
1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 1, 104 p.

STOKES, G. M.
1974. The distribution and abundance of penaeid shrimp in the Lower Laguna Madre of Texas, with a description of the live bait shrimp fishery. Tex. Parks Wildl. Dep., Tech. Ser. 15, 32 p.

SWINGLE, H. A.
1971. Biology of Alabama estuarine areas—cooperative Gulf of Mexico estuarine inventory. Ala. Mar. Res. Bull. 5, 12 p.

SWINGLE, H. A., AND D. G. BLAND.
1974. A study of the fishes of the coastal watercourses of Alabama. Ala. Mar. Res. Bull. 10:17-102.

TAGATZ, M. E.
1968. Biology of the blue crab *Callinectes sapidus* Rathbun, in the St. Johns River, Florida, U.S. Fish Wildl. Serv., Fish. Bull. 67:17-33.

VAN ENGEL, W. A.
1958. The blue crab and its fishery in Chesapeake Bay. Part 1—Reproduction, early development, growth, and migration. Commer. Fish. Rev. 20(6):6-17.

WELSH, B. L.
1975. The role of grass shrimp, *Palaemonetes pugio* in a tidal marsh ecosystem. Ecology 56:513-530.

WILLIAMS, A. B.
1965. Marine decapod crustaceans of the Carolinas. U.S. Fish Wildl. Serv., Fish. Bull 65:1-298.

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DESCRIPTION OF ZOEAE OF COONSTRIPE SHRIMP, *PANDALUS HYPSINOTUS*, REARED IN THE LABORATORY

EVAN HAYNES[1]

ABSTRACT

Zoeae of *Pandalus hypsinotus* from ovigerous females caught in Kachemak Bay, Alaska, were reared in the laboratory. Each of the six zoeal stages is described and illustrated, and a brief description is given for postzoeal Stages VII-IX. The descriptions are compared with descriptions of zoeal stages of *P. hypsinotus* given by other authors.

Although pandalid shrimp form a major fishery resource along the Pacific coast of North America, little has been published on their early life history, especially on identification of the larval stages. Berkeley (1930) described the zoeal stages of five pandalid species from British Columbia, *Pandalus borealis* Krøyer, *P. danae* Stimpson, *P. hypsinotus* Brandt, *P. platyceros* Brandt, and *Pandalopsis dispar* Rathbun. The first zoeal stage of each species was obtained in the laboratory, and various remaining stages were obtained from the plankton. Berkeley also mentioned briefly the growth and distribution of the zoeae. Of 14 species of pandalid shrimps known to occur along the Pacific coast of North America, only two species, *Pandalus jordani* Rathbun and *P. platyceros*, have been reared through all their zoeal stages in the laboratory (Modin and Cox 1967; Price and Chew 1972).

In 1972, the National Marine Fisheries Service began an intensive investigation at its field station at Kasitsna Bay, Alaska, on the early life history of pandalid shrimp in Alaskan waters. The initial objective of the investigation was to describe in detail laboratory-reared zoeae of each pandalid species previously unverified. This report describes and illustrates each of the six zoeal stages of coonstripe shrimp, *P. hypsinotus*, and compares the stages obtained from laboratory-reared zoeae with stages obtained from the plankton by other authors. Brief descriptions of postzoeal Stages VII through IX are also included.

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MATERIALS AND METHODS

Ovigerous *Pandalus hypsinotus* were caught at depths of 54 m (30 fathoms) in shrimp pots in late April 1973. They were kept in plastic buckets filled with seawater for about ½ h and then were put in plastic glass hatching boxes similar to those used by Price and Chew (1972) for rearing zoeae of spot shrimp, *P. platyceros*. The hatching boxes were kept in a biologically filtered recirculating aquarium system containing 190 liters (50 gallons) of refrigerated seawater, of which 19 liters (5 gallons) were exchanged for fresh seawater every other day. Salinity was maintained between 32 and 34‰ and temperature between 6° and 8°C. The quality and quantity of light were not controlled, but direct sunlight was avoided. Most zoeae were released at night but some were released during daytime whenever a female shrimp was stimulated to flex her abdomen rapidly. No predation of zoeae by female shrimp or by the zoeae themselves was noted. No prezoeae were seen.

About 50 zoeae were transferred by large-bore pipette to each of 25 500-ml beakers containing about 400 ml of aquarium seawater. In addition, a zoea was placed in each of 50 25- by 50-mm numbered plastic vials held in compartmented trays. The zoeae in the beakers provided both individual specimens and cast skins of various stages for dissection, and the individual zoeae in the vials provided a continuous sequence of cast skins with a known history. The beakers and vials were both checked daily for exuviae. Seawater in the holding containers was changed every other day and the zoeae were fed newly hatched nauplii of brine shrimp, *Artemia salina*, from San Francisco Bay.

The density of nauplii was controlled only to the extent that a few nauplii remained in the container at the end of each feeding period. The original beakers and vials were used throughout the study because the zoeae also fed on the algae that grew on the sides and bottoms.

All zoeae molted at night. Of the deaths noted, most were caused by failure to complete the molting process; the posterior half was shed successfully, but the anterior half remained attached to the mouth parts and pereopods. Survival was about 90%.

Illustrations were drawn from unstained zoeae and from exuviae stained red with Turtox CMC-S[2] (acid fuchsin stain mountant). Stained exuviae show segmentation and setation more clearly than unstained. Zoeae and exuviae were dissected with the aid of a binocular dissecting microscope. The dissected material was mounted on a slide and drawn to scale with the aid of a camera lucida. Detail was checked with a compound microscope up to 430×.

In the final illustrations (Figures 1-6), for clarity, setules on the setae are usually omitted but spinulose setae are shown. Because the numbers of setae on the surface of the carapace and abdomen are highly variable, especially from Stage IV onward, they are figured only when useful in identification of a stage. For each pair of appendages the left member is figured except for the mandibles, which are drawn in pairs and figured from the right side. Whole zoeae are also figured from the right side. The figures are in part schematic and represent typical setal counts. The setation formulas proceed from the distal to the proximal ends of appendages. Gill development is mentioned in the text but usually not shown in the figures. The terms are defined as follows:

spinose—bearing many spines
spinous—spinelike
setose—set with bristles (setae)
spinulose—set with little spines.

Total length was measured from the anterior tip of the rostrum to the posterior tip of the telson with the aid of a dissecting microscope; the number of specimens used to determine total lengths is given for each stage. A minimum of 10 exuviae of each stage was used to verify segmentation and setation unless noted otherwise. The term "stage" denotes the intermolt period. Nomenclature of larval appendages and gills follows Pike and Williamson (1964) and Berkeley (1930) respectively.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

STAGE I ZOEA

Total length of Stage I zoea (Figure 1A) 5.8 mm (range 5.5-6.2 mm; 50 specimens). Live specimens brightly colored by numerous yellow chromatophores edged reddish brown. A conspicuous yellow chromatophore occurs dorsally on each eyestalk and at base of telson. Smaller but distinct chromatophores occur on nearly all appendages, especially maxillipeds and pereopods. Tips of antennule and antennal scale are tinged reddish brown. Chromatophore pattern of specimens preserved in 5% solution of Formalin and seawater for several days identical to the pattern on live specimens except that yellow color changes to reddish brown after preservation. Rostrum slender, spiniform, without teeth, about one-third length of carapace, and projects horizontally or slightly downward. Carapace with small, somewhat angular dorsal prominence at base of rostrum and a smaller rounded prominence near posterior edge; prominences occur in all zoeal stages. Antennal and pterygostomian spines present, but both usually hidden by sessile eyes; no supraorbital spine.

ANTENNULE (FIGURE 1B).—Antennule (first antenna) consists of a simple unsegmented tubular basal portion, distal conical base, distal conical projection, and a heavily plumose seta on a small conical base; distal conical projection bears four aesthetascs—one long, one short, and two of intermediate length.

ANTENNA (FIGURE 1C).—Antenna consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum two segmented and about one-fourth longer than scale; distal segment is styliform, tipped by a plumose seta and a spine. Distal segment may be partially segmented proximally. Protopodite bears spinous seta at base of flagellum and a spine at base of scale, both of which persist throughout zoeal development. Antennal scale distally divided into six segments (two proximal joints incomplete) and fringed with 10 heavily plumose setae along terminal and inner margins. A small seta occurs on outer margin near base of terminal segments.

MANDIBLES (FIGURE 1D).—Mandibles without palps. Incisor process of left mandible usually bears four teeth in contrast to the distinctly triserrate incisor process of right mandible. Left mandible bears one premolar denticle and right mandible bears two. Two subterminal processes occur on truncated molar process of left mandible but not on right mandible.

MAXILLULE (FIGURE 1E).—Maxillule (first maxilla) bears coxal and basial endites and an endopod. Proximal lobe (coxopodite) bears a stout seta near base and 12 spinulose setae terminally along with a series of extremely fine hairs. Median lobe (basipodite) bears 11 spinulose spines in two rows on terminal margin and several fine hairs subterminally. Endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal setae; three of the five spines are sparsely plumose, the remaining two spinulose. There is no evidence of an outer seta (representing a vestigial exopodite) on maxillule.

MAXILLA (FIGURE 1F).—Maxilla bears plate-like exopodite (scaphognathite) with 16 long, approximately equal, evenly spaced plumose setae along outer margin and one longer and slightly thicker seta (at proximal end). Endopodite has four partly fused segments and bears nine large plumose setae. Basipodite bilobed; each lobe bears eight setae. Bilobed coxopodite bears 16 setae, 4 on distal lobe and 12 on proximal lobe.

FIRST MAXILLIPED (FIGURE 1G).—First maxilliped most heavily setose of natatory appendages. Protopodite partially segmented; bears 7 setae on proximal segment and 18 slightly smaller setae on distal segment; most setae on protopodite plumose but some simple or spinulose. Endopodite distinctly four segmented; setation formula—4, 2, 1, 3. Exopodite a long slender ramus segmented at base; has four terminal and five or six lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (FIGURE 1H). —Protopodite bisegmented; distal segment bears eight sparsely plumose setae, and proximal segment bears a simple seta. Endopodite distinctly five segmented; fourth segment expanded laterally; terminal segment has at least two spinulose setae; remaining setae on endopodite usually sparsely plumose; setation formula—7, 2, 1, 1, 3. Exopodite similar to exopodite of first maxilliped but slightly larger; has 4 terminal setae, 11 or 12 lateral natatory setae. No epipodite.

THIRD MAXILLIPED (FIGURE 1I).—Protopodite bisegmented; distal segment bears four setae. Endopodite distinctly five segmented and nearly as long as exopodite, giving it more pediform appearance than either of the two preceding appendages; setation formula —4, 8, 2, 2, 2. Exopodite similar to second maxilliped but slightly longer; has 3 or 4 terminal setae and 14 lateral natatory setae. No epipodite.

FIRST PEREOPOD (FIGURE 1J).—Endopodite functionally developed and similar in form to third maxilliped but slightly smaller. Endopodite distinctly five segmented; ends in simple conical dactylopodite; setation formula—3, 7, 2, 2, 2. Exopodite naked. Protopodite bisegmented; has four setae. Neither this nor remaining pereopods of this stage have any evidence of epipodite.

SECOND PEREOPOD (FIGURE 1K).—Second pereopod similar to first except that it has fewer setae and fourth or propodal joint is slightly extended to form beginning of chela.

THIRD, FOURTH, AND FIFTH PEREOPODS (FIGURE 1L-N).—These three pereopods essentially identical to each other except that they decrease slightly in size from third to fifth. No exopodites.

PLEOPODS.—No pleopods evident, not even as small buds.

TELSON (FIGURE 1O).—Telson not segmented from sixth abdominal segment; slightly emarginate distally; bears 14 densely plumose setae. Minute spinules at base of each seta; larger spinules along terminal margin between bases of four inner pairs and on the four inner pairs of setae themselves. Enclosed uropods visible. No anal spine.

STAGE II ZOEA

Total length of Stage II zoea (Figure 2A) 6.1

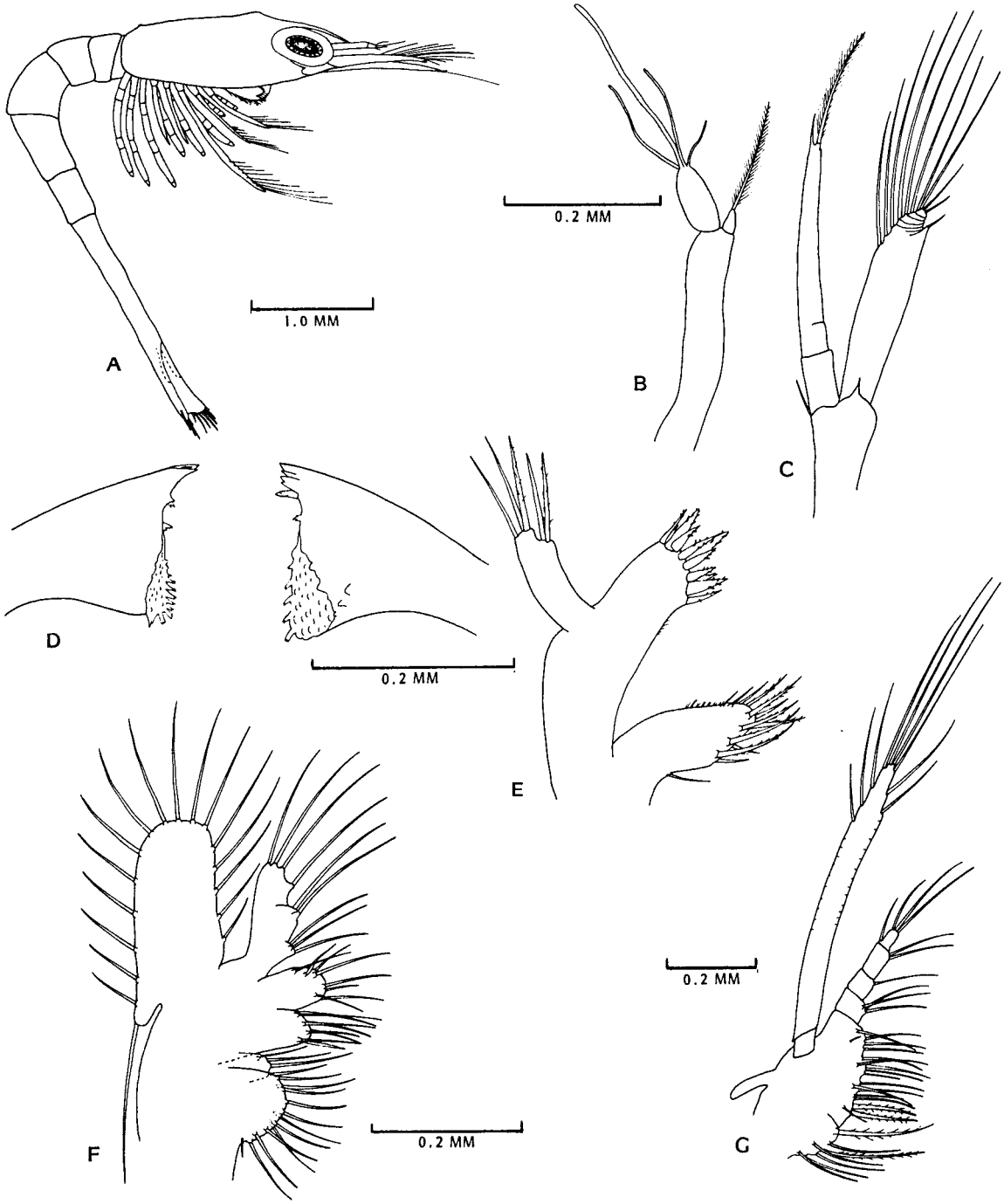
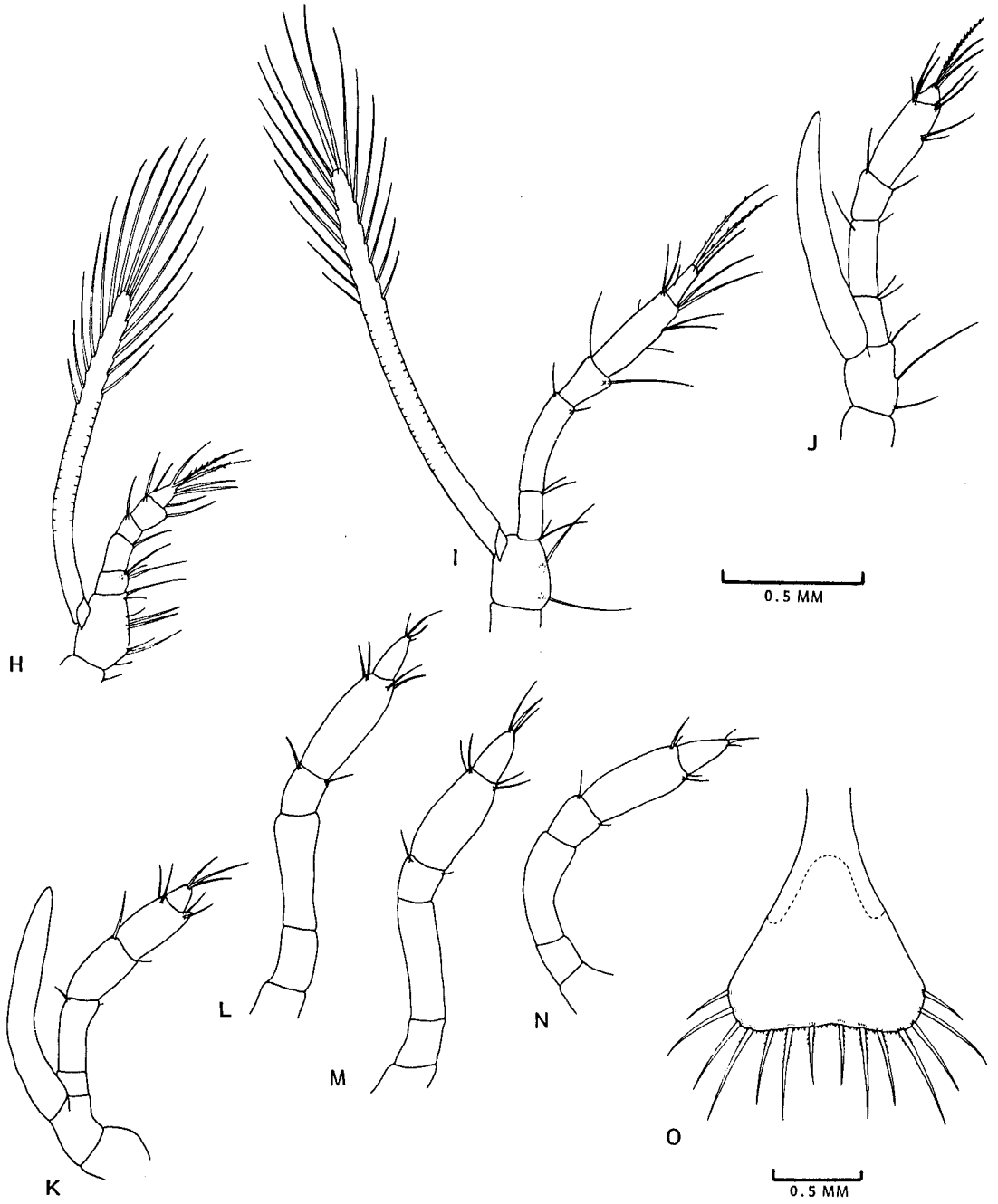


FIGURE 1.—Stage I zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) first maxilliped, (H) second maxilliped, (I) third maxilliped, (J) first pereopod, (K) second pereopod, (L) third pereopod, (M) fourth pereopod, (N) fifth pereopod, (O) telson.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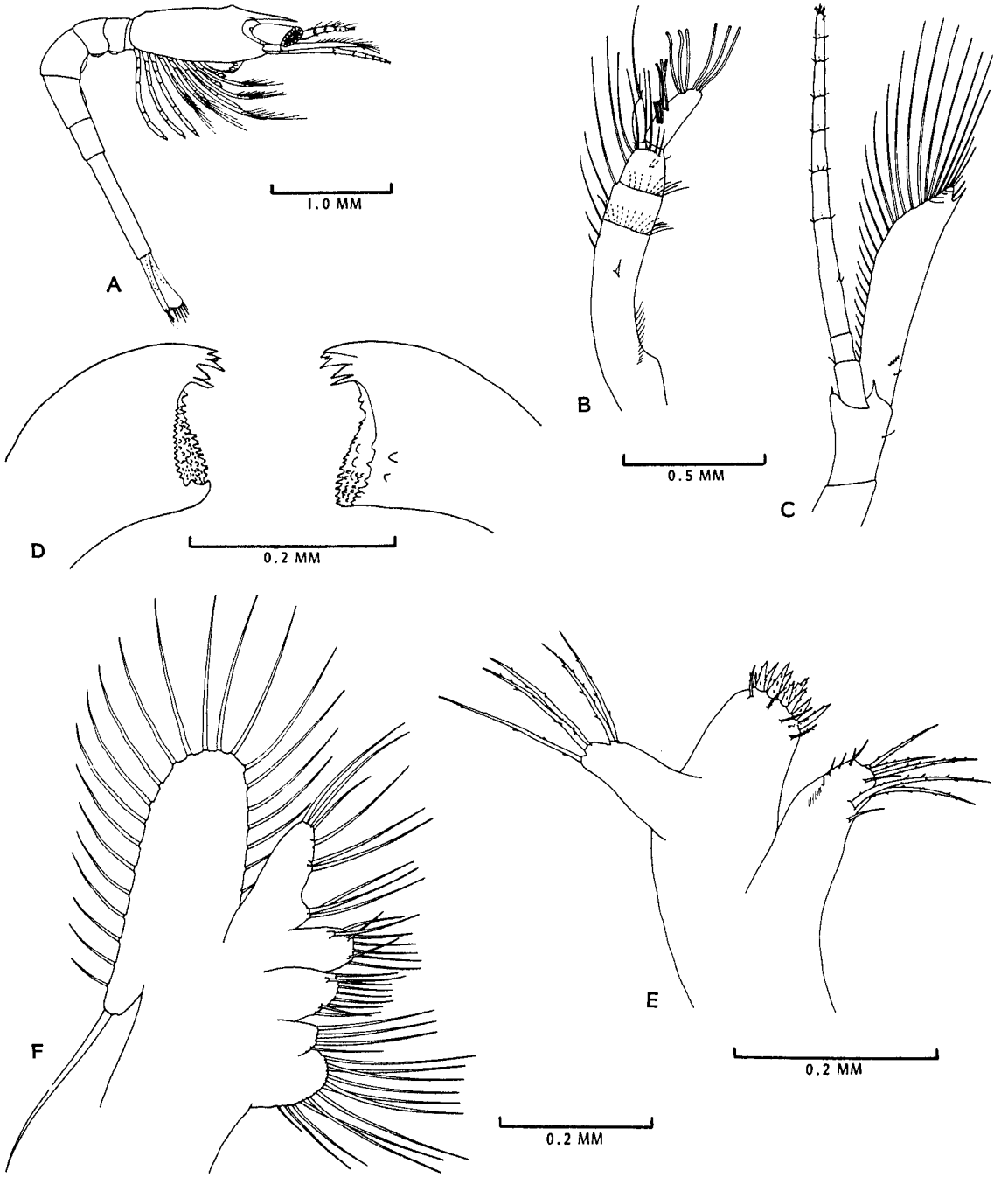
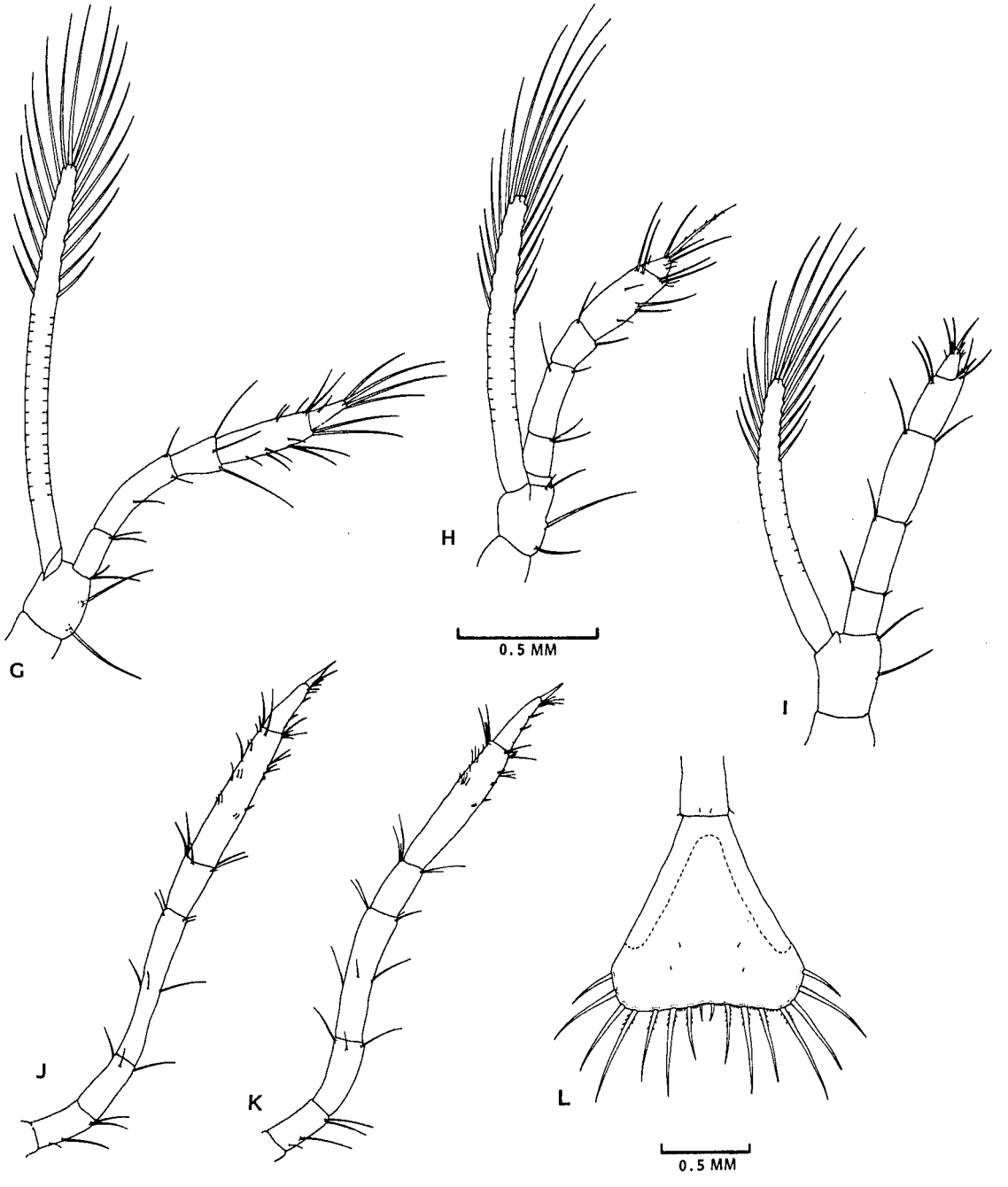


FIGURE 2.—Stage II zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) third maxilliped, (H) first pereopod, (I) second pereopod, (J) third pereopod, (K) fourth pereopod, (L) telson.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mm (range 5.6-6.5 mm; 50 specimens). Chromatophore color and pattern essentially identical to Stage I except ventral surface of abdomen now greenish. Rostrum still without teeth; not curved downward as strongly as in Stage I. Carapace same as Stage I except now has prominent supraorbital spine; antennal and pterygostomian spines clearly visible. Eyes, sessile in Stage I, now stalked.

ANTENNULE (FIGURE 2B).—Antennule shows considerable change from Stage I, now three segmented. It bears on terminal margin a large outer and a smaller inner flagellum, outer flagellum bears four groups of three aesthetascs each, one group terminally and three groups along inner margin; inner flagellum bisegmented and bears three setae terminally, one long and two short; originating at base of these two flagella is a dorsal budlike projection bearing four simple setae (projection and setae not shown in Figure 2B). Proximal segment of antennule laterally expanded at base, with about 12 small setae arranged laterally near expansion; 3 lateral plumose setae and about 14 dorsally projecting but smaller plumose setae ring terminal margin; large spine projects downward from ventral surface. Second segment has 4 lateral plumose setae, 2 long and 2 short, and about 10 dorsal plumose setae ringing terminal margin. Third segment has seven lateral plumose setae—five originating ventrally and the remaining two dorsally—and three simple setae—two dorsal and one lateral.

ANTENNA (FIGURE 2C).—Inner flagellum nine segmented, about twice as long as scale; distal segment tipped by about six small setae. Spine on basipodite at base of inner flagellum reduced in size. Antennal scale fringed with 28-30 long, thin plumose setae along terminal and inner margins. Joints at distal tip reduced to four, three of them incomplete. Distal outer seta of scale a stout spine.

MANDIBLES (FIGURE 2D).—More massive than in Stage I but still without palps. Both mandibles bear pair of premolar serrated denticles, and molar processes are more developed. Truncated end of molar process of right mandible formed into curved lip. Subterminal processes still present on left mandible.

MAXILLULE (FIGURE 2E).—Endopodite essentially unchanged from previous stage. Basipodite bears 10 spinose spines in two rows and five spinous setae on terminal margin, but no fine hairs. Coxopodite bears 12 setae terminally, 5 spinous and considerably longer than remaining 7.

MAXILLA (FIGURE 2F).—Similar to Stage I except exopodite larger and now bearing 21 or 22 marginal plumose setae in addition to plumose seta at proximal end. Lobes of basipodite bear nine setae each instead of eight as in Stage I.

FIRST, SECOND, AND THIRD (FIGURE 2G) MAXILLIPEDS.—Maxillipeds essentially identical to each other and nearly identical to first stage except for an increase in size and a slight variation in numbers of setae.

FIRST PEREOPOD (FIGURE 2H).—First pereopod functionally developed and similar in form to third maxilliped. Exopodites fringed with 15-17 plumose setae. Endopodite six segmented. Propodite projected slightly distally. Setae more numerous than in Stage I, especially on last two segments. This pereopod and the remaining four have a pleurobranchia bud at their base.

SECOND PEREOPOD (FIGURE 2I).—Similar to first pereopod except propodite projection longer and ischiopodite not segmented.

THIRD, FOURTH, AND FIFTH PEREOPODS (FIGURE 2J, K).—Third, fourth, and fifth pereopods essentially identical except for slight differences in size, fifth being smallest. Seven functional segments including dactylopodite. Dactylopodite bears spine at tip and three spines laterally. No exopodite.

PLEOPODS (FIGURE 2A).—Pleopods evident only as slightly swollen areas on abdominal segments.

TELSON (FIGURE 2L).—Telson distinct from sixth abdominal segment; bears 16 densely plumose setae along margin. Spinule arrangement essentially same as Stage I. Dorsal surface bears four small simple setae. Uropods still enclosed but longer than in first stage. No anal spine.

STAGE III ZOEA

Total length of Stage III zoea (Figure 3A) 6.7 mm (range 6.2-7.7 mm, 25 specimens).Chromatophore pattern similar to first two stages but less yellow color and more reddish brown. Rostrum pointing slightly upward with one or two small teeth at base. Supraorbital, antennal, and pterygostomian spines still present on carapace.

ANTENNULE (FIGURE 3B).—Outer flagellum distinctly three segmented; first and second segments have two groups of three aesthetascs each; distal segment has four aesthetascs. Inner flagellum still bisegmented but about twice as long as in Stage II. Remainder of antennule similar to Stage II except it is larger and more setose, and lateral projection on proximal segment is more arcuate.

ANTENNA (FIGURE 3C).—Antennal scale with 32-36 lateral plumose setae; no segmentation at tip in this or later stages. Lateral margin near base now has four additional simple setae. Flagellum about 3 times length of scale; has several additional segments and setae near base.

MANDIBLES (FIGURE 3D).—Both mandibles without palps. Right mandible bears three premolar processes; projections along anterior molar edge stronger and truncated end not curved into lip as in Stage II. Left mandible molar processes also stronger, and subterminal processes present.

MAXILLULE (FIGURE 3E).—Endopodite unchanged from Stage II except two setae particularly spinulose. Basipodite bears an additional plumose seta and a group of small fine hairs subterminally. Coxopodite now bears 14 instead of 12 setae and has more fine hairs than Stage II.

MAXILLA (FIGURE 3F).—Exopodite longer than in Stage II, slightly curved, and bears 27 marginal plumose setae in addition to plumose seta at proximal end. Lobes of basipodite bear 10 setae instead of 9 as in Stage II.

FIRST AND SECOND MAXILLIPEDS.—Epipodite on first maxilliped has rudiment of second lobe. Otherwise, first and second maxillipeds same as Stage II but slightly larger.

THIRD MAXILLIPED (FIGURE 3G).—Similar in shape to third maxilliped at Stage II but larger and more spinous and propodite bears two small spinulose spines. Numbers of setae on endopodites of maxillipeds and pereopods on this and succeeding stages are so highly variable that a specific description of them would not be an aid in identification of stage or species.

FIRST PEREOPOD (FIGURE 3H).—Exopodite still present, more setose than Stage II. Propodite bears a small spinulose spine near base. Pleurobranchia at base of this appendage and remaining four pereopods barely larger than in Stage II.

SECOND PEREOPOD (FIGURE 3I).—Most significant changes are presence of chela on endopodite and an additional segment on base of ischiopodite.

THIRD (FIGURE 3J), FOURTH, AND FIFTH PEREOPODS.—Essentially similar; fifth smallest as usual. Greater development from Stage II shown by well-formed dactylopodite and more setae. An additional segment occurs at base of ischiopodite.

PLEOPODS (FIGURE 3A).—Pleopods evident as small buds.

TELSON (FIGURE 3K).—Uropods free; bear plumose setae and small, randomly located setae on dorsal surface. Telson broader at tip than at base and still slightly emarginate; bears seven pairs of spinous setae and two pairs of lateral spines. Base of telson bears a pair of simple setae that increase in number in later stages and persist in adults. Anal spine appears at this stage.

STAGE IV ZOEA

Total length of Stage IV zoea (Figure 4A) 7.5 mm (range 7.3-8.1 mm, 10 specimens). Chromatophore pattern and color considerably different from previous stages. In general, numerous small wine-red chromatophores occur on carapace, pereopods, and ventral surface of abdomen; small yellow chromatophores occur on carapace, antennules, antennal scale, uropods, telson, and third abdominal segment. Rostrum beginning to acquire adult shape; 11-13 dorsal spines, 2 or 3 small ventral spines, and 1 dorsal spine that may be

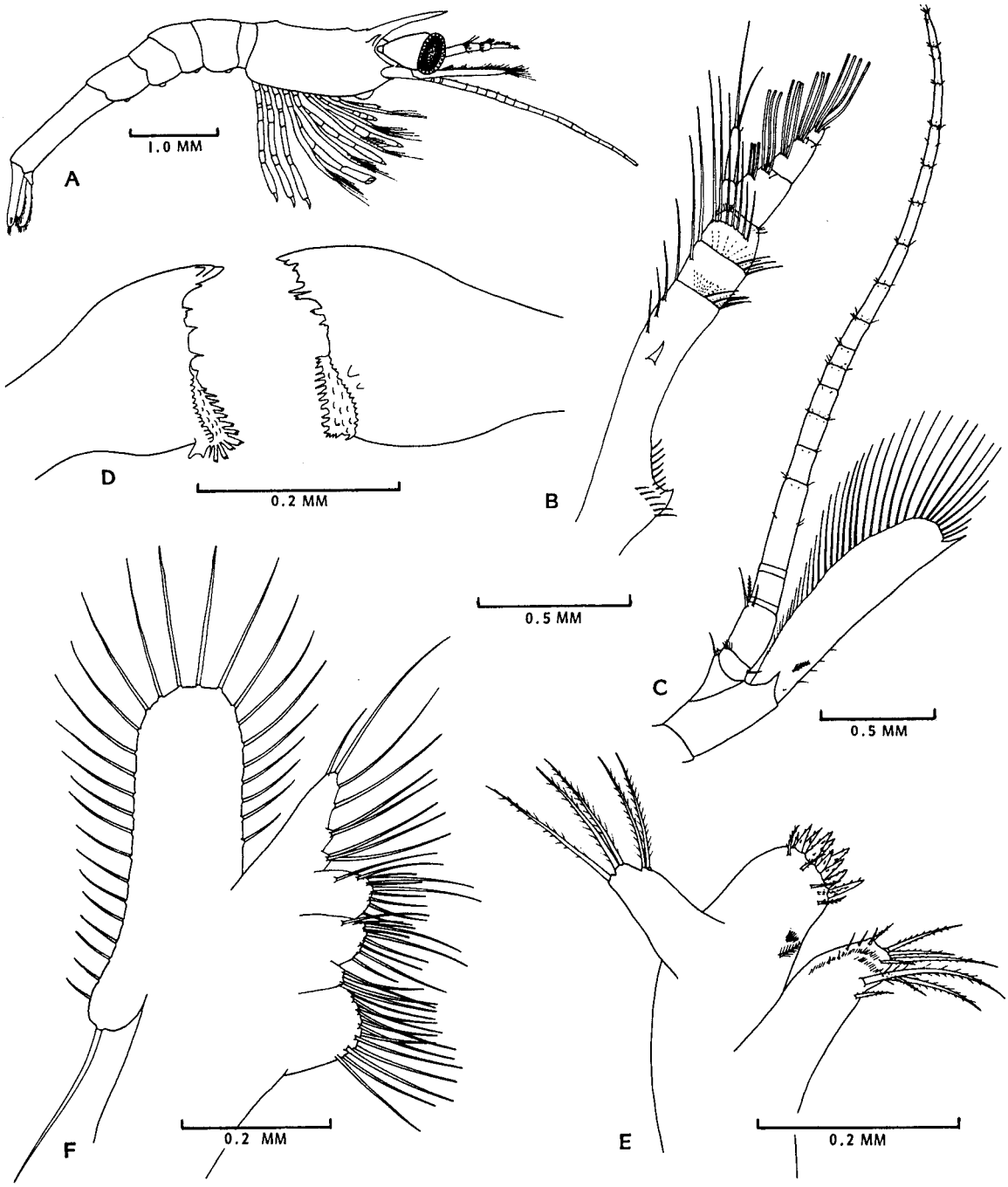
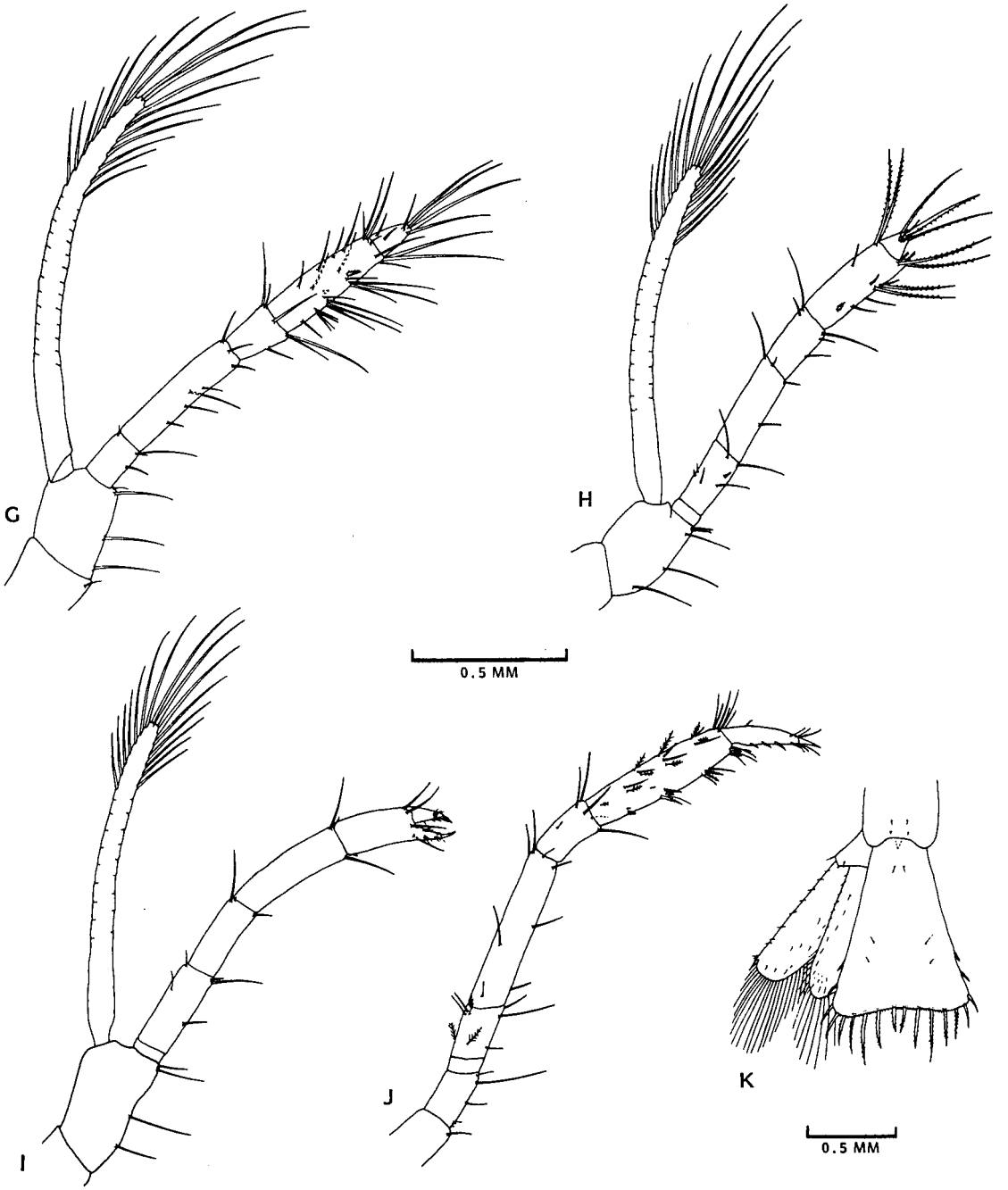


FIGURE 3.—Stage III zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) third maxilliped, (H) first pereopod, (I) second pereopod, (J) third pereopod, (K) telson.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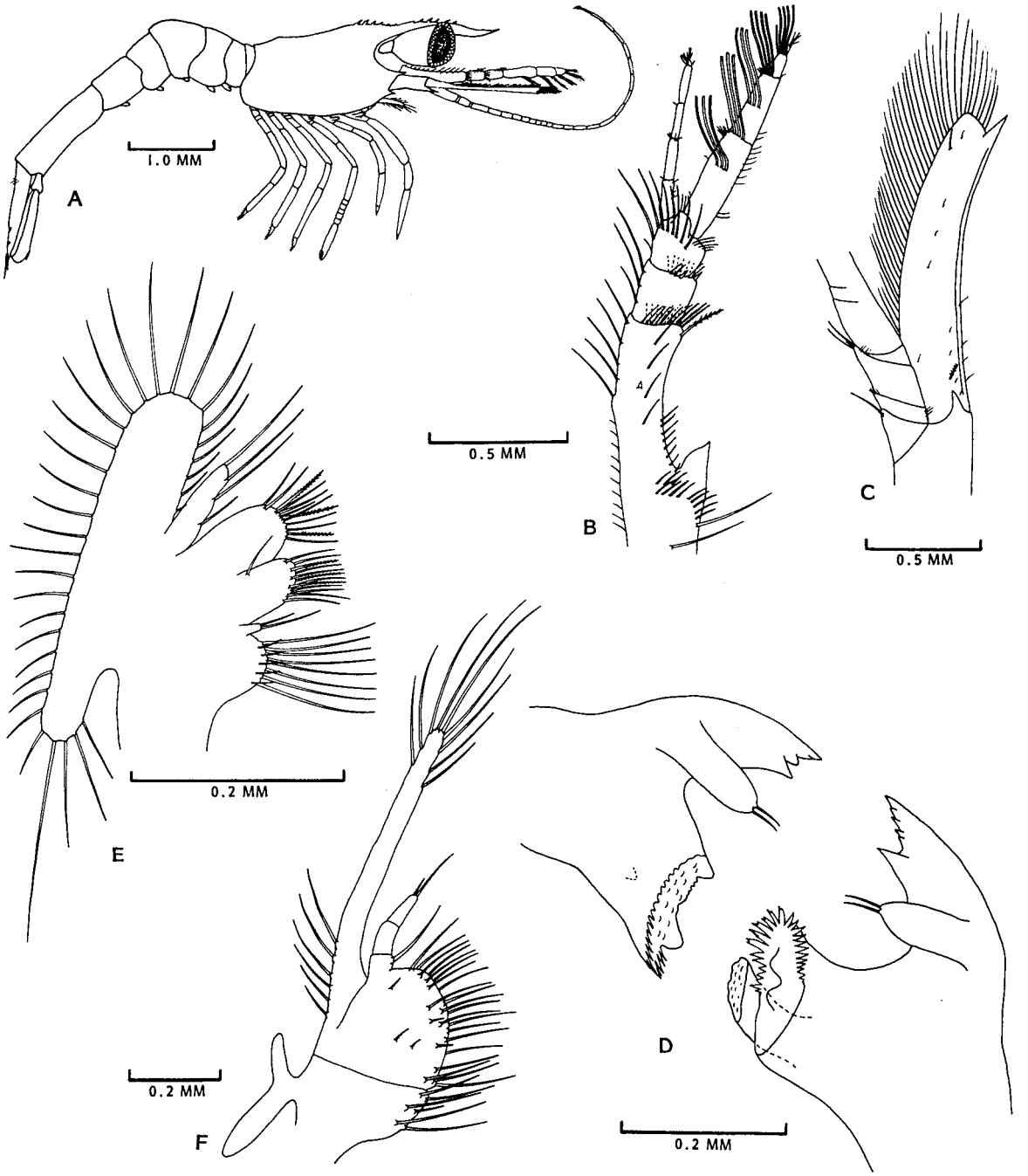
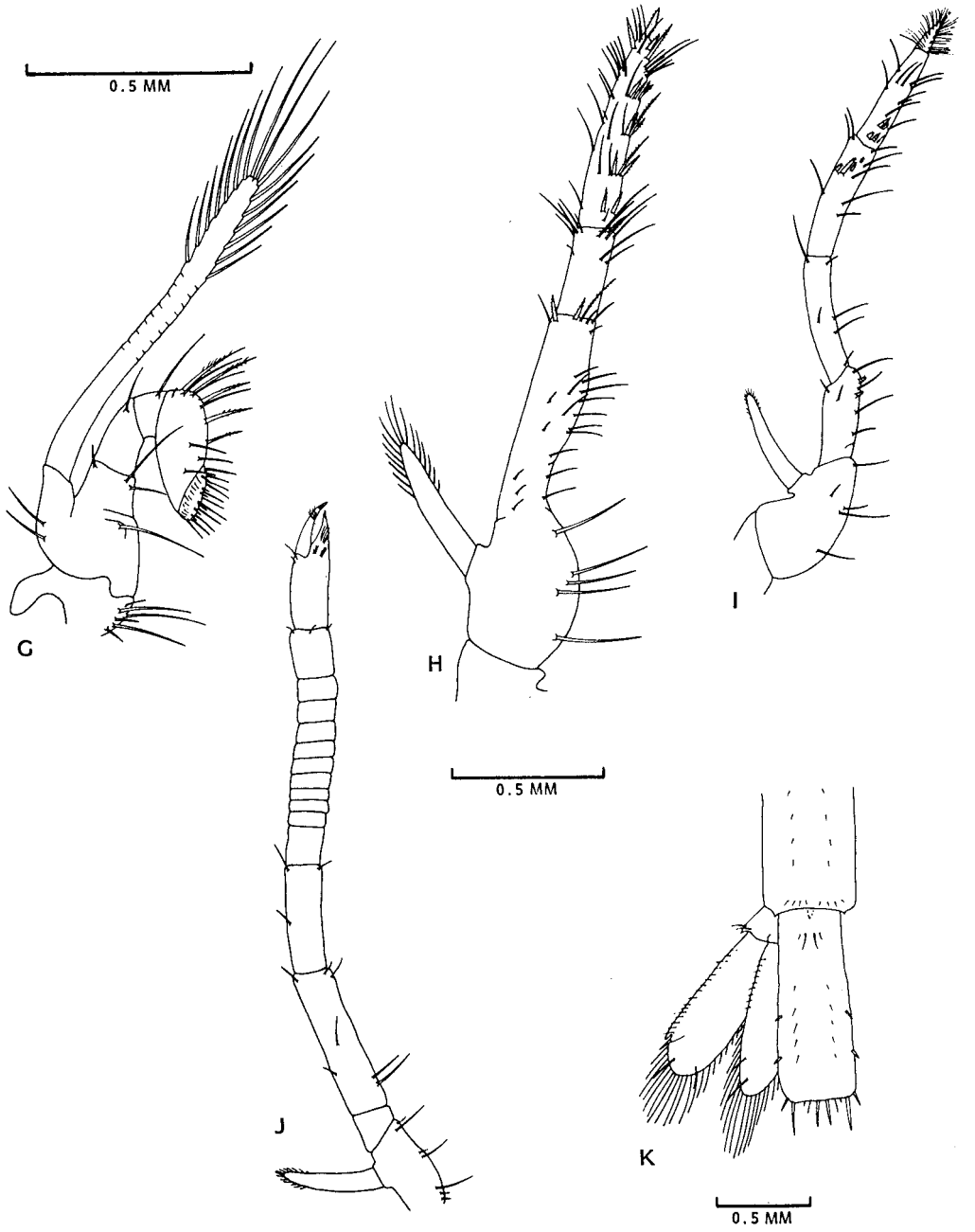


FIGURE 4.—Stage IV zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandible (right and left), (E) maxilla, (F) first maxilliped, (G) second maxilliped, (H) third maxilliped, (I) first pereopod, (J) second pereopod, (K) telson.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faint or distinct near acute tip. No supraorbital spine in this or remaining stages (Figure 4A). Small setae and groups of minute hairs irregularly located on carapace.

ANTENNULE (FIGURE 4B).—Outer flagellum four segmented and longer than in Stage III beginning to acquire slender terminal portion as in adult; five groups of aesthetascs, two groups on first and second segments each and one group on third; groups composed of 3, 3, 3, 4, and 5 aesthetascs. Inner flagellum four segmented, nearly as long as outer flagellum. Rest of antennule similar in shape to Stage III but larger; bears additional spines and setae; lateral projection on proximal segment more pronounced, and ventral spine on proximal segment noticeably smaller than in Stage III.

ANTENNA (FIGURE 4C).—Antennal scale with 32-39 lateral plumose setae and is assuming narrow, slightly curved form of adult; scale bears a few simple setae medially and usually a large seta on inner margin near tip. Inner flagellum not much longer than Stage III, about 3½ times length of scale.

MANDIBLES (FIGURE 4D).—Incisor and molar processes of both mandibles separated by deep cleft, and each mandible has unsegmented palp bearing two setae terminally. Curved lip of right mandible considerably larger than in Stage III.

MAXILLULE.—Similar to Stage III except number of setae somewhat variable. Endopodite usually has one seta but may bear additional small setae. Basipodite has 12 spines and 9-13 setae terminally, 2 or 3 setae subterminally. Coxopodite usually has 15 setae.

MAXILLA (FIGURE 4E).—Exopodite fringed, has 32 plumose setae in addition to plumose seta at proximal end; separated from protopodite by cleft and bears 3 setae along inner margin. Number of setae on endopodite reduced to four. Basipodite bears 12 setae on each lobe; proximal lobe bears additional seta subterminally. Distal lobe of coxopodite reduced in size and bears two setae instead of four as in Stage III; proximal lobe of coxopodite bears eight long and five short setae.

FIRST MAXILLIPED (FIGURE 4F).—Epipodite distinctly bilobed. Protopodite clearly two segmented and bears 6 setae on proximal segment, 26 smaller setae on distal segment. Endopodite three segmented and bears one long seta on first segment and one long and one short setae terminally on third segment. Exopodite bears 6 long plumose setae along proximal outer margin and 9 or 10 natatory setae.

SECOND MAXILLIPED (FIGURE 4G).—Second maxilliped has undergone considerable change from Stage III and now is similar in shape to adult. Endopodite five segmented; terminal segment flattened with many short spinous setae on lateral margins. Epipodite arises from coxopodite and is single lobed.

THIRD MAXILLIPED (FIGURE 4H).—Exopodite considerably reduced. Endopodite heavily setose and spinous. Meropodite slightly enlarged medially; not distinctly segmented from ischiopodite. Basipodite enlarged medially somewhat more than meropodite. Bud of mastigobranchia arises from coxopodite.

FIRST PEREOPOD (FIGURE 4I).—Exopodite reduced as in preceding appendage. Endopodite ends in simple, heavily setose conical dactyl, as in the third maxilliped; ischiopodite articulates somewhat laterally with meropodite. Pereopods of this stage, except fifth pair, bear bud of mastigobranchia. Each pleurobranchia adult in shape and clearly lobulated.

SECOND PEREOPOD (FIGURE 4J).—Exopodite reduced in size as in third maxilliped and first pereopod. Joints appear on carpal segment for first time, 10 or 11 on left and 5-7 on right. Left pereopod slightly longer (about one-tenth) than right pereopod.

THIRD, FOURTH, AND FIFTH PEREOPODS. —Essentially similar to pereopods of Stage III.

PLEOPODS (FIGURE 4A).—Pleopods cleft slightly and without joints or setae.

TELSON (FIGURE 4K).—Lateral margins nearly parallel but spaced slightly wider posteriorly and bear two spines on each margin. Terminal margin straight and bears three pairs of feathered spines, the second pair longest; two

simple setae—one long, one short—occur between first and second pairs of spines. Two pairs of simple setae (inner pair stouter) occur at base of telson and project noticeably at nearly right angles to telson surface (Figure 4A). Both pairs of uropods nearly as long as telson and fully developed; both bear numerous small setae irregularly located on dorsal and ventral surfaces of both pairs in addition to setae figured. Beginning of transverse hinge (diaeresis) of exopodite of uropod faintly evident.

STAGE V ZOEA

Total length of Stage V zoea (Figure 5A) 9.2 mm (range 8.4-10.1 mm, 10 specimens). Numerous small wine-red chromatophores occur primarily on cephalothorax but also along surface of abdomen to base of telson and on dorsal hump of third abdominal segment; large wine-red chromatophore on side of carapace especially pronounced; yellow chromatophores few and minute; occur in head region at base of antennae, on antennules, and on dorsal surface of eyes. Rostrum similar in shape to adult; 15-17 dorsal teeth, in addition to 1 (rarely 2) near acute tip; 4 or 5 ventral teeth. Still no setae between dorsal rostral teeth (Figure 5A).

ANTENNULE AND ANTENNA.—Essentially similar to Stage IV. Inner flagellum of antenna approximately 4 times length of scale.

MANDIBLES.—Mandibles larger but morphology unchanged from Stage IV; mandibular palp row three segmented and bears three or four setae terminally (Figure 5B).

MAXILLULE (FIGURE 5C).—Maxillule adult in shape. Endopodite bears one long seta terminally, sometimes an additional short seta. Basipodite bears 13 spines in two rows along terminal margins: 5 of the spines are relatively long and the remaining 8 short. Seventeen setae of various lengths are distributed terminally and along lateral margin of basipodite. Coxopodite bears five long spinulose setae terminally and a row of five shorter sparsely plumose setae extending proximally; row of fine hairs and a medial seta occur ventrally.

MAXILLA (FIGURE 5D).—Maxilla more adult in shape than previously. Exopodite fringed with 40-44 plumose setae; proximal expansion of exopodite and setae along its inner margin, especially proximal seta, considerably longer than in previous stages. Endopodite shaped as adult; bears three setae. Shape and setation of basipodite and coxopodite similar to Stage IV except distal lobe of basipodite bears 15 setae and proximal lobe of coxopodite bears 7 long and 5 short setae.

FIRST AND SECOND MAXILLIPED.—Similar to Stage IV except endopodite of first maxilliped bears two setae on second segment and three or four on proximal segment.

THIRD MAXILLIPED.—Similar to Stage IV except for a few additional setae, and exopodite is reduced to remnant. Mastigobranchia similar in shape to adult. Arthrobranchia small bud.

FIRST PEREOPOD.—Appendage with few additional setae and spines. Exopodite remnant, distal joint of ischiopodite more pronounced than in Stage IV (Figure 5E). Arthrobranchia minute bud. Mastigobranchia on this and pereopods two to four; adult in shape.

SECOND PEREOPOD.—Exopodite remnant, carpal joints of left and right pereopods 14-16 and 7. No arthrobranchia on this or remaining pereopods.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Distal joints of carpal and basial segments pointed (Figure 5F), no additional joint at basis. Setation essentially as shown in Figure 3J except carpopodite and meropodite each bear a spine.

PLEOPODS (FIGURE 5A).—Pleopods bilobed, segmented, and without setae.

TELSON (FIGURE 5G).—Lateral margins nearly parallel but slightly farther apart at center and bear two spines on each margin. Terminal margin straight; arrangement of spines and setae on margin similar to Stage IV. The two pairs of setae at base of telson noticeably longer than in Stage IV. Transverse hinge of exopodite of uropod complete; numerous small setae located randomly on dorsal and ventral surfaces in addition to those figured.

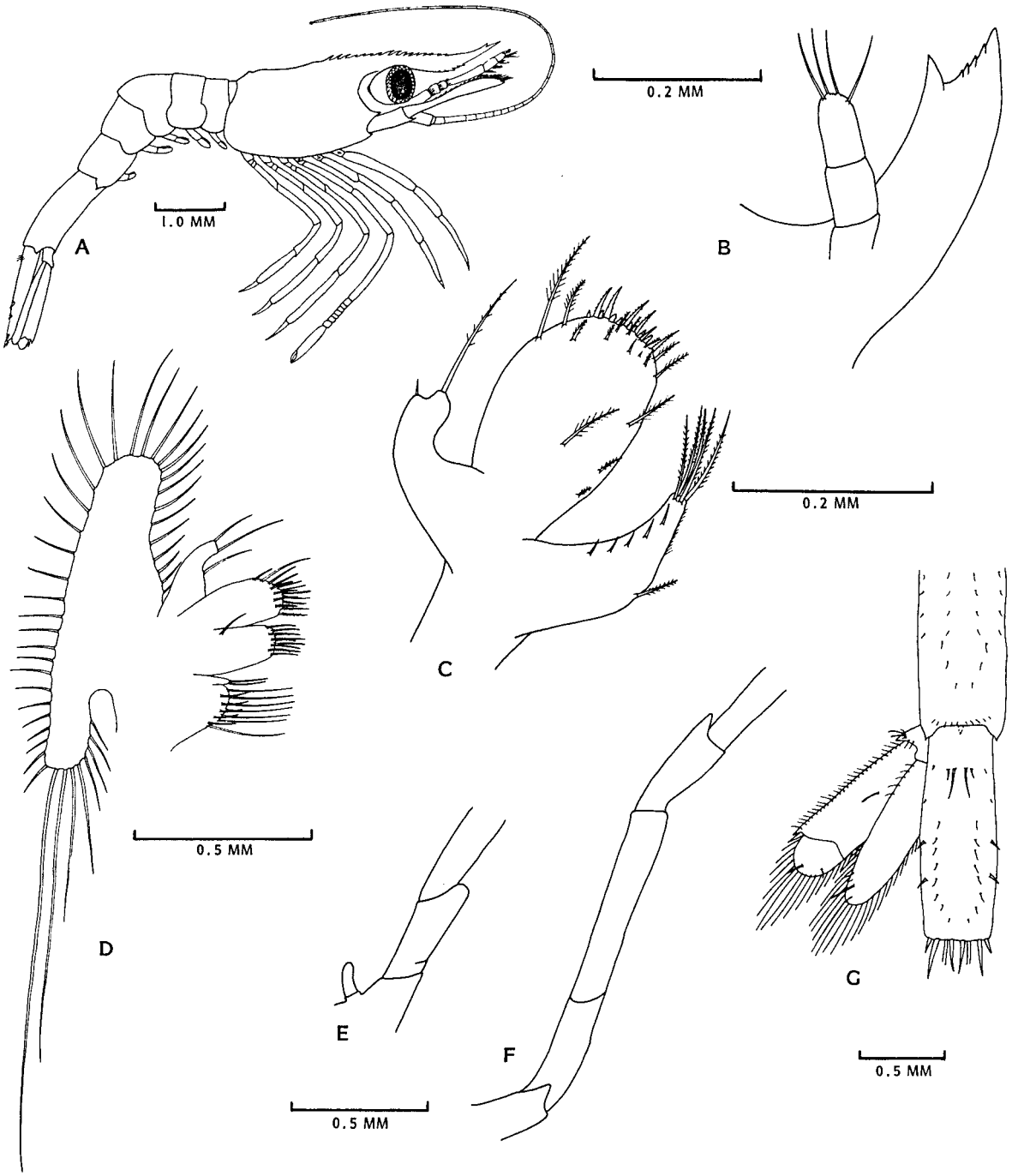

FIGURE 5.—Stage V zoea of *Pandalus hypsinotus:* (A) whole animal, (B) mandibular palp, (C) maxillule, (D) maxilla, (E) first pereopod, (F) fifth pereopod (segmentation only), (G) telson.

STAGE VI ZOEA

Total length of Stage VI zoea (Figure 6A) 10.8 mm (range 10.0-11.8 mm, 10 specimens). General color wine-red, particularly on carapace and pereopods and along ventral abdomen; remainder of telson greenish hue. Most appendages of this stage differ in shape only slightly from those of Stage V and succeeding stages and are not figured in detail. Rostrum with 15-19 dorsal teeth in addition to 1 (usually) but sometimes 2 dorsal teeth near acute tip; 4-7, usually 5, ventral teeth. A seta may occur between two or three dorsal teeth (Figure 6A).

ANTENNULE.—Inner flagellum six segmented (rarely five). Outer flagellum eight segmented; bears seven (rarely eight) groups of three (usually) aesthetascs each.

ANTENNA.—Antennal scale fringed with 40-45 plumose setae; flagellum about 6 times length of scale.

MANDIBULAR PALP.—Three segmented; number of setae variable; setation formula—6-8, 2-3, and 1-3.

MAXILLULE.—Endopodite unchanged from Stage V. Basipodite bears about 20 setae and 13 spines; coxopodite bears 18 setae.

MAXILLA.—Exopodite fringed with 61 or 62 plumose setae. Three setae on endopodite. Setation formula of lobes of basipodite and coxopodite 21-22, 17-19, 2, 11-12.

FIRST MAXILLIPED.—Exopodite has 10 or 11 setae along proximal margin. Setation formula of endopodite 2, 4, 5. Number of setae on protopodite variable—38-61 on basipodite, 7-12 on coxopodite.

SECOND MAXILLIPED.—More setose than in preceding stages; about 50 setae on terminal segment. No podobranchia.

THIRD MAXILLIPED.—No exopodite. Arthrobranchia as two minute rounded buds.

FIRST PEREOPOD.—No exopodite. Arthrobranchia bud at base of each pereopod except fifth.

SECOND PEREOPOD.—No exopodite; carpal joints of left and right pereopods 19 and 7 or 8 respectively. Left and right meropodites with three or four and one or two joints respectively.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Meropodite bears 4-6 spines. Fifth pereopod bears neither bud of arthrobranchia nor epipodite.

PLEOPODS (FIGURE 6B).—All five pairs segmented, biramus, and tipped with setae but nonfunctional. Appendix interna small bud on inner lamella of second and third pleopods only.

TELSON (FIGURE 6C).—Telson shows, for first time, narrow shape similar to adult and bears three pairs of dorsolateral spines. Terminal margin rounded slightly; bears three pairs of feathered spines and a pair of large setae dorsally. Three pairs of stiff setae at base of telson instead of two as in Stage V.

POSTZOEAL STAGES VII-IX

Total length of Stage VII zoea 12.1 mm (range 11.5-12.8 mm, four specimens). Pleopods functional and appendix interna distinct on all pleopods except first pair. Because abdominal propulsion is evident at this stage, it is considered the first postzoeal (megalopa) stage (Williamson 1969). Dorsal rostral spines 19 or 20, 1 or 2 at acute tip; 7 or 8 ventral spines. Seta (usually 1, rarely 2) occurs between each pair of rostral spines. Bud of podobranchia distinct, arises at base of epipodite of second maxilliped; buds of arthrobranchiae on third maxilliped distinct, pointed. Telson bears four pairs of spines along lateral margin, rarely an additional small spine on either margin. Left and right carpal joints of second pereopods 24 or 25 and 10 respectively.

Stages VIII and IX differ only slightly from VII. Total length of Stage VIII zoea 12.4 mm (range 11.1-13.0 mm, four specimens). Gill buds more fully developed in VIII than in VII but not yet lobulated. Left and right carpal joints of second pereopod 28 and 10 or 11 respectively. Total length of Stage IX zoea 13.6 mm (range 13.4-13.8 mm, three specimens). Rostrum with one to three setae between dorsal rostral spines and one to five setae between ventral spines; seta between the two spines at rostral tip. Buds of both podobranchiae and arthrobranchiae nearly lobulated.

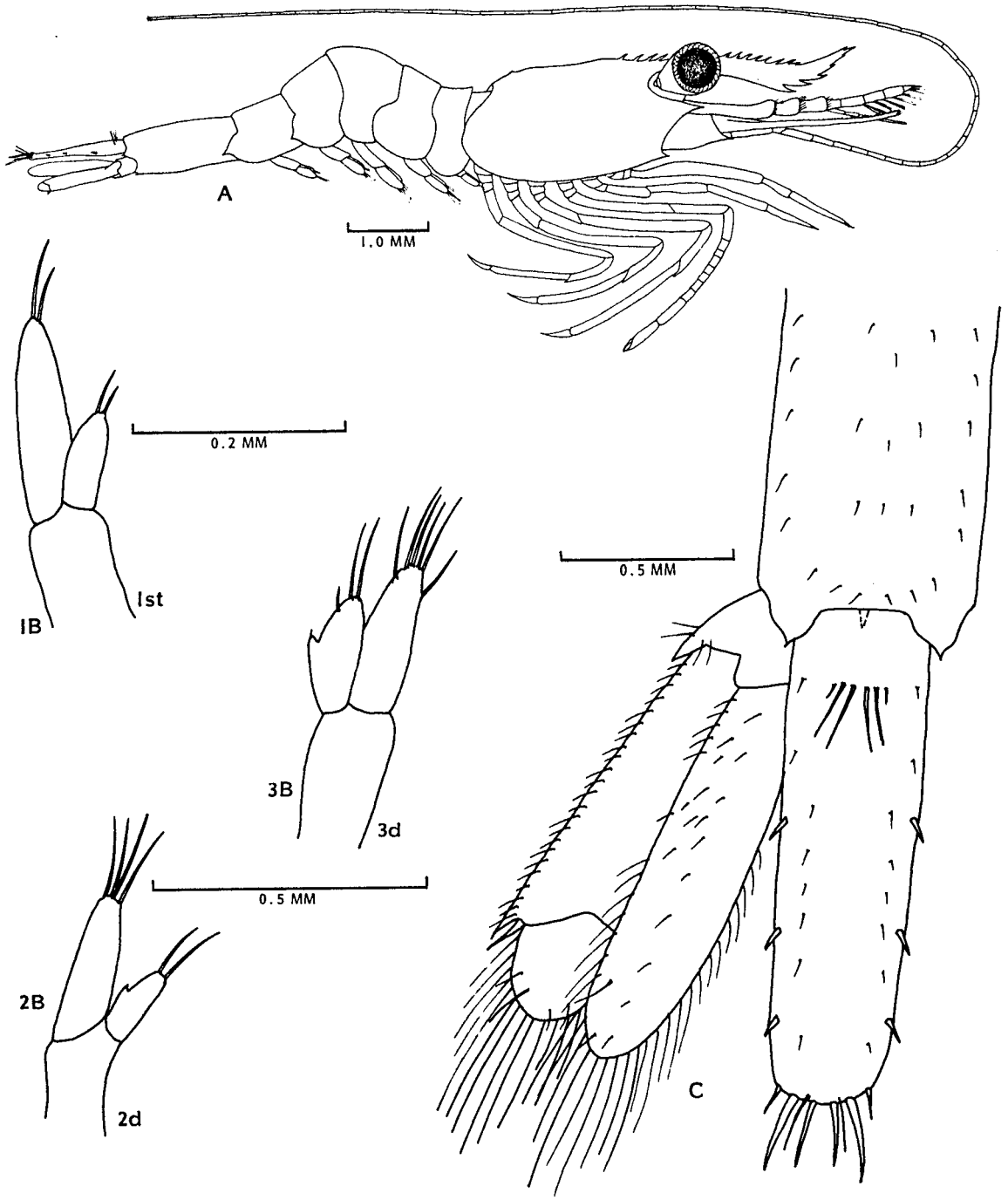

FIGURE 6.—Stage VI zoea of *Pandalus hypsinotus:* (A) whole animal, (B) pleopods (1, 2, and 3), (C) telson.

COMPARISON OF ZOEAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

Berkeley (1930) described and figured the first stage zoeae of *P. hypsinotus* that she reared in the laboratory. She also obtained the probable second and third stages from the plankton, but these were not described. Stage I zoeae reared by Berkeley differed in several respects from mine, but mostly in segmentation and setation of appendages. For instance, Berkeley showed the telson separated from the sixth abdominal segment by a joint whereas I do not. She described the tip of the antennal scale as unsegmented, but my zoeae have the tip divided into six segments. The endopodites of the first and second maxillipeds of her zoeae are unsegmented, and the exopodites of the maxillipeds and first and second pereopods are unjointed at their bases. In my zoeae, the endopodites of the first and second maxillipeds are segmented, and the exopodites of the maxillipeds and first and second pereopods are jointed at their bases. Segmentation of appendages, especially in the early zoeal stages, is most clearly seen in exuviae. Because Berekeley was unable to obtain exuviae from her laboratory-reared specimens, she probably missed seeing the segmentation of most appendages.

Kurata's (1964) description of Stage I zoeae of *P. hypsinotus* was also based on specimens reared in the laboratory; the remaining stages (II-V) he described were obtained from the plankton. The most important differences between Kurata's description and mine are: Stage I—Kurata's zoeae bear a chela on the second pereopod and the antennal scale is four segmented. In my zoeae the chela does not appear until Stage III and the antennal scale is six segmented. Stage II—The tip of the antennal scale is two segmented in Kurata's zoeae but four segmented in mine. Stage III—On Kurata's zoeae, the marginal spines of the telson vary from one to three pairs, and the inner flagellum of the antenna is twice as long as the antennal scale and has 9 or 10 joints. My Stage III zoeae always have two pairs of marginal spines and the inner flagellum of antenna is 3 times the length of the antennal scale and has 19 joints. Stage IV—The telson of Kurata's zoeae decreases in width posteriorly; the inner flagellum of antennule is two segmented; the tip of the first pereopod bears a small chela; and the carapace bears a supraorbital spine. The telson of my Stage IV zoeae increases in width posteriorly; the inner flagellum of antennule is four segmented; the tip of the first pereopod bears a simple dactylopodite in all stages (including adults); and the supraorbital spine occurs only in Stages II and III. Stage V—The telson of Kurata's zoeae bears 6+6 spines terminally; the carpopodites of the second pereopods and the pleopods are without joints; and the carapace still bears a supraorbital spine. In my specimens, the telson bears 3+3 spines terminally; the carpopodites of the left and right second pereopods bear 14-16 and 7 joints respectively; the pleopods are jointed; and the carapace does not bear a supraorbital spine.

The cause for the morphological differences between Kurata's description of the morphology of the zoeae and mine is unknown but apparently is not a result of my zoeae being reared in the laboratory. My zoeae showed no variation in number of zoeal stages and only negligible morphological variation between individuals of the same stage. Also, there were no morphological differences between my zoeae reared in the laboratory and the zoeae of *P. hypsinotus* available from local plankton collections (Stages I-III). The morphological differences between Kurata's zoeae and mine may be due to geographical variation. Berkeley (1930) has shown that pandalid zoeae from the northeast Pacific are further advanced on hatching than those from the Atlantic, although she did not have enough information to compare identical species from both areas. Unfortunately, Kurata's descriptions from Stage II onward were based on specimens from the plankton. Verification of geographical variation in zoeal morphology will be possible only when identification is based upon zoeae of known parentage and the magnitude of variation is established for each stage.

Segmentation of the antennal scale was used by Lebour (1940) as one criterion for classifying the early stages of pandalid zoeae into two groups. The first group includes pandalid species described by various authors as possessing a segmented scale (*Dichelopandalus bonnieri* (Caullery), *Pandalus montagui* Leach, and *P. propinquus* G. O. Sars). The second group includes pandalid species described by Berkeley (1930) as possessing an unsegmented scale (*P. stenolepis* Rathbun, *P. hypsinotus, P. danae*, and *P. platyceros*). Price and Chew (1972) showed Lebour's grouping to be invalid for *P. platyceros*. Kurata (1964) described zoeae of *P. hypsinotus* as hav-

ing a segmented scale. Laboratory-reared Stage I zoeae known by me to possess a segmented scale are *Pandalopsis dispar, Pandalus stenolepis, P. goniurus, P. borealis, P. danae, P. hypsinotus,* and *P. platyceros.* Berkeley obviously failed to recognize the segmented scales on her specimens. Therefore, Price and Chew's (1972) suggestion that Lebour's grouping for classifying the early stages of pandalid zoeae using segmentation of the antennal scale be disregarded is valid.

In most Decapoda, the development of functional pleopods provides a convenient and clear distinction between the zoeal and postzoeal stages because it is accompanied by several other abrupt changes in morphology, such as loss or reduction of some or all of the thoracic exopodites and changes in shape and body proportions. In the Pandalidae, however, there is not always an abrupt metamorphosis at this molt. Pike and Williamson (1964) discussed how in *P. montagui* the pleopods may become fully functional before the exopodites on the pereopods show any reduction; in *P. danae* the exopodites on the pereopods and the third maxilliped degenerate before the pleopods become functional; and in *P. kessleri* Czernaivski the exopodites on the pereopods never become functional. In my zoeae the development of functional pleopods occurred at Stage VII, but other morphological changes normally associated with postzoeal metamorphosis occurred earlier, especially at the molt to Stage IV. Morphological changes that occurred at the molt to Stage VI are reduction of thoracic exopodites; loss of supraorbital spines; changes in color; changes in shape of rostrum, mandibles, and second maxilliped; and segmentation of carpopodite of the second pereopod. Depending upon one's definition of "megalopa," it may be valid to consider Stage VII of *P. hypsinotus* as the megalopa; or one may consider stages IV through VII are all megalopal or the term "megalopa" is not strictly applicable to *P. hypsinotus.*

In addition to the morphological changes noted above, abbreviated development of zoeae of *P. hypsinotus* is also indicated by the occurrence of thoracic exopodites on pereopods 1 and 2. In contrast, most Pandalidae without abbreviated development have thoracic exopodites on pereopods 1-3. A notable exception is zoeae of *P. platyceros,* which have thoracic exopodites on pereopods 1-3 but only four zoeal stages and 8+8 telson setae in Stage I rather than the usual 7+7. Another feature of abbreviated development in *P. hypsinotus* is the proximal extension and occurrence of 17 setae on the exopodite of the maxilla in Stage I. Usually the exopodite of the maxilla in Stage I of the Caridea has no proximal extension and only five setae, as in the protozoea of the Peneidea and most British Pandalidae (Lebour 1940; Gurney 1942). The abbreviated development of zoeae of *P. hypsinotus* agrees with the findings of Berkeley (1930), who noted that zoeae of most Pandalidae of the northeast Pacific tend to be more developed when they hatch than is normal for Caridea.

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LITERATURE CITED

BERKELEY, A. A.
1930. The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. 6:79-163.

GURNEY, R.
1942. Larvae of decapod Crustacea. Ray Soc. Publ. 129, 306 p.

KURATA, H.
1964. Larvae of decapod Crustacea of Hokkaido. 3. Pandalidae. Bull. Hokkaido Reg. Fish. Res. Lab. 28:23-34.

LEBOUR, M. V.
1940. The larvae of the Pandalidae. J. Mar. Biol. Assoc. U.K. 24:239-252.

MODIN, J. C., AND K. W. COX.
1967. Post-embryonic development of laboratory-reared ocean shrimp, *Pandalus jordani* Rathbun. Crustaceana 13:197-219.

PIKE, R. B., AND D. I. WILLIAMSON.
1964. The larvae of some species of Pandalidae (Decapoda). Crustaceana 6:265-284.

PRICE, V. A., AND K. K. CHEW.
1972. Laboratory rearing of spot shrimp larvae *(Pandalus platyceros)* and description of stages. J. Fish. Res. Board Can. 29:413-422.

WILLIAMSON, D. I.
1969. Names of larvae in the Decapoda and Euphausiacea. Crustaceana 16:210-213.

PRESENT AND HISTORICAL SPAWNING GROUNDS AND NURSERIES OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, IN THE DELAWARE RIVER[1]

MARK E. CHITTENDEN, JR.[2]

ABSTRACT

Spawning occurs from late May into July but mainly in a 3-wk period from late May to mid-late June. Spawning ends progressively later proceeding upstream. Light intensity seemed to regulate when spawning began each day. Fish selected shallow riffle areas in preference to pool habitat for spawning. Spawning behavior is described.

Except for the most grossly polluted tidal water, spawning and nursery areas now extend throughout fresh water of the main Delaware and into the East and West branches. The most important spawning grounds and nurseries are now located from Port Jervis, N.Y., to Hancock, N.Y., and extend into the lower East Branch; this has probably been the case since 1910-20. There has been a fundamental upstream shift in the chief spawning grounds and nurseries since the decline of the Delaware River shad runs, because these historically extended downstream from about Delaware Water Gap, Pa., and included tidal water. Reasons for this shift suggest intrastream homing.

Only a small proportion of the historical nursery now contributes to production. Nursery and spawning areas now contribute to production of adults in proportion to their distance from Philadelphia, Pa. The extent of the spawning and nursery area since about 1910-20 has probably expanded and contracted around a core area in the upper Delaware near Hancock. Future prospects of Delaware River shad are discussed. They depend upon water quality in the tidal area and the proposed Tocks Island dam. Extirpation of the remnant runs is a distinct possibility.

The Delaware River basin once supported larger landings of American shad, *Alosa sapidissima*, than any other river system (Stevenson 1899). Annual landings near the turn of the century averaged about 14-17 million pounds but have consistently been much less than 0.5 million pounds since 1920 (Sykes and Lehman 1957; Chittenden 1974). Gross pollution near Philadelphia, Pa. (Figure 1), has been the chief reason for the low abundance since at least 1920 (Ellis et al. 1947; Sykes and Lehman 1957; Chittenden 1969). If pollution were cleared up, shad runs could be largely restored (Chittenden 1969).

Spawning and nursery areas of shad in the Delaware River are not well known, although the U.S. Army Corps of Engineers proposes to construct a dam near Tocks Island, a few kilometers upstream of Delaware Water Gap, Pa. If proposed fishways are not successful, this dam would prevent access to nearly half the 406 km of fresh water between Marcus Hook, Pa., and Hancock, N.Y. Sykes and Lehman (1957) concluded that the chief spawning and nursery areas were located upstream of Tocks Island. Their studies were made in 1950-52 when shad runs were almost nonexistent, however, and their conclusion was necessarily based on extremely limited data. Shad runs markedly resurged during the early mid-1960's when I made extensive collections and observations of adults and young. This paper describes the spawning period, behavior during the spawning period, recent and historical spawning and nursery grounds, and discusses the future prospects of shad in the Delaware River.

MATERIALS AND METHODS

Locations referred to are indicated in Figure 1 or, when first mentioned, by their approximate distances upstream from Marcus Hook, situated about 90 km downstream from the fall line at Trenton, N.J., and near the transition between fresh and brackish water.

Adults (278 males and 250 females) were collected during the spawning runs at Lambertville, N.J., using a 76-mm stretch-mesh, 107-m long and 3.6-m deep haul seine at 3- or 4-day intervals from 5 April to 19 May 1963, 20 March to 18 May 1964, 26 March to 7 May 1965, and 27 March to 19

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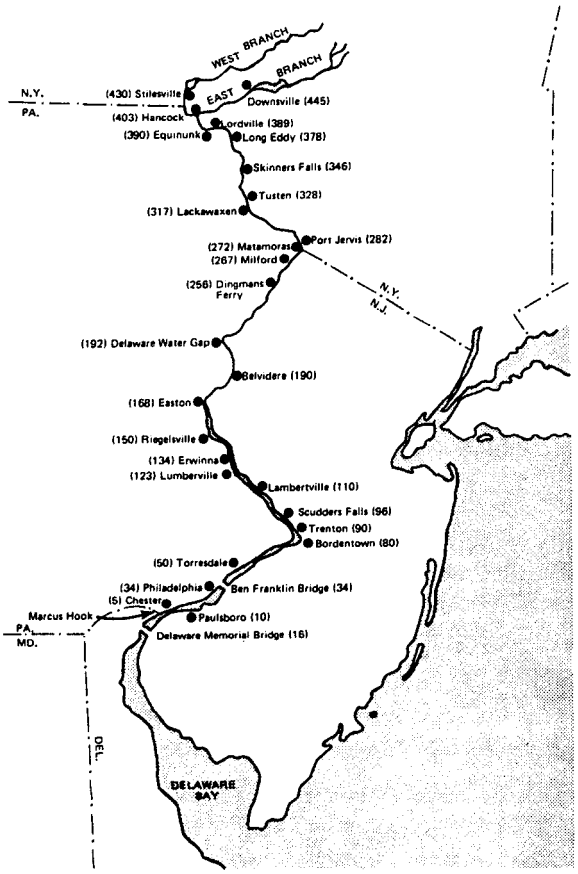

FIGURE 1.—The Delaware River. Numbers in parentheses represent distance in kilometers from Marcus Hook, Pa.

May 1966. Low dissolved oxygen near Philadelphia blocked upstream passage of part of the 1965 spawning run, and few fish were captured at Lambertville (Chittenden 1969); however, 43 dead males and 147 females were collected 21 May-10 June during a fish kill near Paulsboro, N.J. The gonads of all adults collected were examined to assess their degree of maturation following criteria of Leach (1925).

Data on the abundance of adults in the period 1959-62 were obtained from surveys (hereinafter referred to as the Tri-State Surveys) during July and August by the states of New Jersey, New York, and Pennsylvania in cooperation with the U.S. Fish and Wildlife Service. Rotenone was used to collect. After 1962 I made many observations on adult abundance and gonad condition during irregular collections upstream from Dingmans Ferry, Pa., especially during annual float trips in late May between Hancock and Port Jervis, N.Y. Observations on behavior during the spawning period were made chiefly in the East Branch near Hancock.

Young fish were collected in nontidal fresh water from 1963 to 1966 using 12-mm stretch-mesh seines. In 1963, most collections were made from Milford, Pa., upstream into the East and West branches using a 1.8-m deep, 6-m long net or a similar 10.7-m long bag seine. Most seine hauls in 1963 captured few or no young, but a few hauls captured many fish. Quantitative comparisons of abundance were considered unreliable because of the extremely contagious fish distribution. Therefore, techniques were greatly modified in 1964. A 22.9-m long, 1.8-m deep net was paid out from a pram. Lights (900 W for 1 h) were used at night to attract young shad to the shoreline for most collections during 1964 and thereafter. Only one seine haul was made at a station when lights were used, and collection sites were near deep water.

During 1966, night seining with lights was conducted at 2-wk intervals at Lordville, N.Y., Tusten, N.Y., Dingmans Ferry, Belvidere, N.J., Riegelsville, Pa., and Scudders Falls, N.J., from 1-4 August to 27-29 September and weekly thereafter until 14 November following an unreplicated two-way (stations and collections periods) experimental design in which collections were made at each station until the young completely vacated nontidal water. No F tests for significant differences in abundance were possible because of the inherent nature of the study: collecting with lights made catches reliable but replication impossible; intensive seaward movement of the young by mid-late August caused a stations by collection period interaction which negated tests for main effects. Supplementary collections using lights were made during 1966 in the East and West branches and downstream from Dingmans Ferry (Table 1).

Nurseries refer herein to areas the young occupy during July and August. Data for 1963, 1964, and 1966 (after August) are presented in Chittenden (1969, tables 35, 36, 38, 39, 41).

SPAWNING PERIOD

Nearly all spawning apparently occurred within a 3-wk period from about late May to mid-late June, although some spawning extended well into July. No fish had any translucent eggs until early May at Lambertville, and only one running

TABLE 1.—Summary of catch size (*n*) and total lengths (mm) of young American shad collected during July and August 1966.

Date	Location	*n*	Mean	SD	Min	Max
July						
5	Dingmans Ferry[1]	129	37.8	5.30	26	51
6	Belvidere	46	40.4	7.09	32	60
7	Scudders Falls	7	41.0	10.28	28	53
17	Erwinna	0	—	—	—	—
25	Riegelsville	12	51.2	8.39	42	71
25	Scudders Falls	3	68.3	8.50	60	77
August						
1-4	Lordville	208	37.1	4.57	27	52
1-4	Tusten	516	43.5	9.22	26	80
1-4	Dingmans Ferry	193	62.1	9.67	34	82
1-4	Belvidere	83	62.9	8.19	48	90
1-4	Riegelsville	8	62.9	10.86	49	78
1-4	Scudders Falls	0	—	—	—	—
7	East Branch, Hancock[1]	406	—	—	—	—
7	Downsville	0	—	—	—	—
8	Fishs Eddy	2	44.0	4.24	41	47
8	West Branch, Hancock	0	—	—	—	—
15-17	Lordville	363	46.8	9.21	26	79
15-17	Tusten	367	50.8	7.51	34	76
15-17	Dingmans Ferry	1,282	67.5	8.79	42	93
15-17	Belvidere	177	65.9	8.55	46	98
15-17	Riegelsville	16	74.3	10.14	47	90
15-17	Scudders Falls	12	94.8	8.70	82	109
29-31	Lordville	526	53.4	8.64	34	86
29-31	Tusten	45	62.1	9.95	44	87
29-31	Dingmans Ferry	124	70.7	8.80	54	100
29-31	Belvidere	63	75.3	8.61	62	97
29-31	Riegelsville	1	55.0	—	55	55
29-31	Scudders Falls	0	—	—	—	—

[1]The listed *n* was estimated as about half the total catch; large amounts of detritus were mixed with the East Branch, Hancock catch, small fish were hard to find and measurements were not taken.

ripe female was captured as early as 15 May. The gonads of some dead fish collected near Marcus Hook on 21 and 23 May 1965 were nearly ripe. Three females seined at Skinners Falls, N.Y., on 3 June 1964 had partially spawned. In the East Branch near Hancock, I observed much spawning from 10 to 17 June 1964; a few adults moved into a spawning area there after dark on 1 July 1965, suggesting that some spawning occurred then. Most spawning probably occurred before late June, however, because there was a great mortality of adults by then (Chittenden 1976).

Spawning ended at a later date upstream than it did downstream based upon the minimum sizes of young captured (Table 1). Assuming a month between hatching and transformation at about 25 mm (Walburg and Nichols 1967), spawning in 1966 ended about 7 June near Scudders Falls and about 25 June near Riegelsville. At Belvidere, spawning occurred at least until early June and at Dingmans Ferry until 1 July. Spawning ended near Tusten from 1 to 15 July and at Lordville from 15 July to 1 August. Length frequencies of young in July and August 1966 (Chittenden 1969) also show that spawning ended later upstream than it did downstream. However, the spawning period probably varies slightly between years and at different locations depending upon spawning stimuli.

The spawning period is apparently prolonged for individual fish. The ovaries of females captured near Hancock during June 1964 varied in size, many ovaries being about one-third or two-thirds the size of those from prespawning fish captured at Lambertville. This suggests prolonged spawning of individuals as Lehman (1953) concluded from egg diameter measurements.

BEHAVIOR DURING THE SPAWNING PERIOD

During the day, behavior depended upon the habitat occupied. The nontidal Delaware consists of a sequential arrangement of shallow swift riffles and slow-moving deep pools. Shad preferred pools but were frequently observed in riffles about 0.3 m deep. Schools of fish circled slowly in the pools but often formed a V in riffles. The point of the V headed upstream or in the direction of travel and left a readily observed wake. When the school was stationary and facing upstream, the fish at the point of the V moved to the rear after about 30 s. The fish immediately behind these leaders then moved to the point. This behavior spreads energy expenditure among all members of the school and may conserve energy as would the preference for pools. Both may be important to survival. Weight loss during the spawning migration is high (Leggett 1972; Chittenden 1976), and starvation causes a large mortality on the Delaware River spawning grounds (Chittenden 1976).

Adults were observed after dark in the shallows by using a pole to suspend a lantern high in the air. The large schools typical of the day seem to disperse during the evening spawning period, because only one to three fish were usually observed. Several times a behavior was observed which may have been the spawning act: a smaller fish (male?) lined up on either side of a larger fish (female?) bringing their vents in close proximity while swimming; a brief splashing coincident with a rattling sound occurred at or near the surface; and the fish separated after a few seconds. Splashing and rattling noises were continually heard outside the lighted area. This behavior was only witnessed after dark, and it occurred in water as shallow as about 150 mm. Plankton nets were not available to collect fresh eggs to confirm

this was the spawning act. However, the vigorous splashing and noise is similar to the observations of Goode (1888) and Leach (1925) and of Leim (1924) who used plankton nets to collect newly fertilized eggs.

Light intensity seemed to regulate when spawning began each day, and the shad seemed to prefer shallow riffle areas for this activity. Few fish were observed during the day in a shallow riffle spawning site near Hancock, but many fish moved from the upstream pool to the riffle as evening approached. Concentration near the riffle occurred earlier on overcast days than on sunny days. I observed spawning only at night in general agreement with Pennsylvania (1875), Goode (1888), Leim (1924), Leach (1925), Walburg and Nichols (1967), and Marcy (1972). In contrast, Massmann (1952) found spawning at all hours in the Pamunkey River, Va., although possibly more intensively from noon to midnight. Water turbidity probably influences the effect of light in regulating the daily onset of spawning. Spawning probably tends to occur at night in clear water such as the upper Delaware, but seems to begin later during the day or occurs all day long in turbid water typical of tidal areas such as the Pamunkey River. Overcast skies apparently permit spawning to begin earlier in the day.

SPAWNING GROUNDS

Important spawning grounds apparently extend no farther downstream than the Belvidere area. During the Tri-State Surveys, greatest numbers of adults were captured from Minisink Island to Skinners Falls, and none were captured downstream from Manunka Chunk (Table 2). Few adults were captured from Long Eddy, N.Y., upstream. However, these collections were made 10-21 July which is well after most adults move seaward or die (Chittenden 1976). Therefore, the chief spawning grounds may have been farther upstream.

Extensive observations from 1962 to 1968 generally support the Tri-State Survey collections, but in contrast they suggest that the area from Skinners Falls to the lower East Branch was extemely important. Many adults were observed 31 May-1 June 1962 from Milford to Delaware Water Gap, and 30 May-5 June 1963 from Mongaup River (km 296) to a few kilometers above Callicoon, N.Y. (km 360). In 1964, hundreds of adults were observed near Hancock and the lower East Branch 29 May-20 June and (J. Musick pers. commun.) near Milford on 31 May. Fewer adults were observed after 1964, but they consistently appeared from Sparrowbush, N.Y. (km 286), to the lower East Branch in late May and early June.

TABLE 2. — Numbers of adult American shad captured during the Tri-State Surveys.

Station	Distance from Marcus Hook, Pa. (km)	1959	1960	1961	1962
East Branch, Hancock	403	0	0	5	—
West Branch, Hancock	403	0	0	0	—
Long Eddy	378	0	0	23	—
Skinners Falls	346	0	11	107	134
Mongaup Area	292	0	0	271	—
Minisink Island	263	30	0	160	103
Tocks Island	218	0	0	0	0
Manunka Chunk	197	—	32	40	—
Raubs Island	152	—	0	0	—
Marshalls Island	132	—	0	0	0
Scudders Falls	95	—	—	0	—
Trenton Falls	88	—	—	—	0

Some spawning occurs downstream of Philadelphia; however, few fish which pass Philadelphia spawn as far downstream as Lambertville. I collected a nearly spent male on 10 June 1965 at Marcus Hook. This fish undoubtedly had spawned nearby, because low dissolved oxygen would have prevented movement past Philadelphia after April (Chittenden 1969). The Lewis Fishery at Lambertville captured about 6,300 fish from 1963 to 1968, but only 21 were taken after 15 May.

Spawning extends into the lower West and East branches, especially the latter, but dams prevent movement upstream of Stilesville, N.Y., and Downsville, N.Y. Young shad (27 mm total length) were captured in the West Branch at Hancock on 9 August 1963 (Chittenden 1969, table 26). This suggests spawning there because net movement of the young is downstream. Adults were collected in the East Branch at Hancock during the 1961 Tri-State Surveys. Many occurred at least as far upstream as East Branch, N.Y. (km 430), in the runs of 1962-65 (W. Kelly pers. commun.; my observations). I observed spawning in the East Branch near Hancock in 1964 and 1965.

The adults ascend some tributaries, but it is not certain if they spawn there. A female was caught on 16 May 1961 in Big Flat Brook (km 235) about 10 km upstream from the Delaware (Anonymous 1961). Adults ascended several kilometers up the Mongaup River from 1962 to 1964 and 6 km up the Beaverkill River, an East Branch tributary (W. Kelly pers. commun.).

NURSERIES

The chief nursery in 1966 was apparently located upstream from Dingmans Ferry and was especially centered near Tusten and Lordville (Table 1). Areas downstream from Tusten gradually decreased in relative importance. The chief nursery extended into the lower East Branch; many young were captured near Hancock on 7 August, but none were taken at Downsville and few were collected at Fishs Eddy, N.Y. No fish were captured in the West Branch near Hancock on 8 August, suggesting that the lower West Branch was an unimportant nursery in 1966.

Two seemingly aberrant catches affect interpretation of relative abundance upstream from Belvidere. The catch was small at Tusten on 30 August and very large at Dingmans Ferry on 17 August. Hundreds of young were attracted to the lights on 10 and 21 August at Tusten which agrees with the magnitude of catches on 4 and 16 August. The Tusten catch on 30 August probably reflects a seaward exodus of fish after 21 August. A plateau in size formed at Tusten by August 30 (Chittenden 1969, figure 47) when mean total length was 62 mm (Table 1). A plateau represents seaward movement of larger fish, and seaward movement of the young is probable when they reach 64 mm (Chittenden 1969:248). Mean size at Dingmans Ferry was 62 mm on 4 August and 67 mm on 17 August, so that the very large catch at Dingmans Ferry on 17 August probably reflects an influx of seaward moving young from farther upstream.

The Delaware River downstream of Belvidere appears to be a relatively unimportant nursery. Catches during July and August 1966 at Riegelsville and Scudders Falls were consistently much smaller than at stations farther upstream, and a catch at Erwinna, Pa., in July was also small. The largest catch in these 10 collections was 16 young. This is much smaller than the smallest catch in 14 collections at Belvidere, Dingmans Ferry, Tusten, and Lordville.

My collections and observations in 1963-65 generally agree with the nursery patterns of 1966. In 1963, young shad were observed and captured from Dingmans Ferry to the lower East and West branches; many were repeatedly observed and collected in the lower East and West branches at Hancock, and hundreds were observed near Matamoras, Pa., on 19 July and at Skinners Falls on 30 August. In 1964, young were captured from Erwinna upstream to Cochecton, N.Y. (km 354): hundreds were observed or captured at Belvidere, Delaware Water Gap, Worthington Tract (km 217), Flatbrookville (km 235), Dingmans Ferry, Sparrowbush, Pond Eddy (km 301), and Cochecton. No collections were made upstream from Cochecton in 1964 except on 18 August when no young were captured using lights in the West Branch at Hancock. In 1965, young were observed or captured from Belvidere upstream to Pond Eddy; hundreds were observed and captured at Delaware Water Gap on 8 July, at Belvidere on 15 July, and at Dingmans Ferry, Sparrowbush, and Pond Eddy on 21 July. No trips were made upstream of Pond Eddy in 1965.

GENERAL DISCUSSION

Historical Spawning and Nursery Areas

Shad migrated 68 km up the East Branch to Shavertown (Bishop 1936) and 24 km up the West Branch to Deposit in the early 1800's (Gay 1892). A dam constructed at Lackawaxen, Pa., however, blocked access upstream after 1823 (Slack 1874; Smiley 1884; Gay 1892). Spawning grounds then extended downstream from Lackawaxen for about 70 yr until a fishway permitted upstream access in 1891 (Bean 1892, 1903).

Apparently the chief spawning grounds were historically downstream from Lackawaxen. The shad catch along the Atlantic coast is primarily age IV or older fish (Walburg and Nichols 1967). Few Delaware River shad migrate upstream until age III, and most now first do so at ages IV and V (Chittenden 1975). No records exist of size or age composition in the late 1800's-early 1900's when Delaware River landings reached their zenith, except that average weights about 1896 were 3.75 and 3.50 pounds (Stevenson 1899), 3.75 pounds (Townsend 1901), and 4.2 pounds based upon Smith's (1898) report on the numbers and pounds caught. These weights are reasonably similar to the mean weights of males (1,107 g) and females 1,737 g) captured at Lambertville from 1963 to 1965 (Chittenden 1976), so that recent Delaware River data probably closely represent the age structures near the turn of the century. Therefore, renewed access to spawning grounds upstream from Lackawaxen could not have fully affected landings until 1895 or 1896. Except for 1892, annual landings were about 13-14.5 million pounds in the period of 1889-95 and about 13.9-16.8 million pounds from 1896 to 1901 (Chitten-

den 1974). The catches in these two periods are so similar that it would appear that the Lackawaxen Dam had little effect on abundance. The chief spawning grounds may have been located even further downstream than Lackawaxen, however, because Abbott (1868) stated that shad were seldom plentiful upstream from Delaware Water Gap, and this is supported by Smiley's (1884) statement that no shad were seen farther upstream than Milford for 25 yr prior to 1872. Shad were abundant at that time (Slack 1874).

Spawning grounds could have extended downstream to about Marcus Hook, because shad spawn in fresh water (Prince 1907; Leach 1925; Hildebrand and Schroeder 1928; Massmann 1952). Consideration of preferred spawning and nursery habitat and Delaware River morphology suggests that tidal water was historically important: the existence of an extensive tidal nursery (and spawning area) immediately downstream from extensive excellent spawning grounds was probably important to the former abundance of Delaware River shad (Chittenden 1973b). However, the contemporary literature conflicts on the importance of the tidal Delaware (Pennsylvania 1897; discussion session after Meehan 1907; New Jersey 1916).

The potential importance of the tidal Delaware can be judged by comparison with other rivers. Hudson River runs are entirely produced in tidal water, because a dam constructed in 1840 at Troy, N.Y. (Cheney 1896), blocks passage of shad to nontidal water. Annual Hudson River landings were 2-4 million pounds from 1936 to 1949 and catches of about 5 million pounds have been reported (Talbot 1954). Migration of shad in the Potomac River is blocked by Great Falls, 16 km upstream from tidal water, so that most fish are probably from tidal spawning. Spawning grounds in several Virginia rivers are in tidal waters (Massmann 1952). Therefore, it appears that tidal spawning was once very important in the Delaware River, in agreement with Walford [a 1951 memorandum cited by Mansueti and Kolb (1953)] who stated that the principal spawning area once was probably a short distance above Gloucester, N.J. (km 30).

The area near Hancock apparently became an increasingly important spawning area—but eventually for reduced numbers of fish—as the Delaware River shad runs declined. Many fish again moved upstream into the East Branch after installation of the Lackawaxen fishway in 1890 (Bean 1892, 1903). Landings from 1904 to 1913, in general, were only about 3-5 million pounds and consistently have been much less than 0.5 million pounds since 1920 (Sykes and Lehman 1957; Chittenden 1974). In spite of this great decline, many shad (240-350/seine haul) were captured at Hancock until 1915 (Bishop 1936). Catches near Hancock gradually declined after 1915, and a shad fishing club captured only 60-75 fish annually after 1920 and less than 12 in some years (Greeley 1936; Bishop 1936).

Many tributaries, particularly in the tidal area, may have been used for spawning and as nurseries; but their historical importance is not clear. Adults entered many tributaries near Philadelphia (Meehan 1896; Stevenson 1899). The Lehigh and Schuylkill rivers were once famous shad streams (Gay 1892; Meehan 1896), although dams were constructed after 1820 and prevented access to these streams.

Recent Spawning and Nursery Areas

With the probable exception of the most grossly polluted tidal areas, recent spawning and nursery areas have extended throughout fresh water of the Delaware and into the East and West branches. In general, nurseries must be at or downstream of spawning grounds, because the young begin to disperse downstream upon transformation from the post-larval stage—if not sooner (Chittenden 1969).

The chief spawning grounds and nurseries now extend no farther downstream than Belvidere. Gonad condition, the presence of few adults after mid-May, and the location of the chief nurseries, especially during early July, indicate that very little spawning occurs as far downstream as Lambertville. The Delaware between Belvidere and Philadelphia probably now serves as a nursery primarily due to downstream dispersal of the young. The importance of spawning grounds and nurseries now increases proceeding upstream from Belvidere towards Hancock. The most important spawning grounds and nurseries are located from about Port Jervis to Hancock and extend into the lower East Branch.

Tidal water near Philadelphia is no longer suitable as a nursery and probably not for spawning. Although conditions vary slightly between years, in general, the minimum daily dissolved oxygen is at or near 0 mg/liter from about mid-May through early December in the 66-km

stretch from Torresdale, Pa., to the Delaware Memorial Bridge, the most severely affected area being from Chester, Pa., to the Benjamin Franklin Bridge (Chittenden 1969). Minimum daily dissolved oxygen levels of about 2.5-3.0 mg/liter are needed to permit mere survival of shad, and this is not a reasonably normal existence (Chittenden 1973a).

Some spawning probably occurs in fresh water seaward of Philadelphia when low oxygen prevents upstream passage of part of the run. Therefore, this area would be a nursery. The area is limited in extent, however, and survival of fish may be precarious because of daily dissolved oxygen fluctuations due to photosynthesis or tidal movement of polluted water. de Sylva et al. (1962) collected larval shad, but no juveniles, in the Delaware River estuary shore zone even though the euryhaline young can and do utilize brackish nurseries (Chittenden 1973b). Production of shad seaward of Philadelphia, at best, apparently is small because landings in the Delaware Basin have been low for more than 50 yr.

The West Branch is apparently no longer an important nursery. Young shad were repeatedly collected at Hancock in 1963, but none were captured in two collections with lights in 1964 and 1966. Cold water releases from Cannonsville Reservoir, which began after summer 1963, may account for the apparent absence of young in the West Branch thereafter (Chittenden 1972). If so, the East Branch and possibly the Delaware below Hancock may be of precarious suitability for spawning and nursery purposes, because Pepacton Reservoir on the East Branch is also designed for water release from the hypolimnion.

Tributaries act as nurseries and possibly spawning grounds but are probably not important to production today in the Delaware River. Compton (1963) captured 38 young on 23 July 1962 in Big Flat Brook, nearly 1.6 km from the Delaware, and adults have been observed in several tributaries. Tributaries in nontidal water are too small to support many fish, however, except for the Lehigh River (km 168) which is dammed near its junction with the Delaware. Those in tidal water near or upstream of the Philadelphia area are dammed, affected by tidal movement of low oxygen water, or the young produced therein reach Philadelphia too early in summer or fall to successfully pass seaward (Chittenden 1969).

The present findings on spawning and nursery areas agree with Sykes and Lehman's (1957) observations and with their descriptions of unpublished findings of Cable: plankton tows were taken in May 1944 from Bordentown, N.J., to Equinunk, Pa.; the greatest concentration of eggs was above Lackawaxen and no eggs were found below Lumberville, Pa. Therefore, it would appear that the chief spawning grounds and nurseries have remained about the same for at least the last 30 yr and probably since about 1910-20.

Areas Contributing to Successful Production of Adults

It appears that there has been a fundamental shift in the chief spawning grounds and nurseries since the decline of the Delaware River shad runs. Historically the chief spawning grounds were downstream of Delaware Water Gap and included the tidal area. These areas are now of little importance; since the decline, the chief spawning grounds have been upstream of Delaware Water Gap. The most important spawning grounds and nurseries for the last 60 yr or more have seemingly been near the Hancock area.

Implications of the shift in spawning and nursery areas include the existence of an intrastream homing tendency which brings the fish back to spawn in their general area of birth. Chittenden (1969) discussed in detail causes of the decline in abundance of Delaware River shad and why abundance has remained low. I suggested (1969:424) that the shift in spawning and nursery areas occurred because pollution near Philadelphia has selected for an upstream-spawning stock based upon the time when the young reach the Philadelphia area; fish produced farthest downstream have the greatest probability of reaching Philadelphia before dissolved oxygen improves sufficiently to permit successful seaward passage. This implies intrastream homing. Interstream homing exists in shad (Hammer 1942; Hollis 1948; Talbot and Sykes 1958; Nichols 1960), but direct evidence of intrastream homing is desirable.

Spawning and nursery areas near Hancock are apparently the key to maintenance of the remnant Delaware River shad runs, because Chittenden (1969) demonstrated that the last fish to move seaward were, in general, those produced farthest upstream. The extent of the spawning and nursery area since about 1910-20 or earlier has probably expanded and contracted depending upon the size of the run and spawning success.

Important spawning and nursery areas probably extend farthest downstream when the run is large and spawning is successful. The upper Delaware area near Hancock is probably the core around which expansion and contraction occurs.

Downstream sections of the nursery usually contribute little or nothing to production of adults even if the nursery expands. Since 1925, larger shad runs in the Delaware River have depended upon one year class which successfully passed the Philadelphia area (Chittenden 1975). Downstream nurseries contribute to production only when water quality near Philadelphia permits shad passage earlier than normal; there is usually catastrophic destruction of the young as they pass Philadelphia (Chittenden 1969). Therefore, in general, it appears that nursery and spawning areas contribute to production in proportion to their distance from Philadelphia. Only a small part of the historical nursery area now contributes to production of adults.

Future Prospects

Future prospects of shad in the Delware River depend primarily upon water quality in the tidal area and upon a dam near Tocks Island (Chittenden 1969). The present remnant runs appear based upon stocks that spawn far upstream in a small part of their former spawning grounds and whose progeny pass tidal water in late fall when dissolved oxygen increases. A greater area would contribute to successful production if dissolved oxygen increased earlier, because fish spawned farthest downstream pass tidal water first. Therefore, the magnitude of future runs will reflect dissolved oxygen conditions, because the area contributing to production will change accordingly. If recent or typical water quality was maintained, future runs would usually be small. Fortuitous circumstances would occasionally produce larger runs as in the early 1960's.

Construction of a dam near Tocks Island would greatly affect shad. They probably would be extirpated from the Delaware if successful fishways for both adults and young are not provided and water quality in the tidal area is unchanged. Cold water reservoir releases drastically and adversely affect usage of downstream spawning and nursery areas, if only due to avoidance (Chittenden 1972). Cold water releases from a Tocks Island dam would shift spawning and nursery areas far downstream, and spawning grounds under any water release circumstances would be downstream of the area that presently produces adults successfully. Therefore, the young produced would reach tidal water too early to pass seaward successfully. Great water quality improvement would be needed in the tidal area just to maintain the present small runs. Water quality improvement by flow augmentation might be self-defeating, because the young now move downstream even during the summer; and increased discharge and temperature decrease would accelerate this. The potential would be brighter if successful fishways were provided. The reservoir might be an excellent nursery for the young judging from their pelagic habits, their preference for pool habitats, and the former importance of tidal nurseries. This, combined with nurseries upstream from the reservoir, might establish larger runs—if the young passed the dam and tidal water successfully. However, much larger runs would be achieved with less risk at possibly less cost if Delaware River water quality in the tidal area were restored and the dam was not built. Then, the outstanding recreational potential of a clean tidal area in a great population center would be restored—and the outstanding recreational opportunity of an unobstructed Delaware River would not be lost.

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LITERATURE CITED

ABBOT, C. C.
1868. Catalogue of vertebrate animals of New Jersey. *In* Geology of New Jersey, Append. E, p. 751-830.

ANONYMOUS.
1961. Big Flat Brook shad. N.J. Outdoors 12(2):28.

BEAN, T. H.
1892. The fishes of Pennsylvania. Rep. Pa. State Comm. Fish. 1889-90-91:1-149.
1903. Catalogue of the fishes of New York. N.Y. State Mus. Bull. 60:1-784.

BISHOP, S. C.
1936. Fisheries investigations in the Delaware and Susquehanna Rivers. N.Y. State Conserv. Dep., 25th Annu. Rep. 1935, Suppl. 10:122-139.

CHENEY, A. N.
1896. Shad of the Hudson River. Annu. Rep. Comm. Fish. Game For. N.Y. 1895:125-134.

CHITTENDEN, M. E., JR.
1969. Life history and ecology of the American shad, *Alosa sapidissima*, in the Delaware River. Ph.D. Thesis, Rutgers Univ., New Brunswick, N.J., 458 p.
1972. Responses of young American shad, *Alosa sapidissima*, to low temperatures. Trans. Am. Fish. Soc. 101:680-685.
1973a. Effects of handling on oxygen requirements of American shad (*Alosa sapidissima*). J. Fish. Res. Board Can. 30:105-110.
1973b. Salinity tolerance of young American shad, *Alosa sapidissima*. Chesapeake Sci. 14:207-210.
1974. Trends in the abundance of American shad, *Alosa sapidissima*, in the Delaware River Basin. Chesapeake Sci. 15:96-103.
1975. Dynamics of American shad, *Alosa sapidissima*, runs in the Delaware River. Fish. Bull., U.S. 73:487-494.
1976. Weight loss, mortality, feeding, and duration of residence of adult American shad, *Alosa sapidissima*, in fresh water. Fish. Bull., U.S. 74:151-157.

COMPTON, K. R.
1963. Angler harvest comparisons on the fly-fishing only and open fishing stretches of the Big Flatbrook. D. J. Job Compl. Rep. State N.J. Proj. F-20-R-1, 37 p.

DE SYLVA, D. P., F. A. KALBER, JR., AND C. N. SHUSTER, JR.
1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper waters. Univ. Del. Mar. Lab., Inf. Ser., Publ. 5, 164 p.

ELLIS, M. M., B. A. WESTFALL, D. K. MEYER, AND W. S. PLATNER.
1947. Water quality studies of the Delaware River with reference to shad migration. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 38, 19 p.

GAY, J.
1892. The shad streams of Pennsylvania. Rep. Pa. State Comm. Fish. 1889-90-91:151-187.

GOODE, G. B.
1888. American fishes. W. A. Houghton, N.Y., 496 p.

GREELEY, J. R.
1936. Fishes of the area with annotated list. N.Y. State Conserv. Dep., 25th Annu. Rep. 1935, Suppl. 10:45-88.

HAMMER, R. C.
1942. The homing instinct of the Chesapeake shad, *Alosa sapidissima* (Wilson), as revealed by a study of their scales. M.S. Thesis, Univ. of Maryland, College Park, 45 p.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43(1), 368 p.

HOLLIS, E. H.
1948. The homing tendency of shad. Science (Wash., D.C.) 108:332-333.

LEACH, G. C.
1925. Artificial propagation of shad. Rep. U.S. Comm. Fish. 1924. Append. 8, p. 459-486. (Doc. 981.)

LEGGETT, W. C.
1972. Weight loss in American shad (*Alosa sapidissima*, Wilson) during the freshwater migration. Trans. Am. Fish. Soc. 101:549-552.

LEHMAN, B. A.
1953. Fecundity of Hudson River shad. U.S. Fish Wildl. Serv., Res. Rep. 33, 8 p.

LEIM, A. H.
1924. The life history of the shad (*Alosa sapidissima* (Wilson)) with special reference to the factors limiting its abundance. Contrib. Can. Biol., New. Ser. 2:161-284.

MANSUETI, R., AND H. KOLB.
1953. A historical review of the shad fisheries of North America. Chesapeake Biol. Lab. Publ. 97, 293 p.

MARCY, B. C., JR.
1972. Spawning of the American shad, *Alosa sapidissima* in the lower Connecticut River. Chesapeake Sci. 13:116-119.

MASSMANN, W. H.
1952. Characteristics of spawning areas of shad, *Alosa sapidissima* (Wilson) in some Virginia streams. Trans. Am. Fish. Soc. 81:78-93.

MEEHAN, W. E.
1896. Fish, fishing and fisheries of Pennsylvania. Rep. Pa. State Comm. Fish. 1895:108-245.
1907. The shad work on the Delaware River in 1907 and its lessons. Trans. Am. Fish. Soc. 36:105-118.

NEW JERSEY.
1916. Annu. Rep. Board Fish Game Comm. N.J. 1916, 26 p.

NICHOLS, P. R.
1960. Homing tendency of American shad, *Alosa sapidissima*, in the York River, Virginia. Chesapeake Sci. 1:200-201.

PENNSYLVANIA.
1875. Rep. Pa. State Comm. Fish. 1874.
1897. Rep. Pa. State Comm. Fish. 1897.

PRINCE, E. E.
1907. The eggs and early life history of the herring, gaspereau, shad and other clupeoids. Contrib. Can. Biol. 1902-1905:95-110.

SLACK, J. H.
1874. Notes on the shad, as observed in the Delaware River. *In* Notes on the natural history of the shad and alewife, p. 457-459. U.S. Comm. Fish and Fish. Part 2. Rep. Comm. 1872 and 1873.

SMILEY, C. W.
1884. Notes on the shad season of 1884, with references to other species. Bull. U.S. Fish Comm. 4:337-341.

SMITH, H. M.
1898. Report of the Division of Statistics and Methods of the Fisheries. U.S. Comm. Fish and Fish. Part 23. Rep. Comm. 1897:CXXV-CXLVI.

STEVENSON, C. H.
1899. The shad fisheries of the Atlantic coast of the United States. U.S. Comm. Fish and Fish. Part 24. Rep. Comm. 1898:101-269.

SYKES, J. E., AND B. A. LEHMAN.
1957. Past and present Delaware River shad fishery and considerations for its future. U.S. Fish Wildl. Serv., Res. Rep. 46, 25 p.

TALBOT, G. B.
1954. Factors associated with fluctuations in abundance of Hudson River shad. U.S. Fish Wildl. Serv., Fish. Bull. 56:373-413.

TALBOT, G. B., AND J. E. SYKES.
1958. Atlantic coast migrations of American shad. U.S. Fish Wildl. Serv., Fish. Bull. 58:473-490.

TOWNSEND, C. H.
1901. Statistics of the fisheries of the Middle Atlantic States. U.S. Comm. Fish and Fish. Part 26. Rep. Comm. 1900:195-310.

WALBURG, C. H., AND P. R. NICHOLS.
1967. Biology and management of the American shad and status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 550, 105 p.

LARVAL DYNAMICS OF THE DUNGENESS CRAB, *CANCER MAGISTER*, OFF THE CENTRAL OREGON COAST, 1970-71

R. GREGORY LOUGH[1]

ABSTRACT

The larval dynamics of the economically important Dungeness crab, *Cancer magister*, were investigated from plankton samples collected bimonthly during 1970 and 1971 along a trackline near Newport, Oreg. Larvae appeared at maximum densities (8,000/1,000 m^3) within 15 miles of the coast in late January 1970 and remained in the plankton until late May for an approximate larval period of 130 days. The bulk of the larval population was retained in the nearshore area by the strong alongshore and onshore components of the surface currents and to some extent by the behavior of larvae in determining their position in the water column. During the 1971 season, larvae appeared initially at about the same time and densities, but a mass mortality may have occurred in the early zoeal stages coinciding with the unusually severe weather in February and March. A significant difference between the 1970 and 1971 larval populations was suggested by analysis of covariance using sea surface temperature and salinity as environmental variables. However, the effect of the low temperature and salinity values that occurred during the winter of 1971 were not clearly indicated by multiple regression analyses of laboratory experimental data to be the prime factors directly affecting larval survival. Neither did a gut-fullness study of planktonic larvae substantially explain the 1971 larval mortality. Therein various hypotheses are explored in view of the present knowledge of processes affecting larval survival and recommendations are suggested for further research.

It is well known that many species of economically important marine resources fluctuate greatly in number and location. These fluctuations may be explained in part by changes occurring in the larval populations. That the larval stage is the most critical period for the majority of marine animals was originally emphasized by Hjort (1914, 1926) for fish larvae and by Thorson (1946) for marine invertebrate larvae. Survival through this period is usually considered the major factor in determining the strength of the year class. The causes or extent of larval mortality, however, are still relatively unknown.

Bimonthly plankton samples were collected from 1969 through 1971 along a transect off the central Oregon continental shelf to document the species of crab larvae present, their seasonality and abundance, and their onshore-offshore distribution in relation to seasonal changes in oceanographic conditions (Lough 1975b). A major effort was made to assess the larval population of the Dungeness crab, *Cancer magister* Dana, as it supports one of the most important fisheries in the Pacific Northwest.

Cancer magister occurs along the Pacific coast from Unalaska to lower California and ranges from mean low water to 50 fathoms (91 m) (Schmitt 1921). Although it prefers sandy or sandy-mud bottoms of the nearshore area, specimens have been found on all bottom types within estuaries and on the continental slope. Adult females generally reach maturity by their second or third year and may produce three or four broods during a life-span (MacKay 1942; Cleaver 1949; Butler 1960). Egg-carrying females are found in Oregon waters from October to March with essentially one brood produced per year (Waldron 1958). Field observations (Waldron 1958) and laboratory rearings by Poole (1966) and Reed (1969) indicate that larvae hatch off northern California and Oregon from January through March and are present in the nearshore waters through July for a total estimated larval life of 128 to 158 days. *Cancer magister* passes through five zoeal stages and one megalops during its larval development before settling out of the water and metamorphosing to the benthic juvenile.

HYDROGRAPHIC FEATURES OF STUDY AREA

The surface waters along the U.S. west coast are dominated by the California Current; a slow,

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broad, and shallow current flowing equatorward (Wooster and Reid 1963). The nearshore currents vary seasonally and are dependent upon wind direction and strength. During the fall and winter months when the winds are predominantly from the southwest, a subsurface countercurrent flowing northward along the coast develops into the Davidson Current. Drift bottle studies by Wyatt et al. (1972), Burt and Wyatt (1964), and Schwartzlose (1964) indicate that the Davidson Current first develops along the Oregon-Washington coast in September reaching maximum speeds between 0.5 and 2 knots within 20 miles of the coast during the month of November.

The major change in the surface currents from northward to southward occurs in March and April (Wyatt et al. 1972). The phenomenon of coastal upwelling occurs when the northwesterly winds intensify and sometimes persist from May to September. As the surface waters are transported offshore and to the southwest, cold, high salinity waters from below a permanent pycnocline (60-100 m) are brought to the surface (Smith et al. 1966). This zone of active upwelling occurs within 20 miles of the coast but its effects can be observed to the edge of the slope.

The area within 5 miles of the coast has not been studied in much detail but is believed to be dominated by mixing processes (Mooers 1970). The surface currents are generally well correlated with the wind direction, but tidal currents predominate when the wind is reduced. A very strong alongshore current with an onshore component is indicated within 3-5 miles of the coast (Keene 1971; Wyatt et al. 1972; Holton and Elliot 1973).

The dominant processes modifying surface water properties off the Oregon coast during the winter are rainfall and river runoff; while during the summer, the major processes are upwelling in conjunction with heating and mixing with the Columbia River plume water (Pattullo and Denner 1965). Surface temperatures and salinities taken on early life history cruises from June 1969 through August 1971 at stations NH01-NH10 are presented in Figures 1 and 2. Temperatures range annually from about 7° to 17°C and are highest from May through October, peaking in September. More variability is evident during the summer due to surface heating interrupted by local upwelling of near 7°C bottom water. Surface salinity values are generally low during the winter and high in the summer reflecting seasonal precipitation and upwelling, respectively. The annual range of salinity is from about 25 to 35‰. Low salinity values at stations NH03 and NH05 from November through April are probably associated with the Yaquina Bay plume which flows north along the coast during the winter (Kulm and Byrne 1966).

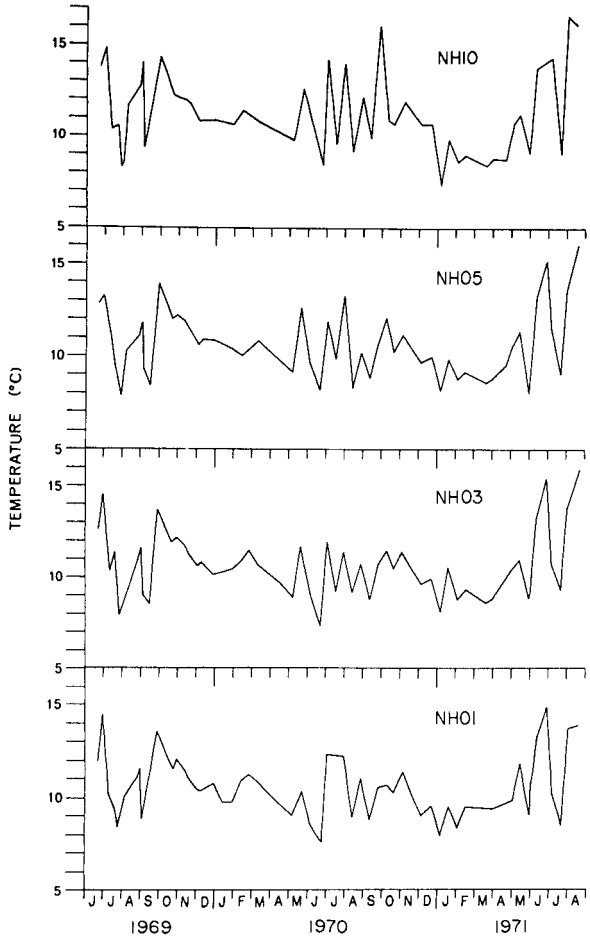


FIGURE 1.—Surface temperature (°C) at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971.

METHODS

Sampling Program and Gear

This study was conducted primarily on a trackline off Newport, Oreg. (lat. 44°39.1′N) across the continental shelf and slope. The 12 sampling stations are designated on the Newport Hydrographic line (NH) in Table 1, which correspond in distance to nautical miles from the

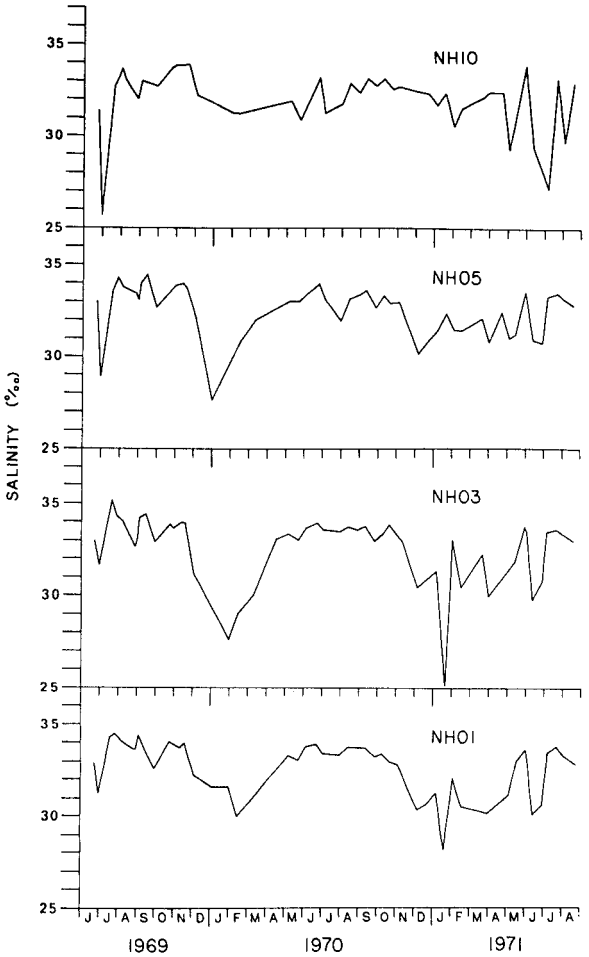


FIGURE 2.—Surface salinity (‰) at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971.

TABLE 1.—Location of plankton sampling stations and bottom depths along the Newport Hydrographic line (NH) off Newport, Oreg.

Station (Lat. 44°39.1'N)	Long.	Depth (m)
NH01	124°05.4'W	20
NH03	124°08.6'W	46
NH05	124°10.7'W	59
NH10	124°17.7'W	85
NH15	124°24.7'W	95
NH20	124°31.7'W	142
NH25	124°38.7'W	330
NH30	124°45.7'W	220
NH35	124°52.7'W	340
NH40	124°59.7'W	1,060
NH50	125°13.7'W	1,300
NH60	125°27.7'W	2,850

coast. Plankton samples initially were collected at the four inshore stations (NH01-NH10) constituting the main series of samples from June 1969 through August 1971. The sampling program was extended offshore to NH60 by 5- or 10-mile intervals beginning with the 3 February 1971 cruise.

A high-speed bongo net sampler (Posgay et al. 1968) with a 0.2-m mouth diameter was used exclusively from 22 June 1969 through 20 October 1970. The two cylinder-cone nets, 1.8 m in length, were constructed of 0.233- and 0.571-mm nylon mesh and had an effective straining surface (pore size area) to mouth area ratio of ca. 10 to 1. A 30-pound lead ball or a 15-pound V-fin depressor was attached to the sampler line.

Starting with the 4 November 1970 cruise, a 0.7-m diameter bongo net sampler was used in conjunction with the 0.2-m sampler to strain a greater volume of water and to reduce avoidance by the larger larvae. The 0.7-m bongo nets had a net length of 5.1 m, were constructed of 0.571-mm nylon mesh, and had an effective straining area ratio of ca. 8 to 1. Both samplers were equipped with TSK[2] flowmeters mounted on brackets 18 cm from the rim of the inside frame. A multiplane kite-otter wire depressor (ca. 80 pounds), modified after Colton (1959), was used with the dual bongo net array to produce a wire angle ratio of 2 to 1. The sampling objective was to make a high speed, oblique, plankton tow, sampling the water column in equal stepped intervals from 150 m depth, or in shallower areas from bottom to surface. Wire was let out and retrieved at 50-75 m/min while the vessel was underway at 2-3 knots. Most of the samples represent daylight (0600-1800) tows ranging in duration from 10 to 25 min. The longer tows were generally made on stations beyond 5 miles. Plankton samples were immediately preserved in 5-10% Formalin and later buffered with sodium borate.

A bathythermograph (BT) cast was made at each station near bottom or to 150 m depth. Surface bucket temperatures also were taken at each station to calibrate the BT readings. Salinity samples were collected on the surface and near bottom or to 150 m depth by a Nansen bottle cast and analyzed by an inductive salinometer. Salinity, temperature, and depth (STD) data from a real-time printout computer were available for several cruises.

The Nekton Cruise of 11-12 April 1970 at station NH45 was included in this study as it is one of the few cruises that sampled the offshore

[2]Tsurumi-Seiki Kosakusho. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

plankton during 1970. The objective of this cruise was to identify those organisms associated with sound scattering layers in the upper 150 m of seawater and, if possible, to follow their day-night migration patterns. Six successive integrated tows of approximately 45 min each were taken to a depth of 150 m (total time: 1852-2355). A standard 6-foot (1.8-m) Isaacs-Kidd mid-water trawl (IKMT) with a 2.9 m^2 mouth opening [1½-inch (3.8-cm) mesh with a ¼-inch (0.6-cm) linear nylon liner] was used for this series. The second series of eight samples alternately sampled from surface to 150 m and from 150 m to surface with an eight-bar electronic multiple plankton sampler (EMPS) attached to the IKMT (Pearcy and Mesecar 1970) (total time: 0134-0514). The cylinder-cone nets were approximately 2.9 m in length with a mouth diameter of 0.4 m and made of 0.571-mm nylon mesh. Another series also used the EMPS to sample eight discrete layers from the surface to 330 m depth covering three bands of scatters (total time: 0640-1113). Scattering layers were located using 12 and 38.5 kHz echo sounders. One automated STD cast was made.

Processing of Plankton Samples

Samples from both mesh sizes of the 0.2-m bongo nets were processed for the nearshore area, stations NH01-NH10. Only one side of the 0.7-m bongo net sampler was processed to examine the offshore area, NH15-NH60. Generally, the entire sample was sorted, however, many required subsampling using an 8-cm diameter plankton splitter (Longhurst and Seiburt 1967). Approximately 22% of the 0.2-m bongo net samples and 39% of the 0.7-m bongo net samples required subsampling. Those samples which required splitting were usually from stations NH01 and NH03.

All crab larvae were removed from the samples and positive identification of *C. magister* larvae was made from the descriptions given by Poole (1966) and from preserved specimens reared by Thomas F. Gaumer, Fish Commission of Oregon, Marine Laboratory, Newport, Oreg. Catches of larvae were first converted by computer to number per 1,000 m^3 of seawater and ordered in a format. Graphs of stage density against time were plotted for the 0.2-m bongo net samples, 0.571-mm mesh, with the aid of a CalComp plotter using the Oregon State University CDC3300 computer.

SAMPLING VARIABILITY

The detailed analyses of the various methods by which sampling variability affected the estimates of larval crab abundance are given by Lough (1975b). Variability estimates and sampler comparisons were made in this study on other species of crab larvae than *C. magister* for the most part, as limited ship time and weather played an important role in determining the objectives and priorities of the sampling program. Analysis of variance techniques were used to estimate the variance of a single observation in the manner of Winsor and Clarke (1940). Confidence limits for a single observation of either sampler usually exceeded the 50-200% range reported by Winsor and Clarke due to the relatively low densities of crab larvae sampled during replicate tows. A range of an order of magnitude was considered necessary to distinguish a real difference between any two observations. There was no significant difference between the total number and kinds of crab larvae caught by the two sides of the different sized samplers. The 0.7-m bongo net sampler gave smaller confidence limits for larval crab catches and was much superior in establishing significant differences between stations than the 0.2-m bongo net sampler.

Most of the nearshore samples (NH01-NH10) were taken during daylight hours; only 8.6% of the 0.2-m bongo net samples were taken at night between 1800 and 0600 h. More (26.7%) of the 0.7-m bongo net samples sorted beyond NH10 were collected at night. Most larvae were caught more abundantly in night tows than day tows for both sized samplers. Day-night differences in larval abundance were greater for the 0.2-m sampler than the 0.7-m sampler. There was a nearly equal distribution in the number of kinds of crab larvae caught between day and night samples using the 0.7-m sampler; however, using the 0.2-m sampler, significantly more kinds of larvae were caught at night.

The results of the Nekton Cruise showed that the larvae of *C. magister* occur in relatively low densities offshore as far as station NH45 during early April 1970. They are most likely to occur in the surface waters above 120 m, the depth of the thermo- and halocline and are probably associated with the first sound scattering layer at 25 to 90 m depth. A Mann-Whitney two sample rank test (Tate and Clelland 1957) retained the null hypothesis that there was no significant dif-

ference between the number of *C. magister* megalopae, or the total number of larvae caught in the first two series of tows. In the second series of samples more larvae were caught towing from surface to 150 m than from 150 m to surface and the total number of larvae decreased with time (0134-0514) for both alternate types of tows. The coefficients of variation (standard deviation/mean) for the total number of larvae were about the same for the first two series of tows (1.25 and 1.31, respectively) indicating a somewhat patchy distribution of the larvae in the upper 150 m of water at night. Very few larvae were caught during the third series of tows.

RESULTS

Distribution and Abundance of *Cancer magister* Larvae

Two larval seasons were encompassed by the sampling program (Figure 3). Zoea 1 larvae made their first substantial appearance during the first season on 29 January 1970 at stations NH03, NH05, and NH10 with maximum densities ranging from 1,000 to 3,000/1,000 m^3. The subsequent zoeal stages were found most abundantly at stations NH05 and NH10. Few zoea 4 and no zoea 5 stages were found at any of the four inshore stations. In general, the number of larvae captured decreased from zoea 1 through 5. However, large numbers of megalopae were found at stations NH01, NH03, and NH05, suggesting a general inshore transport of larvae during this season. Maximum densities of the magalopae ranged from 1,000 to 8,000/1,000 m^3, densities comparable to those of the zoea 1 stage found earlier in the year. Few megalopae appeared in the water column after 22 May 1970 and none after 16 July 1970. This indicates that the length of the larval period in the plankton is approximately 130 days (89-143 days). The summer upwelling conditions did not appear to have any effect on the larvae since the bulk of the megalopae had settled before the onset of intense upwelling.

The major appearance of zoea 1 larvae during the second season occurred at about the same time (18 January 1971) and stations (NH03, NH05, NH10), and at about the same densities (1,000-2,000/1,000 m^3). However, the density of the larvae appeared to decrease more rapidly at zoeal stages 2 and 3, and virtually no larvae of any stage were found after zoea 3. The 30 March 1971 cruise was the last sampling period which caught any significant number of larvae. Very few megalopae were found at any station throughout the summer in day or night samples.

Cancer magister was the most abundant crab larvae caught at station NH45, 11-12 April 1970 (Nekton Cruise). Its megalopae had the highest densities of any larval stage with 19/1,000 m^3, followed by zoea 5 at 12/1,000 m^3. Fewer zoea 4 and 3 were present. Scattered occurrences of all larval stages were present the following year, 1971, to 60 miles offshore in the 0.7-m bongo net samples. Megalopae and zoea 3-5 predominated offshore with densities usually much less than 200/1,000 m^3, suggesting that these larvae had originated nearshore and subsequently drifted offshore. Larvae present at stations NH35 to NH60 are under the influence of the Columbia River plume as indicated by the warmer temperatures and lower salinities measured at these stations during the sampling period.

All observations indicate a dramatic difference in the abundance of megalopae between the 2 yr. Sampling was much more intensive during the 1971 season from the standpoint of day-night replicate tows using both size samplers in the inshore and offshore areas when the megalopae were sparse.

Climate and Hydrography 1970-1971

The winter of 1971 along the Oregon coast was generally more severe than that of 1970. Climatological records (U.S. Environmental Data Service 1970,1971) for Newport and other ports of Oregon show monthly mean air temperatures for February and March 1971 to be substantially lower than the same months during 1970. Also, total precipitation generally was greater during the winter of 1971 but showed considerable variability along the coast. Ocean surface temperatures correspondingly were much colder during this period in 1971 than 1970. Gonor et al. (1970) and Gonor and Elvin (1971)[3] reported Agate Beach, Oreg. mean surf temperatures and Wyatt and Gilbert (1971, 1972) reported monthly mean surface temperatures for various ports along the Oregon coast to be as much as several degrees lower during the later winter of 1971 than 1970.

[3]Gonor, J. J., and D. W. Elvin. 1971. Inshore sea surface temperature and salinity conditions at Agate Beach, and Yaquina Head, Oregon in 1971. Unpubl. data. School Oceanogr. Oreg. State Univ.

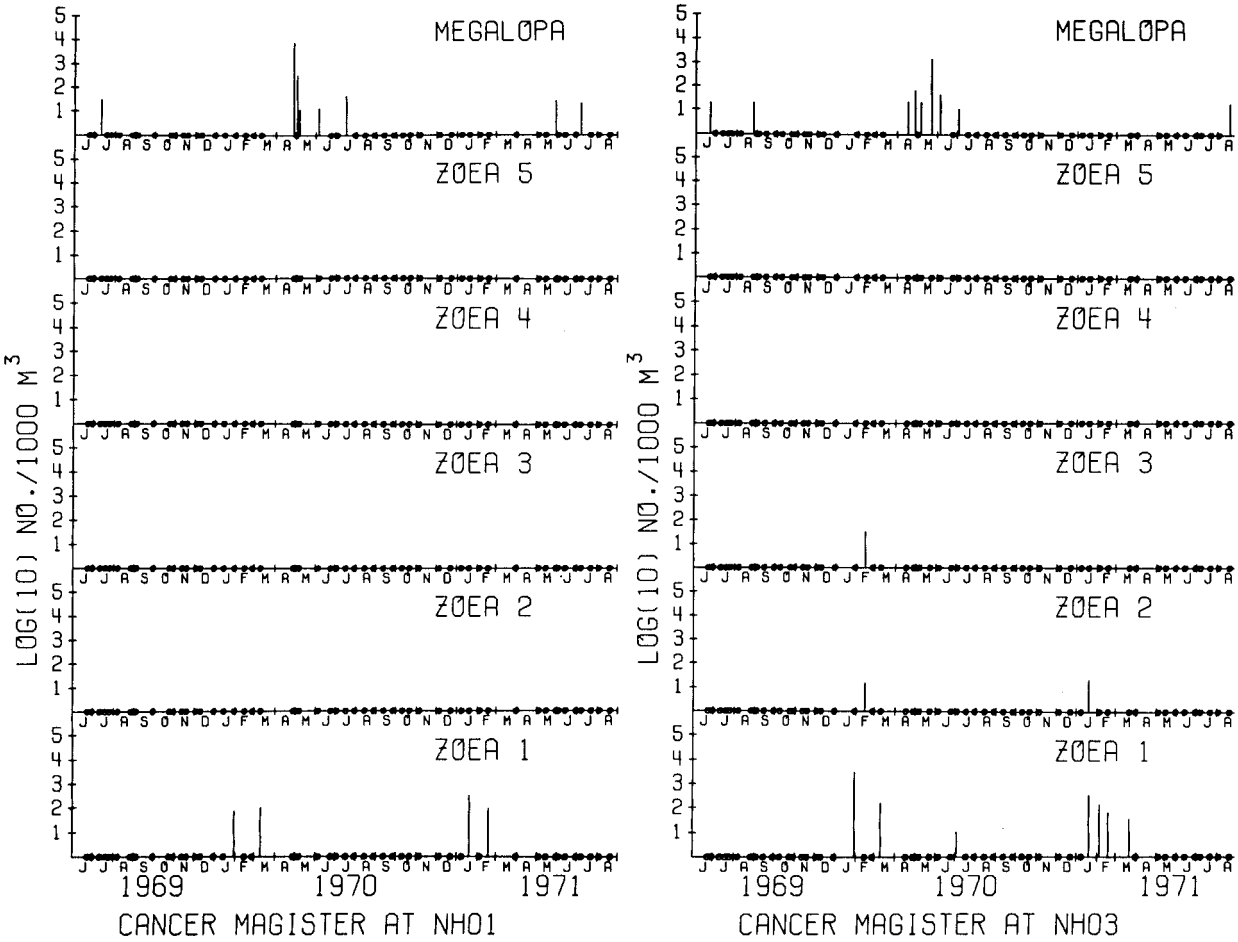
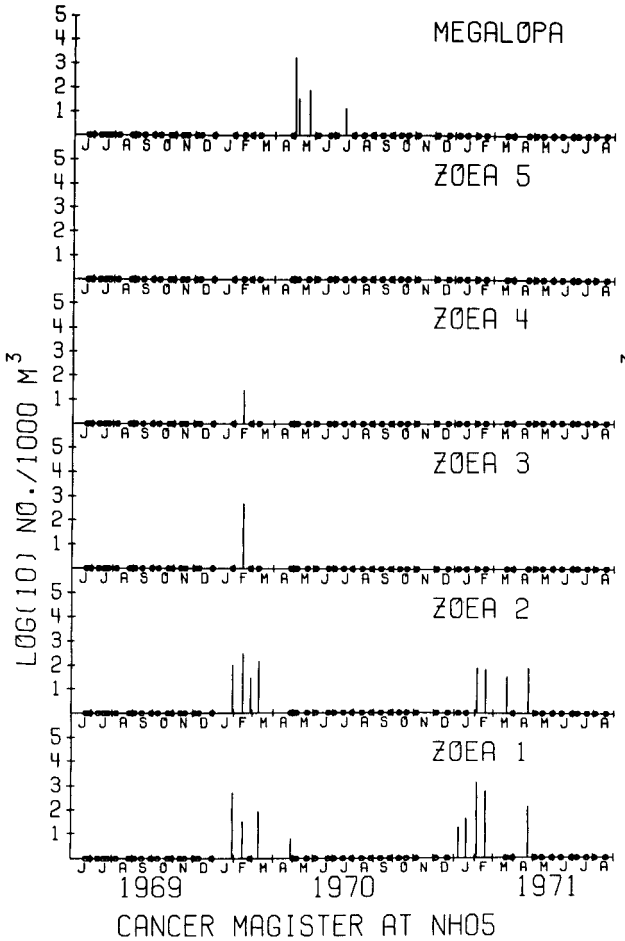
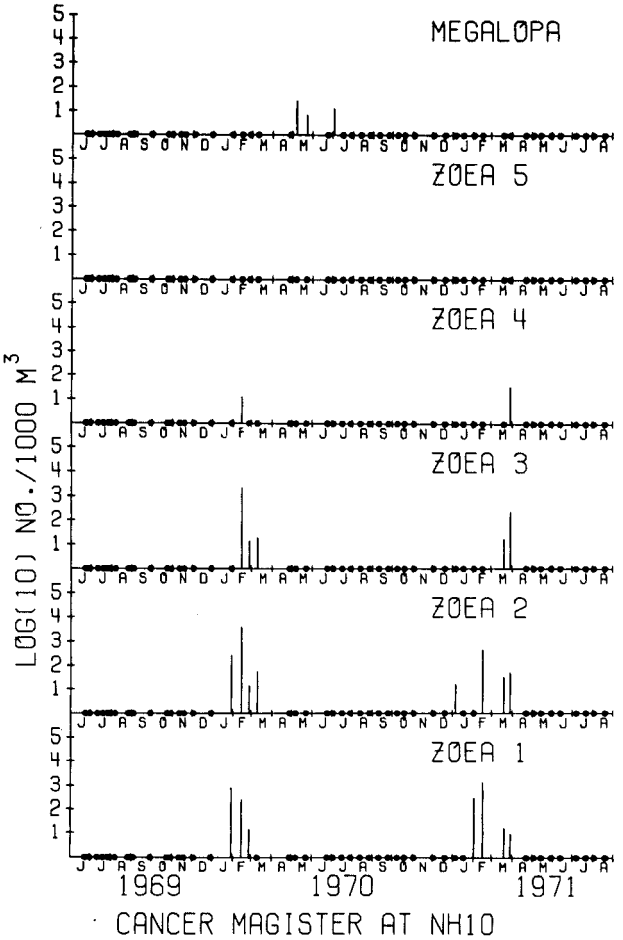


FIGURE 3.—Density of *Cancer magister* larvae at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971, collected with the 0.2-m bongo net sampler, 0.571-mm mesh.

Salinity values showed considerable variability among stations and months such that a generalized trend could not be observed between the two seasons. The anomalous winter of 1971 was further substantiated by Bakun's (1973) indices of coastal upwelling intensity for selected locations along the west coast of North America based on offshore Ekman surface wind transport from monthly mean surface atmospheric pressure data. Positive values indicate periods of coastal upwelling whereas negative values indicate downwelling. January and February of 1970 at lat. 45°N, long. 125°W show significantly greater negative indices (−98 and −71, respectively) than the same period in 1971 (−32 and −16, respectively). High negative values are indicative of strong downwelling along the coast which Bakun stated would accelerate the southward flow. In either case, more offshore surface water would be transported onshore. During the March transition period, the 1970 index was normal (+1); however during 1971 an anomalously high negative index (−49) occurred. This indicates that downwelling and subsequent transport of surface waters was more intense during March of 1971 than 1970. Downwelling also was more intense during March 1971 than in the previous 2 mo of that year. Drift bottle data compiled by Wyatt et al. (1971) reported a 14.7% return for bottles released off Newport from 25 February to 3 March 1970. By contrast, a 28.6% return occurred during 6-9 March 1971. The average percent return of drift bottles on all stations west of Newport, 1961-71, during both February and





March was 18% (Wyatt et al. 1972). High percentages of returns near 30% were observed only during February and March 1961, 1962, 1963, and 1967.

April 1970 showed a high positive index value (+25) indicative of upwelling processes, whereas downwelling was still in process during the same month in 1971 (−2). However, by May 1971 the upwelling intensity was twice the magnitude of that in 1970 (+66 and +33, respectively). In all regards the year 1971 can be considered the most anomalous whereas 1970 can be considered the least anomalous of the sampling period and the most typical over a 20-yr span. Kukla and Kukla (1974) reported large-scale global anomalies in weather patterns developing early in 1971. Snow cover in the northern hemisphere increased dramatically for the months of February, March, April, and September 1971.

Larval Population Analyses Between 1970 and 1971

Despite the rather restricted data set, a rigorous statistical analysis is attempted at this point to explore the relative importance of some environmental variables associated with the *C. magister* larval populations. An attempt is made to examine potential causative factors underlying the difference in larval abundance between 1970 and 1971 seasons. A basic assumption in the analysis is that the larval data collected in a single sampling transect are representative of a much larger homogeneous area. Patches of larvae may be quite localized so that differences in larval abundance from year to year may be due to dispersal and not mortality caused by an environmental variable per se. However, the distribution of adult breeding populations are

confined to shallow waters less than 50 m depth and appear fairly uniform along the Oregon coast based on commercial landings of legal-sized adults (Waldron 1958). This implies that the distribution of larvae along the entire Oregon nearshore area would be relatively homogeneous from year to year. Wind induced turbulence and mixing would tend to increase the homogeneity of the larval population despite any initial patchiness.

If we assume that the total number of *C. magister* larvae combined over the four inshore stations (NH01, NH03, NH05, NH10) is representative of the total population on a local basis, then the question may be asked whether there is a significant difference in the population means between the 2 yr, 1970 and 1971, and can a difference be explained using the concomitant observations of time, temperature, and salinity?

An analysis of multiple covariance was used to test this hypothesis on two sets of data for *C. magister* larvae. The first set of data compares the sampling period from 29 January 1970 to 29 July 1970 with that of 18 January 1971 to 21 July 1971. This period includes, for these 2 yr, the first major larval release through the time at which no megalopae were present in the water column. Larval density estimates from both sizes of mesh of the 0.2-m bongo net sampler were used in the analyses. Surface temperatures and salinities comprised the only complete data set for the two larval seasons and the average values of the four inshore stations were used for each sampling period. Nevertheless, sea surface temperatures and salinities are representative of nearshore subsurface conditions during the winter period from November through March-April as extensive wind mixing occurs in the shallow areas producing isothermal conditions (Renfro et al. 1971). During the spring and summer, a weak thermocline of less than 2°C exists in the nearshore area (<20 m). Larval and environmental data used in the analyses are given in Appendix Table 1.

The mathematical model used for the initial analysis was of the form:

$$Y = b + b_0(y) + b_1(t) + b_2(T) + b_3(S) + b_4(T^2) + b_5(S^2) + b_6(T \times S)$$

where, $Y = \log_{10}(X + 1)$ number of larvae per 4,000 m³ of water, b = a mean effect, y = a year effect, t = a time effect (days elapsed since 1 January), T = linear effect of sea surface temperature (°C), S = linear effect of sea surface salinity (‰), T^2 = quadratic effect of temperature, S^2 = quadratic effect of salinity, and $T \times S$ = interaction effect between temperature and salinity.

The b's in the model were estimated from a general linear hypothesis testing computer program contained in the Oregon State University Statistical Program Library. Various hypotheses can be specified by the user to test the importance of the individual parameters in the model.

A summary of the analysis on the initial run is given in Table 2. A highly significant difference (1% level) was found between y means after being adjusted for all the covariates in the model. However, only t was found to be highly significant in explaining the yearly difference. That is, the appearance of larvae in the plankton was of shorter duration in 1971 than in 1970. Subsequently, a new model was generated using only t as a covariate:

$$Y = b + b_0(y) + b_1(t).$$

The importance of t was again found to be highly significant in explaining the difference between y population means of *C. magister* larvae (Table 3).

TABLE 2. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January through July) by analysis of multiple covariance (full model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	12.983	12.983	15.079**
T	1	1.323	1.323	1.537
S	1	0.120	0.120	0.140
T^2	1	0.513	0.513	0.594
S^2	1	0.296	0.296	0.344
$T \times S$	1	1.303	1.303	1.513
y (adjusted)	1	9.074	9.074	10.538**
Residual	44	37.887	0.861	

**$F_{.99(1,44)} = 7.12$

Fitted model: $Y = -11.313 + 0.470(y) - 0.018(t) - 5.076(T) + 2.576(S) + 0.043(T^2) - 0.060(S^2) + 0.127(T \times S)$.

		Mean of covariates					
Year	Mean Y	t	T	S	T^2	S^2	$T \times S$
1970	2.19518	124.21	10.36	32.23	109.05	1,040.49	333.13
1971	1.57263	109.38	10.01	31.71	102.74	1,007.00	316.70

TABLE 3. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January through July) by analysis of multiple covariance (reduced model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	45.149	45.149	52.336**
y (adjusted)	1	9.448	9.448	11.218**
Residual	49	42.271	0.863	

**$F_{.99(1,49)} = 7.17$

Fitted model: $Y = 3.856 + 4.366(y) - 0.017(t)$.

The second data set compares the sampling period 29 January-2 May 1970 with 18 January-14 May 1971. The period selected compares the larval period prior to summer upwelling, eliminating the erratic surface temperature and salinity fluctuations. Most of the *C. magister* larvae are megalopae by early May.

The same full model was used in the initial run for the second data set and is presented in Table 4. There was a significant difference (5% level) between y means after being adjusted for all the covariates in the model. The covariates, t, T, and $T \times S$ were all significant.

TABLE 4. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January to May) by analysis of multiple covariance (full model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-level
t	1	6.807	6.807	7.073*
T	1	5.277	5.277	5.483*
S	1	0.156	0.156	0.162
T^2	1	0.018	0.018	0.019
S^2	1	0.012	0.012	0.012
$T \times S$	1	5.183	5.183	5.385*
y (adjusted)	1	6.260	6.260	6.504*
Residual	26	25.023	0.962	

*$F_{.95(1,26)} = 4.22$

Fitted model: $Y = 180.944 + 0.712(y) - 0.024(t) - 20.294(T) - 4.907(S) - 0.037(T^2) - 0.022(S^2) + 0.656(T \times S)$.

		Mean of covariates					
Year	Mean Y	t	T	S	T^2	S^2	$T \times S$
1970	2.80494	90.56	10.35	31.76	107.91	1,010.36	328.08
1971	2.09844	80.13	9.59	31.28	92.82	979.08	299.81

The initial model was reduced to the following form:

$$Y = b + b_0(y) + b_1(t) + b^2(T) + b_3(S) + b_4(T \times S)$$

which greatly increased the significance of the parameters in the final model (Table 5). A highly significant difference (1% level) was found between y means after being adjusted for all the covariates. In explaining the difference between y means of *C. magister* larvae, the covariate t was most significant (1% level) followed by T and S, and $T \times S$ at the 5% level.

The foregoing analyses support the contention that there was a significant difference between the *C. magister* larval populations of 1970 and 1971. Fewer larvae appeared in 1971 and they appeared in the plankton for a shorter period of time suggesting widespread larval mortality. This apparent larval mortality was associated by these analyses with the colder surface temperatures and lower salinities that occurred during the winter of 1971. The direct effects of temperature and salinity on larval survival will be explored in the next section.

TABLE 5.—A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January to May) by analysis of multiple covariance (reduced model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-level
t	1	7.629	7.629	8.530**
T	1	5.859	5.859	6.551*
S	1	5.230	5.230	5.845*
$T \times S$	1	5.774	5.774	6.456*
y (adjusted)	1	8.650	8.650	9.672**
Residual	28	25.043	0.894	

*$F_{.95(1,28)} = 4.20$; **$F_{.99(1,28)} = 7.64$

Fitted model: $Y = 201.891 + 0.705(y) - 0.023(t) - 20.547(T) - 6.148(S) + 0.641(T \times S)$.

Temperature-Salinity Tolerance of Laboratory-Reared Larvae

A laboratory study by Reed (1969) determined the effects of temperature and salinity on the larval survival of *C. magister*. However, it was necessary to assess more thoroughly the effects of these factors on survival during development and to extrapolate from Reed's data in order to derive better estimates of larval survival at the low temperatures that occurred during the 1971 season. The response surface technique used in the analysis of his data is not only valuable in its predictive role, but also visually represents any change in response at various stages of development. Details of this response surface technique and its application to the study of marine ecology are discussed by Alderdice (1972).

A multiple regression analysis was applied to Reed's (1969) survival data of *C. magister* after 20, 30, 40, and 50 days of culture at experimental conditions. The mathematical model used in the analysis was of the form:

$$Y = b_0 + b_1(S) + b_2(T) + b_3(S^2) + b_4(T^2) + b_5(S \times T)$$

where, Y = percentage survival, b_0 = a constant, S = linear effect of salinity, T = linear effect of temperature, S^2 = quadratic effect of salinity, T^2 = quadratic effect of temperature, and $S \times T$ = interaction effect between salinity and temperature.

The b's in the model were estimated by a stepwise multiple regression computer program. Further details of the regression analysis are

given by Lough (1975a). The calculated regression coefficients from a particular equation are fitted by computer to a full quadratic equation in temperature and salinity in order to print a contour diagram of the response surface. Temperature and salinity scales on all plots were set to range beyond the experimental conditions in order to facilitate response comparison and to allow the overall form of the surface to be visualized. Contours extrapolated beyond the experimental data lie outside the dotted lines.

A summary of the multiple regression analyses on survival after the various periods of rearing and the response surfaces are given in Table 6 and Figure 4. The analyses indicated that after 20 days of rearing under the experimental conditions S and S^2 were the two most important variables in the model. T and $S \times T$ were of lesser importance but still contributed significantly to the model. Analyses of the later rearing periods of *C. magister* emphasized the effect of temperature and showed the decreasing importance of both S and S^2 and $S \times T$. This trend is more evident when one compares the response surface plots from 20 through 50 days of rearing. After 20 days of rearing, the response surface contours are nearly circular, with a slight tilt to the main axis, indicating a small interaction effect. The axis of the contours tilts progressively towards the temperature axis until, at 50 days of rearing, the contour axis is almost perpendicular to the temperature axis. Also, the survival contours progressively constrict about the temperature axis with time showing the narrowing of the temperature range tolerated by the larvae. Maximum survival (80% contour) at 20 days is predicted to occur between 6.5° and 17.5°C and 21.5 and 35.0‰, while at 50 days, maximum survival is predicted to occur between 9.0° and 15.0°C and above 28.5‰. The area of maximum survival (80% contour) shifts somewhat during the 20- to 50-day period from an initial low salinity-wide temperature range to a high salinity-low temperature tolerance. However, when the 20- and 50-day survival polynomials were tested by an analysis of covariance (Ostle 1963:205), they were not found significantly different in their response (Table 7). In summary, salinity appears to exert an immediate effect on *C. magister* larval survival, while the effect of temperature becomes increasingly important with time.

Survival at a given temperature, salinity, and time can now be estimated using the fitted equations. All of the fitted equations for the four time

TABLE 6. — Multiple regression analyses of *Cancer magister* larval survival in 20 temperature and salinity combinations.

Regression step number	Variable	R^2	F-value	Degrees of freedom	Significance level	Coefficients	t-value	Significance level
				20 days				
1	S	0.505	18.378	(1,18)	1%	29.4369	4.069	1%
2	S^2	0.591	3.723	(2,17)	5%	−0.4720	3.040	1%
3	T^2	0.659	3.030	(3,16)	N.S.	−0.7068	4.635	1%
4	T	0.834	15.819	(4,15)	1%	23.4636	4.559	1%
5	$S \times T$	0.865	3.272	(5,14)	5%	−0.2277	1.809	N.S.[1]
	Constant					−457.6092		
				30 days				
1	S	0.417	12.878	(1,18)	1%	18.3726	2.026	N.S.
2	T^2	0.529	4.044	(2,17)	5%	−0.6903	3.611	1%
3	T	0.702	9.290	(3,16)	1%	23.0272	3.569	1%
4	$S \times T$	0.744	2.443	(4,15)	N.S.	−0.2503	1.586	N.S.
5	S^2	0.768	1.446	(5,14)	N.S.	−0.2340	1.202	N.S.
	Constant					−335.2887		
				40 days				
1	S	0.416	12.830	(1,18)	1%	14.3243	1.602	N.S.
2	T^2	0.491	2.511	(2,17)	N.S.	−0.8113	4.305	1%
3	T	0.744	15.824	(3,16)	1%	25.5095	4.011	1%
4	$S \times T$	0.768	1.509	(4,15)	N.S.	−0.1892	1.217	N.S.
5	S^2	0.779	0.713	(5,14)	N.S.	−0.1620	0.844	N.S.
	Constant					−313.8493		
				50 days				
1	S	0.373	10.717	(1,18)	1%	13.4195	1.687	N.S.
2	T^2	0.432	1.756	(2,17)	N.S.	−0.8265	4.931	1%
3	T	0.757	21.339	(3,16)	1%	25.7928	4.559	1%
4	$S \times T$	0.778	1.451	(4,15)	N.S.	−0.1662	1.201	N.S.
5	S^2	0.791	0.901	(5,14)	N.S.	−0.1620	0.949	N.S.
	Constant					−305.2337		

[1]N.S. = Not significant.

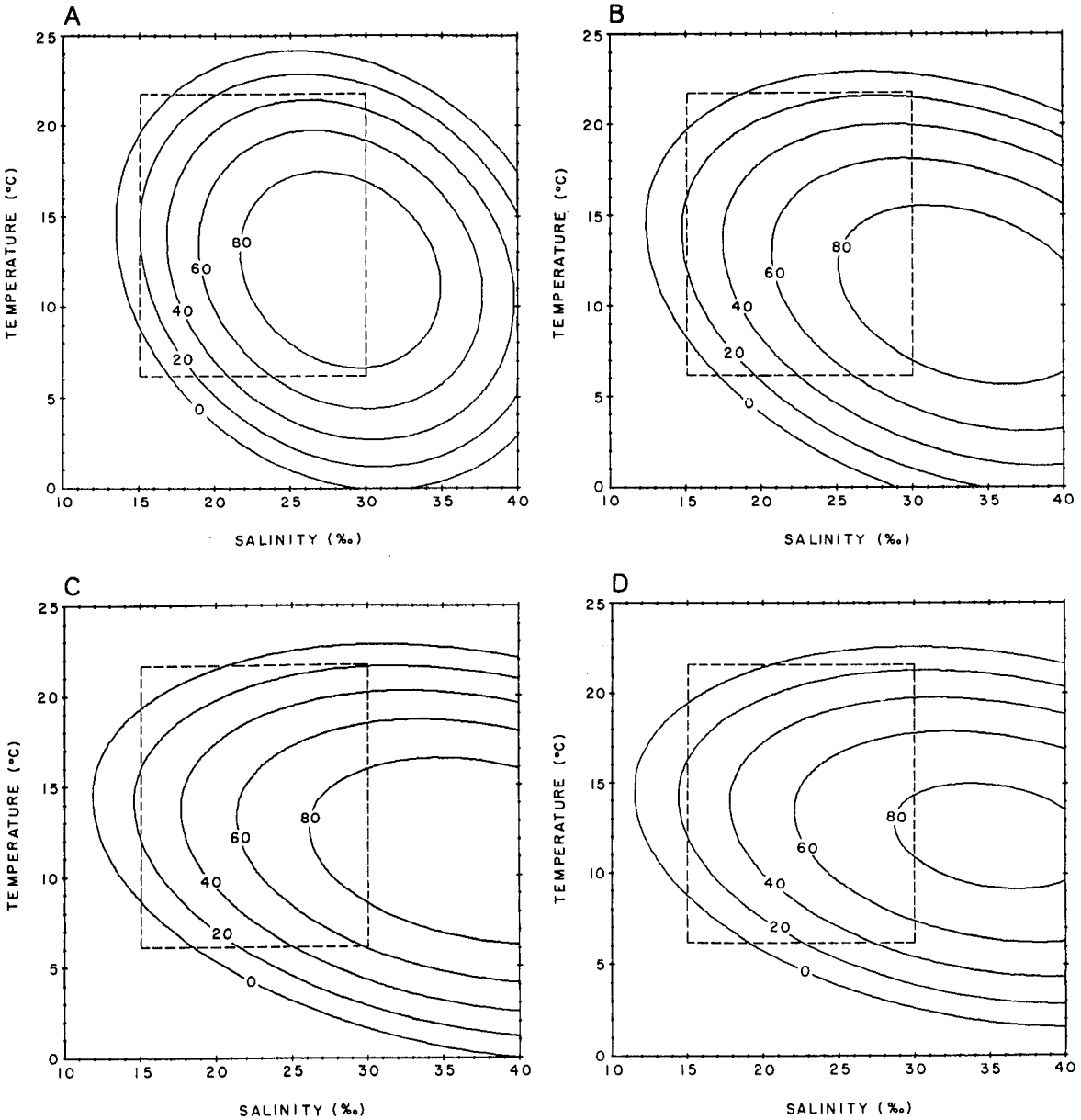


FIGURE 4. — Response surface estimation of percent survival of *Cancer magister* larvae after (A) 20 days, (B) 30 days, (C) 40 days, and (D) 50 days of development at 20 different temperature and salinity combinations.

periods explained a significant 77-87% of the variance in the data. The lowest surface temperature and salinity reported for any sampled station during the 1971 season was 7.4°C and 25.17‰. After 20 days at this combination, 76.8% survival is predicted; after 50 days, 44.6% survival. The monthly mean surface temperature and salinity compiled at the Oregon State University Marine Science Center dock, Newport, is reported by Wyatt and Gilbert (1972) for March 1971 to be 8.81°C and 30.12‰. Survival of 92.3% is predicted at this temperature and salinity combination after 20 days, and 71.0% survival after 50 days. The direct effect of these temperatures and salinities found off the central Oregon coast on the survival of *C. magister* larvae would appear to

TABLE 7. — An analysis of covariance between the 20- and 50-day survival polynomials of *Cancer magister* larvae. Null hypothesis: no significant difference between 20- and 50-day survival polynomials.

Source of variation	df	Sum of squares	Mean square	*F*-value
Polynomial 1: 20-day survival	14	4,217.780		
Polynomial 2: 50-day survival	14	5,096.684		
Total: Polynomial 1 and 2	28	9,314.464	332.659	
Polynomial 3: Combined 20- and 50-day survival	34	13,287.052		
Difference: Polynomial 3 and total	6	3,972.588	662.098	[1]1.99

[1]Not significant, $F_{.95(6,25)} = 2.44$.

be minimal. Forty-five percent survival would still occur, even after an unrealistic period of 50 days at nonconservative temperatures and salinities.

Gut-Fullness Analysis of Planktonic Larvae

The physical appearance of *C. magister* larvae was examined for clues to the difference in the larval populations between the two seasons, 1970 and 1971. Whatever happened to the larvae occurred early in their development during the months of February and March 1971, as a marked decrease in the total larval population was observed by the second zoeal stage. Those larvae examined from the 1971 season appeared more flaccid with a soft exoskeleton, had less eye pigmentation, and were more transparent compared to the larvae caught during the 1970 season. However, these features of appearance could not be readily quantified. Further examination indicated a possible difference on a population basis in the amount of food in their guts among stages, stations, and years. Differences in larval gut-fullness may indicate good versus poor food availability, or possibly a dying larval population weakened by some factor in their environment other than food.

Food and/or feces in the guts could readily be seen through the body wall up to the fourth or fifth zoeal stage and a close estimation of the percentage fullness could be made by noting the proportion of gut segments filled with food. The larval body can be divided into eight equal segments; the thorax constituting twice the length of an abdominal segment. The food or feces was considered to be of the same approximate diameter and could be estimated to within 3% of the total gut length. A sample size of 30 larvae was necessary before any significant difference could be considered.

The 0.2-m bongo net samples were used to compare the 1970 and 1971 larval seasons at stations NH01, NH03, NH05, and NH10. Samples were combined with both meshes of the 0.2-m bongo nets. Only whole larvae were used and usually the entire sample was analyzed. Specimens from the 0.7-m bongo net samples were used to compare inshore-offshore larval gut-fullness between the 12 stations, NH01 through NH60, for the 1971 season.

Zoea 1 larvae from the 1970 season showed maximum mean percentage gut-fullness at stations NH03 and NH10 compared to those from NH01 and NH05 (Table 8). A general decrease in gut-fullness was observed with increasing stage of development. Surprisingly, all zoeal stages of larvae caught during the 1971 season showed an increase in gut-fullness over those of the 1970 season. The notable exception occurred for zoea 1 larvae at station NH03, where the 1971 gut-fullness is significantly lower than that for the 1970 season.

The onshore-offshore comparison showed that the greatest gut-fullness for any larval stage oc-

TABLE 8. — A comparison of *Cancer magister* larval gut-fullness[1] between 1970 and 1971 at four Newport Hydrographic line (NH) stations.[2]

Stage	Year	NH01	NH03	NH05	NH10
Zoea 1	1970	13.19 ± 2.74(4)	31.23** ± 0.06(126)	19.64 ± 0.12(65)	29.53 ± 0.07(106)
	1971	14.26 ± 0.34(19)	9.86 ± 0.10(78)	24.10** ± 0.03(241)	36.13** ± 0.04(187)
Zoea 2	1970		7.56 ± 1.97(5)	15.57 ± 0.10(72)	12.94 ± 0.02(269)
	1971		25.00 ± (1)	23.29** ± 0.24(38)	30.39** ± 0.11(87)
Zoea 3	1970		10.49 ± 10.49(2)	23.76 ± 0.09(81)	14.02 ± 0.02(212)
	1971			18.75 ± (1)	20.20** ± 0.09(51)
Zoea 4	1970			9.40 ± 3.36(4)	15.99 ± 1.19(6)
	1971				19.50 ± 1.61(7)
Zoea 5	1970				
	1971				

[1]Gut-fullness is expressed as a reconverted arcsin$\sqrt{\text{percentage}}$ transformed mean followed by its standard error and the number of observations in parentheses.
[2]The station samples in this table represent the combined specimens from both mesh sizes of the 0.2-m bongo net sampler.
**1% level significant difference between yearly means based on a two-sample *t*-test.

TABLE 9. — A comparison of *Cancer magister* larval gut-fullness[1] between 12 Newport Hydrographic line (NH) stations for 1971.[2]

Station	Zoea 1	Zoea 2	Zoea 3	Zoea 4	Zoea 5
NH01	8.51* ± 1.33(9)				
NH03	10.51** ± 0.06(82)	0.79 ± 0.79(2)	0.0 ± (1)		
NH05	27.89** ± 0.05(134)	17.57** ± 1.09(14)			
NH10	26.51** ± 0.07(137)	29.79** ± 0.07(109)	45.77* ± 0.71(12)		
NH15	23.50** ± 0.07(76)	35.11** ± 0.33(36)	60.77** ± 2.27(8)		
NH20	34.43** ± 0.12(72)	23.69** ± 0.13(69)	20.99 ± 0.12(5)	25.00 ± (1)	43.75 ± (1)
NH25	6.26** ± 0.25(33)	6.41 ± 0.48(20)	3.01 ± 3.01(3)		
NH30	11.51 ± 0.07(56)	7.75 ± 0.39(9)	23.41 ± 0.52(4)		25.00 ± (1)
NH35		12.03 ± 0.99(3)	17.09 ± 0.16(5)	18.75 ± (1)	
NH40	53.14 ± 0.10(2)	0.0 ± (1)	6.70 ± 6.70(2)	6.25 ± (1)	13.92 ± 5.06(3)
NH50		6.25 ± (1)	0.0 ± 0.0 (2)	19.39 ± 19.39(2)	3.02 ± 1.74(8)
NH60	0.71 ± 0.71(3)	0.13 ± 0.13(10)	0.0 ± 0.0 (4)	0.0 ± 0.0(15)	0.0 ± 0.0 (3)

[1]Gut-fullness is expressed as a reconverted arcsin$\sqrt{\text{percentage}}$ transformed mean followed by its standard error and the number of observations in parentheses.
[2]The station samples in this table are from the 0.7-m bongo net sampler exclusively.
*5% level significant difference between successive station means based on two-sample *t*-tests.
**1% level significant difference between successive station means based on two-sample *t*-tests.

curred between stations NH05 and NH20 (Table 9). Any zoeal stage caught within NH03 and farther offshore than NH20 showed a marked decrease in gut-fullness.

DISCUSSION

The initial appearance of *C. magister* larvae in the plankton off the central Oregon coast in late January and early February occurs at a time when sea surface temperatures are generally warming after the yearly mean low in January (Gonor et al. 1970). High densities of early stage zoea caught within 3-10 miles of shore are in agreement with the known distribution of the adults at this time. Relatively few occurrences of early stage larvae were found beyond 10 miles of shore during the sampling period as the northward flowing Davidson Current tends to retain the early developing larvae in the nearshore area. A very strong onshore component of the current has been observed within 5 miles of shore (Keene 1971; Wyatt et al. 1972; Holton and Elliot 1973). During the March and April transition period when the northward Davidson Current is replaced by currents flowing to the south and southwest, the larvae have developed to late stage zoea and megalopae. The bulk of the *C. magister* megalopae settle out of the water and metamorphose to juveniles by April and May before the onset of intense coastal upwelling in June and July, thus reducing the chance of being carried offshore by the resulting Ekman Current. During all seasons along the coast, larvae which occur increasingly closer to shore would be subject to decreasing current transport either alongshore or offshore.

1970 Season

It was observed during the 1970 larval season of *C. magister* that the late zoeal stages "disappeared" or were greatly reduced in numbers in the inshore sampling area, whereupon the megalopae reappeared after the proper time interval in densities comparable to those of the previously sampled zoea. Hypotheses to explain their disappearance and reappearance are as follows: 1) the late zoea were misidentified, 2) some stages are skipped in development, 3) the sampling interval missed those stages, 4) avoidance of the samplers increases with zoeal stages of development but decreases at megalopal stage, 5) the late zoeal larvae are carried offshore or alongshore but upon molting to the megalopal stages are transported onshore or back to their original release point, 6) the larvae were very dispersed at late zoeal development so that the volume of water filtered was not adequate, or 7) late stage zoea are resting on the bottom or below the depth sampled.

The late stages of *C. magister* larvae were not misidentified as they are morphologically distinct by this time and are nearly twice the size of any other local cancrid species. Apparently, the late larval stages of *C. magister* were not skipped in their development since zoea 4 and 5 stages were collected on the offshore stations in late March and early April. It is not believed that the late zoeal stages have greater swimming ability compared to the early zoea and megalopa which would permit them to avoid the samplers to a greater degree. On the contrary, personal observations of the late stage larvae in laboratory culture show them to be sluggish swimmers that

spend considerable time resting on the bottom of the rearing vessel.

A species such as *C. magister*, which has a larval life of approximately 130 days, could conceivably be transported northward about 600 miles along the North Pacific coast as Wyatt et al. (1972) reported that the winter surface currents based on drift bottle studies have a mean speed of 0.2 knots, or a drift of 150 miles per month. The Ekman transport of surface waters due to wind stress decreases exponentially with depth due to frictional resistance, so that when the current has fallen to about one-twenty third that of the surface, this subsurface flow is negligible or reverse to that of the surface currents (Sverdrup et al. 1942). Recent studies indicate wind driven water motion extends to a depth of about 10 m (Bourke et al. 1971). If the larval population resides about 5m below the surface where the wind induced current is about one-quarter that of the surface, then the larvae would only be transported 150 miles in a linear distance. Larvae located in the water column below 5m depth, particularly the later zoeal stages, would experience relatively little transport in any direction. Holton and Elliot (1973) reported the greatest abundance and density of zooplankton containing crab larvae occurred at about 15m depth at nearshore stations off Newport during the daylight hours. Hypothetically, larvae released in January-February could be transported north along the coast in the surface currents and, after the transition period of currents in March, travel south a comparable distance in April and May. Or, taking into consideration the fact that the older stages may reside deeper into the water column, they could conceivably travel north in the surface currents as early zoea and travel south again as late larvae in a weak underlying countercurrent, but this seems unlikely. Huyer et al. (1975) reported the northward currents along the central Oregon coast essentially are constant with depth during the winter and southward at all depths in the spring but stronger at the surface. Larvae occurring within 3-5 miles of the coast probably are caught within a system of eddies and countercurrents characteristic of this zone, retarding large-scale dispersal in any direction. The mechanistic concepts of recruitment seem too contrived and unnecessary if stochastic processes are the general rule for species producing large numbers of expendable young. Most investigators would agree that the great majority of the pelagic larvae of marine invertebrates are lost to the population and that only a very small percentage of annual recruits are normally required to maintain a stable population for longer-lived adults. *Cancer magister* lives 4 or 5 yr so that a population unexploited by man would only require recruitment every other year or so. The fact that the adult populations are not retreating northward supports the view that at least some of the larvae are retained in the same general area as their point of origin.

The low densities of late stage larvae collected in the offshore area indicated that the small volume of water filtered on the inshore stations could account for their disappearance or reduced numbers.

Knowledge of their vertical location within the water column at different stages of development is important in understanding their spatial distribution and local abundance. However, a separate study of the larvae within the upper 150 m was not undertaken. Most crab larvae are photopositive to light in their early stages and migrate to the surface layers, whereas the late stages respond photonegatively and are found in the deeper layers near the bottom as they prepare to molt to juveniles (Thorson 1964). The larvae of *C. magister* appear to follow this same general pattern except that the early megalopal stage shows anomalous behavior as they have been observed to "swarm" near the sea surface along the coast (Cleaver 1949; Gaumer 1971; pers. obs.). Personal laboratory observations, as well as those by MacKay (1942) and others, substantiate the fact that the early zoea and megalopa of *C. magister* are generally photopositive in contrast to the late zoeal stages which are neutral or photonegative.

A scheme is proposed which would explain their distribution and abundance within 10 miles of the coast taking into account the differential behavioral response to light of the various larval stages. Newly hatched zoeal larvae are strongly photopositive and swim to the surface where current transport during the winter is generally onshore. They become progressively heavier and less photopositive with development until in the late zoeal stages they are neutral or responding negatively to light. As a consequence, the late zoeal stages reside in the deeper layers of water, possibly within a few meters of the bottom. They are now maximally dispersed in the nearshore area. Upon molting to the megalopic stage they are temporarily strongly photopositive to light and coupled with their increased powers of

locomotion, they swarm to the surface again and are congregated by the prevailing currents usually in a band within 5 miles of the coast. If the late zoeal larvae do in fact reside near the sea bottom, the onshore drift current within 10-20 m of the bottom would prevent them from being transported offshore. Bottom flow in waters less than 40 m deep is towards the coast in the direction of wave travel throughout the year (Gross et al. 1969). The behavior of the larvae within the water column in relation to the hydrological features of the nearshore area under usual circumstances tends to restrict dispersal of the larvae to any great degree.

1971 Season

The sparseness of *C. magister* late zoeal larvae and megalopae during the 1971 season implies that a mass mortality occurred in the early zoeal stages. This apparent mortality was associated with sea surface temperature and salinity in analyses of covariance, but larval survival predicted through response surface methodology and gut-fullness analysis did not substantially explain their sparseness. The lack of highly supportive evidence leads to further speculation as to the causes of larval mortality in the plankton.

Hypothesis 1: Direct Effects of Temperature and Salinity

Sea surface temperature, and salinity to a lesser degree, were important environmental factors in explaining the difference in yearly larval population means of *C. magister* by analyses of multiple covariance. However, the statistical importance of these factors in determining larval abundance may be misleading. A wide temperature gradient during a larval season, i.e., a steep slope, could be statistically significant, but the range of temperatures may be well within the tolerance limits of an organism. In contrast, the salinity gradient during the same larval season is usually narrow resulting in a statistically nonsignificant slope, which may still occur outside the range tolerated by the larvae. Also, the erratic surface temperature and salinity fluctuations that occurred during the summer upwelling may cancel the effect of a significant gradient that occurred earlier in winter and spring.

Cancer magister larvae were reared by Reed (1969) under various temperature-salinity combinations and he concluded that these factors, as they normally occur off the Oregon coast, would not significantly affect survival. Response surface techniques, using Reed's data, predicted about 45% survival under the extreme temperatures and salinities that occurred during February and March 1971. The sea surface temperatures and salinities used in the analysis probably represent the most extreme long-term conditions that the larvae could have experienced in the field. Larvae several meters below the surface may be protected from the more extreme fluctuations of temperature and salinity, but some degree of exposure seems certain in view of the fact that extensive wind mixing occurs in shallow waters along the coast. The North Pacific is characterized by heavy precipitation during the fall and winter seasons resulting in considerable land drainage and river runoff along the nearshore area. Larvae along the coast, particularly near the mouths of bays and rivers, may lie in the low-salinity plume waters before sufficient mixing occurs. Harder (1968) reported that many planktonic organisms tend to accumulate near density interfaces that frequently occur in natural waters. Some species of copepods were observed under laboratory conditions to react to extremely small changes in density. Whether *C. magister* larvae have the ability to avoid these low-salinity surface waters that may be detrimental to them is not known. The early zoeal larvae would seem most vulnerable to low surface salinity as their behavioral response directs them to the surface and their swimming ability is slight compared to the megalops stage. Early larval ability to avoid low-salinity surface waters would have to be sufficient to overcome the increased storm-induced mixing during this season. The mortality rate of *C. magister* larvae reared in the laboratory under optimum conditions was constant and minimal throughout development (Reed 1969). Mortality increased greatly for larvae reared at 20‰ salinity; early zoeal larvae were killed within a short period in salinities less than 20‰. In addition, both the lower range of salinities and temperatures used in his experiments increased the duration of the larval instars where survival could be monitored for a sufficient time period.

It is difficult to evaluate the extent to which results from laboratory studies approach reality in order to understand how environmental variables may affect survival. Larvae reared at sub-

optimal conditions have been observed to survive for considerable periods of time, apparently unable to molt successfully. These same larvae eventually die, but laboratory experiments often are terminated before full mortality can be observed. Low salinity during the winter of 1971 may have been an important factor resulting in the demise of *C. magister* larvae that year. Subtle changes in the flux and composition of the internal ionic constituents can alter the molting process; larvae which appear normal in early development may mask deficiencies that express themselves later in development. Nevertheless, short-term exposure to extreme conditions may be just as detrimental as slightly suboptimal conditions over a long period of time (cf. Lough and Gonor 1973a, b). Although the nearshore surf salinities on a monthly average are in the range of tolerance by the larvae, daily measurements occasionally drop below 20‰ (Gonor et al. 1970). No larvae survived below 20‰ salinity in Reed's (1969) laboratory study.

The effect of low salinity in conjunction with wider than normal temperatures may play an important role in larval survival as indicated from the analyses. Low and high temperatures greatly accentuated the effects of marginally dilute salinities on *C. magister* larval survival. But again, the ecological significance of a synergistic effect has not been fully established in this study. More detailed, short-term studies of salinity-temperature variability and larval monitoring are needed in the nearshore area. Sastry and McCarthy (1973) observed distinct differences in temperature-salinity tolerances and metabolic responses of the larvae of two species of *Cancer* sympatrically distributed along the east coast of North America. Complete development for *C. irroratus* larvae occurred over a wide range of temperatures, whereas *C. borealis* larvae was restricted to a narrow range. The metabolic-temperature pattern of *C. irroratus* larvae indicated a progessive narrowing in temperature sensitivity. In contrast, the early stages of *C. borealis* initially were sensitive to warmer temperatures but in the later stages sensitivity shifted to colder temperatures. Hatching of the two *Cancer* species is separated in time so that the diverse metabolic responses observed are believed to be adaptations by larvae of the two species to the different temperature conditions encountered.

The combined effects of salinity and temperature have been studied under controlled laboratory conditions on other species of brachyuran larvae by Costlow et al. (1960, 1962, 1966), Costlow and Bookhout (1962), and Costlow (1967). Although the adults inhabit euryhaline waters, specific larval stages have been shown to require restricted ranges of salinity and temperature to varying degrees for complete development. In many cases, both temperature and salinity and the interaction of various combinations of the two environmental variables were observed to affect larval survival and retard development. Salinity generally has an immediate effect on survival while temperature appears to play a modifying role within the extremes of tolerance. Most of their work indicates that mortality was highest during the early zoeal stages and that the megalops stage was the least subject to environmental stress, although exceptions are reported. Recently, Costlow and Bookhout (1971) investigated the effects of cyclic temperatures compared to constant temperatures on the larvae of the estuarine mud crab, *Rhithropanopeus harrisii*. Duration of larval life and survival were about the same but survival was enhanced under cyclic temperatures at the higher end of the experimental range. Short-term fluctuations in temperature or other environmental variables throughout the water column have not been adequately monitored along the North Pacific coast. Their effect on *C. magister* larvae is not known and should be investigated.

Hypothesis 2: Food Quality and Quantity

May (1974) reviewed Hjort's (1914) critical period concept for fish larvae since Marr's (1956) evaluation and concluded from recent work that starvation may be an important cause of mortality, especially during the period immediately following the yolk sac stage. Although crab larvae do not have a strictly comparable yolk sac stage in their planktonic life, adequate food densities for efficient feeding may be of critical importance during a brief period following hatching. There is limited knowledge concerning the types of food organisms normally available and selected by *C. magister* larvae and concerning the densities of these food organisms sufficient for development. Most crab larvae are omnivorous, requiring substantial protein in their diet (Costlow and Sastry 1966; and others). Attempts to distinguish gut contents of field-caught *C. magister* larvae were unsuccessful in the present study. However, the

specific kind of food organism encountered may not be as important as its size. The size of food organisms available for each larval stage must be within a restricted range in order for a larva to successfully capture and ingest. The progression of larval size with development would indicate that the different larval stages can utilize increasingly greater sizes of food organisms. Reed (1969) found in laboratory culture that the larvae of *C. magister* survived well feeding on *Artemia salina* (0.475-0.752 mm length) and *Balanus gladula* nauplii (0.370-0.420 mm length), but would only survive for a limited period on smaller size veliger larvae of *Mytilus edulis* (0.100-0.300 mm length?). He also reported that unfed *C. magister* zoea larvae would only survive for 14 days. This implies that under natural conditions larvae will not survive if a suitable food organism is delayed in its appearance by more than 2 wk, and that certain kinds of food organisms selected by the larvae are nutritionally inadequate for their long-term metabolic needs.

Chamberlain (1961, 1962) reared the larvae of two xanthid crabs, *Neopanope texana sayi* and *Rhithropanopeus harrisii*, on a variety of foods and found that development was retarded when larvae were fed on a mixture of nauplii and algae. Larvae fed algae alone would not molt and only lived 6-10 days in culture. Algae appeared to be nutritionally inadequate for successful development and restricts the intake of more suitable food by indiscriminate larval feeding. Costlow and Sastry (1966) suggested that high mortality of *Callinectes sapidus* larvae at the time of the third zoeal stage in nutritionally inadequate culture may be due to the initial availability of a large pool of free amino acids within the eggs through the first and second zoeal stages. They also pointed out that the variability in tolerance to suboptimal conditions may be related to the size of such a free amino acid pool.

Although the gut-fullness analysis in the present study did not provide insight into the difference in larval abundance between the 2 yr, it did suggest the existence of an optimum zone for adequate feeding between 3 and 20 miles offshore where suitable kinds and densities of food organisms occur. Zooplankton volumes along the Washington coast decrease to a minimum level during the winter and increase to maximum levels during the spring (Frolander 1962). During the winter, the volume of zooplankton and abundance of copepods were greater inshore than offshore as a consequence of the onshore transport of surface waters (Frolander 1962; Anderson 1964; Peterson 1972). Anomalous weather conditions such as occurred during the winter of 1971 may have been ultimately responsible for alterations in the usual types and availability of food organisms encountered during the first few weeks of larval feeding.

Hypothesis 3: Predators and Competitors

The importance of the combined or separate effects of predation and competition on larval populations is difficult to assess. Predation has generally been regarded as the major cause of larval mortality (Thorson 1946, 1950). Lebour (1919a, b, 1920, 1921, 1922, 1923) observed many species of young fish and medusae to prey upon crab larvae as well as most other small organisms in the plankton. Cannibalism is well known in laboratory culture. Knudsen (1960) observed in the laboratory that xanthid first stage zoea were eaten by older zoea and megalops as well as by copepods. Other predators known to feed on marine larvae, such as ctenophores, chaetognaths, euphausiids, and shrimps, appear seasonally in high densities along the North Pacific coast. Their effect on larval populations has not been fully ascertained. Peterson (1972) compared the ratios of copepod nauplii to total copepods off the Washington coast and found that more nauplii were hatched inshore than offshore throughout the year, but fewer developed to adults suggesting greater predation in the inshore area. Predation was reduced during the winter compared to other seasons within the inshore area. These findings might similarly apply to relative predation rates on *C. magister* larvae along the North Pacific coast.

Factors in the environment such as abnormally cold temperatures or lack of food that extend the pelagic life of the larval phase have been considered detrimental due to predation. It has been assumed that the longer the larvae remain in the plankton the more they will be preyed upon, although predation pressure upon their recruitment to the benthic habitat may be just as great, or greater (Thorson 1966). Larvae genetically feeble or weakened by some environmental factors may be more subject to predation so that under usual circumstances, the importance of predation may be secondary in mortality processes. The effect of predation on larval populations

would not seem to be constant in the heterogeneous marine environment, but would more likely vary in intensity both temporally and spatially. Predation may only be a dominant factor in unusual years and/or on a small-scale basis.

Other members of the plankton community undoubtedly feed on the same food organisms as *C. magister* and competition may become an important factor when these food organisms become sparse. One potential competitor was tentatively identified as *C. oregonensis*. Its larvae are very abundant in the inshore area and cooccur with those of *C. magister*. Both species are morphologically similar and pass through the same number of larval stages, except that the larvae of *C. magister* become increasingly larger with development. There are studies showing the antagonistic effects of a mutually shared food resource. Brooks and Dodson (1965), in a study of two species of freshwater *Daphnia*, concluded that the larger species was more efficient in collecting both small and large particles and would competitively exclude the smaller species as long as size dependent predation was of low intensity. Conversely, Schoener (1969), in a theoretical study, concluded that large predators ate an equal or a greater range of food compared to the smaller ones as long as food was at some upper level. But, as food abundance was reduced, the optimal predator size shifted towards the smaller predator. Similar situations could conceivably occur and explain why *C. magister* larvae were less numerous in 1971. The interactions of hierarchies of predators and their prey involving temporal and spatial changes in densities and size frequencies can be exceedingly complex.

Hypothesis 4: Oceanic currents and multiple environmental effects

Planktonic organisms have limited means of locomotion and consequently are subject to the vagaries of oceanic currents. Changes in the strength or timing of these currents can be ultimately responsible for the success or failure of larval populations and their adult stocks (Coe 1956). The transport of entire larval stocks out of their normal environment can have catastrophic results for annual recruitment.

During the winter-spring larval period of *C. magister*, the major nearshore oceanographic feature is the northerly intrusion of the Davidson Current along the Oregon-Washington coast and its reversal in March-April. The strength and duration of the Davidson Current are critical factors in the initiation, development, and persistence of seasonally dominant plankton communities. Southern neritic zooplankton species appear abundant off the Oregon and Washington coasts during fall and winter and are believed to be carried by the northerly surface drift (Cross and Small 1967; Miller 1972; Frolander et al. 1973). Frolander (1962) observed widespread anomalous conditions off the Washington coast during February 1958, compared to the previous year. Lower plankton volumes and a change in plankton species were associated with an increase in the surface temperatures, a decrease in dissolved inorganic phosphate, and unusual weather during the anomalous February. These events were believed to be the result of southerly offshore waters moving into the coastal area to a larger extent that year.

Superimposed upon the nearshore currents with their characteristic water properties, a dominant modifying process results from precipitation and river runoff. A band of low salinity occurs all along the North Pacific coast. Little information is available on the effect of the heavy river runoff on the endemic plankton populations in the neritic zone, but some studies have been done concerning the effect of the Columbia River plume on the physical processes and biota over its range of influence (Anderson 1972). The Columbia River effluent flows north along the coast of Washington during the winter in response to the prevailing southwesterly winds (Barnes et al. 1972). Hobson (1966) and Anderson (1972) observed that chlorophyll and productivity at the surface of the plume and ambient waters were higher than nearby oceanic waters due to the increased stability of the water column providing an environment where phytoplankton could accumulate. The major influence of the Columbia River plume on phytoplankton development is believed to be in the timing of events. Phytoplankton populations can develop 3-5 wk earlier in the plume due to the increased stabilization. Heinrich (1962, 1968) stated that the seasonal cycle of phytoplankton communities are less balanced in the neritic zone and that the phytoplankton populations in this area can vary depending on the timing and differential growth of relative copepod species. Shifts in weather patterns create corresponding changes in nearshore currents resulting in the intrusion and displacement of endemic

planktons. Nearshore modifying processes can change the character of these communities setting forth new interactions among the populations.

Anomalous hydrographic and meteorological conditions were observed along the Oregon coast during the winter of 1971 in the present study. Its effect on the plankton populations to date only have been investigated in relation to *C. magister* larvae. To what extent did the relaxation of onshore transport of surface waters during January and February with subsequent increased transport in March 1971, compared to the same period in 1970, affect the dynamics of the *C. magister* larval population? The circumstantial evidence suggests that heavy mortality of the larvae occurred in 1971. However, the difference in larval abundance for the 2 yr may not be real if the larvae were quite localized in their alongshore distribution and moved out of the study area. Sampling was not conducted in other areas for those years to fully answer this point. In addition, the late zoeal stages were undersampled both years leaving a gap in our knowledge of their true numbers, distribution, and condition. Assuming that a mass mortality of larvae did, in fact, occur in the study area, what are the most likely environmental mechanisms? Did the decreased onshore surface water transport in early winter of 1971 relative to 1970 allow more larvae to be carried offshore that year where food abundance was lower, etc.? Any larvae swept off the shelf area that survived would still probably be beyond successful recruitment to the adult nearshore population. Did the greater onshore transport of surface waters during late winter of 1971 move the bulk of the larval population closer to shore into a suboptimal environment too early in their development? What is the effect of the increased precipitation and river runoff during the winter of 1971 that reduced nearshore salinities? Was a phytoplankton bloom initiated earlier in the season and how did it affect populations of other planktonic organisms utilized as food for *C. magister* larvae? Chamberlain (1961) commented that, for crab larvae feeding indiscriminately on both algae and zooplankton, a phytoplankton bloom initially may retard zoeal development; however, following the increase of the herbivore population, more nutritionally adequate food is available and would accelerate larval development. Do the low-salinity Columbia River plume and other river effluents effectively act as barriers against northerly alongshore transport of larvae? The lower temperatures and salinities in 1971, particularly in the nearshore area, coupled with adverse biological pressures, i.e., increased predation, may have had a synergistic effect on larval mortality. Many alternatives are open in marine ecosystems where stochastic processes prevail producing innumerable permutations. The indirect effect of physical variables on larval food organisms and predator-prey relations can be extremely complex and important. Subtle changes in these relations may have an accumulative effect on a larval population already in a stressed condition and near the point at which recovery diminishes.

Answers to these questions remain conjectural and may only be sought through further comprehensive and detailed studies. However, in conclusion, there is no substantial evidence from this study that the colder winter of 1971 caused a delay in the initial appearance and developmental schedule throughout the larval period of *C. magister*. The generally poor appearance of the early zoeal larvae collected during the 1971 season suggests that whatever factor(s) responsible for the apparent mortality appeared to have an immediate effect on these stages. The first few zoeal stages may be the critical period in the early life history of *C. magister* where the greatest mortality occurs ultimately determining future year class strength.

RECOMMENDATIONS FOR FUTURE RESEARCH

Studies to date have provided a broad overview of knowledge concerning the initial timing, abundance, and dispersal of *C. magister* larvae in relation to major oceanographic events off the central Oregon coast. First approximation estimates of length of larval life, mortality, and feeding have been achieved, but we are still lacking detailed insight into the dynamics of the larvae-plankton-environment matrix. This study points out our limited knowledge and understanding of the physical and biological mechanisms affecting the dispersal and subsequent survival of *C. magister* larvae. An understanding of these processes is necessary for an understanding of the stability and long-term productive potential of the Dungeness crab as a fishery resource in the Pacific Northwest. By studying processes controlling the dispersal and survival of the larvae, we

may be able to gain insight into stock-recruitment relations and be able to predict the effects of long-term environmental changes. Some specific recommendations for further work are listed below.

1. A minimum of three surveys should be conducted between late January and early June to monitor initial hatching, production, rate of development, and dispersal of the larvae. It is imperative that survey coverage be extended along the Oregon coast to observe patchiness and alongshore dispersal. A grid of stations to within 30 miles of the coast from at least Cape Blanco, Oreg. to Cape Flattery, Wash. is recommended. A sufficient time series of data is required to adequately assess yearly changes in the larval populations in order to gain insight into mortality processes. Also, a long-term series is needed as a background of knowledge upon which more specialized short-term studies can be based. Six or seven years of plankton sampling seems to be a minimum time series for establishing trends, although 10-15 yr are required to substantiate significant differences.
2. Intensive close-order grid sampling on a short-term basis, following a fairly well-defined and homogeneous "patch" of larvae, should be conducted to assess in more detail mortality and feeding in good and poor areas.
3. This study emphasizes the need for more detailed oceanographic studies in the nearshore environment and how they affect the population dynamics of organisms living in this zone. In conjunction with larval surveys, circulation studies should be expanded during the winter and spring along the Oregon coast to improve the basis for predicting and evaluating dispersal, primary productivity, etc. A continuous program of temperature, salinity, and current measurements are needed of the nearshore currents during the larval period from January through June and particularly the timing and extent of the March-April transition of the Davidson Current.
4. Short-term exposure of the larvae to environmental variables such as low salinity in combination with varying temperature, food density, etc. and subsequent transfer to optimum conditions for long-term observations in the laboratory are needed to properly evaluate the effects of these factors.
5. Detailed descriptions of the three-dimensional composition of the associated plankton communities are needed in terms of the dominant species, size categories, and diurnal variability. Investigations into the contagious distribution of these organisms, mechanisms of initiation and destruction, are central to understanding prey-predator interaction and attempts to model these phenomena.
6. Fine-mesh (0.165 and 0.053 mm) sampling with the 0.2-m bongo nets should be used concurrently with the 0.7-m bongo nets to examine and answer the questions of food composition and availability utilized by early *C. magister* larvae. In particular, the invertebrate component for both coarse- and fine-mesh samples should be analyzed initially between contrasting years or areas of larval abundance. The use of plankton pumps may be more amenable in this case as fine-mesh nets clog rapidly.
7. The vertical distribution and diurnal movements of *C. magister* larvae throughout its pelagic life is especially important in regard to sampling variability, dispersal, and feeding, and should be studied. Do most of the older zoeal larvae, in fact, reside within a few meters of the bottom in the shallow inshore area?
8. Laboratory studies should be undertaken to analyze the phototactic behavior of the larvae at various stages of development to gain a better understanding of their diurnal movements as may be modified by temperature, hunger state, presence of prey and predators, etc.
9. A new approach is needed in the analysis of larval gut contents. Biochemical techniques of gut material may be used to identify food organisms utilized by the larvae. Energy budgets should be constructed to determine minimum food requirements of the various larval stages. Condition factors indicative of the physiological well-being of larvae may be used to evaluate good versus poor areas and years of feeding.
10. Potential predators that cooccur with *C. magister* larvae should be identified and ingestion rates determined from field and laboratory experiments in order to estimate

their effect on the larval population. Transitional experiments should be carried out in the field to further assess the reality of laboratory studies.

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LITERATURE CITED

ALDERDICE, D. F.
1972. Factor combinations. Responses of marine poikilotherms to environmental factors acting in concert. *In* O. Kinne (editor), Marine ecology, Vol. 1, Part 3, p. 1659-1722. Wiley-Interscience, Lond.

ANDERSON, G. C.
1964. The seasonal and geographic distribution of primary productivity off the Washington and Oregon coasts. Limnol. Oceanogr. 9:284-302.
1972. Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 219-264. Univ. Wash. Press, Seattle.

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BARNES, C. A., A. C. DUXBURY, AND B. A. MORSE.
1972. Circulation and selected properties of the Columbia River effluent at sea. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 41-80. Univ. Wash. Press, Seattle.

BOURKE, R. H., B. GLENNE, AND B. W. ADAMS.
1971. The nearshore physical oceanographic environment of the Pacific Northwest coast. Dep. Oceanogr. Oreg. State Univ., Ref. 71-45, 120 p.

BROOKS, J. L., AND S. I. DODSON.
1965. Predation, body size, and composition of plankton. Science (Wash., D.C.) 150:28-35.

BURT, W. V., AND B. WYATT.
1964. Drift bottle observations of the Davidson Current off Oregon. *In* K. Yoshida (editor), Studies on oceanography, p. 156-165. Univ. Tokyo Press, Tokyo.

BUTLER, T. H.
1960. Maturity and breeding of the Pacific edible crab, *Cancer magister* Dana. J. Fish. Res. Board Can. 17:641-646.

CHAMBERLAIN, N. A.
1961. Studies on the larval development of Neopanope texana sayi (Smith) and other crabs of the family Xanthidae (Brachyura). Chesapeake Bay Inst., John Hopkins Univ., Tech. Rep. 22:1-35.
1962. Ecological studies of the larval development of *Rhithropanopeus harrisii* (Xanthidae, Brachyura). Chesapeake Bay Inst., John Hopkins Univ., Tech. Rep. 28:1-47.

CLEAVER, F. C.
1949. Preliminary results of the coastal crab (Cancer magister) investigation. Wash. Dep. Fish., Biol. Rep. 49A:47-82.

COE, W. R.
1956. Fluctuations in populations of littoral marine invertebrates. J. Mar. Res. 15:212-232.

COLTON, J. B., JR.
1959. The multiplane kite-otter as a depressor for high-speed plankton samplers. J. Cons. 25:29-35.

COSTLOW, J. D., JR.
1967. The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus*. Helgoländer wiss. Meeresunters. 15:84-97.

COSTLOW, J. D., JR., AND C. G. BOOKHOUT.
1962. The larval development of *Hepatus epheliticus* (L.) under laboratory conditions. J. Elisha Mitchell Sci. Soc. 78:113-125.
1971. The effect of cyclic temperatures on larval development in the mud-crab *Rhithropanopeus harrisii*. *In* D. J. Crisp (editor), Fourth European Marine Biology Symposium, p. 211-220. Cambridge Univ. Press., Lond.

COSTLOW, J. D., JR., C. G. BOOKHOUT, AND R. MONROE.
1960. The effect of salinity and temperature on larval development of Sesarma cinereum (Bosc) reared in the laboratory. Biol. Bull. (Woods Hole) 118:183-202.
1962. Salinity-temperature effects on the larval development of the crab Panopeus herbstii Milne-Edwards, reared in the laboratory. Physiol. Zoöl. 35:79-93.
1966. Studies on the larval development of the crab, *Rhithropanopeus harrisii* (Gould). I. The effect of salinity and temperature on larval development. Physiol. Zoöl. 39:81-100.

COSTLOW, J. D., JR., AND A. N. SASTRY.
1966. Free animo acids in developing stages of two crabs, *Callinectes sapidus* Rathbun and *Rhithropanopeus harrisii* (Gould). Acta Embryol. Morphol. Exp. 9:44-55.

CROSS, F. A., AND L. F. SMALL.
1967. Copepod indicators of surface water movements off the Oregon coast. Limnol. Oceanogr. 12:60-72.

FROLANDER, H. F.
1962. Quantitative estimations of temporal variations of zooplankton off the coast of Washington and British Columbia. J. Fish. Res. Board Can. 19:657-675.

FROLANDER, H. F., C. B. MILLER, M. J. FLYNN, S. C. MEYERS, AND S. T. ZIMMERMAN.
1973. Seasonal cycles of abundance in zooplankton populations of Yaquina Bay, Oregon. Mar. Biol. (Berl.) 21:277-288.

GAUMER, T. F.
1971. Controlled rearing of Dungeness crab larvae and the influence of environmental conditions on their survival. Commer. Fish. Res. Dev. Act Prog. Rep., Nov. 16, 1965 to June 30, 1971. Fish. Comm. Oreg., Closing Rep., 43 p.

GONOR, J. J., A. B. THUM, AND D. W. ELVIN.
1970. Inshore sea surface temperature sand salinity conditions at Agate Beach, Yaquina Bay and Whale Cove, Oregon, in 1970. Data Rep. 45. Dep. Oceanogr. Oreg. State Univ., Ref. 70-44, 30 p.

GROSS, M. G., B.-A. MORSE, AND C. A. BARNES.
1969. Movement of near-bottom waters on the continental shelf off the northwestern United States. J. Geophys. Res. 74:7044-7047.

HARDER, W.
1968. Reactions of plankton organisms to water stratification. Limnol. Oceanogr. 13:156-168.

HEINRICH, A. K.
1962. The life histories of plankton animals and seasonal cycles of plankton communities in the oceans. J. Cons. 27:15-24.
1968. On seasonal phenomena in the plankton of the Northeastern Pacific. Okeanologiya 8:287-296.

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer. 20:1-228.
1926. Fluctuations in the year classes of important food fishes. J. Cons. 1:5-38.

HOBSON, L. A.
1966. Some influences of the Columbia River effluent on marine phytoplankton during January 1961. Limnol. Oceanogr. 11:223-234.

HOLTON, R. L., AND W. P. ELLIOTT.
1973. The development of methods for studying physical and biological processes in the nearshore zone on the Pacific coast of the United States. Dep. Oceanogr. Oreg. State Univ., Ref. 73-3, 18 p.

HUYER, A., R. D. PILLSBURY, AND R. L. SMITH.
1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90-95.

KEENE, D. F.
1971. A physical oceanographic study of the nearshore zone at Newport, Oregon. M.S. Thesis, Oreg. State Univ., Corvallis, 91 p.

KNUDSEN, J. W.
1960. Reproduction, life history and larval ecology of the California Xanthidae, the pebble crabs. Pac. Sci. 14:3-17.

KUKLA, G. J., AND H. J. KUKLA.
1974. Increased surface albedo in the northern hemisphere. Science (Wash., D.C.) 183:709-714.

KULM, L. D., AND J. V. BYRNE.
1966. Sedimentary response to hydrography in an Oregon estuary. Mar. Geol. 4:85-118.

LEBOUR, M. V.
1919a. Feeding habits of some young fish. J. Mar. Biol. Assoc. U.K. 12:9-21.
1919b. The food of post-larval fish. No. II (1918). J. Mar. Biol. Assoc. U.K. 12:22-47.
1920. The food of young fish. No. III. (1919). J. Mar. Biol. Assoc. U.K. 12:261-324.
1921. The food of young clupeoids. J. Mar. Biol. Assoc. U.K. 12:458-467.
1922. The food of planktonic organisms. J. Mar. Biol. Assoc. U.K. 12:644-677.
1923. The food of plankton organisms. II. J. Mar. Biol. Assoc. U.K. 13:70-92.

LONGHURST, A. R., AND D. L. R. SEIBERT.
1967. Skill in the use of Folsom's plankton sample splitter. Limnol. Oceanogr. 12:334-335.

LOUGH, R. G.
1975a. A reevaluation of the combined effects of temperature and salinity on survival and growth of bivalve larvae using response surface techniques. Fish. Bull., U.S. 73:86-94.
1975b. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Thesis, Oreg. State Univ., Corvallis, 299 p.

LOUGH, R. G., AND J. J. GONOR.
1973a. A response-surface approach to the combined effects of temperature and salinity on the larval development of *Adula californiensis* (Pelecypoda: Mytilidae). I. Survival and growth of three and fifteen-day old larvae. Mar. Biol. (Berl.) 22:241-250.
1973b. A response-surface approach to the combined effects of temperature and salinity on the larval development of *Adula californiensis* (Pelecypoda: Mytilidae). II. Long-term larval survival and growth in relation to respiration. Mar. Biol. (Berl.) 22:295-305.

MACKAY, D. C. G.
1942. The Pacific edible crab, Cancer magister. Fish. Res. Board Can., Bull. 62:1-32.

MARR, J. C.
1956. The "critical period" in the early life history of marine fishes. J. Cons. 21:160-170.

MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.

MILLER, C. B.
1972. Zooplankton indicators of the seasonal cycle of currents along the Oregon coast. Trans. Am. Microsc. Soc. 91:87.

MOOERS, C. N. K.
1970. The interaction of internal tide with the frontal zone of a coastal upwelling region. Ph.D. Thesis, Oreg. State Univ., Corvallis, 480 p.

OSTLE, B.
1963. Statistics in research. 2nd ed. Iowa State Univ. Press, Ames, 585 p.

PATTULO, J. G., AND W. DENNER.
1965. Processes affecting seawater characteristics along the Oregon coast. Limnol. Oceanogr. 10:443-450.

PEARCY, W. G., AND R. S. MESECAR.
1970. Scattering layers and vertical distribution of oceanic animals off Oregon. *In* G. Brooke Farquhar (editor), Proceedings of an international symposium of biological sound scattering in the ocean, p. 381-394. Maury Cent. Ocean Sci., Dep. Navy, Wash., D.C.

PETERSON, W. K.
1972. Distribution of pelagic copepoda off the coasts of Washington and Oregon during 1961 and 1962. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 313-343. Univ. Wash. Press, Seattle.

POOLE, R. L.
1966. A description of laboratory-reared zoea of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda, Brachyura). Crustaceana 11:83-97.

POSGAY, J. A., R. R. MARAK, AND R. C. HENNEMUTH.
1968. Development and tests of new zooplankton samplers. Int. Comm. Northwest Atl. Fish., Res. Doc. 68/85, ser. 2085, 23 p.

REED, P. H.
1969. Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab

(*Cancer magister*) larvae in the laboratory. J. Fish. Res. Board Can. 26:389-397.

RENFRO, W. C., J. C. MCCAULEY, B. GLENNE, R. H. BOURKE, D. R. HANCOCK, AND S. W. HAGER.
1971. Oceanography of the nearshore coastal waters of the Pacific Northwest relating to possible pollution. Vol. I, II. Water Qual. Off., Environ. Prot. Agency, Grant No. 16070 EOK.

SASTRY, A. N., AND J. F. MCCARTHY.
1973. Diversity in metabolic adaptation of pelagic larval stages of two sympatric species of brachyuran crabs. Neth. J. Sea Res. 7:434-446.

SCHMITT, W. L.
1921. The marine decapod crustacea of California. Univ. Calif. Publ. Zool. 23:1-470.

SCHOENER, T. W.
1969. Models of optimum size for solitary predators. Am. Nat. 103:277-313.

SCHWARTZLOSE, R. A.
1964. Nearshore currents of western United States, Baja, California, as measured by drift bottles. Calif. Coop. Oceanic Fish. Invest., Prog. Rep. 1 July 1960 - June 1962, p. 15-22.

SMITH, R. L., J. G. PATTULLO, AND R. K. LANE.
1966. An investigation of the early stage of upwelling along the Oregon coast. J. Geophys. Res. 71:1135-1140.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans their physics, chemistry, and general biology. Prentice-Hall, N.Y., 1087 p.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

THORSON, G.
1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Oresund). Medd. Komm. Dan. Fisk.-og. Havunders. Ser. Plankton. 4(1):1-523.
1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. (Camb.) 25:1-45.
1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia 1:167-208.
1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3:267-293.

U.S. ENVIRONMENTAL DATA SERVICE.
1970. Climatological data, Oregon. Environ. Sci. Serv. Admin., Dep. Commer. 76.
1971. Climatological data, Oregon. Environ. Sci. Serv. Admin., Dep. Commer. 77.

WALDRON, K. D.
1958. The fishery and biology of the Dungeness crab (*Cancer magister* Dana) in Oregon waters. Fish. Comm. Oreg., Contrib. 24, 43 p.

WINSOR, C. P., AND G. L. CLARKE.
1940. A statistical study of variation in the catch of plankton nets. J. Mar. Res. 3:1-34.

WOOSTER, W. S., AND J. L. REID, JR.
1963. Eastern boundary currents. *In* M. N. Hill (editor), The sea, Vol. 2, p. 253-280. John Wiley & Sons, Inc., Lond.

WYATT, B., AND W. GILBERT.
1971. Surface temperature and salinity observations at Pacific Northwest shore stations during 1970. Data Rep. 47. Dep. Oceanogr. Oreg. State Univ., Ref. 71-8, 19 p.
1972. Surface temperature and salinity observations at Pacific Northwest shore stations during 1971. Data Rep. 51. Dep. Oceanogr. Oreg. State Univ., Ref. 72-2, 15 p.

WYATT, B., D. A. BARSTOW, W. E. GILBERT, AND J. L. WASHBURN.
1971. Drift bottle recoveries and releases off the Oregon coast 1961 through 1970. Data Rep. 50. Dep. Oceanogr. Oreg. State Univ., Ref. 71-36, 57 p.

WYATT, B., W. V. BURT, AND J. G. PATTULLO.
1972. Surface currents off Oregon as determined from drift bottle returns. J. Phys. Oceanogr. 2:286-293.

APPENDIX

TABLE 1. — *Cancer magister* larval abundance for 1970-71 seasons and associated environmental data used in analyses of multiple covariance.

Date	0.2 m-bongo net sampler mesh size (mm)	Larval abundance[1]	Surface temp. (°C)[2]	Surface salinity (‰)
1970:				
1/29	0.571	4,598	10.3	29.55
	0.233	2,607		
2/13	0.571	6,721	11.0	30.25
	0.233	13,276		
2/25	0.571	65	11.4	30.62
	0.233	152		
3/9	0.571	536	10.8	30.99
	0.233	381		
4/16	0.571	88	9.7	33.06
	0.233	0		
4/27	0.571	7,713	9.5	32.98
	0.233	5,267		
5/1	0.571	1,868	9.5	32.98
	0.233	1,847		
5/6	0.571	89	9.2	32.98
	0.233	39		
5/22	0.571	1,817	11.8	32.51
	0.233	1,697		
6/4	0.571	74	9.1	33.62
	0.233	32		
6/23	0.571	0	7.9	33.60
	0.233	26		
7/2	0.571	21	12.5	32.84
	0.233	38		
7/16	0.571	56	9.6	32.73
	0.233	28		
7/29	0.571	0	12.7	32.63
	0.233	0		
1971:				
1/18	0.571	736	9.9	29.50
	0.233	1,007		
2/3	0.571	1,762	8.6	31.80
	0.233	1,930		
2/16	0.571	2,539	9.3	31.00
	0.233	3,408		
3/20	0.571	205	8.5	32.16
	0.233	21		
3/30	0.571	305	8.9	30.81
	0.233	316		
4/22	0.571	390	9.6	32.45
	0.233	999		
5/03	0.571	0	10.4	30.74
	0.233	0		
5/14	0.571	0	11.5	31.76
	0.233	0		
5/29	0.571	26	8.8	33.69
	0.233	25		
6/2	0.571	0	10.1	33.52
	0.233	0		
6/12	0.571	0	13.4	30.04
6/28	0.571	0	15.1	30.75
7/6	0.571	20	11.7	31.83
7/21	0.571	0	9.0	33.53

[1]Number of larvae per 4,000 m^3. Larvae summed over four inshore stations: NH01, NH03, NH05, NH10.
[2]Averaged values over four inshore stations.

SUBTIDAL AND INTERTIDAL MARINE FOULING ON ARTIFICIAL SUBSTRATA IN NORTHERN PUGET SOUND, WASHINGTON[1]

CHARLES H. HANSON[2] AND JONATHAN BELL[3]

ABSTRACT

The design and siting of power plant cooling systems requires detailed information concerning the fouling tendencies of specific organisms on specific construction materials. This study, conducted in the vicinity of Kiket Island, northern Puget Sound, Wash., attempts to provide some of this information.

The sessile community characteristics of five materials exposed at three depths and two locations in the subtidal zone, and of one material in the intertidal zone are described. The degree of biofouling was least for copper-nickel alloy and progressively greater for Plexiglas, wood, steel, and concrete. Media decay and biological accumulation was greatest at the near-surface level, decreasing in intensity with increasing depth. The maximum rate of colonization occurred during the late spring (April-June) and early fall (mid-August-October). The present study, an analysis of biofouling, indicates that if the proposed power plant were to be built at Kiket Island, its cooling system intake should be sited in water deeper than 6 m and should have a safe and adequate fouling control scheme.

The settlement of entrained fouling organisms seriously affects the proper functioning of industrial cooling systems (Dobson 1946; Beauchamp 1966; Holmes 1970). Thus, the design of a cooling system requires detailed information concerning the fouling tendencies of specific organisms on specific construction materials. The present study — conducted in the vicinity of Kiket Island, northern Puget Sound, Wash.—attempts to provide some of this information. At the time, the study area was the proposed site for a 1,000 MW nuclear power plant with a once-through cooling system.

The study analyzed the fouling resistances of several common construction materials both in the subtidal and in the intertidal zones. Colonization in the subtidal zone was examined from April to November 1972, while colonization in the intertidal zone was examined from December 1971 to September 1972. Short-term (series I) and long-term (series II) exposures of test materials provided information about the rate of fouling accumulations and progressive community change. The study also determined the seasonal and vertical distribution of the dominant fouling organisms endemic to the Kiket Island area. These exposures also allowed a determination of the periods of maximum colonization by fouling organisms.

MATERIALS AND METHODS

Subtidal Fouling

Two test sites for the study of subtidal fouling were established offshore from Kiket and Skagit islands (Figure 1), in water of a mean depth of 18 m. At each test site five construction materials were tested for their resistances to fouling. The materials that were tested included a 90% copper-10% nickel alloy, steel, Plexiglas[4] (an acrylic plastic), white pine wood, and concrete. The materials were cut into 10 cm × 10 cm squares—54 squares each of steel, Plexiglas, and wood; 18 squares each of copper-nickel alloy and concrete. The squares or "plates" had two 12.7-mm holes drilled into opposite corners of the plate. Rope was threaded through the holes and the plates were then separated into 18 "test panels"—each panel having three plates of steel, Plexiglas, and wood, and one plate of copper-nickel alloy and concrete. Within each panel there was a random distribution of plates.

The test panels were suspended in the water at mean depths of 1, 6.1, and 15.3 m below the sur-

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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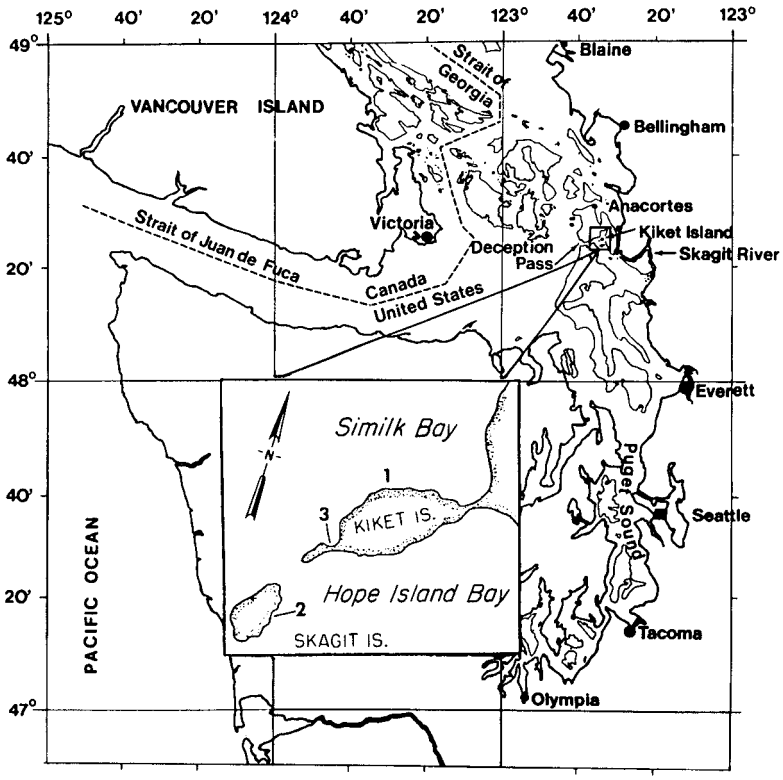

FIGURE 1. — Map of western Washington, with the study areas shown in inset: 1) Kiket Island subtidal site; 2) Skagit Island subtidal site; and 3) intertidal site.

face. The 1-m depth test panels were suspended from a steel surface float. The 6.1- and 15.3-m depth test panels were suspended between a concrete bottom anchor and a steel float moored just below the extreme low water level. At both test sites three panels were deployed at each depth (Figure 2).

Series I test panels were exposed for periods of 41 and 79 days offshore from Skagit Island and were exposed for 58 and 101 days offshore from Kiket Island. Series II test panels were exposed continuously for a period of 8 mo (16 April-29 November 1972) at both locations.

The standard analytical procedure for series I plates involved identification of the organisms, estimation of the percent of plate coverage, and, if possible, a measurement of the size of the organisms. A central square of each plate, measuring 7 cm × 7 cm, was used for analysis. The fouling organisms on each 49-cm^2 central area were scraped onto preweighed filter paper, dried at approximately 100°C for 24 h, and then weighed to 0.01 g. Monthly qualitative observations of series II plates, anchors, lines, and floats were made using scuba.

Intertidal Fouling

An examination was made of the settling rate of intertidal fouling organisms on concrete slabs. The concrete slabs measured 38 cm wide by 76 cm long by 15 cm deep. The slabs were uniform in texture, composition, surface configuration, stability, and resistance to wave action. They were anchored to the beach with steel reinforcing bars imbedded in the concrete. The long dimension was parallel to the water and the top surface was placed horizontal to the plane of the water. The slabs were positioned at the +0.6-, 0-, −0.6-, and −1.2-m water levels relative to mean sea level. Once each month the density of the fouling organisms was determined from a series of randomly chosen 49-cm^2 areas on each concrete slab.

RESULTS

Physicochemical Environment

Seasonal water quality data for the Kiket Island area have been described in detail (Stober et al.

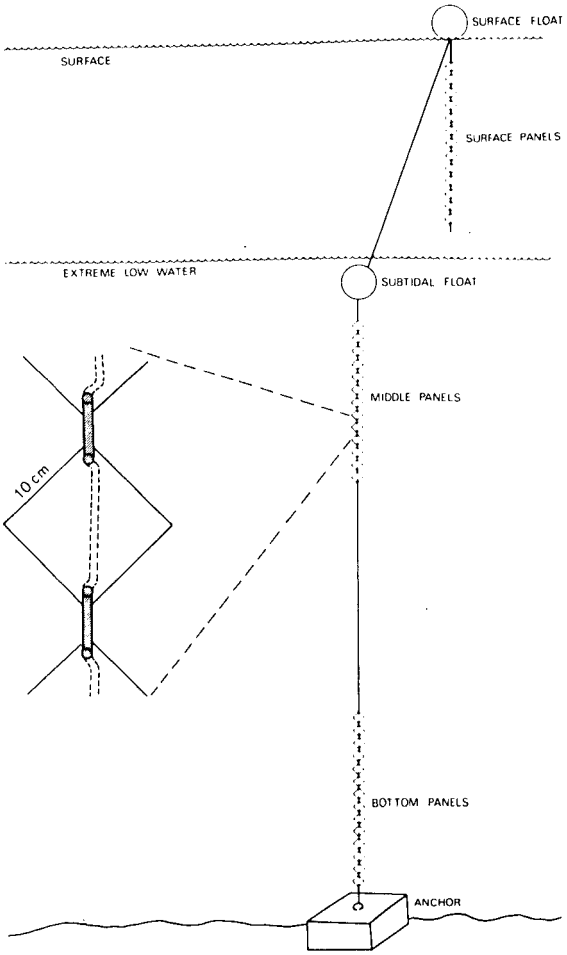

FIGURE 2.—A schematic of the array of subtidal test panels used to measure biofouling with inset showing details of test plate attachment.

1973). Weekly minimum, mean, and maximum temperature and salinity readings are presented in Figure 3. Average weekly temperatures ranged from 6.2°C to 11.8°C. Average weekly salinities ranged from 17.5 to 29.7 g/liter; pH ranged from 7.1 to 8.2; and dissolved oxygen concentrations ranged from 10.5 to 13.3 mg/liter. Lincoln et al. (1970) and Bendiner et al. (1972) have detailed the physical oceanography and vertical stratification of the Kiket Island area. The physicochemical characteristics of North Skagit Bay led Stober et al. (1973) to classify the study area as a well mixed estuary.

Qualitative observations of the study area were made periodically while scuba diving. The bottom in the vicinity of the fouling plates at Kiket Island consisted of soft silt and sediment with a few rock outcroppings. Acorn barnacles, *Balanus crenatus*, densely covered the few rock outcroppings, but were otherwise not present. At a depth of 18 m, light penetration was low and bottom currents appeared to be generally slow. In contrast, the bottom at Skagit Island was virtually free of silt and was predominantly covered with cobble and rock outcroppings. The cobble and rock were densely covered with *B. crenatus*. At 18 m, light penetration was moderate and the bottom currents were consistently more rapid than those at the Kiket Island site.

Fouling Colonization of the Construction Materials

The fouling resistances of the different test materials were compared using the dry weights of organisms collected during periodic sampling. The dry weight data for the 1-m level are shown in Table 1. Weight data of the removable material from the 15.3-m and 6.1-m levels were negligible except for the plates of wood and concrete colonized by *Balanus crenatus* (Table 2).

COPPER-NICKEL ALLOY.—There was no removable material through the first 58 days. The

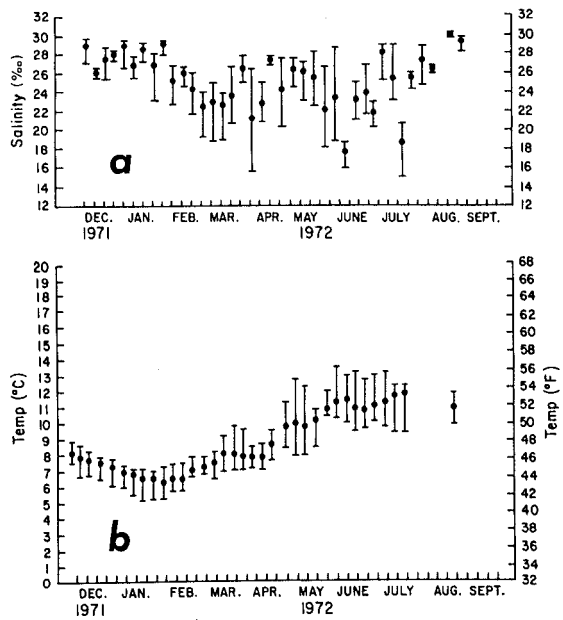

FIGURE 3.—Weekly mean, minimum, and maximum salinity measurements (a) and water temperature (b) recorded in the Kiket Island area (data from Stober et al. 1973).

TABLE 1.—Dry weight in grams of material collected per square centimeter of surface area from five artificial media exposed at the near-surface level for four time periods.

Exposure	Copper-nickel alloy	Steel	Plexiglas	Wood	Concrete
May 26					
41-day exposure	0.00	0.15	0.19	0.13	0.12
June 12					
58-day exposure	0.00	0.26	0.09	0.09	0.07
July 3					
79-day exposure	0.01	0.23	0.08	0.07	0.05
July 25					
101-day exposure	0.01	0.13	0.04	0.05	0.04

TABLE 2.—Density of the barnacle, *Balanus crenatus*, per square centimeter of surface area collected from five artificial media at three depths.

Exposure and depth	Copper-nickel alloy	Steel	Plexiglas	Wood	Concrete
May 26					
41-day exposure					
1 m	0.0	0.0	0.0	0.0	0.0
6.1 m	0.0	0.0	0.0	0.0	0.0
15.3 m	0.0	0.0	0.0	0.0	0.0
June 12					
58-day exposure					
1 m	0.0	0.2	0.1	0.2	2.9
6.1 m	0.0	0.1	0.4	0.3	1.6
15.3 m	0.0	0.0	0.0	0.0	0.4
July 3					
79-day exposure					
1 m	0.0	0.3	0.8	0.4	4.9
6.1 m	0.0	0.0	0.5	4.6	11.3
15.3 m	0.0	0.0	0.0	39	64
July 25					
101-day exposure					
1 m	0.0	0.1	0.2	0.9	2.1
6.1 m	0.0	0.0	0.0	0.0	0.4
15.3 m	0.0	0.0	0.0	0.1	0.0

79-day and the 101-day samples had removable material weighing less than 0.01 g/cm^2. Removable material consisted primarily of diatoms, with small deposits from flaking of the alloy surface. No mussels, barnacles, or green algae were observed.

STEEL.—After 41 days the dry weight of the removable material was 0.15 g/cm^2, after 58 days 0.26 g/cm^2, after 79 days 0.23 g/cm^2, and after 101 days 0.13 g/cm^2. A high proportion of the removable material was rust; biological accumulations consisted of diatoms, barnacles, green algae, and mussels. *Balanus crenatus* densities at the 1-m depth ranged from 0.0 on day 41 to 0.3/cm^2 on day 79. *Balanus* density at the 6.1-m level ranged from 0.0 on day 41 to 0.1/cm^2 on day 58. No *Balanus* were found at the 15.3-m level.

PLEXIGLAS.—After 41 days the dry weight of the removable material was 0.19 g/cm^2, after 58 days 0.09 g/cm^2, after 79 days 0.08 g/cm^2, and after 101 days 0.04 g/cm^2. Removable material consisted of diatoms, green algae, and barnacles. Mussels were not observed on the Plexiglas media. The density of *Balanus crenatus* at the 1-m level ranged from 0.0 on day 41 to 0.8/cm^2 on day 79. At the 6.1-m level *Balanus* densities ranged from 0.0 on day 41 to 0.5/cm^2 on day 79. No *Balanus* were found at the 15.3-m level.

WOOD.—After 41 days the dry weight of the removable material was 0.13 g/cm^2, after 58 days 0.09 g/cm^2, after 79 days 0.07 g/cm^2, and after 101 days 0.05 g/cm^2. Removable material consisted primarily of diatoms and barnacles with small amounts of green algae. No mussels were found. The density of *Balanus crenatus* at the 1-m level ranged from 0.0 on day 41 to 0.9/cm^2 on day 101. *Balanus* density at the 6.1-m level ranged from 0.0 on day 41 to 4.6/cm^2 on day 79. *Balanus* density at the 15.3-m level ranged from 0.0 on day 41 to 39/cm^2 on day 79. *Balanus* achieved 100% of plate coverage on day 79 at the 15.3-m level. No wood borers were found at any level.

CONCRETE.—After 41 days the weight of the removable material was 0.12 g/cm^2, after 58 days 0.07 g/cm^2, after 79 days 0.05 g/cm^2, and after 101 days 0.04 g/cm^2. Removable material consisted of diatoms, barnacles, mussels, and green algae. The density of *Balanus crenatus* at the 1-m level ranged from 0.0 on day 41 to 4.9/cm^2 on day 79. *Balanus* density at the 6.1-m level ranged from 0.0 on day 41 to 11.3/cm^2 on day 79. *Balanus* density at the 15.3-m level ranged from 0.0 on day 41 to 64/cm^2 on day 79. *Balanus* achieved 100% plate coverage on day 79 at the 15.3-m level. Bay mussels, *Mytilus edulis*, achieved a density of 0.4/cm^2 at the 1-m level — none were found in the deeper water samples.

Intertidal Fouling

The colonization of fouling organisms was observed on concrete test slabs positioned at various levels in the intertidal zone of Kiket Island. The principal algae species colonizing the slabs were *Fucus distichus* and *Ulva lactuca*. The dominant animal species included the acorn barnacle, *Balanus glandula*, and the bay mussel. A detailed examination of the natural vertical and seasonal distribution of the intertidal flora and fauna of Kiket Island is presented by Houghton (1973).

Settlement by barnacles (Figure 4) was the most rapid during late May. Barnacle density peaked in June, but subsequently there was a general decrease in the density—probably due to intraspecific competition for the limited growing area. Barnacle settlement was most successful at the −0.6-m level. There was limited settlement at the —1.2-m level and at the 0.0-m level. No barnacles successfully settled at the +0.6-m level.

Settlement by barnacles at the −1.2-m level appeared to be limited by heavy siltation and diatomaceous growth. The absence of barnacles at the +0.6-m level was principally caused by the extensive exposure of the organisms to sunlight. Successful settlement at the −0.6-m level was the result of a limited exposure to sunlight and of the moderate wave action limiting the silt/diatom buildup.

Settlement by *M. edulis* was predominant at the −0.6-m level, where maximum density was 1.3/cm². *Mytilus edulis* were present in lower densities at the 0.0-m and −1.2-m levels. The same factors affecting settlement by barnacles—exposure to sunlight and the silt-diatom buildup—affected settlement by *M. edulis*. Mussels were observed to attach primarily in the late summer and in the fall (July-October); a few individuals were observed in April and May.

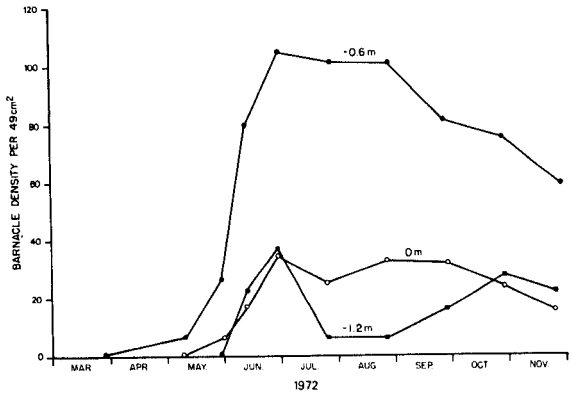

FIGURE 4.—Mean density of *Balanus glandula* attached to concrete substrata exposed in the intertidal zone of Kiket Island (tidal level relative to mean sea level).

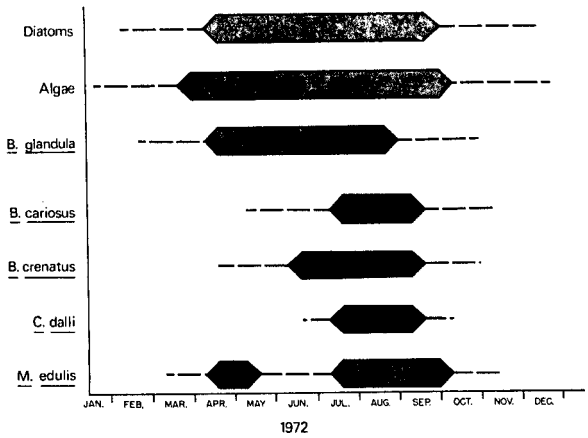

FIGURE 5. — Seasonal distribution of predominant subtidal and intertidal fouling organisms.

Seasonal Distribution of Fouling Organisms

The seasonal distribution of the major sessile fouling organisms found in the Kiket Island area is presented in Figure 5. Conclusions about the distribution of these organisms are based on data collected during a 1½-yr study of intertidal settlement and an 8-mo study of subtidal fouling. Comparable conclusions were reached by DePalma (1966) for Admiralty Inlet.

The first diatoms to appear on the study plates were those of the genus *Melosira*. These diatoms remained dominant throughout the study period. *Navicula* and *Fragilaria,* as well as a large number of unidentified diatoms, also settled on the plates, but were not nearly as abundant as *Melosira*. Although the spores of many diatom species were present all year, settlement occurred predominantly from early spring to midsummer.

Four dominant forms of algae settled on the study plates. *Fucus distichus* and *Ulva lactuca* were dominant in the intertidal zone, while *Ulothrix* sp., *Cladophora* sp., and *Ulva lactuca* were dominant in the subtidal zone. The algae was abundant seasonally—in the spring and summer there was an extensive algal cover on the plates, yet in the fall and winter months the abundance of algae decreased substantially. Many small crustaceans, including copepods, cladocerans, and amphipods, were observed inhabiting the diatoms and algae covering the test plates.

Although barnacles of the genus *Balanus* were present throughout the year, their rate of settlement varied greatly with the different seasons. As a general rule, maximum settlement occurred during the late spring (April-June) and in early fall (mid-August-October). For example, *B. glandula* settled in the intertidal zone from February

through November, but the maximum rate of settlement was observed in May and August. However, in the subtidal zone, *B. crenatus* settled from April to November, but with a peak in late July and early August. Others, like *B. cariosus* and *Chthamalus dalli,* settles sporadically from May to November and peaked in August and September.

Settlement by the bay mussel occurred primarily from August to November, although there was some settlement during April and May. It appears that prior settlement by diatoms, algae, and barnacles is necessary for the establishment of a mussel colony. Cleaned test plates were exposed in both the intertidal and the subtidal zones and were compared with plates already having an established community of diatoms, algae, and barnacles. Only on those plates which were already fouled was there any settlement by mussels. Coe (1932) reported the same phenomenon and concluded that the smooth quality of nonfouled surfaces was not suitable for attachment by the byssus of young mussels.

Vertical Distribution in the Subtidal Zone

At both subtidal test sites there was a distinct vertical pattern to the fouling of the test plates. The greatest number of species settled at the near-surface (1-m) level. At that level there were colonial diatoms of the genera *Melosira, Navicula,* and *Fragilaria,* and three species of the acorn barnacle, *Balanus crenatus, B. glandula,* and *B. cariosus*. Subdominant genera included the green algae, *Ulothrix, Ulva,* and *Cladophora*. Small numbers of the bay mussel were also found at the surface level. At the middle depth (6.1 m) the species composition of the fouling organisms changed. Green algae became rare and diatoms were less dense. *Mytilus edulis, B. glandula,* and *B. cariosus* were absent. *Balanus crenatus* increased in density with increasing depth at Skagit Island, but not at the Kiket Island site.

The 15.3-m level was very different from the two upper levels. The plates had no algae or diatoms. *Balanus crenatus* was the dominant species. Consistently higher densities of *B. crenatus* were observed at the Skagit Island test site. The ratio of densities between Skagit and Kiket Island for *B. crenatus* at the 15.3-m level ranged as high as 50 to 1 for the wood and concrete test plates.

DISCUSSION

Marine fouling presents one of the most serious long-term operational problems for power generating stations using saline waters for cooling (Powell 1933; Dobson 1946; Holmes 1970). Fouling accumulations reduce the carrying capacity of cooling system conduits by increasing the frictional resistance and by reducing the pipeline diameter. In addition, marine fouling reduces the heat transfer efficiency of steam condenser systems and promotes severe corrosion of the condenser system components. The accumulation of fouling debris, such as dead shells, adds to the inefficiency by clogging the condenser tubes.

Data are needed by design engineers in order to determine the probable construction requirements for the control of fouling in a power plant cooling system. Because marine fouling varies considerably from one location to another, an on-site determination of the population dynamics of fouling organisms is desirable. Each site should be studied in order to determine: 1) the species composition of sessile organisms colonizing specific construction materials at various subtidal levels, 2) the types of construction materials least likely to be fouled, 3) the seasonal variations in settlement and abundance, and 4) the times of the year when antifouling procedures must be considered. The present study was, in a sense, an attempt to study all these factors, and although the power plant for which the study was intended may never be built, this report should be a useful guide to future studies of power plant siting.

Data for the present study were collected from test plates suspended at various depths in the water. However, caution must be used in extrapolating studies carried out with these small static test plates. Graham and Gay (1945) reported that plates, 9.8 cm × 9.8 cm, were found to give results just as reliable as larger ones. Holmes (pers. commun.), however, considers that "edge effects and top-to-bottom gradients could be very important in biassing results from such small panels." Although no effort was made in the present study to determine the reliability of the small plates, a 3-cm border zone surrounding the 49-cm^2 examination area was considered sufficient to eliminate any edge effect. There was consistently less than 10% variation in the dry weights of the removable material and in the density of barnacles taken from different plates of the same media at the same water level.

One must also recognize that data collected from static test panels can only give a limited indication of the growth rate of fouling organisms in a continuous-flow cooling system (Dobson 1946). Fouling organisms naturally dependent upon water currents to supply food, may have their growth rates enhanced by the greater water velocities of a continuous-flow cooling system (Dobson 1946; Benson et al.[5]). Mawatari[6] observed, however, that test panels exposed in current velocities of 4 to 7 m/s remained totally free of fouling organisms. Efforts to reduce the influence of static plates have been made by several authors (Smith 1946; Doochin and Smith 1951; Wood 1955), but these efforts have produced conflicting results.

Several additional factors should be mentioned which influence both the growth rate and the species composition of sessile organisms colonizing test plates. The larvae of barnacles and many other fouling organisms have been found to be negatively phototrophic when they attach to a surface. Therefore, these organisms prefer to attach to shaded or dark surfaces (Visscher and Luce 1928; Thorson 1964). Also, surface texture has been shown to affect the rate of attachment of settling larvae (Crisp and Ryland 1960; Pomerat and Weiss[7]). In general, porous and rough surfaces have the greatest fouling accumulation.

All of these factors influenced the results obtained by the present study. For example, the test plates, although they were subjected to natural flow currents of the marine environment, were not subjected to the "unnatural" flow currents of a power plant cooling system. Thus, fouling on the test plates might be somewhat different from the fouling of a cooling system. Yet the test plates offer useful indications as to what will happen in the actual cooling system and therefore they are useful for predictive planning of power plant engineers.

In the present study, variations in the abundance and species composition of fouling organisms were observed for the different construction materials. Accumulation was slow on the copper-nickel alloy plates, but was rapid and complete on the concrete and wood plates. Because the fouling plates were exposed to identical environmental conditions, the differences in fouling resistance must have been dependent upon the differences between the media. Previous research has shown the same results—Woods Hole Oceanographic Institution (1952), for example, found that copper-nickel alloy maintains its fouling resistance for 10 mo, much longer than concrete or wood.

Depth was found to have a significant effect upon the rate of fouling accumulation. For example, the dry weight of removable material from all materials placed below the surface level (1 m) was negligible except for those wood and concrete plates colonized by *Balanus crenatus*. Yet at the surface there was considerable algal and diatomaceous growth on all media except the copper-nickel alloy. The only organism which increased in density as the depth increased was *B. crenatus*, the only organism colonizing the plates at the 15.3-m level. Because these results were similar for all media and because they were corroborated by qualitative examinations made on the ropes, floats, and anchors, it appears that a cooling system intake in the Kiket Island area should be sited in water deeper than about 6 m. Based on biofouling results, the cooling system intake should not be sited at the surface because fouling is greatest at that level.

An analysis of the seasonal distribution of the fouling organisms showed that there was initially an accumulation of brown detrital film and bacterial slime on the fouling plates. Soon a filamentous algae, *Enteromorpha*, and a diatom, *Melosira*, became established. As floral density increased, greater numbers of Crustacea were observed living in the growths on the plates. Barnacle and mussel colonization of the test plates occured throughout the year, but was greatest from April through October. For mussels, at least, it appeared that a previous accumulation of fouling material was required before the mussels would attach to the test plates. Thus, it would appear that fouling control should be greatest during the spring, summer, and early fall. During late fall and winter fouling control need not be so greatly emphasized. It must be remembered that the time for maximum fouling may vary from year to year, and thus fouling control should be regulated by routine observations of larval settlement. In addition, early fouling control may help to deter col-

[5]Benson, P. H., E. L. Littauer, and N. P. Stumbaugh. 1968. Outlook for marine corrosion and fouling protection. Paper presented at Symposium on Ocean Technical Problems of the 1970's. 61st Annu. Meet., Los Ang., Calif., Dec. 1968, 42 p.

[6]Mawatari, S. 1965. Protection of power plants from biological fouling. Unpubl. rep. Research Institute for Natural Resources, Tokyo, Jap.

[7]Pomerat, C. M., and C. M. Weiss. 1946. The influence of texture and composition of surface on the attachment of sedentary marine organisms. Unpubl. manuscr.

onization by mussels, which, according to Hoshiai (1964) and Holmes (1970), are the principal fouling organisms in power plant cooling systems.

The use of intermittent chlorination as a fouling control agent has been noted by Holmes (1970), Morris (1971), and Draley (1972). In general, most investigators feel that the larvae of various marine fouling organisms are more sensitive to chronic low-level concentrations of chlorine than are the adults (Dobson 1946; Turner et al. 1948). Thus, greatest effectiveness results from repeated low-level chlorination, which either kills the larvae directly or creates an unfavorable environment for settlement.

Any fouling control scheme should maintain adequate precautions against excessive interference with organisms inhabiting the receiving water ecosystem. Chemical toxins such as chlorine are objected to as antifouling agents primarily because of the possible detrimental effects on nontarget organisms (Waugh 1964; Hamilton et al. 1970; Stober and Hanson 1974). This effect is particularly true when the treated effluent is discharged directly into the aquatic environment.

The data presented in this study can only be called preliminary. Additional tests should be run which would include at least one complete annual cycle study of subtidal fouling. Yet the present study does indicate that if the proposed plant were to be built at Kiket Island, its cooling system should be in water deeper than 6 m and should have a safe and adequate fouling control scheme. Of the different construction materials tested in this study, it would appear that copper-nickel alloy would most effectively deter fouling and that concrete and wood would be least effective.

It must be emphasized that the present study is an analysis of biofouling. Prior to the siting and final design of the cooling water intake structure, consideration must also be given to the potential effects of entrainment on zooplankton and larval and juvenile fish.

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LITERATURE CITED

BEAUCHAMP, R. S.
1966. Low-level chlorination for the control of marine fouling. Central Electric Res. Lab., Lab. Memo RD/L/M 147, 16 p.

BENDINER, W. P., T. E. EWART, AND E. H. LINGER.
1972. Prediction of excess heat distribution using tracer dye techniques. Final Rep. APL-UW 7206, Univ. Wash. Appl. Phys. Lab., Seattle, 83 p.

COE, W. R.
1932. Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography, La Jolla, California. Bull. Scripps Inst. Oceanogr. Tech. Ser. 3:37-87.

CRISP, D. J., AND J. S. RYLAND.
1960. Influence of filming and of surface texture on the settlement of marine organisms. Nature (Lond.) 185:119.

DEPALMA, J. R.
1966. A study of the marine fouling and boring organisms at Admiralty Inlet, Washington. Inf. Ms. Rep. 0-6-66, Oceanogr. Surv. Dep., U.S. Nav. Oceanogr. Off., Wash., D.C., 32 p.

DOBSON, J. G.
1946. The control of fouling organisms in fresh- and saltwater circuits. Trans. Am. Soc. Mech. Eng. 68:247-265.

DOOCHIN, H., AND F. G. W. SMITH.
1951. Marine boring and fouling in relation to velocity of water currents. Bull. Mar. Sci. Gulf Caribb. 1:196-208.

DRALEY, J. E.
1972. The treatment of cooling waters with chlorine. ANL/ES-12 Feb. 1972. Argonne National Laboratory, Lemont, Ill., 11 p.

GRAHAM, H. W., AND H. GAY.
1945. Season of attachment and growth of sedentary marine organisms at Oakland, California. Ecology 26:375-386.

HAMILTON, D. H., JR., D. A. FLEMER, C. W. KEEFE, AND J. A. MIHURSKY.
1970. Power plants: effects of chlorination on estuarine primary production. Science (Wash., D.C.) 169:197-198.

HOLMES, N.
1970. Marine fouling in power plants. Mar. Pollut. Bull. 1:105-106.

HOSHIAI, T.
1964. Distribution of sessile animals in the intake-duct of the cooling sea water of the Hachinohe thermal power station. Asamushi Mar. Biol. Stn. Bull. 12:42-50.

HOUGHTON, J. P.
1973. Intertidal ecology. *In* Q. J. Stober and E. O. Salo (editors), Ecological studies of the proposed Kiket Island nuclear power site, p. 119-257. Final Rep. to Snohomish County P.U.D. and Seattle City Light. Univ. of Wash. Coll. Fish., Fish. Res. Inst., Seattle.

LINCOLN, J., E. E. COLLIAS, AND C. S. BARNES.
1970. Skagit Bay study, Prog. Rep. 3. Univ. Wash. Dep. Oceanogr. Ref. M70-111, 88 p.

MORRIS, J. C.
1971. Chlorination and disinfection — state of the art. J. Am. Water Works Assoc. 63:769:774.

POWELL, S. T.
1933. Slime and mussel control in surface condensers and circulating water tunnels. Combustion (April):7-13.

SMITH, F. G. W.
1946. Effect of water currents upon the attachment and growth of barnacles. Biol. Bull. (Woods Hole) 90:51-70.

STOBER, Q. J., AND C. H. HANSON.
1974. Toxicity of chorine and heat to pink *(Oncorhynchus gorbuscha)* and chinook salmon *(O. tshawytscha)*. Trans. Am. Fish. Soc. 103:569-576.

STOBER, Q. J., S. J. WALDEN, AND D. T. GRIGGS.
1973. Seasonal water quality in North Skagit Bay. *In* Q. J. Stober and E. O. Salo (editors), Ecological studies of the proposed Kiket Island nuclear power site, p. 7-34. Final Rep. to Snohomish County P.U.D. and Seattle City Light. Univ. of Wash. Coll. Fish., Fish. Res. Inst., Seattle.

THORSON, G.
1964. Light as an ecological factor in the dispersal and settlement of larvae of marine botttom invertebrates. Ophelia 1:167-208.

TURNER, H. J., JR., D. M. REYNOLDS, AND A. C. REDFIELD.
1948. Chlorine and sodium pentachlorophenate as fouling preventives in sea water conduits. Ind. Eng. Chem. 40:450:453.

VISSCHER, J. P., AND R. H. LUCE.
1928. Reactions of the cyprid larvae of barnacles to light with special reference to spectral colors. Biol. Bull. (Woods Hole) 54:336-350.

WAUGH, G. D.
1964. Observations on the effects of chlorine on the larvae of oysters (*Ostrea edulis* (L.)) and barnacles (*Eliminius modestus* (Darwin)). Ann. Appl. Biol. 54:423-440.

WOOD, E. J. F.
1955. Effect of temperature and rate of flow on some marine fouling organisms. Aust. J. Sci. 18:34-37.

WOODS HOLE OCEANOGRAPHIC INSTITUTION.
1952. Marine fouling and its prevention. U.S. Nav. Inst., Annapolis, 388 p.

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OBSERVATIONS ON THE FISH FAUNA ASSOCIATED WITH OFFSHORE PLATFORMS IN THE NORTHEASTERN GULF OF MEXICO

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ABSTRACT

The fish fauna associated with two U.S. Navy research platforms, Stage I and Stage II, in the northeastern Gulf of Mexico off Panama City, Fla., was studied at irregular intervals from 1970 to 1974. Such platforms function as artificial reef habitats and support diverse and abundant fish populations not normally characteristic of the open sandy bottoms in the area.

A total of 101 taxa (identified to family or species) was recorded at the two platforms; 61 species were observed at Stage I in water 32 m deep and 86 taxa at Stage II in water 18 m deep. The greater number of species recorded at the shallower location may be more a result of the greater number of observations made there than of differences in the two habitats. The number of species present at the platforms varies considerably at different times of the day and year. Species numbers are greatest during the summer and fall, but many species begin to move offshore or southward as the water temperature drops, and only about 50-60% of those recorded at the platform remain in December. The number of species diminishes to about 16% in February at Stage II, then increases gradually with the rising water temperature in the spring.

Major species occupying the platform habitats include fishes usually characteristic of pelagic, inshore (coastal or estuarine), and rocky reef environments. At the platforms, the pelagic species and most of the larger predators occupy various levels of the water column, either directly below or surrounding the structure, while most of the other species are associated either with the pilings and cross-members of the platform or with the bottom. For some of the species, the platform provides food and shelter, while for others, it offers only shelter. Some species may be present only to feed on the numerous fishes and other organisms concentrated there. Diel rhythms of activity are obvious for many of the fishes, with some species active only during the day, and others only at night.

Offshore oil drilling platforms are known to attract various species of marine fishes and thus function as artificial reefs (Carlisle et al. 1964; Treybig 1971). Anglers often recognize such platforms as desirable fishing sites. Carlisle et al. (1964) documented the development of fish populations (as well as populations of encrusting organisms) at two platforms constructed off the coast of California. The supporting piles and cross-members of such platforms provide hard substrates for the settling of pelagic larvae of encrusting invertebrates and algae which, with their associated invertebrate populations, provide food and shelter for reef fishes attracted to the structures. In addition, many pelagic fishes congregate about these platforms, attracted either by the solid, reeflike nature of the supporting structures, or by the numerous smaller forage organisms in the area.

Many comparable platforms have been constructed in the Gulf of Mexico since the 1940's, but no studies of their associated fish faunas have been reported, even though they are known to attract numerous species of fishes. Current studies by personnel of the University of Southwestern Louisiana have documented the fish fauna of drilling platforms off the coast of Louisiana (Sonnier et al. 1976). This paper records the fish populations observed around two offshore platforms in the northeastern Gulf of Mexico off Panama City, Fla.

LOCATION AND TIME OF STUDY

Two research platforms operated by the U.S. Navy off the coast of Panama City are referred to as Stage I and Stage II. Stage I is 17.7 km offshore in water 32 m deep (lat. 30°00.5′N, long. 85°54.2′W). Stage II (Figure 1) is 3.2 km offshore in water 18 m deep (lat. 30°07.2′N, long. 85°46.4′W). The pilings of Stage I form a square on the sea bottom with each side measuring 32.6 m, whereas those of Stage II measure 19.1 m. The two platforms were the sites of biofouling studies

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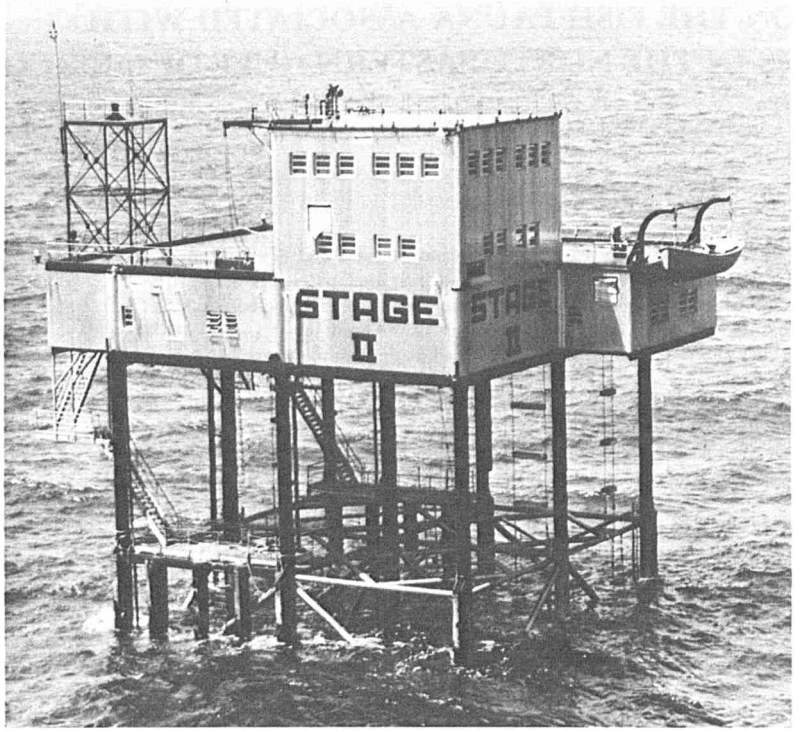

FIGURE 1.—Stage II, the Navy research platform 3.2 km offshore of Panama City, Fla. (U.S. Navy photo.)

by Pequegnat et al. (1967), Pequegnat and Pequegnat (1968), and Culpepper and Pequegnat (1969). Vick (1964) mentioned 13 species of fishes either collected or reported from the stages and vicinity.

These platforms were examined occasionally from 1970 to 1974 by the first and second authors in connection with studies of reef fishes in the northern Gulf of Mexico. During the fall of 1970 (Ogren) and summer of 1972 (Hastings and Mabry), the authors participated in the Scientist-in-the-Sea (SITS I and II) diving program at the Naval Coastal Systems Laboratory in Panama City and were able to make repeated observations at the platforms.

Between September 1970 and January 1974, 10 dives were made at Stage I (including 1 night dive) and 21 dives were made at Stage II to determine the composition of the fish populations under the structures (see Tables 1, 2). During the SITS II program in 1972, a series of dives made at various times during four consecutive 24-h periods (1-4 August) enabled us to determine diel patterns of concentration of fish schools around and under the platforms.

METHODS

During each dive an attempt was made to identify each species of fish present in the area and to estimate its abundance. At the end of a dive a debriefing session was held and notes were compared as to species and numbers observed. Divers often carried hand nets or spears for collecting unusual or difficult to identify species.

Dives were usually conducted on an irregular basis, and the length of the observation period and the area examined varied considerably from one dive to the next. Consequently, no numerical values were assigned to these estimates of abundance. Instead, relative terms such as few, several, common, and abundant were used, simply to indicate the impression received by the divers as to the numbers of each species present. It should be kept in mind, however, when considering these estimates, that such relative terms may have different meanings when applied to different species of fishes. For example, an absolute number such as 100 individuals might be interpreted as few if applied to a schooling species such as *Harengula pensacolae*, but as abundant if applied to a soli-

tary reef species such as *Chaetodon ocellatus*. These estimates (recorded for all dives in Tables 1 and 2) are admittedly subjective but may be useful in describing the seasonal changes in the fish populations around the platforms.

Our dives at Stage II during the SITS II program were scheduled to occur at approximately 5-h intervals from 1 to 4 August 1972. Although this schedule was not always followed because of other diving commitments of the program, we made 10 dives which included at least 2 dives during each quarter of the 24-h day. Times of the dives are presented as Central Standard Time (CST) in this report. During early August 1972, the times of sunrise and sunset at Stage II were approximately 0500 and 1840 CST, respectively.

During the SITS II program, two censusing stations were set up under Stage II: Station 1 on the bottom at 18.3 m; and Station 2 directly above, about 4.6 m below the water surface. Both stations were the same size and were conveniently delimited by the cross-members at one corner of the platform. The stations measured 4.9 × 4.9 × 7.0 m. Counts were restricted to that portion of the water column estimated to extend 1 m upward from the base of the cross-members (corresponding to the bottom at Station 1). Thus, the water volume included within each station was about 12 m^3.

During each dive at the censusing stations the authors attempted to identify and count all species of fishes present within each station. Counts were recorded on plastic slates during the censusing, then transferred to data sheets after surfacing. Times required to make each census varied because of the great variation in the numbers of fishes present, but were usually about 10-15 min for each station. In most cases both stations were censused on each dive, and counts for Station 2 were made about 15-20 min after the counts for Station 1. On dives 1, 9, and 10, only one of the two stations was censused. Some species were so numerous at times that only estimates of their abundance could be made. Such estimates of fish abundance by two divers making counts at the same time were generally in the same order of magnitude.

During nocturnal diving operations, an underwater light was suspended near the surface below a ladder (to facilitate diver return) at the corner of the platform farthest from the censusing stations. It was not visible underwater at the censusing stations and did not appear to affect our counts. Although some fishes were attracted to this light, they were mostly juveniles and larvae of pelagic species.

Nomenclature and arrangement of the families in Tables 1, 2, and 3 follow Bailey et al. (1970).

RESULTS AND DISCUSSION

All species recorded at the two stages during this study are listed in Tables 1 and 2. Table 3 is a list of the species recorded in the two stations at Stage II during the SITS II dives. These tables should be examined in connection with the following synopsis of the results of this study. At least 101 taxa (identified to family or species) were recorded during this study at the two platforms; 61 species were recorded at Stage I during 10 dives, and 86 taxa were recorded at Stage II during 21 dives. The greater number recorded at Stage II is probably primarily a result of the greater number of observations there. In general, the fish faunas of the two stages are quite similar, and most of the species recorded at only one could be expected to occur at both occasionally. Of the 101 taxa recorded, about 75 were frequently observed during the study and could be regarded as characteristic members of the fauna, 41 were recorded as common or abundant. Of the latter group, 27 species were recorded at Stage I and 36 at Stage II.

Faunal Composition

The two stages represent an artificial reef habitat in an area previously characterized by flat sand bottoms. Thus, the fishes inhabiting the stage environment are a mixture of faunal types, including some species usually expected in such flat, sandy areas, but also including many species more characteristic of other habitats of the northern Gulf of Mexico, especially fishes which are attracted to reef environments.

A number of demersal species characteristic of open sand habitats of the northern Gulf of Mexico were frequently recorded at the stages, but these were usually seen over the open sandy areas surrounding the stages. Examples are *Dasyatis* sp., *Raja eglanteria, Arius felis, Ogcocephalus radiatus, Stenotomus caprinus, Hemipteronotus novacula, Prionotus* sp., *Paralichthys albigutta, Lactophrys quadricornis*, and *Chilomycterus schoepfi*. In addition, many species recorded at the stages are pelagic fishes characteristic of open

TABLE 1.—Fishes recorded at Stage I off Panama City, Fla., with estimates of usual abundance and habitat occupied.

Species	Abundance[1]				Habitat[1]
	Spring (Apr.)	Summer-fall (July-Nov.)	Winter Dec.	Winter Jan.	
Carcharhinidae:					
Carcharhinus milberti	—	few	—	—	O
Dasyatidae:					
Dasyatis sp.	—	few	—	—	B
Muraenidae:					
Gymnothorax nigromarginatus	—	few	few	—	B
Clupeidae:					
Sardinella anchovia	—	com-abun	abun	—	U
Ariidae:					
Arius felis	—	sev	—	—	B
Batrachoididae:					
Opsanus pardus	sev	sev	sev	com	B
Antennariidae:					
Antennarius ocellatus	few	few	few	few	B
Ogcocephalidae:					
Ogcocephalus radiatus	—	few	few	few	B
Serranidae:					
Centropristis ocyurus	com	com	com	com	B
Diplectrum formosum	sev	sev-com	sev-com	—	B
Epinephelus nigritus	—	—	—	few	L
Mycteroperca microlepis	—	few-com	few	sev	L
Serranus subligarius	sev	sev-com	sev-com	com	B-P
Grammistidae:					
Rypticus maculatus	—	sev-com	sev	com	B-P
Apogonidae:					
Apogon pseudomaculatus	few	sev-com	—	sev	B
Rachycentridae:					
Rachycentron canadum	—	few	few	—	O-U
Echeneidae:					
Echeneis neucratoides	—	few-sev	—	sev	([2])
Carangidae:					
Caranx crysos	—	com	—	—	U
Caranx hippos	—	sev-com	—	—	O-U
Caranx ruber	—	few-com	few	—	U
Decapterus punctatus	—	com-abun	abun	few	U
Elagatis bipinnulata	—	sev	sev	few	O-U
Seriola dumerili	sev	few-com	com	com-abun	L-O-U
Seriola rivoliana	—	—	few	—	U
Trachurus lathami	—	com	—	—	L
Lutjanidae:					
Lutjanus campechanus	—	few	few	—	L
Lutjanus griseus	few	sev-abun	few	sev	L-U
Rhomboplites aurorubens	sev	com-abun	—	com	L
Pomadasyidae:					
Haemulon aurolineatum	com	com-abun	com-abun	sev	L
Haemulon plumieri	—	—	few-sev	—	L
Sparidae:					
Archosargus probatocephalus	—	few	—	—	U
Lagodon rhomboides	—	sev	—	—	L-U
Sciaenidae:					
Equetus lanceolatus	—	sev-com	—	com	B
Equetus umbrosus	com	sev-com	com	com	B
Equetus sp.[3]	—	few	—	—	B
Kyphosidae:					
Kyphosus sectatrix	—	sev	—	—	U
Ephippidae:					
Chaetodipterus faber	com	sev-com	sev	com	L-U
Chaetodontidae:					
Chaetodon ocellatus	few	few	few	few	B-P
Chaetodon sedentarius	—	few	few	—	B
Holacanthus bermudensis	sev	sev-com	sev	sev	L-U
Pomacentridae:					
Abudefduf saxatilis	—	few-sev	—	sev	P
Chromis enchrysurus	—	few	—	few	B
Chromis scotti	—	sev-com	—	sev	B-P
Pomacentrus partitus	—	few-sev	—	—	P
Pomacentrus variabilis	com	sev-com	sev	com	B-P
Labridae:					
Halichoeres caudalis	com	sev-com	—	few	B
Thalassoma bifasciatum	—	few-sev	—	sev	P
Sphyraenidae:					
Sphyraena barracuda	—	sev-abun	sev	few	O-U
Blenniidae:					
Blennius marmoreus	—	sev	—	—	B-P
Hypleurochilus geminatus	few	few-com	—	—	P

TABLE 1. — Continued.

Species	Abundance[1] Spring (Apr.)	Summer-fall (July-Nov.)	Winter Dec.	Winter Jan.	Habitat[1]
Gobiidae:					
Coryphopterus punctipectophorus	few	few	—	—	B
Ioglossus calliurus	—	sev	—	—	B
Acanthuridae:					
Acanthurus coeruleus	—	—	—	few	P
Scombridae:					
Euthynnus alletteratus	—	sev-com	sev	sev	O-U
Bothidae:					
Paralichthys albigutta	—	few	—	—	B
Balistidae:					
Balistes capriscus	few	few-sev	few	few	L-U
Monacanthus hispidus	—	few-sev	—	—	P
Ostraciidae:					
Lactophrys quadricornis	few	few	few	—	B
Tetraodontidae:					
Canthigaster rostrata	—	few	—	—	B
Sphoeroides spengleri	—	few	—	—	B
Diodontidae:					
Chilomycterus schoepfi	few	few	few	few	B
61 species 100%	21 species 34%	57 species 93%	31 species 51%	32 species 52%	
Number of observations	1	6	2	1	
Temperature range	17°-20°C	23°-29°C	18°-19°C	18°C	

[1]Abbreviations are as follows: sev-several, com-common, abun-abundant, B-on bottom, L-lower water column, P-on pilings, O-open water around platform, U-middle to upper water column under platform.
[2]*Echeneis neucratoides* on *Epinephelus, Sphyaena, Seriola, Balistes,* and *Caretta.*
[3]*Equetus* sp. - an undescribed species listed by Bullis and Thompson (1965) as "*Equetus* sp. nov." and by Struhsaker (1969) as "Blackbar drum *Pareques* sp. (undescribed)."

waters, which are attracted to solid, reeflike structures. Smaller baitfishes, such as *Harengula pensacolae, Sardinella anchovia, Etrumeus teres, Opisthonema oglinum, Decapterus punctatus, Trachurus lathami,* and *Scomber japonicus*, were abundant at times and formed dense schools under the stages. Klima and Wickham (1971) demonstrated the potential for harvesting commercial quantities of these and other species by attracting schools to artificial structures. In research conducted near Stage II during 1969, they found *Decapterus* and *Sardinella* more numerous than *Harengula*, but did not record the other species. *Harengula pensacolae* was usually the most common species at Stage II during our observations made in 1972, while *Decapterus* and *Sardinella* were more common in other years.

Larger pelagic species often recorded at the stages were *Rachycentron canadum, Caranx bartholomaei, C. crysos, C. hippos, C. ruber, Elagatis bipinnulata, Seriola dumerili, Euthynnus alletteratus,* and *Sphyraena barracuda.* These species were recorded at the stages often enough to indicate some attraction to the structures, even though they are characteristic open-water species. Part of the attraction for these larger predators may be the large number of smaller baitfishes which provide much of their food (Wickham et al. 1973). Publications on the attraction of fishes to artificial reefs have noted that pelagic species such as those listed here are attracted to artificial structures in greatest numbers when the structures extend a considerable distance above the bottom or even reach the surface, as do these offshore platforms (Unger 1966; Gooding and Magnuson 1967; Hunter and Mitchell 1967, 1968; Klima and Wickham 1971). Springer and Woodburn (1960) noted that *S. barracuda* occurred near shipwrecks off the Tampa Bay area but not on natural rocky reefs. The occurrence of barracuda may be associated with the higher relief of structures such as shipwrecks or the stages. In this respect the offshore platforms are ideal for attracting large numbers of typically open-water fishes.

Sharksuckers (remoras) were often seen associated with other fish species around the stages (especially the larger pelagic species such as *Caranx hippos* and *S. barracuda*) but were never numerous. The species was probably *Echeneis neucratoides*, although *E. naucrates* could also be expected in the area. Four *Echeneis* were also seen attached to one of two loggerhead turtles, *Caretta caretta caretta*, which were observed asleep on the bottom below Stage I. The remoras were attached to the turtle's plastron and ventral margin of the carapace and were inactive except for movements of their opercula.

TABLE 2.—Fishes recorded at Stage II off Panama City, Fla., with estimates of usual abundance and habitat occupied.

Species	Abundance[1]				Habitat[1]
	Spring (Apr.-May)	Summer-fall (June-Nov.)	Winter Dec.	Winter Feb.	
Carcharhinidae	—	few	—	—	O
Sphyrnidae:					
Sphyrna sp.	—	few	—	—	O
Dasyatidae:					
Dasyatis sp.	—	few	—	—	B
Rajidae:					
Raja eglanteria	—	few	few	—	B
Muraenidae:					
Gymnothorax nigromarginatus	few	few	few	—	B
Congridae	—	—	few	—	B
Ophichthidae:					
Mystriophis intertinctus	few	few	few	—	B
Clupeidae:					
Etrumeus teres	—	sev-com	—	—	U
Harengula pensacolae	—	sev-abun	sev-com	—	L-U
Opisthonema oglinum	sev	com	—	—	U
Sardinella anchovia	com-abun	com-abun	sev-abun	—	U
Engraulidae	—	com-abun	—	—	L-U
Ariidae:					
Arius felis	—	few-abun	—	—	B
Batrachoididae:					
Opsanus pardus	few-sev	few	few-com	—	B
Antennariidae:					
Antennarius ocellatus	few	few	few-com	—	B
Ogcocephalidae:					
Ogcocephalus radiatus	few	few	few	—	B
Syngnathidae:					
Syngnathus sp.	—	few	—	—	O
Serranidae:					
Centropristis melana	few	sev	few-sev	sev	B
Centropristis ocyurus	com	com-abun	com	com	B
Centropristis philadelphica	—	—	few	—	B
Diplectrum formosum	sev-com	few-com	sev	sev	B
Epinephelus morio	few	few	few	—	B-L
Epinephelus sp.[2]	—	few	—	—	B
Mycteroperca microlepis	few	few-sev	few-sev	—	L
Serranus subligarius	sev	sev-com	sev-com	few	B-P
Grammistidae:					
Rypticus maculatus	—	few-com	few-com	—	B-P
Priacanthidae:					
Priacanthus arenatus	—	few	—	—	B
Apogonidae:					
Apogon pseudomaculatus	few	few-com	few-sev	—	B
Pomatomidae:					
Pomatomus saltatrix	few-sev	—	few	—	O-U
Rachycentridae:					
Rachycentron canadum	—	few-sev	—	—	O-U
Echeneidae:					
Echeneis neucratoides	—	few	—	—	([3])
Carangidae:					
Caranx bartholomaei	—	few-sev	few	—	L-U
Caranx crysos	—	sev-abun	few	—	U
Caranx hippos	—	com	sev	—	O-U
Caranx ruber	—	few-com	—	—	U
Decapterus punctatus	com-abun	abun	com-abun	com	L-U
Selar crumenophthalmus	—	sev-com	—	—	L-U
Seriola dumerili	few	few-sev	sev	—	L-O-U
Seriola zonata	few	—	—	—	U
Trachurus lathami	com	com	few-abun	—	L
Lutjanidae:					
Lutjanus campechanus	—	few-sev	sev	—	L
Lutjanus griseus	—	sev	few-sev	—	L-U
Lutjanus synagris	—	few	—	—	L
Rhomboplites aurorubens	sev	sev-com	few-sev	—	L-U
Lobotidae:					
Lobotes surinamensis	—	few	—	—	U
Pomadasyidae:					
Haemulon aurolineatum	com	com-abun	few-com	few	L
Haemulon plumieri	few-sev	few-sev	few	—	L
Orthopristis chrysoptera	com	abun	few-abun	—	L
Sparidae:					
Archosargus probatocephalus	few	sev	few	—	L-U
Calamus-Pagrus	—	few	few	—	L
Diplodus holbrooki	—	few-sev	few	—	U
Lagodon rhomboides	com	sev-com	sev-com	sev	L-U
Stenotomus caprinus	—	com	—	—	B-O

TABLE 2.—Continued.

Species	Abundance[1] Spring (Apr.)	Summer-fall (July-Nov.)	Winter Dec.	Winter Jan.	Habitat[1]
Sciaenidae:					
Equetus lanceolatus	few-sev	few-com	few-com	com	B
Equetus umbrosus	sev	sev-com	few-sev	—	B
Leiostomus xanthurus	—	com	sev	—	B
Sciaenops ocellata		few	few		B
Mullidae	—	few	—	—	O
Kyphosidae:					
Kyphosus sectatrix	—	few-sev	—	—	U
Ephippidae:					
Chaetodipterus faber	sev	few-com	sev	—	L-U
Chaetodontidae:					
Chaetodon ocellatus	—	few	few	—	B
Holacanthus bermudensis	sev-com	few-com	sev-com	sev	L-U
Pomacentridae:					
Pomacentrus variabilis	sev-com	sev-com	few-sev	—	B-P
Labridae:					
Halichoeres bivittatus	few	few-com	few	—	B
Halichoeres caudalis	sev	sev-com	few-sev	sev	B
Hemipteronotus novacula	—	few	few	—	B
Lachnolaimus maximus	—	few	—	—	L
Sphyraenidae:					
Sphyraena barracuda	—	few-sev	—	—	L-O-U
Sphyraena borealis	—	sev	—	—	U
Polynemidae:					
Polydactylus octonemus	—	—	sev	—	O
Blenniidae:					
Blennius marmoreus	few	few-sev	few	—	P
Hypleurochilus geminatus	sev-com	sev-com	—	—	P
Acanthuridae:					
Acanthurus chirurgus	—	few	—	—	B-P
Scombridae:					
Euthynnus alletteratus	sev-com	sev-com	few-com	—	O
Scomber japonicus	com	com	few	—	U
Scomberomorus cavalla	—	sev	—	—	O
Stromateidae:					
Peprilus burti	few-sev	sev	—	—	U
Scorpaenidae:					
Scorpaena brasiliensis	—	few	few	—	B
Triglidae:					
Prionotus sp.	—	few	—	—	B
Bothidae:					
Paralichthys albigutta	sev	few-sev	sev	few	B
Syacium papillosum	—	few	—	—	B
Balistidae:					
Balistes capriscus	few-sev	few-com	few-sev	few	L-U
Cantherhines pullus	—	few	few	—	P
Monacanthus hispidus	—	few	sev	—	L-P
Ostraciidae:					
Lactophrys quadricornis	few	few-sev	few	—	B
Diodontidae:					
Chilomycterus schoepfi	few	few-sev	few	few	B
86 taxa	41 species	81 taxa	57 taxa	13 species	
100%	48%	94%	66%	15%	
Number of observations	3	13	4	1	
Temperature range	17°-20°C	20°-30°C	15°-19°C	13°C	

[1]Abbreviations are as follows: sev - several, com - common, abun - abundant, B - on bottom, L - lower water column, P - on pilings, O - open water around platform, U - middle to upper water column under platform.
[2]*Epinephelus* sp. - A juvenile apparently either *E. flavolimbatus* or *E. niveatus* based upon color pattern (brownish with small white spots on lateral surface and a dark saddle on caudal peduncle, Smith 1971).
[3]*Echeneis neucratoides* on *Caranx* and *Sphyraena*.

A few species recorded at the stages are typical inshore fishes which are characteristic of coastal or estuarine areas. Examples are *Orthopristis chrysoptera, Lagodon rhomboides,* and *Leiostomus xanthurus.* These first two species were important members of the fauna at Stage II, while *L. xanthurus* was common at times but usually remained over the surrounding open sand bottom.

Most of the species recorded at the stages are species characteristic of rocky bottom areas offshore in the Gulf of Mexico. The platforms with their supporting pilings, as well as litter and shell hash which has accumulated in the area immediately surrounding the stages, serve as artificial reef habitat for such species. Some of the important reef species are *Gymnothorax nigromarginatus, Mystriophis intertinctus, Opsanus*

TABLE 3.—Counts of fishes at two stations below Stage II off Panama City, Fla., 1-4 August 1972. (Bold numerals are estimates.)

Family and species	Time of census (CST)									
	0129-0216	0525-0604	0715-0755	1042-1133	1152-1228	1325-1405	1519-1553	1721-1800	1833-1913	2308-2342
Station 1 (bottom)										
Ophichthidae:										
Mystriophis intertinctus	0	0	0	1	0	1	(1)	0	1	0
Clupeidae:										
Harengula pensacolae	0	0	**20**	**100**	**100**	**100**	(1)	**200**	0	0
Batrachoididae:										
Opsanus pardus	1	0	0	0	0	0	(1)	0	0	1
Antennariidae:										
Antennarius ocellatus	2	0	1	1	1	2	(1)	1	2	1
Ogcocephalidae:										
Ogcocephalus radiatus	0	1	0	0	0	0	(1)	0	0	0
Serranidae:										
Centropristis ocyurus	3	8	10	20	18	14	(1)	14	10	4
Epinephelus sp.[2]	0	0	0	0	0	0	(1)	1	0	0
Mycteroperca microlepis	0	0	1	0	0	1	(1)	0	1	0
Serranus subligarius	2	4	8	8	7	12	(1)	9	4	3
Grammistidae:										
Rypticus maculatus	4	5	4	8	1	3	(1)	5	10	6
Apogonidae:										
Apogon pseudomaculatus	2	0	2	3	0	0	(1)	1	7	3
Carangidae:										
Decapterus punctatus	0	0	0	0	0	5	(1)	0	0	0
Seriola dumerili	0	5	0	0	0	0	(1)	0	0	0
Lutjanidae:										
Rhomboplites aurorubens	0	0	2	0	0	0	(1)	4	0	0
Pomadasyidae:										
Haemulon aurolineatum	0	**30**	**200**	**200**	**300**	**300**	(1)	**200**	**100**	1
Haemulon plumieri	1	1	2	3	1	1	(1)	1	1	3
Orthopristis chrysoptera	2	**100**	**100**	**200**	**30**	**200**	(1)	**40**	11	0
Sparidae:										
Lagodon rhomboides	0	0	0	0	0	0	(1)	0	2	0
Sciaenidae:										
Equetus umbrosus	6	2	2	2	3	2	(1)	0	2	3
Kyphosidae:										
Kyphosus sectatrix	0	0	0	0	0	0	(1)	2	0	0
Ephippidae:										
Chaetodipterus faber	0	1	1	0	1	0	(1)	0	1	0
Chaetodontidae:										
Holacanthus bermudensis	0	1	4	5	2	3	(1)	1	1	0
Pomacentridae:										
Pomacentrus variabilis	0	1	10	11	13	14	(1)	12	2	0
Labridae:										
Halichoeres caudalis	0	0	6	12	22	6	(1)	9	1	0
Acanthuridae:										
Acanthurus chirurgus	0	0	1	0	0	0	(1)	0	0	0
Scorpaenidae:										
Scorpaena brasiliensis	0	0	0	1	0	1	(1)	0	1	0
Balistidae:										
Balistes capriscus	1	3	5	0	7	3	(1)	4	2	3
Monacanthus hispidus	0	0	1	1	0	0	(1)	0	0	0
Diodontidae:										
Chilomycterus schoepfi	2	1	2	0	0	1	(1)	0	0	1
Station 2 (subsurface)										
Clupeidae:										
Harengula pensacolae	0	**500**	**50**	(1)	**300**	**500**	**1,000**	**200**	0	(1)
Serranidae:										
Serranus subligarius	1	2	4	(1)	3	7	3	1	1	(1)
Grammistidae:										
Rypticus maculatus	3	0	0	(1)	0	0	0	2	2	(1)
Carangidae:										
Caranx crysos	0	**50**	**30**	(1)	**30**	7	**20**	**10**	0	(1)
Caranx ruber	0	0	1	(1)	0	0	0	0	0	(1)
Decapterus punctatus	0	5	10	(1)	**20**	2	0	0	0	(1)
Sparidae:										
Diplodus holbrooki	0	0	0	(1)	0	0	1	0	0	(1)
Lagodon rhomboides	0	6	11	(1)	12	18	12	14	0	(1)
Kyphosidae:										
Kyphosus sectatrix	5	6	1	(1)	5	2	10	0	2	(1)
Blenniidae:										
Hypleurochilus geminatus	4	2	3	(1)	2	3	2	3	2	(1)
Acanthuridae:										
Acanthurus chirurgus	0	0	0	(1)	0	0	1	0	0	(1)

[1]No census made.
[2]*Epinephelus* sp. - A juvenile apparently either *E. flavolimbatus* or *E. niveatus* based upon color pattern (brownish with small white spots on lateral surface and a dark saddle on caudal peduncle (Smith 1971).

pardus, Antennarius ocellatus, Centropristis ocyurus, Diplectrum formosum, Mycteroperca microlepis, Serranus subligarius, Rypticus maculatus, Apogon pseudomaculatus, Lutjanus campechanus, L. griseus, Rhomboplites aurorubens, Haemulon aurolineatum, H. plumieri, Diplodus holbrooki, Equetus lanceolatus, E. umbrosus, Chaetodipterus faber, Chaetodon ocellatus, C. sedentarius, Holacanthus bermudensis, Chromis enchrysurus, C. scotti, Pomacentrus variabilis, Halichoeres bivittatus, H. caudalis, Blennius marmoreus, Hypleurochilus geminatus, Ioglossus calliurus, Acanthurus chirurgus, and *Balistes capriscus*. A few natural rock outcrops which support reef faunas occur in the area, especially offshore from Stage I, but these are characteristically low in relief and are quite distinct in some ways from the habitats at the stages. They do support populations of the reef species listed above (and usually larger numbers than at the stages), but usually do not attract large masses of pelagic schooling and predatory species.

A few reef species observed at the stage habitats (such as *Abudefduf saxatilis, Pomacentrus partitus, Thalassoma bifasciatum,* and *Acanthurus coeruleus*) do not normally occur on the natural rocky reefs off the northwest Florida coast, but are tropical coral reef species which may be carried into the northern Gulf of Mexico by currents (see Hastings 1972). Such species are not permanent residents of the northern gulf, but are apparently usually killed by low winter temperatures, except for possibly during mild winters.

Comparison of the Two Stages

Although the fish faunas of the two stages were quite similar (Tables 1, 2), there were a few notable differences between the species lists for the two stages which may be significant. The most numerous species at Stage II during the summer and fall were the clupeids, *Harengula pensacolae* and *Sardinella anchovia*, and rather irregularly, *Etrumeus teres* and *Opisthonema oglinum*. These fishes formed dense schools (Figures 2, 3) below the platform during daylight hours, usually also with large numbers of carangids such as *Decapterus punctatus, Selar crumenophthalmus,* and *Trachurus lathami,* and the mackerel, *Scomber japonicus*. Such schools of baitfishes were considerably less abundant at Stage I except for during the fall and early winter (especially November and December) when large numbers of *Sardinella anchovia* and *D. punctatus* were present. Most of these had disappeared by January, however.

As might be expected, typical estuarine species, such as *Orthopristis chrysoptera, Lagodon rhomboides*, and *Leiostomus xanthurus*, were rare or absent at Stage I, even though they were quite numerous at Stage II. In contrast, *Elagatis bipinnulata*, a species typical of open, pelagic waters (Hiatt and Strasburg 1960), was recorded at Stage I, but not at Stage II, although Klima and Wickham (1971) found this species to be the most common jack congregating about artificial structures near Stage II in 1969. Other pelagic species such as *Seriola dumerili* and *Sphyraena barracuda* were also more numerous at Stage I. Similarly, some benthic species, which are characteristic of the deeper water, natural reefs in the northern Gulf of Mexico and may be rare in inshore waters as shallow as 18 m, were occasionally recorded at Stage I, but not at Stage II. Examples are *Chaetodon sedentarius, Chromis enchrysurus, C. scotti, Coryphopterus punctipectophorus,* and *Ioglossus calliurus*.

The tropical coral reef species, such as *Abudefduf saxatilis, Pomacentrus partitus, Thalassoma bifasciatum, Acanthurus coeruleus,* and *Canthigaster rostrata,* were recorded only at Stage I. These tend to be shallow-water species which apparently were able to survive by settling on the pilings and cross-members near the surface at Stage I. Such species are occasionally recorded in inshore artificial reef habitats in the northeastern gulf (Caldwell and Briggs 1957; Caldwell 1959, 1963; Haburay et al. 1969, 1974; Hastings 1972) and should be expected to occur occasionally at both stages.

Winter-Summer Contrast

Seasonal changes in the faunal composition at the stages were striking in some cases. Water temperatures recorded during this study ranged from 17° to 29°C at Stage I and from 13° to 30°C at Stage II. Lowest temperatures were recorded in January at Stage I and in February at Stage II. Highest temperatures were recorded during August and September. Changes in the fish fauna were apparently correlated with temperature, since the largest percentages of species recorded (93% at Stage I; 95% at Stage II) were present during the summer and fall, while the lowest numbers were recorded during either the winter

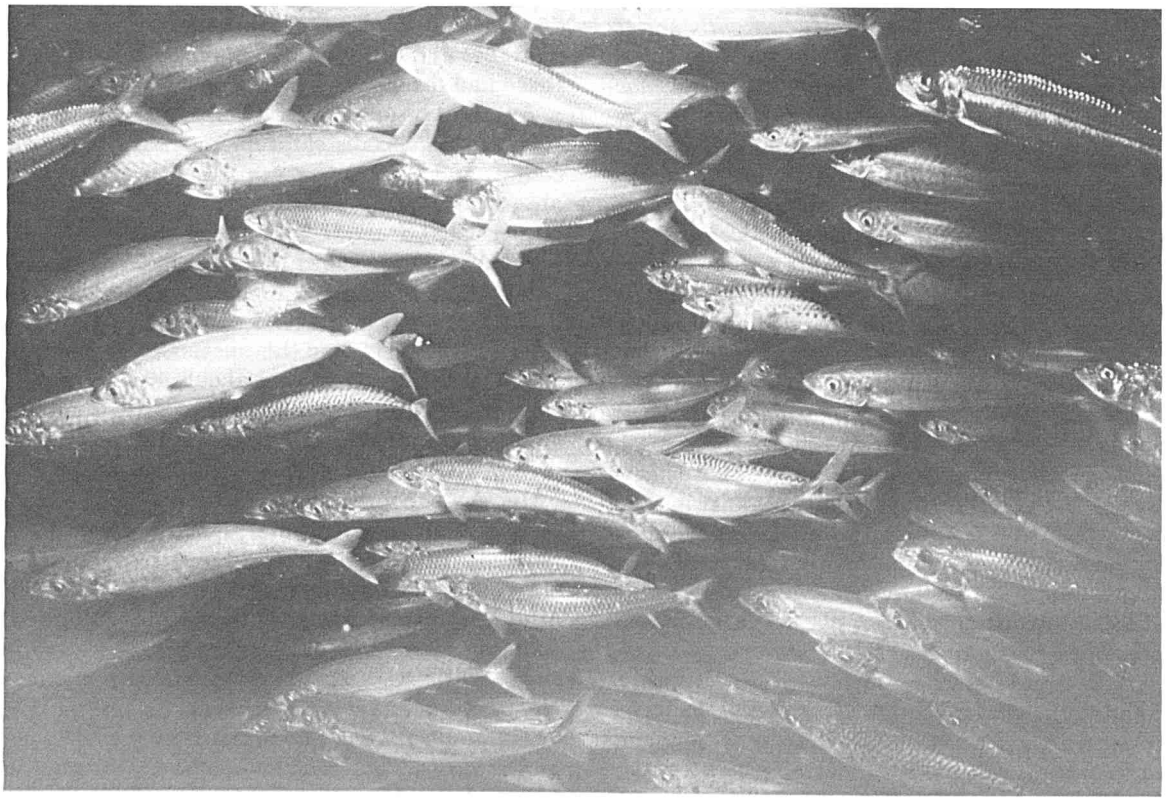

FIGURE 2.—*Sardinella anchovia*, *Decapterus punctatus*, and *Scomber japonicus*, in a mixed school, under Stage II off Panama City, Fla.

or spring. Estimates of abundance during the spring, summer-fall, and winter observations (Tables 1, 2) indicate that most species disappear from the area of the stages during the winter months, then gradually reappear during the spring and summer. They apparently either move offshore to deeper water, or else they migrate southward along the Florida coast (see Hastings 1972). This decrease in number of species (as well as number of individuals) occurred at both stages, but was most profound at Stage II, where temperature extremes were greater. About 50% of the number of species recorded at Stage I were present in December and January, but at Stage II, 67% were present in December and only 15% in February. These seasonal changes were most striking in the schooling clupeids and carangids (such as *H. pensacolae*, *Sardinella anchovia*, and *D. punctatus*) which were extremely numerous during the summer and fall, but usually rare or absent in January or February (although *Decapterus* was common at Stage II during February).

Habitat Occupation and Activity Patterns

The usual habitat occupied by each species in the vicinity of the platforms is indicated in Tables 1 and 2. Station counts for some species at Stage II, indicating diel changes in activity and occurrence at the stage, are shown in Table 3.

The pelagic species which congregate about the stages normally occupied the upper water column, either surrounding or below the platform. The clupeids, *H. pensacolae* and *S. anchovia*, formed dense schools below the platform, usually near the surface but with *Sardinella* usually somewhat deeper. The carangids, *D. punctatus* and *Trachurus lathami*, were also quite numerous, *Decapturus* normally in mid-water or near the surface and *Trachurus* very near the bottom. At times, these and other schooling species of comparable size, such as *Opisthonema oglinum* and *Scomber japonicus*, formed mixed schools under the platform (Figure 2). These species

FIGURE 3.—Large school of *Harengula pensacolae* surrounding a piling of Stage II off Panama City, Fla.

gathered in compact schools below the stage during the day apparently as a defense against predation (Hobson 1965). Station counts at Stage II for *H. pensacolae* and *D. punctatus* indicate that they left the protection of the platform and moved into the open areas surrounding the stage at night. Several species of clupeids and schooling carangids, including *H. pensacolae, Sardinella anchovia, D. punctatus,* and *Selar crumenophthalmus,* have been described as nocturnal plankton feeders (Hobson 1965; Starck and Davis 1966), although some diurnal feeding activity by *Decapterus* and *Sardinella* was observed by us and others (Klima and Wickham 1971). During daylight hours at Stage II, from about 0500 to about 1800 CST, extensive schools of *H. pensacolae* were present around and under the platform, and, at times, were so dense that they darkened the area below (Figure 3). Relatively large numbers were present at the census stations during most daylight dives, but none was observed during any of the night censuses. Similar records were obtained for *D. punctatus*, although the numbers present were considerably less than for *H. pensacolae*. In addition, *D. punctatus* may have left the vicinity of the platform earlier in the evening (about 1500 CST).

The other pelagic species are, in most cases, large predators and are continually on the move in the upper water column surrounding the platforms, occasionally darting into the schools of smaller fishes to feed. Some, such as *Seriola dumerili*, were often seen near the bottom as well. Most of these pelagic predators probably feed to some extent at night as well as during the day, and may follow the bait species, as the bait species disperse at night. However, studies indicate that many such piscivorous fishes are primarily crepuscular, with peaks of feeding activity at dawn and dusk (Hobson 1965, 1968, 1972, 1974; Starck and Davis 1966).

Only *Caranx crysos* was consistently present in the station counts (but only in Station 2 near the surface). These counts show a pattern similar to that of *H. pensacolae*, with fairly large numbers present during daylight hours and none present

at night. Possibly this jack followed the *Harengula* as they dispersed, to continue feeding through the night.

A large number of benthic reef species occupy the bottom below the platform and also the area immediately surrounding the stage, where much litter has accumulated, apparently discarded by workmen on the platform above. Other benthic species were observed on the pilings and cross-members of the platform structure, where encrusting invertebrates and algae provided food and hiding places for smaller species. In addition, habitat for benthic species may be provided by accumulations of shell hash at the bases of the pilings, probably broken loose from the pilings by storms or by the grazing of fishes or predation by other organisms. Some of the more important benthic species at the stages are *Gymnothorax nigromarginatus, Opsanus pardus, Antennarius ocellatus, Ogcocephalus radiatus, Centropristis ocyurus, Diplectrum formosum, Serranus subligarius, Rypticus maculatus, Apogon pseudomaculatus, Equetus lanceolatus, E. umbrosus, Chaetodon ocellatus, Pomacentrus variabilis, Halichoeres caudalis, Blennius marmoreus*, and *Hypleurochilus geminatus*. A few of these, such as *S. subligarius, R. maculatus*, and *P. variabilis,* seemed to be equally at home on the pilings at all levels of the water column, while others were found only near the bottom (*G. nigromarginatus, Opsanus pardus, Antennarius ocellatus, Ogcocephalus radiatus, Centropristis ocyurus, D. formosum, Apogon pseudomaculatus, E. lanceolatus, E. umbrosus,* and *Halichoeres caudalis*) or only on the pilings (*Hypleurochilus geminatus*).

An interesting contrast was noticed among members of the families Pomacentridae and Labridae at Stage I. Those species which are characteristic and permanent members of the northern gulf reef fauna (*Chromis enchrysurus, C. scotti, P. variabilis,* and *Halichoeres caudalis*) were most numerous on the bottom in association with platform supports and other objects. In contrast, species which are not permanent residents of reefs in this area, but are apparently tropical species carried north by currents (*Abudefduf saxatilis, P. partitus*, and *Thalassoma bifasciatum*) were never observed near the bottom, but were always associated with the pilings and cross-members within about 10 m of the surface. These are shallow-water species which apparently do not occur at the greater depths at Stage I (32 m).

At least two species, *G. nigromarginatus* and *Mystriophis intertinctus*, were usually seen partially buried in the substrate, often with only their heads protruding.

Several other species occurring on the bottom were most numerous over the open sandy areas surrounding the stages. *Stenotomus caprinus, Leiostomus xanthurus, Paralichthys albigutta,* and *Lactophrys quadricornis* are examples.

This benthic group includes both diurnal and nocturnal species. Species which are active and apparently feed at night are *R. maculatus, Apogon pseudomaculatus,* and *E. umbrosus*. Benthic species which are diurnal and inactive at night are *Centropristis ocyurus, D. formosum, Serranus subligarius, Chaetodon ocellatus, Pomacentrus variabilis*, and *H. caudalis*. The other species were not observed enough to determine activity patterns.

Generally counts of the nocturnal species were higher during the nocturnal observations. *Rypticus maculatus* was more numerous in Station 1 on the bottom under cross-members or other sheltering objects, but was counted in Station 2 near the surface three times, during each of the nocturnal counts between about 1730 and 0215 CST. Hiding places on the pilings are rather limited and can, in most cases, accommodate only small individuals, so apparently these soapfish were moving up the pilings at night to feed. Other references also report noctural feeding in the grammistids (Hobson 1965; Starck and Davis 1966).

Apogon pseudomaculatus, when observed at night, was active, swimming about in open areas near the bottom, while those observed during the day were always inactive, hiding among shells or other debris or under the stage cross-members. On one occasion a group of about 15 juvenile *Apogon* was seen associated with a diadematid sea urchin below a cross-member at Stage I. These small cardinal fish remained motionless among the long spines of the urchin. Cardinal fishes in general are nocturnal predators (Hobson 1965; Starck and Davis 1966; Livingston 1971).

Species of *Equetus* (or the related *Pareques*) have been reported to remain in small groups in sheltered areas by day, and then feed individually in the immediate vicinity at night (Hobson 1965; Starck and Davis 1966). Similar observations

were made during this study for *E. umbrosus*, which was present during almost every observation at Station 1.

The smaller demersal sea basses (family Serranidae) observed at the stages were relatively inactive fishes which did not exhibit obvious day-night changes in behavior. However, counts of *Centropristis ocyurus* and *S. subligarius* decreased at night, possibly indicating that some had taken shelter under objects or within shells or crevices. Literature records indicate that these and related sea basses are diurnal (Starck and Davis 1966; Bortone 1971).

Chaetodon ocellatus was usually seen swimming about near the bottom during the day and frequently in pairs. One individual observed at night resting on the bottom next to a piling exhibited the typical nocturnal color pattern described by Starck and Davis (1966).

Counts of *Pomacentrus variabilis* and *H. caudalis* at Station 1 were considerably higher during the daylight observations than at night. Daylight counts for *P. variabilis* (10-14) were less variable than those for *H. caudalis* (6-22). *Pomacentrus variabilis* is territorial and probably remains at the same general location throughout the day while *H. caudalis* is less sedentary and tends to move about more. Starck and Davis (1966) stated that *P. variabilis* and other pomacentrids are diurnal feeders which seek shelter at night in sponges, rocks, coral, or other close cover. Most of those at the stage may have taken shelter in and among the many empty mollusk shells which cover much of the bottom at the base of the stage. *Halichoeres caudalis* has not been studied previously, but several species of labrids, including *H. bivittatus* which was also present at times at Stage II, have been reported to bury themselves in sand at night (Breder 1951; Hobson 1965; Starck and Davis 1966), and this may also be the case with *H. caudalis*.

The numerous species of free-swimming fishes occupying the various levels of the water column under the platform apparently include several distinct groups based upon activity patterns and feeding habits. *Mycteroperca microlepis* is a large predator which appeared to be continually moving about under or around the stage, usually near the bottom, but a few inactive individuals were observed at night on the bottom resting against the pilings. Such species are normally described as being opportunistic feeders with peaks of feeding activity during twilight periods when the changeover of activity patterns in prey species makes them more vulnerable (Starck and Davis 1966; Collette and Talbot 1972; Hobson 1972).

Lutjanus griseus (Starck 1971), *Haemulon aurolineatum*, and *Orthopristis chrysoptera* are apparently nocturnal feeders, which utilize the stage only as a shelter during daylight hours, and move out into surrounding areas at night to feed. *Lutjanus griseus* was normally seen schooling during the day in the lower-to-middle water column under the platform. *Haemulon aurolineatum* and *O. chrysoptera* were two of the most numerous fishes in Station 1 at Stage II (Figure 4), although both were rare or absent during the nighttime observations. There may be a difference in the time of major movement for these two species. *Haemulon aurolineatum* apparently began to disperse and move out of the area at or shortly after sunset, and returned shortly after sunrise. *Orthopristis chrysoptera* possibly leaves the area under the stage earlier in the evening (just before sunset) and also may return earlier in the morning. Apparently these grunts feed at night in the open areas surrounding the stage and school under the stage as a defense against diurnal predators (Hobson 1965; Starck and Davis 1966).

Other species (such as *H. plumieri, Diplodus holbrooki, Lagodon rhomboides, Kyphosus sectatrix, Chaetodipterus faber, Holacanthus bermudensis, Acanthurus chirurgus, Balistes capriscus,* and *Monacanthus hispidus*) seemed to feed mostly on benthic organisms attached to the pilings or other objects, and may move up and down in the water column, grazing upon this material. However, some of these were more numerous near the surface (such as *D. holbrooki, L. rhomboides,* and *K. sectatrix*) while others normally remained near the bottom (such as *Haemulon plumieri, C. faber, Holacanthus bermudensis*, and *B. capriscus*). Most of these species are apparently diurnal and become inactive at night. A few *L. rhomboides, H. bermudensis,* and *B. capriscus* were observed near the bottom at night, either resting on the bottom or in protected places below cross-members or between pilings and adjacent objects. *Kyphosus sectatrix* was inactive at night, but remained in the upper water column. In contrast, *Haemulon plumieri* is nocturnal but seemed to remain in the same general area near the bottom throughout the day and night. Such

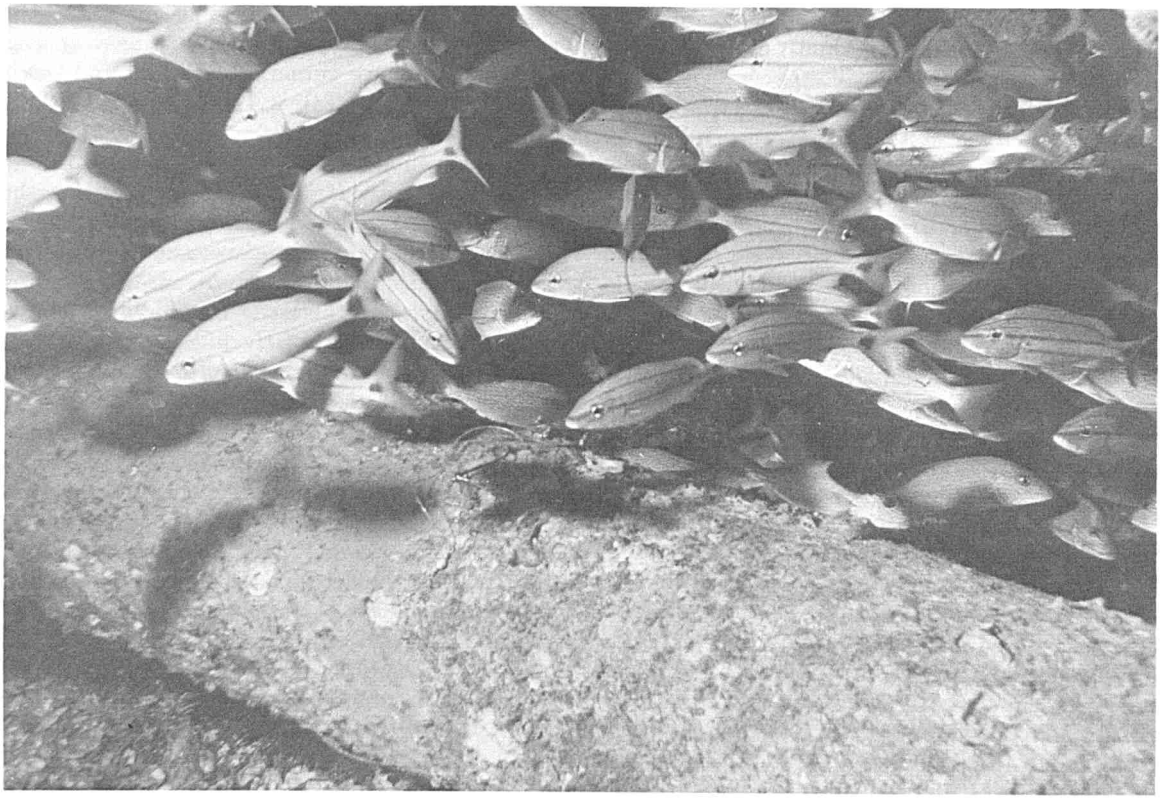

FIGURE 4.—*Haemulon aurolineatum* and *Orthopristis chrysoptera* near the bottom at Stage II off Panama City, Fla.

behavior was also noted by Starck and Davis (1966).

Starck and Davis (1966) emphasized the importance of nocturnal foraging migrations and plankton feeding to the coral reef trophic structure. Similar feeding patterns may contribute to the economy of artificial reef structures such as these offshore platforms, where abundant species of the families Clupeidae, Carangidae, Lutjanidae, and Pomadasyidae feed at night in adjacent areas, but return to the reef by day, and thus contribute to the biomass of the community.

In conclusion, the platform pilings and crossmembers, with their encrusting organisms and associated motile invertebrate fauna, provide food and shelter for numerous fish species. In addition, several diurnally schooling species are abundant beneath the platforms during the day, where they are afforded some protection from predation, but disperse into surrounding open areas at night to feed. Large numbers of piscivorous species also are attracted to the platform habitat to feed on the numerous smaller fishes associated with the structure. As the water temperature drops, many species migrate away from the platforms during the colder months. Repopulation occurs in the spring and summer.

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LITERATURE CITED

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc. Spec. Publ. 6, 149 p.

BORTONE, S. A.
1971. Studies on the biology of the sand perch, *Diplectrum formosum* (Perciformes: Serranidae). Fla. Dep. Nat. Resour., Div. Mar. Sci., Tech. Ser. 65:1-27.

BREDER, C. M., JR.
1951. Nocturnal and feeding behavior of the labrid fish *Xyrichthys psittacus*. Copeia 1951:162-163.

BULLIS, H. R., JR., AND J. R. THOMPSON.
1965. Collections by the exploratory fishing vessels *Oregon, Silver Bay, Combat,* and *Pelican* made during 1956 to 1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510, 130 p.

CALDWELL, D. K.
1959. Observations on tropical marine fishes from the northeastern Gulf of Mexico. Q. J. Fla. Acad. Sci. 22:69-74.
1963. Tropical marine fishes in the Gulf of Mexico. Q. J. Fla. Acad. Sci. 26:188-191.

CALDWELL, D. K., AND J. C. BRIGGS.
1957. Range extensions of western North Atlantic fishes with notes on some soles of the genus *Gymnachirus*. Bull. Fla. State Mus., Biol. Ser. 2:1-11.

CARLISLE, J., JR., C. TURNER, AND E. EBERT.
1964. Artificial habitat in the marine environment. Calif. Dep. Fish Game, Fish Bull. 124, 93 p.

COLLETTE, B. B., AND F. H. TALBOT.
1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *In* Results of the Tektite program: Ecology of coral reef fishes, p. 98-124. Nat. Hist. Mus., Los Ang. Cty., Sci. Bull. 14.

CULPEPPER, T. J., AND W. E. PEQUEGNAT.
1969. A taxonomic and ecological study of selected benthonic gammarid crustaceans from the northeastern Gulf of Mexico. Tex. A&M Univ., Dep. Oceanogr. Proj. 286-6, Ref. 69-3T,102 p.

GOODING, R. M., AND J. J. MAGNUSON.
1967. Ecological significance of a drifting object to pelagic fishes. Pac. Sci. 21:486-497.

HABURAY, K., C. F. CROOKE, AND R. HASTINGS.
1969. Tropical marine fishes from Pensacola, Florida. Q. J. Fla. Acad. Sci. 31:213-219.

HABURAY, K., R. W. HASTINGS, D. DEVRIES, AND J. MASSEY.
1974. Tropical marine fishes from Pensacola, Florida. Fla. Sci. 37:105-109.

HASTINGS, R. W.
1972. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Ph.D. Thesis, Florida State Univ., Tallahassee, 555 p.

HIATT, R. W., AND D. W. STRASBURG.
1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65-127.

HOBSON, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HUNTER, J. R., AND C. T. MITCHELL.
1967. Association of fishes with flotsam in the offshore waters of Central America. U.S. Fish Wildl. Serv., Fish. Bull. 66:13-29.
1968. Field experiments on the attraction of pelagic fish to floating objects. J. Cons. 31:427-434.

KLIMA, E. F., AND D. A. WICKHAM.
1971. Attraction of coastal pelagic fishes with artificial structures. Trans. Am. Fish. Soc. 100:86-99.

LIVINGSTON, R. J.
1971. Circadian rhythms in the respiration of eight species of cardinal fishes (Pisces: Apogonidae): Comparative analysis and adaptive significance. Mar. Biol. (Berl.) 9:253-266.

PEQUEGNAT, W. E., R. S. GAILLE, AND L. H. PEQUEGNAT.
1967. Biofouling studies off Panama City, Florida. II. The two mile offshore station. Tex. A&M Univ., Dep. Oceanogr. Proj. 286-6, Ref. 67-18T, 47 p.

PEQUEGNAT, W. E., AND L. H. PEQUEGNAT.
1968. Ecological aspects of marine fouling in the northeastern Gulf of Mexico. Tex. A&M Univ., Dep. Oceanogr. Proj. 286-6, Ref. 68-22T, 88 p.

SMITH, C. L.
1971. A revision of the American groupers: *Epinephelus* and allied genera. Bull. Am. Mus. Nat. Hist. 146:67-241.

SONNIER, F., J. TEERLING, AND H. D. HOESE.
1976. Observations on the offshore reef and platform fish fauna of Louisiana. Copeia 1976:105-111.

SPRINGER, V. G., AND K. D. WOODBURN.
1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 1, 104 p.

STARCK, W. A. II.
1971. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. Stud. Trop. Oceanogr., Inst. Mar. Sci., Univ. Miami 10:11-150.

STARCK, W. A. II, AND W. B. DAVIS.
1966. Night habits of fishes of Alligator Reef, Florida. Ichthyologica 38(4):313-356.

STRUHSAKER, P.
1969. Demersal fish resources: Composition, distribution, and commercial potential of the Continental Shelf stocks off Southeastern United States. U.S. Fish Wildl. Serv., Fish. Ind. Res. 4:261-300.

TREYBIG, D. L.
1971. How offshore platforms help fishing. Ocean Ind. 6(4):64-65.

UNGER, I.
1966. Artificial reefs. Am. Littoral Soc., Spec. Publ. 4, 74 p.

VICK, N. G.
1964. The marine ichthyofauna of St. Andrew Bay, Florida, and nearshore habitats of the northeastern Gulf of Mexico. Tex. A&M Univ., Dep. Oceanogr. Meteorol. Proj. 286-D, Ref. 64-19T, 77 p.

WICKHAM, D. A., J. W. WATSON, JR., AND L. H. OGREN.
1973. The efficacy of midwater artificial structures for attracting pelagic sport fish. Trans. Am. Fish. Soc. 102:563-572.

EFFECTS OF INCREASED WATER TEMPERATURE ON *DAPHNIA PULEX*

DONOVAN R. CRADDOCK[1]

ABSTRACT

Techniques were developed to study the effects of increased water temperature on certain zooplankters; specific studies were conducted on *Daphnia pulex*, an abundant and important zooplankter of the lower Columbia River. Study methods simulated prolonged exposure to constant high temperatures in thermal discharges and short exposures to increased temperatures in condensers of cooling systems. Effects were evaluated on the basis of survival and reproduction for periods ranging from 34 to 90 days. The time to death of 50% of the *D. pulex*, both mature and young, was less than 24 h at temperatures above 27°C. Temperatures of 27°C and below required an exposure of at least 192 h to cause 50% mortality. The young females were more tolerant of temperature increases than older females. The greatest reproduction by older females was at the control temperature (15°C), whereas reproduction by the young females was low at lower temperatures. No reproduction occurred above 27°C.

Two groups of *D. pulex* (one from the Seattle, Wash., area and the other from the Columbia River) studied at increased temperatures for prolonged periods revealed similar patterns of survival and reproduction, but the Columbia River group appeared less tolerant of increased temperatures. A short exposure (15 min) to increased temperatures up to 30°C had little effect on survival and reproduction.

It was concluded that temperatures should not exceed 26° or 27°C for prolonged periods or 30°C for more than 15 min to protect *D. pulex* populations in the river.

The lower reaches of the Columbia River (below Portland, Oreg.) support extensive and valuable commercial and sport fisheries as well as other types of recreational activities. This section of the river is also becoming increasingly industrialized. Associated with the industrialization is 1) the extensive use of river water for cooling purposes and 2) the discharge of heated cooling water back into the river. This increasing use of the river for industrial cooling has created concern that the aquatic biota is endangered by thermal pollution. North and Adams (1969) have described thermal conditions at outfalls and in condenser cooling systems of some California plants. They pointed out that increases of +10°F (5.6°C) above normal are considered significant biologically at all seasons of the year. Coutant (1970) presented a diagram of the hypothetical time-course of acute thermal shock to any organism entrained in condenser cooling water systems that indicates they could be exposed to the maximum increase (10.8°C) for at least 9 min in diffuser systems and to substantial increases from 12 to 20 min in the discharge canal system. He also noted the average temperature rise reported is about 10.8°C but may be as great as 16°C.

I studied the effect of increased water temperatures on one of the abundant cladocerans of the area, *Daphnia pulex*. It has been found to be important in the diet of valuable stocks of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in certain seasons of the year (Craddock et al.[2]). Cladocerans may be thermally affected by a thermal nuclear power plant where, along with other zooplankton, they may be entrained with intake cooling water and pass through the condenser cooling system encountering sudden and sizable temperature increases. Increased cooling water use by industrial and power plants may increase the temperature of certain areas of the river (bays and eddies) for extended periods and also affect zooplankton.

The specific objectives of the study were: 1) to develop techniques for laboratory study of thermal effects on zooplankton and 2) to assess the

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[2]Craddock, D. R., T. A. Blahm, and W. D. Parente, 1974. Occurrence and utilization of zooplankton by juvenile chinook salmon in the lower Columbia River. Unpubl. manuscr. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

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effect of both prolonged and short exposure to increased temperatures on survival and reproduction of *D. pulex*.

METHODS AND MATERIALS

Two stocks of *D. pulex* were cultured at two acclimation temperatures and subjected to three types of tests to determine their thermal tolerance. One stock was obtained from the Columbia River and the other from a small pond north of Seattle, Wash. They were cultured separately and will be referred to as the Columbia group and the Seattle group. Stock cultures were maintained in 5-liter battery jars of Lake Washington water filtered through No. 25 Swiss silk bolting cloth to remove zooplankton and phytoplankton, but not bacteria. Taub and Dollar (1968) felt that bacteria were important to the nutrition of *Daphnia*, especially in relation to reproduction. Stock cultures were reared and acclimated at either 15° or 20°C in a controlled temperature incubator. Continuous fluorescent lighting (45-50 foot candles, cool white) provided similar lighting in the incubator and in the laboratory and was consistent for all animals, test and control. Algae, *Chlorella* and *Chlamydomonas*, were cultured using medium No. 63 developed by Taub and Dollar (1968) and fed to *D. pulex*. Water in the test vessels was changed weekly, and the animals were fed three times a week.

The test temperatures were maintained by using primary and secondary water baths and immersion heaters activated by temperature controllers (Figure 1). The primary bath was a Plexiglas[3] tank 150 × 30 × 23 cm supplied with flowing water at 10° to 15°C. The secondary baths consisted of six or seven 5-liter battery jars, 23 × 14 × 17 cm, placed in the primary bath. The temperature in each of these secondary baths was raised progressively from the water inlet end to the outlet end of the primary tank. Temperatures in the secondary baths could be maintained from 10° to 36°C ± 0.5°. Air continually bubbling into each secondary bath eliminated stratification. Experimental subjects were held in 50-ml jars of filtered lake water suspended in the secondary baths and equilibrated to the test temperature in those baths.

Parthenogenetically produced animals of the same age, either young females (less than 24 h old) or mature females (approximately 1 wk old), were selected from the stock cultures and held in 10-ml vials for a day before the start of the experiment to check for handling mortality. At the start of an experiment, the bulk of the water in the vials was canted off, and the appropriate number of test animals was poured directly into the 50-ml test chamber at the test temperature. The control groups were treated identically with the others, except that they were held at acclimation temperatures. A large bore pipette was used when individual animals were handled.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

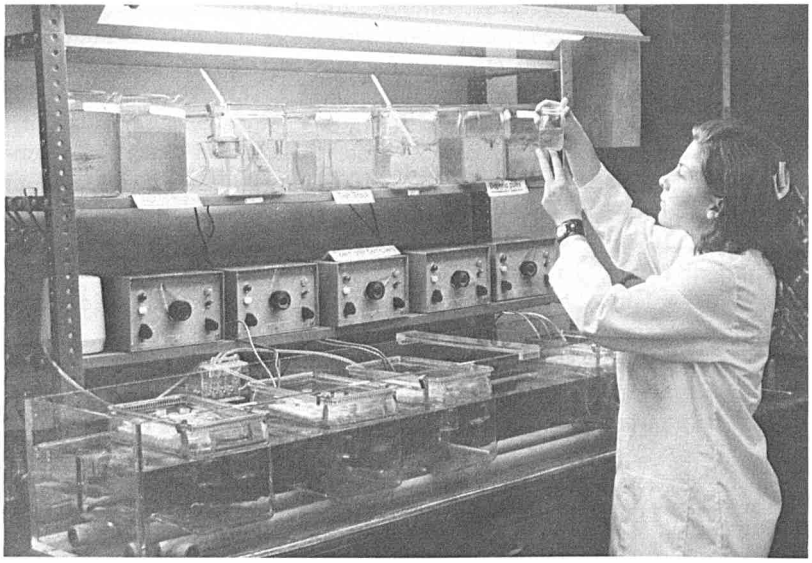

FIGURE 1.—Experimental equipment used to study temperature effects on zooplankton showing primary and secondary water baths, test vessels, and temperature controllers.

Three experiments were conducted to simulate thermal conditions that *D. pulex* might encounter. Two experiments studied the effect of increased temperatures that might be encountered in the area of a heated plant outfall, whereas the third simulated the thermal conditions small organisms could encounter in the condenser cooling system of a thermal power plant.

The first experiment compared the effect of prolonged exposure (50-52 days) to constant temperatures of 15° (control), 18°, 21°, 24°, 27°, 30°, and 33°C. Test organisms were both mature females and young females (at the start of the tests) of the Seattle group acclimated at 15°C. There were 18 mature females per test temperature, 6 per test jar, and 10 young females were tested per test temperature and test jar. Ten *Daphnia* per 50-ml jar were well below the number that would cause harmful metabolic waste buildup or oxygen depletion (Pratt 1943); 10 animals has long been accepted as a standard for bioassays, Doudoroff (1951), American Public Health Association (1971), and Sprague (1973).

The second experiment compared the effect of prolonged exposure (34 days) to temperatures of 20° (control), 23°, 26°, 29°, and 32°C on mature females of the two groups (Seattle and Columbia) acclimated at 20°C. There were 10 animals per test temperature and test jar.

The third experiment subjected mature females of the Seattle group acclimated to 15°C to a short exposure (15 min) to temperatures of 15° (control), 19°, 21°, 24°, 27°, 30°, 33°, and 36°C. Test organisms were then returned to acclimation temperature where they were held and observed for 90 days. Twelve animals were tested at each temperature.

Test animals were examined frequently to determine the effect of increased temperatures, usually hourly during the first 8 h of a test. The next day or two, they were examined two or three times a day and subsequently once each week day. During each observation, the mortalities were noted and removed, and newly born *Daphnia* were counted and removed. The animals were assumed to be dead when they lay on the bottom and there was no detectable movement of the antennae, thoracic legs, or the post abdomen.

Temperature effects were evaluated on the basis of survival and reproduction by animals tested at the various temperatures. In this study, my evaluation criterion was the time at a particular temperature until 50% mortality; therefore, I use the term TD_{50} (time to death of 50% of the test animals at a particular temperature).

RESULTS

Experiments Relating to Discharges of Heated Water

Seattle *Daphnia* Acclimated to Water of 15°C

Death occurred rapidly for both mature and young *D. pulex* at 33°C. Some animals in both groups lost equilibrium within the first hour, TD_{50} occurred before the third hour, and none survived the fourth hour of exposure (Table 1). Mature and young *D. pulex* subjected to temperatures above 27°C reached TD_{50} in less than 24 h. Temperatures of 27°C and below required an exposure of at least 192 h (8 days) to cause 50% mortality. The younger females did not succumb to moderately high temperatures (18°, 21°, and 24°C) as quickly as the older females. Temperatures of 21°, 24°, and 27°C caused TD_{50} among the older females after an average of 238 h, whereas the younger females did not reach TD_{50} until an average of 768 h.

TABLE 1.—Mortality of *Daphnia pulex* introduced as mature and young females and maintained at temperatures of 15° to 33°C (Seattle race, acclimated at 15°C).

Test temp (°C)	Mature females: Hours to 50% mortality[1]	Mature females: % mortality at end of test (50 days)	Young females: Hours to 50% mortality[1]	Young females: % mortality at end of test (52 days)
15	1,008 (42)	67	1,224 (51)	50
18	888 (37)	78	[2]1,248 (51)	40
21	259 (9)	89	1,152 (48)	60
24	192 (8)	100	648 (27)	100
27	264 (11)	100	504 (21)	100
30	19	100	21	100
33	3	100	3	100

[1]Days in parentheses.
[2]50% mortality not reached.

All animals died before producing young at 30° and 33°C; rate of reproduction was highest at 24° and 27°C before all subjects died. Total offspring produced and rate of reproduction varied for the two age-groups of females tested at 21°C or below (Table 2).

First reproduction by the mature females occurred 5 days earlier at test temperatures of 27°, 24°, and 21°C than at the control temperature (15°C). Only one peak of production occurred at 27°C before 100% mortality was reached. Reproduction at 15°C was stable with peaks occurring

TABLE 2.—Reproduction of *Daphnia pulex* introduced as mature and young females and maintained at temperatures of 15° to 33°C (acclimated at 15°C, Seattle race).

Test temp (°C)	Mature females: Total young produced[1]	Mature females: Average no. young/adult per day[2]	Young females: Total young produced[3]	Young females: Average no. young/adult per day[2]
15	1,162	2.20	33	0.09
18	652	1.05	40	0.08
21	244	1.11	286	0.74
24	466	2.61	366	2.67
27	318	3.02	629	3.25
30	0	0.00	0	0.00
33	0	0.00	0	0.00

[1]Total reproduction from 18 animals during 50 days of experiments.
[2]Average reproduction based on number of days survivors remained.
[3]Total reproduction from 10 animals for 52 days of experiments.

regularly at 6-day intervals, whereas at higher temperatures reproduction was erratic. The greatest numbers of offspring were produced by the older females at 15°C and generally decreased with increasing temperatures. The highest rates were at 27° and 24°C where the survivors reproduced rapidly before they all succumbed on the 13th and 27th day, respectively. High temperatures increased the rate of reproduction for a short period before total mortality, but the increased rate was short lived and did not match total production by animals at a more normal temperature (15°C).

Reproduction by females who were young at the start of the experiment increased with increasing temperature, contrary to the trend shown by the older females (Table 2). No reproduction occurred at 15°C until the 34th day; at 18° and 21°C, initial reproduction took place on the 3rd to 6th day but did not resume until the 44th and 22nd day, respectively. At 24° and 27°C, the first reproduction occurred on the 3rd to 6th day, stopped for 3 or 4 days, and then continued at a high rate until the death of all females on the 34th and 27th day, respectively. The low reproduction by the younger females at 15° and 18°C is not explained.

Seattle and Columbia *Daphnia* Acclimated to Water of 20°C

Both Seattle and Columbia *Daphnia* reached TD_{50} within 24 h at 32°C (Table 3); 90% mortality occurred in less than 24 h in the Columbia group and within 48 h in the Seattle group. At 29°C, both groups reached 50% mortality in 120 h. There were significant differences in the length of time to 50% mortality for each of the two groups at 20°, 23°, 26°, and 29°C (Seattle—χ^2 = 37.9, $P<0.01$, 3 df; Columbia—χ^2 = 18.8, $P<0.01$, 3 df). The Columbia group seemed to succumb more rapidly than the Seattle group, but the more rapid demise of the Columbia *Daphnia* at 20°C (the acclimation temperature) casts doubt upon these results. However, a test of homogeneity for temperatures of 23°, 26°, and 29°C indicated significant differences between the two groups in days to 50% mortality (χ^2 = 22.6, $P<0.01$, 2 df).

TABLE 3.—Mortality of *Daphnia pulex* (Seattle and Columbia races) acclimated at 20°C and introduced as maturing females to temperatures of 20° to 32°C.

Test temp (°C)	Seattle race: Hours to 50% mortality[1]	Seattle race: % mortality at end of test (34 days)	Columbia race: Hours to 50% mortality[1]	Columbia race: % mortality at end of test (34 days)
20	[2]>816 (34)	40	216 (9)	70
23	648 (27)	80	456 (19)	100
26	120 (5)	100	48 (2)	100
29	120 (5)	100	120 (5)	100
32	<24 (1)	100	<24 (1)	100

[1]Days in parentheses.
[2]50% mortality not reached.

Comparatively little reproduction took place at temperatures of 26°C and above (Table 4). The greatest reproduction for the Seattle group was at 23°C and for the Columbia group at 20°C. The Columbia animals remaining after the initial unexplained mortality at 20°C outproduced the Seattle animals at the same temperature. The Seattle animals produced 62% of the total young produced by the two groups.

TABLE 4.—Reproduction of *Daphnia pulex* (Seattle and Columbia races) acclimated at 20°C and introduced as maturing females to temperatures of 20° to 32°C.

Test temp (°C)	Seattle race: Total young produced[1]	Seattle race: Average no. young/adult per day[2]	Columbia race: Total young produced[1]	Columbia race: Average no. young/adult per day[2]
20	246	1.12	299	1.82
23	424	1.68	152	1.02
26	0	0.00	3	0.67
29	90	2.14	16	0.32
32	0	0.00	0	0.00
Total	760		470	

[1]Total reproduction by 10 animals for 34 days of experiments.
[2]Average reproduction based on the number of days survivors remained.

Experiments Relating to Water Passing Through Cooling Systems

Exposure for 15 min at temperatures of 30°C or less seemed to have little or no effect upon the survival of *D. pulex* (Table 5). The only mortalities observed during the exposure period were at 36°C: within 5 min, over 50% of the animals at this temperature were dead; all but one died in 15

TABLE 5.—Mortality and reproduction of *Daphnia pulex* (Seattle race) exposed as maturing females for 15 min to various temperatures and returned to acclimation temperature of 15°C.

	Survival		Reproduction	
Shock temp (°C)	Hours to 50% mortality[1]	% mortality after 90 days	Total young produced[2]	Average no. young/adult per day of test[3]
15	1,178 (49)	92	2,051	3.64
19	1,320 (55)	83	1,340	2.30
21	1,008 (42)	92	1,365	3.57
24	1,512 (63)	75	2,640	3.50
27	1,464 (61)	67	1,716	2.26
30	1,536 (64)	92	1,832	2.48
33	792 (33)	100	363	0.78
36	0.083	92	[4]480	5.33

[1]Days in parentheses.
[2]Total reproduction for 90 days of test.
[3]Average daily reproduction per surviving adult.
[4]Produced by the one survivor of the 15-min exposure during the succeeding 90 days.

min. One hour after exposure, one animal had died at 33°C, but TD_{50} took 792 h (33 days) at 33°C and 1,008-1,536 h (42-64 days) after exposure to temperatures below 33°C. Time in days to reach TD_{50} was not statistically significant (χ^2 = 6.89, 5 df) for temperature treatments of 15° to 30°C. A temperature in excess of 30°C for the 15-min exposure was necessary to significantly increase mortality.

The rate of reproduction was not significantly changed by an exposure of 15 min to increased temperatures through 30°C (χ^2 = 0.79, 5 df). The greatest total reproduction was by those *D. pulex* tested at 24°C (Table 5) where survival was also good. Reproduction at 27° and 30°C exceeded the reproduction at 19°C, so it appears that reproduction is not materially affected by a short exposure to temperatures through 30°C that do not seriously affect survival. Reproduction by animals tested at 33° and 36°C was drastically reduced because most of the test animals died.

DISCUSSION

In zooplankton sampling of the Prescott-Kalama section of the Columbia River in 1968-69, *D. pulex* was more abundant during periods of higher water temperature (Craddock et al. see footnote 2). Numbers of *D. pulex* were low during the portion of the year when the temperature remained below 15°C (late fall, winter, and spring), but as water reached and exceeded this temperature the population increased rapidly until the peak abundance was reached at the maximum water temperature (approximately 21°C). The mean daily water temperature in August (the month of highest temperature) ranged from 19.3° to 22.8°C in 1968 and from 19.7° to 21.1°C in 1969 (Snyder and McConnell 1971). Tauson (1931) found temperatures of 16°-22°C favorable for parthenogenetic reproduction by *D. pulex,* but above or below this range production was reduced considerably. The upper limit was 30°C. Ivleva (1969) reviewed literature on the thermal range of *Daphnia* and noted that several researchers reported the optimum temperature range for development of *D. pulex* as 18°-20°C. Ivleva made the general observation that the optimal range varies with age and the young are more resistant to high temperature than the old, as was indicated by my experiments. Other researchers reviewed by Ivleva found that mass mortalities could occur in the range of 28°-32°C. Some of these researchers indicated that when *Daphnia* species are acclimated to higher or lower temperatures over a long period they become more resistant to further increases or reductions in temperature.

My experiments to determine the effect of increased temperature on *D. pulex* that were 1 wk old and 1 day old (i.e., at the start of the experiment) indicated that the younger animals adapted better to increased temperatures. Temperatures of 21°C and above seriously reduced the length of survival of the older females (21°C = TD_{50} in 259 h), whereas temperatures of 24° to 27°C or more were required to have the same effect on the younger females (24°C = TD_{50} in 648 h; 27°C = TD_{50} in 504 h). Temperatures above 27°C caused TD_{50} in a short time (less than 21 h) for both age-groups.

Although the younger females survived better at the control and lower test temperatures (15°, 18°, and 21°C), their eventual production of young was considerably less than that of the mature animals. This difference was not due solely to the 1-wk difference in age, and I do not have an adequate explanation.

My experiment comparing survival and reproduction of the Seattle and Columbia races indicated that the Columbia *Daphnia* may be less resistant to increased temperatures. The results of the tests of Seattle *D. pulex* acclimated at 15° and 20°C are not directly comparable and, although there is some indication that the higher temperature acclimation increases resistance in the mid-range (23°-24°C), the effect was not apparent in the high range (26°-27°C) and no conclusion could be made.

My experiments indicate that an increase of 6°C in the area of an outfall could cause TD_{50} in about 168 h (7 days) among important segments of the reproducing population. To minimize damage to *Daphnia* populations in the Columbia River, the temperature should not be raised more than 6°C above ambient or higher than 26° or 27°C for any prolonged period.

A short exposure (15 min) to increased temperatures as might occur in a condenser cooling system did not cause a significant reduction in time to TD_{50} or in reproduction unless the temperature exceeded 30°C. There is a period from mid-July through September when the lower Columbia River temperatures may exceed 20°C. In these instances, the temperature increase in condenser cooling systems should be less than 10°C if the *Daphnia* are to survive. It must be kept in mind that temperature is only one of several factors including pressure, abrasion, and toxic chemicals that could be acting synergistically to damage zooplankton in a condenser cooling system (Marcy 1973; Becker and Thatcher[4]).

To protect *D. pulex* populations, water temperatures in condenser cooling systems should not exceed 30°C and passage through the system should take less than 15 min.

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[4]Becker, C. D., and T. O. Thatcher. 1973. Toxicity of power plant chemicals to aquatic life. Battelle Mem. Inst., Pac. Northwest Lab., Richland, Wash., rep. for U.S. At. Energy Comm., WASH-1249, UC-11, misc. pagination.

LITERATURE CITED

AMERICAN PUBLIC HEALTH ASSOCIATION.
1971. Standard methods for the examination of water and wastewater. 13th ed. Am. Publ. Health Assoc., Wash., D.C., 874 p.

COUTANT, C. C.
1970. Entrainment in cooling waters: steps toward predictability. Proc. 50th Annu. Conf. West. Assoc. State Game Fish Comm., p. 90-105.

DOUDOROFF, P., B. G. ANDERSON, G. E. BURDICK, P. S. GALTSOFF, W. B. HART, R. PATRICK, E. R. STRONG, E. W. SURBER, AND W. M. VAN HORN.
1951. Bio-assay methods for the evaluation of acute toxicity of industrial wastes to fish. Sewage Ind. Wastes 23:1380-1397.

IVLEVA, I. V.
1969. Mass cultivation of invertebrates. Biology and methods. Izd. "Nauka", Moscow. (Translated by Israel Prog. Sci. Transl., 1973, 148 p.; available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA, as TT 65-50098.)

MARCY, B. C., JR.
1973. Vulnerability and survival of young Connecticut River fish entrained at a nuclear power plant. J. Fish. Res. Board Can. 30:1195-1203.

NORTH, W. J., AND J. R. ADAMS.
1969. The status of thermal discharges on the Pacific Coast. Chesapeake Sci. 10:139-144.

PRATT, D. M.
1943. Analysis of population development in Daphnia at different temperatures. Biol. Bull. (Woods Hole) 85:116-140.

SNYDER, G. R., AND R. J. MCCONNELL.
1971. Subsurface water temperatures of the Columbia River at Prescott, Oregon (River mile 72), 1968-69. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Data Rep. 53, 9 p. on 1 microfiche.

SPRAGUE, J. B.
1973. The ABC's of Pollutant Bioassay using fish. Am. Soc. Test. Mater., Spec. Tech. Publ. 528:6-30.

TAUB, F. B., AND A. M. DOLLAR
1968. The nutritional inadequacy of *Chlorella* and *Chlamydomonas* as food for *Daphnia pulex*. Limnol. Oceanogr. 13:607-617.

TAUSON, A.
1931. Die Wirking der äusseren Bedingungen auf die Veränderung des Geschlechts und auf die Entwicklung von Daphnia pulex De Geer. Wilhelm Roux Arch. Entwicklungsmech. Org. 123:80-131.

LIFE HISTORY, ECOLOGY, AND BEHAVIOR OF *LIPARIS INQUILINUS* (PISCES: CYCLOPTERIDAE) ASSOCIATED WITH THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*[1]

K. W. ABLE[2] AND J. A. MUSICK[3]

ABSTRACT

In the Mid-Atlantic Bight, spawning of *Liparis inquilinus* peaked near shore, away from sea scallop beds, in March and April. In the laboratory, females appeared to initiate spawning activity and each female probably spawned more than once. The eggs are adhesive and demersal and have been found attached to hydroids in nature. The larvae were most abundant in plankton collections inshore in May and averaged 5 mm total length at that time. Larger larvae were found in deeper water, and by 12-13 mm total length they had undergone metamorphosis and descended to the bottom where they became associated with the sea scallop, *Placopecten magellanicus*. They maintained this association from August through December. The population comprises a single year class which leaves the scallops and migrates inshore to spawn as the fish are entering their second year.

Laboratory and field observations indicated that fish were more abundant in the scallops and more scallops contained fish during the day. At night, fish left the scallops to feed on small crustaceans. *Liparis inquilinus* observed in aquaria used the fin rays of the lower lobe of the pectoral fin to detect food. These fin rays have taste buds on the surface of each ray.

Liparis inquilinus is probably protected from predation while inside sea scallops since there are few predators on the scallops of the size usually occupied. Predation while outside the scallop may be minimized by feeding only at night and then returning as soon as the fish becomes satiated. Sea scallops seem to suffer no ill effects from the association and they do not compete for food with *L. inquilinus* since *P. magellanicus* is a microplanktonic filter feeder and the former feeds on small crustaceans.

Little is known of the life history of most species of *Liparis*. Most of the meager information available for North Atlantic *Liparis* is included in Bigelow and Schroeder (1953), Andriyashev (1954), Leim and Scott (1966), and Wheeler (1969). Unfortunately, taxonomic problems remain and some published life history information may be incorrect because of misidentification. Recently, Detwyler (1963) studied the life history and reproductive biology of *L. atlanticus* from New Hampshire and Maine, and Able (in press) commented on the life history of a new species of *Liparis* from the Gulf of Maine. Elsewhere, Nizortsev et al. (1963) noted the stomach contents of *L. koefoedi*, *L. liparis*, and *L. laptevi* in the Barents Sea; Johnson (1969, 1970) reported on food habits and age and growth of *L. pulchellus* off California; Kosaka (1971) described the food habits and seasonal distribution of *L. tanakae* from Japan; Gibson (1972) mentioned the vertical distribution and feeding of *L. montagui*; and Quast (1968) described the food habits of *L. mucosus* off California.

The association between *Liparis* (= *L. inquilinus*, see Able 1973) and the sea scallop, *Placopecten magellanicus*, has been reported by several authors (Bean 1884; Goode 1884; Garman 1892; Goode and Bean 1895; Jordan and Evermann 1898; Welsh 1915; Burke 1930; Bigelow and Schroeder 1953; Leim and Scott 1966) but information is lacking on most aspects of the assocation. The purpose of this paper is to report on the life history, ecology, and behavior of *L. inquilinus*.

MATERIALS AND METHODS

The life history stages, although often overlapping, are defined as follows: larvae—planktonic individuals usually 3-13 mm total length (TL), which have not transformed to adult coloration; juveniles—sexually immature benthic individuals with adult coloration, often associated with the sea scallop, approximately 14-45 mm TL; and adults—sexually mature individuals greater than 33 mm TL. The latter can be distinguished by the presence of prickles on the body of males

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and by the enlarged abdomen of females. Scallop anatomical terminology follows Bourne (1964).

Larval *Liparis* were examined from monthly collections of the National Marine Fisheries Service (NMFS) laboratory at Sandy Hook in the Mid-Atlantic Bight during 1966-67 (Clarke et al. 1969) and from routine plankton sampling on the Woods Hole NMFS RV *Albatross IV* cruises 69-5 and 72-3 off southern New England, in the Gulf of Maine, and on Georges Bank. The larvae of *L. inquilinus* can be distinguished from those of other *Liparis* which occur in the Mid-Atlantic Bight and the Gulf of Maine by differences in pigmentation pattern in combination with size at hatching, disc formation, and notochord flexion (Able 1974). The eggs were identified on the basis of their similarity, in size of the egg and melanophore pattern of the embryo, to eggs deposited by the laboratory population of *L. inquilinus*.

Juvenile *L. inquilinus* were collected from sea scallops which were taken in otter trawls during cruises of the *Sea Breeze* while on charter to the Virginia Institute of Marine Science, and *Albatross IV* cruises 69-11 and 70-6. Other *L. inquilinus* were collected from sea scallops on *Albatross IV* cruises 68-14 and 69-8 with a 3-m scallop dredge with a 5.1-cm ring bag which was towed for 10 min at each station. On *Albatross IV* cruise 68-14, bottom substrate type and amount were estimated from the scallop dredge catch. Size and number of scallops and regular hydrographic data were also recorded. On *Albatross IV* cruise 69-8, scallop dredge tows were replicated every 2 h during a 24-h period on 4-5 August 1969. The same general area was maintained during sampling by using information from depth recorders and loran navigation. The scallop catch at each station was divided into 5-cm height classes and a representative number of scallops were examined for *L. inquilinus* from each size class.

A large series of adult *L. inquilinus* collected off the New Jersey coast in the 1930's was examined from uncatalogued material of the Academy of Natural Sciences of Philadelphia. Other small collections were obtained from a variety of sources that are too numerous to mention here.

Liparis inquilinus and sea scallops were collected between lat. 39°30′ and 40°10′N near Hudson Canyon in depths of 36-95 m and maintained in 10 to 25 gallon aerated aquaria with sand substrates for 15 mo. The aquaria were held in a cold room at 10°-11°C. Winter temperatures in aquaria dropped as low as 4°C because of the absence of heating facilities. Salinity varied from 23 to 42‰. Illumination was provided by a 60-W bulb in one corner of the room. This provided approximately 86 to 280-lx illumination for the aquaria, depending on their location in the room. The light cycle was controlled automatically and approximated that in nature. Occasional power failures caused irregular variation in photoperiod and temperature.

Liparis inquilinus were fed live amphipods, usually *Orchestia platenis* and *Gammarus mucronatus*, and the mysid shrimp *Neomysis americana* and various other small crustaceans. Sea scallops were fed a mixture of algae, *Monochrysis lutheri*, *Isochrysis galbana*, and *Phaeodactylum triconutum*, that was added to the unfiltered aquarium water.

Pectoral fins of *L. inquilinus* were sectioned and stained with Harris' hematoxylin and eosin Y following fixation in 10% Formalin.[4]

LIFE HISTORY OF *LIPARIS INQUILINUS*

In the Mid-Atlantic Bight, spawning of *L. inquilinus* occurs near shore and away from scallop beds in the winter. In the early 1930's, over 700 adult, sexually mature and maturing *L. inquilinus* were collected from mid-December through April (Figure 1) off the coast of New Jersey and Delaware. This species was found from the Brigantine Can Buoy north of Atlantic City, N.J., to near the mouth of Delaware Bay and inside the bay at Old Bare Shoal and in deep holes off Brandywine (Shoal?) and Lewes, Del. Most of the collections were in 7-14 m; however, part of this series was from depths as shallow as 3-4 m "off New England Creek (near Cape May Co.)." Unfortunately, we have been unable to locate this area in New Jersey. Recently (January-March 1971 and January-February 1973) other mature adults were found off New Jersey, especially off Little Egg Inlet in depths from 4 to 7 m. Sea scallops were never taken in the vicinity of these collections (D. Thomas pers. commun.).

The average total length of *L. inquilinus* increases from December through April (Figure 1). Detwyler (1963) attributed an increase in total

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

length of *L. atlanticus* during the winter to the replacement of smaller adults by larger adults as the spawning season progressed. This may occur for *L. inquilinus*, but it seems more likely that sexually immature fish moving inshore in November, December, and January may continue to grow as they become sexually mature. In the laboratory, fish continued to feed during spawning periods. Although the range in total length for collections for each month is large, the variation about and between the means is small (Figure 1). This probably indicates that a single year class is present in each sample.

Spawning in *L. inquilinus* probably peaks in March and April. A single collection of *L. inquilinus* eggs was made on 9 March 1973, approximately 3.5 nautical miles off Holgate, Long Beach Island, N.J. Also, the adult fish represented in Figure 1 were examined for sexual maturity. The percentage of sexually mature fish increased from 12% in January, to 44% in February, and to 67% in March, but decreased to 33% in April, although this last sample was small. Hatching times for other *Liparis* vary from 22-30 days for *L. atlanticus* (Detwyler 1963) to 6-8 wk for *L. liparis* (Breder and Rosen 1966). Therefore, the occurrence of *L. inquilinus* larvae averaging 5 mm in May (Figure 1) infers that spawning probably takes place in March and April, and this is in agreement with the time of occurrence of sexually mature adults in inshore waters.

In the laboratory, reproductive activity and egg laying occurred over many months. During 1969, females distended with eggs and performing prespawning behavior (see below) were present from January through August. Eggs with eyed larvae were first found in late April and egg masses were found through June. Successful hatching occurred only in May. The extensive period of egg deposition and reproductive behavior observed in the laboratory does not agree with the limited reproductive period inferred from field collections. These differences may be attributable to the occasional power failures which affected photoperiod, water temperature, and water quality in the laboratory aquaria or simply to laboratory confinement.

It is likely that the average size of sexually mature males and females is similar and that the sex ratio is 1:1. A single collection of 143 *L. inquilinus* (off New England Creek, 7 m, 22 February 1933) contained 75 mature and maturing males (mean 55.3 mm TL, range 37.1-69.6 mm TL) and 68 females (mean 54.3 mm TL, range 44.3-65.7 mm TL). Neither the ratio of males to females nor the average total length was significantly different.

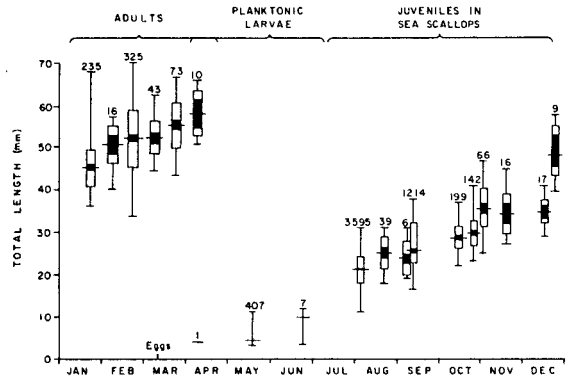

FIGURE 1.—Length-frequency distribution of *Liparis inquilinus* collected from the Mid-Atlantic Bight. For each sample, the range is represented by the vertical line, mean by the horizontal line, one standard deviation on each side of the mean by hollow rectangles and two standard errors on each side of the mean by solid rectangles. Numbers above figure are sample sizes. A single collection of *L. inquilinus* eggs is noted on the horizontal axis.

Female *L. inquilinus* may spawn more than once. In the laboratory, the abdomen of individual fish was observed to decrease in size as more egg masses were found in aquaria and increase again later. Also the egg diameters in ovaries of females from 16 March 1932 and 1933 usually had two well-defined modes. Fourteen ovaries were examined and most eggs were either 1.00-1.30 or 0.01-0.50 mm in diameter. The largest eggs were clear and contained several oil globules and these were more abundant in the center of the ovary. When egg diameter modes in the ovary were not well-defined, egg distribution by size was often random. Counts for the larger eggs ranged from 105 to 1,135 (mean 447) in seven ovaries from females raised in the laboratory and from 231 to 563 (mean 342) for females collected off New Jersey. The high count for females raised in the laboratory may have been due to the failure of the female to spawn and continued development and accumulation of the eggs in the ovary because of disturbances in the laboratory. There seemed to be no correlation between fish size and egg numbers. The average number of eggs is less than the 475 to 700 eggs reported for *L. atlanticus* (Detwyler 1963), a larger species.

Spawning Behavior

Female *L. inquilinus* may initiate spawning activity. In laboratory aquaria females with distended abdomens were the most active. They often swam in quick dashes around the sides of the aquarium then up to the surface and down again. During these dashes, the snout came out of the water and there was considerable splashing. Similar behavior has been reported for *L. atlanticus* females (Detwyler 1963). This activity often lasted several minutes and on one occasion 7 min and 20 s. Occasionally during these excited dashes the females would bump into other fish, both males and females. In a few instances, this activity seemed to excite other females and they also became active. In one instance, a ripe female repeatedly nudged with her snout a fish of unknown sex that was attached to the side of the aquarium. Soon a prominent bulge appeared just posterior to the genital papilla of the female. This has been observed just before spawning in *L. atlanticus* (Detwyler 1963) and *Cyclopterus lumpus* (Cowan 1929). In this instance, the nudged fish did not respond and the female swam away. The bulge receded after about 5 min. Sexually mature males are covered with numerous prickles while the females usually lack these or have only a few. Thus, the female may be able to recognize males by making contact with them. Breeding tubercles and contact organs in fishes may function in maintenance of body contact between the sexes during spawning and stimulation during breeding (Wiley and Collette 1970). The prickles on *L. inquilinus* males may function in these ways also. Spawning was not observed but is probably similar to that in *L. atlanticus* (Detwyler 1963). In the laboratory, *L. inquilinus* deposited small clumps of 20-80 eggs on the bottom of the aquaria and did not guard them. The eggs collected on 9 March 1973 off New Jersey were attached to hydroids as has been reported for *L. liparis* (Ehrenbaum 1905). The larvae that hatched in the laboratory did not survive beyond yolk sac absorption.

Larvae

In the Mid-Atlantic Bight, larvae of *L. inquilinus* are planktonic during the spring. During monthly larval fish surveys in 1966-67 by the Sandy Hook Laboratory, 98% of the *L. inquilinus* larvae were collected in May (Figure 1) from deep and shallow tows. These averaged 5.1 mm TL (range 3.2-12.0 mm TL). Larvae were most abundant in samples collected nearest to shore (Figure 2). Other larvae of the same average size have been collected during May from inshore waters in the Gulf of Maine and on Georges Bank (Table 1, Fig. 3). Larvae larger than 13 mm TL were usually not found in the plankton.

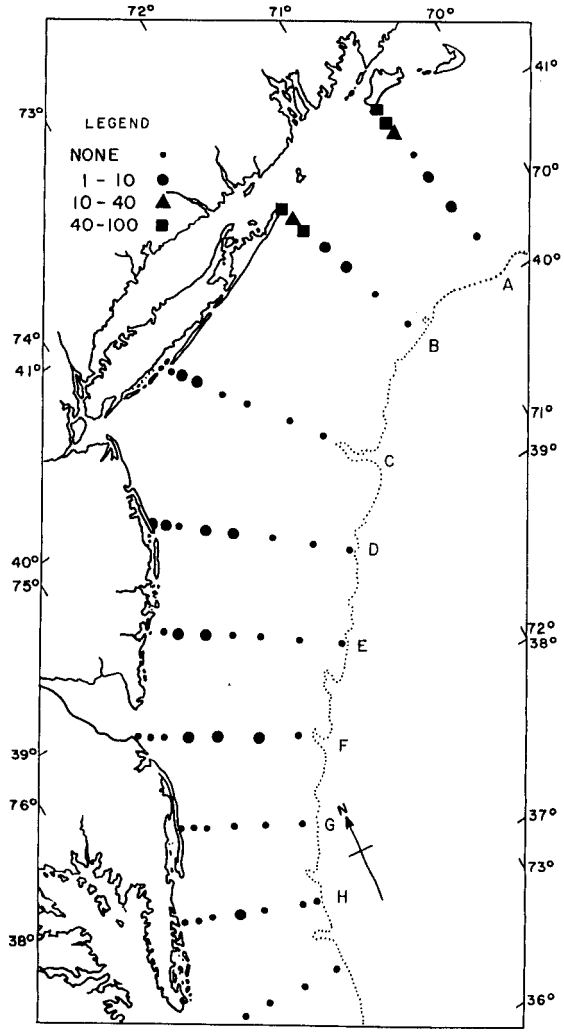

FIGURE 2.—Distribution and abundance of larval *Liparis inquilinus* from *Dolphin* cruise D-66-5 during May 1966.

Juveniles

In the Mid-Atlantic Bight, juvenile *L. inquilinus* are associated with sea scallops from August through December. Stevenson[5] reported

[5]Stevenson, J. A. Fish. Res. Board Can., St. Andrews, New Brunswick, Manuscr. Rep. 373.

TABLE 1.—Collections of larval *Liparis inquilinus* from plankton sampling cruises. Mean followed by range in parentheses.

Item	*Dolphin* 66-3	*Dolphin* 66-5	*Dolphin* 66-7	*Albatross IV* 69-5	*Albatross IV* 72-3
Locality	Mid-Atlantic Bight	Mid-Atlantic Bight	Mid-Atlantic Bight	Georges Bank	Southern New England Gulf of Maine Georges Bank
Date	8 April 1966	12-20 May 1966	18-27 June 1966	22-26 May 1969	6-16 May 1972
Water depth (m)	—	—	—	73.0(65-88)	65.8(36-96)
Number collected	1	414	7	28	73
Number measured	1	269	7	26	32
Total length (mm)	3.8	5.0(4.0-11.0)	9.4(3.4-11.5)	5.8(3.5-15.7)	4.6(3.7-10.0)

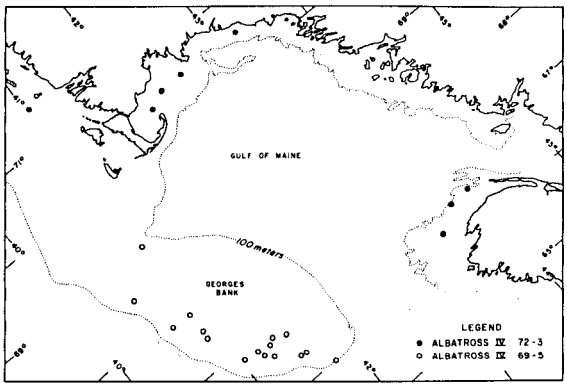

FIGURE 3.—Locations of collections of larval *Liparis inquilinus* from *Albatross IV* cruises 69-5 and 72-3.

Neoliparis (Liparis) atlanticus from sea scallops as early as July in the Bay of Fundy off Digby, Nova Scotia. Specimens we have from sea scallops in that area are all *L. inquilinus*. Juvenile *L. inquilinus* have also been collected from scallops from Georges Bank in July and may be present in sea scallops during July in the Mid-Atlantic Bight as well. The fish found in the scallops during August (Figure 1) corresponded in size with that expected from the earlier collection of planktonic larvae (Figure 1) and represented the same year class. The average total length of fish from scallops increased steadily from August through November (Figure 1). The small variation in each collection indicated that there was a single year class inhabiting sea scallops during a single year. *Liparis inquilinus* have been collected from sea scallops as late as mid-December (17 Dec. 1967, lat. 38°20′N, long. 73°59′W, 66 m and lat. 38°18′N, long. 74°23′W, 42 m) (Figure 1). The absence of fish in the scallops collected in January (18 Jan. 1968, lat. 38°34.5′N, long. 73°36′W, 62 m; 26 Jan. 1968, lat. 38°05′N, long. 74°13′W, 66 m) corresponds with the appearance of *L. inquilinus* inshore off Delaware and New Jersey during the same periods. These mature and maturing fish represent the same year class as the juveniles that were associated with sea scallops. Therefore, *L. inquilinus* reproduces when 1 yr old in the Mid-Atlantic Bight.

Adults may not survive to spawn the following year. Specimens larger than 50 mm have never been taken from May through December. The life history of *L. inquilinus* in the Mid-Atlantic Bight is summarized in Figure 4.

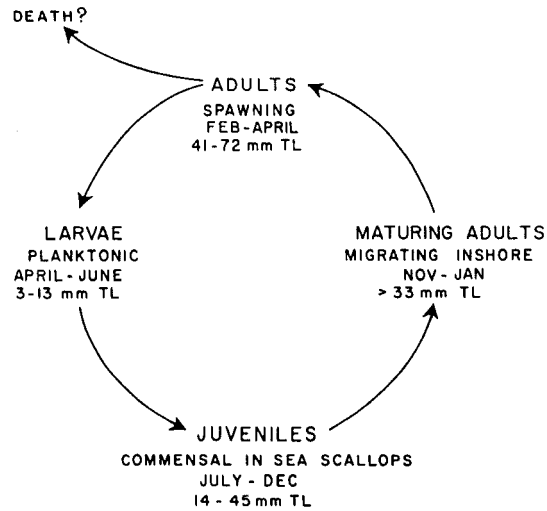

FIGURE 4.—Schematic presentation of the life history of *Liparis inquilinus* in the Mid-Atlantic Bight.

ECOLOGY AND BEHAVIOR OF *LIPARIS INQUILINUS* ASSOCIATED WITH SCALLOP

Resting

In aquaria, *L. inquilinus* preferred an inverted resting position with the disc attached to any smooth substrate such as the side of the aquarium, the interior of mollusk shells, rocks, or glass containers. Once attached, the fish flexed its

tail so that the caudal fin was alongside the head. From 13 November to 20 December 1968, observations were made on the position of fish attached to four hinged sea scallop shells or "clappers." These were positioned on the bottom of an aquarium, with one of each of these pairs placed with the right valve (flat valve) up and the left valve down. One value rested on the bottom and the other was at an angle of approximately 30°-40°. Of 40 observations, 95% of the fish in shells were attached upside-down to the top valve of the clapper with as many as eight attached to the same valve. The inverted resting position was also the most commonly observed during the remainder of the time fish were maintained in the laboratory.

Feeding

Liparis inquilinus has several morphological and behavioral adaptations which may allow it to feed at night. In aquaria, fish swimming over the bottom appeared to depend on reception of tactile and/or gustatory stimuli received by the head and pectoral fins. Swimming resulted from the combined action of the tail and the upper lobe of the pectoral fins. The eight or nine filaments in the lower lobe of the pectoral fins were extended vertically toward and often touched the bottom. When amphipods were placed in aquaria, fish did not appear to respond to visual cues but feeding usually occurred when the head or the lower lobe of the pectoral fin touched an amphipod. If food touched the head, it was immediately ingested. If food touched the pectoral fin, the fish quickly backed up or arched its body to the side and sucked in the prey. The rays in the lower lobe of the pectoral fin of *L. inquilinus* contain dark staining buds along the surface of each ray (Figure 5A) which are most abundant at the tips (Figure 5B). They are identified as taste buds on the basis of their similarity to the figures presented by Bardach and Case (1965). They described the sensitivity of the pelvic fins in *Urophycis chuss* and the pectoral fins in *Prionotus carolinus* and *P. evolans* to gustatory stimuli. Freihofer (1963) suggested that the particular pattern of the ramus lateralis accessorius nerve to the pectoral and pelvic fins in the Liparidae allows the development of these fins as "sensory, locomotor and support appendages." The well-developed cephalic lateralis system of *L. inquilinus* may also function in detecting moving prey. Occasionally fish sucked in amphipods which passed within less than 1 inch of the head.

Liparis inquilinus feeds on benthic prey. Stomachs of fish collected in nature contain almost exclusively small crustaceans and small numbers of sand grains. In the laboratory, sand from the bottom was frequently sucked in with food items and then discharged from the gill opening. A round mouth, as in *L. inquilinus*, is well-adapted to sucking in prey (Alexander 1967).

Behavior of Fish Associated with Sea Scallops

The association between *L. inquilinus* and sea scallops is well-developed and both partners show definite behavioral adaptations. Fish collected from sea scallops were isolated from them for several weeks. Upon reintroduction of fish into aquaria containing acclimated sea scallops, many of the fish swam around and over the scallops but concentrated most of their activity along the scallops' mantles. Most fish alternated between swimming parallel to the mantle with the lower lobe of the pectoral fin extended toward it or swimming with the head oriented directly toward the mantle. The tentacles on the mantle often contracted but the valves did not close. On one occasion a fish "mouthed" a tentacle, an action similar to the acclimitization behavior of some pomacentrid fishes associated with anemones (Mariscal 1966). On two occasions, fish attached to the mantle, and in one of these instances the tentacles of the scallop mantle moved over the body of the fish and depressed the anterior portion of the dorsal fin. There was no reaction by either partner and eventually the fish attempted unsuccessfully to enter the scallop.

The tentacles of the sea scallop are tactile and chemical receptors (Bourne 1964) and may be able to discriminate between *L. inquilinus* and other fishes. In aquaria, sea scallops exposed to individuals of *Gobiosoma bosci* and *Gobiesox strumosus* reacted negatively, when the mantle of the scallop was brushed by either species, by closing the valves. Similar results were observed when *Fundulus heteroclitus* and *Tautogolabrus adspersus*, were exposed to sea scallops (Musick 1969).

Liparis inquilinus occasionally may enter an alternate host species. Hoff (1968) reported a specimen of *L. atlanticus* from the bay scallop, *Aequipecten irradians*, in Buzzards Bay, Mass.

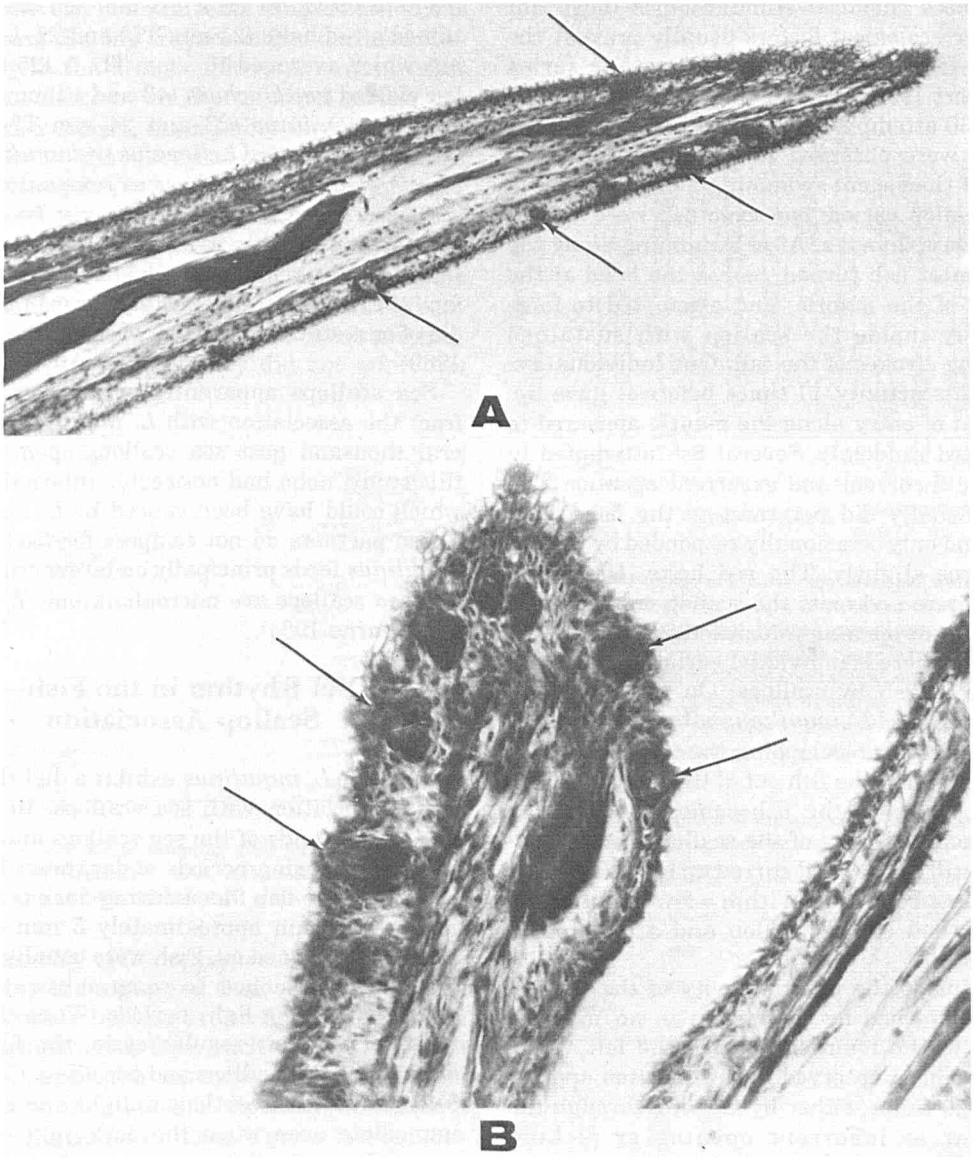

FIGURE 5.—Section through a fin ray from the lower lobe of the pectoral fin of *Liparis inquilinus* stained with hematoxylineosin. Arrows indicate taste buds. A. Taste buds on margin of fleshy portion of fin ray. B. Numerous taste buds at the tips of the fin rays.

We identified a specimen provided by him as *L. inquilinus*. Since that initial occurrence he has collected several other *Liparis*, which are probably also *L. inquilinus*, from bay scallops (pers. commun.). *Liparis inquilinus* originally collected from sea scallops were placed in aquaria with bay scallops to determine if they would attempt to enter the scallops. These scallops were completely ignored and the fish made no attempt to enter or attach to them. When brushed by *L. inquilinus*, the bay scallops either showed no response or closed the valves slightly. Bay scallops are found in much shallower water than the sea scallops, and the occurrence of *L. inquilinus* in depths frequented by bay scallops is unusual. These fish which occur in shallower water may attempt to associate with bay scallops in the absence of their regular host. Confusion in host recognition may

occur where chemical stimulation is important but other ecological factors usually prevent the animal from associating with other forms (Davenport 1955).

Over 30 attempts by *L. inquilinus* to enter sea scallops were observed in the laboratory. The length of time spent swimming along the mantle of the scallop varied, but some fish were able to enter in less than 3 s. After swimming along the mantle most fish turned, placed the head at the margins of the mantle, and attempted to force their way inside the scallop with sustained swimming strokes of the tail. One individual repeated this activity 10 times before it gave up. The point of entry along the mantle appeared to be selected randomly. Several fish attempted to enter the incurrent and excurrent opening. The scallop usually did not react to the fishes' entrance and only occasionally responded by closing the valves slightly. The red hake, *Urophycis chuss,* enters and exits the scallop only through the excurrent opening (Musick 1969).

Perhaps there is individual variation in the acceptance of fish by scallops. On two occasions, scallops rejected *L. inquilinus* after they had entered the scallop by clapping the valves together and thus forcing the fish out of the mantle cavity. In each instance, the fish came to rest a few inches from the edge of the scallop. The fish remained still as the sand stirred up by the scallop's activity settled over it. Within a few minutes, the fish returned to the scallop and attempted to enter again.

Once inside the mantle cavity of the scallop, the fish attached by their discs in an inverted position to the mantle tissue of the left valve. Fish have been observed in this position approximately 20 times, either by viewing through the excurrent or incurrent opening or picking the scallop out of the water and looking in as it clapped. Often several fish were observed in the same scallop simultaneously. This position in the scallop is the same as that preferred by fish attached to clapper shells and other smooth substrates. In approximately 100 other instances, *L. inquilinus* presence in sea scallops was confirmed by their absence elsewhere in the aquaria.

Liparis inquilinus and *U. chuss* apparently cooccur in sea scallops frequently and in considerable numbers. We have collected these fishes together in sea scallops from Georges Bank in September, November, and December. In the Mid-Atlantic Bight (4 August 1969, lat. 39°40′N, long. 73°09′W, 40 m) a 141-mm sea scallop contained a red hake (21 mm TL) and 21 *L. inquilinus* which averaged 16.5 mm TL. A 125-mm scallop yielded two *U. chuss* (43 and 47 mm TL) and two *L. inquilinus* (23 and 24 mm TL). Goode (1884) also reported *L. lineatus* (= *inquilinus*) and *Phycis* (= *Urophycis*) *chuss* as companions in sea scallops. These two fishes may not be in direct competition for this particular habitat since the *L. inquilinus* remain attached to the upper surface of the cavity and *U. chuss* swims in the middle of or rests on the bottom of the cavity (Musick 1969).

Sea scallops apparently suffer no ill effects from the association with *L. inquilinus*. Of several thousand host sea scallops opened during this study, none had noticeable internal damage which could have been caused by *L. inquilinus*. These partners do not compete for food since *L. inquilinus* feeds principally on larger crustaceans and sea scallops are microplanktonic filter feeders (Bourne 1964).

Diel Rhythm in the Fish—Scallop Association

Juvenile *L. inquilinus* exhibit a diel rhythm in their association with sea scallops. In aquaria, fish were outside of the sea scallops and actively swimming during periods of darkness. The color pattern of the fish faded during dark periods but returned within approximately 5 min after the lights were turned on. Fish were usually inside of scallops or attached to some substrate in the aquarium during light periods. When the lights went off on their regular cycle, the fish would often leave the scallops and become active within 5-10 min. These reactions to light and dark were immediate even when the dark-light cycle was changed drastically during a single day. *Liparis inquilinus* which were collected from sea scallops during a 24-h period on 4-5 August 1969 near Hudson Canyon (Figure 6) exhibited the same pattern (Figure 7). During this period, 3,595 *L. inquilinus*, averaging 21.0 mm TL, were collected from 616 of the 841 scallops examined. In one instance, 32 fish were found inside a 139-mm scallop. Fish were more abundant in scallops and more scallops contained fish during the day than at night (Table 2). However, some fish were present in scallops during every sampling period. The greatest increase and decrease in the number of fish per scallop occurred around sunrise and sun-

set respectively. The number of fish per scallop was high during the day (Figure 7) and declined substantially in the first sample after sunset. After the initial decrease in the numbers of fish per scallop after sunset, the number increased regularly up to daytime levels as sunrise approached. The number of fish in scallops was slightly greater than presented in Figure 7. Fish found outside of scallops (122 or 3% of the total) in the collecting buckets or on the deck were not included in the averages. However, these fish were more abundant at stations where the number of fish per scallop was greater so that they did not affect the comparative data.

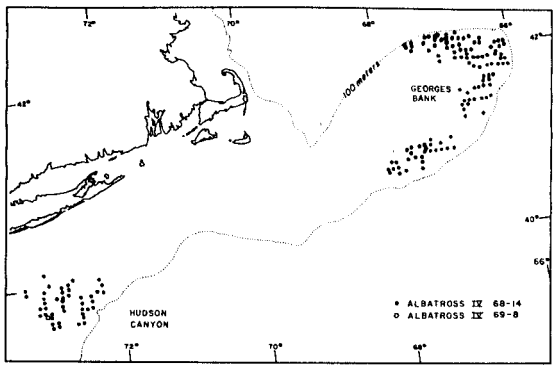

FIGURE 6.—Locations of sampling sites for fish-scallop association on 5-17 September 1968, *Albatross IV* cruise 68-14 and on 4-5 August 1969, *Albatross IV* cruise 69-8.

The majority of *L. inquilinus* leave scallops to feed during the night and then return near sunrise or as they become satiated. Sixty stomachs were examined (five from each sampling period) and were assigned a separate value for relative fullness (0-4) and state of digestion of contents (1-3) with the highest numbers given to stomachs with the most food and the least degree of digestion. When added together, these give a relative value referred to as the stomach analysis index. The maximum value possible is 7, the minimum is 1. The higher values should be from fish which had recently fed, and digestion had not begun or had not progressed very far. The stomach analysis index values increased from 2200 h, with highest values occurring just before and after sunrise (Figure 8). The lowest values were found just before and after sunset (Figure 8). Whole undigested amphipods were found in stomachs of fish taken at night, but after 0800 h stomach contents were in increasingly advanced stages of

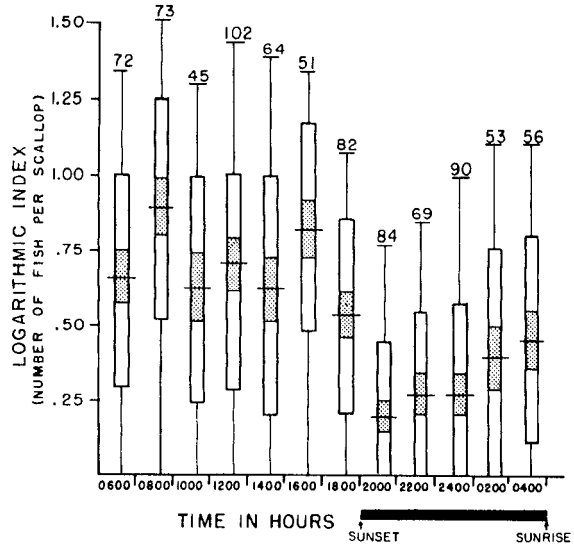

FIGURE 7.—Number of *Liparis inquilinus* per scallop from the combined total of two 10-min tows taken every 2 h over a 24-h period on 4-5 August 1969 at approximately lat. 39°39′N, long. 73°08′W. For each sample, the range is represented by the vertical line, mean by the horizontal line, one standard deviation on each side of the mean by hollow rectangles and two standard errors on each side of the mean by solid rectangles. Numbers above each figure represent the number of scallops sampled.

TABLE 2.—Comparison of the number of *Liparis inquilinus* in sea scallops during the day and night for a 24-h period.

Time	Number of scallops examined	Mean number of fish per scallop	Percent of scallops with fish	Number of replicated stations
Day (0503-1908 h)	489	6.1	86.3	7
Night (1909-0502 h)	352	1.7	57.3	5
Total	841	4.2	73.2	12

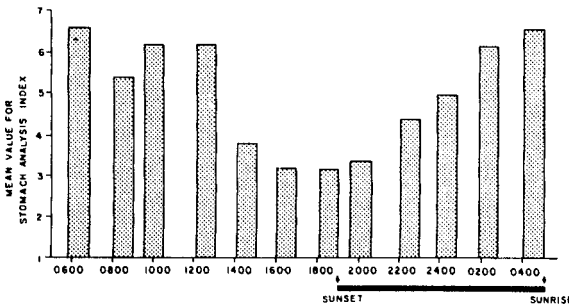

FIGURE 8.—Results of stomach analysis of *Liparis inquilinus* taken from scallops over a 24-h period on 4-5 August 1969. Stomach analysis index value for each stomach was derived from ranking relative fullness (0-4) which is added to the state of digestion of the contents (1-3), with the highest numbers given to stomachs having the most food and the least degree of digestion.

digestion until only unidentifiable material remained in stomachs collected just before and after sunset. Fish with full stomachs and undigested contents were first collected at 2200 and 2400 h. These were probably returning to scallops as they became satiated. All fish do not leave the scallops at sunset (Figure 7). Some may remain if they still have food in their stomachs. Those fish examined around 2000 h did not have completely empty stomachs (Figure 8). None of the fish examined at 0200 and 0400 h had empty stomachs.

The number of *L. inquilinus* occupying sea scallops probably decreases through the fall and early winter. During September 1968, 43 collections near Hudson Canyon (Figure 6), which overlapped the collecting area in August 1969 (Figure 6), yielded fewer fish per scallop (Table 3) than in August. These differences could be due to relative year-class strength or may reflect an actual change in the number of fish occupying scallops later in the year. Mortality of *L. inquilinus* owing to predation or a breakdown in the association as the fish grow larger could explain a decrease of this magnitude. Small numbers of sea scallops collected during the fall and early winter of several years did not yield as many *L. inquilinus* as were collected earlier in the year.

Size of individual sea scallops may be a factor in their selection by fish. In one instance, a 60-mm scallop contained a 21-mm TL fish, but it is the larger scallops which contain the largest number of fish (Figure 9).

TABLE 3.—Abundance and average total length of *Liparis inquilinus* in sea scallops from August 1969 and September 1968.

Collecting dates	Number of scallops examined	Mean number of fish per scallop	Maximum number in single scallop	Average TL of fish (mm)
4-5 Aug. 1969	841	4.2	32	21.0
14-17 Sept. 1968	717	1.7	18	26.1

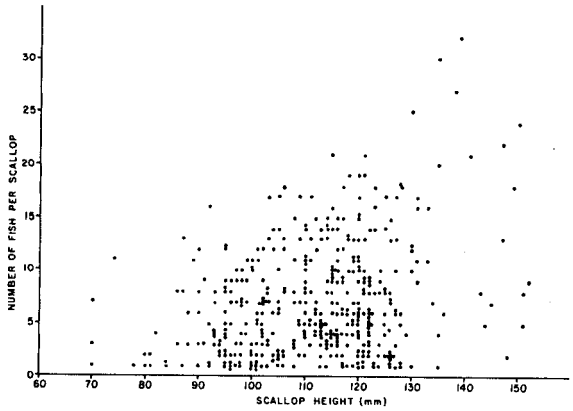

FIGURE 9.—Plot of mean number of fish per scallop versus scallop height (mm) from daytime collections from *Albatross IV* cruise 69-8.

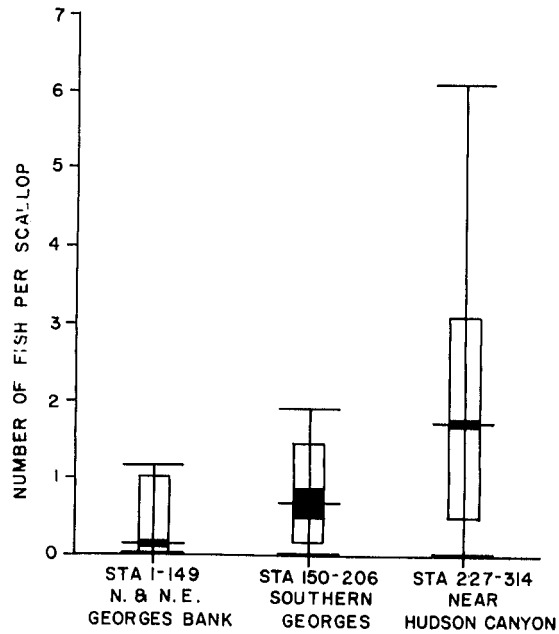

FIGURE 10.—Plot of mean number of fish per scallop at different localities from collections of 5-17 September 1968.

Geographic Variation in Abundance of Fish in Scallops

The abundance of fish in scallops varies with geographic location (Figure 10). On *Albatross IV* cruise 68-14, 155 10-min scallop dredge tows were made as part of a sea scallop survey on Georges Bank and in the Mid-Atlantic Bight near Hudson Canyon (Figure 6). From these, 2,274 *L. inquilinus* were collected from 1,228 of the 5,905 sea scallops examined. The mean number of fish per scallop (Figure 10) and the mean number of fish per station (Table 4) were highest north of Hudson Canyon, lowest on the north and northwest edges of Georges Bank, and intermediate on southern Georges Bank. Although the greatest abundance of fish in sea scallops occurred near Hudson Canyon, where the average depth and bottom temperature were lowest (Table 4), these parameters did not seem to be related to abundance in this area (Figures 11, 12). The average

TABLE 4.—Comparison of the possible parameters affecting *Liparis inquilinus* abundance in sea scallops over a wide geographic area. Given as mean followed by range in parentheses.

Item	Northern and northeastern Georges Bank	Southern Georges Bank	Near Hudson Canyon
No. of stations	83	29	43
Date, 1968	5-10 Sept.	10-12 Sept.	14-17 Sept.
No. of fish per scallop	0.11(0.0-1.1)	0.65(0.0-1.8)	1.74(0.0-6.1)
Scallops with fish (%)	10.1(0.0-90.9)	41.0(0.0-78.9)	59.2(0.0-100.0)
No. of fish per station	4.8(0-31)	20.6(0-64)	27.1(0-82)
TL (mm) of fish in scallops	29.4(14-47)	28.2(16-43)	26.1(17-38)
Depth (m)	77(47-95)	77(62-90)	57(37-77)
Bottom temp (°C)	10.0(4.0-14.5)	9.7(8.2-13.3)	7.8(6.5-10.1)
Clapper shells (bushels)	3.4(1-7)	5.8(2-9)	4.0(2-8)
No. scallops >60 mm per station	152(3-456)	38(10-79)	68(3-311)

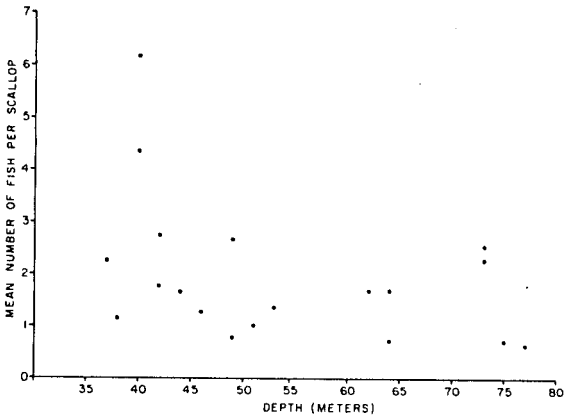

FIGURE 11.—Plot of mean number of fish per scallop versus water depth from daytime collections of 14-17 September 1968 near Hudson Canyon.

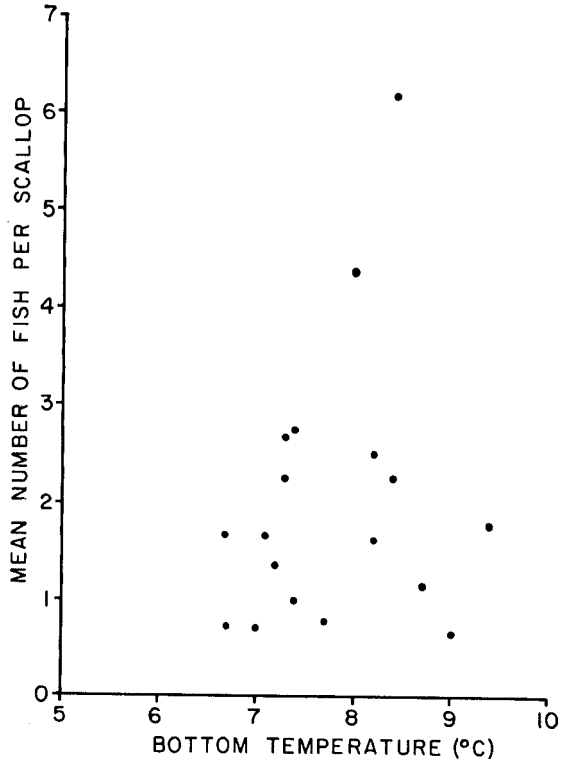

FIGURE 12.—Plot of mean number of fish per scallop versus bottom temperature from daytime collections of 14-17 September 1968 near Hudson Canyon.

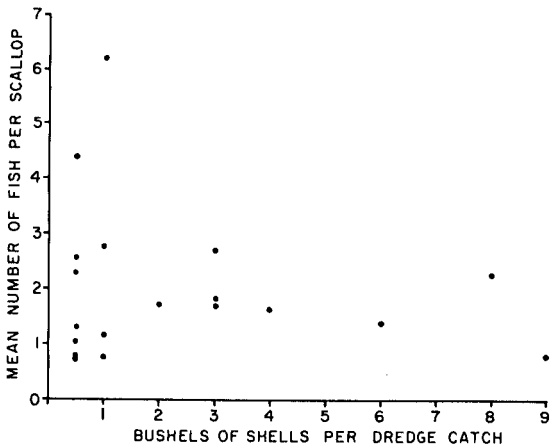

FIGURE 13.—Plot of mean number of fish per scallop from daytime collections versus clapper shell abundance from collections of 14-17 September 1968 near Hudson Canyon.

number of scallops per station for each area was not related to increased abundance of fish in scallops (Table 4). Clapper shell abundance, regardless of species, was originally hypothesized to be important in *L. inquilinus* survival and abundance since *L. inquilinus* readily occupied shells in the laboratory, and this habit may offer protection from predators. A plot of this possible relationship did not suggest a correlation (Figure 13). The similarity of abundance estimates for southern Georges Bank and the area near Hudson Canyon could be attributed to a similarity in bottom types. Both of these areas have smooth bottoms and are quite different from the rough topography of northern Georges Bank (Uchupi 1968). Fish living on smooth bottom would have less chance of concealment and evasion of predators, which would place a greater selective advantage on association with scallops. The simplest explanations for observed differences in abundance are

differences in the year-class strength and differences in actual abundance among different *L. inquilinus* populations.

Possible Advantages of the Association

Liparis inquilinus probably is protected from predation by its association with sea scallops. The only known predators of larger sea scallops which might also ingest *L. inquilinus* are Atlantic wolfish, *Anarhichas lupus*, and Atlantic cod, *Gadus morhua* (Bourne 1964). Wolfish and cod only feed occasionally on scallops and they are rare or only winter inhabitants of the Mid-Atlantic Bight. Also, *L. inquilinus* is not associated with scallops during most of the winter.

Individuals of *L. inquilinus* maximize the period of protection by associating with sea scallops for most of their demersal life. In the Mid-Atlantic Bight, *L. inquilinus* remains associated with sea scallops from the time they leave the plankton until they begin to move inshore to spawn. Also, individuals only leave sea scallops to feed and then return as soon as they become satiated. Nocturnal feeding may also decrease the possibility of detection by predators.

The relative number of scallops may not be a limiting factor for survival of juvenile *L. inquilinus*. In every sample, at any time of the year in which *L. inquilinus* have been taken with sea scallops, some scallops were always empty. However, this assumes that all sea scallops will accept fish. This remains to be proven.

The symbiosis between *L. inquilinus* and *P. magellanicus* should be referred to as a commensal association. Such an association is one in which the population of the commensal benefits and the host is unaffected (Odum 1971).

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LITERATURE CITED

ABLE, K. W.
1973. A new cyclopterid fish, *Liparis inquilinus*, associated with the sea scallop, *Placopecten magellanicus*, in the western North Atlantic, with notes on the *Liparis liparis* complex. Copeia 1973:787-794.
1974. Life history, ecology and behavior of two new *Liparis* (Pisces: Cyclopteridae) from the western North Atlantic. Ph.D. Thesis, College of William and Mary, Williamsburg, 115 p.
In press. A new cyclopterid fish from the western North Atlantic with notes on life history. Copeia.

ALEXANDER, R. M.
1967. Functional design in fishes. Hutchinson, Lond., 160 p.

ANDRIYASHEV, A. P.
1954. Fishes of the northern seas of the USSR. Akad. Nauk SSSR, Zool. Inst., Opredeliteli po Faune SSSR 53, 566 p. (Translated by Israel Program Sci. Transl., 1964, 617 p.; available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as OTS63-11160.)

BARDACH, J. E., AND J. CASE.
1965. Sensory capabilities of the modified fins of squirrel hake (*Urophycis chuss*) and searobins (*Prionotus carolinus* and *P. evolans*). Copeia 1965:194-206.

BEAN, T. H.
1884. List of fishes collected by the U.S. Fish Commission at Wood's Holl, Massachusetts, during the summer of 1881. Rep. U.S. Comm. Fish Fish. 1882:339-344.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BOURNE, N.
1964. Scallops and the offshore fishery of the Maritimes. Fish. Res. Board Can., Bull. 145, 60 p.

BREDER, C. M., JR., AND D. E. ROSEN.
1966. Modes of reproduction in fishes. Nat. Hist. Press, Garden City, N.Y., 941 p.

BURKE, V.
1930. Revision of the fishes of the family Liparidae. U.S. Natl. Mus. Bull. 150, 204 p.

CLARK, J., W. G. SMITH, A. W. KENDALL, JR., AND M. P. FAHAY.
1969. Studies of estuarine dependence of Atlantic coastal fishes. Data Report I: Northern section, Cape Cod to Cape Lookout. R.V. *Dolphin* cruises 1965-66: Zooplankton volumes, midwater trawl collections, temperatures and salinities. U.S. Bur. Sport Fish. Wildl., Tech. Pap. 28, 132 p.

COWAN, D.
1929. Spawning of the lumpsucker. Rep. Dove Mar. Lab., Cullercoats, Northumberland 17:37-38.

DAVENPORT, D.
1955. Specificity and behavior in symbioses. Q. Rev. Biol. 30:29-46.

DETWYLER, R.
1963. Some aspects of the biology of the seasnail, *Liparis atlanticus* (Jordan and Evermann). Ph.D. Thesis, Univ. New Hampshire, Durham, 103 p.

EHRENBAUM, E.
1905. Eier und Larven von Fischen. *In* Nordisches Plankton; Zoologischer Teil, Erster Band, p. 1-216. Verlag von Lipsius & Tischer, Kiel und Leipz.

FREIHOFER, W. C.
1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyol. Bull. 8:80-189.

GARMAN, S.
1892. The Discoboli. Cyclopteridae, Liparopsidae, and Liparididae. Mem. Mus. Comp. Zool. 14(2), 96 p.

GIBSON, R. N.
1972. The vertical distribution and feeding relationships of intertidal fish on the Atlantic coast of France. J. Anim. Ecol. 41:189-207.

GOODE, G. B.
1884. Natural history of useful aquatic animals. Part III, The food fishes of the United States. *In* The fisheries and fishery industries of the United States, Sec. I:163-682.

GOODE, G. B., AND T. H. BEAN.
1895. Oceanic ichthyology. U.S. Natl. Mus., Spec. Bull. 2, 553 p.

HOFF, J. G.
1968. Occurrence of *Liparis atlanticus* in *Aequipecten irradians* in Buzzards Bay, Massachusetts. Trans. Am. Fish. Soc. 97:278.

JOHNSON, C. R.
1969. Contributions to the biology of the showy snailfish, *Liparis pulchellus (Liparidae)*. Copeia 1969:830-835.
1970. Age of the showy snailfish, *Liparis pulchellus*. Jap. J. Ichthyol. 17:121-123.

JORDAN, D. S., AND B. W. EVERMANN.
1898. The fishes of North and Middle America. U.S. Natl. Mus. Bull. 47, Part 2:1241-2183.

KOSAKA, M.
1971. On the ecological niche of the sea-snails, *Liparis tanakai* (Gilbert et Burke) in Sendai Bay. J. Coll. Mar. Sci. Technol., Tokai Univ. 5:27-41.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

MARISCAL, R. N.
1966. The symbiosis between tropical sea anemones and fishes: A review. *In* R. I. Bowman (editor), The Galápagos, p. 157-171. Univ. Calif. Press, Berkeley.

MUSICK, J. A.
1969. The comparative biology of two American Atlantic hakes, *Urophycis chuss* and *U. tenuis* (Pisces: Gadidae). Ph.D. Thesis, Harvard Univ., Cambridge, 150 p.

NIZORTSEV, G. P., V. P. PONOMARENKO, AND R. A. SHASHLOVA.
1963. New data on the representatives of *Liparis* genus in the Barents Sea. (In Russ.) Zool. Zh. 42:1415-1418.

ODUM, E. P.
1971. Fundamentals of ecology. 3rd ed. W. B. Saunders Co., Phila., 574 p.

QUAST, J. C.
1968. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.

UCHUPI, E.
1968. Atlantic continental shelf and slope of the United States—Physiography. U.S. Geol. Surv., Prof. Pap. 529-C, 30 p.

WELSH, W. W.
1915. Note on the habits of the young of the squirrel hake and sea snail. Copeia 18:2-3.

WHEELER, A.
1969. The fishes of the British Isles and north-west Europe. Macmillan Co., Lond., 613 p.

WILEY, M. L., AND B. B. COLLETTE.
1970. Breeding tubercules and contact organs in fishes: Their occurrence, structure, and significance. Bull. Am. Mus. Nat. Hist. 143:147-216.

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FURTHER OBSERVATIONS OF THE FEEDING ECOLOGY OF POSTLARVAL PINFISH, *LAGODON RHOMBOIDES*, AND SPOT, *LEIOSTOMUS XANTHURUS*[1]

MARTIN A. KJELSON AND GEORGE N. JOHNSON[2]

ABSTRACT

The effect of current on feeding, temporal variation in food consumption, and the effect of predator and prey size on food preferences were evaluated for postlarval stages of pinfish, *Lagodon rhomboides* (15-19 mm total length); and spot, *Leiostomus xanthurus* (16-22 mm). Field and laboratory observations indicated that pinfish feeding rates decreased as water current velocity increased. Similar behavior was noted in spot from field observations, but spot feeding rates in the laboratory were highest when a slight current was present. Mean gut contents of postlarvae collected at midday over a 2-mo period ranged from 0.4 to 38 copepods/fish. The mean coefficient of variation for the number of copepods per fish in a single midday sample (n = 20 fish) was 20%. Maximum daily feeding rates were estimated at 17 and 26 copepods/h for spot and pinfish, respectively. Field and laboratory data confirmed that as postlarval size increases the size of their prey also increases. Refined estimates of postlarval evacuation rates and daily rations also are presented. Daily ration estimates as a percent of the fish's wet body weight were 9% for both species. The ration estimates for both species were greater than metabolic needs estimated from oxygen consumption measurements.

Information on the feeding ecology of larval fishes is necessary to understand the role of larvae in ecosystem energetics and community structure and the importance of feeding conditions to year class strength. However, relatively little is known about the feeding of larval fishes. This paper reports four major aspects of postlarval feeding: 1) the effect of current speed on feeding intensity; 2) temporal variation in postlarval food consumption; 3) the relation of feeding rate to food abundance; and 4) the effect of prey and predator size on postlarval food preferences. Refined results concerning postlarval evacuation rates and daily rations also are presented. Our earlier paper (Kjelson et al. 1975) stressed the study of food preferences, feeding intensity and periodicity, evacuation rates, daily rations, and the effect of handling and capturing the fishes on their digestive tract contents.

Pinfish, *Lagodon rhomboides*, and spot, *Leiostomus xanthurus*, constitute a major portion of the fish biomass of southeastern estuaries of the Atlantic coast and thus are important to the structure and function of these ecosystems. Spot are also an important commercial food species. Both species are primarily winter spawners in the Atlantic Ocean with larvae migrating inshore to estuarine waters which serve as nursery grounds between spring and fall. Larval forms (here defined as individuals <11 mm) are rarely found within the estuaries, whereas postlarval stages (here defined as fish between 11 and 22 mm) occur both in nearshore oceanic and estuarine waters.

METHODS

General

Postlarval pinfish (15-19 mm total length (TL)) and spot (16-22 mm) were collected during January and February 1974, from the Newport River estuary, N.C., following their recent immigration into the estuary from the offshore spawning grounds in the Atlantic Ocean. All fish were collected at Pivers Island, 2.5 km inside the Beaufort Inlet. Shore samples were collected with dip nets while those in the adjacent channel were collected with a channel net (Lewis et al. 1970). Fish were anesthetized immediately upon capture in a 0.12 g/liter seawater solution of MS-222[3] (tricaine methanesulfonate) and dissected in the

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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laboratory. Gut contents included material in the total digestive tract, from foregut to anus.

Current Speed and Feeding Intensity

Larval pinfish and spot were collected within 2 m of the shore (depth 0-2 m) where refuge from current was available and in the center of the adjacent channel (depth 5-7 m) approximately 25 m from shore where a current normally was present. Three separate collections were made for pinfish and two for spot. Twenty fish of each species from each collection were measured, dissected, and the mean number of copepods per fish determined. Surface tows for zooplankton were made at the same time and location using a 30 cm in diameter, 0.158-mm mesh net with current meter attached. Observations on copepods throughout this investigation were restricted to adult and copepodid stages. Copepod measurements were made of carapace length. Current velocities were measured with a Gurley current meter.

Feeding rates of pinfish and spot at varied current speeds also were studied in the laboratory. Fish were captured, placed in four donut-shaped, 11-liter tanks (46 cm in diameter, 10- by 10-cm cross-sectional area), and allowed to acclimate overnight in filtered, food-free seawater with no current flow. Two tanks were used as controls (zero current flow) and contained 50 and 100 fish, respectively. The other two tanks, containing 50 fish each, were attached to pumps, providing current velocities of 1.7 and 5.1 m/s, respectively. Current speed was estimated by recording the amount of time required for a minute innate particle to complete one revolution of the donut-shaped tank. At the beginning of each experiment, current flow was started in the two test chambers and *Artemia salina* nauplii (1.0/ml) were provided to each of the four tanks. Fish were allowed to feed for 1 h with additional food provided after 30 min to assume a minimum density of 1 *Artemia*/ml throughout the experiment. Twenty fish were sampled from each tank to calculate the mean number of *Artemia* consumed.

Temporal Variation in Midday Feeding

Day-to-day variation in the feeding intensity of larval pinfish and spot was studied at midday (1100-1300 h) when larval digestive tracts contained the greatest amounts of food. Fifteen collections were made from 21 January to 28 February at one site within 2 m of the shore. Each collection consisted of 20 fish of each species. Total lengths of the fish were measured, the total number of copepods in each gut counted, and a geometric mean of the number of copepods per fish calculated. Geometric means were used as a measure of central tendency because frequency distributions of the copepods or *Artemia* nauplii per fish showed a positive skewness. In addition, a geometric mean was used to limit the bias of a few individuals feeding at a rate not representative of the population because variation increased as the mean values increased.

A zooplankton tow was taken at the time and location of fish capture. The tows were made just below the surface, against the current, and sampled approximately 5 m^3 of water. Estimates of copepod density were made from three 10-ml subsamples of each tow. Twenty copepods per sample were measured for length frequencies.

Evacuation Rates

To refine our information on larval evacuation rates of copepods, two laboratory experiments were performed using pinfish and spot that had been fed an abundance of natural copepods. Four to five hundred fish were starved for 8 to 12 h and then they were allowed to feed for 1 h. Food densities averaged 2.5 copepods/ml for pinfish and 3.0 copepods/ml for spot. Larvae were acclimated and experiments run at ambient estuarine temperatures and salinities. Temperature was 12°C for the pinfish evacuation and 17°C for spot; salinity was 30‰. Following feeding, 30 fish were removed, anesthetized with MS-222 to prevent any possible regurgitation, dissected, and counts made of the numbers of copepods per fish. At the same time, three groups of 100 fish were transferred to separate food-free tanks, and the decrease in their gut contents observed by sampling 10 fish from each tank at 2-h intervals until more than one-half of the fish had empty tracts. Instantaneous evacuation rates were then calculated according to the method of Peters and Kjelson (1975). The amount of food remaining in the stomach at any time can be predicted from the following equation:

$$\log C = \log A + Bt$$

where C = content of gastrointestinal tract + 1

A = amount ingested + 1
B = evacuation rate constant
t = time.

By adding 1 to the amount ingested and to gut contents we were able to include empty gastrointestinal tracts in our calculations. From the above equation, with log base 10:

$$C = e^{2.303\,(\log A\, + Bt)}$$

and the instantaneous evacuation rate

$$\frac{dC}{dt} = 2.303\, Be^{2.303\,(\log A\, + Bt)}$$

or

$$\frac{dC}{dt} = 2.303\, BC.$$

Feeding Periodicity

Diel periodicity of digestive tract contents indicated the intensity and chronology of feeding by the fish. Our purpose was to refine the feeding chronology curve (Kjelson et al. 1975) by taking samples more frequently than in our previous study. Ten fish of each species were collected at 2-h intervals between 0600 and 1800 and at 2100 and 2400 h. Fewer samples were taken at night because our past observations have shown that larval fish cease feeding during darkness. All fish were measured, the copepods they contained counted, and a geometric mean for copepods per fish calculated for each sample.

Daily Rations

One objective of this research was to re-estimate the daily ration of larval fish for comparison with our earlier study. Daily rations were calculated by the same technique (Kjelson et al. 1975) using new information on diel periodicity of gut contents and refined measurements of instantaneous evacuation rates. Our method of calculating daily ration accounts for changes in evacuation rate which accompany diel changes in feeding intensity.

To calculate daily ration, we first estimated the average evacuation rates (in copepods per hour) for each of the 2-, 3-, or 6-h sampling periods in our feeding chronology study. This average rate was the geometric mean of the instantaneous evacuation rates at the beginning and end of each period. The estimate of food evacuated during any period is equal to the number of hours in the period multiplied by the respective average hourly evacuation rate. The total food evacuated per day was computed by summing the nine respective evacuation estimates, and is an estimate of the daily ration because the average ingestion rate must equal the rate at which material in the gut is assimilated or defecated.

Daily rations were calculated initially as copepods per fish per day and then transformed to percent of the larval body weight and calories per fish per day. Dry weights of ingested copepods were estimated from the length-weight relationship: $W = 6.274L - 0.153$ where W is the dry weight in micrograms and L is the copepod length in millimeters, based upon Heinle's (1966) data for all stages of *Acartia tonsa*. Copepod dry weights were converted to wet weights using a factor of 9.1 based upon our measurements of the wet-dry ratio for zooplankton and were compared with wet weights of the fish to compute the daily ration as a percent of live body weight. Daily caloric intake was computed using our estimation of 0.555 cal/mg wet weight of an average size copepod, based on micro-bomb calorimeter measurements of mixed estuarine zooplankton (Thayer et al. 1974).

RESULTS AND DISCUSSION

Effects of Current Speed on Feeding Intensity

Pinfish and spot larvae collected along the shore had more copepods present in their digestive tracts than those collected in midchannel (Table 1). Previous observations (Kjelson et al. 1975) indicated that neither pinfish nor spot regurgitate or defecate food under the stress of capture or handling. Thus, differences in collecting techniques

TABLE 1. — Digestive tract contents of larval fishes collected at midday at midchannel and shore stations in the Newport River estuary, January to February 1974.

Date	Species	Mean number of copepods/fish ± 1 SE		Current speed (m/s) in channel[1]	Tidal stage[2]
		Shore	Channel		
29 Jan.	Pinfish	9.1 ± 1.6	0.8 ± 0.2	1.4	LF
30 Jan.	Pinfish	19.6 ± 2.8	4.1 ± 0.8	0.0	HS
14 Feb.	Pinfish	20.0 ± 2.8	1.8 ± 0.6	3.2	LF
14 Feb.	Spot	14.4 ± 1.7	0.9 ± 0.4	3.2	LF
21 Feb.	Spot	2.7 ± 0.6	0.3 ± 0.2	5.5	ME

[1]No current was observed along the shore on any sample date.
[2]LF = late flood, ME = mid ebb, HS = high slack.

(channel net versus dip net) between areas were not felt to bias the results. We observed no differences in the length of fish sampled (by species) or in the density of copepods at the two locations.

These results indicate that larval feeding rates are limited when the fish are exposed to current. Current speed ranged from 0 to 5.5 m/s in mid-channel where feeding was low, to no measurable current along the shore where more feeding occurred (Table 1). In addition, pinfish collected in the channel on a slack tide contained 4.1 copepods/fish compared with a mean of 1.3 copepods/fish when there was a current present.

Laboratory experiments indicated that current speed affected the food consumption rate of both species (Table 2). Pinfish consumed the most food when there was no current, but spot ate more at a current velocity of 1.7 m/s. Pinfish ate the least food in a 5.1 m/s current while the spot minimum feeding occurred at varied current speeds. Both species fed at a higher rate when fish densities were lower.

The observations from both field and laboratory studies indicate that postlarval pinfish feeding declines as current speed increases. These results suggest that current speed influences the ability of pinfish to capture their prey, although the specific reasons for such altered behavior are unknown. The well-known attack behavior of larval fish, that of visually sighting the prey and of assuming an S-shape prior to striking (Blaxter and Holliday 1963), may be unattainable by postlarval pinfish exposed to higher current speeds. Bishai (1959) found that larval herring drift with a current at speeds less than the current itself. This may suggest that the size, shape, and behavior of a plankter may influence its rate of movement in a current. Prey organisms may move at a faster rate than the fish larvae, which in turn may lessen the ability of the fish to orient to the prey.

Current also may destroy the microstructure of the prey population. Without a strong current, food could aggregate in patches thus producing local areas with high food density and therefore increase the rate of ingestion. This latter explanation is probable in the natural environment; however, it appears unlikely under the laboratory conditions, because the density of *Artemia* in the tanks was very high (1/ml) and prey were replenished to assure that it did not decrease. In addition, the small cross-sectional area (100 cm^2) and volume of the tanks greatly limited the distance a larva had to travel to find food even if prey were in a patch configuration.

Differences in channel versus shoreline feeding by spot in the natural environment (Table 1) are similar to those of pinfish; however, feeding by spot in the laboratory was highly variable and is difficult to explain. Spot fed at the highest rates when a slight current was present and even fed at a high rate when exposed to a maximum current of 5.1 m/s. The spot postlarvae used in the studies were larger than the pinfish and this may explain the ability of spot to feed at a high rate when exposed to current, because increased size usually improves swimming ability which may improve the fish's ability to capture their prey. However, species differences in swimming ability were not apparent: larvae of both species moved freely about the tank when current was absent; oriented into the current or at times drifted with the current at the 1.7 m/s speed; and drifted along with the current in the 5.1 m/s current, although some individuals oriented into the current briefly. Similar behavior by larval fishes exposed to varied current velocities was discussed by Bishai (1959) and Houde (1969). Ryland (1963) indicated that the mechanisms by which larval fishes orient to a current are poorly understood. The lower feeding rate of spot in no current is unexplainable unless this species is adapted in some way to be more effective at capturing prey within a current. Serebrov (1973) also found differences in the feeding intensity of various species (guppy, *Poecilia reticulata,* and European dace, *Phoxinus phoxinus)* when exposed to different current velocities and suggested that the differences were due both to natural adaptation to certain current condi-

TABLE 2.—Digestive tract contents (mean number of *Artemia* nauplii/larva ± 1 SE) of larval fishes following feeding in the laboratory under several current velocities.

Date 1974	Species	Length of fish (mm)	Current velocity			
			[1]5.1 m/s	[1]1.7 m/s	No current[1]	No current[2]
26 Feb.	Pinfish	16-17	2.5 ± 1.8	22.1 ± 3.5	50.9 ± 6.3	35.0 ± 4.0
3 Mar.	Spot	20-22	104.7 ± 7.5	166.0 ± 8.0	72.1 ± 7.7	23.5 ± 5.3
14 Mar.	Spot	19-20	30.3 ± 3.3	90.0 ± 5.5	39.1 ± 4.3	23.1 ± 3.2

[1]Fifty fish.
[2]One hundred fish.

tions and to the stimulation of food grasping activity caused by the increased movement of food in a current.

The highly variable nature of spot feeding in the laboratory also may be explained by the varied current conditions within the tank itself, although conditions were kept as constant as possible during the two studies. Current flow may not have been uniform throughout the tank, although the importance of this factor upon feeding is unknown. The larvae in all experiments were distributed throughout the tank and did not appear to be feeding at specific locations. The low variability in feeding rate between individual fish in each experiment, as shown by the standard errors (Table 2), suggests that all individuals were feeding at a similar rate even though they were dispersed throughout the tank. The distribution of flow across the tank vertically was not measured, although such information would be useful (Ryland 1963). The two treatment groups of spot postlarvae were from separate field collections which may have altered their behavioral characteristics sufficiently to produce the variable results.

Finally, the apparent necessity for low current velocity for feeding to take place may restrict considerably the amount of area suitable for feeding to be successful. This may be particularly true along the channels linking the oceanic habitat to that of the estuarine marsh system where our observations took place. The amount of protected shoreline and bottom habitat characterized by low current velocity along these channels is very limited compared to that present in the broad reaches of the estuary where cordgrass (*Spartina*) marsh shoreline and eelgrass (*Zostera*) beds are extensive.

Temporal Variation in Food Consumption

Considerable day-to-day variation was observed in the mean number of copepods in the plankton and in the larval fish collected at midday (Figure 1). Mean pinfish gut contents ranged from 0.4 to 38 copepods/fish while spot contained from 0.5 to 24 copepods/fish. The coefficient of variation for the number of copepods per fish in single field samples averaged 20% (range 7-40%) for pinfish, and 17% (range 8-40%) for spot. The greatest variability occurred when the average gut contents were low. Copepod density also fluctuated widely from 477 to 3,262 copepods/m^3. These densities are not dis-

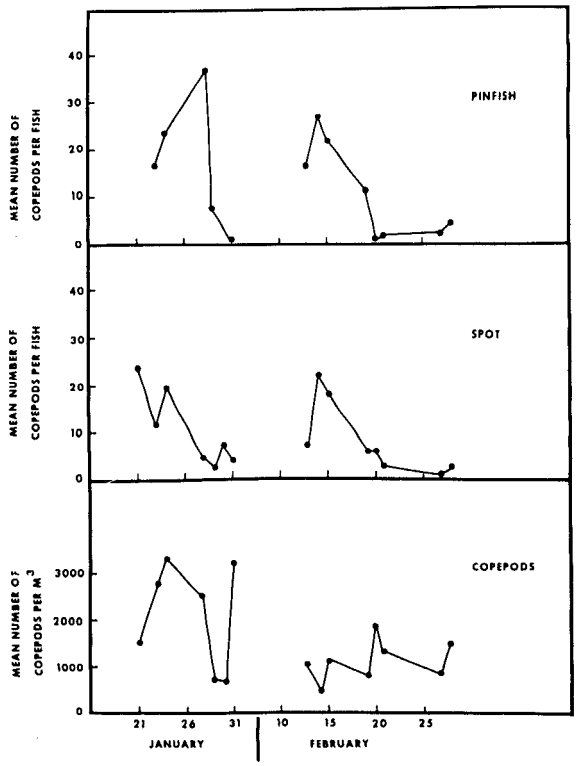

FIGURE 1. — Variation in the numbers of copepods per larval pinfish and spot, and copepods per cubic meter based on midday samples in the Newport River estuary during January and February 1974.

similar from those observed during the same months in the open waters of the Newport River estuary (Thayer et al. 1974). The coefficient of variation of the copepod counts from five tows at the site of larval collections was 24%. Such variation is not high for field sampling and although it represents the variability for only a single sampling date, it does suggest that the precision of the estimate of copepod density is acceptable.

One of our goals was to determine if the amount of food present in larvae was related to copepod density. In our study, the correlation coefficients between copepod concentration and gut contents were very low ($r = +0.08$ for both pinfish and spot), indicating that there was no relationship. Other studies on larval fish populations have shown that feeding incidence may be correlated with food concentration (Berner 1959; Nakai et al. 1966; Bainbridge and Forsyth 1971), while Houde (1967) found no correlation between copepod abundance and feeding rate by larval walleye.

The number of factors influencing larval feeding

rates in an estuary are undoubtedly numerous; therefore, it may be difficult through field measurements to establish a relationship between larval feeding rates and food abundance. For example, the clumped distribution typical of zooplankton populations may affect larval feeding rates, with feeding limited primarily to those periods when the fish are exposed to a dense patch of copepods.

Comparing naturally occurring mean food densities with mean gut contents, to establish a relationship between prey abundance and feeding rate, presents problems if the zooplankton populations are not randomly distributed or if the fish collected were not feeding upon the same prey community sampled by the plankton net (O'Brien and Vinyard 1974). Furthermore, the aggregation of zooplankton discussed earlier may be important in determining the rate of food consumption (Schumann 1965). Ivlev (1961) indicates that patchiness in the distribution of the food material increases the ration by comparison with an even food distribution when the average concentration is the same in both cases. High consumption rates by postlarval pinfish and spot may be possible only when patches of copepods come within the feeding range of the larvae. This hypothesis is discussed by Murphy (1961). The above remarks emphasize that laboratory investigations may be required in understanding the relationships between feeding rates and food abundance.

Size Related Food Preferences

Various investigators have observed selective feeding by larval fish and, at times, definite preference for a specific food form is indicated. Much of the selectivity, however, is due to the size relationship of the larval fish and the available zooplankton (Marak 1960). Information gained from our midday field samples and our laboratory evacuation experiments enabled us to observe the relationship between fish size and the size of prey they consumed. The Wilcoxon test for paired values (Alder and Roessler 1964) was used to determine if the mean size of copepods consumed was significantly different ($\alpha = 0.05$) from those collected in the plankton tows or provided in aquaria.

The spot collected for both field and laboratory studies were significantly larger than the pinfish. Both field and laboratory results indicated that pinfish larvae always ate smaller copepods than the mean size available to them while the reverse was true for spot (Table 3). Each species consumed prey that were proportional to their size with the ratio of the mean copepod length to the average fish length approximately 1:35 based upon laboratory measurements to 1:30 based upon field data.

The above results suggest that, as the larval fish size increases, the size of the consumed prey also increases. Many researchers (Blaxter and Holliday 1963; Blaxter 1965; Ciechomski 1967; Detwyler and Houde 1970; de Mendiola 1974; Marak 1974) also have observed this relationship in a variety of larval fishes. However, the mean size consumed in each study by either pinfish or spot varied considerably (Table 3). Pinfish of similar mean sizes (16 and 16.4 mm) fed upon 590-μm copepods in the laboratory, but the 460-μm prey in the field. This difference in prey size may be explained by the apparent difference in the prey sizes available to the fish in the two studies; laboratory prey had a mean size of 663 μm while those in the field were only 515 μm. Spot size preferences, on the other hand, are difficult to explain in the same manner, because spot consumed larger prey in the laboratory than in the field, although the prey available in the laboratory were considerably smaller than those present in natural waters (Table 3).

TABLE 3.— Mean sizes of copepods eaten by larval pinfish and spot in the field and laboratory compared to the mean sizes of copepods present.

	Mean length of		
Species	Larvae (mm)	Copepods eaten (μm ± 1 SE)	Copepods in aquaria or net tow (μm ± 1 SE)
Laboratory:			
Pinfish	16.0	590 ± 29	663 ± 28
Spot	17.7	669 ± 31	491 ± 68
Field:			
Pinfish	16.4	460 ± 12	515 ± 22
Spot	20.4	581 ± 12	515 ± 22

Comparisons of mean size prey from plankton tows to those from gut contents may be difficult again due to distributional dissimilarities of both predator and prey populations during feeding and prey aggregation patterns (Schumann 1965; O'Brien and Vinyard 1974). However, these problems were lessened in laboratory aquaria where we were able to control the size, density, and distribution of the predator-prey populations.

Two primary factors appear to explain the increase in prey size as larval fish size increases.

First, mouth size usually increases as the length of larvae increases. This relationship has been documented for larval fish of various species by Marak (1960), Blaxter (1965), Ciechomski (1967), Detwyler and Houde (1970), and Shiroto (1970). A few body measurements of pinfish and spot postlarvae showed that the gape of the mouth increased as the size of the fish increased. Pinfish of 16 mm TL were estimated to have a mouth gape of 1.43 mm, while spot of 1.6 mm had a gape of 1.70 mm. The larger gape in spot may explain, in part, their consumption of larger prey. Secondly, swimming speed also increases with an increase in the fish's body size (Houde 1969; Hoagman 1974); hence, the large spot may be capable of capturing larger copepods.

Although this study emphasized the food size preferences of postlarval pinfish and spot, a topic of potential importance in the selective nature of larval fish feeding deals with the selection of specific species of copepods. We did not compare the copepod taxa in the digestive tracts with those found in the plankton tows, but such effort should provide valuable information, because copepod species differences in swimming speed, vertical position in the water, and aggregation behavior may be very important in determining the type of prey available to and finally consumed by larval fish. However, the dominant genera present in the estuary during the study period were *Centropages, Temora, Acartia,* and *Euterpina,* common forms in the Beaufort area during winter and early spring (Thayer et al. 1974). Marak (1960) and Ciechomski (1967) attempted to assess the selectivity of larval fish for individual species of copepods, but did not observe any such preferences.

The size differences in spot and pinfish that we observed in the Newport River estuary may be due either to dissimilar spawning times, different growth rates, or both. Observations made in another North Carolina estuary (the White Oak River estuary) during 1969 indicated that estuarine spot and pinfish larval populations during January and February differed in size and that spot were significantly larger than pinfish (R. M. Lewis, pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.); spot average 18.0 mm in length while pinfish were 15.5 mm. Thus, there appears to be consistancy in the size differences observed in these two species during their influx into North Carolina estuarine waters.

Evacuation Rates

Regression coefficients for the equations describing the evacuation of copepods by larval pinfish and spot are shown in Table 4. The coefficients differ significantly from those calculated earlier (Kjelson et al. 1975). Copepod evacuation in our previous study was determined using fish collected in the estuary, placing them in a food-free environment, and observing evacuation. Those fish contained limited amounts of food at the beginning of the experiments apparently due to a low rate of feeding just prior to capture. Also, there was a 2°C difference between estuarine and laboratory water temperatures, and this may have altered the evacuation rates.

In an effort to measure the evacuation through a wide range of gut quantities and thus, hopefully, achieve a better description of evacuation, our present study used fish that initially had their guts full of copepods (21-57 copepods/fish) as determined from sacrificing 20 fish of each species at the beginning of the experiment. In addition, the possible stress of transport and rapid temperature changes in the earlier study were eliminated by using fish that had been acclimated to laboratory temperatures and that were fed in the laboratory.

The regression coefficients (slopes) achieved from our present study (Table 4) were significantly different from and approximately twice those found during the 1972-73 evacuation experiments. We consider the estimates of evacuation rates in the present study to be more representative of natural evacuation because the techniques used in measuring evacuation were more refined than in the earlier study.

The experimental temperatures, although different for the two species, were within the normal range for larvae immigrating into North Carolina estuaries. The larger negative slope in the regression model for spot compared with that for pinfish (Table 4) is probably due in part to the temperature differences (12°C for pinfish and

TABLE 4.—Linear regressions describing evacuation of copepods in pinfish and spot larvae. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of copepods per larva})$ and t = hours since feeding. n = number of data points.

Species	Size range (mm)	Temperature (°C)	A	B	n	r^2
Pinfish	15-18	12	1.30	−0.18	5	0.98*
Spot	16-20	17	1.84	−0.24	5	0.98*

*$P < 0.01$

17°C for spot), because Peters et al. (1974) showed that evacuation rate of juvenile pinfish and spot is related directly to temperature.

Feeding Periodicity and Feeding Rate

Observations of larval gut contents through 24 h again indicated that these larval fish contained the greatest amount of food during daylight hours (Figure 2). Peaks in gut contents for both pinfish and spot were at 1200 h. Water temperature was 15°C.

The periodicity observed in the gut contents does not represent the actual feeding periodicity. However, if our evacuation data and model are appropriate, the feeding periodicity may be calculated from the periodicity of gut contents. Gut contents at the beginning and end of each sampling interval (Figure 2) differ by an amount equal to the amount consumed minus the amount evacuated during that time period (Peters and Kjelson 1975). Thus, we can add the amount evacuated in each interval from the change in gut content to achieve the amount ingested during the interval. Maximum hourly feeding rates (from the 1000-1200-h sampling interval) were 26 copepods/h for pinfish and 17 copepods/h for spot.

Daily Rations

Estimates of daily ration for pinfish and spot larvae were higher than those obtained from the 1972-73 study. During our earlier study, pinfish ate 38 copepods/day while the present estimate indicates 92. Previous estimates for spot were 47 and 99 copepods/day while our present estimate is 115 (Table 5). The increased ration sizes are attributed to the use of higher instantaeous evacuation rates, and in the case of pinfish, to the presence of greater amounts of food during the feeding periodicity study (Figure 2). Pinfish digestive tracts had an average of 47 copepods/fish at 1200 h during the 1974 sample day whereas during 1972 they only had 10 copepods/fish. Spot gut contents at 1200 h averaged 17, 37, and 27, respectively in the three successive years of the study.

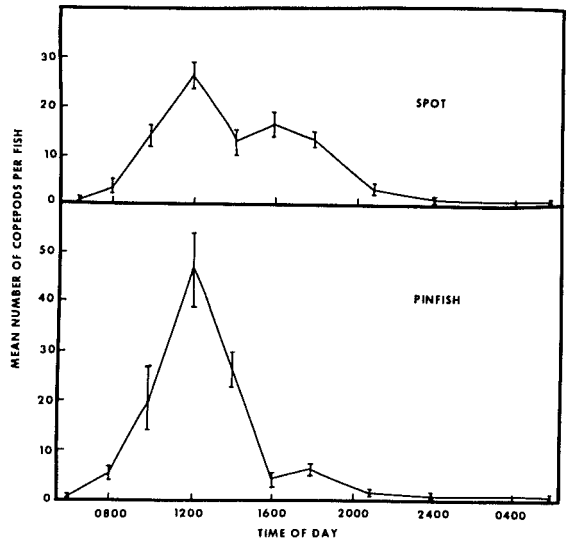

FIGURE 2. — Diel cycle of digestive tract contents in larval pinfish and spot at 15°C based upon the geometric mean of the number of copepods per fish (n = 10 fish per sampling time). Vertical bars are equal to two standard errors.

Based on our daily ration estimates of 1.3 and 2.0 cal/fish per day (Table 5) and the mean weights of the larvae, this was equal to a consumption rate of approximately 0.05 cal/mg fish wet weight per day for both species. The similarity is interesting since the average pinfish weight was only 60% that of spot and suggests that larvae of dissimilar species and sizes have similar consumption on a unit weight basis. Oxygen consumption measurements by D. E. Hoss (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.) indicate that similar respiration

TABLE 5.—Daily rations calculated from feeding studies and O_2 consumption measurements at 15°C for larval pinfish and spot in the Newport River estuary, N.C.

Species	Mean larvae wet wt (mg)	Number copepods/ fish · day	Calories/ fish · day	Calories/fish · day from O_2 consumption[1]	
				Gilson respirometer[2]	Flowing water respirometer[3]
Pinfish	25	92	1.3	0.9	1.0
Spot	42	115	2.0	1.3	2.0

[1]3.38 cal/mg O_2.
[2]Pinfish data from Hoss (1974), spot data from D. E. Hoss (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.).
[3]Pinfish data from W. F. Hettler, Jr. (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.), spot data from Hoss et al. (1974).

values on a per unit weight basis are typical for larvae of different species. Such similarity, however, may not exist for all species and size classes.

Measurements of postlarval metabolic expenditures based on oxygen consumptions at 15°C using a Gilson respirometer (Hoss, pers. commun.) and a flowing water respirometer (W. F. Hetter, Jr., pers. commun., Atlantic Estuarine Fisheries Center) are shown in Table 5. In both cases, fish were deprived of food for 24 h prior to measurement of their oxygen consumption, and the oxygen content of the water was near air saturation. Both Hoss and Hettler consider their measurements to be routine oxygen consumption as defined by Fry (1971), i.e., the mean rate observed in fish whose metabolic rate is influenced by random activity under experimental conditions in which movements are presumably somewhat restricted and the fish are protected from outside stimuli. Postlarval pinfish and spot in the flowing water respirometer were confined in an 11-liter chamber identical to that used for our laboratory current-feeding experiments described earlier and therefore were able to move about considerably.

A major problem exists in most measurements of fish oxygen consumption due to the uncertainty as to the animals state of activity (Altman and Dittmer 1971). Furthermore, measurements of fish respiration under natural conditions, termed normal respiration, have been unattainable; and although many investigators have estimated normal respiration by doubling routine metabolism, such a process is felt to be too subjective by Hoss and Peters (in press).

Considering the requirement for information on fish metabolic needs under natural conditions, it appears that our method of estimating the daily rations of postlarval fishes has potential value. Our estimates of daily rations were higher or equal to those rations estimated from oxygen consumption measurements. The observed differences in rations (Table 5) are reasonable if we assume that oxygen consumption measurements, particularly those of Hoss, are closer to routine respiration than to normal. The Hoss data have the lowest values, followed by the Hettler data. These differences, although probably not significant, are reasonable because the less restrictive system provided in the flowing water respirometer allowed the fish to move about in a manner similar to that in natural water. The lack of feeding activity by fish during respiration measurements and the respective decrease in oxygen consumption (Warren and Davis 1967) also should account for a lesser daily ration.

Based on earlier metabolic measurements, Thayer et al. (1974) estimated a daily ration of 1.04 cal/fish per day for larval fishes in the Newport River estuary during January and February. They indicated that, with larval energy requirements of this magnitude and a 90% assimilation efficiency, the larvae would be required to graze on an average of 10% of the zooplankton population per day. Furthermore, they suggested that this need may indeed have accounted for decreases in zooplankton observed in the estuary during spring. Our daily rations, based on feeding periodicity and evacuation (Table 5), are somewhat larger and tend to support the conclusion, assuming larval densities similar to those presented by Thayer et al. that larval fishes may have a significant impact on copepod populations in this system.

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LITERATURE CITED

ALDER, H. L., AND E. B. ROESSLER.
1964. Introduction to probability and statistics. 3rd ed. W. H. Freeman and Co., San Franc., 313 p.

ALTMAN, P. L., AND D. S. DITTMER (EDITORS).
1971. Respiration and circulation. Fed. Am. Soc. Exp. Biol., Bethesda, 930 p.

BAINBRIDGE, V., AND D. C. T. FORSYTH.
1971. The feeding of herring larvae in the Clyde. Rapp. P.-V Réun. Cons. Perm. Int. Explor. Mer. 160:104-113.

BERNER, L., JR.
1959. The food of the larvae of the northern anchovy *Engraulis mordax*. Inter-Am. Trop. Tuna Comm., Bull. 4:3-22.

BISHAI, H. M.
1959. The effect of water currents on the survival and distribution of fish larvae. J. Cons. 25:134-146.

BLAXTER, J. H. S.
1965. The feeding of herring larvae and their ecology in relation to feeding. Calif. Coop. Oceanic Fish. Invest. Rep. 10:79-88.

BLAXTER, J. H. S., AND F. G. T. HOLLIDAY.
1963. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1:261-393.

CIECHOMSKI, J. DZ., DE.
1967. Investigations of food and feeding habits of larvae and juveniles of the Argentine anchovy *Engraulis anchoita*. Calif. Coop. Oceanic Fish. Invest. Rep. 11:72-81.

DE MENDIOLA, B. R.
1974. Food of the larval anchoveta *Engraulis ringens* J. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 277-285. Springer-Verlag, N. Y.

DETWYLER, R., AND E. D. HOUDE.
1970. Food selection by laboratory-reared larvae of the scaled sardine *Harengula pensacolae* (Pisces, Clupeidae) and the bay anchovy *Anchoa mitchilli* (Pisces, Engraulidae). Mar. Biol. (Berl.) 7:214-222.

FRY, F. E. J.
1971. The effect of environmental factors on the physiology of fish. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 6, p. 1-98. Academic Press, N. Y.

HEINLE, D. R.
1966. Production of a calanoid copepod, *Acartia tonsa* in the Patuxent River estuary. Chesapeake Sci. 7:59-74.

HOAGMAN, W. J.
1974. Vital activity parameters as related to the early life history of larval and post-larval lake whitefish (*Coregonus clupeaformis*). *In* J. H. S. Blaxter (editor), The early life history of fish, p. 547-558. Springer-Verlag, N. Y.

HOSS, D. E.
1974. Energy requirements of a population of pinfish *Lagodon rhomboides* (Linnaeus). Ecology 55:848-855.

HOSS, D. E., W. F. HETTLER, JR., AND L. C. COSTON.
1974. Effects of thermal shock on larval estuarine fish – ecological implications with respect to entrainment in power plant cooling systems. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 357-371. Springer-Verlag, N. Y.

HOSS, D. E., AND D. S. PETERS.
In press. Respiratory adaptation: Fish. Proc. Estuarine Res. Fed. 3rd Int. Bienn. Conf., Oct. 6-9, 1975, Galveston, Tex.

HOUDE, E. D.
1967. Food of pelagic young of the walleye, *Stizostedion vitreum vitreum*, in Onedia Lake, New York. Trans. Am. Fish. Soc. 96:17-24.
1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). J. Fish. Res. Board Can. 26:1647-1659.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes (Translated from Russian by D. Scott) Yale Univ. Press, New Haven, 302 p.

KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON
1975. The general feeding ecology of post-larval fishes in the Newport River estuary. Fish. Bull., U.S. 73:137-144.

LEWIS, R. M., W. F. HETTLER, JR., E. P. H. WILKENS, AND G. N. JOHNSON.
1970. A channel net for catching larval fishes. Cheasapeake Sci. 11:196-197.

MARAK, R. R.
1960. Food habits of larval cod, haddock, and codfish in the Gulf of Maine and Georges Bank area. J. Cons. 25:147-157.
1974. Food and feeding of larval redfish in the Gulf of Main. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 267-275. Springer-Verlag, N. Y.

MURPHY, G. I.
1961. Oceanography and variations in the Pacific sardine population. Calif. Coop. Oceanic Fish. Invest. Rep. 8:55-64.

NAKAI, Z., K. HONJO, S. HATTORI, T. KIDACHI, AND H. SUZUKI.
1966. Further examples of Hjort's hunger theory. 2nd Int. Oceanogr. Congr., Mosc. Abstr. of pap., p. 263.

O'BRIEN, W. J., AND G. L. VINYARD.
1974. Comment on the use of Ivlev's electivity index with planktivorous fish. J. Fish. Res. Board Can. 31:1427-1429.

PETERS, D. S., AND M. A. KJELSON.
1975. Consumption and utilization of food by various post-larval and juvenile North Carolina estuarine fishes. *In* L. E. Cronin (editor), Estuarine research, Vol. 1, p. 448-472. Academic Press, N.Y.

PETERS, D. S., M. A. KJELSON, AND M. T. BOYD.
1974. The effect of temperature on digestion rate in the pinfish, *Lagodon rhomboides;* spot, *Leiostomus zanthurus;* and silverside, *Menidia menidia*. Proc. 26th Annu. Conf. Southeast Assoc. Game Fish Comm., p. 637-643.

RYLAND, J. S.
1963. The swimming speeds of plaice larvae. J. Exp. Biol. 40:285-299.

SCHUMANN, G. O.
1965. Some aspects of behavior in clupeid larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 10:71-78.

SEREBROV, L. I.
1973. Effect of a current on the intensity of feeding in certain fish. Hydrobiol. J. 9(2):68-70.

SHIROTA, A.
1970. Studies on the mouth size of fish larvae. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 36:353-368.

THAYER, G. W., D. E. HOSS, M. A. KJELSON, W. F. HETTLER, JR., AND M. W. LACROIX.
1947. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. Chesapeake Sci. 15:9-16.

WARREN, C. E., AND G. E. DAVIS.
1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. *In* S. D. Gerking (editor), the biological basis of fresh water fish production, p. 175-214. Blackwell Sci. Publ., Oxf.

THERMAL TOLERANCE AND RESISTANCE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

GARY D. BREWER[1]

ABSTRACT

An experimental, flow-through seawater system, constructed to maintain juvenile and adult northern anchovy, *Engraulis mordax*, and rear embryos and larvae through yolk-sac absorption under controlled temperature and photoperiod regimes, was used to determine aspects of thermal tolerance, resistance, rates of acclimation, and some effects of temperature on the development and growth of the anchovy.

Thermal tolerance was determined for juvenile and adult fish, acclimated to six constant temperatures between 8° and 28°C. Thermal resistance (minutes until death for fish exposed to a lethal temperature) was independent of photoperiod and fish size; however, females proved more resistant than males, and resistance decreased at night. Acclimation (as measured by resistance) from 12° to 20°C was nearly complete after 2-day exposure to the higher temperature; acclimation from 20° to 12°C was nearly complete after 5-day exposure to the lower temperature. Fish subjected to fluctuating water temperatures between 12° and 20°C proved less resistant to cold than a 12°C (constant) acclimated group and less resistant to heat than a 20°C (constant) acclimated group.

Thermal tolerance was determined for larvae in the yolk-sac stage, acclimated to four constant temperatures between 12° and 24°C. Although hatching occurred at temperatures as high as 29.5°C and as low as 8.5°C, the percentage of normally developed larvae equaled that of controls (incubated at 16°C) only between temperatures of 27.0° and 11.5°C. Embryos in the blastodisc stage proved most sensitive to acute temperature increases when compared to embryos in the blastopore closure stage and larvae in the yolk-sac stage. These same three stages proved insensitive to acute temperature decreases to 0.5°C for 60-min exposure periods.

Temperature is discussed in relation to anchovy distribution and survival under natural and artificially created thermal conditions.

Research on the effects of temperature on aquatic organisms has been given impetus in recent years as numerous lakes and streams are considered potential heat reservoirs by electric power generating plants and other industrial concerns. As the demands for water as a heat transfer medium continue to increase dramatically, more attention will be turned to the marine environment for large volumes of water and surface areas necessary for the dissipation of excess heat (Naylor 1965; de Sylva 1969; Tarzwell 1972). Unchecked thermal loading of freshwater and nearshore marine ecosystems will inevitably pose a serious threat to the homeostasis and well-being of aquatic communities unless realistic guidelines are established and enforced. Such guidelines must be based on knowledge of how aquatic organisms respond to both acute and chronic temperature changes.

This study details aspects of thermal tolerance and resistance (as defined by Fry 1971) on the embryo, larval, juvenile, and adult stages of the northern anchovy, *Engraulis mordax* Girard. The study was prompted by the proposed discharge of thermal effluent into the Los Angeles-Long Beach Harbor. The biology and fishery of the northern anchovy in the Los Angeles-Long Beach Harbor were described by Brewer (1975a).

The general biology of the northern anchovy has been summarized by Baxter (1967), Messersmith et al. (1969), the California Department of Fish and Game (1971), and Brewer (1975a). A dramatic increase in abundance of *E. mordax* during the past 20 yr (Ahlstrom 1967; Smith 1972) has prompted an intense interest in the biology and fishery potential of this clupeoid. The California Department of Fish and Game (1971:48) considered the anchovy ". . . the most abundant species with immediate harvest potential in the California Current system."

MATERIALS AND METHODS

Experiments were conducted in a small, tem-

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perature and photoperiod controlled, flow-through seawater system. The system delivered filtered, ultraviolet-sterilized seawater from the Los Angeles-Long Beach Harbor to five round, 950-liter, fiber glass aquaria (1.5 m in diameter, 0.6 m high) and a single 400-liter rectangular water table, all housed in a light-tight aluminum cargo container (Figure 1). An exchange rate of 2-6 liters/min was maintained in each aquarium, with overflow drainage provided by standpipes. Wastewater was not recirculated. Temperatures were maintained within ±0.5°C.

Above each aquarium were two incandescent light bulbs controlled by separate dimmer controls and regulated by a 7-day timer to simulate photoperiods. The "day" bulb provided 700 lx and the "night" bulb provided 16 lx to the surface of each aquarium. Oxygen was maintained at or near saturation levels in all acclimation and test tanks by splashing incoming water at the surface and by bubbling air stones in the aquaria. Salinity varied between 31.4 and 33.8‰ (mean 33.1‰) during the study period.

Juveniles and Adults

Juvenile and adult *E. mordax* were obtained from a live-bait dealer. The initial transfer from the bait boat to the 950-liter acclimation tanks caused 20-30% mortality during the first 2-3 days of confinement. Within 2-4 days, healthy fish began to feed and were offered a daily ration, equivalent to approximately 4% of the fish's wet weight, of Trout Chow.[2] This ration was supplemented with chopped anchovy, chopped squid, brine shrimp, or wild plankton equal to approximately 1% of the fish's wet weight. Adjusted fish ate voraciously and mortality became insignificant in acclimation tanks within 1 wk. Acclimation tanks were stocked with between 3 and 7 kg of anchovy. The food ration was withheld for a period of 24 h prior to all thermal tests on juvenile and adult fish.

Ninety-six Hour Tolerance

Standardized techniques for the determination of lethal temperatures (Fry et al. 1942; Brett 1944; Fry 1947) call for a series of experiments in which the animals are acclimated to several different constant temperatures. Acclimated fish are then abruptly transferred to test aquaria previously equilibrated to various high and low temperature extremes. Mortality is monitored and recorded.

This procedure extends the concept of lethal temperatures from two extreme end points, to a family of upper and lower (incipient) lethal levels. The ultimate upper and lower lethal temperatures, which circumscribe the extreme tolerance limits, may be determined by graphic extrapolation—that is, by drawing a line through those high and low test temperatures that proved lethal to 50% of the test animals for each acclimation temperature. The extrapolated line will then

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

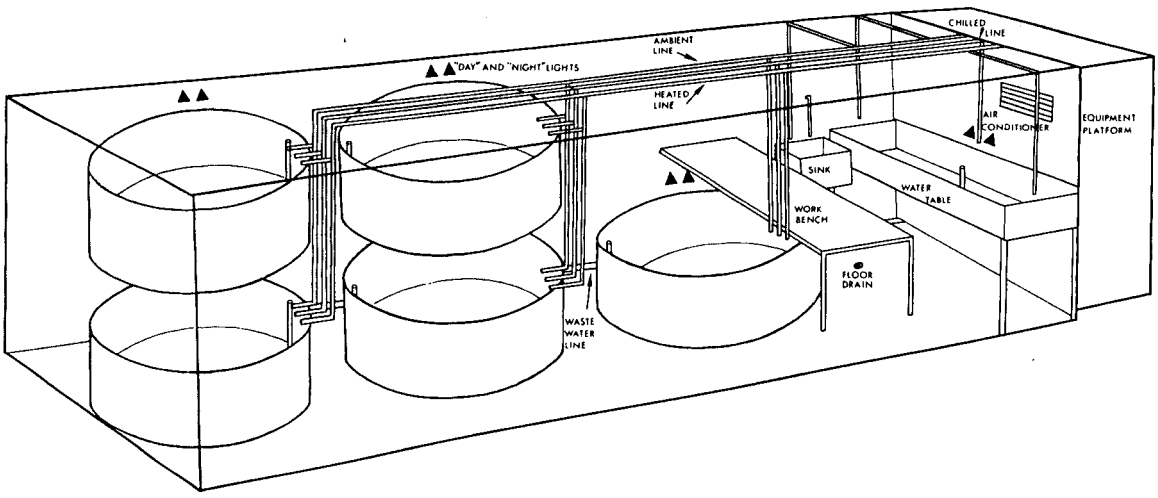

FIGURE 1.—Diagram of the flow-through seawater system used for experiments on *Engraulis mordax*.

intersect a diagonal at the upper and lower extremes, which represents those points where the lethal temperatures equal the acclimation temperatures. Fish cannot be acclimated to temperatures above or below these experimentally determined ultimate upper and lower lethal temperatures, respectively.

Juvenile and adult *E. mordax* between 45 and 139 mm SL (standard length) were held for a minimum of 3 wk at constant temperatures of 8°, 12°, 16°, 20°, 24°, and 28°C and under a light cycle of 12 h light and 12 h dark. Unless otherwise noted, the term "acclimated fish" designates *E. mordax* held under such conditions. "Juvenile" refers to metamorphosed fish less than 100 mm SL, while "adult" refers to fish over 100 mm.

The fish's susceptability to mechanical damage increased at high and low acclimation temperatures. Therefore, each acclimation temperature-test series was accompanied by a series of strict control transfers, and the observed mortalities for each series were adjusted separately, based on the respective control mortalities. Fish were considered dead and were removed when all swimming movements ceased. Ninety-six hour LD_{50} (mean lethal dose) temperatures (i.e., incipient lethal levels) were estimated from regression lines plotted on probit paper (Sokal and Rohlf 1969). Experiments were conducted between February 1973 and November 1974 and included all seasons. About 20 fish were used for each test.

Resistance as a Function of Size, Sex, Time, and Photoperiod

To test the potential influence of photoperiod, sex, size, and diel effects, anchovies were acclimated to 20°C, tested by direct transfer to 30°C, and the time to death (resistance time) determined. As the fish died, they were removed from the test aquaria, measured, and adult fish were sexed. Identical tests were conducted in the morning (0900 h) and in the evening (2100 h). Tests were also conducted after fish had been held under a short-day photoperiod (8 h light) and a long-day photoperiod (16 h light) for periods of 3 wk each. All thermal resistance tests were run during the summer and fall.

Rates of Thermal Acclimation

Juvenile and adult anchovy acclimated to 12°C were subjected to an 8°C temperature change over a 24-h period to 20°C, and then tested for resistance to 30°C on the same day and after 1-, 2-, and 4-day exposure to the 20°C temperature. Moreover, fish acclimated to 20°C were subjected to a temperature decrease to 12°C over a 24-h period, and then tested for resistance to 6°C on the same day and after 2-, 5-, and 9-day exposure to the 12°C temperature. As the fish become acclimated to the new higher or lower temperature, one would expect the mean resistance times for these fish to approach and eventually equal the mean resistance times (e.g., reach a steady-state) of fish acclimated to 20° and 12°C and tested at 30° and 6°C, respectively (controls).

Effects of Cycled Temperatures on Resistance

In view of the observations by Mais (1974) that *E. mordax* may undergo diel vertical migrations and consequently experience fluctuating temperatures, I examined the relative thermal resistance of anchovies subjected to regular changes in temperature from 12° to 20°C over 48-h intervals. Fish acclimated to 20°C were gradually subjected to decreasing temperatures to 12°C over 24 h and then back to 20°C over the next 24 h. The cycle was repeated for 25 days, at which time a sample of fish which had just reached 20°C was tested for resistance to 30°C. The following morning, as the remaining fish reached 12°C, a sample was tested for resistance to 6°C.

Embryos and Larvae

Engraulis mordax eggs, caught in plankton tows in or near the Los Angeles-Long Beach Harbor throughout the year, were utilized for experiments on embryos and larvae. Water temperatures, at time of capture, varied between 13° and 18°C. In the laboratory, eggs in the blastodisc stage were placed into 2-liter glass jars and maintained at 12°, 16°, 20°, or 24°C until transferred to incubation or test vessels which consisted of 250-ml jars containing 60 ml of seawater. Not more than five eggs or larvae were tested per jar.

Twenty-four Hour Tolerance

Larvae in the yolk-sac stage were tested within 1 day after hatching at each acclimation temperature. Larvae were pipetted from each acclimation temperature directly into test vessels ranging

from 6° to 32°C. Mortality was recorded after 24 h. Incipient lethal levels for each acclimation level were estimated as described for the juveniles and adults.

Hatching and Developmental Temperature Limits

Eggs in the blastodisc stage were transferred to a series of incubation vessels, after which the temperatures were gradually raised or lowered from the ambient level of 16°C over a period of 60 min in order to avoid possible shock effects to the developing embryos. Incubation temperatures were then held constant (±0.5°C) between 6° and 12°C, and 26° and 31°C at 0.5°C intervals. A 16°C temperature was used as a control. Development was considered normal only if the larvae were free of obvious deformities (e.g., spinal curvatures) until pigmented eyes and functional jaws were evident, and death had occurred only after yolk reserves were exhausted.

Resistance to Acute Temperature Changes

Embryos in the blastodisc stage (ca. 12-14 h after fertilization at 16°C) and in the blastopore closure stage (ca. 36-38 h after fertilization), and larvae in the yolk-sac stage (within 24 h after hatching) were subjected to temperature shocks for periods of 1, 3, 5, and 60 min. Embryos and larvae were pipetted from incubation vessels maintained at 16°C directly into water at high and low temperature extremes. After the exposure period, the embryos and larvae were returned directly to the incubation vessels at 16°C where they remained for 48 h after hatching. Mortality and developmental abnormalities were recorded.

This procedure was an attempt to simulate what the embryos and larvae might actually experience if entrained by intake pipes of electrical generating plants or LNG (Liquified Natural Gas) vaporization plants (or either thermal plums), subjected to rapid temperature increases and decreases in the heat exchange systems, and subsequently flushed back into the natural environmental temperatures at the outfall.

Development and Growth

Experiments were designed to determine the temperatures required for optimal growth of anchovy larvae. The tests were confined to that period of larval life between hatching and starvation following exhaustion of all stored yolk reserves. No food was offered.

Eggs in the blastodisc stage were reared through hatching in a series of constant temperature baths between 10° and 26°C. On the day of hatching and each subsequent day, approximately 10 larvae were sacrificed from each rearing temperature and measured from the tip of the snout to the end of the notochord with an ocular micrometer to the nearest 0.05 mm. This procedure was continued until all larvae at each rearing temperature died of starvation.

RESULTS

Juveniles and Adults

Ninety-six Hour Tolerance

Experiments on juvenile and adult tolerance encompassed 117 separate 96-h tests and 2,400 fish. Control survival ranged from lows of 81.3 and 87.9% at 8° and 28°C acclimation temperatures, respectively, to 98.3% at the 16°C acclimation temperature.

Figure 2 graphically depicts the lethal temperature relations, with adjusted percent mortality plotted against test temperatures for acclimation levels of 8° and 28°C. Adjusted upper and lower LD_{50} temperatures were plotted against acclimation temperatures in Figure 3 and a thermal tolerance polygon constructed (Fry 1947). Ultimate upper and lower lethal temperatures are estimated by extrapolation (line fitted by eye) to be

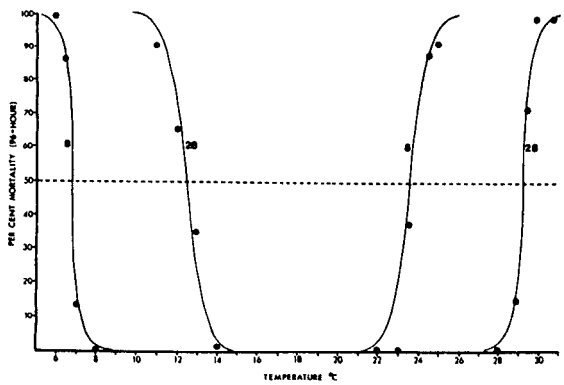

FIGURE 2.—Effects of acclimation temperatures of 8° and 28°C on the upper and lower lethal temperatures of *Engraulis mordax* juveniles and adults (original date in Brewer 1975b).

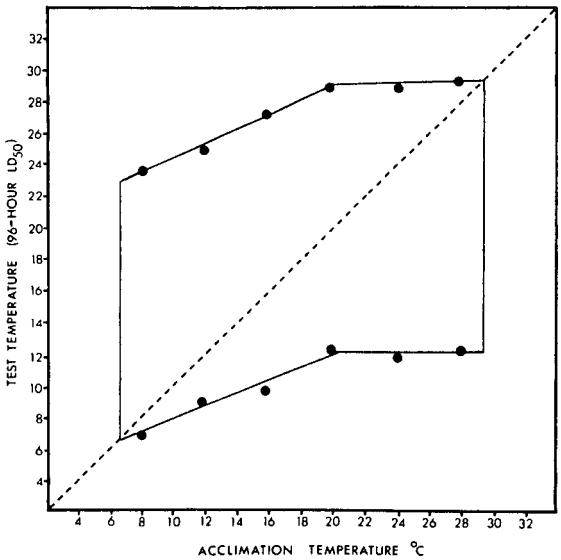

FIGURE 3.—Thermal tolerance polygon for *Engraulis mordax* juveniles and adults. Those points where the extrapolated LD_{50} levels intersect the diagonal represent the extreme (ultimate) tolerance limits and correspond to 6.5° and 29.5°C.

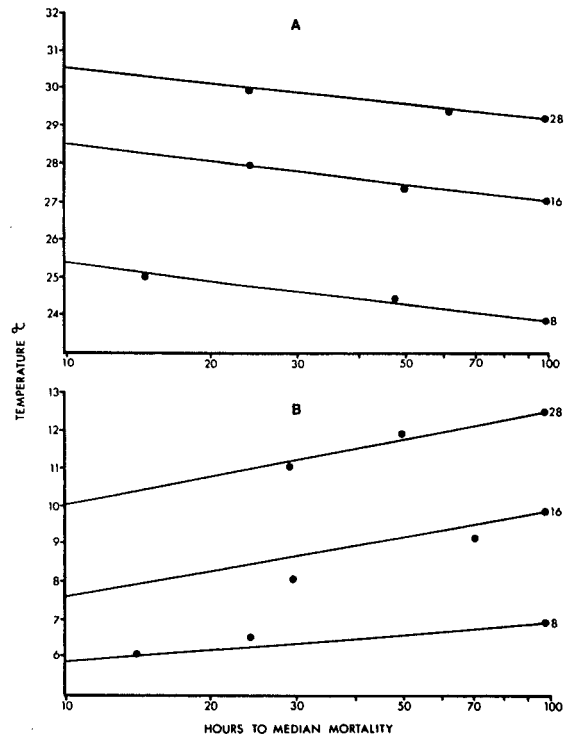

FIGURE 4.—Resistance times to median mortality of juvenile and adult *Engraulis mordax* exposed to high (A) and low (B) lethal temperatures when acclimated to 8°, 16°, and 28°C.

29.5° and 6.5°C, respectively. These temperatures represent the maximum tolerance range of *E. mordax* juveniles and adults sampled from southern California and maintained under laboratory conditions as described. Anchovy cannot be acclimated to temperatures beyond these extremes. Attempts were made to slowly acclimate fish to 29.5° and 6.5°C, but they proved futile.

Figure 4 shows the resistance times to median mortality of juvenile and adult *E. mordax*, acclimated to 8°, 16°, and 28°C, upon exposure to temperatures beyond incipient lethal levels. These curves were derived by plotting cumulative mortality as percentages against exposure time to estimate the time to LD_{50} for each test temperature.

Resistance as a Function of Size, Sex, Time, and Photoperiod

Results of experiments on thermal resistance to 30°C in relation to size, sex, and potential diel and photoperiod effects are summarized in Table 1. Analysis of variance (one-way classification) showed that resistance times to lethal temperatures of 30°C were not significantly different ($P>0.05$) for fishes of different sizes (<79 mm; 80-99 mm; >100 mm) or for fishes maintained under different photoperiods (8, 12, and 16 h light). These results should be verified with larger sample sizes. Resistance times showed highly significant differences ($P<0.01$) for males compared with females, and for tests conducted in the morning as compared with those conducted at night. Females proved more resistant than males, and animals tested in the morning showed greater resistance than those tested in the evening.

TABLE 1.—Comparison of resistance times (minutes until death) for juvenile and adult *Engraulis mordax* acclimated to 20°C and immediately transferred to aquaria at 30°C.

Item	*N*	Range (min)	Mean (min)	SD	SE
Length (mm):					
<79	11	49-285	133.9	74.9	22.6
80-99	22	41-302	149.4	62.3	13.3
>100	12	37-343	141.3	102.9	29.7
Sex:					
Male	20	6-118	40.9	33.1	7.4
Female	36	4-401	116.8	113.6	18.9
Time of test:					
Morning	45	31-343	143.5	76.3	11.4
Evening	38	8-244	72.6	66.7	10.8
Photoperiod (hours of light):					
8	14	6-401	154.5	127.0	34.0
12	34	37-302	141.1	67.6	11.6
16	11	31-343	150.8	102.3	30.9

Rates of Thermal Acclimation

Results suggest that acclimation from 12° to 20°C nears completion within 2 days of exposure to the higher temperature. Mean resistance times for day 2 and day 5 samples exceeded the mean resistance time for the control sample. However, analysis of variance shows that the variation between day 2, day 5, and control samples is not significant ($P>0.05$). The relatively high resistance of some fish in the day 2 and day 5 samples, which exceeded the resistance of control fish, may be due to slight temperature variations (±0.2°C) in the test aquaria, or possibly to "physiological overshoots" to the acclimation process (Prosser 1973). Figure 5 shows the progress toward acclimation with contined exposure to the higher temperature. Most noticeable is the change in shape of the resistance curves with acclimation. Nonacclimated fish succumb to the lethal 30°C temperature quickly, probably as a result of "shock effects" (Scott 1964; Tyler 1966; Allen and Strawn 1971). Acclimation to the higher temperature diminishes the shock effects. Apparently, acclimated fish die from secondary causes termed "direct effects" by Fry (1971). The physiological basis of the shock and direct effects is not clear. Acclimation from warm to cool water (20° to 12°C) appears to be nearly complete by day 5 (Figure 6). As acclimation progresses and resistance to low temperatures is increased, death rate becomes increasingly regular; the graphs approach a straight line and the effects of the initial cold shock are largely eliminated. Because these tests used small sample sizes, statistical differences cannot be demonstrated.

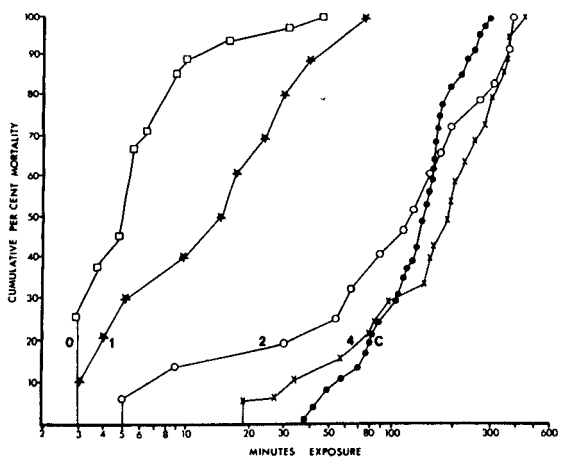

FIGURE 5.—Cumulative percent mortality of *Engraulis mordax* juveniles and adults as a function of exposure to 30°C. The response of a 20°C acclimated control group (C) is compared with that of a 12°C acclimated group after 0-, 1-, 2-, and 4-day exposures to 20°C (original data in Brewer 1975b).

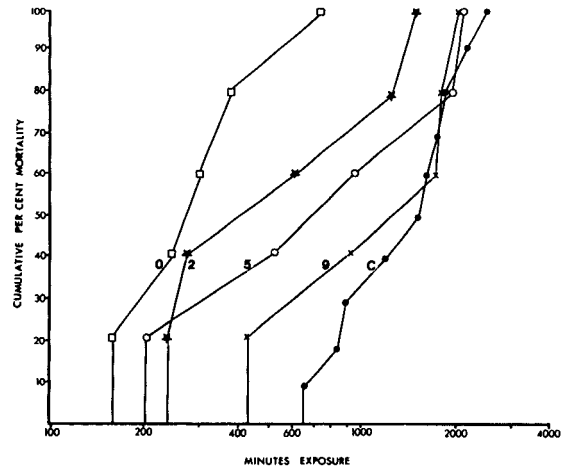

FIGURE 6.—Cumulative percent mortality of *Engraulis mordax* juveniles and adults as a function of exposure to 6°C. The response of a 12°C acclimated control group (C) is compared with that of a 20°C acclimated group after 0-, 2-, 5-, and 9-day exposures to 12°C (original date in Brewer 1975b).

Effects of Cycled Temperatures on Resistance

Results are summarized in Table 2. Mean resistance times to 6° and 30°C for fish subjected to periodic changes in temperature between 12° and 20°C were well below the mean resistance times of fish acclimated to a constant 12°C and constant 20°C, respectively. However, the fish have greater high temperature resistance than those acclimated to 12° and greater low temperature resistance than those acclimated to 20°C.

TABLE 2.—Resistance times (minutes until death) of juvenile and adult *Engraulis mordax* to 6° and 30°C after being subjected to temperature fluctuations between 12° and 20°C on a 48-h cycle for a period of 25 days.

Test temp	Group	*N*	Range (min)	Mean (min)	SD	SE
6°C	12°C acclimated	10	643-2,490	1,419.0	589.0	186.3
	20° to 12°C	10	117-1,111	410.6	374.5	118.4
30°C	20°C acclimated	34	37-302	141.1	67.6	11.6
	12° to 20°C	10	6-68	28.0	22.1	7.0

Embryos and Larvae

Twenty-four Hour Tolerance

Over 600 larvae were tested in the 24-h tolerance experiments. Generally, 10 or more larvae were tested at each temperature. The percentage (normal) survival for controls ranged from 72.7 at the 12°C acclimation level to 86.7 at 16° and 20°C acclimation temperatures.

Apparently the physiological mechanisms for thermal acclimation are little developed in *E. mordax* larvae in the yolk-sac stage. Figure 7 shows the 24-h lethal temperature relations with percent adjusted mortality plotted against test temperatures for acclimation temperatures of 12° and 24°C. Rearing the yolk-sac larvae in warm and cold water does little to increase or decrease their upper or lower lethal temperatures, respectively. Potential effects of parental acclimation temperatures (Hubbs and Bryan 1974) or the exposure of eggs to acclimation temperatures at the time of fertilization require investigation.

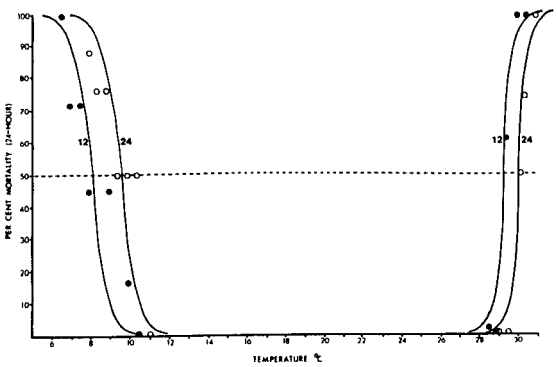

FIGURE 7.—Effects of acclimation temperatures of 12° and 24°C on the upper and lower lethal temperatures of *Engraulis mordax* larvae in the yolk-sac stage (original data in Brewer 1975b).

In Figure 8, adjusted upper and lower LD_{50} temperatures are plotted against respective acclimation temperatures in the construction of a thermal tolerance polygon. Ultimate upper and lower lethal temperatures are estimated to be 30.2° and 7.0°C, respectively.

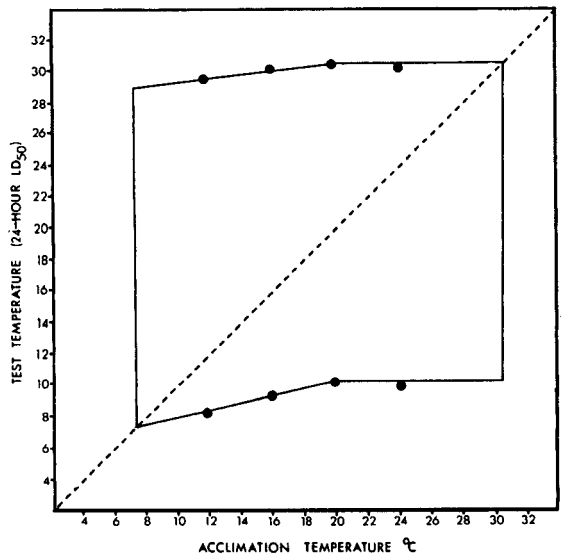

FIGURE 8.—Thermal tolerance polygon for *Engraulis mordax* larvae in the yolk-sac stage. Those points where the extrapolated LD_{50} levels intersect the diagonal represent the extreme tolerance limits and correspond to 7.0° and 30.2°C.

TABLE 3.—Effects of temperature on hatching and development of *Engraulis mordax* through yolk-sac absorption and eye pigmentation of larvae. Temperatures were maintained within ±0.5°C of those shown below.

Rearing temp (°C)	*N*	No. hatching	With normal development		Adjusted survival (%)
			No.	%	
31.0	10	0	0	0	0.0
30.0	10	0	0	0	0.0
29.5	10	3	3	30.0	33.3
29.0	10	3	3	30.0	33.3
28.5	10	8	5	50.0	55.6
28.0	30	27	23	76.7	84.9
27.5	10	9	7	70.0	77.8
27.0	30	28	27	90.0	100.0
26.5	10	8	8	80.0	88.9
26.0	10	9	9	90.0	100.0
[1]16.0	30	29	27	90.0	100.0
7.5	10	0	0	0.0	0.0
8.0	10	0	0	0.0	0.0
8.5	10	2	0	0.0	0.0
9.0	10	3	0	0.0	0.0
9.5	15	3	0	0.0	0.0
10.0	10	6	1	10.0	11.1
10.5	10	5	3	30.0	33.3
11.0	10	8	6	60.0	66.7
11.5	10	9	9	90.0	100.0
12.0	10	10	9	90.0	100.0

[1]Control.

Hatching and Developmental Temperature Limits

Results of this experiment are given in Table 3. Although hatching was observed at temperatures as high as 29.5°C and as low as 8.5°C, 50% (adjusted) normal development occurred between 11.0° and 28.5°C. Only below 27.0°C and above 11.5°C did the percentages of hatching and normal development approach those for the controls.

Resistance to Acute Temperature Changes

Resistance to high temperatures is surprisingly great for embryos and larvae when exposure is of short duration (Figure 9). Blastodisc stage embryos are least resistant while yolk-sac larvae are most resistant; LD_{50} values for the 60-min exposure period for the larvae are within 1.3°C of the extrapolated 24-h tolerance limits determined from Figure 8. *Engraulis mordax* embryos and larvae appear to be insensitive to abrupt temperature decreases down to 0.5°C for short periods (Brewer 1975b).

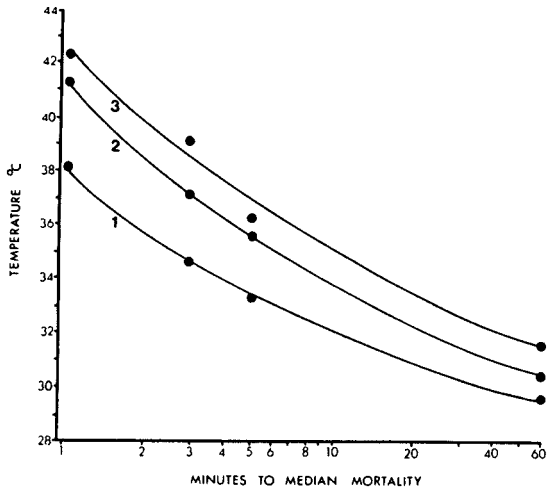

FIGURE 9.—Minutes to median mortality for the blastodisc stage (1), blastopore closure stage (2), and yolk-sac stage (3) subjected to abrupt temperature increases from 16°C (original data in Brewer 1975b).

Development and Growth

Table 4 summarizes data on the growth of larvae at constant temperatures between 10° and 26°C. The maximum size of larvae attained at any temperature before shrinkage due to starvation was 4.16 mm. This is considerably smaller than the value of 4.8 mm given by Lasker (1964) for *E. mordax* larvae reared under similar conditions. Variability in egg size may be responsible for this discrepancy; egg size of the Argentine anchovy, *E. anchoita,* is known to vary by season and location (de Ciechomski 1973).

The highest mean growth response was obtained for larvae reared at 18°C (3.94 mm). Mean larval lengths less than 3.78 mm were considered significantly smaller than the maximum response at 18°C (Least Significant Difference, Sokal and Rohlf 1969). It seems reasonable to assume that larvae reared at temperatures of 12°C or lower and 24°C or higher converted yolk into body tissue at suboptimal levels. Analysis of variance showed that maximum mean lengths attained by larvae reared at 14°, 17°, 18°, and 20°C were not significantly different ($P>0.05$).

TABLE 4.—Comparison of the maximum size attained by *Engraulis mordax* larvae in the yolk-sac stage before shrinkage due to starvation.

Incubation temp (°C)	*N*	Range (mm)	Mean (mm)	SD	SE
10	10	3.37-3.79	3.63	0.13	0.04
12	10	3.31-4.00	3.62	0.21	0.07
14	10	3.63-4.10	3.93	0.18	0.06
17	10	3.63-4.00	3.81	0.15	0.05
18	10	3.63-4.10	3.94	0.16	0.05
20	10	3.52-4.16	3.82	0.18	0.06
24	10	3.52-4.00	3.71	0.14	0.04
26	10	3.42-3.84	3.56	0.13	0.04

DISCUSSION

Figure 10 shows a graphic summary of various field and laboratory-deduced temperature ranges and limits for the distribution and survival of *E. mordax*. A temperature range of about 4.5°C lies between the highest temperatures that anchovy adults have been found in nature (25°C, Baxter 1967) and the experimentally determined upper lethal temperature for juveniles and adults (29.5°C). Anchovy had been maintained in the laboratory at 28°C for weeks with no apparent ill effects. The fish are extremely active at this temperature and their metabolic requirements are undoubtedly considerable. Anchovy maintained at 28°C and fed the standard ration lost weight. The upper environmental temperature limit and southern distributional limit of *E. mordax* may be dictated by metabolic demands which outweigh the ration supplied by the environment. Maximum temperatures off Cabo San Lucas, which is the southern range limit for *E. mordax*, exceeds 25°C (Lynn 1967). Interestingly, 25°C corresponds to the highest temperature that juvenile *E. mordax* would venture into when tested in laboratory thermal gradients (Brewer 1974). Moreover, the plateau in the thermal tolerance polygon (Figure 3) shows that acclimation temperatures of 24°C and above have little effect on increasing the incipient upper lethal temperature. Apparently the anchovy's overall mechanisms for

physiological compensation begin to break down at temperatures above 25°C.

Reid's (1967) observation that *E. mordax* may overwinter at temperatures of 7° or 8°C off British Columbia is of special interest. These fish may be within less than 1°C of their lower lethal temperature. Juvenile and adult anchovy acclimated to 8°C in the laboratory and transferred to 7°C made no effort to consume food offered to them after 5 days at the lower temperature. I have not confirmed this by stomach examination, but feeding, if it takes place at all, is minimal at this low temperature.

It is important to consider the possibility that the thermal tolerance and resistance of *E. mordax* may be different for northern, central, and southern populations. Apparently genetically distinct, these populations were first identified on the basis of meristic characters by McHugh (1951) and later on by serum transferrin analysis conducted by Vrooman and Smith (1971). If the thermal requirements of these populations were distinct, I would anticipate their reproductive temperature ranges to vary accordingly. Richardson's (1973) data on anchovy spawning off Oregon discount this. In any case, thermal resistance experiments on samples from each population would be of interest.

Experiments on the resistance of juvenile and adult anchovy to a high lethal temperature showed no significant difference in the mean resistance times for fish of different sizes or for fish maintained under different photoperiods. However, females were more resistant than males, and animals tested in the morning showed greater resistance than those tested in the evening. Investigators have variously shown significant differences in one or more of the factors tested here, depending on the species. Thermal resistance has been found to vary according to size, with large *Oncorhynchus* (Salmonidae) and *Carassius* (Cyprinidae) more resistant to cold (Brett 1952; Hoar 1955, respectively) and large *Clupea* (Clupeidae) less resistant to heat (Brawn 1960). *Carassius* maintained under long photoperiods were more resistant to high temperatures than fish maintained under short photoperiods, while resistance to cold temperatures was greater for the short photoperiod fish (Hoar 1956). Hoar discovered that male *Carassius* were more resistant to low temperature extremes than females. Heath (1963) observed slight differences in critical thermal

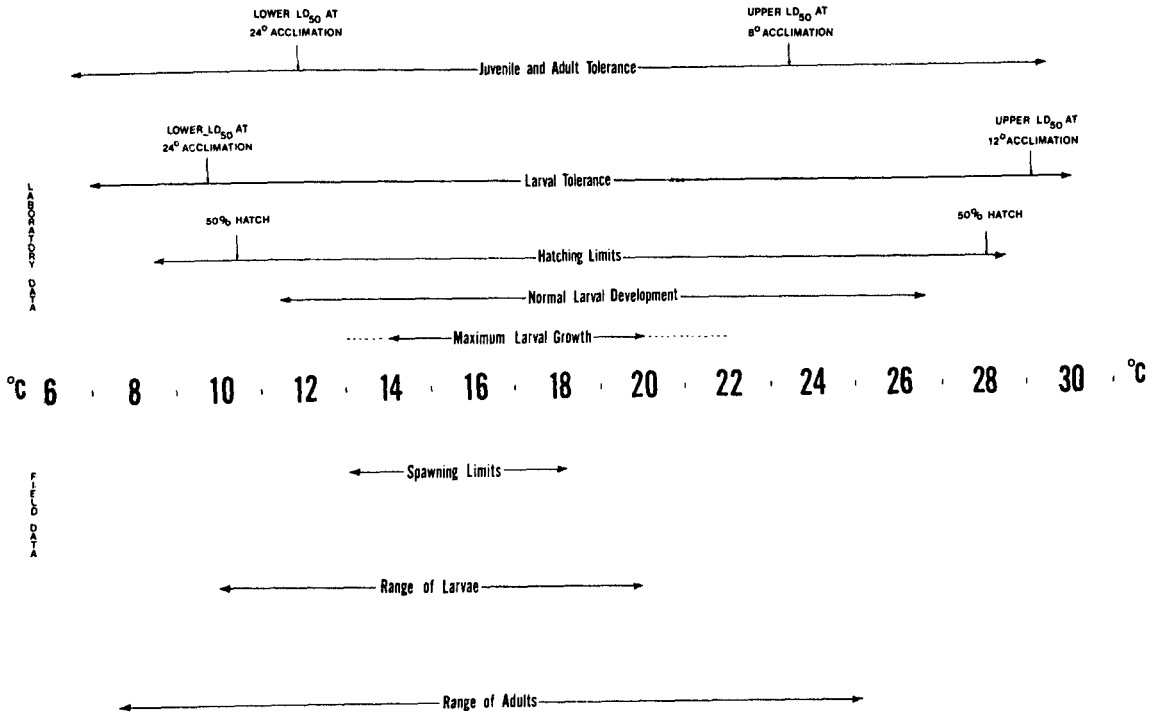

FIGURE 10.—Field and laboratory deduced thermal limits for the distribution and survival of *Engraulis mordax*.

maximum temperatures for *Salvelinus* (Salmonidae), depending on the time the test was conducted. He also noticed that maximum tolerance followed a 24-h cycle and suggested that this was a physiological adaptation to natural habitats with 24-h variations in temperature.

The present experiments on *E. mordax* were conducted in the fall when anchovy presumably ascend from deep water to warm surface waters in the evening (California Department of Fish and Game 1971). If a circadian cycle of thermal resistance existed in anchovy, one might anticipate maximum resistance to high temperatures to occur in the evening. The data in Table 1 suggest that, under laboratory conditions, resistance to high temperature is reduced in the evening.

The embryonic and larval stages of pelagic fishes are potentially the most vulnerable ones to thermal stresses. While juvenile and adult fishes may detect and avoid unfavorable environmental conditions (Bull 1928; Doudoroff 1938; Alabaster and Robertson 1961; Coutant 1969), the eggs and planktonic larvae of fishes such as *E. mordax* are at the mercy of currents which might carry them into environments unfavorable for growth or survival. Reviews by de Sylva (1969) and Brett (1970) have shown that on the average, marine fish larvae are one-third to one-half as tolerant to thermal stresses as their conspecific adults. Normal development of *E. mordax* is inhibited below 11.5°C and above 27.0°C. Larvae held at temperatures below 11.0°C for short periods become inactive, making little effort to avoid capture by pipette.

The survival of pelagic larvae is dependent on the early consumption of prey species and the ability to avoid predators (Lasker et al. 1970). The degree to which these two processes can be accomplished is largely dependent on the optimal development of swimming ability, precise biting reflexes, and visual acuity (Hunter 1972). Since swimming ability is proportional to larval size, the development of maximum growth potential should be of distinct survival value. Maximum growth of larvae in the yolk-sac stage, in turn, is dependent on the efficient utilization of the limited yolk reserve, i.e., its conversion into body tissues.

Growth of anchovy larvae in the yolk-sac stage is maximal in experimental temperatures between 14° and 20°C. Variation within this range may be highly significant but is difficult to test. Although growth rates of anchovy larvae in the yolk-sac stage increase with increasing temperatures, the maximum size attained by the larvae decreased at high temperatures.

Thermal tolerance limits have been determined for anchovy larvae and juveniles and adults by tests that considered the LD_{50} as a lethal end point. LD_{50} temperatures do not represent "safe" levels and have been used merely because of convention. Any temperature level that produces a lethal response significantly greater than the maximum response at control temperatures should be considered excessive. This would represent the most realistic end point to insure environmental quality. The thermal death of even a few individuals at any particular temperature level suggests that the survivors are under severe stress, leaving them unable to compete successfully for limited resources or avoid predation. For acclimation temperatures of 8°, 12°, 16°, 20°, and 24°C, a range of temperatures encountered by juveniles and adults in nature, immediate exposure to high temperatures less than 23.0°, 24.0°, 25.5°, 26.5°, and 27.5°C, respectively, would be tolerated by fish from southern California without significant mortality from the direct effects of temperature alone. Likewise, for the same acclimation temperatures, juvenile and adult anchovy could tolerate lows of 7.5°, 10.0°, 12.5°, 13.5°, and 14.5°C, respectively. Larvae in the yolk-sac stage can tolerate limited exposure (24 h) to any temperature <28.0°C and >12.0°C. Regardless of acclimation temperature, larvae in the yolk-sac stage, juveniles, and adults can endure sudden temperature increases and decreases between the limits of 14.5° and 23.0°C without significant lethality from direct temperature effects alone.

Although the gross effects of high and low temperature extremes have been quantified, the physiological and biochemical factors that are responsible for thermal death and temperature acclimation are poorly understood. Various mechanisms to account for these phenomena have been discussed by Hochachka and Somero (1971) and Hazel and Prosser (1974). Evidence suggests that qualitatively different enzymes (isoenzymes) may be synthesized during thermal acclimation, and "warm" and "cold" enzyme variants have been described (Hochachka 1967; Hochachka and Somero 1968; Hebb et al. 1969). Enzyme inactivation has been suggested as a cause of thermal death, but it is ". . . undoubtedly more subtle than gross protein denaturation" (Hochachka and Somero 1971:139). The reaction velocities (K_m) of enzymes may drop below certain critical levels at

high and low temperatures, resulting in the disruption of basic physiological functions such as osmoregulation, respiration, and overall nervous system integration (Prosser 1973).

It is unlikely that the offshore realm of any ocean could ever be significantly affected by artificial thermal input. Projected energy needs for the decades ahead and their associated requirements for immense volumes of water for cooling (electric power generating) and heating (LNG) may pose a serious environmental threat in nearshore areas, especially bays, harbors, and estuaries. As a case-in-point, juvenile northern anchovy find the confined waters of the Los Angeles-Long Beach Harbor a suitable habitat. Brewer (1975a) found anchovy egg densities as high as 35/m^3 of surface water within 0.5 mile of the harbor breakwater. These areas will be affected by seawater intake pipes, and thermal effluent plumes and *E. mordax* embryos would be highly susceptible to entrainment. Eggs in the blastodisc stage are most sensitive to abrupt changes in temperature. If one considers the high temperature extremes where mortality begins to exceed the control mortality as unsafe, anchovy embryos should not be allowed to remain in temperatures of 35.5°, 30.5°, 30.0°, and 27.5°C for periods longer than 1, 3, 5, and 60 min, respectively. While embryos proved insensitive to the effects of temperatures as low as 0.5°C for 60-min exposures, it is questionable whether these sensitive developmental stages could withstand the turbulence and mechanical shock associated with heat exchange systems or thermal effluent outfalls. In this respect, larvae are most vulnerable, and Lasker (1964) found this vulnerability increased with decreasing temperatures below 14°C for Pacific sardine, *Sardinops*, larvae which are morphologically similar to anchovy larvae. Their thin integument and fragile bodies are easily damaged. Extreme care was taken in the present study when the larvae were transferred from incubation to test jars, but control survival was only 77.5%. Survival of larvae in experiments that did not involve transfer to rearing vessels was over 90%. Serious consideration must therefore be given to the location of intake pipes and effluent discharge to avoid trapping eggs and larvae. These stages are probably too small to be excluded by screening.

Many more experiments are required to understand the dynamics of the thermal requirements of *E. mordax*. It may be unreasonable to assume that there is one optimal temperature for anchovy well-being. Activity cycles or rhythms (e.g., the evening spawning cycle) may be present in natural populations which require diel temperature changes (e.g., achieved through vertical migration). Temperature optima for reproduction or the growth of larvae in the yolk-sac stage may differ from optima for growth of juveniles and adults which must respond to fluctuating food levels. Brett et al. (1969), experimenting with *Onchorhynchus nerka*, found that as food rations were decreased, temperatures required for maximum growth rates also decreased. When food rations were not limiting, growth rates increased as the temperature increased to a certain optimal level, after which growth rates decreased rapidly.

In conclusion, the potential responses of the northern anchovy to temperature are many and varied. They depend upon the degree and rate of temperature change, length of exposure to a particular temperature, the previous thermal experience of the fish, and the effects of interactions among other environmental variables, both biotic and abiotic. Furthermore, these responses vary with ontogeny.

Although expatriated individuals may temporarily tolerate environmental extremes, the distribution and survival of *E. mordax* are ultimately dependent upon those physicochemical characteristics of the environment conducive to spawning. For the present, such an environment is best described as that part of the California Current where surface water temperatures reach 13°-18°C during at least part of the year (Ahlstrom 1956, 1959, 1966, 1967; Richardson 1973).

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LITERATURE CITED

AHLSTROM, E. H.
1956. Eggs and larvae of anchovy, jack mackerel, and Pacific mackerel. Calif. Coop. Oceanic Fish. Invest., Prog. Rep., 1 Apr. 1955 to June 1956:33-42.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish Bull. 60:107-146.
1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1954-64: A summary. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 534, 71 p.
1967. Co-occurrences of sardine and anchovy larvae in the California Current region off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 11:117-135.

ALABASTER, J. S., AND K. G. ROBERTSON.
1961. The effect of diurnal changes in temperature, dissolved oxygen, and illumination on the behaviour of the roach (*Rutilus rutilus* (L.)), bream (*Abramis brama* (L.)) and perch (*Perca fluviatilis* (L.)). Anim. Behav. 9:187-196.

ALLEN, K. O., AND E. STRAWN.
1971. Rate of acclimation of juvenile channel catfish, *Ictalurus punctatus*, to high temperatures. Trans. Am. Fish. Soc. 100:665-671.

BAXTER, J. L.
1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 11:110-116.

BRAWN, V. M.
1960. Temperature tolerance of unacclimated herring (*Clupea harengus* L.). J. Fish. Res. Board Can. 17:721-723.

BRETT, J. R.
1944. Some lethal temperature relations of Algonquin Park fishes. Publ. Ont. Fish. Res. Lab. 63:1-49.
1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Board Can. 9:265-323.
1970. Temperature. *In* O. Kinne (editor), Marine Ecology, Vol. 1, Part 1, p. 515-560. Wiley-Interscience, Lond.

BRETT, J. R., J. E. SHELBOURNE, AND C. T. SHOOP.
1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

BREWER, G. D.
1974. Preliminary observations on the lower minimum temperature requirements of the northern anchovy. *In* D. Soule and M. Oguri (editors), Marine studies of San Pedro Bay, California, Part III, p. 21-43. Allan Hancock Found. Publ., USC-SG-1-74.
1975a. The biology and fishery of the northern anchovy in San Pedro Bay: Potential impact of dredging and landfill. *In* D. Soule and M. Oguri (editors), Marine Studies of San Pedro Bay, California, Part VIII, p. 23-43. Allan Hancock Found. Publ., USC-SG-1-74.
1975b. The biology of the northern anchovy (*Engraulis mordax*), in relation to temperature. Ph.D. Thesis, Univ. Southern California, 205 p.

BULL, H. O.
1928. Studies on conditioned responses in fishes. Part I. J. Mar. Biol. Assoc. U.K. 15:485-533.

CALIFORNIA DEPARTMENT OF FISH AND GAME.
1971. Pelagic wetfish. Northern anchovy. *In* H. W. Frey (editor), California's living marine resources and their utilization, p. 48-51. Calif. Dep. Fish Game, Resour. Agency.

COUTANT, C. C.
1969. Temperature, reproduction and behavior. Chesapeake Sci. 10:261-274.

DE CIECHOMSKI, J. D.
1973. The size of the eggs of the Argentine anchovy *Engraulis anchoita* (Hubbs & Marini) in relation to the season of the year and to the area of spawning. J. Fish Biol. 5:393-398.

DE SYLVA, D. P.
1969. Theoretical considerations of the effects of heated effluents on marine fishes. *In* P. A. Krenkel and F. L. Parker (editors), Biological aspects of thermal pollution, p. 229-293. Vanderbilt Univ. Press, Portland, Oreg.

DOUDOROFF, P.
1938. Reactions of marine fishes to temperature gradients. Biol. Bull. (Woods Hole) 75:494-509.

FRY, F. E. J.
1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser. 55:1-62.
1971. The effect of environmental factors on the physiology of fish. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 6, p. 1-98. Academic Press, N.Y.

FRY, F. E. J., J. R. BRETT, AND G. H. CLAWSON.
1942. Lethal limits of temperature for young goldfish. Rev. Can. Biol. 1:50-56.

HAZEL, J. R., AND C. L. PROSSER.
1974. Molecular mechanisms of temperature compensation in poikilotherms. Physiol. Rev. 54:620-677.

HEATH, W. G.
1963. Thermoperiodism in sea-run cutthroat trout (Salmo clarki clarki). Science (Wash., D.C.) 142:486-488.

HEBB, C., D. MORRIS, AND M. W. SMITH.
1969. Choline acetyltransferase activity in the brain of goldfish acclimated to different temperatures. Comp. Biochem. Physiol. 28:29-36.

HOAR, W. S.
1955. Seasonal variations in the resistance of goldfish to temperature. Trans. R. Soc. Can., Ser. III 49(5):25-34.
1956. Photoperiodism and thermal resistance of goldfish. Nature (Lond.) 178:364-365.

HOCHACHKA, P. W.
1967. Organization of metabolism during temperature compensation. *In* C. L. Prosser (editor), Molecular mechanisms of temperature adaptation, p. 177-203. Am. Assoc. Adv. Sci. Publ. 84.

HOCHACHKA, P. W., AND G. N. SOMERO.
1968. The adaptation of enzymes to temperature. Comp. Biochem. Physiol. 27:659-668.
1971. Biochemical adaptation to the environment. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 6, p. 99-156. Academic Press, N.Y.

HUBBS, C., AND C. BRYAN.
1974. Effect of parental temperature experience on thermal tolerance of eggs of *Menidia audens*. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 431-435. Springer-Verlag, N.Y.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LYNN, R. J.
1967. Seasonal variation of temperature and salinity at 10 meters in the California Current. Calif. Coop. Oceanic Fish Invest. Rep. 11:157-187.

MAIS, K. R.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game, Fish Bull. 162:1-79.

MCHUGH, J. L.
1951. Meristic variations and populations of northern anchovy (*Engraulis mordax mordax*). Bull. Scripps Inst. Oceanogr. 6:123-160.

MESSERSMITH, J. D., J. L. BAXTER, AND P. M. ROEDEL.
1969. The anchovy resources of the California Current region off California and Baja California. Calif. Coop. Oceanic Fish Invest. Rep. 13:32-38.

NAYLOR, E.
1965. Effects of heated effluents upon marine and estuarine organisms. Adv. Mar. Biol. 3:63-103.

PROSSER, C. L. (editor).
1973. Comparative animal physiology, 3rd ed. W. B. Saunders, Phila., 966 p.

REID, J. L., JR.
1967. Ocean environments of the genus *Engraulis* around the world. Calif. Coop. Oceanic Fish. Invest. Rep. 11:29-33.

RICHARDSON, S. L.
1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71:697-711.

SCOTT, D. P.
1964. Thermal resistance of pike (*Esox lucius* L.), muskellunge (*E. masquinongy* Mitchill), and their F_1 hybrid. J. Fish. Res. Board Can. 21:1043-1049.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

TARZWELL, C. M.
1972. An argument for the open ocean siting of coastal thermal electric plants. J. Environ. Qual. 1:89-91.

TYLER, A. V.
1966. Some lethal temperature relations of two minnows of the genus Chrosomus. Can. J. Zool. 44:349-364.

VROOMAN, A. M., AND P. E. SMITH.
1971. Biomass of the subpopulations of the northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 15:49-51.

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NOTES

ISOLATION AND DESCRIPTION OF TWO VIBRIOS PATHOGENIC TO PACIFIC SALMON IN PUGET SOUND, WASHINGTON

Vibrio anguillarum (Bergman 1909) is recognized worldwide as a saltwater pathogen in fish (Anderson and Conroy 1970). Most epizootics caused by marine bacteria have been attributed to this organism (Rucker 1959; Sindermann 1966). This note describes recent mortalities resulting from vibriosis of Pacific salmon in the marine waters of Puget Sound, Wash., and heterogeneity observed in vibrios isolated from diseased fish.

The National Marine Fisheries Service (NMFS) is engaged in the experimental culture of Pacific salmon in salt water at the NMFS Aquaculture Experiment Station near Manchester, Wash. Epizootics caused by marine vibrios have occurred regularly in cultured salmon during the spring and summer months; the organisms were also isolated from diseased fish on a minor scale in every month during fall and winter (Novotny 1975). Vibrios originally isolated from diseased fish at Manchester were typical of *Vibrio anguillarum* (Evelyn 1971); strain 775 was representative.

In November 1973, a commercial salmon farm in the Manchester area suffered a high mortality of pen-reared, 0-age, 250-g coho salmon, *Oncorhynchus kisutch*. Past experience with vibriosis in the area indicated that the first serious outbreaks usually began in April when water temperatures exceeded 9°C and continued until water temperatures dropped below 12°C in early October (Novotny 1975). Water temperatures in November 1973 were 10° to 11°C; therefore, problems from vibriosis were not anticipated.

Mortalities also began to occur at about the same time, although not on an epizootic scale, in coho salmon held at the NMFS facility at Manchester. These fish had been vaccinated in late spring by injecting a heat-killed bacterin prepared from *V. anguillarum* 775. Oral antibiotics were administered, but the period required to bring the disease under control appeared to be almost twice that usually required for *V. anguillarum*.

Diseased fish sampled from the NMFS pens and the commercial farm exhibited the common signs of vibriosis, most notably a hemorrhagic septicemia. Bacteria characterized as vibrios were consistently isolated from dead or dying fish, but the growth rate of the isolated bacteria was markedly different from that of the typical *V. anguillarum*. Also, this bacterium was not agglutinated by rabbit anti-*V. anguillarum* 775 serum in rapid slide agglutination tests.

The new isolates were confirmed as pathogens by injecting pure cultures of them into salmon. All the injected fish died and the organism was routinely re-isolated from kidneys. We designated this bacterium as *Vibrio* sp. 1669.

In June 1974, NMFS conducted cooperative vaccination tests with a second commercial salmon farm in the Manchester area. Approximately 280,000 coho salmon smolts were injected with a heat-killed bacterin of *V. anguillarum* 775 at least 2 wk prior to their transfer to saltwater pens. Mortalities were exceptionally low until late August (less than 6% from all causes and less than 2% from vibriosis). At that time the rate of mortality began to increase and *Vibrio* sp. 1669 was isolated.

Further tests were made in early August 1974, when 450 0-age sockeye salmon, *O. nerka*, smolts were transferred to NMFS saltwater pens. One pen contained 150 unvaccinated control fish, and two pens contained 150 fish each that had been vaccinated in fresh water with a heat-killed *V. anguillarum* 775 bacterin. After 50 days in the saltwater pens, 95% of the unvaccinated fish had died. During the same period the mortalities in the vaccinated lots were 9% and 27% (Figure 1). Vibrios isolated from the vaccinated fish were only of the 1669 type, based on results of slide agglutination tests.

Materials and Methods

Samples of kidney, eye, or spleen from freshly dead or moribund fish were streaked on trypticase soy agar (TSA) (Difco)[1] with 1% salt added, or on 50% seawater cytophaga agar (Pacha and

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

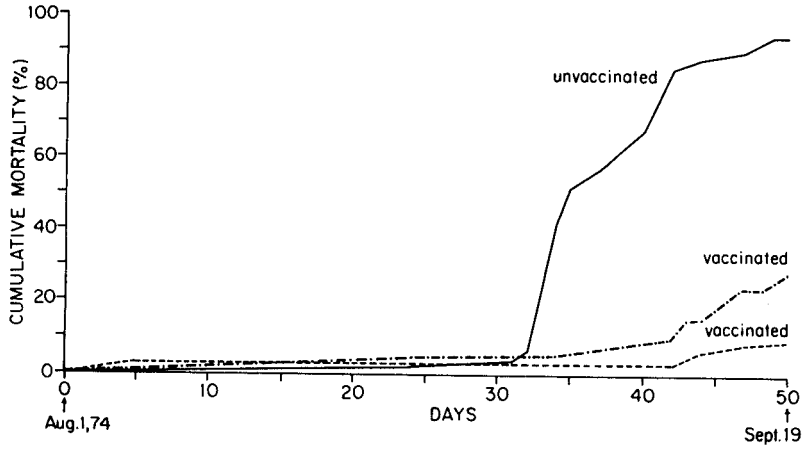

FIGURE 1.—Comparative rate of mortality of three lots of 0-age sockeye salmon raised in net pens at Manchester, Wash. Two of the lots were vaccinated with an intraperitoneal injection of a heat-killed bacterin prepared from *Vibrio anguillarum* 775.

Ordal 1967). Plates were incubated aerobically at 23°C. Presumptive identifications of the bacteria were based on the following tests: gram stain, motility and morphology characteristics under phase contrast microscopy, oxidase test (Kovacs), fermentation or oxidation of glucose, and sensitivity to the vibriostatic compound 0/129 (2,4-diamino-6,7-diisopropyl pteridine phosphate).

Further biochemical characterization included tests in Moeller's media for an alkaline reaction with arginine and for lysine decarboxylase, the production of indole, the production of acetylmethylcarbinol (Voges-Proskauer test), and the ability to ferment arabinose, glycerol, mannitol, sucrose, and galactose. These tests were selected because they were found to be variable among marine vibrio groups established by deoxyribonucleic acid homology characteristics (E. J. Ordal, University of Washington School of Medicine, Seattle, pers. commun.). In all of these tests additional NaCl (1%) was added.

TABLE 1.—Selected properties of *Vibrio anguillarum* 775 and *Vibrio* sp. 1669.

Property	*V. anguillarum* 775	*Vibrio* sp. 1669
Gram reaction	–	–
Motility	+	+
Oxidase (Kovacs) test	+	+
Fermentative (glucose)	+	+
Gas from glucose	–	–
Moeller's media:		
Arginine-alkaline reaction	+	–
Lysine decarboxylase test	–	–
Indole production	–	–
Voges-Proskauer reaction	+	–
Acid from:		
Arabinose	+	–
Glycerol	+	–
Mannitol	+	+
Sucrose	+	+
Galactose	+	–

Antisera for serological comparisons were prepared in both rabbits and coho salmon with heat-killed bacterins of *V. anguillarum* 775 and *Vibrio* sp. 1669 in Freund's complete adjuvant. Rapid slide agglutination tests with the specific antisera were used for initial differentiation. The microtiter system (Cooke Engineering Co.) was used later to determine agglutinin titers, and immunodiffusion techniques were used to further compare antigenic structure and relatedness. Tests were run with unabsorbed antisera and with anti-*Vibrio* sp. 1669 sera absorbed with *V. anguillarum* 775.

Results and Discussion

Vibrio sp. 1669 was typical of the marine vibrio group: it was characterized as a gram negative, motile, curved, asporogenous rod that was oxidase positive, an anaerogenic fermenter, and sensitive to the vibriostatic compound 0/129. A slower rate of growth of *Vibrio* sp. 1669, in comparison to *V. anguillarum* 775, was observed on TSA, as well as variations in certain culture reactions (Table 1).

Coho salmon anti-*V. anguillarum* 775 serum with an agglutinin titer of 512 against the homologous bacterium had a titer of 8 against *Vibrio* sp. 1669. Immunodiffusion also revealed differences between the two vibrios. In Figure 2, the inner precipitin lines demonstrate antigenic cross-reactivity (reaction of identity). An additional antigen unique to *V. anguillarum* 775 is demonstrated by the outer precipitin line which is not present in reactions with *Vibrio* sp. 1669.

After all detectable agglutinin activity against

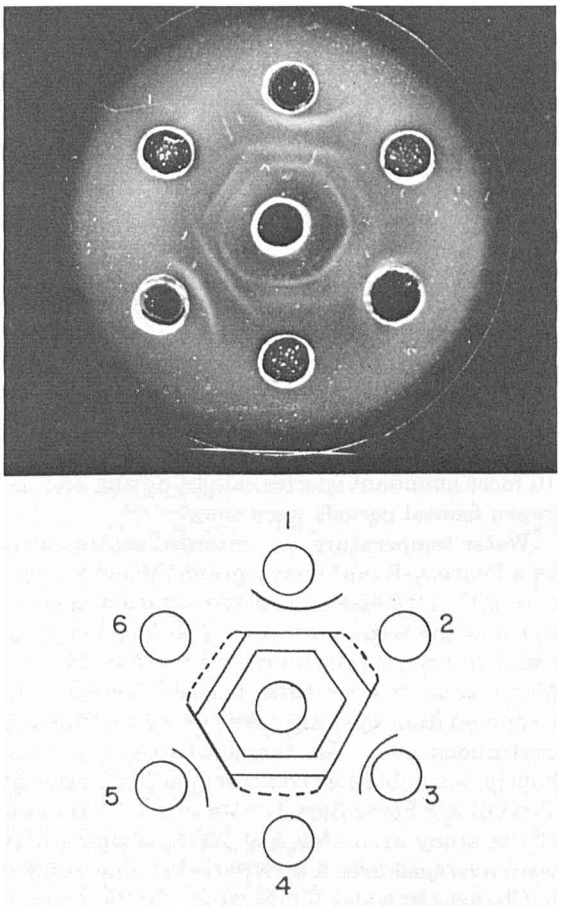

FIGURE 2. —Immunodiffusion comparison of *Vibrio anguillarum* 775 and *Vibrio* sp. 1669. Wells 1, 3, and 5 contain *V. anguillarum* 775 sonicate and wells 2, 4, and 6 contain *Vibrio* sp. 1669 sonicate. The center well contains rabbit anti-*V. anguillarum* 775 serum.

V. anguillarum 775 in rabbit anti-*Vibrio* sp. 1669 serum was removed by absorption, a titer of 16 against 1669 remained (Table 2), indicating that *Vibrio* sp. 1669 also contains antigenic determinants not present on *V. anguillarum* 775.

Whether a vaccine containing antigens from both vibrios would be more protective than vaccines containing antigens from only one of the vibrios is not known. This possibility is currently being investigated. Deoxyribonucleic acid homology experiments are also in progress to better clarify the taxonomic relation of the two vibrios.

TABLE 2. — Agglutinin titers of rabbit anti-*Vibrio* sp. 1669 serum unabsorbed and absorbed with *V. anguillarum* 775 antigen.

Condition	Titer	
	775	1669
Unabsorbed anti-1669 serum	8	32
Anti-1669 serum absorbed with 775	0	16

Literature Cited

ANDERSON, J. I. W., AND D. A. CONROY.
1970. Vibrio disease in marine fishes. *In* S. F. Snieszko (editor), A Symposium on Diseases of Fishes and Shellfishes, p. 266-272. Am. Fish. Soc., Spec. Publ. 5.

EVELYN, T. P. T.
1971. First records of vibriosis in Pacific salmon cultured in Canada, and taxonomic status of the responsible bacterium, *Vibrio anguillarum*. J. Fish. Res. Board Can. 28:517-525.

NOVOTNY, A. J.
1975. Net-pen culture of Pacific salmon in marine waters. Mar. Fish. Rev. 37(1):36-47.

PACHA, R. E., AND E. J. ORDAL.
1967. Histopathology of experimental columnaris disease in young salmon. J. Comp. Pathol. 77:419-423.

RUCKER, R. R.
1959. Vibrio infections among marine and fresh-water fish. Prog. Fish-Cult. 21:22-25.

SINDERMANN, C. J.
1966. Diseases of marine fishes. Adv. Mar. Biol. 4:1-89.

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RELATION OF FISH CATCHES IN GILL NETS TO FRONTAL PERIODS

A study was conducted in 1972 relating gill net catches of fishes to webbing material, time of day, and water depth in St. Andrew Bay, Fla. (Pristas and Trent[1]). While conducting the study, Pristas and Trent observed that catches in the nets appeared to be greater when atmospheric fronts moved through the area in the autumn. We decided to test the hypothesis that catches of fishes in gill nets increase during frontal periods. Experimental data were collected in September-December 1973, and the results of the analysis are presented in this paper.

[1]Pristas, P. J., and L. Trent. 1974. Comparisons of catches of fishes in gill nets in relation to webbing material, time of day, and water depth in St. Andrew Bay, Florida. Unpubl. manuscr.

Study Area and Methods

The study area was located about 300-800 m northwest of Courtney Point in St. Andrew Bay (Figure 1). Hydrological, physical, and sedimentological characteristics of the bay system were described by Ichiye and Jones (1961), Waller (1961), and Hopkins (1966). The bay system exchanges water with the Gulf of Mexico through East and West passes (Figure 1). Prevailing winds are from the southwest in the summer, north and northeast in the autumn, and north and southeast in the winter and spring. Tides are usually diurnal with a mean range of about 0.4 m in St. Andrew Bay (U.S. Department of Commerce 1967).

Eleven gill nets of different mesh sizes were fished for 87 consecutive days from 17 September to 13 December 1973. Each net was 33.3 m long and 3.3 m deep. Stretched mesh sizes ranged from 6.4 to 12.7 cm, the mesh sizes increasing by 0.6-cm increments. The nets were made of #208 monofilament nylon webbing hung to the float and lead lines on the half basis (two lengths of stretched mesh to one length of float line).

Nets were set parallel to each other about 50 m apart, perpendicular to shore, and in water depths (mean low tide) of 2.2 to 2.6 m (Figure 1). Nets remained in the water continuously except for 12 brief periods when they were randomly reset among net locations during the 87-day period. Damaged webbing never exceeded 5% of the total surface area of each net.

Fishes were removed from the nets at sunrise ±2 h and occasionally at sunset ±1 h. The total number of each species caught, including the damaged specimens, was counted. Lengths of the undamaged specimens were determined on a measuring board to the nearest 0.5 cm in fork length (tip of snout to fork of tail) for those fishes having forked tails and in total length (tip of snout to extremity of caudal fin) for Atlantic croaker and sharks.

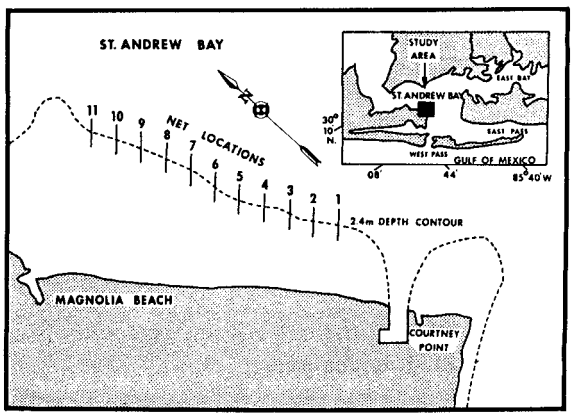

FIGURE 1.—Study area and net locations in St. Andrew Bay, Fla.

Total catch and catches of each of the 10 most abundant species per 24-h period (catches per day) during and between frontal periods were compared using a t-test for unpaired observations (Steel and Torrie 1960). We tested the hypothesis that the mean catch during frontal periods (n = 23) equaled the mean catch between frontal periods (n = 64). We also used the t-test to test the hypothesis that the mean lengths of each of the 10 most abundant species caught during and between frontal periods were equal.

Water temperature was recorded continuously by a Peabody-Ryan[2] thermograph (Model F; accurate within 2% on time and temperature) about 1 m below the water surface at a dockside location about 100 m from the south end of the study area. Mean water temperatures per 24-h period were computed from readings taken every 6 h from the continuous data. Air temperatures, measured hourly, were obtained from the weather station at Tyndall Air Force Base located about 13 km east of the study area. Air and water temperatures were averaged over a 24-h period ending at 0600 h. Changes in water temperature per 24-h period were determined from these means.

Species and Numbers of Fish Caught

A total of 15,398 individuals representing at least 65 species (not all species of *Sphyrna* and none of *Scorpaena* were specifically identified) of marine fishes was caught during the study (Table 1). Catch per day ranged from 10 to 967 individuals and from 6 to 25 species; increases and decreases in the total number of fish caught per day were generally accompanied by similar changes in the number of species of fish caught per day (Figure 2).

The 10 most abundant species comprised 88% of the total catch. The 10 were: Gulf menhaden, *Brevoortia patronus*; spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogon undulatus*; pinfish, *Lagodon rhomboides*; pigfish, *Orthopristis*

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Species and numbers of fish caught in gill nets during September-December 1973 in St. Andrew Bay, Fla.

Species	Number caught
Gulf menhaden, *Brevoortia patronus*	3,467
Spot, *Leiostomus xanthurus*	2,504
Atlantic croaker, *Micropogon undulatus*	2,335
Pinfish, *Lagodon rhomboides*	1,661
Pigfish, *Orthopristis chrysoptera*	905
Sea catfish, *Arius felis*	853
Bluefish, *Pomatomus saltatrix*	594
Spanish mackerel, *Scomberomorus maculatus*	563
Yellowfin menhaden, *Brevoortia smithi*	473
Gafftopsail catfish, *Bagre marinus*	239
Crevalle jack, *Caranx hippos*	212
Blue runner, *Caranx crysos*	211
Little tunny, *Euthynnus alletteratus*	170
Inshore lizardfish, *Synodus foetens*	123
Atlantic sharpnose shark, *Rhizoprionodon terraenovae*	94
Bonnethead, *Sphyrna tiburo*	91
Gulf flounder, *Paralichthys albigutta*	89
Florida pompano, *Trachinotus carolinus*	86
Atlantic bumper, *Chloroscombrus chrysurus*	78
Ladyfish, *Elops saurus*	74
Cobia, *Rachycentron canadum*	46
Blacktip shark, *Carcharhinus limbatus*	40
Blacknose shark, *Carcharhinus acronotus*	39
Harvestfish, *Peprilus alepidotus*	34
Yellow jack, *Caranx bartholomaei*	34
Remora, *Remora remora*	32
Hybrid menhaden, *Brevoortia smithi* × *patronus*	29
Sand seatrout, *Cynoscion arenarius*	29
Skipjack herring, *Alosa chrysochloris*	28
Bighead searobin, *Prionotus tribulus*	22
Spotted seatrout, *Cynoscion nebulosus*	22
Striped mullet, *Mugil cephalus*	22
Leatherjacket, *Oligoplites saurus*	22
Atlantic thread herring, *Opisthonema oglinum*	17
Longnose gar, *Lepisosteus osseus*	16
Florida smoothhound, *Mustelus norrisi*	15
Black drum, *Pogonias cromis*	12
Alabama shad, *Alosa alabamae*	11
Gray snapper, *Lutjanus griseus*	10
Atlantic spadefish, *Chaetodipterus faber*	10
Southern sea bass, *Centropristis melana*	8
Atlantic threadfin, *Polydactylus octonemus*	7
Finetooth shark, *Aprionodon isodon*	7
Sheepshead, *Archosargus probatocephalus*	6
Gulf toadfish, *Opsanus beta*	6
Orange filefish, *Aluterus schoepfi*	5
Gag, *Mycteroperca microlepis*	5
Sand perch, *Diplectrum formosum*	5
Atlantic moonfish, *Vomer setapinnis*	5
Hogchoker, *Trinectes maculatus*	4
White mullet, *Mugil curema*	4
Hammerhead shark, *Sphyrna* sp.	3
Southern stargazer, *Astroscopus y-graecum*	3
Smooth dogfish, *Mustelus canis*	3
Scorpionfish, *Scorpaena* sp.	2
Guaguanche, *Sphyraena guachancho*	2
Striped burrfish, *Chilomycterus schoepfi*	2
Dusky flounder, *Syacium papillosum*	2
Tarpon, *Megalops atlantica*	1
Bull shark, *Carcharhinus leucas*	1
Tripletail, *Lobotes surinamensis*	1
Shrimp eel, *Ophichthus gomesi*	1
Sandbar shark, *Carcharhinus milberti*	1
Bonefish, *Albula vulpes*	1
Halfbeak, *Hyporhamphus unifasciatus*	1
Total	15,398

chrysoptera; sea catfish, *Arius felis*; bluefish, *Pomatomus saltatrix*; Spanish mackerel, *Scomberomorus maculatus*; yellowfin menhaden, *Brevoortia smithi*; and gafftopsail catfish, *Bagre marinus* (Table 1). Catches per day of each of these are shown in Figure 3.

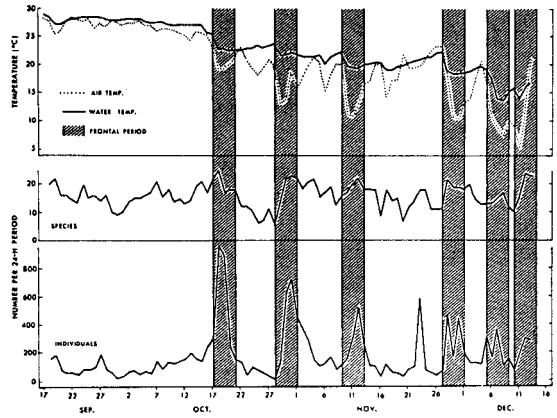

FIGURE 2.—Frontal periods, mean air and water temperatures, and numbers of species and individuals caught per 24-h period in St. Andrew Bay, Fla., September-December 1973.

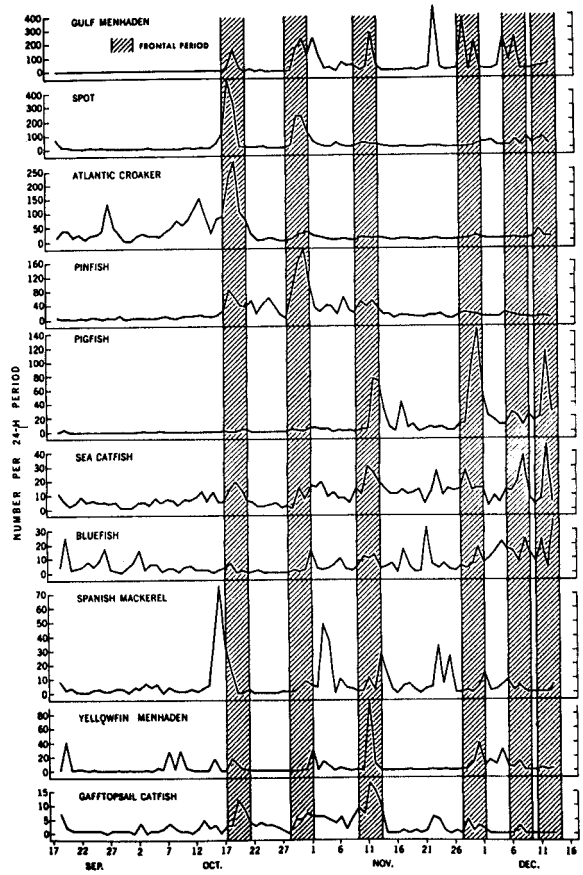

FIGURE 3.—Frontal periods and number of individuals caught by species per 24-h period in St. Andrew Bay, Fla., September-December 1973.

Frontal Periods

A frontal period was arbitrarily defined as any four consecutive days the first of which the water temperature dropped 2°C or more. Four days were selected, because fish catches were generally affected for 2 to 4 days following the initial temperature drop on the first day of a frontal period. Six frontal periods occurred in the study area from 17 September to 13 December (Figure 2). Fronts moved through the study area on 17 October, 28 October, 9 November, 27 November, 5 December, and 10 December (Figure 2). The average decrease of water and air temperatures per 24-h period for the above dates was 2.5°C and 6.4°C, respectively. In addition to decreases of temperatures, fronts passing through estuaries of the northern Gulf of Mexico are also characterized by: 1) rapid changes in barometric pressure, 2) shifts in wind direction and wind speed, 3) changes in tidal heights, and 4) increases in turbidity and velocity of tidal currents (E. J. Pullen, pers. commun., U.S. Corps of Engineers, Galveston, Tex.).

Catch Related to Frontal Periods

Each front was characterized by a marked increase in the numbers of individuals caught. Such a marked increase occurred only once (22-24 November) during a nonfrontal period (Figure 2). The mean number (all species combined) of fish caught per day was 354.7 during frontal periods and 113.1 between frontal periods (Table 2). Mean catches were significantly higher during frontal periods for all species combined and for 8 of the 10 most abundant species., Atlantic croaker and Spanish mackerel (Table 2, Figure 3) were the exceptions. Spanish mackerel was the only species caught in greatest numbers between frontal periods. Mean catches of the nine species ranged from 1.7 to 9.5 times greater during frontal periods than between frontal periods.

Mean lengths of fish caught during frontal periods were not significantly different from those caught between frontal periods for each of the 10 most abundant species (Table 2).

These results suggest that many species of marine fishes become more vulnerable to capture by gill nets in shallow areas of coastal bays during frontal periods in autumn. This increased vulnerability probably results from increased activity, migration, a lessening ability to avoid the net, and one or more of the factors associated with fronts, e.g., changes in temperature, tidal height, turbidity, and current velocity.

Acknowledgments

Our sincere appreciation is extended to J. R. Lara for furnishing climatological data and to D. B. Jester, M. A. Roessler, and J. Y. Christmas for their helpful comments.

Literature Cited

HOPKINS, T. L.
1966. The plankton of the St. Andrew Bay system, Florida. Publ. Inst. Mar. Sci., Univ. Tex. 11:12-64.

ICHIYE, T., AND M. L. JONES.
1961. On the hydrography of the St. Andrew Bay system, Florida. Limnol. Oceanogr. 6:302-311.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to biological sciences. McGraw-Hill, N.Y., 481 p.

TABLE 2.—Comparisons of mean catches per day and mean lengths during and between frontal periods, September-December 1973, St. Andrew Bay, Fla.

Species group or species	Mean number caught per day: During frontal periods	Mean number caught per day: Between frontal periods	*t*-value	Mean length (cm): During frontal periods	Mean length (cm): Between frontal periods	*t*-value
All fish	354.7	113.1	−6.60**	(1)	(1)	(1)
Gulf menhaden	90.4	21.7	−3.46**	21.0	21.5	1.26
Spot	81.7	9.8	−4.66**	20.2	19.6	−1.85
Atlantic croaker	38.6	22.6	−1.43	26.2	25.6	−1.06
Pinfish	41.6	11.0	−4.46**	17.0	16.5	−0.64
Pigfish	30.4	3.2	−5.28**	18.2	18.9	1.36
Sea catfish	16.7	7.3	−5.68**	30.2	30.9	0.78
Bluefish	10.4	5.5	−2.74**	33.6	35.9	0.89
Spanish mackerel	5.0	7.0	0.70	34.9	36.9	1.15
Yellowfin menhaden	10.5	3.6	−2.22*	25.8	26.0	0.65
Gafftopsail catfish	5.0	2.0	−3.98**	42.7	44.2	1.06

[1]Not determined.
*Significant at 5% level.
**Significant at 1% level.

U.S. DEPARTMENT OF COMMERCE.
1967. U.S. Coast Pilot 5, Atlantic Coast, 301 p.
WALLER, R. A.
1961. Ostracods of the St. Andrew Bay system. M.S Thesis, Florida State Univ., Tallahassee, 46 p.

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PHOSPHOGLUCOMUTASE POLYMORPHISM IN TWO PENAEID SHRIMPS, *PENAEUS BRASILIENSIS* AND *PENAEUS AZTECUS SUBTILIS*

In a search for subpopulation differences within species of penaeid shrimp in the northern Gulf of Mexico, Proctor et al. (1974) and Marvin and Caillouet (1976) reported genetically controlled polymorphism in the enzyme phosphoglucomutase (PGM) in *Penaeus aztecus* (brown shrimp) and *P. setiferus* (white shrimp). The brown shrimp were collected in the northern Gulf of Mexico, so they are *P. aztecus aztecus* Ives, according to Pérez Farfante (1969). The white shrimp, collected both from the northern Gulf and from the North Edisto River, S.C., are *P. setiferus* (Linnaeus), according to Pérez Farfante (1969). Our paper describes similar polymorphisms in PGM in two more penaeids, *P. brasiliensis* Latreille and *P. aztecus subtilis* Pérez Farfante.

Methods

Specimens were collected off the coasts of Guyana, Surinam, and French Guiana, South America, on cruise 49 of the *Oregon II*, between lat. 6°13′ and 6°29′N and between long. 53°10′ and 53°36′W, at 22-29 fathoms, on 9 and 10 February 1974. They were stored at −20°C or below until analyzed. Preparation of abdominal muscle extracts, electropherograms of general protein patterns, and PGM zymograms followed procedures used by Procter et al. (1974). Each specimen was identified to species by morphological characteristics, then their distinctive general protein patterns (Figure 1) were used to confirm this identification. To do so, each gel was sliced horizontally into two halves after electrophoresis was complete. One half was treated with PGM specific stain and the other half was stained with Coomassie Blue.[1] Specimens of *P. aztecus aztecus*

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

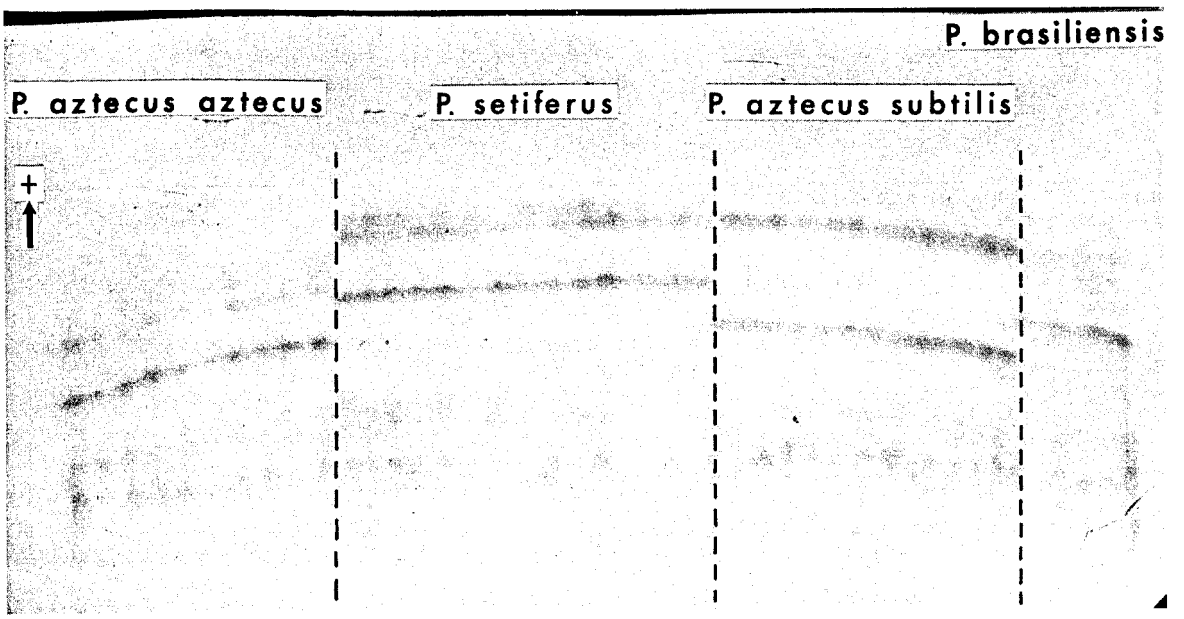

FIGURE 1. — Electropherogram showing general protein pattern of *Penaeus brasiliensis, P. aztecus subtilis, P. aztecus aztecus,* and *P. setiferus.* Stain used was Coomassie Blue. Direction (↑) of protein migration toward the anode (+) is shown.

and *P. setiferus* collected in the northern Gulf were included for comparison with *P. aztecus subtilis* and *P. brasiliensis*.

Results and Discussion

In *P. aztecus subtilis* the zymograms of abdominal muscle extracts exhibited a single region of PGM activity composed of five anodal bands which are labelled a, b, c, d, and e. The same was true for *P. brasiliensis* with the exception that band e was not observed. Bands a, b, c, and d are shown in Figure 2 and bands b, c, and d in Figure 3. Band e, observed in *P. aztecus subtilis*, is shown only diagrammatically (Figure 3). Direct comparison of PGM bands among *P. brasiliensis, P. aztecus subtilis, P. aztecus aztecus*, and *P. setiferus* suggested that bands b, c, and d are similar in these shrimps (Figure 4). This result is supported by Marvin and Caillouet (1976) who showed that *P. setiferus* and *P. aztecus aztecus* have the same five PGM bands. These bands are assumed to be under the control of five codominant allelic genes designated PGM_a through PGM_e (Proctor et al. 1974; Marvin and Caillouet 1976).

Six phenotypes of PGM were observed in *P. brasiliensis* and eight in *P. aztecus subtilis* (Table 1). PGM phenotypes were enumerated from zymograms to determine numerical distributions of phenotypes, and allele (PGM band) frequencies were derived therefrom (Table 1). Two-banded phenotypes (Figures 2-4) observed in some individuals presumably reflect heterozygous individuals. With PGM phenotypes grouped into three categories, cc, cx, and xx (where x includes bands a, b, d, and e), chi-square tests detected no difference ($P>0.05$) in phenotype distribution between the sexes in either species. With the same

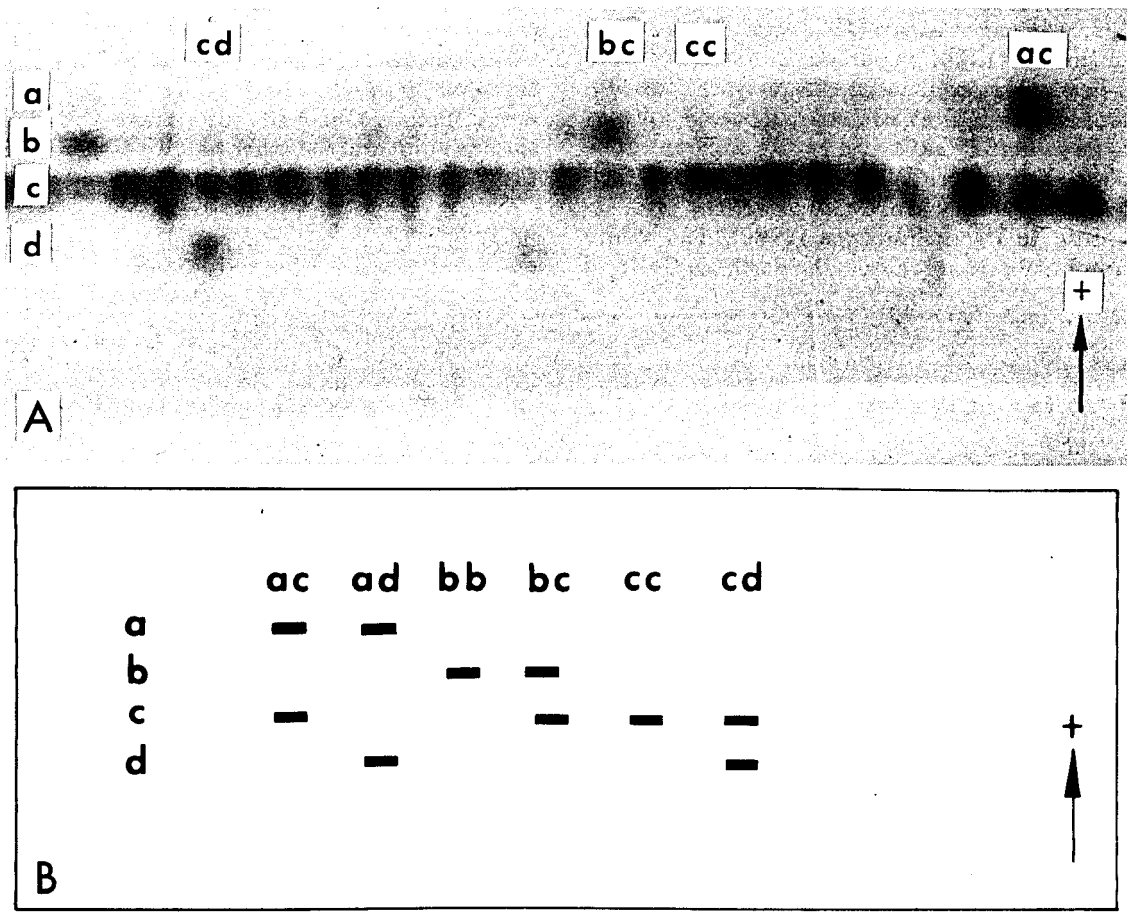

FIGURE 2. — A. Zymogram showing PGM bands a through d (band e not shown) and phenotypes cd, bc, cc, and ac. B. Diagram showing six PGM phenotypes observed in *Penaeus brasiliensis*. Direction (↑) of protein migration toward the anode (+) is shown.

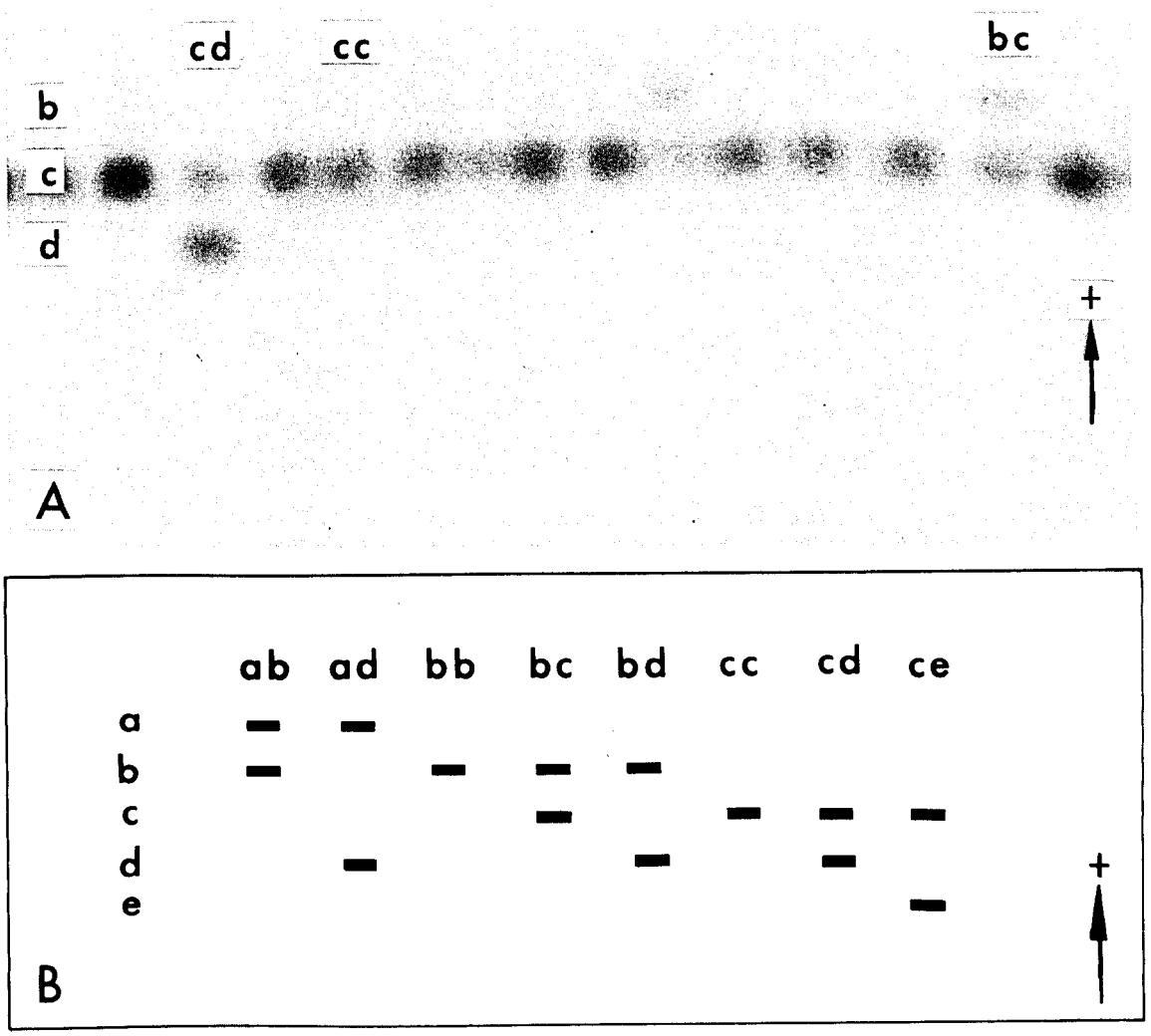

FIGURE 3. — A. Zymogram showing PGM bands b through d (bands a and e not shown) and phenotypes cd, cc and bc. B. Diagram showing eight PGM phenotypes observed in *Penaeus aztecus subtilis*. Direction (↑) of protein migration toward the anode (+) is shown.

TABLE 1. — Distribution (number of specimens) of PGM phenotypes and frequency of PGM alleles in samples of *Penaeus brasiliensis*, *P. aztecus subtilis*, and *P. aztecus aztecus*.

Species	Total length[1] range (mm)	Sex	Phenotypes									Alleles				
			ab	ac	ad	bb	bc	bd	cc	cd	ce	a	b	c	d	e
P. brasiliensis	145-185	Male	0	2	0	1	12	0	172	17	0	0.0049	0.0343	0.9191	0.0417	0.0000
	151-210	Female	0	2	1	0	8	0	161	14	0	0.0081	0.0215	0.9301	0.0403	0.0000
	145-210	Combined	0	4	1	1	20	0	333	31	0	0.0064	0.0282	0.9244	0.0410	0.0000
P. aztecus subtilis	102-152	Male	0	0	2	0	13	2	143	6	0	0.0060	0.0452	0.9187	0.0301	0.0000
	107-175	Female	1	0	0	1	13	0	119	8	2	0.0035	0.0556	0.9062	0.0278	0.0069
	102-175	Combined	1	0	2	1	26	2	262	14	2	0.0048	0.0500	0.9129	0.0290	0.0032
P. aztecus aztecus[2]	60-100	Combined	1	2	0	22	211	5	345	12	2	0.0025	0.2175	0.7642	0.0142	0.0017

[1]Tip of rostrum to tip of telson.
[2]Data adapted from Proctor et al. (1974).

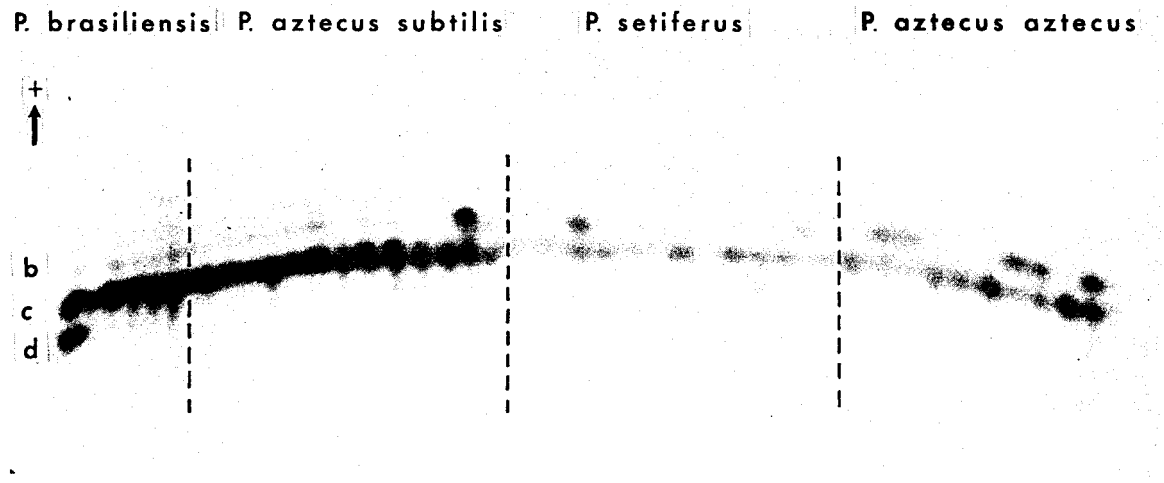

FIGURE 4.—Zymogram comparing PGM bands b through d (bands a and e not shown) in *Penaeus brasiliensis, P. aztecus subtilis, P. aztecus aztecus*, and *P. setiferus*. Direction (↑) of protein migration toward the anode (+) is shown.

phenotype categories, but with data for sexes combined, the phenotype distribution of *P. aztecus subtilis* deviated significantly ($\chi^2 = 7.086$, $0.025<P<0.05$) from that expected from Hardy-Weinberg equilibrium (Stern 1943). The reason for this deviation is not known. Johnson et al. (1974) noted a deviation from Hardy-Weinberg expectation for PGM phenotype distribution of a pandalid shrimp *Pandalus hypsinotus* Brandt, in Alaska, and they suggested that it might be related to depth of capture as found in, Pacific ocean perch, *Sebastodes alutus* (Johnson et al. 1971).

Our study provided an opportunity to compare the subspecies *P. aztecus subtilis* and *P. aztecus aztecus,* therefore distribution of PGM phenotypes and frequency of PGM alleles for the latter subspecies (data adapted from Proctor et al. 1974) also are shown in Table 1. This comparison is based on the assumption that bands a and e as well as bands b, c, and d are similar in the two species. However, even if this is not the case, the small frequencies of the rare a and e alleles would not appreciably affect the comparison. Both subspecies exhibited eight phenotypes, but not all were the same. Phenotype ad was detected in *P. aztecus subtilis* but not in *P. aztecus aztecus.* Phenotype ac was detected in the latter but not in the former. With phenotypes grouped into categories cc, cx, and xx, and with sexes combined, a chi-square contingency test detected a significant ($P<0.05$) difference in phenotype distribution between the subspecies, and this result provides an additional characteristic to existing evidence of differences between these subspecies (see Pérez Farfante 1969).

This and previous studies by Proctor et al. (1974) and Marvin and Caillouet (1976) suggest that zymogram analysis may provide a useful tool in the study of population genetics of the Penaeidae. The wide distribution (Mistakidis 1968), commercial importance, and relatively short generation time of the Penaeidae should make them particularly attractive subjects of study by population geneticists.

Acknowledgments

Through initial efforts by Raphael R. Proctor, Jr., Gulf Coastal Fisheries Center, National Marine Fisheries Service (NMFS), Galveston, Tex., this study was made possible. His helpful suggestions were greatly appreciated. We are grateful to Albert C. Jones, Alexander Dragovich, and Donald M. Allen, Southeast Fisheries Center, NMFS, Miami, Fl., for providing specimens for this study. Fred M. Utter, Northwest Fisheries Center, NMFS, Seattle, Wash., reviewed the manuscript. Frank Patella conducted the statistical analyses for the study.

Literature Cited

JOHNSON, A. G., F. M. UTTER, AND H. O. HODGINS.
1971. Phosphoglucomutase polymorphism in Pacific ocean perch, *Sebastodes alutus*. Comp. Biochem. Physiol. 39B:285-290.

1974. Electrophoretic comparison of five species of pandalid shrimp from the northeastern Pacific Ocean. Fish. Bull., U.S. 72:799-803.

MARVIN, K. T., AND C. W. CAILLOUET.
1976. Phosphoglucomutase polymorphism in white shrimp, *Penaeus setiferus*. Comp. Biochem. Physiol. 53B:127-131.

MISTAKIDIS, M. N. (editor).
1968. Proceedings of the World Scientific Conference on the Biology and Culture of Shrimps and Prawns. FAO Fish. Rep. 57, 4 vol., 1627 p.

PÉREZ FARFANTE, I.
1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.

PROCTOR, R. R., K. T. MARVIN, L. M. LANSFORD, AND R. C. BENTON.
1974. Phosphoglucomutase polymorphism in brown shrimp, *Penaeus aztecus*. J. Fish. Res. Board Can. 31:1405-1407.

STERN, C.
1943. The Hardy-Weinberg law. Science (Wash., D.C.) 97:137-138.

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FIRST RECORD OF THE MELON-HEADED WHALE, *PEPONOCEPHALA ELECTRA*, IN THE EASTERN PACIFIC, WITH A SUMMARY OF WORLD DISTRIBUTION

Peponocephala electra (Gray 1846) is a tropical pelagic delphinid previously known to occur in the eastern Atlantic, Indian, and western and central Pacific oceans. It is also known as the electra dolphin, the Hawaiian blackfish, and the many-toothed blackfish. Since van Bree and Cadenat (1968; localities 1-4, 6-9, 11, 13, 14, 16, 18, and 19 in Figure 1) summarized world records, the species has been reported from Thailand (Pilleri 1973, locality 17), the Philippine Sea near Cebu (W. H. Dawbin pers. commun., locality 15), near Townsville, Australia (G. E. Heinsohn pers. commun., locality 12), the New Hebrides (Rancurel 1974, locality 10), and the Tuamotos-Marquesas region (K. S. Norris pers. commun., locality 5). Records cited by van Bree and Cadenat (1968) as "in litteris" or in press, have subsequently been published (Dawbin et al. 1970, locality 11; Mörzer Bruyns 1971, localities 6-9). The purpose of this note is to report a capture that extends the known range of the species some 3,000 miles into the eastern tropical Pacific off Central America (Figure 1; triangle).

The specimen (Figure 2), a male calf 112 cm long (tip of upper jaw to base of notch in flukes) and weighing 15 kg, was captured in a tuna purse seine that had been set on an aggregation of yellowfin tuna, *Thunnus albacares*, and dolphins, *Stenella* sp., approximately 90 nautical miles (about 167 km) due west of Champerico, Guatemala (lat. 14°20′N, long. 91°52′W), in May 1974. More precise information on date and locality of capture is not available. A crew member found the calf dead in the net, placed it in the ship's freezer, and on return to port donated it to the National Marine Fisheries Service, La Jolla. The specimen was identified using X rays of the dentition. The high tooth count ($\frac{23+|23+}{22+|22+}$), combined with the blunt head and dark coloration, is diagnostic of the species. The specimen was then photographed, measured, weighed, cast in plastic, and sent frozen to the U.S. National Museum (USNM), Washington, D.C., where it was preserved whole

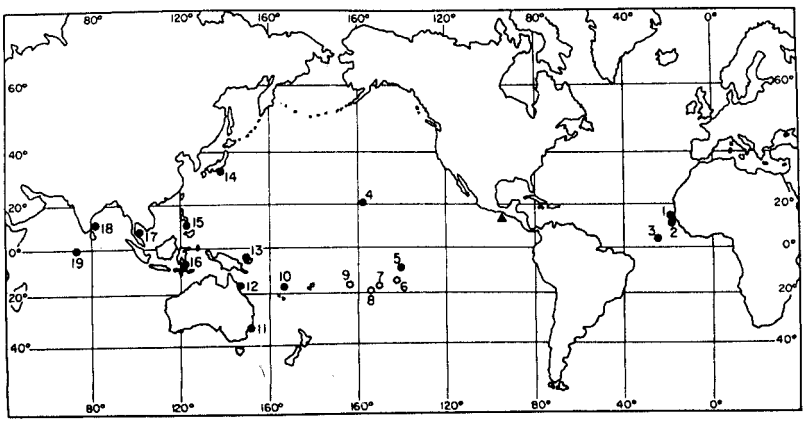

FIGURE 1. — Known distribution of *Peponocephala electra*. Triangle is new record; sources of others in text. Closed circles are specimen localities, open circles are sightings. Some circles represent multiple records from single localities, e.g., Hawaii and Honshu, Japan.

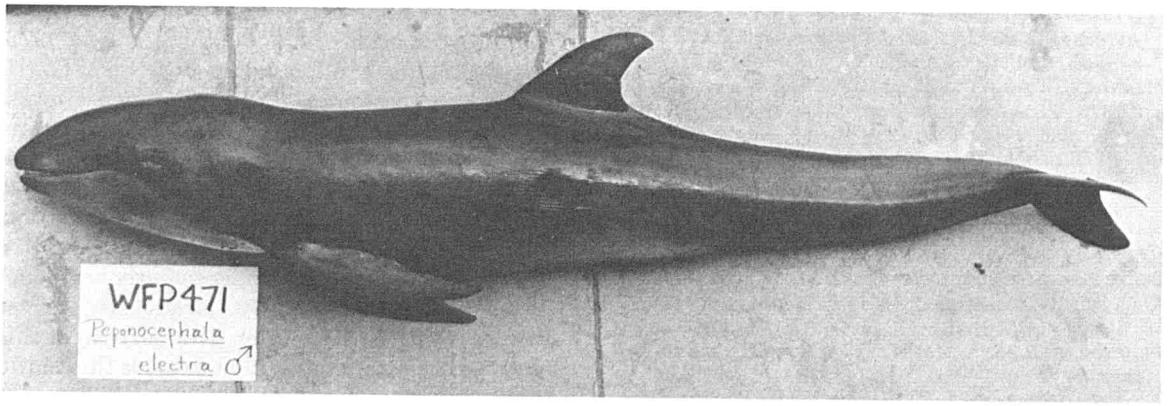

FIGURE 2. — Calf of *Peponocephala electra* collected in eastern tropical Pacific (USNM 504087).

and placed in the marine mammal collection (USNM 504087).

Acknowledgments

I thank Edward Kovalchek and Joseph Madruga for providing the specimen and P. J. H. van Bree for reading the manuscript.

Literature Cited

DAWBIN, W. H., B. A. NOBLE, AND F. C. FRASER.
1970. Observations on the electra dolphin, *Peponocephala electra*. Bull. Br. Mus. (Nat. Hist.) Zool. 20(6):175-201.

MÖRZER BRUYNS, W. F. J.
1971. Field guide of whales and dolphins. C. A. Mees, Amsterdam, 258 p.

PILLERI, G.
1973. Cetologische Expedition zum Indus und Persischen Golf und Forschungsreise nach Goa und Thailand im Jahre 1973. Hirnanatomisches Institut, Waldau-Bern, Switzerland, 52 p.

RANCUREL, P.
1974. Echouage en masse du cétacé *Peponocephala electra* aux Nouvelles-Hébrides. Biol. Cons. 6:232-234.

VAN BREE, P. J. H., AND J. CADENAT.
1968. On a skull of *Peponocephala electra* (Gray, 1846) (Cetacea, Globicephalinae) from Sénégal. Beaufortia 14:193-202.

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FOODS OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, IN THE INSHORE COASTAL WATERS OF BRISTOL BAY, ALASKA, 1966-67

For most living organisms the early portion of life is most critical in determining survival. Anadromous fishes such as Pacific salmon have two critical periods during early life — development and growth in fresh water and subsequent adaptation to a marine environment. The food of juvenile salmon during the first few months of marine life influences growth and condition, which in turn probably influences parasitism, predation, and other factors which ultimately determine marine survival.

Although the sockeye salmon, *Oncorhynchus nerka* (Walbaum), is one of the most valuable commercial fishes in Alaska and has been the object of extensive research, little is known of its early life in the sea. Straty (1974) and Straty and Jaenicke[1] have made the only comprehensive study of early marine life of the sockeye salmon in Bristol Bay, historically the largest sockeye fishery in the North Pacific. Documented studies of sockeye salmon food habits during this period of life are generally limited to brief accounts of Soviet research in Kamchatka waters (Synkova 1951), a study in British Columbia (Manzer 1969), examination of a few specimens from Aleutian and Kodiak waters (Chamberlain 1907), and 45 specimens taken off Cape Seniavin in lower

[1]Straty, R. R., and H. W. Jaenicke. 1971. Studies of the estuarine and early marine life history of sockeye salmon in Bristol Bay, 1965-67. Unpubl. manuscr., 137 p. Northwest Fish. Cent. Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

Bristol Bay (Dell 1963). Recently, Jaenicke and Bonnett[2] completed an extensive study of the foods of some 1,200 seaward-migrating sockeye salmon in Bristol Bay during 1969 and 1970. Most of their samples were taken over deeper waters farther offshore than mine — particularly those off Port Moller.

The purpose of my study was to document the foods of seaward-migrating sockeye salmon along the main migration route on the north side of the Alaska Peninsula in Bristol Bay, Alaska, during 1966 and 1967. Later studies by Straty and Jaenicke (see footnote 1) and Jaenicke and Bonnett (see footnote 2) show that the areas where I took samples of juvenile sockeye salmon (Kvichak to Port Moller — Figure 1) were indeed along the main migration route in the upper and central parts of the bay (Kvichak to Port Heiden). In lower Bristol Bay, however, my sampling area (Port Moller) was inshore from the usual main migration route. In years when unusually cold seawater temperatures prevail, the main migration route in the lower bay shifts to the warmer inshore waters (Straty 1974). The juvenile sockeye salmon I sampled in the Port Moller area were taken in a year (1967) when normal temperatures prevailed and were presumably inshore from the path followed by most migrants that year. However, the foods found in 1967 in these inshore waters may reflect what is usually available to the main body of outmigrants in colder years when their path is altered.

[2]Jaenicke, H. W., and M. B. Bonnett. Food of sockeye salmon outmigrants in Bristol Bay, Alaska, 1969-70. Unpubl. manuscr., 20 p. Northwest Fish. Cent. Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

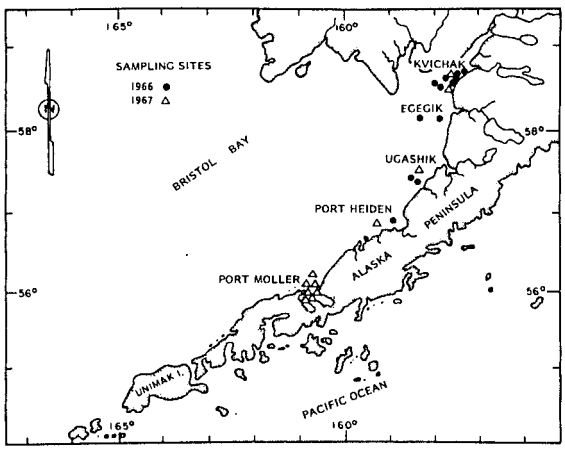

FIGURE 1. — Bristol Bay, Alaska, showing locations where juvenile sockeye salmon were collected in 1966 and 1967 for food habit analyses. Samples in the upper bay (Kvichak and Egegik) were taken in June, and those in the central bay (Ugashik) and lower bay (Port Heiden and Port Moller) were taken from July to September.

Materials and Methods

The samples of juvenile sockeye salmon were collected in 1966 and 1967 in the following areas (Figure 1) and times: Kvichak, June of both years; Egegik, June 1966; Ugashik, July and September 1966 and August 1967; Port Heiden, July 1966 and August 1967; and Port Moller, July and August 1967. All samples were taken during daylight, usually between 1000 and 1900 h.

In 1966, the juvenile sockeye salmon were collected with circular tow nets (2.1 m in diameter) and a small-mesh round haul seine (110 m long by about 7 m deep); in 1967 they were collected in a small-mesh lampara seine (183 m long by about 14 m deep). All sampling was done from the 13-m National Marine Fisheries Service vessel *Sockeye*. Samples were preserved in 10% Formalin[3] solution and processed later.

I analyzed the stomach contents of 160 juvenile sockeye salmon and all but 16 contained food. These 160 fish represented roughly equal numbers of individuals from 1-cm size groups ranging from 6- to 13-cm fork length and were from all five areas of Bristol Bay from Kvichak Bay south to Port Moller — a distance of about 320 km.

The stomach (that portion of the digestive tract from the anterior end of the esophagus to the pylorus) of each specimen was removed, and all food organisms were separated and identified to the lowest taxonomic level practical. All of the food items were air dried overnight at room temperature and weighed to the nearest 0.1 mg the following day.

The eight major categories of food items: copepods, fish, larval crustaceans, euphausiids, amphipods, insects, miscellaneous crustaceans, and zoofauna, are not mutually exclusive. The least specific categories merely reflect the digested condition or incidental importance of a given item, e.g., crustacean remains (recorded as miscellaneous crustaceans) or arachnids (zoofauna), which occurred only once.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

For each sampling area, the weight of each major food category was calculated as the percentage of the total dry weight of all food found. The percentage of occurrences and weights of foods were based only on those specimens containing food.

Results

The foods consumed by seaward-migrating sockeye salmon in Bristol Bay varied in the relative proportion and occurrence of kinds and quantities between months during the summer. The apparent differences between the upper and lower areas of the bay are largely due to date of sampling. The 16 empty stomachs found were collected in June from the upper bay — the Kvichak and Egegik areas.

In early June 1966 in the Kvichak area, 11 of 19 juvenile sockeye salmon contained food. Although fish and insects made up 97% of the bulk (weight), fish occurred in only 5% of the stomachs and insects in 53%. By late June in the same area, 8 of 10 stomachs contained food, most of which was copepods. They made up 89% of the bulk and were found in 70% of the stomachs; miscellaneous crustaceans were found in 60%. In mid-June of the following year (1967), 18 of 21 juvenile sockeye salmon from the Kvichak area contained food. Fish, insects, and copepods made up 93% of the bulk; fish occurred in 19% of the stomachs, insects in 76%, and copepods in 62%.

In mid-June 1966, 20 of 23 stomachs collected farther seaward at Egegik contained very small amounts of food. Euphausiids and miscellaneous crustaceans made up 78% of the bulk, but euphausiids occurred in only 9% of the stomachs and miscellaneous crustaceans in 13%. Insects occurred in 48% of the stomachs, but made up only 4% of the bulk.

In mid-July 1966 at Ugashik, all 20 stomachs collected contained larval crustaceans (79% by bulk and mostly anomurans). Copepods were insignificant in terms of bulk but occurred in 70% of the stomachs. At Port Heiden (farther seaward) on the same date, fish made up 76% of the bulk of the contents of the seven stomachs collected. Fish occurred in 28% of the stomachs, whereas amphipods occurred in 71% and insects in 57%.

At Port Moller in lower Bristol Bay throughout July and on 1 August 1967, copepods made up 71% of the bulk of food in 48 stomachs and occurred in 85%; larval crustaceans occurred in 58%, amphipods in 50%, and fish in 42%.

By mid-August 1967, when most juvenile sockeye salmon have migrated out of Bristol Bay (Straty 1974), the two juveniles taken at Ugashik contained only copepods and insects and two taken at Port Heiden contained mostly fish.

Only eight juvenile sockeye salmon were taken in September 1966 in the Ugashik area. Copepods and fish accounted for 86% of the stomach contents, but only copepods occurred frequently (100% with copepods vs. 25% with fish).

As the young sockeye salmon migrated seaward over successive months, they ate increasing amounts of food. In the Kvichak and Egegik areas during June, 16 of the 73 stomachs examined were empty and the others had only relatively small amounts of food (average of 3-6 mg). Later in the summer and farther at sea (Ugashik and Port Heiden) the average amount of food per stomach was much greater (20-24 mg), and still later in the summer and farther at sea (Port Moller), the amounts were the highest of all (average of 82 mg).

In terms of both bulk and frequency of occurrence, copepods were the most important food of juvenile sockeye salmon in inshore Bristol Bay in 1966 and 1967 (Tables 1, 2). Two genera of calanoid copepods (*Eurytemora* and *Metridia*) made up 98% of the number of copepods in the stomachs of 50 juveniles taken by Straty and Jaenicke (see footnote 1) in 1967 at Kvichak and

TABLE 1.—Percentage total dry weight of foods consumed by juvenile sockeye salmon collected at five areas in Bristol Bay, Alaska, 1966 and 1967.

Food category	Kvichak $N = 50$	Egegik $N = 23$	Ugashik $N = 30$	Port Heiden $N = 9$	Port Moller $N = 48$
Copepods	30.3	8.6	25.4	6.3	71.2
Fish	45.7	4.1	22.6	80.3	11.8
Larval crustaceans	0.1	0.4	44.6	—	5.7
Euphausiids	—	43.1	0.4	—	5.2
Amphipods	0.6	1.0	1.3	4.8	4.7
Insects	18.6	3.9	0.9	0.7	0.8
Miscellaneous crustaceans	2.6	34.9	0.2	0.1	0.5
Zoofauna	2.1	3.3	4.7	6.1	0.2
Other	—	0.8	—	1.8	—

TABLE 2. — Summary of foods eaten by juvenile sockeye salmon (N = 160) in all regions of Bristol Bay, Alaska, between June and September 1966 and 1967.

Food category	Percentage total dry weight	Percentage occurrence
Copepods	60.4	66.7
Fish	17.4	25.0
Larval crustaceans	9.8	35.4
Euphausiids	4.6	6.3
Amphipods	4.0	29.2
Insects	1.6	41.0
Miscellaneous crustaceans	0.9	22.2
Zoofauna	1.1	18.8
Other	0.1	2.8
Empty stomachs	—	10.0

Port Moller. (The 50 specimens were taken at the same time and place as my samples.) Fish were second in importance to copepods in terms of weight of food, and over half the bulk of these fish were Pacific sand lance, *Ammodytes hexapterus*. Larval crustaceans were the only other food of major importance (by bulk) and most of these were anomuran larvae eaten by juveniles in the Ugashik area in July 1966. Other items eaten by juvenile sockeye salmon in significant amounts during their migration out of Bristol Bay were euphausiids, amphipods, and insects. Insects and amphipods occurred frequently in the diet but did not contribute much bulk.

I looked for differences in food selectivity between large and small fish among 144 juveniles (6-13 cm fork length) grouped in 1-cm size categories, but the results were inconclusive.

Discussion

The results of this study generally agree with those of other investigators. The importance of copepods in the diet of juvenile sockeye salmon near shore in Bristol Bay is paralleled in coastal waters of British Columbia (Manzer 1969) and is similar to Kamchatka coasts, where copepods and cladocerans were the predominant foods of juvenile sockeye salmon (Synkova 1951). My findings differ from those of Jaenicke and Bonnett (see footnote 2), who sampled mainly over deeper waters of Bristol Bay farther offshore than I did, and Dell (1963), who sampled off Port Moller in Bristol Bay. Jaenicke and Bonnett examined the food of over 1,200 juvenile sockeye salmon captured during the summers of 1969-70 and found that the main items (in bulk) were young and larval sand lance and euphausiids. Similarly, Dell reported that 45 juvenile sockeye salmon taken in late July 1962 contained mostly larval sand lance and euphausiids.

Nearly all of the insects I found were from juvenile sockeye salmon captured in the Kvichak and Egegik areas in June (Table 1). These areas are contiguous to many rivers that form part of a major sockeye salmon reproductive complex of lakes and steams (Figure 1). According to Hartman et al. (1967), most of the migration from freshwater to Bristol Bay takes place in June. Most of the insects were probably ingested in fresh water when the fish were migrating seaward, suggesting that many of the juveniles taken in these areas were recent immigrants from fresh water. The occurrence of the only empty stomachs and small average weight of food per fish at Kvichak and Egegik suggest that the juveniles eat very little when they first enter salt water. Straty (1974) concluded that the young sockeye salmon did not feed when they entered Bristol Bay or that food was scarce. Reduction of feeding could be caused by a number of factors other than lack of food, including the physiological strain of adjusting osmoregulatory function from a freshwater to a marine environment.

The differences I observed in the types, relative proportions, and amounts of food eaten over successive months by the juvenile sockeye salmon as they progressed seaward can be largely attributed to food availability. Near-surface waters in the Kvichak area contained an average of 27 zooplankters per cubic meter in June, while near Port Moller in July the density was 1,400-8,100 (see footnote 1). Straty (1974) compared zooplankton abundance in the inner part of Bristol Bay (above Port Heiden) and the outer part (below Port Heiden) during 1969-71 and concluded that zooplankton was much more abundant as one progressed seaward.

Acknowledgements

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Literature Cited

CHAMBERLAIN, F. M.
1907. Some observations on salmon and trout in Alaska. Rep. U.S. Comm. Fish. 1906, 112 p. (Bur. Fish. Doc. 627.)

DELL, M. B.
1963. Oceanic feeding habits of the sockeye salmon, *Oncorhynchus nerka* (Walbaum), in Aleutian waters. M.S. Thesis, Univ. Michigan, Ann Arbor, 40 p.

HARTMAN, W. L., W. R. HEARD, AND B. DRUCKER.
1967. Migratory behavior of sockeye salmon fry and smolts. J. Fish. Res. Board Can. 24:2069-2099.

MANZER, J. I.
1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. J. Fish. Res. Board Can. 26:2219-2223.

STRATY, R. R.
1974. Ecology and behavior of juvenile sockeye salmon *(Oncorhynchus nerka)* in Bristol Bay and the eastern Bering Sea. *In* D. W. Hood and E. J. Kelley (editors), Oceanograhy of the Bering Sea, p. 285-319. Inst. Mar. Sci., Univ. Alaska, Fairbanks.

SYNKOVA, A. I.
1951. Food of Pacific salmon in Kamchatka waters. [In Russ.] Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 34:105-121.

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OCCURRENCE OF TWO GALATHEID CRUSTACEANS, *MUNIDA FORCEPS* AND *MUNIDOPSIS BERMUDEZI*, IN THE CHESAPEAKE BIGHT OF THE WESTERN NORTH ATLANTIC OCEAN[1,2]

Living male specimens of *Munida forceps* A. Milne-Edwards and *Munidopsis bermudezi* Chace (Table 1) were collected on the continental slope and rise south of Norfolk Canyon off the coast of Virginia on 18-19 November 1974. An ovigerous female *M. bermudezi* was also collected on 14 September 1975 in the Norfolk Canyon. They were taken with a 15-m shrimp trawl (12-mm stretch mesh inner liner) towed from the RV *James M. Gillis* (University of Miami, Florida).

Munida forceps has been reported from 80 to 338 m within the Gulf of Mexico and in the southwestern Atlantic between lat. 22°46.5′ and 26°37.0′N (Chace 1940, 1942; Springer and Bullis 1956; Bullis and Thompson 1965). Our find is consistent with the previously reported depth range, but it extends the geographic range of the species northward by 10° latitude.

Munidopsis bermudezi has been reported from the coast of Cuba (lat. 21°19′N, long. 76°05′W) at a depth of 2,654 m (Chace 1940, 1942), the Gulf of Mexico (lat. 25°50.5′N, long. 94°27′W) at 3,294 m (Pequegnat and Pequegnat 1970), and north of the Azores (lat. 45°26′N, long. 25°45′W) at 3,171 m (Sivertsen and Holthuis 1956).

The *Munida forceps* sample also included the galatheids *M. iris* A. Milne-Edwards and *M. longipes* A. Milne-Edwards and other decapods including *Bathynectes superbus* (Costa), *Cancer borealis* Stimpson, *C. irroratus* Say, *Homarus americanus* H. Milne Edwards, and penaeidean and caridean shrimps. The association of *M. forceps* with *M. iris* and *M. longipes* in our sample is previously unreported. Some previous records have shown associations with *M. stimpsoni* A. Milne-Edwards (Chace 1942) and with *M. flinti* Benedict and *M. irrasa* A. Milne-Edwards (Milne-Edwards 1880 from Pequegnat and Pequegnat 1970). Others (Benedict 1902; Bullis and Thompson 1965; Pequegnat and Pequegnat 1970) have not specified association of *M. forceps* with other galatheids.

TABLE 1.—Station and morphometric data for *Munida forceps* and *Munidopsis bermudezi* captured near Norfolk Canyon off the coast of Virginia. Length and width measurements in millimeters.

Item	*Munida forceps*	*Munidopsis bermudezi*	
	Male	Male	Female
Station	79	86	35
Collection	C74-499	C74-506	C74-168
Location, lat.	36°43.2′N	36°41.6′N	36°57.9′N
long.	74°38.0′W	73°47.0′W	73°21.5′W
Date of collection	Nov. 1974	Nov. 1974	Sept. 1975
Depth (m)	220-310	2,620-2,650	2,915-2,955
Bottom temperature (°C)	10.6	3.0	2.3
Bottom salinity (‰)	—	34.82	35.11
Total length (rostral tip to posterior margin of telson)	34	81.4	83.2
Carapace width, anterior	7.9	28.4	28.8
posterior	10.4	31.0	31.5
Carapace length (orbit to posterior margin)	13.5	33.5	33.5
Carapace length (including rostrum)	18.5	44.8	43.8
Cheliped (right) length	45	42.4	40.8
Carpus length	4.0	8.5	7.5
Merus length	15.2	14.5	13.0
Propodus length	25.6	19.3	14.3
Propodus width	4.5	8.8	8.0
Dactylus length	15.1	10.5	8.3
Second left pereopod length	28.8	48.7	46.5

[1]Research supported by National Science Foundation Grant GA-37561, J. A. Musick, Principal Investigator and by U.S. Department of Commerce, National Marine Fisheries Service Contract No. 03-4-043-353 for C.E.L. and P.A.H. participation.
[2]Contribution No. 717, Virginia Institute of Marine Science.

In November 1974, *Munidopsis bermudezi* was associated with *M. curvirostra* Whiteaves. Previous accounts did not indicate association of *M. bermudezi* with other galatheids. Other decapods taken in the November sample were *Lithodes agassizii* Smith, *Stereomastis sculpta* (Smith), and penaeidean and caridean shrimps, including *Hymenodora gracilis* Smith, a species occurring in the Azores sample (Sivertsen and Holthuis 1956).

In September, *M. bermudezi* was associated with *M. bairdii* (Smith) and *M. crassa* (Smith), as well as *Lithodes agassizii* and caridean shrimp.

The ovigerous *M. bermudezi* had not shed all eggs onto the pleopods. The 19 external eggs were tan and averaged 2.8 mm in diameter. These eggs were spherical with no visible blastoderm and were recently extruded. The ovary was tan and very well developed. It contained 106 ova averaging 2.7 mm in diameter. All eggs were measured with an ocular micrometer.

We suspect that these species with tropical affinities are normally present, though rare, in the Chesapeake Bight; but they could be accidental migrants. In either case, the probability of detection was raised by the recent increase in sampling intensity in the vicinity of Norfolk Canyon as compared to other areas of the continental slope between Florida and North Carolina. The question of how far north the tropical fauna extends along the southeastern coast of North America is still unanswered (Briggs 1974). Cerame-Vivas and Gray (1966) noted that the inshore fauna of the North Carolina shelf was warm temperate (Carolinian) but that the offshore fauna was tropical. In a study of sea stars of North Carolina, Gray et al. (1968) found 13 species that occurred in a northward extension of the Caribbean Province along the outer shelf and that these species ranged slightly northward past Cape Hatteras.

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Literature Cited

BENEDICT, J. E.
1902. Descriptions of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of the known marine species. Proc. U.S. Natl. Mus. 26:243-334.

BRIGGS, J. C.
1974. Marine zoogeography. McGraw-Hill, N.Y., 475 p.

BULLIS, H. R., AND J. R. THOMPSON.
1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat* and *Pelican* made during 1956 to 1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510, 130 p.

CERAME-VIVAS, M. J., AND I. E. GRAY.
1966. The distributional pattern of the benthic invertebrates of the continental shelf off North Carolina. Ecology 47:260-270.

CHACE, F. A., JR.
1940. The Atlantis expeditions to the West Indies in 1938 and 1939, under the joint auspices of the University of Havana and Harvard University. List of Stations. Woods Hole Oceanogr. Inst., Contrib. 274, 8 p.
1942. Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The anomuran Crustacea. I. Galatheidea (Families Chirostylidae, Galatheidae and Porcellanidae). Torreia (Havana) 11:1-106.

GRAY, I. E., M. E. DOWNEY, AND M. J. CERAME-VIVAS.
1968. Sea-stars of North Carolina. U.S. Fish Wildl. Serv., Fish. Bull. 67:127-163.

MILNE-EDWARDS, A.
1880-81 Reports on the results of dredging under the supervision of *Alexander Agassiz*, in the Gulf of Mexico and in the Caribbean Sea *1887 '78, '79* by the U.S. Coast Survey Steamer "Blake," Lieut.-Commander *C. D. Sigsbee*, U.S.N., and Commander *J. R. Bartlett*, U.S.N., Commanding. VIII. Études préliminaries sur les Crustacés. Bull. Mus. Comp. Zoöl. Harv. Coll. 8:1-68.

PEQUEGNAT, L. H., AND W. E. PEQUEGNAT.
1970. Deep-sea anomurans of Superfamily Galatheoidea with descriptions of three new species. *In* W. E. Pequegnat and F. A. Chace, Jr. (editors), Contributions on the biology of the Gulf of Mexico, Vol. 1, p. 125-170. Gulf Publ. Co., Houston.

SIVERTSEN, E., AND L. B. HOLTHUIS.
1956. Crustacea Decapoda (the Penaeidea and Stenopodidea excepted). Rep. Sci. Result "Michael Sars" North Atl. Deep-sea Exped. 1910 5(12):1-54.

SPRINGER, S., AND H. R. BULLIS, JR.
1956. Collections by the *Oregon* in the Gulf of Mexico. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 196, 134 p.

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EFFECTS OF MERCURY, CADMIUM, AND LEAD SALTS ON REGENERATION AND ECDYSIS IN THE FIDDLER CRAB, *UCA PUGILATOR*

Crabs are capable of autotomizing injured limbs at a preformed breakage plane and subsequently regenerating them. The regenerating limb bud grows in a folded position within a layer of cuticle, and unfolds when the animal molts. The length of regenerating limb buds is generally expressed in terms of "R-value" (Bliss 1956) which is length of limb bud × 100/carapace width. Such a regeneration index is useful for comparisons of crabs of different sizes. Since regeneration always terminates with a molt, the presence of regenerating limbs can affect the timing of ecdysis, and factors which influence ecdysis will also affect regeneration. For example, removal of eyestalks, a source of molt-inhibiting hormones, is a standard way of inducing precocious molting. Such animals will regenerate missing limbs rapidly, but will generally die at ecdysis. Skinner and Graham (1972) have shown that multiple autotomy, producing many regenerating limb buds, can cause accelerated regeneration, also leading to precocious molt.

Heavy metals as pollutants of the marine environment are of great concern. These chemicals are released as a result of industrial processes and tend to be toxic and to accumulate in organisms. Their toxicity to Crustacea has been studied by Corner and Sparrow (1957), Wisely and Blick (1967), Eisler (1971), Vernberg and Vernberg (1972), and O'Hara (1973).

This paper reports on the effects of mercury, lead, and cadmium on regeneration in the fiddler crab, *Uca pugilator*. With its estuarine intertidal habitat, this crab is likely to be subject to heavy metal pollution in industrial areas.

Materials and Methods

Fiddler crabs were collected in July and August from Accabonac Harbor, near East Hampton, N.Y., and brought into the laboratory. Autotomy of one chela and six walking legs was induced by pinching each merus with a hemostat. Immediately after autotomy, crabs were placed in solutions of $Pb(NO_3)_2$ (Reagent grade, Fisher Scientific), $HgCl_2$ (Reagent grade, Fisher Scientific), or anhydrous $CdCl_2$ (Reagent grade, Matheson, Coleman and Bell) at concentrations of 0.1 or 1.0 mg/liter of the metal ion. Crabs were maintained in groups of 10 in 1-liter glass aquaria in 200 ml of filtered seawater (30‰ salinity, room temperature 25°C). Twice weekly the aquaria were washed out and redosed. (In a similar static experimental design, Jackim et al. (1970) determined that the loss of metal ion from solution over a 96-h period was 0% for cadmium, 26% for mercury, and 79% for lead.) Crabs were fed twice weekly with Purina Fly Chow[1]. In all experiments, groups were arranged to have the same mean carapace width and to have equivalent distribution of males and females (5/5).

The growth of limb buds was measured twice weekly under a dissecting microscope with a calibrated ocular micrometer. In all cases, the first walking leg was measured as a representative limb. Values thus obtained were converted to R-values, and the means for each group were compared by the use of the *t*-test. Times of molting were recorded for all animals. Limb buds reached R-values of about 20 just prior to ecdysis.

Whole crabs were analyzed for mercury, cadmium, and lead following 2 wk of exposure to 0.1 mg/liter. Five crabs were used for each assay, which was done by New Jersey Department of Health personnel, using atomic absorption spectrophotometry.

Results

In experiment 1, crabs (mean carapace width 15 mm, range 13-16 mm) were exposed to 0.1 mg/liter of lead, cadmium, and mercury. Ten crabs were in each group, total biomass about 11 g. Cadmium had a retarding effect on regeneration (Table 1) although most individuals had molted by 28 days. The majority of controls molted by 21 days, and the rest completed ecdysis by 24 days. Mercury and lead had no retarding effect.

This experiment was repeated with crabs of a somewhat smaller size (13 mm carapace width, range 11-14 mm). Although cadmium again retarded regeneration, the retardation was less and was not always statistically significant (Table 1). These crabs reached ecdysis at the same time as controls (21 days). No effects of lead or mercury were seen.

In experiment 2, crabs were exposed to lead, mercury, and cadmium at concentrations of 1.0 mg/liter. Carapace width of crabs was 15 mm

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—R-values (mean ± standard error) of first walking legs of crabs after multiple autotomy and treatment with Pb, Hg, and Cd at 0.1 mg/liter.

Chemical	Days 7	10	14	17	21
Carapace width 15 mm:					
Controls	1.8 ± 0.3	7.3 ± 0.6	12.0 ± 0.7	18.4 ± 0.8	60% molt
Pb	2.8 ± 0.5	10.2 ± 0.7	14.7 ± 1.1	20.1 ± 0.6	80% molt
Hg	2.3 ± 0.2	8.8 ± 1.2	13.8 ± 1.3	17.7 ± 0.8	70% molt
Cd	1.0 ± 3.3	3.3 ± 0.7*	8.6 ± 1.2*	11.0 ± 1.3*	13.5 ± 1.5
Carapace width 13 mm:					
Controls	4.8 ± 0.4	10.6 ± 1.0	17.7 ± 1.0	20.2 ± 0.7 40% molt	70% molt
Pb	4.2 ± 0.4	9.2 ± 0.9	17.7 ± 0.8	18.2 ± 0.9 50% molt	90% molt
Hg	3.9 ± 0.7	9.4 ± 0.9	16.2 ± 1.1	17.9 ± 0.5 30% molt	60% molt
Cd	3.5 ± 0.6	8.0 ± 1.0	14.2 ± 1.1*	17.0 ± 0.8* 0% molt	70% molt

*P = 0.05 or less.

(range 14-16 mm). At this concentration, cadmium retarded regeneration to an even greater extent. This concentration of mercury was usually toxic, and the data obtained were from four crabs which survived the duration of the experiment. Regeneration did not take place in these crabs (Table 2). The cadmium, however, was not toxic, and all crabs survived, the majority (60%) completing ecdysis by 28 days. There was no mortality in lead, cadmium, or clean water in any of the experiments. The majority of controls molted by 24 days. A second group of crabs (carapace width 13 mm, range 12-14 mm) was exposed to cadmium and mercury at 1.0 mg/liter. Lead was not used in this experiment. Because of the high mortality in mercury in the previous experiment, 20 crabs were exposed to mercury. By the 17th day, the number surviving in mercury was reduced to eight, the same percentage as survived the previous experiment. The amount of growth in these crabs, though slight, was nevertheless much greater than in the previous experiment. Likewise, the retardation in cadmium was not as striking as in the earlier experiment (Table 2). The majority of controls molted by 21 days, whereas the majority in cadmium molted by 28 days. After 2½ wk, the eight crabs remaining in mercury were transferred to clean water, which was then changed daily, but they did not show evidence of recovery within 4 wk after return to clean water, during which time no significant growth occurred.

Residue analysis revealed that the crabs exposed for 2 wk to 0.1 mg/liter of mercury had absorbed 0.026 ± 0.001 ppm; those exposed to 0.1 mg/liter of cadmium had absorbed 0.50 ± 0.10 ppm; and those exposed to 0.1 mg/liter of lead had absorbed 2.04 ± 0.55 ppm.

Discussion

Retardation of regeneration was a specific effect of cadmium at both 0.1 and 1.0 mg/liter. At 0.1

TABLE 2. — R-values (mean ± standard error) of first walking legs of crabs after multiple autotomy and treatment with Pb, Hg, and Cd at 1.0 mg/liter.

Chemical	Days 7	10	14	17	21	24
Carapace width 15 mm:						
Controls	4.2 ± 0.4	8.0 ± 0.6	13.1 ± 1.0	15.9 ± 0.9	18.1 ± 0.3	70% molt
Pb	2.8 ± 0.6	6.2 ± 0.7	11.4 ± 1.0	14.5 ± 1.2	17.6 ± 0.7	70% molt
Hg	0*	0*	0*	0*	0.01 ± 0.01*	0.01 ± 0.01*
Cd	0.3 ± 0.2*	2.2 ± 0.8*	4.3 ± 1.2*	5.6 ± 1.5*	8.3 ± 2.5*	7.6 ± 2.3* 20% molt
Carapace width 13 mm:						
Controls	4.6 ± 0.5	10.2 ± 0.7	15.7 ± 0.9	18.0 ± 0.6	70% molt	90% molt
Hg	1.0 ± 0.6*	1.5 ± 0.8*	1.6 ± 0.8*	[1]2.1 ± 1.0*	2.7 ± 1.1*	2.9 ± 1.1*
Cd	3.5 ± 0.2	6.8 ± 0.6*	11.5 ± 1.3*	13.8 ± 1.5*	16.0 ± 2.0*	50% molt

[1]Returned to clean water.
*P = 0.05 or less.

mg/liter, mercury was not toxic and did not have an effect on the growth of limb buds. At 1.0 mg/liter, mercury caused almost total inhibition of limb growth, but also proved lethal to 60% of the crabs. Therefore, the inhibition of regeneration may not be a specific effect of the mercury, but just an indication of the toxicity of the metal to the crabs. In this light, *Uca* is seen to be much more resistant to mercury than the porcelain crab, *Petrolisthes armatus*, in which the 96 h LC_{50} (mean lethal concentration) was 0.050-0.064 ppm (Roesijadi et al. 1974). With long-term exposure to mercury, however, *Uca* can tolerate only 0.18 ppm (Vernberg and O'Hara 1972). In the present study, cadmium might have shown a greater effect than mercury at 0.1 mg/liter because it was absorbed to a much greater extent than the mercury. It is possible that exposure to mercury at levels between 0.1 and 1.0 mg/liter could inhibit regeneration without causing mortality. Despite the high amounts absorbed, lead had no effect on regeneration rate.

At both dose levels of cadmium and the higher concentration of mercury, the retarding effects were greater the first time the experiment was performed (July) than the second (August). Since these crabs normally molt in August, it is probable that they have higher titers of ecdysone at that time, and their progress toward ecdysis cannot be inhibited to the same extent. A similar seasonal difference in sensitivity to cadmium was seen in the shrimp *Paratya tasmaniensis*, which showed a threefold higher LC_{50} value in mid-October than in early July (Thorp and Lake 1974).

Thurberg et al. (1973) have found that cadmium reduced the level of oxygen consumption in the crabs *Carcinus maenas* and *Cancer irroratus*. A reduction of oxygen consumption of the gills of the mud crab, *Eurypanopeus depressus*, exposed to cadmium was found by Collier et al. (1973). Reduced metabolism may be responsible for the retardation of regeneration of the crabs in cadmium. Cadmium has been found to inhibit oxygen consumption and metabolism of fishes (Thurberg and Dawson 1974; Jackim et al. 1970) and has similarly been found to retard fin regeneration in fishes (Weis and Weis in press).

In this sort of study it is difficult to extrapolate laboratory findings to the field. In nature, metals would tend to be concentrated in the sediments more than the water, and it would be primarily from the sediments that these estuarine intertidal crabs would pick up the metals. Crabs would not normally be subjected to the loss of many appendages. Loss of a single limb is not particularly debilitating to a decapod. Should many limbs be lost, however, the crab's locomotion would be impaired, and it would be at a disadvantage. It would therefore be advantageous to regenerate the lost limbs as quickly as possible. Crabs which could not regenerate as quickly could be more subject to predation, and the toxic heavy metal pollutant would then be passed on to higher trophic levels.

Acknowledgments

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Literature Cited

BLISS, D. E.
1956. Neurosecretion and the control of growth in a decapod crustacean. *In* K. G. Wingstrand (editor), Bertil Hanström, zoological papers in honour of his sixty-fifth birthday, Nov. 20, 1956, p. 56-75. Zool. Inst. Lund, Swed.

COLLIER, R. S., J. E. MILLER, M. A. DAWSON, AND F. P. THURBERG.
1973. Physiological response of the mud crab, *Eurypanopeus depressus* to cadmium. Bull. Environ. Contam. Toxicol. 10:378-382.

CORNER, E. D. S., AND B. W. SPARROW.
1957. The modes of action of toxic agents. II. Factors influencing toxicities of mercury compounds to certain crustacea. J. Mar. Biol. Assoc. U.K. 36:459-472.

EISLER, R.
1971. Cadmium poisoning in *Fundulus heteroclitus* (Pisces: Cyprinodontidae) and other marine organisms. J. Fish. Res. Board Can. 28:1225-1234.

JACKIM, E., J. M. HAMLIN, AND S. SONIS.
1970. Effects of metal poisoning on five liver enzymes in the killifish (*Fundulus heteroclitus*). J. Fish. Res. Board Can. 27:383-390.

O'HARA, J.
1973. The influence of temperature and salinity on the toxicity of cadmium to the fiddler crab, *Uca pugilator*. Fish. Bull., U.S. 71:149-153.

ROESIJADI, G., S. R. PETROCELLI, J. W. ANDERSON, B. J. PRESLEY, AND R. SIMS.
1974. Survival and chloride ion regulation of the porcelain crab *Petrolisthes armatus* exposed to mercury. Mar. Biol. (Berl.) 27:213-217.

SKINNER, D. M., AND D. E. GRAHAM.
1972. Loss of limbs as a stimulus to ecdysis in Brachyura (true crabs). Biol. Bull. (Woods Hole) 143:222-233.

THORP, V. J., AND P. S. LAKE.
1974. Toxicity bioassays of cadmium on selected freshwater

invertebrates and the interaction of cadmium and zinc on the freshwater shrimp, *Paratya tasmaniensis* Riek. Aust. J. Mar. Freshwater Res. 25:97-104.

THURBERG, F. P., AND M. A. DAWSON.
1974. Physiological response of the cunner, *Tautogolabrus adspersus*, to cadmium. III. Changes in osmoregulation and oxygen consumption. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-681:11-13.

THURBERG, F. P., M. A. DAWSON, AND R. S. COLLIER.
1973. Effects of copper and cadmium on osmoregulation and oxygen consumption in two species of estuarine crabs. Mar. Biol. (Berl.) 23:171-175.

VERNBERG, W. B., AND J. O'HARA.
1972. Temperature-salinity stress and mercury uptake in the fiddler crab, *Uca pugilator*. J. Fish. Res. Board Can. 29:1491-1494.

VERNBERG, W. B., AND J. VERNBERG.
1972. The synergistic effects of temperature, salinity, and mercury on survival and metabolism of the adult fiddler crab, *Uca pugilator*. Fish. Bull., U.S. 70:415-420.

WEIS, P., AND J. S. WEIS.
In press. Effects of heavy metals on fin regeneration in the killifish, *Fundulus heteroclitus*. Bull. Environ. Contam. Toxicol.

WISELY, B., AND R. A. P. BLICK.
1967. Mortality of marine invertebrate larvae in mercury, copper, and zinc solutions. Aust. J. Mar. Freshwater Res. 18:63-72.

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NOTES ON THE EARLY DEVELOPMENT OF THE SEA RAVEN, *HEMITRIPTERUS AMERICANUS*

Egg and larval characteristics of the sea raven, *Hemitripterus americanus* (Gmelin), are distinctive. The species ranges from Labrador to Chesapeake Bay but is nowhere abundant (Bigelow and Welsh 1925). Notes on the fertilized eggs (Bean 1897), newly hatched larvae (Warfel and Merriman 1944), and juveniles larger than 45 mm (Huntsman 1922; Bigelow and Welsh 1925; Bigelow and Schroeder 1936) have been recorded. However, there is no available information dealing with specimens between 12 and 45 mm in length. The present paper attempts, in part, to bridge this gap in previous observations of these larvae.

Methods and Materials

A cluster of nearly 90 eggs was found on the rocky shore of Montauk Point, N.Y. The eggs were collected at the level of the high tide mark at 0930 h on 9 November 1974. They were placed in an open system seawater aquarium at the marine station of Southampton College. In mid-December half of the eggs were transferred to laboratory facilities at the Academy of Natural Sciences of Philadelphia, where they were held in artificial seawater (7°C, 32‰) with a controlled photoperiod of 10.5 h light and 13.5 h darkness. Crude but effective temperature control was achieved by placing the covered rearing container in a water bath. The water bath and rearing container were then placed in a refrigerator. The temperature of the water bath was maintained with a thermostatically controlled aquarium heater. A 7½-W light bulb, controlled by an electric timer, was suspended above the rearing container. Moderate aeration kept the eggs in motion. After hatching, the larvae were maintained in similar conditions but without aeration. The strong current resulting from aeration appeared to be detrimental to the fragile larvae. When the yolk was nearly absorbed, the larvae were presented with food in the form of *Artemia* sp. nauplii and small pieces of *Palaemonetes* sp. and *Littorina* sp. flesh. Only three specimens could be induced to eat the pieces of flesh by placing the food in their mouths. Eventually one specimen ate the *Artemia* sp. nauplii unassisted.

Measurements were made on live material. Egg diameters were measured with dial calipers. Total lengths (TL) of the larvae were measured through a dissecting microscope using an ocular micrometer. Myomere counts were made with the aid of two Polaroid[1] HN 38 × 0.3 inch filters placed above and below the larvae and used in conjunction with a dissecting microscope and substage lamp. Final identification of the larvae was based on a comparison of the largest reared specimen in this study and the specimens collected in the Gulf of Maine by Joanne and Wayne Laroche. All 36 preserved specimens were preserved in 5% buffered Formalin and deposited in the Department of Ichthyology, Academy of Natural Sciences of Philadelphia (ANSP 131947).

Descriptions

Egg and Embryo

Some of the peripheral eggs in the cluster had

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

flattened sides, suggesting the cluster had been part of a larger mass. A small piece of an encrusting sponge, *Halichondria panicea*, was found attached to the eggs. Small tubules (0.14 mm in diameter) were also found on the surface of some of the eggs and were assumed to belong to some species of polychaete. Eggs have been described by Warfel and Merriman (1944). At the time of collection, embryos were already well developed in all of the eggs. Pigmentation on the body consisted of melanophores arranged in vertical bars corresponding to the location of the myomeres. The retina was black and the iris had a silvery appearance. The median fin fold and pectoral buds were formed. The former originated close behind the hindbrain. By 16 December, large melanophores developed on the hindbrain and dorsal half of the yolk sac. The body pigmentation ended abruptly on the caudal peduncle about three-fourths of the total length from the snout. This characteristic pattern, to be referred to as the truncated pigmentation pattern, persisted throughout the development of all specimens. The mouth was formed and open. The single oil globule (ca. 0.8 mm in diameter) inside the yolk sac was located at the anterior confluence of the abdomen and yolk sac.

Newly Hatched Larvae

The larvae (Figure 1) began hatching on 3 January 1975, 55 days after collecting the already well developed eggs, and continued through 30 January. The newly hatched larvae averaged 12.8 mm TL (range 11.7-12.7 mm). Warfel and Merriman (1944) noted the larvae emerged head first. This was not always true in the case of my material. Nearly one-half of the larvae which were observed hatching emerged tail first. The large ovoid yolk extended forward to or beyond the posterior margin of the eye. The head was not flexed over the anterior of the yolk sac. Body pigmentation became more dense and uniform but was lacking over the forebrain, ventral half of the yolk sac, and the posterior one-fourth of the body. Melanophores lined the base of the dorsal fin fold to the level of the truncated body pigment. A few melanophores were present along the post-anal fin fold base, near the posterior margin of the body pigment. The preanal fin fold was barely perceptible. No gas bladder developed. The mouth was very large. The maxillary extended to or slightly behind the middle of the eye. The lower jaw contained four sharply pointed, conical teeth on each side. The fourth tooth was somewhat smaller and located lower on the dentary. Body proportions and total myomeres (38 or 39) were similar to those reported by Warfel and Merriman (1944) at this stage. The larvae remained mostly on the bottom of the container, spending much of the time on their sides possibly as a result of the enlarged yolk sac. Efforts to swim were very awkward and only made when the larvae were disturbed.

Further Development

Near the end of January, the larvae were observed to be positively phototactic. The yolk of many of the larvae was absorbed by the end of the first week in February. The peritoneum appeared silvery through the skin. The pigmentation became uniform olive grey over the body (Figure 2). Specimens ranged between 14.0 and 17.0 mm TL on 6 February. Those longer than 16.1 mm had rudimentary caudal rays. The larvae were more

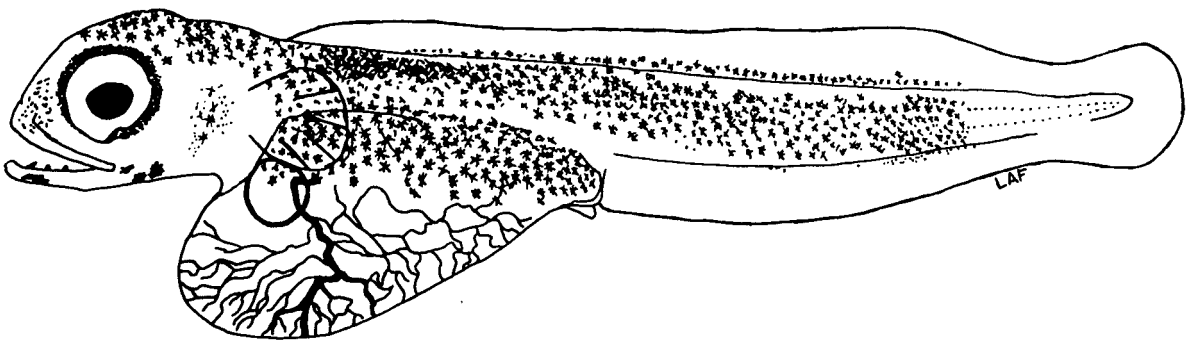

FIGURE 1.—*Hemitripterus americanus*. Prolarva (newly hatched), 8 January 1975: 12.6 mm TL.

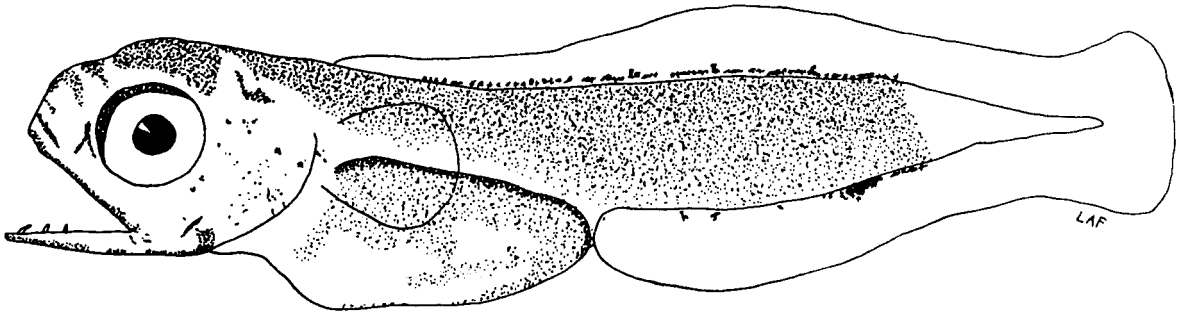

FIGURE 2.—*Hemitripterus americanus*. Early postlarva, 17 February 1975: 15.5 mm TL.

active by this time, but still spent most of the time on the bottom. By 2 March, the larvae were no longer attracted to light.

Toward the end of March, the caudal fin had 8 or 9 ray rudiments. Rays began to develop in the second then first dorsal fins followed by the pectoral fins. The caudal peduncle remained unpigmented. Spines began to form on the preoperculum. Greyish-tan fleshy tabs developed dorsally behind the head and around the occiput.

By 20 April, the largest specimen (Figure 3) had 14 and 11 elements in the first and second dorsal fins, respectively. The anal had 10 rays and the caudal had 12, at about 20 mm TL. Both the dentary and premaxilla had 15 teeth on each side. The preopercular spines became more prominent. The hypural plate began to form. The ratio of the head length to total length was 3.6; of the predorsal length to total length, 3.8; and of the eye diameter to head length, 2.7. The iris became less silvery. Dense pigmentation developed on the interradial membrane of the first dorsal fin between elements 1 through 4 and 8 through 12. Similar pigmentation developed in the second dorsal fin (between elements 3 and 7) and the postanal fin fold (between elements 3 and 6). Few melanophores were scattered between these dense areas of pigment. This larva utilized much of the water column during active periods and spent little time on the bottom.

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Literature Cited

BEAN, T. H.
1897. Notes upon New York fishes received at the New York Aquarium, 1895—1897. Bull. Am. Mus. Nat. Hist. 9:327-375.

BIGELOW, H. B., AND W. C. SCHROEDER.
1936. Supplemental notes on fishes of the Gulf of Maine. Bull. U.S. Bur. Fish. 48:319-343.

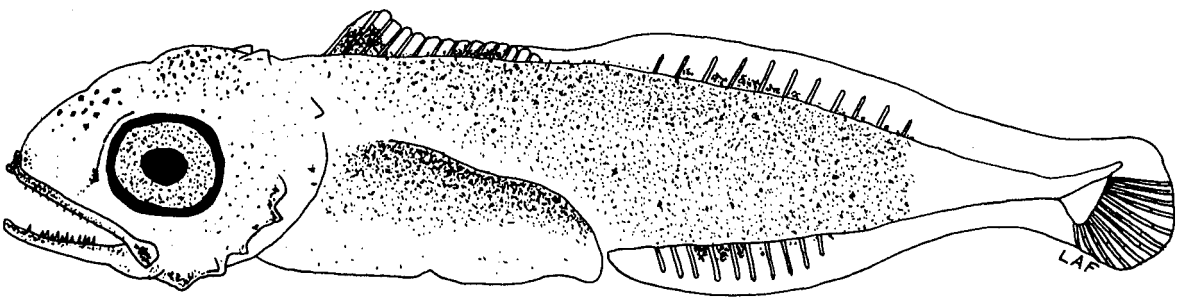

FIGURE 3.—*Hemitripterus americanus*. Postlarva, 20 April 1975: ca. 20 mm TL (the pectoral fin has been deleted for the sake of clarity).

BIGELOW, H. B., AND W. W. WELSH.
1925. Fishes of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(1), 567 p. (Doc. 965.)
HUNTSMAN, A. G.
1922. The fishes of the Bay of Fundy. Contrib. Can. Biol. 1921:49-72.
WARFEL, H. E., AND D. MERRIMAN.
1944. The spawning habits, eggs, and larvae of the sea raven, *Hemitripterus americanus*, in southern New England. Copeia 1944:197-205.

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Fishery Bulletin

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FISH SCHOOLS AS OPERATIONAL STRUCTURES

CHARLES M. BREDER, JR.[1]

ABSTRACT

The interaction of a space lattice, vortex trails, and the lubricity of fish surface mucus is shown to be important to the operation and structure of fish schools and significant in terms of locomotor efficiency. This is independent of the various interpretations of possible survival values, protection from predation, and similar ideas—all of which are extremely difficult to prove, even if valid.

A single type of space lattice is shown to approximate the arrangement of fishes in a school on the basis of geometrical reasoning. This is supported by empirical data.

The vortex trails left by each fish, when the fishes are deployed according to the "fish school" lattice, lead each following fish into a series of vortices at a point where the water flow is traveling in the direction in which they are swimming.

The lubricity of the mucus-water mixture that the fish ahead leaves in its vortices decreases the drag on the following fish.

The advantages of the regimented life in a school, as against the freedom of action common to the more or less solitary life, are evidently related to the effectiveness of the drag-reducing mucus in the vortices. The fishes with the least effective mucus appear to take advantage of the schooling life while those with the most effective mucus are more likely to be solitary.

The past decade has witnessed a considerable increase in output of papers addressed to a better understanding of the numerous phenomona presented by fish schools. These documents have covered a wide variety of the inherent problems. Nonetheless, there remain some basic questions that have proved peculiarly elusive, such as the nature of the evident regularity of the positional relationships of individuals in well organized schools and the nature of influences that hold the school members in their regular patterns. A fish school is considered here as a group of polarized individuals that operates as a unit between the times of its resolution and eventual dissolution. Initially, the activity of the fishes crowding together in their polarized pattern creates the structure of which they form components. Once established, the school efficiently regulates the locomotor activities and general comportment of the organized fishes.

The primary purpose of this paper is to show that both the geometrical pattern of the space lattice approximated by schooling fishes and the surface mucus on their bodies are mutually important elements in the formation and maintenance of fish schools. The physical bearing of these two elements is direct and important, each in its own right, to an understanding of any theory that attempts to explain the origin of schooling without recourse to theoretical interpretations.

How much of the schooling phenomenon observed in modern fishes is a result of interactions between the swimming capabilities of the fishes and the physical restrictions imposed by their environment, as compared with other biological needs, is not readily determined. However, the experiments described here are in some cases suggestive. These experiments, primarily undertaken to establish data relevant to the basic purposes of this study, in each case, have been carried only as far as was necessary to make a point. Many of them could be extended into much greater refinement with the promise of worthwhile further elucidation.

This work leads to a number of lines of possible approach to the problems of school organization. Some of the newer items discussed have had the benefit of recent studies—remote from schooling problems and in some instances remote from biology. This is especially marked in those studies that are dependent on developments in hydrodynamics during the last decade.

FISH SCHOOLS AS SPACE LATTICES

To further the understanding of the physical organization displayed by schools of fishes, a study

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of their geometrical characteristics has been undertaken. Much of the older literature on the distribution of individuals of a population, or smaller group, of animals or plants took for granted that the deployment is stochastic. Clark and Evans (1954) stated, "This assumption is no longer a tenable one and is probably even less applicable to animal populations." It is, of course, doubtful if creatures with well organized locomotor abilities and complex sensory systems are ever distributed in a fully random manner. The systems encountered in nature seem to be mostly those of ordered arrays variously distorted by processes of many kinds, sometimes obvious, but more often obscure or barely discernible. Attempts to measure the structure of assemblages of individuals have been predicated mostly on the idea of showing the extent of their departures from theoretical randomness. Since fully organized fish schools have very obvious structure, it is at least equally appropriate to compare them with mathematically organized patterns, especially where there are good theoretical reasons to expect the presence of some similarity.

Geometrical Models

The establishment of a geometrical model of a fish school is relatively simple, for whatever else a fish school[2] may be, it is essentially a closely packed group of very similar individuals united by their uniformity of orientation. A more explicit definition has been given by van Olst and Hunter (1970) who stated, "The principal characteristics of the organization of fish schools are that the individuals stay together, tend to head in the same direction, maintain even spacing, and the activities of the individuals tend to be synchronized." Because of the nature of fish locomotion it is necessary that a certain amount of swimming room be maintained by each fish (Breder 1965, van Olst and Hunter 1970). Thus each fish and a "shell" of water about it may be considered as a unit, and a school as a packing together of these units. Such structures can be handled by established mathematical procedures. The fact the fishes are all moving forward and, in many instances, often shifting their relative positions merely makes the handling of such data a little tedious, but does not vitiate the basic propositions.

One approach to the analysis of the structure of a fish school, the empirical, can be made by measuring the distance, angle, or other parameter between a given fish and the other members of the school. The mathematical manipulation of such measurements can establish values that may serve as an index to the school's organization. One's imagination alone limits the selection of data. Papers that have employed this type of approach include Keenleyside (1955), Breder (1959, 1965), Cullen et al. (1965), Hunter (1966), van Olst and Hunter (1970), Symons (1971a, b), Healey and Prieston (1973), Weihs (1973a), and Pitcher (1973). Only Cullen et al., Symons, and Pitcher in the above list attempted complete tridimensional measurements. Pitcher's paper has important bearing on the approach developed here on the basis of abstract reasoning. It will be discussed in detail later.

A theoretical approach, equally valid, is based on tridimensional geometrical concepts and constructs for purposes of comparison with fish schools. Since there is an infinite variety of such constructs possible, only those of some conceivable application to this study are discussed here. Unlike the empirical approach, there are evidently no prior papers that have employed this theoretical one. The following treatment has been made especially explicit because of the complex relationships within both space lattices and space packings, as some biologists who might consult these pages may not have instant recall of such details.

It is necessary to introduce some elementary data on tridimensional lattices that are essential to an understanding of their bearing on fish schools.[3] The most readily visualized space lattice is that in which a cube is the element or cell (Figure 1A). It is not the closest possible packing of such points: a closer one can be obtained by figuratively pushing the cubic lattice askew (Figure 1B) so that the special case of cubes with their 90° angles become rhombohedrons with other angles. The dotted arrow in Figure 1B indicates the amount of travel of the point in the upper left front corner of the lattice in attaining

[2]Definitions of this word as used here are given by Breder (1959, 1967). For an extended discussion of this and other usages see Shaw (1970).

[3]Support of all geometric statements made in this section may be found in any formal or informal geometry text covering the area concerned, such as Hilbert and Cohn-Vossen (1952) and Lines (1965).

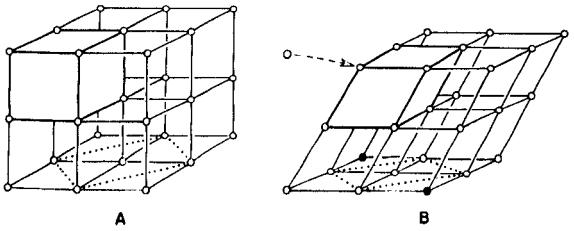

FIGURE 1.—Two space lattices in perspective, each with a single cell shown as a solid. A. The cubic lattice. B. The rhomboidal lattice. The arrow indicates the manner of transformation by which the cubic lattice becomes the rhomboidal lattice.

the transformation from cube to rhombohedron. All the angles in this rhombic lattice are either 60° or 120°, so transformed from the cubic lattice with only angles of 90°. On the floor of the cubic lattice in Figure 1A, the nearest points to the central one, in the same plane, are four in number. These are connected to each other by a dotted line. On the floor of the rhombohedron in Figure 1B, the sides of which have internal angles of 60° and 120°, the nearest points to the central point include four at the corners of the dotted parallelogram plus two more, indicated by the dark points. These define a regular hexagon because the parellelograms are composed of two equilateral triangles.

If models of identical fishes are stationed with their centers at each lattice point, and if all the models are in parallel orientation, the group superficially resembles a fish school. It becomes immediately apparent however that such a lattice of fishes has characteristics that are never seen in a school. If they had ever been seen in such a formation, their appearance would have been so striking that the details of the regimentation would have been recorded long ago. In such a school, viewed from above, fish would be seen in horizontal files and these files would be swimming ahead in rows transverse to their direction of travel. Viewed from the side, each fish within the school would have another directly above and another directly below it, forming columns, except the two fish marking the upper and lower limits of the school in each vertical column of fishes. These two would be without another fish above and below, respectively. Thus we can temporarily put this unschoollike lattice aside.

Fish models positioned at the points of the rhombic lattice do not show the peculiar features seen in the cubic lattice, but have a more distinct resemblance to fish schools. It is difficult to deny that schooling fishes, in most situations, are indeed approximating this configuration, the details of which will be discussed later.

Turning now from space lattices to the packing of space, it is easy to arrive at the above rhombic lattice by a very different route. As a preliminary mathematical simplification, fishes and the immediately surrounding water that envelops each fish individually in a school shall be equated to spheres, the centers of which are located on the axis of the fish midway between the end of the snout and the tip of the tail. Here it is necessary to describe some of the less obvious geometrical features of a mass of spheres packed together as closely as possible. A single layer of identical spheres on a plane surface packed at maximum density may be represented on paper by an equivalent packing of circles (Figure 2). A hexagon may be circumscribed about each circle, one of which is shown in the lower left corner.

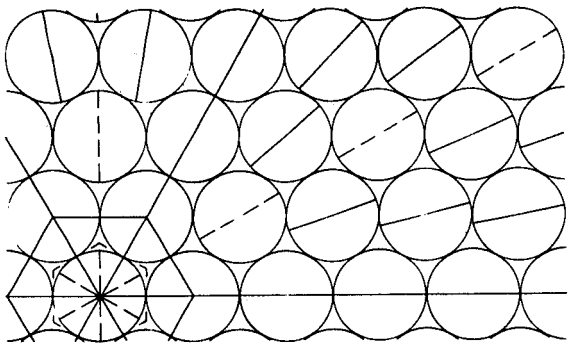

FIGURE 2.—The closest possible packing of a single layer of identical spheres or circles, showing the relationships to hexagons and their six equalateral triangles as well as the disposition of a single diameter in each circle when drawn radiating from the center of the circle with the circumscribed hexagon.

The individual diameters of each circle as shown in Figure 2 lie along radiating lines emanating from the common center of the hexagons.[4] Those lying on the radials passing through the apices of the larger hexagon are continuous lines (major axes), while those passing through the equivalent points on the smaller hexagon are dashed lines (minor axes). If these diameters are all permitted to become parallel to one another, a very different

[4]Although simple, this geometric treatment of transformations of related diameters of packed circles or spheres is evidently original here, or at least no approach to this treatment has been found. No formal proofs are necessary as the usage here is simple enough to be self-evident and would be irrelevant to present purposes.

situation appears. This may be conceptually treated as though the diameters were under some common influence, somewhat like iron filings in a rectilinear magnetic field. Figure 3 shows such an arrangement, where all diameters are in the first case at an angle of 30° to a major axis and 15° in the second case. Obviously the continuous lines of the major axes of Figure 2 are no longer possible except when the diameters are at one of the three angles of the major axes, where in each case such a drawing would show only a series of continuous parallel lines. In any of these parallel arrangements the distances of the diameters from end to end are constant throughout as are the distances from side to side. These two dimensions change only if the angle between the diameters and major axes is changed, as can be seen by comparing Figures 4 and 5 based on a square with Figures 2, 3A, and 3B based on a hexagon.

These two types of packing may now be considered in their more complex form in three dimensional space. The cubic space lattice is very simple and will be referred to later; the rhombic spatial array, more likely to be confusing, is

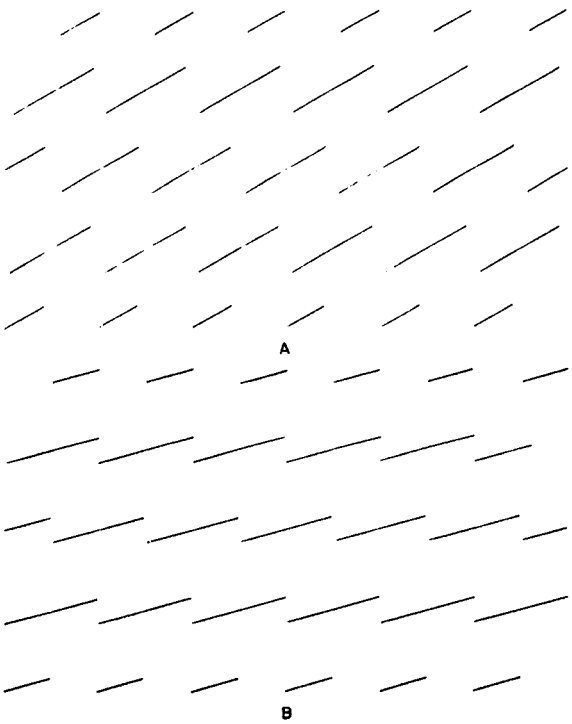

FIGURE 3.—Parallel diameters drawn on the form of Figure 2. A. Based on diameters halfway between two major axes, 30° from either. B. Based on half the angular distance used in A, 15°.

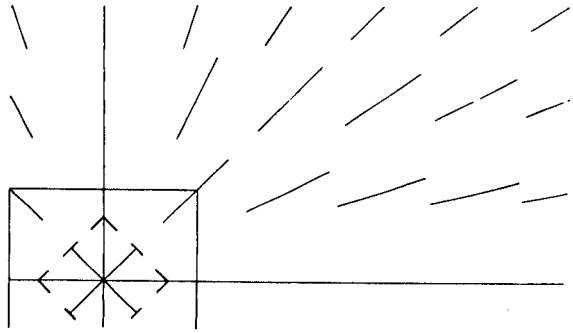

FIGURE 4.—Cubic packing of a single layer of spheres or circles, directly comparable with Figure 2.

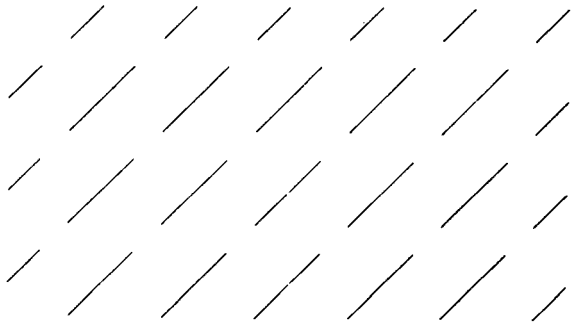

FIGURE 5.—Parallel diameters drawn on the frame of Figure 4, based on diameters halfway between two consecutive axes, 45° from either. Directly comparable with Figure 3.

discussed in sufficient detail for present needs. Starting with the single layer of spheres of Figure 2, another layer may be placed upon it so that each sphere of the second layer rests in the hollow between three adjacent spheres of the first. The second layer automatically has a pattern identical to the first, but the centers of all the spheres of the upper layer are displaced so as to fall over the centers of an equilateral triangle connecting the centers of the supporting first layer spheres. This is shown in Figure 6 where the centers of the first layer spheres are indicated by large circles and those of the second by smaller dark circles. The dash-line hexagon of Figure 6 indicates the displacement of the second layer centers. It also shows that just three second layer sphere centers are within the solid-line hexagon. There are also shown three similar small open circles forming a similar pattern within the hexagon, which indicate the absence of spheres centered by them, and connected by dotted lines to form a hexagon of absences. In the upper left corner of this same

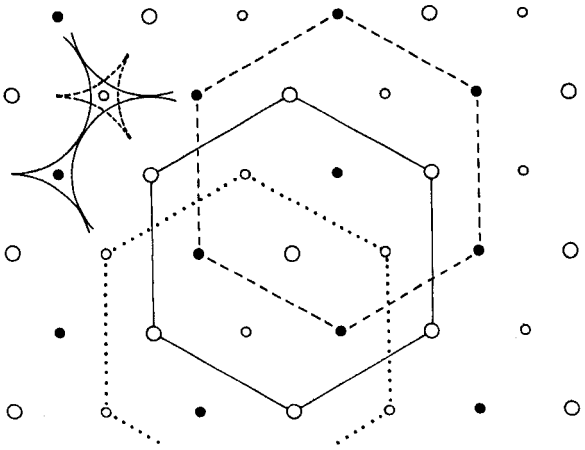

FIGURE 6.–The rhombohedral sphere pack of three layers as viewed from above. Based on Figures 1B and 2. See text for full description.

figure parts of the adjacent outlines of four spheres of the first layer are shown by solid lines. The dotted lines of three overlying spheres of the second layer are also shown. This indicates clear vertical passages through the overlying junctures that permit passage through the two layers of spheres (small open circles) while two are blocked by overlying spheres (small dark circles). The pattern is repeated throughout the system. A third layer of spheres may be identical with the first, a fourth layer identical with the second, and so on indefinitely. This pattern preserves the integrity of the vertical passages, but this need not be the case. If the second layer of sphere centers exchanges the position of the black and open small circles, the clear passages occur where the black circles are now shown and vice versa. As any layer may be so reversed the passages may be blocked in many complicated patterns. The shortest possible passage can be the vertical distance between the level of the centers of two adjacent layers of spheres, otherwise the passage may be indefinitely long.

As these planes, referred to above as layers, form the faces of the generating rhombohedron shown in Figure 1B, these passages run in three intersecting directions, as do the three planes of the lattice. The passages are all interrelated, as altering the relationships of the sphere centers in one plane automatically alters those in the two others.

The above may be simpler to visualize by referring to the perspective illustration of Figure 7.

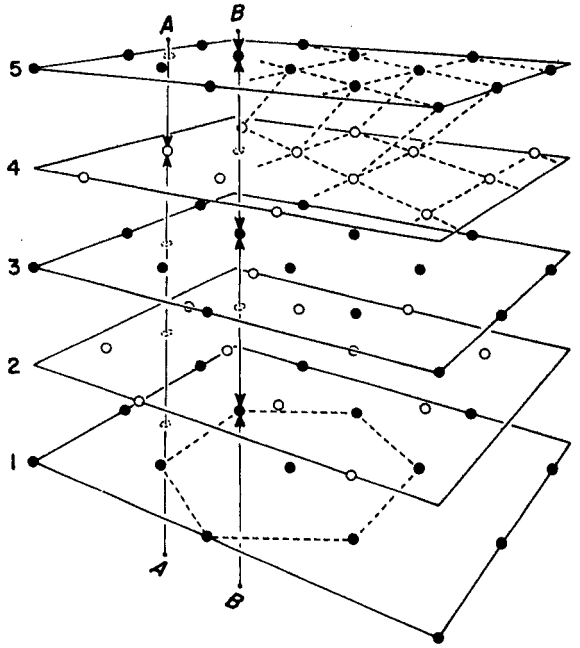

FIGURE 7.–The rhombohedral packing of spheres in perspective, showing only sphere centers. Two other sets of planes could be drawn through these centers at angles determined by the sides of the generating cell, two of which are shown between layers 4 and 5. See text for full explanation.

Here it has been necessary to completely alter the symbols used in Figure 6 owing to other needs. Plane 1 of Figure 7 is identical with the first layer of Figure 6. The hexagon of Figure 6 is shown in Figure 7 as one of dotted lines. Planes 1, 2, and 3 of Figure 7 represent the corresponding layers of Figure 6. The two added planes, 4 and 5, show more realistically the vertical passage running from A to A. It has clearance through the first three planes but is blocked at plane 4 and runs clear through 5. Note that plane 4 is "reversed" from 2, which is the reason for the blockage. The passage from B to B is blocked by planes 1, 3, and 5, but not by 2 and 4.

The indications of the rhombohedral cells by dotted lines between planes 4 and 5 clearly show how two additional sets of planes could be passed through the points.

A perspective view of the simpler cubic packing of spheres is shown in Figure 8 for comparison with Figures 1, 4, 5, and 7. Only four planes are shown, as more are unnecessary. It is evident that the cubic cell and consequent total right angled construction precludes any of the rhombic complications.

These two systems of packing spheres are all

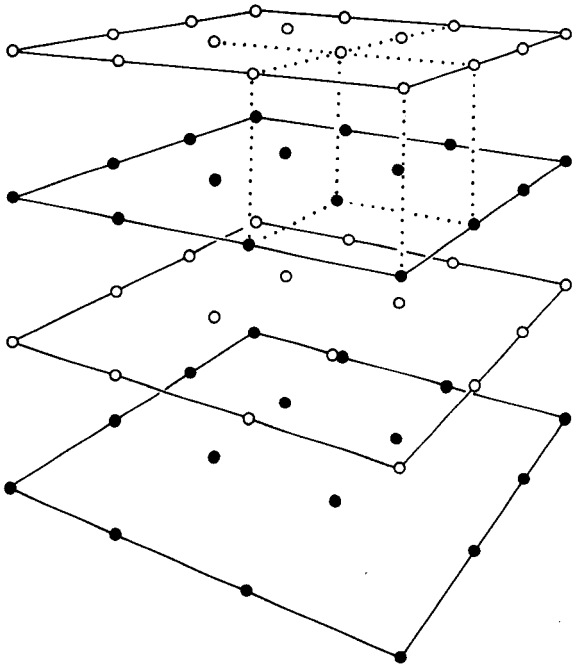

FIGURE 8.—The cubic packing of spheres, directly comparable with Figure 7. See text for full explanation.

that will be considered here, as all others are much looser and are not relevant to this study. The density of these two and the number of contacts that interior spheres have with others are given below.

Packing	Percent of volume occupied	Number of contacts of each sphere
Rhomboidal	0.740	12
Cubic	0.513	6

The number of contacts indicated here are identical with the number of "nearest neighbors" mentioned in reference to the equivalent space lattices.

Pitcher's (1973) data on clusters of spheres presented another way of explaining the complications of close sphere packing. It emphasizes the measurements from center to center, with which he was working, rather than the overall pattern of a larger group, which emphasizes the layering effect of polarized parallel diameters discussed here.

Structure and Functioning of Natural Schools

The series of diagrams in the preceding section is virtually a key to determining what, if any, space lattice a given school of fishes could approximate and it clearly indicates what types of space lattices do not find their embodiment in fish schools. Reason and observation also indicate that school-forming fishes establish their schools rapidly with great unanimity of action. The schools come to stability only after each individual has the common orientation, all normally as close together as the spatial requirements of their individual propulsive acts permit. The organization is strictly one formed in this manner and without any of the differential behavior that more complex lattices would require.

Pitcher (1973), by purely empirical means, arrived at the geometrical relationships of a school of *Phoxinus phoxinus* (Linnaeus) identical with the present formal lattice reached by theory. His fishes fit our theoretical operations even better than any of the fishes checked for this study. Our material all showed some attenuation of the lattice along the axis of travel, which also was the case in Weihs (1973a). This may simply mean that *Phoxinus* keeps a tighter school than any species we checked, or that there is some small effect here that relates to speed of fish and their absolute size. Possibly, however, it may be related to a difference in behavior between a school swimming ahead in quiet water and one holding a stationary position in flowing water, as did Pitcher's fish. In the latter, optical fixation on fellow fishes and some background feature is possible, but in the former, fixation is only possible on other members of the school as the background apparently drifts backward. If this effect does modify the spacing of the fishes, stationary schools in fast flowing rivers where backgrounds are visible should more closely approach the theoretical.

Spacing of Fishes

Using the preceding examination of lattices and the packing of spheres, a preliminary comparison with fish schools may start by continuing the equating of fishes in a school to the diameters of the packed spheres. Schooling fishes should not be expected to space themselves exactly as spheres and they do not do so in precise detail, see Pitcher (1973), but a basic resemblance exists.

If the rigid sphere of geometry be mentally replaced by a soft rubber ball, the approximation comes closer to that of a fish embedded in a school of its fellows. Thus a group of such balls, when packed together, are subjected to slight flattening

and to other minor distortions where contacts are made with other balls, all proportional to the amount of pressure and its direction. The pattern of lattice considered here as closest to the spatial distribution commonly shown by schooling fishes can be reached by very simple transformations.

The calculations that equated the diameters of the spheres to the fishes' lengths can be altered. Here the lengths are changed but the positions of fishes in space remain the same.

A change that evidently does occur regularly involves altering the angles in the quadrilateral mesh composed of two triangles as illustrated in Figure 9, where A and B represent the quadrilaterals in Figure 1, and C represents a quadrilateral that has been used by Weihs (1973a) in connection with his studies on vortex streets. It is called simply a "diamond" by that author. His model resulted from considerations of energy saving requirements. The Weihs (1973a) diamond can be used as a very convenient basic unit or cell[5] characteristic of the fish school lattices, without altering any of concepts discussed here. At this writing, all known changes from the conditions of regular geometrical figures are on the side of increased differences between the two pairs of angles of the diamond. No instances have been found in real fish schools that would lie between case A and B of Figures 1 and 9, unless the widespread separations which have been considered as degenerating schools are included. All other variations found are on the far side of B except for the data of Pitcher (1973), which is precisely at B. In Figure 9, A shows the square pattern with 90°, B shows the 60°, 120° rhombus, and C shows a rhombus with 30°, 150° which depicts a condition frequently seen in fish schools and is, as already indicated, the Weihs (1973a) diamond. Carrying this angular reduction further, the end is reached as the side to side distance between fishes is reduced to zero, so that the total length of the figure becomes a single line equal to twice the length of a side of the diamond. At the other end of this series of quadrilaterals, an increase beyond 90° produces another series. In this case the final result is also a single line, equal to twice the length of a side but at right angles to the one reached at the other extreme of the series, as described above.

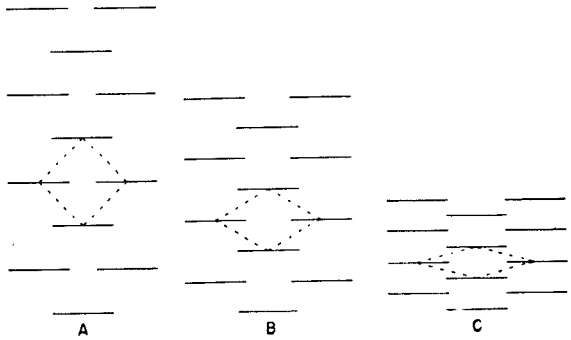

FIGURE 9.—Three quadrilaterals (lattice elements) as related to "diameters" or "fish lengths." See text for full explanation.

Figure 10 shows how these matters relate to the hexagons and how the quadrilaterals relate to an entire school. Each small circle in the upper row of three diagrams represents the midpoint of each fish. The four fishes, each on a diamond point, are represented by heavy horizontal lines representing the fish lengths. The direction of swimming is understood to be from left to right. All the others, shown only by the small circles, are moving parallel to and in the same common direction as the four indicated. Starting at A with a square and passing to B composed of two equilateral triangles, the series terminates at C with acute angles of 30°,

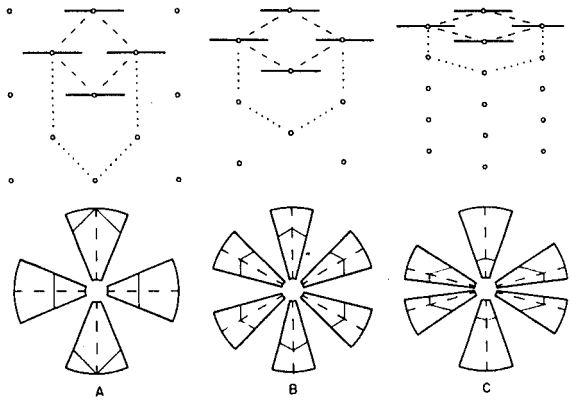

FIGURE 10.—The relations of the three quadrilaterals shown in Figure 9 to the station points in a school and to the corresponding hexagons (upper row). The clear turning sectors and those requiring a too close mutual approach are shown in the lower row. The latter are marked by their two radii and arc by a heavy solid line. Their axes, the lines of contact, are marked by dashed radii. See text for full explanation.

[5]In most schooling fishes two individuals, if isolated from the others, will swim together side by side or with one diagonally ahead of the other. If three fish are so isolated, they will normally form a pattern of three points of a diamond. In this case there is usually much more shifting around than in the case of two, while four fish tend to form a diamond. It has been a common practice for workers in this field to consider these cases of very small schools. From groups of less than four, it is impossible to make any reasonable estimate of the shape of the diamond. Some judgment can normally be obtained from a group of four, although even that might vary somewhat from a school.

which is the most compressed of the three. Also shown are the relations between the quadrilaterals and the corresponding hexagons, as well as the number of fishes in a given area.

Continuing with Figure 10, it is obvious that the direction of travel could be in any other horizontal direction of swimming, than the one shown here. It should be noted however, that the lattice of each shows that if the fish turned so as to be parallel with any edge of their parallelogram, the fishes would all be brought to the nose to tail position, something which does not occur.

In the lower row of three corresponding diagrams in Figure 10 the dashed radial lines show the directions of swimming that would place the fish in contact. The clear spaces indicate where the passages are unobstructed. The enclosed areas, which surround the dotted lines of contact, meet the clear areas at a point halfway between that line and the centers of the clear areas, except in C which is not based on a regular quadrilateral or hexagon. This will be further discussed under Problems of a School Turning.

In any school, a certain minimum distance from the nose of a following fish to the tail of a leading fish is maintained. The evident need for this separation is natatorial. Requirements differ with the various types of fishes that form schools. Although fishes do not leave wakes behind, as does a motor-propelled ship, there is still the matter of dying vortices (Rosen 1959; Breder 1965). This alone could account for the need of a spatial lead. Conceptually, fishes could swim satisfactorily on any of the diameters shown in Figures 2 and 3, except those on the major axial lines. The minimum distances between these diameters (fishes) in a line occur halfway between these axes as in Figure 2. It is to be noted also that the horizontal rows of diameters tend to line up so that the diameters are not all the same distance from each other as in Figure 3A. This change continues with angles less than 15° so that when these diameters become horizontal they are in end-to-end contact, producing a series of parallel lines. This is merely a matter of the geometry of the uniform rotation of the diameters. No schooling fishes would tolerate this condition, but would adjust their positions to lie near midway between the positions of those lateral to them, as shown in the diagrams of Figure 9. Compare Figure 3B with Figure 9C. The apparent differences between the two are entirely owing to the fact that the first diagram is based on rigid circles, or spheres, and the second does not have that heavy stricture. The three quadrilaterals in Figure 9 can be considered as making a closed curvilinear figure, where Figure 9A would be circumscribed by a circle while Figures 9B and 9C would both be circumscribed by ellipses, Figure 9C being much narrower than Figure 9B. This transformation can be brought about by increasing the head-to-tail distances of the fishes in a single file and decreasing the distances between adjacent files.

The greatest width between the tracks of fishes swimming parallel is also at the halfway angle between two successive axes, as shown in Figure 3A. As long as all the fishes are swimming in parallel courses the distance need not vary, as seen in Figure 3A. The closer this angle approaches an axis, the smaller becomes the distance between the parallel tracks, indicated in Figure 3B. The distance between fishes, head to tail, varies inversely as an axis is approached.

Still photographs cannot give the sense of a regular pattern of fishes that is evident on viewing a school or a motion picture. Because of these conditions, in those photographs shown here sufficiently open to see the fishes distinctly, they appear as rather ragged groups. Thus in Figure 11 of *Katsuwonus pelamis* (Linnaeus), only fragments of some regularity of pattern can be seen. Those on the left of center show the pattern of a loose school while those on the right are breaking ranks for feeding. This picture, however, indicates several lines of fish alignment, some running from top downwards to the right and others to the left, from which the relationship to the diagram in Figure 7 can be seen within the limits of a still picture.

Species attaining very large size, such as *Thunnus thynnus* (Linnaeus), tend to have disproportionally greater distances between individuals when large, as compared to their younger and smaller sizes (see Breder 1965). Contrary to this, van Olst and Hunter (1970) showed that other smaller fishes (*Scomber*, *Engraulis*, *Trachurus*, and *Atherinops*) tighten their ranks as they grow from larvae to near adult size, some abruptly and others gradually.

Hunter (1966) presented some data on the organization of fish schools for purposes that do not concern present interests. However these data, based on motion picture analysis shown in his figure 2, have a distinct bearing on some features

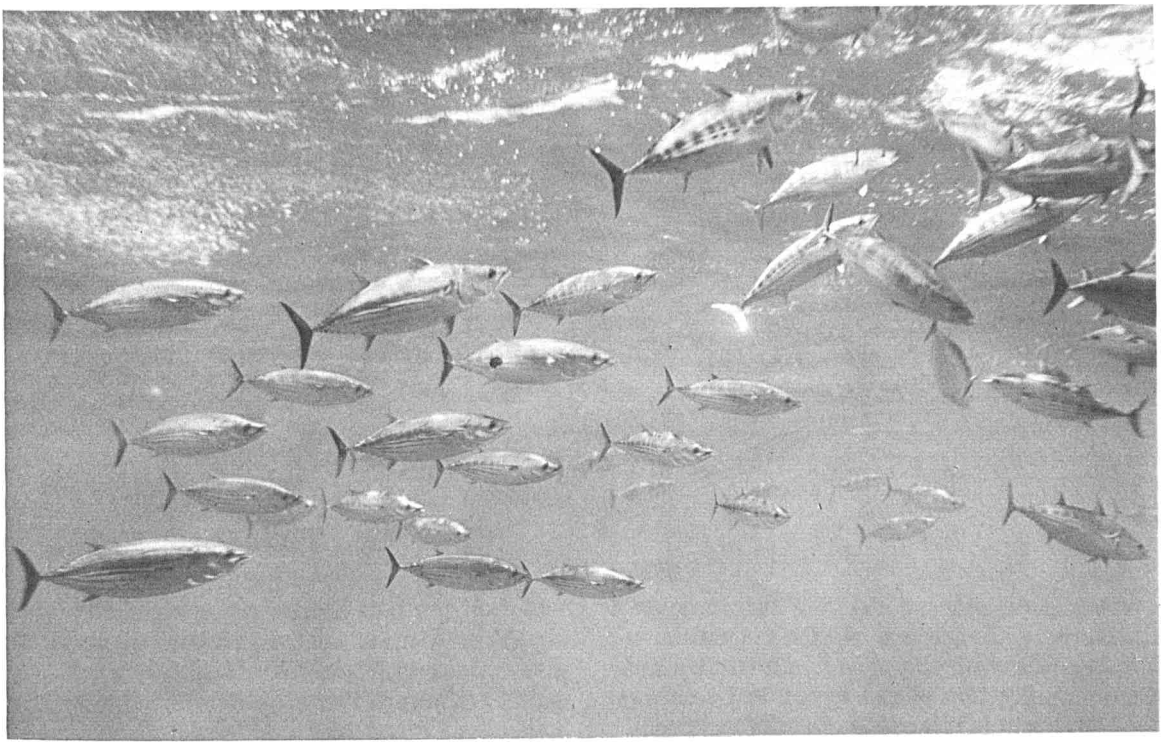

FIGURE 11.—A school of *Katsuwonus pelamis* off the Hawaiian Islands, breaking up for surface feeding. Courtesy of the National Marine Fisheries Service, Honolulu Laboratory, Honolulu, Hawaii.

of this study. Figure 12 is based on Hunter's figure, modified appropriately for this analysis. Although the small group used, six captive individuals of *Trachurus symmetricus* (Ayres), is not large enough to form a well organized school and even has members that do not always stay precisely at the same level as the others, it is exceptionally interesting in that it does display items pertinent to school structure.

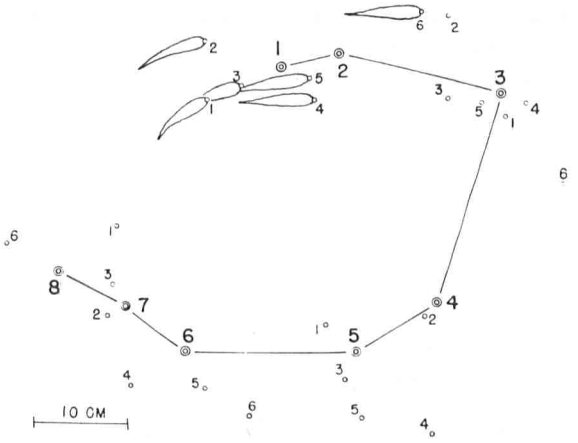

FIGURE 12.—Analysis of the location of six *Trachurus symmetricus* in a school, shown by successive eight steps in their travel. Based on data of Hunter (1966) and his figure 2. Only the odd-numbered positions have the individual fish positions indicated. To show them all would confuse rather than clarify.

Figure 12 represents the progress of the six fish covering 8⅓ s shown on 100 frames of motion picture film exposed at a rate of 12 frames/s. The larger circles indicate the mean values of the eight positions of the snouts of each of the six fish. These means are connected serially by straight lines.[6] The small circles indicate the patterns of positions of the six fish's snouts for four of the eight means. Every other one has been omitted because adjacent patterns overlap enough to be confusing.

Figure 13 indicates the manner in which the values are related to the trajectory of the group.

[6]Hunter (1966) recognized three turns in his figure 2. For present purposes the sequence is given six turns, as indicated in Figure 12 and Table 1. His three indices, mean separation, distance to nearest neighbor, and angular deviation represent other measures of the same activity, all of which relate to the differences of the mathematical approaches involved.

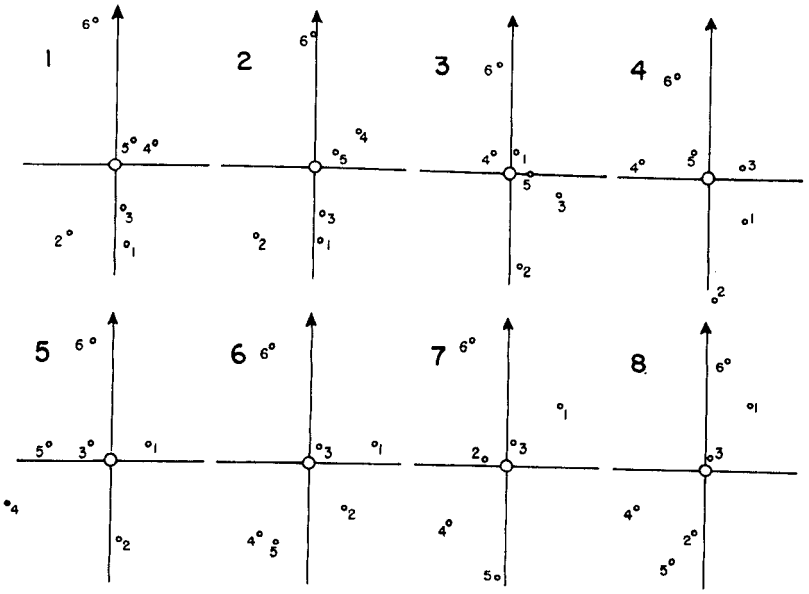

FIGURE 13.—The positions of each of the six fishes (small circles) and their means (large circles). The arrowheads indicate the directions of travel of the group. These lines pass through the means and the transverse lines intersect to divide the field into quadrants.

Also shown is the pattern of each fish's distribution, together with the means,[7] the momentary swimming direction of the school, and a line at right angles to it intersecting at the mean position. This device divides the area in which the fishes occur into quadrants. The data for this are given in the first part of Table 1. The precise positions of the fishes were picked from Hunter's (1966) figure 2 and have been handled by graphic methods in the construction of the diagrams shown in Figures 13 and 14. The numerals attending the positions of the fishes, actually the tips of their snouts, in Figures 12, 13, and 14 are those used by Hunter (1966) to differentiate the individuals and they have no other significance here.

It is immediately apparent that fish number 6 is in the front quadrants continuously. Replotting this data according to the total number of each fish separately as in Figure 14A, other features appear. Figure 14B, which shows the means of Figure 14A, does indeed approximate the Weihs (1973a) diamond.

Considering the manner in which the data have been assembled—captive fishes in a tank, the curvature of their paths, the difficulties in estimating the path of the school, and its generally

[7]These means were obtained by separately spreading each of the eight positions of the six fishes on Cartesian graph paper and determining their X and Y values and the means.

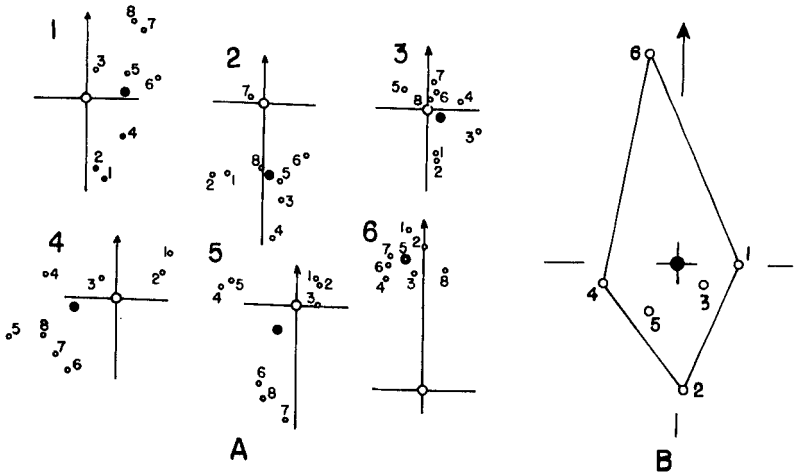

FIGURE 14.—The location of each of the six fishes (small circles) at each of the eight positions. A. The larger light circles with the intersecting lines passing through them are those shown in Figure 13. The large dark circles show the locations of the mean positions of each of the six fishes. B. The large light circles represent the means of the six in A. The small circles show the mean position of each fish (the dark circles of A).

TABLE 1.–Location of individual fishes (*Trachurus*) by quadrants and by halves. Data based on figure 2 of Hunter (1966). (First letters, L and R = left and right. Second letters, F and R = front and rear.)

School's position	Location of each fish (See Figure 13) By quadrants LF	RF	LR	RR	By halves F	R
1	6	4 5	2	1 3	4 5 6	1 2 3
2	6	4 5	2	1 3	4 5 6	1 2 3
3	4 6	1		2 3 5	1 4 6	2 3 5
4	4 5 6	3		1 2	3 4 5 6	1 2
5	3 5 6	1	4	2	1 3 5 6	2 4
6	6	1 3	4 5	2	1 3 6	2 4 5
7	2 6	1 3	4 5		1 2 3 6	4 5
8		1 3 6	2 4 5		1 3 6	2 4 5

Fish no.	Quadrants and halves occupied by individual fishes (See Figure 14) By quadrants LF	RF	LR	RR	By halves F	R
1		3 5 6 7 8		1 2 4	3 5 6 7 8	1 2 4
2	7		1 2 8	3 4 5 6	7	1 2 3 4 5 6 8
3	5	4 6 7 8		1 2 3	4 5 6 7 8	1 2 3
4	4 3	1 2	5 6 7 8		1 2 3 4	5 6 7 8
5	4 5	1 2 3	6 7 8		1 2 3 4 5	6 7 8
6	1-7	8			1-8	

loose nature–it is remarkable that any such approximation to a regular figure could be found. This material indicates that the influence tending to hold schooling fishes to approximating figures this close to geometrical regularity is effective even in assemblages of fishes barely coming within our definition of the word.

Healey and Prieston (1973) brought out a very interesting feature of schools by the application of multivariate analysis. This is evidently closely related to the preceding geometrical study on the data presented by Hunter (1966). The problem of the origins or the reasons for the existence of these individual variations in fish movements within a school is not yet susceptible to a general solution. Clearly some are caused by extrinsic stimuli and some by intrinsic causes, such as the physiological state of the individual. Healey and Prieston (1973) wrote that their data suggested, "... that there may be a short-term and a long-term organization within the school." Possibly this could eventually be referred to equivalently short- or long-enduring stimuli, not grossly evident to the observer. The data of McFarland and Moss (1967) and Moss and McFarland (1970) may represent an intrinsic short-term event, in this case being a reduction in oxygen tension. Alekseeva (1963) showed that various fishes have a greater oxygen consumption when visually isolated from their fellows. Such individuals, if able to see the others, do not. Schuett (1934), Escobar et al. (1936), and Breder and Nigrelli (1938) indicated that individuals of *Carassius auratus* (Linnaeus) swam faster when alone and when crowded, but slower when with a few companions. This should be reflected in their oxygen demand and may account for the results of Alekseeva (1963).

The very short duration of the Hunter (1966) data suggests that the details here might be based on intrinsic sources, as in the case of the fish that kept the leadership of the school and of the one that brought up the rear. It is conceivable that these may be the consequences of the individual physiological states.

In agreement with Bowen (1931, 1932) and Radakov (1972), there is no convincing evidence that the superficial appearance of "leadership," to be seen occasionally, supports such a view. Hunter's (1966) data covered only 8⅓ s. Breder (1959) suggested that "white" *Carassius auratus* (Linnaeus) seem to take the leadership in schools otherwise composed only of "yellow" individuals. This finding of white fishes in leading positions is apparently related to the greater conspicuousness of the white fish as compared with the yellow in a lily pond environment and is not an indication of leadership by any individual.

Radakov's (1972) data, which was extensive and important, considered "leadership" in a rather different sense than the others. He considered numbers of leaders up to 40% of the number of fishes comprising a school. The front fishes, with no other fishes ahead of them, are considered here as leaders. These fishes are in a different physical category as they have none of the advantages of being a following fish.

An exceedingly interesting and simple experiment was undertaken by Radakov (1972) with 21 young *Pollachius virens* (Linnaeus) of 8 to 9 cm. These were placed in a tank measuring 1.6×7×0.3 m. It was divided into two equal compartments by a clear glass partition. All the fish were placed in one compartment. The experiment consisted of transferring the fishes, one at a time, to the other compartment. With 20% or less of the fishes transferred, the smaller group tried continuously to swim through the glass partition in their efforts to rejoin the others. Above that percentage, the two larger groups, between 30 and 40% of the fish on both sides tried to form a common school with the glass partition cutting through it. Continuing the transferring, a reverse series of the attitudes described above was obtained.

Movements of Individuals

The study of travel by individual fishes within a school has difficult and tedious aspects, as is evident from the preceding. The subject has not attracted many investigators as witness the paucity of comments on it in earlier papers. An examination of Figure 12 shows quickly that such internal traveling is neither negligible nor slight, at least in very loosely organized schools, but is probably much less so in very tight schools. Because of this, the geometrical properties of schools have been considered chiefly in a single layer of fishes, i.e., in terms of plane geometry. Schools of greater depth present special difficulties in obtaining adequate field data, as it is necessary to invoke the complications of the third dimension while the fishes are often so closely packed that visual perception within the school is severely restricted. In addition, there are further problems incident to the fishes' continual activity. This is particularly difficult in efforts to recognize the rhombohedron of Figure 1B. The present efforts have yielded some hints that suggest support to our thesis.

The vertical structure of schools and vertical mixing within them is much more difficult to handle. This is evidently owing partly to the greater inherent difficulties in three dimensional plotting and partly in the nature of fish morphology and methods of propulsion. The influences of each fish on the others in the same horizontal plane are greater than in any other direction because both vision and locomotor mechanics operate primarily in that plane. That is, optical axes of schooling fishes lie in that plane and the propulsive mechanism produces forces operating in it.[8]

It is consequently less difficult to compare the relative amount of shifting about in the horizontal plane as compared with that in the vertical. Although we have no clear observations or photographs of a fish sinking to the layer below it or rising up from one below, there are many instances of evidently "uncertain" fishes seen between distinct layers or ones dropping slightly below, as in Hunter's (1966) figure 2.

Shape and Size of Schools

The closed figure that forms the outline of a school is a remarkably flexible boundary subject to continual transformation. These changes are produced by a large variety of influences both intrinsic and, by a vastly greater number, extrinsic. Obviously, the most important intrinsic factor in holding a school together is the impulse that causes fishes of one kind to assemble, respecting each others necessary swimming room and accepting a common polarization.

The fishes that are outermost along the sides of a school do not form a special boundary layer any more than do those at the front form "leaders." Those at the side surfaces differ from the rest only in that they lack fellows on one side. Like those at the front, they are continually changing as their aggregating tendency apparently moves them toward a more central position.

Aside from temporary weakening of the bonds by such things as vigorous feeding, reproduction, the coming of a sufficiently dark night, or a particularly violent disturbance, the basic school structure is continuous in obligate schoolers. In facultative schoolers, the school is periodic or of occasional occurrence. True semipermanent intermediates between these two ordinarily distinct modes are not easy to find and are uncertain at best.

The intrinsic influences divide naturally into two groups, the first being those of nonorganic elements. Common examples of these are light, water currents, shoreline, sharply mottled bottom patterns, and obstructions. Sharp discontinuities of any of these are especially influential. Organic

[8]A comparison of fish schools with those of cetaceans should be illuminating because the propulsive efforts of the latter operate in the vertical plane.

factors include other schools, large predatory fishes, fish-catching birds, and rich plankton streaks.

Theoretically at least, fish schools could take any shape. Considered as three dimensional "blobs," they have been described and photographed in a wide variety of shapes, including even the nearly spherical (Breder 1959). The latter mostly occurs in open water some distance from the influence of the water's surface and the bottom of the body of water. These are rare and suggest almost exactly balanced forces. Under such conditions the school formation in the ordinary sense breaks down.[9] The form of organization within such near-spheres has not been analyzed, nor has their manner of formation or eventual dissolution. Other shapes not readily described in simple geometrical terms, as that shown in Figure 15, seem to illustrate the presence of either spiral arms or "smoke ring" formations.

Much more frequently encountered are schools close to the water's surface or the bottom. These often show a more or less oblate spheroidal form from which a portion has apparently been planed off, where near contact with surface or bottom necessarily caused flattening. Otherwise, the opposite side follows the contour of the flattened side so that the school takes the form of a flattened sheet of rather uniform thickness. These often take the form of a sheet one-fish deep, the school practically reducing to a nearly two-dimensional figure. These all may occur in open water, either near the surface or bottom. They are, however, more usually seen in very shallow water where both surface and bottom influences impinge on the school. These schools in which the horizontal dimensions greatly exceed the small vertical one

[9]There is in this case a question as to the propriety of including this assemblage as a school in any sense. At least the fishes that form this ball are in a solid school formation as they rush in to form these structures.

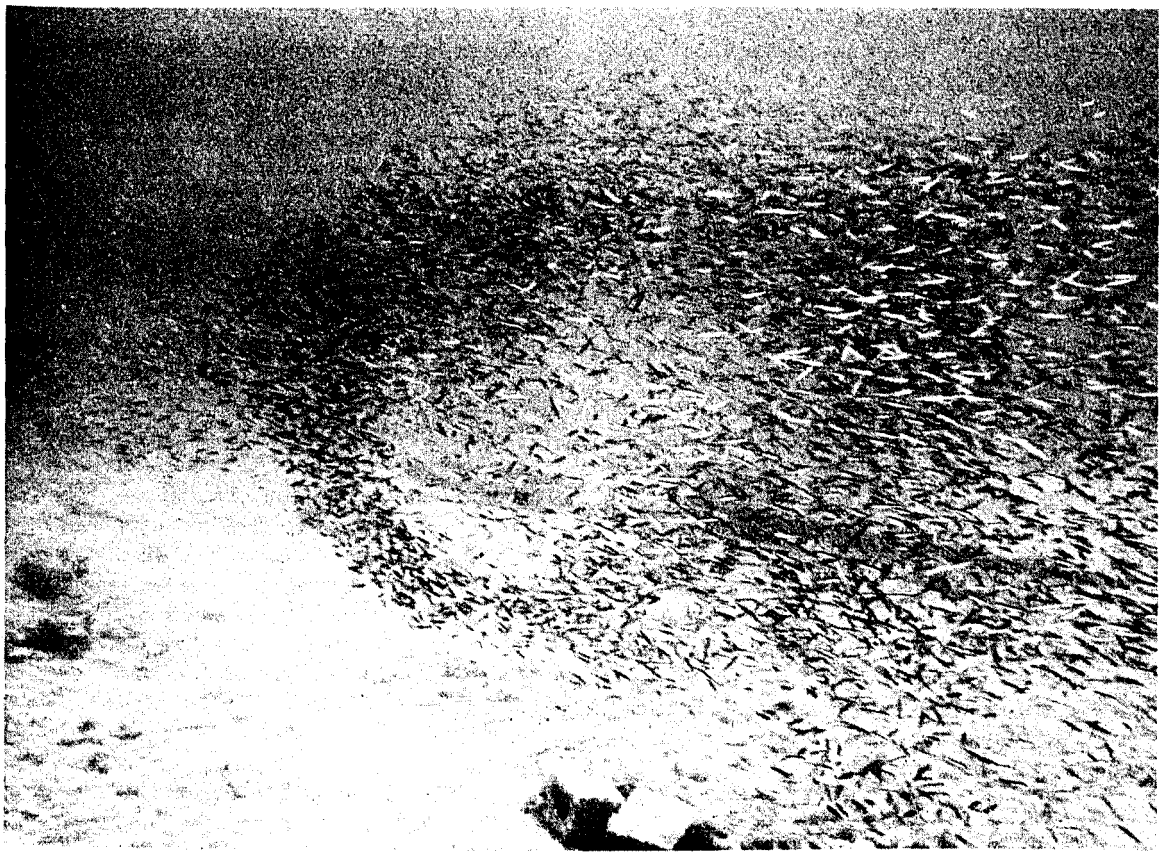

FIGURE 15.—An unusual and not readily explicable maneuver of *Jenkensia stolifera*, seen at Grand Cayman from scuba gear under very calm conditions.

are more accessible for study and the data obtained from them is readily handled by much simpler geometrical methods. Most of the present knowledge of schools is based on observations and analyses of these sheetlike schools, treated as a geometrical surface.

Unless there is mention to the contrary, all statements in this study refer to small or moderate schools. When schools attain huge dimensions, some of these statements require modification. A fish in the central part of such a school, that may have thousands of others between it and open water in any direction, is locked in a position that permits practically no freedom of movement. Such fish are forced to swerve and swim almost as a single block. Thus the turns discussed in the section Problems of a School Turning are not possible. The section Sizes of Fishes in a School discusses conditions involving the amount of size variation of the individuals found in a school. This reaches its maximum in huge schools where size variations are often large enough to break up a lesser school.

Problems of a School Turning

A solitary fish obviously can alter its path from that of a straight line and swim off in any direction. The presence of objects, such as neutrally disposed fishes of the same or other species and same general size, may make little difference except for appropriate course altering. Problems loom as a significant influence only when the density factor becomes relatively large, as in a loose unpolarized aggregation. When fishes become even more crowded by each other, the ability to swim in any direction is severely restricted by the mere presence of the bodies of other fishes. In a dense school this manner of restriction becomes intense. Such closely packed and regimented fish can swim serenely, parallel to each other, in a straight line or in large swinging arcs of a radius down to a value of about as little as five to ten lengths of the fishes involved as shown in Table 2A. If, however, a sharp curve of shorter radius is attempted, complications arise (Table 2B). Such turns are commonly made by small schools up to sizes that are too large to act as a completely cohesive unit.[10] The data shown in Table 2 refer only to these small cohesive groups.

[10]See Breder (1967) for a discussion of the vastly greater complexities inherent in the behavior of enormous schools.

TABLE 2.—Data on two types of turns made by fish schools.

A. Radii of broad curves in *Selar crumenophthalmus*

Radius in fish lengths	Fish lengths in cm			No. of fishes
	Max	Mean	Min	
5.5	30.5	25.4	22.6	11
9.3	25.9	25.4	22.8	9

B. Measurements of sharp curves

Species	Angles of turn in °	Remarks
Menidia berylina	41.5	
Selar crumenophthalmus	135.5	Shown in Figure 17.
	148.0	
	158.0	
	160.0	
	163.0	
	175.±	Turns as in Figure 18.
	177.0	
Trachurus symmetricus	94.0	Note: The 11 numbers not set in boldface refer to Figure 16
	40.5	
	33.0	
	31.5	
	25.0	

Here some disturbance ahead frequently can set off an activity among the leading fishes in which they turn sharply left or right. These are then followed by the others, making their turns in substantially the same place. Normally the maneuver is accomplished with a scarcely apparent and transient slowing of pace. The hydrodynamics of how sharp turns are made by fishes with a minimum of deceleration was discussed in detail by Weihs (1972).

Some of the angles between the initial and subsequent paths of schools making these sharp turns are given in Table 2B, picked from motion picture sequences. Figure 16A indicates that turning at a certain angle could cause following fishes to approach the tail tips of those just ahead, an accident that appears never to happen.

There is nothing inherent in the situation of a school swimming ahead that concerns angles of turning. The features of the diagram in Figure 16A are meaningless to the fishes until they begin to turn. Let the school swim in a straight line and turn 30° to the right at the center of the diagram. Each fish will come out in an occluded sector and find it being brushed by the tail of the fish ahead. If the Weihs (1973a) diamond is elongate along the axis of travel, the fishes will fall a little short of contact but will swim into the wrong side of the vortices shed by the preceding individual. This is evidently sufficient to initiate avoidance reactions.

If they turn at 60°, there will be no problem as they will be well separated by the amount indicated in Figure 3A. The fishes in turning evidently do so only where there is no danger of

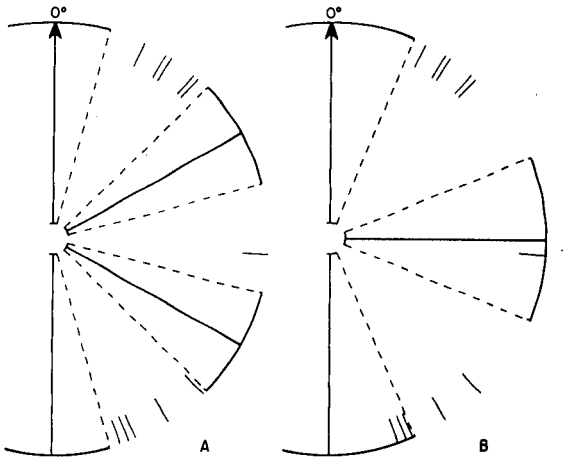

FIGURE 16.—Angles of sharp-turning fish schools. A. Angles compared with the rhomboidal lattice. The four solid radial lines represent the collision paths of turns if the original path is represented by the vertical line marked 0°. This direction of a fish's path is indicated by the arrowhead. The dashed radials marking the end of each arc separate the clear sectors, without arcs, from the occluded. The 11 short radial line segments represent the new path of the fishes after they have made their sharp turn. The numerical values of the angles are given in Table 2B. The same fish turns compared with the cubic lattice. Here the fish paths are not limited to the clear sectors. See text for full explanation.

interfering with each other's swimming. Actual turns of various species keep well away from the critical angle. Which particular clear space is selected is evidently determined, at least in part, by the strength of the deflection-causing stimulus. As such a turn is completed, the fish again start to swim in an essentially straight line while they regain the positions that were somewhat disturbed in turning and the Weihs (1973a) diamond appears again. Thus the outlined sectors in Figure 16A become "forbidden" paths. Since the diagram in this figure is purely a geometrical construction with the occluded and clear sections having equal areas, this is not to say that some intrusion into the outlined sectors is impossible. The axis of the occluded sectors is the worst position for turning and that of the clear sector the best, the areas between grading gradually from one condition to the other. The dotted radii are halfway between the center lines of the clear and the occluded areas. The turns made by real fish schools, measured by motion picture analysis, and shown in Figure 16A and Table 2A indicate the absence of intrusion into the enclosed areas.

This examination of the sharp turnings of fish schools would not have shown these features if they had been organized on some pattern other than that of the hexagonal lattice. If they had been organized on the square lattice, shown in Figure 4, there would have been at least some in the "forbidden" sectors, as is shown in Figure 16B where the same data on turning angles have been placed on a diagram based on the square mesh. Here the same data show less preferential behavior on the part of the fishes toward the clear sectors. All the schools, in the hexagonal case, stayed within the boundaries of the clear sectors (Figure 16A) while only 64+% did in the square case (Figure 16B). Also the intrusion into the occluded sections increased with the increasing angle between the initial course and the new one. These two items are additional reasons for considering the lattice to be basically hexagonal.

A typical turn of the sort discussed is shown in Figure 17 and in Table 2B. This drawing is based on a series of seven motion picture frames (0.44 s). The sequences are of a tight school, the angles between the straight paths, before and after the turn, are based on the mean paths of the fishes. Only a few of the individual fishes are shown in Figure 17 to indicate the nature of the turn at that point. Not shown are the many fishes constituting the bulk of the school.

There is also another type of sharp turn that is not mentioned in the preceding description. It can lead to considerable confusion because superficially it is readily confounded with the foregoing type. It differs primarily in not being concerned with angular limitations, which apparently can be ignored only at the expense of making the turn

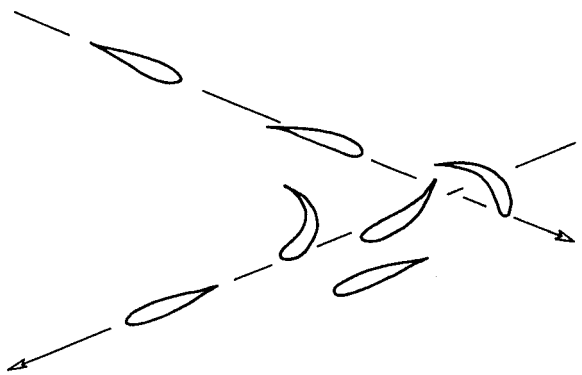

FIGURE 17.—A sharp turn of *Selar crumenophthalmus*. Only the paths before and after the turn are indicated and a few of the turning fishes. The directions of the two paths are indicated by arrowheads. See text for full explanation.

with considerably less alacrity. Once the behavioral differences between the two types of turn are understood, they can be seen in the field if one happens to be looking directly at the point of turning before it begins. This is easier to see in a relatively large school than in a small one because the larger the number of individuals involved the more prolonged the turning maneuver becomes. Also, it is most noticeable where the sudden appearance of something large and "threatening" produces an apparent "panic situation." Instead of what seems to be the beginning of a tight turn, as previously discussed, the action is most often seen as an attempt to retreat over their forward path. Here there develops a "logjam" and confusion. The immediate response is for the clump of fishes to spread out into a more or less circular area, out of which the school is seen to beat a hasty retreat. Figure 18 shows such a performance which theoretically, at least, could move off in any direction but, so far as our observations go, has usually been close to the opposite direction of the abandoned advance. The conventions of Figure 17 have been used and the same number of frames cover this sequence. The seeming difference of speed is simply that badly frightened fish move faster than relatively placid ones and therefore make up much of the time lost in the greater length of their confusion-imposed travel. This area sometimes develops a central clear spot devoid of fishes, and a true "fish mill"[11] is transiently developed.

The angular measurements between the track of a school before the turn and after it can only be precise in photographs taken with the camera pointed straight down. This is nearly impossible with feral fishes because such schools simply move away from anything directly overhead. The photographs on which Table 2 are based are those which approach that position as nearly as possible. This departure from the vertical naturally tends to slightly blur the accuracy of the angles and thus serves to produce a greater spread in the apparent angles. This effect has less influence on the mean values of each clustered group. To help counter this source of error, a transparent dial was prepared with the sectors shown in Figure 16. Hand held, it can be tipped at an angle appropriate to the angular amount of departure from the vertical with which the eye or camera viewed the scene. A

[11]A term used by Parr (1927) to cover the case of a fish school swimming in a more or less circular path, where every fish is following those ahead of it. The clear center that these mills sometimes develop has been discussed by Breder (1951).

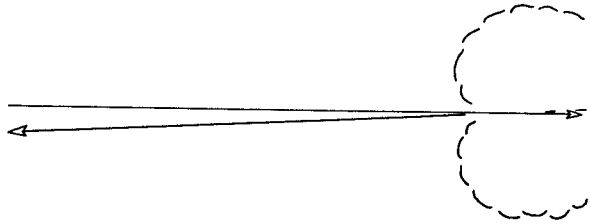

FIGURE 18.—A slower turn of the school shown in Figure 17, with confusion at the turning point. The directions of the two paths, into and away from the melee, are indicated by arrowheads.

variety of items shown in such a film helped establish the needed correction with sufficient accuracy for present purposes. Although little use could be made of it in the direct observations because of the rapidity of the action, it was invaluable in studying strips of motion picture film. Small cues that helped establish the proper angle of tilt of the viewing dial included principally the amount of the sides of the fishes that could be seen plus other objects incidentally included in the photographs.

Absolute turns enforced on schools of *Mugil cephalus* Linnaeus and *Pollachius virens* (Linnaeus) by the end of an aquarium were studied by Radakov (1972). These are in contrast to the preceding studies of turning in open water where the actual cause of the turn was often obscure, but irrelevant to the mechanics of turning. The aquarium studies show nothing like the "sharp turns" but are close to, if not identical with, the present "slower turns" where the school breaks down and reforms on the retreat path. Here and in Radakov's (1972) work, there is considerable mixing and the place of individual fishes in the school after these turns may be grossly altered. In the confines of an aquarium there is practically no choice of turning angle and the complex situation in turning in open water does not exist.

General Traffic Problems

Road traffic of automobiles may seem to be very remote from a school of fishes. Close examination, however, reveals that the two have common roots and that, despite their apparent differences, they are isomorphic. Both cars on a road and fishes in a school can be treated as embodiments of mathematical expressions concerned with mass movements of redundant units. The mathematics of the behavior of automobiles developed along with their proliferation, following the need for

increasing specific and detailed control of their movements. Thus, from a purely empirical beginning these studies have gradually developed into the present traffic theory, most of which has developed in the last 10 yr. Introductions to its considerable literature are given by Ashton (1966) and Gazis (1967).

Some of the similarities and differences between cars and fishes in the attainment of an organization of free-flowing traffic is indicated by the following comparative listing of the two types of redundant units.

Fish	*Automobiles*
1. Fishes, schooling or not, operate freely in three dimensions, but most free-swimming fishes, especially those that form schools, operate mostly parallel (although not necessarily close) to a usually horizontal surface, either the surface of the water or the bottom. These two mark the vertical limits within which the fishes must stay. Horizontal boundaries may vary from too close for schools to exist to practically limitless expanse, in the strictly physical sense. Schooling fishes can go in any direction but only with their school.	1. Cars, in traffic or not, are confined to a surface, which is not necessarily a plane and is often a warped surface, where the extent of warping eventually limits the possibility of use by cars. Cars must stay on their roads but do not necessarily stay with their fellows. They may strike out alone wherever there are connections with other roads, except where accompanied by restrictive road signs forbidding a given maneuver or by the general rules of behavior.
2. Other strictures are those with which only schooling fishes are constrained. Here fishes all swim in a common direction, mostly in parallel paths, and in single files. Collisions are rare or absent, their avoidance evidently being rooted in their highly developed sensory mechanisms: vision, lateral line and cupulae[12] senses, and hearing. There is no provision for "night driving" except in species carrying their own illumination. Others loosen their ranks or break up on nights sufficiently dark to eliminate vision.	2. Other strictures are those with which only cars, especially in traffic are constrained. These controls are maintained by laws to run in an indicated direction in single files or in parallel paths, depending on the width of the road and its indicated number of lanes. Collisions occur with monotonous frequency. The protections are only the sense organs of vision and hearing. Night driving illumination is normally present.
3. Fishes form well-defined patterns; for hydrodynamic reasons they are quadrilaterals.	3. Cars form "diamonds," or if the road has less than three one-way lanes, parts thereof.

In both cases there are valid reasons for not following closely behind the unit directly ahead and for not traveling in tandem positions. The resulting staggered deployment permits passing and lane shifting with a minimum of confusion. It is this arrangement of units and their possible movements that is largely responsible for the irregularities in any instantaneous structure of the swimming patterns.

In the case of a traffic jam of cars or the equivalent conditions of pods[13] of fishes, the pattern formed by units is nearly obliterated.

The shape of the diamond formed by four cars is related to the speed of travel and is determined by the rules of the road covering the increase in distance to be given the car ahead with an increase in speed. Also the rules require the passing car to speed as fast as practicable in passing the slower car. Thus, the faster the traffic, the farther the hexagon or diamond departs from the regular, attenuating along the axis of travel.

That the fish and a car with its human driver are closely comparable should be clear from the preceding and the following outline indicating that the relations between the two dynamic systems do in fact constitute an isomorphism. Two central nervous systems, one of a fish whose body is vehicle, power plant, and pilot, and the other, that of a human who is the pilot, enveloped in a capsule comprising the vehicle and power plant, operationally calls for the same kinematic pattern and trajectories of behavior. As these are both systems with feedback in which all essential variables are evident, the canonical representation and the ordinary algebraic forms of equations can be calculated. This will not be done here as it would

In fishes, the same results are obtained by those ahead leaving both advantageous and disadvantageous water movements in which the followers, by taking the path of least resistance, fall automatically into positions that mark out the diamond. The lengthening of the figures as the fishes' speed increases is very slight as compared with that of the distance increase with cars.

[12]See Cahn (1967) for a survey of the function of these systems.

[13]This term has been defined by Breder (1959).

not be relevant to present purposes and would carry away from the intent of this communication, although the equation of Breder (1954) should be useful to such a study.

The main thrusts of the students of traffic flow have been concerned with such things as problems of delays, queueing, road junction, traffic signals, analogies to fluid movements, and follow-the-leader sequences.

The study of fish schools has not yet reached into these matters, although they all bear a one-to-one resemblance to similar items in schools. This undeveloped area is difficult to enter into deeply partly because there is no facile way to keep track of each individual. The analysis of the behavior of individuals in a school based on the data of Hunter (1966) could be considered as a start in this direction.

Influence of Body Forms

There is a marked positive relationship between schooling and the extent of streamlining of the general contours and of the drag-reducing surface details of fishes that, in the most advanced obligates, can be considered exquisite. Parallel to this is an equally marked negative relationship between schooling and special surface features of the eruptive sort. At this end of the series, the fishes are not schoolers at all, nor even aggregators, but are usually solitary, neutral, or agonistic toward their fellows. All of this can be shown to be related to mechanistic details covering the manner of life of the individuals involved.

For example, we know of no obligate schoolers such as clupeids or scombroids that have any drag-producing extensions, while the vast majority show beautiful fairing even in the manner that the maxillary fits into a matching recess when the mouth is closed and in the slot that the depressed dorsal fin fits into as shown in *Scomberomorus*. Such niceties are not to be found in the facultative schoolers such as most of the Salmonidae, Cyprinidae, and Serranidae. In the essentially nonschooling fishes, the streamlining often becomes less effective and outgrowths from the integument and eruptive structures become more and more extreme as in *Hippocampus*, the Scorpaenidae, Cyclopteridae, and Diodontidae. With this comes slower swimming speeds and an increasing tendency to reduce swimming to a minor roll, as in some of the Scorpaenidae and all of the Antennariidae.

The remainder of fishes to be considered here are those that show a depth[14] equal to or greater than their lengths. These are often facultative schoolers. Families in which this is a usual or frequent condition include the Stromateidae, Ephippidae (including the extreme platacids), Chaetodontidae, and Acanthuridae. Many others show an approach to the condition, as in the Pomacentridae. In addition to these, there are a considerable number of families in which one or a few species have the necessary characteristics, as the Carangidae and Cichlidae.

The schools that are formed by fishes of great body depth are superficially very similar to those formed by fishes with fusiform outlines. A school of deep-bodied fishes is, however, automatically tighter because the greater depth of body intrudes into the swimming areas of the layer of fishes above as well as the layer below.

There is both mechanical and hydrodynamic interference and an optical occlusion that is much more severe because of the greater area of the sides of these fishes. This leads to greater difficulty in making sharp turns. These conditions can only be relieved by loosening the school in the vertical direction. How much mutual swimming facilitation is lost by this loosening is not known. Figure 19 illustrates these conditions with a head-on photograph of an extremely loose school of *Chaetodipterus faber* (Broussonet).

The only other fishes known to form schools are those in which the longitudinal axes do not lie parallel to their line of travel. They include various characins, the "head standers" of aquarists, and some aulostomoids, the best known of which are *Aeoliscus* and *Macrorhamphosus*. These evidently swim with the head up or down (Atz 1962, Klausewitz 1963). There is no data on any aspect of their hydrodynamics nor on their mucus. These forms, therefore, are not discussed here.

Sizes of Fishes in a School.

The variation in the lengths of individuals in a school usually reaches no more than 30%. The difference between the length of the largest fish minus that of the smallest fish in a given school is expressed as a percentage in this notation. Data from Breder (1954), recalculated for present pur-

[14]This is not the body depth of taxonomists, but the vertical depth of the entire profile, including the extent of the dorsal and anal fin in that dimension.

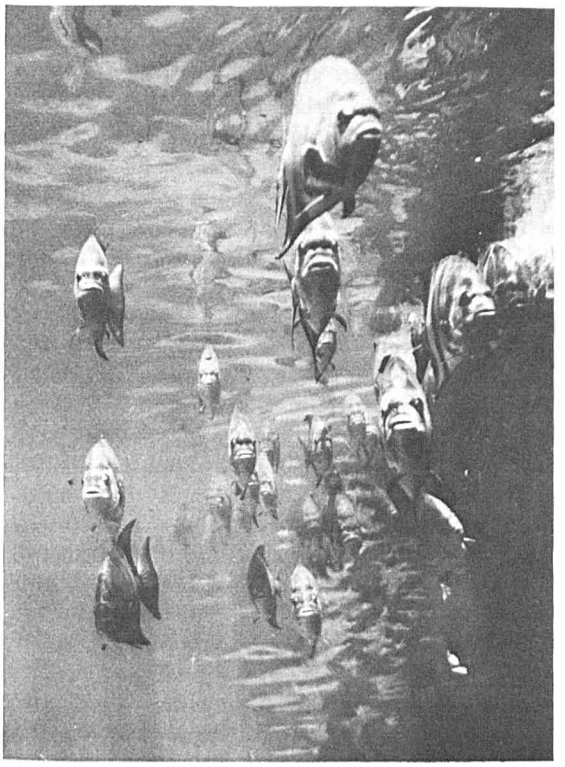

FIGURE 19.—A head on view of a loose school of *Chaetodipterus. faber*. From Herald (1961). Photo by Fritz Goro.

poses, yielded the following comparative values: *Harengula humeralis* (Cuvier) 12.5, *Jenkinsia* sp. 24.2, and *Atherinomorus stipes* (Müller and Troschel) 25.0. Additional data on *Jenkinsia stolifera* (Jordan and Gilbert) taken from Breder and Bird (1975), based on Grand Cayman fishes, gave 31.7. All are below the 30% level of variation except the last. A school of *Ictalurus nebulosus* (LeSueur) still being herded about by their parents, however, had 42.9. It is known that when several family groups are present, the young fish often become mixed. This may well be the cause of this greater variation, a similar feature being found in extra large schools of adult clupeids, as discussed by Breder (1967).

The fate of injured and parasitized schooling fish has not been given much attention and it has generally been assumed that such unfortunates do not long survive. This view has been nurtured by the fact that a captured school of fish most often contains no individuals that show either wounds or evidence of gross parasitism. That there are striking exceptions to this has been shown by Guthrie and Kroger (1974). They reported that individuals of both *Brevoortia tyrannus* (Latrobe) and *B. patronus* Goode, with vitality reduced because of depletion caused by injury or parasitism, are to be found in estuaries schooling with smaller, younger, but healthy individuals normally present in these relatively protected areas. Outside waters yielded no such composed schools.

The relative sizes of the healthy young fishes and the handicapped older ones and the ratios between the largest and smallest individuals are given below as percentages.

	Young	*Old*
Estuarine		
B. tyrannus	52.7	10.4
B. patronus	73.6	44.2
Oceanic		
Both spp.	–	63.4

Only one group has an index of low variation in lengths, 10.4. The others all have indices of high variation reaching to the extreme of 73.6. If the schools of both young and old are each taken as a whole then all groups would show very high variation, i.e., 63.6 for *B. tyrannus* and 80.0 for *B. patronus*.

There is only one way these figures can be interpreted. The schools of both species are a mixed lot of lesser schools, as would be expected of fishes that persist in forming enormous schools that mix broods from different spawning areas and that are hatched at various times in waters of different temperatures. This genus would seem to be the most prodigious gatherer of huge aggregates of a single species on the American Atlantic coast.

In the usual, more uniform schools, where the variation is less than about 30%, the geometric structure is observably more uniform. Theoretically, at least, the smaller the variation in the size of the fishes the nearer the lattice could approach geometrical perfection. Schools of fishes where there is larger variation in size tend to break in direct proportion to the magnitude of the variation. In enormous schools with great size variations breaking up is not always possible but does lead to considerable churning as individuals of similar sizes gravitate together.

Effects of Mirrors

The confronting of animals with mirrors has been practiced for many years, for both trivial and serious purposes. The vast majority of such presentations has been made to one subject at a time,

e.g., Svendsen and Armitage (1973). There have been few cases of mirrors being introduced to groups, such as fish schools. Pitcher (1973), using mirrors for certain photographic purposes, noted some of the reactions of his fish subjects. In both cases above and almost all others, the studies have been made on captive animals.

Information on the reactions of individual fishes within a tightly organized school is not readily obtained. Experiments on captive schools yield results that are naturally suspect, primarily because of the usually gross changes in the behavior of schools confined to small quarters and the length of time in days or weeks, even in a relatively enormous container, that it takes to reach apparent stability. Analysis of motion pictures taken of feral schools cannot be expected to supply much more than occasionally fortunate sequences. One difficulty is the interference of other members of the school or of other species exterior to it. Mirrors introduce something to which fishes generally respond and thus the possibility of reasonably interpreting their responses exists. The experiments and their results follow.

A submerged mirror, 39 × 57 cm, was hung near an observation dock or other suitable location which yielded data on fishes in schools in their native habitats. The school's presence was in no way forced, nor were they present because of any attractiveness mirrors may have, since the sites selected were normally visited daily by these schools.

Four species, three of the Clupeoidei and one of the Mugiloidei, reacted to this mirror, each in a different manner, as follows.

Anchoa hepsetus (Linnaeus) showed the most striking reactions. All the schools of this species were large, at least containing 1,000 fishes and usually far above that number. The schools appeared at this place only during the daylight hours and moved off to deeper water for the night. These movements were independent of the tidal stages. The horizontal component of the tidal flow clearly regimented these fishes because at slack tide they became somewhat disorganized.

If the mirror was submerged while this species was absent, the fishes schooled on arrival would regard it simply as any other solid object, such as a pile, that had to be avoided by changing their course. In doing this, schooling fishes normally leave a clear space between them and the object. In this case it averaged close to 20 fish lengths. If the fishes were present before the mirror could be lowered, it was allowed to slide directly into the school, which produced little disturbance, other than a few transient "shock waves" as the normal space was formed around the mirror. It was noticed early that the distance kept by the fishes from the back of the mirror, painted black, was a little greater than that kept from the face of the mirror.

After the elapse of about 1 h after the introduction of the mirror, the portion of the school opposite the mirror's face made slight "bulges" toward it, which were promptly resorbed. Nothing like this appeared on the part of the school opposite the black backing of the mirror.

After another hour, the school had moved closer to the face of the mirror, approximately 10 fish lengths away. When this was once established, individual fishes would sally forth from the perimeter of the school opposite the mirror and swim to within four fish lengths of the mirror and momentarily run parallel with their reflection. This would be followed by a hasty retreat to the school. The action, repeated frequently by various individuals, would seem to be explicable as follows. A peripheral member of the school could see the school's reflection twice as far as the mirror surface. To join that "other" school required that the adventuresome individual had to negotiate that apparent distance. The fish traveled about nine fish lengths before it turned back. Here the fish found that one fish in the reflection is coming at him and running side-by-side with him, at an apparent distance of two fish lengths. This kind of behavior is not the "normal" in the situation of a few or one fish attempting to join a much larger group, at least in any of the species under study. The usual manner in which one or a few fishes join a large school is to quietly approach the larger body and pick up its rate of speed and slowly merge into the main body. There is never any evident specific act on the part of the affected fishes of the school. They seem to react to the "intruders" as they do to the other members of the school, constantly adjusting their positions by small amounts.

The above is not true of two schools of more nearly equal size when in the process of merging. The smaller will approach the larger at a rate of speed apparently inversely proportional to the volume of the smaller school. The larger school will approach the smaller at a much slower speed also inversely proportional to its volume. When the two schools come within a distance equivalent to about

four fish lengths, both schools show a bulge on the side closest to the other school and in so doing automatically loosen their ranks slightly, but sufficiently to allow the two bulges to merge, forming a single school where there had been two. This type of merging can usually be found between schools that do not differ in size by a factor as large as four.

The above describes what are evidently the normal sequences to expect when two schools of various size relationships have an encounter that may lead to merging. This leads to the idea that the "behavior" of a mirror image is sufficiently unusual to prevent the further development of a process leading to merging, the fishes evidently recognizing a difference between another fish and their own reflection.

Sardinella anchovia Valenciennes and *Brevoortia patronus* Goode avoided coming close enough to the mirror for the development of any further reaction. The first was present frequently in large schools which tended to stay away from the dock area in deeper water, but frequently came into the shallower areas at which time they revealed no indication of "nervousness." The second was seen only as young fish in very small schools of not more than 30 fast-moving individuals, that gave any solid structure a wide berth, which is characteristic of this species, at this place at least. *Brevoortia* in a 10-foot circular concrete tank formed a school of about 30 individuals that averaged about 10 cm in length. They had lived there for about 10 mo. These fish were exposed to the mirror for 1 day in August and 4 continuous days in November. Prior to the introduction of the mirror, the school circled the tank close to its wall. The introduction of the mirror disrupted this path of the school which then formed a tight mill as far away from the mirror as possible. At no time were the fish observed to approach the mirror. Only dropping food close to its reflective surface would cause individuals to move toward the mirror, and then only to snap at the food and retreat rapidly. The fish fed less during the presence of the mirror. After the mirror was removed 6 days passed before the mill broke up and the former swimming pattern was resumed. *Harengula pensacolae* Goode and Bean, not seen around the dock when the mirror was used, behaved not unlike the *Brevoortia* in the concrete pool.

Mugil curema Valenciennes, in its very young surface swarming stage of not over 2 cm, forms very loose schools not at all like those of the adults. These young, on encountering the mirror, would try persistently to swim into the mirror, seemingly disregarding their mirror image that just as persistently "opposed" them. Occasionally when such a group left the mirror for reasons unknown, a single fish would remain and continue to try to swim through the mirror for a long period, evidently almost to exhaustion.

These observations were carried on from 8 June to 10 September 1973, weather permitting, and represent many repetitions of the facts and interpretations. It is impossible to present these notes in a more formal manner at this time. They clearly have bearing on the present study and suggest the desirability of going into this matter further as another project which would in any case lead away from present purposes.

The observations indicate that there is a much wider range of difference in response to the mirror image than had been expected and therefore that the bonds that hold a school together are not identical for each species, even if the total result appears as a very similar geometric structure. It would seem that the response of a fish to a fellow (here its mirror image) that approaches on a true and unswerving collision course from which it will not (cannot) budge is a truly frightening experience. The difference in response between *Anchoa* and *Mugil* in this case is especially striking. *Anchoa* acts in a manner that one might anticipate, while the action of *Mugil* in placing their mouths together has never been seen at any age or size.

LOCOMOTOR PROBLEMS

With large numbers of fishes of one kind swimming closely together in a common direction, the locomotor needs of the participants would obviously have influence on the structural nature of the school, which in turn would also affect some details of the locomotor efforts. Both classical and contemporary hydrodynamics have to be invoked in any attempt to understand this mechanical aspect of school formation and operation.

Flow Patterns

To answer the question of whether water flow induced by the propulsive activity of the fishes themselves can help or hinder other fishes following them depends on the direction and strength of the flow and the angle of entry of a fish encoun-

tering the flow. The solution of such problems lie in the realm of classical hydrodynamics. See Lindgren (1967) for a brief, but explicit statement of the hydrodynamics involved. Fishes leave no wake in the usual sense of the word, but do leave a series of dying vortices, alternately on either side of the swimming axis of their producer. The rotational direction of the flow within the vortices on one side is always the same and is opposite to the rotation of those on the other side. The flow within the vortices is such that, on the side nearest the axis of the fish producing them, the flow is opposite to the direction of travel of that fish, while on the side away from the axis the flow is in the same direction of travel as the fish. These rotational directions are opposite to those of vortices formed in a typical Karman trail produced by a rigid solid. A following fish thus has the choice of swimming through the side that would help it on its way or the other that would retard it. Swimming through a vortex center would push the head of the fish to one side before the center was reached and to the other side after the center had been passed. The fish that follows is normally found in the water flow that is in its direction of swimming, see Rosen (1959), Breder (1965), and Weihs (1973a). This arrangement evidently helps the locomotor efforts of all but the lead fishes. As the energy in the vortices dissipates rapidly it is doubtful if more than the immediately following fishes benefit significantly. As each fish produces a similar short-lived set of vortices there is no appreciable additive effect of successive rows of fish ahead. Thus all the fishes after the first transverse row receive approximately the same energy input from the vortices, so long as they remain in the specified positions. The value of this has not been measured as yet or even estimated.

These friction reducing effects evidently influence small fishes to sometimes closely associate with much larger, usually solitary, fishes of other affinities. The small attendant fishes evidently gain locomotor advantages that are otherwise only obtained by schooling with their own kind. Many authors, including Breder (1959, 1965, 1967) and Aleev (1963), have noted a variety of such fishes. These fishes station themselves close to and in definite positions relative to the larger fish, often a shark. The behavior is habitual, as in *Seriola*, but may be occasional, as in *Caranx*. Shuleikin (1958) discussed the hydrodynamics of *Naucrates ductor* (Linnaeus) in its persistent association with large sharks.

Weihs (1973a) indicated additional energy saving advantages consequent on fish swimming his diamond pattern; the channeling effect of rows of similar fishes, the effects of the phase of the tail-wagging of one fish with respect to the tail phases of its near neighbors, and the extent of length variations in the participating fishes. He calculated this variation as up to 50%. Actually over 60% variation has been found in unquestionable schools (Breder 1954), although it is impossible from this data to determine the permanency of such groups or the efficiency loss at this greater range of variation.

Active fishes, especially schooling types, lack the protuberances and hollows often present on the bodies of sluggish fishes. Aleev (1963) enumerated many instances of the latter. He indicated that this lack of streamline integrity leads to the production of minor vortices and that these disturbances, depending on their size and point of origin, could lower the locomotor efficiency of a fish. The utility of the larger terminal vortices, here under discussion, could be reduced or destroyed, thus eliminating one of the advantages of school formation.

Turbulent Friction Reduction

Until recently, students of fish locomotion were not in agreement concerning what function in relation to swimming, if any, was served by the presence of the mucus that covers the bodies of living fishes. Aleev (1963), in a well-documented review, indicated that he agreed with Richardson (1936) and Gero (1952) that whatever part it may play, the effect must be very small. That this could not be so was mentioned by Rosen (1959) and Walters and Liu (1967). Recent advances in hydrodynamics now indicate clearly that it has a very considerable role.

Polysaccharides are known to be released by a variety of aquatic organisms, both plant and animal. One of the effects of the presence of those forming long-chain molecules is friction reduction in turbulent water flow. Some of the history of the development of this information was recorded by Newton (1960), Barnaby and Dorey (1965), and Hoyt (1966, 1968, 1972, 1975). These papers discussed naturally occurring polysaccharides from algae as well as synthetic high polymers, some of the latter being used for very practical purposes as very efficient reducers of turbulent friction. The application of extremely small amounts of such materials can reduce drag by over 60%.

Rosen and Cornford (1970, 1971) had shown by means of a special type of rheometer that there are great differences in the friction reducing abilities of the slime of various species of fishes. See Jakowska (1963) for a discussion on the extent of the wide variety of other kinds of utility ascribed to the mucus of various fishes. It would seem to be certain that these effects are dependent on the polysaccharides inherent in fish mucus, although for present purposes it is not necessary to know just what components of fish mucus account for friction reduction.

Successive dilutions of fish slime with the water of the individual's habitat have been plotted against reduction of friction in terms of percent by Rosen and Cornford (1970, 1971). In some cases the curve rises extremely rapidly, reaching a reduction of turbulent friction of over 60% with water dilution to only 5% mucus. Others, with evidently less potent slime, show a much smaller rise in friction reduction, reaching 50% or less with a water dilution to 50% or more of slime. The most extreme case reaches only 8% reduction in friction with full strength slime.

It is notable that the two species with the fastest rise in friction reduction are rapacious and strike at relatively large prey. These fish can move from a resting position to their highest speed in a remarkably short time. The three species at the other end of the friction reduction series feed on much smaller organisms in proportion to their own size, for which violent pursuit is completely unnecessary. The two species with the most efficient drag reduction do not form obligate schools and are often solitary, while the three with the least effective mucus are schoolers and only one drops to the facultative status.

The preceding data on the reduction of turbulent friction by means of long-chain polymers, and the demonstration of the great effectiveness of the mucus exuded by some fishes, as well as the geometrical patterns in which schooling fishes arrange themselves, leaves little room for doubt that the fishes so organized may attain a locomotor advantage from the mucus trail trapped in the vortices left by the fishes that preceded them.

The fishes with sharp rise in friction reduction in Table 3 and Figure 20 are all nonschoolers or at most facultative: *Paralichthys californicus* (Ayers), *Sphyraena argentea* Girard,[15] and *Micropterus dolomieui* Lacépède. Those with a slow rise in friction reduction are all schoolers and are primarily obligate[16] schoolers: *Scomber japonicus* Houttuyn, *Sarda chiliensis* (Cuvier), with *Salmo trutta* Linnaeus and *S. gairdneri* Richardson as facultatives. The nonschoolers are capable of showing a sudden acceleration from a resting position and apparently attain their highest possible speed in a matter of seconds or less. The hydrodynamic aspects of extreme acceleration from a position of rest, shown by slender fishes such as barracuda, are treated by Weihs (1973b). This can be critical in overtaking relatively large prey. Schooling fishes that normally swim at a continued steady pace evidently cannot perform in such a manner and even the marginal members seldom try.

Uskova and Chaikovskaya (1975) noted, in a paper on the chemical nature of the protein com-

[15]It is recognized that the Pacific *Sphyraena argentea* tends to form schools more readily than the larger Atlantic *S. barracuda* which is usually solitary. The smaller Atlantic congeners approach *S. argentea* in this respect.

[16]A term defined by Breder (1967).

TABLE 3.—Drag reduction by fish mucus, based on data from Rosen and Cornford (1970, 1971).

Species	Drag reduction (%)	Mucus concentration (%)	Length (cm)
1 *Salmo gairdneri* Richardson (Rush Creek)	61.8	50	28
2 *S. gairdneri* (Grant Lake)	62.0	50	33
3 *S. gairdneri* (Lundy Lake)	20.5	50	23
4 *S. trutta* Linneaus	63.2	25	33
5 *Sphyraena argentea* Girard	65.9	5	76-79
6 *Scomber japonicus* Houttuyn	56.9	50	38-41
7 *Sarda chiliensis* (Culvier)	6.4	100	73
8 *Micropterus dolomieui* Lacépède	62.0	50	33-42
9 *Pomoxis annularis* Rafinesque	61.7	20	—
10 *Lepomis machrochirus* Rafinesque	60.1	20	15.3-20.4
11 *Paralabrax clathratus* (Girard)	58.7	25	43
12 *P. nebulifer* (Girard)	17.4	20	33±
13 *Paralichthys californicus* (Ayres)	60.9	5	53

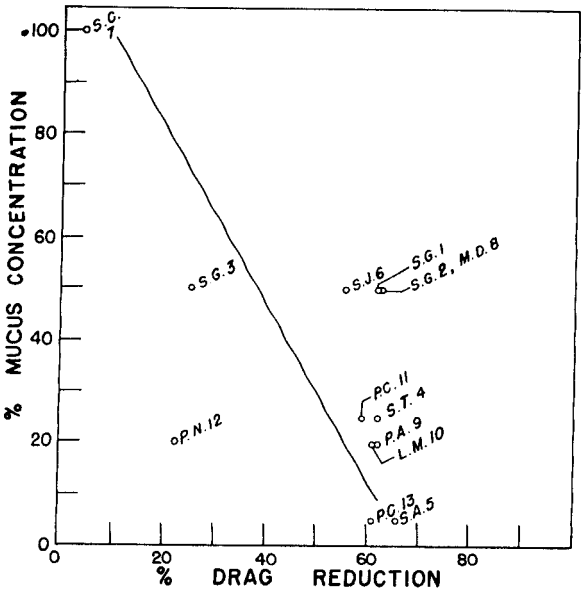

FIGURE 20.–Graph of the effectiveness of fish mucus on drag reduction. Based on the data of Rosen and Cornford (1970, 1971). The numbers and letters at each point are explained in Table 3, giving the name and number of each fish in the left hand column. See text for full explanation.

ponents of fish mucus, that the hydrodynamic efficiency of the fishes they studied varied directly with the extent of the basicity of their surface mucus. The fishes measured were Atlantic bonito, *Sarda sarda* (Bloch), sea bass, *Serranus scriba* (Linnaeus), and stargazer, *Uranoscopus scaber* (Linnaeus), given here in the order of descending basicity. This is consistent with the present studies based on the lubricity of certain polymers.

The mucus of a fish in a school does more than reduce the drag on its producer since it washes over those that follow. This means that the "leaders" have only their own mucus to ease their passages while the "laggards" receive all the benefits bestowed by those ahead of them. The net effect is to produce a lubricity gradient from zero to the maximum which is dependent on the size of the school. To maintain a steady pace, fishes in the forepart of the school must use more muscular power than the others while the last members require the least effort to hold their positions. As fatigue sets in, the "front runners" would have a choice of accelerating their efforts or holding a steady pace and thus permit those following to pass ahead of them until they find a place requiring an effort compatible with the magnitude of their tiring, which could carry them to the trailing end positions of the school, if necessary. Zuev and Belyaev (1970) indicated that in a school of *Trachurus*, the individuals in the front part beat their tails faster than those in the rear. This condition would naturally follow the lattice-vortex-mucus thesis as developed here.

Thus, this condition of graded positions in respect to ease of swimming and the matter of muscular fatigue may be a large factor in the maintenance of the integrity of a school and explain the internal churning so often seen in fish schools. The very general changes in positions of individuals within the structure of a school could thus be impelled to a large extent by the individual urge to attain a position demanding the least swimming effort. Also this urge would insure the usual prompt reassembly of a school after being violently dispersed and suggests that the closed figure "mills" of schooling fishes, that would otherwise seem to be trivial and pointless, form a relatively quiescent rest period in a favored place. Fish mills have been noted by many students, beginning with Parr (1927). They can be developed from many other sources than the one noted above. Often they are derived directly from extrinsic events, as discussed by Breder (1965). The development of an evidently intrinsic mill is shown there by three photographs that may truly represent the formation of a true "resting mill" as suggested above.

There is too little known about the complexities of fish mucus to permit much further progress into the details of its relation to school formation and maintenance or its importance to other matters. For instance, how constant are its characteristics and are there rhythmic variations in them related to season, reproductive periods, or type of food ingested? Are there changes in the mucus with age or condition of the fish? Is the mucus of marine fishes more stable than that of freshwater fishes? Since ocean water is chemically more uniform than fresh water it might be expected that these features were reflected in the mucus.

Experiments with Drag-Reducing Polymers

Fish mucus, in the amounts necessary for these experiments, is difficult, if not impossible, to obtain and handle without some decomposition and reduction of the long-chain molecules. Additives of some bacteriostatic chemical or refrigeration merely introduces other difficulties that could make interpretations uncertain.

Furthermore, the drag reduction of a fish slime diluted with water that produced a 25% reduction just after its removal from the fish, was inert 3 h later, according to Hoyt (1975). He also gave a hydrodynamic explanation on why it is possible for very small fishes to gain an advantage from their mucus although the operational mechanics are different than those available to larger fishes. This concerns differences in the boundary-layer transition from laminar to turbulent flow in relation to the Reynolds numbers. Fish mucus does not dilute easily with water by mere contact, but does so easily with agitation. Rosen (1959) used the term "reluctance" to designate this condition. Polymers, especially those manufactured to have high drag-reducing characteristics as measured on a rheometer, have drag reduction features that are comparable to or exceed those of fishes' surface mucus in the small quantities required to obtain maximum effects.

The material used was a water soluble resin, a high polymer of ethylene oxide, from the Union Carbide Corporation, and generally known by its trade name Polyox[17]. The significant characteristics, as given by Hoyt (1971) follow

Polyox F.R.A. (Lot 1163)

Molecular weight	*Max drag reduction (%)*	*Concentration (%)*	
		Max D.R.	*½ max D.R.*
6,000,000 (ca.)	67.8	15	1

This particular grade of Polyox was used because of its unusually high molecular weight as the purpose here was merely to establish whether such products would induce a change in the swimming efficiency of the fishes. Hoyt (1975) considered a minimum molecular weight of 50,000 of the drag-reducing element to be necessary for friction reduction to be expected.

Polyox is reported to have very low, if any, toxicity, (Smyth, et al. 1970, Wade 1970). For the purposes of this study, toxicity tests were also run on a variety of fishes. Nothing whatever occurred that would suggest any physiological disturbance on any of the test fishes. Both *Poecilia reticulata* Peters (fresh water) and *Hippocampus erectus* Perry (salt water) produced young when subjected to concentrations far higher than any required here. The only item showing obvious adjustments to the change in lubricity of the water was that mature examples of *Hippocampus erectus* were unable to use their prehensile tails effectively on the smaller supports provided in their aquaria. That is, they simply slipped off plastic rods, of circular cross section, if the rod diameters were below a certain magnitude relative to the grasp of their tails. With larger rods they had no trouble and were readily able to "grasp" the supports and hold on in normal fashion. Those that could not find a suitably sized "perch" coiled their tails so that about three-quarters of a circle was formed at right angles to the body axis and then "sat" with the partial circle laid on the bottom of their aquarium. Apart from being somewhat restless, they apparently were just as well off as the others. The *Poecilia* moved about in what appeared to be their normal random manner, but whether they moved a little faster or not could have only been determined with great difficulty and would not have contributed to the problems under study. None of the fishes tested after the preceding preliminaries showed any distress from the addition of Polyox.

The Gulf menhaden, *Brevoortia patronus* Goode, was used for tests on drag reduction. This species is an obligate schooler and, as with many such schoolers, the ability to spread its caudal fin is severely limited. There is a strong possibility that none of them exercised this slight ability at all. Also, these fish accommodate well to aquarium life if provided adequate swimming room and a few companion fishes, a feature not common in many members of this family. The fishes selected for testing were first established in a circular concrete tank 4+ m diameter, with a water depth of 1 m.

Specially made aquaria were used for these experiments. They measured 25 × 25 × 90 cm and were filled with synthetic seawater[18] to a depth of 20 cm providing a total water volume of 45,000 cm^3. These were established in a perfectly light-tight room, actually a Navy Sea Van without windows, remote from vibrations and sounds. Lights were controlled by a time switch for day and night effects and a thermostat controlled the temperature. The test aquarium was placed on the floor and the others on rocks at a convenient height. Precautions were taken to protect the fishes from being startled by motions, vibrations, or other

[17]Kindly supplied gratis. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[18]Kindly supplied gratis under the name "Instant Ocean" by Aquarium Systems, Inc.

disturbances outside their container. There is no reason to suppose that the results were so influenced.

Two grams of the dry granular Polyox were dissolved in a small portion of the synthetic seawater. This was then returned to the test aquarium by allowing it to drip back by means of a siphon tube nearly closed by a screw clamp. The final concentration of Polyox in the aquarium became approximately 42 ppm.

A motion picture camera facing down was erected so that its optical axis was over the geometric center of the tank. Photo floodlights were set up as required. The view included most of the aquarium, omitting only the ends of the tank where the fishes were forced to turn back, as these tests must be made with the fishes moving in a nearly straight line. Also included in the camera's coverage were tapes marked in centimeters. One ran along the top edge of the tank and the other along its bottom, thus providing an index to the lengths of the fishes and their distances of travel. The aquarium had its sides blocked with bluish cardboards, except on the sides toward the lights. These were higher than the aquarium and off to one side sufficiently to eliminate reflections into the camera's lens. The test fish were added and allowed to adjust to the new situation for about 1 h. The tank in which they had lived for at least 1 wk was identical with the test tank, except that it had all four sides covered with similar cardboard guards.

Photographs were taken after the lights had been turned on gradually to full voltage. It was found by experience that normal film speed was fully adequate for our analysis. Sufficient footage was exposed to insure an adequate number of straight runs of single fish.

When the above procedures were completed, the Polyox was allowed to drip into the tank, which took about 10 min. After 1 h had elapsed, its mixing was considered completed, for in addition to the aerating devices, the four very active fishes provided continuous mixing. After this time interval the photographic procedures were repeated and the experiment was terminated.

The results of these experiments are given in Table 4 and their analysis is illustrated by graphs in Figure 21. Graphs A and C clearly show the difference between fishes swimming in synthetic seawater, initially devoid of any long-chain polymers, and in the same water to which the polymer has been added. The speed of the fishes is approximately double in the latter, as are the tail beats. In this experiment, after the first run (S1) was made in synthetic seawater, the tank with its contained fishes was left as it was until 2 days later when another run (S2) was made. The new speed readings were a little higher, but the proportional corrections were not. If more refined measurements show that a small difference is measurable, it should be due to the additions of organic substance in the interim, consisting of the body wastes of the fish as well as their own surface slime produced in this period. Added to this must be the dissolved matter from the food given to the fishes. To minimize all this, all particles not consumed directly were meticulously removed. The manner of handling data was that of Bainbridge (1958). The greater refinements of the methods of Hunter and Zweifel (1971) were not deemed necessary for the present simple purposes. Because of the large differences between the speeds of fishes in the same water, with and without long-chain polymers, the slight possible spreading of the caudal fin in this species could not increase the area of the tail by more than a negligible amount in these experiments. Later another set of four

TABLE 4.—Calculations based on experiments on drag reduction in *Brevoortia* by polymers. TL = total length. TB = tail beats.

Date 1973	Water state	Fish TL (cm)	Run length (cm)	Run time (s)	No. of tail beats	Speed (cm/s)	TB/s	cm/s TL
13 Sept.	Synthetic	6.30	19.50	1.33	6	14.58	4.51	2.31
		6.60	25.00	1.67	7	14.90	4.19	2.26
11 Oct.		7.10	23.30	1.95	6	11.99	3.08	1.69
		9.00	23.00	1.44	4	15.10	2.78	1.68
	+ Polyox	7.50	15.00	0.89	4	16.85	4.49	2.25
		7.90	29.00	0.89	7	32.58	7.87	4.12
		7.50	35.00	1.11	8	31.53	7.21	4.20
		8.00	32.00	1.11	6	28.83	5.41	4.80
6 Nov.	Bay	7.00	34.00	1.11	9	30.63	8.11	4.37
		6.60	10.00	0.78	3	12.82	3.85	1.94
	+ Polyox	10.00	36.00	2.00	4	18.00	2.00	1.80
		6.60	47.00	1.11	5	42.34	4.50	6.42
		10.00	44.00	1.06	8	41.51	4.55	4.15

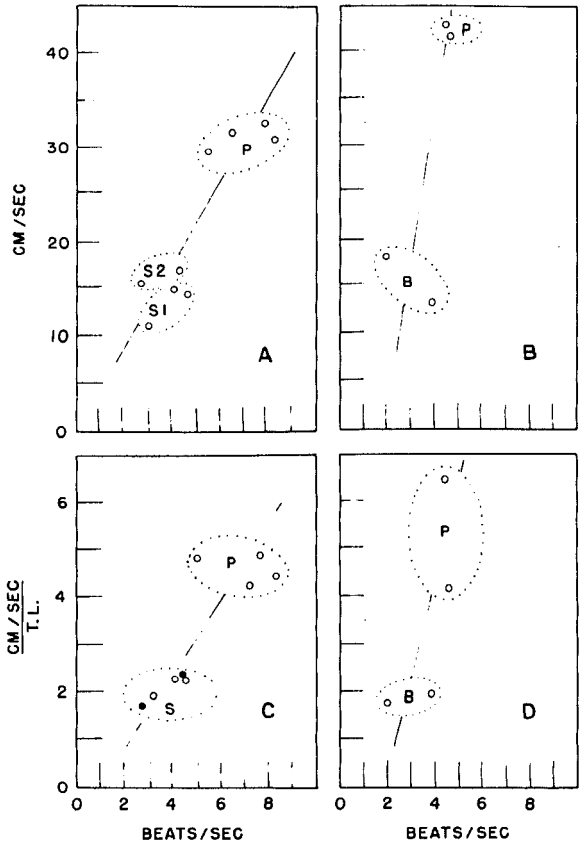

FIGURE 21.–Graph of experimental analysis of the relationship of tail beats to speed in waters of various degrees of lubricity. S = synthetic sea water. B = bay water. P = Polyox added. S2 in graph A is shown in graph C by black spots. See text for explanation.

fishes were similarly tested. These were somewhat larger than the first. Grossly polluted but sand-filtered bay water was used. The results were in good accord with the first set, the readings running a little higher and the slope of proportionality being a little steeper.

Measures of the varying amplitudes reached by swings of the tails were not made as they vary with the tempo of the cycles, as noted by Bainbridge (1958), and contribute no additional information germane to this study.

A direct result of these experiments is very clear. The fishes had a choice of two possible extreme responses to an increase in the water's lubricity. They could maintain their former speed by appropriately reducing the frequency of the tail cycles, or they could so increase their tail beat rate and thus their rate of translation. Obviously they could respond by some intermediate response by partially using each of the above two responses. Present data cannot be used to determine these finer distinctions. However, the amounts of the speed increase in both cases strongly suggests that most, if not all, of the gain was by increase of speed.

It might be thought that the fishes were swimming at their accustomed rate in the situation of these experiments and so would not change their rate of swimming even when the changed drag effects reduced the effort required. The phrase "accustomed rate" may or may not be the same as their "optimum speed" as defined by Weihs (1973a). As they did change their pace it seems most probable that the fish were swimming close to their maximum, possibly induced by the increased illumination.

The differences in speed of the fishes between the nontreated water and that with Polyox added, expressed in percentages, is impressive. Experiments 1 to 5 and 6 to 9 (synthetic seawater) show a mean increase of 66+%. Experiments 10 to 11 and 12 to 13 (bay water) show a mean increase of 63+%. The crude percentage figures show no significant differences between the two cases. The equivalent figures, using the correction values for size of the individual, follow: Synthetic seawater, experiments 1 to 9, mean increase 58+%. Bay water, experiments 10 to 13, mean increase 35+%. Further analysis may show this to be a real difference.

Cahn's (1972) studies tend to confirm the importance of both the hydrodynamic and mucus elements in the formation and maintenance of schools of *Euthynnus affinis* (Cantor). The fish used by her were about 40 cm in total length and the project was concerned with lateral line studies. She found that placing a transparent plastic partition between two fish that had been swimming in parallel courses with the partition, with one somewhat ahead of the other as the first point and one of the side points of Weihs' (1973a) diamond, resulted in the fishes changing to a side to side position. Without questioning the value of the lateral line organs, there is also the value of the mucus and vortices and the "cues" from them which may be handled by the lateral line system. How much these sense organs are directly involved with the maintenance of fish schools is not yet clear. Williams (1967)[19] did not, " . . . believe

[19]Williams (1964), followed by Hamilton (1971), believes that schooling is primarily a matter of cover seeking.

that the lateral line is important in schooling behavior." In the same publication Walters and Liu (1967) ". . . postulate that the boundary layer acts as a hydrodynamic amplifier . . ." that is involved in transferring precise information on changes in water movement that the fish encounters as it swims ahead, reaching the fishes brain via the lateral line system. In a school, much of such information concerns the water movements produced by the swimming activities of the fishes ahead, probably by the bending of the cupulae that indicate the direction of flow of the currents and its strength. Other experiments carried out by different investigators point the same way as, for instance, the work of Pitcher (1973) with mirrors. This is not in discord with the related work reported here and both can be accounted for by the effects of the lattice pattern and the hydrodynamic and the mucus cues. Also the work of Shaw and Tucker (1965) and the interpretation of their results by van Olst and Hunter (1970), based on an optomotor device, indicated that the test fish reacted more to the fishes ahead of it than to the moving target spot.

Another source of possible information has been pointed out by Smith (1930) in some little-noticed studies. These have shown that *Carassius auratus* (Linnaeus) can draw samples of the surrounding water into its lateral line canals and expel them as new samples are drawn in. This behavior certainly suggests the possibility of a chemical or other sensory device that could distinguish the concentration of the mucus of preceding fishes. Present understanding of the relation of the sensory possibilities related to schooling organization clearly suggests that such activity of the lateral line could be a part, or even an important element, in a following fish's ability to locate the most favorable position to be stationed in respect to the mucus of the preceding individual.

Fish at the front of a school receive locomotor benefits from only their own production of mucus. All the rest receive benefits from the mucus of those ahead; those at the very end of a school thus receive the most benefit. This is sufficient to account for the "churning" sometimes seen in schools, the leaders falling back while others press ahead, all of which helps maintain the integrity of the school as previously noted.

The peripheral individuals in a school often keep trying and usually do eventually attain a more central position, evidently for reasons similar to those given above. The rapid reorganization of a school after violent disruption is apparently similarly motivated.

The existence of fish mills, as noted in the prior section, may not be the trivial phenomenon it is generally thought to be. Instead, in the present view, it may be a resting device with an important purpose. If the fishes reach a point of fatigue that would slow the school down to an extent inimical to the schools integrity, the mill formation would supply that necessary respite.

All three of the preceding observable items of activity, as noted, have a consolidating effect on a school and none show any tendency toward school dispersion.

The works of Belyaev and Zuev (1969), Zuev and Belyaev (1970) and Weihs (1973a) discussed the hydrodynamic effects of one fish on another in a school, considering only the water movements induced by the swimming efforts of each member of the school. This is all in basic agreement with the present theoretical treatment of the school organization. Adding to this, the effects of the drag reducing abilities of the mucus released by the fishes involved can only result in much higher efficiency.

Furthermore, there is no evidence that more mucus cannot be released by fishes to ease their muscular efforts when necessary. There are, however, strong probabilities that such abilities are indeed present. Species that use their mucus for other purposes have this faculty developed to a high degree, as in *Rypticus* (Maretzki and del Castillo 1967), that exudes a toxic mucus in great quantities when attacked or handled or many of the parrotfishes that envelope themselves in a "cocoon" of congealed mucus on nightfall (Winn 1955). Quality control is also possible with many fishes under appropriate stimulation. All calculations at this time involving mucus production are somewhat uncertain and must remain so until it is known whether the mucus is exuded at a rather steady rate or is subject to wide fluctuations, somewhat after the manner of perspiration in various mammals.

It is possible that the closing up of ranks, when a school is in flight from some danger, may destroy the assistance of both vortices and mucus. Under this kind of emergency, involving maximum energy expenditures, this loss may have to be accepted. Possibly such a situation could call for an extra outpouring of mucus.

DISCUSSION

The two basic purposes of this paper are the establishment of the primary space lattice formed by schooling fishes and the role that their surface mucus plays. Both features are supported by theory and empirical data and both expedite the swimming efforts of the fishes. This alone gives sufficient reasons for the formation and the maintenance of schools.

The question of how much of the schooling phenomenon is a simple following of the paths of least resistance, with automatic avoidance of other fishes, how much is social imitation, and how much is mediated by communication between individuals is not answered here. The phrase "social imitation" is discussed at length by Radakov (1972) as is the status of the term "communication" discussed by Tavolga (1974). The latter indicated that the mechanisms involved can begin as the optomotor orientations of Shaw (1960, 1961). He added that possibly the responses of the fishes "... even as adults may be primarily taxic." The rheotactic response to vortices and to fish mucus, reported here, may be equal to or of greater influence than the optical response, since they are fully operable in the dark, but not nearly as precise as the visual response. This could account for the fact that schooling fishes do not fully lose contact with each other in darkness even in species not given to sound production (Breder 1967).

It is recognized, of course, that there is more to the activity of any fish than efforts to avoid possible physical exhaustion. An evaluation of the importance of other activities or even an enumeration of those that are more evident will not be attempted here. However, another approach to the overall problem is noted as follows. The "following reaction" of Crook (1961), based on bird flocks, has been discussed in connection with fish schools by Shaw (1960, 1962), Hemmings (1966), and van Olst and Hunter (1970). The expression is evidently very nearly, if not completely, identical with the "social imitation" of Radakov (1972).

These data suggest a hypothesis that could go as follows. A group of fossil fishes, not living in schools, but within swimming distances of each other, may form the background. One fish crossing in back of another and encountering its vortex trail would find that self-propulsion required less effort. It is not unreasonable to suppose that after a few such encounters, a tendency to follow would develop. This might be without any instinct to follow or imitate but not without prior experience with the vagaries of water currents, which each fish encounters on its first feeble swimming attempts as a hatchling; nor is there any reason to dismiss the alternative, that the order is opposite. In Recent fishes the latter is most probably the case. However in the early fishes, which are considered above, the first move to follow could have been solely on a hydrodynamic basis. From here on, with the establishment of a primitive school, its continued existence and development or extinction would be regulated by selective processes, depending basically on whether schooling hindered or enhanced the species' ability to survive. It is visualized that this process could have taken place many times in various groups, especially among fishes with relatively scanty mucus production. Also, this process would probably be easily reversible so that fish schools could appear and disappear according to environmental or physiological changes that made schooling or a solitary life favor a species' survival.

Detailed conparisons between schools of various taxa, or between schools formed by a single species at various times, or under varied conditions have not been made. It would seem however, that all schools are not necessarily isomorphic but are probably at least homomorphic, in the sense of Ashby (1956).

In a fully theoretical paper, Hamilton (1971) supported the view of Williams (1964, 1967), that most types of animal aggregations owe their existence basically to each animal (vertebrate or invertebrate) trying to hide behind another. With this we have no argument (Breder 1967) and our presentation here, on the locomotor utility of fish schools, exists comfortably with or without it. The question of which came first, hiding or benefiting from an enhancement of swimming efforts, involves no interference. They could have developed together or independently, each little advancement of one helping the development of the other.

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LITERATURE CITED

ALEEV, Y. G.
1963. Function and gross morphology in fish. [In Russ.] Izd. Akad. Nauk SSSR. Moscow, 245 p. (Translated by Israel Program Sci. Transl., 1969, 268 p., available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as TT 67-51391.)

ALEKSEEVA, K. D.
1963. Role of vision in group behavior of some Black Sea fishes. [In Russ.] Vopr. Ikhtiol. 29:726-733.

ASHBY, W. R.
1956. An introduction to cybernetics. Chapman and Hall, Ltd., Lond., 295 p.

ASHTON, W. D.
1966. The theory of road traffic flow. Methuen's monographs on applied probability and statistics. John Wiley and Sons, Inc., N.Y., 178 p.

ATZ, J. W.
1962. Does the shrimpfish swim head up or head down? Anim. Kingdom 65:175-179.

BAINBRIDGE, R.
1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. Exp. Biol. 35:109-133.

BARNABY, K. C., AND A. L. DOREY.
1965. A towing tank storm. Trans. R. Inst. Nav. Archit. 107:265-272.

BELYAEV, V. V., AND G. V. ZUEV.
1969. Hydrodynamic hypothesis of school formation. [In. Russ.] Vopr. Ikhtiol. 57:716-725.

BOWEN, E. S.
1931. The role of the sense organs in aggregations of *Ameiurus melas*. Ecol. Monogr. 1:1-35.
1932. Further studies of the aggregating behavior of Ameiurus melas. Biol. Bull. (Woods Hole) 63:258-270.

BREDER, C. M., JR.
1951. Studies on the structure of the fish school. Bull. Am. Mus. Nat. Hist. 98:1-27.
1954. Equations descriptive of fish schools and other animal aggregations. Ecology 35:361-370.
1959. Studies on social groupings in fishes. Bull. Am. Mus. Nat. Hist. 117:393-482.
1965. Vortices and fish schools. Zoologica (N.Y.) 50:97-114.
1967. On the survival value of fish schools. Zoologica (N.Y.) 52:25-40.

BREDER, C. M., JR., AND P. M. BIRD.
1975. Cave entry by schools and associated pigmentary changes of the marine clupeid, *Jenkinsia*. Bull. Mar. Sci. 25:377-386.

BREDER, C. M., JR., AND R. F. NIGRELLI.
1938. The significance of differential locomotor activity as an index to the mass physiology of fishes. Zoologica (N.Y.) 23:1-29.

CAHN, P. H. (editor).
1967. Lateral line detectors. Indiana Univ. Press, Bloomington, 496 p.

CAHN, P. H.
1972. Sensory factors in the side-to-side spacing and positional orientation of the tuna, *Euthynnus affinis*, during schooling. Fish. Bull., U.S. 70:197-204.

CLARK, P. S., AND F. C. EVANS.
1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

CROOK, J. H.
1961. The basis of flock organization in birds. *In* W. H. Thorpe and O. L. Zangwill (editors), Current problems in animal behaviour, p. 125-149. Cambridge Univ. Press, Lond.

CULLEN, J. M., E. SHAW, AND H. A. BALDWIN.
1965. Methods for measuring the three-dimensional structure of fish schools. Anim. Behav. 13:534-543.

ESCOBAR, R. A., R. P. MINAHAN, AND R. J. SHAW.
1936. Motility factors in mass physiology: Locomotor activity of fishes under conditions of isolation, homotypic grouping, and heterotypic grouping. Physiol. Zool. 9:66-78.

GAZIS, D. C.
1967. Mathematical theory of automobile traffic. Science (Wash., D.C.) 157:273-281.

GERO, D. R.
1952. The hydrodynamic aspects of fish propulsion. Am. Mus. Novit. 1601, 32 p.

GUTHRIE, J. F., AND R. L. KROGER.
1974. Schooling habits of injured and parasitized menhaden. Ecology 55:208-210.

HAMILTON, W. D.
1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

HEALEY, M. C., AND R. PRIESTON.
1973. The interrelationships among individuals in a fish school. Fish. Res. Board Can. Tech. Rep. 389, 15 p.

HEMMINGS, C. C.
1966. Olfaction and vision in fish schooling. J. Exp. Biol. 45:449-464.

HERALD, E. S.
1961. Living fishes of the world. Doubleday and Co., Inc., Garden City, N.Y., 304 p.

HILBERT, D., AND S. COHN-VOSSEN.
1952. Geometry and the imagination. (Translated from Ger. by P. Nemenyi.) Chelsea Publ. Co., N.Y., 357 p.

HOYT, J. W.
1966. The friction-reducing effects of high polymers. Nav. Res. Rev. 19(10):16-21.
1968. Microorganisms-Their influence on hydrodynamic testing. Nav. Res. Rev. 21(5):18-21.
1971. Drag-reduction effectiveness of polymer solutions in the turbulent-flow rheometer: a catalog. Polym. Lett. 9:851-862.
1972. The effect of additives on fluid friction. Trans. Am. Soc. Mech. Eng., J. Basic Eng. 94D:258-285.
1975. Hydrodynamic drag reduction due to fish slimes. *In* T. V. T. Wu, C. J. Brokaw, and C. Brennen (editors), Swimming and flying in nature, Vol. 2, p. 653-672. Plenum Press, N.Y.

HUNTER, J. R.
1966. Procedure for analysis of schooling behavior. J. Fish. Res. Board Can. 23:547-562.

HUNTER, J. R., AND J. R. ZWEIFEL.
1971. Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. Fish. Bull., U.S. 69:253-266.

JAKOWSKA, S.
1963. Mucus secretion in fish—a note. Ann. N.Y. Acad. Sci. 106:458-462.

KEENLEYSIDE, M. H. A.
1955. Some aspects of the schooling behaviour of fish. Behaviour 8:183-248.

KLAUSEWITZ, W.
1963. Wie schwimmt der Schnepfenfisch? Nat. Mus. 93:69-73.

LINDGREN, E. R.
1967. The lateral line from the point of view of a fluid dynamicist. *In* P. H. Cahn (editor), Lateral line detectors, p. 448-450. Indiana Univ. Press, Bloomington.

LINES, L.
1965. Solid geometry. Dover Publ., 202 p. Corrected reprint of the 1935 publ.

MCFARLAND, W. N., AND S. A. MOSS.
1967. Internal behavior in fish schools. Science (Wash., D.C.) 156:260-262.

MARETZKI, A., AND J. DEL CASTILLO.
1967. A toxin secreted by the soapfish *Rypticus saponaceus*. Toxicon 4:245-250.

MOSS, S. A., AND W. N. MCFARLAND.
1970. The influence of dissolved oxygen and carbon dioxide in fish schooling behavior. J. Mar. Biol. 5:100-107.

NEWTON, R. N.
1960. Standard model technique at Admiralty Experiment Works, Hasler. Trans. R. Inst. Nav. Archit. 102:435-470.

PARR, A. E.
1927. A contribution to the theoretical analysis of the schooling behavior of fishes. Occas. Pap. Bingham Oceanogr. Collect. 1:1-32.

PITCHER, T. J.
1973. The three-dimensional structure of schools in the minnow, *Phoxinus phoxinus* (L.). Anim. Behav. 21: 673-686.

RADAKOV, D. V.
1972. Schooling in the ecology of fish. Izdatel. "Nauka", Moscow. [In Russ., Engl. transl., 1973, 173 p. Israel Program Sci. Transl. Publ. John Wiley and Sons, N.Y.]

RICHARDSON, E. G.
1936. The physical aspects of fish locomotion. J. Exp. Biol. 13:63-74.

ROSEN, M. W.
1959. Water flow about a swimming fish. U.S. Naval Ordnance Test Stn., China Lake, Calif., Tech. Publ. NOTS TP 2298, 94 p.

ROSEN, M. W., AND N. E. CORNFORD.
1970. Fluid friction of the slime of aquatic animals. Nav. Undersea Res. Dev. Cent., Tech. Publ. NUC TP 193, 45 p.
1971. Fluid friction of fish slimes. Nature (Lond.) 234:49-51.

SCHUETT, F.
1934. Studies in mass physiology: The activity of goldfishes under different conditions of aggregation. Ecology 15:258-262.

SHAW, E.
1960. The development of schooling behavior in fishes. Physiol. Zool. 33:79-86.
1961. The development of schooling behavior in fishes. II. Physiol. Zool. 34:263-272.
1962. The schooling of fishes. Sci. Am. 206:128-134, 137-138.
1970. Schooling in fishes: Critique and review. *In* L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt (editors), Development and evolution of behavior, p. 452-480. W. H. Freeman and Co., San Franc.

SHAW, E., AND A. TUCKER.
1965. The optomotor reaction of schooling carangid fishes. Anim. Behav. 13:330-336.

SHULEIKIN, V. V.
1958. How the pilot fish moves with the speed of the shark. Dokl. Adad. Nauk SSSR 119:140-143.

SMITH, G. M.
1930. A mechanism of intake and expulsion of colored fluids by the lateral line canals as seen experimentally in the goldfish (*Carassius auratus*). Biol. Bull. (Woods Hole) 58:313-321.

SMYTH, H. F., JR., C. S. WEIL, M. D. WOODSIDE, J. H. KNAAK, L. J. SULLIVAN, AND C. P. CARPENTER.
1970. Experimental toxicity of a high molecular weight poly(ethylene oxide). Toxicol. Appl. Pharmacol. 16:422-445.

SVENDSEN, G. E., AND K. B. ARMITAGE.
1973. Mirror-image stimulation applied to field behavioral studies. Ecology 54:623-627.

SYMONS, P. E. K.
1971a. Spacing and density in schooling threespine stickelbacks (*Gasterosteus aculeatus*) and mummichog (*Fundulus heteroclitus*). J. Fish. Res. Board Can. 28:999-1004.
1971b. Estimating distances between fish schooling in an aquarium. J. Fish. Res. Board Can. 28:1805-1806.

TAVOLGA, W. N.
1974. Application of the concept of levels of organization to the study of animal communication. *In* L. Krames, T.

Alloway, and P. Pliner (editors), Nonverbal communication, Vol. 1, p. 51-76. Plenum Press, N.Y.

USKOVA, E. T., AND A. V. CHAIKOVSKAYA.
1975. Heterogeneity and chemical nature of protein components in sea fish mucus coats. [In Russ.] Gidrobiol. Zh. 11(3):38-42.

VAN OLST, J. C., AND J. R. HUNTER.
1970. Some aspects of the organization of fish schools. J. Fish. Res. Board Can. 27:1225-1238.

WADE, R. H.
1970. Pollution potential of drag-reducing polymers. NUC symposium on environmental preservation. Nav. Undersea Cent., Tech. Publ. 215:131-143.

WALTERS, V., AND R. K. LIU.
1967. Hydrodynamics of navigation by fishes in terms of the mucus-water "interface." *In* P. H. Cahn (editor), Lateral line detectors, p. 437-446. Indiana Univ. Press, Bloomington.

WEIHS, D.
1972. A hydrodynamical analysis of fish turning maneouvres. Proc. R. Soc. Lond. B Biol. Sci. 182:59-72.
1973a. Hydromechanics of fish schooling. Nature (Lond.) 241:290-291.
1973b. The mechanism of rapid starting of slender fish. Biorheology 10:343-350.

WILLIAMS, G. C.
1964. Measurement of consociation among fishes and comments on the evolution of schooling. Publ. Mus. Mich. State Univ., Biol. Ser., 2(7):351-383.
1967. Comments from panelists. *In* P. H. Cahn (editor), Lateral line detectors, p. 476-477. Indiana Univ. Press, Bloomington.

WINN, H. E.
1955. Formation of a mucous envelope at night by parrot fishes. Zoologica (N.Y.) 40:145-148.

ZUEV, G. V., AND V. V. BELYAEV.
1970. An experimental study of group swimming in fish with reference to horse-mackerel *Trachurus mediterraneus ponticus* Aleev. [In Russ.] Vopr. Ikhtol. 63:733-739. [Transl. in J. Ichthyol. 10:545-549.]

ESTIMATION OF FISHING EFFORT IN THE WESTERN NORTH ATLANTIC FROM AERIAL SEARCH DATA

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ABSTRACT

Three estimators of days fished were developed from aerial search data obtained by fisheries surveillance operations over the northwest Atlantic off the northeast coast of the United States. These algorithms estimate fishing effort by applying functions of past aerial observations and past reported effort to aerial data from the time period for which effort is to be calculated. An estimator based on the relation of the average number of fishing vessels that were observed per flight and days fished as reported has produced easily calculated estimates of days fished to within ±0.50 of the reported value in 90% of all cases, 1971-73. An estimator based on the probability of a day fished if not sighted by fisheries surveillance operations provided an estimate of fishing effort to within ±0.50 in 95% of all cases. An algorithm based on the probability of a day on fishing grounds, if not actually observed, and on the ratio of days fished to days on grounds enabled the calculation of days fished with largest error (within ±0.50 in approximately 80% of all cases).

Prior to 1961, the waters off the northeast coast of the United States were fished exclusively by the domestic fleet. However, in 1961 distant water fishing fleets of other nations began fishing this area. Concern for the presence of these fishing vessels prompted the United States to observe and record the activities and magnitude of such fleets. These observations over the 160,000 km^2 fishing grounds were made from land-based aircraft; one to several flights were made each month. Although fisheries statistics are reported by fishing nations, such statistics are only available at least 6 mo after the close of the reporting period. Overflight observations are therefore the only available up-to-date information on that fishery.

The fishery in these waters is regulated by the International Commission for the Northwest Atlantic Fisheries (ICNAF), a fisheries management directed treaty organization. Under the objective of maintaining a maximum sustained catch, the Commission sets regulations "to achieve the optimum utilization of the stocks of those species of fish which support international fisheries in the convention area."[2] Intensive fisheries harvest regulations by that agency[3] have required progressively larger cutbacks in fishing by fleets other than the United States and Canada in these waters. (ICNAF Statistical Subareas 5 and 6, Figure 1.)

The United States has expressed its concern to ICNAF as to adherence to these fisheries regulations in 1974.[4] This concern originated from preliminary examination of the fisheries overflight data.

As a consequence, stochastic methods to monitor the fishery through the analysis of overflight data are of chief importance. In response to such needs three estimators of fishing effort are presented. These estimators of days fished are based on the aerial surveillance data and concomitant reported fishing effort. (Fishing effort as reported by each ICNAF member nation is published annually, usually about 1 yr following the reporting period. Such statistics used in this study were obtained from the ICNAF Statistical Bulletin, Vol. 19-23, Dartmouth, N.S.) In each estimation method, functions developed from aerial surveillance and reported data in a previous time interval are used to calculate fishing effort during a future time interval for which only aerial surveillance data are available.

METHOD

Fisheries surveillance flights were approximately 12 h or less in duration and were carried out

[1]Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]ICNAF. 1974. ICNAF Handbook. Dartmouth, N.S., Can., 78 p.

[3]ICNAF. 1974. Proceedings of the third special meeting, October, 1973, N.S., Can., 34 p.

[4]ICNAF. 1975. Proceedings of the fifth special meeting, November, 1974, N.S., Can., 40 p.

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FISHERY BULLETIN: VOL. 74, NO. 3, 1976.

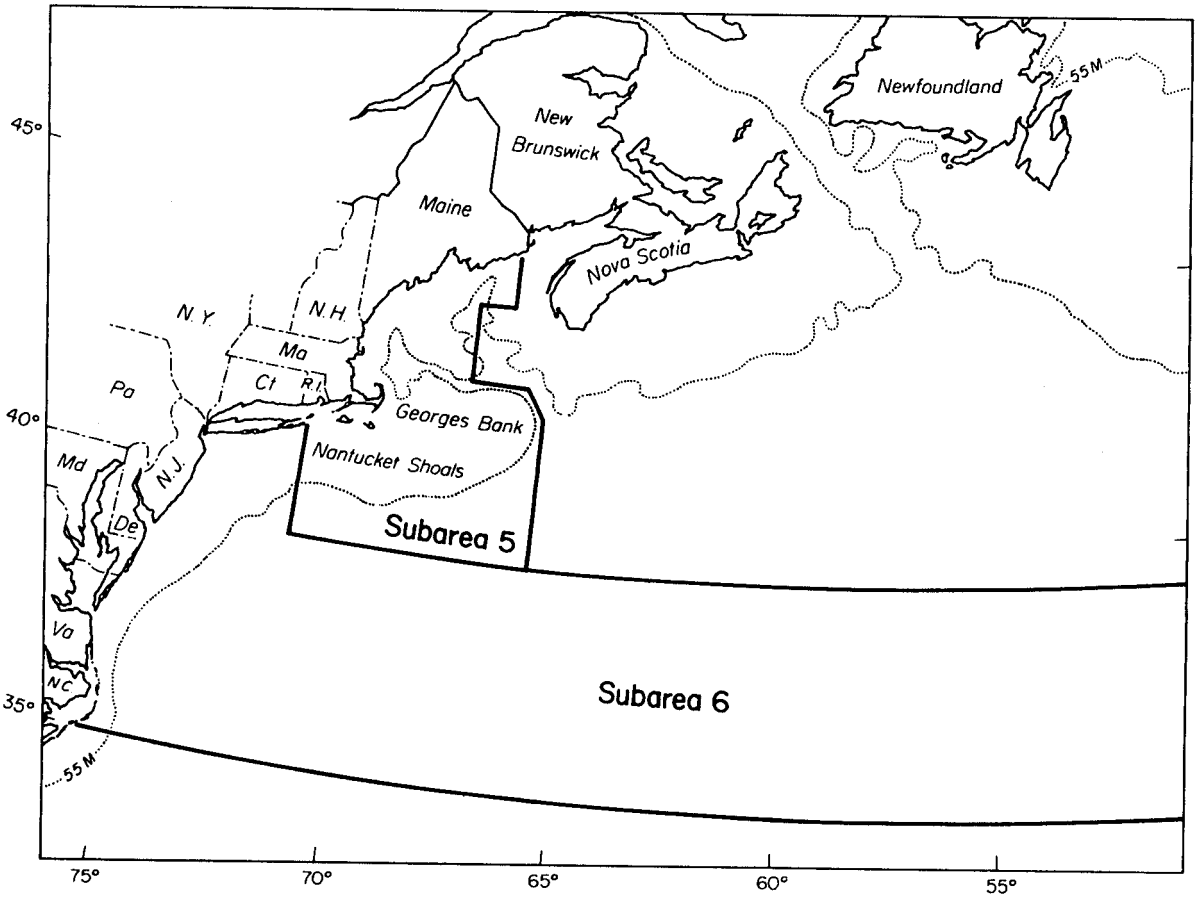

FIGURE 1.–ICNAF Subareas 5 and 6.

during daylight hours. The primary objective of each of the flights was to observe as many vessels as possible. (U.S. and Canadian vessels were not considered to be of major concern and therefore were not sought out.) Flight paths were therefore not set as required by a probability sampling scheme; rather, a searching technique was employed. Flights were first directed to areas of likely fleet concentration. Such areas were determined from seasonal fleet locations observed on overflights in preceding years and the reports of current fleet locations by U.S. fishers. In the event that major fleet concentrations were not encountered at the expected location or on the way to it, the area was searched as extensively as the range of the aircraft would permit.

During late winter and early spring these distant-water fishing fleets were concentrated from off New Jersey southward, so that fishing surveillance operations based in Virginia covered these fishing grounds. In late spring, the fleets moved northward to fishing grounds off New Jersey and New York, and flight paths were directed to those areas. During the summer and fall, surveillance flights originating on Cape Cod, Mass., monitored fishing areas on Georges Bank, Nantucket Shoals, and, to some extent, areas in the Gulf of Maine. The fleets moved southward with winter so that fisheries surveillance again became concentrated in areas off New York and New Jersey.

Upon encountering a cluster of fishing vessels, fisheries surveillance agents recorded the hull identification number, name, and nationality of each vessel. Other information including the fishing gear in use and operational mode (i.e., engaged in fishing operations or in other activities) at the time of sighting was also recorded. Vessels were judged to be fishing if any evidence was apparent that fishing had occurred on that day. Since ICNAF defines a day fished as a day in

which any fishing occurred, an observation of a vessel fishing was logically defined as an observed day fished. Although the majority of vessels sighted were in some phase of fishing operations, some vessels were observed to be in other operational modes such as drifting, steaming, anchored, loading, unloading, or jogging in heavy seas.

These observations therefore allowed certain fishing effort variables to be derived by nationality and gear type. They include: 1) the number of times any vessel was observed on the grounds (i.e., observed days on grounds), 2) the number of times those same vessels were observed fishing (i.e., observed days fished), and 3) the number of vessels.

These overflight data were subject to limitations which were accounted for in the analysis. First, some observed vessel days have probably been incorrectly categorized. Surveillance flights usually occurred before midday; consequently a sighted vessel that did not fish until late in the day was recorded as not fishing. Such an event was therefore interpreted in the analysis as an observed day on grounds but not as an observed day fished as would have actually been the case. This limitation, as will be explained later, has little effect on the estimation of days fished if such inaccuracies are constant in magnitude through time. These data were further limited in that incorrect vessel identifications sometimes occurred. Adverse weather conditions, dense fleet concentrations, hull scripts of poor visibility, and inaccurate interpretations of non-Roman script resulted in the recording of incorrect individual vessel identifications. Lists received from certain countries (Japan, Romania, Spain) made possible the verification of hull scripts observed during 1974. The comparison of these reported hull identifications with those recorded on overflights during 1974 determined that individual vessel identifications recorded two or more times on fisheries surveillance operations were almost always correct; those recorded only once were almost always incorrect. For example, 40 Spanish stern trawlers were in ICNAF Subarea 5 and Subarea 6 (Figure 1) during the first 10 mo of 1974[5]. During that period, 39 separate Spanish stern trawlers were recorded on fisheries surveillance activities more than once. The number of vessels in the area during a time period of interest was therefore established by considering only vessel identifications observed by fisheries surveillance personnel more than once over the period 1965-74.

Knowledge of each country's fishing effort, both total and by types of gear used, and of the total effort expended by all countries, is of prime concern in existing fisheries management regimes. Separate estimates were therefore made for each country and vessel-type, as were estimates of each country's total effort and estimates for each of the total stern trawl and total side trawl fleets.

In addition it was hypothesized that the relation between reported and observed effort for the various gear and nationality components could be different. Stern trawlers are larger and were expected to be of greater visibility than smaller vessels. Also, surveillance searching operations were likely directed towards certain national fleets as a result of their greater size, their presence in an area closed to fishing, or because their catches were of particular immediate concern. If such relationships are different, separate estimates of functions of sighted and reported effort for each fleet component would logically increase estimation accuracy.

Estimator I

The ratio of reported days fished to the average number of sighted days on grounds per flight were easily computed for time periods when reported fishing effort was available:

$$R = f/\bar{g}' \tag{1.1}$$

where $$\bar{g}' = \left(\sum_{i=1}^{A} g_i' \right) \div A,$$

A = the number of flights made during the time period,

g_i' = the number of sighted days on grounds during the ith flight, and

f = the number of days fished during the time period as reported to ICNAF.

This ratio may then be applied to aerial observations in some future time period to estimate days fished before the value is reported:

$$\hat{f} = R \cdot \bar{g}'. \tag{1.2}$$

R is computed from previous data and $\bar{g}'$ is cal-

[5]ICNAF. 1974. Comments of the Spanish delegation on the U.S. memorandum annexed to ICNAF Comm. Doc. 74/41. Special Meeting ICNAF Comm. Doc. 74/44, Ser. No. 3422.

culated from overflight data from the time period for which the estimate is to be made.

Estimator II

Days on grounds reported to ICNAF (g) were correlated with observed days on grounds (g') and fleet size (V) as established from aerial surveillance data to estimate the probability of a day on grounds that was not sighted [$P(G/N)$] for any desired time period (Δt):

$$P(G/N) = (g - g') \div ((V \cdot \Delta t) - g'). \qquad (2.1)$$

(See Appendix for the derivation of this probability and for the resulting estimator for days fished.) In addition, the relation between days fished (f) and days on grounds (g) may also be established from reported effort:

$$K = f \div g. \qquad (2.2)$$

Fishing effort may then be estimated for some future time period from overflight data by assuming the K and $Pr(G/N)$ previously established:

$$\hat{f} = K\,[P(G/N) \cdot (V \cdot \Delta t - g') + g']. \qquad (2.3)$$

Estimator III

The probability of a day fished if not observed [$P(F/N)$] may be computed for any time period (Δt) for which reported days fished (f), the number of vessels present (V, as determined from vessel identification numbers observed on overflights), observed days on grounds (g'), and observed days fished (f') are available:

$$P(F/N) = (f - f')/((V \cdot \Delta t) - g'). \qquad (3.1)$$

(See Appendix for derivation of this probability and of the resulting estimator.) If this computed probability is assumed for some future time period for which reported effort is not available, days fished for that time period may be estimated:

$$\hat{f} = P(F/N) \cdot ((\Delta t \cdot V) - g') + f'. \qquad (3.2)$$

In order to develop this algorithm, it was assumed that a vessel did not fish at all during the day it was sighted if it was observed in the nonfishing mode. Since surveillance flights were usually completed before afternoon, it is possible, as noted earlier, that evidence of fishing was not observable if the vessel did not fish until late in the day so that the above assumption may have been violated in some cases. If this occurred the $P(F/N)$ is incorrectly calculated, a situation having no effect on the estimates of days fished if such inaccuracies are constant from one time period to another. Since vessels are usually engaged in fishing operations whenever sea conditions permit, such inaccuracies can occur only during days when sea conditions disallow fishing during morning hours (when surveillance flights usually occur) and permit fishing later during the day. If the frequency of such weather conditions are assumed to be constant the magnitude of these inaccuracies may also be expected to be unvarying.

RESULTS

Reported effort and aerial observation data from 1969-73 (Table 1) were used in the various equations to compute R(estimator I), $P(G/N)$(estimator II), K(estimator II), and $P(F/N)$(estimator III). The number of surveillance flights (A, Equation 1.1) is required to calculate R. The numbers of flights for 1969-73 were 64, 66, 91, 105, and 109, respectively. The $P(F/N)$ and R were computed for each gear-country category, for each country, and for all stern trawlers and all side trawlers for each year, 1969-73 (Table 2). Since days on grounds were not consistently reported except by the German Democratic Republic (GDR) and in fact were never reported by some countries, K and $P(G/N)$ could not be calculated in many cases.

The variables R, $P(F/N)$, and $P(G/N)$ exhibit no trends of increase or decline through the years examined; however, these values varied, at times substantially, from year to year. Therefore, in order to decrease estimation error, these variables were averaged whenever possible over years preceding the year for which the estimate was made. The average value was then used to make the estimate. These variables for 1969-72 were averaged to make the 1973 estimates; 1969-71 were averaged to make the 1972 estimates; 1969 and 1970 were averaged to make the 1971 estimates; and the 1969 values were used to make the 1970 estimates.

As stated above, days on grounds were infrequently reported so that such sequential averaging of the $P(G/N)$(estimator II) was not possible except in the case of the GDR. The Union of Soviet

TABLE 1.—Reported days fished (f), reported days on grounds (g), observed days fished (f'), observed days on grounds (g'), and fleet size (v), 1969-73.

Country and gear	1969					1970					1971				
	f	g	f'	g'	v	f	g	f'	g'	v	f	g	f'	g'	v
USSR															
Total	35,922	45,391	2,623	2,901	518	23,856	—	2,167	2,478	434	26,673	—	3,049	3,726	511
Side trawl	26,518	32,527	1,987	2,130	401	20,173	—	1,757	1,982	331	17,468	—	1,891	2,356	332
Stern trawl	7,342	9,476	528	610	106	2,972	—	392	452	90	7,880	—	1,095	1,279	172
Purse seine	2,024	3,349	41	82	11	676	—	17	24	13	710	—	17	40	7
Not known	38	39	67	79	—	35	—	1	20	—	615	—	46	51	—
Poland	—	—	—	—	—										
Total	6,880	10,679	448	491	75	9,346	—	646	768	82	10,599	—	966	1,221	98
Side trawl	5,738	9,032	332	366	52	6,339	—	430	507	54	5,852	—	498	619	56
Stern trawl	1,142	1,647	116	125	23	3,007	—	216	261	28	4,747	—	441	558	42
Not known	—	—	—	—	—	—	—	—	—	—	—	—	27	44	—
GDR[1]															
Total	3,750	4,075	249	289	65	2,096	2,723	200	237	48	3,619	4,297	429	511	53
Side trawl	787	848	57	61	22	778	1,022	87	98	21	1,950	2,457	265	304	24
Stern trawl	2,963	3,227	192	228	43	1,318	1,701	113	139	27	1,669	1,840	156	198	29
Not known	—	—	—	—	—	—	—	—	—	—	—	—	8	9	—
FRG[2]															
Stern trawl	1,929	—	127	102	31	2,093	—	166	205	30	1,285	—	75	128	17
Japan															
Stern trawl	1,233	—	37	41	11	1,097	—	89	99	16	1,535	—	70	78	18
Spain															
Total	—	—	—	—	—	—	—	—	—	—	909	—	102	116	24
Stern trawl	—	—	—	—	—	—	—	—	—	—	410	—	17	21	6
Paired trawl	989	1,247	91	91	18	464	—	61	81	29	499	—	85	95	18
Bulgaria															
Stern trawl	145	—	4	6	2	217	—	13	17	4	1,261	—	111	147	13
Romania															
Stern trawl	51	55	2	3	1	195	—	4	11	4	438	—	47	50	8
TOTAL															
Side trawl	33,043	—	2,565	2,557	475	27,290	—	2,274	2,587	406	25,270	—	2,654	3,279	412
Stern trawl	14,805	—	1,014	1,183	217	10,899	—	1,002	1,200	205	19,225	—	2,012	2,459	305

Country and gear	1972					1973				
	f	g	f'	g'	v	f	g	f'	g'	v
USSR										
Total	29,492	39,631	2,264	3,263	498	20,948	29,049	1,147	2,024	392
Side trawl	17,307	22,753	1,214	1,725	278	9,244	13,594	276	601	168
Stern trawl	8,680	10,986	1,016	1,341	197	7,630	10,134	734	1,039	200
Purse seine	2,727	4,629	23	133	23	4,074	5,321	133	344	24
Not known	778	1,263	11	64	—	—	742	4	40	—
Poland										
Total	10,000	—	754	973	104	6,036	—	358	589	84
Side trawl	5,058	—	380	451	58	1,733	—	67	93	23
Stern trawl	4,942	—	371	518	46	4,303	—	283	484	61
Not known	—	—	3	4	—	—	—	8	12	—
GDR[1]										
Total	4,954	5,675	543	656	55	4,220	4,642	285	362	60
Side trawl	1,825	2,361	242	284	23	1,427	1,651	121	151	26
Stern trawl	3,129	3,314	300	360	32	2,793	2,991	164	209	34
Not known	—	—	1	12	—	—	—	0	2	—
FRG[2]										
Stern trawl	1,020	—	99	121	15	859	—	55	68	18
Japan										
Stern trawl	1,787	1,821	64	76	14	2,274	—	112	145	17
Spain										
Total	1,552	1,828	102	114	32	2,405	2,595	201	222	60
Stern trawl	1,017	1,194	27	30	6	2,024	2,106	94	107	25
Paired trawl	535	634	75	84	26	381	489	107	115	35
Bulgaria										
Stern trawl	1,325	—	134	189	14	993	—	43	70	12
Romania										
Stern trawl	305	—	15	22	7	333	389	19	25	7
TOTAL										
Side trawl	24,190	—	1,913	2,543	359	12,450	—	516	913	238
Stern trawl	22,205	—	2,026	2,657	331	21,209	—	1,504	2,147	374

[1]GDR = German Democratic Republic.
[2]FRG = Federal Republic of Germany.

TABLE 2.–Estimation parameters for Equations 1.2, 2.3, and 3.2.

Country		Stern trawl 1969	1970	1971	1972	1973	Side trawl 1969	1970	1971	1972	1973
USSR	*P(F/N)*	0.18	0.08	0.11	0.11	0.10	0.17	0.16	0.13	0.16	0.15
	P(G/N)	0.23			0.14	0.13	0.21			0.21	0.21
	R	770.30	434.00	560.70	679.60	800.50	796.80	671.80	674.70	1,053.50	1,676.50
	K	0.77			0.79	0.75	0.82			0.76	0.68
Poland	*P(F/N)*	0.12	0.28	0.29	0.28	0.18	0.29	0.31	0.27	0.23	0.20
	P(G/N)	0.18					0.47				
	R	584.70	760.40	774.20	1,001.80	969.10	1,003.40	825.20	860.30	1,177.60	2,031.20
	K	0.69					0.64				
GDR[1]	*P(F/N)*	0.18	0.12	0.15	0.25	0.22	0.09	0.09	0.20	0.19	0.14
	P(G/N)	0.20	0.16	0.16	0.26	0.23	0.10	0.12	0.25	0.25	0.16
	R	831.70	625.80	767.10	912.60	1,456.60	825.70	524.00	583.70	674.70	1,030.10
	K	0.92	0.77	0.91	0.94	0.93	0.93	0.76	0.79	0.77	0.86
Spain	*P(F/N)*			0.18	0.46	0.21	[2]0.14	[2]0.04	[2]0.07	[2]0.05	[2]0.07
	P(G/N)				0.54	0.22	[2]0.18			[2]0.06	[2]0.03
	R				1,776.70	2,061.80	[2]781.40	[2]850.70	[2]825.60	[2]668.80	[2]851.10
	K				0.95	0.96	[2]0.79			[2]0.84	[2]0.78
Japan	*P(F/N)*	0.30	0.18	0.23	0.34	0.36					
	P(G/N)				0.35						
	R	1,924.70	731.30	1,790.80	2,468.90	1,709.40					
	K				0.98						
Bulgaria	*P(F/N)*	0.19	0.14	0.25	0.24	0.21					
	R	1,546.70	842.50	780.60	736.10	1,546.20					
FRG[3]	*P(F/N)*	0.16	0.18	0.20	0.17	0.12					
	R	762.10	673.80	913.60	885.10	1,376.90					
Romania	*P(F/N)*	0.14	0.13	0.14	0.11	0.12					
	P(G/N)	0.14									
	R	1,088.00	1,170.00	797.20	1,455.70	1,451.90					
	K	0.93				0.86					
Total	*P(F/N)*	0.18	0.13	0.16	0.17	0.14	0.18	0.17	0.15	0.17	0.14
	R	800.90	598.10	711.50	877.50	1,076.70	827.00	696.20	701.30	998.80	1,486.40

Country		Purse seine 1969	1970	1971	1972	1973	Total of all gears 1969	1970	1971	1972	1973
USSR	*P(F/N)*	0.50	0.14	0.28	0.31	0.47	0.18	0.14	0.13	0.15	0.14
	P(G/N)	0.83			0.54	0.59	0.23			0.20	0.19
	R	1,579.70	1,859.00	1,615.30	1,076.40	2,152.90	792.50	635.40	636.40	949.00	1,128.10
	K	0.60			0.59	0.77	0.79			0.74	0.72
Poland	*P(F/N)*						0.24	0.30	0.28	0.25	0.17
	P(G/N)						0.38				
	R						896.80	803.20	789.90	1,079.10	1,117.00
	K						0.64				
GDR[1]	*P(F/N)*						0.15	0.11	0.17	0.23	0.18
	P(G/N)						0.16	0.14	0.20	0.26	0.20
	R						673.40	583.70	644.50	792.90	1,270.70
	K						0.92	0.77	0.84	0.87	0.91
Spain	*P(F/N)*						0.14	0.04	0.06	0.05	0.02
	P(G/N)						0.18			0.15	0.11
	R						781.40	397.70	713.10	1,429.50	1,180.00
	K						0.79			0.85	0.93
Japan	*P(F/N)*						0.30	0.18	0.23	0.34	0.36
	P(G/N)									0.35	
	R						1,924.70	731.30	179.80	2,468.90	1,709.40
	K									0.98	
Bulgaria	*P(F/N)*						0.19	0.14	0.25	0.24	0.21
	R						1,546.70	842.50	780.60	736.10	1,546.20
FRG[3]	*P(F/N)*						0.16	0.18	0.20	0.17	0.12
	R						762.10	673.80	913.60	885.10	1,376.90
Romania	*P(F/N)*						0.14	0.13	0.14	0.11	0.12
	P(G/N)						0.14				0.14
	R						1,088.00	1,170.00	797.20	1,455.70	1,451.90
	K						0.93				0.86
Total	*P(F/N)*										
	R										

[1]GDR = German Democratic Republic.
[2]Paired trawl.
[3]FRG = Federal Republic of Germany.

Socialist Republics (USSR) reported days on grounds in 1969 and 1972 only, so that estimates for 1970-72 were based on calculations of $P(G/N)$ and K from 1969 data. The 1973 estimate was based on the average of the 1969 and 1972 values. Spanish paired trawl days on grounds were reported in these same years so that calculations via estimator II were achieved in the same way as for the USSR. Spanish stern trawl and Japanese days on grounds were first reported in 1972 so that the 1973 calculation of days fished by estimator II was based on the 1972 data only. Poland and Romania reported days on grounds in 1969 only, so that all calculations by estimator II were based on $P(G/N)$ and K values computed from 1969 data.

Estimates of days fished were then made for each country-gear partition, for each country's total effort, and for all stern trawlers combined and all side trawlers combined (Table 3). Estimator II was not used to estimate effort for Bulgaria, the Federal Republic of Germany (FRG), Japan for 1970 and 1971, and Spanish stern trawlers in 1972 because of the absence of reported days on grounds which is required by the estimator.

A coefficient of estimation error was calculated to establish a measure of estimator performance:

$$\epsilon = (\hat{f} - f)/f. \qquad (4.0)$$

This error coefficient, then, is the difference between the estimated days fished ($\hat{f}$) and the reported days fished (f) expressed as a proportion of the reported value. An error coefficient was computed for each estimate made and these coefficients (Table 4) were then evaluated to establish the results of partitioning, to compare the relative abilities of the three estimators, and to establish estimator dependability.

Inspection of error coefficients indicated that they decreased considerably (especially those of estimators II and III) after 1970, likely as a result of the averaging of estimation parameters. Since the error coefficients then tended to stabilize, only values of ϵ for the 1971-73 period were used to analyze estimator performance.

The frequency distribution of ϵ for estimator II is slightly negatively skewed, a characteristic also exhibited by the distribution of ϵ for estimator III (Figure 2). This indicates a positive bias in both estimators (approximately 10% in each case). Each of these two distributions is also noticeably leptokurtic indicating a marked clustering of error coefficients in the interval ± 0.10. The distribution of ϵ for estimator I appears to be approximately symmetrical and without the pronounced peakedness exhibited by the other two. Statistics were computed from the calculated error coefficients to establish the probability that the ϵ came from normal distributions. (These statistics, a and b_1, and tables of their probabilities are given by Pearson and Hartley 1956:61-62, 183.) In the case of the error coefficients of estimators II and III, the probability that the error coefficients come from normal distributions is extremely remote,

TABLE 3.—Estimated days fished calculated by three different algorithms.

	1970 Estimate			1971 Estimate			1972 Estimate			1973 Estimate		
	I	II	III	I	II	III	I	II	III	I	II	III
USSR	29,754	30,069	30,063	29,234	35,896	30,410	21,384	34,848	29,293	13,988	25,635	22,488
Side trawl	23,928	22,156	21,970	19,010	22,462	21,200	11,737	18,696	16,417	4,406	10,184	9,627
Stern trawl	5,275	6,156	6,188	8,462	12,009	9,041	7,375	13,717	9,712	5,825	11,321	9,312
Purse seine	574	2,367	2,397	756	2,367	827	2,134	4,209	2,561	5,684	3,617	2,754
Poland	10,435	7,565	7,624	11,405	9,162	8,485	7,691	9,620	10,846	4,821	7,671	8,369
Side trawl	7,708	6,047	6,007	6,219	6,303	6,172	3,850	6,986	6,393	825	2,533	2,336
Stern trawl	2,312	1,233	1,452	4,124	2,096	2,230	3,485	2,248	4,155	3,465	2,874	5,595
GDR[1]	2,418	2,786	2,792	3,530	2,608	2,877	3,960	3,312	3,326	2,237	3,894	3,839
Side trawl	1,226	786	7,567	2,254	941	1,037	1,743	1,243	1,278	903	1,432	1,468
Stern trawl	1,752	1,861	1,857	1,585	1,579	1,731	2,542	2,100	1,998	1,504	2,421	2,293
Spain							685		1,161	2,182	3,205	2,362
Paired trawl	912	1,526	1,513	615	994	661	395	1,737	201	635	1,363	1,027
Stern trawl	—	—	—	—	—	—	508		956	2,619	4,718	1,079
Japan	2,887		1,817	1,138		1,617	1,073		1,246	2,300	2,200	1,693
Bulgaria	398		294	1,930		884	1,902		1,098	627		934
FRG[2]	2,367		1,902	1,010		1,111	902		1,065	504		1,211
Romania	181	203	200	620	204	430	213	359	355	259	361	346
Total side trawl	32,418		28,424	27,444		28,500	17,959		23,600	6,750		15,086
Total stern trawl	14,563		14,255	18,903		18,886	17,802		20,541	14,714		23,002

[1]GDR = German Democratic Republic.
[2]FRG = Federal Republic of Germany.

TABLE 4.—Error coefficients of three estimates of days fished.

		1970 Estimator			1971 Estimator			1972 Estimator			1974 Estimator		
Country	Gear type	I	II	III	I	II	III	I	II	III	I	II	III
USSR	All	0.247	0.260	0.260	0.092	0.346	0.140	−0.275	0.182	−0.007	−0.332	0.223	0.074
	Side trawl	.186	.098	.089	.088	.286	.214	−.322	.080	−.051	−.523	.081	.041
	Stern trawl	.775	1.071	1.082	.074	.524	.147	−.150	.580	.119	.237	.484	.220
	Purse seine	−.151	2.502	2.546	.064	2.502	.164	−.217	.544	−.061	.395	.112	.324
Poland	All	.117	−.191	.184	.076	−.136	−.092	−.231	−.038	.085	−.201	.271	.387
	Side trawl	.216	−.046	.052	.063	.077	.026	−.239	.381	.264	−.524	.462	.348
	Stern trawl	−.231	−.107	−.517	−.131	−.558	−.259	−.295	−.545	−.195	−.195	−.332	.300
GDR[1]	All	.154	.329	.332	−.025	−.279	−.205	−.201	−.331	−.329	−.470	−.077	−.090
	Side trawl	.576	.011	.302	.156	−.052	−.468	−.045	−.319	−.300	−.360	.003	.029
	Stern trawl	.314	.412	.342	−.050	−.054	.037	−.187	−.329	−.361	−.462	−.133	−.179
Spain	All	.965	2.289	2.299				−.589		−.252	−.093	.333	−.018
	Side trawl				.233	.993	.327	−.263	.119	−.802	.664	2.578	1.697
	Stern trawl							−.050		.787	.244	1.331	−.467
Japan	All (stern trawl only)	1.632		.656	−.258		.053	−.400		−.303	.011	−.032	−.256
Bulgaria	All (stern trawl only)	.836		.355	.536		.299	.435		−.171	−.368		−.059
FRG[2]	All (stern trawl only)	.131		−.091	−.214		.136	−.115		.045	−.413		.410
Romania	All (stern trawl only)	−.070	.045	.027	.416	.045	−.017	−.306	.179	.166	−.223	.084	.038
All	Side trawl	−.188		.042	−.086		.128	.258		−.024	.458		.211
All	Stern trawl	−.339		.308	.017		−.018	.198		−.075	.306		.085

[1]GDR = German Democratic Republic.
[2]FRG = Federal Republic of Germany.

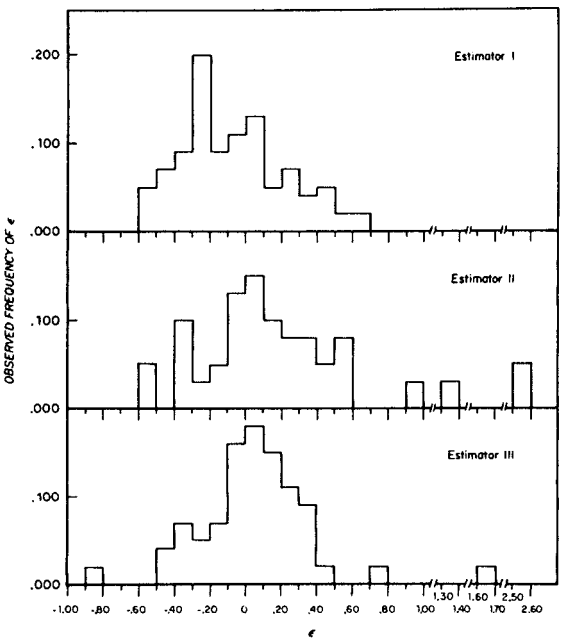

FIGURE 2.—Observed frequency of error coefficients (ϵ) of three estimators of days fished.

less than 0.01. In the case of error coefficients of estimator I, that probability is 0.05.

An analysis of variance for a one-way layout with unequal replication (Steel and Torrie 1960:112-114) was employed to investigate possible differences in the mean values of estimation error in regards to the kinds of category estimated. Here, a separate analysis was carried out for each of the three estimators. All error coefficients for estimates of total days fished by country, all gear types combined, were considered as a single group; error coefficients of estimates of days fished by each gear type (i.e., estimates of days fished by all side trawls and by all stern trawls) as another group; and error coefficients of estimates of days fished for gear-country categories as the final group. F-tests indicated a high probability (>0.25) that errors were the same among these groups in the cases of estimators I and III. Estimation of gear totals (i.e., total stern trawl and total side trawl) was not possible via estimator II because days on grounds were not reported for all countries. The analysis for estimator II therefore included two groups, i.e., gear-country categories and country totals. As before, the likelihood that error rates were the same among these two groups was high (>0.25).

Although application of the F-test requires that normality assumptions be made, the test is robust in regard to violations of these assumptions (Scheffé 1959:361-364) so that limited deviations from normality are likely to be of limited consequence. However, the nonparametric Kruskal-

Wallis one-way analysis of variance (Siegel 1956: 184-194) was also applied and indicated the same general results. The probability of obtaining the calculated test statistic under the hypothesis of no difference among these groups with respect to means is 0.553, 0.410, and 0.872 for estimators I, II, and III, respectively. Both parametric and nonparametric tests, then, indicate that the error rates of each estimator are of the same magnitude regardless of the kind of category estimated.

Analyses for possible differences in error coefficients among estimators were carried out in the same manner. All error coefficients of estimator I were considered as one group, of estimator II as another, and of estimator III as the third group. Both parametric analysis of variance and nonparametric techniques indicated that the different estimators probably produced different error coefficients. The likelihood of obtaining the calculated F statistic under the hypothesis of no difference among the groups is low (0.006). The Kruskal-Wallis analysis technique also indicated a low probability of obtaining the calculated statistic under that hypothesis (0.007).

Cumulative frequency distributions of the ϵ from 1971-73 estimates were used to compare estimator performances and to establish estimator dependability. These frequency distributions were established in the following way. Arbitrary bounds or intervals (μ) were set up so that the first bound included error coefficients from -0.049 to +0.049, the second from -0.099 to +0.099, and so on. The number of error coefficients from Table 4 falling in each interval was counted; these counts were then divided by the total number of coefficients calculated for that estimator to establish the percent of occurrences in each interval. These proportions were then interpreted to be the likelihood of the error coefficient occurring within each bound ($\Phi\mu$, Table 5). Graphs of these probabilities (Figure 3) indicate that estimator III is the most desirable. Its error coefficient is most likely to occur within set error bounds of ±0.50 or less. For error bounds greater than ±0.50, estimator I was superior. Estimator II was always inferior to estimator III, but for very narrow error bounds (±0.20 and less) estimator II was superior to estimator I.

Although estimator II produced the least desirable calculations of days fished, a like algorithm also based upon $P(G/N)$ estimated days on grounds acceptably well:

TABLE 5.—Frequency of error coefficients of estimates of days fished, 1971-73.

Interval of error		Frequency of occurence					
		Estimator I		Estimator II		Estimator III	
From $-\mu$	To $+\mu$	Nos.	Φ	Nos.	Φ	Nos.	Φ
0.049	0.049	4	0.073	4	0.103	10	0.182
.099	.099	14	.255	11	.282	20	.364
.149	.149	16	.291	15	.385	25	.455
.199	.199	21	.382	17	.436	31	.565
.249	.249	31	.564	18	.462	35	.636
.299	.299	36	.655	21	.538	40	.727
.349	.349	40	.727	26	.667	47	.855
.399	.399	43	.782	28	.718	49	.891
.449	.449	47	.855	28	.718	50	.909
.499	.499	50	.909	30	.769	52	.945
.549	.549	53	.964	33	.846	52	.945
.599	.599	54	.982	35	.898	52	.945
.649	.649	54	.982	35	.898	52	.945
.699	.699	55	1.000	35	.898	52	.945
.749	.749			35	.898	52	.945
.799	.799			35	.898	53	.964
.849	.849			35	.898	54	.983
.899	.899			35	.898	54	.983
.949	.949			35	.898	54	.983
.999	.999			36	.923	54	.983
1.049	1.049			37	.949	54	.983
1.699	1.699			37	.949	55	1.000
2.549	2.549			38	.974		
2.599	2.599			39	1.000		

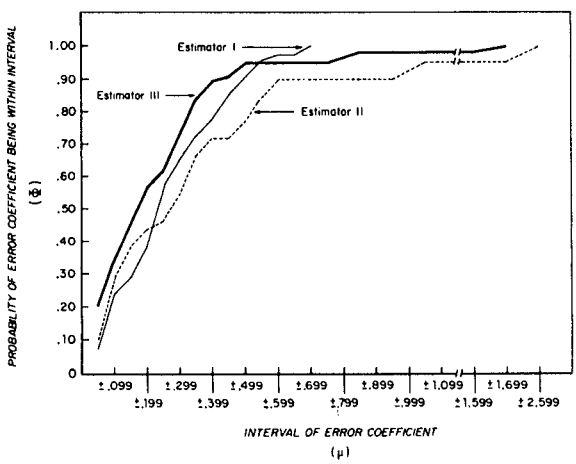

FIGURE 3.—Probabilities of error coefficients occurring within set bounds for three estimators of days fished.

$$\hat{g} = P(G/N)\,(V \cdot \Delta t - g') + g' \qquad (5.1)$$

where $\hat{g}$ is estimated days on grounds and other symbols are as before. Comparisons of calculated days on grounds to reported days on grounds were made when reported values were available (Table 6). These comparisons indicate that the error was less than ±0.50 for 83% of such estimates.

Approximations of estimation dependability may be established from the calculations of

TABLE 6.–Reported and estimated days on grounds and estimation error rates.

		1970		1971		1972		1973	
		Estimate	Error	Estimate	Error	Estimate	Error	Estimate	Error
USSR	Total					43,998	11.0	32,449	11.7
	Side trawl					22,799	0.2	13,400	−1.4
	Stern trawl					17,768	62.5	14,337	41.5
	Purse seine					7,015	51.6	6,130	15.2
GDR	Total	3,028	11.2	3,387	−21.2	3,941	30.6	4,476	−3.6
	Side trawl	845	−17.2	1,238	−49.6	1,573	−33.4	1,859	12.6
	Stern trawl	2,023	18.9	2,051	11.5	2,308	−30.4	2,576	−13.9
Spain	Total							3,426	32.0
	Paired trawl					1,779	180.6	1,181	−43.9
	Stern trawl							6,937	1,318.6

probabilities of error ($\Phi\mu$, Table 5). The probability statement

$$Pr(-\mu < \epsilon < \mu) = \Phi\mu$$

defines these calculated values. Here, ϵ is the error coefficient (Equation 4.0), μ is an arbitrary limit of acceptable error, and $\Phi\mu$ is the likelihood of ϵ being within the interval $-\mu$ to $+\mu$. By substitution (i.e., $\epsilon = (\hat{f}-f)/f$) and reduction of terms:

$$Pr\left(\frac{\hat{f}}{1-\mu} > f > \frac{\hat{f}}{1-\mu}\right) = \Phi\mu.$$

Bounds on points estimates can therefore be calculated:

$$\text{upper limit} = \hat{f}.\ \frac{1}{1-\mu}$$

$$\text{lower limit} = \hat{f}.\ \frac{1}{1+\mu}$$

and values of $\Phi\mu$ from Table 5 can be used to approximate the likelihood that the reported days fished (f) will fall within the interval. For example, if estimator III calculated days fished to be 100, it may be stated that there is a 0.945 probability that the reported value of days fished is within the interval 67 to 200, i.e.,

$$Pr\left(\frac{100}{1-0.499} > f > \frac{100}{1+0.499}\right) = 0.945.$$

It is important to note, however, that the figures in Table 5 were computed directly from the frequency distributions of error rates of estimates made in the past (i.e., 1971-73). Therefore, estimation bounds may be correctly approximated on future point estimates only if it is assumed that future distributions of error coefficients are correctly represented by these past performance data.

DISCUSSION

Of the methods presented, estimator I (based on the ratio between days fished as reported and sighted days-on-grounds) and estimator III (based on the probability of a day fished given that it was not observed) exhibited the least error. Estimator III was consistently most accurate (especially in the last 2 yr) although the difference between the two is small. This estimator may be expected to calculate days fished to within ±0.50 approximately 95% of the time. Estimator I has value in that it does not require sophisticated analysis of overflight data (only the numbers of sightings and numbers of flights are needed) and is less likely than other estimators to produce error coefficients greater than 0.50. It may be expected to produce estimates within ±0.50, 90% of the time.

Estimator II, based on the probability of a day on grounds if it was not sighted, was consistently the poorest of the three. Its poor performance is likely the result of insufficient instances of reported days on grounds. These parameters allow computations of $P(G/N)$ and K, on which the estimate is based. In the case where complete data was available (GDR), effort was estimated very well by estimator II and, in fact, the error coefficient did not exceed 0.42. A similar estimator also based on $P(G/N)$, however, produced acceptable calculations of days on grounds for all countries that were within ±0.50 of the reported value in approximately 80% of all cases.

Estimation error can result from sources which are known to have occurred in the past and are, therefore, of a magnitude predictable by the proposed methods for approximating probability limits on point estimates. The probabilities of fishing ($P(F) = f/(V \cdot \Delta t)$) from data in Table 1 were found to be highly correlated with the $P(F/N)$

(Table 2) as theoretically should occur. Therefore, when countries change fishing patterns from one time period to the next so that $P(F)$ differs, $P(F/N)$ also changes, thus introducing error in the estimates made by estimator III, a condition also true for $P(G)$ and $P(G/N)$ on which estimator II is based. This results from changes in the mean number of days fished (or days on grounds in the case of estimator II) per vessel, a likely occurrence if a particular fleet experiences difficulties in finding fish, if weather conditions are unusually unsuitable for fishing, or if equipment repair or modifications demand excessive lost time in a certain time period.

Although these changes theoretically should not produce changes in the ratio of reported to observed fishing effort (R, estimator I), other factors can conceivably produce such variation of that ratio. Changes in visibility due to weather can likely be an important factor. If fog or other visibility-restricting weather conditions are more prevalent in one time period than another, R may be expected to be larger during that period. Likewise, varying success of overflights in locating fleet concentrations is a factor. Unusually successful searching may be expected to produce ratios smaller than average while low success will tend to increase R.

In addition, changes in the accuracy of reported effort (f and g) will result in corresponding changes in the accuracy of calculations of $P(F/N)$, $P(G/N)$, R, and K for particular time periods. Since reporting accuracy cannot be measured, such deviations have been included in the error coefficients as have the above listed sources of error.

Although a method of calculating probability limits on estimates is presented, the methodology utilizes the observed past performance of each estimator to establish the probability of error. It must be assumed, therefore, that the frequency distribution of estimation error is correctly represented by these past data. Although this assumption can reasonably be made if fisheries surveillance flight patterns and fishing fleet movements are generally constant, caution should be exercised in this regard. If flight patterns or seasonal fleet movements change drastically, the probabilities of not sighting fishing effort (estimators II and III) and the ratio of reported to sighted effort (estimator I) will likewise change so that they are not correctly represented by the range of past values. Aberrant values will result if the fleets are extensively concentrated in different areas than in the past. Fleets will not be located by fisheries surveillance flights as well as in the past and, therefore, effort will not be observed to the same extent as in the past. As a result, values of $P(F/N)$, and R will be much greater than past values. Sizable underestimates of days fished will occur with probabilities greater than those represented by past error frequencies. Conversely, if fleet locations are anticipated by surveillance flight personnel much more accurately than in the past, these estimation constants will be much smaller than represented by past data, so that probabilities of overestimation will be much greater than represented by past performance data.

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LITERATURE CITED

HOEL, P. G.
1962. Introduction to mathematical statistics, 3rd ed. John Wiley and Sons, Inc., N.Y., 427 p.

PEARSON, E. S., AND H. O. HARTLEY (editors).
1956. Biometrika tables for statisticians, Vol. I. Cambridge Univ. Press, Lond., 238 p.

SCHEFFÉ, H.
1959. The analysis of variance. John Wiley and Sons, Inc., N.Y., 477 p.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, N.Y., 312 p.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill, N.Y., 481 p.

APPENDIX

Estimators II and III are based on probabilities of not sighting daily units of fishing effort (i.e., vessel days which were on grounds or on grounds and fishing). These estimates require the calculation of these probabilities during some time period when reported days on grounds and days fished are available which can be correlated with sighted days on grounds, sighted days fished, and fleet size as determined from surveillance overflight data. These estimators were fashioned by considering the possible daily events, constructing the probability space in units of vessel days from reported and observed effort, and then deriving needed probabilities from the constructed space. Let the possible events be symbolized:

G = the daily event of a vessel on the grounds;
F = the daily event of a vessel on the grounds and fishing;
E = the daily event of a vessel not on the grounds, i.e., elsewhere;
S = the daily event of a unit of daily effort observed on overflights; and
N = the daily event of a unit of daily effort not observed on overflights.

Further, by defining the fleet size during some time period Δt, where t is in days, as the number of vessels that were present at some time during that period, the total event space (which is the sum of all possible events) is easily calculated:

$$n = V \cdot \Delta t$$

where n = the total number of all possible daily events,
Δt = the time period in days, and
V = the fleet size.

Even though certain cells in the event space (of little consequence to us) cannot be observed directly, the possible events defined in units of vessel days may be broken down:

Item	*Observed* (S)	*Not seen* (N)	*Total*
On the grounds (G)	g'	$g'' = g - g'$	g
Fishing (F)	f'	$f'' = f - f'$	f
Not fishing	$o' = g' - f''$	$o'' = o - o'$	$o = f - g$
Elsewhere (E)	e' = zero	e''	$e = n - g$
Total	g'	$n - g'$	n

From effort reported to ICNAF and from that observed on overflights, the number of daily events in each cell is easily defined. The number of events of vessel days fished (f) are reported to ICNAF and are either observed on overflights (f') or are not seen on overflights (f''). The number of events of vessel days on grounds (g) may be reported to ICNAF and are either observed on overflights (g') or not observed on overflights (g''). The event of a vessel day on grounds spent not fishing (o) is either observed (o') or not observed (o''). It is important to note that if a vessel day on grounds was fished but was observed on an overflight as not in the fishing mode, which may possibly occur if fishing operations were not initiated until late in the day after the flight occurred, that event would be incorrectly categorized as o' rather than as f'. The effect of this occurrence on estimator III will be discussed; it has no effect on estimator II. If a possible daily event were not on the grounds, then it was elsewhere (e) and was not observed (e''). It was not possible for a vessel day elsewhere to be observed; overflights were directed within the fishing grounds so that e' is zero in all cases. The numbers of daily events, then, are categorized as on the grounds (g) and fishing (f) or not fishing (o), or as elsewhere (e). The numbers of daily events in each category are symbolized by a single prime ($'$) if observed on overflights, as a double prime ($''$) if not observed, and without a symbol if the value is a total number of events.

Estimator II is best explained by considering the probability of a day on grounds:

$$\begin{aligned} {}^{6}P(G) &= P(G,S) + P(G,N) \\ &= P(G,S) + P(G/N) \cdot P(N). \end{aligned}$$

From the above event space, the probabilities of on grounds and observed [$Pr(G,S)$], of on grounds if not observed [$\mathrm{Pr}(G/N)$], and of not observed [$P(N)$], are easily defined:

$$\begin{aligned} P(G,S) &= g' \div n, \\ P(G/N) &= g'' \div (n - g'), \text{ and} \\ P(N) &= (n - g') \div n. \end{aligned}$$

Then by substitution

$$P(G) = (g' \div n) + [(g - g') \div (n - g')] \cdot (n - g') \div n$$

[6]For an explanation of probabilities and the theorems used in the development of these expressions, see Hoel (1962:4-17).

which reduces to

$$P(G) = g \div n;$$

so that the equation may be solved for days on grounds:

$$g = n \cdot P(G).$$

Then by substitution

$$g = n[(g' \div n) + P(G/N) \cdot (n - g') \div n], \text{ or}$$
$$g = g' + P(G/N)\,(n - g').$$

Estimator II is then derived by inclusion of the ratio of days fished to days on grounds, $K = f \div g$, so that the above algorithm may be expressed in terms of days fished:

$$\hat{f} = K\,[g' + P(G/N) \cdot (n - g')].$$

An estimate of days fished ($\hat{f}$) may be made, then, from surveillance overflight data if calculations of R and $P(G/N)$ can be made from past data.

Estimator III is deduced from the event space according to the same rationale. The likelihood of an event of a vessel day fished expressed as observed and not observed is expanded to calculate days fished. From the event space it is apparent that:

$$P(F) = P(F, N) + P(F, S)$$

where $P(F)$ is the probability of a vessel day fished, $P(F, N)$ is the probability of a vessel day fished and not observed on overflights, and $P(F, S)$ is the probability of a vessel day fished and observed on overflights. Further, by application of the multiplication theorem of probabilities

$$P(F, N) = P(F/N) \cdot P(N)$$

where $P(F/N)$ is the probability of a vessel day fished given that it was not observed on overflights, and $P(N)$ is the probability that a possible vessel day (regardless of location or operational mode) was not observed on overflights. The first expression therefore can be written as

$$P(F) = P(F/N) \cdot P(N) + P(F, S).$$

Although all possible probabilities can be expressed in terms of the number of events in each category of the event space, those of interest are:

$$P(F, S) = f'/n,$$
$$P(N) = (n - g')/n, \text{ and}$$
$$P(F/N) = (f - f')/(n - g').$$

By substitution and reduction of terms

$$P(F) = f/n.$$

The number of vessel days fished, then, is the product of the entire event space and the probability of fishing, i.e.,

$$f = n \cdot P(F).$$

Then, by substitution, estimator III easily follows so that days fished are estimable from overflight data if $P(F/N)$ can be predetermined from past data:

$$\hat{f} = f' + P(F/N) \cdot (n - g').$$

From possible algorithms derivable from the event space, this form makes most use of overflight data and is least dependent on functions calculated from past data.

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FOOD AND FEEDING OF LARVAE OF THREE FISHES OCCURRING IN THE CALIFORNIA CURRENT, *SARDINOPS SAGAX*, *ENGRAULIS MORDAX*, AND *TRACHURUS SYMMETRICUS*[1]

DAVID K. ARTHUR[2]

ABSTRACT

The size, number, and types of food particles eaten by larvae of Pacific sardine, *Sardinops sagax*; northern anchovy, *Engraulis mordax*; and jack mackerel, *Trachurus symmetricus*, were determined by an examination of gut contents of larvae captured in plankton samples from the California Current. Food particles found in larvae of the three fishes were predominantly the eggs, nauplii, and the copepodid stages of the smaller species of copepods. These increased in width as the larvae grew though not so uniformly for the anchovy as for sardine and jack mackerel. Particles ingested by anchovies at first feeding were slightly larger than were those ingested by sardines, while jack mackerel could eat particles three times wider than sardines of equal length. The smallest individuals of each species were the most euryphagous, especially anchovies. Feeding incidence of sardine and anchovy declined during the early larval period while that of jack mackerel increased. Sardine and anchovy larvae fed only during the day. The data were not analyzed for day-night feeding for jack mackerel.

The relative body depth and relative weight of laboratory-grown anchovy larvae increased throughout the larval periods examined, whereas, the relative body depth of most ocean-caught anchovy larvae decreased during the first half of this period, possibly as a result of the poorer ration obtainable in the ocean. The decline in relative body depth of ocean-caught anchovy larvae may be related to the decline in feeding incidence and to the apparent lack of increase in size of the food particles ingested.

Owing to the impending collapse of the Pacific sardine, *Sardinops sagax*, fishery, a biological-oceanographic survey program, which later became known as the California Cooperative Oceanic Fisheries Investigation (CalCOFI), was initiated in March 1949. Instrumental in initiating a program to study the food of the sardine larva was the concept developed by Hjort (1914) that the success of a year's spawning may be determined at the critical period when the fragile larvae must secure sufficient food from their environment. For a recent and thorough review of the literature concerning this subject, the reader is directed to May (1974).

To explore the possibilities proposed by Hjort (1914), 10,408 sardine larvae from 398 samples were examined. Food of two potential competitors, namely the northern anchovy (*Engraulis mordax*, 2,350 specimens, 69 samples) and the jack mackerel (*Trachurus symmetricus*, 750 specimens, 65 samples) was also investigated (Arthur 1956). Larvae of these three fishes were supplied to me by Elbert H. Ahlstrom and came from samples taken during early years of the CalCOFI program.

Sardines no longer support a viable fishery, but anchovies have increased in numbers to fill, in part, the ecologic if not economic void. Increasing attention, therefore, will be paid in this paper to this fish and to other species of the genus *Engraulis* which occupy coastal environments of many parts of the world (Reid 1967).

METHODS

Specimens were examined in glycerin because of its advantages over water. Its clearing qualities aid in the detection of food particles within the gut, and the greater viscosity of this medium dampens the movement of particles during dissection. Also, when in glycerin, larvae seem to be more pliable and the intestinal walls do not tend to fragment so readily.

At first the entire intestinal tract of each sardine larva was dissected from the body. This

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procedure proved to be difficult, unnecessary, and, at times, actually misleading. It was unnecessary because no food was ever found in the thin walled anterior intestine which forms about half of the total length of the digestive tract. Also, to view the anterior intestine, the liver which surrounds most of it must be carefully teased away resulting in the production of many fragments which may be confused with possible food particles. Schumann (1965) observed that food particles pass through this portion of the gut in about 25 s in laboratory-reared sardine larvae. The intestines of jack mackerel larvae are not as readily observable as in sardine or anchovy larvae because they are covered by well-developed pelvic fins and because of the earlier development of substantial body walls.

The presence of a single food particle in larval sardines or anchovies can usually be detected by a localized swelling of the surrounding gut wall. When several food particles are present, the posterior intestine may be highly expanded over its entire length. Food particles were dissected out of the gut by means of an instrument consisting of a pig's eyelash, bevelled cut to form a chisel point, and mounted in beeswax in one end of a glass tube. Food particles were identified to taxa as far as their condition allowed.

Each organism found in the intestine was measured as to the maximum cross section that the larva would have to encompass for ingestion. Herring larvae have been shown to ingest crustacean food particles "head on" by Hardy (1924), Bowers and Williamson (1951), and Blaxter (1965). This maximizes the ingestible size of the organism and positions appendages, spines, and setae to the rear of the food organism during its transit through the intestines.

To facilitate a consideration of changes in food with respect to growth, the size ranges of larvae of each of the three species of fishes being considered here have been subdivided into three length groups. The length intervals used in these subdivisions are based on the distribution of sizes in the collections rather than on any definite changes in the larvae with respect to age.

FOOD OF SARDINE LARVAE

Type of Food

The qualitative results of the examination of food material from intestines of larval sardines are presented in Table 1. Length of sardine larvae at the end of the yolk-sac stage is variable. One as small as 3.4 mm contained food, others as long as 5.5 mm still had yolk, but no larva was observed containing both yolk and ingested food organisms. Eggs, nauplii, and juvenile stages of copepods composed almost all of the identifiable food. Copepodid stages in the diet increased in percentage by a factor of 100 through the successive size groups of the larvae. This is undoubtedly due to the severe size restrictions placed on the young larva by the small size of its mouth. As the larva increased in size, its mouth likewise increased in gape, and consequently a larger range of the size spectrum of plankton became available.

TABLE 1.—Food of sardine larvae.

	Size group					
	End of yolk-sac stage to 5.5 mm		6.0 to 9.5 mm		10.0 to 25 mm	
Food items	No.	%	No.	%	No.	%
Copepod eggs	141	22.0	35	10.8	10	28.6
Copepod nauplii:						
Calanoid	40		18		3	
Cyclopoid	68		39		3	
Harpacticoid	62		42		2	
Unidentified	179		149		5	
Total nauplii	349	54.5	248	76.3	13	37.1
Copepodid stages:						
Calanoid			1		7	
Cyclopoid	2		7		3	
Harpacticoid			2		1	
Unidentified			1			
Total copepodids	2	0.3	11	3.4	11	31.4
Dinoflagellates	5	0.8				
Tintinnids	20	3.1				
Foraminifera	3	0.5				
Unidentified crustacean eggs					1	2.9
Unidentifiable material	120	18.8	31	9.5		
Total number of food particles	640		325		35	

Size of Food

Although they are not always of the largest ingestible size, the food particles increased in size isometrically with the increased length of sardine larvae (Figure 1). A larva in doubling its length from 4 to 8 mm likewise doubled its maximum ingestible food size from 80 to 160 μm.

Feeding Incidence

The percentage of fish containing at least one food particle is termed the "feeding incidence" for

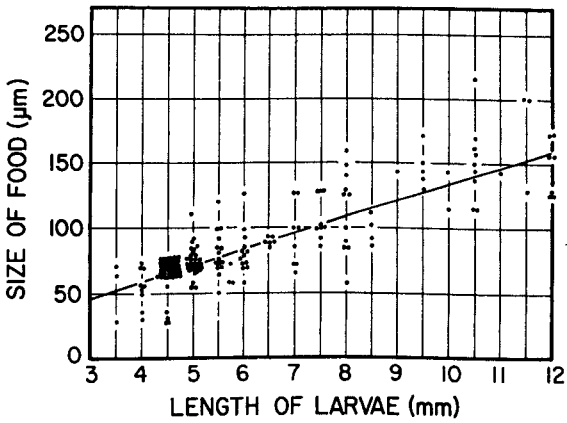

FIGURE 1.–Food size of Pacific sardine larvae. The line is a least squares fit to all data points and is expressed by the equation: $\hat{S} = 13.04L + 5.70$, where $\hat{S}$ is width of food in microns and L is standard length of larvae in millimeters. The correlation coefficient r is 0.813 and the coefficient of determination r^2 implies that 66% of the variation in food size can be explained by larval size alone.

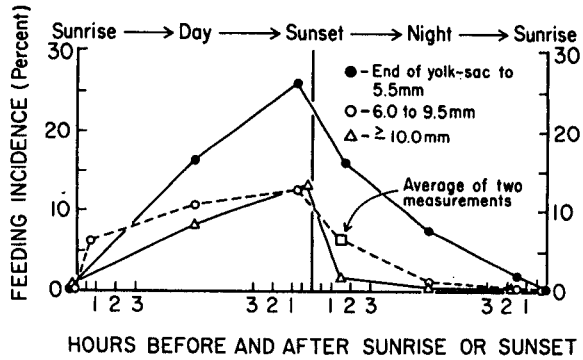

FIGURE 2.–Diurnality of feeding incidence of Pacific sardine larvae. Only those intervals in which at least 50 larvae coming from at least 5 samples are included.

a particular sample and is considered a measure of a larva's ability to obtain food in the environmental circumstances at the time of sampling.

The available data permit an inspection of the average hour-by-hour series of trophic events for sardine larvae (Figure 2). The data were divided into 16 intervals composed of: the first half hour, the second half hour, the second hour, and the third hour both before and after sunrise, and both before and after sunset. There were also midday and midnight intervals which vary in length according to the season. Only those intervals in which at least 50 larvae from at least five samples were included. Feeding incidence of all three size groups increased throughout the day. This could have resulted from accumulation of food in the gut, or perhaps to the success of larvae in finding more suitable feeding conditions as the day progressed. The largest size group demonstrated the fastest return to a low feeding incidence at night which probably reflects faster digestive rates for older larvae, as has been shown for plaice larvae (Yasunaga 1971). The lower feeding incidence of older larvae may, therefore, be partly due to an increased digestive rate.

Figure 2 illustrates the diurnal nature of feeding which is due to the visual feeding sardine larva requiring light to detect its prey. (Schumann 1965). This results in diurnal changes of the intestine. The posterior intestine of larvae captured during the early morning is visibly striated. In late afternoon and early evening, the posterior intestines of many larvae, especially the smaller ones, are expanded and have no visible striations. The intestinal wall contains large vacuoles of clear fluids. During this period of the day, it is common to capture larvae with greatly expanded intestines but with no identifiable food organisms. Often such larvae contain some granular material floating about in the intestinal lumen which is comparatively large due to the expansion of the surrounding wall. During the night, intestinal expansions disappear and by sunrise almost all of the larvae have returned to the compact, striated intestinal condition. This rhythm is most pronounced in the smallest size group where, as indicated in Figure 2, the amplitude of the diurnal feeding incidence is at a maximum.

FOOD OF ANCHOVY LARVAE

Type of Food

No larva was found containing both yolk and ingested food. The diet of anchovy larvae (Table 2) is very similar to that of the sardine. The most striking difference is that very young anchovies are more euryphagous. About 40% of their diet (by numbers) consists of noncrustacean food particles. A food category entitled "unidentified spheres" is represented by small (about 20 μm) objects, probably of plant origin. Copepod nauplii become increasingly important as anchovy larvae increase in length and compose the bulk of particulate food when all sizes of larvae are considered.

Copepod eggs and nauplii were found to be the most important element in the diet of larvae of

TABLE 2.–Food of northern anchovy larvae.

	Size group					
	End of yolk-sac stage to 4.5 mm		5.0 to 6.5 mm		7.0 to 9.0 mm	
Food items	No.	%	No.	%	No.	%
Copepod eggs	15	15.3	4	14.3		
Copepod nauplii:						
Calanoid	10		6		3	
Cyclopoid	13		11		6	
Harpacticoid	4		1		1	
Unrecognizable	15		1			
Total nauplii	42	42.9	19	67.9	10	90.9
Copepod adults:						
Calanoid					1	9.1
Clam larvae	2	2.0				
Foraminifera	2	2.0				
Tintinnids	3	3.1				
Dinoflagellates	7	7.1	1	3.6		
Ciliates	2	2.0	2	7.1		
Coccolithophores	4	4.1				
Unidentified spheres	21	21.4	2	7.1		
TOTAL	98		28		11	

Engraulis mordax (Berner 1959), of *E. anchoita* (Ciechomski 1967), and *E. ringens* (Rojas de Mendiola 1974). Berner and Rojas de Mendiola found considerably more eggs than nauplii while Ciechomski reported about equal numbers.

An unusual example of feeding by both anchovy and sardine larvae was called to my attention by Elbert H. Ahlstrom because of the obvious gorged intestines of some of the larvae. This sample was taken about 38 km off the coast of central Baja California approximately 6 h after sunset and 1½ h after setting of a "first quarter" moon. Unusual aspects of the sample were that most of the larger larvae of the two species contained food at night and that they were literally crammed with the pteropod *Limacina bulminoides*. Of the larvae over 10 mm in length, the 26 feeding sardines averaged 24 pteropods per gut with a maximum of 54 in one 23-mm larva, and the 19 feeding anchovies averaged 18 per gut with a maximum of 26 in a 14-mm individual. Compared to the one or two food particles usually found in a feeding anchovy or sardine larva, the number of pteropods was surprising. The only other molluscs found in either sardine or anchovy larvae in this investigation were two bivalve larvae, one each in two very young anchovies. No molluscs were reported in the extensive investigations of the food of anchovy larvae by Berner (1959), Ciechomski (1967), or Rojas de Mendiola (1974). It cannot be determined whether the larvae found filled with *Limacina* reflected beneficial feeding conditions where they were found, or a hazardous situation in which the larvae had ingested material they could not digest and void.

Because the number of pteropods found in this one sample is larger than the total number of food particles found in the larger sardine and anchovy larvae of all other samples examined, they were not included in the overall tabulations for these fish. The size of the pteropods was used to establish the upper ingestible size of food particles for older anchovies (Figure 3a).

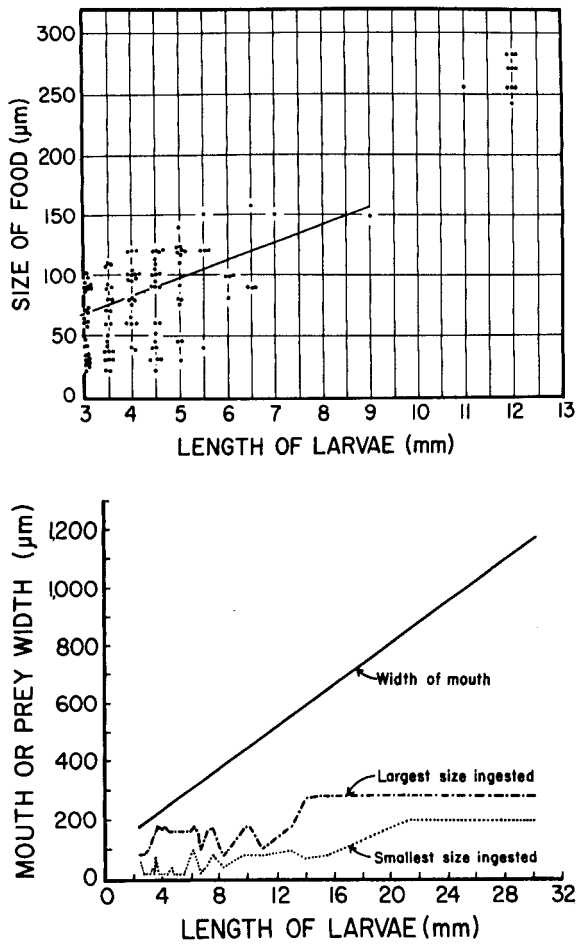

FIGURE 3.–(a) Food size of northern anchovy larvae. The line is a least square fit to all data points from 3 to 9 mm inclusive and is expressed by the equation: $\hat{S} = 16.16L$, where $\hat{S}$ is width of food in microns and L is standard length of larvae in millimeters. The correlation coefficient r is 0.473 and the coefficient of the determination r^2 implies that 22% of the variation in food size can be explained by larval size alone. (b) Food size of anchoveta (*Engraulis ringens*) larvae. Adapted from Rojas de Mendiola (1974).

Size of Food

Food particles of young anchovy larvae are not selected from those near the largest ingestible size as are those of young sardine larvae, though there is a trend to increase particle size as larvae increase in length. The correlation coefficients (Figures 1, 3a) suggest that food size of sardines is more controlled by larval size (0.813^2 or 66% of variance explained) than of anchovies (0.473^2 or 22% of variance explained). The extensive data, including many older larvae, reported by Ciechomski (1967) and Rojas de Mendolia (1974) indicate a sharp increase in food size between the larval lengths of about 3 to 4 mm but relatively little increase for most of the remainder of the larval period. Rojas de Mendiola's data (Figure 3b), including food sizes of 2,088 feeding larvae 3.1 to 5.0 mm in length, are used to illustrate this important point. These data indicate that food size roughly doubles (from approximately 100 to 200 μm) while larvae grew from 4 to 16 mm. Assuming that both larvae and food particles increased in size isometrically, then their volumes increased by the cube of their increase in length or width. Food particles in doubling in width increased 8 times in volume, while larvae increasing 4 times in length increased 64 times in volume. Therefore, the nutritional equivalent of a 200-μm food particle to a 16-mm larva is only one-eight of that of a 100-μm particle to a 4-mm larva. Although Berner (1959) measured the length rather than the width of food particles and his data are not directly comparable, they do indicate that while anchovy larvae increased in length from 3 to 10 mm (an increase of 37 times in volume) their average food size increased from 68 to 128 μm (an increase of only 6⅔ times in volume).

Feeding Incidence

Anchovy larvae also are daytime feeders (Figure 4). The disparity between night and day values for feeding incidence is greater for anchovies than for sardines during their youngest larval stages. This difference perhaps is due to a faster digestive rate for the anchovy.

FOOD OF JACK MACKERAL LARVAE

Type of Food

The jack mackerel larva first starts to feed when

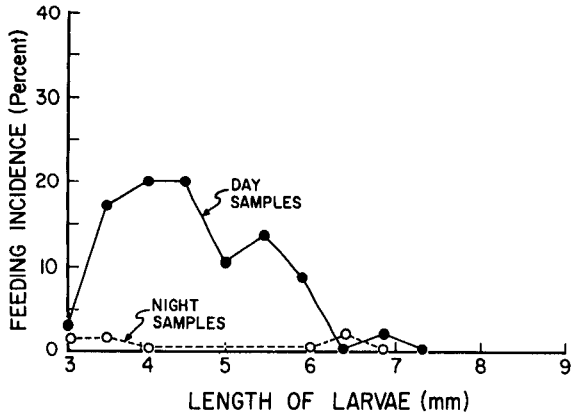

FIGURE 4.—Diurnality of feeding incidence of northern anchovy larvae.

it is about 3.25 mm long. By the end of the yolk-sac stage, the jack mackerel has attained a robustness which contrasts sharply with the slender early larval sardine or anchovy. Its body shape, in general, is more substantial and its mouth is proportionately larger. No jack mackerel larva was found with both yolk and ingested food organisms.

Just as for sardine and anchovy larvae, copepods contributed the greatest bulk of its food (Table 3). Eggs and naupliar stages, however, are much less important. The "egg sacs," appearing under the title of copepod eggs, were probably ingested attached to adult copepods and so represented a coincidental fraction of the food. Copepod nauplii seemed to be significant in numbers only in larvae of the smallest size group.

Copepodid stages of copepods make up the bulk of particulate food, increasingly so as the larva grows older. By the time the larva is 7.0 mm long, 96.0% (by number) of its food is composed of various species of copepods. The most significant feature of the diet is the very high percentage of occurrence of *Microsetella norvegica*, one of the few planktonic species of harpacticoid copepods. This probably represents a definite selection, as this species of copepod, though ubiquitous, never achieved numerical importance in our plankton hauls. Jack mackerel (*Trachurus trachurus*) larvae were reported by Sinyukova (1964) to have an "inborn ability" to select two species of copepods from the mass of plankton living in the Black Sea. On the other hand, the respective behavior of the early jack mackerel larvae and *M. norvegica* may cause the two species to be locally aggregated,

TABLE 3.–Food of jack mackerel larvae.

Food items	Size group: End of yolk-sac stage to 4.5 mm		5.0 to 6.5 mm		7.0 to 10.5 mm	
	No.	%	No.	%	No.	%
Copepod eggs:						
Single eggs	5	4.3	9	4.4		
Egg sacs	1	0.9	4	2.0	1	0.6
Copepod nauplii:						
Calanoid	3		3			
Cyclopoid	5		2		1	
Harpacticoid	7		2			
Total nauplii	15	12.8	7	3.4	1	0.6
Copepod adults:						
Calanoid:						
Calanoid spp.	7		15		60	
Metridia sp.	1					
Candacia sp.					1	
Cyclopoid:						
Oithona sp.	1				3	
Corycaeus sp.	3		3		5	
Oncaea sp.	6		29		39	
Harpacticoid:						
Microsetella norvegica	46		130		56	
Microsetella rosea	1					
Clytemnestra rostrata					1	
Unidentified					4	
Total copepods	65	55.6	117	86.3	169	96.0
Euphausiid:						
Nauplii	1	0.9			2	1.1
Calyptopi			2	1.0	1	0.6
Cladocera			1	0.5		
Unrecognizable crustacean remains	10	8.5				
Peteropods	3	2.6	4	2.0	2	1.1
Tintinnids	16	13.7	1	0.5		
Foraminifera	1	0.9				
Total number of food particles	117		205		176	

perhaps at the surface, thereby allowing the larva a disproportionate chance of securing individuals of this copepod.

Jack mackerel larvae may perceive food organisms by their color, since *M. norvegica*, and species belonging to the genera *Corycaeus* and *Oncaea*, are among the most brightly colored or least transparent of copepods. Species of the two latter genera also enter into the diet of jack mackerel larvae. Calanoid copepods become more important in the diet of larger larvae, perhaps because of an increased visual acuity, or their larger mouths, or a change in their vertical distribution. Whereas each feeding sardine or anchovy larva normally contains only one or two food particles, feeding jack mackerel larvae usually contain more. Some intestines contained *M. norvegica* in numbers as high as a dozen with no other observable food items.

Size of Food

The relatively large mouth of jack mackerel larvae is reflected in the larger food particles ingested (Figure 5). The preponderance in numbers of particles at a size of 120 μm (greatest cross-sectional dimension) is due to the apparent selection of *M. norvegica*. The gape of the larva apparently increases isometrically with increasing length of the larva. At 3.5 mm long, it can ingest particles up to 225 μm in cross section. Doubling its length to 7.0 mm also doubles its ingesting capacity to particles of about 435 μm in cross section.

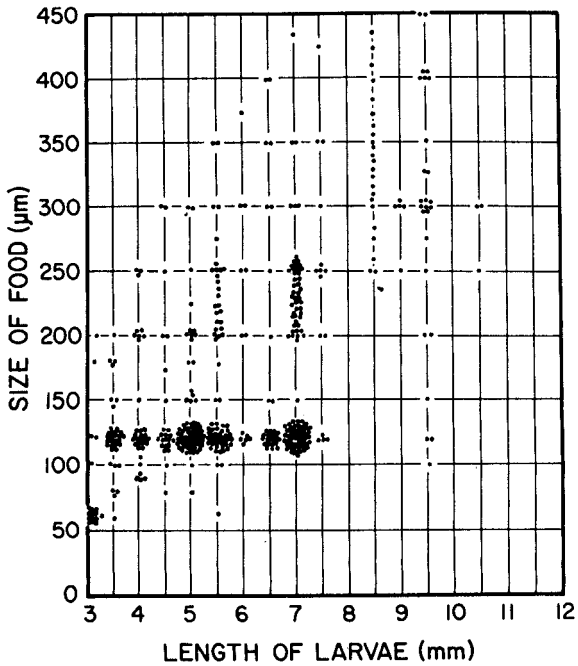

FIGURE 5.–Food size of jack mackerel larvae.

COMPARISONS

Type of Food

The three species may be characterized as primarily crustacean feeders as larvae (Table 4) and the youngest larvae are the most euryphagous. Crustacean food is predominant in all size groups of the larvae of all three species and, furthermore, becomes increasingly so as the larvae increase in size. Only in the smallest anchovies is noncrustacean food an important part of the diet.

TABLE 4.–Crustaceans as percentage of total number of identifiable food particles. Size groups of larvae–small = end of yolk-sac stage to 4.5 mm, middle = 5.0 to 6.5 mm, and large = 7.0 to 9.0 mm.

Species	Size group of larvae		
	Small (%)	Middle (%)	Large (%)
Sardine	96	100	100
Anchovy	58	82	100
Jack mackerel	83	98	99

Size of Food

Figure 6 compares the size ranges of food particles ingested by the three larvae. Because of their larger mouth, jack mackerel larvae can ingest particles about 3 times larger in diameter than can sardine larvae of the same length. This represents a difference in bulk of about 27 times between maximal ingestible sizes for the two larvae. The small anchovy can ingest particles about 40 to 50 μm larger than the maximum-sized particles of the sardine but does not appear to feed as frequently on organisms near to the maximum ingestible size as the sardine does.

Feeding Incidence and Its Relation to Type of Intestine

Feeding incidence increases with length in the jack mackerel but decreases with length in the anchovy and sardine (Figure 7). The high percentage of jack mackerel larvae containing food may indicate that either they are more voracious feeders, or their digestive rate is slower, or perhaps they are less apt to void their guts while being caught and preserved. Feeding incidence of larval fish appears to be associated with the morphology of the gut. The intestine of the sardine and anchovy remains long and straight with little observable differentiation until the larva is about 20 to 25 mm long. On the other hand, when the jack mackerel has attained a length of about 4.25 mm, a portion of its gut forms a loop. This loop divides the larval gut into definite functional parts. Based on a long-range study of feeding habits of fish in the Black Sea, Duka (1967) classified the larval gut into three types: long straight, short straight, and looped. Duka noted also that larvae with looped guts usually contained much more food than larvae with straight guts. Ciechomski and Weiss (1974) noted that the feeding incidence of *E. anchoita* larvae (0-28.0%) was much lower than of hake larvae (63.3-94.5%) taken in the same plankton samples and that intestines of hake larvae are not straight but have several folds.

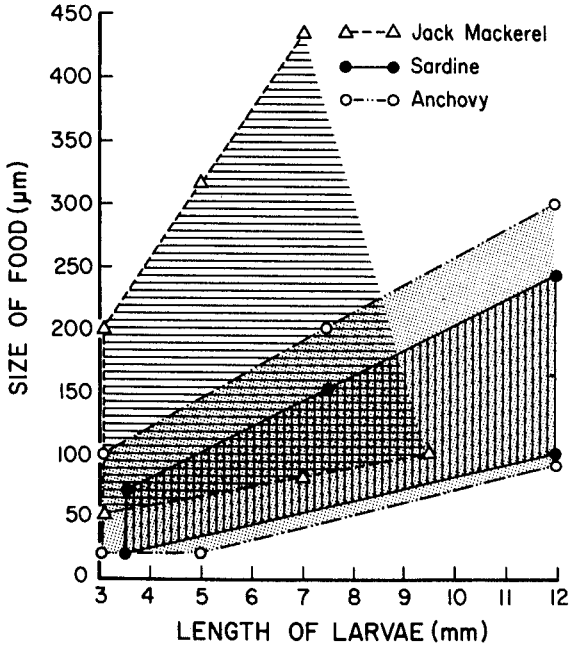

FIGURE 6.–Size range of food particles ingested by larvae of Pacific sardine, northern anchovy, and jack mackerel.

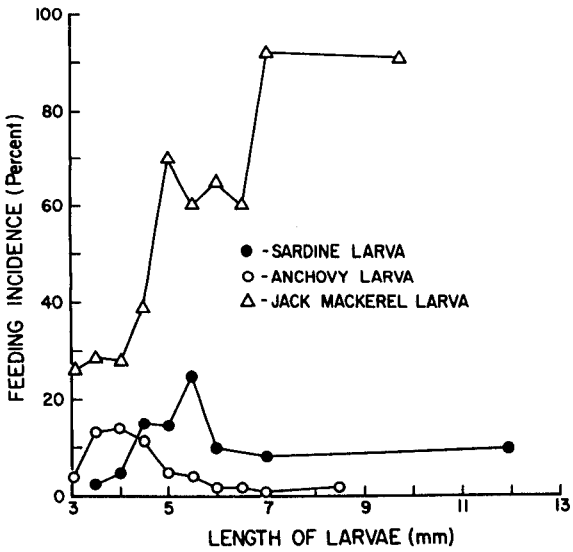

FIGURE 7.–Comparison of feeding incidence of Pacific sardine, northern anchovy, and jack mackerel larvae. Values for sardine and anchovy larvae are averages of day and night feeding incidences. Values for jack mackerel larvae are for all samples combined.

DISCUSSION

Significance of Feeding Incidence

For the past half century, there has been a discussion in progress concerning the significance of feeding incidence. Lebour (1921) called attention to the low feeding incidence of young clupeoids and attributed this to rapid digestion of food in the larval intestine. She was soon challenged by Hardy (1924) who, after observing herring larvae defecating after capture, assumed the low value to be an artifact produced by most larvae voiding their guts. The subject has attracted increasing interest recently. June and Carlson (1971) and Kjelson et al. (1975) observed older larvae of the menhaden, *Brevoortia tyrannus*, defecating after rough handling and fixation. Anchovy larvae have been observed defecating rotifers and *Gymnodinium* while being handled in the laboratory (John Hunter pers. commun.). *Gymnodinium* is eaten by *E. mordax* larvae in the laboratory (Lasker et al. 1970) and probably so in the ocean (Lasker 1975). Rotifers and the veligers of various species of molluscs in combination with *Gymnodinium* sustain anchovy larvae in the laboratory up to about 25 days of age (Lasker et al. 1970; Theilacker and McMaster 1971). Blaxter (1965), however, in attempts to assess the effect of Formalin [3] on food retention of herring larvae was able to demonstrate that only 10% of the larvae empty their guts due to Formalin fixation. Detwyler and Houde (1970) studying laboratory-grown larvae of scaled sardine *Harengula pensacolae*, and bay anchovy, *Anchoa, mitchilli*, found almost all of even the first feeding stages contained food after samples of them were taken from the plankton rich rearing tank and preserved in 5% Formalin. Feeding incidence of clupeoid larvae captured in plankton nets has been positively correlated with the availability of food by Pavlovskaia (1958), Nakai et al. (1966), Burdick (1969), Nakai et al. (1969), Bainbridge and Forsyth (1971), and Schnack (1974). Blaxter (1965) cited the wide variation and observed feeding incidence in the literature concerning herring larvae. I believe that much of the confusion has resulted from many authors failing to consider the time of day when larvae were caught (Figure 2) or the age of the larvae (Figure 4). When these variables are taken into account, a series of observations of feeding incidence can reveal valuable insights into the tropho-dynamics of larvae. Feeding incidence must be viewed only as an indicator of feeding success because of the errors likely to be produced by defecation or to the difficulty in detecting soft bodied items such as *Gymnodinium*.

Comparison of the feeding incidence in four species of *Engraulis* (Figure 8) shows an increase in feeding incidence over larval lengths of 3 to 4 mm. Following this relatively high incidence at 4 mm, there is a drastic drop in this value until lengths of about 7 or 8 mm are reached. The mean feeding incidences for the four curves in this length range are 7 times higher for the 4-mm than for the 8-mm larvae. Feeding incidence remains low but relatively constant over the length range from 8 mm to about 14 mm at which point it begins to increase steadily over the remainder of the larval period. The value for the 20-mm length of *E. ringens* is based on only 12 specimens and, therefore, is not as reliable as values for other lengths.

The available data for sardine larvae suggest the same U-shaped curve. When the values for the sardine (Figure 7) are compared to Figure 8 it is seen that feeding incidence in relation to size falls roughly between *E. ringens* and *E. anchoita*, except that the decrease at intermediate sizes is not as precipitous. Yamashita (1955) reported the following feeding incidence values for larval *Sardinops melanosticta*: for about 14 mm = 8%, 21 to 30 mm = 56%, and 31 to 40 mm = 81% . The upward trend of these data is similar to those of larger anchovy larvae; however, the values are not comparable because the time of day of sampling was not reported. It seems significant that the shape of the curves of the four anchovy species (Figure 8) are so uniform in their relation to each other. *Engraulis ringens* is considerably higher than all others (except for the value at 20 mm). This probably is related to the rich plankton conditions of its habitat.

Clupeoid larvae visually detect prey, approach it, and then strike from a characteristic S-shaped posture. Proficiency of capture increases with age as observed in the laboratory for the larvae of herring and pilchard (Blaxter and Staines 1971), sardine (Schumann 1965), and anchovy (Hunter 1972). These investigators also noted that the volume of water searched increases with larval age. Feeding incidence should, therefore, increase markedly with age. Why, then, does the observed feeding incidence drop so drastically for anchovy

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

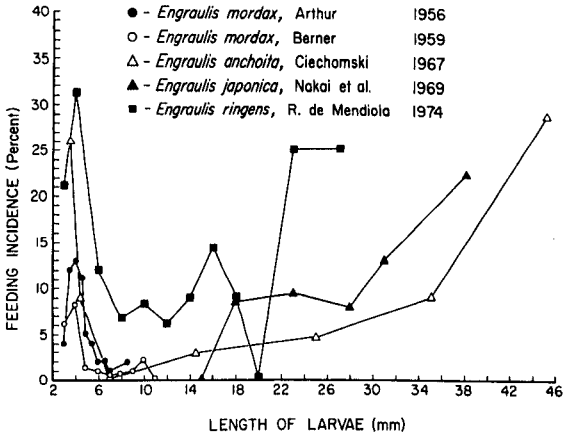

FIGURE 8.—Feeding incidence of larvae of various species of anchovy. Values are the average of day and night feeding (day values are divided by two because young anchovy larvae do not feed at night). Berner's data were recalculated to read "feeding incidence per length of larva" rather than "percent of feeding larvae occurring per length."

living in their natural environment? This could be partly a result of a faster digestive rate of older larvae as indicated for sardine larvae (Figure 2). It also could result if either the ambient food density decreases with time or the larval feeding activity decreases with age. There are reasons to suspect that both of these might occur and at the same time.

Decrease in Food Density

Sardine and anchovy larvae may initiate their first feeding in higher concentrations of food than they will experience several days later. Hand and Berner (1959) found that 74% of the food of adult sardines, when filter feeding at night, were small species of copepods, presumably the same species that produce the small nauplii so important in the diet of the sardine and anchovy larvae. Furthermore, they found that organisms in stomach contents had a high correlation with organisms in plankton samples taken at the same time and place. The adult anchovy, when feeding at night, is probably also a filter-feeding zooplanktivore although it does have more omnivorous tendencies (Loukashkin 1970), and the type of feeding, either biting or filtering, is controlled by the size of the food particles available (Leong and O'Connell 1969; O'Connell 1972). Both species also are selective feeders on larger organisms when visual conditions permit. As a consequence, filter-feeding adults by actively searching for rich feeding conditions for themselves also prospect areas suitable for their larvae. More sardine and anchovy larvae were shown to occur in samples where both species were collected than in hauls where they occurred alone (Ahlstrom 1967); he concluded that these samples were collected near centers of heavier spawning for both species. It would appear that spawning adults of the two species were seeking out the same conditions. Sardines (Ahlstrom 1954), northern anchovies (Bolin 1936), and Argentine and other anchovies (Ciechomski 1965) spawn at night. Both spawning and filter feeding take place at night; therefore, the eggs may be laid near concentrations of suitably sized copepods (assuming spawning and feeding occur on the same night). However, as soon as the eggs have been spawned, they begin to be dispersed by water movement from each other and from organisms they will need for food several days hence. Sardine eggs are spawned in dense patches according to Smith (1973), who calculated that the horizontal mean distance between nearest neighbor eggs is of the order of 1 to 2 cm at spawning and changes to 15- to 20-cm mean distance for several-day-old larvae. These larvae may experience a diminution of their early feeding conditions as a result of diffusion as well as of grazing by the various predators. These ideas are presented to suggest how a general dilution of the co-occurrence of egg and plankton patches could occur in time. Lasker (1975) has recorded how rich larval feeding conditions can be destroyed overnight by a single storm.

Condition of Ocean-Caught and Laboratory-Grown Anchovy Larvae

There are differences in physical condition of the average ocean-caught and laboratory-grown anchovy larvae. These differences are probably a result of the available food.

Ahlstrom et al.[4] have presented a series of measurements of anchovy larvae and juveniles taken randomly from samples of the CalCOFI program. Figure 9 is a scatter diagram of relative body depths (body depth measured just anterior to pectoral fin base ÷ standard length) calculated from the above date. This diagram demonstrates that relative body depths of ocean-caught anchovy

[4]Ahlstrom, E. H., D. Kramer and R. C. Counts. Egg and larval development of the northern anchovy, *Engraulis mordax*. Unpubl. manusc.

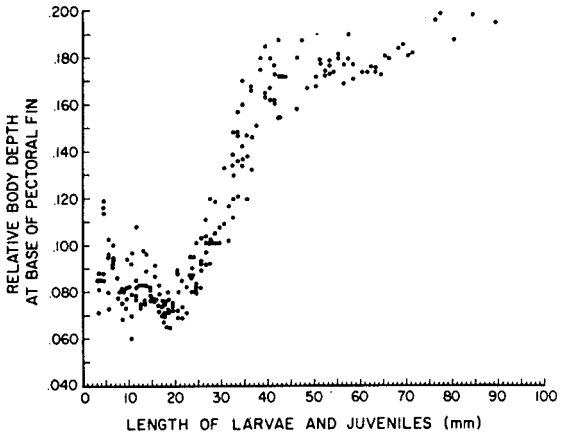

FIGURE 9.–Relative body depth of ocean caught northern anchovy larvae and juveniles calculated from Ahlstrom et al. (see text footnote 4).

larvae generally decrease until they are 17 to 18 mm long. Figure 10 compares relative body depth, averaged per millimeter of length, of the above ocean-caught anchovy larvae to that of larvae grown in the laboratory. These are larvae grown by Kramer and Zweifel (1970, experiment 17-II) at 17°C on a diet of wild plankton and with a feeding incidence described as "high." At the 10-mm length the two curves are different at the 0.05 significance level (*t*-test) and they differ with greater significance at increasing lengths.

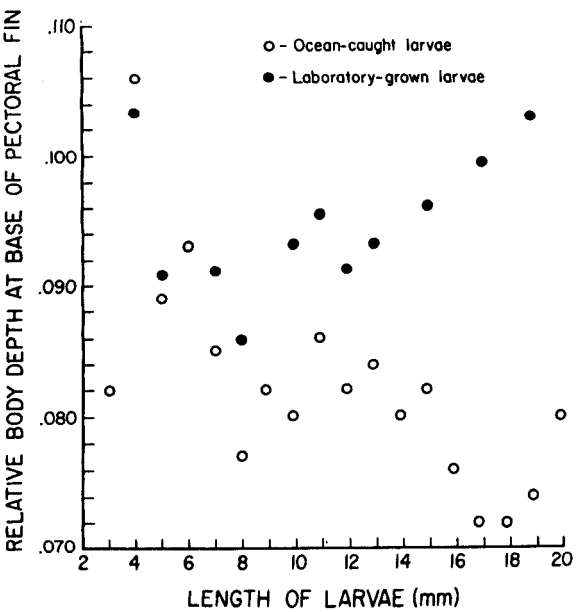

FIGURE 10.–Comparison of relative body depth of ocean caught and laboratory grown northern anchovy larvae. Each point represents an average of at least four larvae.

Condition factor (weight ÷ length^3) for laboratory-grown anchovies increases throughout the larval period as calculated from weight-length relationships presented by Lasker et al. (1970) and Hunter (1976).

Condition factor for ocean-caught *E. anchoita* larvae as calculated from wet weight data recorded by Ciechomski (1965) is at its lowest value between 15 and 20 mm.

The available data, therefore, indicate that relative body depths and weights of well-fed laboratory-grown anchovy larvae increase allometrically throughout the larval period, whereas these values for average ocean-caught larvae are at a low value at some midlarval period, followed by an increase through metamorphosis. This increase is probably related to the start of transformation to the juvenile stage but may also be accelerated by improving nutrition.

A relationship between gut thickness and feeding conditions was reported for ocean-caught larval sardine *Sardinops melanosticta* (Nakai 1960, 1962). The relationship of body depth to the nutritional level of fish larvae has been recorded for *E. japonicus* (Honjo et al. 1959; Nakai et al. 1969) together with relative body weight for herring larvae (Blaxter 1965, 1971). Blaxter attributed the low value of body weight for ocean-caught herring larvae to scarce plankton and to few feeding hours in the Clyde area at the time of sampling. The 14- to 15-mm long laboratory-grown herring larvae when deprived of food died at relative body weights that were higher than those of living ocean-caught individuals. This may be a result of the ocean-caught larvae having survived on suboptimal rations most of their existence whereas the laboratory-grown larvae had ample rations until the time they were suddenly deprived of food. The observed decrease in condition with size might also be an index of the increasing ability to resist starvation. The rich feeding conditions of successful laboratory-rearing experiments probably seldom obtain in the ocean (Lasker 1975; Hunter in press), and this may be reflected in the condition of the average ocean-caught larva.

The sardine larva initiates its first feeding activities in a nutritional deficit (Lasker 1962). This may also be indicated by the increasing thinness of the average ocean-caught *E. mordax*

larva until about midway through its larval existence. Further research is required to determine if the decline in relative physical condition indicates a state of serious malnutrition and, if so, how far from the well-fed state can the condition of the individual vary without resulting in mortality. It is also possible that laboratory-reared larvae have abnormally large relative body depths.

Food Size, Feeding Incidence, and Condition of Anchovy Larvae

The foregoing discussion points to three significant trophic features of the average ocean-caught anchovy larva. These features are:

1. A lack of increase in food particle size proportional to the increase in length for larvae larger than 4 mm (Figure 3b).
2. A steep decline in feeding incidence beginning at 4.5 mm followed by an increase in this value during the second half of the larval period (Figure 8).
3. A decline in relative morphological condition at lengths from at least 10 mm to 17 or 18 mm, followed by an abrupt increase (Figure 9).

Feature 1 must partly reflect the size spectrum of the available plankton. Arthur (1956) and Beers and Stewart (1970) have shown that there are far more food particles of the size taken by the first feeding larvae (50-100 μm) than there are of larger particles suitable for older larvae (i.e., 200 μm). Sardine and jack mackerel larvae, however, are able to secure increasingly larger food particles (Figures 1, 5). When features 1 and 2 are considered together, it would appear that the average oceanic anchovy larva does not sustain its original feeding intensity.

Growth of laboratory-grown anchovy larvae becomes asymptotic at 6 mm long when fed only *Gymnodinium* and at 20 mm when fed only a combination of *Gymnodinium* and rotifers. This was noted by Hunter (in press), who concluded that it is physically impossible for larvae to ingest enough prey in order to grow when the prey are below a certain size. Therefore, the decrease in relative body depth of the ocean-caught anchovy larva (feature 3) could be directly related to the insufficient increase in food particle size (feature 1).

Feeding intensity of clupeoid larvae decreases with malnutrition (Blaxter and Ehrlich 1974; Hunter in press). If the decline in relative body depth does denote a condition of malnutrition, then the decrease in feeding incidence (feature 2) is correlated with this decline, and might be the causative factor. This might also result in larvae spending a longer residence time at these lengths which would introduce a bias in mortality estimates.

It is important to keep in mind that we are considering larvae which have grown in the ocean and have also been caught by plankton nets. This is the reason that the expression "ocean-caught" rather than "ocean-grown" has been used herein. It might be reasoned that the decline in physical condition is a sampling artifact produced by the plankton net catching an increasing percentage of sick or malnourished specimens of the larger larvae as a result of the larger healthy larvae being more capable of dodging the net. The same reasoning could be applied to the decline in feeding incidence. An examination of the physical condition of over 5,000 sardine larvae (Arthur 1956) revealed that there is a higher percentage of larvae in poor shape (e.g., with liver deterioration) taken in day hauls when healthy larvae can avoid the plankton net. Such evidence led Isaacs (1964) to theorize that day-caught sardine and anchovy larvae represent an approximation of the percentage of the population removed by natural mortality. Assuming this sampling bias, however, it then becomes difficult to explain the increase in both relative body depth and feeding incidence of the older larvae taken by the same sampling methods. Burdick (1969), while examining Hawaiian anchovy (*Stolephorus purpureus*) larvae, observed no difference of feeding incidence or physical condition between samples taken concurrently with 1-m net and a plankton purse seine. Assuming the plankton purse seine captures all larvae, sick or well, he concluded that there is no bias produced by only the healthy larvae being able to avoid the 1-m net.

The average ocean-caught anchovy is significantly less robust at its midlarval lengths than its laboratory counterpart, owing presumably to differences in their respective rations. The first feeding (4-day-old) laboratory-reared anchovy larva spends 85% of the daytime in intermittent swimming, 7% in feeding, and 4% at rest (Hunter 1972). Perhaps the undernourished average ocean-caught larva, in response to the usual suboptimal

food densities, conserves its dwindling energy resources by increased resting and waiting for prey to appear within its range.

Hjort (1914, 1926) hypothesized that large-scale mortality will result if the proper food is not available in sufficient quantity at the "critical period" when newly hatched fish larvae require their first feeding, and that the numerical strength of a year class, therefore, might be determined at this time. The increasingly thin shape of young ocean-caught anchovy larvae suggests that feeding problems may exist for sometime into the larval period. Saville (1971) proposed that a "critical stage" might occur at any stage between hatching and metamorphosis and that the detection of same would allow one to specify the earliest stage at which reliable indices of year-class strength could be determined. The end of the decline in relative body depth of the average ocean-caught larva might mark the point in the larva's development when the danger of starvation has diminished and perhaps, as suggested by Saville, is the earliest stage at which estimates of recruitment might be made.

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LITERATURE CITED

AHLSTROM, E. H.
1954. Distribution and abundance of egg and larval populations of the Pacific sardine. U.S. Fish Wildl. Serv., Fish. Bull. 56:83-140.
1967. Co-occurrences of sardine and anchovy larvae in the California Current region off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 11:117-135.

ARTHUR, D. K.
1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Ph.D. Thesis, Univ. California, Scripps Inst. Oceanogr., La Jolla, 231 p.

BAINBRIDGE, V., AND D. C. T. FORSYTH.
1971. The feeding of herring larvae in the Clyde. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 160:104-113.

BEERS, J. R., AND G. L. STEWART.
1970. Numerical abundance and estimated biomass of microzooplankton. *In* J. D. H. Strickland (editor), The ecology of the plankton off La Jolla, California, in the period April through September, 1967, p. 67-87. Bull. Scripps Inst. Oceanogr. Univ. Calif. 17.

BERNER, L., JR.
1959. The food of the larvae of the northern anchovy *Engraulis mordax*. Inter-Am. Trop. Tuna Comm., Bull. 4:3-22.

BLAXTER, J. H. S.
1965. The feeding of herring larvae and their ecology in relation to feeding. Calif. Coop. Oceanic Fish. Invest. Rep. 10:79-88.
1971. Feeding and condition of Clyde herring larvae. Rapp. P-V. Réun. Cons. Int. Explor. Mer 160:128-136.

BLAXTER, J. H. S., AND K. F. EHRLICH.
1974. Changes in behaviour during starvation of herring and plaice larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 575-588. Springer-Verlag, Berl.

BLAXTER, J. H. S., AND M. E. STAINES.
1971. Food searching potential in marine fish larvae. *In* D. J. Crisp (editor), Fourth European Marine Biology Symposium, p. 467-485. Cambridge Univ. Press.

BOLIN, R. L.
1936. Embryonic and early larval stages of the California anchovy, *Engraulis mordax* Girard. Calif. Fish Game 22:314-321.

BOWERS, A. B., AND D. I. WILLIAMSON.
1951. Food of larval and early post-larval stages of autumn-spawned herring in Manx waters. Annu. Rep. Mar. Biol. Stn. Port Erin 63:17-26.

BURDICK, J. E.
1969. The feeding habits of neju (Hawiian anchovy) larvae. M.S. Thesis, Univ. Hawaii, 54 p.

CIECHOMSKI, J. D. DE.
1965. Observaciones sobre la reproducción, desarrollo embrionario y larval de la anchoíta argentina (*Engraulis anchoita*). Bol. Inst. Biol. Mar. Mar del Plata 9, 29 p.
1967. Investigations of food and feeding habits of larvae and juveniles of the Argentine anchovy *Engraulis anchoita*. Calif. Coop. Oceanic Fish. Invest. Rep. 11:72-81.

CIECHOMSKI, J. D. DE, AND G. WEISS.
1974. Estudios sobre la alimentacion de larvas de la merluza, *Merluccius merluccius hubbsi* y de la anchoita, *Engraulis anchoita* en la mar. Physis Rev. Asoc. Argent. Cienc. Nat. 33:199-208.

DETWYLER, R., AND E. D. HOUDE.
1970. Food selection by laboratory-reared larvae of the scaled sardine *Harengula pensacolae* (Pisces, Clupeidae) and the bay anchovy *Anchoa mitchilli* (Pisces, Engraulidae). Mar. Biol. (Berl.) 7:214-222.

DUKA, L. A.
1967. Struktura I dinamika soobshchestv (Adaptive features in the feeding of pelagic larvae of fish living in different ecological conditions). Akad. Nauk Ukr. SSR, p. 136-143. (Translated by Natl. Lending Libr. Transl. Program RTS 5162.)

HAND, C. H., AND L. BERNER, JR.
1959. Food of the Pacific sardine (*Sardinops caerulea*). U.S. Fish Wildl. Serv., Fish. Bul. 60:175-184.

HARDY, A. C.
1924. The herring in relation to its animate environment. Fish. Invest., Minist. Agric. Fish Food. (G.B.), Ser. II, 7(3), 53 p.

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 20:1-228.
1926. Fluctuations in the year classes of important food fishes. J. Cons. 1:5-38.

HONJO, K., T. KITACHI, AND H. SUZUKI.
1959. On the food distribution and survival of post larval iwashi-1 - Distribution of food organisms, the food of the anchovy and ecologically related species along the southwestern Pacific coast of Honshu, Sept.-Nov. 1958. Reports on the major coastal fish investigations, and the investigations for forecasting of oceanographic conditions and fisheries (preliminary report), February 1959. (Engl. transl. by S. Hayashi.)

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
In press. Behavior and survival of northern anchovy, *Engraulis mordax*, larvae. Symposium on Fishery Science. Ciencias Pesquera, Spec. Suppl.

ISSACS, J. D.
1964. Night-caught and day-caught larvae of the California sardine. Science (Wash., D.C.) 144:1132-1133.

JUNE, F. C., AND F. T. CARLSON.
1971. Food of young Atlantic menhaden, *Brevoortia tyrannus*, in relation to metamorphosis. Fish. Bull. U.S. 68:493-512.

KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON.
1975. The general feeding ecology of postlarval fishes in the Newport River estuary. Fish Bull., U.S. 73:137-144.

KRAMER, D., AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

LASKER, R.
1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine *Sardinops caerulea* (Girard). J. Fish. Res. Board Can. 19:867-875.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEBOUR, M. V.
1921. The food of young clupeoids. J. Mar. Biol. Assoc. U.K. 12:458-467.

LEONG, R. J. H., AND C. P. O'CONNELL.
1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). Fish. Res. Board Can. 26:557-582.

LOUKASHKIN, A. S.
1970. On the diet and feeding behavior of the northern anchovy, *Engraulis mordax* (Girard). Proc. Calif. Acad. Sci., Ser. 4, 37:419-458.

MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, Berl.

NAKAI, Z.
1960 Changes in the population and catch of the Far East sardine area. Proc. World Sci. Meet. Biol. Sardines, Related Species. 3:807-853.
1962. Studies relevant to mechanisms underlying the fluctuations in catch of the Japanese sardine, *Sardinops melanosticta* (Temminck & Schlegel). Jap. J. Icthyol. 9:1-113.

NAKAI, Z., H. KOJI, H. SHIGEMASA, K. TAKASHI, AND S. HIDEYA.
1966. Further examples of Hjorts hunger theory. (Abstr.) Second Int. Oceanogr. Congr., p. 263.

NAKAI, Z., M. KOSAKA, M. OGURA, C. HAYASHIDA, AND H. SHIMOZONO.
1969. Feeding habit, and depth of body and diameter of digestive tract of *shirasu*, in relation with nutritious condition. [In Jap., Engl. abstr..] J. Coll. Mar. Sci. Tech. Tokai Univ. 3:23-34.

O'CONNELL, C. P.
1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish Res. Board Can. 29:285-293.

PAVLOVSKAIA, R. M.
1958. The survival of anchovy larvae in the northwest and certain other regions of the Black Sea in 1954-55 in relation to food conditions. Doklady Akad. Nauk SSSR. Biol. Sci. Sect. (Transl.) 120:346-348.

REID, J. L., JR.
1967. Oceanic environments of the genus *Engraulis* around the world. Calif. Coop. Oceanic Fish. Invest. Rep. 11:29-33.

R. DE MENDIOLA, B.
1974. Food of the larval anchoveta *Engraulis ringens* J. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 277-285. Springer-Verlag, Berl.

SAVILLE, A.
1971. The larval stage. *In* A. Saville (editor), Symposium on the biology of early stages and recruitment mechanisms of herring, p. 52-55. Rapp. P-V. Réun. Cons. Int. Explor. Mer 160.

SCHNACK, D.
1974. On the biology of herring larvae in the Schlei Fjord, western Baltic. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 166:114-123.

SCHUMANN, G. O.
1965. Some aspects of behavior in clupeid larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 10:71-78.

SINYUKOVA, V. I.
1964. The feeding of Black Sea horsemackerel larvae. Tr. Sebastopol Biol. Stn. Acad. Sci., USSR. 302-325. (Translated by Lillian Vlymen.)

SMITH, P. E.
1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 164:282-292.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

YAMASHITA, H.
1955. The feeding habit of sardine, *Sardinia melanosticta*, in the waters adjacent of Kyushu, with reference to its growth. [In Jap., Engl. Abstr.] Bull. Jap. Soc. Sci. Fish. 21:471-475.

YASUNAGA, Y.
1971. Studies on the feeding habit and growth of the plaice, *Paralichthys olivaceus*, in the larval stage. [In Jap., Engl. Abstr.] Bull. Tokai Reg. Fish. Res. Lab. 68:31-43.

OBSERVATIONS ON THE COMMERCIAL FISHERY AND REPRODUCTIVE BIOLOGY OF THE TOTOABA, *CYNOSCION MACDONALDI*, IN THE NORTHERN GULF OF CALIFORNIA

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ABSTRACT

Information gathered from fishers and records of the failing totoaba, *Cynoscion macdonaldi*, commercial fishery demonstrate the ability of the three principal ports to fully exploit the dwindling population during its annual breeding migration to the mouth of the Colorado River. Gonadal maturation, daily catch, and capture incidence data document the timing and route of the migration, provide evidence for a tendency toward unisexual schooling in its early phase, and point to the possibility that totoaba may form large aggregations before spawning is initiated. A trend toward reduction in the length of the migratory and spawning period, from 5 or 6 mo in 1965 to 1 mo in 1972 is documented with data from the port of Golfo de Santa Clara. In surveys of the hypothesized nursery area, 28 juvenile totoaba (6-12 cm standard length) were collected at 4 of 14 sampling sites. The four collection sites were commonly characterized only by depth (<1 m) and substrate type (soft clay-silt sediments). Three hypothesized causes of the decline of this commercial fishery are examined by statistical analyses of Colorado River flow and annual totoaba catch data: overfishing, loss of spawning grounds, and loss of nursery grounds. Overfishing was found to be the most likely cause of the decline. Recent trends of catch data among the principal commercial fleets, and evidence that regulatory measures may have resulted in temporary recovery of totoaba production, provide further support for the overfishing hypothesis. The journey of the migrant population along a known route and its concentration into a predictable small area, its hypothesized requirement for dense aggregations prior to spawning, and the added mortality of juveniles taken by shrimp trawls in the near-delta waters are important points of vulnerability that render this endemic species particularly susceptible to fishing pressure. The possibility of the extinction of *Cynoscion macdonaldi*, without continuation of the newly decreed prohibition of fishing, is reiterated.

The totoaba,[2] *Cynoscion macdonaldi* Gilbert 1891, is the largest species of the family Sciaenidae, with maximum reported lengths of almost 2 m (Berdegué 1956) and weights exceeding 135 kg (Cannon 1966); the larger females in present-day commercial catches approximate 1.5 m and 35 kg (Arvizu and Chávez 1972). The species is endemic to the Gulf of California, where it used to support a fishing industry and popular sport fishery based on its annual spring breeding migration to the shallow, formerly brackish waters of the Colorado River Delta region at the extreme northern end of the gulf. The major portion of the catch was exported from Mexico to the United States (principally San Diego) and brought a high price per pound under the influence of apparently unlimited demand. Presently an indefinite closed season on the totoaba, declared by the Government of Mexico on 2 August 1975, prohibits all capture of this species by both commercial and sport fisheries (H. Chávez, pers. commun.).

Although the species has been heavily exploited, its life history, population dynamics, and general ecology are poorly known. Species accounts are given in Jordan and Evermann (1898, 1902), Jordan et al. (1930), Gabrielson and Lamonte (1954), and Lanham (1962). The totoaba was included in accounts of commercial sciaenid species by Croker (1932) and Fitch (1949). Aside from these references and others cited here, little has been published on the totoaba; remaining incidental references may be found in Arvizu and Chávez (1972), the most recent summary of all available information on this species. Although notes on the ecology of the totoaba were first published in 1916 by Jordan, most of the presently accepted life history information is based on fisher's lore. These beliefs were first documented by Berdegué in his 1955 study of the fishery in which he also examined scale annuli series and published the only derived

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[2]The common name is often spelled "totuava" by writers from the United States for no known reason. The spelling used here is that preferred and used by Mexicans; it should become the established spelling.

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growth estimates for this species. His work concluded with a warning that the totoaba is a declining species, in danger of extinction from a combination of overfishing and the disappearance of brackish water spawning grounds due to diversion of Colorado River waters for agricultural and other purposes. Gause (1969) and Sotomayor (1970) later echoed this view.

In this paper we present a short history of the commercial fishery and report new information on totoaba life history. We summarize what is known about the ecology of the species and speculate on consequences of the present small population size and the intense fishing effort to which the fish have been exposed. We discuss the three most probable causes for the decline in the fishery: degradation of spawning grounds, degradation of nursery grounds, and overfishing. We examine Colorado River flow data and annual catch data in the light of these hypotheses, and discuss our results. In conclusion, we draw together all these elements in an attempt to assess the present and future status of this commercial population.

HISTORY OF THE FISHERY

Until about 1920, commercial exploitation of the totoaba was confined to export of dried air bladders to the Orient as an ingredient of a gourmet soup (Chute 1930). Craig (1926) reported the first export of totoaba flesh to the United States. In these early, developing years, the totoaba fishery was directly responsible for the establishment of three northern gulf fishing villages: Golfo de Santa Clara and Puerto Peñasco in the State of Sonora, Mexico, and San Felipe in the State of Baja California Norte (Berdegué 1955). Analysis of registered catches by all Mexican ports for the 1966-70 period shows that these three ports produced from 94.9 to 97.7% of the total catch (H. Chávez, pers. commun.).

From 1929 (when Mexican Government statistics were first collected) onward, the fishery responded to a growing U.S. market by developing transportation and refrigeration capabilities and by improving fishing gear and boat facilities. Annual yield began to increase rapidly in 1934 and the catch peaked at 2,261 metric tons[3] in 1942

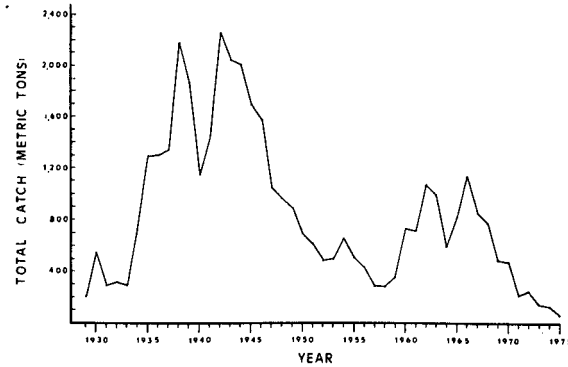

FIGURE 1.—Yield of commercial totoaba fishery, northern Gulf of California for the 1929-75 period. Figure modified from Arvizu and Chávez (1972). Data for 1971-75 were obtained from H. Chávez (pers. commun.).

(Figure 1). After 1942, despite intensified fishing effort and increased gear efficiency, the annual yield exhibited erratic fluctuation to the all-time minimum of approximately 58 metric tons in 1975 (H. Chávez, pers. commun.[4]).

Fishing methods evolved from spearing out of dugout canoes and primitive handlining in the early years, through dynamiting and primitive gill netting, to the use of efficient nylon gill nets. The usual modern net has a stretched mesh size of approximately 25 cm and measures 100-200 × 4-5 m. Gill nets were managed from diesel-powered shrimp trawlers (12-18 m, some temporarily diverted from shrimping during prime season totoaba fishing), and from 4.5- to 7.5-m wooden or fiber glass "pangas" (launches) fitted with outboard motors. The activities of commercial fishers have been largely limited to the prime breeding season (January-March) when the spawning adults are in the shallow waters of the extreme northern gulf. Prior to the 1975 total protection of totoaba, the prime fishing season ended with the advent of an official closed season, 1 April-15 May (Arvizu and Chávez 1972), a protective measure enacted by the Mexican Government in about 1955 (Berdegué 1955).[5] At the same time, a sanctuary was designated at the mouth of the Colorado

[3]We follow the example of Arvizu and Chávez (1972) in giving yields as weights of cleaned fish lacking heads and viscera unless specifically designated otherwise. To convert to whole weights, multiply by 1.1 (H. Chávez, pers. commun.).

[4]The 1975 yield reported here is based on catch from principal ports for the prime season only (through the month of March). The final figures may be as much as 10% higher.

[5]According to Berdegué (1955), before 1955 there was a closed season extending from 20 March to 1 May; the prohibited period was changed to the later dates because active spawning was observed after 1 May. In 1969 and 1970 the beginning of the closed season was delayed 15 days in response to the fishers' petitions when breeding schools had not appeared by the end of March (H. Chávez. pers. commun.).

River. All fishing was prohibited north of an imaginary line extending from Bahía Ometepec on the Baja California coast to the mouth of the Río Santa Clara on the Sonora coast.

In addition to the standard commercial fishery, the Seri Indians of the Bahía Kino and Punta Chueca areas of Sonora were alleged to capture totoaba in coastal waters during the fall and winter, but we have been unable to confirm this by personal observation. Further pressure was exerted on the stocks by an enthusiastic sport fishery, based largely on the Baja California side of the northern gulf, which took unknown numbers of breeding adults during the prime season. In recent years when diminution of the stocks caused the success rate to drop, sport fishing virtually disappeared. At the peak of the sport fishery, large numbers of immature fish resident in the upper gulf waters were also reportedly taken, usually unrecognized as totoaba. For a time, a deepwater handline commercial fishery and accompanying sport fishery continued out of San Felipe during the summer after the adult fish had left the spawning grounds, but this activity also declined in recent years. Craig (1926), Chute (1928), and Berdegué (1955) provided further information on the history of the fishery and contain most of the documented information on the sport fishery.

METHODS AND MATERIALS

The junior author began field studies on the species in 1970 with the primary objective of gathering life history information for conservation purposes. The results reported here derive primarily from data collected by the senior author during three cruises aboard commercial fishing vessels from Puerto Peñasco in March and April 1972. Fishing patterns during these cruises included most of the Gulf of California north of lat. 31°N; with few exceptions, the locations were selected by the fishing captain.

The data were gathered by direct observation of catch and, in a few cases, by reports from fishers on "companion" vessels (as many as five other boats in the cooperating group, in one instance). During 22-24 March 1972 we also collected data from the panga fleet at Golfo de Santa Clara as the catch was landed and cleaned at the port. In both circumstances, our data consisted of information on location, time and size of catch, number of operational net hours, time and state of tide, sexual composition of the catch, and reproductive state of the individual.

All fish examined by us were breeding adults. They were classified according to three mutually exclusive categories of gonadal development: If not running eggs or milt at the time of capture (or within 24 h of capture in the case of several individuals kept alive for a period of hours), they were classified as "unripe"; if milt or hydrated eggs ("applesauce" color and texture) could be expressed with light pressure, they were classified as "ripe"; females with flaccid ovaries and running ripe males taken in the same catch with such females were classified as "spent."

Effort data are reported as the number of operational net hours rather than total time (man-hours or boat-hours) spent fishing because many of the large boats "hunt" for schools suitable for encircling with their nets during the day and then set their gill nets in the usual manner to fish overnight. We believe that recent daytime hunting for schools to encircle was practiced more in memory of times past than as a practical matter of probability. In approximately 50 days aboard such vessels, we have never seen a school located, although one heard of such catches each season. The method persisted because, if successful, it can yield very high tonnage. The larger, diesel-powered trawlers with ice-filled holds frequently stayed at sea for more than a week and commonly traveled considerable distances back to their home ports to land the catch. This is in marked contrast to the methods of the fishers of Golfo de Santa Clara, who fished primarily from pangas and who customarily inspected their nets each day by passing the net over the boat, leaving the weighted ends in place. Such nets "fished" continually, except for occasions when they were taken up to be moved to alternate spots. Lacking storage and refrigeration facilities, the pangas had to return to port each day with their catch from one or two gill nets. Catch in kilograms was recorded by a Mexican government fisheries inspector for each panga, each day. Although we attempted to calculate catch per unit effort, we were unable to resolve its heterogeneous nature. Here we present only our analysis of effort from the panga fishery of Golfo de Santa Clara.

In late May and early June 1972, a number of Sonora and Baja California sites around the perimeter of the extreme northern gulf were surveyed for juvenile totoaba, using both commercial trawl nets and beach seines. Many of these sites

were revisited in June 1973. Observations were made of water temperature, salinity, turbidity, and substrate character; associated faunas at each site were sampled. A few juveniles were transported alive back to Tucson, Ariz., and maintained there for about 80 days. Information on distribution and habitat of the juveniles is presented here; notes on behavior of the juveniles in captivity will be reported elsewhere (C. A. Flanagan in prep.).

In our discussion of the hypotheses for the decline of the totoaba fishery, we present statistics of Colorado River flow and annual totoaba yield. The annual yield data are those already presented (Figure 1). For flow, we have attempted to estimate the amount of water delivered to Mexico in the main river channel at the southerly international boundary on the assumption that it will bear some regular relationship to the volume of fresh water entering the Gulf of California. This assumption becomes tenuous with the development of lowland agriculture in Mexico and with significant groundwater pumping in the United States, both in evidence since about 1960. Suitable effort data for the totoaba fishery are unavailable but we have assumed that, following the peak catch in 1942, effort was constant or increasing. This assumption is probably warranted given the demand and high price paid for totoaba flesh. The limitations imposed by our assumptions are that no catch datum before 1942 and no flow datum after 1960 may be considered in these analyses.

RESULTS AND DISCUSSION

Breeding Migration

The fishers believe that the annual migration of totoaba is prompted by the urge to reproduce and is guided by the search for a suitable estuarine spawning environment. According to their beliefs the breeding population, seeking areas of reduced salinity, leaves deep water in the mid-gulf and follows the Sonora coastline northward; eventually the schools reach the mouth of the Colorado River, where they spawn. Following spawning, the totoaba supposedly seek out the clearer, deeper waters to which they are more accustomed and follow the Baja California coastline on their return migration southward. These beliefs are based upon commercial catch experience dating back to the late 1920's.

Localities and dates of capture observed by the senior author in 1972 (Figure 2 and Table 1) appear to document a pattern consonant with the above hypothesis, as do observations by the junior author in earlier years. The regular port statistics also implicitly support the hypothesis, with catches each year reported chronologically first by Puerto Peñasco, then by Golfo de Santa Clara, and last by San Felipe fleets. The data in Figure 2 represent but a small fraction of the total 1972 fishing effort, however, and in the most conservative interpretation demonstrate only that experienced fishers

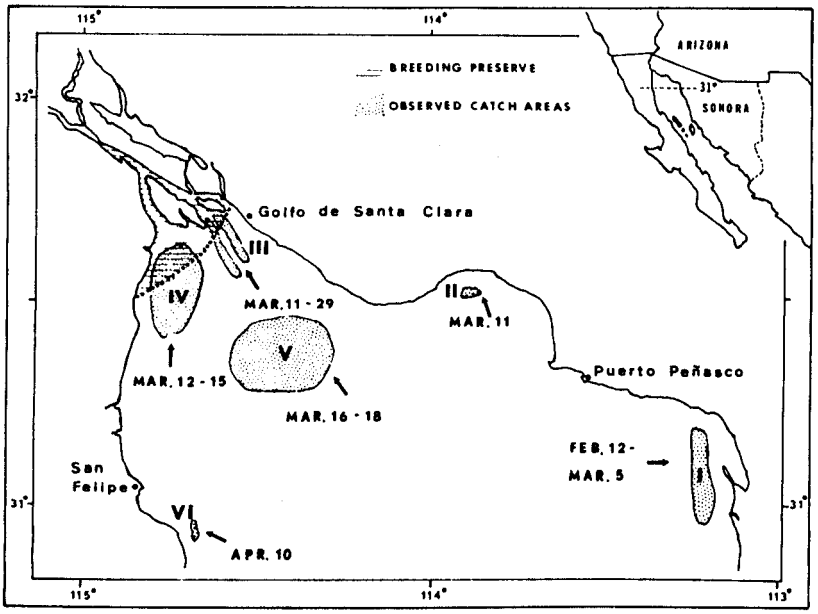

FIGURE 2.–Locations and dates of observed commercial catches of totoaba during the 1972 prime fishing season. Catch information in terms of tonnage by day, boat, and area were also obtained from Fisheries Inspectors. These latter data are reflected in the early capture date of 12 February and the extended capture period of 11-29 March in areas I and III, respectively. Chart shows Gulf of California north of lat. 31°N (see locater in upper right-hand corner).

TABLE 1.–Totoaba captures observed in 1972 (see Figure 2 for areas and timing). The figures shown here are personal observations of the senior author.

Area	No. of observed net sets	No. of successful net sets	Total no. of totoaba caught
I	5	1	1
II	1	1	1
III	(no data)	[1]149	([1])
IV	9	8	42
V	6	5	18
VI	11	1	1

[1]These data are displayed in Figure 5. Although catch data are available for area III only in terms of tonnage, not head count of fish taken, use of the 35-kg average per fish would give a conservative estimate of at least 2,500 individual fish taken in area III during 1972.

know where and when to find fish. Ideally, Figure 2 should reflect the results of an even pattern of standard net sets through the February-June period.

To our knowledge, no one has investigated the salinity preferences or tolerances of spawning adults, but this raises the question of totoaba spawning sites in estuarine areas of other major gulf rivers. Spawning totoaba have never been reported from locations other than the Colorado River mouth. While further investigation is clearly warranted, at present we accept the fisher's hypothesis as an adequate predictor of population migratory patterns.

Spawning Concentration

Because the annual breeding migration results in a high density of fish within a limited area, it has become the single most important aspect of the fishery: total prime season catch is a function of the number of fish arriving in the spawning area before 31 March in an average year. The appearance of migrant schools of totoaba in shallow coastal waters, as signaled by catches from exploratory boats which have ventured out in anticipation of their arrival, usually occurs in mid-February, but may take place as early as December or as late as the end of March.

Three references exist in the literature regarding the spawning period. Nakashima (in Jordan 1916) said that the main spawning period was in early May, while Berdegué (1955) reported the reproductive season as extending from the end of February or early March until early June. Observations by D. A. Thomson (1969) and the junior author over the last four seasons indicate peak spawning as late as April and early May but, more commonly, in mid- to late March. Historical data and existing statistics confirm the fisher's claims that the period of concentrated catch (which apparently coincides with peak spawning) has become progressively abbreviated during the past 20 yr. The monthly catch data for Golfo de Santa Clara for the 1964-72 period show a clear reduction in length of season from 5 or 6 mo to an abbreviated period in March-April at present (Figure 3). We believe (see below) that the catch of the Golfo de Santa Clara fleet is a good reflection of spawning activity and suggest that a pattern of repeated spawnings formerly extending from January-February to May and June has collapsed to a single event which coincides with the old temporal mode. A small remnant population might be expected to react more uniformly to environmental cues than would a large one, a factor leading to progressively shorter migratory and spawning periods. This is consistent with our observation of breeding population residence time of only 18 days on the spawning grounds in 1972 (from 11 March to 29 March, see discussion below).

A limited amount of qualitative data on gonadal maturation, collected during the 1972 prime fishing season (Figure 4), indicates that males ripen before females and retain spawning readiness for longer periods of time–a common occurrence among fishes. It also provides evidence for a

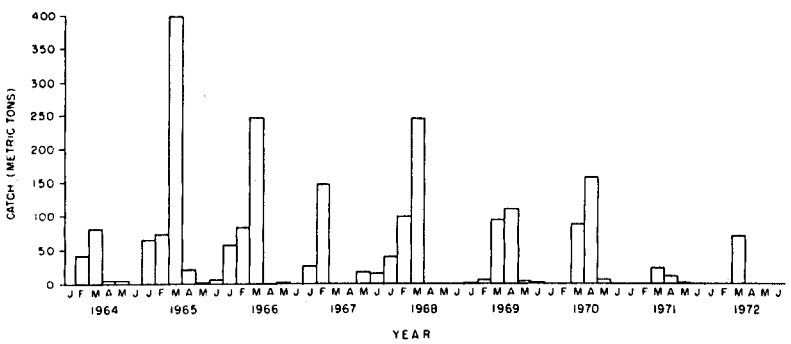

FIGURE 3.–Monthly yield in metric tons of totoaba, port of Golfo de Santa Clara. Data for 1966-70 from Arvizu and Chávez (1972); H. Chávez (pers. commun.) supplied data for 1964-65 and 1971. The 1972 catch data were obtained from F. Aguilera, Fisheries Inspector (15 additional metric tons recorded in 1972 are not shown because month of capture was uncertain).

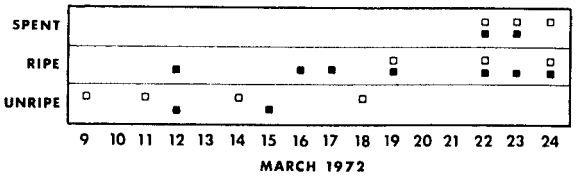

FIGURE 4.—Degree of gonadal maturation observed on specific days during the 1972 prime fishing season. See text for explanation of maturation categories. Each symbol represents one or more individual fish. Open squares represent females; solid squares represent males.

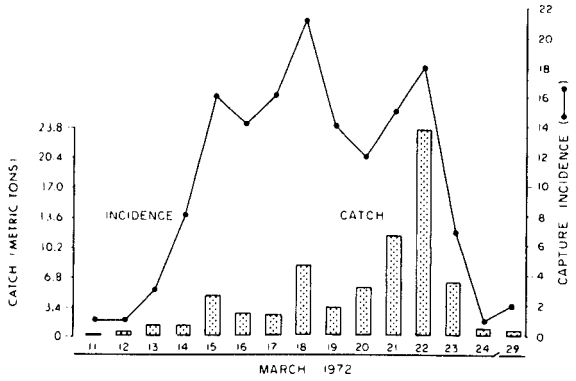

FIGURE 5.—Golfo de Santa Clara catch and capture incidence plotted against days of March for 1972 prime fishing season. See text for explanation of capture incidence unit. Between 15 and 22 March the number of individually successful nets remained comparatively constant, despite the peak catch on 22 March. Official statistics indicate that 15 metric tons in addition to the total of 71 metric tons shown in Figure 3 were recorded for this port in 1972 (H. Chávez, pers. commun.). These additional data cannot be traced to daily catch for inclusion in this figure.

tendency toward sexually segregated schooling, at least in the case of male fish. It will be noted that all the records for the early portion of the period portrayed in Figure 4 show a single sex per catch, while the records for the later portion of the period show both sexes in all but one instance. It must be clearly understood that some of the catch records portrayed in Figure 4 represent single fish, making those data points meaningless in this context, but a majority of the data points represent multiple individuals. This apparent sexual separation of prespawning schools conforms with general observations by Hendrickson in years before 1972 and with the caption for figure 84 in Chute's (1928) paper describing the earlier hook-and-line fishery: "Practically all of the fish in this picture were males . . . ." (the figure, depicting the butchering process, shows about 15 large fish caught by three men in 3 h).

Success of the Golfo de Santa Clara panga fishery is related to the size of the migrant totoaba population, the length of the period in residence on the fishing grounds, and population behavioral patterns. Because the fishing grounds are identical with, near to, or in the path to the spawning grounds, analysis of the panga fishery catch statistics can yield valuable insight into the breeding biology of this species. We have used "capture incidence" as a measure of fishing success, employed here to give a quantitative indicator of the presence of breeding adults on or near the suspected spawning grounds (Figure 5). One capture incident is defined as the catch of at least one totoaba per panga per day; the daily total reflects the number of individually successful net sets. We assume that: 1) fishing effort is constant after a given date within the prime season and 2) fishers individually and collectively fish in the same area each day throughout the period. These assumptions are in keeping with the nature of the Golfo de Santa Clara fishery. This village waited in readiness each year for the arrival of the migrant population and, within a few days of the first catches by exploratory nets, virtually all available gill nets were deployed for fishing of totoaba. Despite daily success or failure, fishing effort continued at this level until the season closed on 1 April. Most of the panga fishers worked a definable area of the delta where "canals" (extensions of Colorado River channels) deep enough to accommodate the large totoaba gill nets are separated by shallow mud bars (see area III in Figure 2).

In 1972 the first catch off Golfo de Santa Clara occurred on 11 March and was followed by a period of increasing catch and capture incidence due to increasing effort until 15 March (Figure 5). During the March 15-22 period, capture incidence was relatively constant and high. During this same period, catch varied somewhat erratically and peaked on 22 March, after which both catch and capture incidence fell off drastically despite no reduction in fishing effort. The 22 March catch amounted to 27% of Golfo de Santa Clara's yield for that year and represented 9% of the total recorded yield from all ports for 1972. The average Golfo de Santa Clara net must have contained over twice as many fish on 22 March as on 21 March and 3-5 times as many as on other "good" days in the prime season.

What factors in totoaba reproductive biology might explain these results? Catch per net may be considered an index of migrant arrivals if we

suppose that, as breeding adults reach the northern end of the gulf, they immediately move up into the channels at the mouth of the Colorado River. The arrival of the largest population segment would then be indicated by the peak catch. Alternatively, the peak catch may have signaled a peak of spawning activity by an already-resident breeding population, becoming more vulnerable to the nets by virtue of spatial concentration and/or behavior. While the data do not allow firm conclusions, we favor the second alternative.

A period of behavioral stimulation in schools to induce the spawning act is suggested by the fact that enormous numbers of individuals allegedly used to gather in this relatively small area to spawn (Jordan 1916; Berdegué 1955). Although the population has been drastically reduced, the fish apparently continue this habit. If the release of reproductive behavior patterns depends upon mutual stimulation within large aggregations (consistent with their sound-producing air bladder; see Breder and Rosen 1966), the present small population might be experiencing some breakdown in the behavioral sequence with consequent lowered reproductive success.

Although the significant yields of 21 and 22 March may indicate a peak in spawning activity, this does not preclude the possibility that other fish were later in arrival and that spawning also occurred in April (during the closed season). The Golfo de Santa Clara fleet's near-failure to catch fish during the 25-31 March period, and our failure to find adult fish during the April cruise lend doubt to this possibility, but the existence of more than one breeding population should not be ruled out.

Juvenile Totoaba Distribution, Habitat, and Diet

The microhabitat and residence time of juvenile totoaba on the nursery grounds are largely unknown. Berdegué (1955) reported that juveniles remain in the shallow waters near the Colorado River mouth until they begin a southward migration to join the parent population. The Colorado River Delta is heavily exploited by the shrimp fishery during parts of the year (effort was observed to be especially intense during April, May, and June), and Berdegué first called attention to the increased mortality of juvenile totoaba due to shrimp trawling activity.

In our experience, the juveniles captured in shrimp trawls are individuals ranging in length from about 15 cm to about 45 cm. The holotype in the U.S. National Museum is approximately 25 cm long and was taken in 20 fathoms of water (Gilbert 1891). To our knowledge, the first collection of really small juveniles (6-12 cm size range) which were positively identified as totoaba was made in 1970 near San Felipe, B.C., and described by Chávez (1973). We surveyed probable northern gulf sites for the presence of such small juveniles during May and June 1972 and 1973 (Figure 6).

Substrate and depth appear to be more important than either temperature or salinity in characterizing the habitat of the captured juveniles. For all sites, surface water temperatures ranged from 25° to 29°C and salinities were recorded between 35 and 40‰. Sites where we collected juveniles were shallow as compared to the other sampling locations, and none were collected from depths greater than 1 m. Substrates were composed of fine clay-silt sediments, devoid of sand;

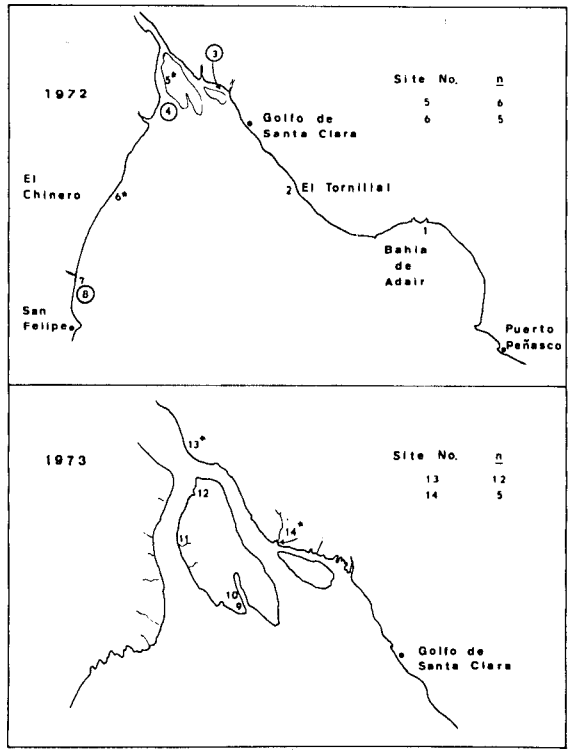

FIGURE 6.—Sites sampled in northern Gulf of California for presence of juvenile totoaba in 1972 and 1973. Circled numbers indicate offshore areas sampled by otter trawl. All other locations are shore stations sampled by seine. Sites where juvenile totoaba were found are indicated by stars. Numbers captured are shown at upper right of each map.

the mud surface layer was very soft. No small juvenile totoaba were collected over firm mud sediments or sandy substrates, as is often the case with the larger individuals taken in shrimp trawls.

Guevara (1974) is presently analyzing the distribution of juvenile totoaba captures in shrimp trawls. Most of his specimens are larger than ours, implying that the fish move into deeper water as their growth continues. Tidal currents in the area are extreme and these may also play a significant role in juvenile distribution.

Juveniles collected in 1972 were examined for stomach contents. Remains of amphipods and other small crustaceans common to the habitat were recognizable, in addition to remains of juvenile fishes which we identified as *Micropogon* sp., *Mugil cephalus*, and *Leuresthes sardina*. Within the limits imposed by size, the diet of juvenile totoaba as small as about 6 cm standard length is comparable in these items with the diet of the large adults.

Decline of the Fishery

We have traced the growth and decline of the totoaba fishery and discussed its present status and methodology. We have presented data on aspects of totoaba life history and raised questions concerning possible reproductive behaviors which may have a bearing on reproductive potential. Although these have significance, if we consider the resource from a management perspective one fact becomes clear: the annual breeding migration to the mouth of the Colorado River emerges as the primary source of vulnerability for this declining population. It serves to concentrate adults in a predictable small area where they may be fished with efficiency during a critical phase of their life cycle. To recruit, the juveniles must traverse an area of intense shrimp trawling activity which artificially increases juvenile mortality and leads to further reduction of this already-depleted stock.

The precise factors responsible for the decline of the totoaba stock cannot be identified with certainty, but we can enumerate the three most probable causes as: degradation of the spawning grounds, degradation of the nursery grounds, and overfishing. The first two are a result of replacement of brakish waters by saline waters in and around the mouth of the Colorado River. Both alternatives may be explored by examining Colorado River flow data and annual totoaba yield over the critical period of declining catch and significant flow reduction. We might expect a relationship to exist between flow and annual yield if the density of the resident breeding population (as measured by catch) varies with some unknown but flow-related quality of the spawning ground. Relation between flow and catch n years later (with n years corresponding to age at recruitment) would indicate the importance of some flow-related quality of the nursery ground. Although tests of overfishing using these data are ambiguous, if catch is statistically related to catch n years later we might expect a depletion of the breeding population resulting from lowered recruitment levels.

The decline in catch with declining, erratic flow is evident for the 1942-58 period (Figure 7). Following 1958, the catch increased to a secondary peak and then crashed to the present all-time minimum, though flow varied little in the same period. For reasons given earlier, we discuss separately the pre-1958 and post-1958 periods.

For the years 1942-58 we have plotted catch against flow (Figure 8). Linear regression of the data reveals a highly significant correlation of annual flow and catch for this period ($P < 0.001$). However, the river flow data are derived from a different base after 1951; analysis of these data in two segments, before and after this change point, shows no significant relationship between catch and flow for either the 1942-50 period or the 1951-58 period. These results suggest that the highly significant correlation of flow and catch for the total 1942-58 period may be spurious and due only to the artificial pairing of declining catch and declining flow functions. Despite these results, we cannot ignore the fact that the totoaba congregate only in the Colorado River estuary (so far as known), and the salient feature distinguishing this from other estuaries in the northern gulf is the (former) discharge of large quantities of fresh water from the Colorado River. Therefore, accepting the tentative nature of the flow-catch relationship, we explore its possible biological basis.

The mechanism could lie in olfactory cues from the river system (physiological responses to either fresh water or substrate "odor"). Given the present agricultural scene, such cues may no longer be present. The present Colorado River surface flow to the Gulf of California is close to zero for all practical purposes and this situation is likely to continue in the future. A conspicuous bar now exists across the channel upstream from the delta

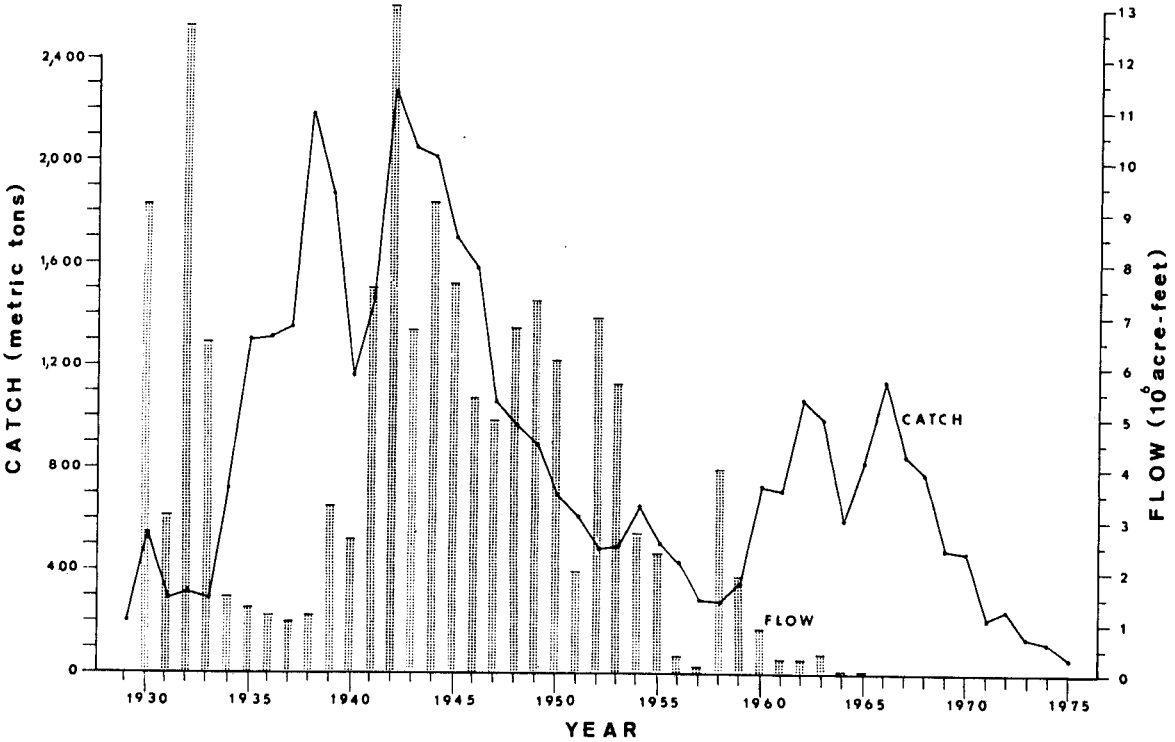

FIGURE 7.–Colorado River flow in thousands of acre-feet and totoaba fishery annual yield in metric tons for the 1930-75 period. Totoaba annual yield data are those of Figure 1. Flow data were calculated from records published in Water Supply Papers 1313, 1733, and 1926 (U.S. Geological Survey, respectively, 1954, 1964, and 1970). Flow data for 1966-75 are not shown but we do not expect them to deviate beyond the 1960-65 variation above. We have calculated the flow delivered to Mexico at the southerly international boundary (near San Luis, Ariz.) as follows (data sources are cited only on first mention): 1930-36: Colorado River at Yuma (1954:710) + Yuma Main Canal Wasteway (1954:717) + Calif. Drainage Canal (1954:723) – Alamo Canal (1954:724) + Eleven-mile Wasteway (1954:726) + Cooper Wasteway (1954:726); 1937-50: Colorado River at Rockwood Gate, Calif. (1954:712) - Alamo Canal + Eleven-mile Wasteway + Twenty-one Mile Wasteway (1954:727) + Cooper Wasteway; 1951-65: Colorado River at southerly boundary, near San Luis (1964:563; 1970:519-521).

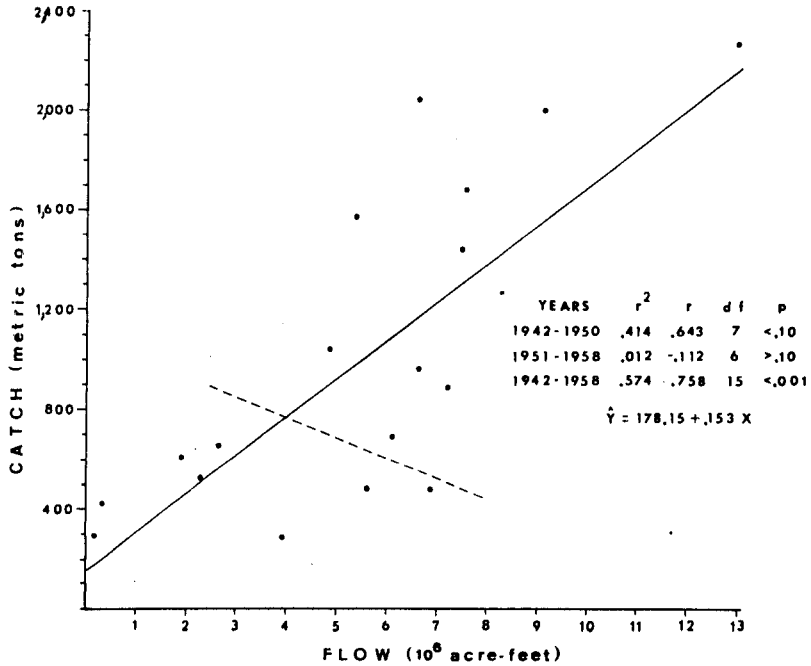

FIGURE 8.–Plot of annual totoaba yield and annual Colorado River flow for the 1942-58 period. Data are those displayed in Figure 7. The points below the dashed line represent the 1951-58 flow years. Though the relationship between catch and flow for the 1942-58 period are highly significant, the disparity between the r^2 levels for the component periods 1942-50 and 1951-58 invites caution in interpretation of these results.

islands, and flow measurements at the southernmost Mexican hydrographic station known as El Marítimo, formerly considered the best single index of actual surface input to the gulf (Schreiber 1969), were discontinued in 1968 for lack of meaningful data.[6] Further, the extensive use of all available water from the lower Colorado River drainage system for irrigation has resulted in hypersalinity of return flows and is a major problem on both sides of the international boundary. Water returned to the river channel which may reach the gulf is now likely to be at least as saline as the marine water it joins. Thompson (1968:8), summarizing the history of Colorado River flow and effects of exploitation on detrital loads, concluded, "Probably little river detritus has reached the northwestern Gulf of California in the last 55-60 years." Thus, if odor is not carried beyond upstream dams and fields where the detrital load stops, it must originate from reworking of the massive deltaic deposits by the strong tidal currents of the uppermost gulf. If Thompson's estimate is correct, this may have been occurring during the developing years of the fishery; the rate of decay of such a process is unknown.

The post-1958 flow and catch data (Figure 7) contrast with those of the previous period. We feel that the secondary peak in totoaba production may be attributable to extraneous factors such as changes in effort or efficiency (availability of nylon gill nets?) which produced a temporary increase in catch. Another possible reason may have been the enforcement of the 1955 breeding preserve regulations which offered some temporary relief from exploitation. If fishing in the sanctuary were to resume after a period of time, the yield might recover and fall in the observed manner.

We now consider the second hypothesis, that the cause of stock depletion is degradation of the nursery ground. When annual totoaba yield is compared with river flow in earlier years (e.g., the 1951 totoaba catch compared with the 1942 river flow, etc.), lag times ranging from 6 to 10 yr all give significant negative correlations ($P<0.05$) using standard linear regression techniques. The relationship is most distinct (Figure 9) when the lag time is 9 yr ($P<0.01$). The 6- to 10-yr periods correspond with estimated ages of recruitment employed below.[7] We find this negative relationship of flow and (lagged) totoaba yield highly interesting, though puzzling. The relation could be taken to imply that survival of young stages is a critical factor, since it couples increased river flow in any one year with reduced recruitment of that year class to the population. This interpretation discounts hypotheses of larval and juvenile physiological dependence on waters of lowered salinity (Berdegué 1955, 1956; Cannon 1966; Gause 1969; Sotomayor 1970). An alternate analysis using flow data only for the March-July period over the years of catch decline would be a better test of the effect of flow on larvae and small juveniles.

We know that successful reproduction still continues in the northern gulf as demonstrated by our ability to find juvenile fish on the nursery grounds. Despite searching, we have found no conspicuous subsurface freshwater seeps which might have provided local areas for limited successful spawning. We believe that reproduction occurs over the entire ancestral spawning grounds. Thus, we conclude that adverse effects of salinity changes must operate in a relative and not an absolute manner. The advantages realized by potential recruits on the nursery ground may be those of reduced predation and abundant food

[6]Nishikawa-Kinomura, K. A. 1973. Flow of the Colorado River into the Gulf of California. *In* S. Álvarez-Borrego et al., Preliminary report to the Secretariat of Hydraulic Resources on the second stage of the chemical study on insecticide contamination at the mouth of the Colorado River, p. 15-19. Unpubl. rep. Mar. Sci. Unit, Inst. Oceanol. Res., Univ. Baja Calif., Ensenada, Mex.

[7]The senior author has reviewed the published estimates of growth curves and ages of recruitment (see Arvizu and Chávez 1972, for a summary of this literature). Apparent discrepancies between reported lengths at different ages and serious disagreement between Berdegué's (1955) growth estimates and the distribution of lengths in observed commercial catches in 1963 (Arvizu and Chávez 1972) encouraged closer scrutiny of these data. The variation in lengths at particular ages and in maximum lengths reported by different authors and summarized by Arvizu and Chávez appear to derive from use of both standard length and total length measurements without discriminating between the two. The senior author calculated von Bertalanffy growth curves using a resolved maximum standard length of 1,600 mm and the intermediate lengths reported by Berdegué (1955). The new growth curves indicate that the best estimate of recruitment age is 6 or 7 yr; they also produce a length series which corresponds well with that observed in commercial catches. Male and female totoaba may vary significantly in growth rates and therefore may recruit at different ages. This variation allows extension of the possible recruitment age to 10 yr. J. E. Fitch (pers. commun.) has examined totoaba otoliths and concluded that totoaba first spawn at age 8. If totoaba do not accompany the migrant population until reproductively mature, his results are consistent with the ages of recruitment used here. However, his overall ages as read from otoliths indicate that these new growth curves may contain a wide margin of error in terms of predicted age at length observed. Fitch has also found that totoaba scales are of little use for growth studies after about age 8; this may explain the maximum lengths at age 8 or 9 reported by Nakashima (Jordan 1916), which we now believe to be erroneous. It also may account for errors in Berdegué's (1955) estimates, since he relied heavily on age determinations from scales.

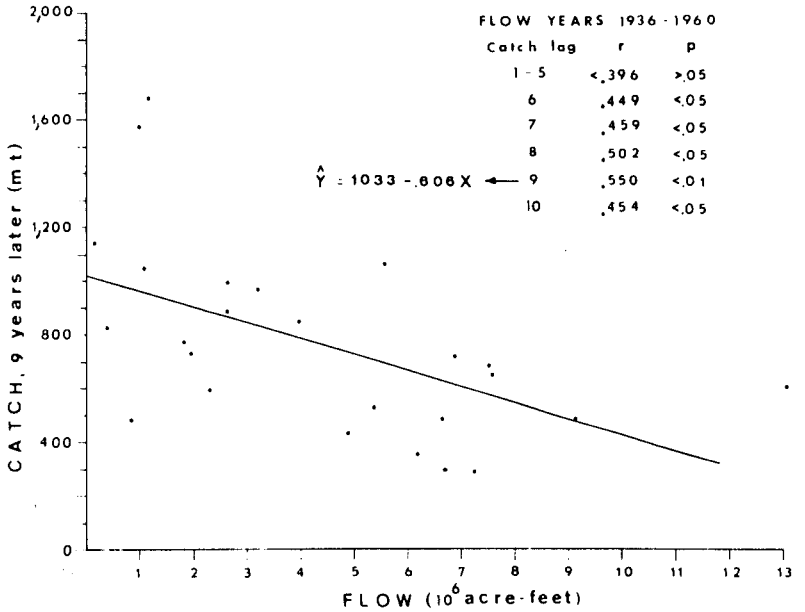

FIGURE 9.—Plot of annual totoaba yield (metric tons) 9 yr following the annual recorded flow, for the 1936-60 period. This plot displays the suggested relationship between flow and recruitment level. Linear regression calculations employing lag times from 1 to 10 yr are significant only for those years corresponding to estimated ages of recruitment (6-10 yr).

resources, both of which are directly related to substrate and shallowness, and indirectly related to flow.

The final cause suggested for the decline in totoaba stock is overfishing of the breeding population. We have examined the relationship of catch with catch n years later. If catch is a good indicator of population size, then we would expect a linear, positive relationship between population size and the size one recruitment age later. Alternatively, if catch is partially a function of sociopolitical constraints (e.g., enforcement of a preserve area and closed season resulting in a catch which significantly underrepresents the population size), we might expect a more complicated plot with a distinct cluster of years corresponding to periods of fishing regulations. We have analyzed plots of catch against catch for recruitment periods ranging from 6 to 10 yr and have found significant relationships which satisfy both of the above predictions. Graphs for all estimated ages of recruitment from 6 to 10 yr showed essentially the same pattern (Figure 10). However, we note inconsistencies which advise against drawing strong conclusions of either overfishing or the demonstrated worth of enforced regulatory measures. For example, increases in catch occur 2-3 yr earlier than is consistent with our assumption that regulatory measures were not enforced until 1955, given that the minimum age of recruitment is 6 yr. The question of a change in gear efficiency, effecting a realized increase in effort, serves to confound the analysis; although catch would increase, this factor alone could not explain recovery of catch to such high levels. We can visualize a combination of factors giving rise to the significant second peak in totoaba production (increase in gear efficiency acting on an increased population size following the period of regulation) but lacking effort data throughout the period, our hypothesis must remain speculative.

Support for the overfishing hypothesis may lie in the recent trend of the relative catches of the three main totoaba fishing fleets. Historically, the

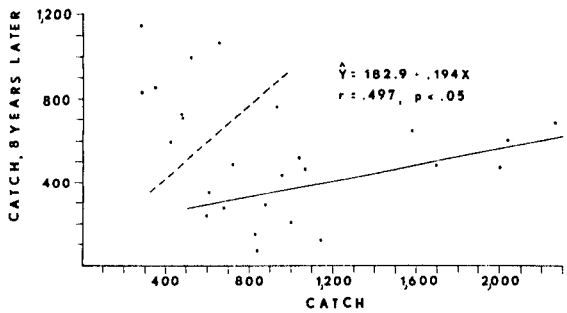

FIGURE 10.—Totoaba catch plotted against catch 8 yr previous. This examines for evidence of reduction in breeding stock by overfishing. All data are from Figure 1, in metric tons. Points above dashed line are for the 1952-59 period. The breeding sanctuary was established in 1955 and the points corresponding to the years 1955-59 may reflect enforcement of this regulation (see text).

TABLE 2.—Prime season catch,[1] in metric tons, of the three principal totoaba fishing ports, 1964-75. Data for 1965-70 period are from Arvizu and Chávez (1972). Data for 1971-75 were provided by H. Chávez (pers. commun.). The 1974-75 data are preliminary but are not expected to increase by more than 10% from these figures.

Year	Puerto Peñasco	Golfo de Santa Clara	San Felipe
1964	72.7	128.4	277.7
1965	97.0	561.2	57.0
1966	177.5	388.6	488.7
1967	188.3	173.4	334.7
1968	37.9	385.7	290.0
1969	60.2	213.8	160.9
1970	27.2	248.7	169.4
1971	69.0	46.0	95.0
1972	52.0	86.0	104.0
1973	88.0	21.0	37.0
1974	51.0	17.0	52.0
1975	49.0	4.0	5.0

[1]Catch is calculated by adding January-April yields as recorded in the official statistics.

Puerto Peñasco fleet catches fewer totoaba than either the San Felipe or Golfo de Santa Clara fleets (Table 2). This is a logical result of the fishing methods and areas worked by the three fleets. However during the last 3 yr, Puerto Peñasco has equalled or exceeded the other ports in recorded totoaba yield despite no apparent increase in effort. Our interpretation of this new trend is that the migrant population, encountered first by the Puerto Peñasco fleet along the Sonora shore, is being decimated before reaching the spawning grounds.

CONCLUSIONS

Our review of the history of exploitation of the stock, our data on spawning concentrations, breeding migration, and juvenile habitat, and our analyses of proposed hypotheses for the decline of the fishery have emphasized points of population vulnerability. Fleets of the three major ports are highly skilled at finding the migrant schools of totoaba. They have, in a sense, specialized to exploit the ascent, resident, and descent phases of the breeding migration, both by nature of their vessels and their port facilities, and by consequence of their geographic locations. This level of exploitation is possible only because the fishers are able to predict with accuracy the migration pattern. In the past, the commercial population level was high and the temporal nature of the port specializations was not a factor in the ranking of port yields. Now, when the population level has reached an all-time low, the Puerto Peñasco fleet seems to have some new advantage.

The totoaba breeding behavior we describe serves to render the resident spawning population especially vulnerable to fishing effort. Frenzied spawning in dense aggregations following a period of behavioral stimulation insures that when a net is encountered, the capture rate will be particularly high. Our capture incidence, daily catch, and gonadal maturation data confirm the consequences of these attributes. The bathymetry of the delta restricts the spawning schools to highly limited areas. These areas, or channels, are the prime fishing sites for the Golfo de Santa Clara fleet. They appear to lie (by our estimate) partially within the breeding sanctuary established by the Mexican Government.

We reiterate here the artificial fishing mortality suffered by juveniles in their forced crossing of the near-delta waters as they make their way south from the nursery grounds. We have documented some known nursery sites and have suggested characteristics of the juvenile habitat which may have predictive value in future surveys of the area.

We have examined the three most probable factors responsible for the decline in totoaba stock. Subject to the limitations of our catch and flow data, our results suggest that overfishing has played the most significant role during the pre-1958 catch period. We speculate that the low yields of the 1956-59 period may have been due to enforcement of the breeding sanctuary regulation and that this partial temporary relief from exploitation may, together with increased gear efficiency, have been responsible for the second peak in totoaba production. If this is true, then the power of regulatory measures for recovery of this commercial stock has been demonstrated. The correlation of annual yield with annual Colorado River flow, though weakened by statistical irregularities, attests to the importance of some flow-related quality of the spawning grounds. Degradation of the spawning grounds, possibly in the ability to provide olfactory cues, also may have resulted in a decline of the commercial population. According to our results, degradation of the nursery grounds, through deterioration of some unknown flow-related quality, has probably not played a significant role in the fishery's decline.

Although it may be possible to ignore statistical analyses and the conclusions therefrom, one cannot deny that the annual yield in 1975 was the minimum recorded in the history of the fishery, a mere 2.5% of the highest recorded catch. The area of the fishery has shrunk to a small fraction of its

former size, and catch events have become sporadic and undependable. The span of the breeding period has been reduced from several months to a period of only 18 days within the open season of 1972. Of those 18 days, a majority of the catch occurred on 21 and 22 March. Although data are scarce, the average size of adult fish is reduced and in recent years most commercially caught individuals have probably been first- or second-year spawners. These harsh facts are indications of a fish population struggling unsucessfully for survival under pressure.

The future of the species is uncertain. Until the recent action of the Mexican Government in establishing a total closed season, the outlook was bleak, indeed. While the commercial fishery was ready to crash before its legal cancellation (a number of financial failures were reported to us), and would presumably never have hunted down and eliminated the last reproductive pair of these magnificent animals, the continued rising prices for totoaba in a seller's market would have guaranteed continued maximum pressure. If there are behavioral elements in the reproductive pattern of the species which require mutual stimulation in large schools for reproductive success, a threshold may have already been crossed which will drive the totoaba the way of the passenger pigeon. The trends produced by irreversible change of the spawning ground may prove more important than we have speculated. In either of the last two circumstances, the ability of the stocks to rebound upon release of fishing pressure may be critically impaired.

We suggest three meaningful measures at this stage: 1) Continuation of the total closed season which has been imposed, until intensive studies document a strong and vigorously increasing population. We suggest an enforcement period of about 1½ times our estimated 6-yr minimum recruitment age, or 10 yr. 2) Action by the U.S. Government (the major market area) complementing the Mexican action by declaring the totoaba an endangered species, to facilitate enforcement of the neighbor country laws by removing much of the stimulus for poaching and smuggling. 3) Intensive scientific investigation to provide knowledge of the species' autecology and behavior with potential application to all facets of management, ranging from environmental manipulation to hatchery techniques. Failing these, we conclude that the probability of extinction of *Cynoscion macdonaldi* by the year 2000 is high.

ACKNOWLEDGMENTS

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LITERATURE CITED

ARVIZU, J., AND H. CHAVEZ.
1972. Sinopsis sobre la biología de la totoaba, *Cynoscion macdonaldi* Gilbert, 1890. FAO (Food Agric. Organ. U.N.) Fish. Synop. 108, 21 p.

BERDEGUE, A. J.
1955. La pesqueria de la totoaba (*Cynoscion macdonaldi* Gilbert) en San Felipe, Baja California. Rev. Soc. Mex. Hist. Nat. 16:45-78.
1956. Peces de importancia comercial en la costa noroccidental de Mexico. Secre. Mar., Dir. Gen. Pesca Ind. Conexas, 345 p.

BREDER, C. M., JR., AND D. E. ROSEN.
1966. Modes of reproduction in fishes. Natural History Press, Garden City, N.Y., 941 p.

CANNON, R.
1966. The Sea of Cortez. Lane Magazine and Book Co., Menlo Park, Calif., 283 p.

CHAVEZ, H.
1973. Descripción de los ejemplares juveniles de totoaba, *Cynoscion macdonaldi* Gilbert. Rev. Soc. Mex. Hist. Nat. 34:293-300.

CHUTE, G. R.
1928. The totuáva fishery of the California Gulf. Calif. Fish Game 14:275-281.
1930. Seen Kow, a regal soup-stock. Calif. Fish Game 16:23-35.

CRAIG, J. A.
1926. A new fishery in Mexico. Calif. Fish Game 12:166-169.

CROCKER, R. S.
1932. The white sea-bass and related species that are sold in California fish markets. Calif. Fish Game 18:318-327.

FITCH, J. E.
1949. Mexican corbina and totuava. *In* The commercial fish catch of California for the year 1947 with an historical review 1916-1947, p. 83-84. Calif. Dep. Fish Game, Fish Bull. 74.

GABRIELSON, I. N., AND F. R. LAMONTE.
1954. The fisherman's encyclopedia. Stackpole Co., Harrisburg, Pa., 730 p.

GAUSE, C. I.
1969. A fish threatened. Underwater Nat. 6:28-31.

GILBERT, C. H.
1891. Scientific results of the explorations by the U.S. Fish Commission steamer Albatross. No. XII—A preliminary report on the fishes collected by the steamer Albatross on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proc. U.S. Natl. Mus. 13:49-126.

GUEVARA, S.
1974. Sobre le eclogía de los juveniles de totoabe *Cynoscion macdonaldi* Gilbert. (Abstr.) *In* Resúmenes Quinto Congreso Nacional de Oceanografia, 22 Oct. 1974, p. 7. Guaymas, Sonora, Mexico.

JORDAN, D. S.
1916. Notes on the totuava (*Cynoscion macdonaldi* Gilbert). Copeia 1916:85.

JORDAN, D. S., AND B. W. EVERMANN.
1898. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47, Part 2:1241-2183.
1902. American food and game fishes. Doubleday, Page & Co., N.Y., 573 p.

JORDAN, D. S., B. W. EVERMANN, AND H. W. CLARK.
1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. U.S. Bur. Fish., Rep. U.S. Comm. Fish. 1928. Part II. Append. 10, 670 p. (Doc. 1055.)

LANHAM, U.
1962. The fishes. Columbia Univ. Press, N.Y., 116 p.

SCHREIBER, J. F., JR.
1969. Changes in Colorado River flow. *In* D. A. Thomson et al. (editors), Environmental impact of brine effluents on Gulf of California, p. 83-87. U.S. Dep. Int., Off. Saline Water, Res. Dev. Prog. Rep. 387.

SOTOMAYOR, C.
1970. La totoaba, una especia que se extingue lentamente. Téc. Pesq. 3:22-25.

THOMPSON, R. W.
1968. Tidal flat sedimentation on the Colorado River Delta, northwestern Gulf of California. Geol. Soc. Am., Mem. 107, 133 p.

THOMSON, D. A.
1969. The commercial fisheries industry. *In* D. A. Thomson et al. (editors), Environmental impact of brine effluents on Gulf of California, p. 100-103. U.S. Dep. Int., Off. Saline Water, Res. Dev. Prog. Rep. 387.

U.S. GEOLOGICAL SURVEY.
1954. Compilation of records of surface waters of the United States through September 1950. Part 9. Colorado River Basin. [U.S.] Geol. Surv. Water-Supply Pap. 1313, 749 p.
1964. Compilation of records of surface waters of the United States, October 1950 to September 1960. Part 9. Colorado River Basin. [U.S.] Geol. Surv. Water-Supply Pap. 1733, 586 p.
1970. Surface water supply of the United States 1961-65. Part 9. Colorado River Basin. Vol. 3. Lower Colorado River Basin. [U.S.] Geol. Surv. Water-Supply Pap. 1926, 571 p.

UPTAKE, DISTRIBUTION, AND DEPURATION OF ^{14}C-BENZENE IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND STRIPED BASS, *MORONE SAXATILIS*

SID KORN,[1] NINA HIRSCH,[2] AND JEANNETTE W. STRUHSAKER[2]

ABSTRACT

The uptake, distribution, and depuration of water-soluble, monocyclic hydrocarbon contained in petroleum and refined products was studied in two species of marine fish. Mature northern anchovy, *Engraulis mordax*, and juvenile striped bass, *Morone saxatilis*, were exposed to sublethal concentrations of ^{14}C-benzene for 48 h. Residues in tissues exhibiting a high lipid content or representing apparent major metabolic sites were measured during the exposure and afterwards when the fish were transferred to clean seawater. Fish exhibited a rapid uptake over a wide range of benzene concentrations in the water column. Accumulation in anchovy was considerably greater than in striped bass. Results indicate that the pathway of hydrocarbons through the liver, gallbladder, intestines, and colon is a major depuration route. Residues were depurated rapidly after cessation of exposure; in striped bass tissues most residues were undetectable by 7 days.

Increased drilling, transportation, and refining of crude oils near or on coastal waters has led to the need for research on the effects of oil on estuarine biota. Considerable public concern has evolved from such occurrences as tanker spills and the Santa Barbara well blowout. However, long-term sublethal effects of low levels of oil in inshore areas may be of greater importance to marine populations than short-term lethal effects of high levels resulting from catastrophic events such as tanker spills and drilling blowouts. It is important to study the effects of chronic oil exposure on marine organisms.

Benzene is a principal aromatic oil component (up to 6.75 ppm in the water-soluble extract [Anderson et al. 1974]) that is relatively water soluble (1,993 μl/liter [Benville and Korn 1974]) and has significant effects on fishes (Brocksen and Bailey 1973; Korn et al. in press). The preceding studies demonstrated the effects of benzene on the nervous system, respiration, and growth of fish. Brocksen and Bailey showed latent effects of benzene on respiratory response lasting up to 6 days after fish were placed in clean water.

Concentrations of highly volatile monocyclic aromatics such as benzene are not thought to be very high in areas subject to chronic exposure to oil. However, measurements of monocyclic aromatics in such situations are scarce. Our preliminary measurements in San Francisco Bay indicate a maximum range from 1 to 10 μl/liter benzene in relatively unpolluted bay areas. Although the chronic levels are low, if fish accumulate benzene over field concentrations and if energy is required to metabolize, detoxify, and depurate accumulated aromatics, detrimental long-term physiological effects are possible.

Investigators such as Lee, Sauerheber, and Benson (1972); Lee, Sauerheber, and Dobbs (1972); Anderson et al. (1974); and Lee (1975) examined uptake of higher aromatics in invertebrates and fish, but no work has been done with benzene.

The fish we studied were San Francisco Bay species but also occur widely in other areas where chronic oil pollution may pose a problem. Striped bass, *Morone saxatilis*, is an important recreational species on the west and east coasts, while northern anchovy, *Engraulis mordax*, is not only a major forage fish for striped bass but also constitutes the greatest biomass of any fishery in the California Current.

The objective of this study was to determine the uptake, distribution, and depuration of benzene in these two species of fishes.

METHODS

Adult northern anchovies were obtained from a local bait dealer and acclimated under controlled

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environmental conditions comparable to those used in experiments. Juvenile striped bass were obtained from the water diversion facilities of the Bureau of Reclamation at Tracy, Calif. Fish were acclimated in 2,000-liter circular tanks for at least 2 wk before testing and fed ground squid once daily to satiation.

In all uptake studies, an appropriate number of fish (Table 1) were transferred into oval 200-liter test tanks and further acclimated for 1 wk. The number of fish per tank was limited to the number (≤1 g/liter) that could be maintained during a 48-h static exposure period when oxygen is a limiting factor. The 48-h static exposure period instead of an open-system constant exposure was necessitated by the expense of the ^{14}C-benzene required for a relatively large volume of water. Except for the 48-h static exposure period, a flow of 1 liter/min of filtered seawater was maintained throughout. During flow periods the salinity and temperature of the water were monitored and controlled by the seawater system components (Korn 1975), whereas temperature was not controlled during the static exposure period.

Stock benzene solutions used for dosing the exposure tanks were prepared as follows: A saturated benzene solution (1 ml benzene in 250 ml seawater) was prepared in a separatory funnel by vigorous shaking and then allowed to settle for 1 h. The resulting solution was analyzed by the gas chromatography method of Benville and Korn (1974). Next, ^{14}C (99.9% ring-labeled benzene, specific activity, 85 μCi/mmol) was mixed with another 200 ml of seawater to make a stock solution and was kept frozen until used. The saturated benzene solution was then mixed with ^{14}C stock solution to the proper specific activity, and the appropriate volume was poured into each tank and mixed by gentle stirring. After mixing, 1-ml water samples were added to a scintillator (10-ml Packard Instagel)[3] and the benzene concentration was measured. Carbon 14 counting was done on a Packard Model 2008 Tri-Carb liquid scintillation spectrometer system. Internal standardization yielded 85% counting efficiency, and all water values were corrected accordingly.

Uptake, distribution, and depuration were determined by sampling fish, rinsing them externally with methanol to remove adsorbed benzene, dissecting out tissues, weighing tissue samples (<200 mg), placing each tissue in a vial with tissue digester solution (1 ml/100 mg tissue Packard Soluene-100), and allowing 48-h digestion at room temperature. Scintillator (10-ml Packard Dimilume) was added to these samples and ^{14}C radioactivity measured. Approximate mean counting efficiencies of 60% and 67% were calculated from spiked samples and used to correct anchovy and striped bass tissue residue values respectively. Water and tissue samples yielding below 40 counts per minute were considered below the detectable limits of our system.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.–Summary of experimental conditions for ^{14}C-benzene uptake and depuration tests with northern anchovy and striped bass. Salinity was 24-26‰

Species and test number	Specific activity (cpm/nl)	Initial mean benzene concentration[1] (μl/liter)	Tanks per concentration	Fish per tank	Time of tissue sampling[2] (days)	Total wet wt (g) Mean	Total wet wt (g) SD	Type of tissue examined
Northern anchovy:								
1	0.11	3.7	3	8	0.042, 0.125, 0.25, 1, 2	17.03	6.55	Liver, brain, gill, muscle
2a	5	0.11	4	8	0.042, 0.25, 1, 2, 4	12.93	5.04	Liver, brain, gill, muscle, gallbladder, intestine
2b	5	0.0097	4	8	0.042, 0.25, 1, 2, 4	11.70	4.74	Liver, brain, gill, muscle, gallbladder, intestine
3a	40	0.0048	4	8	0.25, 1, 2, 3, 4, 7	12.74	3.35	Liver, brain, gill, muscle, gallbladder, intestine
3b	320	0.00069	4	8	0.25, 1, 2, 3, 4, 7	13.94	4.46	Liver, brain, gill, muscle, gallbladder, intestine
Striped bass:								
4	5	0.088	9	5	0.25, 1, 2, 3, 4, 5, 6, 7, 8, 9	76.87	34.60	Liver, brain, gill, muscle, gallbladder, intestine, mesenteric fat, colon, heart, stomach

[1]Exposure to ^{14}C-benzene was static for 48 h followed by resumption of water flow for the duration. Recent analyses by gas-liquid chromatography yielded 0.00015-0.0010 μl/liter background benzene concentration in the seawater at this facility which is not included in these values.

[2]One fish per tank at each sampling time.

Water samples were taken first; then tissues were sampled until open flow was reestablished. Tissues were sampled as noted for each of the four experiments included in this report (Table 1). It is recognized that the residues reported may contain metabolites and degradation products in addition to benzene.

The original data on declining seawater concentrations of benzene during tests and on decreasing concentrations of residues in fish tissues during depuration were first analyzed with a least-squares curve-fitting computer program to determine if the hypothesized function was the best fit. Linear regression analyses were then performed on logarithmically transformed data, and regression coefficients were tested for significance of differences between slopes and a pooled regression coefficient (Snedecor and Cochran 1968).

RESULTS

There were no deaths during the tests. The benzene concentration in the seawater declined exponentially ($\hat{Y} = ae^{-0.0183X}$, where $\hat{Y}$ is concentration and X is time) during all tests. After 24-h exposure, 48-65% remained; after 48 h, 30-43% remained, at which point the water flow was renewed (Table 2).

In general, accumulation in striped bass was greatest in the gallbladder, followed by mesenteric fat, colon, intestine, liver, brain, gill, heart, stomach, and muscle (Table 3). Anchovy exhibited similar results minus the mesenteric fat, colon, heart, and stomach tissues, which were not sampled. The order of decreasing accumulation varied slightly according to experiment. The gallbladder accumulated 53.4-8,450 times the initial water concentration, while muscle accumulated 1.11-135 times the initial water concentration. Maximum concentrations were obtained in the tissues from 0.25 to 4 days after starting exposure. Mesenteric fat, gallbladder, liver, and intestine usually reached a maximum accumulation later than the other tissues.

Accumulation in anchovies was considerably greater than in striped bass in the tissues measured in both species (Figures 1, 2; Table 3). The pattern of uptake in the gill and gallbladder was

TABLE 2.–Benzene concentration during 48-h exposure period. Exponential decline ($Y = ae^{-bX}$); coefficients for each experiment from least-squares curve fitting.

Test no.	Benzene-seawater actual initial concentration µl/liter	nl/liter	n	a	b	Percentage remaining after 24 h	48 h
1	3.7	3,700	15	3.53	−0.1997	54	30
2a	0.110	110	16	0.104	−0.02381*	54	31
2b	0.097	9.7	16	0.094	−0.01262*	65	—
3a	0.0048	4.8	12	0.00457	−0.01983	48	42
3b	0.00069	0.69	12	0.000692	−0.01847	62	42
4	0.088	88	27	0.0991	−0.01813	65	43

*No significant difference between slopes (at $\alpha = 0.05$) except between tests 2a and 2b.
The equation $Y = ae^{-0.0183X}$ describes the exponential decline in benzene, using a pooled regression coefficent.

TABLE 3.–Mean maximum concentration factors[1] in various tissues and days elapsed (numbers in parentheses) from beginning of exposure for northern anchovy and striped bass.

Species and test number	Initial mean benzene-seawater concentration (µl/liter)	Concentration factor in tissue of: Gill	Brain	Muscle	Fat	Heart	Stomach	Liver	Gall-bladder	Intestine	Colon
Northern anchovy:											
1	3.7	34.3 (2)	30.0 (2)	22.7 (1)	—	—	—	45.1 (1)	—	—	—
2a	0.11	41.8 (1)	41.8 (1)	10 (1)	—	—	—	54.6 (0.25)	4,360 (2)	209 (2)	—
2b	0.0097	113 (1)	113 (1)	29.9 (0.25)	—	—	—	309 (2)	8,450 (2)	505 (2)	—
3a	0.0048	7.92 (0.25)	7.5 (0.25)	5.42 (4)	—	—	—	66.7 (4)	229 (2)	60.4 (2, 3)	—
3b	0.00069	7.1 (0.25)	9.13 (0.25)	135 (4)	—	—	—	31.9 (2)	116 (3)	34.8 (2)	—
Striped bass:											
4	0.088	5.57 (1)	7.16 (0.25)	1.11 (0.25)	1.14 (0.25)	2.95 (0.25)	2.72 (0.25)	9.77 (0.25)	53.4 (2)	5.45 (0.25)	14.8 (0.25)

[1]Factor X (benzene-seawater concentration in microliter per liter) = actual nanoliters per gram mean tissue value or (benzene in nanoliters) / (tissue wet weight in grams).

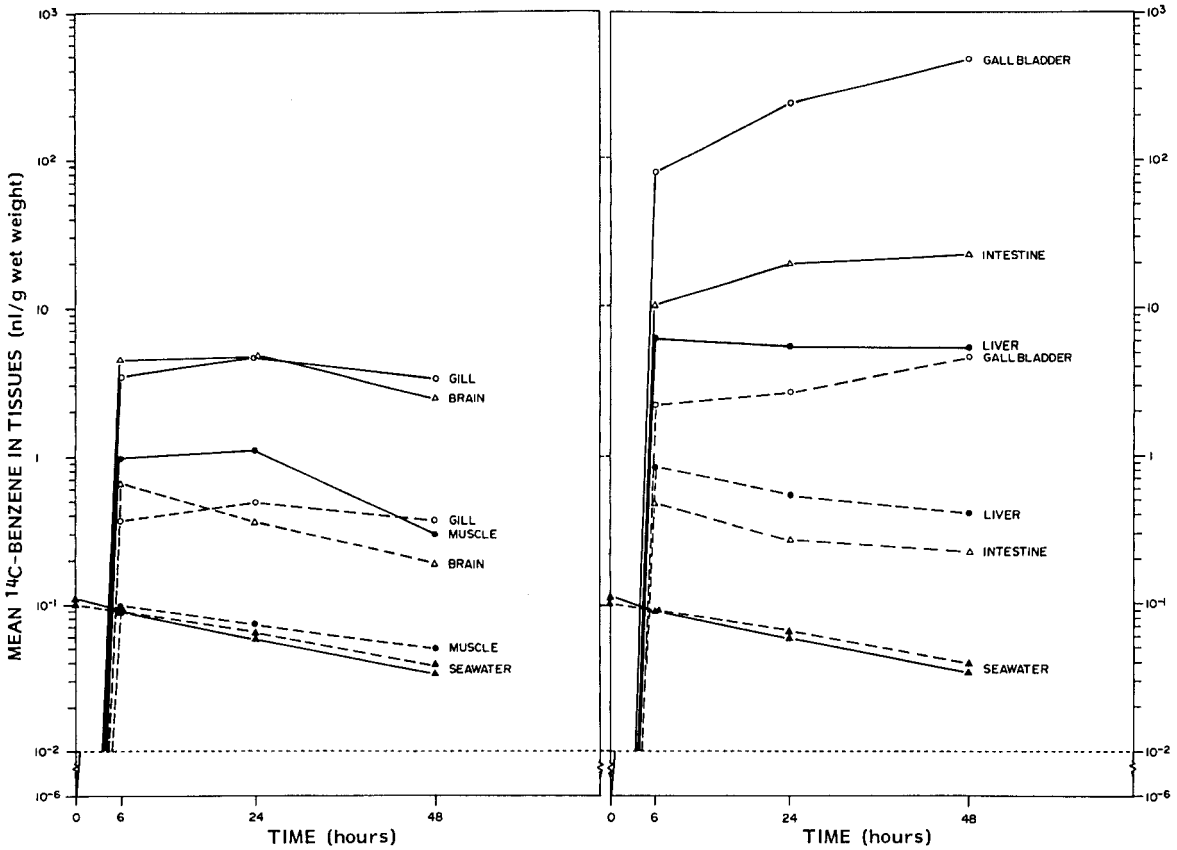

FIGURE 1.–Mean ^{14}C-benzene uptake in tissues (nl/g wet weight) in anchovy (solid lines) and striped bass (dashed lines); sample number: three or four fish. Also shown are mean ^{14}C-benzene concentrations in seawater in anchovy tanks (solid lines) and in striped bass tanks (dashed lines); sample number in Table 2. The concentrations on the Y-axis are calculated from total ^{14}C radioactivity and may include metabolites of benzene.

similar between species, while in the brain, liver, muscle, and intestine, a maximum level was maintained longer in the anchovy. In both species, the greatest rate of uptake occurred in the first 6 h.

Residues were depurated rapidly after cessation of exposure (Table 4). Gallbladder, mesenteric fat, liver, and gill maintained residues the longest. Depuration appeared to occur more rapidly in striped bass than in anchovies in some tissues. In striped bass, depuration is generally described by the logarithmoc form of a power function ($\ln \hat{Y} = \ln a + b \ln X$) after cessation of exposure on day 2 until day 4 or 5 (Figure 3). Subsequently, several of the tissues showed a secondary increase and decrease in concentration. In muscle tissue, residues were undetectable 24 h after exposure ended.

DISCUSSION

Accumulation levels are based solely on radiometric analysis. This analytical technique does not distinguish between ^{14}C-labeled benzene and derived ring metabolites. Complementary analysis by thin-layered chromatography or gas chromatography could have determined some of the actual compounds present, but it was not performed during these experiments. It is hypothesized that fish are capable of excreting and metabolizing benzene. Although there is no direct evidence, the residues reported in selected tissues may be representative of the unchanged parent benzene or associated metabolites and degradation products. Any or all of these may be toxic to fish.

Benzene and/or metabolites accumulate

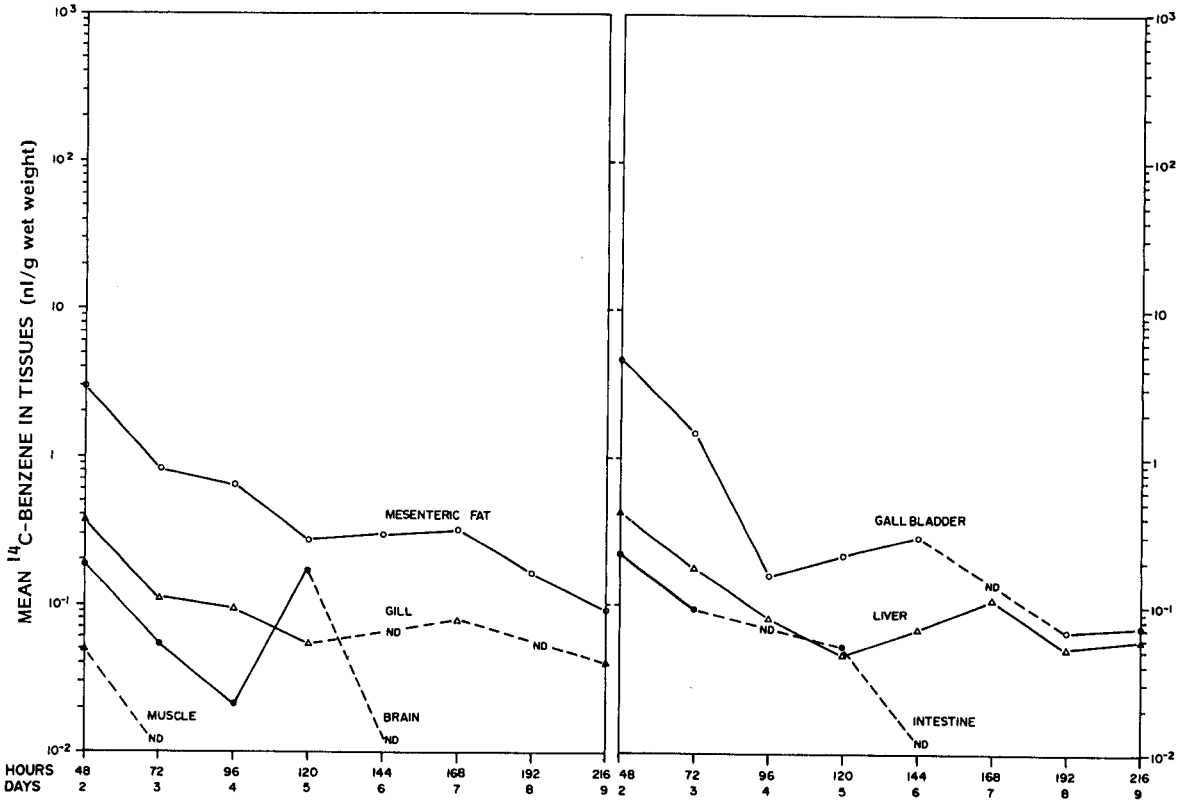

FIGURE 2.–Mean ^{14}C-benzene depuration from tissues (nl/g wet weight) of striped bass; sample number in Table 4. ND = nondetectable level (see Methods). The concentrations on the Y-axis are calculated from total ^{14}C radioactivity and may include metabolites of benzene.

predominantly in tissues that exhibit a high lipid content or represent apparent major metabolic sites. Thus, lipid-rich mesenteric fat and brain tissues had high accumulations; while liver, gallbladder, intestine, and colon (which are tissues associated with the metabolic breakdown and excretion of benzene) also accumulated benzene to higher levels (Table 3).

TABLE 4.–Percent residues[1] remaining in northern anchovy and striped bass after termination of 48-h exposure to benzene. (Sample sizes in parentheses.)

	Northern anchovy[2]		Striped bass[2]						
	Test 2a	Test 2b	Test 4						
	Days from termination of exposure								
Tissue	2	2	1	2	3	4	5	6	7
Gill	61(3)	26(2)	30(3)	25(3)	14(2)	ND[3]	21(3)	ND	11(1)
Brain	22(4)	42(1)	29(2)	11(1)	95(2)	ND	ND	ND	ND
Muscle	93(3)	ND	ND	ND	ND	ND	ND	ND	ND
Fat	—	—	28(2)	21(2)	9.0(4)	9.7(4)	11(4)	5.3(4)	3.0(2)
Heart	—	—	38(1)	ND	ND	ND	ND	ND	ND
Stomach	—	—	ND	ND	35(1)	ND	ND	ND	106(1)
Liver	70(4)	13(2)	43(3)	20(3)	11(3)	16(3)	26(3)	12(2)	14(1)
Gallbladder	69(4)	63(3)	32(4)	3.4(2)	4.7(3)	6.2(3)	ND	1.4(2)	1.3(1)
Intestine	70(4)	17(3)	42(4)	ND	24(1)	ND	ND	ND	ND
Colon	—	—	44(3)	26(2)	ND	ND	ND	ND	ND

[1]Actual nanoliters per gram tissue residues = (benzene in nanoliters) / (tissue wet weight in grams) (mean tissue residue) / 48-h mean tissue residue) (100% residue).
[2]The initial mean benzene seawater concentrations (ul/liter) were 0.11 for test 2a, 0.0097 for test 2b, and 0.088 for test 4.
[3]ND = nondetectable.

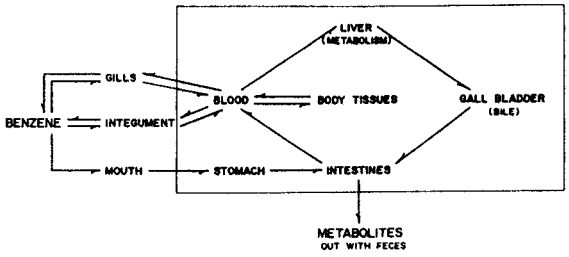

FIGURE 3.–Hypothetical pathway and distribution of benzene in fish.

Figure 3 shows a hypothetical distribution and pathway of benzene in fish which is substantiated by our results. Benzene is absorbed across the gills into the blood where, being lipid soluble, it attaches to the erythrocytes and lipoproteins (Gerarde 1960). It is then translocated via the blood to the tissues where it either accumulates or is metabolized. Parke (1968), Meyers (1970), and Lee, Sauerheber, and Dobbs (1972) described metabolism of benzene to phenol in the liver of fish and mammals. The metabolites are excreted from the liver with the bile and stored in the gallbladder. From the gallbladder the bile is excreted into the intestine and finally eliminated through the colon with the feces. Our results show high accumulation in the liver and gallbladder. Lee, Sauerheber, and Dobbs (1972) also found the gallbladder of fish to be a storage site for polycyclic aromatic compounds. Our results indicate that the pathway through the liver, gallbladder, intestine, and colon is a major depuration route. These tissues take the longest to accumulate and depurate. This is probably due to the time needed for metabolism of benzene. The gill also was one of the tissues which depurated later. Some unchanged benzene metabolites are probably excreted across the gills.

The secondary increase in ^{14}C radioactivity (days 4-7) observed after initial depuration (days 2-4) in several striped bass tissues (Figure 3) is difficult to interpret. One explanation may be that the metabolism of benzene is limited to a certain rate and that until the initial metabolism is complete, some benzene accumulates in nonmetabolic tissues and is not totally metabolized until later. The secondary increase in residues in fat and brain tissues, however, suggests that perhaps metabolites such as phenol are accumulating in the tissues for a period before they too are depurated. Additional work with uptake and depuration in herring tissues shows a similar pattern. Further research must be done to clarify this point.

The low accumulation tissues such as heart, muscle, and stomach are also low in lipid content and apparently do not directly contribute to the metabolism of benzene. Lee, Sauerheber, and Dobbs (1972) found similar results with naphthalene and benzopyrene in fish. Later work at Tiburon has demonstrated that little benzene and/or metabolites accumulate in the kidney tissue of herring. Because of this and the fact that fish in salt water excrete little urine, we feel the kidneys are not a major depuration pathway in fish from saline waters. Further study of urinary depuration is needed.

Northern anchovies are schooling fish, and they swam constantly during the tests–striped bass were more sedentary. This difference in activity might explain the higher accumulation in anchovies.

The short duration of low-level water column exposures of benzene in these experiments did not reveal obvious detrimental effects on behavior or physiology of fish. However, equilibrium accumulation levels have not been obtained because of the static exposure with decreasing benzene-water concentration. During chronic exposures, higher accumulations of benzene and toxic metabolites (such as phenol) with deleterious effects are possible. Further, because of the rapid uptake rate over a wide range of concentrations, it is conceivable that both species could accumulate significant benzene levels after brief exposure during an oil spill. The severity of effects at chronic and acute levels will depend greatly on the energy requirements of the fish and the degree of stress to which they are already subjected. Fish in spawning condition are particularly susceptible to additional stress from pollutants (e.g., spawning Pacific herring [Struhsaker[4]]). Further study of uptake in the lipid-rich mature ovaries of fish should be done.

The rapid depuration of benzene the first day after exposure ended appears to be due to metabolism and excretion via the liver-intestine route. Because of this rapid depuration, the possibility of bio-amplification in fish does not appear

[4]Struhsaker, J. W. Effects of benzene (a toxic component of petroleum) on spawning Pacific herring. Manuscr. in prep. Southwest Fish. Cent. Tiburon Lab., Natl. Mar. Fish. Serv., NOAA, Tiburon, CA 94920.

likely, at least after exposure from the water. Exposure from the ingestion of food organisms may result in a different metabolic process, however, and this work should be done before further conclusions are made. Our results from uptake studies with a rotifer (*Brachionus plicatilus*) (Echeverria[5]) and those of Lee, Sauerheber, and Benson (1972) and Lee (1975) with mollusks and zooplankton indicate that some invertebrates may be unable to metabolize aromatic hydrocarbons—accumulating them to very high levels and depurating them slowly. Fish feeding on such organisms may be exposed to high and potentially damaging levels of aromatics.

Additional chronic uptake studies under continuous-flow conditions are needed. Analyses of metabolites are proceeding and will be reported later.

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LITERATURE CITED

ANDERSON, J. W., J. M. NEFF, B. A. COX, H. E. TATEM, AND G. M. HIGHTOWER.
1974. Characteristics of dispersions and water-soluble extracts of crude and refined oils and their toxicity to estuarine crustaceans and fish. Mar. Biol. (Berl.) 27:75-88.

BENVILLE, P. E., JR., AND S. KORN.
1974. A simple apparatus for metering volatile liquids into water. J. Fish. Res. Board Can. 31:367-368.

BROCKSEN, R.W., AND H. T. BAILEY.
1973. Respiratory response of juvenile chinook salmon and striped bass exposed to benzene, a water-soluble component of crude oil. *In* Proceedings of joint conference on prevention and control of oil spills, p. 783-791. Am. Pet. Inst., Environ. Prot. Agency, U.S. Coast Guard, Wash., D.C.

GERARDE, H. W.
1960. Toxicology and biochemistry of aromatic hydrocarbons. Elsevier Publ. Co., N.Y., 329 p.

KORN, S.
1975. Semiclosed seawater system with automatic salinity, temperature, and turbidity control. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-694, 5 p.

KORN, S., J. W., STRUHSAKER, AND P. BENVILLE, JR.
1976. Effects of benzene on the growth, fat content, and caloric content of striped bass, *Morone saxatilis*. Fish. Bull., U.S. 74: 694-698.

LEE, R. F.
1975. Fate of petroleum hydrocarbons in marine zooplankton. *In* American Petroleum Institute, 1975 Conference on Prevention and Control of Oil Pollution. Proceedings March 25-27, 1975 San Francisco, Calif., p. 549-553. Am. Pet. Inst., Environ. Prot. Agency, U.S. Coast Guard.

LEE, R. F., R. SAUERHEBER, AND A. A. BENSON.
1972. Petroleum hydrocarbons: Uptake and discharge by the marine mussel Mytilus edulis. Science (Wash., D.C.) 177:344-346.

LEE, R. F., R. SAUERHEBER, AND G. H. DOBBS.
1972. Uptake, metabolism and discharge of polycyclic aromatic hydrocarbons by marine fish. Mar. Biol. (Berl.) 17:201-208.

MEYERS, F. H.
1970. Review of medical pharmacology. Lange Medical Publishing Co., Los Altos, Calif., 155 p.

PARKE, D. V.
1968. The biochemistry of foreign compounds. Pergamon Press, Oxf., 269 p.

SNEDECOR, G. W., AND W. G. COCHRAN.
1968. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

[5]Echeverria, T. Uptake, storage and depuration of ^{14}C-labeled benzene in the rotifer, *Brachionus plicatilis*. Manuscr. in prep. Southwest Fish. Cent. Tiburon Lab., Natl. Mar. Fish. Serv., NOAA, Tiburon, CA 94920.

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VON BERTALANFFY GROWTH CURVES FOR STRIPED MARLIN, *TETRAPTURUS AUDAX*, AND BLUE MARLIN, *MAKAIRA NIGRICANS*, IN THE CENTRAL NORTH PACIFIC OCEAN

ROBERT A. SKILLMAN AND MARIAN Y. Y. YONG[1]

ABSTRACT

The growth of striped marlin, *Tetrapturus audax*, and blue marlin, *Makaira nigricans*, was described by fitting von Bertalanffy growth curves (an assumed age model and a length-increment model) to the progression of age-groups, by quarters, through the Hawaiian longline fishery from 1960 to 1970. For striped marlin, the sexes grew at about the same rate and had similar predicted asymptotic maximum fork lengths, 277.4-314.4 cm for males and 288.7-326.2 cm for females. For blue marlin, the sexes grew at about the same rate until 250 cm. Above this length, the growth rate of males declined and an asymptotic maximum length of 298.8-368.0 cm was predicted. For females above 250 cm, the growth continued at a rapid rate; exhibiting little tendency toward an asymptote over the range of ages available to the study.

While blue marlin, *Makaira nigricans* Lacépède, are important in the U.S. sport fishery in California, Florida, and Hawaii and striped marlin, *Tetrapturus audax* (Philippi), are important in California and Hawaii, little is known about their population characteristics or parameters. In particular, growth of these species has received little attention. In this paper, the growth of striped and blue marlins is described by fitting von Bertalanffy growth curves to age-groups separated from length-frequency data collected in Hawaii.

A review of the literature revealed four papers dealing with the growth of marlins. In them, growth was examined by plotting the progression of mean sizes for age-groups separated from size-frequency data by month or some other time interval; the fitting of a functional growth model (e.g., von Bertalanffy or Gompertz) was not discussed or attempted. Royce (1957) studied striped marlin in the Hawaiian longline fishery (1949-52) and concluded that small (13.6-17.7 kg) and large (45.3-49.4 kg) size classes grew about 13.6 kg per year. De Sylva (1957) studied the growth of sailfish, *Istiophorus platypterus* (Shaw and Nodder), in the Atlantic from records obtained primarily from sport catches. His growth curve, fitted by eye, showed an extremely rapid rate of growth: 180 cm total length in the first year of life and 30 cm in the second. Maximum age was estimated as IV. De Sylva and Davis (1963) compared data for the white marlin *T. albidus* Poey, and the sailfish and concluded that white marlin live longer than sailfish. Koto and Kodama (1962), studying the growth of sailfish caught near Japan, found an annual growth of 35 cm for a 140-175 cm eye orbit-fork length group, 20 cm for a 176-195 cm group, and 15 cm for a 196-210 cm group.

The objective of this study was to quantitatively describe the growth of striped and blue marlins using a model that adequately followed the observed data and provided estimates of growth parameters, which could be incorporated into analytical models of population dynamics. Since the von Bertalanffy growth model satisfied these conditions, it was used in this study. Specifically for striped marlin, growth parameters were sought by sex for individual cohorts and then for data pooled over all years. For blue marlin, growth parameters were sought by sex only for data pooled over all years because the data were insufficient to work with individual cohorts. By pooling across years, the assumption was made that the populations under study were in or tending toward a steady state. As such, yearly variations in mean lengths of age-groups as well as variations in growth parameters between cohorts were treated as homogeneous sets of responses to variations in the environment.

MATERIALS

From April 1960 through April 1970 at the

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auction blocks of the fresh fish markets in Honolulu, the staff of the Honolulu Laboratory, National Marine Fisheries Service, NOAA, collected weight and sex data from large pelagic species caught by the Hawaiian longline fleet. Details of the longline fishery are given by June (1950) and Otsu (1954). All fish were weighed to the nearest whole pound. Due to the nearly complete utilization of marlin by the dealers, only a small incision could be made in the abdominal wall in order to examine the gonads. At best, a small section of gonad could be cut off and examined; no microscopic determinations were made. Thus, it is possible that some misidentification of the sex of these fish occurred, especially preceding sexual maturity for both species and following spawning for blue marlin.

METHOD OF ANALYSIS

Briefly, the analyses consisted of 1) transforming the data into usable form by (a) calculating length-weight relationships using functional regressions (Ricker 1973), (b) converting weights to lengths, and (c) grouping the lengths by sex, quarter, year, and length interval; 2) separating age-groups from the frequency distributions and estimating their mean lengths; 3) setting up the progressions of mean lengths and corresponding age structures; and 4) fitting von Bertalanffy growth models to the progressions of mean lengths. Following these steps, tests were performed to determine whether the yearly samples were homogeneous and could be pooled. These tests consisted of a series of nonparametric Friedman two-way analyses of variance (Hollander and Wolfe 1973:139) performed on the number of age-groups, the mean lengths of age-groups, and the percent representation of age-groups separated for each year sampled, as well as on the growth parameters of the different cohorts. Also, a sign test (Siegel 1956:68) was used to test for trends in mean length between sexes; and a series of one sample runs tests (Siegel 1956:52) was used to test for trends in mean length among cohorts. If heterogeneity was not found, the transformed yearly data were pooled, that is, the year designation was ignored, and steps 2-4 above were repeated on the pooled data.

An initial inspection of the blue marlin length-frequency distributions revealed some unusually large specimens identified as males weighing up to 328 kg, whereas it had been contended that male blue marlin in the Atlantic (Erdman 1968) and in the Pacific (Strasburg 1970) do not exceed about 136 kg. An examination of data collected under ideal sampling conditions at Hawaiian International Billfish Tournaments revealed only 5 out of 385 individuals in 12 yr that exceeded 136 kg. Four of these were under 143 kg while one fish weighed 171 kg. On the basis of these data, we accepted Erdman's and Strasburg's contention as essentially correct, assumed that all males over 143 kg were misidentified due to the difficult sampling conditions at the auction sites, and reclassified all males over 143 kg as females (56 were reclassified out of 2,710 specimens originally classified as males).

Transformation of Data

Observed weights were converted from pounds to kilograms and then to fork lengths in centimeters (tip of bill to middle point on the posterior margin of the middle caudal rays, FL). Length-weight relationships used for the latter conversions were calculated as functional regressions from Skillman and Yong (1974) following the recommendations of Ricker (1973). Briefly, the differences between functional and the commonly used predictive (linear) regressions, which are of importance to this application, are as follows. First, the predictive regression applies where it is hypothesized that one variable is linearly related to or dependent on a second variable, the independent variable. Whereas, the functional regression applies where it is hypothesized that two variables are interdependent, and the effect of one cannot be disentangled from the effect of the other. Second, the predictive regression tends to systematically underestimate the magnitude of the regression coefficient as the sample range truncates the real range of the variates; the functional regression does not do so. For striped marlin, the data were insufficient to calculate functional length-weight relationships for each sex; therefore, a single relationship ($FL = 73.4429\ W^{0.2858}$) was applied to each sex separately. For blue marlin, separate functional length-weight relationships were calculated ($FL_{\text{FEMALE}} = 65.4502\ W^{0.3030}$, and $FL_{\text{MALE}} = 56.8780\ W^{0.3318}$). As expected, the coefficients of allometry calculated using functional regressions increased over those calculated in Skillman and Yong (1974) using predictive regressions, and the difference between sexes decreased by 36%.

In order to efficiently separate age-groups from the frequency distributions, the data were grouped and length intervals set up (Simpson et al. 1960). Lengths for striped marlin were grouped by sex, year, quarter, and 3-cm interval, and these groupings resulted in a maximum of 96-length intervals per quarter. Blue marlin lengths were grouped by sex, quarter, year, and 5-cm interval, and these groupings resulted in a maximum of 73-size intervals per quarter.

Separation of Age-Groups

The computer program ENORMSEP (Yong and Skillman 1975) was used to separate the grouped, length-frequency data into constituent age-groups and to calculate estimates of the mean length, variance, percent representation, and numerical size of the age-groups. Essentially this computer program automates the Cassie-Harding probability paper method (Harding 1949; Cassie 1954) and enters intermediate results into NORMSEP which performs the actual separation of age-groups.

Progression of Age-Groups

The estimates of mean lengths for age-groups were plotted by quarter in order to check for reasonable progression and to assign age. Ages were assigned by determining the time of peak spawning, estimating the age at recruitment, and then merely assigning ages progressively as the age-groups passed through the fishery.

The time of spawning is not well established for either striped or blue marlin. For striped marlin, Nakamura (1949) stated that the time of peak spawning seemed to be from April to May in the South China Sea near the Republic of China and from May to June near the Bonin Islands. Royce (1957) stated that testes with free flowing milt were collected in the equatorial central Pacific in March. Kume and Joseph (1969) estimated, on the basis of gonad index of females taken in the eastern tropical North Pacific, that peak spawning occurs in May and June. From specimens landed in southern California and northern Mexico, Eldridge and Wares (1974) indicated that gonad index was highest in June and July, but they did not have samples for August or September. Hence, we took June 1st as the time of peak spawning and assigned an age of 1.46 yr to the 151-cm male and 152-cm female age-groups recruited in the fourth quarter.

For blue marlin, Royce (1957) stated that males with free flowing milt were collected from February through October in the equatorial Pacific, and cited Nakamura (1942) as indicating that spawning occurs east of Luzon (Philippines) from May to July. Kume and Joseph (1969), on the basis of gonad index of females taken in the eastern tropical Pacific, concluded that spawning occurs in December and January; however, most of their samples were collected from south of the equator. We arbitrarily took June 1st as the time of peak spawning and assigned an age of 0.71 yr to the 55.5-cm female age-group recruited in the first quarter.

Von Bertalanffy Growth Model

Two computer programs, BGC3 and BGC4, assembled by Abramson (1971) and written by Patrick Tomlinson were used in this paper to obtain estimates of von Bertalanffy growth parameters. The computer program for model 1, BGC3, fits the von Bertalanffy model by the least squares method to lengths from fish of known or, in this case, assumed age. The basic model is the familiar equation

$$L_t = L_\infty(1 - e^{-K(t - t_0)}) \quad (1)$$

where L_t = length at age t
L_∞ = a parameter depicting asymptotic maximum length
K = a parameter indicating the rate of proportional growth
t_0 = a parameter depicting the theoretical age at which the fish has zero length given the adult growth form.

The computer program for model 2, BGC4, a version of the size-increment method proposed by Fabens (1965), fits the von Bertalanffy model by the least squares method to observed lengths, using data on growth increment in known time intervals but making no assumptions about absolute age. Parameter estimates using this method are included in the tables so that any future estimates of striped or blue marlin growth from tagging data can be compared directly to our results. For model 2, the von Bertalanffy model is written as

$$L_t = L_\infty(1 - be^{-Kt}) \quad (2a)$$

where $b = 1 - \frac{L_0}{L_\infty}$ = a parameter depicting the theoretical proportion of potential growth in length that occurs after hatching;

or by substituting $t = t + \Delta t$ and $be^{-Kt} = 1 - \frac{L_t}{L_\infty}$ into Equation (2a)

$$L_{t+\Delta t} = L_t e^{-K\Delta t} + L_\infty (1 - e^{-K\Delta t}) \quad (2b)$$

where Δt = time increment between points of measured length.

GROWTH OF STRIPED MARLIN

Results—Analysis of Cohorts

Age-groups were successfully separated by sex and by quarter, within years, using the computer program ENORMSEP (Table 1). In general, the mean length estimates for females were slightly larger than those for males of the same age-groups. Quantitatively, the goodness of fit of the separated age-groups to the observed frequency distribution can be assessed with the chi-square values in Table 1. The largeness of the chi-square values indicated poor fit, but it was found that the tails of the distribution, having frequencies too small for the separation of age-groups, contributed disproportionately to the total chi-square value. Qualitatively, the goodness of fit was deemed adequate for the following reasons. In all years there was close agreement between sexes in the number of age-groups separated within quarters: approximately 2, 3, 4, and 3 age-groups for the first through fourth quarters, respectively. There was also close agreement among years and between sexes in the mean lengths and length composition of age-groups within quarters.

The progressions of mean lengths were set up as depicted by the connected open circles in Figure 1. In the third quarter of every year for both sexes, there was an age-group with mean length of about 167 cm that did not fit into the progression of age-groups. By assigning the same assumed age to this age-group as to a similar size group in the first quarter, and allowing the same time between spawning and the attainment of this age, this age-group could have resulted from a spawning in January. On the basis of gonad indices, Kume and Joseph (1969) believed that striped marlin from the eastern South Pacific spawn from November to December, and Royce (1957) indicated that striped marlin with ripe gonads have been collected in February in the equatorial region of the central Pacific. Hence, we concluded that this age-group belonged to a different spawning stock and should not be used in the calculation of the von Bertalanffy growth curves for the central North Pacific stock. Also, for females there were two age-groups having mean lengths of 267.5 and 200.0 cm in the third quarter 1964 and 1966, and for males there were four age-groups having mean lengths of 204.6 and 272.0 cm in the third quarter of 1968, 271.8 cm in the fourth quarter 1968, and 266.0 cm in the second quarter 1969. These could not be assigned with certainty to any cohort.

Several qualitative aspects of the observed growth of the cohorts were noteworthy (Figure 1). First, there seemed to be a cyclical pattern in the mean size at recruitment but no upward or downward trend. Second, the progression of age-groups during the first year in the fishery was fairly smooth and consistent between cohorts. Third, after about a year and a half in the fishery, there seemed to be a regression or slowing down in the apparent growth that persisted for two or three quarters. Fourth, the mean length of the last age-group in each cohort varied considerably.

There were a sufficient number of age-groups for the 1959-65 cohorts to fit a von Bertalanffy growth curve but not for the 1957-58 and 1966-68 cohorts. The calculated growth curves were shown as smooth curves in Figure 1. As expected from the variation shown in the progression of the observed mean sizes in Figure 1, the standard errors of estimates were moderate, and there was variation in parameter estimates between cohorts (Table 2).

To investigate the variation in estimates of mean length for age-groups shown in Table 1 and in growth parameters shown in Table 2, a series of nonparametric Friedman two-way analyses of variance was performed. No difference in the number of age-groups by sex, quarter, or sample year could be demonstrated (all S test statistics were insignificant with probability $P>0.05$, Hollander and Wolfe 1973:139). In testing the effect of sex on the mean length of age-groups within quarters, three significant effects ($S=5.44$, $P\leq0.05$; $S=8.99$, $P\leq0.01$; and $S=5.44$, $P\leq0.05$) were found out of 16 comparisons. However, using a sign test for trends in mean length between sexes showed that females tended to be larger than males (test statistic $P = 0.00005$, or probability $P\leq0.01$, for data from all years). In

TABLE 1.—Estimates of striped marlin age-groups (numbers do not indicate age) by sex and by year and quarter of sampling. Estimates of mean fork length, $\overline{FL}$; percent of total sample comprising a particular age-group, %; and chi-square goodness of fit value, χ^2, were obtained from the computer program ENORMSEP.

			Age-group 1		Age-group 2		Age-group 3		Age-group 4		Age-group 5		
Year	Quarter	Sex	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	χ^2
1960	4	M	150.9	3.4	205.7	86.6	220.8	10.0	—	—	—	—	64.2
		F	154.0	3.4	208.2	85.5	228.7	11.1	—	—	—	—	44.7
1961	1	M	160.2	50.4	208.7	49.6	—	—	—	—	—	—	16.4
		F	162.2	65.2	213.5	34.8	—	—	—	—	—	—	32.1
	2	M	176.5	27.5	215.7	72.5	—	—	—	—	—	—	70.6
		F	172.5	26.2	223.5	56.0	231.1	17.8	—	—	—	—	39.6
	3	M	161.1	18.7	184.7	26.9	203.3	14.8	223.6	39.6	—	—	20.8
		F	159.3	39.4	197.4	17.6	224.2	31.6	247.4	11.4	—	—	35.1
	4	M	156.7	11.2	207.8	72.8	220.6	16.0	—	—	—	—	8.6
		F	158.0	13.4	211.1	71.8	225.8	14.8	—	—	—	—	28.0
1962	1	M	175.8	49.4	211.9	50.6	—	—	—	—	—	—	18.7
		F	170.6	45.9	213.7	54.1	—	—	—	—	—	—	32.5
	2	M	181.7	15.9	215.2	81.0	238.4	3.1	—	—	—	—	47.7
		F	175.9	17.6	217.9	40.4	232.3	42.0	—	—	—	—	28.5
	3	M	169.0	28.7	191.4	37.1	213.4	30.7	225.0	3.5	—	—	24.8
		F	170.3	39.9	193.5	41.5	212.6	18.6	—	—	—	—	24.2
	4	M	149.7	45.4	209.1	49.4	218.8	5.2	—	—	—	—	79.5
		F	150.2	47.1	209.6	48.4	241.1	4.5	—	—	—	—	67.3
1963	1	M	162.9	76.6	210.3	23.4	—	—	—	—	—	—	61.9
		F	163.1	80.2	210.7	19.8	—	—	—	—	—	—	47.1
	2	M	173.9	35.4	217.8	62.8	230.7	1.8	—	—	—	—	66.2
		F	168.4	32.9	225.4	33.4	228.8	33.7	—	—	—	—	61.8
	3	M	171.0	3.4	187.2	19.9	217.4	76.7	—	—	—	—	10.8
		F	173.0	9.0	194.8	33.0	219.9	21.0	239.5	37.0	—	—	12.4
	4	M	151.0	14.7	202.0	59.0	216.5	26.3	—	—	—	—	32.0
		F	153.4	24.3	206.2	53.5	219.0	22.2	—	—	—	—	58.6
1964	1	M	173.5	76.7	206.3	23.3	—	—	—	—	—	—	77.4
		F	173.7	69.3	198.7	30.7	—	—	—	—	—	—	97.4
	2	M	186.3	38.8	209.7	52.8	227.3	8.4	—	—	—	—	63.2
		F	179.5	35.5	216.9	56.0	242.1	8.5	—	—	—	—	35.6
	3	M	164.3	26.0	191.3	21.3	205.3	49.1	228.7	3.6	—	—	15.3
		F	168.8	48.7	192.3	10.3	215.2	39.4	267.5	1.6	—	—	43.6
	4	M	160.7	1.9	203.5	94.2	217.2	3.9	—	—	—	—	99.8
		F	158.6	0.8	206.0	91.5	222.2	7.7	—	—	—	—	137.1
1965	1	M	159.8	3.2	203.2	96.8	—	—	—	—	—	—	49.3
		F	164.1	4.7	206.8	95.3	—	—	—	—	—	—	44.6
	2	M	172.7	7.5	212.5	90.9	232.4	1.6	—	—	—	—	34.3
		F	171.4	11.5	220.3	84.7	235.0	3.8	—	—	—	—	22.0
	3	M	164.6	27.0	193.8	18.3	211.7	40.2	230.6	14.5	—	—	6.7
		F	164.3	29.8	206.1	40.4	224.0	28.0	248.0	1.8	—	—	26.4
	4	M	144.5	3.0	205.9	88.5	225.5	8.6	—	—	—	—	47.3
		F	148.4	4.4	207.9	83.9	222.8	11.7	—	—	—	—	117.9
1966	1	M	158.6	14.3	207.7	85.7	—	—	—	—	—	—	37.0
		F	165.1	18.2	212.1	79.0	250.5	2.8	—	—	—	—	30.0
	2	M	182.3	23.6	215.5	76.0	249.6	0.4	—	—	—	—	32.1
		F	177.7	25.7	220.8	64.8	244.0	9.5	—	—	—	—	26.4
	3	M	171.3	17.0	198.6	69.2	218.6	10.8	234.6	3.0	—	—	15.5
		F	193.8	74.2	200.0	16.5	209.8	2.8	240.8	6.5	—	—	21.1
	4	M	147.9	3.4	206.5	94.0	236.3	2.6	—	—	—	—	142.0
		F	131.0	3.6	208.8	84.0	214.6	12.4	—	—	—	—	52.4
1967	1	M	159.4	6.2	204.3	93.8	—	—	—	—	—	—	44.8
		F	165.7	4.3	207.8	95.7	—	—	—	—	—	—	40.1
	2	M	171.9	1.5	208.2	97.8	233.0	0.7	—	—	—	—	24.8
		F	174.1	5.5	221.4	87.3	249.1	7.2	—	—	—	—	60.2
	3	M	168.3	27.7	192.8	53.7	213.4	3.5	232.5	15.1	—	—	10.5
		F	166.9	30.1	185.1	25.6	204.5	44.3	—	—	—	—	9.8
	4	M	168.7	0.7	202.7	93.4	218.9	5.9	—	—	—	—	82.9
		F	162.8	0.4	202.8	97.4	225.8	2.2	—	—	—	—	98.4
1968	1	M	161.7	1.6	200.7	98.4	—	—	—	—	—	—	37.6
		F	165.6	3.1	202.3	94.8	242.6	2.1	—	—	—	—	48.4
	2	M	174.6	2.2	208.1	97.5	242.0	0.3	—	—	—	—	58.1
		F	182.0	2.3	215.8	97.3	222.7	2.4	—	—	—	—	45.6
	3	M	169.0	9.4	194.7	63.7	217.1	16.0	204.6	6.7	272.0	4.2	30.9
		F	164.5	9.5	193.8	63.6	213.4	19.5	235.1	7.4	—	—	18.4
	4	M	157.7	5.3	205.5	93.9	271.8	0.7	—	—	—	—	79.4
		F	153.9	8.0	209.4	89.3	242.5	2.7	—	—	—	—	66.4

Table 1.—Continued.

Year	Quarter	Sex	Age-group 1 $\overline{FL}$	Age-group 1 %	Age-group 2 $\overline{FL}$	Age-group 2 %	Age-group 3 $\overline{FL}$	Age-group 3 %	Age-group 4 $\overline{FL}$	Age-group 4 %	Age-group 5 $\overline{FL}$	Age-group 5 %	X^2
1969	1	M	157.8	8.9	203.5	91.1	—	—	—	—	—	—	31.1
		F	156.6	12.6	206.6	87.4	—	—	—	—	—	—	32.2
	2	M	179.0	9.1	211.8	90.6	266.0	0.3	—	—	—	—	34.1
		F	182.0	0.4	212.0	97.0	221.9	2.6	—	—	—	—	39.4
	3	M	161.0	0.5	195.4	62.2	220.0	25.2	235.9	12.1	—	—	15.5
		F	174.7	8.3	196.8	71.2	221.0	13.8	241.4	6.7	—	—	40.2
	4	M	154.5	5.8	206.6	92.5	233.0	1.7	—	—	—	—	33.9
		F	155.3	4.8	206.0	93.4	236.2	1.8	—	—	—	—	70.9
1970	1	M	164.1	45.3	210.4	54.7	—	—	—	—	—	—	28.2
		F	164.2	47.4	208.2	52.6	—	—	—	—	—	—	35.9

testing significance of differences between the growth parameters, the analysis of variance failed to demonstrate an effect of either cohort or sex on L_∞, K, or t_0 (all S values insignificant with $P>0.05$). We concluded that there were no significant effects of either cohort or sex on the number of age-groups or growth parameters, and that females tended to be statistically larger at successive ages even though the magnitude of the differences was not significant.

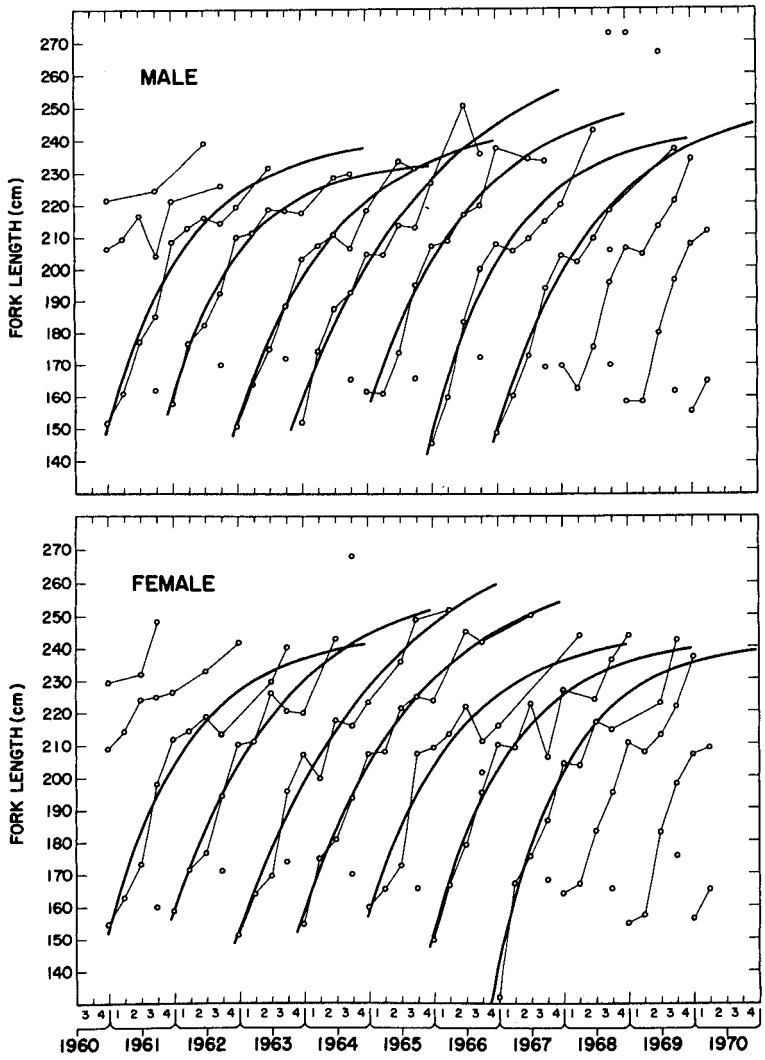

FIGURE 1.–Striped marlin von Bertalanffy growth curves (heavy lines) by sex for the 1959-65 cohorts. Observed mean lengths for age-groups, represented by circles connected with light lines, were used in fitting the growth curves.

TABLE 2.–Striped marlin von Bertalanffy growth parameters by cohort and sex. The parameter estimates, L_∞ (asymptotic maximum fork length), K (rate of proportional growth), and t_0 (theoretical time at which the fish would have zero length), are given for model 1 (upper row) and model 2 (lower row).

Year-class	Sex	L_∞ (cm)	K	t_0 (yr)	Standard error of estimate
1959	Male	241.0	0.812	0.297	5.1
		251.1	0.651		6.1
	Female	245.0	0.809	0.294	6.6
		255.1	0.626		7.3
1960	Male	233.7	0.929	0.260	3.6
		233.5	0.986		4.7
	Female	261.7	0.584	−0.096	6.0
		290.0	0.437		8.0
1961	Male	247.0	0.640	0.007	4.6
		250.9	0.630		5.3
	Female	283.3	0.428	−0.304	6.0
		265.7	0.574		8.6
1962	Male	274.4	0.448	−0.435	6.8
		248.2	0.873		9.0
	Female	265.7	0.554	−0.125	3.7
		261.9	0.664		6.0
1963	Male	256.0	0.622	−0.004	6.2
		244.2	0.655		7.9
	Female	245.5	0.729	0.091	9.1
		258.7	0.607		10.9
1964	Male	243.7	0.818	0.351	7.1
		275.5	0.570		6.7
	Female	243.3	0.803	0.282	7.0
		234.9	1.067		9.8
1965	Male	253.3	0.630	0.086	4.3
		258.1	0.585		5.3
	Female	239.8	0.914	0.542	6.5
		231.5	1.267		8.9

Results—Analysis of Pooled Data

In the preceding section, it was shown that there were no demonstrable differences in the growth parameters between different cohorts; hence, the estimates for L_∞, K, and t_0 could be averaged to provide a pooled estimate. In addition, it was not possible to consistently show significant differences between quarters or years in the number of age-groups separated ($S=11.78$, $P>0.05$), the mean lengths of age-groups ($S=15.51$, $P\leq0.05$, for males in third quarter, all seven remaining S values had $P>0.05$), or the percent representation of age-groups ($S=57.18$, $P\leq0.01$, for males in the second quarter, $S = 49.57$, $P\leq0.01$, for females in the third quarter, all six remaining S values with $P>0.05$). Neither was it possible to show a trend in mean lengths among cohorts using a series of sample runs tests (one test out of 18 deviated from random at the 0.05 level). We interpreted these results to mean that the yearly samples were homogeneous and that at least approximately a steady state existed. Therefore, the yearly frequency data were pooled; and ENORMSEP was used to separate age-groups.

The mean lengths and percent representation of age-groups by quarter (Table 3) were quite similar to the values found using the yearly data (Table 1). Quantitatively evaluating the goodness of fit, the chi-square values were found again to be rather large. Qualitatively, however, the shape of the frequency distributions was consistent between sexes within quarters and generally so between quarters within each sex (Figure 2). The plots for the third quarter, the off-season for striped marlin in Hawaii, did not show much of a pattern at all. Also, the shapes of the plots for the pooled data analysis were similar to those for the analysis of individual cohorts (not shown).

Mean lengths for females and males exhibited a fairly smooth progression (Figure 3). As in the analysis of cohorts, there was an age-group with mean length of about 167 cm in the third quarter that did not fit into the progression of age-groups. Again, it was assumed that this age-group belonged to a different spawning stock and should not be used in the calculation of the growth curve. For females, there were 11 age-groups in the progression whereas there were 10 or 12 but never 11 for the analysis of cohorts. For males, there were 12 age-groups in the progression whereas there were 9 to 11 in the analysis of cohorts. The smallest fish were recruited into the fishery in the fourth quarter and progressed through the fishery until the largest fish passed from it in the third

TABLE 3.–Statistics for striped marlin age-groups by quarter and sex, pooled over all years. Estimates of mean fork length, $\overline{FL}$; percent representation of the age-group, %; the numerical sample for size of the age-group, n; the total sample size, N; and the chi-square goodness of fit value, χ^2, were obtained from the computer program ENORMSEP.

Quarter	Age-group	Male $\overline{FL}$	Male %	Male n	Female $\overline{FL}$	Female %	Female n
1	1	166.6	36.2	1,480	167.1	42.6	1,568
	2	204.7	63.8	2,613	207.2	57.4	2,115
	N			4,093			3,683
	χ^2	114.1			183.8		
2	1	177.3	17.5	1,020	174.4	21.0	852
	2	212.5	81.5	4,746	219.7	69.7	2,827
	3	228.0	1.0	57	238.4	9.3	377
	N			5,823			4,056
	χ^2	97.2			54.0		
3	1	167.1	17.0	178	166.7	22.7	190
	2	195.3	52.6	551	194.0	50.1	419
	3	215.2	19.9	208	217.5	19.4	162
	4	231.6	9.1	96	236.2	7.8	65
	5	260.0	1.4	14	—	—	—
	N			1,047			836
	χ^2	71.6			45.1		
4	1	151.3	7.1	421	152.2	8.7	431
	2	204.7	87.0	5,162	207.0	83.0	4,113
	3	222.6	5.9	352	222.7	8.3	413
	N			5,935			4,957
	χ^2	130.1			192.3		

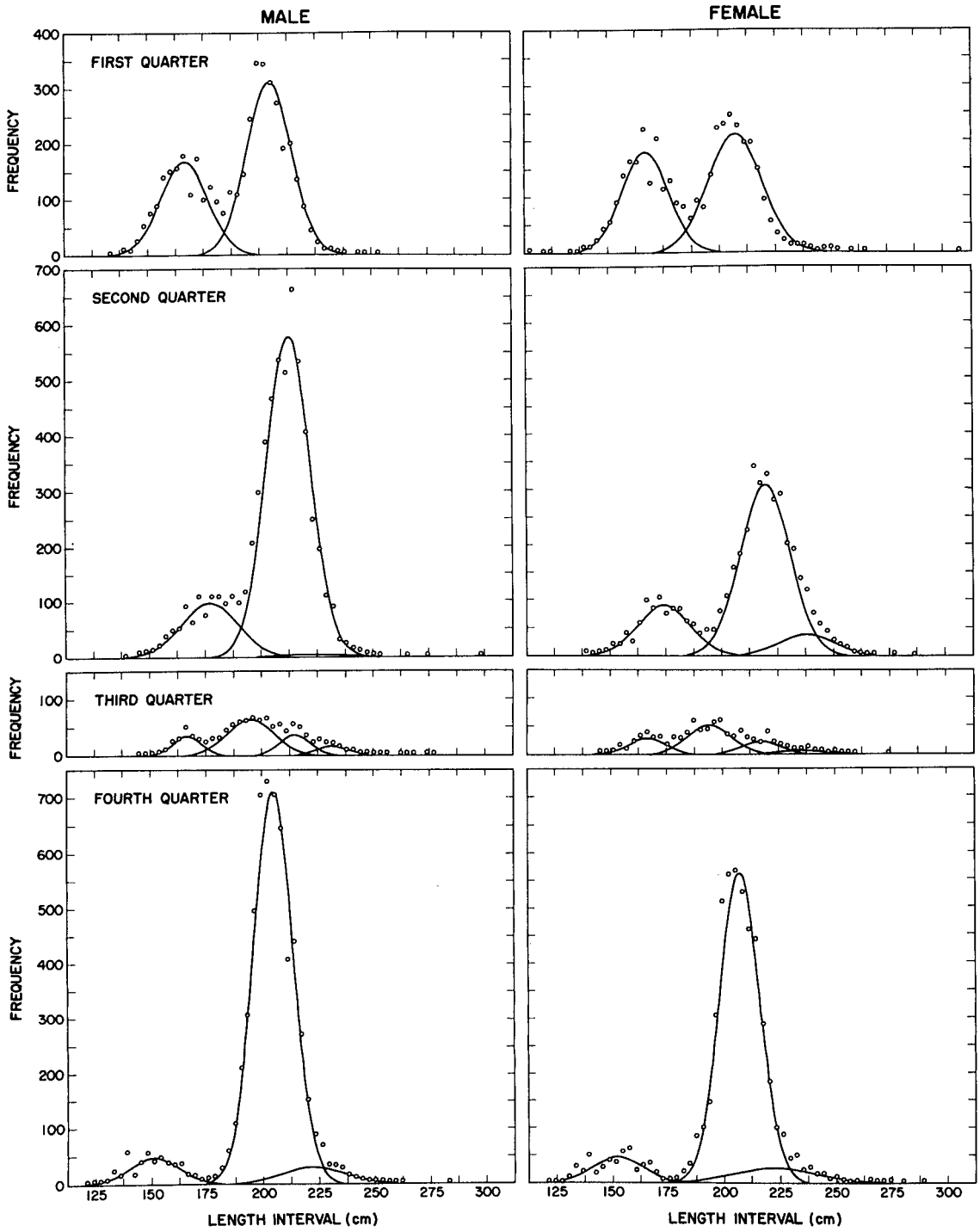

FIGURE 2.–Striped marlin length composition by sex and quarter for the analysis of pooled data. The smooth curves represent age-groups separated by the computer program ENORMSEP, and circles represent observed values.

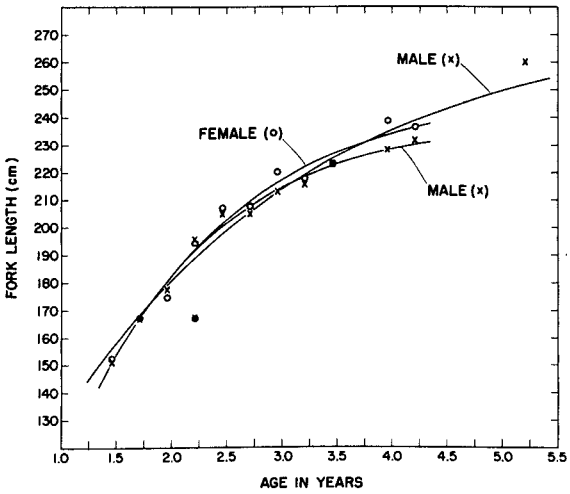

FIGURE 3.–Striped marlin von Bertalanffy growth curves by sex, for the analysis of pooled data. Male and female growth curves having the same length were obtained using 11 age-groups while the longer male curve was obtained using in addition an age-group 1 yr older. Observed mean lengths for male and female age-groups are given. As explained in the text, the outliers at age 2.46 yr were not used in fitting the growth curves.

quarter 3 yr later for females and 4 yr later for males.

Discussion

We felt that the parameter estimates from the analysis of pooled data provided better estimates of population parameters than those from the analysis of individual cohorts because pooling smooths out variation in individual curves. In addition, the less well-represented age-groups, having small and large mean lengths and being recruited to or escaping from the fishery, were estimated more accurately given the larger sample size after pooling.

Since estimates of mean lengths at age were used in the fitting of the growth curves, estimates of growth parameters are in terms of these average values. Likewise, estimates of length at age derived from these models (Table 4) will actually be average values and should only be calculated for the range of ages used in fitting the models. In fact, the greatest utility of these models will be to predict length at ages within the range of the observed data. The accuracy of the estimation of L_∞ is dependent on the range of values used, and it should be remembered that the data used here included fish only up to the onset of sexual maturity.

TABLE 4.–Striped marlin von Bertalanffy growth parameters by sex for analysis of pooled data. The parameter estimates, L_∞ (asymptotic maximum fork length), K (rate of proportional growth), and t_0 (theoretical time at which the marlin would have zero length) are given for model 1 (upper row) and model 2 (lower row).

Sex	Case	L_∞ (cm)	K	t_0 (yr)	Standard error of estimate
Male	All age-groups	277.4	0.417	−0.521	5.5
		314.4	0.315		5.5
Male	Less oldest age-group	239.7	0.810	0.235	2.8
		240.0	0.809		3.7
Female	All age-groups	251.0	0.696	0.136	4.2
		251.8	0.709		6.2

The estimation of population L_∞ was complicated by the fact that males and females were not represented in the fishery for the same length of time. Obviously, the length of time (number of age-groups) that the sexes were in the fishery had an effect on the estimation of L_∞, as well as K and t_0 (Table 4). We believed that the parameter estimates for males using all 12 age-groups provided the most accurate estimates because a greater part of the growth curve was measured. We must admit that the estimates may not be very precise because the estimated sample size of the last age-group was 14 individuals, and the standard error of the estimate for the growth curve was larger when all age-groups were included. The estimates of L_∞ for males using models 1 and 2 were 277.4 and 314.4 cm, respectively. In order to obtain estimates for females that can be compared to those for males, the differences found between females and males using 11 age-groups, 11.3 and 11.8 cm for models 1 and 2, respectively, were added to the estimates of L_∞ for males, giving 288.7 and 326.2 cm, respectively. These estimates seemed reasonable when compared to the largest striped marlin measured by personnel from the Honolulu Laboratory: 296 cm for males, 305 cm for females, and 310 cm for sex undetermined.

Both the analysis of cohorts and the pooled data analysis (though less so) were plagued by apparent negative growth or at least by very slow growth during some quarters about a year and a half after recruitment. Accepting the general growth progression as valid, this problem probably biased the estimates of L_∞ downward and K upward and contributed to the size of the standard errors of estimates. We do not believe that this period of apparent negative growth resulted from some physiological change in the form of growth for which the von Bertalanffy model could not account

and, therefore, is invalid, but rather that the apparent change in growth was caused by seasonal changes in availability of the stock due to some seasonal size-age migration phenomenon or possibly by changes in the selectivity of the fishery. Preliminary examination of Japanese longline statistics suggested that the striped marlin stock available to the Hawaiian fishery shifts its center of density northward in the months with the warmest water temperature and becomes less available to the local fishery (Heeny S. H. Yuen, Southwest Fisheries Center, pers. commun.). The decreased growth most commonly seen in the third quarter might then be due to smaller fish being associated with the periphery of the stock.

There are of course other possible explanations. For example, one reviewer suggested that this period of slow or negative growth represented an asymptote followed by the initiation of a new growth phase. Fitting a two-cycle Gompertz growth curve to the pooled data, this reviewer found both sexes tending toward an asymptote at age 2.46 yr followed by another growth phase where females tended toward an asymptote at 320 cm, but no solution was found for males. Such changes in growth phase are common at sexual maturity and at other times when body form changes. Change in growth form is commonly accompanied by a corresponding change in the length-weight relationship, and Skillman and Yong (1974) found no indication of a change in the length-weight relationship over the range 142.2-310.1 cm. Also, the age of fish in the Hawaiian fishery, having a calculated mean length corresponding to length at first maturity found by Eldridge and Wares (1974) and Kume and Joseph (1969) for the eastern tropical Pacific, was 4.2 yr. This age is nearly double the hypothesized age of first asymptotic growth. Thus, while it is possible to fit a segmented growth curve to the data, biological evidence given above does not support such a procedure.

Another possible explanation involves the separation of age-groups. The aberrant growth occurred most frequently in the third quarter, and since the sample size was smallest in this quarter, the precision of the estimates is probably less than for the other quarters. However, the aberrant growth did not always occur in this quarter, and its repeated occurrence among cohorts suggested that it was real and not an artifact of the estimation procedure per se. With any probabilistic means of separating age-groups from a mixed distribution, there is always the danger that age-groups from different cohorts of the same spawning stock will be so similar in size that they cannot be separated, especially with increasing age and varying growth rates of the cohorts. We acknowledge that this may be a problem, but if it is, it would seem from Figure 1 to be more important for the growth period following the period of aberrant growth. This problem would be increased if there were more than one spawning stock involved, and this seems to be the case for some quarters. In spite of the small sample sizes in the third quarter, there seemed to be little doubt that the 167-cm age-group was real, since its mean length is quite removed from that of the next age-group at about 194 cm and since the age-group was found for the pooled data analysis and for 8 out of 9 yr for females and for all years for males in the analysis of yearly data. Because the two spawning stocks would continue to have quite different lengths for the next couple of quarters and no comparable age-groups were separated in these quarters, it was reasonable to assume that this other secondary stock was not represented in the catches in the subsequent fourth, first, and probably second quarters. But what about the following third quarters? If similar growth curves are assumed for this other stock, then the 200.0-cm female age-group in the third quarter of 1966 and the 204.6-cm male age-group in the third quarter of 1968 could also belong to the secondary spawning stock. If this secondary stock was present in other years but in numbers too small to be separated out, it would tend to bias downward the estimates of the similar-sized age-group of the primary spawning stock. With the accuracy of the present set of data, it is impossible to comment on the likelihood or importance of this possibility.

The occurrence of these age-groups at approximately 167 cm in the third quarter presents an additional problem. Where do they come from? If the male and female growth curves are used to back calculate the probable time of spawning for the age-group at approximately 167 cm in the pooled data analysis, January is estimated as the time of peak spawning. We hypothesize that these fish could come from a stock spawning in the equatorial region, probably north of the equator, during months corresponding to the southern summer. It is hard to visualize a hypothesis that would account for a stock spawned 6 mo out of

phase migrating poleward, but at lower latitudes, at the same time as the primary stock. Possibly these fish associate with blue marlin of about the same size that migrate into Hawaiian waters in the third quarter.

Estimates of von Bertalanffy growth parameters for both sexes were first obtained using for females and using 12 and 11 (deleting oldest) age-groups for males (Table 4, smooth curves in Figure 3). The standard errors of estimates were slightly smaller than those for the individual cohorts but still not what could be considered small. When the oldest age-group for males was deleted from the calculations, L_∞ for females was 11 to 12 cm greater than for males. Using all of the age-groups for males, the estimate of L_∞ increased substantially.

Although this paper deals with growth, the length composition and age of striped marlin as found in this study have some relevancy to the problem of migration. First, Matsumoto and Kazama (1974) hypothesized that striped marlin migrate out of Hawaiian waters to spawn, most likely to the western North Pacific. The calculated mean length of the last female age-group found in the Hawaiian fishery (age 4.2 yr) corresponded to the length at first maturity found by Eldridge and Wares (1974) and Kume and Joseph (1969) for the eastern tropical North Pacific. Thus, our data established that as striped marlin reached the length corresponding to sexual maturity, they became unavailable to the local fishery. Second, Kume and Joseph (1969) indicated that there was a tendency for average length to increase in the southern areas of the Japanese longline fishery in the eastern tropical North Pacific, and it seemed to us from their charts that there was also a western component to the increasing average lengths. Eldridge and Wares (1974) believed that maturing striped marlin moved out of the range of the sport fisheries based in southern California and Mexico; and Squire (1974) suggested that the movement of striped marlin away from the Baja California area might be to the area of the Revilla Gigedo Islands where fish with ripe gonads have been collected and where behavior suggestive of spawning activity has been observed by the Japanese. While the range of our length data was similar to that found in the eastern tropical Pacific, the last age-group recognizable in our data comprised less than 10% of the total frequency whereas similar-sized fish seemed to be well represented in the southern and western areas of the eastern tropical North Pacific longline fishery. Thus, it seems apparent that the fish leaving the fishery off the American coast do not migrate through the Hawaiian fishery in any appreciable numbers. However, the capture of a striped marlin, tagged off Baja California, 322 km southwest of the Hawaiian Islands indicates that some eastern Pacific fish move into the vicinity of the Hawaiian Islands. Finally, our analyses do not provide any information on the direction of emigration from the Hawaiian fishery.

GROWTH OF BLUE MARLIN

Results—Analysis of Pooled Data

The number of age-groups, as separated by the computer program ENORMSEP, varied from three in the third quarter for males to as many as eight in the first quarter for females (Table 5). The

TABLE 5.—Statistics for blue marlin age-groups by quarter and sex for analysis of pooled data. Estimates of mean fork length, $\overline{FL}$; percent representation of the age-group, %; the numerical sample size for the group, n; the total sample size, N; and the chi-square goodness of fit value, χ^2, were obtained from the computer program ENORMSEP.

		Male			Female		
Quarter	Age-group	$\overline{FL}$	%	n	$\overline{FL}$	%	n
1	1	123.0	3.3	2	55.5	0.6	1
	2	172.7	8.7	5	145.9	1.8	3
	3	225.0	57.2	34	190.5	3.0	5
	4	240.5	20.0	12	232.8	7.4	12
	5	281.8	10.8	7	286.8	31.5	52
	6	—	—	—	333.5	32.9	55
	7	—	—	—	366.1	22.2	37
	8	—	—	—	415.5	0.6	1
	N			60			166
	χ^2	16.8			33.2		
2	1	180.5	0.3	1	205.7	5.9	28
	2	220.0	65.4	172	298.3	76.2	365
	3	250.1	31.7	84	345.4	13.0	62
	4	278.0	2.6	7	377.2	4.9	24
	N			264			479
	χ^2	22.0			34.1		
3	1	163.6	1.4	9	158.8	0.4	3
	2	227.7	77.6	486	213.5	7.3	48
	3	255.8	21.0	131	292.6	53.1	352
	4	—	—	—	327.1	24.2	160
	5	—	—	—	362.9	15.0	100
	N			626			663
	χ^2	33.2			38.5		
4	1	175.5	8.4	32	101.7	0.9	4
	2	228.7	80.7	304	180.8	9.2	41
	3	264.0	10.4	39	225.1	11.3	51
	4	285.5	0.5	2	280.0	33.5	151
	5	—	—	—	307.6	14.2	64
	6	—	—	—	342.1	27.4	123
	7	—	—	—	390.8	3.5	16
	N			377			449
	χ^2	26.2			69.3		

shape of the frequency distribution differed substanially between sexes (Figure 4). The 240.5-cm male age-group separated in the first quarter that had zero variance (Table 5) was regarded as false and was not used in subsequent calculations. Quantitatively, the chi-square values do not indicate very good fit; however, as was the case with striped marlin, the tails of the frequency distributions, having frequencies too small for the separation of age-groups, contributed disproportionately to the total chi-square value. Qualitatively, as can be seen from Figure 4, the shape of the frequency distribution was similar from quarter to quarter, especially for males.

Progressions of mean lengths were set up for males and females as depicted in Figure 5. The smallest blue marlin recruited into the fishery in the first quarter were females, with males being recruited 1 yr later. Males were present in the fishery for 3¾ yr and females for 7 yr. Several age-groups represented by one or two individuals were separated for both sexes. The existence of these age-groups was tentatively accepted, but the accuracy of their estimated mean lengths was viewed with skepticism in calculating growth parameters. The mean length estimates of male and female age-groups were in close agreement until about 250 cm (S = 0.50, P>0.05). From 250 to 300 cm, the mean lengths for female age-groups were larger than estimates for males. Above 300 cm, only female age-groups were found, and these formed an irregularly increasing progression.

Estimates of von Bertalanffy growth parameters for both sexes were first obtained using

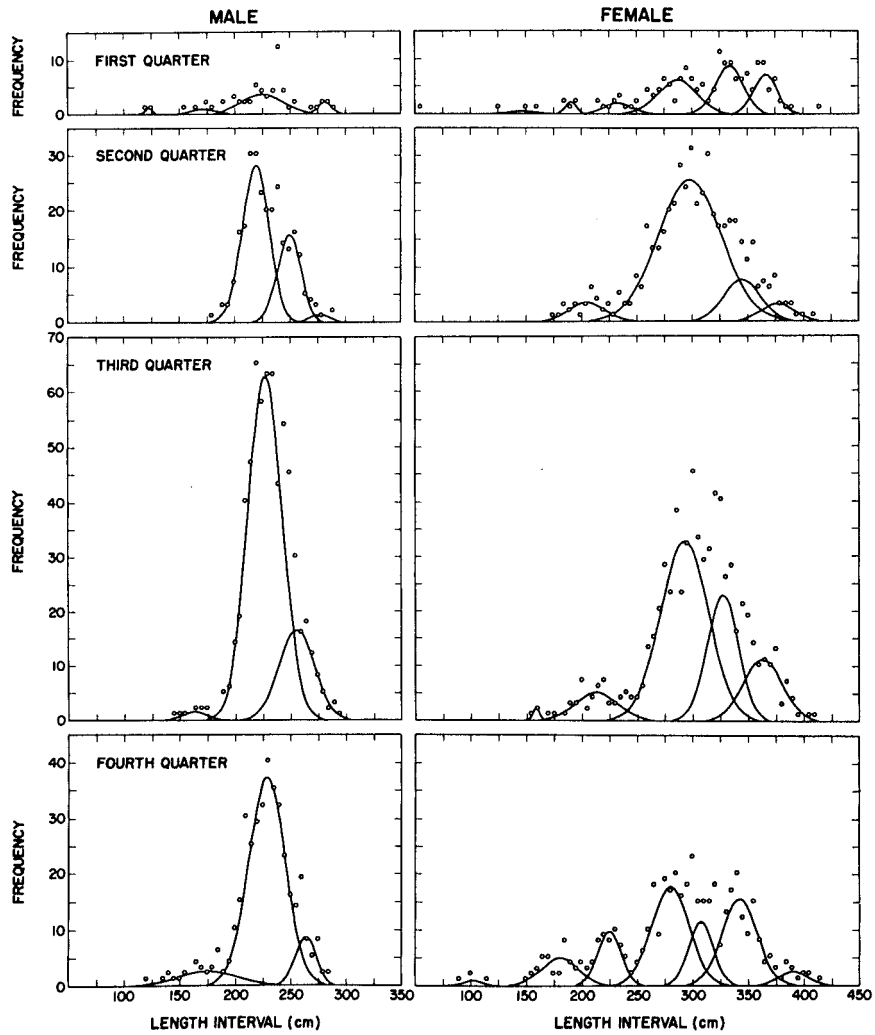

FIGURE 4—Blue marlin length composition by sex and quarter for the analysis of pooled data. The smooth curves represent age-groups separated by the computer program ENORMSEP, and circles represent observed values.

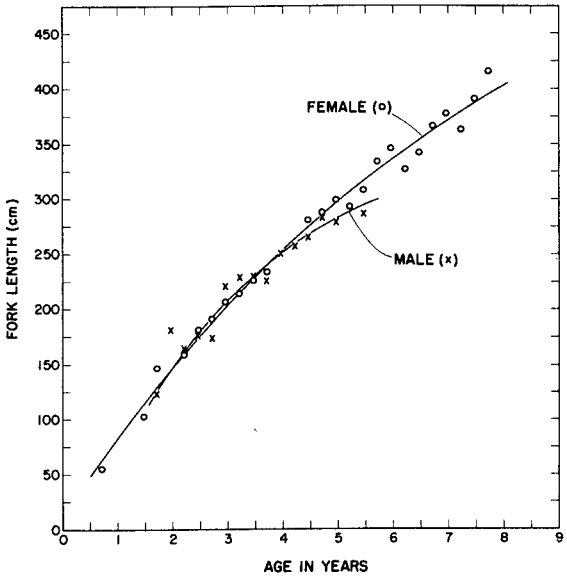

FIGURE 5.—Blue marlin von Bertalanffy growth curves by sex for the analysis of pooled data. Observed mean lengths for female and male age-groups are given.

all age-groups, and then using only those with estimated numerical representations greater than two individuals. Further analyses were done using age-groups for females, over the same age span as for males, with numerical representation greater than two individuals (Table 6). For males, parameter estimates were similar using all age-groups and those age-groups represented by more than two individuals. The standard error of estimate was smaller for the latter than it was for the case using all age-groups. For females, again the parameter estimates were similar for the two data sets, and the standard errors of estimates did not change appreciably. The estimates for L_∞ were nearly doubled those for males. In addition, the estimate of L_∞ for females, using the same age-groups as for males with age-groups represented by more than two individuals, was nearly 3½ times that for males.

Discussion

The estimates of von Bertalanffy growth parameters for male blue marlin differed little whether all of the age-groups were used or whether the less well-represented age-groups were deleted (Table 6). Because the standard errors of estimates were generally smaller for the reduced data sets, we felt that these fits provided

TABLE 6.—Blue marlin von Bertalanffy growth parameters by sex for the analysis of pooled data. The parameter estimates, L_∞ (asymptotic maximum fork length), K (rate of proportional growth), and t_0 (theoretical time at which the fish would have zero length) are given for model 1 (upper row) and model 2 (lower row).

Sex	Case	L_∞ (cm)	K	t_0 (yr)	Standard error of estimate
Male	All age-groups	371.1	0.285	0.106	12.7
		282.3	0.815		18.6
Male	Age-groups with more than two individuals	368.0	0.315	0.390	9.9
		298.8	0.560		15.0
Female	All age-groups	659.1	0.116	−0.161	10.2
		807.8	0.091		13.8
Female	Age-groups with more than two individuals	626.6	0.123	−0.202	9.1
		540.2	0.175		14.0
Female	Same age-groups as for males with more than two individuals	1,248.1	0.048	−0.674	4.0
		875.2	0.086		5.2

better estimates of parameters. Although the standard errors of estimates were larger than desirable, they varied from less than 1% to only 7% of the estimated L_∞. Thus, the von Bertalanffy growth model described the data satisfactorily. The mean length estimates for the poorly represented age-groups, which were the youngest and oldest in our samples, should be viewed as approximate.

For males, estimates of L_∞, 368.0 and 298.8 cm for models 1 and 2, respectively, bracketed the commonly accepted asymptotic length of about 300 cm. If our assumption of a knife-edge limit of 143 kg (approximately 300 cm) for males was incorrect, the progression of age-groups would have been expected to increase in length up to this point without approaching an asymptote. Since an asymptote was found, we felt our assumption was valid.

For females, the von Bertalanffy growth curves seemed adequate for describing the data, but the estimates of growth parameters were not biologically reasonable. Using the same range of age-groups as used for males, the estimates of L_∞ were around 1,000 cm, confirming the visual impression that there was little tendency towards an asymptote over this range of ages. Using all of the data, estimates of L_∞ were 626.6 and 540.2 cm for models 1 and 2, respectively, or approximately 1,729 and 1,060 kg, respectively. While these results suggested that there was some tendency towards an asymptote, which is not visually apparent in the data, we do not believe that enough older age-groups were included in the regressions

to obtain valid estimates of L_∞ or K. Among fishery biologists, there seems to be less of a consensus on the maximum size of females than of males, but generally it is thought that female blue marlin have a maximum weight of less than 900 kg. Hence, our estimates of L_∞ seemed too large.

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LITERATURE CITED

ABRAMSON, N. J. (compiler).
1971. Computer programs for fish stock assessment. FAO Fish. Tech. Pap. 101, [149 p.]

CASSIE, R. M.
1954. Some uses of probability paper in the analysis of size frequency distributions. Aust. J. Mar. Freshwater Res. 5:513-522.

DE SYLVA, D. P.
1957. Studies on the age and growth of the Atlantic sailfish, *Istiophorus americanus* (Cuvier), using length-frequency curves. Bull. Mar. Sci. Gulf Caribb. 7:1-20.

DE SYLVA, D. P., AND W. P. DAVIS.
1963. White marlin, *Tetrapturus albidus*, in the Middle Atlantic Bight, with observations on the hydrography of the fishing grounds. Copeia 1963:81-99.

ELDRIDGE, M. B., AND P. G. WARES.
1974. Some biological observations of billfishes taken in the eastern Pacific Ocean, 1967-1970. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers, p. 89-101. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

ERDMAN, D. S.
1968. Spawning cycle, sex ratio, and weights of blue marlin off Puerto Rico and the Virgin Islands. Trans. Am. Fish. Soc. 97:131-137.

FABENS, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.

HARDING, J. P.
1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. John Wiley and Sons, Inc., N.Y., 503 p.

JUNE, F. C.
1950. Preliminary fisheries survey of the Hawaiian-Line Islands area. Part I - The Hawaiian long-line fishery. Commer. Fish. Rev. 12(1):1-23.

KOTO, T., AND K. KODAMA.
1962. Some considerations on the growth of Marlins, using size-frequencies in commercial catches. I. Attempts to estimate the growth of Sailfish. [In Jap., Engl. abstr.] Rep. Nankai Reg. Fish. Res. Lab. 15:97-108.

KUME, S., AND J. JOSEPH.
1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130°W. Bull. Far Seas Fish. Res. Lab. (Shimizu) 2:115-162.

MATSUMOTO, W. M., AND T. K. KAZAMA.
1974. Occurrence of young billfishes in the central Pacific Ocean. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers, p. 238-251. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

NAKAMURA, H.
1942. On the ecology of the istiophorid fishes of Taiwan waters. [In Jap.] Suisan Gakkwai Hō 9:45-51.
1949. The tunas and their fisheries. Takeuchi Shōbo, Tokyo, 118 p. (Translated from Jap. by W. G. Van Campen, 1952. U. S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 82, 115 p.)

OTSU, T.
1954. Analysis of the Hawaiian long-line fishery, 1948-52. Commer. Fish. Rev. 16(9):1-17.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

ROYCE, W. F.
1957. Observations on the spearfishes of the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 57:497-554.

SIEGEL, S.
1956. Nonparametric statistics for the behavorial sciences. McGraw-Hill, N.Y., 312 p.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN.
1960. Quantitative zoology. Revised ed. Harcourt, Brace and Co., N.Y., 440 p.

SKILLMAN, R. A., AND M. Y. Y. YONG.
1974. Length-weight relationships for six species of billfishes in the central Pacific Ocean. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers, p. 126-137. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

SQUIRE, J. L., JR.
1974. Migration patterns of Istiophoridae in the Pacific Ocean as determined by cooperative tagging programs. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers, p. 226-237. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

STRASBURG, D. W.
1970. A report on the billfishes of the central Pacific Ocean. Bull. Mar. Sci. 20:575-604.

YONG, M. Y. Y., AND R. A. SKILLMAN.
1975. A computer program for analysis of polymodal frequency distributions (ENORMSEP), FORTRAN IV. Fish. Bull., U.S. 73:681.

TROPHIC INTERACTIONS AMONG FISHES AND ZOOPLANKTERS NEAR SHORE AT SANTA CATALINA ISLAND, CALIFORNIA[1]

EDMUND S. HOBSON AND JAMES R. CHESS[2]

ABSTRACT

Predation pressures from fishes have influenced major evolutionary trends among shallow-water zooplankters, as concluded from study at Santa Catalina Island, Calif. The predominant zooplanktivorous fishes near shore are actinopterygians, an evolutionary line that has centered around generalized visually feeding, large-mouthed predators. Historically, zooplankters threatened by these fishes have faced selective pressures favoring reduced size, transparency, and/or nocturnal planktonic habits. At present, most zooplankters in the nearshore water column by day are very small (<2 mm, approximately); included are cladocerans, copepods, and various larval forms. Their small size precludes capture by most large-mouthed fishes, thus providing protection in daylight, when the visual sense of generalized predatory fishes is most effective. Larger zooplankters in the water column by day, for example chaetognaths, tend to be transparent. The advantage of transparency to organisms threatened by visually feeding predators is obvious, and is only briefly mentioned here. Zooplankters having sizes (most >2 mm) and other features making them vulnerable to large-mouthed fishes tend to enter the water column only at night, when darkness offers some security from visually feeding predators. Included are polychaetes, mysids, cumaceans, gammaridean and caprellid amphipods, tanaids, isopods, and carideans.

Because successful defensive features of prey create pressures that modify the offensive features of predators, the tendencies toward reduced size and nocturnal habits among zooplankters have generated appropriate adaptations among planktivorous fishes. Fishes that prey as adults on zooplankters during the day (e.g., blacksmith, *Chromis punctipinnis*) have specialized features, including a small highly modified mouth, that permit even relatively large individuals to take the tiny organisms which constitute the daytime zooplankton. Some other fishes are diurnal planktivores only as small juveniles and assume different feeding habits as they grow larger (e.g., kelp perch, *Brachyistius frenatus*; señorita, *Oxyjulis californica*; smaller juvenile olive rockfish, *Sebastes serranoides*). Fishes that prey on zooplankters at night (e.g., larger juvenile olive rockfish; kelp rockfish, *Sebastes atrovirens*; queenfish, *Seriphus politus*; walleye surfperch, *Hyperprosopon argenteum*; and salema, *Xenistius californiensis*) take the larger organisms that join the zooplankton after dark. In their feeding morphologies and body form, these large-mouthed fishes have diverged less than their diurnal counterparts from the generalized predators that give rise to them all. They have, however, acquired specialized features, including large eyes, suited to detect and capture prey in the dark.

Interactions among predators and their prey are best recognized by viewing assemblages of animals that occur together in nature. Furthermore, many trophic interactions become apparent only upon considering the changes that occur from day to night, and from one season to another. These convictions shaped studies of feeding relations among tropical reef fishes undertaken between 1962 and 1970 (Hobson 1965, 1968, 1972, 1974), and similarly influenced work done in warm temperate waters from 1972 to 1975. This more recent work centered on the inshore habitats at Santa Catalina Island, Calif. (lat. 33°28′N, long. 118°29′W), where most of the attention was directed at fishes that forage on the benthos (Hobson and Chess in prep.). The present report, however, deals with that segment of the work involving certain fishes and trophically related zooplankters that interact in the water column near shore.

Only a few studies have considered feeding habits in natural assemblages of marine fishes. Limbaugh (1955) and Quast (1968) made the major contributions in southern California, but these important studies represent only a beginning.

The present study goes beyond earlier investigations by considering the organisms taken by the fishes as prey against a broader consideration of the array of similar forms present that would seem to have been equally accessible. The selection of specific prey, however, is only partially developed in discussing these data. Selectivity will

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be treated in depth later (Hobson and Chess in prep.), when these data can be reconsidered along with the data on organisms simultaneously accessible on the sea floor and other substrata, as well as in the water column above habitats different from those described here.

TERMINOLOGY

In this report, the term zooplankton encompasses all the varied small organisms we collected with a plankton net during day and night, and (most important to this study) which proved to include the major foods of a well-defined assemblage of fishes. All the organisms that we consider within this definition belong to groups included in most general accounts of the zooplankton (e.g., Newell and Newell 1963; Wickstead 1965).

Nevertheless, some planktologists would exclude from zooplankton forms like large caridean shrimps that irregularly enter the water column at night. But among crustaceans such distinctions fail to establish where, along the continua of size, mobility, and time spent in the water column, forms like large carideans are apart from those minute calanoid copepods that are zooplankters by any definition. A number of terms defining certain ecological categories among zooplankton have been proposed (e.g., holoplankton, meroplankton, tychoplankton, etc.), but while such terms are useful in certain contexts, we have seen none that define categories meaningful to the concepts developed in this paper (see Discussion).

STUDY AREA

The study area is 25 to 75 m off the western shore of Big Fisherman's Cove (Figure 1). Most of the area is open water about 5 to 15 m deep over a sandy sea floor largely overgrown by the brown alga *Dictyopteris zonariodes* (most of which is anchored to tubes of the polychaete *Chaetopterus variopedatus* (Figure 2)). From the seaward edge of the study area, the bottom falls sharply to the greater depths (more than 30 m) that lie at the center of the cove. Shoreward, and at the mouth of the cove, lies a forest of giant kelp, *Macrocystis pyrifera*. This large brown alga grows to the water's surface from a rocky bottom that slopes up to the shoreline from depths of about 8 m (Figure 3). Water temperatures during the study ranged from lows around 12°C in spring, to highs around 20°C in late summer.

FISHES STUDIED

The fishes studied are those that, during either day or night, swim in the water column and feed principally on zooplankters. They are:

Family Scorpaenidae: scorpionfishes
- Olive rockfish, *Sebastes serranoides* (Eigenmann and Eigenmann)
- Kelp rockfish, *S. atrovirens* (Jordan and Gilbert)

Family Pomadasyidae: grunts
- Salema, *Xenistius californiensis* (Steindachner)

Family Sciaenidae: drums
- Queenfish, *Seriphus politus* Ayres

Family Embiotocidae: surfperches
- Walleye surfperch, *Hyperprosopon argenteum* Gibbons
- Kelp perch, *Brachyistius frenatus* Gill

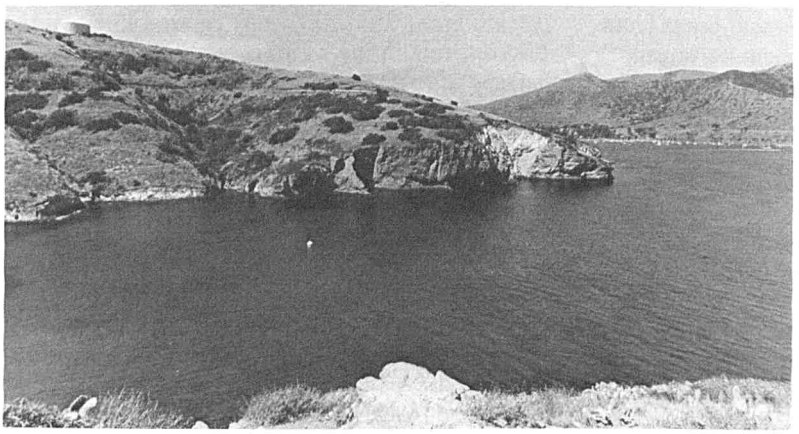


FIGURE 1.—Big Fisherman's Cove, Santa Catalina Island. The study site lies near the opposite shore, between the buoy and the headland.

FIGURE 2.—The *Dictyopteris* field, bordered by the *Macrocystis* forest.

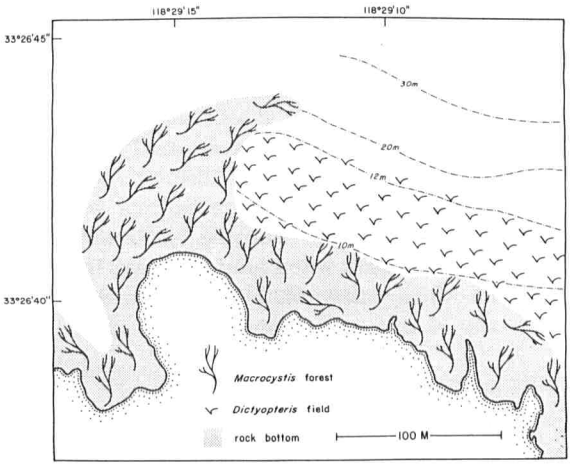


FIGURE 3.—The study area at Santa Catalina Island.

Family Labridae: wrasses
Señorita, *Oxyjulius californica* Günther)
Family Pomacentridae: damselfishes
Blacksmith, *Chromis punctipinnis* (Cooper)

Only two other species in the study area have similar zooplanktivorous habits: the topsmelt, *Antherinops affinis* (Ayres), and the shiner perch, *Cymatogaster aggregata* Gibbons. These two, however, are more characteristic of other habitats, where the species composition of available prey is different. Although for this reason they will be described in separate reports later, their activities are entirely consistent with what is reported and discussed below.

METHODS

Direct Observations

We used scuba and snorkeling (167 h underwater) to observe activity of the fishes and trophically related organisms during all periods of day and night. Except when collecting specimens, we tried to avoid influencing the organisms or their environment.

Collecting Zooplankters

During the same period that we collected fishes for the food-habit study, organisms in the water column that might be their prey were sampled with a 1-m plankton net (0.333-mm mesh) that we pushed through the water for 5-min periods (Figure 4). In this way, a series of paired collections sampled the waters above the *Dictyopteris* field during September 1973, February 1974, and May 1974. Of each pair, the first sampled the water column midway between the water's surface and the sea floor (in 10 to 15 m of water); and the second, which followed immediately, sampled the base of the water column to within about 10 cm above the bottom. During each sampling month, we made a set of eight collections—four at full moon, and four at new moon. Each set included a pair at night (between 2 and 4 h after last evening light), and a pair the following day (between 1200 and 1400 h). In addition, we made one set of collections in the kelp forest bordering the study

FIGURE 4.—Collecting plankton at middepths.

area: a pair at night, under a full moon (when there was enough light to maneuver among the kelp columns), and a pair the following midday.

Because diving lights probably influence organisms in the water column, we turned them off when collecting with the plankton net at night. At these times the moon provided ample light to navigate when it was present, but on dark nights we depended on the luminous dials of our compasses and depth gauges.

Collecting Fishes

To determine the food habits of the fishes, we speared 521 specimens of the eight species and then examined their gut contents. All specimens were taken in the study area between September 1973 and May 1974—the same period over which we sampled the zooplankton. Most of these specimens were collected either at night, within the 2 h before sunrise, or during the afternoon—times that best show differential day or night feeding. All measurements of fish size noted in this report are of standard length.

Sample Analysis

Zooplankton Samples

Generally the samples were analyzed within 2 wk after collection. Sample volumes, which ranged from 0.2 to 36.0 ml ($\bar{x}$ = 8.3), were determined after they had settled for 5 min in a graduated cylinder. The entire sample was analyzed when its volume was less than 5 ml. When the sample was larger, 5-ml aliquots were analyzed, and numbers for the entire sample then extrapolated. Whenever less than the entire sample was analyzed, the balance was searched for forms missing from the aliquot; when found—always in small numbers—these were counted and added to the list.

Fish Gut-Content Samples

The digestive tract of each fish specimen was removed immediately after collection, and preserved in a 10% Formalin[3] solution. For analysis, the contents were examined under a binocular dissecting microscope, and, when necessary, a binocular compound microscope. A note was made of the position in the digestive tract of the various items. A list was then composed of the items in the gut, with the species identified when feasible. The following data were then noted for the items in each listed category: 1) their number; 2) their size range; 3) the extent they had been digested (subjectively assessed on a scale of five, from fresh to well-digested); and 4) an estimate of their representation in the gut as percent by volume of the contents.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Volumes of Zooplankters, Day and Night

Our collections with the plankton net were too few, and spaced over too much time, to attach much significance to the differences in volume between various samples. Nevertheless, certain characteristics probably are meaningful.

The volumes of samples taken day and night at full moon compared with day and night at new moon are as follows: FULL MOON–daytime, middepths (n = 3): 1 to 18 ml, $\bar{x}$ = 8.3; daytime, near bottom (n = 3): 0.2 to 5 ml, $\bar{x}$ = 4; nighttime, middepths (n = 3): 2 to 13 ml, $\bar{x}$ = 4; nighttime, near bottom (n = 3): 5 to 15 ml, $\bar{x}$ = 10.3. NEW MOON–daytime, middepths (n = 3): 2 to 5 ml, $\bar{x}$ = 4; daytime near bottom (n = 3): 1.2 to 5 ml, $\bar{x}$ = 3.7; nighttime, middepths (n = 3): 3 to 13 ml, $\bar{x}$ = 8; nighttime, near bottom (n = 3): 9 to 36 ml, $\bar{x}$ = 19.6.

Thus, during the day the volumes of collections made at the middepths generally were greater than those made near the bottom, whereas the situation was reversed at night. Furthermore, volumes tended to be greater at night than during the day, with the greatest volumes of all taken near the bottom on dark nights.

Activity Patterns of the Zooplankters, Day and Night

The zooplankters are here grouped into a series of categories (Tables 1, 2),[4] most of which represent phylogenetic classes or subclasses.

Radiolarians

Based on the collections made with the plankton net (Tables 1, 2), radiolarians are consistently present in the water column during both day and night, sometimes in large numbers.

Polychaetes, Swimming

We saw polychaetes in the water column only at night. Highly motile epitokous nereids were especially prominent when they swam at middepths during reproductive periods. Polychaetes are underrepresented in the plankton collections (Tables 1, 2), however, because their mobility permitted many to evade our net.

Mollusk Larvae

Based on specimens taken in the plankton net (Tables 1, 2), mollusk veligers occur in the water column in similar numbers during both day and night.

Cladocerans

Cladocerans (Figure 5C) were consistently present in the collections during both day and night (Tables 1, 2), although they were more numerous in the daytime collections.

Ostracods

We saw ostracods in the water column at night, but never during the day. Our daytime plankton collections took only a few individuals, these close to the bottom (Table 3). At night, however, several species were consistently numerous in both middepth and near-bottom collections (Table 3). The most numerous ostracod, *Parasterope* sp. A (Figure 5H), was numerous in the surface layers of the sand during the day (Hobson and Chess in prep.), and during the middle of the night we observed and collected it concentrated at the water's surface.

Calanoid and Cyclopoid Copepods

Calanoid and cyclopoid copepods were numerous in the water column during both day and night, based on our observations in the water as well as on our collections (Tables 1, 2). Indeed, calanoids were the most numerous of all organisms larger than about 1 mm taken in the net. Calanoids and cyclopoids were collected in greater numbers at night (Table 2), but because the plankton is generally richer after dark, they represented a smaller percentage of the sample volumes at night than during the day (Table 1).

The vast majority of calanoids and cyclopoids in the collections were subadults, and some species could be recognized only as adults. Of those identified, the major calanoids were *Acartia tonsa* (Figure 5F) and *Calanus pacificus*, with others

[4]The data in Tables 1 and 2 are from collections with the plankton net made above the open field of low benthic algae adjacent to the kelp forest. A set of day-night collections was also made within the forest (see Methods), where the fishes discussed below spend part (in some cases most) of their time. Because the data from these collections are essentially like those shown in the tables, they are not presented.

TABLE 1.–Organisms collected in the plankton net, day and night, showing size and mean percent of total volume represented by organisms in major taxonomic categories.

Organism category	Size (mm)	Day: Middepth collections (n = 6)	Day: Near-bottom collections (n = 6)	Night: Middepth collections (n = 6)	Night: Near-bottom collections (n = 6)
Radiolarians	0.1- 1.0	5.9	7.2	2.1	0.6
Polychaetes	1.0-55.0	0.3	0.3	0.3	2.1
Mollusk larvae	0.4- 0.8	0.2	0.2	0.2	0.1
Cladocerans	0.3- 1.0	11.2	1.0	0.9	0.5
Ostracods	0.5- 2.0	0.1	<0.1	0.8	1.9
Calanoids and cycloipods	0.6- 4.0	62.5	66.0	29.1	15.3
Harpacticoids	0.6- 1.0	0.2	1.3	0.6	0.8
Other copepods	1.0- 3.0	0.2	<0.1	0.1	0.1
Cirripedian larvae	0.6- 1.0	0.3	1.6	0.2	0.1
Nebaliaceans	3.0- 8.0	0.0	0.0	0.3	0.2
Mysids	1.0-12.0	0.0	0.7	39.1	47.3
Cumaceans	2.0- 5.0	0.0	0.0	2.0	3.7
Tanaids	1.0- 3.0	0.0	0.0	0.3	0.3
Isopods	1.0-10.0	0.0	0.3	1.7	2.4
Gammarideans	1.0- 5.0	0.1	0.2	10.0	14.2
Caprellids	3.0-18.0	0.0	0.0	0.4	0.8
Euphausid larvae	1.0- 3.0	0.6	1.0	0.5	0.3
Euphausid adults and juveniles	12.0-14.0	0.0	0.0	0.2	0.1
Caridean larvae	1.0- 5.0	2.0	2.3	4.8	3.9
Caridean adults and juveniles	4.0-10.0	0.0	0.0	1.0	0.7
Reptantian zoea	0.5- 4.0	0.4	0.6	0.9	0.7
Brachyuran megalops	2.0- 3.0	0.0	0.1	0.4	0.5
Bryozoan larvae	0.5- 1.0	0.7	0.6	0.7	0.5
Chaetognaths	4.0-10.0	1.3	3.4	0.6	0.3
Larvaceans[1]	1.0- 4.0	0.5	0.4	0.1	0.1
Fish eggs	0.6- 2.0	12.1	12.2	1.1	1.3
Fishes	3.0-11.0	1.6	1.9	1.5	1.2

[1]Underrepresented in collections, see text.

TABLE 2.–Organisms collected in the plankton net day and night, showing occurrence and mean number of individuals of organisms in major taxonomic categories.

Organism category	Day: Middepth collections (n = 6) % freq.	Day: Middepth collections (n = 6) Mean no. indiv.	Day: Near-bottom collections (n = 6) % freq.	Day: Near-bottom collections (n = 6) Mean no. indiv.	Night: Middepth collections (n = 6) % freq.	Night: Middepth collections (n = 6) Mean no. indiv.	Night: Near-bottom collections (n = 6) % freq.	Night: Near-bottom collections (n = 6) Mean no. indiv.
Radiolarians	100	~500	100	~550	83	~3,500	83	~1,800
Polychaetes	0	0	0	0	33	<1	50	5
Mollusk larvae	33	3	33	2	50	3	50	4
Cladocerans	100	1,227	83	49	100	146	83	46
Ostracods	17	1	33	<1	100	20	100	73
Calanoids and cyclopoids	100	2,414	100	1,978	100	3,730	100	2,203
Harpacticoids	33	2	50	<1	83	23	100	41
Other copepods	17	1	17	1	17	1	17	1
Cirripedian larvae	50	6	50	30	50	5	17	2
Nebaliaceans	0	0	0	0	33	6	66	2
Mysids	0	0	50	1	100	1,100	100	1,721
Cumaceans	0	0	0	0	100	31	100	105
Tanaids	0	0	0	0	33	6	50	9
Isopods	0	0	33	3	100	23	100	49
Gammarideans	17	<1	17	3	100	436	100	2,121
Caprellids	0	0	0	0	50	4	50	15
Euphausid larvae	100	16	83	21	50	12	50	11
Euphausid adults and juveniles	0	0	0	0	17	<1	17	<1
Caridean larvae	83	31	67	45	100	200	100	220
Caridean adults and juveniles	0	0	0	0	50	25	83	10
Reptantian zoea	67	5	83	9	100	58	100	30
Brachyuran megalops	0		17	<1	50	2	67	4
Bryozoan larvae	83	71	83	12	100	117	67	21
Chaetognaths	100	35	83	31	83	7	33	4
Larvaceans[1]	67	7	50	7	17	2	17	2
Fish eggs	100	137	100	90	100	36	100	59
Fishes	67	19	50	5	83	33	83	19

[1]Underrepresented in collections, see text.

TABLE 3.—Ostracods collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Parasterope sp. A	1-2	0	0	0	0	100	10.2	83	33.8
Cycloleberis lobiancoi	1-2	0	0	0	0	67	3.5	83	18.2
Vargula americana	1-4	0	0	0	0	50	4.8	100	12.2
Philomedes sp. A	1	0	0	0	0	17	0.5	33	3.5
Unidentified species A	1	0	0	0	0	17	0.8	17	0.2
Euphilomedes carcharodonta	1-2	0	0	0	0	50	0.5	0	0
Cythereis sp.	1	0	0	17	0.2	17	0.5	0	0
Philomedes sp. B	1	0	0	0	0	17	0.5	0	0
Conchoecia sp.	1	0	0	17	0.3	0	0	0	0
Unidentified species B	2	0	0	0	0	0	0	17	0.2

present including *Candacia* spp., *Clausocalanus* sp., *Ctenocalanus* sp., *Euchaeta* sp., *Labidocera* spp., *Lucicutia* sp., *Metridia pacificus*, *Paracalanus* sp., and *Rhincalanus nasutus*. The major cyclopoid was *Coryceus* sp. (Figure 5E), but others, including *Oithona* sp., were present.

Harpacticoid Copepods

Our daytime collections took relatively few harpacticoids, all near the bottom. They were more numerous in the night collections, however, when they appeared in both middepth and near-bottom samples. One form predominated, a species of *Porcellidium*, probably undescribed, designated *Porcellidium* species A (Figure 5G). Our night middepth collections (n = 6) took $\bar{x}$ = 21.6 specimens of this species, whereas the near-bottom collections (n = 6) took $\bar{x}$ = 37.3. During the day *Porcellidium* species A was absent in all middepth collections (n = 6), but the near-bottom collections (n = 6) took $\bar{x}$ = 16. Only one other harpacticoid was collected in daylight, a form here designated as harpacticoid species A. Our daytime middepth collections (n = 6) took $\bar{x}$ = 1.8 specimens of this species, but it was absent in all daytime near-bottom collections, and all collections made at night. Three other forms—a second species of *Porcellidium*, and two species of *Eupelta* (all probably undescribed)—were taken only at night: a combined mean of 0.7 in the middepth collections, and a combined mean of 3.2 in near-bottom collections.

Other Copepods

No other copepods were seen in the water column, and very few were taken in the plankton net. An occasional caligoid or monstrilloid appeared in the collections, but were too few to suggest a pattern.

Cirripedian Larvae

Most of the tiny cypris larvae of the barnacles (Figure 5D) are smaller than 1 mm. Their occurrence in the collections (Tables 1, 2) was irregular, and without consistent differences between day and night, or between middepth and near-bottom samples.

Nebaliaceans

At night we occasionally observed and collected one species, probably *Nebalia pugettensis* (Figure 5J; see Smith and Carlton 1975). However, they were neither seen nor taken during the day.

Mysids

Siriella pacifica (Figure 5M) was the most widespread mysid over the study area. It remained sheltered on the sea floor and close to kelp during the day, but during late twilight moved into open water, where it spent the night (Table 4). On five evenings we noted when *S. pacifica* had first risen as much as 1 m above the bottom, and found this level attained 29 to 42 ($\bar{x}$ = 37.6) min after sunset. On six mornings, the last individual 1 m above the bottom was seen 32 to 50 ($\bar{x}$ = 38.7) min before sunrise. The stomach contents of 30 *S. pacifica* collected during day and night were examined: DAYTIME—of 10 (8.5-10.5 mm, $\bar{x}$ = 9.6) collected amid giant kelp during midafternoon (5 from the

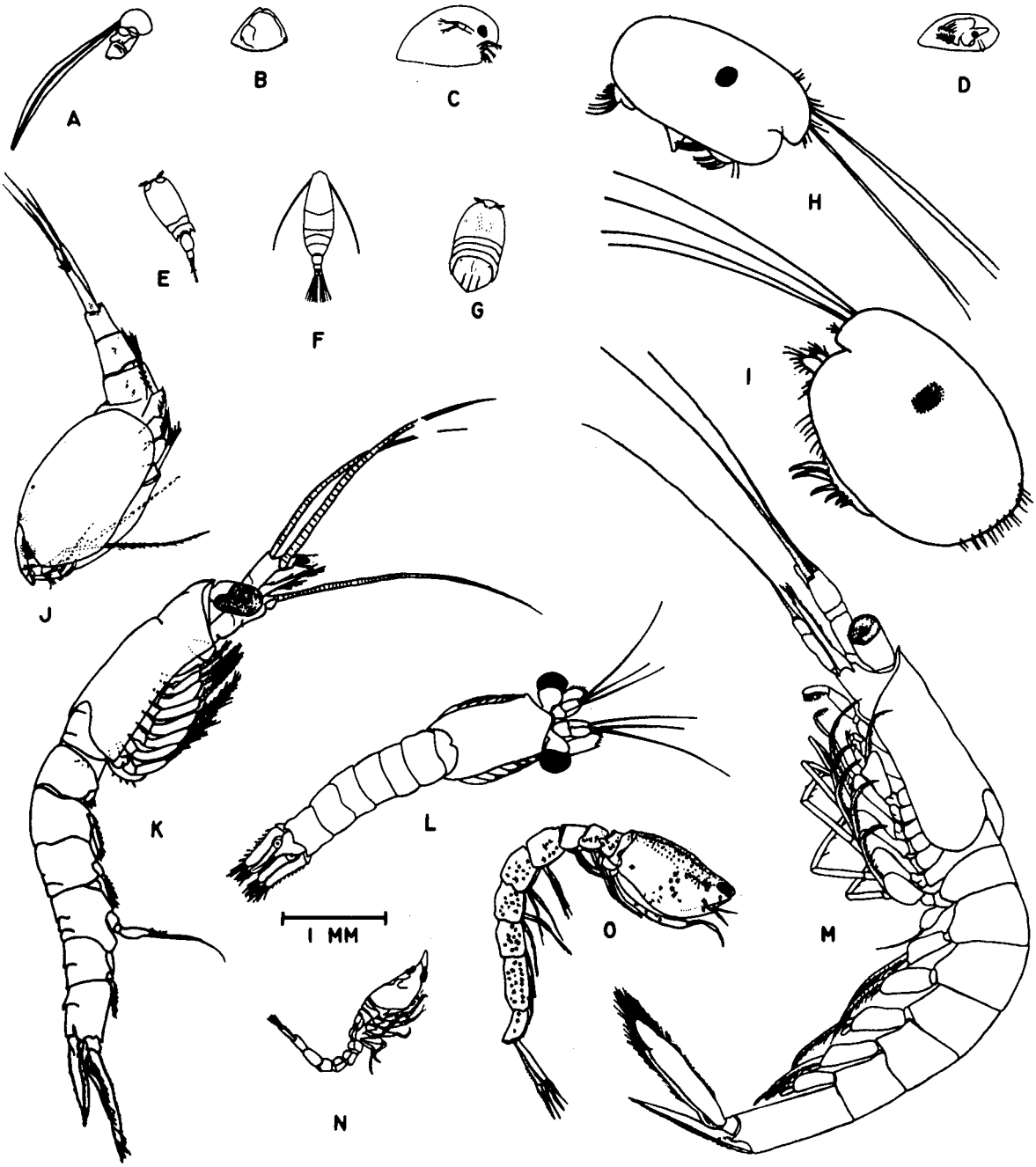
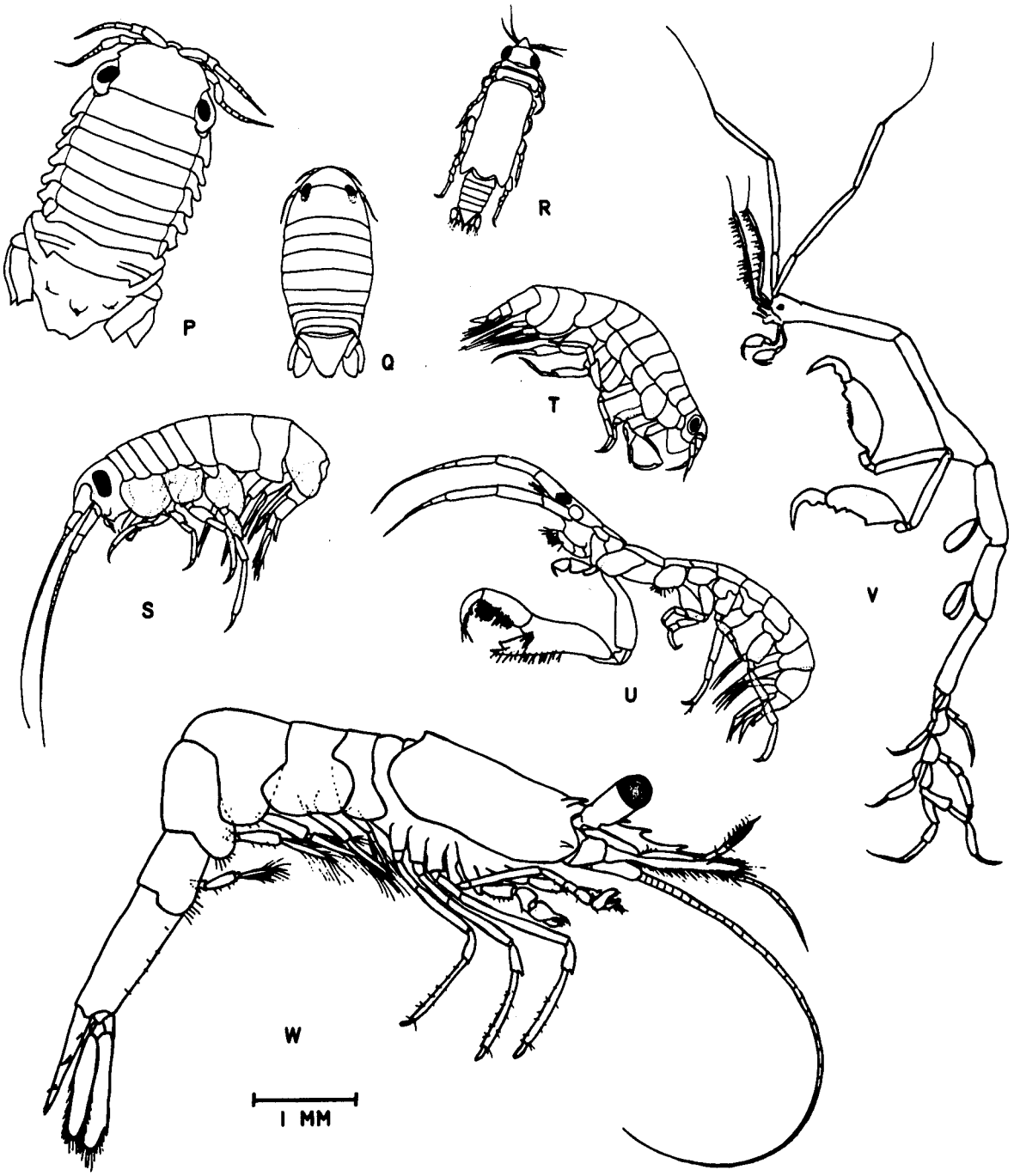


FIGURE 5.—Relative sizes of some of the zooplankters involved in this study. A to F are full-time inhabitants of the water column; G to W are species that rise into the water column after dark (R is occasionally there during daylight). A. larvacean *Oikopleura* sp.; B. bryozoan larva, cyphonautes; C. cladoceran *Evadne* sp.; D. barnacle larva, cypris; E. cyclopoid copepod *Coryceus* sp; F. calanoid copepod *Acartia tonsa*; G. harpacticoid copepod *Porcellidium* sp.; H. ostracod *Parsterope* sp. A; I. ostracod *Cycloleberis lobiancoi*; J. nebaliacean *Nebalia pugettensis*; K. mysid *Acanthomysis sculpta*; L. mysid erythropinid sp.; M. mysid *Siriella pacifica*; N. cumacean *Cumella* sp. A; O. cumacean *Cyclaspis nubila*; P. isopod *Paracercies* sp. (♀); Q. isopod *Cirolana diminuta*; R. isopod gnathiid (♀); S. gammaridean amphipod *Batea transversa*; T. gammaridean amphipod *Gitanopsis vilordes*; U. gammaridean amphipod *Ericthonias braziliensis*; V. caprellid amphipod *Caprella pilidigita*; W. caridean decapod *Hippolyte clarki*.



canopy, 5 from the lower portions of the plants), 7 were empty and 3, whose stomachs averaged 13% full, contained crustacean fragments (55% of total volume) and unidentified material. NIGHTTIME–20 individuals (7-12 mm, $\bar{x}$ = 10.5) taken at middepth 2 h before first morning light had stomachs averaging 82% full, and containing crustacean fragments (100% of total volume), including copepods and cladocerans. Clearly, *S. pacifica* is a nocturnal predator.

TABLE 4.–Mysids collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Siriella pacifica	2-12	0	0	0	0	100	693.0	100	1,242.2
Erythropinid sp.	1- 6	0	0	17	5.3	100	400.3	100	468.3
Acanthomysis sculpta	4- 8	0	0	0	0	33	6.2	17	2.0
Unidentified sp.	3- 8	0	0	0	0	0	0	17	1.0

An unidentified erythropinid species (Figure 5L) behaved much like *S. pacifica*, but was seen less often. Although one daytime near-bottom collection took 32 individuals (probably the net sampled a diurnal aggregation close to the sea floor), generally the species was taken in the plankton net only at night. During the day we found it numerous amid the flocculent material that often accumulates in shallow depressions on sandy bottom (Hobson and Chess in prep.)

The predominant mysid observed and collected in the canopy of the kelp forest was *Acanthomysis sculpta* (Figure 5K), which aggregated in small openings among the kelp fronds during the day. (*Siriella pacifica* also was numerous in the kelp canopy, but not the erythropinid.) At night some *A. sculpta* moved out over the adjacent open regions sampled by our net (Table 4), but most stayed close to the kelp. The stomach contents of 20 *A. sculpta* collected during day and night were examined: DAYTIME–All 10 (8.5-11 mm, $\bar{x}$ = 10.0) collected amid the canopy of giant kelp during midafternoon contained food, with their stomachs averaging 85% full. All 10 contained plant material, apparently *Macrocystis* (69% of diet volume), while 7 contained crustacean fragments, mostly copepods, (30% of diet volume). NIGHTTIME–All 10 (8-11 mm, $\bar{x}$ = 9.6) collected in the kelp canopy 30 min before first morning light contained food, with their stomachs averaging 82% full. All 10 contained plant material, apparently *Macrocystis* (56% of diet volume), and 9 contained crustacean fragments, mostly copepods (44% of diet volume). Thus, *A. sculpta*, which does not join the other two mysid species in their mass movement into open water after dark, seems to feed on plants and animals during both day and night.

Cumaceans

Cumaceans were numerous in the water column at night, but absent there during the day. On four evenings we noted the first one to rise as much as 1 m above the bottom, and found this level attained 26 to 41 ($\bar{x}$ = 32.3) min after sunset. On four mornings we noted the last individual 1 m above the bottom, and recorded this event 37 to 50 ($\bar{x}$ = 41.3) min before sunrise. Usually we were unable to determine the species of cumaceans seen swimming in the water, but our plankton collections (Table 5) took only two species in substantial numbers: *Cumella* sp. A (Figure 5N) and *Cyclaspis nubila* (Figure 5O). Both of these species were numerous in samples of sand taken from the surface of the sea floor during the day (Hobson and Chess in prep.).

Tanaids

Tanaids were absent in the daytime collections, but one species, *Leptochelia dubia*, was collected at

TABLE 5.–Cumaceans collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Cumella sp.A	1-2	0	0	0	0	100	11.7	100	73.5
Cyclaspis nubila	2-5	0	0	0	0	67	17.8	100	29.2
Unidentified sp.	2	0	0	0	0	50	0.7	67	1.7

night. The nighttime middepth collections (n = 6) took $\bar{x}$ = 5.8 *L. dubia*, and the nighttime near-bottom collections (n = 6) took $\bar{x}$ = 9.5. We found this species in tubes of cemented sand grains in daytime dredge samples from sandy bottom (Hobson and Chess in prep.).

Isopods

Isopods generally were absent from the water column during the day, although the plankton collections show that at least some juvenile and female gnathiids (Figure 5R) are present. After dark, however, a number of isopods occurred in the mid-waters (Table 6). *Paracercies* spp., in particular, were numerous. Most of the specimens of *Paracercies* were juveniles or females (Figure 5P), and their identity remains uncertain. Based on the occurrence of males, *P. cordata* is by far the most numerous species of this genus in the study area, but at least one other is present.

Gammaridean Amphipods

Gammaridean amphipods were generally absent from the water column during the day, although *Gitanopsis vilordes*, which lived principally amid the dense surface canopy of the kelp forest bordering the study area (Hobson and Chess in prep.), was collected in small numbers (Table 7). At night, however, we saw gammarideans throughout the water column, and, with *Batea transversa* (Figure 5S) predominating, they were a major component of our catch in the nighttime collections (Table 7). *Batea transversa* was numerous during the day amid the low benthic algae that floors most of the study area (Hobson and Chess in prep.).

TABLE 6.–Isopods collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Gnathiid juveniles	1-3	0	0	33	3	100	9.8	100	32.5
Paracerces sp.	1-3	0	0	0	0	50	11.3	67	11.2
Cirolana harfordi	2	0	0	0	0	33	1.5	17	2.0
Cirolana diminuta	3-5	0	0	0	0	17	0.2	33	0.8
Eurydice caudata	2-3	0	0	0	0	0	0	33	0.8
Excorallana kathae	10	0	0	0	0	17	0.3	17	0.2
Cirolanid sp.	3	0	0	0	0	0	0	17	0.2
Exospheroma rhomburum	3	0	0	0	0	0	0	17	0.2
Limnoria sp.	3	0	0	0	0	0	0	17	0.2

TABLE 7.–Gammaridean amphipods collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Batea transversa	1-4	0	0	0	0	100	400.7	100	1,978.2
Gitanopsis vilordes	1-3	17	0.8	17	2.3	83	11.3	100	41.7
Ericthonias braziliensis	2-4	0	0	0	0	17	0.7	17	2.0
Synchelidium sp.	3	0	0	0	0	17	0.3	33	1.3
Orchomene sp.	2-4	0	0	0	0	17	0.2	50	1.3
Aoroides columbaie	3-4	0	0	0	0	0	0	33	1.3
Pleustes platypa	2	0	0	0	0	33	0.7	0	0
Ampithoe spp.	8	0	0	0	0	17	0.2	17	0.5
Podocerus cristatus	2	0	0	0	0	0	0	33	0.3
Oedocerotid sp.	3	0	0	0	0	0	0	17	0.3
Phoxocephalid sp.	2	0	0	0	0	0	0	17	0.2
Unidentified[1]	1-4	0	0	0	0	83	79.7	100	95.5

[1]Many of the unidentified specimens are juveniles, probably at least many being of the species listed above.

On four evenings we noted the first gammaridean seen as much as 1 m above the bottom, and found this level attained 27 to 39 ($\bar{x}$ = 34) min after sunset. On each occasion, individuals had been visible close among the bottom algae for about 5 min before any of them rose to the 1-m level. The final return to the sea floor at daybreak was monitored on four mornings, when the last individual was seen 1 m above the bottom 26 to 41 ($\bar{x}$ = 35) min before sunrise. Similar to the evening situation, individuals continued to be visible close above the bottom algae for an additional 5 min, or so.

To roughly determine the proportion of gammarideans that rise from the sea floor at night, we compared the amphipods in a sample of benthic algae at night, with a similar sample taken in the same place the following day (both samples, loosely packed in a 2.3-liter plastic bag, were taken immediately after plankton collections). Both samples contained 2.5 ml of animals (including other forms besides amphipods). Nevertheless, the limited data (Table 8) indicate that the numbers of some gammarideans on the algae, notably *B. transversa*, dropped sharply after dark, those of others, including *Ericthonias braziliensis* (Figure 5U), experienced a lesser decline, and those of still others remained essentially unchanged. Data from the collections (Table 7) and direct observations indicate that there were fewer amphipods on benthic algae after dark because many have risen into the water column. But the tendency to leave the sea floor clearly varies between species and in perhaps no species is it absolute. Probably at least many individuals make only short excursions into the water column.

TABLE 8.—Gammaridean amphipods collected in samples of benthic algae, day and night.

Species	No. of individuals Day	Night
Species known from plankton collections		
Batea transversa	10	0
Ericthonias braziliensis	25	8
Ampithoe spp.	15	11
Aoroides columbiae	2	0
Pleustes platypa	2	0
Podocerus cristatus	1	0
Total	55	19
Species unknown from plankton collections		
Hyale nigra	10	9
Photis brevipes	2	0
Elasmopus antennatus	0	1
Heterophlias seclusus	1	0
Total	13	10
Unidentified forms[1]	26	22

[1]At least some of the unidenitfied forms probably are juveniles of the species listed above.

Caprellid Amphipods

We never saw caprellids above the bottom during the day, but saw them, though infrequently, in the water column at night. Consistent with these observations, caprellids were collected in the plankton net at night, but never during the day. The nighttime middepth collections (n = 6) took $\bar{x}$ = 3.2 *Caprella pilidigita* and $\bar{x}$ = 0.2 *C. californica*, whereas the near-bottom collections (n = 6) took $\bar{x}$ = 9.7 *C. pilidigita* and $\bar{x}$ = 5.2 *C. californica*. In addition, a single unidentified juvenile was taken in one nighttime middepth collection. Size ranges of specimens: *C. pilidigita* 4 to 18 mm, *C. californica* 6 to 10 mm, and the unidentified juvenile 3 mm. Both *C. californica* and *C. pilidigita* (Figure 5V) were at all times numerous amid the low benthic algae that floors most of the study area.

Euphausid Larvae

The calyptopis larvae of euphausids occurred regularly in both day and night collections.

Euphausid Adults and Juveniles

Euphasid adults and juveniles were neither seen nor collected in the water column during the day, but occasionally swarmed around our lights at night. The few individuals collected in the plankton net (Tables 1, 2) are of one species: *Thysanoessa spinifera*. The numbers collected, however, underrepresent the numbers we saw in the water (all of which appeared to be *T. spinifera*), probably because this relatively large, motile animal effectively evaded our net. Rather than rising from the sea floor at nightfall, as do so many other nocturnal components of the plankton discussed above, this euphausid seems to move in from deeper water. Unlike the other forms, euphausids were not taken in our extensive diurnal sampling of the benthos (Hobson and Chess in prep.).

Caridean Larvae

Based on the collections (Tables 1, 2), caridean larvae are numerous in the plankton during both day and night, but more so at night. Furthermore, there are more larger individuals in the water

column after dark. We made no attempt to identify our specimens to species, but probably many are larvae of the two species discussed as adults and juveniles, below.

Caridean Adults and Juveniles

Caridean adults and juveniles were observed in the water column only at night. On the one evening that the event was noted, the first individual seen rising as much as 1 m above the bottom attained this level 39 min after sunset. Adult and juvenile carideans are absent in the daytime collections, but *Hippolyte clarki* (Figure 5W), was sometimes numerous in collections made after dark. The nighttime middepth collections ($n = 6$) took $\bar{x} = 25.2$ *H. clarki*, and the near-bottom collections ($n = 6$) took $\bar{x} = 10$. Only one other adult caridean was collected, this a single *Eualus herdmani* in a nighttime near-bottom sample. The specimens of *H. clarki* were 4 to 10 mm long, the single *E. herdmani* 12 mm. *Hippolyte clarki* is numerous during the day in the kelp forest bordering the study area, where it concentrated in the dense surface canopy and upper regions of these massive plants. At the same time *E. herdmani* predominated in the lower regions of the same plants (Hobson and Chess in prep.).

The stomach contents of 20 *H. clarki* collected during day and night were examined. DAYTIME–Of 10 (8-16 mm, $\bar{x} = 10.8$) collected from giant kelp plants during midafternoon, 4 were empty, and the other 6, whose stomachs averaged 17% full, contained only extensively macerated fragments. NIGHTTIME–Of 10 (8-17 mm, $\bar{x} = 12$) collected close to giant kelp 1 h before first morning light, 1 was empty, and the other 9, whose stomachs averaged 34% full, contained a variety of prey, some of it fresh: mollusk veligers in 4 (28% of total volume); foraminiferans in 3 (9% of total volume); shrimp larvae in 1 (11% of total volume); and extensively macerated material in 7 (52% of total volume). These limited data indicate this animal is primarily a nocturnal predator, but only a relatively few seem to swim far from algal cover.

Reptantian Zoea

Based on the collections (Tables 1, 2), zoea were consistently present in moderate numbers at all levels of the water column during both day and night, but were most numerous there after dark. Usually we failed to notice zoea in the water, but one night observed them in dense swarms close to the bottom.

Brachyuran Megalops

Our plankton collections (Tables 1, 2) indicate that brachyuran megalops were frequently present, if not numerous, in the water column at night, but only infrequently present during the day.

Bryozoan Larvae

The cyphonautes larvae of bryozoans (Figure 5B) were consistently taken in substantial numbers by middepth and near-bottom collections both day and night.

Chaetognaths

Our collections regularly took chaetognaths both day and night (Tables 1, 2), but even though these animals are relatively large, we failed to see them in the water, presumably because they are largely transparent. Chaetognaths probably were more numerous in the study area than our collection data indicate, owing to a mobility that would permit many to evade our net.

Larvaceans

We collected larvaceans in our plankton net both day and night, but only in small numbers (Tables 1, 2). It became clear that these numbers far underrepresented the numbers present, however, when we examined the gut contents of the blacksmith (recounted below). Most larvaceans in the area are less than 0.5 mm in diameter, and apparently their pliable bodies readily squeeze through the 0.333-mm mesh of our net. So we made a midday tow in the study area using a 0.25-m net with a 0.253-mm mesh. Significantly, larvaceans, most being of the genus *Oikopleura* (Figure 5A), made up 20% of the sample. There was one larvacean to about every six copepods (calanoids and cyclopoids), and they ranged from 1 to 3 mm long, with a diameter of about 0.2 to 0.5 mm. Significantly, active individuals throughout much of this size range were observed passing through a piece of 0.333-mm mesh net placed among them in a petri dish. Because these animals are transparent, and so small, we failed to see them in the water.

Fish Eggs

Fish eggs were a regular component of both middepth and near-bottom plankton collections during both day and night (Tables 1, 2). Owing to their small size and transparency, however, they went unseen by us in the water.

Fish Larvae

Fish larvae were consistently seen and collected at middepths and near the bottom both day and night (Tables 1, 2).

Activity Patterns of Planktivorous Fishes, Day and Night

Having described the zooplankters that occur in the water column during both day and night, we now consider the feeding activities of the fishes that find prey there.

Sebastes serranoides—olive rockfish

Small juveniles of this species first appeared inshore during midsummer when about 30 mm long. They remained here throughout the ensuing year, growing to about 100 to 110 mm long. Although their numbers declined sharply during the following summer, when the next crop of small juveniles arrived, many remained in the area well into a second winter, and some stayed longer. Nevertheless, few olive rockfish exceeding about 120 mm occurred in the study area. Larger individuals (to well over 200 mm) were numerous in deeper water, but were not considered in this study. Limbaugh (1955) noted: "The young appear in large schools, from May through September. The schools form behind protective reefs, in bay entrances, and in the lee of islands." Other data on this species presented by Limbaugh, and also by Quast (1968), pertain generally to individuals larger than those discussed here. The species is reported to reach 610 mm (Miller and Lea 1972).

The activity pattern of this fish changes markedly during its first year inshore. Most of the smaller juveniles are active by day and relatively inactive at night. Beginning among those about 55 mm long, however, there is a general shift toward feeding after dark. Nocturnal habits are characteristic among individuals larger than about 65 mm (to at least 120 mm—the largest considered here). This report, therefore, recognizes three size categories, and treats each separately:

1) small juveniles, which are predominantly diurnal, are those shorter than 55 mm; 2) intermediate juveniles, which represent a transition to the nocturnal mode, are those between 55 and 64 mm; and 3) large juveniles, most of which are nocturnal, are those 65 mm and longer.

SMALL JUVENILES.—During daylight, the small juveniles generally hovered in small aggregations at middepths in less than 5 m of water. In the study area they were most numerous along the shoreward margin of the kelp forest, close to rising stands of *Macrocystis* and other large algae.

The small juveniles appeared in the water column each morning, beginning about 40 min before sunrise, after a night spent sheltered under cover of algae or rocks. They occurred first as solitary individuals, but soon assembled in aggregations that were well-formed by 30 min before sunrise. Only after sunrise, however, did they feed appreciably. Then, sporatically at first, but with steadily increasing frequency, they began to snap at objects in the water indistinguishable to a human observer a few meters away.

The onset of feeding in the morning is illustrated by the decreasing incidence of empty guts in specimens collected during this period from the mid-water aggregations. Empty guts occurred in 84% of those sampled during the 40 min before sunrise (52 of 62 specimens; 42-54 mm, $\bar{x}$ = 49), in 58% of those collected during the 15 min following sunrise (7 of 12 specimens; 41-53 mm, $\bar{x}$ = 48), in 25% of those taken 15 to 30 min after sunrise (2 of 8 specimens; 45-53 mm, $\bar{x}$ = 50), and in none of those collected 30 to 60 min after sunrise (10 specimens; 41-54 mm, $\bar{x}$ = 50).

Intermittent observations throughout the day showed consistent feeding activity. The guts were full in all 11 specimens (40-51 mm, $\bar{x}$ = 45) sampled from aggregations during midafternoon. Items they had taken, combined with items taken by the 31 specimens containing food that were collected during early morning (a total sample of 42 fish), document the food habits of these small juveniles.

Prey of the 44 small juveniles that had identifiable material in their guts are listed below in order of their rank as prey. (The same format is used in presenting the gut contents of the other fish species, below.) In this list, the major num-

bered categories are the same as those in which the zooplankters are organized in Tables 1 and 2 and in the text above. The few additional major categories include various nonplanktonic organisms that some of these fishes had taken in small numbers. Listed under each major category, according to rank within that category, are the species and species groups that are the actual prey of the fish. Following most entries throughout the listing are sets of three values in parentheses; these values relate certain characteristics of the entry to the food habits of the fish. (The values were derived from calculations based only on fish that contained identifiable material. Fish with empty guts or containing only unidentifiable material were not considered.) The first value in parentheses is the percent of fish that contained the item(s); the second value is the mean number of individuals of the item(s) that were taken, and the third value is the mean percent of the diet volume represented by the item(s). Rank as prey was determined by a ranking index, which is not shown, but which is the product of the first and third values in parentheses.

Following the above format, the prey organisms are:

1. CALANOID AND CYCLOPOID COPEPODS (83: 44.4: 59.5)
   calanoids, including *Acartia tonsa* and *Labidocera* sp. (81: 40.3: 54.9); cyclopoids, including *Corycaeus* sp. (38: 4.1: 4.6).
2. GAMMARIDEAN AMPHIPODS (29: 0.4: 11.4)
   Batea transversa (18: 0.3: 7.6); unidentified fragments (11: 0.1: 3.8).
3. CARIDEAN LARVAE (20: 0.4: 3.2)
   unidentified species.
4. MYSIDS (11: 0.3: 4.5)
   Acanthomysis sculpta (3: 0.1: 2.0); erythropinid sp. (3: 0.1: 0.5); unidentified fragments (7: 0.1: 2.0).
5. CLADOCERANS (20: 1.1: 2.4)
   Evadne sp.
6. OTHER COPEPODS (18: 0.3: 2.2)
   unidentified monstrilloids.
7. EUPHAUSID ADULTS AND JUVENILES (11: 0.1: 1.3)
   unidentified fragments.
8. BRACHYURAN MEGALOPS (5: 0.1: 4.8)
   unidentified.
9. HARPACTICOID COPEPODS (18: 0.4: 1.2)
   harpacticoid sp. A (7: 0.1: 0.7); *Porcellidium* sp. B (5: 0.1: 0.2); *Porcellidium* sp. A (2: 0.1: 0.1); unidentified fragments (5: 0.1: 0.2).
10. TANAIDS (10: 0.2: 2.4)
    Leptochelia dubia (7: 0.1: 1.2); unidentified fragments (3: 0.1: 1.2).
11. REPTANTIAN ZOEA (11: 0.1: 1.3)
    unidentified.
12. FISHES (5: 0.2: 2.0)
    unidentified larvae.
13. ISOPODS (2: <0.1: 1.1)
    Paracercies sp.
14. GASTROPODS (2: 0.4: 0.5)
    Tricolia sp.
15. EUPHAUSID LARVAE (2: <0.1: 0.1)
    calyptopsis.
16. CIRRIPEDIAN LARVAE (5:<0.1: <0.1)
    cypris.
17. BRYOZOAN LARVAE (2: <0.1: <0.1)
    cyphonautes.

Small juveniles took calanoid copepods as their major prey from the time they began feeding at sunrise until they ceased feeding at the end of the day. In 10 specimens collected during May and June (the only times for which calanoids in this material were identified to species), about 22% of the calanoids were *Acartia tonsa*, and although the rest remained unidentified (except for a single specimen of *Labidocera* sp.), many probably were immature individuals of this same species.

A number of the prey listed above occurred only in specimens collected during early morning. These are: the gamaridean amphipods, the tanaids, the euphausids, the lone isopod, the megalops, and all mysids except those in one individual (see below). Most of these items were extensively digested, in sharp contrast to the freshness of the calanoids and other food materials in the early-morning specimens. Clearly, they had been in the guts for some time, probably since the previous night. Nevertheless, judging from the empty guts in most individuals of this size at daybreak it would seem that nocturnal feeding is insignificant.

Only later than about 30 min after sunrise did the olive rockfish begin taking *Evadne* sp., but this cladoceran then became a consistant component of the diet for the rest of the day. *Evadne* is slightly smaller and more transparent than the other prey organisms, and to capture it the rockfish may need more light. The only mysid taken during the day was *Acanthomysis sculpta*, of which two individuals that appeared recently ingested were found in one olive rockfish during midafternoon.

INTERMEDIATE JUVENILES.—Individuals between about 55 and 65 mm long were highly inconsistent in so far as whether they fed by day or by night (many did both). The nocturnal situation among intermediate individuals is represented by 18 specimens (55-63 mm, $\bar{x}$ = 58) collected before sunrise from open water during the hour before first morning light, and also from developing

aggregations of juveniles more than 30 min before sunrise. Of these, 13 (72%) were full of prey in varying stages of digestion, demonstrating nocturnal feeding, whereas 5 (28%) were empty, indicating they had been inactive that night. All the empty fish were from the developing aggregations, but many of those containing food were also taken from those aggregations. Items taken at night by the 13 intermediate juveniles containing food were as follows, with the format being that used for the small juveniles, above.

1. GAMMARIDEAN AMPHIPODS (69: 2.9: 28.5)
   including *Batea transversa* and *Ericthonias braziliensis*.
2. CUMACEANS (54: 2.7: 26.3)
   Cyclaspis nubila (46: 2.6: 26.1); *Cumella* sp. A (8: 0.1: 0.2).
3. MYSIDS (38: ?: 16.2)
   Siriella pacifica (23: 0.3: 13.1); unidentified fragments (15: ?: 3.1).
4. FISHES (15: 7.1: 5.4)
   unidentified larvae.
5. CAPRELLID AMPHIPODS (8: 0.5: 6.2)
   Caprella pilidigita.
6. POLYCHAETES, SWIMMING (8: ?: 5.0)
   unidentified fragments.
7. OSTRACODS (8: 0.1: 0.8)
   Parasterope sp. A
8. BRACHYURAN MEGALOPS (8: 0.5: 0.4)
   unidentified.

The diurnal feeding situation, as well as the changeover from day to night, is represented by 12 individuals (55-62 mm, $\bar{x}$ = 58), all with full guts, collected from among feeding aggregations of small juveniles within 1 h after sunrise. Almost all the food items in this sample were either fresh or well-digested—there was little in between. Presumably, the fresh items were those that had been taken after feeding began within the previous hour, whereas the extensively damaged items had been taken during the night before. (One would expect specimens taken as early in the morning as these to contain evidence of any nocturnal feeding they might have done, and this proved true here.) Seven of the 12 individuals sampled contained both fresh and well-digested material in large numbers, always with the fresh items forward in the gut (often in the esophagus), and the well-digested items well back in the posterior region. Clearly, these individuals had fed substantially during both day and night (a conclusion strengthened by the kinds of prey among the fresh and well-digested segments of the diet, see below). Three of the other five specimens contained only fresh items, indicating diurnal feeding exclusively, whereas two contained just well-digested material, indicating only nocturnal feeding. Food items in this material are identified below, but with fresh items listed separately from well-digested items.

FRESH ITEMS

1. CALANOID AND CYCLOPOID COPEPODS (83: 65.9: 47.8)
   calanoids (83: 65.7: 47.5); cyclopoids (17: 0.2: 0.3).
2. CLADOCERANS (33: 0.8: 0.8)
   Evadne sp.
3. OSTRACODS (8: 0.1: 1.7)
   Cycloleberis lobiancoi.
4. OTHER COPEPODS (8: 0.1: 0.4)
   monstrilloids.
5. ISOPODS (8: 0.1: 0.4)
   gnathiid juveniles.
6. HARPACTICOID COPEPODS (8: 0.2: 0.2)
   Porcellidium sp. A.
7. CARIDEAN LARVAE (8: 0.1: 0.3)
   unidentified.

WELL-DIGESTED ITEMS

1. GAMMARIDEAN AMPHIPODS (50: 1.3: 1.1)
   including *Batea transversa*.
2. CARIDEAN LARVAE (33: 2.2: 12.9)
   unidentified.
3. EUPHAUSID ADULTS AND JUVENILES (17: 0.7: 10.7)
   unidentified fragments.
4. FISHES (17: 1.0: 9.2)
   unidentified larvae.
5. REPTANTIAN ZOEA (17: 0.3: 2.0)
   unidentified.
6. BRACHYURAN MEGALOPS (8: 0.3: 1.3)
   unidentified.
7. INSECTS (8: 0.1: 0.8)
   unidentified.
8. CAPRELLID AMPHIPODS (8: 0.1: 0.4)
   unidentified.

The fresh items apparently represent diurnal feeding, the well-digested items nocturnal feeding. Thus, among individuals within the intermediate size range there obviously are many that forage during both day and night.

LARGE JUVENILES.—During the day, olive rockfish more than about 65 mm long generally hovered in small aggregations low in the water column beneath the kelp canopy within the seaward part of the forest (Figure 6). Aggregations composed of relatively large individuals (exceeding a length of about 100 mm) sometimes hovered above others of the same size seated on the rocks below.

In contrast to the small individuals described above, large juveniles generally showed no sign of feeding during the day, an observation supported

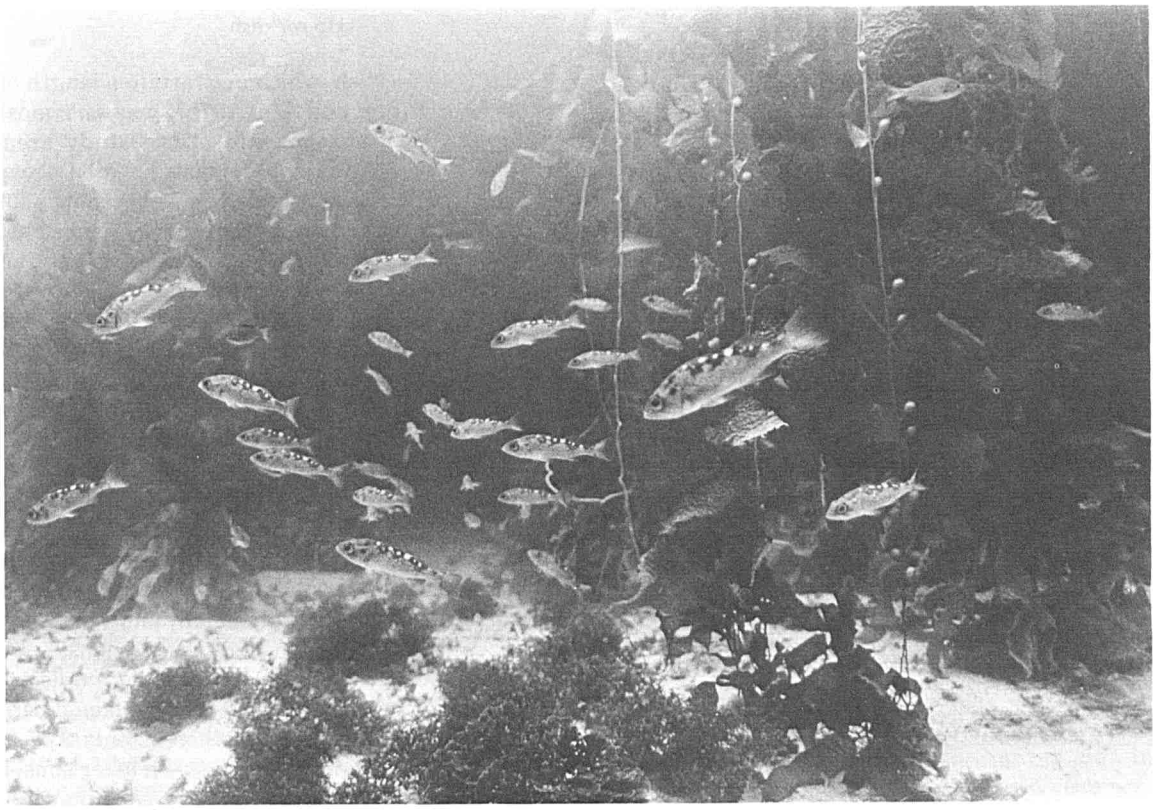


FIGURE 6.—A daytime aggregation of large juvenile olive rockfish, *Sebastes serranoides*. Many nocturnal fishes spend the day in quiet schools.

by examination of gut contents. Of 42 specimens (65-120 mm, $\bar{x}$ = 91) collected from aggregations during midafternoon, 28 (67%) had empty guts, and 8 (19%) contained only well-digested fragments. Six (14%), however, contained relatively fresh prey probably captured earlier that day: the mysid *Acanthomysis sculpta* (50: 15.7: 32.5); the caridean shrimps *Hippolyte clarki* (50: 0.5: 14.2) and *Eualus herdmani* (17: 0.2: 5.2); the cladoceran *Evadne* sp. (17: 4.3: 10.0); calanoid copepods (17: 1.5: 5.2); euphausid larvae, calyptopis stage (17: 0.5: 1.6); and harpacticoid copepod *Porcellidium* sp. A (17: 0.2: 0.1). Also present were extensively digested fragments of cumaceans, tanaids, euphausids, and mysids (33: ?: 20.5) that probably had been taken the night before (a judgment influenced by knowledge of nocturnal food habits, defined below). All of the cladocerans, calanoids, and euphausid larvae among this material constituted the entire gut contents of one 82-mm individual, and the contents suggest a mode of feeding like that of the small juveniles above.

Beginning about 20 min after sunset, large juveniles began leaving the sites of their daytime aggregations. They moved away from the kelp forest, and dispersed over the adjacent field of *Dictyopteris*. Many of them rose into the upper part of the water column, but most remained within 5 m of the sea floor. They remained in these positions throughout the night, often assuming a tail-down attitude, now and then darting a few centimeters forward and snapping at objects in the dark water. The few that remained in the kelp forest usually hovered high in the water column beneath sizeable breaks in the kelp canopy. They began returning to the forest at first morning light, and by 30 min before sunrise were back in their daytime aggregations.

Clearly, olive rockfish of this size feed chiefly at night. This conclusion is supported by study of gut contents from 72 specimens (65-157 mm, $\bar{x}$ = 85) collected in this area at night—later than 4 h after sunset, and before first morning light. Only two of these (less than 3%) had an empty gut, a contrast

to the high incidence of empty guts (67%) among specimens collected during the afternoon. More significant, the gut of all 70 other specimens contained many fresh items, all organisms present in the water column after dark.

Major categories of prey with included species and species groups, are listed below in order of their rank as prey.

1. GAMMARIDEAN AMPHIPODS (90: 16.9: 43.9)
   Batea transversa 76: 8.5: 21.9); *Ericthonias braziliensis* (19: 1.1: 2.6); *Ampithoe* spp. (20: 1.3: 2.4); *Photis brevipes* (14: 1.2: 0.8); *Ampelisca* sp. (3:<0.1: 1.6); *Synchelidium* sp. (9: 0.1: 0.6); *Aoroides columbiae* (9: 0.1: 0.4); *Hyale nigra* (3: 0.1: 0.3); *Monoculoides* sp. (3: 0.3: 0.2); *Podocerus cristatus* (4: <0.1: 0.1); phoxocephalid sp. (3: <0.1: 0.1); lysianassid spp. (1: <0.1: 0.1); *Paraphoxus* sp. (1:<0.1: 0.1); *Pleustes platypa* (1: <0.1: 0.1); unidentified gammarideans, including unknown forms and those unrecognized due to damage (73: 3.9: 12.6).
2. MYSIDS (69: 2.7: 12.5)
   Siriella pacifica (47: 1.7: 9.2); erythropinid sp. (40: 0.9: 3.1); *Acanthomysis sculpta* (3: <0.1: 0.2).
3. CUMACEANS (57: 4.9: 8.4)
   Cyclaspis nubila (37: 4.1: 7.2); *Cumella* sp. (40: 0.8: 1.1); unidentified (3: <0.1: 0.1).
4. POLYCHAETES, SWIMMING (36: 0.5: 8.6)
   at least most of them nereids.
5. CAPRELLID AMPHIPODS (36: 1.4: 7.0)
   Caprella pilidigita (24: 0.8: 4.2); *C. californica* (19: 0.5: 2.6); *C. brevirostis* (1: <0.1: 0.1); unidentified species (1: 0.1: 0.1).
6. OSTRACODS (43: 1.6: 3.8)
   Parasterope sp. A (37: 1.0: 2.9); *Vargula americana* (9: 0.3: 0.5); *Philomedes* sp. (4: 0.1: 0.2); *Cycloleberis lobiancoi* (3: <0.1: 0.1); unidentified (1: <0.1: 0.1).
7. ISOPODS (39: 1.7: 3.3)
   Paracercies sp. (27: 0.8: 2.1); gnathiid juveniles and females (21: 0.8: 0.8); *Idotea* spp. (4: 0.1: 0.1); *Cirolana diminuta* (3: <0.1: <0.1); *Limnoria lignorum* (1: <0.1: 0.1); *Excorallana kathae* (1: <0.1: <0.1).
8. CARIDEAN ADULTS AND JUVENILES (24: 0.4: 4.1)
   Hippolyte clarki (20: 0.2: 2.2); *Eualus herdmani* (6: 0.2: 1.9).
9. TANAIDS (26: 0.5: 1.2)
   Leptochelia dubia (25: 0.4: 1.0); unidentified (4: 0.1: 0.2).
10. EUPHAUSID ADULTS AND JUVENILES (7: 0.1: 2.0)
    Thysanoessa sp. (1: <0.1: 0.7); unidentified (6: 0.1: 1.3).
11. FISHES (9: <0.1: 1.6)
    unidentified larvae.
12. BRACHYURAN MEGALOPS (10: 0.2: 0.7)
    unidentified.
13. CARIDEAN LARVAE (9: 4.0: 0.6)
    unidentified.
14. HARPACTICOID COPEPODS (13: 0.2: 0.2)
    Porcellidium sp. A.
15. REPTANTIAN ZOEA (6: 0.6: 0.4)
    unidentified.
16. CALANOID AND CYCLOPOID COPEPODS (4: <0.1: 0.2)
    unidentified cyclopoids.
17. OTHER COPEPODS (1: <0.1: 0.1)
    unidentified caligoids.
18. NEBALIACEANS (1: <0.1: <0.1)
    Nebalia pugettensis.

Sebastes atrovirens—kelp rockfish

The kelp rockfish, which may attain a length of 425 mm (Miller and Lea 1972), was the most numerous adult scorpaenid in the study area. During the day, a few individuals hovered above the sea floor in shadow under the kelp canopy, but most spent the daytime seated on rocky substrata within the forest—quiet but alert. At night this fish generally hovered in mid-water close to the rising kelp stipes (Figure 7), and often amid the kelp canopy, near the water's surface. Occasionally at night it hovered in open water close along the seaward margin of the forest. Differences in activities between day and night have gone unnoted in previous reports of this species. Limbaugh (1955) reported that it lives in the lower levels of the kelp and among the rocks, and feeds on "crustaceans and small fish." Quast (1968), on the other hand, reported that it ranges all the way from the bottom to the kelp canopy and apparently utilizes "all available foods in these regions."

Of 29 specimens (89-240 mm, $\bar{x}$ = 175) collected for study of food habits, all 6 (100%) taken during midafternoon were empty, whereas only 3 of 23 (13%) taken at night (more than 4 h after sunset) were empty. Clearly, this fish is predominantly a nocturnal feeder. Quast (1968) noted that many of the kelp rockfish he examined had an empty stomach but did not suggest nocturnal feeding. He noted that his specimens "appeared quite thin," and though recognizing this may be a natural condition, thought perhaps "the high frequencies of empty stomachs and the broad variety of food items found may indicate malnutrition." The kelp rockfish of our study area, we have noted, often have deeply concaved bellies during the day, which we assume is due to the emptiness of their guts at this time.

Almost all food materials taken by this fish were from the water column. The major food categories, which included species and species groups, are listed below in order of their rank as prey.

1. MYSIDS (90: 22.3: 39.5)
   Acanthomysis sculpta (60: 18.3: 30.1); *Siriella pacifica* (65: 3.6: 9.2); erythropinid sp. (15: 0.4: 0.2).
2. CARIDEAN ADULTS AND JUVENILES (85: 7.0: 16.2)
   Hippolyte clarki (65: 4.4: 10.0); *Eualus herdmani* (40: 2.6: 6.2).
3. GAMMARIDEAN AMPHIPODS (95: 13.8: 13.7)
   Batea transversa (95: 9.3: 9.5); lysianassid spp. (50: 1.2: 1.1); *Ampelisca* sp. (10: 1.4: 1.3); *Pleustes platypa* (25: 0.3: 0.3); *Podocerus cristatus* (5: 0.1: 0.2); *Ampithoe tea* (5: 0.1: 0.2);

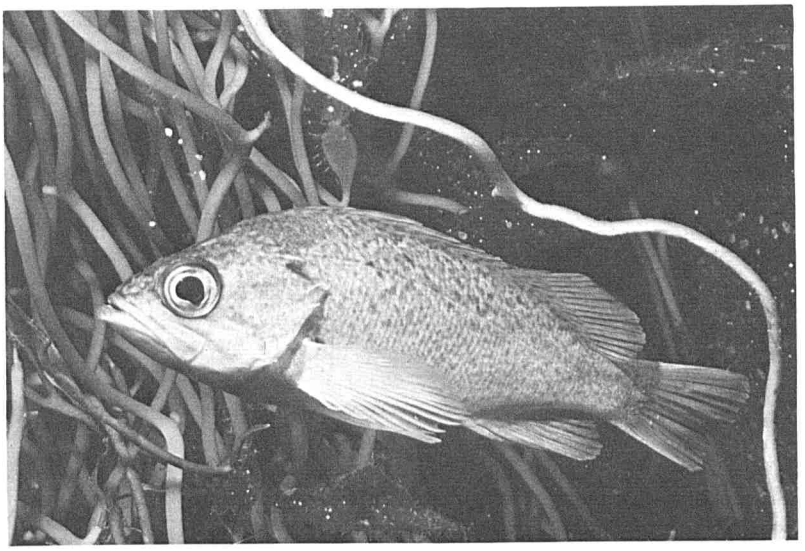


FIGURE 7.—A solitary kelp rockfish, *Sebastes atrovirens*, close to rising stipes of a giant kelp plant at night.

Aoroides columbiae (15: 0.2: 0.1); *Hyale nigra* (5: 0.1: 0.1); *Ericthonias braziliensis* (5: 0.2: 0.1); unidentified (40: 0.9: 0.8).

4. ISOPODS (75: 3.7: 14.3)
   Paracercies sp. (75: 3.3: 11.8); *Pentidotea resecata* (5: 0.1: 1.8); gnathiid juveniles (10: 0.1: 0.3); *Cirolana harfordi* (10: <0.1: 0.2); *Idotea rectolineata* (5: <0.1: 0.2).
5. POLYCHAETES, SWIMMING (20: 0.3: 7.1)
   unidentified, but only certain epitokous nereids were significant, these being prominent in the guts on nights when they swam in mid-water.
6. BRACHYURAN ADULTS (10: 0.1: 4.2)
   all *Pugettia producta*.
7. OSTRACODS (30: 0.5: 0.9)
   Cycloleberis lobiancoi (20: 0.2: 0.5); *Vargula americana* (10: 0.2: 0.3); *Parasterope* sp. A (5: 0.1: 0.1).
8. FISHES (15: 0.1: 1.2)
   larvae (10: 0.1: 0.8); scales (5: ?: 0.4).
9. NEBALIACEANS (5: 0.1: 1.1)
   Nebalia pugettensis.
10. CUMACEANS (5: 0.3: 0.7)
    all *Cyclaspis nubila*.
11. GASTROPODS (5: 0.1: 0.1)
    Lacuna unifasciata.
12. EUPHAUSID ADULTS AND JUVENILES (5: 0.1: 0.1)
    unidentified.

Xenistius californiensis—salema

We never saw salema in the study area during the day, but at night frequently encountered solitary individuals (Figure 8), or loosely spaced groups of four to six. Usually they swam high in the mid-waters above the open fields of *Dictyopteris* within 10 m of the forest. Their first appearance in the evening consistently occurred about 40 min after sunset, apparently after they had come from some distance away. The relatively few times we saw this species in daylight (always more than 400 m from the study area), it swam in schools of more than 50 individuals, closely spaced and seemingly inactive, at middepths within the forest. Reportedly this fish reaches 255 mm (Miller and Lea 1972).

Fresh material filled the stomachs of all five specimens (163-180 mm, $\bar{x}$ = 170) collected for study of food habits. They were taken at night, more than 3 h after sunset, and before daybreak, and so nocturnal feeding is apparent. All three

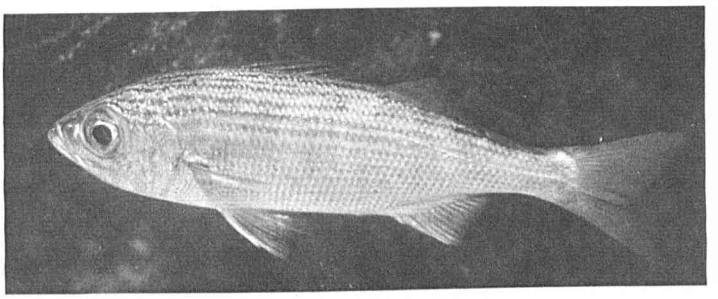


FIGURE 8.—A solitary salema, *Xenistius californiensis*, swims above the sea floor at night.

taken before midnight had their intestines empty; this, considering also the inactive appearance of those in diurnal schools, suggests lack of daytime feeding. Quast (1968) reported a high incidence of empty stomachs in specimens that he collected during the day, but did not relate this to nocturnal feeding.

All food material in the guts of specimens collected during this study are organisms that occured in the water column. Major categories of prey, which included species and species groups, are listed below in order of their rank as prey.

1. GAMMARIDEAN AMPHIPODS (100: 44.8: 38.2)
   Batea transversa (100: 26.0: 30.0); *Ampithoe plumulosa* (20: 5.2: 3.0); *Ericthonias braziliensis* (20: 2.0: 1.0); lysianassid spp. (20: 0.2: 0.4); *Gitanopsis vilordes* (20: 0.2: 0.2); *Ampithoe* spp. (20: 4.0: 1.0); unidentified species (60: 7.2: 2.6).
2. MYSIDS (100: 22.0: 28.0)
   Siriella pacifiica (100: 20.2: 26.8); erythropinid sp. (60: 1.8: 1.2).
3. POLYCHAETES, SWIMMING (40: ?: 20.0)
   unidentified species, mostly epitokus nereids.
4. CUMACEANS (60: 2.0: 2.6)
   Cyclaspis nubila (60: 1.6: 2.2); unidentified juveniles (20: 0.4: 0.4).
5. CAPRELLID AMPHIPODS (40: 5.6: 3.0)
   Caprella pilidigita (40: 4.4: 1.8); *C. californica* (40: 1.2: 1.2).
6. OSTRACODS (80: 2.2: 1.0)
   Parasterope sp. A (60: 1.2: 0.6); *Cycloleberis lobiancoi* (20: 0.6: 0.2); *Vargula americana* (20: 0.4: 0.2).
7. NEBALIACEANS (20: 1.0: 3.0)
   Nebalia pugettensis.
8. ISOPODS (40: 2.4: 1.2)
   Cirolana harfordi (20: 0.8: 0.4); *Paracercies* sp. (20: 1.0: 0.2); *Excorallana kathae* (20: 0.4: 0.2); gnathiid juveniles (20: 0.2: 0.4).
9. FISHES (20: ?: 1.8)
   scales.
10. CARIDEAN LARVAE (20: 1.2: 0.6)
    unidentified.
11. CARIDEAN ADULTS AND JUVENILES (20: 1.2: 0.6)
    unidentified.
12. REPTANTIAN ZOEA (20: 3.6: 0.4)
    unidentified.
13. CALANOID AND CYCLOPOID COPEPODS (20: 0.2: 0.2)
    calanoid, *Labidocera* sp.

This list indicates a diet much like that of salema collected from a kelp bed near La Jolla by Quast (1968), although Quast questioned the validity of his data because of the collecting methods used.

Seriphus politus—queenfish

The queenfish, which can grow to 304 mm (Miller and Lea 1972), consistently appeared in the study area about 40 min after sunset and remained active there throughout the night. Generally, solitary individuals, or loosely spaced groups of two to six swam several meters above the sea floor, usually close to the seaward edge of the kelp forest, but frequently above the open fields of *Dictyopteris*. Then, shortly after first morning light, 40 to 50 min before sunrise, they abruptly left the area.

During the day queenfish hover in dense, relatively inactive schools close to shore (Figure 9), but we have not seen them within 1.5 km of the study site in daylight. Limbaugh (1955), presumably assessing the daytime situation, stated:

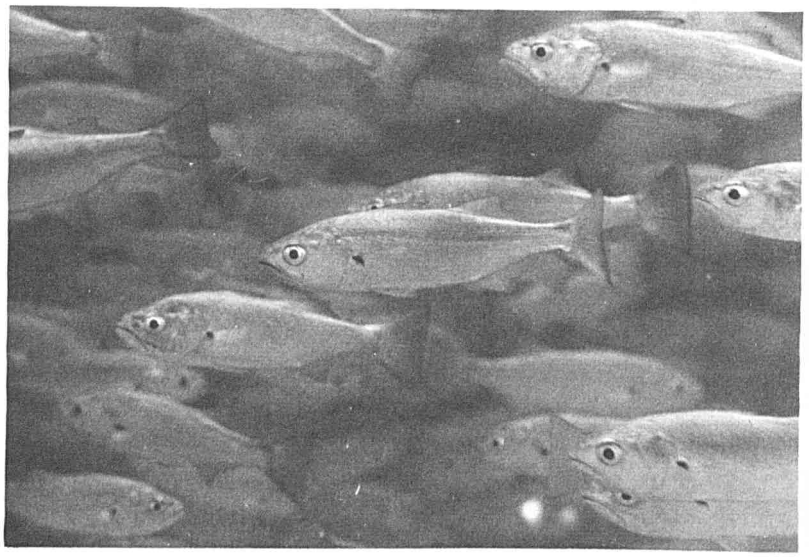


FIGURE 9.—A daytime aggregation of queenfish, *Seriphus politus*.

"Queenfish school in tightly packed aggregations over sandy bottom."

Four of five individuals (124-171 mm, $\bar{x}$ = 148) collected shortly after they had arrived in the study area at nightfall had an empty gut, and the fifth contained just a single freshly ingested shrimp (unidentified). We conclude that these individuals had passed the previous day without feeding. The evidence further suggests they do not feed while en route from daytime schooling sites to their feeding ground in the study area.

All 31 specimens (114-193 mm, $\bar{x}$ = 151) sampled in the study area at night, later than 3 h after sunset and before first morning light, had material in their guts—much of it fresh. All prey belonged to groups known to occur in the water column. Limbaugh (1955) reported that this species feeds on "small free-swimming crustaceans and fish." Below are ranked the species and species groups taken as prey by this fish.

1. MYSIDS (84: 22.5: 44.7)
   Siriella pacifica (84: 21.0: 39.6); *Acanthomysis sculpta* (52: 1.4: 5.0); erythropinid sp. (6: 0.1:<0.1).
2. GAMMARIDEAN AMPHIPODS (89: 16.0: 21.6)
   Batea transversa (84: 15.6: 20.2); *Ampelisca* sp. (9: 0.2: 0.3); lynsianassid spp. (6: 0.1: 0.2); *Ampithoe* sp. (3: 0.1: 0.1); unidentified (3: <0.1: 0.8).
3. POLYCHAETES, SWIMMING (31: 0.8: 21.8)
   Epitokous nereids (22: 0.7: 18.4); unidentified (9: <0.1: 3.4).
4. CARIDEAN ADULTS AND JUVENILES (44: 0.7: 5.9)
   Eualus herdmani (28: 0.4: 2.0); *Hippolyte clarki* (19: 0.3: 2.0); unidentified (3: <0.1: 1.9).
5. ISOPODS (34: 0.7: 3.6)
   Paracercies sp. (22: 0.5: 1.7); gnathiid juveniles (13: 0.1: 0.2); *Limnoria* sp. (3: 0.1: 1.1); *Excorallana kathae* (3: <0.1: 0.5); *Cirolana harfordi* (3: <0.1: 0.1).
6. FISHES (6: 0.6: 1.4)
   scales.
7. NEBALIACEANS (6: 0.1: 0.2)
   Nebalia pugettensis.
8. OSTRACODS (13: 0.3: 0.2)
   Vargula americana (6: 0.1: <0.1); *Cycloeberis lobiancoi* (3: 0.1: <0.1); *Parasterope* sp. A (3: 0.1: <0.1).
9. CARIDEAN LARVAE (3: <0.1: 0.3)
   unidentified.
10. BRACHYURAN MEGALOPS (3: <0.1: 0.2)
    unidentified.
11. EUPHAUSID ADULTS AND JUVENILES (3: <0.1: <0.1)
    unidentified.
12. CUMACEANS (3: <0.1: <0.1)
    Cyclaspis nubila.

A single small juvenile queenfish, 38 mm long, was collected on 2 November shortly before first morning light as it swam alone close over the sand. Its full gut contained mysid *Siriella pacifica*, gammaridean amphipod *Batea transversa*, and isopod *Limnoria* sp. All of these forms are also prey of larger queenfish, but those taken by this small individual were less than half the size of prey routinely taken by the larger fish.

Material that we collected at La Jolla in 1971 included some information on smaller juveniles. Ten individuals (10-27 mm, $\bar{x}$ = 19) were collected on the same day during the hour before first morning light—all from the stomachs of larger individuals of their own species. Of these, only the two largest, 23 and 27 mm, contained prey of the types taken by larger conspecifics: mysids and gammaridean amphipods constituted 99% of the diet of these two, with calanoid copepods representing the remainder. In contrast, calanoid copepods were the major prey of the seven smaller individuals (in six, 80% of the total diet). Fish larvae (in one, 11% of the total diet), and cladocerans (in one, 9% of the total diet), constituted the rest. These limited data indicate that the queenfish, like the olive rockfish above, changes as it grows from a diet of copepods to one of mysids and other plankters that appear after dark. The queenfish, however, seems to make the change at a smaller size, perhaps because it has a larger mouth. Moreover, the data fail to show that the queenfish, like the olive rockfish, feeds by day when subsisting on copepods.

Hyperprosopon argenteum— walleye surfperch

The walleye surfperch, which can grow to 304 mm (Miller and Lea 1972), consistently schooled during the day in about 2 to 5 m of water over sand at the edge of the forest at the head of Fishermen's Cove. Usually these schools included 20 to more than 100 closely spaced individuals. Members of these schools appeared inactive, an impression supported by the eight empty guts found in nine individuals (115-173 mm, $\bar{x}$ = 140) taken during midafternoon (and the ninth contained only well-digested fragments). Presumably describing the daytime situation throughout southern California, Limbaugh (1955) stated: "They school in an aggregate cloud . . . over sand patches among rocks."

The schools dispersed at nightfall, and many individuals spread along the seaward edge of the forest at the perimeters of the cove. They swam individually (Figure 10) or in small groups 1 to 3 m above the bottom, usually over sand within a few meters of, but sometimes within, the forest. Of the 35 (60-151 mm, $\bar{x}$ = 111) collected in the study area between 4 h after sunset and daybreak, only one

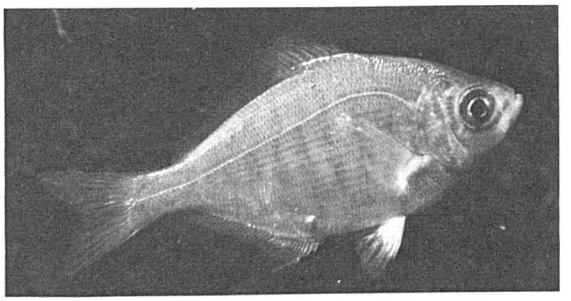


FIGURE 10.—A solitary walleye surfperch, *Hyperprosopon argenteum*, swims in the water column at night.

was empty; the rest were full of prey, much of it fresh.

Clearly, this is a nocturnal fish. Those seen in the study area at night, however, tended to be smaller on the average than those seen in the diurnal schools, suggesting that the larger fish might range farther away. All prey in the 34 individuals containing identifiable material were organisms that occur in the water column, as listed below.

1. GAMMARIDEAN AMPHIPODS (100: 63.6: 47.0)
   Batea transversa (85: 39.8: 24.2); *Ampithoe* spp. (41: 3.3: 3.8); *Hyale nigra* (9: 2.8: 2.9); *Ericthonias braziliensis* (15: 0.5: 1.1); *Ampelisca* sp. (15: 0.6: 1.0); *Synchelidium* sp. (24: 0.4: 0.3); lysianassid spp. (15: 0.6: 0.2); *Heterophilias seclusus* (6: 0.1: 0.1); *Photis* sp. (3: <0.1: 0.1); *Paraphoxus* sp. (3: <0.1: <0.1); *Aoroides columbiae* (3: <0.1: 0.1); unidentified (91: 15.4: 13.2).
2. CUMACEANS (85: 52.9: 25.2)
   Cyclaspis nubila (76: 51.2: 24.8); *Cumella* sp. A (18: 1.7: 0.4).
3. ISOPODS (72: 21.1: 10.2)
   Paracercies sp. (65: 19.5: 7.6); gnathiid juveniles (21: 1.0: 0.6); *Pentidotea resecata* (15: 0.2: 0.6); *Excorallana kathae* (3: 0.1: 1.0); *Cirolana diminuta* (15: 0.2: 0.2); *Rocinella belliceps* (6: <0.1: 0.2); *Exospheroma* sp. (6: <0.1: <0.1); idoteid sp. (3: <0.1: 0.1).
4. CAPRELLID AMPHIPODS (41: 2.1: 6.0)
   Caprella pilidigita (24: 1.4: 4.7); *C. californica* (21: 0.7: 1.2); *C. penantis* (3: <0.1: <0.1); *Tritella laevis* (3: <0.1: <0.1).
5. POLYCHAETES, SWIMMING (35: <0.7: 6.4)
   epitokous nereids (9: 0.7: 5.5); unidentified fragments (26: ?: 0.9).
6. OSTRACODS (62: 1.7: 1.6)
   Parasterope sp. A (38: 0.7: 0.6); *Cycloleberis lobiancoi* (23: 0.5: 0.4); *Philomedes* sp. (9: 0.4: 0.4); species O (3: <0.1: <0.1); species N (3: <0.1: <0.1).
7. MYSIDS (21: 0.6: 1.3)
   Siriella pacifica (15: 0.5: 1.2); *Acanthomysis sculpta* (3: <0.1: <0.1); unidentified fragments (3: 0.1: <0.1).
8. CARIDEAN ADULTS AND JUVENILES (21: 0.9: 0.9)
   Hippolyte clarki (3: 0.2: 0.1); unidentified (24: 0.7: 0.8).
9. BRACHYURAN MEGALOPS (26: 0.7: 0.5)
   unidentified.
10. TANAIDS (15: 0.5: 0.5)
    Leptochelia dubia (6: 0.2: 0.3); unidentified (9: 0.3: 0.2).
11. NEBALIACEANS (6: <0.1: <0.1)
    Nebalia pugettensis.
12. CARIDEAN LARVAE (3: <0.1: <0.1)
    unidentified.

Brachyistius frenatus—kelp perch

The kelp perch, which Miller and Lea (1972) claimed can attain a length of 214 mm, was numerous close among the rising stands of giant kelp. It often aggregated immediately under the canopy (Figure 11), but occurred along the entire length of the plants from water's surface to the

FIGURE 11.—Kelp perch, *Brachyistius frenatus*, aggregated close to kelp, pluck zooplankters from the water column during the day.

sea floor, with larger individuals mostly in the lower regions. Far fewer numbers also occurred close above low fields of benthic algae some distance from the kelp forest. It assumed similar attitudes in the same places during both day and night, but after dark there seemed to be more of them in the mid-waters along the outer edge of the kelp.

Most kelp perch feed by plucking material from the surface of algae, but plankton-feeding is widespread, especially among those aggregated in the mid-waters at the edges of the forests. Limbaugh (1955) reported that the kelp perch feeds on small crustaceans, particularly those that occur on giant kelp. Quast (1968) also reported a predominantly crustacean diet, with a preponderance of amphipods, but also including mollusks and bryozoans.

Preliminary assessment of our food-habit data, along with direct observations, showed that in this species it is primarily the smaller individuals that feed on plankton. Consequently, we consider for this paper only those less than 100 mm long, leaving the larger individuals for a later paper. This point is drawn somewhat arbitrarily, although plankters generally become noticeably less prevalent in the diet at about this size. With kelp perch more so than with the other species treated in this paper, however, many of the individuals considered had mixed a diet of plankters with organisms plucked from a substrate. Bray and Ebeling (1975) reported that kelp perch feed mainly on tiny plankters, mostly copepods, based on a sample of predominantly small individuals (43-142 mm, $\bar{x}$ = 103).

All 35 specimens (40-99 mm $\bar{x}$ = 81) collected during the afternoon as they swam over various locations in the study area, usually close to kelp, contained food, much of it fresh. On the other hand, of 34 specimens (38-99 mm, $\bar{x}$ = 76) collected during the 2 h of night before first morning light 25 (74%) were empty. The other nine, however, contained food, including relatively fresh items. Thus, although the kelp perch within this size range clearly fed mostly by day, some apparently fed at night. Individuals evidencing nocturnal feeding ranged from 81 to 99 ($\bar{x}$ = 95) mm long, and so were among the larger ones in the sample.

Recognizing that the contrasting conditions between day and night undoubtedly influenced the composition of the diet, food data from individuals collected during the afternoon (when presumably most fresh items in the gut had been taken by day) were considered separately from food data from individuals collected during the last hours of the night (when presumably most fresh items in the gut had been taken after dark).

In addition to the high incidence of empty guts in kelp perch collected at night, the guts of those that had taken prey after dark averaged 50% full, compared with an average of 72% full for the day feeders. Furthermore, the night feeders contained an average of 38 prey items, compared with an average of 252 for the day feeders (at least in part, however, this difference reflects the larger size of nocturnal prey). These data strengthen our conclusion that over the size range studied, nocturnal feeding is relatively unimportant to this species. Bray and Ebeling (1975) also noted that kelp perch feed mainly by day.

Foods taken by individuals that had been feeding during the day are ranked below:

1. CALANOID AND CYCLOPOID COPEPODS (94: 157.7: 49.1)
   calanoids, including *Calanus pacificas*, and *Rhincalanus nasutus* (71: 137.2: 44.2); cyclopoids, including *Corycaeus* sp. and *Oncea* sp. (74: 20.5: 4.9).
2. GAMMARIDEAN AMPHIPODS (63: 57.9: 37.0)
   Microjassa litodes (46: 23.1: 15.1); *Ericthonias braziliensis* (14: 3.9: 2.6); *Gitanopsis vilordes* (11: 3.0: 0.1); *Ampithoe* spp. (3: 0.1: 0.2); *Hyale nigra* (3: 0.3: 0.2); *Batea transversa* (3: 0.1: 0.1); unidentified (63: 27.4: 18.7).
3. CLADOCERANS (37: 26.1: 6.9)
   Evadne sp.
4. CIRRIPEDIAN LARVAE (31: 1.8: 0.9)
   cypris stage.
5. POLYCHAETES, NONSWIMMING (11: 0.4: 1.9)
   Spirorbis sp. (9: 0.4: 1.8); unidentified (3: 0.1: 0.1).
6. HARPACTICOID COPEPODS (14: 1.6: 0.7)
   Porcellidium sp. A (11: 1.5: 0.6); *Porcellidium* sp. B (3: 0.1: 0.1).
7. OSTRACODS (26: 0.6: 0.6)
   Cythereis sp. (17: 0.3: 0.2); *Philomedes* sp. B (11: 0.2: 0.1); unidentified sp. C (3: 0.1: 0.3).
8. CAPRELLID AMPHIPODS (9: 0.3: 0.7)
   Caprella pilidigita (6: 0.2: 0.4); *C. californica* (3: <0.1: 0.3).
9. FISH EGGS (14: 0.4: 0.3)
   unidentified.
10. PELECYPODS (11: 0.4: 0.3)
    Hiatella arctica (9: 0.3: 0.3); *Halodakra brunnea* (3: <0.1: <0.1).
11. ISOPODS (14: 0.7: 0.2)
    Paracercies sp. (6: 0.5: 0.1); gnathiid juveniles (6: 0.1: <0.1); unidentified fragments (3: 0.1: 0.1).
12. BRYOZOAN LARVAE (9: 0.1: 0.2)
    cyphonautes.
13. CARIDEAN LARVAE (9: 0.2: <0.1)
    unidentified.
14. FISHES (6: 0.2: <0.1)
    unidentified larvae.

15. MYSIDS (3: <0.1: <0.1)
    Siriella pacifica.
16. CUMACEANS (3: <0.1: <0.1)
    Cyclaspis nubila.
17. CARIDEAN ADULTS AND JUVENILES (3: <0.1: <0.1)
    Hippolyte clarki.

Although these fish preyed heavily on zooplankters, clearly many of the organisms in the above list were plucked from a substrate. The major gammaridean, *Microjassa litodes*, was never seen or taken by us in the water column, but was a predominent form on the surface of giant kelp (Hobson and Chess in prep.) Similarly, the many forms known to occur in the water column only at night, e.g., *Siriella pacifica*, *Cyclaspis nubila*, *Paracercies* sp., *Batea transversa*, and *Hippolyte clarki* were probably plucked by these day feeders from the algae or sand where they occur in the daytime.

Foods taken by individuals that had been feeding at night are ranked below.

1. GAMMARIDEAN AMPHIPODS (100: 33.8: 71.1)
   Batea transversa (66: 8.1: 22.1); *Ericthonias braziliensis* (44: 0.9: 2.6); *Microjassa litodes* (22: 1.6: 1.7); *Ampithoe* spp. (22: 0.3: 0.9); *Hyale nigra* (11: 0.4: 0.9); *Aoroides columbiae* (11: 0.1: 0.3); unidentified, at least some probably juveniles of the above (100: 22.4: 42.6).
2. CAPRELLID AMPHIPODS (66: 4.4: 15.0)
   Caprella californica (55: 2.0: 9.5); *C. pilidigita* (11: 2.0: 4.1); unidentified (22: 0.4: 1.4).
3. ISOPODS (44: 0.5: 6.6)
   Paracercies sp.
4. CARIDEAN ADULTS AND JUVENILES (55: 0.7: 5.1)
   unidentified.
5. MYSIDS (22: 0.2: 1.1)
   Siriella pacifica (12: 0.1: 1.0); erythropinid sp. (11: 0.1: 0.1).
6. POLYCHAETES, NONSWIMMING (22: 0.2: 0.3)
   Spirorbis sp.
7. OSTRACODS (22: 0.2: 0.2)
   Parasterope sp. A (12: 0.1: 0.1); *Cytheresis* sp. (11: 0.1: 0.1).
8. FORAMINIFERANS (11: 0.1: 0.2)
   unidentified.
9. HARPACTICOID COPEPODS (11: 1.0: 0.1)
   Porcellidium sp. A.

Two specimens also contained fragments of algae (*Macrocystis* in one, *Sargassum* in the other) that probably had been taken incidentally along with prey. Clearly this fish took at least some of its nocturnal prey from a substrate—*Spirorbis* sp., for example. Nevertheless, because the diet is comprised mostly of organisms that swim in the water column at night, we believe this was probably where most of them were taken. Most of these prey organisms also occurred on rocks and algae after dark, but if substrate-feeding had predominated, we would have expected a greater proportion of strictly substrate-dwelling forms.

Oxyjulis californica—señorita

The señorita, which can attain a length of 250 mm (Miller and Lea 1972), is perhaps the most widespread fish in nearshore habitats at Santa Catalina Island. It is strictly a diurnal species that, like other labrids, rests under cover on the sea floor at night (Hobson 1971). Often during the day it swims in large assemblages 1 to 2 m above the sea floor (Figure 12).

Most señoritas feed by plucking material from the surface of algae—often from algae drifting as fragments in the mid-waters—but plankton-feeding is widespread, and predominates in smaller juveniles. Limbaugh (1955) concluded that the señorita is an omnivorous carnivore that feeds "on almost any animal protein." Hobson (1971) found that specimens between 110 and 195 mm long had fed primarily on bryozoans that encrust algae, and on caprellid amphipods. Quast (1968) reported the principal foods to be small gastropods and crustaceans commonly associated with algae, but noted that specimens 50 to 60 mm long had fed heavily on copepods, ostracods, and bryozoan larvae.

Direct observations, complemented by our food habit data (see below), agree that smaller individuals mostly pluck their prey from the water column, whereas larger individuals mostly pluck their prey from some substrate. In this respect, then, the señorita is similar to the kelp perch, described above. So, as with the kelp perch, this paper considers only those individuals less than 100 mm long, leaving the larger individuals for a later paper. We have better reason for drawing the dichotomy at this point with the señorita than with the kelp perch: the smallest señorita we found containing prey obviously plucked from a substrate was 101 mm long, and although planktivorous habits predominated in certain individuals up to 175 mm (which were among the largest taken), most over 100 mm seemed to feed primarily on a substrate. So unlike the diverse feeding habits of smaller kelp perch, the smaller señoritas seemed strictly planktivorous. Bray and Ebeling (1975) stated: "Unlike kelp perch, señoritas did not exploit the plankton as a major source of food." Although this view would seem to disagree with our findings, their samples of the two species were not comparable on this point. Most of their kelp

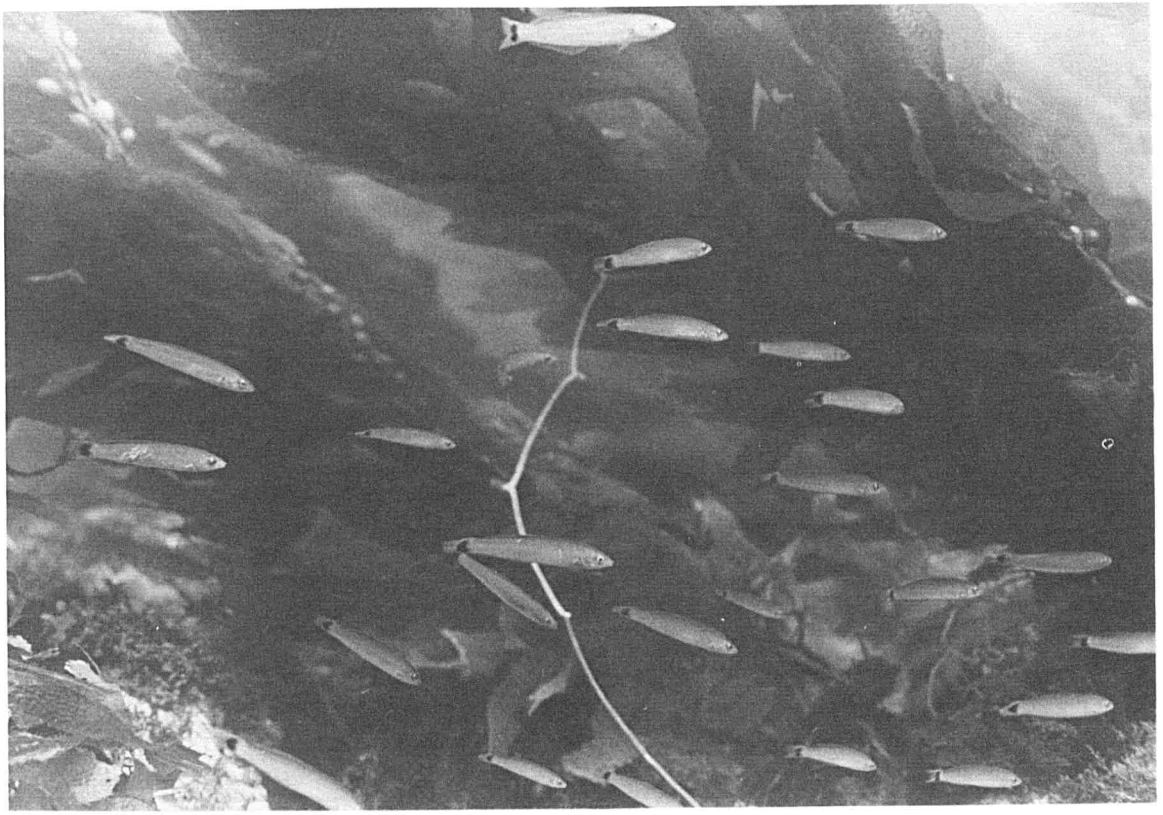


FIGURE 12.—An aggregation of señoritas, *Oxyjulis californica*, passes along the edge of a kelp forest during the day.

perch were small, as noted above, whereas their señoritas were relatively large (110-223 mm, $\bar{x}$ = 169).

All 24 specimens (19-99 mm, $\bar{x}$ = 51) collected during the afternoon as they swam in groups above the sea floor were full of relatively fresh prey, as ranked below:

1. CALANOID AND CYCLOPOID COPEPODS (100: 68.7: 74.1)
   calanoids (75: 44.3: 43.8); cyclopoids, including *Corycaeus* sp. and *Oncaea* sp. (67: 24.4: 30.3).
2. BRYOZOAN LARVAE (58: 7.3: 4.3)
   cyphonautes.
3. HARPACTICOID COPEPODS (42: 7.1: 4.8)
   Microsetella sp. (25: 3.1: 2.1); *Porcellidium* sp. A (8: 0.1: 0.2); unidentified spp. (21: 3.9: 2.5).
4. CIRRIPEDIAN LARVAE (46: 2.8: 2.8)
   cypris stage.
5. GAMMARIDEAN AMPHIPODS (25: 1.8: 4.7)
   unidentified fragments.
6. CLADOCERANS (21: 4.8: 5.4)
   Evadne sp.
7. MOLLUSK LARVAE (46: 1.1: 1.0)
   veligers.
8. FISH EGGS (4: 0.1: 0.3)
   unidentified.
9. RADIOLARIANS (4: 0.1: <0.1)
   unidentified.

With the likely exception of the gammarideans, which were unidentifiable, all of the items in the above list are organisms present in the water column at the time these fish were feeding.

Chromis punctipinnis—blacksmith

The blacksmith, which can attain a length of 300 mm (Miller and Lea 1972), is probably the most numerous fish in the nearshore waters at Santa Catalina Island. During the day it concentrated along the seaward edge of the kelp forests, but occurred in varying numbers in most nearshore habitats, usually aggregated in the mid-waters (Figure 13). At nightfall it sheltered among the rocks, often considerable distances inshore from where it spent the day.

Other species of the genus *Chromis* are widespread in tropical seas, where they are known to be planktivores, e.g.: West Indies (Randall 1967); Gulf

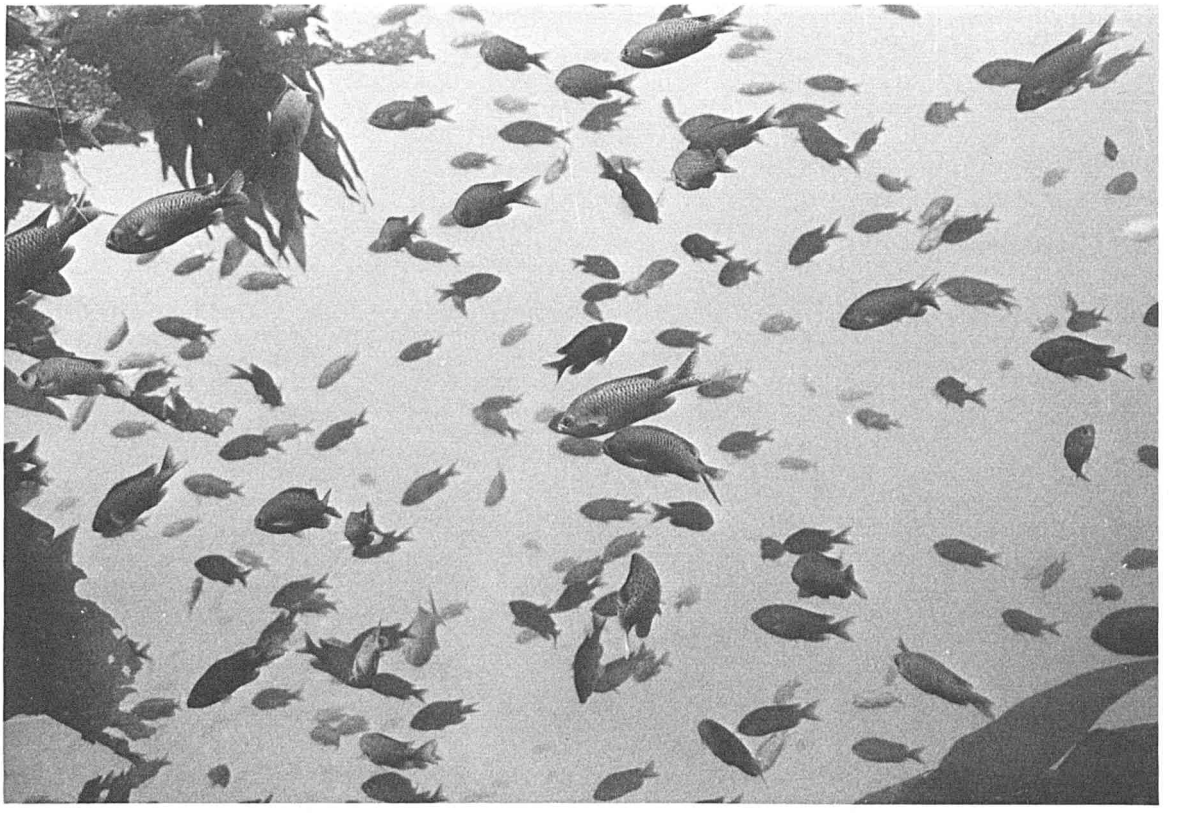


FIGURE 13.—Blacksmiths, *Chromis punctipinnis*, aggregated at the edge of a kelp forest, pluck zooplankters from the water column during the day.

of California (Hobson 1968); Hawaii (Swerdloff 1970; Hobson 1974). It is also well-known that *C. punctipinnis* is a planktivore. Limbaugh (1955) noted that it feeds on "particulate plankton such as small fish, squid, and crustaceans," and "may materially affect the amount of plankton entering kelp beds because they eat it as it enters." Quast (1968) listed the principal food of the blacksmith as "minute swimming crustacea and crustacean eggs and larvae gleaned from open water species of kelp beds and over rocky areas." In taking its tiny prey from the water column in what seems a visually directed action, the blacksmith suddenly thrusts both of its highly protrusible jaws forward, then immediately retracts them, presumably sucking plankters into its rapidly expanding oral cavity. This way of feeding has also been noted among its tropical congeners (Swerdloff 1970; Hobson 1974).

Aggregations of blacksmiths feeding on plankton occurred throughout the water column, with each member of an aggregation acting independently. They aggregated according to size: the discrete aggregations of small juveniles (which first appeared inshore during late summer, when about 15 to 25 mm long) generally were closer to the sea floor than were aggregations of the adults.

Blacksmiths fed throughout the day, but the rate at which they ingested prey varied. In the tropical Atlantic, *Eupomacentrus partitus*, another planktivorous pomacentrid, feeds more rapidly with increased light and with increased current (Stevenson 1972). Blacksmiths, too, feed more rapidly in a current than at slack water, presumably (as Stevenson suggested of *E. partitus*) because they receive more plankters. To measure this effect, we counted the characteristic mouth movements of feeding adult blacksmiths, first in a moderate current, and then at slack water. The observations were made during midafternoon under a clear sky at a depth of 5 m in 10 m of water. The fish were part of an aggregation with members ranging from about 109 to 130 mm long (these being the sizes of the two in-

dividuals collected later judged to be the largest and smallest in the group). In the moderate current, with the giant kelp lying over at about 25° (attempts to measure the current in this habitat proved unsatisfactory owing to complex eddy systems), 10 individuals (selected haphazardly) plucked at plankters 50 to 73 ($\bar{x}$ = 58) times during 1-min periods. One hour later, when there was no discernible current, 10 individuals in a similar, if not the same aggregation, each plucked at plankters 30 to 51 ($\bar{x}$ = 39) times during 1-min periods. Probably there is an optimum current speed beyond which the fish find the increasing difficulty of maintaining station outweighs the advantage of added food. We lack data on feeding rates, but have noted that in strong currents blacksmiths abandon the open places within the forest, where they had been dispersed and feeding, and concentrate in dense numbers close in the lee of individual kelp columns.

Of 41 adults (92-145 mm, $\bar{x}$ = 118) collected from aggregations in the water column throughout the study area during the afternoons, 36 were full of food, much of it fresh. The other 5, all collected during midafternoon along the margin of the forest bordering the inshore edge of the *Dictyopteris* field, were empty. All prey taken by these blacksmiths, ranked below, are forms we have collected in the water column during the day.

1. LARVACEANS (100: 448.1: 57.5)
   most of them *Oikopleura* spp.
2. CALANOID AND CYCLOPOID COPEPODS (100: 256.3: 33.7)
   calanoids, including *Calanus pacificus*, *Acartia tonsa*, *Labidocera* sp., and *Rhincalanus nasutus* (100: 253.6: 32.4); cyclopoids, including *Corycaeus* sp., *Oncaea* sp., and *Oithona* sp. (72: 2.7: 1.3).
3. FISH EGGS (69: 17.9: 4.1)
   unidentified.
4. CLADOCERANS (75: 24.6: 2.5)
   Evadne spp.
5. CARIDEAN LARVAE (33: 1.4: 0.9)
   unidentified.
6. EUPHAUSID LARVAE (33: 5.1: 0.6)
   calyptopis stage.
7. CIRRIPEDIAN LARVAE (33: 3.5: 0.6)
   cypris stage.
8. BRYOZOAN LARVAE (17: 1.2: 0.2)
   cyphonautes.
9. CHAETOGNATHS (3: 0.1: 0.5)
   unidentified.
10. REPTANTIAN ZOEA (3: 0.4: 0.1)
    unidentified.
11. HARPACTICOID COPEPODS (3: <0.1: <0.1)
    Microsetella sp. A.
12. FISHES (3: <0.1: <0.1)
    unidentified larvae.
13. ISOPODS (3: <0.1: <0.1)
    gnathiid juvenile.

In feeding so heavily on larvaceans, their major prey, these adult blacksmiths differ from other species treated in this report. Significantly, however, larvaceans are also major prey of other species of *Chromis* elsewhere, e.g., in Hawaii (Hobson 1974) and in the West Indies (Randall 1967). Probably larvaceans are important food of the blacksmith throughout its range, even though they have gone unreported in previous food-habit studies of this species. Larvaceans are difficult to recognize, especially if digestion is advanced or preservation faulty, and this may account for them going unreported.

Because juvenile blacksmiths were in feeding aggregations distinct from those of the adults, we analyzed their gut contents separately. Of 14 juveniles (16-47 mm, $\bar{x}$ = 34) collected from aggregations during the afternoon, all were full of food, much of it fresh. All prey, ranked below, are forms that we have collected from the water column during the day.

1. CALANOID AND CYCLOPOID COPEPODS (100: 394.4: 54.1)
   calanoids, including *Acartia tonsa* (100: 366.2: 50.5); cyclopoids, including *Corycaeus* sp. and *Oncaea* sp. (93: 28.2: 3.6).
2. LARVACEANS (93: 48.9: 26.4)
   most of them *Oikopleura* spp.
3. CLADOCERANS (100: 108.8: 12.5)
   Evadne spp.
4. CIRRIPEDIAN LARVAE (79: 63.6: 4.6)
   cypris stage.
5. BRYOZOAN LARVAE (79: 63.6: 4.6)
   cyphonautes.
6. HARPACTICOID COPEPODS (57: 6.4: 0.8)
   Microsetella sp. A.
7. FISH EGGS (43: 2.1: 0.7)
   unidentified.

Differences in the diet between juvenile and adult blacksmiths can be related to the sizes of the various organisms in the water column. Most prey of the juveniles were less than 0.5 mm long. Compared to the prey of adults these included more cladocerans, copepods, and larvae of barnacles and bryozoans, but fewer larvaceans and fish eggs (there were no larvaceans in the smallest blacksmith, 16 mm long, and no fish eggs in all six <34 mm).

During the day, the heaviest concentrations of adult blacksmiths in the vicinity of the study area were at the mouth of the cove seaward of the kelp

forest. The sea floor in this region is sand, and lies under more than 30 m of water. Because blacksmiths habitually settled among rocks at night, the offshore feeders migrated to resting areas inshore at day's end. At the migration's peak, groups of 100 or more blacksmiths spaced perhaps 50 m apart streamed along established routes.

As the migrators swam between feeding grounds and shelter areas, they passed among many other blacksmiths, most of which were actively feeding and which gave the migrators no overt notice. Most of the blacksmiths in the vicinity of the study area were nonmigrators that found nocturnal shelter among rocks lying below their mid-water feeding grounds.

Most of the blacksmiths within the forest bordering the study area began descending toward the sea floor by sunset, and by 35 min after sunset the vast majority had taken shelter among the rocks. They rested here throughout the night, and their lack of feeding during this period is indicated by the empty guts we found in all 11 individuals (111-143 mm, $\bar{x}$ = 122) collected among rocks during the 2 h immediately before first morning light.

In the morning, blacksmiths among the rocks became noticeably active about 40 min before sunrise. They began to rise among the kelp columns about 25 to 30 min before sunrise, and to feed about 5 to 10 min later. At about the same time that blacksmiths within the forest were rising into the water column, the migrating individuals streamed along their courses to the offshore feeding grounds, reversing the courses they had followed inshore the night before.

DISCUSSION

Trophic relationships among the fishes and zooplankters near shore at Santa Catalina Island differ strikingly between day and night (Table 9), broadly paralleling the situation described earlier in the water column above tropical reefs (Hobson 1965, 1968, 1972, 1973, 1974). This section discusses these differences and their evolutionary implications.

The Mid-Waters in Daylight

Zooplankters populating the nearshore water column at Santa Catalina during the day—including radiolarians, cladocerans, copepods, and

TABLE 9.—Percent of each fish species that took prey in each major food category.

	Day feeders					Night feeders					
	1. olive rockfish <55 mm, n = 42	2. kelp perch <100 mm, n = 35	3. señorita <100 mm, n = 24	4. blacksmith >90 mm, n = 36	5. blacksmith <50 mm, n = 14	1. olive rockfish >65 mm, n = 70	2. kelp rockfish, n = 20	3. salema, n = 5	4. queenfish, n = 32	5. walleye surfperch, n = 34	6. kelp perch <100 mm, n = 9
Major food category	1	2	3	4	5	1	2	3	4	5	6
Radiolarians	0	0	4	0	0	0	0	0	0	0	0
Polychaetes, swimming	0	0	0	0	0	36	20	40	31	35	0
Mollusk larvae	0	0	46	0	0	0	0	0	0	0	0
Cladocerans	20	37	21	75	100	0	0	0	0	0	0
Ostracods	0	26	0	0	0	43	30	80	13	62	22
Calanoid and cyclopoid copepods	83	94	100	100	100	4	0	20	0	0	0
Harpacticoid copepods	18	14	42	3	57	13	0	0	0	0	11
Other copepods	18	0	0	0	0	1	0	0	0	0	0
Cirripedian larvae	5	31	46	33	79	0	0	0	0	0	0
Nebeliaceans	0	0	0	0	0	1	5	20	6	6	0
Mysids	11	3	0	0	0	69	90	100	84	21	22
Cumaceans	0	3	0	0	0	57	5	60	3	85	0
Tanaids	10	0	0	0	0	26	0	0	0	15	0
Isopods	2	14	0	3	0	39	75	40	34	72	44
Gammaridean amphipods	29	63	25	0	0	90	95	100	89	100	100
Caprellid amphipods	0	9	0	0	0	36	0	40	0	41	66
Euphausid larvae	2	0	0	33	0	0	0	0	0	0	0
Euphausid adults and juveniles	11	0	0	0	0	7	5	0	3	0	0
Caridean larvae	20	9	0	33	0	9	0	20	3	3	0
Caridean adults and juveniles	0	3	0	0	0	24	85	20	44	21	55
Reptantian zoea	11	0	0	3	0	6	0	20	0	0	0
Brachyuran megalops	5	0	0	0	0	10	0	0	3	26	0
Bryozoan larvae	2	9	58	17	79	0	0	0	0	0	0
Chaetognaths	0	0	0	3	0	0	0	0	0	0	0
Larvaceans	0	0	0	100	93	0	0	0	0	0	0
Fish eggs	0	14	4	69	43	0	0	0	0	0	0
Fishes	5	6	0	3	0	9	15	20	6	0	0
Other	2	22	0	0	0	0	15	0	0	0	33

various larval forms (see Tables 1, 2)—tend to be less than 2 mm in their greatest dimension. Forms appreciably larger than this—including chaetognaths and some larvaceans—tend to be transparent. These organisms are equally numerous in the water column at night, and none are residents of the study area. The species are widespread in the water columns of the various inshore habitats, and also offshore.

This assemblage resists a common label. Most of the species have been considered holoplankton (planktonic throughout the whole of their life histories: Newell and Newell 1963), but this term excludes the larval forms so prominent here. The larval forms generally are considered meroplankton (planktonic during some stage in their life histories, but benthonic during some other: Newell and Newell 1963), but this term has been used in general reference to organisms that are planktonic at night, but benthonic by day (e.g., Williams and Bynum 1972). As noted above, we do not use these terms because they fail to define categories meaningful to the concepts developed in this paper.

Fishes that forage in the water column by day have certain characteristics relating to the problems they face as diurnal planktivores. Significantly, of the four diurnal planktivores studied at Santa Catalina, three—the señorita, the kelp perch, and the small juvenile olive rockfish—outgrow this habit. Apparently as they grow larger they find the tiny organisms in the mid-waters increasingly inappropriate as prey. We believe that each is limited in taking very small prey by the size and structure of its mouth, a problem solved by changing either feeding place, or feeding time. Thus, the señorita and kelp perch (noted by Hubbs and Hubbs 1954, to have similar dentition and feeding habits) increasingly abandon the water column as a hunting ground as they grow and shift to prey on organisms that live on algae. The small juvenile olive rockfish, on the other hand, continues to feed in the water column, but assumes nocturnal habits that bring it into contact with the larger organisms that rise above the sea floor at night (see below). The señorita and kelp perch, both relatively small-mouthed species, generally shift their food habits when about 100 mm long; the olive rockfish, with a much larger mouth (compare Figures 6, 11, 12), generally shifts when under 65 mm long.

The fourth diurnal planktivore studied at Santa Catalina, the blacksmith, retains its planktivorous diet through adulthood. It does so despite growing to a relatively large size because it has, among other adaptive features, a small mouth specialized for this habit. Judging from its numbers, the blacksmith is highly successful in the warm temperate waters of southern California. But it does not range far into the colder waters northward, and all its many congeners live in the tropics. The blacksmith embodies morphological features uncharacteristic of temperate-zone fishes, but which are widespread among tropical species. In writing of reef fishes in the tropical Atlantic Ocean, Davis and Birdsong (1973) described morphological specializations adaptive for foraging on small organisms in the mid-waters, and although they do not make the point, all their examples are species that feed by day. Especially striking are the modifications of head and jaws, including dentition, that permit even relatively large individuals to effectively capture tiny prey in open water.

The Mid-Waters at Night

The nocturnal zooplankton include, in addition to the organisms also present during the day, a large array of forms that rise at the onset of darkness from daytime shelters on, in, or close to the sea floor or other cover. These nocturnal additions to the zooplankton include various polychaetes, mysids, cumaceans, gammaridean and caprellid amphipods, isopods, tanaids, carideans, and others (see Tables 1, 2). Most exceed 2 mm in their greatest dimension, and many are 7 to 10 mm, and longer. Unlike the full-time zooplankters, which have no particular relation to the study area, these part-time zooplankters are local residents that rise at night from substrata they are closely associated with during the day.

The nocturnal components of the zooplankton seem to have reasons for rising into the water column at night that are as diverse as their morphologies. Because they have diverse habits that are little known, we feel that terms defining ecological categories among them are premature. Bousfield (1973), and others, have referred to many such forms as tychoplankton, but this term implies that presence in the water column is by chance, or accident—a description that fits very few, if any, of the forms considered here. Many are nocturnal feeders; e.g., when the mysid *Siriella pacifica* moves into the mid-waters after dark, it feeds on copepods and other smaller zooplankters. Similar-

ly, nocturnal foraging may be the rule among species like the ostracod *Perasterope* sp. A, the cumacean *Cumella* sp. A, and the amphipod *Batea transversa*, where it seems the majority spend most of the night in the water column. Working in the tropical Atlantic Ocean, Emery (1968) noted that polychaetes, cumaceans, and zoea rise into the water column at night after spending the day under reef shelter and speculated that they make this ascent to forage. But most of the polychaetes entering the water column after dark at Santa Catalina are epitokus nereids, whose mid-water activities probably relate to reproduction.

Williams and Bynum (1972) doubted the nightly ascents of amphipods in North Carolina estuaries relate to feeding because they subsist on detritus. But detritus can be available to zooplankters in the water column, as reported by Gerber and Marshall (1974) from a coral atoll in the central Pacific. Significantly, however, many of the amphipods that enter the mid-waters at night appear morphologically maladapted for swimming. The oedicerotids (including *Monoculodes* and *Synchelidium*), for example, are modified for burrowing in unstable sand (Bousfield 1973), and the caprellids (Figure 5V) seem especially unsuited for existence in mid-water. It is unlikely that such forms are in the water column to feed, especially as relatively small proportions of their populations are up there. Probably these and similar forms make only brief, or infrequent excursions into the water column for reasons yet undetermined. Williams and Bynum (1972) suggested that relative numbers of caprellids entering the water column may correlate with seasonal deterioration of their benthic habitats. They also felt that among gammaridean amphipods the tubicolous forms (e.g., *Ampelisca* and *Ericthonias*) may facilitate reproduction by entering the water column, where mating pairs would have free access to each other.

We reject Williams and Bynum's additional suggestion that the nightly ascent may be an attempt to escape from predatory bottom-feeding fishes. Most bottom-feeding fishes that prey heavily on amphipods (and other similar organisms) are diurnal. (Some of the relatively few fishes that prey on amphipods at night, and the circumstances surrounding this predation, will be discussed later; Hobson and Chess in prep.) Most predaceous fishes feed visually, and tiny, cryptically hued forms on dark substrata seem to go unseen in the low levels of illumination that prevail at night (Hobson and Chess in prep.; see also Hobson 1968, 1974, for accounts of the same situation on tropical reefs). For whatever the reason, most amphipods that fall prey to predatory fishes after dark are species that rise into the water column.

Compared to their diurnal counterparts, the nocturnal planktivorous fishes are of relatively large sizes and have large mouths—both characteristics reflecting the relatively large size and accessibility of organisms in the mid-waters after dark.

Evolutionary Implications

Since early in the Mesozoic period, the evolution of actinopterigian fishes has centered on a mainstream of generalized predators (Schaeffer and Rosen 1961). Because such predators are adapted for straightforward attacks at prey in exposed positions, the water column, with its absence of cover, has been a risky place for smaller organisms throughout the evolution of modern nearshore marine communities. In discussing the earliest actinopterigian fishes, Schaeffer and Rosen stated that food was probably first obtained by biting and was swallowed whole. Although advances in mouth structure have refined their means of seizing food (Schaeffer and Rosen 1961; Gosline 1971), generalized teleosts have continued to take their prey intact. Consequently, these fishes have found appropriate prey to be organisms large enough for them to entrap in their relatively large mouths, yet small enough for them to swallow whole. As demonstrated at Santa Catalina, prey of appropriate size include animals that rise into the nearshore water column after dark—mysids, amphipods, isopods, and others.

The present situation at Santa Catalina Island suggests that since early times predation pressures from large-mouthed, generalized predators have influenced major evolutionary trends among shallow-water zooplankters. Most apparent are trends toward nocturnal planktonic activity in those zooplankters that would spend only part of their time in the water column, and toward reduced size among those zooplankters that would spend all of their time in the water column. At the same time it would appear that each of these trends has elicited an evolutionary response among planktivorous fishes, as discussed below. We do not suggested that pressures exerted in predator-prey interactions have been the only force shaping these trends, but we believe their

impact has been significant. (A trend toward transparency, most developed in the larger zooplankters present in the water column during the day, is obviously adaptive for organisms threatened by visually feeding predators. Although this trend is only briefly mentioned here, its importance in defense against predators is emphasized by Hamner et al. 1975.)

Because most generalized predaceous fishes probably have been visual feeders since early times, their prey would have long since found water-column activities most safely performed under cover of darkness. Not surprisingly, the zooplankters that are vulnerable to large-mouthed fishes are mostly nocturnal forms that spend the daytime amid benthic cover. But only organisms that have the capacity to leave the water column can enjoy the advantage of cover during vulnerable periods.

The organisms that spend all their time in the water column have had to adapt to being fully exposed during daylight, when the visual sense of their predators is most effective. Under this circumstance one would expect long-established selective pressures favoring sizes smaller than those that can be entrapped by the relatively large mouths of generalized predators. That such selective pressures operate today among zooplankters in daylight is well documented. Brooks and Dotson (1965), for example, described the larger zooplankters in a lake being eliminated by the planktivorous clupeoid fish *Alosa pseudoharengus*, reported by Emery (1973) to feed by day.

Because successful defenses in prey create pressures that modify the offenses of predators, early tendencies in prey toward nocturnal habits or reduced size would have generated appropriate evolutionary responses among predators. Certainly a long-standing selection for nocturnal capabilities is evidenced by the many large-mouthed predaceous fishes that forage in the mid-waters at Santa Catalina after dark, including the walleye, the salema, and the queenfish. Large eyes, an obvious advantage in predators that hunt at night, have been widely acquired by these fishes (see Figures 6-10). Similarly, the small mouth and other specialized features of diurnal planktivorous fishes, like the blacksmith, clearly are adaptive for feeding on the very small organisms that constitute the diurnal zooplankton (see Figures 11-13). In their feeding morphologies and body forms, the nocturnal planktivores have diverged less than have their diurnal counterparts from the generalized predators that gave rise to them all. This does not necessarily mean that the diurnal planktivores are more recently evolved. Each is the product of an equally long evolution, and while the diurnal planktivores have been molded by selective pressures favoring the capacity to take tiny organisms, the nocturnal species have been influenced during the same period by selective pressures favoring the capacity to detect and capture prey in the dark.

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LITERATURE CITED

BOUSFIELD, E. L.
1973. Shallow-water gammaridean Amphipoda of New England. Cornell Univ. Press, Ithaca, 312 p.

BRAY, R. N., AND A. W. EBELING.
1975. Food, activity, and habitat of three "picker-type" micro-carnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BROOKS, J. L., AND S. I. DODSON.
1965. Predation, body size, and composition of plankton. Science (Wash., D.C.) 150:28-35.

DAVIS, W. P., AND R. S. BIRDSONG.
1973. Coral reef fishes which forage in the water column. Helgoländer wiss. Meeresunters. 24:292-306.

EMERY, A. R.
1968. Preliminary observations on coral reef plankton. Limnol. Oceanogr. 13:293-303.
1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Board Can. 30:761-774.

GERBER, R. P., AND N. MARSHALL.
1974. Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. Limnol. Oceanogr. 19:815-824.

GOSLINE, W. A.
1971. Functional morphology and classification of teleostean fishes. Univ. Press Hawaii, Honolulu, 208 p.

HAMNER, W. M., L. P., MADIN, A. L. ALLDREDGE, R. W. GILMER, AND P. P. HAMNER.
1975. Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. Limnol. Oceanogr. 20:907-917.

HOBSON, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep.73, 92 p.
1971. Cleaning symbiosis among California inshore fishes. Fish. Bull., U.S. 69:491-523.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1973. Diel feeding migrations in tropical reef fishes. Helgoländer wiss. Meeresunters. 24:361-370.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HUBBS, C. L., AND L. C. HUBBS.
1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an embiotocid fish of the Californias. Calif. Fish Game 40:183-198.

LIMBAUGH, C.
1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif. Inst. Mar. Resour., IMR Ref. 55-9, 158 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

NEWELL, G. E., AND R. C. NEWELL.
1963. Marine plankton. Hutchinson, Lond., 221 p.

QUAST, J. C.
1968. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.

RANDALL, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.

SCHAEFFER, B., AND D. E. ROSEN.
1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. Am. Zool. 1:187-204.

SMITH, R. I., AND J. T. CARLTON (editors).
1975. Light's manual: Intertidal invertebrates of the central California coast. 3rd ed. Univ. Calif. Press, Berkeley, 716 p.

STEVENSON, R. A., JR.
1972. Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus partitus* Poey) by environmental factors. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals. Vol. 2: Vertebrates, p. 278-302. Plenum Press, N.Y.

SWERDLOFF, S. N.
1970. The comparative biology of two Hawaiian species of the damselfish genus *Chromis* (Pomacentridae). Ph.D. Thesis, Univ. Hawaii, 202 p.

WICKSTEAD, J. H.
1965. An introduction to the study of tropical plankton. Hutchinson and Co., Lond., 160 p.

WILLIAMS, A. B., AND K. H. BYNUM.
1972. A ten-year study of meroplankton in North Carolina estuaries: Amphipods. Chesapeake Sci. 13:175-192.

PROTEIN TAXONOMY OF THE GULF OF MEXICO AND ATLANTIC OCEAN SEATROUTS, GENUS *CYNOSCION*

MICHAEL P. WEINSTEIN[1] AND RALPH W. YERGER[2]

ABSTRACT

Taxonomic relationships among the western North Atlantic seatrouts, genus *Cynoscion*, were investigated utilizing acrylamide gel electrophoresis. Several tissues (blood serum, eye lens, and muscle) were incorporated in this study to gain a better taxonomic overview than would be attainable with a single protein system.

Blood serum exhibited considerable variation in banding patterns. Because direct interspecific comparisons were not possible, a phenetic analysis was employed. Eye lens and muscle patterns, however, were directly comparable. Based on the overall results, three taxonomic conclusions may be drawn. First, with the exception of a single taxonomic distance (d_{jk}) value calculated in the phenetic analysis, the relationships established by electrophoresis reflect the phyletic relationships proposed by Ginsburg. This "aberrant" value is believed to result from the small sample size and the possibility of ecological convergence. Second, the data indicate that *Cynoscion nebulosus* is the most divergent of the four forms, supporting previous morphological and ecological conclusions. Third, as suggested by previous studies, the taxonomic status of *C. arenarius* as a distinct species is again questioned. Electrophoretic patterns indicate that it should be regarded as a subspecies of *C. regalis*.

Investigation of general protein systems has often proven useful in elucidating taxonomic relationships. Species-specific banding patterns have been reported for numerous taxa including fishes (Tsuyuki and Roberts 1965; Perrier et al. 1973). Nyman and Westin (1969) studied serum patterns of cottid fishes from the Baltic Sea and concluded that the patterns reflected the commonly accepted scheme. Species and group (genus, family, class) specificities have also been described for eye lens proteins of several fishes (Rabaey 1964, Bon et al. 1964, Cobb et al. 1968). Recently Eckroat (1974) compared members of the pike family (Esocidae) using this tissue. Myogens have proven particularly useful in reviews of several groups in the families Catostomidae (Tsuyuki, Roberts, and Vanstone 1965; Tsuyuki et al. 1967; Huntsman 1970), Salmonidae (Tsuyuki, Roberts, Vanstone, and Markert 1965; Tsuyuki et al. 1966) and Scorpaenidae (Tsuyuki et al. 1968; Johnson et al. 1972).

In this study we have investigated taxonomic affinities among the western North Atantic seatrouts, genus *Cynoscion*. Four species are currently recognized: spotted seatrout, *C. nebulosus* (Cuvier); weakfish, *C. regalis* (Bloch and Schneider); silver seatrout, *C. nothus* (Holbrook); and sand seatrout, *C. arenarius* Ginsburg. *Cynoscion arenarius* is restricted to the Gulf of Mexico; specimens have been captured from Campeche, Mexico, eastward to the southwest coast of Florida. *Cynoscion regalis* has been generally considered to be limited to the Atlantic coast. Guest and Gunter (1958) described its southernmost occurrence as the St. Lucie estuary, Fla. We now have evidence which conclusively proves its presence in the Gulf of Mexico.

Cynoscion nebulosus occurs from New York to Mexico (Bay of Campeche); its center of abundance is in Florida and the Gulf States (Pearson 1929). *Cynoscion nothus* is found from Chesapeake Bay, Md., to the Bay of Campeche but is uncommon at the southern extremity of its range. It is relatively abundant on the gulf coast and from the east coast of Florida to North Carolina.

Several tissues (blood serum, eye lens, and muscle) were utilized in order to achieve a better taxonomic overview. Since it is difficult (if not impossible) to construct a phylogeny solely on the basis of biochemical differences, our results have been compared with the existing phylogenetic schemes of Ginsburg (1929) who recognized *C. arenarius* and *C. regalis* as cognate species, and Mohsin (1973) who placed *C. arenarius* and *C. nebulosus* in one phyletic line, and *C. regalis* and *C. nothus* in another.

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MATERIALS AND METHODS

Spotted seatrout were obtained by hook and line at seven localities from Corpus Christi, Tex., to Indian River, Fla. Weakfish were caught by hook and line in Peconic Bay, N.Y., and together with silver seatrout in otter trawls in Wassaw Sound, Ga. Sand seatrout were collected by hook and line at Pensacola, Fla., and by shrimp trawl in the vicinity of Carrabelle, Fla.

Preparation of serum and eye lens samples and electrophoretic methods are identical to those recently described by Weinstein and Yerger (in press). Samples were electrophoresed in 7% acrylamide gel, using a modified Davis (1964) technique. Diluting tissue preparations with 10% glycerol avoided the tedius requirement of producing three-layered gels, yet allowed highly satisfactory resolution.

Soluble muscle proteins were prepared by homogenizing 1-g tissue samples with 2 volumes of ice cold 0.05 M phosphate buffer (pH 7.4). Homogenates were centrifuged in a Sorvall[3] RC-2 refrigerated centrifuge at 20,000 rpm for 20 min. Fifty microliters of supernate were combined with an equal volume of 10% glycerol, and 50 μl of the mixture layered on each gel. During electrophoresis the dye band was allowed to migrate to within 0.5 cm of the end of each gel.

RESULTS

Serum Proteins

Although serum protein patterns varied intraspecifically both in the frequency of occurrence of particular bands, and occasionally in their composition (intensity), species specificity was evident. Differences among patterns were not so pronounced as to prevent assigning a given pattern to the proper taxon. Typical results obtained from the four seatrouts are shown in Figure 1, and are diagrammed in Figure 2. All bands observed in the total number of electrophoresed samples are indicated. Their position on the diagrams is also an accurate representation of the relative distances (on the gels) that each band migrated.

We follow the standard method of defining protein zones (α, β, γ, albumin, prealbumin). The various designations were derived from a population study on *C. nebulosus* (see Weinstein 1975).

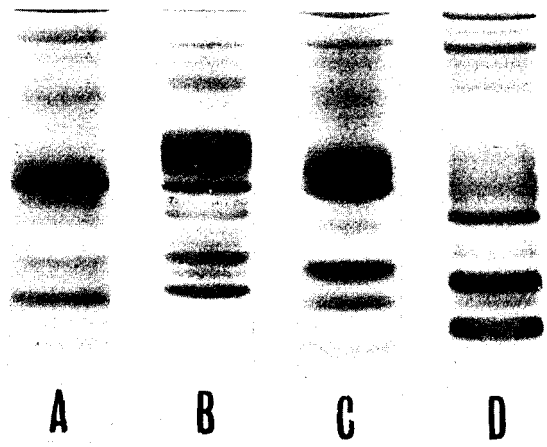

FIGURE 1.–Serum protein electropherograms derived from whole sera of four seatrouts. (A) *Cynoscion nothus*, (B) *C. arenarius*, (C) *C. regalis*, (D) *C. nebulosus*.

Because of the widespread variation observed in the blood serum patterns, direct comparison between the species investigated was difficult. In order to "sum" the intraspecific variation observed and subsequently to use the composites for direct comparison, the taxonomic distance (d_{jk}) measure of Sokal (1961) was utilized. In this formula

$$\overline{d_{12}^2} = \frac{1}{n} \sum_{i=1}^{n} (\xi_{i1} - \xi_{i2})^2$$

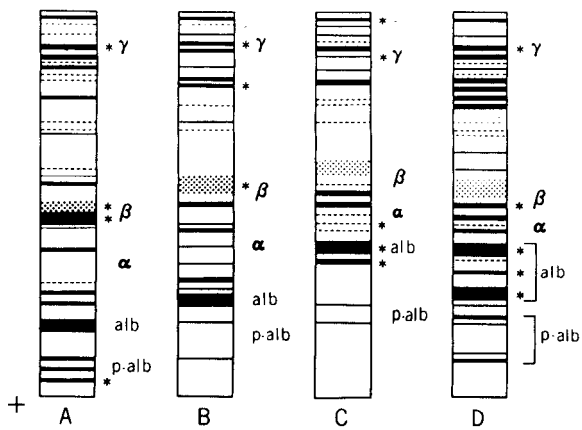

FIGURE 2.–Diagrammatic representation of protein bands occurring in serum electropherograms of four seatrouts. Protein zones are as follows: γ = immunoglobin zone; β = β-globulin zone; α = α-globulin zone; alb = albumins; p-alb = prealbumins. * indicates band present in 100% of samples. (A) *Cynoscion nothus*, (B) *C. arenarius*, (C) *C. regalis*, (D) *C. nebulosus*.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

all of the bands observed on the gels were taken as "characters" and their percent occurrence as "character states." The data utilized in computing taxonomic distances are summarized in Table 1, and the results of such an analysis in Table 2. All data were "standardized" to have a mean of 0 and a variance of 1 (indicated by ξ). Values of d are interpreted as follows, "The larger the distance, the smaller the degrees of association or correlation between taxa." (Sokal 1961). Based on the calculated distances (Table 2), *C. nebulosus* has diverged to a larger extent than any other member of the genus and differs from the others by about the same order of magnitude. *Cynoscion nothus* and *C. regalis* apparently share a closer relationship in blood protein patterns than do *C. regalis* and *C. arenarius*, a result comparable to that based on osteological similarity (Mohsin 1973). It also seems apparent that the close correlation between *C. nothus* and *C. regalis* (44.0) and between *C. arenarius* and *C. regalis* (54.7) should imply a similar distance between *C. nothus* and *C. arenarius*. Such is not the case; and the value 63.8 apparently indicates that their differences are even greater than their similarities.

TABLE 1.–Percent occurrence of banding patterns derived from whole serum samples of seatrouts (*Cynoscion*). A dash indicates the absence of that band.

Serum band	*C. nothus* $n = 34$	*C. arenarius* $n = 19$	*C. regalis* $n = 19$	*C. nebulosus* $n = 500$
1	81.1	83.3	100	74.5
2	70.3	75.0	7.7	—
3	81.1	91.7	76.9	96.5
4	—	100	30.8	—
5	100	50.0	84.6	100
6	8.1	—	—	—
7	54.1	—	100	—
8	67.6	75.0	84.6	30.0
9	10.8	—	—	92.4
10	—	—	—	23.9
11	86.5	50.0	92.3	18.4
12	—	—	—	88.9
13	78.4	100	53.8	94.3
14	—	8.3	76.9	11.2
15	—	—	—	67.3
16	78.4	50.0	15.4	70.6
17	59.5	50.0	—	76.0
18	45.9	—	—	66.4
19	—	—	—	63.9
20	43.2	—	92.3	46.1
21	24.3	100	—	—
22	24.3	—	—	—
23	—	—	—	89.1
24	100	—	15.4	—
25	—	—	84.6	—
26	—	91.7	69.2	100
27	100	—	38.5	89.8
28	48.6	16.7	100	20.0
29	—	91.7	15.4	90.4
30	94.6	66.7	100	100
31	—	—	—	8.4
32	—	91.7	—	100
33	75.7	91.7	100	—
34	24.3	16.7	—	100
35	91.9	50.0	92.3	13.8
36	—	—	—	77.6
37	78.4	66.3	23.0	24.8
38	—	—	—	2.1
39	73.0	91.7	—	80.5
40	21.6	—	—	—
41	100	—	—	—

TABLE 2.–Taxonomic distances (d_{jk}) calculated for interspecific comparisons among four seatrouts (*Cynoscion*). The larger the value, the smaller the degree of association or correlation between taxa (Sokal 1961).

Species compared	d_{jk}
C. nothus versus *C. arenarius*	63.8
C. nothus versus *C. regalis*	44.0
C. nothus versus *C. nebulosus*	78.5
C. arenarius versus *C. regalis*	54.7
C. arenarius versus *C. nebulosus*	67.3
C. regalis versus *C. nebulosus*	72.9

Eye Lens Proteins

Eye lens preparations exhibited considerable uniformity of pattern (Table 3, Figure 3). Four bands designated by arabic numerals were shared in common by the seatrouts; however, the amount of protein in each band differed significantly. For example, *C. regalis* had a greater protein concentration in band 1 than did any of the others. The quantity of protein in this band was not observed to differ significantly in any of the samples processed. Bands 1 and A in *C. nebulosus* ($n = 275$)

TABLE 3.–Percent occurrence of banding patterns derived from eye lens nuclei of seatrouts (*Cynoscion*). A dash indicates the absence of that band.

Band	*C. nothus* $n = 35$	*C. arenarius* $n = 12$	*C. regalis* $n = 16$	*C. nebulosus* $n = 275$
1	100	100	100	100
A	—	—	—	12.7
2	100	100	100	100
3	100	100	100	100
B	—	—	—	14.1
C	—	33.0	—	—
4	100	100	100	100
D	17.0	42.0	—	59.7
E	—	—	—	19.0

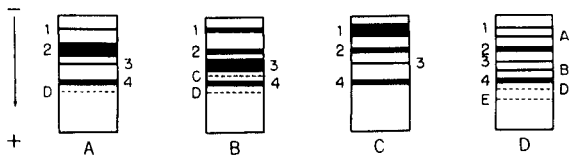

FIGURE 3.–Diagrammatic representation of protein bands occurring in eye lenses of four seatrouts. Arabic numerals indicate bands shared by all taxa (similar electrophoretic mobility). Letters indicate bands that are either unique or not shared by all members of the genus. (A) *Cynoscion nothus*, (B) *C. arenarius*, (C) *C. regalis*, (D) *C. nebulosus*.

together contained approximately the same quantity of protein as found in band 1 of *C. arenarius*. We believe that band 1 (100% occurrence) in *C. nebulosus* contains at least one protein which exhibits polymorphism. Since other proteins (frequency 100%) in this band mask the identity of the protein in question, it is not possible at the level of sensitivity of this system to distinguish the mode of inheritance for this polymorphism. The same situation seems to be true of bands 3 and B in this species.

Band 1 is consistently found in lower concentration in *C. nothus* (n = 35), but the reverse is true of band 2, which exhibits continuously greater concentration than the comparable band in any other seatrout. Band 3 is found in the highest concentration in *C. arenarius* (n = 12); a slightly lower concentration occurs in the composite of bands 3 and B in *C. nebulosus*, and a still lower concentration is found in *C. regalis* and *C. nothus*. Band 4 is present in approximately the same concentration in all four species. It should be emphasized that these are average values; small intraspecific differences were noted from sample to sample.

Qualitative pattern differences were also noted. Bands A and B are unique to *C. nebulosus*. A third band, designated C, was found in 2 of 12 samples of *C. arenarius*, but not in any other species. A fourth variant, designated D, was found in *C. nebulosus*, *C. arenarius*, and *C. nothus*, but not in *C. regalis*. Lastly, a band migrating farthest anodally in *C. nebulosus* was designated E. These qualitative as well as quantitative differences in eye lens patterns are summarized in Table 3.

Myogens

Electropherograms derived from soluble muscle proteins provided the most clearly discernible measure of biochemical relationship. Compared with serum patterns, only minor intraspecific variations were evident. A typical grouping from the four seatrouts is shown in Figure 4, and the patterns are diagrammed in Figure 5. The broken lines indicate two minor bands that occurred in a variable manner and in relatively low frequencies; hence, they were not considered further. All other bands occurred in 100% of the samples and are designated as comprising the typical species-specific patterns. A remarkable degree of similarity in the patterns is obtained for *C. regalis* and *C. arenarius*; they share not only 12 and 13 bands in

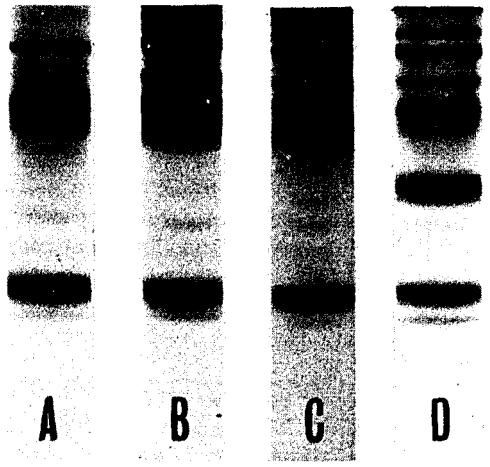

FIGURE 4.—Electropherograms derived from protein extracts of epaxial musculature. (A) *Cynoscion nothus*, (B) *C. arenarius*, (C) *C. regalis*, (D) *C. nebulosus*.

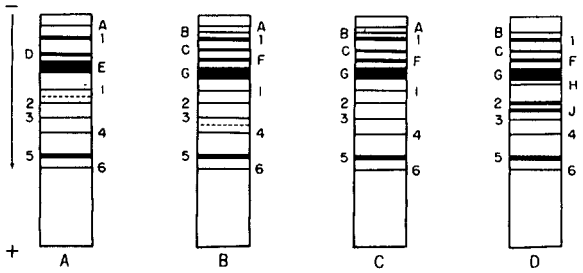

FIGURE 5.—Diagrammatic representation of the protein bands occurring in myogen extracts of four seatrouts. (A) *Cynoscion nothus*, (B) *C. arenarius*, (C) *C. regalis*, (D) *C. nebulosus*.

common (as indicated by electrophoretic mobility and sieving characteristics), but also compare favorably in the quantities of protein comprising each band (Figure 6). Although some variation occurred in relative peak heights from sample to sample (within a species), the densitometer tracings shown in Figure 6 are representative of each species. A close relationship clearly exists between *C. regalis* and *C. arenarius* both in the distance of migration and in the quantity of protein making up the individual bands (Figures 5, 6). Although the other two species shared the same general generic pattern, they varied in the composition of several major bands. *Cynoscion nebulosus* always has a high concentration in band 2 in each of the 12 samples processed, and has a second band immediately adjacent of the same thickness (denoted J on Figure 5). These bands (2 and J) were not resolved as separate peaks in a series of densi-

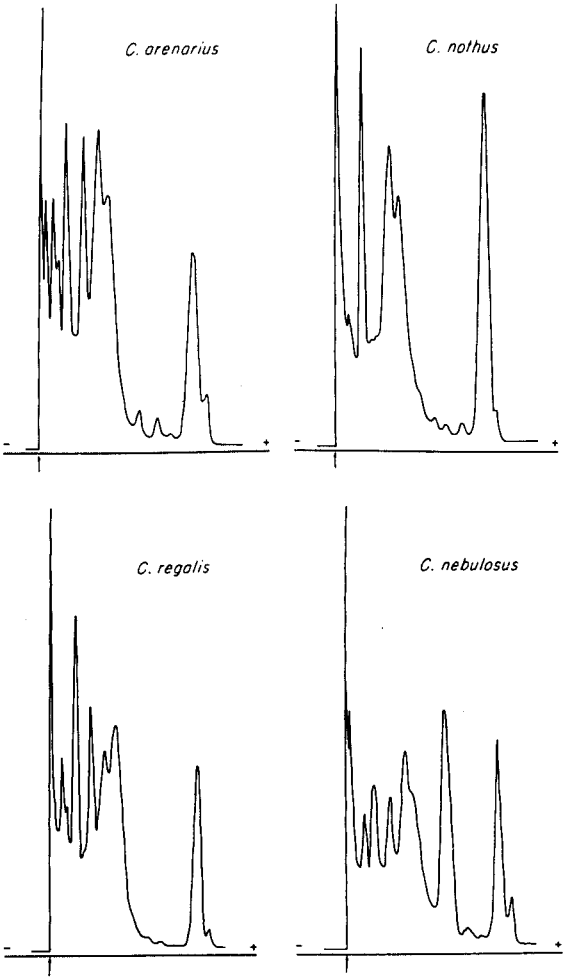

FIGURE 6.—Densitometer tracings of representative myogen patterns of four seatrouts (*Cynoscion*). Intensity of particular bands are indicated by relative peak heights.

tometer tracings; however, observation of gels and photographs clearly indicated their double nature. Band 1 was not present in any of the samples of *C. nebulosus*; however, a band designated as H occurred in a more cathodal direction (above position I).

Bands D and E in *C. nothus* are slightly displaced; i.e., they have a slightly different electrophoretic mobility from their "counterparts" (F and G) in the other three species. This difference could be an artifact, but duplicate experiments indicate otherwise. *Cynoscion nothus* also lacks bands B and C found in the other species. Band A is absent in *C. nebulosus*, but present in the other seatrouts.

DISCUSSION

Morphological Taxonomy

In his review of the seatrouts of the Atlantic and Gulf coasts of the United States, Ginsburg (1929) recognized *C. nebulosus* as the most distinctive morphologically on the basis of its color pattern and its scaleless dorsal and anal fins. *Cynoscion nebulosus* also differs ecologically from the other *Cynoscion;* it is primarily an estuarine form while the others have a closer affinity to the marine environment.

The remaining species are less easily distinguished. Of the many criteria used, size and color are most important. *Cynoscion regalis* is readily recognized in the adult stage by the longitudinal rows of small spots on its back, which produce a mottled appearance. The paler, *C. arenarius* of the gulf lacks conspicuous pigmentation. *Cynoscion nothus* is similar in color to *C. arenarius*, but differs in several other respects including vertebral and anal-fin ray counts. *Cynoscion nothus* may not attain as large a maximum size as *C. arenarius*, although this observation may be a sampling artifact. Gunter (1945) noted that *C. nothus* occurs at slightly greater depths than the other seatrouts. Therefore, the main populations of *C. nothus* may not have been adequately sampled.

Taxonomically, the status of *C. arenarius* has never been satisfactorily resolved. Guest and Gunter (1958) accorded full species rank for *C. arenarius*, as does the current list of the American Fisheries Society (Bailey et al. 1970), and the recent investigation by Mohsin (1973). However, the original description leaves room for considerable doubt. Ginsburg (1929) stated in a footnote that, "An unbiased study of the data here presented shows, I believe, that there is room for difference of opinion as to the degree of difference between this form [*C. arenarius*] and *ragalis* [*regalis*] from the Atlantic coast—whether they should be regarded as species or subspecies." Furthermore, by Ginsburg's (1938) own criteria of the "arithmetical" definition of a species, the 18% intergradation of the most "divergent" character (the number of articulated dorsal rays) would give the two forms only subspecific status.

Protein Taxonomy

Our primary purpose in this study has been to

provide biochemical evidence for the taxonomic relationship among four members of the genus *Cynoscion* (including the degree of divergence), and to compare this information with existing phylogenetic schemes. Although no attempt has been made to construct a phylogeny based on biochemical data, qualitative differences (and similarities) allow some taxonomic conclusions to be drawn.

Serum Proteins

Environmentally induced changes in blood serum components have been well substantiated (Thurston 1967). This evidence, nonetheless, would not preclude blood serum patterns from being a useful taxonomic tool if one additional step is taken. It is obvious that the classical morphologists in comparing populations of animals (or plants) are including the influence of the environment in the range of variation they are describing. For example, it is commonly observed that counts of meristic characters (fin rays, scales, etc.) increase in the northerly direction of the animal's range (in the Northern Hemisphere). This, however, will not affect the conclusions drawn as long as sufficient samples are taken to cover the full (or nearly so) range of variation in the population. Once adequate samples are obtained, accurate modes may be calculated for each character and the relationship between two forms established. Within this framework utilization of highly variable patterns such as that found for serum proteins are justified.

In this study we have been able to sample only a relatively small number of each species, with the exception of *C. nebulosus* (Table 2). Hence, any conclusions regarding the biochemical relationship among the four taxa must be provisional.

Although the blood patterns of the species of *Cynoscion* are somewhat more variable than has been reported for many fishes and other vertebrates, we can present evidence for relationships among the Gulf of Mexico and Atlantic Ocean seatrouts. The Taxonomic distances calculated for members of this genus are listed in Table 2. The value (54.7) for the alleged cognates, *C. arenarius* and *C. regalis*, is surpassed only by the value (43.9) for *C. nothus* and *C. regalis*. Only 10 bands of the 41 present were unique to one of the four species; 7 were found in *C. nebulosus*, 2 in *C. nothus*, and 1 in *C. regalis*. *Cynoscion arenarius* did not display any species-specific bands. Therefore, a considerable portion of the differences among the four seatrouts, as expressed by d_{jk}, are generated by different percentage compositions of the serum proteins.

The similar values obtained for *C. regalis* and *C. nothus* may be interpreted in three ways: 1) these species may actually be more closely related than are *C. regalis* and *C. arenarius*; 2) similar environmental selection pressures have produced an example of ecological convergence; 3) sample size may be insufficient to yield accurate results. Three of the 19 samples of *C. regalis* were taken from the same estuary (Wassaw Sound) as were all samples of *C. nothus*; the remaining sera from *C. regalis* were collected in an estuary (Peconic Bay) sharing several physical and chemical parameters with Wassaw Sound (Odum et al. 1974). Thus, a measure of ecological convergence may be involved. Similar reasoning might explain the d_{jk} calculated for *C. arenarius* versus *C. nothus*; the value (63.8) might be reduced if several other gulf populations of *C. nothus* were added to the total sample.

It could be argued that the much larger sample of *C. nebulosus* ($n=500$) was responsible for most of the difference in the taxonomic distance value since rare bands are being included. This could only be the case for band 38 which occurred in only 2.1% of the specimens sampled. The values (percent occurrence) of the remaining six unique bands (8%, 23%, 66%, 67%, 89%, 89%) argue against this possibility. The average value of 72.8 is therefore taken to mean that *C. nebulosus* is the most divergent of the four species investigated. Possible reasons for this observation have been elaborated previously.

A significant observation in our study is that relatively few species-specific (i.e., unique) proteins have been detected, a phenomenon not without precedence, however (Lewontin 1974). In a study of 10 species of *Drosophila*, the number of unique proteins ranged from 2.6 to 28.2%, with an average of 14.3% (Hubby and Throckmorton 1968). Our own figures compare favorably with these: *C. nebulosus*, 23%; *C nothus*, 7%; *C. regalis*, 5%; and *C. arenarius*, 0%.

Eye Lens Proteins

In a review of intraspecific variation in lens proteins, Day and Clayton (1973) detected no polymorphisms and concluded that observed differ-

ences were almost wholly quantitative rather than qualitative. Data from other studies indicate two further conclusions. First, lens proteins on the whole express a high degree of conservatism. Secondly, in cases where evidence of polymorphisms have been obtained, fishes have been most often implicated. Smith and Goldstein (1967), Smith (1969, 1971), and Smith and Clemens (1973) reported intraspecific variations in the lens patterns of numerous species. Barrett and Williams (1967) detected a polymorphism in the lens proteins of the bonito *Sarda chiliensis*. Eckroat and Wright (1969) and Eckroat (1973) provided direct evidence of polymorphisms in the eye lens of the brook trout, *Salvelinus fontinalis*, and demonstrated simple Mendelian inheritance for several characters.

Previous observations for eye lens proteins and the conclusions stated above are reflected in our work on the patterns derived from the genus *Cynoscion*. Lens protein patterns displayed considerable convervatism among the four seatrouts. Four bands from a total of eight occur in all taxa and are probably high molecular weight α- and β-crystallins. Only a single band (E in *C. nebulosus*, Figure 3) is unique and is found in either very low frequency or not at all in four of the seven estuaries sampled. Its relatively high frequencies in Corpus Christi, Galveston, and Florida Bay (36, 39, and 50%, respectively) indicate a possible relationship to high turbidity and low light intensities characteristic of these three areas.

Although intensity patterns did not vary significantly within a species (with the exception of two bands involved in a suspected polymorphism in *C. nebulosus*), the quantities of protein in bands with the same mobility were quite different and species-specific (Figure 3). The selective forces which control the quantity of protein present in a given band are not easily recognized. The geographic ranges of these four species overlap considerably althouth their centers of abundance are quite different. *Cynoscion nothus* is found farther offshore than its congeners; *C. nebulosus* is primarily restricted to the estuarine habitat. All seatrouts probably experience a similar range of water color and turbidities in their respective habitats. None is considered to be more diurnal or nocturnal than the others. Their temperature ranges overlap considerably. Therefore, it is somewhat puzzling as to the cause of the common observation that variations in patterns both within a species and between them is restricted mainly to intensity differences. Presently the advantages of different proportions of crystallins and other eye lens protein in a particular species are poorly known.

Myogen Proteins

The general application of myogen proteins to systematic studies has been reviewed by Tsuyuki (1974). Perhaps no other tissue investigated has displayed such an overall lack of intraspecific variations. Only a few species of fishes have exhibited detectable polymorphisms (e.g., Nyman 1967; Tsuyuki et al. 1968; Gray and McKenzie 1970), and it is noteworthy that most of these are "tetraploid" species. The majority of investigations on other forms reveal virtually no intraspecific variation, an observation in direct contrast with other protein systems which generally display polymorphisms. Various estimates of proportions of polymorphic alleles in vertebrate species are placed at from 10 to 20% (Selander and Kaufman 1973). The constancy maintained in myogen proteins in the presence of selective forces is indeed remarkable.

The general conservatism displayed in myogen patterns was observed in our own work, but with several important differences. As previously described, *C. nothus* and *C. nebulosus* differed in the presence or absence of one or more major (by staining intensity) bands. Band J (Figure 5), unique in *C. nebulosus*, is found in all samples, and produces a large characteristic peak on densitometer tracings. The absence of several bands, notably B and C (Figure 5), characterizes *C. nothus*.

On the basis of myogen patterns, we suggest that *C. arenarius* and *C. regalis* are more closely related to each other than are any other combination of species under consideration and should be treated as conspecific. Thus, we reject the phylogeny based on slight osteological differences proposed by Mohsin (1973). The gulf form (*C. arenarius*) should be recognized as a subspecies of *C. regalis*, a conclusion strengthened by recent confirmation of specimens of *C. regalis* from the Gulf of Mexico.

Earlier reports of *C. regalis* in the gulf generally lacked documentation, or were misidentifications of *C. arenarius*. The report of Jordan and Eigenmann (1889) from Mobile Bay, Ala., was based on specimens of *C. arenarius*, a form not recognized

until 45 yr later. Rivas (1954) mentioned the weakfish in the gulf but provided no specific data. Hutton et al. (1956) reported *C. regalis* from Boca Ciega Bay at St. Petersburg, Fla., but Springer and Woodburn (1960) listed only *C. arenarius* from Tampa Bay. No specimens of *C. regalis* from the gulf are in the reference fish collection of the Department of Natural Resources at the St. Petersburg Marine Laboratory (Moe et al. 1966).

Two adult *C. regalis* (266 and 298 mm standard length) were captured by personnel from the Marco Ecology Laboratory in the vicinity of Marco Island, on the southwest coast of Florida on 21 July 1972 (Florida State University Fish Collection, catalog number 24023). The documentation of the weakfish in the Gulf of Mexico together with the extremely close morphological and biochemical characteristics shared by *C. regalis* and *C. arenarius* suggest that gene exchange between the Atlantic Ocean and gulf coast populations is feasible although we have no proof of their interbreeding. Nevertheless, the evidence points to the same series of events which characterize the evolutionary history of other marine geminate species in Florida. When the peninsula split the ancestral population into two, the Gulf population differentiated from that in the Atlantic (see Ginsburg 1952; Walters and Robins 1961). Whether or not isolation was complete or only partial, the present distribution indicates that at least one form (*C. regalis*) has been successful in moving around the tip of the peninsula into southeastern gulf waters and in establishing secondary contact with the other (*C. arenarius*). The status of *C. arenarius* should be investigated in depth. Perhaps an extensive enzyme study would be appropriate, the results of which could be compared by statistical analyses (Avise 1974) to determine the level of differentiation between two forms.

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LITERATURE CITED

AVISE, J. C.
1974. Systematic value of electrophoretic data. Syst. Zool. 23:465-481.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc., Spec. Publ. 6, 150 p.

BARRETT, I., AND A. A. WILLIAMS.
1967. Soluble lens proteins of some scombroid fishes. Copeia 1967: 468-471.

BON, W. F., P. L. SWANBORN, G. J. C. M. RUTTENBERG, AND A. DOHRN.
1964. Comparative investigation of the soluble proteins of the eyelens of fish. Publ. Stn. Zool. Napoli 34:59-65.

COBB, B. F., III, L. CARTER, AND V. L. KOENIG.
1968. The distribution of the soluble protein components in the crystalline lenses of fishes. Comp. Biochem. Physiol. 24:817-826.

DAVIS, B. J.
1964. Disc electrophoresis–II. Method and application to human serum proteins. Ann. N.Y. Acad. Sci. 121:404-427.

DAY, T. H., AND R. M. CLAYTON.
1973. Intraspecific variation in the lens proteins. Biochem. Genet. 8:187-203.

ECKROAT, L. R.
1973. Allele frequency analysis of five soluble protein loci in brook trout, *Salvelinus fontinalis* (Mitchill). Trans. Am. Fish. Soc. 102:335-340.
1974. Interspecific comparisons of lens proteins of Esocidae. Copeia 1974: 977-978.

ECKROAT, L. R., AND J. E. WRIGHT.
1969. Genetic analysis of soluble lens protein polymorphism in brook trout, *Salvelinus fontinalis*. Copeia 1969:466-473.

GINSBURG, I.
1929. Review of the weakfishes (Cynoscion) of the Atlantic and Gulf coasts of the United States, with a description of a new species. Bull. U.S. Bur. Fish. 45:71-85.
1938. Arithmetical definition of the species, subspecies and race concept, with a proposal for a modified nomenclature. Zoologica (N.Y.) 23:253-286.
1952. Eight new fishes from the Gulf coast of the United States, with two new genera and notes on geographic distribution. J. Wash. Acad. Sci. 42:84-101.

GRAY, R.W., AND J. A. MCKENZIE.
1970. Muscle protein electrophoresis in the genus *Salmo* of eastern Canada. J. Fish. Res. Board Can. 27:2109-2112.

GUEST, W. C., AND G. GUNTER.
1958. The sea trout or weakfishes (genus *Cynoscion*) of the Gulf of Mexico. Gulf States Mar. Fish. Comm., Tech. Summ. 1, 40 p.

GUNTER, G.
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. Univ. Tex. 1:1-190

HUBBY, J. L., AND L. H. THROCKMORTON.
1968. Protein differences in Drosophila. IV. A study of sibling species. Am. Nat. 102:193-205.

HUNTSMAN, G. R.
1970. Disc gel electrophoresis of blood sera and muscle extracts from some catostomid fishes. Copeia 1970: 457-467.

HUTTON, R. F., B. ELDRED, K. D. WOODBURN, AND R. M. INGLE.
1956. The ecology of Boca Ciega Bay with special reference to dredging and filling operations. Part I. Fla. State Board Conserv., Tech. Ser. 17, 87 p.

JOHNSON, A. G., F. M. UTTER, AND H. O. HODGINS.
1972. Electrophoretic investigation of the family Scorpaenidae. Fish. Bull., U.S. 70:403-413.

JORDAN, D. S., AND C. H. EIGENMANN.
1889. A review of the Sciaenidae of America and Europe. Rep. Comm., U.S. Comm. Fish Fish. 1886: 343-451.

LEWONTIN, R. C.
1974. The genetic basis of evolutionary change. Columbia Univ. Press, N.Y., 346 p.

MOE, M. A., JR., P. C. HEEMSTRA, J. E. TYLER, AND H. WAHLQUIST.
1966. An annotated listing of the fish reference collection at the Florida Board of Conservation Marine Laboratory. Fla. State Board Conserv. Mar. Lab., Spec. Sci. Rep. 10, 121 p.

MOHSIN, A. K. M.
1973. Comparative osteology of the weakfishes (*Cynoscion*) of the Atlantic and Gulf coasts of the United States (Pisces-Sciaenidae). Ph.D. Thesis, Texas A&M Univ., 147 p.

NYMAN, C
1967. Protein variations in Salmonidae. Rep. Inst. Freshwater Res. Drottningholm 47:5-38.

NYMAN, L., AND L. WESTIN.
1969. Blood protein systematics of *Cottidae* in the Baltic drainage area. Rep. Inst. Freshwater Res. Drottningholm 49:164-174.

ODUM, H. T., B. J. COPELAND, AND E. A. MCMAHAN (editors).
1974. Coastal ecological systems of the United States. Vol. I. Conservation Foundation, Wash., D. C., 533 p.

PEARSON, J. C.
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.

PERRIER, H., J. P. DELCROIX, C. PERRIER, AND J. GRAS.
1973. An attempt to classify the plasma proteins of the rainbow trout (*Salmo gairdnerii* Richardson) using disc electrophoresis, gel filtration and salt solubility fractionation. Comp. Biochem. Physiol. 46B: 475-482.

RABAEY, M.
1964. Comparative study of tissue proteins (lens and muscle) in fish. Protides Biol. Fluids, Proc. Colloq. 12:273-277.

RIVAS, L. R.
1954. The origin, relationships, and geographical distribution of the marine fishes of the Gulf of Mexico. *In* P. S. Galtsoff (coordinator), Gulf of Mexico, its origin, waters, and marine life, p. 503-505. U.S. Fish Wildl. Serv., Fish. Bull. 55.

SELANDER, R. K., AND D. W. KAUFMAN.
1973. Genic variability and strategies of adaptation in animals. Proc. Natl. Acad. Sci. 70:1875-1877.

SMITH, A. C.
1969. Protein variation in the eye lens nucleus of the mackeral scad (*Decapterus pinnulatus*). Comp. Biochem. Physiol. 28:1161-1168.
1971. Genetic and evolutionary analysis of protein variation in eye lens nuclei of rainbow trout (*Salmo gairdnerii*). Int. J. Biochem. 2:384-388.

SMITH, A. C., AND H. B. CLEMENS.
1973. A population study by proteins from the nucleus of bluefin tuna eye lens. Trans. Am. Fish. Soc. 102:578-583.

SMITH, A. C., AND R. A. GOLDSTEIN.
1967. Variation in protein composition of the eye lens nucleus in ocean whitefish, *Caulolatilus princeps*. Comp. Biochem. Physiol. 23:533-539.

SOKAL, R. R.
1961. Distance as a measure of taxonomic similarity. Syst. Zool. 10:70-79.

SPRINGER, V. G., AND K. D. WOODBURN.
1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 104 p.

THURSTON, R. V.
1967. Electrophoretic patterns of blood serum proteins from rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 24:2169-2188.

TSUYUKI, H.
1974. Muscle proteins of fishes. *In* M. Florkin and B. T. Scheer (editors), Chemical zoology, Vol. 8, p. 287-305. Academic Press, N.Y.

TSUYUKI, H., AND E. ROBERTS.
1965. Zone electrophoretic comparison of muscle myogens and blood proteins of artificial hybrids of Salmonidae with their parental species. J. Fish. Res. Board Can. 22:767-773.

TSUYUKI, H., E. ROBERTS, R. H. KERR, J. F. UTHE, AND L. W. CLARKE.
1967. Comparative electropherograms of the family Catostomidae. J. Fish. Res. Board Can. 24:299-304.

TSUYUKI, H., E. ROBERTS, R. H. LOWES, W. HADAWAY, AND S. J. WESTRHEIM.
1968. Contribution of protein electrophoresis to rockfish (Scorpaenidae) systematics. J. Fish. Res. Board Can. 25:2477-2501.

TSUYUKI, H., E. ROBERTS, AND W. E. VANSTONE.
1965. Comparative zone electropherograms of muscle myogens and blood hemoglobins of marine and freshwater vertebrates and their application to biochemical systematics. J. Fish. Res. Board Can. 22:203-213.

TSUYUKI, H., E. ROBERTS, W. E. VANSTONE, AND J. R. MARKERT.
1965. The species specificity and constancy of muscle myogen and hemoglobin electropherograms of *Oncorhynchus*. J. Fish. Res. Board Can. 22:215-217.

TSUYUKI, H., J. F. UTHE, E. ROBERTS, AND L. W. CLARKE.
1966. Comparative electropherograms of *Coregonus clupeaformis*, *Salvelinus namaycush*, *S. alpinus*, *S. malma*, and *S. fontinalis* from the family Salmonidae. J. Fish. Res. Board Can. 23:1599-1606.

WALTERS, V., AND C. R. ROBINS.
1961. A new toadfish (Batrachoididae) considered to be a glacial relict in the West Indies. Am. Mus. Novit. 2047, 24 p.

WEINSTEIN, M. P.
1975. Electrophoretic investigation of the Gulf of Mexico and Atlantic Ocean seatrouts of the genus *Cynoscion*, with special reference to the population structure of the spotted seatrout, *Cynoscion nebulosus*. Ph.D. Thesis, Florida State Univ., 115 p.

WEINSTEIN, M. P., AND R. W. YERGER.
In press. Electrophoretic investigation of subpopulations of the spotted seatrout, *Cynoscion nebulosus* (Cuvier), in the Gulf of Mexico and Atlantic Coast of Florida. Comp. Biochem. Physiol.

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PREHATCH AND POSTHATCH GROWTH OF FISHES—A GENERAL MODEL

JAMES R. ZWEIFEL AND REUBEN LASKER[1]

ABSTRACT

The developmental stages of fish eggs and the growth of larval fishes of several species can be represented by a Gompertz-type curve based on the observation that in widely different living systems, exponential growth tends to undergo exponential decay with time. Further, experimental studies and field observations have shown that the effect of temperature on the growth process follows the same pattern, i.e., the rate of growth declines exponentially with increasing temperature. Evidence suggests that prehatch growth rates determine ideal or optimum trajectories which are maintained after hatch in the middle temperature range but not at either extreme. Also, posthatch growth exhibits a temperature optimum which is not apparent in the incubation period. These studies have also shown that for the same spawn both the prehatch and yolk-sac growth curves reach asymptotic limits independent of temperature. Other biological events (e.g., jaw development) occur at the same size for all temperatures.

The growth of post-yolk-sac larvae follows a curve of the same type and hence the posthatch growth trajectory may be represented by a two-stage curve. For starving larvae, the second stage shows a decline in size but maintains the same form, i.e., the rate of exponential decline decreases exponentially with time.

Recent success in spawning and rearing marine fish larvae at the Southwest Fisheries Center (SWFC) (Lasker et al. 1970; May 1971; Leong 1971) has made possible a much more fundamental examination of the growth process than has heretofore been possible. Controlled laboratory experiments can now be utilized to investigate both the inherent nature of the growth process as well as the effect of some environmental factors.

Considerable care is required, however, in constructing a model[2] which is meaningful both mathematically and biologically. For example, almost all growth models currently in use can be derived as variations of the differential equation:

$$\frac{dW}{dt} = \eta W^m - \kappa W^n \tag{1}$$

or

$$\frac{dL}{dt} = \eta' L^{m'} - \kappa' L^{n'} \tag{1a}$$

(von Bertalanffy 1938; Beverton and Holt 1957; Richards 1959; Chapman 1961; Taylor 1962) where W is weight, L is length, and η, κ, m, n, m', and n'are arbitrary constants. These are the equations used most often to describe growth as a function of anabolic and catabolic processes of metabolism. The rate of anabolism, η, is considered to be proportional to W^m and the rate of catabolism, κ, proportional to W^n. Equation (1a) requires, in addition, the allometric relationship $W = qL^p$, where again q and p are arbitrary constants. In practice a dilemma arises from the fact that while such models yield a good empirical fit to the data, the estimates of parameters η and κ are often negative, thereby negating the assumptions on which the model is based. For $n = 1$ and $m = 0, 1, 2$, respectively, Equation (1) gives rise to the von Bertalanffy growth in length, Gompertz, and logistic growth functions. Although we have not as yet made any extensive comparisons, the fact that for $m>1$ and $n = 1$, η and κ must be negative, suggests that in many instances the Gompertz and logistic rather than the von Bertalanffy functions may provide more appropriate models of fish growth. In particular, the simple von Bertalanffy growth model has no inflection point and hence curves such as the generalized von Bertalanffy, Gompertz, or logistic must be used when an inflection in the growth trajectory is evident.

Laird et al. (1965) have presented a Gompertz-type mathematical model of growth based on the

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[2]A model is here conceived to be a mathematical representation of change in length or weight with time under measureable environmental conditions.

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observation that the specific growth rate dW/Wdt of animals and their parts tends to decay exponentially with increasing age. They have shown that this relation offers a practical means of analyzing the growth of parts of embryonic and postnatal animals (Laird 1965a), the growth of tumors (Laird 1964, 1965b), whole embryos of a number of avian and mammalian species (Laird 1966a), and early stages of postnatal growth of a variety of mammalian and avian organisms (Laird 1966b). Further, Laird (1966b, 1967) has shown that postnatal growth of a variety of mammalian and avian organisms can be fitted by compounding this model with a linear growth process beginning at birth and extending on beyond the asymptotic limit of the underlying Gompertz growth process. Overall growth is assumed to be genetically determined by programming only the initial specific growth rate and the rate of exponential decay, these governing growth processes then act on a genetically determined original mass to produce the observed course of growth to a final limiting size characteristic of the species and individual.

Mathematically, these assumptions are described by the two equations:

$$\frac{dW(t)}{dt} = \gamma(t)W(t)$$

and[3]

$$\frac{d\gamma(t)}{dt} = -\alpha\gamma(t)$$

which have the solution

$$W(t) = W_0 e^{\frac{A_0}{\alpha}(1-e^{-\alpha t})}, \qquad (2)$$

where W_0 is weight at $t = 0$, A_0 is the specific growth rate at $t = 0$, α is the rate of exponential decay and the specific growth rate at time t, $A_t = A_0 e^{-\alpha t}$.

Laird et al. (1965) indicated that an additional growth component not included in the Gompertz equation may be due to the accumulation of products that are not self-reproducing or to renewal systems that are not in exact physiological equilibrium and suggested the compound growth curve:

$$W = W_G + \beta \int_0^t \frac{W_G}{M}\, dt \qquad (3)$$

where W_G is the mass due to the Gompertz growth process, β is the rate of linear growth, and M is the asymptotic limit of the growth process. She also suggests that this linear process starts in the early embryonic period, if not at conception. For the age interval covered in this paper, however, the linear growth component ($W - W_G$) was not found to be important.

Several characteristics of the curve are worthy of mention:

1. The asymptotic limit M is $W_0 \operatorname{Exp}(A_0/\alpha)$.
2. The point of inflection $(t_I, W_I) =$
$$\left[\frac{1}{\alpha}\ln(A_0/\alpha),\ W_0 \operatorname{Exp}\left(\frac{A_0}{\alpha} - 1\right)\right].$$
3. The zero point on the time scale may be shifted to any point t_Δ without changing the form of the equation with new parameters $W_\Delta = W(\Delta)$, $A_\Delta = A_0 e^{-\alpha\Delta}$ where α remains unaltered.

The fundamental concept of the Laird-Gompertz model is one of change in weight or mass with time, being due primarily to the self-multiplication of cells and genetically determined limitations on the growth parameters. The use of length as the measured variable is thus a matter of convenience due to the fact that weight measurements are much more time consuming, especially in early larval growth, but also in juvenile and adult fishes. As indicated in Equation (1a), if a true allometric relationship existed, the choice would be unimportant. However, all experimental evidence indicates that both length and weight can be described by a Gompertz-type curve. Hence, it can be shown that 1) the growth rate for both changes continually with time and 2) the form of the length-weight relationship will change continually except for two special instances. Laird et al. (1968) has shown that this occurs only when the rates of exponential decay are the same and either the two measured variables begin growth at different times at the same initial rate or at different rates at the same time. In all other cases the allometric plot will be nonlinear. For

$$L = L_0 e^{K_L(1-e^{-\beta t})}$$

and

$$W = W_0 e^{K_W(1-e^{-\alpha t})}$$

[3]In the usual Gompertz representation the rate of exponential growth is assumed to decline logarithmically as W approaches the asymptote $M = W_0 e^{\frac{A_0}{\alpha}}$, i.e., $\frac{dW}{dt} = \alpha W \ln(M/W)$.

the length-weight relationship is

$$\ln W = \ln W_0 + K_W\left[1-\left(\frac{K_L-\ln(L/L_0)}{K_L}\right)^{\alpha/\beta}\right]. \quad (4)$$

Only when $\alpha = \beta$ does the relationship reduce to the linear form

$$\ln W = \ln W_0 + \frac{K_W}{K_L}\ln(L/L_0).$$

As shown in Figure 1, departure from linearity will not always be great, but for extrapolation the effect of overestimation at larger sizes may become serious.

Throughout this paper, growth will, by necessity, be measured in terms of length rather than weight even though the model equation is developed from the opposite point of view. It should be remembered, however, that no allometric relationship is assumed, i.e., no relationships among the two sets of parameters are assumed except as they are jointly a function of age.

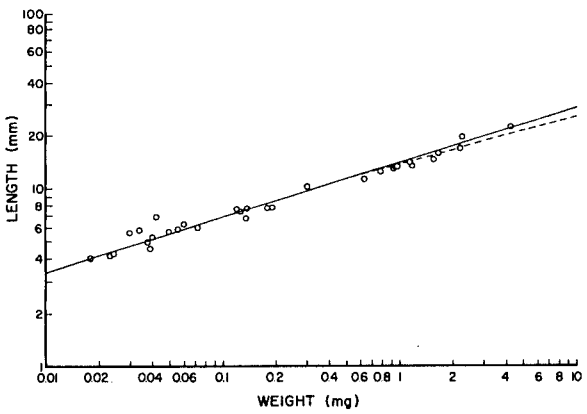

FIGURE 1.–Length-weight relationship in larval anchovies: Solid line fitted from log $W = a + b \log L$; dashed line fitted from Equation (4); estimates are coincident up to 10 mm.

INITIAL ESTIMATES

Equation (2) may be rewritten as follows:

Let $K = A_0/\alpha$

and $M = W_0 e^K$,

then $W(t) = Me^{-Ke^{-\alpha t}}$,

or $\ln[-\ln(W(t)/M)] = \ln K - \alpha t$,

and hence the logarithm of the logarithm of the ratio of size to the asymptotic limit M with the sign changed will be linearly related to time t with parameters $\ln K$ and $-\alpha$. W_0 may be obtained from the relationship $\ln M = \ln W_0 + K$. Note: For decreasing curves, use the reciprocal of the observed values.

VARIABILITY, ESTIMATION, AND TRANSFORMATION BIAS

It is an unfortunate circumstance that the determination of the "best" estimation procedure can rarely be separated from the determination of the "best" mathematical model, i.e., there is no recognized best estimation procedure except in some specialized instances. This is brought about by the fact that almost all parametric estimation procedures assume some information concerning the form and stability of the "error" distribution. This requires, at the very least, the knowledge that the variance is constant and, at the most, the exact form of the error distribution. Since the term "error" in the biological sciences takes a meaning quite different from that in the physical and mathematical sciences in that it represents, in the main, natural variability rather than measurement or experimental error and since natural variability is large (especially so in cold-blooded organisms), few a priori assumptions can be made.

Since most estimation procedures assume a normal distribution of errors at each point along the curve with equal variance (homoscedasticity), the obvious approach, when no more plausible alternative is available, is to fit the situation to this mold.

Some general recommendations are helpful. "Although no clear rule may be safely offered for the taking of logarithms to reduce data to manageable configurations, nevertheless, this transformation (logs) is probably the most common of all. Almost all data that arise from growth phenomenon, where the change in a datum is likely to be proportional to its size and hence errors are similarly afflicted, are improved by transforms to their logarithms" (Acton 1959: 223). Specifically, it can be shown that the logarithmic transformation will induce homoscedasticity in those instances

where the standard deviation is proportional to the population mean, i.e., $\sigma = \beta\mu$ or $\log \sigma = \log \beta + \log \mu$. Hence, a plot of $\log \sigma$ on $\log \mu$ will have a slope of unity and the antilog of the intercept will define the proportionality constant. Plots of $\log \sigma$ on $\log \mu$ were made for several experiments where data were available for extended periods of time. None of the regression coefficients was significantly different from unity. These experiments cover a variety of life stages and environmental situations from controlled laboratory experiments on larval anchovies (Lasker et al. 1970) to large tank feeding of anchovies captured from the wild at 75 mm (Paloma, SWFC, unpubl. data) to samples of adult sardines obtained from bait boats (Lasker 1970). Growth for the 75-mm anchovies was slow and much more uniform than for the other experiments as indicated by the mean square errors in Table 1. The analysis of covariance (Table 1) shows no difference in slope for either length or weight from larval, juvenile, and adult fishes. The average slopes are 0.9981 for larvae and adults and 1.1061 for juveniles. With a slope of unity, the proportionality constant can be estimated by Exp ($\overline{\ln\sigma}$ - $\overline{\ln\mu}$). The results from the several experiments are shown below:

	σ/μ	
	Length	*Weight*
Lasker et al. (1970):		
Experiment 1	0.12	0.39
Experiment 2	0.12	0.33
Paloma[4]	0.06	0.20
Lasker (1970)	0.04	0.13

Not unexpectedly, variation in weight exceeds that of length and both decrease with increasing age.

The question of normality and its relationship to homoscedasticity is more tenuous, but again some help is available. In practical work, it is generally assumed that both x and $\log x$ can be regarded as normally distributed as long as the coefficient of variation $C = \sigma/\mu < 1/3$ or $\sigma_{\log x} < 0.14$ (Hald 1952: 164). This allows transformation for one desideratum without noticeably affecting another.

Paloma (see footnote 4) collected one or two samples per month of laboratory-reared anchovies for a period of nearly 2 yr. Approximately 25 fish were taken for each sample. We examined normality in terms of skewness (G_1) and kurtosis (mean absolute deviation A). Although sample sizes are small, in terms of positive (>mean) and negative (< mean) coefficients, the transformation was effective in normalizing both fish weight and length as shown below:

		L	*log* L	W	*log* W
$G_1(\mu_{G_1} = 0)$	>	19	17	24	16
	≤	14	16	19	17
$A(\mu_A = 0.7979)$	>	18	17	17	17
	≤	15	16	16	16

For these same samples, length and weight were assumed bivariate–log normal and confidence regions were calculated for each sample. On the average, 96% of the observations fell within the 95% confidence ellipse.

In summary, there is strong evidence that the logarithmic transformation will be required to stabilize the variability in all phases of fish growth and that such a transformation will support the assumption of a normal distribution at least in the intermediate size range (75-100 mm) and most likely at other sizes as well.

Seemingly then, the conditions have been met for implementation of either the maximum likelihood or least squares estimation process. However, two problems remain, neither of which has an entirely satisfactory solution. The first, the absence of an explicit solution of the normal equations, arises because the parameters enter the model in a nonlinear manner and, as is usual in

TABLE 1.—The relationship of mean and standard deviation for both length and weight measurements in fishes.

	$\log \sigma = \alpha + \beta \log \mu$		Analysis of covariance deviations from regression		
	α	β	df	s.s.	m.s.
Larvae and adults:					
Length[1] exp. 1	−1.5568	1.6979	6	0.3308	0.0551
exp. 2	−0.8003	0.8281	8	0.7167	0.0896
Weight[1] exp. 1	−0.4192	1.0373	6	0.1572	0.0262
exp. 2	−0.4852	1.0077	8	0.4241	0.0530
Length[2]	−1.6093	1.0848	60	2.2933	0.0382
Weight[2]	−0.4748	0.7906	60	2.5913	0.0432
		Within	148	6.5134	0.0440
		Between	5	0.1425	0.0285
		Common	153	6.6559	
F = 0.0285/0.0440 = 0.65					
Juveniles:					
Length[3]	−1.3975	1.1644	31	0.3658	0.0118
Weight[3]	−0.8000	1.1029	31	0.1511	0.0048
		Within	62	0.5169	0.0083
		Between	1	0.0002	0.0002
		Common	63	0.5171	
F = 0.0002/0.0083 = 0.02					

[1]Lasker et al. (1970), larval anchovies.
[2]Lasker (1970), adult sardines.
[3]Paloma: unpublished data available at SWFC, juvenile anchovies.

[4] Paloma, P. Unpublished data available at SWFC.

situations of this kind, an iterative procedure is required. The one employed for this paper is Marquardt's algorithm (Conway et al. 1970). Procedures such as this are usually justified on the basis that for large samples and independent observations the estimates obtained are "very close" to those which would be obtained by plotting the likelihood function itself (Box and Jenkins 1970: 213). In truth, the small sample bias and variability of such estimates remains unknown. In growth data the second problem is that sequential observations are not likely to arise from entirely independent processes. This fact is usually manifested as a series of runs above and below a fitted curve rather than random variation. One simple explanation is that growth is in reality a series of asymptotic curves and that oscillations around a fitted curve indicate more than one growth cycle. In this case, the basic assumption of the estimation procedure and the likelihood function itself will not be met. No satisfactory solution to this problem has been proposed and none is proffered here. However, since the same larvae were not measured at different ages and since correlated observations usually have little effect on the estimates of mean values, such estimates will likely not be seriously biased. Using these estimates, "goodness of fit" is examined through the magnitude of the residual mean square and the pattern of residuals along the growth curve, rather than using significance tests or confidence intervals.

One further point often considered but left unsaid is the effect of transformations on the estimated means. Such changes of scale can lead to serious biases and errors in interpretation, especially when the coefficient of variation is large. When the exact form of the error distribution is known the bias can usually be determined mathematically. For the log normal, for example, it is necessary to add one-half of the error mean square before calculating the antilog mean. Unfortunately, in practical work, it is generally impossible without very large samples, to determine the distributional form. As stated above, for many situations, x and $\log x$ can both be considered to be normally distributed. In these intermediate cases, however, the bias correction for $\log x$ will be small so, that as a general rule, one can state that whenever a transformation is made, the correction for transformation bias should be used.

RESULTS

Growth Cycles

Previous work on the growth of larval anchovies (Kramer and Zweifel 1970) suggested that the Laird form of the Gompertz equation might provide a useful model of larval growth. Figure 2 reveals several phenomena found to be almost universal in larval growth: 1) there is a moderate increase in length during the interval following hatch that is followed by 2) a period of minimal growth accompanied by nearly uniform variability, and 3) at the onset of feeding, the mean size increases rapidly with variability proportional to the square of the mean size.

Farris (1959) noted the rapid leveling off in growth following hatch for the Pacific sardine and three other species and approximated the growth rate by two discontinuous curves and indicated that "a more detailed study would probably reveal a nonlogarithmic continuous growth function."

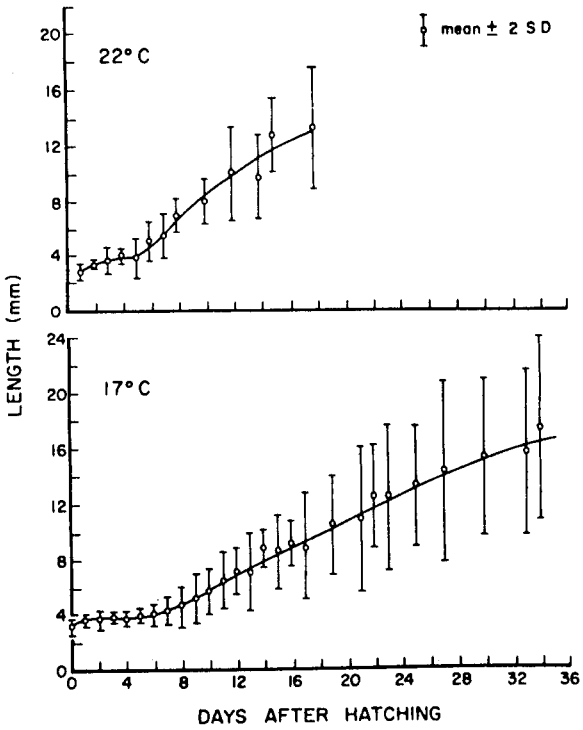

FIGURE 2.—Change in length of yolk-sac and feeding larval anchovies at two temperatures, 17° and 22°C from Kramer and Zweifel (1970); curves are two-cycle Laird-Gompertz.

Although the single stage model used by Kramer and Zweifel (1970) provides an adequate growth curve, two growth cycles are evident: one extending from hatching to the depletion of the yolk sac and the other a more rapid growth at the onset of feeding. Thus, a two-stage model was used to obtain the curves in Figure 2. The fitting procedure is outlined in the Appendix.

It is evident that early larval growth of this species can be represented by a two-stage Laird growth curve. The charcteristics of the growth curves of feeding larvae, i.e., the second cycle, may be related to several environmental factors of which the two most important are probably food ration and temperature. However, an examination of data available on nonfeeding larvae (Figure 3) indicated that even in food-limited situations, change in size may be represented by the two-stage Laird curve.

Growth From Hatch to Depletion of Yolk Sac

The characteristics of the early posthatch growth of larval fishes is more completely described by Lasker (1964). In this series of experiments, growth in length of the Pacific sardine, *Sardinops sagax*, was measured for up to 10 days following hatching at 12 temperatures in the range 11°-21.3°C. The parameters of a single stage Laird curve (Equation 2) were estimated for each of these experiments. Data only up to the day preceding the first decrease in size were used in the calculations.

Even though for such short time series, the parameters are highly correlated due to near-redundancy of one of the parameters, two observations were striking; there was a nearly constant estimated hatching length of about 3.75 mm and a nearly constant estimated maximum length of about 6.1 mm. Accordingly, those experiments with hatching lengths near 3.75 mm and a measured increase in size of at least 3 days were fitted to the reparameterized model:

$$L(t)_T = L_0 e^{K(1 - e^{-\alpha_T t})}$$

where $$K = A_{0_T} / \alpha_T$$

and the T subscript indicates temperature in °C. A plot of α_T on temperature revealed another Laird-Gompertz curve approaching an asymptote at higher temperatures.

A five parameter model:

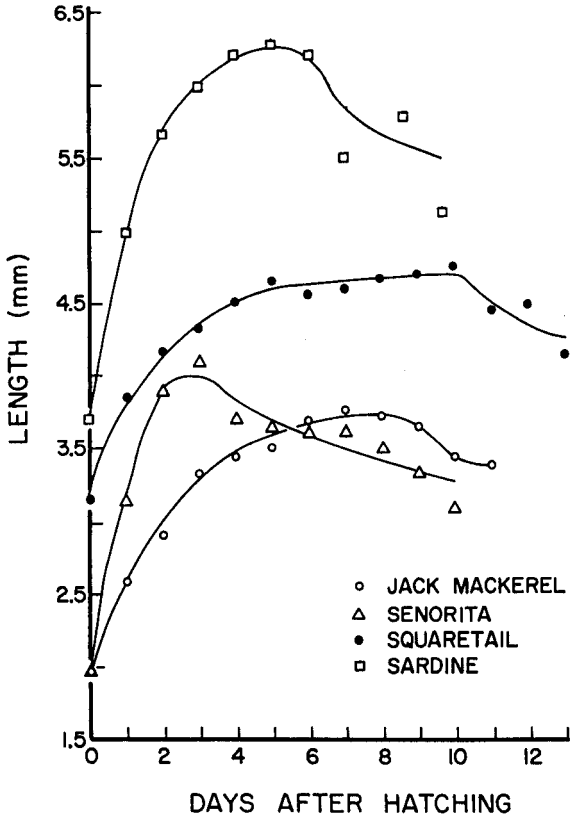

FIGURE 3.—Change in length of yolk-sac and starving larvae; curves are two-cycle Laird-Gompertz.

$$L(t)_T = L_0 e^{K(1 - e^{-\alpha_T t})} \quad (5)$$

where $$\alpha_T = \alpha_0 e^{m(1 - e^{-\beta T})} \quad (5a)$$

was used to fit the growth data from all experiments and provided an excellent fit except at the highest temperature where growth was always overestimated. This suggested a temperature optimum with growth rates decreasing as the absolute difference $|T - T_{opt}|$ increases. Following Stinner et al. (1974), who used a different temperature function, we assumed symmetry around the optimum.

Using Equation (5a), the origin of the temperature scale may easily be shifted to the optimum T_{opt} by the relationships:

$$\alpha_{opt} = \alpha_0 e^{m(1 - e^{-\beta T_{opt}})}$$

and $$m_{opt} = m e^{-\beta T_{opt}}$$

and letting $\Delta = |T - T_{opt}|$

we have the symmetric relationship

$$\alpha_T = \alpha_{opt} e^{m_{opt}(1 - e^{-\beta\Delta})}. \quad (5b)$$

Substituting Equation (5b) for Equation (5a) and treating T_{opt} as an unknown parameter, a six parameter model was fitted to the growth data with the results shown in Table 2.

TABLE 2.–Growth in length of yolk-sac larvae of the Pacific sardine at several temperatures.

Length					
Observed[1]	Estimated[2]	SE	Age (days)	Temperature (°C)	N
3.76	3.72	0.15	0.00	11.00	7
4.30	4.27	0.27	1.00		4
4.78	4.71	0.50	2.00		4
4.97	5.06	0.25	3.00		2
3.77	3.72	0.20	0.00	12.00	9
4.50	4.40	0.24	1.00		11
4.71	4.91	0.29	2.00		8
5.04	5.28	0.44	3.00		6
5.50	5.54	0.36	4.00		3
3.73	3.72	0.16	0.00	13.00	8
4.50	4.55	0.23	1.00		17
4.97	5.12	0.41	2.00		11
5.46	5.49	0.45	3.00		9
4.80	4.72	0.20	1.00	14.00	22
5.39	5.33	0.27	2.00		19
5.65	5.67	0.36	3.00		9
3.93	4.08	0.13	0.30	14.20	11
4.08	4.09	0.13	0.30	14.30	5
5.14	4.89	0.44	1.00	15.00	17
5.59	5.51	0.35	2.00		20
5.96	5.81	0.32	3.00		10
3.71	3.72	0.25	0.00	16.00	21
5.01	5.07	0.25	1.00		19
5.68	5.67	0.26	2.00		23
5.99	5.91	0.15	3.00		11
6.23	6.00	0.11	4.00		9
3.74	3.72	0.22	0.00	16.80	14
5.20	5.21	0.16	1.00		16
5.77	5.78	0.20	2.00		22
6.14	5.97	0.20	3.00		13
3.69	3.97	0.10	0.10	17.80	5
5.27	5.38	0.19	1.00		16
5.86	5.88	0.23	2.00		22
6.06	6.01	0.22	3.00		19
3.71	3.72	0.21	0.00	18.80	4
5.46	5.53	0.18	1.00		18
5.98	5.95	0.21	2.00		25
6.09	6.04	0.15	3.00		18
3.73	3.72	0.10	0.00	19.60	4
5.36	5.58	0.19	1.00		18
5.73	5.97	0.17	2.00		15
5.93	6.04	0.25	3.00		16
5.10	4.83	0.12	0.50	20.50	12
5.46	5.45	0.16	1.00		12
5.43	5.32	0.03	1.00	21.30	3
5.90	6.00	0.13	3.00		5

[1]From Lasker (1964).
[2]Calculated from Equations (5) and (5b) with parameters L_o = 3.716, K = 0.4872, α_{opt} = 1.8523, m = 3.3878, β = 0.0490, and T_{opt} = 19.38.

Growth From Fertilization to Hatch

Coincident to the investigation of early larval growth, a study of the incubation times for the sardine showed that they also could be characterized by a Laird-Gompertz curve. The fitting of Equation (5a) with α_T being incubation time showed no bias at any point along the curve (Figure 4). Unlike the posthatch growth curves, however, no evidence of a temperature optimum was found, i.e., incubation time did not increase at high temperatures. One possible explanation is that larvae which expire cannot be included and hence mortality introduces a negative bias in the estimate of average or median incubation time.

The question arises whether changes in growth rates occur at hatching, i.e., is there a single curve from fertilization to onset of feeding? It can be shown that under the Laird-Gompertz model where growth is approaching a common asymptote from a common origin, i.e. fertilization, the incubation time I_T is simple multiple of the decay rate α_T. From Equation (5) we may solve for the time to hatch I_T at size L_h to obtain:

$$I_T = \ln\left(\frac{K}{K - \ln(L_h / L_0)}\right) / \alpha_T .$$

Since incubation times were not available for all temperatures used in the growth experiment, the sardine curve from Figure 4 was used to convert all data taken at temperatures less than optimum to time from fertilization and fitted to Equation (5).

The results for sardines indicated an increasing size at hatch with increasing temperature which was not evidenced by the observed data and an overestimate of size at temperatures less than 14°C. It was thus concluded that a change in growth rate occurs at hatch, the more noticeably at extreme temperatures and that the prehatch curve must be estimated separately.

The parameters of the prehatch growth curves were obtained by fitting the equation

$$L_h = L_0 e^{K(1 - e^{-\alpha_T I_T})} \quad (6)$$

to only data obtained less than 12 h following hatch. The average estimated hatching size was 3.73 mm and the asymptotic limit was 6.13 mm. The plot for several selected temperatures is shown in Figure 5. Laird (1965a) has shown that the length scale may be standardized and logically simplified by expressing size relative to the asymptotic limit. Biological events such as

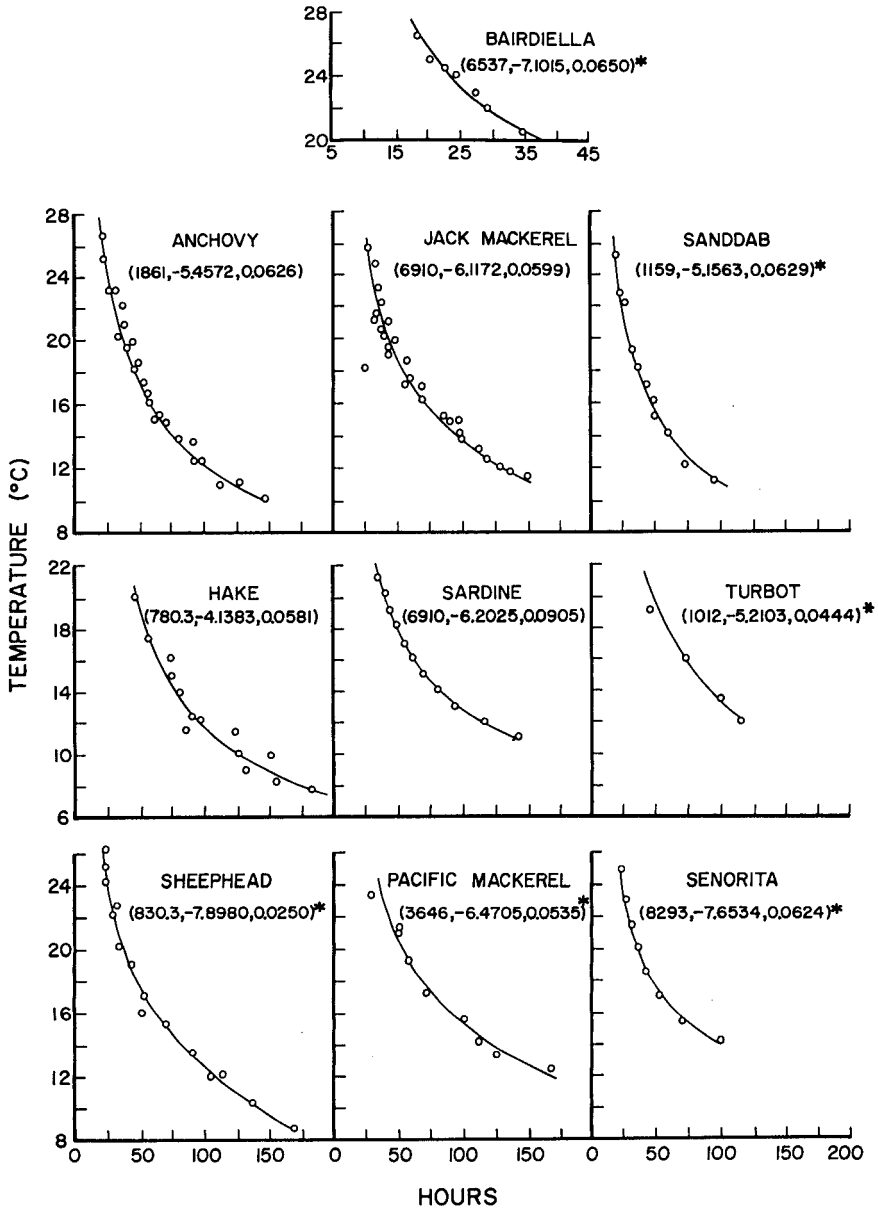

FIGURE 4.—Observed (0) and estimated (curve) (parameters in parentheses are I_0, m, and β for the equation $I_T = I_0 e^{-m(1 - e^{-\beta T})}$ and * indicates time from stage III eggs) incubation times for anchovy, *Engraulis mordax* [combined data from Lasker (1964) and Kramer (unpubl. data) available at SWFC]; hake, *Merluccius productus*; sheephead, *Pimelometopon pulchrum*; bairdiella, *Bairdiella icistia*; jack mackerel, *Trachurus symmetricus*; sardine, *Sardinops sagax*; Pacific mackerel, *Scomber japonicus* (Watanabe 1970); sanddab, *Citharichthys stigmaeus*; turbot, *Pleuronichthys decurrens*; señorita, *Oxyjulis californica*.

developmental egg stages, hatching, and development of the functional jaw occur at fixed points along the curves. Ahlstrom (1943) reported time to several developmental egg stages at different temperatures from field observations. In addition, Lasker (1964) showed incubation times and time to the development of the functional jaw for a wider range of temperatures. Each of these events can

be identified as a fixed percentage point in Figure 5 or the estimated value

$$t_{L_T} = \ln\left(\frac{K}{K - \ln(L_T/L_0)}\right)/\alpha_T \qquad (7)$$

as shown in Table 3.

Lasker (1964) found that the functional jaw did not develop at the lowest two temperatures in agreement with the result that the critical size would not be reached until well after yolk absorption.

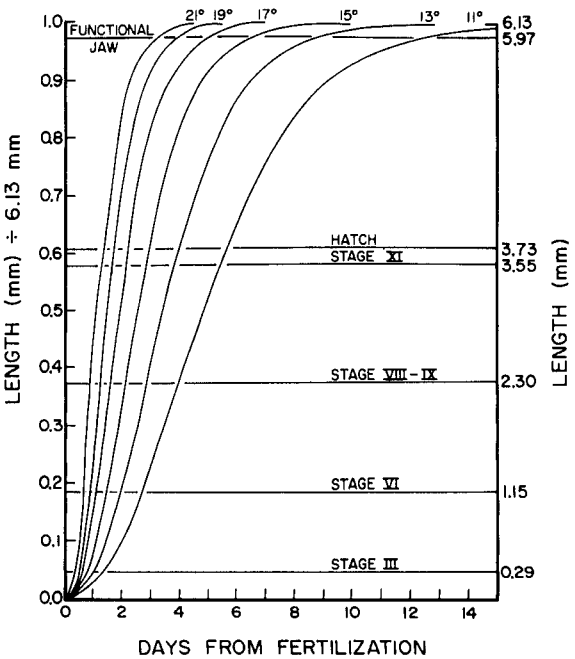

FIGURE 5.–Prehatch growth curves estimated from Equations (5) and (5a) for the Pacific sardine.

Incubation Times

Incubation times were available for several other species. The fitting of Equation (5a) for each species showed no clear bias at any point along the curve (Figure 4). As for the sardine, no evidence of a temperature optimum appeared for any of the species in the temperature ranges used in the experiments. However, it was observed that the decay parameter was relatively constant varying from 0.03 to 0.09 with a mean value of 0.05. When Equation (5a) was fitted with the temperature decay parameter, β, the same for all species, incubation times were closely approximated by Equation (5a) with parameters as shown in Table 4.

The incubation curves used here differ significantly from those calculated from the classical Arrhenius equation: log (incubation time) = a + b/absolute temperature. Using this method, nearly all species showed a characteristic underestimate at the temperature extremes and overestimates in the middle range as shown for the northern anchovy, *Engraulis mordax* (Figure 6).

Prehatch Growth Curves for Other Species

In addition to incubation times for the northern anchovy, Kramer[5] recorded time to several developmental egg stages. Also, Lasker (1964) provided time to hatch from stage IV[6] (Table 5). Further, Hunter (pers. commun.) indicates that

[5]Unpublished data available at SWFC.
[6]Stages of embryological development are those described by Ahlstrom (1943).

TABLE 3.–Observed (Obs.) and estimated (Est.)[1] time in hours to developmental egg stages[2], hatch, and appearance of the functional jaw of the Pacific sardine.

Ahlstrom (1943)									Lasker (1964)				
Temp. (°C)	Stage III		Stage VI		Stages VIII-IX		Stage XI		Temp. (°C)	Incubation time		Functional jaw	
	Obs.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.		Obs.	Est.	Obs.	Est.
13.5	20.4	20.1	41.8	42.9	62.5	63.2	82.6	85.4	11	140	135	—	—
14.0	18.9	18.6	39.1	39.7	58.3	58.5	77.2	79.0	12	115	114	—	—
14.5	17.4	17.3	36.6	36.8	59.4	54.3	72.2	73.3	13	93	96	213	216
15.0	16.2	16.1	34.3	34.2	50.7	50.4	67.5	68.1	14	78.5	82.4	179	185
15.5	14.9	15.0	32.1	31.9	47.2	46.9	63.1	63.4	15	68.1	71.0	156	160
16.0	13.8	14.0	30.0	29.7	44.0	43.7	59.0	59.1	16	60.2	61.6	136	138
16.5	—	—	28.1	27.7	41.1	40.8	55.1	55.2	17	53.7	53.8	119	121
17.0	—	—	26.3	26.0	—	—	51.5	51.6	18	48.4	47.3	105	106
									19	43.2	41.8	94	94
									20	39.3	39.2	85	84
									21	34.0	33.2	77	75

[1]L_0 = 0.0341, K = 5.20, α_0 = 0.0317, m = 6.19, and β = 0.0489.
[2]Egg stages are defined in Ahlstrom (1943).

TABLE 4.—Parameters for estimating incubation time I at centigrade temperature T from the relationship $I_T = I_0 e^{m(1-e^{-\beta T})}$ for several fishes where β is the same for all species.

Species	I_0	m	β
Señorita *Oxyjulis californicus*	[1]6,103	−7.9531	0.0527
Bairdiella *Bairdiella icistia*	[1]3,170	−6.8216	0.0527
Pacific mackerel *Scomber japonicus*	3,580	−6.4896	0.0527
Jack mackerel *Trachurus symmetricus*	1,854	−6.2486	0.0527
Pacific sardine *Sardinops sagax*	2,121	−6.2322	0.0527
Northern anchovy *Engraulis mordax*	1,389	−5.5218	0.0527
Speckled sanddab *Citharichthys stigmaeus*	[1]984.6	−5.4258	0.0527
California sheephead *Pimelometopon pulchrum*	[1]1,316	−5.4194	0.0527
Turbot *Pleuronichthys decurrens*	[1]1,065	−4.7059	0.0527
Pacific hake *Merluccius productus*	699.2	−4.1772	0.0527

[1]Time from stage III eggs.

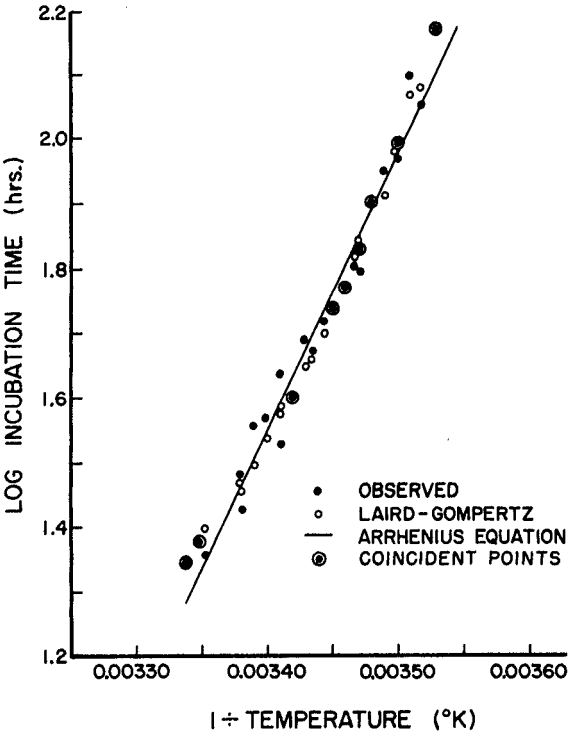

FIGURE 6.—A comparison of two methods of fitting the temperature-incubation time relationship in the northern anchovy.

larval anchovy, on the average, hatch at about 2.9 mm.

Prehatch growth curves were obtained by fitting Equation (6) to hatch sizes of 2.85 at all observed temperatures as shown in Figure 7.

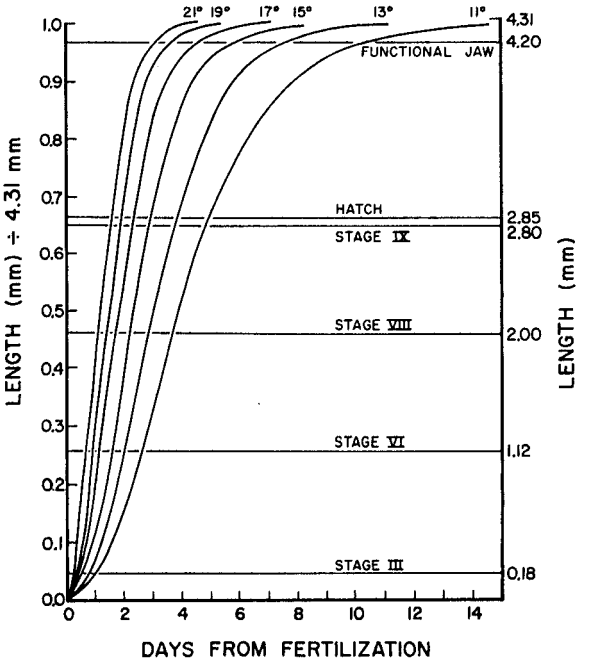

FIGURE 7.—Prehatch growth curves estimated from Equations (5) and (5a) for the northern anchovy.

Comparison with the sardine curves indicate that similar events (i.e., stages of development) occur relatively later for the anchovy. Observed and estimated event times are shown in Table 5.

Except for size at hatch, development data for the prehatch stage was not available for any other species. The curves may, if desired, be easily constructed from the parameters as shown in Table 6.

DISCUSSION

Nothing seems more true than the statement of Thompson (1942:158), "Every growth-problem becomes at last a specific one, running its own course for its own reasons. Our curves of growth are all alike—but no two are ever the same. Growth keeps calling our attention to its own complexity. . . . not least in those composite populations whose own parts aid or hamper one another, in any form or aspect of the struggle for existence."

The truth of this statement has been realized in the disappointing search for growth models derived from physiochemical processes. While it is true that the mathematical form of some equations arrived at from metabolic considerations are the same as those derived in other ways, more

TABLE 5.–Observed (Obs.) and estimated (Est.)[1] time in hours to developmental egg stages[2], hatch, and appearance of the functional jaw of the northern anchovy.

Kramer (unpubl. data)											Lasker (1964)		
Temp. (°C)	Stage III		Stage VI		Stage VIII		Stage XI		Incubation time		Temp. (°C)	Stage IV to hatch	
	Ops.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.		Obs.	Est.
11.1	—	—	—	—	—	—	—	—	113	118.8	11	81	83
12.5	—	—	—	—	—	—	—	—	98	95.1	12	65	71
13.8	20	15.2	42	41.8	58	59.4	78	77.1	80	78.2	13	58	61
15.2	15	12.6	35	34.6	50	49.1	65	63.7	63	64.7	16.8	38	37
16.6	10	10.6	26	29.0	39	41.2	51	53.4	55	54.2	17.8	34	33
18.0	9	9.0	24	24.6	35	35.0	44	45.4	49	46.0	18.8	31	29
19.4	8	7.7	21	21.1	33	30.0	39	39.0	40	39.5	19.6	28	26
20.8	6	6.7	19	18.4	28	26.1	35	33.8	36	34.3	20.5	25	24

[1]Estimates obtained from Equation (7) with parameters as shown in Table 6.
[2]Egg stages are defined by Ahlstrom (1943).

TABLE 6.–Mathematical parameters for prehatch growth curves of six fishes. See text for notation.

Species	L_o	K	α_o	m	β	Average size at hatching
Trachurus symmetricus	0.0005	9.0986	0.0226	5.8338	0.0588	1.95
Sardinops sagax	0.0341	5.1918	0.0317	6.1876	0.0490	3.74
Engraulis mordax	0.0250	5.1493	0.0412	5.5338	0.0546	2.86
Citharichthys stigmaeus	0.1814	5.0600	0.0270	6.2898	0.0319	1.97
Oxyjulis californicus	0.0425	4.7164	0.0572	7.2126	0.0260	1.89
Pleuronichthys decurrens	0.1843	3.2915	0.0480	4.5184	0.0528	3.00

often than not no meaningful biological interpretation of the metabolic parameters can be made. The essence of the growth equation used here is genetically programmed processes of exponential growth and of exponential decay of the specific growth rate. The most probable source of exponential growth is, of course, self-multiplication of cells, the causes of decay are many but not well understood. Laird (1964, 1965a, b, 1966a, b, 1967) has shown that this kind of relationship offers a practical means of analyzing growth of all tumors, as well as embryonic and postnatal growth of a number of avian and mammalian species. We have shown that at least the early stages of the growth of fishes follows a similar pattern.

As with other organisms, several growth cycles exist in fishes. The number of such cycles which will be recognized is determined by the time scale of measurements. We have used three cycles: 1) from fertilization to hatching, 2) from hatch to onset of feeding, and 3) feeding larvae.

In addition, we have observed that the temperature specific growth follows a similar pattern, i.e., exponential increase with an exponential decay of the temperature specific growth rate. In some instances a temperature optimum exists beyond which the specific growth rate begins to decline, although this may be related to food requirements at onset of feeding. Further, we have observed that for the same spawn 1) the asymptotic limit of each growth cycle is independent of temperature and 2) the biological events such as developmental egg stages, hatching, functional jaw development, etc., occur at the same size at all temperatures.

Figure 8 shows posthatch growth curves of the sardine as 1) extrapolated from the prehatch curves and 2) obtained from posthatch data. Although the curves are quite similar at higher temperatures, differences in the lower temperature range are large. Nevertheless, the time to development of the functional jaw is much more accurately determined from the extrapolated curve, indicating an intrinsic process independent

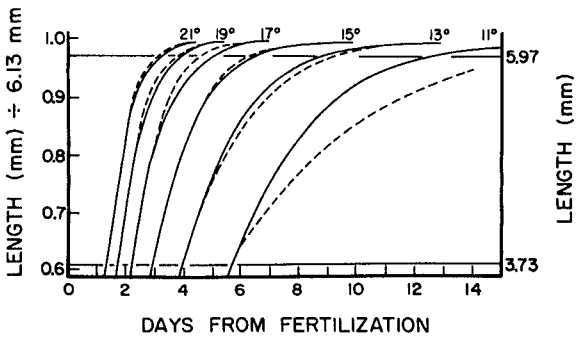

FIGURE 8.–Posthatch growth curves of the northern anchovy. Solid lines are extrapolated from prehatch curve. Broken lines are fitted to actual growth data.

of actual realized size. Comparison of the extrapolated curves for the sardine and anchovy, Figures 5 and 7, shows that for the same temperature and relative to the asymptotic size, hatching occurs later for the anchovy, but jaw development and first feeding occur at about the same time.

In summary, each growth cycle may be represented by an equation of the form

$$L = L_0 e^{K(1 - e^{-\alpha_T t})}$$

with

$$\alpha_T = \alpha_0 e^{m(1 - e^{-\beta T})}$$

or

$$\alpha_T = \alpha_{opt} e^{m_{opt}(1 - e^{-\beta \Delta})}$$

with

$$\Delta = |T - T_{opt}|$$

when a temperature optimum exists. The time required to attain a given size S is

$$t_S = \ln \left[\frac{K}{K - \ln(S/L_0)} \right] / \alpha_T$$

which has the same form as the original equation.

Most of the data available were from studies of two species, *Sardinops sagax* and *Engraulis mordax*, so that generalizations must be made with caution. Nevertheless, incubation times for several other species fit the model well.

Finally, it seems worthwhile to repeat that every growth problem becomes at last a specific one depending on many factors known or unknown, measureable or not. For example, time of fertilization will often not be known and age determinations will be inexact. Further, Hunter and Lenarz[7] have shown that egg size is a measurable and probably important factor in growth and survival of anchovy larvae. For feeding larvae, the quantity and quality of food is critical. Egg size appears to affect growth by a simple scale factor, all events being shifted up or down in proportion to the egg size. Variation in food may result in many "artificial" cycles when nutritional and caloric requirements are not met. Nevertheless, it seems clear that at least the early growth of many fishes may be described in terms of genetically determined but dynamically changing growth rates as defined by the Laird-Gompertz growth function.

[7]Hunter, J., and W. Lenarz. 1974. A discussion on the adaptive values of variation of fish egg sizes. Unpubl. manuscr., 7 p. Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

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LITERATURE CITED

ACTON, F. S.
1959. Analysis of straight-line data. John Wiley and Sons, Inc., N.Y., 267 p.

AHLSTROM, E. H.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4.–Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 23, 26 p.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 19, 533 p.

BOX, G. E. P., AND G. M. JENKINS.
1970. Time series analysis forecasting and control. Holden-Day, San Franc., 553 p.

CHAPMAN, D. G.
1961. Statistical problems in the dynamics of exploited fisheries populations. Proc. Fourth Berkeley Symposium on Mathematical Statistics and Probability 4:153-168.

CONWAY, G. R., N. R. GLASS, AND J. C. WILCOX.
1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

FARRIS, D. A.
1959. A change in the early growth rates of four larval marine fishes. Limnol. Oceanogr. 4:29-36.

HALD, A.
1952. Statistical theory with engineering applications. John Wiley and Sons, Inc., N.Y., 783 p.

KRAMER, D., AND J. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

LAIRD, A. K.
1964. Dynamics of tumor growth. Br. J. Cancer 18:490-502.
1965a. Dynamics of relative growth. Growth 29:249-263.
1965b. Dynamics of tumor growth: Comparison of growth rates and extrapolation of growth curve to one cell. Br. J. Cancer 19:278-291.
1966a. Dynamics of embryonic growth. Growth 30:263-275.
1966b. Postnatal growth of birds and mammals. Growth 30:349-363.
1967. Evolution of the human growth curve. Growth 31:345-355.

LAIRD, A. K., A. D. BARTON, AND S. A. TYLER.
1968. Growth and time: An interpretation of allometry. Growth 32:347-354.

LAIRD, A. K., S. A. TYLER, AND A. D. BARTON.
1965. Dynamics of normal growth. Growth 29:233-248.

LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.
1970. Utilization of zooplankton energy by a Pacific sardine population in the California Current. *In* J. H. Steele (editor), Marine food chain, p. 265-284. Oliver and Boyd, Edinb.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MAY, R. C.
1971. Effects of delayed initial feeding on larvae of the grunion, *Leuresthes tenuis* (Ayres). Fish. Bull., U.S. 69:411-425.

RICHARDS, F. J.
1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

STINNER, R. E., A.P. GUTIERREZ, AND G. D. BUTLER, JR.
1974. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106:519-524.

TAYLOR, C. C.
1962. Growth equations with metabolic parameters. J. Cons. 27:270-286.

THOMPSON, D'ARCY WENTWORTH.
1942. On growth and form. 2nd ed. Cambridge Univ. Press, 464 p.

VONBERTALANFFY, L.
1938. A quantitative theory of organic growth (inquiries on growth laws. II). Human Biol. 10:181-213.

WATANABE, T.
1970. Morphology and ecology of early stages of life in Japanese common mackerel, *Scomber japonicus* Houttuyn, with special reference to fluctuation of population. [In Engl. and Jap.] Bull. Tokai Reg. Fish. Res. Lab. 62, 283 p.

APPENDIX

The estimation procedure of Conway et al. (1970) is a least squares procedure which requires only the definition of the functional relationship and the first derivative with respect to each parameter. Although not stated explicitly, constant variance is assumed and, hence, the logarithmic form will be used throughout. For a single-cycle Laird-Gompertz curve the equations are as follows:

$$\ln F = \ln F_0 + A[1 - \mathrm{Exp}(-\alpha t)]/\alpha$$

$$\frac{\partial \ln F}{F_0} = 1/F_0$$

$$\frac{\partial \ln F}{A} = [1 - \mathrm{Exp}(-\alpha t)]/\alpha$$

$$\frac{\partial \ln F}{\alpha} = A[(\alpha t + 1)\,\mathrm{Exp}(-\alpha t) - 1]/\alpha^2$$

For a two-cycle curve with the second cycle beginning at $t = t^*$ the equations are:

$$\ln F = \ln F_0 + A[1 - \mathrm{Exp}(\alpha\Delta_1)]/\alpha + B[1 - \mathrm{Exp}(-\beta\Delta_2)]/\beta$$

$$\frac{\partial \ln F}{\partial F_0} = 1/F_0$$

$$\frac{\partial \ln F}{\partial A_0} = [1 - \mathrm{Exp}(-\alpha\Delta_1)]/\alpha$$

$$\frac{\partial \ln F}{\partial \alpha} = A[(\alpha\Delta_1 + 1)\,\mathrm{Exp}(-\alpha\Delta_1) - 1]/\alpha^2$$

$$\frac{\partial \ln F}{\partial \beta} = [1 - \mathrm{Exp}(-\beta\Delta_2)]/\beta$$

$$\frac{\partial \ln F}{\partial \beta} = \beta[(\beta\Delta_2 + 1)\,\mathrm{Exp}(-\beta\Delta_2) - 1]/\beta^2$$

$$\frac{\partial \ln F}{\partial t^*} = [A\,\mathrm{Exp}(-\alpha\Delta_1) - B\,\mathrm{Exp}(-\beta\Delta_2)]$$

where $\Delta_1 = \mathrm{MIN}\,(t, t^*)$

$\Delta_2 = \mathrm{MAX}\,(t - t^*, 0)$.

FORTRAN programs are available for fitting single-cycle, temperature-dependent and multicycle, temperature-dependent curves at SWFC.

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NORTH AMERICAN CRAB FISHERIES: REGULATIONS AND THEIR RATIONALES

R. J. MILLER[1]

ABSTRACT

Because of similarities in species' life histories, fishing and processing methods, economics of fishing and processing, and political systems among jurisdictions, managers of North American crab fisheries share many common problems. This review is presented to suggest options to those delegated the responsibility for managing crab fisheries.

The review is organized by fishery and management problems. Six fisheries in 12 government jurisdictions are included. Regulations are grouped into management problems of 1) conservation, 2) allocation of landings among commercial fishermen, 3) stability of landings, 4) conflict over grounds or resource, 5) processing economics, and 6) administration. A final section discusses procedures in eight jurisdictions by which public or government representatives may effect changes in regulations.

If the rationale for each regulation (or at least each new one) and the name of the group requesting it are appended to copies distributed to users, more informed discussion of management problems and more reasoned support for regulations may result.

Problems of managing crab fisheries change as established fisheries develop and new fisheries emerge. Because of similarities in species' life histories, fishing and processing methods, economics of fishing and processing, and political systems within which both government employees and fishing industries must operate, managers of North American crab fisheries share many common problems. This review of North American crab fishery regulations and their rationales is presented to suggest options to those delegated the responsibility for managing crab fisheries. While these regulations may not be optimum according to either biological or economic criteria, they have met the very demanding test of political feasibility.

This review is organized by fishery and management problems. The classification of management problems is necessarily arbitrary. Justifications for a given regulation may make it applicable to more than one problem in the same governmental jurisdiction or applicable to different problems in different jurisdictions. The classification is an attempt to make the presentation more user-oriented, as a search for regulations is commonly prompted by a particular management problem. A final section contains procedures for eight jurisdictions whereby either public or government representatives may recommend changes in regulations.

METHODS

Information on regulations and their rationales was provided by government biologists and resource managers in interviews on the west coast and in correspondence on the east coast. Table 1 lists these contacts and their agencies.

The regulations are not a complete set for any jurisdiction but do represent a large sample of the types of controls in force. Some regulations are omitted because I judged them not to be of general application or my contacts did not know their rationales; the latter is understandable considering the time period over which most sets of regulations evolved. Sampling was least complete for the blue crab fishery. There are 16 States with regulations governing this fishery and several were not included because of the similarity among their regulations.

I have not commented on the success of enforcement of regulations as this would have required firsthand knowledge of each fishery or extensive field interviews with enforcement officers and fishery participants.

The management problems into which regulations have been grouped are listed and defined below.

Conservation: to prevent resource waste,

[1]Department of the Environment, Fisheries, and Marine Service Biological Station, St. John's, Newfoundland, Canada, AIC 1A1.

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TABLE 1.–Sources of information.

Fishery	Contact	Agency
Alaska king crab	Guy C. Powell	Alaska Dep. Fish and Game
	Duane E. Phinney	
Alaska snow crab	Duane E. Phinney	Alaska Dep. Fish and Game
	Guy C. Powell	
West coast Dungeness crab	Duane E. Phinney	Alaska Dep. Fish and Game
	T. H. Butler	Canadian Fisheries & Marine Serv.
	Herb C. Tegelberg	Washington Dep. Fisheries
	C. Dale Snow	Oregon Fish and Wildlife Commission
	Walter Dahlstrom	California Dep. Fish and Game
Eastern Canada snow crab	Author (R. J. Miller)	Canadian Fisheries & Marine Serv.
East coast blue crab	Richard W. Cole	Delaware Dep. Natural Resources & Environmental Control
	William A. Outten	Maryland Dep. Natural Resources
	Dennis L. Spitsbergen	North Carolina Dep. Natural and Economic Resources
	Edwin A. Joyce	Florida Dep. Natural Resources
	Edgar A. Hughes	Alabama Dep. Conservation & Natural Resources
	Terrance R. Leary	Texas Parks and Wildlife Dep.
Florida stone crab	Edwin A. Joyce	Florida Dep. Natural Resources

principally by fishermen, and to maximize physical yield.

Allocation of landings among commercial fishermen: to partition the annual catch of a single species among participants, usually by area or gear restrictions.

Stability of landings: to even out annual landings over good and bad years of resource recruitment.

Conflict over grounds or resource: to resolve competition among classes of users for fishing grounds or fishery resources. Sport-commercial conflicts over the same species are included in this category.

Processing economics: to limit landings to crabs that can be processed at a profit acceptable to processors.

Administration: licensing and registration of boats, men, and gear, and collection of statistics.

RESULTS

Alaska King Crabs (*Paralithodes camtschatica*, *P. platypus*, *P. brevipes*, and *Lithodes aequispina*)

Exploitation of American stocks of king crabs was sporadic prior to 1953, but annual landings increased from 5 to 159 million pounds from 1953 to 1966, sharply decreased, then recovered to 90 million pounds in 1974 and 1975 (Rothschild et al. 1970; D. E. Phinney, pers. commun.). The American fishery is pursued along most of the Alaskan coast from the Bering Sea pack ice to the northern end of Vancouver Island over a depth range of 20 to 100 fathoms (Idyll 1971). The catch is predominately *P. camtschatica*. Although Japanese and Russian fleets formerly took large catches from the Bering Sea, their efforts are now concentrated in the western North Pacific. The following regulations are those of Alaska.

Conservation

Seasons are set to prevent the taking of soft-shelled crabs during and immediately after the molting season. Soft-shelled crabs provide a low meat yield, the quality of meat is poor, and the handling mortality is high.

Harvest levels (i.e., variable catch quotas) and minimum sizes ensure that enough mature males are left on the fishing grounds for breeding. Males are sexually mature for an average of 2 yr before reaching the minimum size. The minimum size also helps maximize yield as determined from growth and mortality rates.

Most females are protected by the minimum size but a separate regulation prevents their being retained to leave them for reproduction.

Gear type is limited to traps, ring nets (a type of baited trap), and diving to prevent use of destructive trawls and tangle nets. The latter two types of gear result in unacceptable levels of mortality of noncommercial crabs returned to the water and of commercial crabs before they reach the processing plant.

One nursery area is always closed to fishing to prevent repeated handling of undersized and female crabs.

To help enforce seasons and harvest levels, tunnel eyes, i.e., entrances of traps, must be at least 5 inches high. This is so that king and snow

crab traps can be distinguished and to prevent king crab fishing in seasons for snow crab fishing only.

A second season in a year in the Kodiak area has a larger minimum crab size than the primary season. This encourages boats to fish areas where catch per trap is lower than in more productive areas but where large, old crabs have accumulated because the areas have been underfished.

A subsistence or sport limit of six crabs per day limits waste that might result from higher catches.

Allocation of Landings Among Commercial Fishermen

There are seven exclusive and two nonexclusive registration areas. A boat may register before the season opens to fish in only one exclusive area but in either or both nonexclusive areas in addition. To enforce this regulation and to prevent fishing before the season opens, a boat must have its hold inspected prior to fishing to verify that no king crabs are on board. If a boat wishes to land its catch outside its registration area, it must report by radio to a designated authority the size of its catch, and it may be required to submit to a hold inspection before leaving its registration area. The boat may at the time of landing have no more or less king crabs on board than were present at the time of reporting or inspection. To revalidate its registration, a boat must be reinspected in its registration area prior to resuming fishing. As the exclusive areas are more accessible to harbors and population centers, they are easier to fish than nonexclusive areas. By limiting boats to one exclusive area the larger, more mobile boats must take part of their catch from more remote areas less accessible to small boats. The small-boat operations are economically viable because of their versatility to participate in other fisheries, e.g., salmon, halibut, and shrimp. A boat operator is limited to operating only one boat in one exclusive area although he may operate the same or additional boats in nonexclusive areas. This excludes one-operator fleets from exclusive areas.

Trap limits per boat in some areas favor small boats because large boats cannot operate as economically if their fishing power is restricted.

Local boats are favored as an ancillary effect of the second season mentioned above. The catch per trap is lower and the weather less favorable than in the primary season, and nonlocal boats are often unwilling to fish for the lower returns.

Stability of Landings

Harvest levels are set to ensure that at least two year-classes are well represented in any year's landings. This helps dampen the effect on landings of uneven annual recruitment to commercial size.

Conflict Over Grounds or Resource

Trap sanctuaries off limits to towed gear have been negotiated with foreign groundfish trawlers. Foreign trawlers have also agreed to area closures and to use rollers on trawls to reduce the catch of king crabs. Domestic shrimp trawlers and scallop draggers are excluded from some prime king crab grounds.

Processing Economics

Crabs are hard shelled much longer than the time required for the fishery to take the annual harvest levels. There is, however, a slight improvement in meat yield as the hard-shelled period progresses with the best yield occurring in most areas at times when the weather is unfavorable for fishing. The season opening within the hard-shelled period is a compromise between the respective interests of fishermen and processors.

Administration

Boats are licensed and registered each year and boats and crab-trap buoys must clearly display registration numbers. Plants are obligated to report area of catch, number of trap lifts, and landings by boat. These regulations are necessary to enforce fishing-area and harvest-level restrictions as well as to provide economic and biological data on the fishery.

Alaska Snow Crabs (*Chionoecetes bairdi*, *C. opilio*)

Although *Chionoecetes bairdi*, *C. opilio*, and *C. tanneri* are all referred to as snow crabs, the current domestic fishery consists of about 98% *C. bairdi* and 2% *C. opilio*. Alaskan landings have increased rapidly from 3 million pounds in 1968 to 61 million pounds in 1973. This fishery operates from the Bering Sea to southeastern Alaska over a depth range of 20 to 140 fathoms (Brown[2]). As in

[2]Brown, R. B. The development of the Alaskan fishery for tanner crab, *Chionoecetes* species, with particular reference to the Kodiak area. Unpubl. manuscr., 15 p. Alaska Dep. Fish Game, Kodiak.

the king crab fisheries, Japan and the USSR formerly took arge quantities from the Bering Sea, but the USSR has not fished since 1971 and the Japanese catch is limited by bilateral treaty to about 22 million pounds per year (D. E. Phinney, pers. commun.). Alaska is the only North American jurisdiction with regulations for this fishery.

Conservation

The following regulations serve the same purpose as in the king crab fishery. Seasons prevent fishing when crabs are soft shelled; fishing gear is limited to traps, ring nets, and diving; harvest levels help ensure enough males are left on the grounds for breeding; females may not be taken; and subsistence fishing is limited to 30 crabs per day. Trap tunnel eyes must be less than 5 inches high when the king crab season is closed to distinguish between snow and king crab traps and to reduce the incidental catch of king crabs.

Cone-shaped traps with a single top entrance may be used for snow crabs in addition to the rectangular king crab trap modified with a smaller tunnel entrance.

Location of Landings Among Commercial Fishermen

As in the king crab fishery, there are exclusive (two) and nonexclusive (three) fishing areas. A boat may register for either one exclusive area or any number of nonexclusive areas. A boat must have its hold inspected to validate its registration and must report prior to landing its catch in an area other than where it is fishing. There are also trap limits for some areas. The rationale for these is the same as in the king crab fishery.

Stability of Landings

Annual harvest levels by area dampen the effect on landings of variable recruitment to commercial size.

Conflict Over Grounds or Resource

As with the king crab fishery, foreign trawlers have agreed to area closures and to use rollers on trawls to restrict the incidental catch of snow crabs. The trap sanctuaries for king crabs also protect the snow crab fishery in many cases.

Processing Economics

The season within the hard-shelled period is set for the convenience of fishermen and processors.

Although there is no minimum size restriction, most immature males are returned to the water on the fishing grounds because they are too small to be processed economically.

Administration

The regulations are similar to those for the king crab fishery.

West Coast Dungeness Crab (*Cancer magister*)

This is an old fishery with commercial exploitation since at least 1917 (Cleaver 1949). Landings are quite variable ranging from 14 to 60 million pounds in the 1970's alone.[3] The fishery operates from southwest Alaska to central California over a depth range of 1 to 20 fathoms.[4] Only United States and Canada fish this species.

Conservation

Closed seasons for the commercial fishery protect soft-shelled crabs in at least some areas of all jurisdictions. Seasons also apply to the sport fishery in California and ocean beaches in Oregon. In addition to a season, Washington specifically prohibits the landings of soft-shelled crabs: "A soft-shelled crab is defined as a crab whose shell, including covering of the legs, is not fully hardened and said shell is flexible and depresses to digital pressure." This regulation has been upheld in Washington courts.

Females may be retained by commercial fishermen only in British Columbia and by sportsmen only in California and British Columbia provided they exceed the minimum legal size. They are protected for breeding purposes (Alaska, Washington, Oregon, California) and because of processing considerations (Washington, Oregon).

Traps left unattended for over 2 wk must have bait removed and doors secured open as protection against ghost fishing (Alaska).

[3]Anon. 1974. Crab review. Fisheries and Fish Prod. Div., Fisheries and Food Prod. Br., Dep. Industry, Trade, and Commerce, Ottawa, 83 p.

[4]Anon. 1972. Pacific edible crab. Fishery Fact Sheet, 2 p. Dep. Environ., Ottawa.

Types of gear are regulated by stating either what may or what may not be used. The effect is to limit the commercial fishery to traps and ring nets, and the sport fishery to traps, ring nets, dip nets, handlines, and diving. Sharp instruments, tangle nets, and usually trawls are excluded to avoid unacceptable levels of crab mortality. To allow escapement of subcommercial-sized crabs, one or two rings of at least 4-inch diameter must be set in the trap mesh in all jurisdictions. This is usually required to be in the upper half of the trap to reduce the chance of openings being covered by drifting sand.

The minimum size is regulated in all jurisdictions. It allows males to mate at least once before reaching legal size although opinions among jurisdictions differ as to whether their respective minimum sizes are biologically optimum. To help enforce size regulations, crabs must be landed whole.

Allocation of Landings Among Commercial Fishermen

Alaska has trap limits which vary considerably among areas. The low limits discourage participation of large boats and reserve the resource for small and local boats. British Columbia limits commercial gear in one area to ring nets or dip nets and traps are excluded in five bays in Oregon to eliminate large commercial operators.

Alaska has both exclusive and nonexclusive fishing areas as in the king and snow crab fisheries, for the same reasons and with the same supporting regulations. As in the snow crab fishery, a boat may not be registered in both exclusive and nonexclusive areas whereas in the king crab fishery a boat may register in one exclusive plus nonexclusive areas.

Conflict Over Grounds or Resource

All jurisdictions have a small catch quota for sport fishermen, ranging from 20 crabs per day in Alaska to 6 per day in British Columbia and Washington. Sport fishermen are limited to three traps or three ring nets in Oregon and two traps or two ring nets in Washington. These regulations serve to differentiate between sport and commercial fishermen and, in some areas, to divide the available catch among many sport fishermen.

There are a number of concessions to sport fishermen in British Columbia, Washington, Oregon, and California for this very accessible species. The fishery is open to only sport fishermen in a marine park in British Columbia, in Hood Canal in western Puget Sound in Washington, and in bays, harbors, and near jetties in California. A 20-trap commercial limit imposed in Dungeness Bay, Wash., controls competition with sport fishermen. A slightly smaller minimum crab size is applied to sport than to commercial catches in Washington and Oregon to increase the sport share of the catch. This size difference is significant because in areas available to the commercial fishery over 80% of the legal-sized crabs are generally caught in the first few months of the season.

Salmon troller operators and crab fishermen in Oregon have an informal agreement to divide the grounds at the 15-fathom contour to resolve incompatible use of the fishing grounds. California trawlers are permitted to land up to 500 pounds of legal-sized male crabs per trip during the crab season. This discourages trawling directed at Dungeness crabs but allows them to retain incidental catches.

Processing Economics

In addition to protection of their reproductive role, females may not be retained in Washington and Oregon because the meat yield and quality are lower than for males.

Some areas near the City of Vancouver, B.C., are closed to both commercial and sport crab fishing because of polluted water.

Administration

A commercial fishing license specifically for crabs is required in Alaska and Washington, while only a general commercial license is required in British Columbia, Oregon, and California. Although this provides a small amount of revenue, it is primarily for records on participants.

Eastern Canada Snow Crab (*Chionoecetes opilio*)

This fishery has two centers of operation, the western Gulf of St. Lawrence and eastern Newfoundland. The first significant commercial landings were taken in the Gulf of St. Lawrence in 1967 and in Newfoundland in 1969. Landings from both areas totaled 23 million pounds in 1974 with

further expansion expected only in Newfoundland. The fishery operates in depths of 40 to 70 fathoms in the Gulf of St. Lawrence and 90 to 200 fathoms in Newfoundland. Only Canada is engaged in this fishery and there is no sport fishery.

Regulations for this fishery have only recently been implemented, so, although they have cleared public service and political hurdles, they have yet to be tested by performance.

Conservation

Any specified area may be closed to the fishery at any time for conservation reasons. Justifications could be an abundance of soft-shelled or sublegal-sized crabs in the catches. Periodicity of soft-shelled abundance is not predictable enough to set annual seasons.

Fishing is permitted only by traps to exclude the wasteful bottom trawl and tangle net gears. A minimum mesh-size regulation allows escapement and eliminates handling of a large portion of the sublegal-sized crabs. A minimum crab size is set (Newfoundland only) in hope of maximizing the yield per recruit, to ensure the presence of enough mature males for mating success, and to satisfy processing requirements. The minimum size excludes all females.

A regulation requires that soft-shelled crabs be returned to the water on the fishing ground. They are unacceptable for processing because of low meat yield, poor quality meat, and poor survival while being held for processing. If landed, they are discarded by processors.

Allocation of Landings Among Commercial Fishermen

Trap limits in the Gulf of St. Lawrence limit the fishing effort per boat.

Any new boats entering the fishery after 1974 must be recommended by a crab management committee composed of representatives from fishermen, processors, Provincial governments, and the Federal government, and approved by a Regional Director of Fisheries. New entrants are considered for underexploited areas only.

Stability of Landings

A single quota for all of Newfoundland is intended to dampen the effects on landings of variable recruitment to commercial size.

Processing Economics

With present technology and product prices, crabs smaller than the legal minimum cannot be processed economically.

Administration

Crab boats must be licensed specifically for crab fishing to control entry and to provide economic data on the fishery. In Newfoundland, boats must report their fishing area to provide a history of yields by area.

East Coast Blue Crab (*Callinectes sapidus*)

This species has supported a commercial fishery since at least 1890 (Newcombe 1945). Landings have been about 140 million pounds annually in the 1970's (footnote 3). The fishery operates along most of the U.S. Atlantic coast and all of the Gulf of Mexico coast, but the bulk of the landings and the most extensive fishery regulations are from the mid-Atlantic States. The depth range of the fishery is between less than 1 to 10 fathoms and the fishery is prosecuted entirely from the United States.

Conservation

Generally, egg-bearing females must be returned to the water to allow them to release their progeny. This is requested by the fishing industry (Delaware, Maryland, Florida, Texas) although there may be no biological evidence establishing a relationship between the size of the parent stock and strength of the resulting year-classes (Delaware, Florida, Texas).

To allow escapement of small crabs, Maryland requires that the wire mesh covering traps be a minimum of 1 by 1 inch, Florida requires that an escape hole near the bottom of traps be a minimum of 2 by 2 inches, and Texas requires that crab trawls have a minimum mesh size of 5 inches (stretch measure).

Seines must be hauled up in the water rather than on shore in Maryland to help ensure that unwanted animals such as small crabs and fish are returned to the water rather than left on the beach.

Hard-shelled crabs must be a minimum of 5-inch

width in Delaware, Maryland, and one county in Florida. This is slightly over the average size at maturity and allows crabs to spawn at least once before being subject to depletion by the fishery. One bushel of undersized crabs is permitted in a daily catch in Delaware.

A 150-trap limit is enforced in small bays just inland from Maryland's ocean beaches as the peeler-crab (crab about to molt) fishery has recently become intensive on the small populations in these bays. Baiting traps with live males ensures a high proportion of females in the catch which molt, then copulate. Effort control through trap limits is an attempt to prevent rates of female removal that would affect the ability of the population to replace itself.

Allocation of Landings Among Commercial Fishermen

A 150-trap limit for some areas in Delaware is near the maximum most boats can fish per day and controls the fishing power of the few fishermen who would choose to fish more traps.

North Carolina prevents the use of dredges operated by power winches in one area. This controls the fishing power of boats using dredges for any species but was aimed primarily at the oyster fishery.

Conflict Over Grounds or Resource

Sport fishermen have gear and catch limits to control their competition with commercial fishermen and to distribute the available landings among many sport fishermen. Limits are two traps, four handlines, and one-bushel catch per day in Delaware; one-bushel catch per day in Maryland; one trap which may not be fished from a boat in North Carolina; and five traps in Florida.

Most Maryland streams emptying into Chesapeake Bay are off limits to traps to reserve the areas for crab fishermen using trot lines. In North Carolina, crab traps are excluded from some areas from 1 April through 30 November to reserve the areas for haul seines and shrimp trawls. Other areas in North Carolina are designated for fixed gears only, however, to protect them from towed gears.

Traps may not be set in marked navigation channels (Delaware, Maryland, North Carolina), may not be set in water shallower than 4 feet at mean low tide (Maryland), or may not be larger than 24 inches on a side (Maryland) because of the hazard to navigation. Traps may not be set near bathing beaches in Maryland because the presence of fishing boats, discarded bait, and discarded dead crabs interfere with the recreational use of the beaches.

Crab dredges (also rakes and scrapes) may not be used on bottom leased for oyster propagation except by the lease holder (Delaware) or on public oyster grounds where oysters or shells have been planted by the State (North Carolina). Dredging is not permitted from 16 March to 15 December (Delaware) or 1 April to 30 November (North Carolina) since crabs are not buried in the bottom during this time, and dredging is destructive to both commercial molluscs and noncommercial benthos. Maximum dredge weight is 100 pounds in North Carolina and 40 pounds in Maryland to limit destruction of bottom organisms by the gear.

North Carolina and Texas restrict crab trawling because of possible damage to shrimp stocks. Some shrimp nursery areas are closed to crab trawling since the resulting turbidity may be lethal to shrimp (North Carolina). Mesh size on trawls may not be smaller than 3-inch stretch measure when used for hard-shelled crabs nor smaller than 2-inch stretch measure when used for soft-shelled crabs to allow shrimp to escape (North Carolina). The 5-inch minimum mentioned earlier serves the same purpose in Texas. Trawls used for soft-shelled and peeler crabs are limited to 25 feet in width (float line length) to control damage to sea grass beds where most of this fishing occurs (North Carolina).

Crab trawling is prohibited from 2000 h on Saturday to 2000 h on Sunday to eliminate the time conflict with fishers of men (North Carolina).

Processing Economics

Processors have requested that egg-bearing females not be landed because of their low meat yield (Texas). North Carolina prohibits trawling in ocean inlets to interior bays from 1 April to 31 August because females incubating eggs are concentrated in these areas: females are uneconomical to process.

Minimum shell width for hard-shelled crabs is 4 inches (Alabama) or 5 inches (Maryland, North Carolina–10% undersized permitted). This protects the processor from pressure to accept small crabs which are unprofitable to process.

Soft-shelled crabs and peelers have legal minima of 3½ inches and 3 inches, respectively, in Delaware and Maryland compared to a 5-inch minimum for hard-shelled crabs. Because of the greater molting frequency of smaller crabs, the smaller size limit permits a greater volume of this relatively high-priced product. Soft-shelled crabs are sold and eaten whole so the economics of meat extraction is not a consideration. Crabs with a shell just starting to harden (paper shell) may not be landed as they are not suitable for the soft-shell market and the meat yield is too low for processing as hard-shelled crabs (Maryland).

In Maryland, dredges are permitted only from 15 April to 31 October (compare with summer closure in Delaware and North Carolina in the previous section). The crabs are not buried in the sediment in this period and have had time to clean themselves of attached mud making them a more desirable product.

Administration

A commercial license is required specifically for blue crab in Delaware and Maryland, while a general commercial license will suffice in North Carolina and Texas. No license is required in Alabama and only a permit number is required in Florida. Traps are generally required to be buoyed and must have the boat permit or license number displayed on buoys in Florida, Maryland, and Delaware. This is to reduce the navigation hazard of traps and to help enforce seasons and registration requirements.

Florida Stone Crab (*Menippe mercenaria*)

This species has supported a commercial fishery in Florida for approximately 25 yr. Landings have recently increased from 1 million pounds in 1965 to 2.1 million pounds in 1973. The fishery operates around most of Florida's coast over less than 1 to 8 fathoms depth, but 80% of the landings are taken from the Keys and the southwest coast. The fishery does not exist in other areas of the United States but does extend into the Caribbean.

Conservation

This fishery has a unique regulation requiring that only the claw may be retained. The remainder of the crab must be returned live to the water. The crab market accepts only the claw. A small percentage of declawed animals survive to spawn and a small percentage regenerate the claw to commercial size. The minimum size for propodus length of the claw is 2¾ inches. Data on growth and natural mortality indicate that this is near the optimum size for maximum yield per recruit.

Crab fishing is closed for 5 mo over the spawning season. Fishermen reason that this closure yields better recruitment to the fishery although this is not supported by present biological data. The effort restriction does produce higher catches per unit effort during the open season, however.

It is unlawful to fish with spears, hooks, or other gear that might kill the crabs.

Administration

Each trap must have a buoy, and traps and boats must be clearly marked with a permit number and color code unique to each boat. These regulations help in enforcement of seasons and boat registration requirements. Traps marked with buoys also reduce their hazards to navigation. Boats must be registered specifically for the stone crab fishery.

PROCEDURES FOR CHANGING LAWS AND REGULATIONS

To this point no distinction has been made between laws and regulations. Laws are passed by an elected legislative body whereas regulations are approved by a department's secretary or minister, or an appointed commission. Recommendations for changes in laws or regulations usually follow the same route whether they originate within the public service or the fishing industry.

Alaska

Regulations are made by a seven-member Board of Fisheries composed of fishermen and businessmen and appointed by the State Governor. Proposed changes for regulations are submitted to the board by the Department of Fish and Game staff and the public at least 60 days before their annual shellfish meeting. Thirty days before the meeting a printed list of all proposals is sent to fishermen, processors, government representatives, and any other interested parties. During its meeting, which is public, the board solicits comments from the public and the staff of the department on each recommendation. Following the

discussion, each recommendation is voted upon by the board in the meeting before proceeding to the next item.

District management officers have authority to adjust seasons and harvest levels and to open and close fishing areas by field announcement.

British Columbia and Eastern Canada

Regulations in these areas, excluding Quebec, are under Federal control. Proposals from any party are submitted to the regional resource management group who drafts regulations. These are forwarded to a resource management group in Ottawa who checks for consistency with existing regulations and considers the justification offered in light of their experience. The Justice Department then checks for contraventions of existing laws, especially the human rights code. It then passes through senior management levels of the Fisheries and Marine Service to the Minister of State for Fisheries. If approval is granted, the Minister finally seeks approval from the Federal Cabinet. Regional Directors of Fisheries have authority to adjust seasons and quotas.

Washington

The Director of the Department of Fisheries has authority to establish many types of fishery regulations, e.g., seasons, gear restrictions, and size limits, after holding public hearings. The State legislature has exclusive authority in setting license fees and can legislate in areas normally the responsibility of the Director.

Oregon

Staff biologists submit proposals to the Marine Fisheries Regional Supervisor who in turn forwards them to the State Fisheries Director. If approved at both these levels, proposals are submitted to a seven-member commission at a public hearing. The commission hears staff and public testimony and accepts, rejects, or modifies the proposal. If accepted, it is registered with the Secretary of State and goes in force. Any citizen of the State may request a public hearing of the commission to consider his views on fisheries regulations. The commissioners are appointed by the Governor and may be any private citizens of the State except an officer in a sportsmen's organization or an affiliate of the commercial fishing industry.

California

A staff biologist submits his proposed law change to his regional manager of the Department of Fish and Game, who in turn submits it to the Department Director. The Director enlists the cooperation of a State senator or representative to sponsor a bill in the legislature where it must be passed by both houses and signed by the Governor. An industry representative may begin at any level in this sequence.

Delaware

The Division of Fish and Game drafts new laws at their own initiative or in response to requests from the public. These drafts of new laws are submitted to a Natural Resources Committee composed of State legislators who in turn brings the recommendations to the legislature for a vote. The laws that have been passed by the legislature are finally signed by the State Governor.

The Division of Fish and Game may also initiate resolutions. These are not enforceable but are desirable policy in the view of the division. Hearings are held by the division to solicit public opinion. Final approval is required from only the Secretary of State.

Maryland

Recommendations for changes in regulations are submitted to a Fisheries Administration staffed by government employees. After the legality of the submission is ensured, public hearings are held by the Fisheries Administration in areas which would be affected by the change. A legislative board of review composed of State legislators must finally approve changes.

Fishery laws are dealt with in the State legislature and are submitted for their consideration by either government or private sources. A legislative committee holds public hearings on proposed changes before they are brought to a vote in the legislature.

North Carolina

A nine-member Fisheries Advisory Board appointed by the Governor is staffed by three representatives each from recreational fisheries, commercial fisheries, and the scientific community. This is a source group which advises a seven-member Fisheries Commission. The latter group,

also appointed by the Governor, includes representatives from the tourist industry, seafood processors, sport fishermen, commercial fishermen, and scientists. Recommendations for changes in regulations may be brought to either body although only the Fisheries Commission has authority to make changes. They are obligated to hold public hearings on changes and advertise the hearings in news media a minimum of 10 days before a hearing. Following the hearings, and solicitation of advice from the Fisheries Advisory Board and the Division of Commercial and Sports Fisheries, changes are passed by majority vote.

Texas

The Parks and Wildlife Department accepts recommendations from its staff or the public. Once each year a public hearing is held by the Parks and Wildlife Department in each county affected by suggested changes. A six-man Parks and Wildlife Commission appointed by the Governor then considers staff recommendations and the public reaction at its monthly public meeting when setting regulations. Laws are enacted in the State legislature in response to requests from the government or the public. Fisheries in 15 of 19 coastal counties are controlled by regulations while those in the remaining 4 are controlled by laws.

SUMMARY AND CONCLUSIONS

Management problems and applicable regulations are summarized below.

1. Conservation:
   a. soft-shelled crabs: season protecting soft shells, taking soft shells prohibited;
   b. protection of breeding crabs: no females, no egg-bearing females, fishing closed during spawning season, trap limits to control catches of mature females, minimum size which excludes some mature males, catch quotas to leave a significant portion of commercial-sized males, all stone crabs returned live to water;
   c. ghost fishing: traps must be attended at least every 2 wk;
   d. handling subcommercial sized crabs: escape holes in trap mesh, minimum mesh size in traps and trawls, fishing excluded in nursery areas, seines must be hauled up in water rather than on shore;
   e. wasteful gear: sharp instruments, tangle nets, and trawls excluded; and
   f. optimize yield per recruit: minimumn crab size, second season with larger minimum size.
2. Allocation of landings among commercial fishermen: trap limits, trap type (ring nets only), registration area, limited entry of boats.
3. Stability of landings: catch quotas (harvest levels) by area.
4. Conflict over grounds or resource: areas reserved for sport fishery; smaller size limit for sport; limits on catch, gear type, and gear quantity for sport; areas for traps only, set gear only (traps or lines), or mobile gear only (trawls or seines); traps may not be set in navigation channels, in less than 4 feet depth, or near beaches; limit on crab catch by groundfish trawlers; weight limit on dredges; seasons and area limits for crab dredging; shrimp nursery areas closed to crab trawling; shrimp trawling; groundfish trawling, and scallop dragging excluded from good crab fishing areas.
5. Processing economics: minimum crab size, females or egg-bearing females excluded, areas of female concentration closed, soft-shelled crabs excluded, areas of polluted water closed, dredging prohibited when crabs buried in sediment.
6. Administration: registration of boats, men, and gear; marking boats and gear with registration number; reporting fishing area, number of trap lifts, and quantity of landings.

Many resource managers agree that some regulations are unsupportable on either conservation or economic grounds. This is understandable since there is an inevitable time lag between the collection of information and the updating of regulations, and since groups or individuals are sometimes able to influence regulations by weight of authority without supporting rationale.

I recommend that copies of regulations (or at least each new regulation) provided to enforcement officers, fishermen, processors, etc., have the rationale for each regulation as well as the group requesting it appended. This procedure has the following possible benefits:

1. Fishery participants would be informed as to the benefits of the regulations, i.e., why they are expected to observe them.
2. They could be at least partially educated to the tools and rationale of fisheries management.
3. Providing participants with a background for informed discussion should help to involve them in managing their fishery.
4. Making the concerns of different vested interests public would hopefully provoke the fishing industry, regulatory authorities, and legislators to provide reasoned support for regulations.

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Considering the amount of detail in the sets of regulations included and the unusual (for someone not trained in the field) legal terminology employed, some errors are inevitable. I accept responsibility for these.

LITERATURE CITED

CLEAVER, F. C.
1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Wash. Dep. Fish., Biol. Rep. 49A:47-82.

IDYLL, C. P.
1971. The crab that shakes hands. Natl. Geogr. 139:254-271.

NEWCOMBE, L. L.
1945. The biology and conservation of the blue crab, *Callinectes sapidus* Rathbun. Va. Inst. Mar. Sci., Educ. Ser. 4, 39 p.

ROTHSCHILD, B. J., G. POWELL, J. JOSEPH, N. J. ABRAMSON, J. A. BUSS, AND P. ELDRIDGE.
1970. A survey of the population dynamics of king crab in Alaska with particular reference to the Kodiak area. Alaska Dep. Fish Game, Inf. Leafl. 147, 149 p.

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VERTICAL DISTRIBUTION AND OTHER ASPECTS OF THE ECOLOGY OF CERTAIN MESOPELAGIC FISHES TAKEN NEAR HAWAII

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ABSTRACT

Data on abundance, size, depth and time of capture, and sexual development are presented for 37 species of 15 families of rare to moderately abundant mesopelagic fishes taken in the central Pacific. These exhibit a wide variety of patterns of vertical distribution and diel migration. Several undertake migrations similar in extent to those of most myctophids and migrating stomiatoids, while others remain at depth both day and night. In between are species where occurrence or extent of migration are related to size. A trend for juveniles to occur shallower than adults, already noted in myctophids and stomiatoids, is present in most species covered here regardless of migration pattern. Sexual differences in adult size and uneven sex ratios are indicated for several species. The interplay between sexual dimorphism, size difference, and sex ratio and the consequences to reproductive strategy are briefly discussed.

Most ecological studies of mesoplagic fishes have dealt primarily or exclusively with the two groups which dominate the fauna in most parts of the ocean—the family Myctophidae and the stomiatoid fishes. Because other forms are generally collected in small numbers, our knowledge of their ecology is limited to minor parts of general reports (e.g., Badcock 1970) or short notes on a few new specimens. Systematic or zoogeographic studies have assembled data from earlier collections, but in most cases the ecological value of such data is limited because sampling programs were not designed with ecological objectives in mind. Also the gear used was in many cases undoubtedly ineffective at sampling many forms and was fished without really good knowledge of depth of tow.

Recent, ecologically designed collections in the central Pacific Ocean near Hawaii by our program and that of R. E. Young have yielded a large amount of material involving some 225-250 species of mesopelagic fishes. Data on the myctophids and certain stomiatoids have already been reported (Clarke 1973, 1974), and material including many of the remaining species, which has been passed to other investigators, will eventually be covered in broader reports, e.g., family revisions, etc.

In this paper we report on a rather heterogeneous group of rare to moderately abundant fishes taken in these collections. Included are representatives of several families which are present and often moderately abundant in most parts of the world ocean, but of which knowledge of even the depth distribution is rather poor. Even though we are able to consider only a few other ecological parameters in detail for most of these, we feel that presentation of this data contributes to a broader understanding of the patterns of life history exhibited by the diverse mesopelagic fauna.

MATERIALS AND METHODS

Most of the specimens considered herein were taken near Oahu, Hawaii in a series of collections described in detail in Clarke (1973). These included six approximately quarterly series of extended horizontal tows with 2-m (one series) and 3-m Isaacs-Kidd midwater trawls (IK) and a series of samples in the upper 250 m with the larger Cobb Pelagic Trawl (CT). Because the program was designed primarily for study of vertically migrating species, the upper 250 m at night and the 400-1,200 m zone by day were covered most thoroughly; effort in the deeper zone at night was roughly one-fourth that by day. Thus for some of the nonmigrating species considered here, we have examined deep night collections made by R. E. Young with an opening-closing Tucker Trawl (TT). We have also examined collections from

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seven TT collections taken between 1,200 and 2,300 m. Finally, to present as much data as possible on rare species, we have included more recent collections with 3- and 5-m IK, deep-day and shallow-night TT collections, and a variety of CT and IK tows made by the National Marine Fisheries Service (NMFS).

The lower depth limits given are subject to question because most of the specimens considered were taken by the IK or CT, neither of which were equipped with opening-closing devices. As discussed in Clarke (1973, 1974), this problem is not great in dealing with abundant species, but for rare species—as were many considered here—there is no basis upon which to discriminate captures made at the principal towing depth from those made in transit to and from towing depth. Consequently, some of our conclusions about depth ranges and vertical migration must be regarded as tentative.

Lengths of all specimens were measured to the nearest millimeter. For each species discussed individually, the total number examined and the length range in millimeters are given in parentheses after the species name. (Unless noted as TL-total length, SL or standard length is used.) Gonads were examined under a dissecting microscope to estimate size at maturity (defined here as the smallest female with well-developed ova), seasonal trends in gonad development, and sex ratios. For rarely taken species, we examined all specimens and have reported results for undamaged specimens large enough to be reliably sexed by our routine technique. In species where we examined only a fraction of the total available material, we selected tows taken from throughout the day and night depth range and from all seasons and examined all individuals of the size range of interest from these selected tows. Hopefully this procedure minimized any potential bias due to sexual differences in depth distribution, etc. In all cases where we discuss population sex ratio, at least 50% (usually 70-80%) of the total individuals of the appropriate size range were sexed.

Numbers of specimens captured per tow were, for all species considered here, too low to treat in a rigorous quantitative fashion. Consequently, we have pooled data from all seasons to estimate depth ranges, pooled fish from all depths to consider seasonal changes in abundance, etc. Since both depth coverage and effort were roughly equal for each of the seasonal series of collections, it is unlikely that any serious bias resulted from our procedures.

Specimens of all species considered here will be deposited in the National Museum of Natural History, Washington, D.C.

TABLE 1.—Lengths and capture data for 11 species taken near Hawaii (lat. 22°20-30′N; long. 158°20-30′W) and two specimens (*) taken in the central equatorial Pacific (lat. 3°30′N; long. 145°W). Total length is given for *Isistius* and *Snyderidia*; standard length for the others. For horizontal tows, the most frequently fished depth is given; oblique tows are noted by 0-maximum depth. Catches by opening-closing trawl are noted by (OC).

	Length (mm); depth (m)	
Family, species	Night (2000-0500)	Day (0700-1800)
Squalidae:		
Isistius brasiliensis	355; 70 398; 0-500 492; 170	
Argentinidae:		
Microstoma microstoma		89; 490
Nansenia sp.	85; 525 (OC)	46; 560 73; 0-1,100 86; 725 107; 620
**Xenophthalmichthys danae*	ca. 75; 300	
Opisthoproctidae:		
Rhynchohyalus natalensis	61; 600 156; 0-400	80. 0-1,100 85; 0-800 107; 530 (OC)
**Winteria telescopa*	41; 450	
Rondeletiidae:		
Rondeletia loricata	15; 190 21; 200 28; 175 38; 450 85; 100	30; 800 33; 1,150 47, 69 (2); 775 86; 0-1,900 52; 925
Barbourisiidae:		
Barbourisia rufa	125; 800 276; 750 314; 0-1,200	67; 750
Zoarcidae:		
Synderidia canina	176; 0-350 188; 150 227; 500 ca. 240 (3); 0-500	79; 0-1,160 188, 247 (2); 800
Gempylidae:		
Lepidocybium flavobrunneum	15; 200 29; 0-350	
Nesiarchus nasutus	22; 370 67; 170	
Scombrolabrax heterolepis	10; 190 26; 25 26 (2); 250	18, 26 (2); 800 27; 1,000 27, 29 (2); 750
Trichiuridae:		
Aphanopus carbo	19; 170 40; 150 59; 190	197; 1,100 252; 660

RESULTS

Table 1 gives length and capture data for 11 rare and sporadically taken species from our collections near Hawaii. We also have included in Table 1 capture data for two rather infrequently collected species of argentinoid fishes which were taken by a series of IK trawls in the central equatorial Pacific (cruise 47 of the NMFS RV *Townsend Cromwell*). Other species are considered under individual headings below.

Opisthoproctidae

Opisthoproctus soleatus Vaillant (150; 28-84 mm)

Almost all *O. soleatus* were taken at 450-600 m during the day; highest catch rates were at 500-550 m. Large (> 50 mm) fish were caught throughout the day depth range, but smaller fish were taken mostly above 550 m. Only six specimens were taken at night—also in the same depth range. The day:night ratio of total trawling time in this depth range was about 4:1; thus the difference in catch is only partially explained by differences in effort. Since the night catches did not indicate that *O. soleatus* is spread more thinly over a broader depth range, the difference in catch per effort indicates that this species avoids the net better at night.

Female *O. soleatus* mature at about 60 mm. Data for each season were few, but there was no indication of seasonality in gonad ripeness, size composition, or abundance.

Opisthoproctus sp. (3; 11-17 mm)

A 17-mm specimen, tentatively identified as *O. grimaldii* Zugmayer, was taken in a day tow at 500 m in September. Two smaller specimens (11 and 15 mm) taken in June are apparently *O. soleatus*. One was taken at night in an oblique tow from 0 to 350 m; the other was caught, possibly in transit, by a day tow which fished at 725 m.

Alepocephalidae

Photostylus pycnopterus Beebe (12; 62-113 mm)

Photostylus pycnopterus was taken within the same depth range day and night. Five day catches were at 750-975 m, and the two night catches at 750 and 875 m. Five other day catches were from oblique tows which fished to 800-1,000 m.

Photostylus pyncopterus appears to mature at about 100 mm and to spawn relatively few but large eggs. Goodyear (1969) recorded a 93-mm female with eggs 1.4 mm in diameter and two specimens (84 and 96 mm) with much smaller eggs. Our three largest females (101-113 mm) carried eggs about 1.75 mm in diameter. One undamaged specimen had only 80 eggs in the ovaries. Another apparently had spawned some already; there were 26 eggs—mostly in the anterior sections of the ovaries. The gonads of two large males (106 and 110 mm) filled most of the body cavity. The remaining specimens (62-89 mm) were clearly immature.

The eggs of *P. pycnopterus*, both absolutely and relative to body size, were larger than those of any other species examined from our collections. Mead et al. (1964) have pointed out that other species of Alepocephalidae also have large eggs.

Giganturidae

Bathyleptus lisae Walters (89; 49-195 mm)

Although a few *B. lisae* were caught as shallow as 500 m, the majority were taken at 750-1,000 m both day and night. Of the 70 specimens taken in horizontal tows, only 7 were taken above this range and 3 deeper. There was no apparent trend in size with depth.

Female *B. lisae* appear to reach much greater size than males. Of 26 fish sexed, there were 14 females of all sizes (67-195 mm) and 12 males—all between 63-81 mm. All nine specimens over 81 mm were females. Of these, only one (171 mm) appeared mature.

Eurypharyngidae

Eurypharynx pelecanoides Vaillant (34; 89-575 mm TL)

Except for two day captures of small individuals (126 and 155 mm at 425 and 550 m, respectively) *E. pelecanoides* was taken between 650 and 1,300 m. Twenty-five specimens were taken during the day within this range. Of the 14 less than 300 mm, only 2 were taken below 1,000 m, and all over 300 mm were taken below 1,000 m. Thus, the small fish appear to occur shallower than the large ones. There were only seven night catches in horizontal tows, but these agreed with the size-depth pattern apparent in the day data.

Among 19 specimens that could be sexed, there were 8 males and 11 females. The seven largest fish included two males (440 and 507 mm), three apparently mature females (ca. 490-575 mm), and two nearly mature females (464 and 494 mm).

Bregmacerotidae

Two species of the genus *Bregmaceros* were taken in our collections. One fits published data (D'Ancona and Cavinato 1965) on *B. japonicus* Tanaka reasonably well, while the other is closest to but not identical with *B. macclellandi* Thompson. The latter is apparently distinct from another form similar to *B. macclellandi* which has been taken in the southern Pacific (E. H. Ahlstrom and J. E. Fitch, pers. commun.). The exact identity of all of these must await a thorough review of this badly confused genus.

The two Hawaiian forms were, however, quite distinct from each other. Dorsal and pectoral ray counts were 56-62 and 19-21 for *B. macclellandi* vs. 50-54 and 17-19 (rarely 20 or 21), respectively, for *B. japonicus*. The latter was the more slender species with SL/greatest body depth of 7.3-10.0 vs. 6.5-7.3 in *B. macclellandi*. *Bregmaceros japonicus* adults were distinctly darker dorsally, while *B. macclellandi* were not countershaded. The isthmus and pelvic fins of all larger *B. macclellandi* were grey, while in juveniles (<25-30 mm), the isthmus was covered with small melanophores. In most *B. japonicus* the isthmus and pelvics were totally unpigmented. A few small (ca. 20-25 mm) specimens whose counts fit *B. japonicus* had a few large melanophores on the isthmus.

Bregmaceros japonicus Tanaka (284; 18-52 mm)

The great majority of *B. japonicus* were taken at 25-125 m at night; however, 40 specimens, possibly contaminants, were taken at 125-200 m. Those under 30 mm were taken mostly above 100 m, while larger individuals were taken with roughly equal frequency throughout the 25- to 125-m range. Only 32 specimens were taken during the day; most (25) were large individuals (>35 mm) and taken at 600-800 m. This suggests that during the day the juveniles may occur shallower than the upper limit of our day samples (ca. 300 m).

Female *B. japonicus* appear to mature at about 40 mm, and almost all specimens over this size carried well-developed ova at all seasons. Small fish (<30 mm) were most abundant in March; they made up about 50% of the catch then as opposed to less than 10% at other seasons.

Bregmaceros cf. *macclellandi* Thompson (274; 14-94 mm)

Bregmaceros macclellandi occurred between 100 and 250 m at night. Most individuals less than 30 mm were caught about 150 m, and most 30-50 mm above 175 m, but larger fish were taken with roughly equal frequency throughout the night depth range. Day catches were mostly between 600 and 1,000 m with those less than 30 mm occurring above 800 m. Seven specimens (65-80 mm) were taken in tows that fished between 1,200 and 1,400 m; three of these were from an opening-closing trawl.

Bregmaceros macclellandi over about 35 mm appear to avoid the IK. Of the total specimens, 152 were taken by the CT in March 1971. Of these only about 12% were less than 35 mm, whereas, about half of the IK specimens were less than 35 mm for either the March data alone (12/23) or the total IK collection (56/122).

Females mature at about 60 mm. There were so few mature females in most series that no trends in gonad ripeness could be ascertained. The size composition of the catch showed no obvious seasonal changes.

Melamphaidae

Scopelogadus mizolepis mizolepis (Günther) (201; 7-74 mm)

Ebeling and Weed (1963, 1973) concluded from their data that *S. mizolepis* does not undertake diel vertical migrations and gave the upper depth limit of "adults" (66-94 mm) as 500 m. Our data, in contrast, clearly indicate that *S. mizolepis* of all sizes undertake a definite vertical migration. During the day, *S. mizolepis* occurred between 600 and 1,000 m and possibly deeper (the few tows below 1,000 m do not allow us to guess whether IK catches there were made in transit). Most of the fish less than 25 mm were taken between 600 and 800 m, and most larger ones at 700-1,000 m. At night the smallest fish occurred at 100-180 m, those 25-50 mm mostly at 150-250 m, and the larger ones at 200-400 m. There were no night catches between 400 and 600 m, but several specimens of all sizes

were taken at night within the daytime depth range, suggesting that a small fraction of the population does not migrate.

We examined the gonads of 127 specimens. Of 39 females (19-74 mm), those less than 50 mm were clearly immature, 2 56-mm fish were nearly mature, and 8 of the 10 largest (57-74 mm) carried well-developed ova. The 88 males were 18-60 mm.

There were too few mature females to consider any seasonal trends in ripeness. Juveniles (7-12 mm) were taken in March, June, and September, and made up the largest fraction of the catch (59%) in March. There were other peaks in size-frequency distributions at all seasons, but none could be clearly traced from season to season.

Poromitra crassiceps (Günther) (57; 16-130 mm)

All sizes of *P. crassiceps* occurred shallower at night than during the day. Day catches were between 750 and 1,000-1,200 m. No specimens over 60 mm were caught above 900 m. At night, two small fish were caught near the day depth, the remaining small fish (19-51 mm) at 150-400 m, and the larger fish (84-128 mm) between 340 and 825 m.

The seven smallest fish (16-25 mm) were taken in March, June, or July, and 16 intermediate-sized individuals (27-35 mm) were all taken in September. The others (39-130 mm) were scattered seasonally. Twenty-four specimens were 80 mm or larger. Nineteen of these (80-101 mm) were males; several of those over 90 mm appeared, subjectively, to be mature or nearly so. The five females were 97-130 mm, and none were mature.

Poromitra megalops (Lütken) (56; 13-41 mm)

All but one *P. megalops* were either 13-21 mm or 28-41 mm. Four of the small fish were caught at 625-1,000 m during the day. At night, five were taken at 250-380 m, and five at 690-775 m. Of the large fish, 27 were taken at 725-1,000 m during the day and 13 at 640-850 m at night. Thus some of the small fish undertake a fairly substantial upward migration at night, but the large fish appear to shift upwards only slightly, if at all. There were no obvious seasonal trends in size composition of the catches; specimens of both size groups were present at all seasons.

Of the 34 specimens sexed, there were 18 females (26-41 mm) and 16 males (28-39 mm). The 5 smallest females (26-35 mm) were immature, while the 13 large ones (37-41 mm) appeared mature. Ebeling and Weed (1973) reported the size range of mature *P. megalops* as 45-62 mm. Possibly, *P. megalops* matures at a smaller size in certain parts of its range. (Ebeling and Weed did not give specific geographic data for their mature specimens.)

Poromitra oscitans Ebeling (19; 44-71 mm)

Poromitra oscitans is a deep-living, nonmigrating species (Ebeling 1975). It occurred only at the lower edge of the depth range sampled in detail. One specimen each was taken at 750 and 850 m; the others were caught in nine tows all of which fished below 1,000 m. Four of these were taken in opening-closing TT tows which fished only below 1,350 m. Three were males (44-53 mm), and the others, immature females (45-71 mm).

Scopeloberyx opisthopterus (Parr) (93; 14-38 mm)

Scopeloberyx opisthopterus was taken between 540 and 1,200 m during the day. Night catches by the IK were at 650-1,175 m, and one specimen was taken by the TT fished open between 1,300 and 1,450 m. There was thus no evidence of any diel change in depth range. Most small specimens (<25 mm) were taken above 800 m and most large ones below 750 m.

Out of 55 specimens (25-38 mm) sexed, there were 10 immature females (26-30 mm), 24 mature females (31-38 mm), 7 males (27-33 mm), and 4 (25-29 mm) that were too small to sex with certainty but which were probably males. Mature females were taken at all seasons except December (when only four *S. opisthopterus* were taken). There were two rough size groups in the catch; all but seven specimens were either 14-20 mm or over 26 mm. Representatives of the smaller group were absent from samples taken in July and nearly absent in June, suggesting possible seasonality in recruitment.

Scopeloberyx robustus (Günther) (120; 12-31 mm)

Scopeloberyx robustus was taken at 550-1,200 m during the day. With the exception of three small (14-20 mm) specimens taken at 340-425 m, the night depth range was similar—600-1,175 m. Thus there is no indication that any but the small *S. robustus* vertically migrate. There was a distinct increase in size with depth. With few exceptions, fish less than 20 mm were caught above 800 m,

those 20-25 mm at 750-1,000 m, and those over 25 mm below 900 m.

Of 41 specimens (21-31 mm) sexed, 24 were females of which 6 (29-31 mm) were mature. The 17 males were 22-30 mm. Fish less than 16 mm were taken only in July and September. There were no seasonal trends in abundance of the larger fish.

Melamphaes danae Ebeling (627; 11-22 mm)

During the day, *M. danae* occurred principally at 750-1,200 m; a few were taken as shallow as 650 m. Fish less than 15 mm were almost all taken above 1,000 m, while larger ones occurred throughout the day depth range. Most night captures were between 75 and 200 m; the small fish were mostly taken at 75-100 m, while the larger ones occurred throughout the depth range. There were no night captures between 400 and 650 m, but 27 specimens of all sizes were taken at night in tows that fished within the day depth range. Although this catch was numerically small, and possibly due to in transit captures, it was large enough relative to effort to suggest that a small, but not insignificant fraction of the population did not regularly migrate.

Female *M. danae* matured at about 17-18 mm. Mature females were present in comparable numbers and percentages at all seasons, but the size composition of the catches indicated that juveniles were recruited primarily in the spring and early summer. For the series where the proper depth ranges were adequately and roughly equivalently sampled, the small (11-14 mm) fish made up 27% of the total catch in March, 15% in June, and 42% in July as opposed to 1% in September and 2.5% in December.

Melamphaes simus Ebeling (4; 14-24 mm)

Data on *M. simus* indicate little more than that it is present in low abundance in the area. The two night captures were at 300 and 800 m, while the two day captures were at ca. 700-800 m (the latter depths are estimates from wire out; depth records for both day tows were invalid).

Melamphaes indicus Ebeling (20; 16-55 mm)

Eleven *M. indicus* were taken at night at 125-150 m—nine of these in one tow. Nine specimens were taken during the day at 640-900 m. Two large females (51 and 55 mm) were mature, and four males (47-53 mm) appeared mature or nearly so.

Melamphaes sp. (*janae?* Ebeling) (10; 17-54 mm)

Seven *M.* "*janae*" were taken at night at 190-250 m and three during the day between 650 and 900 m. All were taken in September or November. The two largest specimens (43 and 54 mm) were both males and larger than the maximum size of this species given by Ebeling (1962). Ebeling, however, did note geographic differences in size at maturity. Our specimens fit the description of *M. janae* in other respects and could be reliably distinguished from similar-sized individuals of *M. indicus*. Study of more specimens will be necessary to determine whether *M. janae* is more variable in size than Ebeling noted or more than one species is involved.

Melamphaes sp. (*longivelis?* Parr) (2; 18, 20 mm)

Two small specimens of the "*typhlops*" group are tentatively identified as *M. longivelis*. The smaller was taken at 625 m at night, the larger at 640 by day.

Melamphaes polylepis Ebeling (10; 17-57 mm)

One *M. polylepis* was taken at night at 930 m; the remainder were taken during the day at 640-1,150 m. They included two mature females (56 and 57 mm), six males (46-56 mm), and two juveniles (17 and 19 mm).

Anoplogasteridae

Anoplogaster cornuta (Valenciennes) (93; 3-126 mm)

Juvenile *A. cornuta* undertake a substantial upward migration at night. At least some of the large fish also move upwards, but occur deeper than the juveniles both day and night. Seventy-two specimens were small (3-24 mm) and were taken in February-March. Fifty-eight were taken at night between 135 and 185 m; the remaining 14 were taken during the day—12 at 650 m and 2 at ca. 800 m. Larger specimens (all >70 mm) were taken throughout the year. At night six (77-87 mm) were taken between 275 and 475 m, one each at ca. 600 m (108 mm), 900 m (109 mm), and in an oblique tow to

980 m (94 mm). The 12 large (77-126 mm) individuals taken during the day were from 750-1,150 m.

Among the 18 fish sexed, there were 12 males (80-109 mm) and 6 females (78-126 mm). None appeared mature. The collection of so many small individuals in one of the seasonal series indicates that *A. cornuta* has a rather short spawning season.

Stylephoridae

Stylephorus chordatus Shaw (19; ca. 60-315 mm)

Seven *S. chordatus* (ca. 60-315 mm) were taken at night between 300 and 600 m. Eleven (63-282 mm) were taken between 625 and 800 m during the day, and one at dusk at 500 m. Thus *S. chordatus* appear to migrate about 200-300 m upward at night.

Two females (282 and 315 mm) appeared mature; the next largest female was 147 mm. The four largest males were 235-243 mm.

Gempylidae

Gempylus serpens Cuvier (29; 7-148 mm)

All but two *G. serpens* were taken at night in the upper 250 m; 19 were from 30-100 m. During the day, a 60-mm specimen was taken at 450 m and a 30-mm one at 800 m. It seems likely that the latter or both of the day catches were made in transit and that *G. serpens* migrates downward only a short distance, if at all, during the day. None were near maturity.

Nealotus tripes Johnson (95; 7-173 mm)

Most *N. tripes* were small (9-41 mm) taken at 50-200 m at night. Seventy-three were taken in December—58 in three tows at 170-200 m and 12 in a tow at 250 m. The CT collected four large specimens at night, three (75, 168, 173 mm) at 100 m and one (68 mm) at 250 m, while only one (49 mm at 150 m) was taken by the IK. No small fish and only three large ones were taken during the day. The CT captured a 49-mm individual at ca. 350 m, and the IK took two (63, 105 mm) in separate tows at ca. 750 m. The small *N. tripes* apparently stay in the upper layers both day and night. Since the larger fish were obviously inadequately sampled by the IK and there were no deep day tows made with the CT, it is not clear whether adults descend or not. The two deep day catches by the IK may well have been coincidentally taken in transit by tows which fished the same depth.

Diplospinus multistriatus Maul (224; 8-239 mm)

Most of the *D. multistriatus* were small individuals caught at night at two depth zones and at two separate seasons. Of the 100 specimens taken in December, 78 (8-30 mm) were taken in three tows at 170-200 m. In July, 62 specimens were taken; 31 (7-18 mm) were from four tows at 100-110 m. Other small fish taken at night were mostly from the upper 200 m with a few, probably captured in transit, taken in deeper tows. Of the 18 larger (35-239 mm) specimens taken at night, 13 were taken in the upper 130 m, 4 at 200-300 m, and 1 probably captured in transit, at 500 m.

Only 37 were taken in day tows, all but 2 between 500 and 1,000 m. Only one of these (11 mm) was in the size range which dominated the night catches. Three specimens were slightly larger (36-42 mm) and the remainder 68-221 mm. Most less than 140 mm were taken above 800 m, and most over 140 mm were taken below 700 m.

The near absence of small *D. multistriatus* in the day samples suggests that they either remain in the upper layers during the day (and were not sampled by our tows) or occur deeper and avoid the net during the day. The latter seems improbable for such small fish. Assuming the former is true and considering the data on larger fish, it appears that *D. multistriatus* occurs in the upper 100-200 m at night and that the larger sizes migrate to progressively greater depths by day.

Of the 46 specimens sexed, 12 were males (93-207 mm) and 34 females (75-239 mm). Eight females (163-239 mm) were mature.

DISCUSSION

Vertical Distribution and Migration

The diverse group of fishes considered here, as might be expected, exhibit a greater array of vertical distribution patterns than the myctophids and stomiatoids which occur in the study area. Most species of the latter two groups undertake substantial diel vertical migrations. The remaining species do not vertically migrate at all. Among the species considered here, migrators and nonmigrators are about equally represented, and

almost every conceivable intermediate pattern is represented as well.

Four of the common species, *Bregmaceros japonicus*, *B. macclellandi*, *Scopelogadus mizolepis*, and *Melamphaes danae*, are typical migrators. Both juveniles and adults move from well below 500 m during the day into the upper 250 m at night. The data indicate that four rarer species, *Rondeletia loricata*, *Melamphaes indicus*, *M. "janae,"* and *Scombrolabrax heterolepis* probably perform similar migrations.

The first four species were the most abundant of all considered here and ranked with all but the 8-10 most abundant myctophids and migrating stomiatoids (see Clarke 1973, 1974). The night size-depth patterns of the four were similar to the general types observed in the latter groups. *Bregmaceros japonicus* cooccurred with similar-sized individuals of several abundant myctophid species and *Vinciguerria nimbaria*, while *B. macclellandi* and the melamphaids had patterns similar to those of deeper-living species, e.g., *Lampanyctus niger* and *Gonostoma* spp. In the case of the *Bregmaceros* spp. and *M. danae*, the adults occurred throughout the depth range instead of primarily at the lower end as was usually the case with the other fishes.

During the day, the four migrating species exhibited a trend for increased size with depth. The day depth range of *B. japonicus* was similar to those of many other migrating species, but the other three were the only migrating species besides the myctophid *Lampanyctus nobilis* whose day depth range extended well below 1,000 m. *Lampanyctus nobilis*, *B. macclellandi*, and *Scopelogadus mizolepis* are relatively large species, but *M. danae* is one of the smallest species of fishes encountered in our study area.

The species for which there was no indication of diel change in vertical distribution are a rather heterogeneous group. *Opisthoproctus soleatus* inhabited a relatively shallow depth range and cooccurred with several stomiatoid species with similar, and probably convergent, morphological features (see Clarke 1974). Other nonmigrating species (*Scopeloberyx* spp.; *Poromitra oscitans*, *Photostylus pycnopterus*, *Bathyleptus lisae*, *Eurypharynx pelecanoides*, and probably *Barbourisia rufa*) occurred mostly below 600 m. Many of these species are commonly referred to with the too casually used adjective "bathypelagic," which has the connotation (if not always the denotation) of extremely great depths well removed from direct influences of surface phenomena. Our data indicate that most of these should more properly be considered members of the mesopelagic community. Even taking into account the relatively few hours of sampling below 1,000-1,200 m, the only species which appear to occur in any abundance below this depth are *Poromitra oscitans* and *E. pelecanoides* (of course, other fishes not covered here do occur deeper and some, e.g., certain ceratioids and the eel *Cyema* appear to occur only below 1,000-1,200 m). In fact, *B. lisae*, the *Scopeloberyx* spp., and probably all the others except *P. oscitans* have their primary centers of abundance above 1,000-1,200 m. During the day, they cooccur and presumably interact with vertically migrating species. Thus at least some aspects of their ecology must be affected by diel light changes.

Four species showed limited diel changes in depth distribution. *Stylephorus chordatus* moved somewhat shallower at night, but did not occur in the upper 250 m. Juveniles of *P. crassiceps* and *Anoplogaster cornuta* undertook fairly substantial upward migrations at night, but the adults shifted only slightly shallower. Juvenile *P. megalops* occurred somewhat shallower at night, but there was no conclusive evidence that the adults moved at all. Juvenile *Scopeloberyx robustus*, considered a "nonmigrator" above, may also move up at night. Since only *P. crassiceps* and *P. megalops* were taken in even moderate numbers, the patterns for the other species must be regarded as tentative. Size-related differences in migration have been noted for some myctophids and stomiatoids (Clarke 1973, 1974). As examples, the adults of *Bolinichthys distofax* (identified as *B. superlateralis* in Clarke 1973) appear not to migrate while the juveniles do, and the larger individuals of *Gonostoma elongatum* appear to occasionally remain at depth during the night.

Interpretation of data on the gempylid-trichiurid species is limited because, with the exception of *Diplospinus*, only the small juveniles were collected, and even these either avoided the net during the day or occurred so shallow that they were not sampled by our program during the day. The data indicate that all sizes of *Gempylus serpens* (to 148 mm) and *Nealotus tripes* (to 173 mm) collected probably remain in the upper layers during the day. Although the deep day catches of small *Scombrolabrax heterolepis* may have been made in transit, the absence of this species from day tows above 750 m suggests that it may mi-

grate. *Diplospinus multistriatus* exhibited a pattern opposite to that of *P. crassiceps*; the small fish either remain in the upper layers or descend only slightly during the day while the larger juveniles (>ca. 60 mm) and adults undertake a substantial migration.

Avoidance

With the exception of the gempylid-trichiurid species, there were few obvious indications of sampling error due to avoidance, but in most cases data were too few to even discuss the subject. The failure to capture mature specimens of the two large *Poromitra* spp. indicates avoidance by these and probably a fraction of the populations of other large melamphaids. *Bregmaceros japonicus* was apparently undersampled during the day, and the large *B. macclellandi* were sampled better by the CT than by the IK. It is not unexpected that avoidance was indicated for the larger, more "solidly built" species rather than for small species such as *M. danae* and the *Scopeloberyx* spp. or species such as *Bathyleptus lisae* and *Eurypharynx pelecanoides* which do not appear "designed" for swimming ability. The most puzzling indication of avoidance was that suggested for *Opisthoproctus soleatus*. This species not only has few characteristics indicating swimming prowess, but was undersampled at night rather than during the day as one might expect if vision were involved.

Sexual Dimorphism and Sex Ratio

In several species, the males appeared to be smaller than females (Table 2). The extreme case was *Bathyleptus lisae* where the largest female was about 2.5 times longer than the largest male. In *Scopelogadus mizolepis*, the females mature at about the size of the largest males observed and reach somewhat larger maximum size. A similar trend is suggested by the data for *Anoplogaster cornuta* and two other large melamphaids, *Poromitra crassiceps* and *P. oscitans*, but the numbers involved are too small to confirm it here. In two smaller species of the same family, *P.*

TABLE 2.—Summary of data on sex ratio and sexual differences in size for 10 species of fishes. Under Population sex ratio and left hand column gives the number and size ranges of all males in the population with 95% confidence limits (read to the nearest 0.01 from Chart 3 in Tate and Clelland 1957). Sex ratio was considered significantly different from 1:1 if these limits did not cross 0.50. Under Size Difference similar figures are given for only those specimens larger than the smallest mature female (since all *Melamphaes danae* were as large or larger than the smallest mature female, the data are the same for both pairs of columns). For *Bathyleptus lisae*, where the smallest mature female was much larger than the largest male, and for three melamphaids, where no mature females were taken, we have given only the number and size range of females larger than the largest male.

Species	Population sex ratio		Size difference	
	No. examined (Size range, mm)	Proportion of males (95% limits)	No. examined (Size range, mm)	Proportion of males (95% limits)
Bathyleptus lisae	12♂ (63-81)	0.46	9♀ (90-195)	—
	14♀ (67-195)	(0.26-0.67)		
Scopelogadus mizolepis	88♂ (18-60)	0.69	2♂ (60)	0.17
	39♀ (19-74)	(0.60-0.77)	10♀ (57-74)	(0.02-0.47)
Poromitra crassiceps	19♂ (80-101)	0.79	4♀ (121-130)	—
	5♀ (97-130)	(0.57-0.96)		
Poromitra megalops	16♂ (26-39)	0.47	3♂ (37-39)	0.19
	18♀ (28-41)	(0.29-0.66)	13♀ (37-41)	(0.04-0.47)
Poromitra oscitans	3♂ (44-53)	0.16	10♀ (53-71)	—
	16♀ (45-71)	(0.03-0.41)		
Scopeloberyx opisthopterus	21♂ (25-33)	0.38	8♂ (31-33)	0.25
	34♀ (26-38)	(0.25-0.53)	24♀ (31-38)	(0.11-0.45)
Scopeloberyx robustus	17♂ (22-30)	0.41	4♂ (29-30)	0.40
	24♀ (21-31)	(0.24-0.58)	6♀ (29-31)	(0.12-0.70)
Melamphaes danae	282♂ (17-22)	0.65	—	—
	144♀ (17-22)	(0.60-0.70)		
Anoplogaster cornuta	12♂ (80-109)	0.67	3♀ (110-126)	—
	6♀ (78-126)	(0.41-0.87)		
Diplospinus multistriatus	12♂ (93-207)	0.26	3♂ (184-207)	0.23
	34♀ (75-239)	(0.13-0.42)	10♀ (163-239)	(0.05-0.55)

megalops and *Scopeloberyx opisthopterus*, the maximum size of females was only slightly greater than that of males, but there were relatively few males larger than the smallest mature female. Thus there appears to be a slight but real difference in size of the two sexes. The two smallest melamphaids, *Melamphaes danae* and *S. robustus* showed no sexual differences in size. In all cases, except *P. crassiceps* and *P. oscitans*, there were sufficient small females to indicate that the size differences were not due to protandrous hermaphroditism.

Sexual differences in size have been reported for many species of dioecious mesopelagic fishes. Large differences comparable to that observed in *Bathyleptus* occur in the ceratioid anglerfishes (Bertelsen 1951) and the stomiatoid *Idiacanthus* (Gibbs 1964). Differences of the order observed for some of the melamphaids are known for several stomiatoids: *Stomias* (Gibbs 1969), *Echiostoma* (Krueger and Gibbs 1966), and *Cyclothone* (Kobayashi 1973). The usual explanation of the adaptive significance of smaller males (Marshall 1971) is that in a food limited environment—such as the deep-sea probably is—the energy required by the population is lowered without diminished fecundity.

Sexual dimorphism (as opposed to differences only in size) is quite common among meso- and bathypelagic fishes. Males of several groups exhibit better developed swimming muscles or sensory apparatus than the females (Marshall 1971). In many myctophids and stomiatoids, there are sexual differences in light organs. In most cases, sexual dimorphism seems related to increasing reproductive success by increasing the probability of heterosexual encounter.

No obvious external sexual dimorphism was observed in any of the species considered here (with the exception of *Isistius*), but at least two species appear to have uneven sex ratios (Table 2), an adaptation which, like the dimorphisms noted above, serves to increase the probability of a female meeting a conspecific male. Actually, the sex ratios of five species were significantly different from 1:1, and *Anoplogaster cornuta* showed a nearly significant trend. However, it seems wise to view the estimates for *Poromitra crassiceps*, *P. oscitans*, and *Diplospinus multistriatus* with suspicion since numbers were rather low and biases due to inadequate sampling and avoidance may be involved.

For both *Melamphaes danae* and *Scopelagadus mizolepis*, the numbers involved are relatively high and there is no indication that the populations were not adequately sampled. The estimated sex ratios for these two species indicate that the probability of an individual female encountering a male is about twice that expected for a population with the same density of females and 1:1 sex ratio. (The probability of an individual male encountering a female is lowered, but this has no consequences to population reproductive success.) In the case of *M. danae*, where the sexes are the same size, population fecundity would be less than that of a population of equal total biomass and 1:1 sex ratio because about two-thirds of the biomass are males. The males of *S. mizolepis* are, however, smaller than the females. Consequently, the effect of uneven sex ratio on population fecundity is to some extent balanced by the more nearly even division of population biomass between males and females. Better data on stages of maturity—particularly for males—and size distribution of mature fish of each sex would be needed to quantitatively describe the "trade off" between uneven sex ratio and sexual size difference.

The difference between *M. danae* and *S. mizolepis* may simply be due to the fact that *M. danae* is already a "dwarf" species—the smallest at maturity of all mesopelagic fishes in our collections. There may be other factors which select against the males being smaller than the already tiny females. On the other hand, *M. danae* may in some sense be less "food-limited" than *S. mizolepis* and thus able as a population to afford having two-thirds of the biomass as males. Further study of the interplay between sexual dimorphism, differences in size, and departure of sex ratio from 1:1 might prove to be a fruitful approach toward understanding the diverse life history features shown by mesopelagic fishes.

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LITERATURE CITED

BADCOCK, J.
1970. The vertical distribution of mesopelagic fishes collected on the Sond cruise. J. Mar. Biol. Assoc. U.K. 50:1001-1044.

BERTELSEN, E.
1951. The ceratioid fishes: Ontogeny, taxonomy, distribution, and biology. Dana Rep. Carlsberg Found. 39, 276 p.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.
1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 72:337-351.

D'ANCONA, U., AND G. CAVINATO.
1965. The fishes of the family Bregmacerotidae. Dana Rep. Carlsberg Found. 64, 92 p.

EBELING, A. W.
1962. Melamphaidae. I. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. Dana Rep. Carlsberg Found. 58, 164 p.
1975. A new Indo-Pacific bathypelagic-fish species of *Poromitra* and a key to the genus. Copeia 1975:306-315.

EBELING, A. W., AND W. H. WEED III.
1963. Melamphaidae. III. Systematics and distribution of the species in the bathypelagic fish genus *Scopelogadus* Vaillant. Dana Rep. Carlsberg Found. 60, 58 p.
1973. Order Xenoberyces (Stephanoberyciformes). *In* Fishes of the western North Atlantic. Part Six, p. 397-478. Mem. Sears Found. Mar. Res., Yale Univ. 1.

GIBBS, R. H., JR.
1964. Family Idiacanthidae. *In* Fishes of the western North Atlantic. Part Four, p. 512-522. Mem. Sears Found. Mar. Res., Yale Univ. 1.
1969. Taxonomy, sexual dimorphism, vertical distribution, and evolutionary zoogeography of the bathypelagic fish genus *Stomias* (Stomiatidae). Smithson. Contrib. Zool. 31, 25 p.

GOODYEAR, R. H.
1969. Records of the alepocephalid fish *Photostylus pycnopterus* in the Indian and Pacific oceans. Copeia 1969:398-400.

KOBAYASHI, B. N.
1973. Systematics, zoogeography, and aspects of the biology of the bathypelagic fish genus *Cyclothone* in the Pacific Ocean. Ph.D. Thesis, Univ. California, San Diego, 487 p.

KRUEGER, W. H., AND R. H. GIBBS, JR.
1966. Growth changes and sexual dimorphism in the stomiatoid fish *Echiostoma barbatum*. Copeia 1966:42-49.

MARSHALL, N. B.
1971. Explorations in the life of fishes. Harvard Univ. Press., Camb., 204 p.

MEAD, G. W., E. BERTELSEN, AND D. M. COHEN.
1964. Reproduction among deep-sea fishes. Deep-Sea Res. 11:569-596.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Danville, 171 p.

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DISTRIBUTION, FOOD, AND FEEDING OF THE THREESPINE STICKLEBACK, *GASTEROSTEUS ACULEATUS*, IN GREAT CENTRAL LAKE, VANCOUVER ISLAND, WITH COMMENTS ON COMPETITION FOR FOOD WITH JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*

J. I. MANZER[1]

ABSTRACT

The distribution, relative abundance, and food of the threespine stickleback, *Gasterosteus aculeatus*, was studied in Great Central Lake on Vancouver Island, B.C., in 1970 and 1971 as part of a multidisciplinary study on the production of sockeye salmon, *Oncorhynchus nerka*, following controlled additions of inorganic nutrients (1970-73 inclusive) to an oligotrophic sockeye nursery lake. Stickleback appeared along shore in relatively low numbers prior to mid-April and most were between 30 and 59 mm long. Following spawning in June and July, initially stickleback were smaller, but as fish of the year became more available, both the number and average size of stickleback increased. They were absent in the littoral zone by November, but their presence in the pelagic zone in winter could not be established. Over the diel cycle the larger individuals apparently move offshore during the day. The populations in the 2 yr did not differ greatly in size.

In each of the 2 yr stickleback had a wide but similar diet. They predominantly fed on two cladocerans (*Holopedium gibberum*, *Bosmina coregoni*), two copepods (*Epischura nevadensis*, *Diaptomus oregonensis*), and a cyclopoid copepod (*Cyclops bicuspidatus*). Larvae and pupae of the family Chironomidae were also of some importance. Other food items, but of minor importance, included harpacticoid copepods, insects, pelecypods, ostracods, acarids, Araneida, planaria, Odonata, and fish. Variations in diet in relation to season, size and sexual maturity of stickleback, and time of day were observed. The daily ration for stickleback was estimated to be 6.55% of their body weight in July and 7.80% in October.

Stickleback and juvenile sockeye salmon in the littoral zone exhibited considerable dietary overlap, especially during the late spring and summer. However, since sockeye salmon in this zone are relatively few in number, and stickleback do not inhabit the limnetic zone, serious interspecific competition for food in the lake is probably lacking, especially in years of abundant food supply.

Along the Pacific coast of North America, threespine stickleback, *Gasterosteus aculeatus*, hereafter referred to as stickleback, occur in many coastal lakes, rivers, and streams ranging from western Alaska to lower California (McPhail and Lindsey 1970). In British Columbia and Alaska, large populations have been reported in some nursery lakes of young sockeye salmon, *Oncorhynchus nerka* (Greenbank and Nelson 1959; Ruggles 1965). Separate studies on the food of young sockeye salmon (Ricker 1937; Narver 1970; Barraclough and Robinson 1972) and stickleback (Greenbank and Nelson 1959) in British Columbia and Alaska lakes have generally shown that both species feed mainly on planktonic crustaceans and insects. Rogers (1968) compared the food of both species residing in the same lake in Alaska and, after finding a great similarity in diet, concluded that potential interspecific competition for food exists. Krogius and Krokhin (1956) and Ruggles (1965) studied production of young sockeye salmon in different lakes where the two species were present and observed that sockeye salmon production was inversely related to stickleback abundance.

In 1969, the Pacific Biological Station of the Department of the Environment, Canada, started a multidisciplinary investigation to determine if the production of juvenile sockeye salmon in Great Central Lake on Vancouver Island, B.C., (Figure 1) would be increased by controlled additions of inorganic nutrients. Approximately 100 tons of inorganic nutrients were added from late spring through summer for 4 yr beginning in 1970, usually in 5-ton weekly lots with the ultimate

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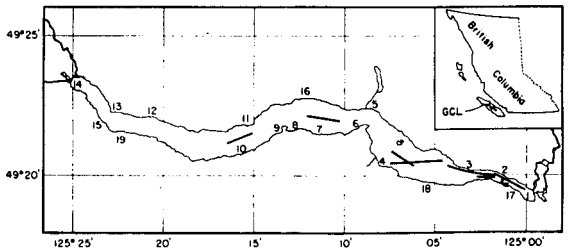

FIGURE 1.—Map of Great Central Lake, British Columbia, showing the location of beach seining (numbers) and mid-water trawling (lines) stations.

purpose of increasing the food resource for young sockeye salmon without significantly altering water quality. Preliminary results for 1970 when compared with 1969 (untreated year), indicate that primary production was increased without substantially changing the nature of the food chain (Parsons et al. 1970; Parsons et al. 1972). Zooplankton standing stock from May through October was approximately 10 times higher (LeBrasseur and Kennedy 1972). Young sockeye salmon generally consumed the important zooplankters in the lake and underyearling sockeye salmon were 30% heavier in weight (Barraclough and Robinson 1972). Considering the results of earlier studies by other investigators on the food of young sockeye salmon and stickleback, and the uncertainty of the response of the stickleback population to lake enrichment, a study on the biology of stickleback with special emphasis on diet and feeding habits was carried out in 1970 and 1971 as part of the overall fertilization experiment in Great Central Lake. This paper reports on the results of studies on distribution, relative abundance, and food and feeding of stickleback, and in addition contains comments on stickleback as a competitor of juvenile sockeye salmon for the food resource in the lake.

DESCRIPTION OF GREAT CENTRAL LAKE

Great Central Lake is an ultra-oligotrophic lake situated in the central part of Vancouver Island, B.C. The lake is approximately 34 km (21 miles) long, varies between 1 and 2.5 km (0.6 and 1.5 miles) in width, and has a surface area of 5,100 hectares. The maximum depth is approximately 250 m (800 feet). The shoreline varies from gentle sloping beaches to rocky, precipitous ledges. The littoral area in comparison to lake perimeter is relatively small and depths of 25 m or more only a few meters from shore are common. Beach cover ranges from small pebbles to rocks and boulders. Water inflow is by two major streams at the west end and several minor streams around the lake, as well as by snow melt in the spring months. The lake is drained at its east end by the Stamp River, which flows approximately 30 km before emptying into the sea at the head of Alberni Inlet. Surface water temperatures in the lake ranged from 4° to 21°C in 1970 and from 4° to 24°C in 1971. Minimal temperatures occur in February; maximal temperatures in late July. In general warm-up is slower in the western end, but once maximum temperatures are reached in July, surface water cools off at approximately the same rate. In some winters, the lake is ice-covered for varying periods of time, more often at the western end.

The fish community consists of at least eight species. Young sockeye salmon are by far the most abundant, followed by stickleback. Other species caught in considerably fewer numbers are juvenile coho salmon, *O. kisutch*; cutthroat trout, *Salmo clarki*; rainbow trout, *S. gairdneri*; Dolly Varden, *Salvelinus malma*; prickly sculpin, *Cottus asper*; pumpkinseed, *Lepomis gibbosus*; and river lamprey, *Lampetra ayresi*.

TAXONOMY

Two morphologically different forms of *G. aculeatus* occur along the Pacific coast of North America: a heavily plated form, *trachurus*, that is usually marine, and a partially plated freshwater form, *leiurus*. McPhail and Lindsey (1970) provided nomenclatural and taxonomic details regarding the *G. aculeatus* complex. Recent studies on isolated freshwater populations indicate considerable geographic variation with the result that their taxonomic status is of considerable uncertainty and interest (Hagen 1967; Narver 1969; Miller and Hubbs 1969; Hagen and McPhail 1970; Hagen and Gilbertson 1972). Hagen and Gilbertson (1972) consider that at least three plate morphs are present in permanent freshwater populations of *Gasterosteus*, namely low plated (3-7), partially plated (8-29), and fully plated (30-35).

The stickleback morph in Great Central Lake was identified from samples collected prior to the spawning season at four stations (3, 5, 13, and 14, see Figure 1) located along the length of the lake. The individual samples contained from 14 to 20

stickleback. The length of the stickleback in the combined samples ranged from 45 to 79 mm. Lateral plates along the left side and caudal keel were counted, using a probe and binocular microscope. Since all individuals in the samples exceeded 30 mm in length, plate formation was considered complete (Hagen and Gilbertson 1972). Analysis of variance revealed no significant difference in plate counts between stations (F = 3.15; df = 3, 66; P>0.05). The mean plate count for the combined samples was 25.17. Considering plate counts, it can be concluded that the stickleback population in Great Central Lake is a freshwater population more representative of the *trachurus* than the *leiurus* form.

DISTRIBUTION AND RELATIVE ABUNDANCE

Methods

Distribution and estimates of relative abundance of stickleback were determined from catches made with a purse seine used as such in mid-lake waters or as a beach seine along the shoreline, in 1970 and 1971. A description of the gear and its operation as a beach seine was provided by Manzer (1971). The net sampled an area between 450 and 550 m^2, or approximately 10 m of shoreline.

The field program in 1970 was carried out over eight surveys between 22 April and 27 November. Some purse seining and sighting were carried out in the early season but most effort was devoted to beach seining along shore. Here 18 different locations representing typical but different shoreline habitats were fished between 0830 and 1730 h (Pacific daylight time). Eleven of these stations were established as key stations. Coverage was more complete between late June and late August when surveys were conducted at 2-wk intervals. The fishing program in 1971 was essentially the same as in 1970. Five secondary stations sampled in 1970 were deleted and one new station was added to provide better coverage of the lake. Seven surveys were carried out between 18 February and 30 November, approximately at monthly intervals beginning in May. Fishing was conducted between 0630 and 1830 h. No fishing was done in September in either 1970 or 1971. The beach seining stations are shown in Figure 1 and grouped by character below, the stations in boldface being key stations.

Description	*Station*
Gentle slope, gravel bottom	**1, 4, 5, 9, 10, 14**
Gentle slope, rocks and boulders	6, 12, 15, 16, 17, 18
Rock slope, sharp dropoff	2, 3, 7, 8, 11, 13, 19

Information on the winter distribution of stickleback was obtained from purse seining operations carried out on 18 February and from mid-water trawling on 23 and 24 March in the pelagic zone, using a mid-water trawl routinely employed to catch age-0 sockeye salmon in the lake (Barraclough and Robinson 1972). Ice cover restricted fishing to the eastern one-half of the lake.

Results

Sighting surveys, purse seining, and beach seining were conducted in the eastern part of the lake in April and June 1970. The purpose of these operations was to determine the distribution of stickleback in proximity to the shoreline. It was considered that the results of these operations would be applicable to the lake as a whole. Stickleback were readily observed in varying numbers close to shore apparently moving at random and feeding in waters from less than 1 foot (0.3 m) to several feet (ca. 2 m) deep. They were rarely seen in offshore waters. This general pattern of distribution was confirmed by purse seine and beach seine catches. Eight "blind" (i.e., uncorroborated by sightings) purse seine sets in the limnetic zone yielded three stickleback. The net was considered effective to a depth of 3-4 m. In contrast, 16 beach seine sets at shore areas ranging from shallow beaches to precipitous slopes yielded stickleback on all but three occasions. As many as 350 stickleback were caught in a single set. Their virtual absence in offshore waters was indicated by the results of townetting for young sockeye salmon in the lake. A total of 480 tows made during 1969-73 in the limnetic zone of the lake at various depths (0-60 m) with trawl nets with mouth openings of approximately 18 m^2 and 4 m^2 yielded 21 stickleback (D.G. Robinson pers. commun.). From these operations it is concluded that stickleback were primarily concentrated close to shore.

Catches of stickleback by beach seining operations are given in Table 1 by survey and location. Catches in each year ranged from zero or a few fish to estimates of 2,500. In 1970, 105 sets were made and 10,727 stickleback were caught. Twenty-one sets failed to catch stickleback. In 1971, 89 sets were made and 10,806 stickleback were caught. Of

TABLE 1.–Beach seine catches of the threespine stickleback in Great Central Lake, 1970 and 1971, by survey and location. Multiple sets shown in parentheses. Estimated catch shown by asterisk.

	1970									1971							
Location	22, 30 Apr.	24, 25 June	8, 9 July	22, 23 July	5, 6 Aug.	19, 20 Aug.	2 Oct.	26, 27 Nov.	Total	18 Feb.	12, 20 May	10, 17 June	9 July	10 Aug.	14 Oct.	30 Nov.	Total
1	74	—	20	—	81	—	—	—	175	—	—	—	—	—	—	—	—
2	—	2(2)	13(2)	459(2)	7(2)	21(2)	63	0(2)	565	—	3	86(2)	12(2)	23	39(2)	0	163
3	—	200*	—	56(2)	95	225	600	3(2)	1,179	0	36	69	24	10	75	8	222
4	1	8(2)	2(3)	384(2)	279	158	300*	0(2)	1,132	0	121(3)	3(2)	145(2)	21	1,000(2)*	8(2)	1,298
5	350	1	—	18	649	2,000*	200*	2	3,220	0	4	26	28	800	293	36	1,187
6	—	—	—	15(2)	—	237	2,000*	0	2,252	0	8(2)	200*	13(2)	500	2,500	—	3,221
7	—	—	—	2	56(2)	—	—	—	58	—	2	16	6	29	—	0	53
8	—	1	—	16	0	2(2)	0	0	19	—	0	—	—	—	—	—	0
9	—	0(2)	—	11	29(2)	15(2)	0(2)	0(2)	55	—	10(2)	3(2)	500	100	27	0	640
10	—	—	—	500(2)	159(2)	300(2)	—	0(2)	959	—	2	134(2)	31	71	77	0	315
11	—	—	—	—	181	124(2)	500*	0	805	—	4(2)	52	296	23	125	1	501
12	—	—	—	1	79(2)	27(2)	—	—	107	—	—	—	—	—	—	—	—
13	—	—	—	—	12	5	—	—	17	—	13	35	400	6	—	—	454
14	—	—	—	0(2)	50	12	—	—	62	—	—	500*	107	8	—	—	615
15	—	—	—	7(2)	21(2)	25	—	—	53	—	—	—	—	—	—	—	—
16	—	—	—	—	—	—	30	2	32	—	13(2)	250	9	9	1,800	0	2,081
17	—	27(2)	—	—	—	—	—	—	27	—	—	—	—	—	—	—	—
18	—	10(2)	—	—	—	—	—	—	10	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—	15	34	7	—	—	56
Total	425	249	35	1,469	1,698	3,151	3,693	7	10,727	0	216	1,389	1,605	1,607	5,936	53	10,806
No. sets	3	13	6	19	20	19	10	15	105	4	18	17	16	13	11	10	89
Arith. mean catch	141.7	19.2	5.8	77.3	84.9	165.8	369.3	0.5	102.2	0	12.0	81.7	100.3	123.6	539.6	5.3	121.4
Geom. mean catch	37.41	4.14	3.89	11.07	12.28	21.68	48.53	1.27	9.31	0	1.34	25.24	34.04	33.27	109.20	2.39	12.19

these, 12 sets failed to catch stickleback. Most of the sets which failed to catch stickleback (21 of 33) were made in February and November. Arithmetic and geometric means of the numbers caught in each survey are also provided. The latter are included because of the skewness of the catch data and were obtained from log (n + 1) transformation of the data where n is the stickleback count in each set. This transformation permitted utilization of zero catches in the computations: in all likelihood during the spring to fall months at least one stickleback would have been caught had fishing been repeated.

The distribution and relative abundance of stickleback and size composition of the catches according to small (<30 mm), medium (30-59 mm), and large (60+ mm) stickleback are illustrated in Figure 2. (The size-groups were arbitrarily chosen but in general approximate age-groups: <30 mm = 0 age; 30-59 = 1 yr old; 60+ mm = 2 yr and older.) Gear efficiency was assumed to be reasonably constant, although a few sets were made under conditions of relatively strong wind and current. It was further assumed that after spawning (July and later) stickleback were catchable regardless of size. Abundance levels just prior to spawning may have been higher than catches indicate because of the decreased vulnerability of mature individuals, especially males which repair to nesting areas.

Some differences in survey dates, especially in the early part of the year, and some changes in the sampling sites in the 2 yr prevent a strict time and place comparison of the data. Nevertheless some general conclusions on distribution and relative abundance can be made from Table 1 and Figure 2. Seasonally, stickleback appeared along shore prior to mid-April. Their abundance at this time was low and appeared to vary between locations. Most stickleback in almost all localities ranged in length between 30 and 59 mm. A few larger individuals were caught but none smaller. In both years it was obvious that in all areas stickleback progressively increased in numbers, from July through October, although apparently they were less abundant off rock slopes than on gentle sloping beaches covered by either gravel or boulders. This increase is due to the recruitment of fish of the year as evidenced by the large proportion of fish less than 30 mm in July and August. The average seasonal catch was largest in October and consisted of stickleback measuring between 30 and 59 mm long. Fish belonging to the small and large size groups also were present in considerable numbers, and in some areas small fish predominated (for example, the central part of the north shore). The small or zero catches made in November suggest that stickleback prior to winter had abandoned the shore areas.

Observations on diel size variation in stickleback along the shore were made in conjunction with diel feeding habits, which are described in a later section. Paired samples taken 100 m and 15 min apart were collected at station 1 at 3-h intervals between 0700 and 1900 h in October 1970 and through the 24-h cycle in July 1971. Diel size changes observed during each series are illustrated in Figure 3 using the graphic method developed by Dice and Leraas (Simpson and Roe 1939). At each site and date the size of stickleback decreased from dawn to midday and then increased again by dusk, suggesting that the large fish are less available in the littoral area during the day. This trend is most clearly shown by fish in July at site B. Here, stickleback at midday are significantly smaller than at either dawn or dusk.

Stickleback virtually abandon the shore areas by November, but their presence in numbers in the pelagic zone of the lake during the winter could not be established. Limited purse seining (four sets) in February in the pelagic zone of the eastern part of the lake failed to yield any stickleback. Mid-water trawling in March, along transverse and longitudinal axes of the lake over a lineal distance of 22 km and at depths ranging from 10 to 100 m in the eastern half of the lake, resulted in the capture of one stickleback; ice cover prevented trawling in the western half of the lake. This stickleback measured 37 mm long and could have been caught at some depth down to 50 m. From the results of these fishing operations stickleback apparently either leave the lake or retreat to areas where they cannot be caught for the winter months, becoming available again between February and April.

Reliable estimates of the size of the stickleback population could not be made from the available catch data. Within any survey, catches varied widely between locations. In addition, local variance in the catches is not precisely known, although judging from a few instances when two sets were made in the same location the numbers caught can vary greatly. The catch data are considered more informative for the period beginning in July when coverage was more complete and stickleback availability increased. Assuming that factors contributing to variability in

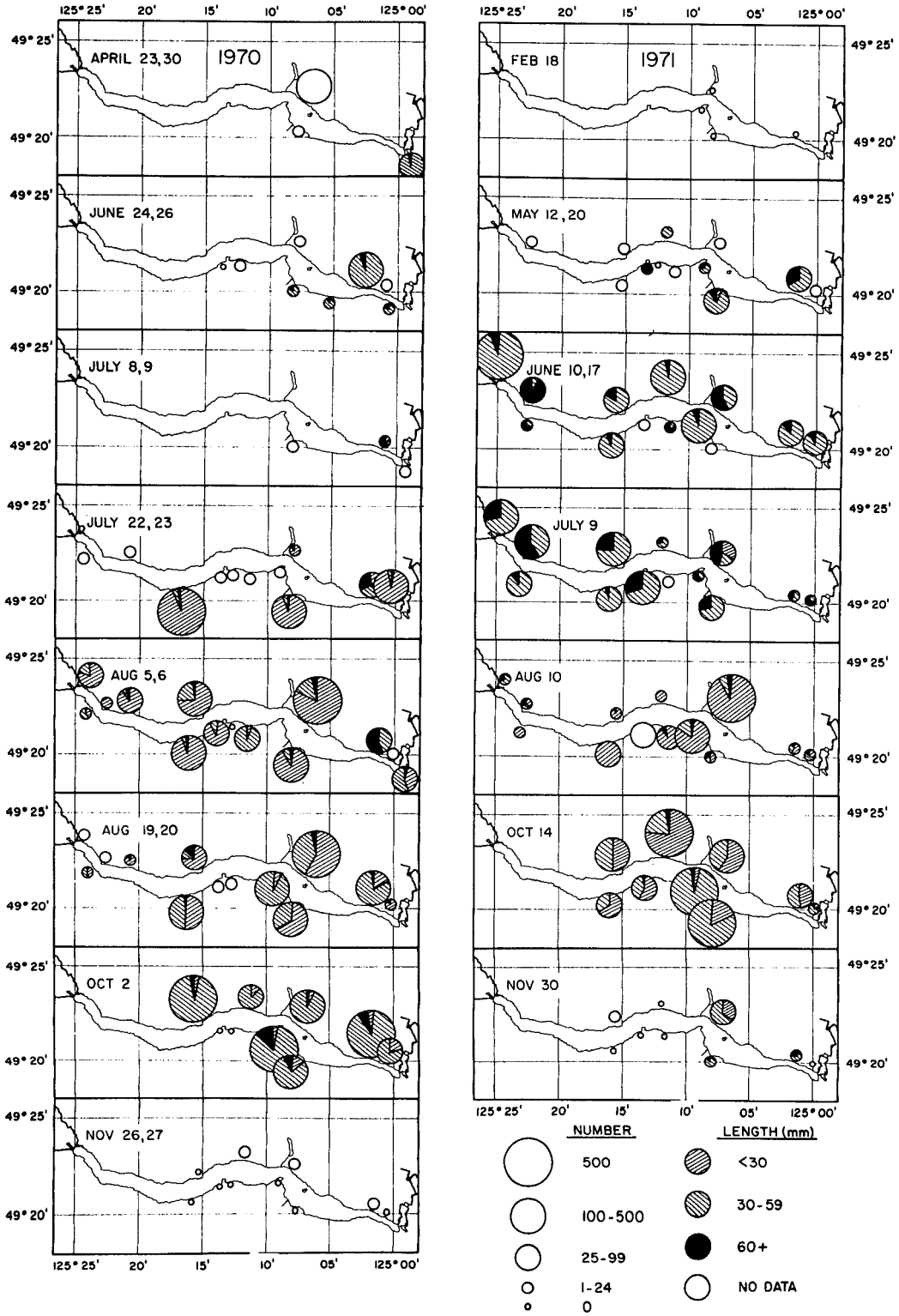

FIGURE 2.–Distribution and size composition of catches of threespine stickleback in Great Central Lake, 1970 and 1971.

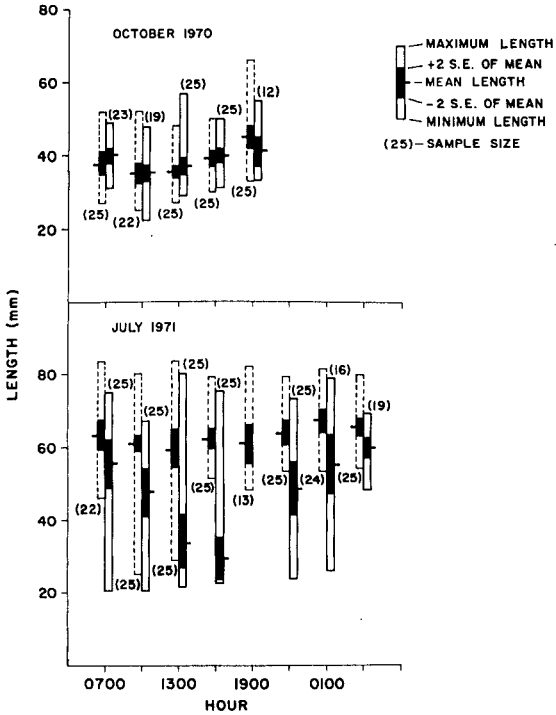

FIGURE 3.—Diel changes in the length of threespine stickleback as indicated by paired catches at station 1, October 1970 and July 1971. Open bars = length range; solid bars = ±2 SE of mean; dash = mean length. Site A = left bar, site B = right bar.

the catches in the 2 yr averaged out, the mean catch for surveys in 1971 was consistently higher than that for the same period in 1970. The difference between yearly mean catches was only 20%, suggesting that the stickleback populations in the 2 yr were approximately similar in size.

Discussion

Seasonal changes in abundance and distribution have been described for several lake populations of threespine stickleback. Greenbank and Nelson (1959), on the basis of beach seine catches, reported that in Bare and Karluk lakes, Alaska, from late May into September stickleback in varying numbers essentially inhabited shallow waters. A few were sighted on the surface of Karluk Lake at a considerable distance from shore, and some were caught by fyke nets at depths of 30 and 80 feet (approximately 9 and 25 m) but not in sets at 126 or 200 feet (approximately 39 and 61 m). Ruggles (1965), while studying juvenile sockeye salmon in Lake Owikeno, B.C., observed that during April to October, stickleback were most abundant in areas suitable for spawning and were taken in two netting operations in midlake surface waters in considerable numbers. Stickleback fry were caught throughout the spring to fall seasons but largest catches were made in the spring. In some years, a secondary increase in abundance occurred in the fall. In Lake Aleknagik, Alaska, Rogers et al. (1963), and Rogers (1968) using beach seines, trawls, and tow nets, observed stickleback in the spring and early summer to inhabit mainly the littoral area. By midsummer, fish of age I and II became pelagic while age 0 and III tended to remain inshore. Observations on stickleback distribution, movement, or numbers during the late fall and winter are lacking for these lakes, presumably because of ice cover. Markovtsev (1972), however, in Lake Dalnee from January through August observed that stickleback are present over winter in the pelagic zone and the population started moving from the pelagic to the littoral zone about May and resumed pelagic residence in the summer.

The seasonal occurrence of threespine stickleback in Great Central Lake is generally similar to those described for other lake populations along the Pacific coast, but their distribution during summer appears to be somewhat different. In other lakes, beginning in midsummer, some stickleback leave the littoral area to inhabit pelagic waters; those in Great Central Lake remain relatively close to or along the shore throughout lake residence. The reason for this apparent difference in distribution patterns is not known although it seems unlikely that it is the result of different fishing gears and methods employed by various investigators. The distribution patterns in the different lakes may be related to lake bathymetry. By comparison with other lakes studied Great Central Lake has relatively little littoral area. Expanses of water exceeding 25 m or more in depth only a few meters from shore are common. This bathymetric feature may provide stickleback with a food supply close to shore thus making it unnecessary for them to move into offshore feeding areas.

The virtual absence of stickleback in the pelagic zone in Great Central Lake does not conflict with the documented onshore-offshore movements of larger individuals during midsummer and fall. Offshore movement during the day and corresponding onshore movements at night were reported for marine threespine stickleback in the

Baltic (Meek 1916). The stimulus for this size-related behavioral difference remains unknown. In Great Central Lake some survival or feeding advantage may accrue to smaller individuals remaining close to shore but the affinity for shore shown by large individuals in July is probably associated with reproduction because virtually all these fish were physically mature or gravid.

FOOD AND FEEDING

Methods

Feeding Relationships

Seasonal and spatial differences in stickleback diet were determined from catches or samples of catches, if large, made during each fishing survey in 1970 and 1971. By coincidence, stomachs from 544 stickleback, or approximately 5% of the total number caught in each year, were examined for content. Stickleback examined in 1970 ranged in length from 15 to 78 mm; in 1971, from 14 to 86 mm. The numbers of fish examined from each station and by survey in the 2 yr are given in Table 2.

Fork length (millimeters), body weight (milligrams, minus the weight of the body cavity parasite, *Schistocephalus*, if present), and stomach content weight (to nearest 0.2 mg) were obtained. Stomach content weight was determined by first weighing the stomach with food and then without. The stomach contents were identified to species when possible, and counted using a binocular microscope. The content weight expressed as a percent of body weight was used as an index of feeding intensity. Gravid females were excluded from the analyses because they appeared to feed less intensively, judging from the occluded stomachs of many individuals. Supplementary information on feeding periodicity was also obtained by subjectively classifying stomachs as either full, three-fourths full, one-half full, one-fourth full, trace of food, or empty, and noting whether the contents were fresh, partially digested, or digested and therefore unidentifiable. The basic data are reported by Manzer (1971, 1972).

Three methods were used to determine the importance of organisms as food:

a. Occurrence—the percent of stickleback feeding on a particular organism.
b. Numerical—mean number of a particular organism per stomach.
c. Points—relative importance of organisms considering size and numbers.

The relative merits of these methods have been discussed by Hynes (1950) and Windell (1968). For the points method, the equivalent units assigned different organisms are given in Table 3. The units for common planktonic crustacea are in the ratio of their wet weight, as determined from zooplankton studies in Great Central Lake (LeBrasseur and Kennedy 1972). Equivalent units for other organisms, including insects, were determined by inspection and assigned the same unit value as other organisms or groups of organisms of similar volume, assuming a common specific gravity. Since individual size of a given organism

TABLE 2.—Numbers of threespine stickleback stomachs examined, by survey and location, 1970 and 1971.

		Location																		
Survey	Date	1	2	3	4	5	6	7	9	10	11	12	13	14	15	16	17	18	19	Total
1970:																				
1	22, 30 Apr.	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15
2	24, 25 June	—	—	23	8	—	—	—	—	—	—	—	—	—	—	—	15	10	—	56
3	8, 9 July	—	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13
4	22, 23 July	—	30	20	10	10	—	—	—	10	—	—	—	—	—	—	—	—	—	80
5	5, 6 Aug.	19	—	15	32	36	—	—	10	25	15	13	12	10	10	—	—	—	—	197
6	19, 20 Aug.	—	13	20	13	22	10	—	—	10	10	10	—	—	10	—	—	—	—	118
7	2 Oct.	—	15	10	10	10	10	—	—	—	10	—	—	—	—	—	—	—	—	65
Total		34	71	88	73	78	20	—	10	45	35	23	12	10	20	—	15	10	—	544
1971:																				
1	12, 20 May	—	—	20	20	3	8	—	10	—	3	—	—	—	—	10	—	—	—	74
2	10, 17 June	—	10	10	—	10	10	10	—	10	10	—	10	10	—	10	—	—	10	110
3	9 July	—	10	10	20	15	6	—	10	10	10	—	10	10	—	9	—	—	10	130
4	10 Aug.	—	9	10	10	12	11	10	—	10	10	—	6	8	—	9	—	—	—	105
5	14 Oct.	—	11	10	10	12	10	—	11	10	10	—	—	—	—	15	—	—	—	99
6	30 Nov.	—	—	8	8	10	—	—	—	—	—	—	—	—	—	—	—	—	—	26
Total		—	40	68	68	62	45	20	31	40	43	—	26	28	—	53	—	—	20	544

TABLE 3.—Equivalent units of important dietaries.

Organism	Bulk units	Organism	Bulk units
Alona	2	Nauplius	0.2
Holopedium	3	Copepodids	1
Bosmina	1	Harpacticoid	1
Daphnia	2	Chironomid larva	5
Epischura	11	Chironomid pupa	50
Diaptomus	2	Egg, zooplankton	1
Cyclops	1	Egg, stickleback	2

was reasonably uniform with time, seasonal adjustment of equivalent units appeared unnecessary. Items which averaged less than one per stomach or less than 1.0% of the bulk were recorded as trace (T) quantities.

Stomachs of large stickleback frequently contained several hundred organisms. In such cases, contents were identified and enumerated from a weighed portion of the total bolus and the resulting counts were then prorated to the total weight to estimate the numbers of organisms consumed. The remaining portion of the bolus was examined for food organisms not represented in the sample. Correlation analysis indicated a very significant positive relationship between actual and estimated counts of major food items ($r = +0.964$, $P<0.01$, $n = 15$).

Major features of the stickleback diet were adequately described from examinations of 10 stomachs per sample. In a few cases, smaller numbers were examined to eliminate gaps in time or place. On the basis of two separate tests of association between stomach contents of 10 and 25 fish samples from the same catch, ranked by numbers, Spearman's rank correlation test (Siegel 1956) gave r_s values of $+0.943$ and 1.000. The extent of lake coverage in the 2 yr, especially 1970, differed between surveys. The dietary agreement among stickleback taken at different locations within surveys was examined using Kendall's coefficient of concordance test (Siegel 1956). For each survey, the most common food items at each location were ranked according to mean number in the sample, excluding material rendered unidentifiable through digestion. Corrections were made for items tied in rank and W, the index of divergence of observed from perfect agreement, and related chi-square values were calculated. For eight of the nine surveys tested (four in 1970 and five in 1971) the agreement observed in rankings of dietaries among locations was higher than it would be by chance ($P = 0.05$) (Table 4). Therefore, it seemed reasonable to combine the data for all locations by survey to facilitate detection of possible seasonal changes in diet. From plankton studies conducted in Great Central Lake in 1970, LeBrasseur and Kennedy (1972) stated that "the epilimnion is well mixed, thus assuring a nearly uniform dispersal of planktonic organisms along the lake."

Diet in relation to sexual maturity was determined from combined samples of stickleback caught during the first three surveys (mid-May to early June) in 1971. Mature and immature females were separated on the basis of size, 60 mm being used as the dividing length. Of 54 females 60 mm or larger examined, 4 were immature and 50 were mature. Of the latter group, 28 were ripe. Blue coloration of the iris and red coloration of the pelvic region were used to separate mature from immature males (Craig-Bennett 1931; Greenbank and Nelson 1959). Because female sticklebacks are larger than males of equivalent age (Greenbank and Nelson 1959; van Mullem and van der Vlugt 1964) males larger than 60 mm were considered to be sexually mature. From testes inspection, ripe males were few in number and accordingly no attempt was made to treat functional and nonfunctional males separately. The relative scarcity of ripe males is believed due to their behavior of attending spawning females or nests.

Diel Feeding Rhythm

Diel feeding periodicity and food composition studies were based on paired catches made at station 1 on 1-2 October 1970, and 21-22 July 1971 at two sites (A and B), approximately 100 m apart. In the October series, fishing started at 1300 h 1 October and during the next 24-h period was conducted at 1600, 1900, 2200, 0630, and 1000 h.

TABLE 4.—Summary of results of Kendall coefficient of concordance (W) tests (Siegel 1956) for agreement in diet of threespine stickleback at different sampling locations.

Survey date	Number of locations (k)	Number of food categories (N)	W	Chi-square	P level
1970:					
22-23 July	5	12	0.566	31.13	0.01
5-6 Aug.	11	9	0.383	26.12	0.001
19-20 Aug.	9	12	0.498	49.30	0.001
2 Oct.	6	12	0.581	41.83	0.001
1971:					
12, 20 May	5	9	0.220	8.80	0.70
10, 17 June	10	9	0.317	25.36	0.01
9 July	12	9	0.450	43.20	0.001
10 Aug.	10	6	0.230	11.50	0.05
14 Oct.	9	9	0.629	45.29	0.001

Fishing at 2200 h at each site failed to yield any stickleback, presumably because of inefficient operations under conditions of total darkness. As a consequence further sampling was suspended until 0630 h 2 October. Fishing during the July series began at 0700 h and was repeated at 1000, 1300, 1600, 1900, 2200, 0100, and 0400 h. Gear problems precluded fishing at site B at 1900 h. During each series, the time interval between fishing at the two sites at any time of day was approximately 15 min and for practical purposes can be considered concurrent.

The target sample size for each site and time of day was 25 fish. Except for sampling times already indicated, this number was achieved or closely approximated. The smallest sample contained 12 fish (site B, 1900 h). All fish in the sample were processed in accordance with methods described earlier and 10 fish, selected at random, were examined for stomach contents. A total of 226 stickleback were examined for the October series, 334 for the July series. The sizes of stickleback by sample are illustrated in Figure 3.

Mean feeding intensity indices (food weight/body weight × 100) for paired samples were similar, and data for each series were pooled by time of day.

Daily Ration and Maximum Meal Size

In this study, daily ration is defined as the weight of food consumed over a 24-h period expressed as a percent of body weight. Daily rations were estimated from the diel feeding rhythm curve, using a modification of the method developed by Keast and Welsh (1968). Essentially, differences between maximal and minimal feeding indices during successive periods over a 24-h cycle were determined and these values and the residual content were summed. The method is most applicable to species which completely empty their stomachs between meals.

Maximum individual meal size was determined from regression analysis of stickleback taken during the maximal feeding period in July and which were judged to have "full" stomachs according to the subjective "fullness" scale described earlier.

TABLE 5.—Seasonal change in the diet of threespine stickleback in Great Central Lake, 1970.

Date	22, 30 Apr.			24-25 June			8-9 July			22-23 July			5-6 Aug.			19-20 Aug.			2 Oct.		
No. fish examined	15			56			13			80			197			118			65		
% empty	0			3.6			15.4			13.7			3.6			3.4			0		
Size range (mm)	33-63			36-72			16-70			18-75			15-74			19-76			27-76		
Mean size (mm)	48			49			51			43			33			35			39		
Mean content wt (mg)	34.6			27.4			14.6			25.4			15.3			14.3			17.4		
Organism	1[1]	2[2]	3[3]	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Rotifera	—	—	—	46	15	T	62	91	T	26	47	T	75	52	T	76	67	T	59	56	T
Cladocera:																					
Holopedium	—	—	—	41	39	12	46	37	63	53	95	60	76	115	60	75	141	61	88	129	47
Bosmina	100	2,419	95	73	235	24	77	37	21	60	14	3	65	18	3	79	88	13	98	116	14
Daphnia	—	—	—	11	1	T	8	T	1	—	—	—	T	T	T	2	T	T	2	T	T
Alona	—	—	—	5	T	T	23	2	2	16	1	T	44	2	T	46	4	1	23	1	2
Copepoda:																					
Epischura	40	2	T	55	46	51	31	1	6	45	10	23	63	17	33	36	7	5	29	4	5
Diaptomus	—	—	—	—	—	—	—	—	—	6	1	T	4	T	T	19	9	3	49	98	24
Cyclops	100	88	3	16	T	T	—	—	—	1	T	T	3	T	T	42	4	T	60	38	4
Copepodids	—	—	—	—	—	—	—	—	—	4	T	T	19	6	1	32	27	4	57	20	2
Nauplii	—	—	—	—	—	—	—	—	—	13	1	T	21	10	T	38	32	T	35	9	T
Harpacticoid	—	—	—	9	T	T	—	—	—	14	T	T	4	T	T	22	2	T	19	1	T
Insecta:																					
Chironomid larvae	—	—	—	27	5	2	15	T	T	39	3	3	25	1	T	33	5	4	14	1	T
Chironomid pupae	—	—	—	50	2	10	8	T	T	26	1	10	14	T	T	28	1	7	5	T	T
Other	—	—	—	11	T	T	—	—	—	4	T	T	8	T	T	10	T	T	8	T	T
Eggs - zooplankton	93	18	T	19	4	T	62	10	6	9	T	T	26	1	T	45	8	1	34	8	1
Other:																					
Pelecypoda	—	—	—	11	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda	—	—	—	—	—	—	15	T	T	8	T	T	1	T	T	11	T	T	T	T	T
Acari	—	—	—	—	—	—	—	—	—	3	T	T	3	T	T	5	T	T	5	T	T
Planaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	T	T	T	T	T
Odonata	—	—	—	—	—	—	—	—	—	—	—	—	1	T	T	—	—	—	—	—	—
Fish	—	—	—	—	—	—	8	T	T	5	T	T	3	T	T	—	—	—	—	—	—
Unidentifiable %									25						3			4			1

[1]% stomachs with item.
[2]Mean no. items per stomach examined.
[3]Item = % of total bulk units. T = Trace = < 1 organism or < 1%.

RESULTS

Feeding Relationships

Seasonal Variations in Diet

Data on size and stomach contents of stickleback examined in 1970 and 1971 are summarized by survey in Tables 5 and 6. The predominant features regarding seasonal change in diet are depicted in Figure 4. Observations for 1970, except for August when almost all stations were sampled, are based mainly on samples taken from the eastern part of the lake. Observations for 1971 are based on samples from most of the key sampling stations except in November when fishing was confined to the eastern end of the lake.

Although the numbers of stickleback examined differed by survey, a similar seasonal trend in the proportion of fish with empty stomachs was observed for the 2 yr: low in the spring and early summer, highest in midsummer, and again low in the fall. The mean weight of stomach contents fluctuated in each year but generally was higher in the spring and early summer. The higher mean values in the early part of the year are probably related to fish size. On the average, stickleback were larger in the spring and early summer than in the late summer and fall. The relatively high proportion of fish with empty stomachs in midseason can be explained by feeding behavioral differences associated with sexual maturity.

In each of the 2 yr stickleback had a wide but rather similar diet. They predominately fed on five species of organisms: two cladocerans (*Holopedium gibberum*, *Bosmina coregoni*), two copepods (*Epischura nevadensis*, *Diaptomus oregonensis*), and a cyclopoid copepod (*Cyclops bicuspidatus*). Larvae and pupae of the family Chironomidae were also of some importance. The distinction between zooplankton eggs and fish eggs in 1971 represents a qualitative refinement in analysis of the data, rather than any difference in diet. Other kinds of organisms consumed at various times but of minor importance were harpacticoid copepods, insects, pelecypods, ostracods,

TABLE 6.—Seasonal change in the diet of threespine stickleback in Great Central Lake, 1971.

Date	12, 20 May			10, 17 June			9 July			10 Aug.			14 Oct.			30 Nov.		
No. fish examined	74			110			130			105			99			26		
% empty	2.7			4.5			18.5			19.1			8.1			3.8		
Size range (mm)	29-86			33-82			15-86			14-80			23-77			24-78		
Mean size (mm)	54			54			58			33			38			34		
Mean content wt (mg)	26.1			45.3			28.0			16.5			18.6			13.9		
Organism	1[1]	2[2]	3[3]	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Rotifer	—	—	—	10	1	T	40	15	T	44	27	T	74	35	T	31	12	T
Cladocera:																		
Holopedium	1	T	T	34	14	1	59	47	16	57	22	28	89	163	67	65	20	35
Bosmina	47	10	2	37	2	T	19	T	T	40	10	4	89	85	12	69	43	25
Daphnia	—	—	—	—	—	—	—	—	—	—	—	—	19	1	T	—	—	—
Alona	5	T	T	4	1	T	2	3	T	54	17	14	20	1	T	23	1	1
Copepoda:																		
Epischura	1	7	19	56	286	95	50	55	68	6	6	28	19	1	1	—	—	—
Diaptomus	—	—	—	10	2	T	—	—	—	5	2	2	71	28	8	54	10	12
Cyclops	40	75	19	49	68	2	35	4	T	4	T	T	65	20	3	42	6	3
Copepodids	40	13	3	23	8	T	40	12	1	6	T	T	48	52	7	50	38	22
Nauplii	32	22	T	—	—	—	13	6	T	—	—	—	28	2	T	—	—	—
Harpacticoid	10	1	T	9	13	T	3	T	T	8	T	T	1	T	T	4	T	T
Insecta:																		
Chironomid larvae	19	1	T	6	T	T	9	T	T	11	T	T	1	T	T	4	T	—
Chironomid pupae	23	3	38	11	T	T	7	1	6	2	T	T	—	—	—	—	—	—
Other	12	1	13	9	T	T	16	1	6	5	1	21	3	T	T	4	T	T
Eggs - zooplankton	5	1	T	19	3	T	39	22	2	1	T	T	54	15	2	31	3	2
Fish	1	T	T	3	T	T	4	T	T	1	T	T	—	—	—	—	—	—
Other:																		
Amphipoda	4	T	T	2	T	T	2	T	T	—	—	—	—	—	—	4	T	T
Pelecypoda	8	1	2	3	T	T	T	T	T	—	—	—	—	—	—	—	—	—
Ostracoda	—	—	—	2	T	T	4	T	T	17	1	T	—	—	—	8	T	T
Acari	8	T	T	4	T	T	—	T	T	22	1	2	—	—	—	—	—	—
Araneida	1	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fish	—	—	—	—	—	—	—	—	—	—	—	—	1	T	T	—	—	—
Coleoptera	2	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ceratopogonidae	11	T	T	3	T	T	—	—	—	—	—	—	—	—	—	—	—	—
Isopoda	1	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentifiable %		51			47			38			24			36			34	

[1]% stomachs with item.
[2]Mean no. items per stomach examined.
[3]Item = % of total bulk units. T = Trace = < 1 organism or < 1%.

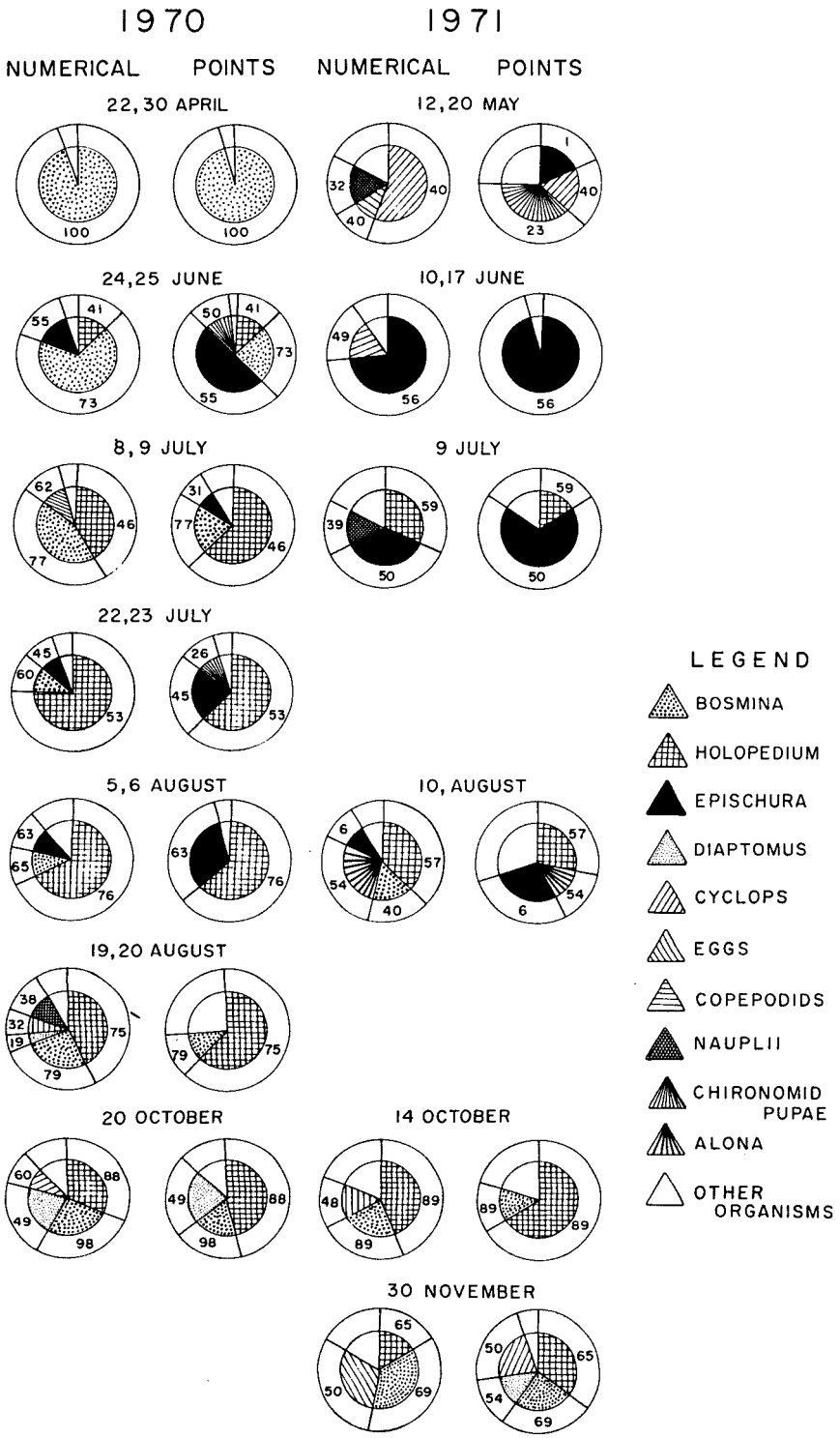

FIGURE 4.—Seasonal change in the predominant food items of threespine stickleback in Great Central Lake, 1970 and 1971. Figures in the periphery of each pie diagram represent the percent of stickleback stomachs containing the particular item.

acarids, Araneida, planaria, Odonata, and fish (cottids).

The different food organisms differed seasonally in their dietary importance. Considering items of major importance, in 1970 in late April, virtually all stickleback stomachs examined contained *Bosmina*, *Cyclops*, and zooplankton eggs, but *Bosmina* was most important, averaging 2,419 individuals per stomach and making up 95% of the bulk. By late June, *Bosmina* was still the dominant food item but had declined somewhat in importance as indicated by an increasing proportion of stickleback feeding on *Epischura* (55%), *Holopedium* (41%), and chironomids, especially pupae. Of these *Epischura* was most important, forming almost 50% of the bulk. Through July and August, *Bosmina* was consumed by a high proportion of stickleback (no less than 60%) but *Holopedium* progressively became the dominant food organism (approximately 60% by bulk). During these two months, the number of stickleback feeding on *Alona*, copepod copepodids and nauplii, and *Diaptomus* increased but none of these items was important quantitatively. In October, *Holopedium* continued to be the dominant food item in terms of bulk, but more stickleback fed on *Bosmina* (98%). *Diaptomus* and *Cyclops* were present in about 50% of the stomachs examined and were of minor importance. Rotifers and eggs were present virtually throughout the study period, the former item occurred rather frequently (26-76%), but were unimportant in terms of bulk. Judging from size, the eggs were from both zooplankton and stickleback. Since stickleback spawn between late June and early August, eggs encountered at other times of the year presumably were zooplankton eggs.

In May 1971, about one-half of the stickleback had *Bosmina*, *Cyclops*, and copepodids in their stomachs. *Cyclops* was most important in terms of numbers per stomach (75) but chironomid pupae, because of relative size of individuals, was important in terms of bulk (38%). By mid-June, more stickleback were feeding on *Epischura* (56%) and *Holopedium* (34%), but *Epischura* was the dominant food organism (95% of total stomach contents). About the same number (49%) of stickleback fed on *Cyclops* as in May, and although the item ranked second in incidence, it accounted for only 2% of the total stomach content. In July, *Epischura* declined in importance but still maintained dominant position among the other food organisms. *Holopedium* continued to increase in importance. This inverse trend in the importance of these two food items was observed into October. In October, *Holopedium* was the dominant food item and *Bosmina* ranked second in bulk and were consumed by as many stickleback as were *Holopedium*. In terms of occurrence, *Diaptomus* (71%), *Cyclops* (65%), copepod copepodids (48%), and zooplankton eggs (54%) were of secondary importance. At the end of November, *Holopedium*, *Bosmina*, and copepod copepodids formed the major part of the diet of stickleback and individually were of about equal importance.

The stickleback diet in 2 yr showed some marked seasonal similarities and differences. *Bosmina* was not as important in the early part of 1971 as in 1970. Another difference is the greater importance of *Epischura* later into 1971 than 1970, and the greater importance of *Holopedium* in July and August in 1970. A feature common to both years is the late season resurgence of *Bosmina* as an important food organism. It is not known for certain whether these differences and similarities represent annual differences in abundance levels of the various kinds of organisms or in sampling dates.

Diet in Relation to Stickleback Size

A total of 205 stickleback taken from the eastern end of the lake on 22 July and 5 August 1970, and ranging in length from 15 to 78 mm were examined for diet differences in relation to size. The stickleback were arbitrarily divided into four size groups: <30 mm, 30-49 mm, 50-69 mm, 70+ mm. Data on diet for the same size group for the 2 days were pooled since samples were obtained in the same general area within a short time interval (Table 7).

A high proportion of the stickleback (75, 65, and 68% respectively) in the <30 mm group consumed *Bosmina*, Rotifera, and *Holopedium*. *Alona*, *Epischura*, and chironomid larvae occurred in about one-half of the stomachs. Of the remaining items consumed only copepod nauplii, chironomid pupae, and zooplankton eggs were of any importance, occurring in 18, 16, and 13% of the stomachs, respectively. Larger stickleback, excluding the 70+ mm group of which only 11 were examined, tended to feed more on *Holopedium*, *Epischura*, chironomid pupae, and zooplankton eggs, and less on Rotifera (except those in the 30-49 mm group), *Bosmina* and *Alona*. Copepod nauplii apparently were not consumed by larger stickleback, but fish

TABLE 7.–Occurrence (percent) of different organisms in the diet of threespine stickleback of four size groups– <30 mm group contained 100 fish; 30-49 mm, 34 fish; 50-69 mm, 60 fish; and 70+ mm, 11 fish. Based on samples taken on 22 July and 5 August 1970.

Organism	Size group (mm) <30	30-49	50-69	70+
Rotifera	65	85	49	9
Cladocera:				
Holopedium	68	88	81	71
Bosmina	75	50	36	28
Alona	46	19	19	—
Copepoda:				
Epischura	50	79	83	57
Diaptomus	3	6	2	—
Cyclops	4	—	—	—
Copepodids	7	—	2	—
Nauplii	18	—	—	—
Harpacticoid	7	10	8	—
Insecta:				
Chironomid larvae	42	22	21	14
Chironomid pupae	16	35	21	—
Other	7	5	7	—
Eggs - zooplankton	13	29	23	28
Other:				
Pelecypoda	—	—	2	—
Ostracoda	6	6	3	—
Acari	2	—	—	—
Araneida	—	3	—	—
Fish	—	—	10	—
Isopoda	—	—	3	14

larvae were, the largest, a cottid, measuring 14 mm. It is reasonably clear that a positive relationship exists between food size and stickleback size. This relationship is also apparent when for each stickleback size-group the different food organisms, especially the common items (namely, *Bosmina*, *Holopedium*, and *Epischura*), are expressed as a percent of the total stomach content for that group (Table 8).

Diet in Relation to Sexual Maturity

Mature males showed a higher incidence of feeding (90%) than did gravid females (61%) (Table 9), the difference being statistically significant. ($\chi^2 = 13.811, n = 2, P = <0.01$).

Nongravid females, gravid females, and mature males fed on a variety of similar kinds of organisms (Table 9) and, except for *Epischura*, none of the items were of great importance as food. Since *Epischura* is the largest planktonic form, its predominance in the diet of large individuals is not unexpected. *Epischura* formed more than 90% of the bulk units and the mean number ingested was very much higher than for any other single item. In contrast to 54% of gravid females which had eaten this item, its occurrence in nongravid females and in males was considerably less, 18 and 16%, respectively. Planktonic crustaceans, insects,

TABLE 8.–Relative importance (percent) of food organisms of different bulk units in the diet of threespine stickleback of four size groups– <30 mm group contained 100 fish; 30-49 mm, 34 fish; 50-69 mm, 60 fish; and 70+ mm, 11 fish. Based on samples taken on 22 July and 5 August 1970.

Bulk units	Size group (mm) <30	30-49	50-69	70+	Item
≤ 1	48	29	26	8	Rotifera, nauplius, *Bosmina*, *Cyclops*, copepodids, harpacticoids, zooplankton eggs
2	3	1	1	3	*Alona*, *Daphnia*, *Diaptomus*, stickleback eggs
3	39	64	67	77	*Holopedium*
5	1	1	1	T	Chironomid larvae
11	8	8	6	12	*Epischura*
≥50	T	T	T	0	Chironomid pupae, fish

TABLE 9.–Stomach contents of nongravid and gravid females and sexually mature male threespine stickleback, Great Central Lake, 12 May-9 July 1971.

	Female						Male		
	Non-gravid			Gravid					
No. examined	22			28			81		
Percent with food	73			61			90		
Organism	1[1]	2[2]	3[3]	1	2	3	1	2	3
Rotifera	9	2	T	—	—	—	10	4	T
Cladocera:									
Holopedium	23	6	1	32	75	7	17	13	1
Bosmina	—	—	—	4	T	T	6	1	T
Alona	5	1	T	—	—	—	2	2	T
Copepoda:									
Epischura	18	141	94	54	268	92	16	230	94
Diaptomus	—	—	—	—	—	—	1	T	T
Cyclops	14	3	T	11	T	T	22	11	T
Harpacticoid	5	T	T	—	—	—	4	T	T
Copepodids	5	2	T	—	—	—	9	1	T
Insecta:									
Chironomidae L	27	4	1	4	T	T	17	1	T
Chironomidae P	18	T	1	11	T	T	15	2	3
Coleoptera	5	T	T	—	—	—	1	T	T
Ceratopogonidae	14	1	2	—	—	—	11	T	T
Other	18	T	T	14	T	T	15	T	T
Araneida	—	—	—	—	—	—	1	T	T
Acari	—	—	—	—	—	—	9	T	T
Ostracoda	5	T	T	—	—	—	5	T	T
Pelecypoda	—	—	—	—	—	—	15	T	T
Isopoda	—	—	—	—	—	—	1	T	T
Amphipoda	5	T	T	4	T	T	7	T	T
Eggs:									
Zooplankton	9	5	T	14	13	T	19	8	T
Stickleback	—	—	—	4	T	T	9	2	T
Detritus	—	—	—	1	—	—	13	—	—

[1]Percentage of stomachs with item.
[2]Mean number of items per stomach examined.
[3]Item = percent of total bulk units. T = Trace = < 1 organism or <1%.

eggs of zooplankton and stickleback, and other miscellaneous taxonomic groups, some of which are littoral in habitat, made up most of the remainder of the stomach contents. Males ate more benthic and epibenthic forms, as well as detritus (mainly sand and twigs), than did females. Detritus in individual male stomachs made up from 10 to 100% of the contents and was

present in 13 stomachs, compared with 1 for females. The ingestion of detritus by males is probably related to its role in nest building and not to feeding behavior per se.

Diel Feeding Rhythm and Variation in Diet

Despite some size differences in stickleback at sites A and B (station 1), feeding intensity indices (food weight/body weight × 100) for stickleback caught at a specific sampling time were similar during October and July. Active feeding took place mainly during postdawn and predusk hours, leading to two daily alternating feeding and "nonfeeding" periods (Figure 5). Differences between the mean indices for different times of day in the October and July series were subjected to the Kruskal-Wallis test (Siegel 1956) and found to be significant (October, $H = 25.71$, 4 df, $P = <0.0001$; July, $H = 28.97$, 7 df, $P = <0.001$). This periodicity in feeding was corroborated by the mean number of organisms present in stomachs at different times of day (Table 10).

The kinds of organisms consumed and their importance at different times of the diel cycle are presented in Table 10 for both the October and July series. Information for October is based on stickleback ranging in mean length from 37 to 44 mm. Stickleback examined in the July series were less uniform in size and ranged in mean length from 49 to 63 mm.

Considering the important food items, the composition of the diet changed through the daily cycle in October and July (Table 10). In October, *Bosmina* and *Holopedium* occurred in a very high percentage of the stomachs examined, regardless of sampling time. In terms of numbers consumed and bulk units, *Holopedium* was the dominant item, especially between 0700 and 1000 h. Between 1300 and 1900 h the relative importance of *Holopedium* was reduced somewhat by the increased consumption of *Bosmina*, *Alona*, *Epischura*, and eggs of zooplankton.

In July, *Holopedium* was the dominant food organism throughout the daily cycle. Although not as important as *Holopedium* in terms of numbers or bulk, eggs of zooplankton were present in a large proportion of the stomachs examined, ranging from 40% (0100 h) to 100% (1000 h), with consumption being greatest in the morning. *Epischura* was present in stomachs at most times of the day, but their contribution to the diet was highest during peak feeding times.

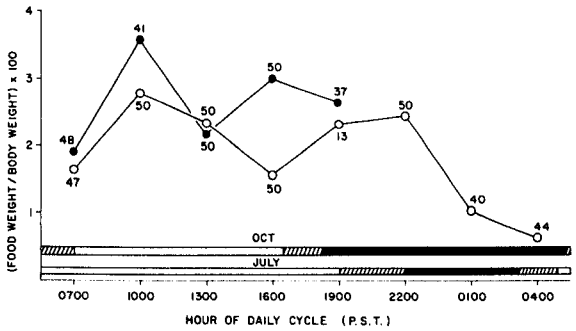

FIGURE 5.—Diel fluctuations in feeding intensity of threespine stickleback in October 1970 (closed circles) and July 1971 (open circles). The number associated with each datum point represents sample size. The horizontal bars indicate periods of daylight and darkness.

Rotifera were present in a large proportion of the stomachs throughout the diel cycle in October and July and were numerous compared to most other items. Their individual small size would tend to depress their importance as a food item.

Daily Ration and Maximal Meal Size

The described diel fluctuations in feeding intensity indicate that in July at least, consumption and evacuation occurred alternately over periods of approximately 6-h duration. On the average, a particle of food required about 6 h to pass through the stomach. Stomachs were least full at 0400 h when the contents amounted to 0.65% of the mean body weight but they were, on the average, never devoid of food, suggesting that feeding was continuous in the population. Freshly ingested organisms were present in some stomachs even during dark hours.

Recognizing two periods of consumption and stomach evacuation each of approximately 6-h duration, and the presence of "residual" content, the daily ratio (DR) in July can be calculated by the formula:

$$DR = R + P_1 + P_2$$

where R = residual content × food particle evacuation time,
P_1 = Major feeding index - residual content,
P_2 = Minor feeding index - residual content.

Substituting actual values indicated in Figure 5, the food consumed by stickleback in July amounted to (0.65 × 24/6) + (2.80 - 0.65) + (2.45 - 0.65) =

TABLE 10.–Occurrence, mean number, and relative importance in bulk units of various organisms consumed by threespine stickleback in Great Central Lake, October 1970 and July 1971. Data for sites A and B combined.

Month	Item	0700 h			1000 h			1300 h			1600 h			1900 h			2200 h			0100 h			0400 h			Total		
		1[1]	2[2]	3[3]	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
October	No. of fish		20			20			20			20			20													
	Mean length (mm)		39.2			37.1			38.8			41.1			43.8													
	Organisms:																											
	Rotifera	75	50	T	75	87	T	60	60	T	75	87	T	80	75	T										73	359	T
	Cladocera:																											
	Alona	—	—	—	45	4	1	—	—	—	30	19	7	20	32	13										19	55	6
	Bosmina	80	6	2	95	17	3	80	38	38	90	31	6	75	20	8										84	112	6
	Daphnia	25	T	T	5	T	T	5	T	T	—	—	—	15	T	T										10	T	T
	Holopedium	70	70	87	90	149	85	80	10	30	60	43	26	75	70	43										75	342	56
	Copepoda:																											
	Copepodids	10	T	T	15	T	T	55	4	4	55	15	3	25	5	1										32	24	1
	Cyclops	5	T	T	55	7	1	5	T	T	—	—	—	10	1	T										15	8	T
	Diaptomus	5	T	T	50	21	8	5	T	T	—	—	—	25	3	1										17	24	2
	Epischura	30	2	9	20	T	T	50	2	22	55	25	55	60	10	23										43	39	23
	Harpacticoid	—	—	—	35	T	T	20	T	T	35	T	T	—	—	—										18	T	T
	Insecta:																											
	Chironomid larvae	—	—	—	10	T	T	20	T	T	5	T	T	5	T	T										8	T	T
	Chironomid pupae	—	—	—	—	—	—	10	T	T	5	T	T	—	—	—										3	T	T
	Ceratopogonidae larvae	—	—	—	5	T	T	—	—	—	5	T	T	—	—	—										2	T	T
	Eggs - Zooplankton	55	3	1	55	3	T	45	2	2	35	2	T	55	42	8										49	52	29
	Other:																											
	Ostracoda	5	T	T	15	T	T	10	T	T	15	T	T	10	T	T										11	T	T
	Oligochaeta	—	—	—	15	T	T	—	—	—	15	T	T	—	—	—										6	T	T
	Turbellaria	—	—	—	10	T	T	5	T	T	—	—	—	—	—	—										3	T	T
	Pelecypoda	—	—	—	—	—	—	5	T	T	—	—	—	—	—	—										1	T	T
	Sum of means		131			348			116			222		258													1,015	
July	No. of fish		20			20			20			20			10			20			20			20				
	Mean length (mm)		58.8			57.2			50.5			49.4			59.8			54.4			59.6			63.1				
	Organisms:																											
	Rotifera	65	20	T	75	48	T	55	120	T	45	92	T	80	152	T	72	208	T	35	19	T	55	43	T	59	702	T
	Cladocera:																											
	Alona	—	—	—	45	56	3	15	T	T	15	T	T	10	T	T	4	13	1	10	3	7	5	16	14	9	88	1
	Bosmina	5	T	—	10	1	T	30	T	T	35	T	T	30	1	T	46	T	T	5	T	T	5	T	T	22	2	T
	Daphnia	—	—	—	10	T	T	—	—	—	10	T	T	—	—	—	—	—	—	—	—	—	—	—	—	T	T	T
	Holopedium	90	471	85	95	825	86	60	182	81	40	148	86	70	396	47	75	496	92	40	22	83	70	56	77	68	2,596	77
	Copepoda:																											
	Nauplii	—	—	—	20	6	T	50	33	1	25	2	T	—	—	—	—	—	—	—	—	—	—	—	—	12	41	T
	Copepodids	—	—	—	15	3	T	30	6	1	10	T	T	10	2	T	—	—	—	—	—	—	—	—	—	8	11	T
	Cyclops	35	6	T	55	17	T	15	T	T	5	T	T	—	—	—	25	1	T	—	—	—	—	—	—	18	24	T
	Diaptomus	5	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	T	T	T
	Epischura	40	18	12	70	20	7	35	9	14	20	4	8	50	113	50	25	2	1	15	T	T	—	—	—	30	166	18
	Harpacticoid	—	—	—	5	T	T	—	—	—	10	T	T	10	T	T	—	—	—	5	T	T	—	—	—	3	T	T
	Insecta:																											
	Chironomid larvae	5	T	T	—	—	—	—	—	—	—	—	—	10	T	T	4	T	T	—	—	—	—	—	—	T	T	T
	Chironomid pupae	15	T	T	—	—	—	—	—	—	5	T	T	—	—	—	—	—	—	—	—	—	10	T	T	3	T	T
	Other	20	T	T	—	—	—	5	T	T	—	—	—	—	—	—	4	T	T	10	T	T	5	T	T	6	T	T
	Eggs:																											
	Zooplankton	95	33	2	100	45	1	65	20	3	45	26	5	8	53	2	72	75	4	40	7	8	65	16	7	70	275	2
	Stickleback	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	T	T	—	—	—	T	T	T
	Other:																											
	Ostracod	5	T	T	5	1	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	T
	Fish	—	—	—	—	—	—	5	T	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	T	T	T
	Sum of means		548			1,022			370			272			717			795			51			131			3,906	

[1]Percent of stomachs with item. [2]Mean number of organisms per stomach. [3]Item = percent of total bulk units.

6.55% of their body weight. Some digestion would have occurred during consumption so this is a minimal value.

For October, failure to obtain feeding indices between 1900 and 0700 h over the diel cycle precluded similar estimation of the daily ration. However, if the residual content is assumed to be 0.65% of the body weight during periods lacking observations, the daily food consumption can be estimated to be 2.60 + 2.90 + 2.30 = 7.80% of the mean body weight.

Estimates of maximum meal size were obtained by plotting feeding indices for only those fish which were judged to have "full" stomachs during the postdawn feeding period (i.e., the most intensive feeding time of day) against length (Figure 6A). Data for stickleback in July were used because of their wide range in length. Despite considerable individual variation between fish of the same length obviously feeding intensity was inversely related to length (r = -0.788, df = 26, P <0.01). From the regression line fitted by the method of least squares, it can be predicted by extrapolation that, on the average, larval stickleback, which measure approximately 8 mm upon hatching, consume 7.5% of their body weight in a single meal, and that consumption in relation to body weight decreases 0.8% per 10 mm increase in length. As would be expected, large fish in a single meal eat more than do small fish and the relationship is of the positive exponential form (Figure 6B).

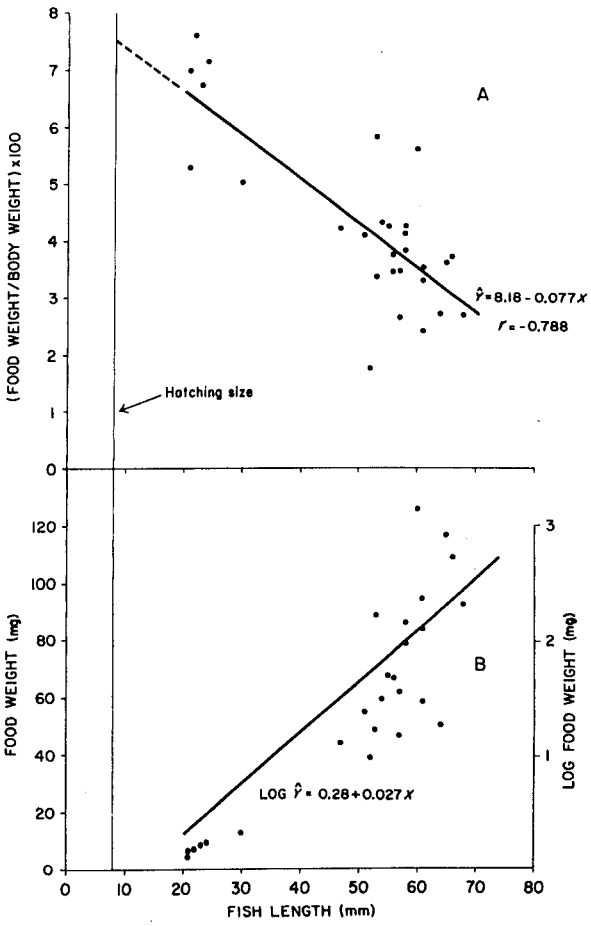

FIGURE 6.—The relation between maximum size of single meal (A) and weight of stomach contents (B) with length of threespine stickleback.

For stickleback in October and July (assuming mean lengths of 40 mm and 60 mm, respectively), the average meal size was approximately 5 and 3.5% of their body weight, respectively. Assuming two feeding periods per day, the daily ration becomes 10 and 7% of body weight. These values are in reasonable agreement with daily ration estimates based on diel fluctuations in stomach contents.

Discussion

During 1970 and 1971, the first 2 yr of a fertilization program attempting to increase sockeye salmon production in Great Central Lake, stickleback were observed to feed on a variety of organisms with planktonic crustaceans (cladocerans and copepods) and insects (chironomid pupae and larvae), to a lesser degree, being the main food organisms. These findings are consistent with observations on food of stickleback in a variety of freshwater habitats made by other investigators (Hartley 1948; Hynes 1950; Greenbank and Nelson 1959; Rogers 1968). From a trophic standpoint, the species is a secondary consumer.

The literature on feeding of fishes in both laboratory and in nature is replete with evidence that consumption is influenced by a multitude of factors. In the present study effort was focussed on examining seasonal and diel changes in feeding habits, possible influencing factors being limited to size and sexual maturity.

The most pronounced feature observed in the feeding of stickleback was the seasonal change in the importance of different kinds of organisms consumed. Although the food resource was not sampled in conjunction with the food studies, some general comments on food availability and selec-

tivity by stickleback in 1970 can be made using results of zooplankton studies by LeBrasseur and Kennedy (1972) (Figure 7). A more precise method of measuring the use of major planktonic forms in relation to availability would have been the employment of Ivlev's (1961) "electivity index," taking into account the comments of O'Brien and Vinyard (1974) regarding distribution of predator and prey. *Bosmina*, *Holopedium*, and *Diaptomus* were consumed approximately in relation to their abundance, although in the early part of the year relative utilization was highest for *Bosmina*. *Cyclops* and *Bosmina* were approximately equally abundant and exhibited somewhat similar seasonal fluctuations but utilization of *Bosmina* was sharply restricted during July and early August whereas *Cyclops* was relatively unutilized throughout the summer. Consumption of *Epischura*, a less abundant form which occurred mainly between May and September, was highest in June during the early part of the "bloom."

The reasons for the apparent differences in the relative utilization of the major food items would appear to differ. The shift from *Epischura*, despite rather uniform abundance, to smaller organisms, mainly *Holopedium* and *Bosmina*, through the season may be due to the decrease in average size of stickleback that occurred in midsummer. *Epischura*, which equals 11 bulk units compared with 3 and 1 for *Holopedium* and *Bosmina*, respectively, may have been too large an item to be consumed by the majority of stickleback present after July. Greenbank and Nelson (1959) and Rogers (1968) observed that feeding habits of *G. aculeatus* in Alaskan lakes changed through the summer and differed between individuals of different size. The disparity in relative utilization of *Bosmina* and *Cyclops*, which were of comparable abundance and individual size, cannot be thus explained. Rather, it would appear that the difference in their dietary importance may be explained by differences in spatial distribution affecting availability: *Cyclops*

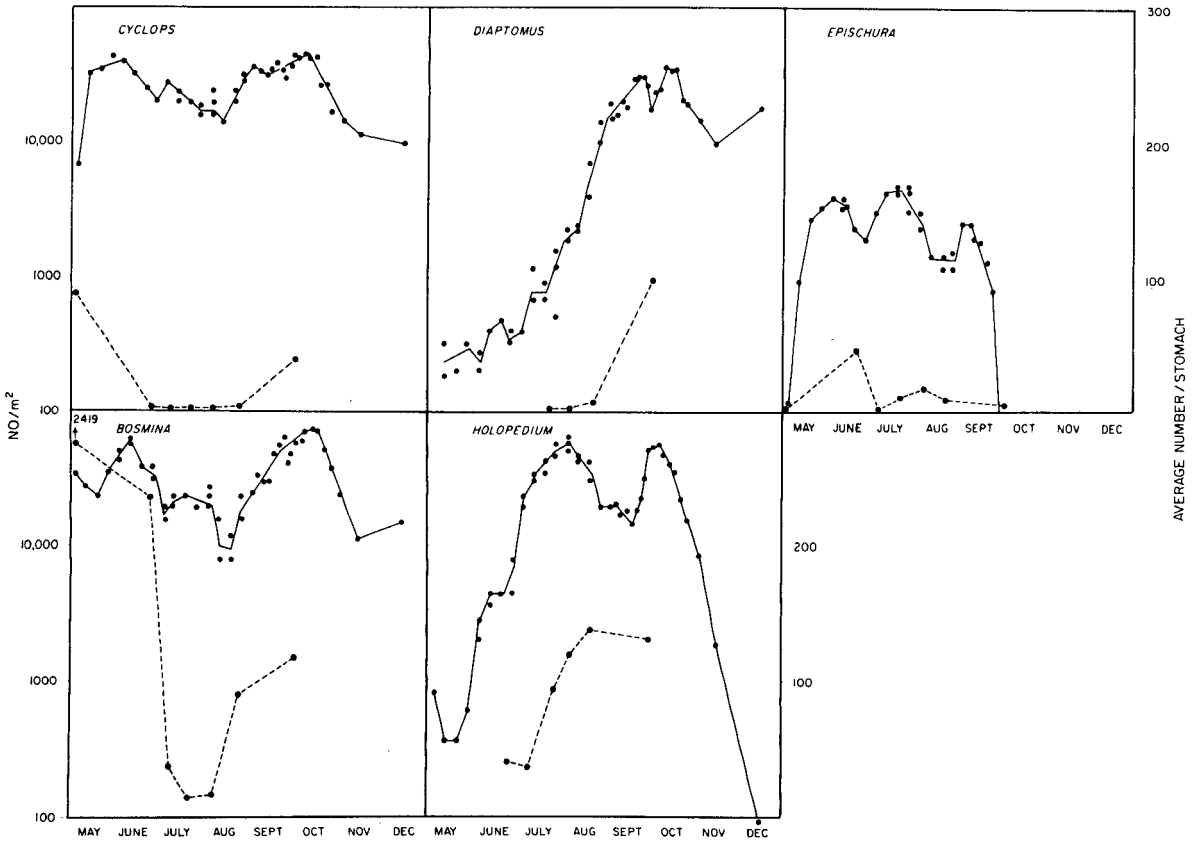

FIGURE 7.—Seasonal change in the biomass (unbroken line) of important prey species for threespine stickleback and the average number present per stomach. Graphs representing biomass were taken from LeBrasseur and Kennedy (1972) and are shown in logarithmic scale.

were hypolimnetic whereas *Bosmina* were mainly epilemnetic (LeBrasseur and Kennedy 1972, Figure 2). If temperature influences their distribution as is suggested by their distribution in relation to the thermocline, one might reasonably infer that *Cyclops* was less available than *Bosmina* to stickleback inhabiting the littoral and nearshore areas where water temperatures generally are highest. Consumption of *Holopedium* increased rapidly as the summer progressed. Consumption of *Diaptomus* increased during August and September. The appearance of these approximately similar sized species in the diet of stickleback paralleled their occurrence in population succession and maximum abundance in the relatively warm surface waters.

The diel feeding rhythm observed during July and October has not been described for *G. aculeatus* in fresh water but the pattern is exemplary of feeding periodicities described for a variety of freshwater and marine fishes. The association of peak feeding with postdawn and predusk periods in summer and late fall when the number of daylight hours differs suggests that feeding is light-dependent.

The literature on meal size and daily ration for *G. aculeatus* is rather scant considering the number of studies on the feeding biology of the species. Krokhin (1957) using the O_2 consumption method estimated that stickleback averaging 4.5 g in summer (August) consumed 5.1% of their body weight daily. Beukema (1968) feeding stickleback (2.5 g mean weight) Tubifex worms concluded that the contents of a well-filled stomach equalled 5.5% of the body weight, and that daily intake amounted to 12% of the body weight. Beukema recognized that the daily ration was rather high for adult fish and suggested that rapid digestibility of the food offered may have been responsible for the rather high food intake value obtained. The mean daily ration estimated in the present study from diel feeding rhythm curves for stickleback in July (mean length = 55 mm, mean weight = 2.4 g) and in October (mean length = 39 mm, mean weight = 0.7 g) was 6.5% and 7.8%, respectively, of their body weight. These estimates are only slightly less than those derived by doubling the maximum meal size of individuals of corresponding length (see Figure 6A), namely 7.8% and 10%. Considering that food intake is influenced by several factors such as size, physiology and behavior of individual, food deprivation, previous meal size, temperature, and prey digestibility (Darnell and Meierotto 1962; Davis and Warren 1968; Keast and Welsh 1968; Swenson and Smith 1973), one may conclude that the mean daily rations determined in this study are in close agreement with those obtained from experimental studies.

FEEDING RELATIONSHIP BETWEEN STICKLEBACK AND JUVENILE SOCKEYE SALMON

Information on competition between stickleback and juvenile sockeye salmon for food must be based on samples of each species from the same catch. Further, it must be assumed that individuals of each species taken together fed in the same area. In 1970, 7 of 105, or 6.6% of the sets yielded both species. Sockeye salmon equalled 5% of the two species combined. In 1971, the two species were caught together in 18 of 89, or 20.2% of the sets, and sockeye salmon equalled 2.2% of the combined catch.

Sockeye salmon and stickleback caught in the littoral zone in October 1970 and May-July 1971 were used in this comparative study (Tables 11 and 12). Only catches containing 5 or more individuals of each species were considered and a maximum number of 10 individuals of each species was examined from any one catch. For convenience, the catches were grouped according to the following time periods: October 1970, May-June 1971, and July 1971.

Stickleback through this period increased in average size as a result of seasonal growth. By contrast, sockeye salmon, although larger, decreased in average size. This decrease in size reflects the emigration from the lake of the larger individuals as smolts in the following spring. The relatively high percentage (20%) of stickleback with empty stomachs in July can be explained by the presence of the gravid females.

In general, stickleback and young sockeye salmon taken together exhibited considerable dietary overlap (Tables 11 and 12). Stomach contents of sockeye salmon were treated and analysed in accordance with methods used for stickleback. The degree of similarity in diet during each period was determined from occurrence data using Spearman's rank correlation coefficient, r_s (Siegel 1956). The r_s value indicates agreement in rank of food items and can range from + 1.0 for complete agreement to -1.0 for total disagreement. The tests were restricted to items which were not rendered unidentifiable through digestion and

TABLE 11.—Stomach contents of threespine stickleback in Great Central Lake, October 1970-July 1971.

Date	October 1970			May-June 1971			July 1971		
No. examined	25			46			56		
Percent empty	0			9			20		
Size range (mm)	27-76			40-86			42-86		
Mean length (mm)	39.5			54.0			59.8		
Food item	Percent of stomachs with item	Average no.[2] per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk
Rotifera	64	17	T[3]	17	2	T	48	10	T
Cladocera:									
Holopedium	100	77	59	39	27	2	63	33	3
Bosmina	100	37	9	46	4	T	14	T	T
Daphnia[1]	4	T	T	—	—	—	—	—	—
Alona	36	1	T	11	3	T	1	T	T
Copepoda:									
Epischura	40	5	14	59	109	40	57	69	22
Diaptomus	16	6	3	22	4	T	—	—	—
Cyclops	60	13	3	59	81	2	32	4	T
Copepodids	56	24	6	41	13	T	41	8	T
Nauplii	8	T	T	—	—	—	12	10	T
Harpacticoid	44	3	T	24	30	1	1	T	T
Insecta:									
Chironomid L	32	2	3	13	1	T	7	T	T
Chironomid P	2	T	T	9	T	T	5	T	T
Other	16	T	T	7	T	T	14	1	1
Mites	4	T	T	4	T	T	—	—	T
Eggs:									
Zooplankton	—	—	—	26	3	T	48	14	T
Fish	—	—	—	1	T	T	1	T	T
Other:									
Amphipoda	—	—	—	—	—	—	4	T	T
Pelecypoda	—	—	—	—	—	—	1	T	T
Ostracoda	—	—	—	7	T	T	1	T	T
Unidentifiable			0.0			52.0			72.0
Total			100.0			100.0			100.0

[1]Mainly *D. pulex*.
[2]Based on stomachs in which condition of contents permitted counts of various dietaries.
[3]T = Trace = < 1% of bulk.

which were present in at least 10% of the stomachs of one or the other foraging species. Infrequent ties in rank were broken in favor of the larger food item.

The r_s values for May-June and July samples were significant at $P = 0.05$ but that for October was not (Table 13). In October *Bosmina*, *Cyclops*, and copepodids were common items in the diet of stickleback compared to the larger *Epischura* and *Holopedium* in the sockeye salmon diet. A possible explanation for the difference between stickleback and sockeye diets in October may be that larger predators feed on larger prey: in October, sockeye salmon on the average measured 74.6 mm, stickleback 39.5 mm.

The observed dietary overlap indicates the existence of potential competition between stickleback and sockeye salmon for food in May-June and July. Accurate assessment of actual competition is contingent not only on information on food and feeding habits of the two foraging species but on other factors, such as their temporal and spatial associations during different life history stages and their abundance and growth in relation to food supply. For this study, data essential for quantitative assessment of competition during different seasons are inadequate or unavailable, although competition in winter is precluded by the apparent absence of stickleback. It is known however that when the two species occur together it is near shore or in the littoral zone, and that relative to stickleback sockeye salmon are few in number: sockeye salmon are almost the exclusive inhabitants of the limnetic zone (D. Robinson, pers. commun.). From the distribution patterns of the two species, it can be inferred that stickleback in Great Central Lake are not serious competitors of sockeye salmon for food despite their similarity in diet. Additionally, during this study the zooplankton abundance had increased substantially as a result of nutrient additions (LeBrasseur and Kennedy 1972) and the growth rate in sockeye salmon was faster than that observed under untreated lake conditions (Barraclough and Robinson 1972). However, in lakes where both species are abundant and overlap extensively in spatial distribution, utilization of a common food resource may affect production of one or both of the foraging species, especially during periods of reduced or limited food supply.

TABLE 12.–Stomach contents of young sockeye salmon in Great Central Lake, October 1970-July 1971.

Date	October 1970			May-June 1971			July 1971		
No. examined	18			40			35		
Percent empty	0			3			3		
Size range (mm)	58-95			28-82			37-75		
Mean length (mm)	74.6			63.0			60.0		
Food item	Percent of stomachs with item	Average no.[2] per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk	Percent of stomachs with item	Average no. per stomach	% of total bulk
Rotifera	11	T[3]	T	—	—	—	24	2	T
Cladocera:									
Holopedium	89	360	22	35	4	T	74	33	8
Bosmina	61	19	T	25	1	T	24	T	T
Daphnia[1]	56	2	T	—	—	—	—	—	—
Alona	6	T	T	—	—	—	—	—	—
Copepoda:									
Epischura	100	234	53	68	52	37	56	32	28
Diaptomus	22	T	T	15	2	T	—	—	—
Cyclops	11	T	T	43	50	3	35	5	T
Copepodids	11	T	T	45	11	T	35	8	T
Nauplii	—	—	—	—	—	—	15	2	T
Harpacticoid	—	—	—	5	T	T	—	—	—
Insecta:									
Chironomid L	—	—	—	3	T	T	—	—	—
Chironomid P	—	—	—	15	T	T	—	—	—
Diptera (pupae & adult)	11	3	3	30	T	T	6	T	T
Araneida	—	—	—	5	—	T	—	—	—
Remains	—	—	—	—	T	T	—	—	—
Other	—	—	—	—	—	—	3	T	T
Eggs - Zooplankton	6	4	T	15	1	T	24	5	T
Unidentifiable			21.0			57.0			62.0
Total			100.0			100.0			100.0

[1]Mainly *D. pulex*.
[2]Based on stomachs in which condition of contents permitted counts of various dietaries.
[3]T = Trace = < 1% of bulk.

TABLE 13.–Similarity in diet of threespine stickleback and young sockeye salmon in the littoral zone, Great Central Lake, October 1970-July 1971. Similarity was measured by Spearman's rank correlation coefficient (r_s). Rotifers are excluded from the calculations.

Time period	No. food items considered	r_s
October 1970	11	−0.068
May-June 1971	12	0.629*
July 1971	8	0.738*

*Significant at $P = 0.05$.

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LITERATURE CITED

BARRACLOUGH, W. E., AND D. G. ROBINSON.
1972. The fertilization of Great Central Lake. III. Effect on juvenile sockeye salmon. Fish. Bull., U.S. 70:37-48.

BUKEMA, J. J.
1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): The influence of hunger and experience. Behaviour 31:1-126.

CRAIG-BENNETT, A.
1931. The reproductive cycle of the three-spined stickleback, *Gasterosteus aculeatus*, Linn. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 219:197-279

DARNELL, R. M., AND R. R. MEIEROTTO.
1962. Determination of feeding chronology in fishes. Trans. Am. Fish. Soc. 91:313-320.

DAVIS, G. E., AND C. E. WARREN.
1968. Estimation of food consumption rates. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 204-225. IBP (Int. Biol. Programme) Handbook No. 3. Blackwell Sci. Publ., Oxf., Engl.

GREENBANK, J., AND P. R. NELSON.
1959. Life history of the threespine stickleback *Gasterosteus aculeatus* Linnaeus in Karluk Lake and Bare Lake, Kodiak Island, Alaska. U.S. Fish Wildl. Serv., Fish. Bull. 59:537-559.

HAGEN, D. W.
1967. Isolating mechanisms in threespine sticklebacks (*Gasterosteus*). J. Fish. Res. Board Can. 24:1637-1692.

HAGEN, D. W., AND L. G. GILBERTSON.
1972. Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific Northwest, America. Evolution 26:32-51.

HAGEN, D. W., AND J. D. MCPHAIL.
1970. The species problem within *Gasterosteus aculeatus* on the Pacific coast of North America. J. Fish. Res. Board Can. 27:147-155.

HARTLEY, P. H. T.
1948. Food and feeding relationships in a community of fresh-water fishes. J. Anim. Ecol. 17:1-14.

HYNES, H. B. N.
1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of

methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. (Translated from the Russian by Douglas Scott.) Yale Univ. Press, New Haven, 302 p.

KEAST, A. H., AND L. WELSH.
1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. 25:1133-1144.

KROGIUS, F. V., AND E. M. KROKHIN.
1957. Causes of the fluctuations in abundance of sockeye salmon in Kamchatka. (Tr. Probl. Temat. Soveshch. Zool. Inst. Akad. Nauk SSSR, 1956, 6:144-149.) Fish. Res. Board Can. Transl. Ser. 92, 5 p.

KROKHIN, E. M.
1957. [Determination of the daily food ration of young sockeye and three-spined stickleback by the respiration method.] [In Russ.] Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 44:97-110.

LEBRASSEUR, R. J., AND O. D. KENNEDY.
1972. The fertilization of Great Central Lake. II. Zooplankton standing stock. Fish. Bull., U.S. 70:25-36.

MANZER, J. I.
1971. Data on catch, size and food of the three-spined stickleback in Great Central Lake, British Columbia in 1970. Fish. Res. Board Can. Manuscr. Rep. 1145, 43 p.
1972. Data on catches, size, and food of the three-spined stickleback in Great Central Lake, British Columbia, in 1971. Fish. Res. Board Can. Manuscr. Rep. 1166, 52 p.

MARKOVTSEV, V. G.
1972. Feeding and food relationships of young sockeye and three-spine stickleback in Lake Dalnee. Izv. Tinro 82:227-233.

MCPHAIL, J. D., AND C. C. LINDSEY.
1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Board Can., Bull. 173, 381 p.

MEEK, A.
1916. The migrations of fish. Edward Arnold, Lond., 427 p.

MILLER, R. R., AND C. L. HUBBS.
1969. Systematics of *Gasterosteus aculeatus*, with particular reference to intergradation and introgression along the Pacific Coast of North America: A commentary on a recent contribution. Copeia 1969:52-69.

MULLEM, P. J. VAN, AND J. C. VAN DER VLUGT.
1964. On the age, growth and migration of the anadromous stickleback *Gasterosteus aculeatus* L. investigated in mixed populations. Arch. Néerl. Zool. 16:111-139.

NARVER, D. W.
1969. Phenotypic variation in threespine sticklebacks (*Gasterosteus aculeatus*) of the Chignik River system, Alaska. J. Fish. Res. Board Can. 26:405-412.
1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27:281-316.

O'BRIEN, W. J., AND G. L. VINYARD.
1974. Comment on the use of Ivlev's electivity index with planktivorous fish. J. Fish. Res. Board Can. 31:1427-1429.

PARSONS, T. R., C. D. MCALLISTER, R. J. LEBRASSEUR, AND W. E. BARRACLOUGH.
1972. The use of nutrients in the enrichment of sockeye salmon nursery lakes (a preliminary report). *In* M. Ruivo (editor), Marine pollution and sea life, p. 519-525. Fishing News (Books) Ltd., Surrey and Lond., Engl.

PARSONS, T. R., K. STEPHENS, AND M. TAKAHASHI.
1972. The fertilization of Great Central Lake. I. Effect on primary production. Fish. Bull., U.S. 70:13-23.

RICKER, W. E.
1937. The food and the food supply of sockeye salmon (*Oncorhynchus nerka* Walbaum) in Cultus Lake, British Columbia. J. Biol. Board Can. 3:450-468.

ROGERS, D. E.
1968. A comparison of the food of sockeye salmon fry and threespine sticklebacks in the Wood River lakes. *In* R. L. Burgner (editor), Further studies of Alaska sockeye salmon, p. 1-43. Univ. Wash. Publ. Fish., New Ser. 3.

ROGERS, D. E., M. O. NELSON, J. J. PELLA, AND R. L. BURGNER.
1963. Relative abundance and distribution of fish species in Lake Aleknagik. Res. Fish. Fish. Res. Inst. Univ. Wash. 1962:14-15. (Univ. Wash. Coll. Fish. Contrib. 147.)

RUGGLES, C. P.
1965. Juvenile sockeye studies in Owikeno Lake, British Columbia. Can. Fish Cult. 36:3-21.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Toronto, 312 p.

SIMPSON, G. G., AND A. ROE.
1939. Quantitative zoology. McGraw-Hill Book Co., Inc., N.Y., 414 p.

SWENSON, W. A., AND L. L. SMITH, JR.
1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30:1327-1336.

WINDELL, J. T.
1968. Food analysis and rate of digestion. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 197-203. IBP (Int. Biol. Programme) Handbook No. 3. Blackwell Sci. Publ., Oxf., Engl.

PREDATOR-PREY RELATIONSHIP BETWEEN PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*, LARVAE AND A PREDATORY HYPERIID AMPHIPOD, *HYPEROCHE MEDUSARUM*[1]

HEIN VON WESTERNHAGEN AND HARALD ROSENTHAL[2]

ABSTRACT

Predatory efficiency of *Hyperoche medusarum* (Hyperiida, Amphipoda) on yolk-sac larvae of Pacific herring, *Clupea harengus pallasi*, was studied in the laboratory under continuous light conditions: 1, 5, 10, and 50 herring larvae were exposed to 1, 2, 4, 8, and 16 hyperiids in 500-ml beakers. It was found that the number of attacked larvae per unit time increased with rising predatory and/or prey density. Individual mean predation rate was found to decline with increasing predator as well as prey densities, prolonged exposure times, and the presence of alternative prey.

Aside from starvation (Sette 1943; Schnack 1972), one major cause of mortality in marine fish larvae is assumed to be predation (Stevenson 1962), the predators frequently being crustaceans, as described by Garstang (1900), Lebour (1925), Davis (1959), Lillelund (1967), Rosenthal (1967), Kabata (1970), Lillelund and Lasker (1971), Theilacker and Lasker (1974), and others. The pelagic hyperiid amphipod *Hyperoche medusarum* occurs commonly off the Oregon coast (Lorz and Pearcy 1975), in Californian waters (Hurley 1956), in the North Atlantic (Shoemaker 1930; Bowman et al. 1963; Dunbar 1963), in the North Sea (Sars 1895; Evans and Sheader 1972), and in New Zealand waters (Hurley 1955). In British Columbia waters it occurs commonly in the upper layers (<30 m) of the water column (Bowman 1953), and in Departure Bay (Vancouver Island) its juveniles are frequently found clinging to the exumbrellae of hydromedusae (Westernhagen 1976).

The cooccurrence of large numbers of juvenile *H. medusarum* with newly hatched larvae of the Pacific herring, *Clupea harengus pallasi*, was incidentally discovered in 1974 at the pier of the Pacific Biological Station, Departure Bay. Field observations indicated that *Hyperoche* juveniles preyed on herring larvae and occasionally on other fish larvae. Since this was the first record on a possible predator-prey relationship between *H. medusarum* and marine fish larvae, this study was initiated to shed some light on the predatory efficiency of this amphipod.

MATERIAL AND METHODS

For prey, yolk-sac larvae (8.0-9.5 mm TL (total length)) of the Pacific herring incubated in the laboratory were used. Immature *H. medusarum* (1.48-1.80 mm TL) which had aggregated beneath a light at night were caught with a pail and separated from other plankton organisms with a large bore pipette.

Experiments were performed in filtered seawater in 500-ml beakers (salinity 28‰; temperature 9°C; constant light). The water surface of the beakers was covered with 300-μm mesh size nylon gauze in order to keep the amphipods from breaking through the surface. Because *Hyperoche* specimens in their natural habitat were occasionally found resting on the exumbrellae of medusae, a strip of nylon gauze (50×20 mm) hanging from the surface cover provided attachment for the amphipods when needed.

Different numbers of herring larvae 1, 5, 10, and 50 were exposed to 1, 2, 4, 8, and 16 hyperiids for three exposure periods (2, 4, and 8 h). The number of replicates for all predator/prey ratios were 4, 6, and 5 for the 2-, 4-, and 8-h exposure periods. Some additional experiments with 6- and 10-h exposure periods were used for the computation of a mean attack rate on the basis of 111 h of observation. Eleven trials using 25 herring and 25 flatfish larvae with 16 amphipods were also conducted. One additional control vessel (50 herring larvae, no

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amphipods) was used for each exposure period. Mortality of larvae was measured every 2, 4, and 8 h by means of direct counts. All remaining larvae were removed, and healthy, wounded, and dead larvae were counted. The original number of herring larvae then was restored before a new experiment was started. Between experiments, the hyperiids were provided with food in order to reduce cannibalism.

RESULTS

Swimming and Feeding Behavior of *Hyperoche medusarum*

Two modes of swimming were observed: 1) quick darting movements with the body kept in a horizontal position; and 2) slow hovering, in which the body was held in a vertical position, and the pleopods beat continuously. The latter mode of swimming was maintained for periods longer than 20 min, but the speed of swimming was slow (about 10 cm/min). It was only during swimming that *Hyperoche* would, by chance encounter, capture a herring larva. The amphipod usually grasped the tail but attacks at the head and the midportion of the larva also occurred. An attacked larva did not survive long. The larva attempted to shake the amphipod off for a few minutes, then sank to the bottom where it was eaten by the *Hyperoche*. Larvae were not always consumed. Frequently, amphipods clung to a larva for only a few seconds but the wound inflicted during this process inevitably lead to the death of the larva. Wounded larvae which were removed after termination of the experiment never survived for more than 4-5 h when kept in separate beakers.

Between swimming activities, the amphipods either remained on the bottom (probably an artifact due to the small size of the beakers—in large enough containers *Hyperoche* juveniles swam continuously (Westernhagen 1976)), or attached themselves with the posterior pereiopods to the nylon gauze provided in the beakers for this purpose and assumed a resting posture. This posture has been described for *Hyperia galba* by Bowman et al. (1963) and for *Hyperoche medusarum* by Evans and Sheader (1972). The latter authors defined the posture as an "inactive curled position head and urus directed away from the substrate it (the animal) sits on." Larvae that bumped into resting amphipods were not pursued or captured.

Predatory Efficiency of *Hyperoche medusarum*

The results of all experiments were summarized and presented as the number of larvae attacked per hour at different predator and prey densities (Figure 1). The number of wounded and killed larvae was dependent on two factors, the density of the herring larvae and the density of hyperiids. With increasing numbers (predator or prey) larval mortality per hour increased, reaching a value of more than two larvae killed or wounded per hour at the 16 *Hyperoche* and 50 herring larvae combination.

The number of larvae attacked per unit time (1 h) depended to a great extend on the duration of the experiment (Figure 2). Experiments with short exposure times (2 h) yielded for all larvae and hyperiid combinations higher attack rates per hour than experiments lasting 4 or 8 h. The mean predatory efficiency of the hyperiids was affected also by their density in each beaker. The number of larvae attacked per unit time decreased as the density of the predators increased (Figure 3). It is for this reason that there are different values for the number of herring larvae attacked per hour by one hyperiid (Figure 4), (A) for the observation of one single hyperiid, and (B) for the calculated mean predation rate of a hyperiid from experiments with 1, 2, 4, 8, and 16 *Hyperoche*. Yet both curves show that an increase of a potential prey in a constant environment beyond a certain density

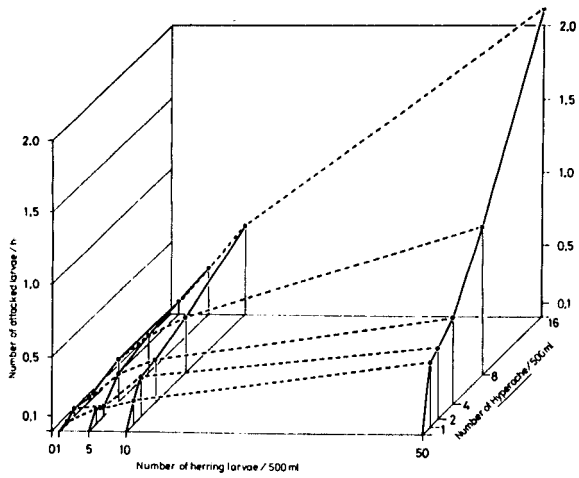

FIGURE 1.—Predatory efficiency of *Hyperoche medusarum* on yolk-sac larvae of *Clupea harengus pallasi* at different predator and prey densities. Water temperature: 9°C; total observation time: 111 h; observation periods: 20.

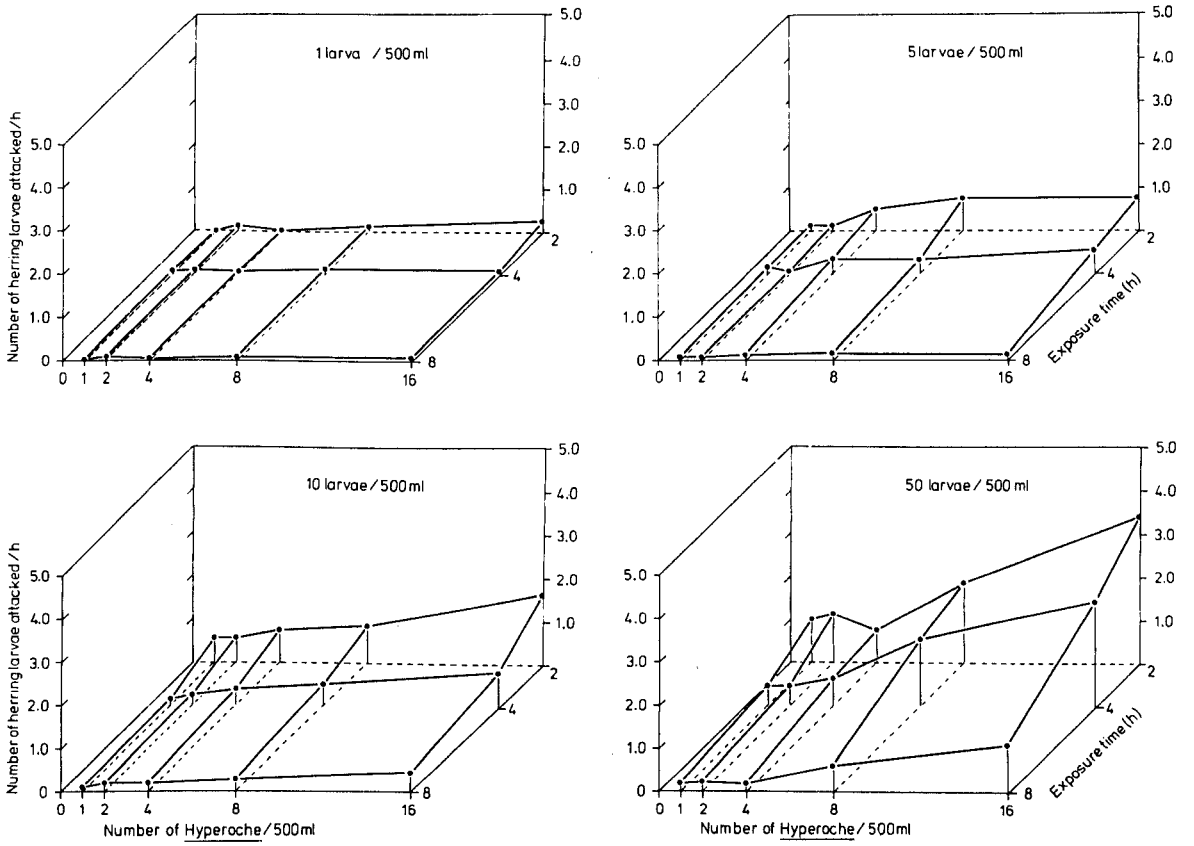

FIGURE 2.–Mean number of yolk-sac larvae of *Clupea harengus pallasi* attacked by *Hyperoche medusarum* after different exposure times. Water temperature 9°C.

does not necessarily lead to a corresponding increase in predation. At herring larvae densities of 5/500 ml and 10/500 ml, one individual hyperiid attacked 0.1 larvae/h and 0.16 larvae/h, respectively. At 50 larvae/500 ml the attack rate was 0.45 larvae/h. Assuming a linear increase in attack rate, we would have expected rates of 1.0 and 0.8 larvae/h.

Alterations in predation rates of *Hyperoche* were obtained when heterogenous prey was offered (25 herring larvae + 25 flatfish larvae), and Figure 3 shows that predation on larvae was remarkably reduced. Of the 0.07 larvae attacked per hour by one hyperiid, 0.055 (78%) were herring larvae and 0.015 (22%) flatfish larvae, thereby showing a pronounced preference for herring.

DISCUSSION

Figure 1 shows a clear, direct relationship between number of attacked larvae and both larval and hyperiid density. Increase in larval as well as predator density lead to increasing attack rates per hour. Because searching and contacting are random, this response was expected and has been described by Murdoch (1971) for predator-prey interaction. That relatively more larvae are attacked per hour during short exposure periods than during long ones (Figure 2) can be partially explained by a rapid thinning out effect on prey in confined containers, a problem discussed by Murdoch (1969) for the predation of *Thais* and *Acanthina* on *Mytilus* and *Balanus*. These data suggest that short observation periods are preferable in experiments of this type, a point frequently neglected in experiments with exposure times of 20 and more hours (Lillelund 1967; Lillelund and Lasker 1971; Theilacker and Lasker 1974; Ambler and Frost 1974), leading to an underestimate of the actual possible predation rate. An additional factor may be the degree of satiation, which could be shown for invertebrates to

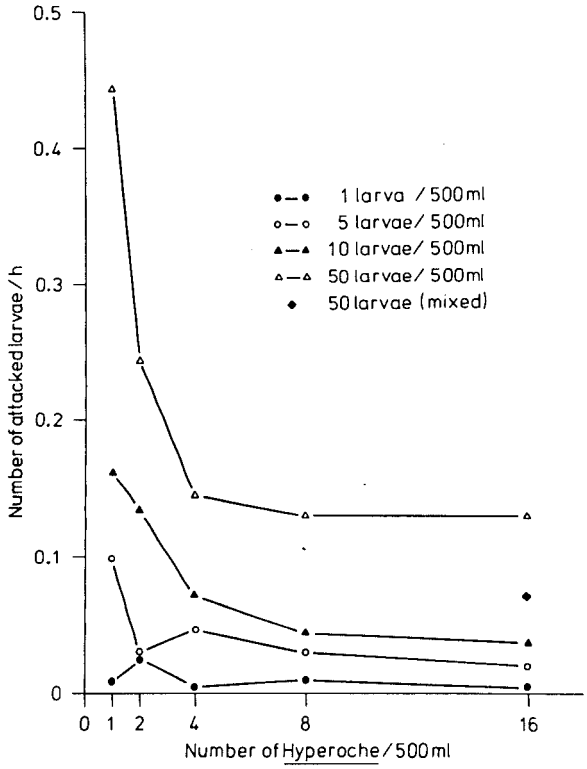

FIGURE 3. – Mean number of yolk-sac larvae of *Clupea harengus pallasi* attacked by *Hyperoche medusarum* during 1-h exposure time in an experimental volume of 500 ml at different larval concentrations. Water temperature 9°C. the "mixed" trial was provided with 25 herring and 25 flatfish larvae (11 replicates, 64 h total observation time).

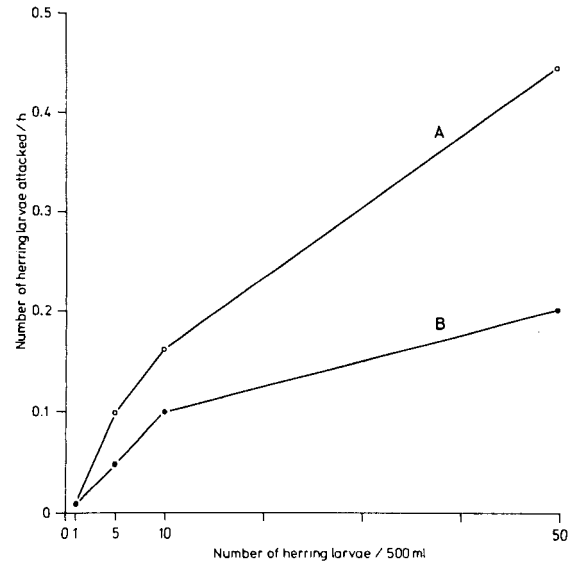

FIGURE 4.–Mean number of yolk-sac larvae of *Clupea harengus pallasi* attacked per hour by one *Hyperoche* at different larval densities:
A. data of actual experiments with single hyperiids;
B. data obtained from mean values for experiments with 1, 2, 4, 8, and 16 hyperiids/500 ml.

reduce the rate of predation (Holling 1966; Brandl and Fernando 1974).

It became evident through the experiments that predation rate was also influenced by the number of predators present in an experimental beaker (Figure 3). Calculated mean individual predation rates in experiments using 50, 10, and 5 larvae decreased as the number of hyperiids in one container increased. Lillelund (1967) observed the same phenomenon in his experiment using cyclopids preying on larvae of *Osmerus eperlanus*, and Salt (1967) noted the same trend in experiments using the predatory protozoan *Woodruffia metabolica* preying on *Paramecium*. We consider this phenomenon an artifact caused by more than one predator feeding on the same prey, an event frequently observed at higher predator densities. This is unlikely to occur in the natural habitat, because a herring larva once killed by its predator which is still attached to it would sink down to the bottom out of the reach of the other *Hyperoche*.

The number of herring larvae attacked did not increase proportionally with an increase of herring larvae available for the predators (Figure 4). This phenomenon has been termed "functional response" (type 2 response) by Holling (1966), and is believed to occur commonly in preying invertebrates. Similar responses are displayed by the house cricket, *Acheta domesticus* (Pimentel and Cranston 1960); *Podiscus maculiventris* (Morris 1963); *Acanthina* sp. (Murdock 1969); *Tortanus discaudatus* (Ambler and Frost 1974); and *Euphausia pacifica* (Theilacker and Lasker 1974). In a typical functional response curve, the number of prey eaten or attacked per predator increases to reach or approach a maximum at an asymptote (Murdoch 1971). Although the curves in Figure 4 do not yet approach an asymptote due to insufficient prey density, the trend towards a maximum attacking rate at a given prey density is noticeable.

Hyperoche medusarum exposed to two species of fish larvae clearly discriminated disproportionately between these two. In Figure 3, the total number of larvae attacked in trials providing alternate prey at equal densities is given as 0.7 individuals/h. Of these, 0.055 were herring larvae and 0.015 flatfish larvae. Discrimination between two prey species, which is likely to occur only in predators with searching and food selection

behavior (Murdoch and Marks 1973), might be either caused by different distribution of prey species (Oaten and Murdoch 1975), differences in palatibility (Holling 1965), avoidance behavior of the prey, or conditioning and/or training of the predator (Murdoch 1969; Oaten and Murdoch 1975) in cases of weak preferences.

Although generally *H. medusarum* was considered to lead a parasitic life on medusae (Sars 1895) such as *Cyanea capillata* (Bowman et al. 1963) or *Pleurobrachia pileus* (Evans and Sheader 1972), the results of our experiments show that even in the presence of alternate prey this amphipod displays considerable predation on herring larvae.

Unlike another carnivorous hyperiid, *Parathemisto gaudichaudi*, which hunts moving plankton visually (Sheader and Evans 1975), *H. medusarum* depends on random encounters with its prey. Many carnivorous copepods display the same behavior (Dziuban 1937; Fryer 1957; Lillelund 1967; Rosenthal 1972; Brandl and Fernando 1974; Ambler and Frost 1974). This mode of hunting requires a relatively high density of prey individuals which at times is provided by the enormous numbers of newly hatched herring larvae. During this investigation, herring larvae density during the day at the water surface was frequently above 2 larvae/100 cm^2 (direct observations). Simultaneous mass occurrences of *H. medusarum* suggest that the amphipods could possibly contribute considerably to herring larvae mortality, especially since conditioning to abundant prey organisms is comprehensible as could be shown by Sheader and Evans (1975) for *P. gaudichaudi* and its feeding on fish larvae. In fact stomach-content analyses of *H. medusarum* captured during this study period revealed that the amphipods had eaten considerable amounts of fish larvae (Westernhagen 1976).

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LITERATURE CITED

AMBLER, J. W., AND B. W. FROST.
1974. The feeding behavior of a predatory planktonic copepod, *Tortanus discaudatus*. Limnol. Oceanogr. 19:446-451.

BOWMAN, T. E.
1953. The systematics and distribution of pelagic amphipods of the families Vibiliidae, Paraphronimidae, Hyperiidae, Dairellidae, and Phrosinnidae from the northeastern Pacific. Ph.D. Thesis, Univ. California, Los Ang., 430 p.

BOWMAN, T. E., C. D. MEYERS, AND S. D. HICKS.
1963. Notes on associations between hyperiid amphipods and medusae in Chesapeake and Narragansett Bays and the Niantic River. Chesapeake Sci. 4:141-146.

BRANDL, Z., AND C. H. FERNANDO.
1974. Feeding of the copepod *Acanthocyclops vernalis* on the cladoceren *Ceriodaphnia reticulata* under laboratory conditions. Can. J. Zool. 52:99-105.

DAVIS, C. C.
1959. Damage to fish fry by cyclopoid copepods. Ohio J. Sci. 59:101-102.

DUNBAR, M. J.
1963. Amphipoda. Sub-order: Hyperiidea Family: Hyperiidae. Cons. Perm. Int. Explor. Mer, Fiches Identification Zooplankton 103:2-4.

DZIUBAN, N. A.
1937. On the nutrition of some *Cyclopidae* (*Crustacea*). C.R. (Dokl.) Akad. Sci. URSS, Nour. Sér. 17:319-322.

EVANS, F., AND M. SHEADER.
1972. Host species of the hyperiid amphipod *Hyperoche medusarum* (Krøyer) in the North Sea. Crustaceana (Suppl.) 3:275-276.

FRYER, G.
1957. The feeding mechanism of some freshwater cyclopoid copepods. Proc. Zool. Soc. Lond. 129:1-25.

GARSTANG, W.
1900. Preliminary experiments on the rearing of sea-fish larvae. J. Mar. Biol. Assoc. U.K. 6:70-93.

HOLLING, C. S.
1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45:1-60.
1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48:1-86.

HURLEY, D. E.
1955. Pelagic amphipods of the sub-order *Hyperiidae* in New Zealand waters. I.–Systematics. Trans. R. Soc. N.Z. 83:119-194.
1956. Bathypelagic and other Hyperiidae from Californian waters. Allan Hancock Found., Occas. Pap. 18, 25 p.

KABATA, Z.
1970. Crustacea as enemies of fishes. *In* S. F. Snieszko and H. A. Axelrod (editors), Diseases of fishes. Vol. 1, p. 128-133. T.F.H. Publ. Inc., Jersey City, N.J.

LEBOUR, M. V.
1925. Young anglers in captivity and some of their enemies. A study in a plunger jar. J. Mar. Biol. Assoc. U.K. 13:721-734.

LILLELUND, K.
1967. Experimentelle Untersuchungen über den Einfluss carnivorer Cyclopiden auf die Sterblichkeit der Fischbrut. Z. Fisch. Hilfswiss. 15:29-43.

LILLELUND, K., AND R. LASKER.
1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull., U.S. 69:655-667.

LORZ, H. V., AND W. G. PEARCY.
1975. Distribution of hyperiid amphipods off the Oregon coast. J. Fish. Res. Board Can. 32:1442-1447.

MORRIS, R. F.
1963. The effect of predator age and prey defense on the functional response of *Podisus maculiventris* Say to the density of *Hyphantria cunea* Drury. Can. Entomol. 95:1009-1020.

MURDOCH, W. W.
1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39:335-354.
1971. The developmental response of predators to changes in prey density. Ecology 52:132-137.

MURDOCH, W. W., AND J. R. MARKS.
1973. Predation by coccinellid beetles: Experiments on switching. Ecology 54:160-167.

OATEN, A., AND W. W. MURDOCH.
1975. Switching, functional response, and stability in predator-prey systems. Am. Nat. 109:299-318.

PIMENTEL, D., AND F. CRANSTON.
1960. The house cricket, *Acheta domesticus*, and the house fly, *Musca domestica*, as a model predator-prey system. J. Econ. Entomol. 53:171-172.

ROSENTHAL, H.
1967. Parasites in larvae of the herring (*Clupea harengus L.*) fed with wild plankton. Mar. Biol. (Berl.) 1:10-15.
1972. Über die Geschwindigkeit der Sprungbewegungen bei *Cyclops strenuus* (Copepoda). Int. Rev. Gesamten Hydrobiol. 57:157-167.

SALT, G. W.
1967. Predation in an experimental protozoan population (*Woodruffia-Paramecium*). Ecol. Monogr. 37:113-144.

SARS, G. O.
1895. An account of the crustacea of Norway. Vol. 1. Amphipoda. Alb. Cammermeyers Forlag, Copenh., 711 p.

SCHNACK, D.
1972. Nahrungsökologische Untersuchungen an Heringslarven. Ber. Dtsch. wiss. Komm. Meeresforsch. 22:273-343.

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including the growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv., Fish. Bull. 50:149-237.

SHEADER, M., AND F. EVANS.
1975. Feeding and gut structure of *Parathemisto gaudichaudi* (Guerin) (Amphipoda, Hyperiidea). J. Mar. Biol. Assoc. U.K. 55:641-656.

SHOEMAKER, C. R.
1930. The amphipoda of the Cheticamp expedition of 1971. Contrib. Can. Biol. Fish. 5:221-359.

STEVENSON, J. C.
1962. Distribution and survival of herring larvae (*Clupea pallasi* Valenciennes) in British Columbia waters. J. Fish. Res. Board Can. 19:735-810.

THEILACKER, G. H., AND R. LASKER.
1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 287-299. Springer-Verlag, Berl.

WESTERNHAGEN, H. VON.
1976. Some aspects of the biology of the hyperiid amphipod *Hyperoche medasarum*. Helgoländer wiss. Meeresunters. 28:43-50.

ESTIMATES OF RATES OF TAG SHEDDING BY NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*

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ABSTRACT

Type-I (immediate) and Type-II (instantaneous) rates of tag shedding by North Pacific albacore, *Thunnus alalunga*, are estimated using data from a double-tagging experiment. Type-I shedding is estimated to be about 0.12 and Type-II to be between 0.086 and 0.098 on an annual basis. The paper also contains a discussion on the accuracy of the estimates, and a method is developed to estimate possible bias due to fishermen reporting double tag recoveries as single tag recoveries. The possible bias is estimated to be low.

A tagging program was initiated in 1971, and is continuing, on North Pacific albacore, *Thunnus alalunga* (Bonnaterre), to examine their migration patterns, to obtain information for use in population studies, and to estimate rates of mortality. Because loss of tags through shedding can cause estimates of mortality to be biased upwards unless corrected for, part of the tagging program in 1972 consisted of an experiment in which 788 albacore were double-tagged to evaluate tag shedding by this species.

Chapman et al. (1965) developed a formulation of the return of single- and double-tagged fish which includes instantaneous loss rates due to fishing mortality, other mortality, and tag shedding. They then solved for the instantaneous rate of tag shedding given data from double-tagging experiments. Bayliff and Mobrand (1972) extended the work of Chapman et al. to provide estimates of the portion of tags which are retained after immediate shedding occurs. Results of the use of the Bayliff and Mobrand procedure to estimate rates of tag shedding from the double-tagging experiment on North Pacific albacore are presented in this paper.

METHODS

The tagging program is being conducted jointly by the National Marine Fisheries Service[2] (NMFS), NOAA, and the albacore fishing industry through the American Fishermen's Research Foundation[3] (AFRF).

Albacore were caught by commercial jig boats and a bait boat on charter to the AFRF. Fishing operations on jig boats were conducted with standard commercial albacore feathered jig-fishing equipment and commercial trolling methods. Most of the fish that were tagged and released from the bait boat were caught by the "winging" method of live-bait, pole-and-line fishing, whereby a fish is caught on an anchovy-baited barbless hook on the end of a short line attached to a stout pole. Immediately after hooking, the fish is lifted out of the water, swung toward the fisher, and caught under the arm of the fisher, who then removes the hook. A small number of the fish tagged from the bait boat were taken by trolling feathered jigs and on rod-and-reel using live anchovy as bait.

Special care was exercised to tag and release only fish judged to be in very good condition. Fish which showed signs of severe bleeding, which were hooked through the roof of the mouth or which showed signs of extreme exhaustion, were not tagged. For each tagged and released fish records were kept of the number of the tag, the date and time of tagging, the length of fish to the nearest lower centimeter, condition of fish, and sea surface temperature. A fish caught by pole and line was measured with a large caliper and tagged with two tags inserted almost simultaneously by a technician while the fisher held the fish under his arm. A fish caught on trolling gear and rod-and-reel was

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[3] AFRF administers revenues derived from an assessment paid on U.S. - landed albacore.

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measured on a Naugahyde-covered foam measuring pad and tagged by a technician while it was on the pad. In order to tag an albacore on each side, using this method, the fish had to be turned from side-to-side.

Spaghetti-dart type Floy[4] tags are being used in the tagging program. The tags are made of yellow Resinite tubing, 12 to 13 cm long and similar in structure to those described by Yamashita and Waldron (1958) and identical to those used by Fink (1965). The tags were inserted on both sides of the fish below the second dorsal fin with the aid of a beveled stainless steel piece of tubing, 14 to 16 cm long and 0.135- or 0.156-inch inside diameter. The tags were inserted so that the barb of the tag was lodged around the pterygiophores of the second dorsal fin.

We estimated rates of tag shedding using the notation and methodology of Bayliff and Mobrand (1972) for yellowfin tuna as did Lenarz et al. (1973) in a similar study on bluefin tuna. Bayliff and Mobrand's equations for returns of tags are:

$$n_{ddk} = F\tau N_D \pi \rho^2 e^{-(F + X + 2L)t_k} \quad (1)$$

and

$$n_{dsk} = 2F\tau N_D \pi \rho \, (1 - \rho e^{-Lt} k) e^{-(F + X + L)t_k} \quad (2)$$

where

t_k = time at the middle of the kth recovery period of length τ days ($k = 1, 2$);

n_{ddk} = number of returns of double-tagged fish retaining both tags during the period centered at t_k;

n_{dsk} = number of returns of double-tagged fish retaining only one tag during the period centered at t_k;

N_D = number fish released with double tags;

π = portion of tagged fish which remain alive after the immediate mortality, including Type I tagging mortality, has taken place;

ρ = portion of the tags which are retained after Type-I (immediate) shedding has taken place;

F = instantaneous rate of fishing mortality;

X = instantaneous rate of other mortality (other included natural mortality, Type-II (long-term) tagging mortality, and apparent mortality due to migrations from the fishery); and

L = instantaneous rate of tag shedding (Type-II shedding).

Bayliff and Mobrand (1972), using Equations (1) and (2), showed that

$$\ln \frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = -Lt_k + \ln \rho = y_k \quad (3)$$

where y_k is an estimate of the natural logarithm of the proportion of tags retained up to time t_k. Note that the first factor of the right-hand side of Equation (2) is the integer 2. Both Bayliff and Mobrand (1972) and Lenarz et al. (1973) mistakenly left this multiplier out of the equation in their papers. However, the error was typographical and did not affect their derivations or results. Given n_{ddk}, n_{dsk}, and t_k, L and ρ are estimated using simple linear regression; or as in the case of this study when only two recovery periods are used, the solution of two simultaneous equations. Equations (1) and (2) assume that L and the total of F and X are constant over t_k. Since the albacore fishery is seasonal, the assumption is likely to be violated. The effect of the violation has not been examined.

RESULTS

Release and return data through 1973 are shown in Table 1. The number of returns in 1974 was insufficient for analysis. A chi-square test indicated that gear type did not have a significant effect on the proportions of single- and double-tag returns in 1972 ($\chi^2 = 1.117$, df = 1). Data from both gears were combined for the remainder of the analysis.

Estimates of ρ and L are shown in Table 2. Only returns that could be specified to the nearest week are included in Table 1. Precise dates of recovery

TABLE 1.–Tag releases and returns with information on date of recovery for North Pacific albacore and double-tag study.

Gear type	1972 double-tag releases	1972 returns: Double (n_{dd1})	1972 returns: Single (n_{ds1})	1972 returns: Average days out (t_2)	1973 returns: Double (n_{dd2})	1973 returns: Single (n_{ds})	1973 returns: Average days out (t_2)
Jig	330	10	5	—	12	5	—
Bait	448	22	5	—	2	3	—
Total	778	32	10	54.71	14	8	451.55

[4]Floy Manufacturing Company, Seattle, Wash. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.–Estimates of rates of tag shedding, $\hat{L}$ (on an annual basis), retention, $\hat{\rho}$, from 1972 North Pacific albacore double-tag study.

Item	$\hat{L}$	$\hat{\rho}$
Undated returns excluded	0.098	0.88
Undated returns included	0.086	0.88

could not be assigned to seven double-tag and two single-tag returns in 1972 and one double-tag return in 1973. We assumed that t_k was the same for the returns shown in Table 1 and the returns with unspecified recovery dates and included the 10 additional returns in a recalculation of $\hat{\rho}$ and $\hat{L}$ The results of the recalculations are similar to the original (Table 2). We estimated ρ to be about 0.88 and L on an annual basis to be between 0.086 and 0.098. This means that if no mortality occurs, 8.2 to 9.3% of all unrecovered tags are expected to be lost through shedding annually.

Our estimate of ρ is similar to the results obtained for yellowfin tuna ($\hat{\rho}$ = 0.913) by Bayliff and Mobrand (1972) and bluefin tuna ($\hat{\rho}$ = 0.973) by Lenarz et al. (1973). However, our estimate of L is considerably lower than that obtained for yellowfin tuna ($\hat{L}$ = 0.278) and bluefin tuna (L = 0.310).

Methodology for estimation of the variance of L and ρ when only two periods of recovery are available has not been published. However, we believe that the number of tag returns available for this study is too low for accurate estimates of ρ and L. We made the following calculations to illustrate the relative level of accuracy. If we arbitrarily assume that the returns of double- and single-tagged fish in 1973 were from a binomial distribution with the probability of a returned fish having only one tag being 0.5, the probability of having 8 or fewer fish returned with only one tag out of a sample of 22 fish from such a population is about 0.14. If 11 fish were returned with single tags (the expected value from the assumed distribution) instead of the 8 observed, our estimates of ρ would be 0.895 and our estimate of L would be 0.172. Thus it appears that there is a reasonable chance that our estimate of L (about 0.09) could be considerably lower than the true value.

We are not aware of any other data available from double-tag studies on albacore. However, there is a considerable amount of data available from single-tag studies conducted in recent years on albacore in the eastern North Pacific (Table 3). Return rates in the year after release were 0.018

TABLE 3.–Tag releases and returns from North Pacific albacore single-tag studies.

Year of release	Number released	Number returned 1971	1972	1973	1974
1971	887	0	16	11	6
1972	1,304		27	47	14
1973	1,806			13	59
1974	2,490				35

for the 1971 releases, 0.036 for the 1972 releases, and 0.033 for the 1973 releases of single-tagged fish, for an average of 0.029. If the return rates are divided by 0.88 to account for Type-I tag shedding, the average becomes 0.033. The return rate in the year after release for the double-tag study was 0.027. If the rate is divided by 0.99 $(1 - (1 - \hat{\rho})^2)$ to account for Type-I shedding of both tags, the return rate is 0.027. Thus the return rates from the single-tag studies give further evidence that Type-II shedding is insignificant, because if it were not, return rates adjusted for Type-I shedding from the single-tag releases should be lower than return rates from the double-tag releases, provided mortality rates were similar for these years.

The above estimates are based on the assumption that all double-tag recoveries are reported as double-tag recoveries. A possible source of error is that some fishers may return only one tag from a double-tag recovery. These fishers might return only one tag because of their interest in albacore migrations, but retain the second tag as a souvenir. This would result in our underestimating the value of ρ. To illustrate the extreme case assume that ρ is actually 1.0, but we estimate it to be 0.88 because of incomplete reporting. Then assuming ρ = 1, Equations (1) and (2) become

$$n_{ddk} = F \tau N_D \pi B e^{-(F + X + 2L)t_k} \quad (4)$$

and

$$n_{dsk} = 2F \tau N_D \pi (1 - e^{-Lt}k) e^{-(F + X + L)t_k} + (1 - B) F \tau N_D \pi e^{-(F + X + 2L)t_k} \quad (5)$$

where B = minimum proportion of double-tag recoveries that are reported as double-tag recoveries.

Manipulation of Equations (4) and (5) results in

$$\frac{(n_{dd2} + n_{ds2})(n_{dd1})}{(n_{dd1} + n_{ds1})(n_{dd2})} = \frac{2e^{Lt_2} - 1}{2e^{Lt_1} - 1} \quad (6)$$

and

$$B = \frac{(2e^{Lt_k} - 1)(n_{ddk})}{n_{ddk} + n_{dsk}}. \quad (7)$$

An estimate of L is obtained from an iterative solution of Equation (6). An estimate of the minimum value of B is obtained from substitution of the estimate of L into Equation (7). Our estimate of L and the minimum value of B, where only returns with specified dates are included in the calculations, are 0.087 and 0.78, respectively. When all of the return dates are included we estimate L to be 0.077 and B to be 0.78. Thus, it appears that the rate of reporting double-tag recoveries as single-tag recoveries is less than 0.22 $(1 - B)$.

However, we have no evidence to indicate that fishers have returned only one tag from fish recovered with two tags. We believe that fishers have turned in both tags of fish recovered with two tags based on interviews with those who have recovered tagged fish, the very good cooperation that we have received from them during the tagging program, and the fact that tags from recovered fish may be returned to the fisher if he wishes to have them.

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LITERATURE CITED

BAYLIFF, W. H., AND L. M. MOBRAND.
1972. Estimates of the rates of shedding of dart tags from yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 15:441-462.

CHAPMAN, D. G., B. D. FINK, AND E. B. BENNETT.
1965. A method for estimating the rate of shedding of tags from yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 10:333-352.

FINK, B. D.
1965. A technique, and the equipment used, for tagging tunas caught by the pole and line method. J. Cons. 29:335-339.

LENARZ, W. H., F. J. MATHER III, J. S. BECKETT, A. C. JONES, AND J. M. MASON, JR.
1973. Estimation of rates of tag shedding by northwest Atlantic bluefin tuna. Fish. Bull., U. S. 71:1103-1105.

YAMASHITA, D. T., AND K. D. WALDRON.
1958. An all-plastic dart-type fish tag. Calif. Fish Game 44:311-317.

NOTES

PARALYTIC SHELLFISH POISONING IN TENAKEE, SOUTHEASTERN ALASKA: A POSSIBLE CAUSE

PSP (paralytic shellfish poisoning) has been reported from much of the west coast of North America. Recent reviews (Halstead 1965: 157-240; Quayle 1969) summarizing many aspects of the problem have emphasized its causative organism, *Gonyaulax catenella* (and possibly *G. acatenella*).

Chemical studies (Schantz and Magnusson 1964) indicate that the poison is chemically similar throughout the range of *G. catenella*—California through Alaska. Because of this similarity, and the reported occurrence of *G. catenella* in Alaska (Meyers and Hilliard 1955; Sparks 1966; Neal 1967), it has often been assumed that this species is the cause of PSP in Alaska. This assumption has not been well verified, however. A 2-yr study in southeastern Alaska by the University of Alaska failed to find a significant correlation between the occurrence of PSP and *G. catenella* (Chang 1971). Sparks (1966) and Neal (1967) reported a correlation in their occurrence near Ketchikan, but the number of *G. catenella* was so low that very long toxification periods would have been required to cause lethal clams.

The difficulty in verifying the relationship results, in part, from the very low densities of *G. catenella* in Alaska plankton (Schantz 1966; Chang 1971). Sparks (1966) stated that it has even been difficult to demonstrate that *G. catenella* occurs in Alaska waters. Since toxic shellfish occur quite frequently in southeastern Alaska, some observers (Schantz and Magnusson 1964; Neal 1967; Chang 1971) have concluded that organisms other than *G. catenella* might also cause PSP.

We believe the events reported in this paper provide the first demonstration of a localized *G. catenella* bloom followed by a PSP outbreak in Alaska waters.

Methods and Results

On 20 September 1973, 5 days before an outbreak of shellfish poisoning in humans occurred, very high bioluminescence was seen in Tenakee Harbor (lat. 57°48′N; long. 135°14′W). During darkness, glowing outlines of large individual fish and schools of fish were clearly seen moving in the water. Long-time residents remarked that it was the greatest amount of "phosphorous" (bioluminescence) they had ever seen there.

The RV *Maybeso*, Alaska Department of Environmental Conservation, was in the area at the time, and curiosity about the bioluminescence prompted the crew to collect a small (100-cm^3) water sample, which was preserved with Formalin.[1] Water temperature at the time of collection was 11.5°C, and salinity was 22.18‰. The water could not be microscopically examined until 1 October, when the *Maybeso* returned to Juneau. At that time the sample was given to the senior author, who was coordinating a PSP research program for the Department of Environmental Conservation. Large numbers (235,000/liter) of *G. catenella* were found in the sample. Other dinoflagellate species were present but only in trace amounts. No organism other than *G. catenella* was found in high enough numbers to cause intense bioluminescence.

We learned that on 25 September 1973, several families had dug the butter clam, *Saxidomus giganteus*, near the boat harbor in Tenakee. After eating the clams, two people reported severe symptoms of PSP to the Alaska Department of Health and Social Services. When interviewed, the victims, as well as other Tenakee residents, stated that they had eaten clams from the same area earlier in the year without any toxic reactions.

Using conventional methods (Quayle 1969; Prakash et al. 1971), the Alaska Division of Public Health Southeast Regional Laboratory determined that the level of toxin in the uneaten portion of some of the cooked clams from Tenakee was 4,550 μg/100 g. The toxin was distributed throughout the body and was not concentrated in the siphons. Indeed, one of the illnesses was caused by ingesting clams from which the siphons had been removed before cooking.

We flew to Tenakee on 5 October, about 2 wk after the outbreak, but found no *G. catenella* in the water. We did not test any clams for toxin levels at that time, but the mussel, *Mytilus edulis*, growing on harbor pilings had high levels of toxin (2,300 μg/100 g).

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Discussion

The fact that toxin was distributed throughout the bodies of the clams, rather than being concentrated in the siphons, indicates that the contact between the clams and the toxin-producing organisms had been recent. The lack of a concentration of toxin in the siphon may even indicate that toxification was in progress (Quayle 1969). The high toxin levels in mussels also reinforces the probability that toxification had occurred recently; mussels lose their toxin rapidly (Prakash et al. 1971) and the high levels indicate that the toxicity was acquired shortly before our sampling.

There is presently no information on the pumping rate, particle retention, or assimilation efficiency of *Saxidomus giganteus* (K. Chew pers. commun.). Pumping rates of the American oyster, *Crassostrea virginica*, can be as high as 20 liters/h and probably average about 10 liters/h (Loosanoff and Engle 1947; Galtsoff 1964). By using the rate of 10 liters/h, which is conservative for the larger *S. giganteus*, and assuming a particle retention of 25%, which is also conservative when particles the size of *G. catenella*, 25-55 μm, are ingested (Loosanoff and Engle 1947), a toxification period may be calculated.

Approximately 3,000 *G. catenella* will produce one mouse unit (approximately equal to 0.2 μg) of toxin (see discussion in Neal 1967). Filtering 10 liters/h of water containing 235,000 *G. catenella* /liter and retaining 25% of the *G. catenella* will result in an increase of 40 μg of toxin/h in each clam. The *Saxidomus* sampled at Tenakee contained 4,500 μg/100 g or approximately 2,250 μg/clam (an average clam probably weighs less than 50 g). Thus, using these conservative figures, it would have taken slightly more than 2 days (57 h) of filtering to reach the levels found in Tenakee clams.

From the known background of this event, it is apparent that the shellfish must have become toxic shortly before the illnesses were reported. The occurrence of the *G. catenella* bloom approximately 1 wk before the PSP outbreak indicates that even though this species is normally found in very low densities in Alaska, it can occur in high enough numbers to rapidly toxify clams.

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Literature Cited

CHANG, J. C. C.
1971. An ecological study of butter clam (*Saxidomus giganteus*) toxicity in Southeast Alaska. M.S. Thesis, Univ. Alaska, College, 94 p.

GALTSOFF, P. S.
1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Fish Wildl. Serv., Fish. Bull. 64:1-480.

HALSTEAD, B. W. (editor).
1965. Poisonous and venomous marine animals of the world. Vol. 1. U. S. Gov. Print. Off., Wash., D.C., 994 p.

LOOSANOFF, V. L., AND J. B. ENGLE.
1947. Effect of different concentrations of micro-organisms on the feeding of oysters (*O. virginica*). U. S. Fish Wildl. Serv., Fish. Bull. 51:30-57.

MEYERS, H. F., AND D. R. HILLIARD.
1955. Shellfish poisoning episode in False Pass, Alaska. Public Health Rep. 70:419-420.

NEAL, R. A.
1967. Fluctuations in the levels of paralytic shellfish toxin in four species of lamellibranch molluscs near Ketchikan, Alaska, 1963-1965. Ph.D. Thesis, Univ. Washington, Seattle, 164 p.

PRAKASH, A., J. C. MEDCOF, AND A. D. TENNANT.
1971. Paralytic shellfish poisoning in eastern Canada. Fish. Res. Board Can., Bull. 177, 87 p.

QUAYLE, D. B.
1969. Paralytic shellfish poisoning in British Columbia. Fish. Res. Board Can., Bull. 168, 68 p.

SCHANTZ, E. J.
1966. Chemical studies on shellfish poisons. *In* W. Felsing (editor), Proceedings of joint sanitation seminar on North Pacific clams, p. 18-21. Alaska Dep. Health Welfare and U. S. Dep. Health, Educ., Welfare, Public Health Serv.

SCHANTZ, E. J., AND H. W. MAGNUSSON.
1964. Observations on the origin of the paralytic shellfish poison in Alaska butter clams. J. Protozool. 11:239-242.

SPARKS, A. D.
1966. Physiological ecology of the causative organisms including mechanisms of toxin accumulation in shellfish. *In* W. Felsing (editor), Proceedings of joint sanitation seminar on North Pacific clams, p. 10-11. Alaska Dep. Health Welfare and U.S. Dep. Health, Educ., Welfare, Public Health Serv.

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OIL AND GREASE: A PROPOSED ANALYTICAL METHOD FOR FISHERY WASTE EFFLUENTS

The published procedures (American Public Health Association 1971:407-413; Environmental Protection Agency 1974) for determining oil and grease in industrial wastes are generally unsuitable for fish-processing waste effluents, especially for such high-load effluents as occur during the processing of salmon for canning. These wastes cannot be filtered satisfactorily by the method described. In addition, a Soxhlet extraction of the fish proteinlike material after drying for 30 min gives low values because of the inefficient extraction of protein-bound lipids.

These inadequacies of the published methods for the analysis of oil in fish-processing waste streams indicate a need for an alternate method that is simple and accurate. Accordingly, a method was worked out using portions of the published oil and grease methods and using techniques developed by Kelley and Harmon (1972) for the analysis of carotenoids. The method involves a precipitation of protein and particulate matter to allow easy filtration and subsequent extraction of oil from the residue under anhydrous conditions, using 2-propanol (IPA) and petroleum ether (PE). The method is proposed as an alternate method for determining oil and grease in fishery waste effluents.

Materials and Methods

Reagents and Equipment

Celite[1] 503, Johns-Mansville (filter aid): For best results, Celite should be washed with water and solvents because a slight oil residue may carry over into the oil fraction. Blend about 100 parts of Celite by weight with 500 parts water, filter, reblend with 500 parts (vol) IPA, filter, reblend with 500 parts (vol) PE, filter and apply suction until reasonably dry. Air dry and store in a jar. Filter paper dispersion: Blend 20 7-cm filter paper disks (Whatman 1 or 40) with distilled water in a blender for 5 - 10 min. Bring volume to 2,000 ml. Sodium hexametaphosphate in water: 250 mg/ml, use 1 ml per analysis, i.e., 250 ppm. Other materials required are: filter flasks (250 ml and 2,000 ml), graduated cylinder (1,000 ml), filter pump (water aspirator), filter funnel (fritted disc, 350 ml coarse, 150 ml medium), blender and jars (Virtis Model 23 and 200-ml blender jars), rotating evaporator with 250-ml flask, film to seal cylinder (parafilm "M," American Can Company, Marathon Products), 50% acetic acid, anhydrous magnesium sulfate (powdered), reagent grade IPA, and reagent grade PE (bp 40°-60°C).

Preparation of Filter Funnel

Assemble filter flask and a 350-ml "c" sintered glass filter funnel. Add about 3 g filter aid and 100 ml filter paper dispersion directly to the funnel. Fill funnel with water, stir and allow to partly drain without vacuum. Apply vacuum, rinse briefly, and press down along edge of mat to ensure a good seal.

Preparation of Sample and Filtering Step

Pour well-mixed sample of effluent to the 1,000-ml mark in the graduated cylinder. Add 3 to 6 g filter aid to aid precipitation. In its absence, flotation and precipitation both occurred. Add 1 ml hexametaphosphate solution, seal cylinder with film, and mix by inverting cylinder about 12 times. Add 2 ml acetic acid. The amount of acid will vary with the type of effluent and is not critical provided enough is added; the pH must be lower than 4.2, but precipitation works equally well at several levels between pH 2.1 and 4.2. Invert three or four times. Excessive mixing inhibits rate of precipitation. Wait about 2 min and add more acid if top inch or so is not clear. Solids in salmon waste effluents are slow to settle and are best handled by allowing the mixture to settle overnight in the refrigerator. Salmon waste, after 2-h settling, can be filtered but with difficulty. If filtration is started too soon, the sample often must be discarded because it will not filter. Shrimp and crab waste usually can be filtered in 15 to 30 min. Filter clear supernatant fluid under vacuum through the prepared filter funnel (very rapid), and transfer more slowly the precipitate (50-75 ml vol) and rinsings to the funnel. Use about 200 ml water to remove excess acid and to rinse graduate and filter. Continue vacuum 5 to 10 min to remove as much water as possible because the next step, the extraction, must be anhydrous.

Extraction of Oil

Carefully transfer solid material, including

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Celite and filter paper, to the 200-ml blender jar plus about 15 g anhydrous $MgSO_4$ and 75 ml IPA. The desiccating step with $MgSO_4$ is not effective if volumes of IPA are excessive. In addition, all volumes should be maintained as specified to allow rinsing without exceeding the capacity of the 250-ml evaporating flask. The IPA should be measured in the liter graduate and shaken or rotated to wash cylinder. Blend at high speed for 5 min, then pour contents of blender jar into 150-ml dry filter funnel (M-porosity), apply vacuum until dripping ceases, rinse briefly with PE (wash bottle), then repeat extraction with 75 ml PE. The second extraction with PE removes about 2.5% of the total oil.

Quantitatively transfer filtrate to a pre-dried and weighed 250-ml 24/40 standard taper round-bottom flask, and flash evaporate using a rotating vacuum evaporator and warm water bath. This method takes from 5 to 10 min, but other techniques of evaporating would be suitable. When solvents are removed, add about 10 ml PE to determine if water or solid materials are present. If clean, evaporate to dryness, wipe outside of flask, and place in drying oven for exactly 30 min to remove traces of solvent or water. Cool in air for 1 h and weigh. Subtract tare weight and record weight of oil directly as milligrams per liter. The common practice of storing the dry flasks in a desiccator was not necessary because there was little change in weight with subsequent exposure to air. The oil apparently reached nearly constant weight (oxidation) during the 0.5-h drying step. Exposure of the dry oil and the flasks to air for 15 and 40 min resulted in 2.2 and 2.6 mg gain in weight for 1,684 mg oil and only 3.2 mg gain with overnight exposure. Consequently, because the 250-ml round-bottom flasks were difficult to weigh in a rapid manner, weights were obtained after oven drying for 0.5 h and air cooling for 1 h.

If the above PE solution is not free of water or solid particles, add 10-15 g anhydrous sodium sulfate and sufficient PE to mix well. Let sit a few minutes, and filter through sodium sulfate on a 60-ml medium- or fine-porosity fritted-glass funnel, rinse with PE, and transfer back to evaporating flask. The pre-weighed 250-ml flask should be washed out with water and solvents before reuse. This step is time-consuming and is never necessary if the previous extraction and desiccating steps are done properly.

Accuracy and Precision

The results of replicate analyses on eight effluent samples indicate that the proposed method gives acceptable precision (Table 1).

The mean standard deviation of these data on three different species is 5.3, and the mean is 552 mg/liter. The published mean standard deviation for the three methods given in the Environmental Protection Agency (EPA) manual is 1.1, with a mean of 15.0 mg/liter. To compare standard deviations with different means, the coefficient of variation (*CV*) is used, and for the data in this paper the *CV* is 1 as compared with 7 for the data given in the EPA manual. This means that a sample of waste effluent having 100 mg oil and grease/liter will have a comparative standard deviation of 1 or 7 mg/liter, depending on the method used.

The accuracy of the proposed method was evaluated by comparing the EPA Soxhlet method with the method given in this paper, using seven grab samples of king crab, snow crab, and shrimp waste effluents. The data in Table 2 show that the official EPA Freon 113 Soxhlet method gave oil and grease values that were consistently low, varying from 6 to 48% and averaging about 30%.

The filtrates from the EPA method of filtration from samples 3, 4, 5, 6, 7 were precipitated and

TABLE 1.—Oil and grease values expressed as milligrams per liter for eight effluent samples.

Sample	Replicate oil and grease values I	II	III
1. Snow crab effluent	158	154	153
2. Snow crab effluent	251	250	248
3. Shrimp effluent	397	399	
4. Shrimp effluent	432	404	
5. Salmon effluent	844	847	
6. Salmon effluent	231	221	
7. Salmon effluent	923	925	
8. Salmon effluent	1,200	1,190	

TABLE 2.—Comparison of oil and grease values expressed as milligrams per liter determined by the EPA Soxhlet method and the proposed method.

Sample analyzed	EPA method A	B	Proposed method C	D
1. King crab effluent	41	39	68	70
2. King crab effluent	37	28	59	54
3. King crab effluent	([1])	([1])	225	225
4. King crab effluent	([1])	164	221	225
5. Shrimp effluent	179	182	215	209
6. Snow crab effluent	161	164	174	174
7. Snow crab effluent	5	8	12	13

[1]Samples 3A, 3B, and 4A could not be filtered except by changing filters.

extracted by the method of this paper to give recoveries of 49 mg (23%), 56 mg (25%), 18 mg (10%), and 6 mg (50%), respectively. Thus, the official method of filtration resulted in an average loss of oil and grease of 25% of the values determined by the proposed method.

Two effluents (3 and 4) were precipitated by the method in this paper but extracted by the Soxhlet method and gave 16 and 5% low values, respectively. In addition, contamination of the oil fraction with Celite and fiber is apparent in the EPA Soxhlet method and oil and grease values are estimated to be 5-10 mg lower than reported.

Discussion

Different precipitation techniques were used in developing this method and gave valid results for specific waste effluents. For freshwater-processed shrimp, Celite, alum (200 ppm), and Magnafloc 835A (2 ppm) resulted in complete precipitation in about 15 min. The alum technique also worked on waste effluents from saltwater-processed shrimp and on snow crab, but precipitation was slower and filtration was more difficult. In general, the hexametaphosphate precipitation is the preferred technique because it resulted in a more firm, dense floc that filtered more rapidly than the alum system. In addition, the soluble proteins along with their oil content are recovered in the hexametaphosphate precipitate and included in the analysis. The soluble proteins generally are not recovered with the alum system or by the EPA method. Presumably, any reagent can be used for precipitation provided there is no carry-over into the oil fraction. Sulfuric acid was used to develop this method, but it occasionally resulted in a dark oil after drying. Consequently, the use of sulfuric acid was discontinued in favor of acetic acid. The proposed method should be tested further in comparison with the standard EPA methods for oil and grease to determine its applicability to other fishery waste effluents.

Literature Cited

AMERICAN PUBLIC HEALTH ASSOCIATION.
1971. Standards for the examination of water and wastewater. 13th ed. Am. Publ. Health Assoc., Wash., D. C., 874 p.

ENVIRONMENTAL PROTECTION AGENCY.
1974. Oil and grease. *In* Methods for chemical analysis of water and wastes, p. 226-235. Environ. Prot. Agency, Off. Technol. Transfer, Wash. D.C.

KELLEY, C. E., AND A. W. HARMON.
1972. Method of determining carotenoid contents of Alaska pink shrimp and representative values for several shrimp products. Fish. Bull., U.S. 70:111-113.

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OCCURRENCE OF VOLATILE N-NITROSAMINES IN JAPANESE SALMON ROE

Consumer interest and concern about food additives is as strong in Japan as in the United States. The possibility that secondary or tertiary amines and nitrites in fish roe products (sujiko) might combine to produce *N*-nitrosamines, known carcinogens, has received much attention and publicity. If the use of nitrites is curtailed in Japan, American salmon canners would be hurt because of loss of sales or decreased prices for roe sold to Japanese processors operating in the Pacific Northwest. The value of this business to the U.S. salmon industry is from $10 to $15 million each year.

Investigations by Howard et al. (1970) and Fazio, Howard, White, and Watts (1971) showing trace quantities of *N*-nitrosodimethylamine (NDMA) from samples of chub, sable, salmon, and shad prompted the National Marine Fisheries Service (NMFS) to be concerned about *N*-nitrosamines in smoked nitrite-treated fishery products. This concern was shared by the National Canners Association (NCA) in connection with nitrite-treated salmon roe products. Various samples of salmon roe commercially produced in canneries in the northwestern United States and Alaska were obtained by the NCA for analysis of volatile *N*-nitrosamines.

In addition to the analysis for nitrosamines which was carried out by NMFS, samples were also analyzed by NCA for residual nitrite and chloride concentrations. The results of these findings are presented in this report.

Experimental

Background

For a number of years, Japanese companies

have maintained salmon roe processing operations at canneries in the northwestern United States and Alaska. The processing of salmon roe is an art rather than a formulated production procedure, and numerous minor differences are found in the various recipes employed. The following is, of necessity, a generalized description of the production operation.

Roe from the butchered salmon is received in the egg house, cleaned of extraneous fish material, and rinsed to remove blood. From 27 to 38 kg of roe are placed in a vat containing 200 liters of saturated brine into which has been added either 0.02-0.05% nitrate or 0.05-0.07% nitrite (equivalent to 500-700 ppm.).

The mix is agitated mechanically for approximately 20 min. The actual length of time is determined by technicians who consider a range of variables, such as the size of roe, the freshness of fish from which roe was obtained, and temperature of brine solution. Larger roe, as from king or chum salmon, are held in the brine longer. Brine batches may be used for several changes of roe; normally, they are changed four or five times in an 8-h day.

After removal from the vat, the roe are drained and graded by size and color. Nitrite level of the roe at this time is about 50 ppm. The roe are then packed in 10-kg wooden boxes which are lined with sheets of plastic. After each layer is packed, it is lightly salted with a fine grind sodium chloride. The boxes are slightly overfilled, and the lids placed on without nailing. They are then stacked with weights on top to form a press. The boxes are cured in this fashion for as long as 7 to 10 days, depending on ambient temperature conditions. During the curing period, the desirable red color of sujiko develops, and nitrite residuals drop to less than 5 ppm. It is possible that the color enhancing action of the nitrite may be due to its inhibiting effect on color destroying oxidative enzymes in the roe.

Following pressing and curing, the product is inspected. If satisfactory, the lids are nailed down, and the boxes are stored at -5°F (-20.6°C) at the cannery and placed aboard transport vessels to Japan. In Japan, the same storage conditions apply until the product is sold to the retail markets.

Production Survey

Duplicate 10-kg samples of commercially produced red and pink salmon roe products were obtained from four of the five major sujiko processors. The processing plants were located on Kodiak Island in the Gulf of Alaska, southwest of Anchorage; Hawk Inlet in the Admiralty Islands, west of Juneau; Cook Inlet, large inlet which Anchorage is at the head of; and Ketchikan, southeast Alaska on the south side of Revillagigedo Island. Duplicate 10-kg samples of roe from three species of salmon—red, chum, and king—were obtained from the fifth major producer located at Puget Sound, Wash. All of these samples were obtained after their delivery to Japan. It was decided to sample the roe in Japan so that storage conditions would be more nearly identical to those received by the product going to consumers. Upon return of the samples to this country, NCA delivered them to NMFS. The samples were composited in a Hobart silent cutter, packaged in Mylar[1] bags, and sealed. A portion of the composite sample was returned to NCA for determinations of residual nitrites and NaCl content.

Experimental Pack

Using roe from the same batch of fish, one test pack and one control pack of salmon roe were prepared by NCA. The test pack was prepared in a saturated brine containing 700-ppm. nitrite, while only a saturated brine was used to prepare the control pack. The packs were cured at a temperature of 60°F (15.6°C) for 7 days and then stored for 6 mo at -5°F (-20.6°C).

Materials

The solvents—methylene chloride, pentane, and ethyl ether—were purified by distillation. Solvents, silica gel, and Celite 545 were tested prior to use to assure the absence of interfering peaks.

Analytical

The multidetection method for the analysis of volatile *N*-nitrosamines in foods developed by Fazio, Howard, and White (1971) was used in this investigation. Because of the high phospholipid content of the salmon egg samples, William T. Roubal of the Northwest Fisheries Center, NMFS, NOAA, found it necessary to make some preliminary modifications in the procedure (Fazio,

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Howard, and White 1971). Very briefly, these modifications were as follows:

1. Initial digestion of product—30 g of KOH were employed in the digestion, and the methanolic KOH solution was refluxed for 2-5 h.
2. Distillation step—8 g of $Ba(OH)_2$ was utilized. The distillation was carried out with the aid of a magnetic stirrer.

Briefly, the procedure involved digestion of the sample in methanolic KOH, liquid-liquid extraction of an aliquot of the digest with methylene chloride, distillation of the nitrosamines from alkaline solution with further cleanup by solvent partitioning and column chromatography on silica gel and Celite 545 columns followed by GLC (gas-liquid chromatography) analysis.

A victoreen Model 4000 GLC Chromatograph equipped with a Coulson Electrolytic Conductivity Detector and an Autolab System IV Computing Integrator was employed in the analysis of salmon roe extracts. A 9 foot (2.74 m) × 4 mm inside diameter glass column coated with 10% Carbowax 1540 + 3% KOH on 80/100 mesh gas chrom Q was used. The following parameters were maintained throughout all analyses.

Temperature of injector block - 190°C
Carrier gas (helium) flow rate - 70 ml/min
GC (gas chromatograph) oven temperature - ambient for 540 s; GC oven door was closed and brought to 80°C (held at 80°C for 180 s); 80°-180°C at a program rate of 5°C/min.

Conditions of Coulson Electrolytic Conductivity Detector operated in reductive mode were:

Hydrogen flow rate - 83 ml/min
Venting helium flow - 70 ml/min
Furnace temperature - 820°C
Venting block temperature - 190°C
Conductivity bridge - 30 V
Attenuation - 1.

Moisture, nitrite, and chloride determinations were made according to the official methods of analysis of the Association of Official Analytical Chemists.

Results and Discussion

During the survey, recovery studies were conducted. A mixture of six *N*-nitrosamines was used. The *N*-nitroso compounds were NDMA, diethylamine (NDEA), dipropylamine (NDPA), dibutylamine (NDBA), piperidine (NPi), and pyrrolidine (NPy). Prior to recovery runs, however, the salmon roe samples were examined for *N*-nitrosamines. Several of the cleaner samples were fortified at the 10-ppb (parts per billion) level. In instances where a nitrosamine was found under study, appropriate adjustments were made in the recovery values. Recovery of the *N*-nitrosamines at the 10-ppb level ranged from 67 to 88%.

Representative chromatograms obtained from a fortified pink salmon roe extract together with those obtained from the corresponding unfortified samples are shown in Figure 1. This figure shows the recovery of six nitrosamines after the silica gel cleanup step. Usually, the interferences occurring at a retention time of NPy were removed by further cleanup on the acid-Celite column. During the course of this investigation, blank runs (without a salmon roe sample) were made, and the minute GLC peak (3-15 mm) with the same retention time of NDMA observed with all roe samples was not apparent in the blank. As shown in Table 1; if the peaks are calculated as NDMA, the levels range from 0 to 3 ppb. Residual nitrite and chloride concentration are also shown.

A total of 24 salmon roe samples were analyzed in duplicate. All samples contained less than 5 ppb of NDMA. The demonstrated sensitivity of the method was shown to be 10 ppb. A peak with a retention time of NDEA was found (< 1 ppb). No attempt was made to confirm the identity of NDMA or NDEA in any of the samples since all were too low for mass spectrometric confirmation. Some samples were carefully concentrated down

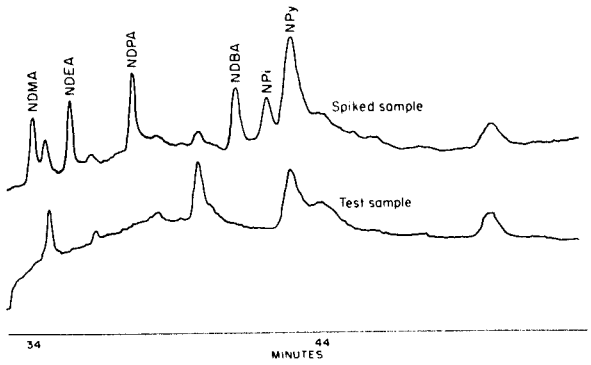

FIGURE 1.—Gas chromatograms of spiked and unspiked extracts of pink salmon.

TABLE 1.–DMNA, nitrite, and NaCl content of salmon roe samples prepared from different species of salmon at various processing plants in the Pacific Northwest.

Species	Location of processing plant	NaCl (%)	Residual nitrite (ppm.)	Apparent DMNA found (ppb)
	Production survey			
Red	Kodiak Island	8.42	0.3	1
Red	Kodiak Island	8.01	Trace	1
Red	Cook Inlet	8.75	Trace	2
Red	Cook Inlet	7.07	Trace	2
Red	Ketchikan	8.73	Trace	1.5
Red	Ketchikan	8.50	0.85	1.5
Red	Hawk Inlet	7.89	Trace	2
Red	Hawk Inlet	8.56	Trace	2
Pink	Kodiak Island	9.38	0.3	1.8
Pink	Kodiak Island	7.94	Trace	1.5
Pink	Cook Inlet	9.34	0.2	2.5
Pink	Cook Inlet	9.16	0.3	2.5
Pink	Ketchikan	9.01	0.60	2
Pink	Ketchikan	9.58	0.3	2
Pink	Hawk Inlet	9.58	0.3	2
Pink	Hawk Inlet	8.82	Trace	2
King	Puget Sound	5.19	Trace	3
King	Puget Sound	5.30	Trace	3
Chum	Puget Sound	9.53	Trace	2
Chum	Puget Sound	10.97	Trace	2
Red	Puget Sound	8.46	0.3	2
Red	Puget Sound	9.16	0.3	2
	Experimental pack			
Red	Control, NCA	9.5	Trace	0
Red	Test, NCA	8.8	Trace	3

to 100 μl. The chromatograms showed few, if any, indications of other volatile *N*-nitrosamines studied.

The multidetection method of Fazio, Howard, and White (1971) was used to prepare four runs of the same sample. The eluants from four silica gel columns were combined into a 1-liter Kuderna-Danish apparatus and concentrated to 1 ml and an aliquot injected for GLC analysis. The concentrate represented 100 g/ml of roe instead of the usual 25 g/ml. The increase in the area and height of the NDMA peak was very pronounced. The extract was submitted to an acid-Celite column cleanup. Interferring peaks were removed, but the suspected NDMA was still present (Figure 2).

In view of the above findings, it can be concluded that less than 5 ppb of apparent NDMA was found in salmon roe products of the different species of salmon having been processed at five major locations, and that no other nitrosamines were evident.

Acknowledgments

We express our appreciation to Donald M. Crosgrove of NCA, Northwest Laboratories, for furnishing us with the salmon roe samples and the respective residual nitrite and chloride data.

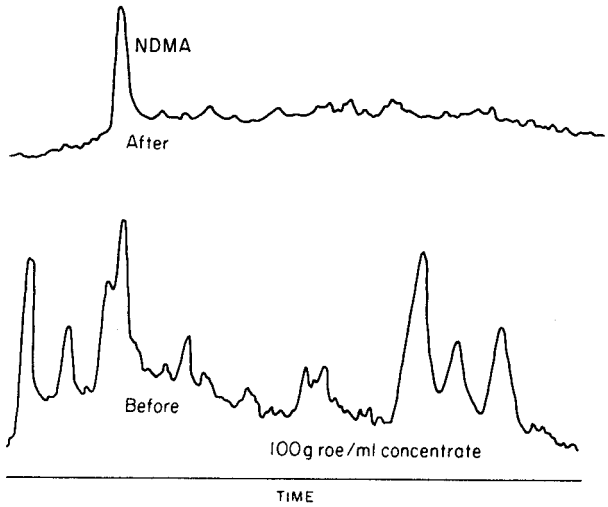

FIGURE 2.–Chromatograms of an extract of nitrite-treated salmon roe before and after being cleaned up on a column of acid Celite.

Literature Cited

FAZIO, T., J. N. DAMICO, J. W. HOWARD, R. H. WHITE, AND J. O. WATTS.
1971. Gas chromatographic determination and mass spectrometric confirmation of *N*-nitrosodimethylamine in smoke-processed marine fish. J. Agric. Food Chem. 19:250-253.

FAZIO, T., J. W. HOWARD, AND R. H. WHITE.
1971. Multidetection method for analysis of volatile *N*-nitrosamines in foods. Proc. Heidelb. Meet. Nitrosamines, Int. Agency Res. Chem., 13-15 Oct.

HOWARD, J. W., T. FAZIO, AND J. O. WATTS.
1970. Extraction and gas chromatographic determination of *N*-nitrosodimethylamine in smoked fish: Application to smoked nitrite-treated chub. J. Assoc. Off. Anal. Chem. 53:269-274.

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UNDERWATER PAINT MARKING OF PORPOISES[1]

Identification of individual animals has always been a problem in cetacean behavioral research. Only a small part of the animal is ordinarily visible, and individuals within a pod of whales or porpoises may all look very much alike, and, for that matter, very much like all the individuals in all neighboring pods. How does one mark (or label) an animal at sea?

Our radio tagging experiments and flashing light systems (Schevill and Watkins[2]) were designed to provide a partial solution to this problem, and, more recently, radio transmitters have been attached to animals by means of harnesses or other fastenings (Evans 1974; Norris and Gentry 1974; Norris et al. 1974). Conspicuous visual marks have often been suggested, and a few have been successfully contrived for particular experiments, including freeze-branding, brightly colored buoyant lines, buoys, and plastic numbered buttons toggled through dorsal fins (Norris and Pryor 1970; Evans et al. 1972)

We have been loath to use acoustic tags on animals that react to the noise of ships, and even to low-level pingers (Watkins and Schevill 1975). Frequencies that are above their hearing would be useful only at short ranges because of attenuation of high frequencies in seawater.

Ideally, we wanted a mark that was highly visible, that could be varied, that had no effect on the behavior of the animal, that would last for long periods of time, and that was easy to apply at sea. Even a temporary mark permitting positive identification for only a few hours would be a boon. Paint seemed an answer (Schevill 1966).

Materials and Methods

Several standard paint formulations were tried; some could be applied to a wet surface, and some would set relatively quickly underwater. Application of these paints was easiest by pressurized spray. We experimented with spray volumes, velocities, propellants, and methods of controlling the paint. A propellant that mixed well with the paint carried it in a discrete stream, preventing immediate mixing with the water, and higher volumes of the paint mixture provided more effective displacement of the water on the surface to be painted. In our most satisfactory marking system, we used 186-g (6-ounce) pressurized cans of paint with a fire-extinguisher type of valve to deliver short bursts of paint at about 125 g/s. A nozzle 3 cm long with a 3.5-mm orifice was fabricated to actuate the valve and direct the paint in a coherent stream (in air, 2 or 3 m horizontally). An internal modification to the standard container removed the dip tube so that the can could be used in an inverted position. For ease in handling and to allow the stream of paint to be brought close to a passing animal (as from the bow of a ship), a holder for the paint can was mounted at the end of a pole.

Paint bounced off most hard-surface materials before it could set underwater, unlike human or porpoise skin which appeared to have approximately equivalent temporary reactions to paint. But paper masking tape (3M-Scotch 183),[3] which has a softer surface, reacted somewhat like skin to both the paint and the water, and was used as an underwater test surface.

Two paints were selected: a red lacquer based on a nitrocellulose/alkyd vehicle and a red-orange fluorescent based on an acrylic ester resin vehicle.[4] These paints solidify by removal of the solvents rather than by oxidation, as in the usual paint preparations. The paint containers were capped at about 4.2 kg/cm^2 (60 lb/in^2) at room temperature. A 5% change of pressure can be expected with each 5°C change in ambient temperature; can temperature is critical for adequate pressure.

Tests were conducted in a 3-m^3 tank of flowing seawater, and water temperatures were controlled from 20.9°C in steps of a degree or less to 3.45°C, and a comparison was made for each temperature at several depths. Both paints penetrated the water in a coherent stream, adhered to the test surface, and set (hardened) underwater. The red lacquer set within a second or two, but was considerably dulled when applied through the water. The fluorescent red-orange was largely unaffected by underwater application, except that its setting time was extended by 10-15 min. Patches of both

[1]Contribution No. 3586 from the Woods Hole Oceanographic Institution.

[2]Schevill, W. E., and W. A. Watkins. 1966. Radio-tagging of whales. Unpubl. manuscr., 15 p. Woods Hole Oceanogr. Inst. Ref. No. 66-17.

[3]Reference to trade names and manufacturers does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]These two paints are similar to formulation AL-98 and V-129 by Lenmar, Inc., 150 South Calverton Road, Baltimore, Md. These and other formulations and colors recommended by Lenmar have been tested and appear to have equivalent underwater characteristics.

paints applied underwater and kept immersed for 13 days and 7 h at 3.5°C showed only slight differences from short-term tests. There was little difference in the painted surfaces down to a temperature of 4.0°C. Below this, less paint adhered, and the color of the painted surface was duller. The paint maintained a coherent stream to greater depths in warmer water, perhaps because of associated higher air temperature and therefore greater pressure in the can. With the apparatus above water, penetration and marking (at 15°C) occurred to a depth of about 40 cm, and with increasing depth progressively less paint adhered. Comparisons of application of these paints in both seawater and fresh water showed little difference, at least on a short-term basis.

Since only a portion of the paint actually adhered underwater, the residue of these paints floated as an inert scum in temperatures of 5°C or warmer, generally not sticking to anything. This was in sharp contrast to many other paints that often floated as soft globules on the water, and for hours thereafter would coat any objects they contacted.

Results

On 16 December 1974, we tested both paints on a captive *Tursiops* (one of two in a tank) at the Naval Undersea Center, San Diego, Calif. The porpoise swam slowly past with all but its dorsal fin underwater. The holder for the paint can was hand-held about 20 cm above the water, and the paint stream was directed downward at the animal, about 20° from the vertical. The stream penetrated the water by as much as 15-20 cm, marking a streak 6-8 cm wide (at each pass) on the animal's back, as well as on the right side of the dorsal fin.

The paint contrasted sharply with the dark gray color of the animal and provided a conspicuous mark that was brightly visible 8 h after application, although patches of it had disappeared. Twenty-four hours after painting, only a small strip of paint (at the leading edge of the dorsal fin) remained, and much of this residue was still there 56 h after application, though quite dulled.

Of the two *Tursiops* in the tank only one was painted, yet no obvious behavioral changes could be noted; they both seemed to ignore the whole process and behaved as before. There was no obvious reaction to either the painted animals or to the excess paint floating on the water.

A *Lagenorhynchus acutus* was successfully marked in the open ocean on 8 May 1975, 8 to 10 km northeast of Race Point, Cape Cod, Mass. Though *L. acutus* usually is shy of ships and difficult to approach (Schevill 1956), we found about 30 of these animals and were able to get close to a subgroup of six porpoises. They would not surface within reach of our vessel (13-m RV *Asterias*), so the paint was applied through 15 to 20 cm of water. The paint mark was a 10-cm circular red spot at the after part of the buff-colored stripe on the right side. We were able to follow this porpoise for only 30 min, but during this time, the mark provided a highly visible tag which permitted rapid identification of the marked individual as well as the subgroup of animals. This subgroup appeared to stay together even when mingling with others of the larger porpoise aggregation. Again, the paint mark appeared to be ignored by all of the animals. The next day, two schools of *L. actus* (probably including the same animals) were studied, but no mark could be found.

Discussion

We suppose that the paint on the leading edge of the dorsal fin of the captive porpoise persisted longer than elsewhere because of the roughness and scarring of the skin there. The disappearance of the paint from the smooth surfaces on both the captive and wild animals was apparently because of the normally rapid sloughing of surface layers of skin. Palmer and Weddell (1964: 555) noted that cells in *Tursiops* skin undergo mitosis 250 to 290 times as rapidly as human skin, and Harrison and Thurley (1972) also reported that cells in the surface layer are desquamated in large numbers. Presumably, the paint came loose because the surface cells sloughed off. The relative stiffness and greater mass of the cells coated with paint would have accelerated their removal, but after the paint had worn off, no difference in the skin surface could be noted. We could find no indications of any adverse effects. Since the paint lasted so much longer on the rough part of the fin, we anticipate that similar nonsloughing surfaces on the other cetacean species also would hold a paint mark well (e.g., the highly barnacled portions of a gray whale, or perhaps right whale bonnets). In addition, we anticipate that such paints could usefully mark other aquatic animals (turtles, seals, manatees, etc.).

Little is known about color vision in porpoises,

though it has been assumed that they could see color because of the relative numbers and arrangement of rods and cones in the retina of *Tursiops* (Perez et al. 1972). But since very little in the animals' open ocean experience involves much color, the painted marks may hold small significance for them.

Since our purpose was to test the feasibility of paint marking of porpoises, no attempt was made to create an ideal paint, though a paint formulated specifically for marking doubtless would have been better than those we used. Our experiments began with available paints, and those that were found to coat wet surfaces were modified for use in pressurized containers with high volume valves. Paint manufacturers generally are prepared to process only large volume orders, but we found that smaller specialty companies were able to prepare formulations to order and modify small quantities of pressurized paint containers.

Conclusions

Paint marking of porpoises provides a satisfactory short-term tag that can be applied at sea. The paint has not modified the animals' behavior and it seems not to be detrimental in any way. The high visibility of the colors we tried often made it possible to locate the marked animal when other porpoises of the school were obscured. The underwater paint marking technique would appear to be potentially useful in the study of other aquatic animals.

Acknowledgments

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Literature Cited

EVANS, W. E.
1974. Radio-telemetric studies of two species of small odontocete cetaceans. *In* W. E. Schevill (editor), The whale problem, p. 385-394. Harvard Univ. Press, Camb., Mass.

EVANS, W. E., J. D. HALL, A. B. IRVINE, AND J. S. LEATHERWOOD.
1972. Methods for tagging small cetaceans. Fish. Bull., U.S. 70:61-65.

HARRISON, R. J., AND K. W. THURLEY.
1972. Fine structural features of delphinid epidermis. (Abstr.) J. Anat. 111:498-500.

NORRIS, K. S., W. E. EVANS, AND G. C. RAY.
1974. New tagging and tracking methods for the study of marine mammal biology and migration. *In* W. E. Schevill (editor), The whale problem, p. 395-408. Harvard Univ. Press, Camb., Mass.

NORRIS, K. S., AND R. L. GENTRY.
1974. Capture and harnessing of young California gray whales, *Eschrinchtius robustus*. Mar. Fish. Rev. 36(4): 58-64.

NORRIS, K. S., AND K. W. PRYOR.
1970. A tagging method for small cataceans. J. Mammal. 51:609-610.

PALMER, E., AND G. WEDDELL.
1964. The relationship between structure, innervation and function of the skin of the bottle nose dolphin *(Tursiops truncatus)*. Proc. Zool. Soc. Lond. 143:553-567.

PEREZ, J. M., W. W. DAWSON, AND D. LANDAU.
1972. Retinal anatomy of the bottlenosed dolphin (*Tursiops truncatus*). Cetology 11:1-11.

SCHEVILL, W. E.
1956. *Lagenorhynchus acutus* off Cape Cod. J. Mammal. 37:128-129.
1966. Comments. *In* K. S. Norris (editor), Whales, dolphins, and porpoises, p. 487. Univ. Calif. Press, Berkeley and Los Ang.

WATKINS, W. A., AND W. E. SCHEVILL.
1975. Sperm whales *(Physeter catodon)* react to pingers. Deep-Sea Res. 22:123-129.

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GRAZING OF FRESHWATER AND ESTUARINE, BENTHIC DIATOMS BY ADULT ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

The diet of the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), varies with stages in metamorphosis and the availability of food resources, but it has been characterized consistently in the literature as derived from the particulate organic components of planktonic ecosystems (Reintjes 1969; June and Carlson 1971; Jeffries 1975; Peters and Kjelson 1975; Durbin and Durbin 1975). Menhaden larvae feed primarily by selective predation on the larger estuarine zooplankters. Their metamorphosis into prejuveniles brings about the

development of a functional branchial filtering apparatus which promotes a grazing of phytoplankton and suspended detritus. Late juveniles and adults are primarily herbivores also but retain the ability to eat zooplankton.

The stimulus for this investigation was a shoreline observation of adult menhaden grazing directly on the benthic microbial communities covering the rocks in the headwaters of a Massachusetts estuary. The fish were observed to bite or rip off chunks of the benthic community film and swallow them. This film was composed primarily of diatoms and detritus. Subsequent gut analyses of the fish and the epilithic diatom assemblage confirmed the field observations. Additionally, ingestion of these benthic primary producers and their associated detritus by juvenile menhaden is postulated from a reinterpretation of previous reports on their diet.

Methods

In the early afternoon of 19 September 1974, nine adult menhaden (25-34 cm fork length) were collected in the oligohaline region of the Slocum River estuary, Mass. (Hoff et al. 1969). The fish were sampled with a 10-m, 64-mm mesh haul seine from a school of about 150, which was observed feeding on the bottom within a 500-m^2 area about 1 m deep for the 15 min prior to collection. The pyloric stomachs were excised, opened, and their fullness visually estimated. The stomach contents of each fish were maintained and examined separately; they were preserved in 3% formaldehyde solution. A preliminary microscopic examination of the contents was made to determine the presence of diatoms and other components of the diet. Diatoms were prepared for detailed examination by a nitric acid-dichromate oxidation of an aliquot of the sample followed by washing of the cleaned frustules and mounting in Hyrax[1] (Hohn and Hellerman 1963). Diatom populations in each sample were identified and enumerated from a random sample of about 200 frustules, which were observed using oil-immersion phase-contrast optics at a magnification of 1000×.

On 21 September 1974, a 20-cm diameter rock was removed from the same region of the estuary in which the menhaden had been observed feeding. The diatom assemblage on the rock was air-dried, then scraped off and subjected to the same procedures of preparation and examination as those derived from the stomachs.

All samples and slides have been deposited in the Hellerman Diatom Herbarium at Southeastern Massachusetts University according to the following collection numbers: HH918-HH926 (stomach samples) and HH927 (epilithic sample).

The diatom populations were classified as freshwater, brackish, or marine based on the habitat in which they grow optimally. This classification was derived primarily from the works of Hustedt (1937-1938, 1939), Patrick and Reimer (1966), Foged (1947, 1954), and Cleve-Euler (1951-1955). Only those populations identified without reservation to the species level were classified ecologically. Additionally, in an ecological classification of diatoms, identification of populations to the level of variety is desirable among multivarietal species, because frequently different varieties of the same species have different optimal habitats.

The terms "common" and "rare," as employed in this paper, differentiate diatom populations having greater than 1% or less than 1% mean relative abundance, respectively, in the stomach samples.

Results

All fish stomachs were completely full or nearly so. Amorphous detritus and diatoms composed the bulk of the material with the detritus accounting for the greater portion, but as estimated microscopically, from 5 to 25% of the volume was diatomaceous. Most larger diatom cells were broken and without contents, but many smaller diatoms retained their chromatophores in structurally intact frustules. Other microorganisms, particularly filamentous blue-green algae and nematodes, were evident, and the remnants of some microcrustaceans were noted in a few stomachs.

The examination of about 1,800 diatom individuals from the stomachs revealed 163 populations of which 134 were identified to species or variety. Twenty-three populations were common and only three of them were not assignable to a particular species (Table 1). The rare populations which were unidentified constituted less than 2% of all individuals. Practically all the populations are benthic. Eight of them, particularly *Skeletonema costatum* and *Thalassiosira* spp., are considered planktonic, but they contained less than 7% of all individuals and were found also on the rock. Freshwater populations composed 50% of the common and nearly 70% of all populations (Table

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—The relative abundance (%) and the optimal habitats of the common diatoms occurring both in the stomachs of Atlantic menhaden and on a rock from the Slocum River estuary, Mass. Only those populations having greater than 1% mean relative abundance in the stomachs are listed.

Diatoms	Fish stomachs		Rock	Optimal habitat[1]
	Mean	Range		
Nitzschia frustulum var. *perminuta* Grun.	8.0	4.1-13.3	2.3	F
N. subtilis var. *paleacea* Grun.	8.0	1.5-13.5	0.5	F
Navicula cincta (Ehr.) Ralfs	6.8	3.6- 9.6	5.0	B
Melosira nummuloides (Dillw.) Ag.	6.7	1.8-18.9	1.4	B
Skeletonema costatum (Grev.) Cl.	4.5	1.9- 6.3	0.5	B/M
Cyclotella sp. cf. *glomerata* Bachm.	4.2	1.5- 8.7	4.6	?
Eunotia pectinalis (Dillw.) Rabh. var. *pectinalis*	3.0	1.4- 4.5	2.7	F
Achnanthes minutissima Kütz.	2.9	0.5- 5.9	1.4	F
Bacillaria paradoxa Gmel.	2.8	0.9- 5.1	1.8	B
Cyclotella sp. cf. *atomus* Hust.	2.8	0.5- 5.8	5.5	?
Melosira varians Ag.	2.8	0.9- 5.0	0.5	F
Navicula diserta Hust.	2.3	0.0- 4.1	0.5	M
Navicula capitata var. *hungarica* (Grun.) Ross	2.2	0.5- 4.0	1.4	F
Eunotia pectinalis var. *minor* (Kütz.) Rabh.	2.1	0.9- 5.9	2.7	F
Fragilaria construens var. *venter* (Ehr.) Grun.	2.0	0.0- 5.0	2.7	F
Navicula gregaria Donk.	2.0	0.0- 4.0	1.4	B
Rhoicosphenia curvata (Kütz.) Grun.	1.9	1.4- 2.7	1.8	F/B
Nitzschia sigma W. Sm.	1.7	0.9- 4.4	1.4	M
Thalassiosira sp. cf. *nana* Hust.	1.7	0.5- 1.9	0.5	?
Achnanthes weissiae Reim.	1.5	0.9- 2.8	0.9	F
Nitzschia parvula Lewis	1.5	0.0- 1.5	25.6	F
Cyclotella striata (Kütz.) Grun.	1.3	0.5- 3.0	4.1	B
Fragilaria construens var. *intercedens* (Grun.) Hust.	1.1	0.0- 2.7	1.8	F
Total	73.8		71.0	

[1]F = freshwater, B = brackish, M = marine.

2). They accounted also for more than 50% of all individuals. Brackish and marine populations were present in about equal numbers, but more common populations were brackish. Nearly 35% of all individuals belonged to brackish populations. All common populations in the stomachs were at least present on the rock, and 17 of the 23 also accounted for greater than 1% relative abundance in the epilithic assemblage (Table 1). Additionally, 24 rare populations were found in both the stomach and the epilithic samples. The greater number of rare populations found in the stomachs as compared to the rock is attributable to the greater sample size associated with the stomachs. These rare populations were primarily species of *Achnanthes*, *Amphora*, *Cocconeis*, *Cymbella*, *Eunotia*, *Fragilaria*, *Gomphonema*, *Navicula*, *Nitzschia*, and *Synedra*.

TABLE 2.—The distribution of numbers of common and rare diatom populations from the stomach and epilithic assemblages among their optimal habitats (F = freshwater, B = brackish, M = marine). Populations interpreted as growing equally well in two habitats are divided equally between them.

Diatom populations	Stomachs[1]				Rock[2]			
	F	B	M	Total	F	B	M	Total
Common	11.5	6.0	2.5	20.0	11.5	6.0	2.5	20.0
Rare	79.5	15.0	19.5	114.0	12.0	2.5	8.5	23.0
All	91.0	21.0	22.0	134.0	23.5	8.5	11.0	43.0

[1]Total sample size ≈ 1,800 individuals.
[2]Total sample size ≈ 200 individuals.

Based on the examination of about 200 individuals from the epilithic assemblage, 43 populations were identified to species or variety. Twenty identified and three unidentified populations were common in the fish stomachs (Table 1). Only four other populations were unidentified, and they represented less than 3% of all individuals in the sample. All populations are benthic. Given the means of collection of the epilithic assemblage, those populations usually considered planktonic were clearly benthic. They accounted for about 7% of the total number of individuals in the assemblage, as they did in the stomach samples. Nearly 90% of all populations found on the rock were recorded in the stomachs. Freshwater populations accounted for about 50% of both the common and all populations (Table 2). Brackish and marine populations occurred equally among all populations, but among the common ones, brackish populations were more frequent. A population of the freshwater diatom, *Nitzschia parvula*, constituted 25% of the whole assemblage.

Discussion

The benthic microbial communities of estuaries and the adjacent freshwater reaches of rivers, as

well as probably those of shallow marine coastal waters, are utilized directly as a food resource by adult and juvenile menhaden. Our field observations of their grazing habits, the preponderance of benthic diatoms in their stomachs, and the taxonomic and ecological similarity of the diatom assemblages in their stomachs with that of the benthos support this conclusion. The composition of the stomach and epilithic samples is commensurate with the expectations of random sampling of the benthos in this region of the estuary. The quantitative characteristics of estuarine benthic diatom assemblages can be extremely variable within a small space, even on similar substrates (McIntire and Overton 1971; Round 1971; Main and McIntire 1974), and so the expectation of quanititative identity among random samples is low. But, much greater qualititative similarity is expected of samples from similar substrates in the same area.

The data of other investigators, but not their conclusions, support our findings. In a study of the diet of juvenile menhaden collected between April and June 1961, in Delaware, June and Carlson (1971) found most frequently eight genera of diatoms present in their guts: "*Pleurosigma, Navicula, Nitzschia, Cyclotella, Melosira, Amphora, Gyrosigma,* and *Surirella.*" All these genera are characteristically benthic in marine and estuarine ecosystems. Compared to the list of diatom genera they reported from the phytoplankton, which they sampled between November 1960 and May 1961, in the same area, the eight genera accounted on the average for less than 10% of the total number of diatom phytoplankters. Furthermore, they reported that *Skeletonema, Coscinodiscus, Rhizosolenia, Thalassiosira,* and *Thalassiothrix* composed on the average 75% of the diatom phytoplankton, but all were unrecorded from their gut analyses of the fish. We conclude from their data that the juvenile menhaden they collected were not grazing primarily on the plankton but rather on the benthos. Likewise, Mulkana (1966) reported six diatom genera from the stomachs of juvenile menhaden collected in Rhode Island estuaries, and four of the six are usually benthic: *Gyrosigma, Grammatophora, Achnanthes,* and *Navicula.* Although the diatoms, whether planktonic or benthic, appear to constitute a less significant portion of the diet of juveniles and adults in estuaries than does detritus (Jeffries 1975; Peters and Kjelson 1975), they accurately reflect the immediate source of the detritus, because they are good habitat labels (Round 1964, 1971).

Both juvenile and adult menhaden tolerate salinities of less than 1‰ (Reintjes 1969), but we know of no records other than our own of their feeding on primarily freshwater or oligohaline resources.

The Atlantic menhaden is among the commercially most important species in the United States fishery, and consequently, the factors which regulate its population size are of considerable interest. Assuming that human and other predators are prudent, trophic energy availability is likely to be limiting. McHugh (1967) has postulated that "the rate of plankton production will limit the numbers of menhaden . . . that a particular body of water can support." If we interpret the concept of the plankton liberally, including the living organisms plus the suspended detritus, the idea is certainly tenable; however, it is conditional upon the menhaden's grazing being restricted to the plankton. Also, adult menhaden's minimum-size threshold for filtration of particles appears to be around 15 μm with the consequence that a substantial portion of the phytoplankton will be unavailable to them (Durbin and Durbin 1975). But, considering the productivity of benthic primary producers and the quantities of sedimented detritus in shallow estuaries (Darnell 1967; Odum 1971; Smayda 1973), the menhaden's exploitation of the benthos, potentially, at least, doubles the energy available to it. Unfortunately, the quantitative significance of their benthic grazing habits and their ability to assimilate the ingested materials during the estuarine portions of their life cycle are unassessed.

Jeffries (1975) has characterized the menhaden as an adaptable species capable of switching from one food resource to another, and thus compensating for the variability in the availability of estuarine food resources. In general, this apparent switching in juveniles and adults is more the product of a fine-grain feeding in resource-different habitats than of coarse-grain feeding on the plankton. Our observations extend this mode of feeding in menhaden to include benthic habitats.

Literature Cited

CLEVE-EULER, A.
1951-55. Die Diatomeen von Schweden und Finnland. K. Sven. Vetenskaps akad. Handl., Ser. 4, I,2(1):1-163, (1951);

II,4(1):1-158, (1953); III,4(5):1-255, (1953); IV,5(4):1-232, (1955); V,3(3):1-153, (1952).
DARNELL, R. M.
1967. Organic detritus in relation to the estuarine ecosystem. *In* G. H. Lauff (editor), Estuaries, p. 376-382. Am. Assoc. Adv. Sci. Publ. 83.
DURBIN, A. G., AND E. G. DURBIN.
1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. Mar. Biol. (Berl.) 33: 265-277.
FOGED, N.
1947. Diatoms in water-courses in Funen. II. Lindved AA (The Lindved Brook). III. Odense AA (The Odense Brook). Dan. Bot. Ark 12(6):1-69. 1954. On the diatom flora of some Funen lakes. Folia Limnol. Scand. 6, 75 p.
HOFF, J. G., P. BARROW, AND D. A. MCGILL.
1969. Some aspects of the hydrography of a relatively unpolluted estuary in southeastern Massachusetts. Proc. 24th Ind. Waste Conf., Purdue Univ. Eng. Exten. Ser. 135:87-98.
HOHN, M. H., AND J. HELLERMAN.
1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. Trans. Am. Microsc. Soc. 82:250-329.
HUSTEDT, F.
1937-1938. Systematische und ökologische Untersuchungen uber die Diatomeen-Flora von Java, Bali and Sumatra. Arkiv Hydrobiol. Suppl.-Bd. XV: "Tropische Binnengewässer," 506 p.
1939. Die Diatomeenflora des Kustengebeites der Nordsee vom Dollart bis zur Elbe-mundung. Abh. Naturwiss. Ver. Bremen 31:572-677.
JEFFRIES, H. P.
1975. Diets of juvenile Atlantic menhaden (*Brevoortia tyrannus*) in three estuarine habitats as determined from fatty acid composition of gut contents. J. Fish. Res. Board Can. 32:587-592.
JUNE, F. C., AND F. T. CARLSON.
1971. Food of young Atlantic menhaden, *Brevoortia tyrannus*, in relation to metamorphosis. Fish. Bull., U.S. 68:493-512.
MAIN, S. P., AND C. D. MCINTIRE.
1974. The distribution of epiphytic diatoms in Yaquina Estuary, Oregon (U.S.A.). Bot. Mar. 17:88-99.
MCHUGH, J. L.
1967. Estuarine nekton. *In* G. H. Lauff (editor), Estuaries, p. 581-620. Am. Assoc. Adv. Sci. Publ. 83.
MCINTIRE, C. D., AND W. S. OVERTON.
1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. Ecology 52: 758-777.
MULKANA, M. S.
1966. The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Res. Rep. 2:97-167.
ODUM, E. P.
1971. Fundamentals of ecology. 3rd ed. W. B. Saunders, Phila., 574 p.
PATRICK, R., AND C. W. REIMER.
1966. The diatoms of the United States exclusive of Alaska and Hawaii. Vol. 1: Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. Monogr. Acad. Nat. Sci. Phila. 13, 688 p.
PETERS, D. S., AND M. A. KJELSON.
1975. Composition and utilization of food by postlarval and juvenile fishes of North Carolina estuaries. *In* L. E. Cronin (editor), Estuarine Research. Vol. 1, p. 448-472. Academic Press, N.Y.
REINTJES, J. W.
1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv., Circ. 320, 30 p.
ROUND, F. E.
1964. The ecology of benthic algae. *In* D. F. Jackson (editor), Algae and man, p. 138-184. Plenum Press, N.Y.
1971. Benthic marine diatoms. Oceanogr. Mar. Biol., Annu. Rev. 9:83-139.
SMAYDA, T. J.
1973. Phytoplankton. *In* Coastal and offshore environmental inventory: Cape Hatteras to Nantucket Shoals, Sec. 3, 100 p. Mar. Publ. Ser. 2, Univ. Rhode Island, Kingston.

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ELECTROPHORETIC EVIDENCE OF HYBRID SNOW CRAB, *CHIONOECETES BAIRDI* × *OPILIO*

Karinen and Hoopes (1971) and Hoopes et al. (1972) reported finding snow (Tanner) crabs in the southeastern Bering Sea which possessed morphological characteristics that were atypical for either *Chionoecetes bairdi* or *C. opilio* and, instead, were intermediate. The females of this form appeared to have reduced reproductivity, as many were nongravid at maturity, and those that were gravid possessed abnormally small egg clutches containing large numbers of dead eggs. These conditions were presented as evidence of hybridization. Hybrid-type males constituted 1.0% of all male snow crabs captured, while hybrid-type females made up 0.4% of the females captured.

Karinen (1974) confirmed the above reports and found that hybrids made up 4.6% of the snow crabs collected in the Bering Sea and were most abundant west of lat. 166°W. The carapace width frequency of the hybrids was intermediate between *C. bairdi* and *C. opilio*—providing additional evidence of hybridization.

The purpose of the present study was to determine if electrophoretic differences between the parent species and the hybrid could be detected.

The samples used were collected from the southeastern Bering Sea in July 1974, identified, and frozen by National Marine Fisheries Service (NMFS) personnel. The general proteins of leg

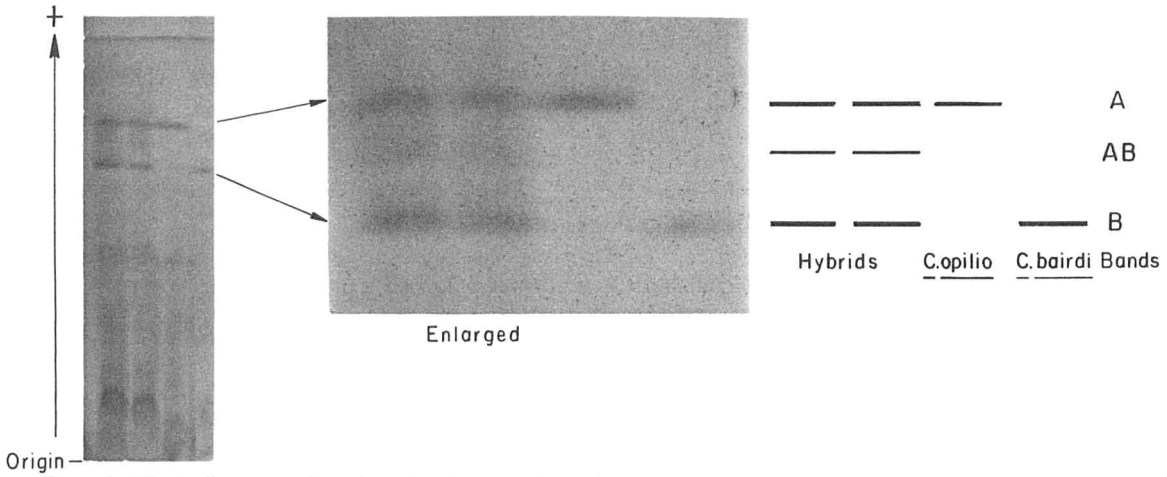

FIGURE 1.—Electropherogram of starch gel showing general muscle protein patterns of *Chinoecetes bairdi*, *C. opilio*, and hybrids.

muscle tissue from 10 *C. bairdi*, 5 hybrids, and 10 *C. opilio* were examined electrophoretically using the methods of Johnson et al. (1972) and the buffer system of Ridgway et al. (1970).

The electrophoretic patterns of general muscle proteins are shown in Figure 1. All *C. opilio* patterns possessed a single band (A), while all *C. bairdi* showed a slower anodally migrating band (B). The five hybrids possessed three bands: A, B, and an intermediate band AB which indicates hybridization between *C. bairdi* and *C. opilio*.

The intermediate band (AB) was less intense than either of the other bands (A or B). A 1:2:1 ratio is expected in random combination of dimeric protein. I thus assume that there is nonrandom association between the protein units.

Further investigation is needed to determine if the electrophoretic patterns reported here are evident in all possible crosses between the two parent species and that the parental patterns are invariant throughout their ranges.

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Literature Cited

HOOPES, D. T., J. F. KARINEN, AND M. J. PELTO.
1972. King and Tanner crab research. Int. North Pac. Fish. Comm., Annu. Rep. 1970:110-120.

JOHNSON, A. G., F. M. UTTER, AND H. O. HODGINS.
1972. Electrophoretic investigation of the family Scorpaenidae. Fish. Bull., U.S. 70:403-413.

KARINEN, J. F.
1974. King and Tanner crab research, 1971. Int. North Pac. Fish. Comm., Annu. Rep. 1972:102-111.

KARINEN, J. F., AND D. T. HOOPES.
1971. Occurrence of Tanner crabs (*Chionoecetes* sp.) in the eastern Bering Sea with characteristics intermediate between *C. bairdi* and *C. opilio*. (Abstr.) Proc. Natl. Shellfish Assoc. 61:8-9.

RIDGWAY, G. J., S. W. SHERBURNE, AND R. D. LEWIS.
1970. Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99:147-151.

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EFFECTS OF BENZENE ON GROWTH, FAT CONTENT, AND CALORIC CONTENT OF STRIPED BASS, *MORONE SAXATILIS*

The San Francisco Bay area is a major terminus and refinery area for crude oil, and oil-related activities in the area are expected to increase because of the Alaska pipeline and expanded drilling on the outer continental shelves of California and Alaska. The San Francisco Bay-delta region supports a number of fisheries, including the most important recreational striped bass, *Morone saxatilis*, fishery on the west coast. Information on the toxicity of aromatics in crude oil to striped bass and other fisheries is needed.

The aromatic hydrocarbon, benzene, is one of the major water-soluble components of crude oil. Anderson et al. (1974) reported 6.75 and 3.36‰ in the water-soluble fractions of south Louisiana and Kuwait crude oil standards respectively. In addition to being relatively soluble in water (1,780 ‰ – McAuliffe 1966), benzene is one of the most toxic components of petroleum.

The acute 96-h, TL-50 lethal level (10-11 μl/liter) of constant benzene exposure for juvenile striped bass was determined previously at our laboratory by Meyerhoff (1975). The objective of experiments described here was to see if sublethal levels of benzene, although not inducing death, would inhibit efficient energy utilization by the fish as measured by growth (wet weight, dry weight), fat content, and caloric content. Because the experimental period of 4 wk was relatively short, the juvenile striped bass were exposed to mean high-sublethal concentrations (3.5 μl/liter, SD 1.4; 6.0 μl/liter, SD 1.6) to determine the effects of benzene on growth.

Methods

Juvenile striped bass (mean standard length 18.1 cm, SD 2.3; mean total wet weight 3.39 g, SD 1.1) were obtained from the Tracy pumping plant operated by the Bureau of Reclamation, Tracy, Calif. After being transported by truck to our facility (Korn 1975) the fish were changed to saline water (26‰) during a 3-day period. Juvenile fish occur naturally at this salinity as well as in fresh water. The fish were acclimated for 2 wk to test conditions (salinity 26‰, temperature 15°-16°C, pH 7.8). Thirty-five fish were then placed into each of nine 80-liter fiber glass aquariums and acclimated for one more week. Halver's diet (1957) in pelleted form (5.350 kcal/g) was fed at the rate of 3% of fish body weight per day.

Benzene concentrations were maintained in three aquariums at 3.5 μl/liter benzene and in three at 6 μl/liter benzene; three others served as controls (0 μl/liter). Relatively constant benzene concentrations were maintained using the method of Benville and Korn (1974). The input of benzene-saturated air was balanced by a continuous 2 liters/min water flow through the aquariums.

Benzene concentrations were monitored daily using the gas chromatograph procedure of Benville and Korn (1974). Water quality conditions during the test were as follows: temperature, 15.2°-16.4°C; oxygen, 7.5-7.9 mg/liter; salinity, 25-26‰; pH, 7.7-7.8; ammonia, <0.5 mg/liter.

Seven fish were sampled from each aquarium at 0, 7, 14, 21, and 28 days. The animals were anesthetized with MS-222,[1] killed by severing the spinal cord, blotted dry, weighed individually, dried in a 70°C oven for 4 days, cooled in a desiccator, and reweighed. Three of the fish were then processed for caloric analyses and four for fat analyses.

Calorimetric content was analyzed by individually processing three fish in a Parr adiabatic calorimeter, model 1241.

For fat analyses, the four dried fish were blended with 150-ml MF Freon (monoflourotrichloromethane) in a high-speed blender. The mixture was poured and rinsed into a Buchner vacuum filter through No. 1 filter paper. The filtrate was put into preweighed beakers and evaporated in a hood to dryness. After reweighing the beakers, fat content was calculated.

Data were analyzed with an analysis of variance for factorial design program (BMD 02V–Dixon 1973). The independent factors of tank, week, concentration, and their interactions were tested for significance of effect on the dependent variables of wet weight, dry weight, fat content, and caloric value. Duncan's new multiple-range test (Duncan 1955; Pachares 1959) was used to determine the significant differences between means of levels for treatments found significant in the analysis of variance.

Results

Benzene concentrations varied because of fluctuations in water flow caused by particulate material clogging the valves. The high-level treatment varied from 3.6 to 8.1 μl/liter during the 4-wk test; the low-level treatment varied from 1.5 to 5.4 μl/liter. Analysis of variance of the benzene water concentration showed a significant ($P<0.01$) increase at both levels over the test period. However, the means of low (3.5 μl/liter, SD 1.4) and high (6.0 μl/liter, SD 1.6) concentrations were significantly different ($P<0.01$).

The start of benzene exposure caused pronounced hyperactivity at the high level and a moderate effect at the low level. The fish reacted by attempting to jump out of the water. Fish exposed to the high level attempted to feed but were unable to locate and consume their ration. Random jerking movements were observed when

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food was introduced. Fish exposed to the low level had some success locating the food, and approximately 50% of the pellets were consumed. Control fish successfully consumed all of their ration within 5 min.

After 1 wk, feeding success on low- and high-dose fish started improving gradually. At the end of the study, the control and low-level fish fed normally, while the high-level fish consumed 50% of their ration.

Analyses of variance of wet weight, dry weight, kilocalories per gram ash-free dry weight, and percent fat between concentrations, weeks, and tanks yielded the following results (Tables 1, 2). There was a significant decrease in wet weight ($P<0.05$), dry weight ($P<0.01$), and percent fat ($P<0.01$) with increasing concentration (Table 2). Concentration levels varied significantly ($P<0.05$) (Table 1): Wet weight was less at 6.0 μl/liter than controls and did not vary significantly between 3.5 μl/liter and controls or between 3.5 and 6.0 μl/liter. Dry weight was less at 6.0 μl/liter than at 3.5 μl/liter and controls but did not vary significantly between controls and 3.5 μl/liter. Percent fat was less at 6.0 and 3.5 μl/liter than in controls. There was no significant difference in percent fat between 6.0 and 3.5 μl/liter.

There was a significant increase in dry weight ($P<0.05$) during the last week at all exposures (Table 2, Figure 1). There was no significant difference between treatments in kilocalories per gram ash-free dry weight (Table 2). The significant interaction between concentration and tank ($P<0.05$–Table 2) is a result of experimental design in which certain tanks were always at a high or low concentration. No significant variation occurred between tanks.

TABLE 1.–Mean wet wet and dry weights and fat caloric content of one control and two test groups of striped bass, *Morone saxatilis*, exposed to benzene for 4 wk.

Treatment mean concentration (μ l/liter)	Variable[2]			
	Wet weight (g)	Dry weight (g)	Fat (%)	Ash-free dry weight (kcal/g)
Control	2.7135	0.8721	39.2	6.8123
Low level (3.5)	2.6062	0.8137	34.1	6.8435
High level (6.0)	2.3951	0.7242	32.2	6.7451
Total number of fish	315	315	45	45

[1]The three treatments used three replicate tanks per treatment sampled at 0, 1, 2, 3, and 4 wk. Tests for wet and dry weights had seven fish/tank per week; tests for percent fat had four fish/tank per week; and tests for kilocalories/gram ash-free dry weight had three fish/tank per week.

[2]Duncan's new multiple-range test of differences between means of treatment levels was performed. Means grouped above with same bar are not significantly different at the 5% level. Means not grouped with same bar are significantly different at the 5% level (Duncan 1955; Pachares 1959).

Discussion

Although acclimated, fish in all treatments were stressed from crowding and insufficient water movement. This was unavoidable because space and equipment were limited. Consequently, the control fish did not grow at the same rate as similar fish held in larger tanks at this facility. In spite of these limitations, significant relative changes in growth rate and fat content did occur between exposure treatments. Wet weight, dry weight, and fat content decreased with increasing concentration as expected. This was probably due

TABLE 2.–Analysis of variance of treatment effects of benzene concentration (μl/liter), week, and tank number on wet weight (g), dry weight (g), kilocalories per gram ash-free dry weight, and percent fat of juvenile striped bass, *Morone saxatilis*.

Dependent variable and source of variation	df	Sum of squares	Mean square	F ratio	Probability
Wet weight:					
Concentration	2	5.511	2.756	3.16	$P<0.05$
Week	4	7.750	1.938	2.20	NS
Tank	2	3.050	1.525	1.75	NS
Concentration-week	8	11.673	0.909	1.04	NS
Concentration-tank	4	11.255	2.814	3.22	$P<0.05$
Week-tank	8	11.673	1.459	1.67	NS
Concentration-week-tank	16	15.516	0.970	1.11	NS
Within (error)	270	235.675	0.873	—	—
Total	314	302.103	—	—	—
Dry weight:					
Concentration	2	1.165	0.583	5.40	$P<0.01$
Week	4	1.232	0.308	2.85	$P<0.05$
Tank	2	0.420	0.210	1.94	NS
Concentration-week	8	0.933	0.117	1.08	NS
Concentration-tank	4	1.214	0.304	2.81	$P<0.05$
Week-tank	8	1.367	0.171	1.58	NS
Concentration-week-tank	16	2.166	0.135	1.25	NS
Within (error)	270	29.137	0.108	—	—
Total	314	37.634	—	—	—
Kilocalories per gram ash-free dry weight:					
Concentration	2	0.076	0.038	0.50	NS
Week	4	0.404	0.101	1.33	NS
Tank	2	0.284	0.142	1.87	NS
Concentration-week	8	1.177	0.147	1.93	NS
Concentration-tank	4	0.147	0.037	0.49	NS
Week-tank	8	0.667	0.083	1.09	NS
Residual (error)	16	1.222	0.076	—	—
Total	44	3.977	—	—	—
Percent fat:					
Concentration	2	383.902	191.951	13.42	$P<0.01$
Week	4	99.539	24.885	1.74	NS
Tank	2	52.878	26.439	1.85	NS
Concentration-week	8	138.843	17.355	1.21	NS
Concentration-tank	4	55.000	13.750	0.96	NS
Week-tank	8	190.733	23.842	1.67	NS
Residual (error)	16	228.929	14.308	—	—
Total	44	1,149.824	—	—	—

NS = not significant.

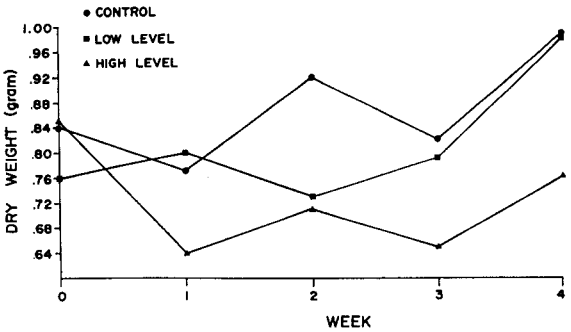

FIGURE 1.—Average weight of each of three groups of striped bass, *Morone saxatilis*, exposed to three concentrations of benzene (0, 3.5, and 6.0 μl/liter) for 4 wk. The dry weight of high-level exposure fish was significantly less ($P<0.01$) than the other two groups at the end of the first week and thereafter. The dry weight of the three groups combined was significantly higher ($P<0.05$) than in previous weeks.

mostly to impaired food localization at higher concentrations. A similar effect on the nervous system is documented by Brocksen and Bailey (1973). The energy required to metabolize benzene could also decrease efficient utilization of energy for growth and fat deposition.

There was an apparent acclimation of the fish to benzene at the low level (3.5 μl/liter) by the end of the 4-wk exposure, as reflected by the dry weight of the fish (Figure 1). After 4 wk at high level (6.0 μl/liter), fish also appeared to begin to recover from effects. This was substantiated by observations of improved feeding response in exposed fish as the experiment progressed. Nevertheless, definite effects of benzene on growth parameters were noted at 6.0- and 3.5-μl/liter levels of benzene. Although the fish may be able to adapt by metabolic detoxification and depuration of benzene and metabolites, after more prolonged periods the competitive effects on energy utilization may not only decrease growth but also increase mortality or reduce ability to withstand environmental stress.

The parameters measured in this study show effects at the low μl/liter levels. In most situations, it is unlikely that fish would be exposed to benzene above the nl/liter level except shortly after catastrophic spills. Anderson et al. (1974) obtained a concentration of several μl/liter benzene in water-soluble extracts of crude oils. In the marine environment, dilution and volatilization of benzene would probably lower the concentration of benzene rapidly. Research on effects at the nl/liter level is needed along with monitoring information on actual concentrations of benzene in chronically polluted environments. Such situations may induce a reduction in growth rate and fat deposition which would have implications in the reproductive potential of exposed species. Studies of chronic effects of low concentrations of benzene on reproduction, including fecundity, egg size, embryonic development, and larval survival, are indicated. Some of these studies have been completed at the Tiburon Laboratory and will be reported on later.

Acknowledgments

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Literature Cited

ANDERSON, J. W., J. M. NEFF, B. A. COX, H. E. TATEM, AND G. M. HIGHTOWER.
1974. Characteristics of dispersions and water-soluble extracts of crude and refined oils and their toxicity to estuarine crustaceans and fish. Mar. Biol. (Berl.) 27:75-88.

BENVILLE, P. E., JR. AND S. KORN.
1974. A simple apparatus for metering volatile liquids into water. J. Fish. Res. Board Can. 31:367-368.

BROCKSEN, R. W., AND H. T. BAILEY.
1973. Respiratory response of juvenile chinook salmon and striped bass exposed to benzene, a water-soluble component of crude oil *In* Proceedings of Joint Conference on Prevention and Control of Oil Spills, p. 783-791. Am. Pet. Inst., Environ. Prot. Agency, U.S. Coast Guard, Wash., D.C.

DIXON, W. J. (editor).
1973. BMD biomedical computer programs. Univ. Calif. Press, Berkeley, 773 p.

DUNCAN, D. B.
1955. Multiple range and multiple *F* tests. Biometrics 11:1-42.

HALVER, J. E.
1957. Nutrition of salmonid fishes. III. Water-soluble vitamin requirements of chinook salmon. J. Nutr. 62:225-243.

KORN, S.
1975. Semiclosed seawater system with automatic salinity, temperature, and turbidity control. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-694, 5 p.

MCAULIFFE, C.
1966. Solubility in water of paraffin, cycloparaffin, olefin, acetylene, cycloolefin, and aromatic hydrocarbons. J. Phys. Chem. 70:1267-1275.

MEYERHOFF, R. D.
1975. Acute toxicity of benzene, a component of crude oil, to

juvenile striped bass (*Morone saxatilis*). J. Fish. Res. Board Can. 32:1864-1866.
PACHARES, J.
1959. Table of the upper 10% points of the studentized range. Biometrika 46:461-466.
PARR INSTRUMENT CO.
1969. Instructions for D41 and D42 adiabatic calorimeters. Man. 142. Parr Instrum. Co., 211 53d St., Moline, Ill., 23 p.

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FERTILIZATION METHOD QUANTIFYING GAMETE CONCENTRATIONS AND MAXIMIZING LARVAE PRODUCTION IN *CRASSOSTREA GIGAS*

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Most workers obtain oyster larvae by using experimental methods similar to those reported by Galtsoff (1964). Although useful in most hatchery or laboratory investigations, these methods do not quantify gamete concentrations. To obtain specific larval concentrations, most researchers dilute dense postfertilization concentrations.

This paper reports on a method of estimating sperm concentrations of Pacific oyster, *Crassostrea gigas*, using colorimetric techniques, and on a method of fertilization using small volumes of seawater and known gamete concentrations. We also present an index which may be useful in evaluating the efficiency of fertilization. These methods were developed during 1973 and should prove useful in the study and production of cultured oysters.

Materials and Methods

Pacific oysters were obtained from Fowler Oyster Co. on Yaquina Bay, Newport, Oreg. Sand-filtered seawater of 25-32‰ salinity and pH 7.0-8.1 was collected at the Oregon State University Marine Science Center (MSC) at Newport, exposed to ultraviolet light (3.785 liters/min), diluted (when necessary) to 25‰ with distilled water, and stored in Nalgene carboys. This salinity is within the range recommended for *C. virginica* by Davis and Calabrese (1964), and was used for maintenance of oysters and for experiments on fertilization and early larval development. In laboratory procedures, all glassware was initially acid-washed; used glassware was carefully cleaned and rinsed several times first in tap water and then in distilled water; all polyethylene tubing was Tygon[1] R3606 (nontoxic by bioassay, Breese, MSC, unpubl. data); gametes and larvae were confined in glass containers only (except for momentary exposure to stainless steel syringe needles and nylon screen); all seawater used in fertilization experiments was Millipore-filtered (0.47 μm) and stored in glass screw-cap bottles with Parafilm-lined caps (nontoxic by bioassay, Breese unpubl. data).

Procurement of Gametes

To enhance gonad development, we conditioned mature oysters in seawater at 16.0° ± 1.0°C for 3-6 wk (Loosanoff and Davis 1963). To identify test oysters, we drilled a 0.8-mm (1/32-inch) hole in the umbo and attached a 6.4- × 15.9-mm numbered plastic tag (Howitt Plastics Co., Mollala, Oreg.) with monofilament. After conditioning, access to the gonads was made by drilling a 1.2-mm (3/64-inch) hole in the posterodorsal region of the right valve. We extracted gametes with a 2.5-cm^3 glass syringe fitted with a 20-gauge 38-mm needle containing about 0.5 ml of seawater (Lannan 1971). Oysters containing either intensively motile sperm or eggs greater than or equal to 36 μm were kept for fertilization experiments. To prevent spawning after extractions, we isolated individual oysters for 12-24 h in 3-liter beakers containing seawater at 12°C.

Prior to gamete extraction we raised the temperature of all donor oysters to 27.0° ± 0.5°C, a temperature within the range recommended by Davis and Calabrese (1964) for fertilization and larval development. Oysters were transferred from the conditioning tray to an 18.9-liter (5-gallon) tank containing 11.4 liters (3 gallons) of seawater at 16.0° ± 1.0°C; a 100-W aquarium heater

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

connected to a thermostat slowly increased the temperature to 27.0° ± 0.5°C. After 30-60 min at this temperature, we extracted gametes by syringe (as above) for use in fertilization experiments. To protect gametes from large pressure changes during gonad extractions, we maintained a gentle and constant negative pressure in the syringe; gametes drawn abruptly into the syringe were discarded. Only extractions which entered the syringe as dense white cords were used; more diffuse or cloudy extractions were also discarded. Samples of gonad extractions and all seawater and glassware used were stored at 27.0° ± 0.5°C.

Gamete Concentrations and Fertilization

Extractions from the gonads of 3-5 males were transferred to and lightly agitated in a Klett-Summerson sample tube containing 5-8 ml of seawater. Using a Klett-Summerson colorimeter with a green (#54) filter, we measured light diffusion through diluted extractions. We then diluted subsamples, placed them in a hemacytometer, and counted the number of sperm. Comparisons were then made between the Klett reading (K) and the actual sperm counts.

Gonad extractions from 3-5 females were similarly pooled, transferred to a Nytex screen (36-μm mesh), and rinsed with seawater to remove small debris and reduce the possibility that some component of the eggs (released from any ova broken during extraction) would cause sperm to agglutinate (Galtsoff 1964). We then rinsed the cleaned eggs into a 250-ml beaker containing 20-50 ml of seawater, counted samples of eggs using a dissection microscope, diluted samples with seawater until reaching the desired concentration, and maintained the egg-seawater suspension at 27.0° ± 0.5°C. We discarded eggs remaining in seawater for more than 1 h to reduce the possibility of sperm agglutination resulting from secretions.

Using a Pasteur pipette (45 drops of seawater/ml), we transferred various sperm concentrations (Table 1) to numbered Syracuse watch glasses, then with an automatic pipette added 0.2 ml of egg-seawater suspension containing 100 ± 4 eggs. The pH of 7.8 ± 0.1 was in the range recommended by Humphrey (1950). After introduction of the egg-seawater suspension, we added 7 ml of seawater at different time intervals (flooding time, Table 2) to dilute the sperm concentrations and to reduce the possibility of polyspermy. The watch glasses were stacked to reduce evaporation and incubated at 27.0° ± 0.5°C. Because the number of swimming lavae did not increase after 6 h postfertilization time, the number of fertilized eggs was obtained by counting unfertilized eggs remaining on the bottom at 6 h and subtracting this figure from 100 (the number of eggs originally present). After 24 h we transferred the watch glasses to a 4°C refrigerator; within 30 min the D-shaped (straight-hinged) larvae settled to the bottom and were easily counted.

Although none of the 460 oysters examined appeared hermaphroditic, sperm-free controls were used in all experiments. We did not observe fertilization in any of the controls.

TABLE 1.—Range and mean of percent fertilization (%Z) and percent of larvae developing to the D-shape stage (%D) resulting from different sperm concentrations combined with fresh eggs (100 ± 4/0.2 ml) of *Crassostrea gigas*.[1]

Sperm		%Z		%D			
Concn.	Vol (ml)	Range	Mean	Range	Mean	$L_{\bar{x}}$[2]	CI[3]
1.1×10^4	0.02	0- 58	27.6	0-56	25.0	2.60	0.74
3.3×10^4	0.07	10- 55	34.4	10-50	29.2	5.20	0.64
5.5×10^4	0.11	41- 86	57.4	36-73	48.0	9.40	0.99
1.1×10^5	0.22	55-100	77.2	50-93	58.6	18.60	0.91
2.4×10^5	0.02	60-100	72.6	47-88	58.2	14.40	1.05
7.3×10^5	0.07	75-100	87.0	51-94	68.8	18.20	1.16
1.2×10^6	0.11	78-100	89.0	35-70	45.2	43.80	0.33
2.4×10^6	0.22	80-100	89.2	13-72	29.0	60.20	0.12
5.0×10^6	0.50	80-100	92.4	8-43	21.9	70.50	0.06
1.1×10^7	1.00	87-100	96.0	0-23	15.0	81.00	0.03

[1]Seawater of salinity 25‰ and pH 7.8 ± 0.1; temperature 27° ± 0.5°C; gametes diluted with 7 ml of seawater at 10 min postfertilization; 5 repetitions per sperm concentration.

[2]$L_{\bar{x}}$ = Mean percent larvae losses = ($\%Z_{\bar{x}}$ minus $\%D_{\bar{x}}$).

[3]CI = Compatibility index = $\frac{(\%D_{\bar{x}})^2}{\sqrt{L_{\bar{x}}(\%Z_{\bar{x}})}} \times 10_{\bar{x}}^2$.

TABLE 2.—The range and mean of percent fertilization (%Z) and percent of larvae developing to the D-shaped stage (%D) obtained by different flooding times[1] after combining the gametes of *Crassostrea gigas*.[2]

Flooding time[1] (min)	%Z		%D		
	Range	Mean	Range	Mean	$L_{\bar{x}}$[3]
1	41- 88	67.2	41-72	62.0	5.2
5	73-100	85.4	65-94	73.0	12.4
10	75-100	87.8	51-94	68.2	19.6
15	78-100	89.8	0-68	47.0	42.8
30	82-100	96.4	0-20	8.8	87.6

[1]Flooding time = time (min) between the combination of gametes and the addition of 7 ml of seawater to the gamete mixture.

[2]Using seawater of salinity 25‰ and pH 7.8 ± 0.1, 100 ± 4 eggs in 0.2 ml of seawater were added to 7.3×10^5 sperm in 0.07 ml of seawater; 5 repetitions/flooding time were used.

[3]$L_{\bar{x}}$ = Mean percent larvae losses = ($\%Z_{\bar{x}}$ minus $\%D_{\bar{x}}$).

Results and Discussion

The relationship between K and the number of

sperm counted is linear (r = 0.996) from about K = 10 to about K = 80 (Figure 1). Because this method of estimation is sufficiently precise and accurate and because attempts to minimize gonadal debris (and thus minimize a variable in colorimetric evaluation) by gravity filtration or centrifugation usually resulted in broken tails and agglutination, respectively, we consider our methods of sperm procurement and estimation useful. Measuring light diffusion through a sample of *C. gigas* eggs did not accurately estimate egg numbers because they settled rapidly.

We estimate that about one-half the number of sperm counted had little or no observable motility; we may have withdrawn immature sperm or damaged mature sperm during extraction. Inactive sperm were not agglutinated, an indication that the acrosome reaction was not the major cause of immotility. Although not directly equating fertilization capacity with high motility, our assumption is that relatively immotile sperm are incapable of fertilizing viable eggs. Similarly, extractions from females often included small and presumably immature eggs (Galtsoff 1964). Sperm concentrations reported in Figure 1 and Tables 1 and 2 are observed values and do not reflect estimates of immotile cells; only "mature-sized" eggs were used because eggs less than 36 μm were rinsed through the cleaning screen.

Within the limits of this investigation, mean percent fertilization ($\%Z_{\bar{x}}$) increased as the number of sperm/100 eggs increased (Table 1). The mean percent of larvae developing to the D-shape stage ($\%D_{\bar{x}}$) increased until 7.3 × 10^5 sperm were used; $\%D_{\bar{x}}$ decreased with further increases of sperm concentration (Table 1). Because Glatsoff (1964) reported that high sperm concentrations may result in polyspermy and because in our experiments resulting in large

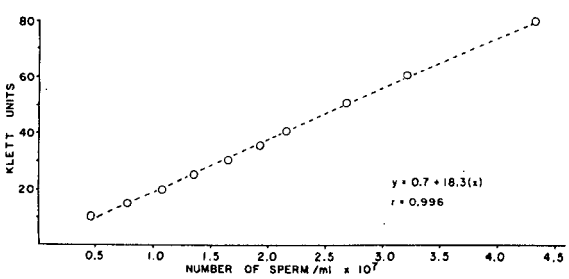

FIGURE 1.–Correlation between mean (N = 5) number of *Crassostrea gigas* sperm and Klett units (light diffusion readings) on a Klett-Summerson colorimeter.

losses of larvae ($L_{\bar{x}}$ [where $L_{\bar{x}}$ = $\%Z_{\bar{x}}$ minus $\%D_{\bar{x}}$]) aberrant forms were observed (e.g., swimming chains of cells, and trochophores persisting beyond 48 h), we assume polyspermy was responsible for the increasing $L_{\bar{x}}$.

Using 7.3 × 10^5 sperm/100 eggs, we observed that $\%Z_{\bar{x}}$ increased as flodding time increased (Table 2). $L_{\bar{x}}$ also increased as flooding time increased, and maximum $\%D_{\bar{x}}$ was obtained using a flooding time of 5 min.

Although most workers need only to maximize $\%D_{\bar{x}}$ without regard to $L_{\bar{x}}$, some investigators may need to minimize $L_{\bar{x}}$ due to limited spawning stock or other problems. Thus, to achieve maximum efficiency it is necessary to maximize $\%D_{\bar{x}}$ and minimize $L_{\bar{x}}$. Under different conditions (e.g., water quality and gamete viability may differ at different locations or at different times), the optimal sperm concentration and flooding time will vary in response to the environment. Increases in $\%D_{\bar{x}}$ (by increasing sperm concentration or flooding time) also produce undesirable increases in $L_{\bar{x}}$, thus a subjective decision usually is made to evaluate the efficiency of fertilization and larvae production. To reduce the subjectivity of this evaluation, we suggest the following formula reflects a compatability between maximum $\%D_{\bar{x}}$ and minimum $L_{\bar{x}}$:

$$\text{Compatability index (CI)} = \frac{(\%D_{\bar{x}})^2}{\sqrt{L_{\bar{x}}\ (\%Z_{\bar{x}})}} \times 10^{-2}.$$

In our lab, values greater than or equal to 1 were desirable, and 1.16 was the maximim value obtained (Table 1). CI values can be high for relatively low $\%D_{\bar{x}}$ if $L_{\bar{x}}$ is unusually low (e.g., where $\%Z_{\bar{x}}$ = 30, and $\%D_{\bar{x}}$ = 28, CI = 1.01). Low $L_{\bar{x}}$ values will normally be associated with low $\%D_{\bar{x}}$; however, if a low $L_{\bar{x}}$ occurs concommittantly with a "reasonable" $\%D_{\bar{x}}$, we assume that the evaluation would be based more on the desired $\%D_{\bar{x}}$ rather than on CI. Further, due to the often dramatic differences in conditions at different labs and hatcheries, or at different times, attempts to establish a desirable CI value or range under specified conditions may prove useful.

During a 4- to 6-wk period we made 8-12 extractions from individual oysters, but did not observe a deterioration of gametes. Data from experiments using gametes from initial extractions were consistent with those of later extractions. The pooling of extractions may have reduced observable changes. After about 8 wk, eggs were easily broken and we noticed free yolk in extrac-

tions. Although deterioration of male gonads was less evident, we noted that the sperm concentration decreased after about 8 wk, presumably as a result of resorption. The mortality rate for oysters repeatedly used for gamete extractions and maintained without food or biological filters in 113.6-liter (30-gallon) tanks containing recirculating seawater (25‰) at 16.0° ± 1.0°C was about 10% during the 8-wk period.

Because high concentrations and large numbers of gametes can repeatedly be extracted from the gonads of individual oysters without apparent detriment and because gamete extraction obviates artificial spawning and its inherent problems, we suggest our method of gamete procurement can be useful in many investigations and hatchery situations. Our method also permits repeated use of the gametes of selected oysters, and this together with the possible use of cryopreserved sperm (Staeger 1974) reduces variability and increases control and management of hatchery production or biological investigations.

Acknowledgments

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Literature Cited

DAVIS, H. C., AND A. CALABRESE.
1964. Combined effects of temperature and salinity on development of eggs and growth of larvae of *M. mercenaria* and *C. virginica*. U.S. Fish Wildl. Serv., Fish. Bull. 63:643-655.

GALTSOFF, P. S.
1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Fish Wildl. Serv., Fish. Bull. 64:1-480.

HUMPHREY, G. F.
1950. The metabolism of oyster spermatozoa. Aust. J. Exp. Biol. Med. Sci. 28:1-13.

LANNAN, J. E.
1971. Experimental self-fertilization of the Pacific oyster, *Crassostrea gigas*, utilizing cryopreserved sperm. Genetics 68:599-601.

LOOSANOFF, V. L., AND H. C. DAVIS.
1963. Rearing of bivalve mollusks. Adv. Mar. Biol. 1:1-136.

STAEGER, W. H.
1974. Cryobiological investigations of the gametes of the Pacific oyster, *Crassostrea gigas*. M.S. Thesis, Oregon State Univ., Corvallis, 45 p.

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DEPARTMENT OF COMMERCE • UNITED STATES OF AMERICA

Fishery Bulletin

National Oceanic and Atmospheric Administration • National Marine Fisheries Service

Vol. 74, No. 4 October 1976

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Seattle, Washington

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DAY VERSUS NIGHT ACTIVITY OF REEF FISHES IN A KELP FOREST OFF SANTA BARBARA, CALIFORNIA

ALFRED W. EBELING AND RICHARD N. BRAY[1]

ABSTRACT

Vertical distributions and feeding activities of residential kelp-bed fishes were compared between day and night in an area of reef and kelp off Santa Barbara, Calif. Abundances and positions of fishes within four vertically oriented zones were observed during 42 paired day and night scuba transects made throughout the year along a line secured to a high-relief rocky reef located about 1.6 km offshore. Feeding activity was determined for surfperches (Embiotocidae) from the proportion of fish collected during the day or night having empty "foreguts," and inferred for other fishes from general observations of individuals. Although almost all of the 25 common fish species recorded were seen both day and night, the number seen and the degree of activity of most of these species decreased considerably at night. Many fishes that fed and moved about in mid-water well above the reef during the day were found in holes and crevices in the reef at night; others that foraged on or just above the bottom during the day showed little change in their position; and still others tended to disperse to adjacent areas of the reef. Daytime aggregations of fishes centered around the crest of the reef and other productive prominences and invariably dispersed at night. Unlike tropical communities of reef fishes, the kelp-bed community included neither a broad replacement for diurnal planktivores in the night shift nor a contingent that moves out over nearby sand flats to forage at night. Kelp-bed fishes showed considerable intraspecific variability in behavior. Thus, the kelp-bed community appears to be more loosely "programmed" even though it follows the same basic pattern of diel activity as the tropical-reef community. The kelp-bed species that belong to primarily tropical families tended to be quite specialized in their nocturnal sheltering behavior. Yet the primarily temperate surfperches, for example, simply became somewhat lethargic and remained exposed at night.

Day-night variations in the activities of reef fishes have received considerable attention recently, especially as these variations may relate to foraging methods (Hobson 1975), and to sharing of limited space (Smith and Tyler 1972). Direct observations of coral reef fishes have shown that, although most species are active mainly during the day, a substantial number are active only during the night (Hobson 1965, 1968, 1974; Starck and Schroeder 1965; Smith and Tyler 1972). In both instances, fish forage mainly during their active periods and school and/or seek shelter during their inactive periods (Hobson 1972). Dawn and dusk are important transitional periods when fishes that had been active seek shelter, when fishes that had been resting begin foraging, and when piscivores become most effective (Hobson 1972; Collette and Talbot 1972; Domm and Domm 1973).

The assemblage of fishes at a particular place on a tropical reef at night may differ markedly from the assemblage gathering at the same place during the day because foraging and sheltering activities do not always occur in the same area. For example, some surgeonfishes (Acanthuridae) and damselfishes (Pomacentridae), which shelter at night in the shallower portions of coral reefs, migrate offshore at dawn to their feeding grounds in deeper water (Hobson 1972). Nocturnal predators may undergo even more extensive migrations. Some snappers (Lutjanidae) and grunts (Pomadasyidae) are among a considerable number of species that move away from the reef at night to forage over surrounding sand flats (Hobson 1968, 1972). For many planktivores, however, the change in activity simply involves vertical movements from foraging areas in the water column to underlying sheltering sites (Hobson 1973). Thus the important events during the transition period between day and night include vertical as well as horizontal movements of fish.

Less is known about the nocturnal activities of temperate kelp-bed fishes. Some information has been available on a few species: the garibaldi, *Hypsypops rubicundus* (By Clarke 1970); the California sheephead, *Pimelometopon pulchrum* (by Wiley 1974); the kelp perch, *Brachyistius frenatus*; white seaperch, *Phanerodon furcatus*,

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and señorita, *Oxyjulis californica* (by Bray and Ebeling 1975); and the horn shark, *Heterodontus francisci*, and swell shark, *Cephaloscyllium ventriosum* (by Nelson and Johnson 1970). More recently, Hobson and Chess (1976) presented more comprehensive comparisons of the day and night feeding activities of fish off Santa Catalina Island: in particular, of the blacksmith, *Chromis punctipinnis*; the walleye surfperch, *Hyperprosopon argenteum*; the kelp rockfish, *Sebastes atrovirens*; the olive rockfish, *S. serranoides*; the queenfish, *Seriphus politus*; and the salema, *Xenistius californiensis*, as well as some of the others mentioned above. Therefore, we initiated a comparative day and night survey of the fishes inhabiting an area of reef and kelp off Santa Barbara, Calif., to see if the fish community undergoes a substantial diel change in its composition, vertical distribution, and activity.

METHODS

Naples Reef is a large rocky outcrop located 24 km west of Santa Barbara (lat. 34°25′N, long. 119°57′W). The reef measures 275 m by 80 m (2.2 hectares) and lies 1.6 km offshore. The substratum consists of a series of sandstone rills and ridges that run parallel to the coast. Depths across the reef average 8 to 10 m, although some prominences project to within 5 m of the surface. The bottom surrounding the reef is 16 to 20 m deep and is comprised of sand with rocky outcrops inshore, or sand and cobbles offshore. The assemblage of plant and animal life on and about the reef is among the richest along the Santa Barbara coast. Giant kelp (*Macrocystis*) is always present on the reef, although kelp densities fluctuated throughout the study period. Temperatures along the top of the reef ranged from 11°C in the spring to 19°C in the fall. Underwater visibility averaged 5 m at the transect line.

A transect line consisting of two 40-m segments was staked along either side, shoreward and seaward, of a high-relief ridge with a crest at 6 m. Day and night counts of fishes along the line were made by scuba divers. For each day-night pair of samples, we counted fish within 2 m on either side of the line. To minimize the effect of nondiel fluctuations on our observations, we always made the night transect member of a pair within 12 h of the day transect. A special effort was made to insure that the night counts of fish were made throughout approximately the same reef area and overlying volume of water as were the day counts. Powerful 10-cell underwater hand lights, fitted with reflectors to illuminate the data sheets, were used intermittently during the day to inspect holes, and used continuously throughout the night dives.

We evaluated the diel activities of fish species by observing the fishes' vertical distribution and feeding habits. During the transects, fish sightings were tallied in separate columns on our plastic data sheets according to the zone in which each individual was observed (Table 1).

The use of dive lights at night may have attracted or repelled fish depending on the species and/or altered their state of activity. Yet fishes normally inactive at night did not seem to be affected by brief exposures to dive lights. Species normally active at night responded in various ways, from showing hyperactivity to apparent immobilization. Other nighttime observations of reef fishes off California (Nelson and Johnson 1970) and in tropical waters (Hobson 1965; Starck and Davis 1966; Smith and Tyler 1972) also indicate that night-active fishes often respond unpredictably to artificial illumination.

Day and night differences in the feeding habits of many species were inferred either from direct observations of foragers or from changes in the fishes' vertical distribution and activity level (i.e., whether the fish were exposed and responsive to our presence or sheltered and unresponsive). We feel that such observations of fish activity by themselves were sufficient to distinguish feeding from nonfeeding periods for many of the more prominent species. However, such observations proved to be inadequate indicators of foraging activity for surfperches (Embiotocidae), which comprise the most abundant and diverse foraging guild of the fishes on Naples Reef. To test for diel differences in feeding activity of surfperches, therefore, we speared during all hours of day and night approximately 400 adults of the five common demersal species: the black perch, *Embiotoca jacksoni* (median standard length 195 mm, range

TABLE 1.—Zones of vertical orientation in which fish were observed along a transect line

Zone	Extent of zone
IV Mid-water	Greater than 1.0 m above the bottom, in open water and/or near kelp stipes
III Suprabenthic	Within 1.0 m of the bottom
II Bottom	In physical contact with the bottom yet exposed
I Shelter	In holes, crevices, or under ledges

86-244 mm); striped seaperch, *E. lateralis* (200, 110-280); rubberlip seaperch, *Rhacochilus toxotes* (279, 165-400); pile perch, *Damalichthys vacca* (210, 97-260); and rainbow seaperch, *Hypsurus caryi* (159, 114-253). Immediately after each dive, individuals were either iced and later frozen, or slit ventrally and fixed in 10% Formalin.[2] The procedure for gut analysis followed the method of Bray and Ebeling (1975), except that the surfperch's gut, which is simple and tubular and lacks a well defined "stomach," was divided into quarters. Fullness of the "foregut," defined as the first quarter of the length of the entire gut, was scored subjectively from 1 (empty) to 5 (full), and plotted against time of collection. Since fish were sampled throughout the year, their times of collection were seasonally adjusted relative to actual times of sunrise and sunset as determined from solar tables.

RESULTS

We identified 25 species of fishes from 21 paired day-night transects made between April 1972 and September 1973. Most of the fishes seen along the transect line were adults. The only abundant juveniles were of the blue rockfish, *Sebastes mystinus*. Hence for blue rockfish only, juveniles and adults were counted separately. We excluded from the analysis all species that could not be consistently observed, such as some of the more cryptic and secretive fishes that blend with their surroundings and hide in kelp and rocks, and species that occur only near the water surface outside our field of vision.

It appeared that our visual counts adequately sampled all of the more conspicuous kelp-bed fishes. The rank order of abundance of fishes recorded in the 21 daytime transects was highly correlated with that of fishes observed in a photographic survey consisting of 125, 2.5-min motion pictures (Ebeling, Larson, and Alevizon unpubl. data) filmed over the same area (Kendall's tau coefficient of rank correlation = 0.65; $P<0.001$).

The species composition of seasonally pooled samples and the relative abundances of the different species varied surprisingly little during the 17-mo study period. Almost all species were seen throughout the year, and rank orders of species abundances, pooled over day and night samples, were significantly concordant among seasonal periods that correspond roughly to annual oceanographic periods defined by Brown (1974) (Table 2).

During the day, almost 4,000 fishes representing 11 families of teleosts and 1 family of sharks were counted along the transect line. The two dominant groups—surfperches (Embiotocidae) and rockfishes (*Sebastes*)—were represented by six species each. The most abundant species was *S. mystinus* whose juveniles accounted for 44% of the individuals sighted during the day (Table 3).

Most individuals of all species of fishes (66%) were observed in the mid-water zone higher than 1 m off the bottom (Table 4). The two most abundant species in the mid-water zone, *S. mystinus* and *Chromis punctipinnis* often formed large, mixed aggregations above rocky prominences and around columns of giant kelp. Besides *S. mystinus* and *C. punctipinnis*, more than 80% of the individuals in several other species were observed in the mid-water zone: the kelp bass, *Paralabrax clathratus*; *Oxyjulis californica*; opaleye, *Girella nigricans*; and *S. serranoides* (Table 4). But 10 of the total of 19 species recorded from the mid-water zone were more abundant in other zones.

Some 25% of the total individuals of all species were observed in the suprabenthic zone, within 1 m of the rocky bottom (Table 4). This zone included the most species (21) and was dominated by surfperches: 71% of the individuals observed in the suprabenthic zone were surfperches, as compared with but 12% in the mid-water zone. Nearly half the individuals were *Embiotoca jacksoni* or *E. lateralis*.

Less than 10% of the total individuals recorded during the day were observed either in the bottom zone, contacting the reef in an exposed position, or in the shelter zone, occupying a crevice or hole (Table 4). Most of these were demersal, "ambusher-type" predators, e.g., rockfishes and sculpins (Cottidae), although a few of the mid-water species, e.g., *S. mystinus* and *C. punctipinnis*, were also observed in these zones in small numbers.

We recorded substantially fewer individuals at night than during the day (Table 3). Day to night decreases in total numbers were consistently significant among the 21 pairs of day-night samples (Wilcoxon signed-ranks test for paired observations, $P<0.005$). Also, lists of species, ranked by abundance, differed at night. All 21 rank correlations for the day-night sample pairs (tau = -0.32 to +0.22), as well as the single rank correla-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Seasonal variation in relative abundance of fishes observed along a transect line. Samples are pooled over day and night transects by trimonthly intervals generally coinciding with periods of oceanographic change off Santa Barbara. Kendall's W coefficient of rank concordance among seasons = 0.77 (P<<0.005).

Species	Percent of total individuals by season			
	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Sebastes mystinus (juvenile)	29.5	29.4	45.3	25.2
Chromis punctipinnis	21.3	11.1	14.5	14.9
Embiotoca jacksoni	14.5	10.9	8.75	14.5
Oxylebius pictus	5.61	3.97	2.05	3.71
Embiotoca lateralis	4.97	2.34	1.49	1.86
S. carnatus	3.71	4.69	2.33	3.12
Hyperprosopon argenteum	3.29	2.71	1.40	8.27
S. mystinus (adult)	2.09	6.40	1.77	9.20
Pimelometopon pulchrum	1.95	0.36	0.84	0.42
Damalichthys vacca	1.86	3.07	2.98	2.36
Rhacochilus toxotes	1.44	1.89	0.47	1.27
Hypsypops rubicundus	1.30	1.17	1.86	1.94
Coryphopterus nicholsii	1.25	0.18	0	0.84
Paralabrax clathratus	1.21	0.36	1.30	1.86
S. chrysomelas	1.21	0.81	0.65	1.10
Medialuna californiensis	0.97	0.09	0.28	0.17
Scorpaenichthys marmoratus	0.84	0.27	0.09	0.08
Hypsurus caryi	0.56	13.6	3.17	1.86
Oxyjulis californica	0.56	2.34	1.12	2.62
Phanerodon furcatus	0.51	2.89	4.28	0.17
Ophiodon elongatus	0.46	0.18	0.09	0
Girella nigricans	0.37	0.27	2.70	3.04
Sebastes serriceps	0.19	0.36	0.37	0
S. serranoides	0.14	0.09	1.77	0.76
Cephaloscyllium ventriosum	0.19	0.09	0	0.34
S. atrovirens	0.05	0.45	0.37	0.34
Total no. of individuals	2,150	1,109	1,074	1,185
Total no. of transects	14	10	10	8

TABLE 3.—Day-night variation in abundance of fishes observed along a transect line. Samples are pooled over seasonal intervals (see Table 2). Symbols in the "Difference" column indicate for each species whether the numbers of individuals observed during the day, ordered among all transects, were significantly greater than (>), less than (<), not significantly different from (=), or too few to compare with (NC) the numbers observed at night (Wilcoxon signed-rank test for paired observations, $P \leq 0.05$).

Species	No. of individuals		Percent of total individuals		Difference day vs. night
	Day	Night	Day	Night	
Sebastes mystinus (juvenile)	1,730	8	43.80	0.51	>
Embiotoca jacksoni	492	207	12.40	13.20	>
Chromis punctipinnis	253	662	6.40	42.30	<
Oxylebius pictus	215	16	5.44	1.02	>
S. mystinus (adult)	210	34	5.31	2.17	>
Hypsurus caryi	188	31	4.75	1.98	=
Embiotoca lateralis	134	37	3.39	2.37	>
Damalichthys vacca	112	22	2.83	1.41	>
Phanerodon furcatus	91	0	2.30	0	>
Oxyjulis californica	81	0	2.05	0	>
Girella nigricans	70	6	1.77	0.38	>
Paralabrax clathratus	65	2	1.64	0.13	>
S. carnatus	56	138	1.42	8.82	<
Hypsypops rubicundus	55	29	1.39	1.85	>
Pimelometopon pulchrum	41	19	1.04	1.21	=
Coryphopterus nicholsii	38	1	0.96	0.06	>
Rhacochilus toxotes	31	41	0.78	2.62	=
S. serranoides	21	11	0.53	0.70	=
Medialuna californiensis	19	8	0.48	0.51	=
S. chrysomelas	17	38	0.43	2.43	<
Scorpaenichthys marmoratus	12	11	0.30	0.70	=
Ophiodon elongatus	10	3	0.25	0.19	=
Sebastes atrovirens	7	7	0.18	0.45	NC
S. serriceps	4	8	0.10	0.51	=
Cephaloscyllium ventriosum	2	11	0.05	0.70	NC
Hyperprosopon argenteum	0	214	0	13.70	<
Total no. of individuals	3,954	1,564	100.0	100.0	
Total no. of transects	21	21	21	21	

TABLE 4.—Vertical-zone variation in numbers of fishes observed along a transect line compared between day and night. Vertical zones are defined in Table 1; the Δh measure of a species' change in vertical position between day and night is defined in the text.

	Day				Night				
Family and species	Mid-water	Supra-benthic	Bottom	Shelter	Mid-water	Supra-benthic	Bottom	Shelter	Δh
Scyliorhinidae:									
Cephaloscyllium ventriosum	0	1	0	1	0	1	6	4	0.27
Serranidae:									
Paralabrax clathratus	54	11	0	0	1	0	0	1	1.33
Kyphosid-like fishes:									
Girella nigricans	65	5	0	0	0	2	4	0	1.60
Medialuna californiensis	6	13	0	0	0	3	4	1	1.07
Embiotocidae:									
Damalichthys vacca	32	76	2	2	10	10	2	0	−0.13
Embiotoca jacksoni	101	386	4	1	66	84	51	6	0.18
E. lateralis	26	108	0	0	10	15	10	2	0.30
Hyperprosopon argenteum	0	0	0	0	213	1	0	0	—
Hypsurus caryi	97	90	1	0	7	6	16	2	0.93
Phanerodon furcatus	64	27	0	0	0	0	0	0	—
Rhacochilus toxotes	8	19	4	0	16	20	4	1	−0.12
Pomacentridae:									
Chromis punctipinnis	210	30	0	13	5	9	38	610	2.62
Hypsypops rubicundus	8	32	5	10	0	0	1	28	1.66
Labridae:									
Oxyjulis californica	73	8	0	0	0	0	0	0	[1]2.91
Pimelometopon pulchrum	29	10	0	2	0	0	0	19	2.61
Gobiidae:									
Coryphopterus nicholsii	0	0	32	6	0	0	1	0	−0.16
Scorpaenidae:									
Sebastes atrovirens	2	3	1	1	2	2	2	1	0.14
S. carnatus	3	6	32	15	0	10	84	44	0.19
S. chrysomelas	0	0	10	7	0	0	19	19	0.09
S. mystinus (adult)	178	21	10	1	4	2	8	20	2.08
S. mystinus (juvenile)	1,606	119	0	5	0	1	1	6	2.55
S. serranoides	18	3	0	0	9	0	0	2	0.40
S. serriceps	0	0	1	3	0	0	2	6	0
Hexagrammidae:									
Ophiodon elongatus	2	4	4	0	0	0	0	3	1.80
Oxylebius pictus	4	24	179	8	0	0	6	10	0.74
Cottidae:									
Scorpaenichthys marmoratus	0	1	10	1	0	0	10	1	0.09
Total no. of individuals	2,586	997	295	76	343	166	269	786	
Percent of day or night total	65.4	25.2	7.46	1.92	21.9	10.6	17.2	50.3	
Total no. of transects	21	21	21	21	21	21	21	21	

[1]Individuals are assumed to bury themselves at night.

tion for the day-night contrast with samples pooled (tau = 0.13), were nonsignificant (P>0.05). A Wilcoxon signed-ranks test for paired (day-night) observations indicated that numbers of eight species did not differ significantly between day and night, while numbers of four species actually increased (Table 3).

Two species commonly observed during the day were either seldom or not seen at night: *Phanerodon furcatus* and *Oxyjulis californica*. Although we often saw individuals of *P. furcatus* browsing on bryozoan-encrusted algae (mainly *Gelidium* sp.) along a crest of the reef during the day, we rarely observed them at night along the crest and never observed them during regular transects. We commonly saw small groups of *O. californica* in the mid-water zone above the transect lines during the day. At dusk, however, *Oxyjulis* individuals bury themselves in rubble and sand on the reef and remain covered until dawn (Herald 1961; Feder et al. 1974; Bray and Ebeling 1975).

Only one species was seen at night but never during the day. *Hyperprosopon argenteum* was the second-most abundant species recorded at night, although it was never seen around the transect line during daylight hours. In over 6 yr of observations, we have seen this species in kelp beds on only a few occasions during the day. Schools of *H. argenteum* commonly occur in shallow waters along sandy beaches and shallow reefs during the day, so it appears that at least some of the larger individuals migrate offshore to kelp beds at dusk. To reach Naples Reef, fish near the surf would have to swim approximately 1.6 km offshore.

Resemblance between the day and night samples of S = 25 species within each of the four vertical zones was measured by coefficients of similarity or "overlap" (cf. Colwell and Futuyma

1971). Similarity (C) is scaled from 0 (no resemblance at all) to 1.0:

$$C = 1.0 - \tfrac{1}{2} \sum_{i=1}^{s} |P_{ij} - P_{ik}|,$$

where P_{ij} = the proportionate abundance of species i in day sample j, and P_{ik} = that in night sample k.

Though the mid-water zone abounded with fishes during the day, it appeared sparsely populated at night (Table 4). Day-night similarity within the mid-water zone was the least (C = 0.12) for the four zones. Six of the 10 species recorded from the mid-water zone at night were surfperches, while three of the remaining four were rockfishes. *Hyperprosopon argenteum* accounted for 62% of the total fish recorded in this zone. *Damalichthys vacca*, along with *Sebastes serranoides* and adult *S. mystinus*, were often seen scattered in the water column at night.

Although the suprabenthic zone underwent a substantial reduction in fish abundance at night, its day-night species similarity was the highest (C = 0.67) for the four zones. During both day and night, the suprabenthic zone was dominated by surfperches. At night, surfperches comprised the four most abundant species, accounting for almost 80% of the total fishes observed in the suprabenthic zone (Table 4). Although Pacific electric rays (*Torpedo californica*) were never recorded over the transect lines, they were often encountered nearby, swimming slowly and hovering above the bottom (Bray, Hixon, and Ebeling unpubl. data). Swell sharks (*Cephaloscyllium ventriosum*), whose nocturnal activities were investigated by Nelson and Johnson (1970), were occasionally seen swimming just above the reef at night.

Fish observed in the bottom zone increased from 7.4% of the total individuals recorded from all zones during the day to 17.1% of the total at night (Table 4). The zone's relatively low day-night species similarity (C = 0.28) was due to variations in numbers of the demersal ambusher-type predators and increases in numbers of "resting" surfperches. Among the ambusher-type species, e.g., numbers of painted greenling, *Oxylebius pictus*, decreased from 179 counted during the day to only 6 at night, and numbers of two common rockfishes increased: the black-and-yellow, *S. chrysomelas*, almost doubled and the gopher, *S. carnatus*, almost tripled (Table 4).

At night, most fishes were observed in the shelter zone. Although only 2% of the day total of fishes were seen in holes and crevices, 50% of the night total were observed there (Table 4). Day-night species similarity was fairly low (C = 0.36), largely because of the increase in numbers of individuals of *Chromis punctipinnis* observed in holes: from only 13 counted during the day to 610 counted at night (Table 4). Individuals of *Pimelometopon pulchrum* and *S. mystinus* were also commonly seen in the shelter zone at night.

These counts of fishes inhabiting holes, especially at night, may be conservative because we could not completely census the numerous deep holes and crevices along the transect line. This problem certainly influenced our counts of individuals of *O. pictus* and juvenile *S. mystinus*. Nocturnal counts of both species were much lower than those made during the day, and the individuals that were observed at night were invariably hiding deep in holes. Subsequent nighttime applications of small amounts of the anesthetic quinaldine to holes that first appeared vacant often yielded several *O. pictus* and 5 to 20 juvenile *S. mystinus*. Similar applications of this anesthetic during the daytime occasionally revealed these fishes, but in far smaller numbers.

The vertical positions of the 25 species of fishes during the day and night are summarized in Table 4. Data on some species are fragmentary because individuals of these species were rarely encountered along the transect line. However, general observations made during hundreds of hours of diving during both day and night tend to substantiate conclusions based on these data. For example, we saw but two kelp bass along the transect line at night, one in mid-water, the other on the bottom. In surrounding areas, we saw many individuals resting on the bottom, several in mid-water, but very few in holes. Eighteen of 24 species recorded during the day were most common in the suprabenthic and mid-water zones above the reef. Only the treefish, *S. serriceps*, was most common in the holes of the shelter zone. Of the 23 species recorded at night 16 were most common in contact with the reef, either in the open positions of the bottom zone or in the holes of the shelter zone. Only two species, *Hyperprosopon argenteum* and *S. serranoides*, were most common in the mid-water zone.

The day-night differences in the activities of many species involved considerable shifts among

the four zones. These shifts are measured in Table 4 by values of Δh:

$$\Delta h = \sum_{i=1}^{4} \left[(p_{i\,\mathrm{day}})(i) - (p_{i\,\mathrm{night}})(i) \right],$$

where $p_{i\,\mathrm{day}}$ is the proportion of individuals of a species observed during the day in zone i (i = 1,2, 3, or 4 for the shelter through mid-water zones, respectively) and $p_{i\,\mathrm{night}}$ is the proportion observed at night. The Δh's range from +3.0, when all observed individuals of a species undergo a maximum shift downward from the mid-water zone during the day to the shelter zone at night, to -3.0, when all individuals undergo the reverse maximum shift upward. A Δh = 0.0 indicates little or no shift, in that the species' proportional distribution among zones does not change from day to night.

Fish species varied considerably in the degree to which they changed zones between day and night, although the patterns of shifting upward or downward were similar within families (Table 4). Some species changed their vertical position little if at all: several species of rockfishes; the cabezon, *Scorpaenichthys marmoratus*; *Rhacochilus toxotes*; *Damalichthys vacca*; and blackeye goby, *Coryphopterus nicholsii*. Other species changed their vertical position markedly between day and night. Individuals of *Chromis punctipinnis* and *Pimelometopon pulchrum*, which had near-maximum positive values of Δh, move about in the water column during the day and shelter in holes at night. No individuals of *Oxyjulis californica* were seen at night (recall that they descend from mid-water to bury themselves in sand or gravel patches). Assuming that burying individuals are in the "shelter zone," Δh for *Oxyjulis* = 2.91. No species had a large negative value of Δh, i.e., no species mostly contained individuals that rose from the bottom to mid-water at night. Hobson and Chess (1976) noted that during the day most *Sebastes atrovirens* were "seated on rocky strata" whereas at night they "hovered in mid-water." In the present study, the Δh of *S. atrovirens* was small but positive (Table 4); however, this species was relatively rare in our transects.

Several lines of evidence indicate that many of the kelp-bed fishes observed become less active and do not regularly feed at night. The levels of activity often could be inferred from direct observations. Many species that swam about and fed on or above the reef during the day were found deep in holes and crevices at night and would flee from their shelter only when vigorously disturbed. These species included *Hypsypops rubicundus*, *C. punctipinnis*, *P. pulchrum*, and juvenile *S. mystinus*. Some individuals of *P. pulchrum* reportedly secrete a mucous envelope about themselves (Wiley 1974), and we often found this fish wedged deep in crevices in an apparent state of torpor at night. Individuals of *Girella nigricans* were also found in holes or on the bottom but were more responsive to our presence. Previous diel analyses of gut contents substantiate our present impressions that the following species are strictly daytime feeders: *H. rubicundus* (by Clarke 1970), *O. californica* (by Bray and Ebeling 1975), juvenile *S. mystinus* (by Thomas Bailey unpubl. data), and *C. punctipinnis* (by Hobson and Chess 1976; Bray unpubl. data).

Our analyses of fish-gut emptiness revealed that even many of the kelp-bed fishes not undergoing such obvious diel changes in vertical position may stop feeding at dusk (Figure 1, Table 5). Although all five demersal surfperches (*Embiotoca jacksoni*, *E. lateralis*, *Hypsurus caryi*, *Damalichthys vacca*, and *Rhacochilus toxotes*) generally remain in the suprabenthic and bottom zones both day and night, their diel patterns of gut emptiness indicate that all but *R. toxotes* do not feed at night. Median scores of gut fullness for *E. jacksoni* reached maximum values in the afternoon and declined after sunset; at dawn, all guts examined were empty (Figure 1a). Fully 88% of the fishes speared during daylight hours contained food in their foreguts (Table 5). Although 39% of the fishes collected at night contained food, 89% of these were collected before midnight. Thus it is likely that the food contained in the foreguts of these individuals was eaten before nightfall and had not yet passed into the second quarter of their guts. Foreguts of *E. lateralis*, *H. caryi*, and *D. vacca* show the same pattern (Figure 1b-d). In fact, all four species had significantly less food in their guts during the night than during the day (Table 5). Gnose (1968) also observed that individuals of *E. lateralis* collected from off Oregon had empty guts at dawn. Additionally, two other kelp-bed surfperches that commonly occur in mid-water, *Phanerodon furcatus* and *Brachyistius frenatus*, which is rare at Naples Reef, feed mainly during the day (Bray and Ebeling 1975; Hobson and Chess 1976).

In contrast, median scores for fullness of *R. toxotes* reached maximum values at night, and many foreguts were empty during the day (Figure

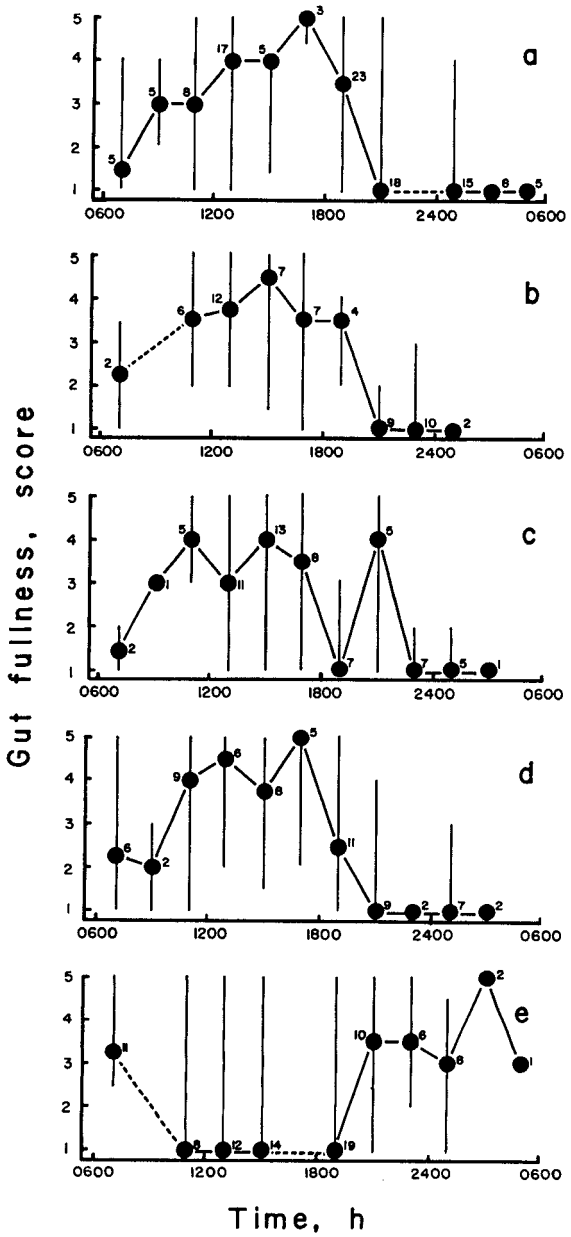

FIGURE 1.—Scored fullness (1, empty-5, full) of foreguts of five demersal surfperches: a, *Embiotoca jacksoni*; b, *E. lateralis*; c, *Hypsurus caryi*; d, *Damalichthys vacca*; and e, *Rhacochilus toxotes*. Each point represents the median score and each vertical line the range of scores for (n) individuals collected over a 2-h interval. Time is measured relative to sunrise (0600 h) and sunset (1800 h).

1e). Some 67% of the fish collected at night contained food in their foreguts, and 49% of those collected during the day also contained food, although this difference was not significant (Table 5).

TABLE 5.—Day-night variation in "foregut" emptiness for the five species of demersal surfperches. Values of chi-square with 1 df were calculated from day-night, empty-not empty values in contingency tables for each species.

Species	Day: No. examined	Day: % empty	Night: No. examined	Night: % empty	Day vs. night: χ^2	Day vs. night: P
Embiotoca jacksoni	43	12	69	61	26.4	<0.005
E. lateralis	34	5.9	25	64	23.0	<0.005
Hypsurus caryi	40	10	25	60	18.6	<0.005
Damalichthys vacca	36	8.3	31	71	27.9	<0.005
Rhacochilus toxotes	45	51	46	33	3.2	≈0.07

It is likely that many of the large-mouthed demersal species feed any time that suitable prey are available. Included among these species are various rockfishes (*Sebastes carnatus*, *S. chrysomelas*, and *S. serriceps*) and *Scorpaenichthys marmoratus*, all of which are cryptically patterned and probably ambush much of their prey. Analyses of gut fullness and states of digestion relative to time of day may be of little value in determining the feeding chronology of these fishes, especially larger individuals. Kariya (1969) showed that food items may take days rather than hours to pass through the stomach of *Sebastes inermis*, a species from Japan; and Larson (pers. commun.) found that small majid crabs (10 mm carapace width) were still intact in the stomachs of adults of *S. carnatus* up to 10 h after ingestion. However, other lines of evidence indicate that they feed at night. We saw more individuals of *S. carnatus* and *S. chrysomelas* at night, probably because they were more active then, and the types of food items included in their diets suggest they feed at night as well as during the day. Their diets include medium-sized crustaceans (crabs, shrimps, etc.) and cephalopods (Quast 1968b; Larson 1972); both prey were far more active and exposed along the transect line at night. We have observed individuals of *S. carnatus* and *S. chrysomelas* at night with live, struggling crabs and octopi protruding from their mouths. Also, individuals of these species often consumed small fishes that escaped from our collecting spears during night dives. Finally, all of these fishes can be caught by hook and line at night as well as during the day (Milton Love, pers. commun.).

Along the transect line during the day, fishes congregate in mid-water to pick plankton and browse on kelp surfaces. At night, on the other hand, almost all of the foraging by fishes occurs on

or near the bottom. *Hyperprosopon argenteum* was an exception in that individuals of this species occurred alone or in small, loose groups in mid-water at night. Hobson and Chess (1976) and Bray (unpubl. data) found that guts of specimens speared at night were full of recently ingested prey, whereas almost all guts from individuals speared during the day were empty. However, the fact that this fish constitutes a large portion of the catch made by shore fishermen (Frey 1971) indicates that at least some individuals feed during the day.

We know little about the feeding periods of the remaining six species seen along the transect line. The halfmoon, *Medialuna californiensis*, often appeared to be more sensitive to our presence than were individuals of other species near the bottom, and we cannot deny the possibility that *Medialuna* feeds at night. It reportedly eats mainly algae supporting a variety of attached epiphytic animals and much smaller quantities of free animals (Quast 1968b; Follett et al. 1960). The fact that two small demersal species, *Coryphopterus nicholsii* and *Oxylebius pictus*, were seen much less often at night suggests that they retreat deep into holes and crevices then. Larger individuals of lingcod, *Ophiodon elongatus*; *Paralabrax clathratus*; and *S. mystinus* eat cephalopods as well as fishes and other prey (Love 1974; Miller and Geibel 1973; Quast 1968c), so it is reasonable to suspect that they too feed, at least occasionally, at night.

DISCUSSION

During the day, large numbers of fishes pervade the study area of reef and kelp off Santa Barbara. Most fishes inhabit the mid-water zone well off the bottom, while smaller numbers of ambusher-type predators remain in contact with the reef bottom. In contrast, the same kelp forest appears almost abandoned at night. Most notably, large numbers of fishes disappear from mid-water, while the numbers of fishes increase markedly in the shelter zone of holes and crevices.

Although day-night changes in fish abundance may be partly attributable to sampling error caused by our use of lights at night, etc., these changes most certainly reflect differences in the fishes' requirements and distributional patterns between their periods of activity and inactivity. During the day, the area in the vicinity of our transect line seems to constitute a focal point of fish activity. Daytime fish diversity and abundance appeared to be greater along the transect line than in adjacent areas, 5 to 10 m away. Loose aggregations of juvenile *S. mystinus* and, less frequently, *Chromis punctipinnis*, *P. clathratus*, and *Girella nigricans*, formed in the water column above the transect line. Likewise, other fishes gathered closer to the bottom. Perhaps this local richness relates to the position of the transect about the reef crest. The transect line was attached to one of the highest rocky prominences on the reef, and it ran along the inner margin of a dense stand of giant kelp. Quast (1968a) noted that the combination of high-relief rocks and kelp augments the surface area available for invertebrates, the principal food of the fishes, and serve as orientation points for fishes throughout the water column. Also, inshore and offshore margins of kelp beds often demonstrate the "edge-effect," in that the fauna is richer there than in areas on either side (Feder et al. 1974). At Naples Reef, surfperches, especially individuals of *Embiotoca lateralis* and *Phanerodon furcatus*, tend to congregate about the reef crest and the south dropoff 20 m away where thick stands of *Gelidium* and other red algae flourish. Individuals of *E. lateralis* gorge themselves on the caprellid amphipods that occur in great numbers amongst the algae (Robert Cowen and David Laur, pers. commun.). Also we noticed that fishes tend to aggregate in sunlit areas like the reef crest and avoid the shaded areas on either side. In tropical reefs, diurnally schooling fishes that migrate to adjacent sand flats at night return in daylight to the same prominent topographic features on the reef (Hobson 1973). Other factors that influence local fish abundance and diversity are: availability of food (e.g., Hobson 1968, 1972, 1974), proximity to shelter (e.g., Low 1971; Sale 1972), and the presence of "cleaner" fish that rid larger fish of their ectoparasites (Slobodkin and Fishelson 1974). At least some of these factors may also have contributed to the high numbers of fish along our transect line.

After dark, fishes that seek shelter and/or become inactive are no longer attracted by richer feeding grounds and orientation points characteristic of the reef crest. As darkness falls, mid-water aggregations of *C. punctipinnis*, *Paralabrax clathratus*, *Girella nigricans*, and young *S. mystinus* dissolve as the fish disperse singly or in small groups over the bottom to shelter in the many holes and crevices in surrounding areas. During the day, for example, individuals of *C.*

punctipinnis occur patchily in small mid-water aggregations over the transect line and in much larger aggregations along the outer margins of the kelp bed. At night, however, they shelter in holes throughout the entire study area. In freshwater lakes of Ontario at night, day-active fishes move into shallow water where there is sufficient cover for sheltering (Emery 1973), but in the tropics, most day-active reef fishes shelter in holes deep in the coral and so their exposed numbers decrease at night (see Hobson 1974).

The decrease in nocturnal abundance of fishes in the transect area might have been caused by their migrations to nearby areas of sand. Over coral reefs, many of the more prominent fishes seen in large stationary schools during the day are actually nocturnal species that leave the reef at dusk (Hobson 1968). Among these are croakers (Sciaenidae), snappers (Lutjanidae), and grunts (Pomadasyidae), which move to surrounding sand flats to feed on their invertebrate prey during the night (see papers by Hobson). However, we found no evidence of a pronounced nocturnal migration of fishes from reef and kelp to the surrounding sand. Essentially all of the fishes observed during the day were accounted for at one part or another of the reef at night. On several occasions at night, while swimming considerable distances over the surrounding sand flats, we saw only species that occur commonly at kelp-bed margins and do not actively forage at night (e.g., *Phanerodon furcatus* and *Damalichthys vacca*), or that typically inhabit sandy bottoms (e.g., the spotted cusk-eel *Chilara taylori*, and various skates and rays). We have occasionally seen relatively inactive schools of black croaker, *Cheilotrema saturnum*, on the reef during the day, and although we have not seen the fish at night, it is possible that they migrate to adjacent sandy areas to feed. Limbaugh (1961) reported that they are most active at night.

In a study of the night habits of coral reef fishes, Starck and Davis (1966) noted that the feeding times of reef fishes are closely related to the type and activities of their prey. Microcarnivorous and omnivorous fishes that browse and pick at sessile organisms are generally active only during the day. Mesocarnivorous fishes (i.e., those that feed on larger motile invertebrate prey) are largely nocturnal, because their prey (e.g., crustaceans) are active and exposed at night. Planktivorous fishes feed during both day and night, the nocturnal species having larger eyes than their diurnal counterparts. Piscivorous fishes feed opportunistically during the day and night, but are most active at dawn and dusk when their prey fish are exposed while moving to and from foraging and sheltering areas. This feeding pattern has also been observed in other tropical areas (Hiatt and Strasburg 1960; Collette and Talbot 1972; Hobson 1974) and in freshwater lakes (Emery 1973).

Kelp-bed fishes also tend to show this general feeding pattern, though perhaps not so distinctly. Small-mouthed microcarnivores that pick or graze sessile invertebrates and hidden prey from off the bottom and other substrates are generally active only during daylight hours. Such foragers, including most of the surfperches, as well as *Oxyjulis californica*, *Pimelometopon pulchrum*, and *Hypsypops rubicundus*, readily converge on urchins broken open during the day, but completely ignore such chum at night.

Also as in the tropics, though less extensively so, different planktivores feed in the mid-water zone of kelp beds during the day and night. The most visible daytime planktivores, *Chromis punctipinnis* and juvenile *S. mystinus*, often form mixed aggregations of individuals that pick small zooplankton from the incoming currents. At night, neither was seen exposed outside its shelter, and individuals collected by spear and later examined had empty stomachs. Instead, the mid-water zone is dominated at night by the large-eyed species, *Hyperprosopon argenteum*, which darts about, actively feeding throughout the water column. Though we have little data on kelp-bed mesocarnivores, some, such as various rockfishes, *Scorpaenichthys marmoratus*, and *Ophiodon elongatus*, may feed at night.

We emphasize the fact that many kelp-bed fishes show considerable intraspecific variability in vertical distribution and feeding activity. Although a large majority of the population of *C. punctipinnis* usually feeds in mid-water during the day, e.g., a few individuals can usually be found in holes. Likewise, a small proportion of the day-sampled individuals of *Embiotoca jacksoni* had empty foreguts even though the species is strictly a diurnal forager. Even more variable is the feeding schedule of *Rhacochilus toxotes*. Most individuals probably have empty guts at any daylight hour, although others are satiated. We have observed that at any given time during the day, most of these surfperch assemble as schools of varying sizes just above the bottom or even in mid-water (see also Alevizon 1975). However, a lone individual may suddenly leave the school to

feed rapidly over the bottom for several minutes before rejoining the same or another school of lazily swimming, nonfeeding fish. But we do not know yet if any particular individuals tend to feed in this sporadic manner during the day to a greater extent than do most others which may feed more consistently during the night. Hobson (1971, 1976) stressed the probably widespread occurrence of individual variation in the tendency of fishes to "clean" ectoparasites from larger host species. Specifically, Hobson (1976) observed that even though cleaning is not considered to be characteristic of the rock wrasse, *Halichoeres semicinctus*, this feeding mode was repeatedly a major activity in what was probably the same individual. Thus, as far as fish activities are concerned, the behavior of an individual is not always predictable from the general characteristics of its species.

Temperate-Tropical Differences

Some phenomena that characterize the day-night change in activities of fishes inhabiting tropical coral reefs appear less well developed or absent in the activity cycles of the Santa Barbara kelp-bed fishes. For one thing, no kelp-bed species that we observed forms inactive schools over the reef during the day and disperses elsewhere to feed at night, as do snappers and grunts in tropical systems. Another noticeable lack in the kelp forests is the widespread replacement of daytime mid-water planktivores by nighttime counterparts. In tropical areas, this replacement involves more species and, to some extent, occurs vertically: at night, the diurnal planktivores (a few pomacentrids, the unusual labrid *Clepticus*, etc.) take refuge in reefs that had provided shelter for the nocturnal planktivores (some holocentrids, apogonids, priacanthids, etc.) during the day (Hobson 1968, 1972; Collette and Talbot 1972). In our kelp-bed system at Naples Reef, however, the only noticeable replacement of the abundant daytime mid-water planktivores is *Hyperprosopon argenteum*, which, moreover, is probably a "horizontal replacement" from inshore areas. In this system, the only common fish that shelters during the day and may emerge at night is *Cephaloscyllium ventriosum*, a rather slow-moving piscivore that probably eats sheltering or inactive prey (Nelson and Johnson 1970). The cryptic demersal mesocarnivores (i.e., carnivores that feed on medium-sized prey, e.g., rockfishes, *Scorpaenichthys marmoratus*, etc.) may shelter either day or night between feeding bouts.

However, feeding on plankton at night may be more widespread in areas farther south. Hobson and Chess (1976) concluded that several species eat plankton at night off Santa Catalina Island. Though they are relatively rare at Naples Reef, for example, individuals of *Sebastes atrovirens* and larger juveniles of *S. serranoides* are important mid-water planktivores at night in kelp beds off Santa Catalina. Also, *Xenistius californiensis* picks plankton in the relatively clear waters around this island, but this species does not commonly occur as far north as Santa Barbara. Naples Reef is located just south of a faunal boundary at Point Conception (cf. Hubbs 1960; Quast 1968; Briggs 1974). Also, our mainland assemblage differs noticeably from nearby insular communities (Ebeling et al. unpubl. data). Nonetheless, it is reassuring to find that many of our results parallel those of Hobson and Chess.

Figure 2 summarizes the day-night distributions of kelp-bed fishes from an evolutionary point of view. Fish are depicted as being distributed vertically, based on their proportionate abundances in each of the four zones, from the mid-water zone to the shelter zone, and as comprising four ecological groups, based on their habits and phylogenetic origins. Belonging to taxa with temperate origins, all species in group A are demersal species of the bottom-habitat group, which generally move but little from their perches on the bottom during the day or night (see Table 4, $\bar{\Delta}h = 0.42$). Groups B, C, and D are composed of more active species that commonly occur in the suprabenthic zone and in mid-water during the day, but there the similarity ends. Also with temperate origins, species in group B are large-mouthed generalized predators, which can switch from plankton to larger prey including small fishes as the occasion arises (Love 1974), and simply descend to rest on the bottom at night ($\bar{\Delta}h = 1.92$). Group C and D species are small-mouthed microcarnivores of mixed origins, which either forage over the substrate or pick plankton from mid-water. Group C fishes are all surfperches with a common temperate origin, whose day-night change in vertical position is relatively slight ($\bar{\Delta}h = 0.22$), and whose nocturnal behavior is relatively unspecialized, in that the fish simply slow down over the bottom and do not generally seek shelter in holes and crevices. But in contrast with all the others, group D fishes appear to be rela-

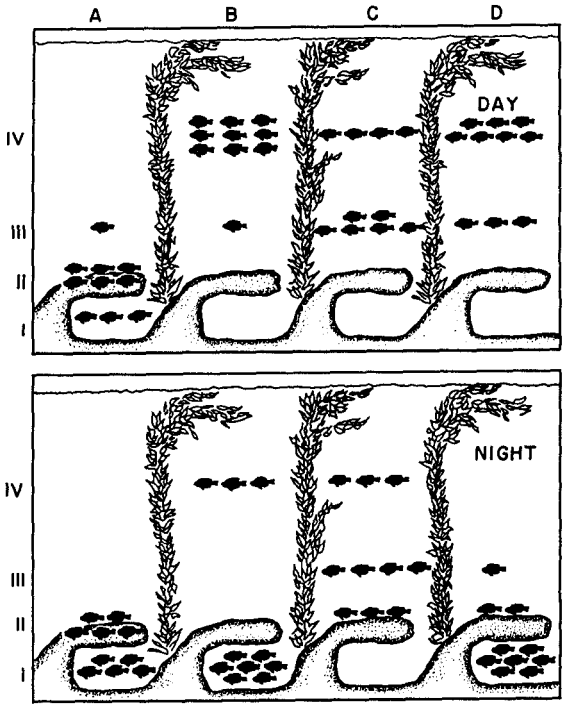

FIGURE 2.–Day and night positions of four ecological groups of fishes inhabiting Santa Barbara kelp beds: A) demersal species (*Coryphopterus nicholsii, Ophiodon elongatus, Oxylebius pictus, Sebastes carnatus, S. chrysomelas, S. serriceps,* and *Scorpaenichthys marmoratus*); B) large-mouthed generalized predators (*Paralabrax clathratus, Sebastes serranoides,* and adult *S. mystinus*); C) surfperches (*Embiotoca jacksoni, E. lateralis, Hypsurus caryi, Phanerodon furcatus, Rhacochilus toxotes,* and *Damalichthys vacca*); D) small-mouthed grazing and picking tropical derivatives (*Chromis punctipinnis, Hypsypops rubicundus, Medialuna californiensis, Oxyjulis californica,* and *Pimelometopon pulchrum*). Vertical zones (I-IV) are defined in Table 1. Each fish symbol represents 10% of the total individuals in the group expressed proportionally to the relative abundances of the different species in the group.

tively recent derivatives of primarily tropical families (Pomacentridae, Labridae, etc.), and essentially all show extreme changes in their vertical distribution ($\bar{\Delta}h$ = 2.07) as they actively seek the shelter zone refuge. Some at least, like *Chromis punctipinnis*, are specialized to the extent that they tend to "home" to the same hole on successive nights (Bray unpubl. data).

Thus, in the kelp beds, there is no broad replacement for the "day shift" of fishes at night, even though the fishes' invertebrate prey appear to be more active and exposed then. And, in general, after the dusk period of intensified activity, the notably lackluster night life gives the kelp forest an aura of desolation, as compared with the pictures of renewed (albeit lessened) activity painted of the community of coral reef and outlying sand-flat fishes at night (Starck and Davis 1966; Collette and Talbot 1972; etc.). Perhaps the relatively clear and well-lighted tropical waters are more conducive to nocturnal activity for the many visually oriented fish. Denied much of the moonlight by the dense kelp canopy and frequent low clouds, the relatively turbid, temperate waters are often a dark and gloomy place at night. In fact, even during the day when the water is particularly turbid, the usually active planktivores, grazers, and browsers tend to stop foraging and often seek shelter, as do their tropical counterparts under similar conditions (Collette and Talbot 1972).

It is paradoxical that the "tropical derivatives" (Figure 2D) persist in their complex nocturnal shelter-seeking while many primarily temperate fishes remain exposed. One explanation assumes that selection pressures brought about by nocturnal (or crepuscular) predation are either different or more relaxed in our temperate system of kelp forest and reef than in the tropical reef system. Observing a similar set of circumstances, Hobson (1972) noted that Hawaiian reef fishes, which enjoy a relative dearth of crepuscular predators, show the same specialized sheltering behavior during twilight as do their close relatives in the Gulf of California, which have many such predators. He suggested that these complex behavior patterns may evidence historic selection pressures from predators. These patterns may persist on Hawaiian reefs today even though they are currently perhaps less critical to the survival of the refuge-seeking species than in reef systems elsewhere. An alternative explanation holds that crepuscular and nocturnal predation by, e.g., the Pacific electric ray, is important in kelp beds, but that the tropical derivatives compete more successfully against the primarily temperate species for shelter.

CONCLUSIONS

As indicated by paired day-night observations along a transect line, kelp-bed fishes occur in about the same relative abundances throughout the year in an area of reef and kelp along the mainland side of the Santa Barbara Channel. During the day, most fishes occupy the "mid-water zone" higher than 1 m off the bottom. Far fewer are "exposed on the bottom" or in the "shelter zone" of holes and crevices in the reef itself. During the night, when

the number of individuals appears reduced by more than half, most fishes occupy the bottom and shelter zones.

Thus, like that of tropical reefs, the vertical distribution of fishes changes markedly between day and night. Planktivores that pack the mid-water zone during the day virtually abandon the area at night to rest on the bottom or seek shelter in reef holes. The vacated mid-water space is only partly reoccupied by a relatively sparse population of nocturnal planktivores and a few remaining generalized carnivores. The largest relative increase of individuals occurs in the shelter zone, where superabundant daytime planktivores, such as the blacksmith, hide at night. With so many fishes commuting extensively between the mid-water and shelter zones, it is understandable that the intervening suprabenthic zone shows the greatest species similarity between day and night. Many ambusher-type foragers are always oriented to the bottom and change their positions relatively little for the night shift.

It seems likely, therefore, that at night feeding on plankton decreases and most of the foraging by fishes takes place over the bottom. The large-mouthed demersal ambushers—various rockfishes, the cabezon, and others—probably feed almost any time that suitable prey are available. The rubber-lip seaperch may actually feed more actively at night. Nonetheless, many of the fishes that wander over the bottom at night may stop feeding at dusk. Most demersal surfperches remain exposed at night, although their foreguts soon empty, and the fish appear more lethargic than they do during the day when they are actively foraging.

Focal points of daytime fish activity, such as the productive crest of the reef and other prominent landmarks, appear to lose their attractiveness at night. Most aggregations disappear at dusk as fishes generally disperse out over the reef bottom. But unlike many tropical-reef fishes, kelp-bed species do not normally move off the reef to forage over the adjacent sand flats.

Kelp-bed fishes often show considerable intraspecific variation in vertical distribution and feeding activity. During the day, e.g., noticeable numbers of typically mid-water species invariably seek shelter, while at night some individuals remain in the water column. And fishes differ in the intensity at which they feed during any given period during the day. All this suggests that certain individuals may assume and even maintain distinctive habits that differ from the species "norm," i.e., the behavior of a particular fish is not always predictable from the general characteristics of its species.

Thus, in comparing the diel behavior of kelp-bed fishes as a group with that of their tropical counterparts, it becomes apparent that even though both groups follow the same basic patterns, the kelp-bed community is the more loosely "programmed." In the kelp-bed system, for example, there is less large-scale replacement of fishes between discrete areas or vertical zones at dusk. Here, the night shift offers no real substitute for the dense aggregations of daytime planktivores or demersal microcarnivores, even though these fishes' invertebrate prey are active and exposed at night. Perhaps the better lighted tropical waters allow more specialized activities because here the visually oriented fishes can better see what they are doing, even by moonlight. In the kelp forest, the level of fish activity decreases even during the day when the water becomes very turbid, as often happens with the onset of dense blooms of phytoplankton during the spring and summer.

The kelp-bed species that belong primarily to tropical families tend to show the same specialized pattern of nocturnal shelter seeking as do their close tropical relatives, even though the general program of diel activity in the kelp forest appears to be comparatively unstructured. Perhaps the specialized refuge-seeking procedures of kelp-bed pomacentrids and labrids are simply "evolutionary holdovers" that contribute relatively little to the present fitness of these fishes. But alternatively, the "tropical derivatives" may actually compete more successfully against primarily temperate species such as surfperches for shelter on the reef. Even though the intensity of predation at twilight and perhaps at dark may be somewhat less in our temperate system than in the tropics, a few ingenious and effective predators, such as the Pacific electric ray, patrol the Santa Barbara kelp forests throughout the night.

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LITERATURE CITED

ALEVIZON, W. S.
1975. Spatial overlap and competition in congeneric surfperches (Embiotocidae) off Santa Barbara, California. Copeia 1975:352-356.

BRAY, R. N., AND A. W. EBELING.
1975. Food, activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BRIGGS, J. C.
1974. Marine zoogeography. McGraw-Hill, N.Y., 475 p.

BROWN, D. W.
1974. Hydrography and midwater fishes of three contiguous oceanic areas off Santa Barbara, California. Los Ang. Cty. Mus. Contrib. Sci. 261:1-30.

CLARKE, T. A.
1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda*. Ecol. Monogr. 40:189-212.

COLLETTE, B. B., AND F. H. TALBOT.
1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 98-124. Bull. Los Ang. Cty. Nat. Hist. Mus. Sci. 14.

COLWELL, R. K., AND D. J. FUTUYMA.
1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

DOMM, S. B., AND A. J. DOMM.
1973. The sequence of appearance at dawn and disappearance at dusk of some coral reef fishes. Pac. Sci. 27:128-135.

EMERY, A. R.
1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Board Can. 30:761-774.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in Southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

FOLLETT, W. I., D. GOTSHALL, AND J. G. SMITH.
1960. Northerly occurrences of the scorpid fish *Medialuna californiensis* (Steindachner), with meristic data, life-history notes, and discussion of the fisheries. Calif. Fish Game 46:165-175.

FREY, H. W. (editor).
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game Spec. Publ., 148 p.

GNOSE, E. C.
1968. Ecology of the striped seaperch, *Embiotoca lateralis*, in Yaquina Bay, Oregon. M.S. Thesis, Oregon State Univ., 51 p.

HERALD, E. S.
1961. Living fishes of the world. Doubleday and Co., Inc., Garden City, N.Y., 304 p.

HIATT, R. W., AND D. W. STRASBURG.
1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65-127.

HOBSON, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.
1971. Cleaning symbiosis among California inshore fishes. Fish. Bull., U.S. 69:491-523.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1973. Diel feeding migrations in tropical reef fishes. Helgoländer wiss. Meeresunters. 24:361-370.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:951-1031.
1975. Feeding patterns among tropical reef fishes. Am. Sci. 63:382-392.
1976. The rock wrasse, *Halichoeres semicinctus*, as a cleaner fish. Calif. Fish Game 62:73-78.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

HUBBS, C. L.
1960. The marine vertebrates of the outer coast. *In* Symposium: The biogeography of Baja California and adjacent seas. Part 2, p. 134-147. Syst. Zool. 9.

KARIYA, T.
1969. The relationship of food intake to the amount of stomach contents in mebaru, *Sebastes inermis*. Bull. Jap. Soc. Sci. Fish. 35:533-536.

LARSON, R. J.
1972. The food habits of four kelp-bed rockfishes (Scorpaenidae, *Sebastes*) off Santa Barbara, California. M.A. Thesis, Univ. California Santa Barbara, 56 p.

LIMBAUGH, C.
1961. Life-history and ecologic notes on the black croaker. Calif. Fish Game 47:163-174.

LOW, R. M.
1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology 52:648-654.

LOVE, M. S.
1974. Food habits of three midwater kelp-bed predators. M.A. Thesis, Univ. California Santa Barbara, 50 p.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

NELSON, D. R., AND R. H. JOHNSON.
1970. Diel activity rhythms in the nocturnal, bottom-

dwelling sharks, *Heterodontus francisci* and *Cephaloscyllium ventriosum*. Copeia 1970:732-739.

QUAST, J. C.
1968a. Fish fauna of the rocky inshore zone. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 35-79. Calif. Dep. Fish Game, Fish Bull. 139.
1968b. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.
1968c. Observations on the food and biology of the kelp bass, *Paralabrax clathratus*, with notes on its sportfishery at San Diego, California. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 81-108. Calif. Dep. Fish Game, Fish Bull. 139.

SALE, P. F.
1972. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus*. Ecology 53:741-744.

SLOBODKIN, L. B., AND I. FISHELSON.
1974. The effect of the cleaner-fish *Labroides dimidiatus* on the point diversity of fishes on the reef front at Eilat. Am. Nat. 108:369-376.

SMITH, D. L., AND J. C. TYLER.
1972. Space resource sharing in a coral reef fish community. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 125-170. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 14.

STARCK, W. A., II, AND R. E. SCHROEDER.
1965. A coral reef at night. Sea Front. 11:66-79.

STARCK, W. A., II, AND W. P. DAVIS.
1966. Night habits of fishes of Alligator Reef, Florida. Ichthyol. Aquarium J. 38:313-356.

WILEY, J. W.
1974. Observations on the use of mucus envelopes by the California sheephead, *Pimelometopon pulchrum*, on southern California rock reefs. Copeia 1974:789-790.

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INCIDENCE OF CULL LOBSTERS, *HOMARUS AMERICANUS*, IN COMMERCIAL AND RESEARCH CATCHES OFF THE MAINE COAST[1]

JAY S. KROUSE[2]

ABSTRACT

Data obtained by port sampling the Maine commercial lobster catch (1968-74) and the natural lobster population near Boothbay Harbor, Maine, with research gear (1969-74) indicate that 6.5% of the commercially harvested lobsters have lost at least one claw while 21.0% of the lobsters (all sizes) in the natural population have missing and/or regenerating claws. An assessment of variations in cull frequencies associated with different seasons, fishing localities, and lobster size distributions suggests a direct relationship between fishing intensity and the incidence of culls. This information further supports Krouse and Thomas' recommendation that all lobster traps be equipped with an escape vent thus minimizing fishermen's needless handling of excessive numbers of sublegal-sized lobsters.

Over the years the occurrence of American lobster, *Homarus americanus*, with a missing and/or regenerating cheliped in the commercial landings has undoubtedly resulted in a significant financial loss to the fishing industry due to the culls' reduced weight and marketability (retail price of culls is less per pound). Scarratt (1973) reported that commercially caught lobsters from ports off Nova Scotia and Prince Edward Island had incidences of missing claws ranging from 5 to 19%. Although claw loss could not be attributed to a single factor, causes related to fishing such as rough handling by fishermen and movement of traps over the seabed were cited. Recognizing the importance of this situation, I have analyzed cull data provided by the Maine Department of Marine Resources Lobster Research Program's research catches (Krouse 1973) and sampling of the commercial catch (Thomas 1973). In this paper I attempt to assess the magnitude of the cull problem along the Maine coast, some of its causes, and a possible solution to diminish the number of culls.

METHODS

From June 1969 through December 1974, the occurrence of lobsters with missing and/or regenerating claw(s) in daily catches of research gear was noted. Carapace length in millimeters, weight in grams, and sex were recorded for each lobster. Wire lobster traps (2.54 × 2.54 cm mesh) were fished throughout the 6-yr period, whereas modified wooden traps with plastic escape vents of 3.81, 4.13, and 4.45 cm were not used until July 1972. Most experimental fishing was conducted in the vicinity of Capitol, Squirrel, and Damariscove islands in the Boothbay region of Maine (Figure 1).

Information pertaining to the frequency of culls in the Maine commercial catch from 1968 through 1974 was obtained from the probability sampling program described by Thomas (1973).

A length-weight relationship was calculated for 297 lobsters with a regenerating claw and for 225 lobsters with a missing claw collected near Boothbay Harbor, 1972-73. All lobster culls used in this determination had one normal sized claw. The regression of weight on carapace length for these two cull categories was fitted by the method of least squares using the logarithmic transformation $\log_{10} W = \log_{10} a + b \log_{10} L$.

RESULTS AND DISCUSSION

Seasonal and Size Variation in Cull Frequency

From the research catches I have calculated the percentage of culls by month and 5-mm size groups for 1969 through 1974 (Tables 1, 2). Fluctuations in the monthly percentages of culls seem to follow a seasonal pattern, i.e., the number of culls peaked

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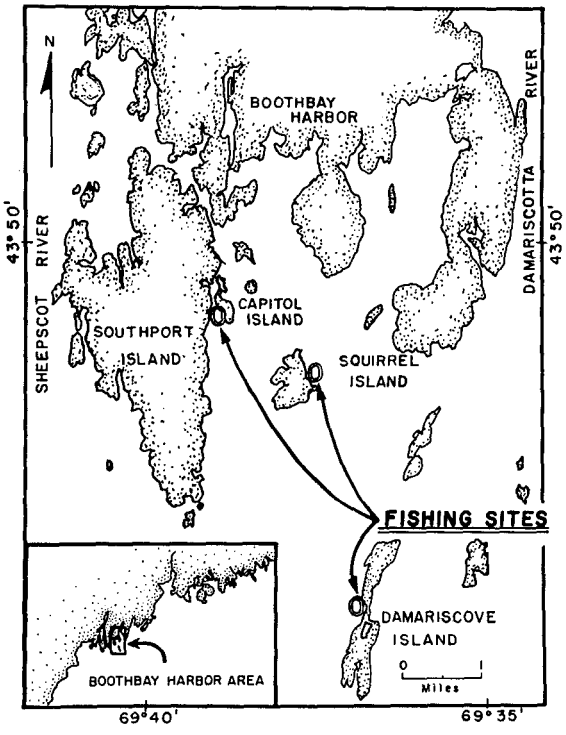

FIGURE 1.—Map showing the areas fished near Boothbay Harbor, Maine.

in the catch during winter-spring (26.9-31.3%), then subsided in July-August (18.1-19.4%), and increased in the fall (17.7-25.6%—variations in fall percentages may be due to sporadic shedding during this season). These seasonal changes might be related to the time of molting (July-September) associated with temporal fluctuations in fishing pressure. If we assume that a high percentage of the total number of culls are caused by fishing operations as suggested by earlier observations of fishermen's needless handling of excessive numbers of sublegal size lobsters (Krouse and Thomas 1975), then the decline in cull frequency during July and August (peak of shedding) may be explained, in part, by: 1) some culls losing this status after shedding and regenerating normal size claws, and 2) small lobsters (usually nonculls by virtue of their nonvulnerability to fishing gear) being recruited into the fishery at this time as a result of shedding. Even though the catch data of this study reveals that a high percentage of lobsters <45 mm carapace length were culls, most of these smaller culls probably acquired this condition while confined in our lobster traps.

TABLE 1.—Monthly incidence of lobster culls in research catches near Boothbay Harbor, Maine, 1969-74.

Month	Total no. examined	Culls (%)	Month	Total no. examined	Culls (%)
Jan.	16	31.3	Aug.	2,164	19.4
Feb.	26	26.9	Sept.	1,266	23.1
Mar.	34	29.4	Oct.	504	19.0
Apr.	83	26.5	Nov.	129	25.6
May	296	24.0	Dec.	62	17.7
June	805	24.0	Total	6,417	21.0
July	1,032	18.1			

TABLE 2.—Percentage of lobster culls by 5-mm size groups in research catches near Boothbay Harbor, Maine, 1969-74.

Carapace length (mm)	Total number caught	Culls (%)	Carapace length (mm)	Total number caught	Culls (%)
36- 40	19	26.3	76- 80	1,403	22.7
41- 45	77	33.8	81- 85	406	22.7
46- 50	160	21.9	86- 90	240	17.9
51- 55	333	19.5	91- 95	119	8.4
56- 60	542	23.2	96-100	20	10.0
61- 65	802	22.8	≥101	18	11.1
66- 70	1,046	19.3	Total	6,417	21.0
71- 75	1,232	19.2			

The frequency of culls by 5-mm increments (Table 2) indicated that culls are most prevalent at carapace lengths ≤45 mm and progressively less numerous at lengths ≥86 mm. The high incidence of culls for small lobsters can be attributed, at least in part, to these lobsters being particularly defenseless to claw loss inflicted by larger lobsters within the trap. On several occasions we have either caught small lobsters with recent claw losses in traps containing larger lobsters or actually witnessed larger lobsters destroying the claw of their diminutive opponent. To further substantiate this explanation of the two cull categories, i.e., regenerating and missing claws, the missing claw group predominated for lobsters ≤50 mm; however, for sizes ≥51 mm, lobsters with regenerating claws usually outnumbered those without claws (Table 3). This disparity was more pronounced for wood traps within the 81- to 85- and 86- to 90-mm groupings. Considering that legal-sized lobsters are handled only once and therefore are probably less prone to claw loss, then one would expect these larger lobsters to have a higher incidence of regenerating claws. Conversely, those sublegal-sized lobsters between 76 and 80 mm that are repeatedly discarded from the fishermen's catch have a preponderance of missing claws for catches with wire and wood traps.

The decline in the incidence of culls at the legal sizes (Maine minimum legal size is 81 mm carapace length) is manifested not only by the research

TABLE 3.—Percentage of lobster culls with missing claws by 5-mm size groups for research catches of wire and wooden traps.

Carapace length (mm)	Wire traps: Number of lobsters: Regenerating claw	Wire traps: Number of lobsters: Missing claw	Wire traps: Missing claw (%)	Wood traps: Number of lobsters: Regenerating claw	Wood traps: Number of lobsters: Missing claw	Wood traps: Missing claw (%)
36-40	2	3	60.0	—	—	—
41-45	2	15	88.2	—	—	—
46-50	7	15	68.2	—	—	—
51-55	15	15	50.0	—	—	—
56-60	50	34	40.5	—	—	—
61-65	62	45	42.1	—	—	—
66-70	65	51	44.0	2	8	80.0
71-75	74	55	42.6	16	15	48.4
76-80	57	74	56.5	59	66	52.8
81-85	14	17	54.8	30	17	36.2
86-90	4	2	33.3	20	10	33.3
≥91	1	1	50.0	5	5	50.0
Total	353	327	48.1	132	121	47.8

catches (Table 2) but also by the commercial catches for 1968-74 (Table 4). For both catches, more legal-sized culls occurred in the 81- to 85-mm size group while the percentage of culls gradually decreased for carapace lengths >85 mm. If, once again, it is assumed that fishing operations often cause culled lobsters and knowing that legal lobsters are handled only once and not repeatedly as may be the case for sublegal-sized lobsters, one would expect fewer culls amongst legal lobsters along with a gradual reduction in culls for sizes >85 mm. Since this study's data demonstrate this very pattern, my contention concerning the possible injurious effects of fishing activities on lobsters <81 mm is strengthened. Certainly there is a greater likelihood of a lobster becoming injured when as a result of fishing operations this lobster is: 1) crowded with other cannibalistic lobsters in a trap; 2) held captive in a trap which may undergo rigorous movement during a storm; 3) hauled boatside with appendages dangling between the trap's laths; and 4) removed from the trap while clinging to the trap, fishermen, or another lobster and eventually released for a descent to the ocean floor during which predation may occur.

TABLE 4.—Incidence of lobsters with missing claws by 5-mm size groups occurring in the commercial catch along the Maine coast (1968-74).

Carapace length (mm)	Total number caught	Culls (%)	Carapace length (mm)	Total number caught	Culls (%)
81- 85	5,322	8.1	106-110	219	3.7
86- 90	7,373	6.2	111-115	109	1.8
91- 95	5,580	5.2	116-120	41	4.9
96-100	1,208	3.7	≥121	6	0
101-105	368	4.3	Total	20,226	6.5

Effect of Fishing Intensity on Cull Frequency

The relationship of fishing intensity and its influence on cull incidence was investigated by calculating the frequencies of culls caught with wire and wood lobster traps (Table 5) at three different fishing sites near Boothbay Harbor (Figure 1). In addition, length-frequency histograms were constructed by 1-mm increments of the catches for each of the sampling sites (Figure 2). This analysis revealed that catches off Capitol Island, the most intensively fished area, contained more culls (23.3% for wire and 22.0% for wood traps) than either the catch of Damariscove (21.2%) or Squirrel islands (12.7% for wire and 17.9% for wood traps) which had the fewest culls. Although Damariscove and Squirrel islands appeared to have similar trap concentrations based on visual sightings of pot buoys, appreciably more culls were trapped at Damariscove. Possible reasons for this difference may be related to: 1) lobsters being maimed by excessive movement of traps over the substrate during storms off the more exposed seaward shoreline of Damariscove (waters fished at Squirrel were more sheltered); 2) Damariscove's greater abundance of small lobsters which are more vulnerable to injury [average size of lobsters in Damariscove catch was smaller than those of the other two areas (Figure 2), and the percentage of lobsters with missing claws was highest at Damariscove (Table 5)]; and 3) perhaps, an error in our rather subjective determination of nearly equal fishing intensities for both islands. Nevertheless, there does appear to be a positive

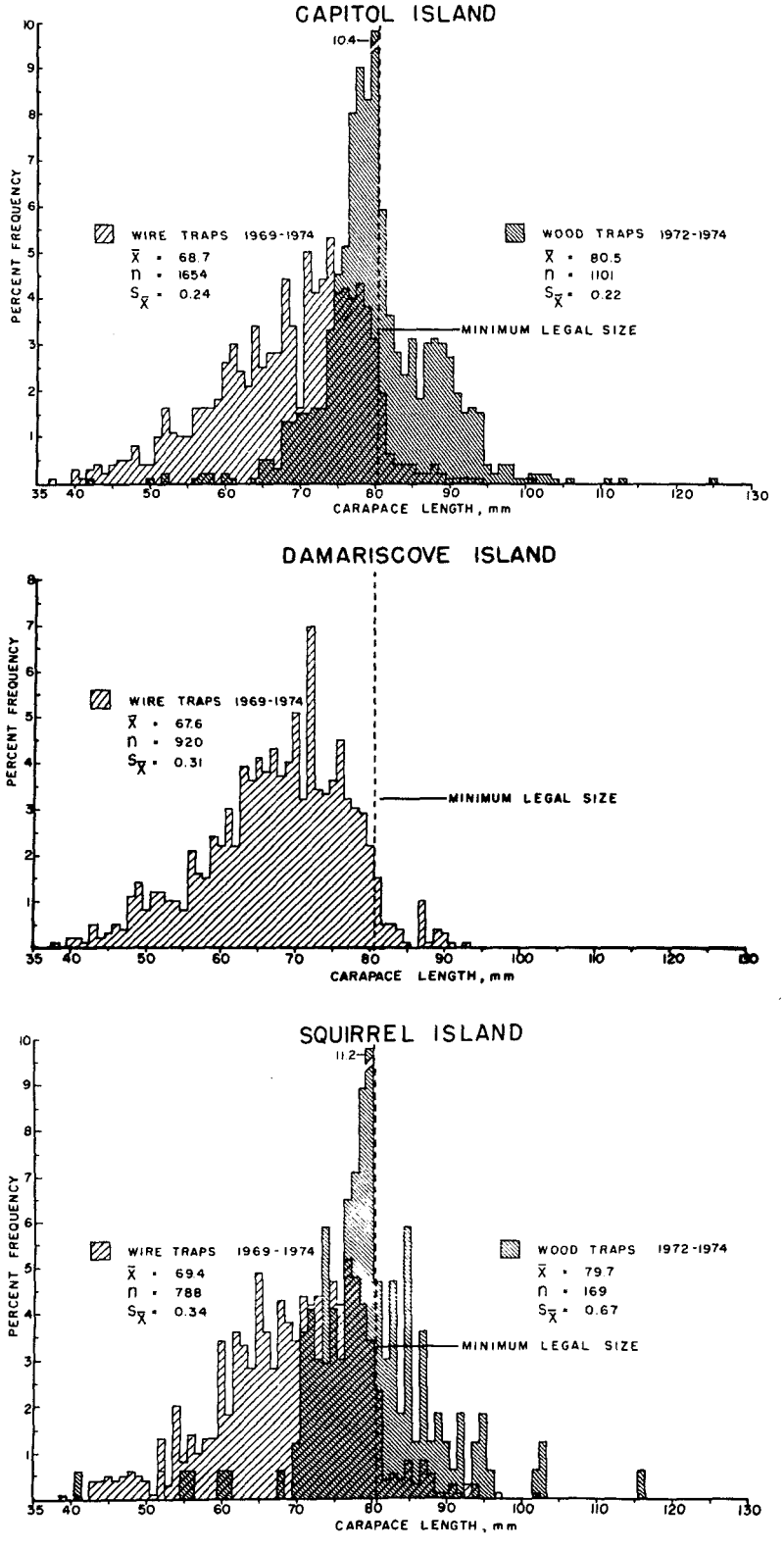

FIGURE 2.—Length-frequency histograms for the lobster catches with wire and wood traps for each of the three sampling sites near Boothbay Harbor, Maine.

TABLE 5–Comparison of the incidence of lobster culls in catches of wire and wood traps for various areas near Boothbay Harbor, Maine, 1969-74.

Gear and area	Total no. lobsters	Culls (%)	Regenerating claw (%)	Both claws regenerating (%)	Missing claw (%)	Both claws missing (%)	Regenerating and missing claws (%)
Wire traps:							
Capitol	1,627	23.3	10.6	1.8	9.1	1.1	0.7
Damariscove	920	21.2	8.4	1.0	10.0	1.0	0.5
Squirrel	787	12.7	6.9	0.5	5.1	0.1	0.1
Wood traps:							
Capitol	1,125	22.0	10.0	1.4	8.4	1.3	0.8
Squirrel	162	17.9	8.6	1.9	5.6	1.9	0

correlation between fishing intensity and incidence of culls; however, this does not preclude other factors such as predation, intraspecific competition, molting difficulties, and storm related damages.

Loss of Value of Catch Due to Culls

At the beginning of this paper I mentioned that culls have perennially detracted from the landed value of the lobster catch. To assess this situation, the regressions of weight for lobsters with missing and regenerating claws on carapace length for sublegal- and legal-sized lobsters were calculated. These curves were then compared to the length-weight relationship for noncull lobsters (Krouse 1973) (Figure 3). These comparisons reveal that noncull lobsters are about 14 to 20% heavier than those lobsters with regenerating and missing claws. Knowing these weight differentials and that about 6.5% of the lobsters in the commercial catch are missing at least one claw (Table 4) and that at least an equal percentage (6.5) of lobsters must have regenerating claws, the cull loss to the fishery can now be quantified. From the 1974 Maine Landings which reported a lobster catch of 16,457,666 pounds valued at $23,212,808, I estimated that the annual catch without any culls could have been increased by about 363,700 pounds (2.2%), adding $512,800 to the landed value. Unfortunately, there probably is no way to eliminate culls completely; however, proper size escape vents in all traps would be beneficial in effecting a marked reduction in the incidence of culls (Krouse and Thomas 1975). This reduction in culls would be the result of decidedly fewer numbers of sublegal-sized lobsters being handled by fishermen as indicated by the conspicuous disparity between the size composition of research catches with wire and vented wooden traps (Figure 2). Even if the cull loss could be lessened by only 25%, the industry would still realize an annual increase of about $128,000.

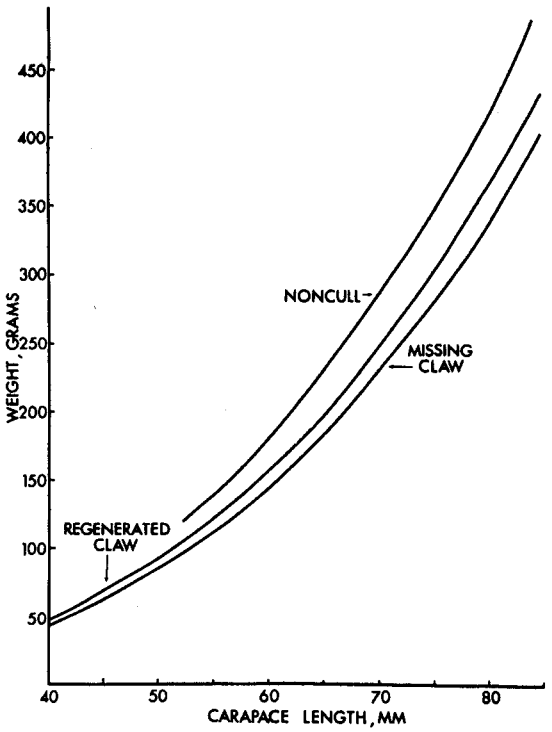

FIGURE 3.–Comparison of the calculated length-weight relationships for lobsters with regenerating, missing, and normal claws (noncull). The regression equations are: 1) regenerating claws: $\log_{10} W = -2.99 + 2.91 \log_{10} L$; 2) missing claws: $\log_{10} W = -3.03 + 2.92 \log_{10} L$; and 3) noncull: $\log_{10} W = -2.91 + 2.90 \log_{10} L$.

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LITERATURE CITED

KROUSE, J. S.
1973. Maturity, sex ratio, and size composition of the natural population of American lobster, *Homarus americanus*, along the Maine coast. Fish. Bull., U.S. 71:165-173.

KROUSE, J. S., AND J. C. THOMAS.
1975. Effects of trap selectivity and some population parameters on size composition of the American lobster, *Homarus americanus*, catch along the Maine coast. Fish. Bull., U.S. 73:862-871.

SCARRATT, D. J.
1973. Claw loss and other wounds in commercially caught lobsters *(Homarus americanus)*. J. Fish. Res. Board Can. 30:1370-1373.

THOMAS, J. C.
1973. An analysis of the commercial lobster *(Homarus americanus)* fishery along the coast of Maine, August 1966 through December 1970. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-667, 57 p.

FISHERY WASTE EFFLUENTS: A METHOD TO DETERMINE RELATIONSHIPS BETWEEN CHEMICAL OXYGEN DEMAND AND RESIDUE

JEFF COLLINS AND RICHARD D. TENNEY[1]

ABSTRACT

Researchers and the fishing industry have experienced difficulty in applying the Environmental Protection Agency's standard tests to industrial fishing waste effluents, especially for total suspended and settleable solids, and oil and grease.

The relationship between chemical oxygen demand and residue was determined on a limited number of samples from four types of screened waste effluents from November 1973 to September 1974: shrimp using fresh or salt water processing, snow crab, and canned salmon. In addition to chemical oxygen demand and residue, tests for settleable solids, total suspended and settleable solids, oil and grease, protein, and salt were also performed. Based on these relationships, a method is suggested to develop a system for the analysis of pollutants that will be more economic and give more meaningful data than currently obtainable under Environmental Protection Agency's methods. The method requires that base data on a plant be obtained to relate chemical oxygen demand with residue values using regression lines and equations. A subsequent routine monitoring program need only test for total residue and chemical oxygen demand of the filterable residue. Substitution into the equations gives the other residue fractions and their chemical oxygen demand values, i.e., total chemical oxygen demand, chemical oxygen demand of the particulate matter, filterable residue, and nonfilterable residue.

This laboratory has modified and studied in detail a number of analytical techniques to measure pollutants (Tenney)[2]. We have considered the methods of testing specified by the Environmental Protection Agency (EPA) to monitor fishery pollutants and are of the opinion that the monitoring program and analytical methods specified under the National Pollutant Discharge Elimination System (NPDES) program could be improved for application to seafood-processing effluents (Pojasek 1975). The purpose of this paper is to suggest different tests for monitoring effluents with certain prerequisites that would satisfy the intent of the law, yet recognize both the technical and economic problems associated with the fishing industry's efforts to comply with the monitoring regulations.

Since laboratory space, equipment, and labor necessary to conduct a waste-monitoring program are quite expensive to the fishing industry, economics suggest the use of a minimum number of tests to do the job, and where possible, the use of inexpensive equipment. In some analyses, the time required to complete any analysis is important, as in the 5-day test for biological oxygen demand (BOD). In this instance, the chemical test (chemical oxygen demand–COD) provides quick results and has better application. The limited level of laboratory experience and equipment generally found in seafood-processing plants and their diverse and often remote locations also suggest that the regulations and permit system should reflect these limitations and require only fairly simple tests to measure pollutants. At the same time, however, analytical techniques used to measure pollutants must be accurate, have good precision, and be a meaningful measure of pollutants.

In this study we have evaluated the relationship between COD and residue of the screened effluents of four plants. Based on these correlations, a monitoring system is suggested that enables the results of two analyses to provide data on six pollutant parameters.

EXPERIMENTAL

Identification and Definition of Terms

BOD (*Biochemical oxygen demand*): oxidation by bacteria.

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[2]Tenney, R. D. 1972. COD for Industrial Waste Water, Tech. Rep. 97, 5 p.; 1972. Chemical Oxygen Demand, Tech. Rep. 101, 12 p.; 1973. Shrimp Waste Streams and COD, Tech. Rep. 104, 3 p. Unpublished, intralaboratory reports, Kodiak Utilization Research Laboratory.

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FISHERY BULLETIN: VOL. 74, NO. 4, 1976.

COD (*Chemical oxygen demand*): oxidation by potassium dichromate.

Residue: This term does not necessarily mean solids, rather it is the results of or the substance remaining from a separation process such as filtering or drying. For example, if a solvent is evaporated from oil, the resulting residue is a liquid, not a solid.

TR (*Total residue*): is the weight of material remaining from a sample of the original screened effluent after overnight drying at 103°C.

FR (*Filterable residue*): is the residue of the filtrate (GF/A glass filter) dried at 103°C. Drying seafood effluents at 180°C (Environmental Protection Agency 1974) produced results that could not be related to the TR and nonfilterable residue.

NFR (*Nonfilterable residue*): is the residue remaining on the glass filter after drying at 103°C. Since the three residue terms are related and provided drying conditions are the same, NFR can be determined indirectly, i.e., TR - FR.

SS (*Settleable and floatable solids*): This term has caused considerable trouble to the industry and researchers. By custom, the volume of the settled portion in the Imhoff cone is measured and considered SS. However, this measurement does *not* actually measure SS, because floatables are not included in the reading. The term only has correct meaning when SS is determined in milligrams/liter by difference: the NFR minus the NFR of a sample taken from near the center of the Imhoff cone after 1 h of settling.

Sus. Sol. (*Suspended solids*): are the particulate matter suspended in the center of the Imhoff cone, i.e., the NFR of that area.

TSS (*Total suspended nonfilterable solids*): This term has also caused confusion. It means the dry weight of all particulate matter (settleable, suspended, floatable), i.e., the NFR. For both technical and grammatical reasons, NFR is the preferred term.

O&G (*Oil and grease*): content was determined by a method in which the precipitated, filtered-solids material plus Celite[3] (used as a precipitation aid) is extracted directly under anhydrous conditions, using 2-propanol and petroleum ether (Collins 1976). This technique extracts all lipidlike material, including carotenoids.

Protein: The nitrogen content was determined by the macro-Kjeldahl method on 100- to 200-g samples and expressed as protein by multiplying N by 6.25 (Horwitz 1965:273).

Salt: Chloride was determined by the standard $AgNO_3$ method and expressed as NaCl (Horwitz 1965:273).

Subscripts: In this paper, we use subscripts to identify the particular portion of the sample tested. For example, COD_{TR} is the COD of the screened waste effluent, and COD_{FR} is the COD of the FR, i.e., the filtrate, not the actual dried FR. If no subscript is used, we are referring to the test in general or to the test on the original screened sample, i.e., COD is the same as COD_{TR}.

Industrially screened shrimp and crab effluents were obtained from November 1973 through February 1974 and from salmon effluents July through September 1974. Since our purpose was to compare data rather than characterize the level of pollution in a plant, we took grab samples at specific times during the production to get a useful range of values. The following analyses were made: COD_{TR}, COD_{FR}, TR, FR, NFR (i.e., TSS), SS, protein, O&G, salt, and the COD of a sample from the center of the Imhoff cone after 1 h of settling.

In conducting these analyses we used the methods of the Environmental Protection Agency (1974), unless otherwise indicated. The particulate matter in our samples of fishery waste was so high that the filter clogged frequently before the entire sample had been filtered. For this reason, sample sizes were reduced, where necessary, to 25 ml.

The degree of pollutant in an effluent is affected by the processes employed, species processed, and the use of fresh or salt water in varying degrees during processing. Mechanical shrimp peelers use about 7 gallons of water per pound of shrimp. Salt water from wells close to the shore or from the ocean is sometimes used on the mechanical peelers. The two main types of peelers vary in their relative waste load. The Model A peeler peels raw shrimp and generally has a higher waste load than the Model PCA peeler that peels a steam-blanched shrimp.

RESULTS

Study 1—Shrimp: Analyses of effluents from a shrimp plant processing with fresh water and mechanical peelers (Model A).

Over a 10-day period in December 1973, eight samples of waste effluents were taken from the underflow of the Bauer Hydrasieve (tangential screen, 0.04-inch) and analyzed (Table 1). Averages for COD by analysis are as follows:

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

a. COD, screened effluent 3,257 mg/liter
b. COD, center of Imhoff cone 3,043 mg/liter
c. COD, filtrate of NFR test 1,616 mg/liter

By calculation, the COD of the particulate matter and its percentage contribution to the total COD are:

COD of NFR (a - c) = 1,641 mg/liter 50.4%
COD of SS by weight
(a - b) = 214 mg/liter 6.6%
COD of Sus. Sol.
[(a - c) - (a - b)] = 1,426 mg/liter 43.8%

By analysis and calculation, data were also obtained for the means of other residue tests:

By analysis:
d. Total residue (TR) 2,381 mg/liter
e. Filterable residue (FR) 1,577 mg/liter
f. Settleable solids (SS) 5.6 ml/liter
g. Nonfilterable residue (NFR) 769 mg/liter

By calculation: NFR, i.e., (d - e) or TR - FR = 804 mg/liter.

By weight, the FR was 66.3% of the TR, but the COD of the FR was only 49.6% of the total COD. The NFR, however, contributed only 33.7% to the TR by weight but contributed 50.4% as COD.

The standard deviations (SD) in Table 1 show relatively large values in agreement with practical experience. The higher average concentration and lower SD for the NFR determined by difference suggests that this is a better method for determining the concentration of NFR than is the direct analysis.

Study 2—Shrimp: Analyses of effluents from a shrimp plant processing with salt water and mechanical peelers (Models A and PCA).

Ten samples of waste effluent were taken from the underflow of the 0.7-mm Dorr-Oliver screen. The individual results are given in Table 2, and the average analytical data are as follows:

a. COD, screened effluent 2,643 mg/liter
b. COD, center of Imhoff cone 2,338 mg/liter
c. COD, filtrate from NFR test 1,519 mg/liter
d. Settleable solids (SS) 7.8 ml/liter
e. Nonfilterable residue (NFR) 684 mg/liter

TABLE 1.—Analyses of shrimp waste effluents from a plant processing with fresh water and mechanical peelers (Model A). All values are in milligrams per liter except SS in milliliters per liter.

Date of sample	Screened effluent		Filtrate (glass filter)		By difference		Center Imhoff	SS	Direct analysis
Dec. 1973	COD_{TR}	TR	COD_{FR}	FR	COD_{NFR}	NFR	COD	Vol	NFR
11	3,070	2,370	1,492	1,640	1,578	730	2,856	8.0	880
12	3,364	2,660	2,040	1,990	1,324	670	3,212	7.0	840
13	3,068	2,290	1,580	1,540	1,488	750	2,912	3.0	656
14	2,516	1,970	1,240	1,350	1,276	620	2,312	7.0	796
18	3,353	2,280	1,405	1,360	1,948	920	2,956	11.0	892
19	2,660	1,790	1,080	1,010	1,580	780	2,418	2.0	120
20	2,962	2,040	1,588	1,420	1,374	620	2,841	2.5	660
21	5,065	3,650	2,500	2,310	2,565	1,340	4,836	4.0	1,308
Mean	3,257	2,381	1,616	1,577	1,642	804	3,043	5.6	769
SD	789	578	455	407	428	238	781	3.2	332

TABLE 2.—Analyses of shrimp waste effluents from a plant processing with salt water and mechanical peelers (Models A and PCA). All values are in milligrams per liter except SS in milliliters per liter.

Date of sample	Screened effluent		Filtrate (glass filter)		By difference		Center Imhoff	SS	Direct analysis
	COD_{TR}	TR	COD_{FR}	FR	COD_{NFR}	NFR	COD	Vol	NFR
18 Nov. 1973	3,264	33,500	—	—	—	—	2,915	8.0	993
27 Nov.	4,050	—	2,690	—	1,360	—	3,883	3.0	—
7 Dec.	2,090	25,550	1,212	25,360	878	190	1,882	4.0	580
10 Dec.	3,161	34,090	1,729	33,780	1,432	310	2,935	9.0	1,212
2 Jan. 1974	3,143	27,730	1,733	—	1,410	—	2,849	8.0	1,008
9 Jan.	2,364	23,314	1,353	—	1,011	—	2,021	9.0	180
1 Feb.	2,890	23,300	1,363	23,100	1,527	200	2,487	10.0	616
4 Feb.	1,948	26,610	1,100	—	848	—	1,640	9.5	476
7 Feb.	2,442	23,940	1,659	—	783	—	1,806	9.5	896
15 Feb.	1,080	25,240	828	25,200	252	40	960	8.0	192
Mean	2,643		1,519		1,056		2,338	7.8	684
SD	836		534		415		839	2.4	367

By calculation, the COD of the particulate matter and its percentage contribution to the total COD are:

COD of NFR	(a - c) =	1,124 mg/liter	42.5%
COD of SS	(a - b) =	305 mg/liter	11.5%
COD of Sus. Sol.	[(a - c) - (a - b)] =	819 mg/liter	31.0%

Some figures were also collected on the concentration of residues by direct analysis and are included in the table to illustrate the problems associated with monitoring plants that process with salt water. Residue values were not determined by calculation because of the high and variable salt content. It is questionable that meaningful data for NFR can be obtained because of errors that can occur when the salt values of about 25,000 mg/liter are subtracted from the mean TR values of about 27,000 mg/liter.

Study 3—Snow Crab: Analyses of effluents from a plant processing both meats and sections in fresh water.

Over a 2-wk period in February 1974, six samples of waste effluent from a plant processing snow crab using fresh water were taken from the underflow of Dorr-Oliver 0.4-mm screen and analyzed (Table 3). Average values by analysis are as follows:

a.	COD, screened effluent	1,426 mg/liter
b.	COD, center of Imhoff cone	1,332 mg/liter
c.	COD, filtrate from NFR test	824 mg/liter
d.	Total residue (TR)	1,393 mg/liter
e.	Filterable residue (FR)	1,086 mg/liter
f.	Settleable solids (SS)	4.2 ml/liter
g.	Nonfilterable residue (NFR)	277 mg/liter

By calculation, the mean values for COD of the particulate matter and its percentage contribution to the total were:

COD of NFR	(a - c) =	602 mg/liter	42.2%
COD of SS	(a - b) =	94 mg/liter	6.6%
COD of Sus. Sol.	[(a - c) - (a - b)] =	503 mg/liter	42.2%

By calculation, the mean value for NFR is: (d - e) = 307 mg/liter.

Study 4—Salmon: Analyses of effluents from a plant processing canned salmon.

During the summer of 1974, ten samples of

TABLE 3.—Analyses of snow crab waste effluents from a plant processing both meats and sections in fresh water. All values are in milligrams per liter except SS in milliliters per liter.

Date of sample Feb. 1974	Screened effluent		Filtrate (glass filter)		By difference		Center Imhoff	SS	Direct analysis
	COD_{TR}	TR	COD_{FR}	FR	COD_{NFR}	NFR	COD	Vol	NFR
6	680	880	506	770	174	110	599	1.3	126
8	888	960	650	850	238	110	868	0.5	41
11	1,056	1,230	746	1,030	310	200	974	5.0	143
14	1,560	1,590	870	1,280	690	310	1,408	4.0	462
19	1,988	1,900	1,077	1,500	911	400	1,889	7.5	540
25	2,383	1,800	1,093	—	1,290	—	2,254	7.0	348
Mean	1,426	1,393	824	1,086	602	226	1,332	4.2	277
SD	668	433	235	303	442	127	640	2.9	202

TABLE 4.—Analyses of salmon waste effluents from a plant processing canned salmon. All values are in milligrams per liter.

Date of sample 1974	Salmon	Screened effluent					Filtrate — glass filter				By difference	
		COD_{TR}	TR	Protein	O&G	Salt	COD_{FR}	FR	Protein	Salt	COD_{NFR}	NFR
30 June	Red	5,716	3,695	2,197	1,190	574	1,365	1,513	1,044	545	4,351	2,182
7 July	Red	2,908	2,076	1,500	330	373	1,212	1,135	656	273	1,696	941
8 July	Red	4,069	2,368	1,453	918	253	1,131	1,078	744	247	2,938	1,290
11 July	Chum	2,070	1,125	1,179	308	—	797	350	531	453	1,273	775
14 July	Chum	6,294	4,450	2,980	—	728	2,687	2,560	1,775	436	3,607	1,890
17 July	Pink	9,513	7,102	—	—	596	4,020	3,655	3,346	465	5,493	3,447
30 July	Chum	9,101	6,315	3,346	1,407	397	3,420	2,813	—	—	5,681	3,502
13 Aug.	Pink	5,236	3,595	2,378	845	493	1,462	1,465	1,009	459	3,774	2,130
14 Aug.	Pink	2,647	2,148	1,518	226	344	1,822	1,570	1,168	292	825	578
22 Aug.	Mixed	6,219	4,874	3,263	924	642	2,615	2,722	1,938	556	3,604	2,152
Mean		5,377	3,775	2,201	769	489	2,053	1,886	1,357	414	3,324	1,889
SD		2,557	1,937	840	437	157	1,078	1,007	885	115	1,664	1,026

salmon cannery waste effluent were taken from the underflow of a Bauer screen (0.03-inch) (Table 4). The average values by analysis and calculation are as follows:

a.	COD, screened effluent	5,377 mg/liter
b.	COD, filtrate of NFR test	2,053 mg/liter
c.	COD, of NFR (a - b)	3,324 mg/liter
d.	Total residue	3,775 mg/liter
e.	Filterable residue	1,886 mg/liter
f.	Nonfilterable residue (d - e)	1,889 mg/liter
g.	O&G, screened effluent	769 mg/liter
h.	Protein, screened effluent	2,201 mg/liter
i.	Salt, screened effluent	489 mg/liter

The NFR is 50% of the TR, but the COD of the NFR is 62% of the total COD.

DISCUSSION

The following discussion is concerned with monitoring parameters previously suggested or currently in effect under EPA effluent limitations for seafood processing and with the suggestion of a more precise and simpler monitoring system. The present EPA requirements, however, for use of alternative analytical methods must be considered. Under EPA rules (Title 40 "Code of Federal Regulations," Parts 136.4 and 136.5), any person wishing to use alternative analytical methods for the parameters listed must follow variance procedures specified under the NPDES permit system.

Current permits require monitoring for SS, COD (i.e., COD_{TR}), TSS (i.e., NFR), O&G, flow, and pH. SS is imprecise and contributes so little to the pollution load in seafood processing that it has relatively little value as a measure of pollution, although it has merit as a check on the efficiency of screen operation. As discussed later, total COD can be determined more accurately in an indirect manner. The O&G analysis is difficult to do, and this value, too, can be obtained more accurately through calculation. Data in this paper suggest that the indirect analysis for NFR (i.e., TSS) was more accurate than the direct method. The FR is an important parameter because this fraction contributed about 50% to the total COD or TR and will need to be considered in the design of future treatment systems.

To develop an improved monitoring system, we plotted the COD and residue data of Table 1 to illustrate the correlation between the COD of the residue and the concentration of the residue (Figure 1). The regression lines and equations were determined by the method of least squares. The TR and FR regression lines were obtained through direct analyses, and the NFR line was obtained by difference. The maximum deviation of any COD value from the regression line was 260 mg/liter. This is slightly less than the possible error of the analytical method (± 8%) (Moore et al. 1949). On the average, the individual values were within 107 mg COD of the regression line.

The correlations shown in Figure 1 can be used to calculate COD and residue values. In the following, the first three equations are the regression lines of Figure 1 and the next three are derived equations to solve for residue rather than for COD. Of course, these equations are valid only for this group of data and for this particular plant. If the TR and COD_{FR} are determined by analysis, the other values can be derived from the equations or the regression line and from the expression TR = FR + NFR.

$$COD_{TR} = 1.32\,TR + 113 \quad (1)$$
$$COD_{FR} = 1.08\,FR - 96 \quad (2)$$
$$COD_{NFR} = 1.78\,NFR + 210 \quad (3)$$

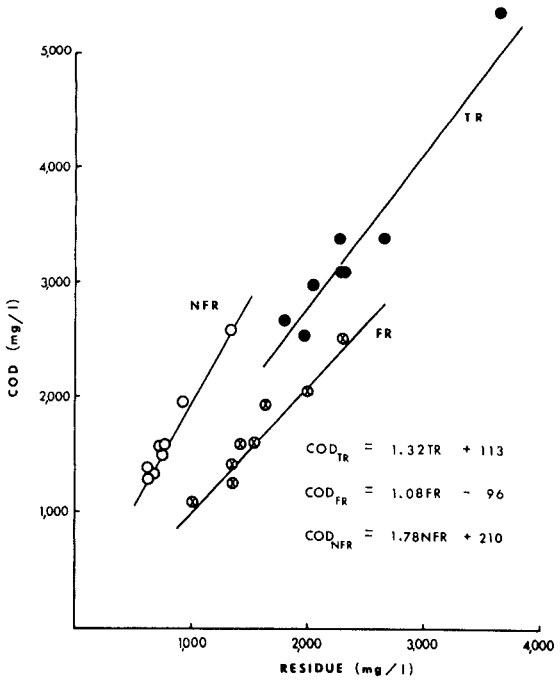

FIGURE 1.–Relationship between the COD of the residue and the concentration of the residue from shrimp processed on Model A peelers using fresh water.

$$TR = 0.76\ COD_{TR} - 86 \quad (4)$$
$$FR = 0.93\ COD_{FR} - 89 \quad (5)$$
$$NFR = 0.56\ COD_{NFR} - 118 \quad (6)$$

When salt water was used in processing, such as in the second plant study (Table 2), the residue values included salt. Since salt values were not determined, COD and residue data were not correlated for this plant.

In the third plant study of snow crab effluent, the data (Table 3) were plotted similarly to the shrimp data (Figure 2). The basic equations for snow crab can also be used to calculate from two analyses the other COD or residue values. The equations are listed in Figure 2.

Data for the fourth plant study of salmon-waste effluents (Table 4) were also plotted, and the regression lines and equations were similarly determined (Figure 3). The regression lines for salmon are less precise because of the variable salt content of the effluent and the high levels of COD and residue. Salt varied because of the erratic operation of the salmon egg-processing room. These regression lines (salmon) should not be used to calculate or interpolate COD or residue values unless a check is first made on salt content. If salt content of the effluent is about normal (500 mg/liter), the calculation is valid since these equations are derived from data with a high standard deviation for salt. A check is made to ensure that the level is not 1 or 2% as it could be if a brine tank were dumped. A routine composite sampling program for the plant, of course, would reduce salt variation.

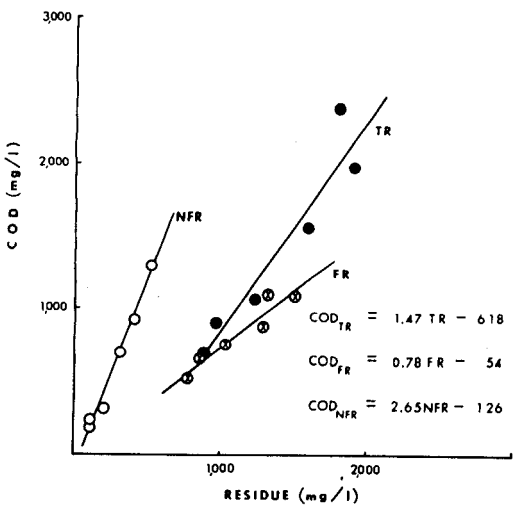

FIGURE 2.—Relationship between the COD of the residue and the concentration of residue from the processing of snow crab meats and sections.

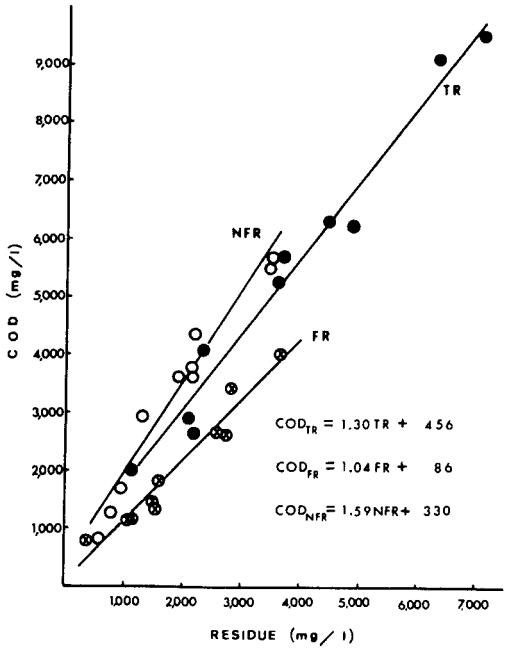

FIGURE 3.—Relationship between the COD of the residue and the concentration of the residue for canned salmon processing.

A SIMPLIFIED MONITORING SYSTEM

The data of the first plant study (Table 1) and the six equations listed earlier may be used to illustrate how a simplified monitoring system can be set up for a particular plant.

Since COD is difficult to determine on the original effluent (particulate matter causes dilution problems) and impractical to determine on a solid sample, COD should be determined on the filterable residue sample before drying. Equation (5) is then used to calculate FR in milligrams per liter. It is not necessary to actually finish the FR test. The next analysis most logically should be the total residue test. It is an easy test to do and is accurate. Equation (1) is used to calculate the COD of the TR, and the previously calculated FR is subtracted from TR to give the NFR in milligrams per liter. Equation (3) is then used to calculate the COD of the NFR. Thus, two analyses plus several calculations give three COD and three residue values.

The two analyses recommended (COD_{FR} and TR) are logically the most accurate of the six

possible, thus the other calculated values that are based on an ideal regression line should be more valid than those obtainable by direct analysis. Although this system may suggest doing the FR rather than the COD_{FR}, we believe that one direct analysis for COD is desirable, since the effect of oxygen demand on the receiving water is an important parameter of a monitoring program. Although O&G were not specifically considered except for salmon, for which we had limited data, the COD and residue data imply that O&G are related and that a regression line could be calculated.

In conclusion, it appears that in-plant monitoring for COD_{FR} and TR and the application of proper correlation factors and equations previously determined for the plant effluent will give reportable data on COD_{TR}, COD_{NFR}, COD_{FR}, TR, FR, and NFR. The suggested analyses can be done at reasonable cost with simple equipment, are capable of good precision and accuracy, and can be conducted by quality assurance personnel in the fishing industry. We suggest, recognizing the limitations of our data and obvious and known differences between processing plants and processing methods, that if regression lines or correlations similar to those given in this paper were determined, the resulting monitoring system would be simpler and more accurate than that currently in use.

In a subsequent paper, we will report regression data for protein and O&G similar to that suggested in this paper and a method using a simultaneous equation to calculate protein and O&G from TR and COD data.

LITERATURE CITED

COLLINS, J.
1976. Oil and grease: A proposed analytical method for fishery waste effluents. Fish. Bull., U.S. 74:

ENVIRONMENTAL PROTECTION AGENCY.
1974. Methods for chemical analysis of water and wastes. Environ. Prot. Agency, Off. Tech. Transfer, Meth. Dev. Qual. Assurance Res. Lab., Natl. Environ. Res. Cent. 298 p.

HORWITZ, W. (chairman and editor).
1965. Official methods of analysis of the Association of Official Agricultural Chemists. 10th ed. Association of Official Agricultural Chemists, Wash., D.C., xx+ 957 p.

MOORE, W. A., R. C. KRONER, AND C. C. RUCHHOFT.
1949. Dichromate reflux method for determination of oxygen consumed. Anal. Chem. 21:953-957.

POJASEK, R. B.
1975. NPDES permits and water analyses. Environ. Sci. Technol. 9:320-324.

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POPULATION BIOLOGY OF *EUPHAUSIA PACIFICA* OFF SOUTHERN CALIFORNIA

EDWARD BRINTON[1]

ABSTRACT

Euphausia pacifica was observed with respect to reproduction, growth and development of cohorts, and successions in population structure and biomass during 4 yr, 1953-56. The southern California eddy and its upwelling regime serve as a reproduction refuge for a warm-temperate population of this euphausiid. Three size classes spawn there during a year—the largest in April-June, an intermediate in June-February, and small, newly mature females usually in August-January. There were year-to-year differences.

The largest densities of larvae were observed about a month after egg peaks (one survey later) or appeared coincident with them. In 1953 there was strong spring recruitment, abruptly subsiding with an early decline in upwelling—the index of environmental enrichment used. During 1954 only one substantial cohort was recorded, in June at the height of a poor upwelling season. In 1955 repeated spawning occurred during the long upwelling season, but recruitment after July was poor. The year of most intense upwelling, 1956, yielded three strong cohorts—the last, July-October, being exceptionally strong. Smallest larvae were usually in 12°-16°C waters. Ripe females were concentrated at high densities at these same temperatures during August-March but were distributed over a broader range at 10.5°-19°C during April-July.

Growth was estimated to be about 3 mm body length per month, slowing during September-January or after about 17 mm. Females appeared to grow slower in breeding seasons. Maturity can be at 11 mm, but reproduction is not general until 15-16 mm. Here, maximum size was 21 mm after about 7 mo for early-year recruits and a year for summer recruits. Survival rates appeared higher in the latter. Growth rates were similar to those reported for *E. pacifica* off Oregon and higher than in the subarctic Pacific. Survivorship was lowest for furcilia larvae, increased in juvenile and young adult phases, then decreased after reproduction became regular. Slowed growth and increased survivorship at life interphases appeared to cause regular frequency and biomass maxima at lengths of 7, 10-12, and 15 mm. Sex ratio favored females. Males apparently accomplished multiple fertilizations.

Euphausia pacifica Hansen is a temperate North Pacific euphausiid crustacean, composing a substantial part of the zooplankton of the North Pacific Drift, lat. 40°-50°N, and ranging southward along the coast of North America as far as lat. 25°N (Brinton 1962a). In the cooler part of the California Current, it occurs in association with the euphausiids *Nematoscelis difficilis* and *Thysanoessa gregaria*. Depth ranges of the three species overlap daily as *E. pacifica* and *N. difficilis* engage in distinctive vertical migrations while *T. gregaria* does not migrate (Brinton 1967a). Horizontal ranges are sufficiently similar so that these species, together with *E. gibboides*, were considered the euphausiids of a California Current-Transition Zone plankton assemblage (Brinton 1962a).

Euphausia pacifica performs extensive vertical migrations. Off California it lives at daytime depths of 200-400 m, entering the surface layer at night. It is an omnivore (Lasker 1966) and possesses thoracic food-gathering limbs which are nearly uniform in length and in setation of the filtering screens.

Euphausia pacifica is usually the most abundant euphausiid. Its maximum densities are often centered relatively near to the coast of California. The low-latitude part of the population of *E. pacifica* is the object of this study. Aspects of its life history have been observed in the more typically temperate regime to the north of lat. 40°N (Nemoto 1957; Ponomareva 1963; Smiles and Pearcy 1971) where environmental characteristics show stronger seasonality than to the south. The extent to which the downstream portion of this distributional range is maintained by local processes has not been previously investigated.

The study was organized in relation to existing knowledge of the physical-chemical characteristics of the area and of the species distributions.

Surveys of the region of the California Current since 1949 have provided a reservoir of hydrographic data and plankton samples that lend

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themselves to time-series studies of biological and environmental developments. The CalCOFI (California Cooperative Oceanic Fisheries Investigations) Atlas series (Numbers 1-24) presented varied material, including euphausiid distributions derived from the program. Charts of distributions of *E. pacifica* based on the data that are the subject of the present analysis are included in Brinton and Wyllie (in press). Smith (1971) described the distribution of zooplankton biomass.

Description of the Study Area

The southern California eddy is the southernmost area in which *E. pacifica* is still both abundant (commonly 10-1,000 individuals beneath 1 m^2 of sea = 10-1,000 mg wet weight) and dominant among the larger zooplankters (Brinton 1967a, b). The eddy may be considered bounded on the north by Point Conception, lat. 34°N, and on the south by about lat. 30°N. Its east-west extent is about 250 km; beyond its western limits, flow is consistently from the north and apparently contributes relatively little water and biota to the eddy.

The sluggish circulation off southern California evidently permits substantial autonomy for the resident populations. The currents are commonly 5-10 cm/s and rarely as much as 25 cm/s, both at the surface and at 200 m depth (Wyllie 1966). Direction of flow sometimes reverses between these two levels. These are, respectively, the night and day depth levels occupied by vertically migrating *E. pacifica* (juvenile and adult) in the area; larvae remain near the surface day and night (Brinton 1967a).

Circulation of the eddy is cyclonic. Within it, therefore, there is upward transport of enriched water. The center of the eddy (no surface flow) is, on the average, near San Nicholas Island (lat. 33°15′N, long. 119°30′W), 100 km off the midpoint of the southern California coast. The study area was centered here. Farther east, mean flow is northwesterly along the coast. To the west, flow is southeasterly, angling toward the coast near lat. 30°N.

About 150 km south of Point Conception, mean geostrophic flow approaches 135°, averaging 10 cm/s. A parcel of water entering the eddy from the northwest would, at that speed, take 100 days to move around the eddy back to Point Conception, flow permitting. Average velocities within the eddy are much less. Places where substantial advection takes place across margins of the area are determinable from the flow diagrams in a relative sense. Northerly surface flow into and out of the area is characteristic of winter months when the Davidson Countercurrent is developed. Southerly flow into or through the western part of the area is usually strongest in April-July. The eddy persisted in almost all of the months studied.

Upwelling enhances the temperate character of the area during spring and summer, usually intensifying during April-June (Bakun 1973) when annual temperature minima are usually found. It is responsible for much of the local nutrient enrichment (Reid et al. 1958). Seasonal periodicity is evident when water temperature is averaged for the area of the eddy as a whole: August-October is generally warmest and January-April coolest (Anonymous 1963). The area contains a scatter of islands which provide substantial shoal grounds, regarded off Oregon to be areas best suited for *E. pacifica* (Smiles and Pearcy 1971). Such islands also provide topography for the formation of downstream eddies which are enrichment centers (Uda and Ishino 1958). They also serve as centers of upwelling. Here, upwelling is less dependent on the direction of the wind than on its intensity. However, the coast from Point Conception eastward remains the main focus of upwelling during the period of prevailing northwest winds, February-June. According to the indices derived by Bakun from extrapolated atmospheric pressure gradients at the sea surface, upwelling off southern California is the most intense to be found in the California Current.

For this initial life-history study, the period chosen (1953-56) was one of generally stable oceanic climate and hydrographic conditions, compared with the years immediately following, which included times of more extreme fluctuations in temperature and flow characteristics. During 2 of the 4 yr, 1955 and 1956, upwelling was inferred by Bakun (1973) to be more intense than the 1946-71 mean; however, during 1954 it was less, and during 1953 upwelling commenced early but barely achieved the June peak of mean intensity and was greatly diminished in the summer months.

Thus it was anticipated that the study period would yield observations of low annual variability in the population of *E. pacifica*, thereby providing a baseline against which eventually to measure events in years of known extremes in ocean climate, e.g., 1957-59 (Brinton 1960).

Previous Investigations

In addition to the observations on the life history of *E. pacifica* (Nemoto 1957; Ponomareva 1963; Smiles and Pearcy 1971), aspects of the energy budget and physiology of this species have been studied. Lasker (1964, 1966) measured moulting frequency, feeding rates, respiration and carbon utilization by specimens maintained in the laboratory, and observed growth rate in juveniles and adults. Fowler et al. (1971) considered effects of temperature and size on moulting. Small et al. (1966) measured respiration at different temperatures and discussed energy flow, while Small (1967) further examined energy flow. Paranjape (1967) made observations on moulting and respiration. Aspects of depth-habitat and pressure in relation to respiration were considered by Small and Hebard (1967), Pearcy and Small (1968), and Childress (1971). Gilfillan (1972) studied oxygen uptake in relation to laboratory controlled temperatures and salinities.

Total oocytes in a large female were counted by Ponomareva (1963). Clutch size estimates and the vertical distribution of different age groups were given in Brinton (1962b and 1967a, respectively).

Limitations of the Study

Understanding the population biology of an oceanic species depends in large part upon the extent to which a representative part of the population can be representatively sampled. In the planktonic environment, currents not only tend to transport the organisms across an observer's horizon, but also cause relative horizontal displacement of life stages because, in many species, the various stages of development live at different depths and experience different horizontal transport. This is true of euphausiids. Species undergoing both ontogenetic and daily vertical migrations, such as *E. pacifica*, are further subject to differential horizontal transport. Thus, water movement is a variable which complicates any plan for temporal continuity in sampling a population. The area covered and the time spent in carrying out an assessment of a population does not need to be great if the waters are restricted geographically and if growth and development of the population is measurable between successive assessments. Clearly, a gyre of circulation, such as the eddy lying off southern California, may be expected to harbor elements of a population that persists locally. This study area has proven practical in size according to the logistics of CalCOFI.

MATERIALS AND METHODS

Samples were obtained by oblique tows, 0-140 m depth (except where the water was shallower), using the CalCOFI standard net, 1-m mouth diameter and 0.55-mm mesh width (Ahlstrom 1948). The mesh width of the cod end and of a 40-cm section in front of it was 0.25 mm. The volume of water strained through a net was determined with a TSK (Tsurumi-Seiki Kosakusho) flowmeter.[2] Most volumes were in the range of 300-400 m^3. The net was towed at about 75 cm/s. The 1953-56 cruises provided month-to-month data, including more frequent surveys off southern California in late 1955 (four in September, three in November). Station positions and collecting data together with displacement volumes of the plankton samples are from annual listings of CalCOFI plankton sampling 1953-56 (South Pacific Fishery Investigations 1954, 1955, 1956; Thrailkill 1957).

Specimens smaller than 3 mm in length are able to pass through the meshes of the net and therefore were not representatively sampled. Smaller specimens (2 mm) are nevertheless retained by the fine meshes of the cod end of the net and counts of these are included as indicative of the presence of the small calyptopis larvae. Free floating eggs of *E. pacifica* are not retained by this net. Estimates of egg production are derived from examination of the ripe females sampled, as described in the discussion of fecundity below.

A total of 819 samples from 48 cruises, 5301 (January 1953) through 5612 (December 1956), were examined (Figure 4d). Only nighttime samples were used since juveniles and adults are not representatively sampled in the daytime, owing to vertical migration and avoidance of the net (Brinton 1967a). Between 7 and 43 nighttime samples were collected in the study area during each cruise. "Night" was considered to be the period from 1 h after sunset to 1 h before sunrise. A few sunrise and sunset samples were analysed if they were collected under overcast skies. A sample marginal to, but outside of, the area was studied when such a sample was from a locality nearer to the closest boundary of the area than any of the

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

sampled localities within the area. Thus, some samples from station lines 77 (northern) and 97 (southern), or designated 80.80 (western), were occasionally used.

The samples were examined in the following manner. An aliquot containing 100-200 *E. pacifica* was counted; the specimens were measured to the nearest millimeter of body length (tip of frontal plate to tip of telson); adults were sexed; and the degree to which the reproductive products were developed was recorded. If, for adults (specimens >10.5 mm in length), the initial aliquot contained fewer than three specimens of any particular length, a second aliquot of equal size was examined for specimens of that size or larger. In this way, increasingly large fractions of the sample were examined for specimens of those length intervals which were progressively determined to be fewest in the sample. This procedure made it possible to count the rarer, large specimens with a degree of accuracy comparable with that to which the consistently more abundant small specimens were counted. Usually, the entire sample was examined for specimens of more than 14-mm body length. This procedure was facilitated by the use of the Folsom plankton splitter which, through successive splitting operations, provides aliquots of ½, ¼, ⅛, . . . $1/n$. All counts were standardized for 1,000 m^3 of water strained by the net.

After standardization, the counts for a sample (station) were weighted according to the proportion of the survey area represented by that station. When the nearest area surrounding the station was equal to a 65×65 km square (a usual spacing for CalCOFI stations), the weighting factor was 1.0. When areas represented by stations were greater or less than 65×65 km, weighting factors were proportionally greater or less than 1.0. The study area was equal to 19 65×65 km squares. Therefore the sum of the weighted abundances (for each size of *E. pacifica*) was divided by 19, providing a mean standardized abundance for the area for the given survey. (The night stations were not at the same localities on each cruise, though tracks followed by the vessels were generally repeated. Furthermore, as is to be expected, clusters of day stations tend to alternate with clusters of night stations. Unsampled parts of the area are expected to be better represented by samples from stations nearest to that unsampled part than by samples from more distant localities.)

Females were classified as 1) with ripe eggs (Mauchline's [1968] egg phase IV) and with attached spermatophore, 2) with ripe eggs and no spermatophore, 3) with ripening eggs (approx. Mauchline's phase II), or 4) ovary weakly developed. Adult males were categorized as 1) with ripe spermatophores, either protruding or internal, or 2) without ripe spermatophores.

Biomass was calculated using abundance at each body length (1-mm increment). Values are in terms of wet displacement volume (wet weight) of *E. pacifica*, given per body length increment in Miller (1966). The following conversion factors from Lasker (1966) may be applied:

Dry weight	= 17.2% of wet weight
Carbon	= 42 ± 1.7% of dry weight
Carbon	= 7.2% of wet weight

RESULTS

Southern California Eddy in Relation to the Rest of the California Current

October 1955 data (cruise 5510) illustrated characteristics of flow and temperature in the current, and occurrences of *E. pacifica* larvae (Figure 1a-c). These were general to fall-winter 1953-56 and placed the southern California area in broader geographical perspective. At that time the landward portion of the current, slow and cool, supported five centers of recruitment of *E. pacifica* (Figure 1c): 1) off San Francisco, probably related to the September peak off Oregon obsrved by Smiles and Pearcy (1971), 2) north of Point Conception, 3) southern California, 4) Point Colnett (lat. 31°N), and 5) Point Canoas (lat. 29°N). The three centers off California were then associated with current reversals while the two centers off Baja California were places where upwelling was conspicuous. A Punta Eugenia center, farther south (lat. 27°-28°N), usually supports *E. pacifica* earlier, during the local peak of spring coastal upwelling, May-June.

Direction and intensity of coastal flow tends to vary on a seasonal basis. During cruise 5510 and through ensuing fall and winter months, coastal currents off California provided means of northerly transport for portions of southern populations. During spring and summer, intensified southerly currents off northern California are expected to bring elements of the northern population into the southern California area via the offshore route west of Point Conception, diverting shoreward near lat. 32°N.

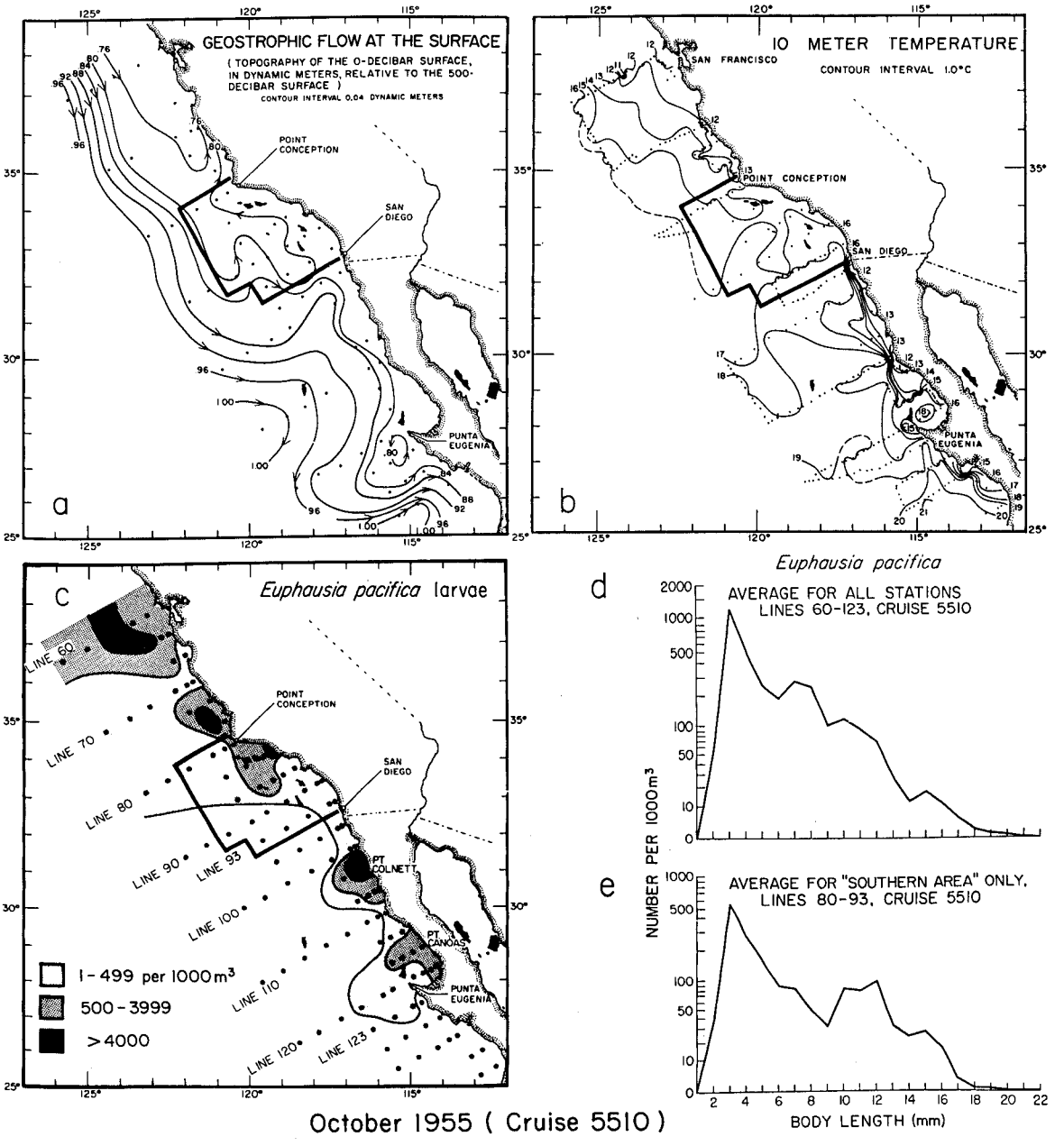

FIGURE 1.–October 1955 data (cruise 5510). **a**, Surface streamlines showing areas of current reversals off California and **b**, 10-m temperatures indicating upwelling centers along Baja California, both associated with **c**, aggregations of *Euphausia pacifica* larvae. Length-frequency distributions of *E. pacifica* are averages for **d**, all nighttime stations and **e**, stations within southern California area.

The length-frequency (L-F) diagram for *E. pacifica* in the California Current as a whole (cruise 5510) shows four modes present in the overall population: 3-4 mm (larvae), 7-8 mm, 10-12 mm, and 15-16 mm (Figure 1d). Time progressions in such modes are used below to estimate population development, including growth and mortality. The southern California part of the population is characterized by small (10-12 mm) and large adults (15-16 mm). It will be shown below that each of these two October 1955 modes is distinguishable within a month-to-month L-F sequence of cohort

development; the 10-12 mm group, most characteristic of the southern California area in Figure 1e, was of a cohort which remained locally dominant from its inception in July 1955 until January 1956.

The 7-8, 9-12, and 15-16 mm modes are described below as being common to *E. pacifica* because they are at body lengths at which life-phase changes and growth slows; therefore frequencies of those sizes increase, particularly during fall-winter periods of reduced food supply.

L-F curves for individual stations show the clear 7-8 mm mode along an "offshore" north-south track (Figure 2a, c) in the axis of the fastest part of the current (Figure 1a). It dominates the 9-10 mm mode as the transect, following the steamlines, angles shoreward along the southern edge of the southern California area, until lat. 35.5°N (station 97.50) where the 7-8 mm mode becomes inconspicuous and the 9-10 mm mode assumes dominance. Thus offshore, where southerly population transport would be expected on the basis of the observed current, dissipation of the L-F characteristic of the northern population takes place along the western limit of the study area. This is considered evidence that such transport then contributed little to the area's population, relative to more nearshore, local contributions.

Individual stations along a "nearshore" north-south transect (Figure 2b) showed a dense heterogeneous population of *E. pacifica* off San Francisco (station 63.55, lat. 37°N). Off central California (stations 70.55, 77.55), 7-8 mm juveniles became conspicuous (cf. Figure 3). Farther south, particularly in the southern California area (stations 83.51-90.28), 7-10 mm individuals were much reduced in numbers, while the frequency of the 11-12 mm size increased, appearing as a clear L-F mode. In October, larvae were few off northernmost Baja California where oceanic water typically moves eastware compressing shoreward the faunistic connection of the southern California area to more southern upwelling centers. To the south along the Mexican coast, the 11-12 mm mode characteristic of the study area reappeared, coincident with areas of production of larvae. Farthest south (off Punta Eugenia; stations 120.45, 123.40), modes were at 9-10 mm and at 3-mm larvae. These 9-10 mm specimens may be poorly nourished individuals, corresponding in age to 11-12 mm individuals occupying the area immediately to the north—an area which appears relatively fertile with respect to production of larvae. The same relationship was observed locally off northernmost Baja California; there the population having a 9-10 mm mode included few larvae (Figure 1c) and occupied an easterly incursion of oceanic water (Figure 1a), being bounded on the north and south by cooler and presumably more fertile areas in which both 11-12 mm and larval modes were again conspicuous.

At this time (October 1955) the range of *E. pacifica* terminated near Punta Eugenia, but it can extend to lat. 23°S (Brinton 1967b). These far downstream parts of the population appear reproductive, but to the south of southern California they are impermanent (Brinton 1967b, 1973). Mature or maturing individuals are expected to be intermittently injected from the north, particularly during the March-June period when southerly flow is intensified. These individuals may find local places of refuge in cool, slowly moving, productive coastal waters from Point Conception southward in association with upwelling centers. The southern California eddy is the largest such refuge, serving also as a major population center which has both coastal and oceanic dimensions.

Spawning and Recruitment

Spawning intensity was estimated indirectly since free-floating eggs were not sampled. Females bearing ripe eggs provided a means of estimating incipient spawning. All females having an attached spermatophore also carried ripe eggs in the ovary. From the several thousands of these counted, 373 of different body lengths were examined with respect to number of ripe eggs carried. The relationship between body length and mean number of ripe eggs was linear between 11 and 20 mm length (means were encompassed by 95% confidence limits of regression line), with the mean number of eggs extending from 20 to 212 across this range (Figure 3). Disproportionately small numbers of eggs were observed in the largest (>20 mm) females. Mean values for each body length were applied to the numbers of each length of ripe female counted in the plankton samples to estimate the spawning potential for each sampling period. These are underestimates since, for 60% of the surveys, the predicted values are not high enough to have produced the density of larvae found at the time of the next survey—even presuming only 50% mortality between surveys (Figure 4c). Evidently some eggs

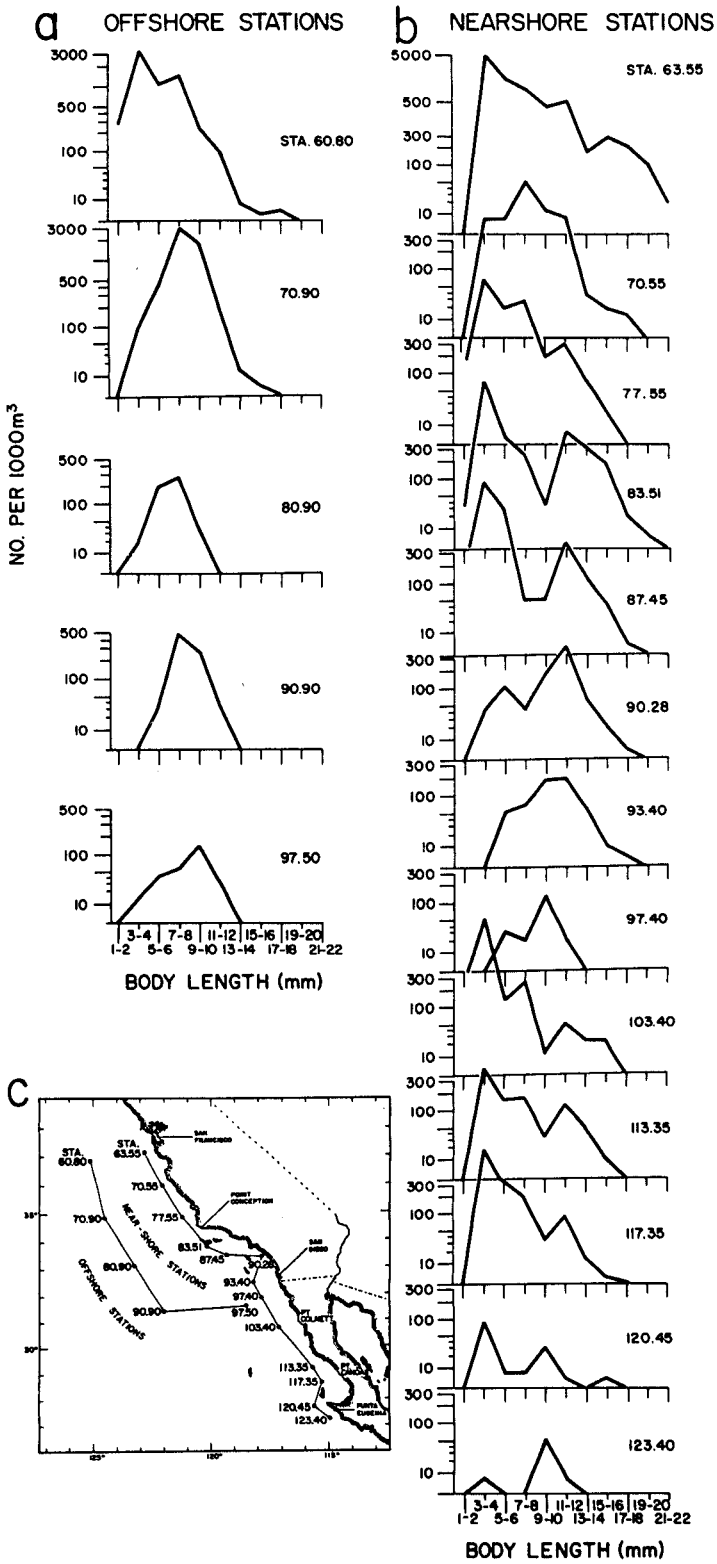

FIGURE 2.—Length-frequency distribution of *Euphausia pacifica* along north-south axes of California Current (cruise 5510). a, Approximately 250 km offshore; b, <100 km offshore; c, positions of stations.

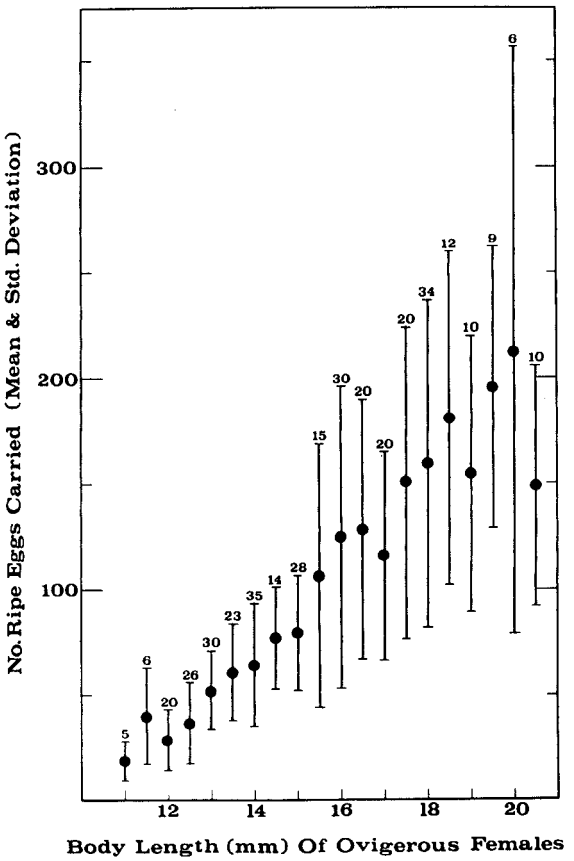

FIGURE 3.–Number of mature eggs in ripe spermatophore-bearing *Euphausia pacifica* in relation to body length. Numbers of individuals examined are indicated.

found to be immature at time of counting, either in ripe or other females, mature in time to contribute to the monthly spawn. The egg estimates are therefore regarded as only relative, month to month.

The production of eggs and larvae in each year (Figure 4c) was considered in relation to four parameters: 1) annual upwelling cycle in the southern California area inferred from atmospheric parameters (Figure 4a) and from minimum water temperatures (Figure 4b), 2) size structure of the spawning stock (Figure 4d), 3) zooplankton biomass (Figure 5a), and 4) *E. pacifica* biomass (Figure 5b).

1953

Upwelling began early (February, cruise 5302) with above-average intensity, accompanied by spawning in February and April. The February spawn, mainly by females of medium length (12.6-16.5 mm), led to discernable recruitment of larvae in March. The April spawn, mainly by large females (16.6-21.5 mm) led to the year's maximum recruitment in May-June. Upwelling peaked in June, and diminished to an unseasonably low intensity thereafter (Figure 4a), accompanied by local variability in water temperature through October (Figure 4b).

Substantial egg production during June-August, by medium-sized and small (10.6-12.5 mm) spawners, led to less recruitment than in April when spawning was of similar intensity. April was the start of the general spring zooplankton bloom (Figure 5a), presumably a response to the greater availability of phytoplankton food in the spring. Spawning diminished after August although larvae were evident in September and November. Small females became predominant after September when they became important contributors to the production of eggs.

These estimates of relative spawning are supported by a consistent relationship of egg peaks to larva peaks. Three of the four egg peaks in 1953 were followed by larva peaks a month later. Under conditions of laboratory hatching and rearing, euphausiids live as larvae for about 29 days (Gopalakrishnan 1973).

1954

Upwelling commenced in March (Figure 4a), a month later than in 1953. Local temperature minima, however, showed that this process was not obvious until April (Figure 4b). By both criteria, spring upwelling in 1954 was the least intense to be observed during 1953-56. (According to Bakun (1973), it was the least observed during 1953-71, though substantially greater than during 1947-52.) Production of eggs was initiated in March, evidently by a stock of large females derived from the September 1953 recruitment (see sections on growth and survival below, and Figure 9). Recruitment became intense only during June-July, associated with the one peak in spawning observed during 1954.

1955

As in 1954, upwelling started in March (following Bakun 1973, Figure 4a) or in April (using temperature minima, Figure 4b). There was a gradual increase in egg production begin-

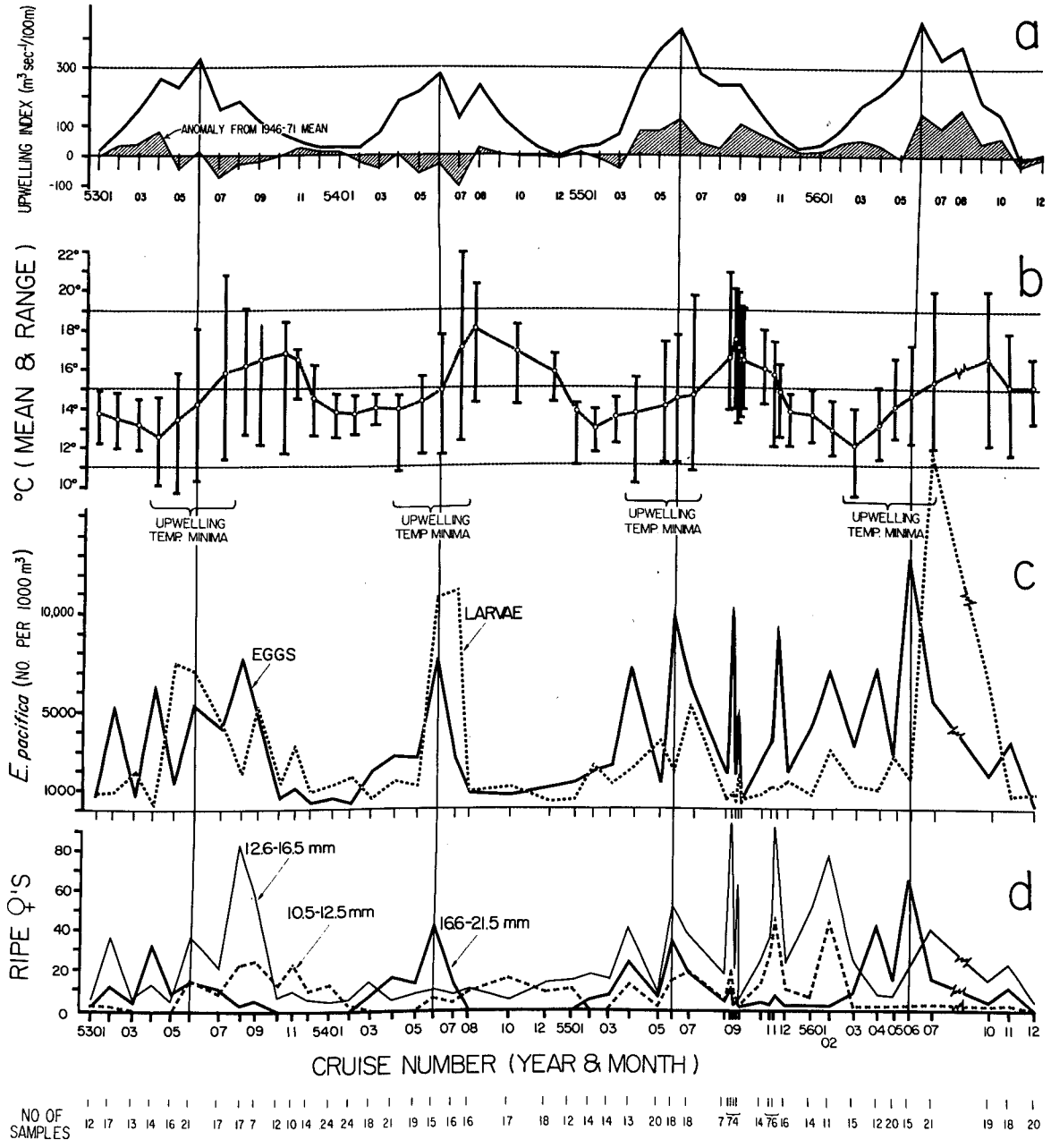

FIGURE 4.—**a**, Inferred monthly index of upwelling intensity per 100 m of southern California coastline, 1953-56 (from Bakun 1973). **b**, Temperature range and mean, by cruise, in study area. **c**, Estimated densities of ripe eggs and <4.5 mm larvae of *Euphausia pacifica* in area. **d**, Densities of ripe females, three body-length groups. Number of samples examined are indicated by cruise.

ning in December 1954, and the first significant recruitment was in February (cruise 5502). This increase in spawning continued through March, but recruitment did not increase markedly until May, following an April egg maximum. Thereafter egg production peaked in alternate months, June (the annual upwelling maximum), September, and November—but recruitment was generally low (<2,500 larvae/1,000 m³ in the area) except during May and July. July yielded the year's peak in

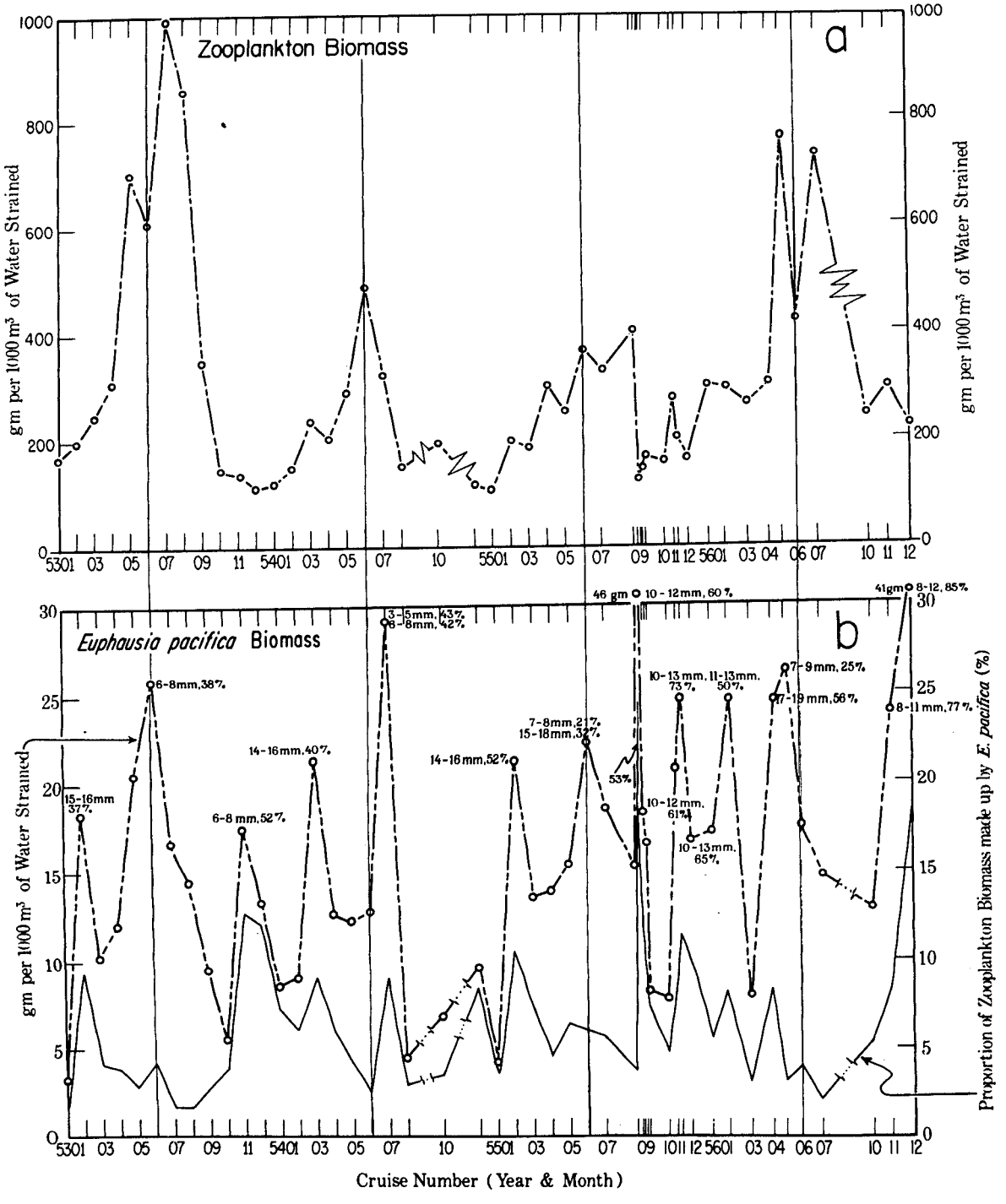

FIGURE 5.—Mean biomass, by cruise, of a, zooplankton in southern California area, based on same samples examined for euphausiids; and b, biomass of *Euphausia pacifica* and its proportion of zooplankton biomass, with dominant body lengths indicated.

larvae. Large and medium-sized spawners were substantial contributors to this recruitment. The latter were predominant and continued to be throughout 1955. This differed from 1953, 1954, and 1956 when small or large spawners were predominant during at least part of the year.

In September a brief increase in larvae closely followed the year's peak in potential egg production, as observed during four September cruises closely spaced in time. This was at the time of maximum water temperatures (Figure 4b). The November peak in eggs, to which small spawning females contributed importantly for the only time in 1955, led to a slight increase in recruitment in December. This November activity was associated with residual upwelling that was significantly more intense than the 20-yr November mean.

1956

Upwelling began early in February as in 1953. February spawning was also high, as in 1953 and differing from 1954-55. Spawners were small and medium-sized females (Figure 4d). Larvae peaked during the same month. Following a March decline in eggs and larvae, April spawning returned to the February level associated with the usual spring appearance of large spawners. This egg maximum was followed in May by a small peak in larvae. In June, egg production reached a peak for the 4-yr period (13,000 eggs/1,000 m^3) at the same time as a 4-yr peak in the upwelling index which, however, was not confirmed by the observed temperature minima (Figure 4a, b). In July 1956, larvae showed strong survival from the June spawn with a density of 17,000/1,000 m^3. While the upwelling index continued to be well above average through August, CalCOFI sampling did not resume until October. Therefore, August-September recruitment was not recorded. High numbers of larvae observed from 28 September to 5 October (5,000/1,000 m^3) together with record numbers of 8-11 mm juveniles appearing in November-December (Figure 10) indicated that August-September spawning was heavy and greater than the substantial August-September spawn of 1953.

An increase in egg production in November 1956 resulted in little recruitment in December, after upwelling had stopped. An explanation may be inferred from the fact that, though zooplankton biomass had peaked earlier (May-July, 5505-07), the euphausiid part of the biomass became extremely high (24-41 g/1,000 m^3) only in November-December, consisting largely of 8-12 mm juveniles and young adults (Figure 5b). *Euphausia pacifica* then made up a larger proportion than ever before of the total biomass (15-20%), indicating a diminished amount of organisms of other taxa, such as salps and copepods. These, like larval euphausiids, depend heavily upon primary production for food. Their reduced numbers suggest diminished phytoplankton food (unless their mortality was not food related), hence the poor December survival of *E. pacifica* larvae emerging from the November spawn. Additional evidence of diminished food in November-December will be seen in the negligible rate of growth during November-December of the massive population of 8-12 mm *E. pacifica*. Alternatively, this population may have consumed the November larvae as well as their food, but this presumption is not supported by its low growth rate.

Recruitment Efficiency and Spatial Aggregation of Eggs

The relationship of spawning potential (density of ripe eggs) to larvae subsequently recruited is irregular, although a trend (Figure 6) indicated that efficiency of recruitment from available eggs was better during spring and summer (March-September) than during fall and winter (October-February). In 1953 the spring-summer peaks in

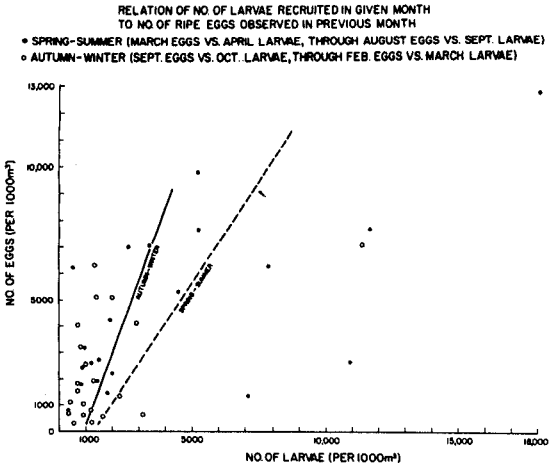

FIGURE 6.—Density of <4.5 mm *Euphausia pacifica* larvae in given month in relation to ripe unspawned eggs observed previous month, 1953-56 data. Regressions (Bartlett's test) for spring-summer (March-September) and autumn-winter (October-February) data are not significantly different.

egg production were followed by proportionately high peaks in larvae, relative to 1955 and early 1956 (January-April) (Figure 4c). Both the one peak in eggs in 1954 (June) and the highest peak in 1956 (June) led to particularly heavy recruitment.

Incipient spawners and larvae were both unevenly distributed in the study area, the larvae usually more patchy than the spawners (Brinton and Wyllie in press). A possible effect of relative aggregation of spawners on recruitment was considered. A monthly index of survival of newly hatched larvae was determined as the ratio of the mean density of larvae observed on a given cruise to the density of ripe eggs calculated for the previous month—usually one cruise earlier. (As noted above, this ratio is >1.0 in about one-third of the instances, indicating that spawning is underestimated. The indices are, therefore, regarded only as relative to each other.) Cruise-to-cruise differences in patchiness of spawners were estimated by comparing, among cruises, variances of number of ripe eggs carried by incipient spawners. Each variance was derived by use of numbers from all stations of a cruise. The regression of patchiness in relation to survival of calyptopis larvae showed a slope not significantly different from zero (Figure 7). Evidently, differences in the degree of aggregation of spawners on the scale observed (32-64 km between stations) did not affect survival of newly hatched larvae.

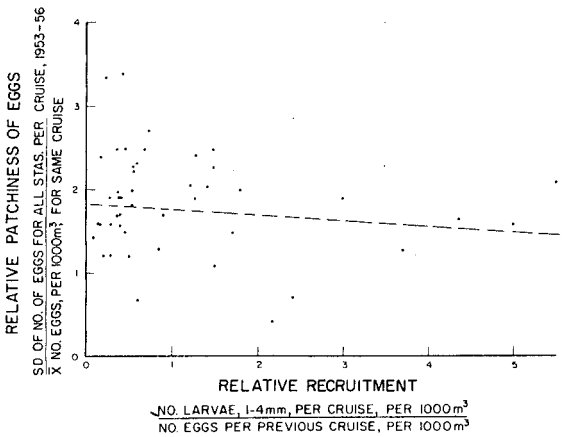

FIGURE 7.—Index of patchiness of ripe unspawned eggs of *Euphausia pacifica* in relation to index of recruitment during succeeding month. Slope of regression not significantly different from 0 ($P>0.05$, t-test). Standard deviation is used as a measure of dispersion and in no way assumes normality of the data.

Temperature Relationships of Spawners and Larvae

Abundances of spawners and recently hatched larvae (calyptopes of <2.5 mm) were plotted in relation to ambient temperature at 10 m depth (Figure 8). A relationship of spring-summer upwelling to maxima in reproduction, however indirect, was evident in foregoing observations. Therefore, data for the months of strong upwelling (April-July) are separated from those of the other months.

Both spawners and larvae occurred across a range 10°-21.6°C, virtually the available range. When lumped by 0.5°C increments, close to 40% of the stations yielded some calyptopis larvae and 40% yielded incipient spawners. During August-March (Figure 10a) larvae were most concentrated within the range of 12°-16.5°C, the same as the spawners. There, mean densities of larvae were 50-200/1,000 m³. During April-July (Figure 8b), maximum densities of larvae, 200-7,000/1,000 m³,

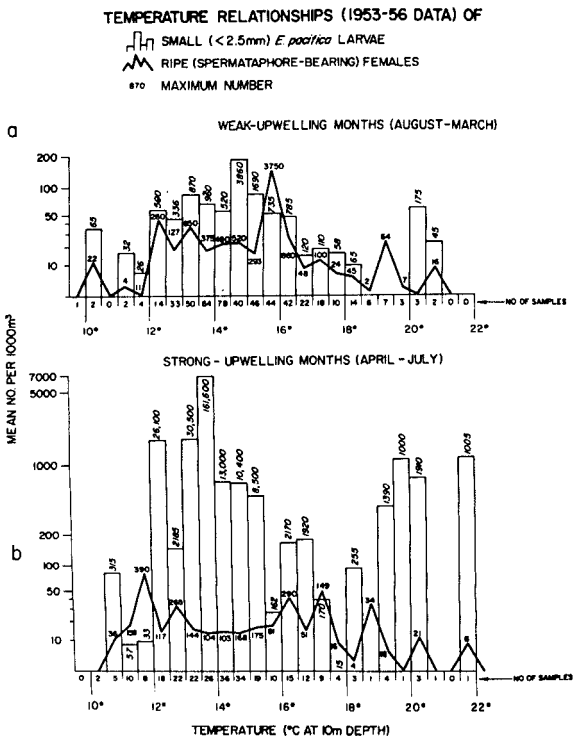

FIGURE 8.—Densities of *Euphausia pacifica* larvae <2.5 mm length and ripe females in relation to water temperature at 10 m depth. a, August-March; b, April-July.

were within a somewhat narrow range of temperature, 12°-15.5°C, as compared with the weak-upwelling period, and most spawners were within a broader range, 11.5°-17.5°C.

By years, during 1953, 1955, and 1956 the mean maxima of larvae were at 14°-15°C. In 1954 there were maxima at both 13°-14°C and 14.5°-16°C. Occurrences of larvae and spawners at temperatures >18.5°C during January-March and August-December were only during 1955, the year in which spawning extended on into September and November. Occurrences of April-July larvae at temperatures >18°C were all during 1954, the year of weakest upwelling, except for a single record in 1953.

Overall frequency of spawners did not differ between the periods of strong and weak upwelling, in contrast to large differences in the frequency of recruits. This implies that factors other than temperature are important to recruitment—probably the production of food associated with the upwelling period. Patchy local increases in surface nutrients associated with the upwelling season of 1969 are described in the Discussion.

It is also noteworthy that during periods of both strong and weak upwelling, mean maxima of spawners occurred at or just outside the limits of the optimal temperature range for recruits: during weak upwelling months, at 12°-12.5°C and 15.5°-16°C; and during strong upwelling months, at 11.5°-12°C and 17°-17.5°C. This implies that stations showing maximum densities of larvae and those showing maxima of spawners were mutually exclusive—an impression gained earlier during counting. Removal of adults from the region where they might fortuitously feed upon their young could be brought about by the vertical migration of the adults and their consequent differential transport at greater daytime depths, in accordance with the hypothesis of Hardy (1956).

Growth

Monthly L-F polygons for *E. pacifica* consistently peak at larvae 3-4 mm in length (Figures 9, 10). In the stream of continuous recruitment, a month-class is first distinguishable as high numbers of larvae relative to those produced in the months before and after. Subsequent growth can be traced through successive months as an L-F mode, either in the form of a crest, irregularity in slope, or change in height relative to the month before. Observations of growth and survival appear most reliable when cohorts are traced that begin as densities in excess of 2,000 larvae per 1 mm length increment per 1,000 m^3.

A cohort is designated by the year-month (e.g., 5303) in which its larva maximum is observed. Presumed relationships of egg maxima (Figure 4c) to subsequent recruitment are indicated in Figure 12.

When presented in terms of biomass (Figures 9, 10), population composition differs from that indicated by length frequency. For example, biomass modes may increase in height with time owing to growth, while corresponding L-F modes decrease in height because of mortality. As a consequence, cohorts are often more conspicuous when plotted as biomass. Biomass is plotted on a linear scale while abundances (length frequency) were plotted on a logarithmic scale to accommodate fluctuations in the many larvae and the few large adults. The biomass of larvae was generally low but periods of heavy recruitment are conspicuous.

1953 Cohorts

A small February 1953 cohort (Figures 9, 12) was tentatively traced through April as 10-11 mm adolescents. More substantial recruitment occurred in March from the February egg maximum, followed by little recruitment in April; growth appears to have been to 7-8 mm in April, 10 mm in May, 13 mm in June, 15-17 mm in July, 18 mm in August, and 18-19 mm in September.

Production of larvae first became intense during May-July 1953 (cuises 5305-5307), resulting in a broad mode recognizable as 3-7 mm in June (enclosed by a pair of dashed lines in Figure 11, one originating at 3 mm in May and the other at 3 mm in June). July larvae appeared to show poor survival, as shown in the reduced 5-7 mm component of the population in August. This is interpreted as leading to graphic separation of the May-June cohort as a conspicuous L-F mode, first observed in August (5308) as 8-13 mm juveniles and young adults (Figures 9, 11a), persisting into September at 12-15 mm, and perhaps surviving without growth into October, though decimated. Development of this cohort is even more conspicuous through the sequence of biomass modes.

An increase in recruitment in September (5309) over August, followed by low production in October, yielded a particularly conspicuous cohort

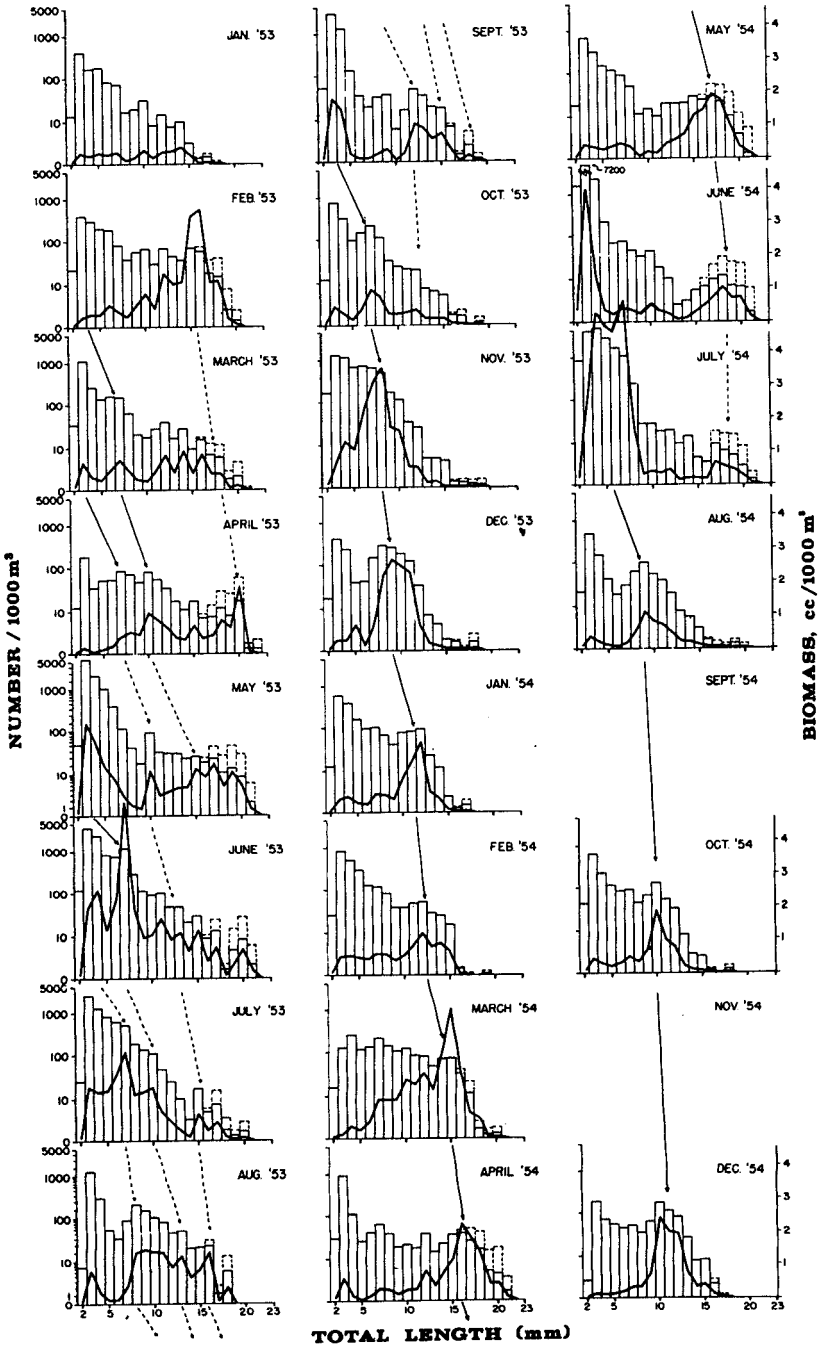

FIGURE 9.—Length-frequency (histograms) and biomass (line graphs) distributions, of *Euphausia pacifica*, 1953-54 cruises. Dotted boxes appended to histograms for body lengths 16-21 mm are corrections for net avoidance using Isaacs' (1965) factors derived for anchovy larvae of those sizes. Corrections are not applied to biomass. Arrows trace development of cohorts. Solid arrows trace sequences considered clear, dashed arrows trace those less clear.

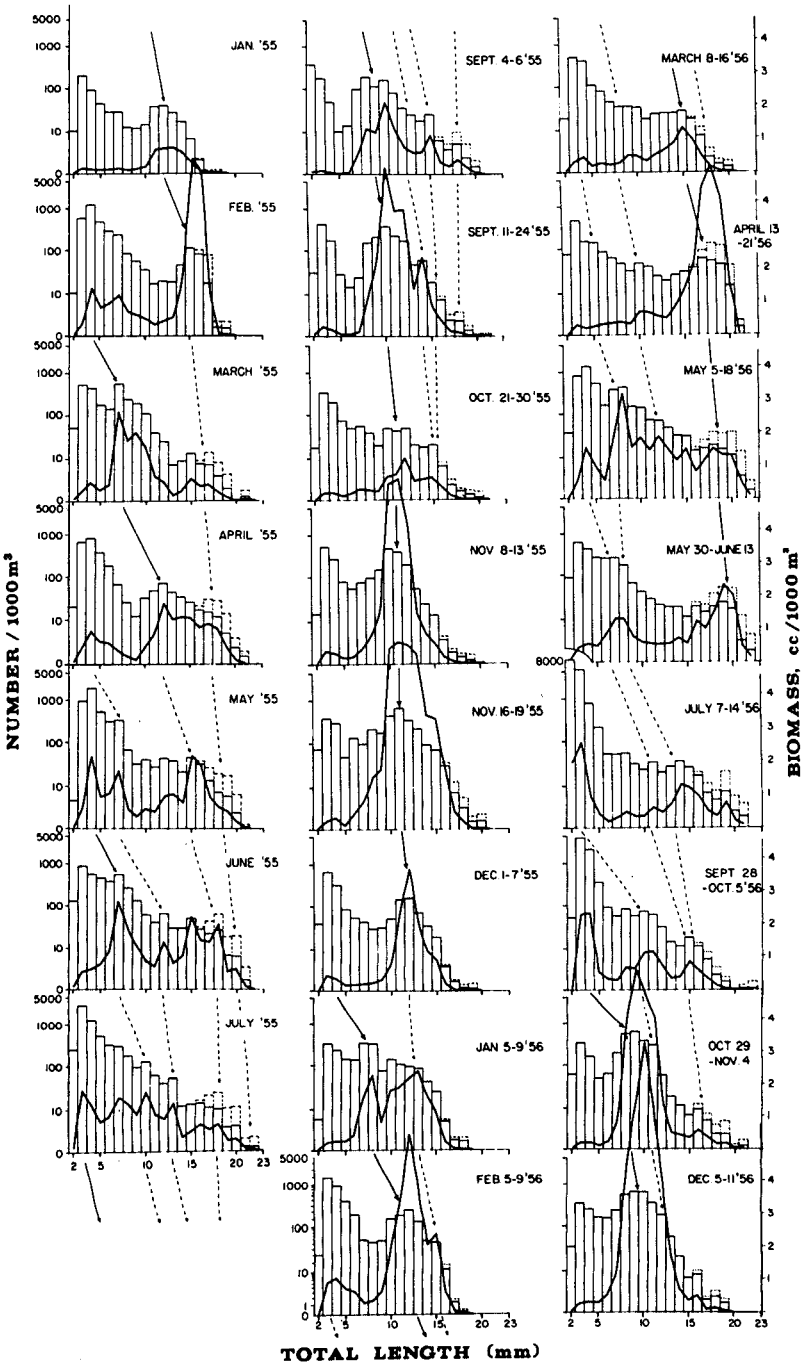

FIGURE 10.—Length-frequency (histograms) and biomass (line graphs) distributions, of *Euphausia pacifica*, 1955-56 cruises. Dotted boxes appended to histograms for body lengths 16-21 mm are corrections for net avoidance using Isaacs' (1965) factors derived for anchovy larvae of those sizes. Corrections are not applied to biomass. Arrows trace development of cohorts. Solid arrows trace sequences considered clear, dashed arrows trace those less clear.

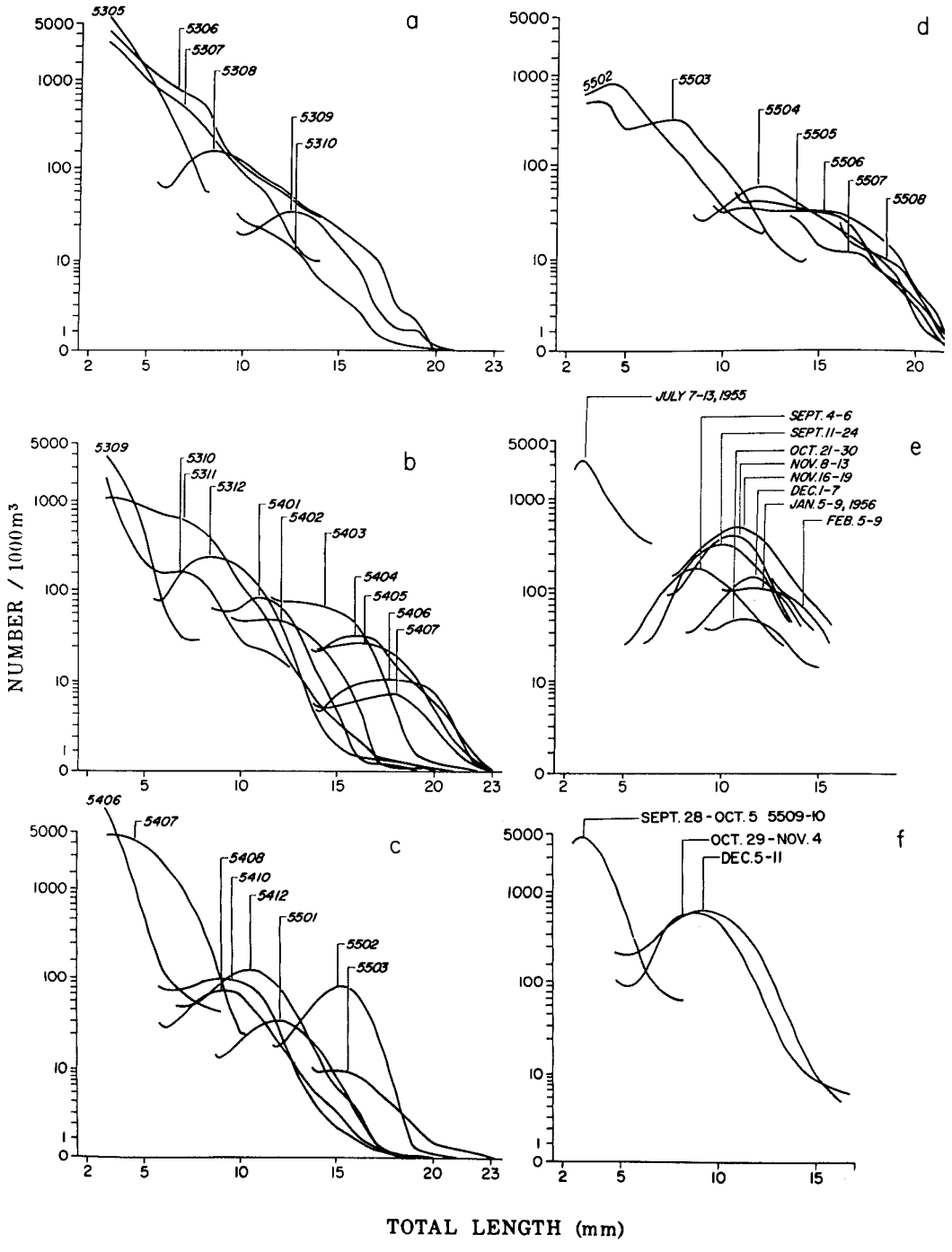

FIGURE 11.–Cohort development of *Euphausia pacifica*, shown as progressions of length-frequency modes. Curves are three-point running averages of portions of histograms in Figures 9 and 10. Cohort is identified by date (cruise) at appearance of conspicuous mode of 2-3 mm larvae. **a**, 5305; **b**, 5309; **c**, 5406; **d**, 5502; **e**, 5505; **f**, 5509-10.

traceable for 10 mo through July 1954 (5407) when it had achieved large-adult size, 17-20 mm (Figures 9, 11b, 12). Separate L-F curves for males and females (Figure 13), commencing at the onset of maturity ca. 11 mm, show that the modes for the 5309 cohort illustrated in Figures 9 and 11b actually are made up of paired overlapping peaks, for females regularly at a larger body-length increment by about 1 mm and for males where the difference in absolute frequency between males and females is greatest.

It is not likely that females, upon maturity, have undergone sudden, relatively rapid growth so as to exceed males in size. The curves (Figure 13) show larger females to be at a relatively greater frequency than males and the converse would be expected with increased female growth-rate. (Average male/female ratio is probably 1:1 at onset of adulthood, discussed under Sex Ratio.) Rather, the most mature females—those at the leading edge of the mode-cohort at the onset of February-March breeding—are growing slower than before, thereby appearing more numerous. At the same time, decreasing relative male survivorship could contribute to the increasing inequality in sex ratio. At body lengths >16 mm, females tend to dominate by 2:1 or more, indicating that they then spend twice as long as males at given sizes, at least while breeding, or that their survivorship is then greater, or that males remain below sampling depths at night. These alternatives are considered in the discussion of Sex Ratio, below.

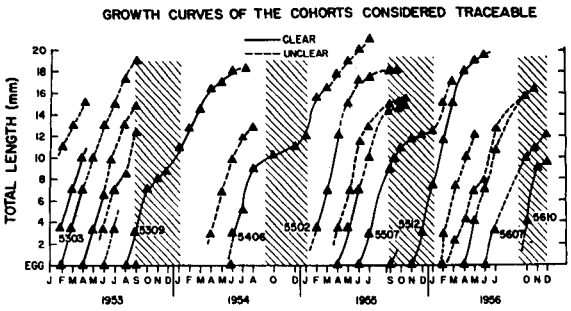

FIGURE 12.—Growth curves of *Euphausia pacifica* inferred from length-frequency modes. Clear (solid lines) and unclear (dashed lines) sequences as in Figures 9 and 10. Times of egg production are extrapolated, see Figure 4c. Fall-winter period of slowed growth is crosshatched.

1954 Cohorts

The single intense spawn of 1954 (June) led to strong June-July recruitment, establishing a cohort (5406) that was followed through a 10-mo period to 17-19 mm in April 1955 and, with less certainty, to 20 mm in June (Figures 9, 10, 11c, 13).

1955 Cohorts

Conspicuous 1955 cohorts arose in February (5502) and July (5507). The former appeared to attain 18 mm after 7 mo (September) and the latter reached 17-18 mm after 8 mo, following slowed growth during October-January (Figures 11d-e, 12). This cohort appeared at too-low density in October (5510) relative to a month later. This may be due either to sampling variability or to "piling up" at the 11-12 mm increment in November owing to growth being faster into the newly adult phase than out of it, energy then being diverted to gonad development. Nevertheless, it is noteworthy that the 5502 and 5507 cohorts appeared to be distinguishable in October (5510) as modes of 10-12 mm and 15-16 mm, Figure 1e, discussed earlier when the southern California area was compared with the California Current as a whole.

The December 1955 cohort was the only distinct year-end cohort observed during 1953-56 (Figures 10, 12, 13). It grew rapidly at 4 to 5 mm/mo during December-February and 3 to 4 mm/mo during February-April, apparently attaining 18 to 20 mm length by June 1956.

1956 Cohorts

These were scarcely traceable except for that appearing as 8-11 mm individuals in early November and as 8-12 mm in December. This mode doubtless derives from extremely dense larvae sampled during 5507 and 5509-10, its crest appearing to relate mainly to the latter. The small biomass peak at 10-11 mm during 29 September-5 October is clearly derived from the very heavy July recruitment. It subsequently becomes indistinguishable during November and December from the biomass of 8-12 mm juvenile-adults considered to have grown from 5509-10 larvae. The 29 October -4 November peak appears most likely to have derived from the 5509-10 larvae.

Survivorship

The average L-F distribution for all samples (Figure 14) shows that decline in density with body length is roughly exponential. The decline is

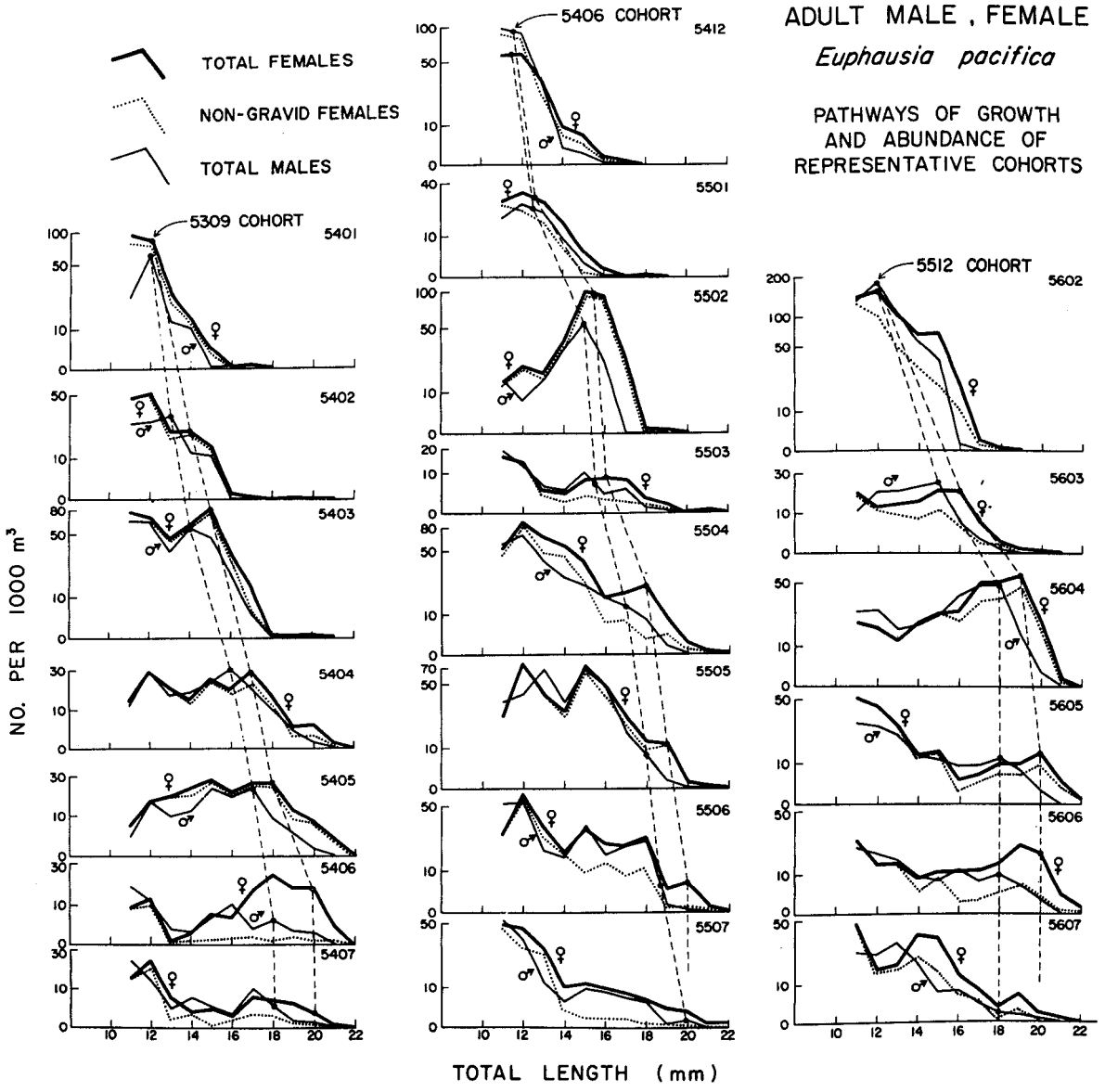

FIGURE 13.–Length-frequencies of adult males and females of *Euphausia pacifica*. Dashed lines trace development in males and females. Frequencies of females without ripe eggs are indicated (pertinent to discussion of Sex Ratio).

rapid during the larval phase and slower thereafter until large adulthood, 18-19 mm. Positive perturbations appear at 6-7 mm, 9-10 mm, and 14-15 mm. Average survivorship is 16% during the 1 mo furcilia larva phase, as seen in the decline in mean population density from 1,850 to 300/1,000 m^3 (Figure 14) between 3 mm and about 6 mm in body length which Boden (1950) has shown to be larval phase. For juveniles, 6 mm through 9 mm, survivorship is near 67%/mo over about 2 mo.

For adolescents and young adults of 9-14 mm, average survivorship remains nearly the same, 64%/mo, then decreasing to 60%/mo through 18 mm. After that, population decline appears rapid, possibly because sampling of such large individuals is not representative. Apparent

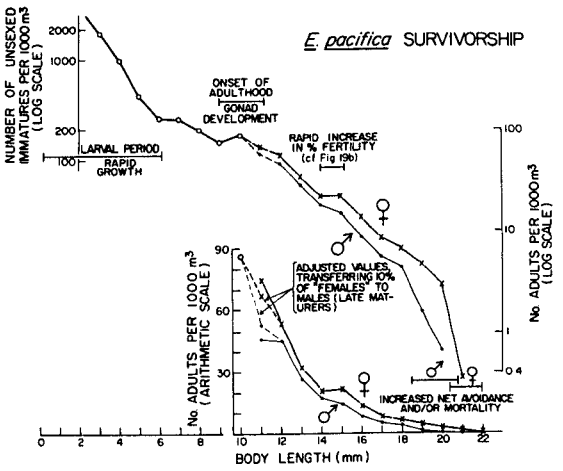

FIGURE 14.–Catch curves for all *Euphausia pacifica* sampled, densities shown on logarithmic and linear (adults only) scales. Periods of changing slope (changing survivorship, net avoidance and/or growth rates) indicated as related to life phases. Scale used for density of sexed adults (right) is doubled for lumped immatures (left).

differences in survivorship between males and females (Figure 14) are discussed below under Sex Ratio.

Survival rates for individual cohorts were approximated from relative amplitudes of month-to-month modes in the sequences used to trace growth (e.g., Figure 11). Percent survivorship plotted against estimated age shows cohort curves to be similar (Figure 15a). A positive change in slope consistently occurs within the range of 8-12 mm body length encompassing adolescence. However, regressions of $\log_{10}$ density on age take two forms:

1) Mean life-span survival rate calculated as a single linear regression for individual cohorts is highest among those recruited during June-December (06-12). For example, it is 51%/mo for the 5512 cohort, 58% for 5610, and 59% for 5309. In such late-year cohorts most of the juvenile-adult phase is during August-March, the period of reduced food and slowed growth. For example, the cohort 5507 attained adolescence (9-10 mm) in September and large adulthood (17 mm) in March (Figure 15b), having an estimated life span of 10 mo. (Egg stage to 3 or 4 mm length is considered the first month.) The cohort 5406 (Figure 15c) attained adolescence at 9 mm in August, appeared to show strong survival through 15-16 mm in February, and was distinguishable at 20 mm size in June–a life span of 13 mo. Thus those cohorts which attained 15-16 mm with densities >50/1,000

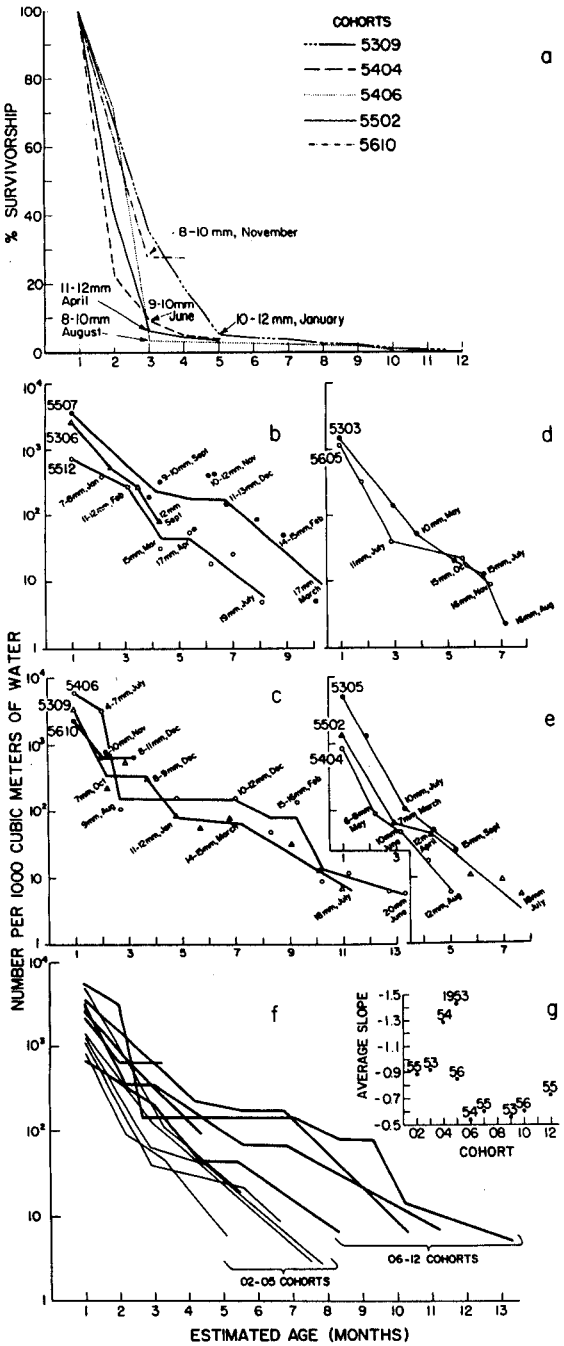

FIGURE 15.–Survivorship of cohorts of *Euphausia pacifica*, from amplitudes of length-frequency modes. **a**, Percent survivorship showing rapid decline until adolescence, ca. 9-11 mm. **b**, **c**, Age-frequency distributions of 06-12 cohorts smoothed for apparent piling up at times of slowed growth. **d**, **e**, Age-frequency distributions of 02-05 cohorts. **f**, Curves seen in b-e, clustered. **g**, Average slopes (from straight line regressions) for 02-05 cohorts seen as steeper than for 06-12 cohorts.

m³ by February-March continued to be evident on into the spring bloom.

Two exceptionally large cohorts, 5406 and 5507, were initiated during late June-July. At first, these survived poorly, 8-10%/mo for 5406 through August-September and 40%/mo for 5507 through October (Figures 11c, f; 15b, c). Growth apparently then stopped after 9-11 mm body length, and the density had declined to 100/1,000 m³. This took place when the onset of maturity was in September-October. This is presumably the start of the fall-winter period during which food supply is inadequate to permit both gonad development and size increase. During October-December, the 10-12 mm sizes increased in frequency, indicating continuing growth into that range by younger elements of the overall population and much reduced growth out of it. Therefore survivorship of the 5406 and 5507 cohorts during September-December could not be determined, but it appears to have been high. By January, body-length growth of these cohorts, now numerically enhanced, resumed. Survivorship of "5406" prevailed at about 47%/mo through June 1955 (21 mm), and for "5507" at 40%/mo as before September.

The large 5607 and 5610 cohorts appear to have undegone similar development (Figure 10), appearing to coalesce at 9-12 mm during November-December, with much increased frequencies at those body lengths.

2) Survival rate is poorer, 26-45%/mo, for recruits produced earlier in the year, February-June. Mean life-span survival was 43%/mo for the 5303 cohort, 26% for 5305, 37% for 5306, 30% for 5404, 44% for 5502, and 45% for 5605. Nonlinear details of survivorship in these cohorts are depicted in Figure 15d, e, while differences between early-year and late-year cohorts in mean slope of survivorship regressions are seen in Figure 15g. Coincidence of the juvenile-adult phases of early-year cohorts with the productive period May-September evidently accounts for the observed rapid growth during this period, hence the poor survival rate. These cohorts were traced to body lengths of 16-18 mm after 7.5-8 mo (5502, 5303, 5605) or to 13-15 mm after 4-5 mo (5404, 5305). Having declined to densities <10/1,000 m³ during summer-fall, they were no longer recognizable in winter sampling.

Annual Biomass

Annual biomass by body length shows year-to-year similarities (Figure 16). Peaks are at 1) 3-4 mm, owing to consistent abundances of larvae in early furcilia phase; 2) 7 mm (except 1956), the onset of juvenile phase; 3) 10-12 mm (9-11 mm in 1956) the onset of adult phase; and 4) 15 mm, early in the peak reproductive phase. It was noted (Figure 5b) that monthly biomass peaks were usually dominated by one or another of these four body lengths. The larva peak occurs in spite of rapid early growth. The other three peaks are at ages when slowed body-length growth would be

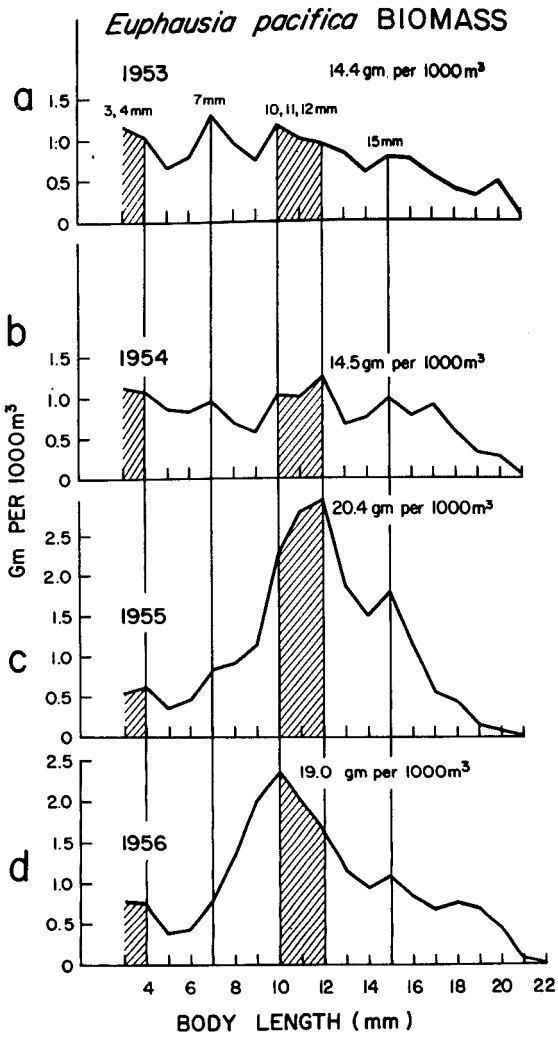

FIGURE 16.—Biomass, annual mean values for *Euphausia pacifica* and distributions per 1 mm body length. **a, b,** Uniform distributions for 1953, 1954, with modes at 3-4 mm, 7 mm (onset of juvenile phase), 10-12 mm (onset of adulthood) and 15-16 mm (start of maximum egg production, cf. Figure 21b). **c, d,** Distributions, strongly peaked at adolescence, biased by large 5507 and 5609-10 cohorts respectively.

expected: onset of juvenile phase, onset of gonad development, and time of maximum gamete production.

Biomass on body-length distribution was most even during 1953 and 1954 (Figure 16a, b). Recruitment in May and September 1953 led to the 7-mm peak of that year, and the September cohort was the main contributor to the 10-12 mm peak. The 1954 crest at 10-12 mm stemmed mainly from October and December sampling of the June 1954 cohort.

In 1955 and 1956, 3-4 mm larvae were reduced in average biomass compared with 1953 and 1954 while biomass of 9-12 mm adolescents was two times greater. The November 1955 stock of 11-12 mm stages (5507 cohort) was mainly responsible for the 1955 biomass peaks. The November-December 1956 stock of 9-11 mm stages (5609-10 cohort) provided much of the 1956 peak.

Large 18-20 mm adults showed their greatest biomass in 1956 following the strong upwelling year 1955, and lowest in 1955 following least productive year 1954.

Monthly changes in biomass are traced for each of three conspicuous sizes (Figure 17). Small (7 mm) juvenile bulk is greatest within May-July following spring recruitment. Other high values for the 7-mm size are not consistent seasonally, occurring during October-March.

Adolescents (10 mm), considered representative of the 9-12 mm juvenile-adult phase change, tend to be at greatest volume during August-January (when the smallest spawners, 10.6-12.5 mm, were also observed to peak, Figure 4d). Increased survivorship and slowed growth during fall-winter maturation of spring cohorts, discussed above, are considered responsible.

Subsequent February-March peaking of biomass at 15-mm size occurs as egg development accelerates. (This is preliminary to the appearance of the large >16.5 mm spawners during April-June, Figure 4d.)

A close relationship is evident (Figure 17) between biomass of each of the three sizes and their percent of the total *E. pacifica* biomass. This indicates that a given month's increase in biomass of the 7-mm size (or of the 10-mm or 15-mm size) is not accompanied by proportionate increase in the composite biomass of all other sizes. Therefore, the periodic peaks in biomass shown in Figure 5b should be largely due to peaks at these or very similar sizes, which was indeed the case.

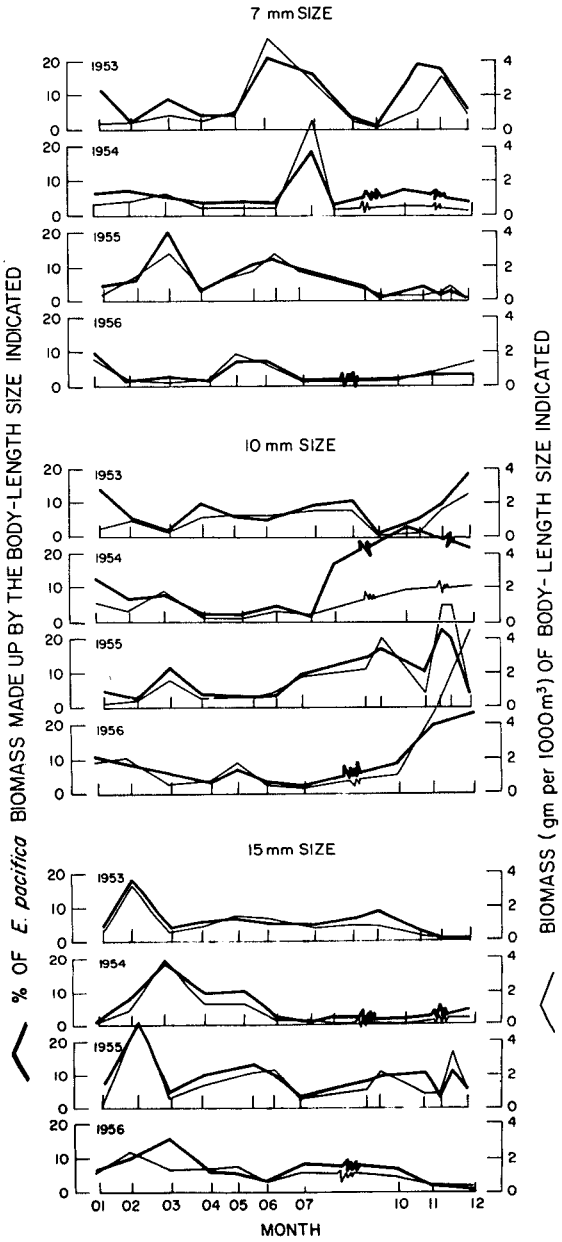

FIGURE 17.—Annual length-biomass modes of *Euphausia pacifica* analyzed by months. The 7-mm size peaks heavily in June-July (May-June in 1956), with other peaks in March and November-January; the 10-mm size peaks September-January; and 15-mm size peaks February or March.

There are variations from this relationship: 1) moderate increase in biomass of 10-mm size during August-December 1954 caused a disproportionately large percent-increase in it—an effect of the single large 1954 cohort (5406-07) developing

unaccompanied by other substantial cohorts (Figure 16b); 2) the converse, when November-December 1955 biomass of 10-mm size (together with 11-12 mm, Figure 16c) increased extremely but the percent increase did not keep pace because of strong survival from extended July-September recruitment, seen as piling up in December across 8-12 mm range.

Rate of growth (body length) was seen, above, to be generally steady (Figure 12). Slowed growth was commonest when adolescence or late adulthood took place during fall-winter. Exceptionally high biomass of 10-12 mm sizes in 1955 and 1956 was attributed to greatly slowed growth of adolescents of large cohorts during November-December of both years.

Regular, less extreme peaking of biomass at the four body lengths just descibed as prominent may be interpreted in terms of differing survival rates among life phases:

If body-length growth is steady during a given life phase, such as the larval period, biomass growth would proceed as the cube of body length, while population size would be expected to decline exponentially. This inequality leads to a biomass peak at a particular body length which depends on survival rate (Figure 18a). A survival rate of about 24%/mo for the larval phase is found to yield such a peak at 4 mm length in the biomass on body-length distribution, a size at which biomass regularly peaks during *E. pacifica* development.

Other survival rates were extrapolated from a cluster of age-density curves so as to yield biomass peaks which coincide with real average peaks shown in Figure 16: 43%/mo was found to peak at 7 mm, 54%/mo at 10-11 mm, and 66%/mo at 15 mm. A derived age-biomass distribution, linear scale (Figure 18b), is composed of segments based on the above sequence of survival rates. Segments end at 5.8 mm (end of larval phase), 9.3 mm (end of juvenile phase), and 13.2 mm (start of intensive reproduction, after Figure 21b).

The derived distribution is similar in shape to the observed average annual biomass distributions for 1953 and 1954 (Figure 16a, b). (Growth rates of 1953 cohorts were relatively steady, Figure 12. Those of 1954 appeared less steady but were still without the massive November-December pile-ups of adolescents noted in 1955 and 1956.) However, except for the larval period for which the derived and observed mean survival rates (from Figure 14) were both about 23%/mo; other derived rates had to be different from the

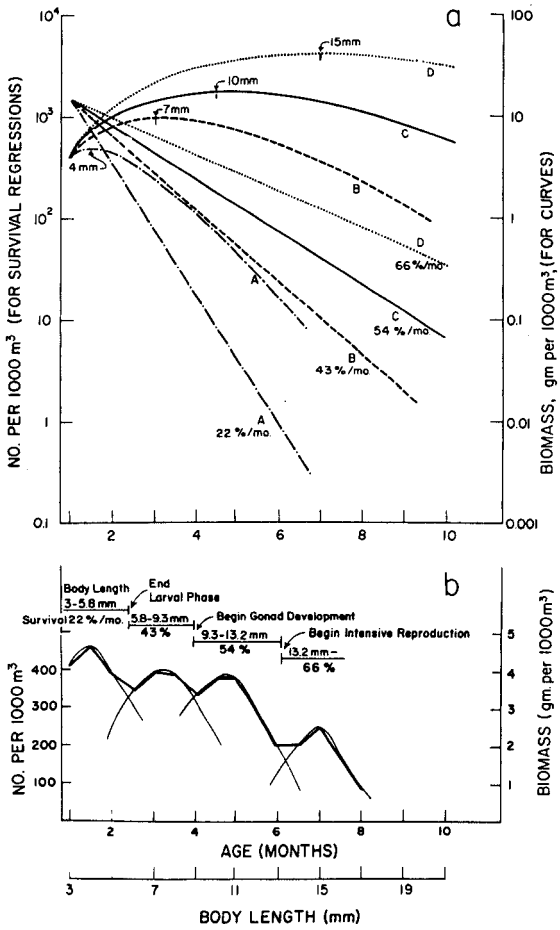

FIGURE 18.—Hypothetical age-frequency and age-biomass distributions of *Euphausia pacifica* assuming uniform body-length growth. **a**, Constant survivorship at each of four rates, selected to yield biomass peaking at 4, 7, 10, and 15 mm, respectively. **b**, An approximation of annual length-biomass distributions shown in Figure 17, obtained by changing survivorship at life-phase change.

mean observed rates so as to yield the observed peaks at 7, 10-11, and 15 mm length. These were lower by 24% and 10% for the juvenile and young adult phases respectively, and higher by 6% for the 14-18 mm sizes. This means that after the larval phase observed, mean survivorship decreased phase-to-phase by about 4%/mo, whereas in the derived distribution it increased by 11-12%/mo at phase change. This is attributed to deviations from evenness in real growth rates. However, there is a tendency toward progressively positive inflexion with age in certain of the survivorship curves of individual cohorts (Figure 15b-g).

Sex Ratio

Fifty percent of the estimates of prespawned eggs were two to four times greater than the estimates of larvae in the plankton a month later. The other 50% of egg/larva ratios were even lower than two (Figures 4d, 6). Further evidence that spawning was underestimated is seen in an examination of ratio of the sexes and state of their reproductive products.

The ripe male *E. pacifica* stores two spermatophores in a pair of ducts. The fertilized female possesses a single attached spermatophore (Brinton in press). This discrepancy might be attributed to a sex ratio in which females predominate, or to a need for more than one fertilization when spawning is protracted or intermittent across days, intermolt periods or longer. If such multiple fertilizations take place, males transfer one spermatophore to each of two females, probably quickly because single ripe spermatophores were not observed in males. The paired spermatophores in males were observed always to be of equal size, color, and readiness for extrusion. (Ready spermatophores may be easily expelled with gentle external pressure in the laboratory.) A continuing preponderance of ripe males, as shown in Figure 19, would tend to insure fertilization of females whenever they ripen. Mauchline and Fisher (1969) have explained, with reference to *Meganyctiphanes norvegica*, that fully formed spermatophores may be stored in the ejaculatory ducts for some time.

Here, ripe and unripe females outnumber males by about 1.5 times at 15 mm, and 3 times at 20 mm (See Figure 21a). Ponomareva's (1963) data on *E. pacifica* from the Sea of Japan showed females to be 56% of the adult population, and from the Okhotsk Sea 63% in April, 62% in June-July, and 44% in October. Four factors may contribute to the apparently greater number of females:

1) In the present data, apparent dominance by females (all body lengths lumped, Figure 20) is partly due to periods in which the population included late-maturing individuals of 10.5-11.5 mm length, some males of which were as yet without petasmas and were therefore categorized as females. (Secondary sexual characters of *E. pacifica* are usually evident at this size.) For example, this apparently happened during counting of material from cruises 5401 and 5402 (Figure 13), and cruises 5610-12 (Figure 20) when

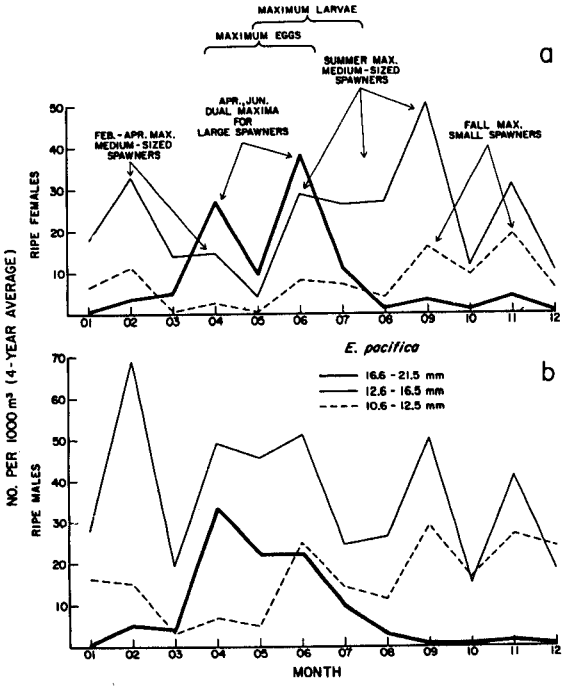

FIGURE 19.—a, Densities of ripe female *Euphausia pacifica* by months, three body-length groups, 1953-56 data combined from Figure 6d. b, Densities of males with ready spermatophores, same body-length groups.

"females" dominated the dense population of 8-12 mm individuals.

2) Increasing mortality in males relative to that in females may take place after 12 mm body length. Since the ratio of males to females decreases with body length, multiple fertilizations by males would be increasingly important with increasing size. (Mates are probably of similar size, in view of large spermatophores being attached to large females and small spermatophores to small females.)

3) Large males and unripe females may be more underestimated than egg-bearing females if the latter are less able to avoid net capture. For anchovy larvae, Isaacs (1965) hypothesized that avoidance of the 1-m net becomes significant after 15 mm body length. Similar differential avoidance might contribute to the female/male bias here. For 3 of the 4 yr, the average percentage of females that are ripe crested at 15-16 mm (Figure 21b). It remained high, 40-60%, through the larger size groups. The 1954 data differed in that the proportion of ripe/unripe females remained low through 16 mm body length. This is also seen in Figure 4d in which the 12.6-16.5 mm group showed

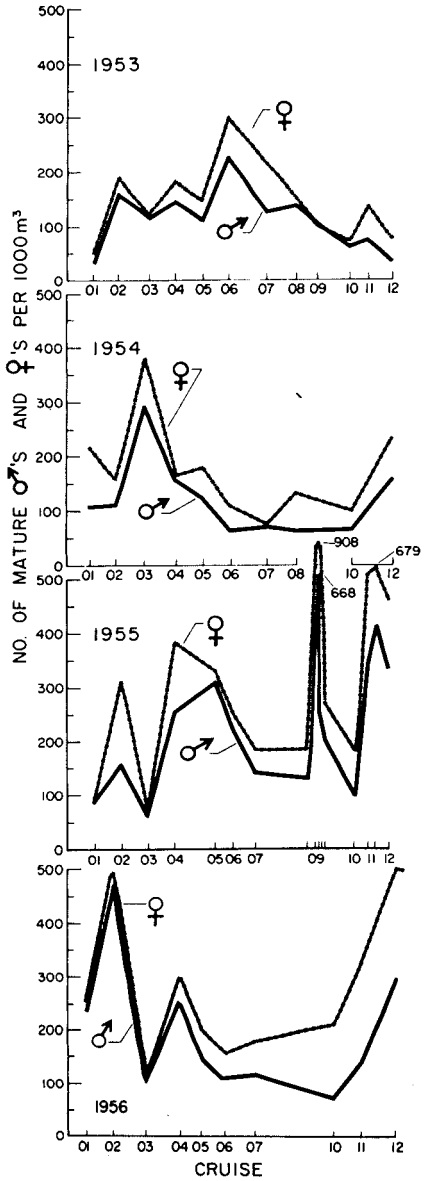

FIGURE 20.—Mean densities of presumed mature (>10.5 mm) male and female *Euphausia pacifica*, by month.

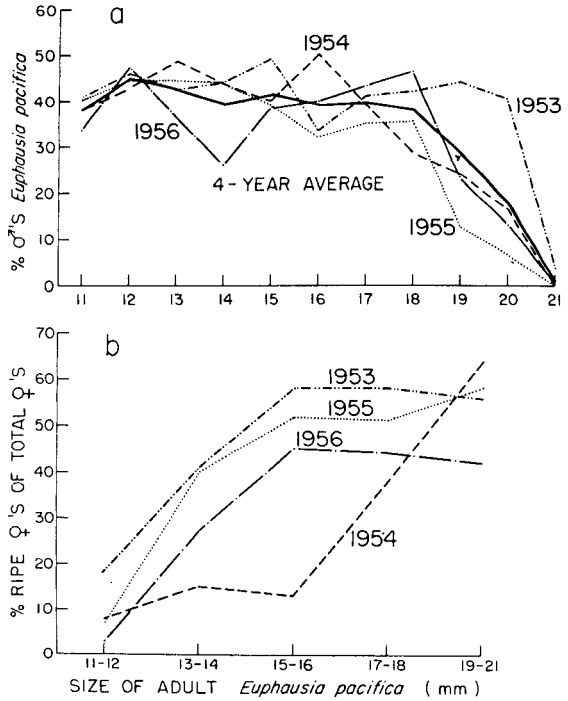

FIGURE 21.—a, Sex ratios for *Euphausia pacifica* by 1 mm body length, all data for each year averaged and 4-yr average. b, Annual gravidity ratios, by body length.

low reproductive activity. Furthermore, in 1954 the sex ratios for 13, 14, and 16 mm body length were 1:1, as compared with other years (Figure 21a). However, no relationship was seen (Figure 13) between numbers of gravid females of a given size and the difference between numbers of males and total females of the same size. Therefore, the observed increase with body length (at least to 15-16 mm) in the ratio of gravid to nongravid females appears natural, attributable either to higher frequency or longer duration of egg production with increasing body length.

4) An increase with body length in female/male ratio may be due to their differing growth rates. Both sexes tend to mature at the same size, ca. 11 mm. Thereafter, females grow slower, appearing increasingly numerous relative to males at successive body-length increments (Figures 14, 21a). Nemoto's (1957) data suggested that the adult male of *E. pacifica* tends to be smaller than the female of the same age, and Mauchline (1960) stated this to be the case in *Meganyctiphanes norvegica*. Slower growth rate in females indicates shorter life span for males, probably by 1 or 2 mo, since females grow to 21 mm length off southern California (rarely more) compared with 20 mm for males.

In summary, reasons were sought for a) underestimation of spawning, b) paired spermatophores in males, and c) apparent imbalance in sex ratio. These explanations were considered: eggs can ripen and females can spawn more often than the frequency of the surveys, applicable to a) and b); the bias in sex ratio favoring females is real and develops either with higher male mortality at

all sizes after maturity, applicable to b) and c), or because females grow slower and live longer, also applicable to b) and c); and the bias is an artifact of reduced net avoidance by ripe females and of observations during seasons when some males mature relatively late, resembly females for a time, applicable to c). Evidence supports each of the above. With regard to the increasing female/male ratio with body size, there are particularly strong indications of relatively slow growth in females, apparently leading to better survival than in males at given sizes and ages.

DISCUSSION

The predominance of *E. pacifica* among zooplankters off southern California appears related to the spring-early summer upwelling regime, which coincides with heaviest spawning. Recruitment consistently crested during May-July following annual surface temperature minima in April or May. Although this species may range southward along California and Mexico because of currents and the cool (10°-18°C) water, sole dependence on temperature effect in the southern California area for reproductivity is not likely because the area as a whole is coolest during December-April and the most substantial recruitment is later.

That the dependence is partly effected by food, as indicated by the seasonal pattern in availability of nutrients (plants), was shown in charts of the California Current region for 1969 for nutrients (Thomas and Seibert 1974) and for chlorophyll *a* (Owen 1974). The assumption is made that timing of the seasons in 1969 agrees enough with 1953-56 so that the April-June buildup in upwelling applies to both periods. Off southern California nutrient concentrations intensified in April and peaked in May in a patchy distribution corresponding to the areas of low surface temperature. For example, PO_4-P (integrated through 0-50 m depth) was in the range of 10-40 mg-at./m^2 during January-February and August-December but increased to 40-60 mg-at./m^2 during April-June. Silicate-Si peaked at 400-1,000 mg-at./m^2 during April-June; during the other months concentrations >400 mg-at./m^2 were rare.

Correspondingly, during the main upwelling period, April-September, chlorophyll *a* in the surface waters inhabited by newly hatched euphausiid larvae showed the patchy pattern of extreme concentrations shown also by the nutrients. Values peaked at 3.0 mg/m^3 during April-September compared with 2.0 mg/m^3 for January-March and 0.5 mg/m^3 for October-December. The possible importance of shallow (12-19.5 m), intense (to 50 μg/liter) chlorophyll maxima—particularly those containing the dinoflagellate *Gymnodinium splendens*—to first feeding of anchovy larvae was put forward by Lasker (1975). These maxima were found during March-April 1974 within 15 km of the southern California coast. Such layering of food particles could have broad significance to feeding and survival of zooplankton larvae.

Most larvae of *E. pacifica* are found in nearshore areas described above as recruitment refuges where upwelling prevails and currents are sluggish. Similarly, off Oregon (Smiles and Pearcy 1971), more larvae were in nearshore upwellings than in offshore water characterized by a summer productivity minimum typical of the region. Also working off Oregon, Peterson and Miller (1975) found no relationship between year-to-year (1969-71) intensity of summer upwelling and abundances of euphausiid eggs and larvae (not identified to species).

Evidence that larvae occupying southern California waters are produced locally is seen in the time of the upwelling season along the coast. Upwelling peaks off southern Baja California in February-March. Progressing northward, its maximum off Oregon is during August-September. Hence maximum spawning and recruitment, if upwelling induced, should develop along the same northerly track, counter to the direction of main flow in the California Current during this period of relatively consistent northeast winds. This is the case: recruitment off mid-Baja California, lat. 27°-29°N, is mainly February-April (Brinton 1967b, 1973), in Monterey Bay it is both spring and summer (Barham 1957), off southern California it is mainly May-July, and off Oregon, August-December.

Although ripening of ovaries, spawning, and recruitment reach maxima as consequence of upwelling-associated events, the southern California population includes ripe females and newly hatched larvae year-round (Figures 4c, d; 19). Off Oregon, *E. pacifica* also includes some larvae at all times (Smiles and Pearcy 1971); while in the Sea of Japan (lat. 40°-50°N) and south of Kamchatka, Alaska (lat. 50°-55°N), in areas enriched by winter mixing of the water column, *E. pacifica* possesses ripe gonads in May-June, the

presumed breeding period (Ponomareva 1963), though eggs were abundant in August nearby in the Sea of Okhotsk. To the north and south of the eastern Aleutian Islands, Nemoto (1957) found females of *E. pacifica* with attached spermatophores during July.

Dominance of the southern California population by the particular cohorts followed in the analyses of growth tends to obscure the regular contribution of small classes, including those of fall-winter in which densities of larvae are usually 1,000-2,000/1,000 m^3.

Such continuous recruitment of variable intensity is seen as an adaptation to midlatitude irregularity in oceanographic conditions, both seasonal and year-to-year, as compared with cycles at high latitudes. Continuous recruitment permits the stock to always include a wide spectrum of sizes and maturity stages, providing a potential for one or another to adapt to periods of poor climate or food availability, of differing duration or amplitude. For example, in 1954, a year of weak upwelling, recruitment was all but limited to June-July; nevertheless, spawning resumed at high intensity during four different periods in 1955.

Periodicity was observed in maxima of spawning and recruitment, and recruitment is appropriately out of phase with the inferred spawning (Figure 4c), implying substantial synchrony among breeders. Spawning apparently pulses at a 2-mo frequency during the period of maximum gamete generation, which also must be the period of maximum food use by breeders and larvae. This is to be compared with the annual (or at most, semiannual) frequency of breeding noted in the subarctic North Pacific. Thus it appears possible that, under optimal feeding conditions off southern California, a female might spawn every 2 mo: first at about 11.5 mm length (20-50 eggs), second at 16 mm (50-200 eggs), and third at 20 mm (100-400 eggs), during which time an individual might be expected to produce a maximum of 650 eggs. This is compatible with an observation of 1,400 oocytes (all stages of development) in ovaries of an *E. pacifica* in the springtime in the northeastern Pacific (Ponomareva 1963) where spawning is concentrated into one season, and with Lasker's observation, reported in Mauchline and Fisher (1969), that an *E. pacifica* from southern California shed 230 eggs after capture.

The long duration of maturity—probably half of this species' life expectancy—further contributes to population stability and continuity. In conjunction with substantial horizontal transport, the capacity to breed several times enhances genetic integration across the distributional range.

The first observations on growth in *E. pacifica* were from specimens maintained in the laboratory by Lasker (1966) at 10°C with excess food. In small juveniles, growth was steady at 2.5 or 2.9 mm during 2 mo, from about 5 to 8 mm length. In the southern California field populations, growth of juveniles of this size was consistently in the range of 3-3.5 mm/mo. However, the 5309 cohort, having reached 5 mm by the start of the fall period of reduced growth, then grew only 3 mm in 1.5 mo.

Larger *E. pacifica* were observed by Lasker to grow somewhat slower. A 6.5-mm specimen grew 1.5 mm in 70 days, but added only 1.5 mm in 230 more days before dying, not having reached fully adult size. A 7.9-mm specimen grew 1.5 mm in 75 days, an 8.0-mm specimen grew 1.5 mm in 130 days, and an 8.4-mm specimen grew 1.0 mm in 160 days. These rates are smaller than those for the local field populations. They are closer to those supposed for *E. pacifica* in the northeastern Pacific where environmental enrichment is not by intermittent upwelling but by winter mixing followed by spring stability in the water column, hence not a continuing process.

In the analysis of growth, cohorts are considered as normal L-F distributions representing broods continuously hatched during a few days to a month or more. Observation on duration of reproduction is limited by the character of the sampling, here in approximately 1-wk period with a 2-3 wk interval between surveys. Only in a few of the months can a pulse in recruitment by recognized as distinct to that month. In most months, the larvae derive from the beginning, continuation, or end of a period of cohort formation which extends beyond one survey period and into another. Recruitment found less than in past or succeeding months is neither recognizable initially as a cohort nor traceable thereafter.

The area's population, therefore, is constantly polymodal in character, being compounded of individuals belonging to different age-groups and sexes. The possible difference in size between the sexes after about 15 mm length was not taken into consideration in the growth study.

The simplest method of analyzing growth and survival is that of following obvious modes, survey to survey. This is probably the most significant means biologically. Nevertheless, certain im-

precise trends in development of presumed cohorts provide growth rates which corroborate the more obvious trends. Some pathways of development indicated in Figures 9 and 10 may appear imaginary unless the shapes and amplitudes of the related L-F distributions, adjacent in time, are closely compared. When such indistinct modes are followed, precision and accuracy in recognizing rates of development are reduced. Graphical procedures for mathematically defining cohorts composing irregular L-F polygons (e.g., Harding 1949) required some subjectivity in recognizing modes and were employed only in an exploratory way.

There can be important inaccuracies in field estimates of growth rate when reliance is upon time-sequences in L-F modes. Even with steady, uniform recruitment, peaks or troughs would appear in the L-F distribution owing to differing growth rates and survivorship among life phases or between sexes. With unsteady recruitment, such peaks may sometimes lie in phase with the cohort being traced, but the cohort nevertheless becomes compounded by younger individuals when its growth is differentially slowed or by older individuals when accelerated.

It is possible that the individuals composing a mode could be totally replaced in the course of its time progression, although the modal assemblage persists as a size group, presumably feeding and mating as a unit. I have noted above that spring-summer cohorts tend to "pile up" in fall-winter when growth of adolescents appears to be food limited.

In tracing growth, reliance is therefore upon the more substantial cohorts. Although these can be masked, their frequent appearance as modes at sizes not associated with life-phase changes gives credence to the method.

Growth rates of *E. pacifica* off southern California appear similar to those off Oregon (Smiles and Pearcy 1971). Figure 22 shows generalized growth curves for this species from four areas in the North Pacific. The Oregon population showed steady growth after September recruitment. The juvenile and adolescent phases were during the winter and 13 mm was reached by February. About 22 mm was attained after 1 yr. This parallels development of a winter cohort (5512) off southern California which grew to 12 mm in 3 mo and was traced to about 21 mm after 8 mo.

Spring (5406) and summer (5309) cohorts off southern California grew at rates similar to the

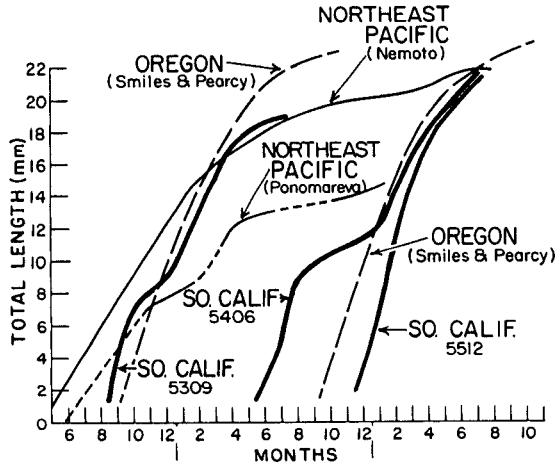

FIGURE 22.—Representative growth curves from southern California area compared with curves previously derived for *Euphausia pacifica* and illustrated by Smiles and Pearcy (1971).

winter cohort, except for slowing during October-December—5406 during adolescence and 5309 during the juvenile phase.

Here, life expectancy appears to be about 8 mo for winter and early-spring cohorts, to sizes of 18-20 mm by August-October. December-January populations never included individuals larger than 19 mm. Life expectancy is up to 12 mo for late-spring and summer cohorts, which grew to 21-22 mm by the following April-July. This agrees with estimates of 12 mo for September cohorts off Oregon.

Growth in other euphausiid species, mostly summarized in Smiles and Pearcy (1971), is similar. Several reach about 22 mm after 1 yr: *E. superba* (Ruud 1932; Bargmann 1945; Marr 1962), *E. triacantha* (Baker 1959), *Thysanoessa raschii* (Mauchline 1966), *Meganyctiphanes norvegica* (Ruud 1936; Einarsson 1945; Mauchline 1960; Matthews 1973), and *Thysanopoda acutifrons* (Einarsson 1945). Most of these species have a life expectancy of 2 yr, reproducing in each and growing slowly or not at all in winter.

During winter in the westernmost North Pacific (Sea of Okhotsk), Ponomareva (1963) found *E. pacifica* to be 8 mm (considered to have hatched the previous summer) and 14-15 mm (considered 2 yr old). In the spring it was 12-13 mm (1 yr old) and 19 mm (2 yr old). Both groups bred in June. Off nearby Kamchatka in the summer, Nemoto (1957) found a size range of 12-22 mm, much like that found by Ponomareva, but with most at 14-20 mm. There were no larvae, but females with spermatophores were present in September, as off Oregon.

South of the Aleutian Islands in September, he found a 6-12 mm group interpreted as having hatched in the spring or early summer. Maximum numbers of adult females were 16-19 mm in May, 17-21 mm in June, and 18-22 mm in September.

Thus growth of *E. pacifica* is inferred to be slower and of longer duration in the Subarctic seas than off Oregon and California (Figure 22). Nemoto's (1957) estimate from south of the Aleutians was intermediate between Ponomareva's (1963) from the western Pacific and those from the American coast. Ponomareva's finding that sexual maturity is attained by 15-17 mm, with some mature at only 11-12 mm, agreed with the observations off southern California.

During *E. pacifica*'s main reproductive season there is similarity in surface water temperatures (Sverdrup et al. 1942; Anonymous 1963) among the five North Pacific areas from which information on life history comes; there is less agreement in winter temperatures:

Sea of Okhotsk	10-13°C (Aug.),	0°C (Feb.)
Off Kamchatka	9-11°C (Aug.),	0°- 1°C (Feb.)
South of Aleutians	10-12°C (Aug.),	2°- 4°C (Feb.)
Off Oregon	10-14°C (Sept.),	9°-11°C (Feb.)
Off southern California	10-18°C (June),	12°-15°C (Feb.)

Winter temperatures in the three subarctic areas are near 0°C whereas off Oregon and California they differ little from spring-summer temperatures influenced by upwelling. An overall temperature regime for *E. pacifica* is thereby described in which low temperature does not limit occupancy but in which 9°-16°C is suitable for reproduction, food permitting. In the subarctic region reproduction takes place at 9-13°C, the highest annual temperatures there. To the south of the California Current off mainland Mexico, food seems to be abundant, but other factors (temperatures >20°C, oxygen concentrations <0.1 ml/liter, different current systems) appear there to curtail the species' range.

The serial biomass representations included here clearly show rise and decline of cohorts, but are less exact than length frequency in determining growth and do not serve in estimating survivorship. It is evident that biomass of the species fluctuates month-to-month, with recruitment and growth not balancing mortality in any regular way. However in 34 of the 48 mo, the biomass was within the range of 8-22 g/1,000 m^3.

The intense densities of *E. pacifica* at 8-12 mm, also appearing as conspicuous biomass peaks, are the rule rather than the exception. Therefore, such regular concentrating at the adolescence interphase, particularly in fall-winter, may be other than an incidental consequence of reduced food. It appears as a means of increasing size uniformity in the population, hence improved breeding efficiency, by the time of the spring bloom—a condition fulfilled by stricter seasonality in the high-latitude populations of *E. pacifica*.

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LITERATURE CITED

AHLSTROM, E. H.
1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 54, 75 p.

ANONYMOUS
1963. CalCOFI atlas of 10-meter temperatures and salinities 1949 through 1959. Calif. Coop. Oceanic Fish. Invest., Atlas 1, 297 p.

BAKER, A. DE C.
1959. The distribution and life history of *Euphausia tricantha* Holt and Tattersall. Discovery Rep. 29:309-340.

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BARGMANN, H. E.
1945. The development and life-history of adolescent and adult krill, *Euphausia superba*. Discovery Rep. 23:103-176.

BARHAM, E. G.
1957. The ecology of sonic scattering layers in the Monterey Bay area, California. Ph.D. Thesis, Stanford Univ., 192 p.

BODEN, B. P.
1950. The post-naupliar stages of the crustacean *Euphausia pacifica*. Trans. Am. Microsc. Soc. 69:373-386.

BRINTON, E.
1960. Changes in the distribution of euphausiid crustaceans

in the region of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 7:137-146.

1962a. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8: 51-269.

1962b. Two new species of Euphausiacea, *Euphausia nana* and *Stylocheiron robustum* from the Pacific. Crustaceana 4:167-179.

1967a. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

1967b. Distributional atlas of Euphausiacea (Crustacea) in the California Current Region, Part I. Calif. Coop. Oceanic Fish. Invest. Atlas 5, 275 p.

1973. Distributional atlas of Euphausiacea (Crustacea) in the California Current region, Part II. Calif. Coop. Oceanic Fish. Invest. Atlas 18, 336 p.

In press. Observations of spermatophores attached to pleopods of male euphausiids. Crustaceana.

BRINTON, E., AND J. G. WYLLIE.

In press. Distributional atlas of Euphausiacea, Part III. Developmental stages of euphausiids in the region of the Southern California eddy, 1953-1956. Calif. Coop. Oceanic Fish. Invest., Atlas 24.

CHILDRESS, J. J.

1971. Respiratory rate and depth of occurrence of midwater animals. Limnol. Oceanogr. 16:104-106.

EINARSSON, H.

1945. Euphausiacea. 1. North Atlantic species. Dana Rep. Carlsberg Found. 27, 185 p.

FOWLER, S. W., L. F. SMALL, and S. KEČKEŠ.

1971. Effects of temperature and size on molting of euphausiid crustaceans. Mar. Biol. (Berl.) 11:45-51.

GILFILLAN, E.

1972. Reactions of *Euphausia pacifica* Hansen (Crustacea) from oceanic, mixed oceanic-coastal and coastal waters of British Columbia to experimental changes in temperature and salinity. J. Exp. Mar. Biol. Ecol. 10:29-40.

GOPALAKRISHNAN, K.

1973. Developmental and growth studies of the euphausiid *Nematoscelis difficilis* (Crustacea) based on rearing. Bull. Scripps Inst. Oceanogr., Univ. Calif. 20:1-87.

HARDING, J. P.

1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

HARDY, A. C.

1956. The open sea. Its natural history: the world of plankton. Houghton Mifflin Co., Boston, 335 p.

ISAACS, J. D.

1965. Larval sardine and anchovy interrelationships. Calif. Coop. Oceanic Fish. Invest. Rep. 10:102-140.

LASKER, R.

1964. Molting frequency of a deep-sea crustacean, *Euphausia pacifica*. Nature (Lond.) 203:96.

1966. Feeding, growth, respiration, and carbon utilization of euphausiid crustacean. J. Fish. Res. Board Can. 23:1291-1317.

1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

MARR, J.

1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Rep. 32:33-464.

MATTHEWS, J. B. L.

1973. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of *Meganyctiphanes norvegica* (Crustacea, Euphausiacea) in 1968 and 1969. Sarsia 54:75-90.

MAUCHLINE, J.

1960. The biology of the euphausiid crustacean, *Meganyctiphanes norvegica* (M. Sars). Proc. R. Soc. Edinb., Sect. B., Biol. 67:141-179.

1966. The biology of *Thysanoessa raschii* (M. Sars), with a comparison of its diet with that of *Meganyctiphanes norvegica* (M. Sars). *In* H. Barnes (editor), Some contemporary studies in marine science, p. 493-510. George Allen and Unwin Ltd., Lond.

1968. The development of the eggs in the ovaries of euphausiids and estimation of fecundity. Crustaceana 14:155-163.

MAUCHLINE, J., AND L. R. FISHER.

1969. The biology of euphausiids. Adv. Mar. Biol. 7, 454 p.

MILLER, J. K.

1966. Biomass determinations of selected zooplankters found in the California Cooperative Oceanic Fisheries Investigations. Scripps Inst. Oceanogr. SIO Ref. 66-15, 18 p.

NEMOTO, T.

1957. Foods of baleen whales in the northern Pacific. Sci. Rep. Whales Res. Inst. 12:33-90.

OWEN, R. W., JR.

1974. Distribution of primary production, plant pigments and Secchi depth in the California Current region, 1969. Calif. Coop. Oceanic Fish. Invest. Atlas 20:xi-xiv, charts 98-117.

PARANJAPE, M. A.

1967. Molting and respiration of euphausiids. J. Fish. Res. Board Can. 24:1229-1240.

PEARCY, W. G., AND L. F. SMALL.

1968. Effects of pressure on the respiration of vertically migrating crustaceans. J. Fish. Res. Board Can. 25:1311-1316.

PETERSON, W. T., AND C. B. MILLER.

1975. Year-to-year variations in the planktonology of the Oregon upwelling zone. Fish. Bull., U. S. 73:642-653.

PONOMAREVA, L. A.

1963. Euphausiids of the North Pacific, their distribution and ecology. Akad. Nauk SSSR Inst. Okeanol. (Translated by Israel Program for Scientific Translations, Jerusalem 1966, IPST Catalog No. 1368, 154 p.)

REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE.

1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest., Prog. Rep., 1 July 1956 to 1 Jan. 1958, p. 27-57.

RUUD, J. T.

1932. On the biology of southern Euphausiidae. Hvalradets Skr. 2, 105 p.

1936. Euphausiacea. Rep. Dan. Oceanogr. Exped. 1908-1910 Mediter. Adjacent Seas 2D6 (Biol.), 86 p.

SMALL, L. F.

1967. Energy flow in *Euphausia pacifica*. Nature (Lond.) 215:515-516.

SMALL, L. F., AND J. F. HEBARD.

1967. Respiration of a vertically migrating marine crustacean *Euphausia pacifica* Hansen. Limnol. Oceanogr. 12:272-280.

SMALL, L. F., J. F. HEBARD, AND C. D. MCINTIRE.
1966. Respiration in euphausiids. Nature (Lond.) 211:1210-1211.

SMILES, M. C., JR., AND W. G. PEARCY.
1971. Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. Fish. Bull., U.S. 69:79-86.

SMITH, P. E.
1971. Distributional atlas of zooplankton volume in the California Current region, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest., Atlas 13: v-xvi, 144 p.

SOUTH PACIFIC FISHERY INVESTIGATIONS.
1954. Zooplankton volumes off the Pacific Coast, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 132, 38 p.
1955. Zooplankton volumes off the Pacific coast, 1954. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 161, 35 p.
1956. Zooplankton volumes off the Pacific coast, 1955. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 177, 32 p.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans, their physics, chemistry and general biology. Prentice Hall, N.Y., 1087 p.

THOMAS, W. H., AND D. L. R. SEIBERT.
1974. Distribution of nitrate, nitrite, phosphate and silicate in the California Current region, 1969. Calif. Coop. Oceanic Fish. Invest., Atlas 20:vii-x, charts 2-97.

THRAILKILL, J. R.
1957. Zooplankton volumes off the Pacific coast, 1956. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 232, 50 p.

UDA, M., AND M. ISHINO.
1958. Enrichment pattern resulting from eddy system in relation to fishing grounds. J. Tokyo Univ. Fish. 44:105-119.

WYLLIE, J. G.
1966. Geostrophic flow of the California Current at the surface and at 200 meters. Calif. Coop. Oceanic Fish. Invest. Atlas 4, 288 p.

PRODUCTION OF JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN A HEATED MODEL STREAM[1]

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ABSTRACT

Temperature was elevated approximately 4°C in a model stream, compared with an unheated but otherwise similar control stream. The streams were located outdoors and received identical amounts of exchange water from a nearby creek. Diel and seasonal temperature fluctuations were similar to those of area streams. Juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, were introduced into each stream either as eyed eggs or fry and allowed to remain for approximately 1 yr. Two consecutive year classes of juvenile salmon were studied. Their production was measured triweekly and related to changes in temperature, food availability, and other environmental factors. Ancillary experiments utilizing water from the model streams permitted measurement of differences in growth rate of salmon fed various rations.

Salmon production in the control stream exceeded that in the heated stream. In 1972, total production in the control stream was twofold greater and, in 1973, it was approximately 30% greater than in the heated stream. Elevated temperature resulted in reduced growth rates of the fish especially as food became less abundant and at times also resulted in lower biomasses of food organisms, either because the temperature increase directly affected survival and growth of benthic invertebrates or because increased sedimentation associated with heavier growth of filamentous algae made riffle substrate less suitable for certain species. Beneficial effects of increased temperature appeared to include protection from infestation by a trematode parasite (*Nanophyetus salmincola*) and, possibly, increased tendencies of some invertebrates to enter the drift.

Studies of the effects of elevated temperature on stream dwelling organisms have been largely confined to short-term laboratory experiments or to field surveys associated with man-caused thermal increases. We have employed two large model streams, one heated and one unheated, to examine the effects of constantly elevated temperature on production of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), under conditions similar to natural streams, but where temperature could be controlled. Identifying the factors governing productivity of the streams that were influenced by increased temperature and measuring the impact of the addition of a known amount of heat on chinook salmon production were the two main objectives of the research.

Temperature change can affect salmonid fishes in two general ways. First are the direct effects, e.g., accelerated developmental rates, altered food conversion efficiencies, and, under certain conditions, lethality. These kinds of effects have received considerable attention in laboratory experiments. Less well understood are the indirect effects, one of the most important being resultant changes in the abundance of food organisms. In a previous study involving the same streams, Iverson (1972) found that the production of juvenile coho salmon, *O. kisutch*, was significantly reduced in the heated stream compared with the unheated control, and he attributed this reduction mainly to lower biomasses of immature stages of insects in the heated stream. Evaluating the importance of indirect consequences of temperature elevation on juvenile chinook thus became one of our major concerns, for water quality guidelines relating to the temperature requirements of salmon and trout are based primarily upon knowledge of direct effects and to a much lesser extent upon possible indirect or secondary effects.

MATERIALS AND METHODS

Physical Characteristics of the Streams

The model streams were located at the Oak Creek Laboratory of Biology near Corvallis in

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western Oregon. They consisted of two large wooden channels interconnected at the ends by pipes (Figure 1). Within each stream were four riffle-pool sections of equal size; the total surface area available to fish and other organisms was 22 m^2. Minor differences in substrate composition, water velocity and depth, and shading from terrestrial vegetation existed among the riffle-pool sections. These variations were sufficient to prevent the sections from being treated as replicates; therefore, samples from each of the four sections were composited.

The slope of each stream was approximately 1.9% so that water pumped into the upstream ends flowed downstream at velocities typical of natural streams (approximately 60 cm/s in the riffles to near 0 cm/s at the bottom of the pools). A 2-horsepower centrifugal pump forced water from the downstream end of one channel to the upstream end of the other. A gate valve controlled the flow rate, which was maintained at approximately 1.35 m^3/min.

Complete freedom of movement for the fish was allowed between the two channels. Individuals could pass downstream or upstream through the pipe from one side to the other; they were, however, prevented from entering the pump by a screen at the downstream end of the lowermost pool. Movement of the fish from the streams took place through a 6-cm diameter outlet pipe that originated at the screen and terminated in a partitioned trap. Fish that entered the trap were returned to the uppermost riffle both to avoid fortuitous losses and to provide the fish with an adequate opportunity to establish residence.

Substrate consisted of a layer of rocks approximately 7 cm deep. Following Cummins' (1962) terminology, cobbles and pebbles composed more than 95% of the substrate, both in the riffles and pools, while larger sand was almost absent. No large boulders were present, although a few cobbles projected above the water. A difference in the amount of very fine sediments existed between the two streams; this difference will be discussed in connection with their invertebrate faunas.

Temperature Regulation

Water temperature in the unheated control followed natural diel and seasonal cycles (Figure 2). Two 6-kw stainless steel heaters regulated by a variable input timer facilitated temperature elevation in the heated stream. Continuous recordings of the temperature were made by Partlow RFT thermographs.[4] Differences between monthly means ranged from 3.3°C (August 1972) to 4.9°C (December 1972): the average temperature difference between the streams was 3.9°C.

Both streams received 10-20 liters/min of unfiltered water from a small spring-fed creek that contained aquatic invertebrates and algae, but no fishes. During periods of low stream flow, the water supply was supplemented by a mixture of well water and unfiltered water pumped from a large nearby creek. The model streams have been operating continuously at approximately the same temperature differential since completion of construction in 1969 (Iverson 1972). However, in December 1972 unusually cold weather caused

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

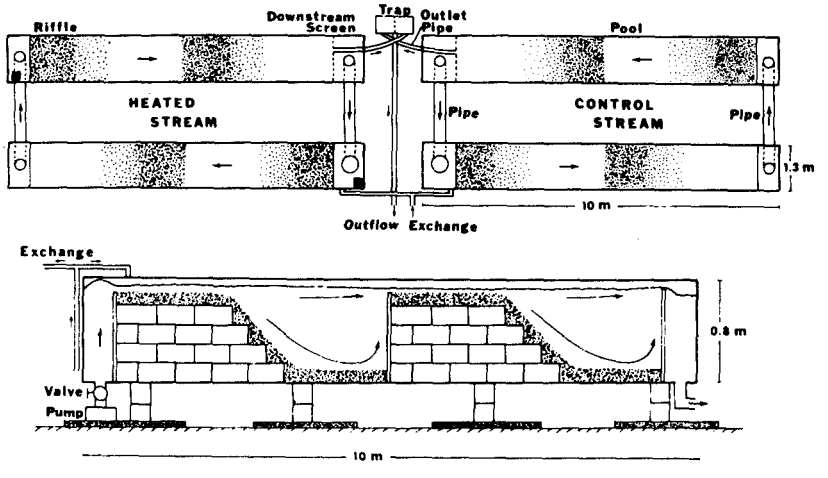

FIGURE 1.—Top. Plan view of model streams. Arrows indicate direction of water flow and black squares in the heated stream denote location of heating units. Bottom. Cross section of one of the channels in a model stream.

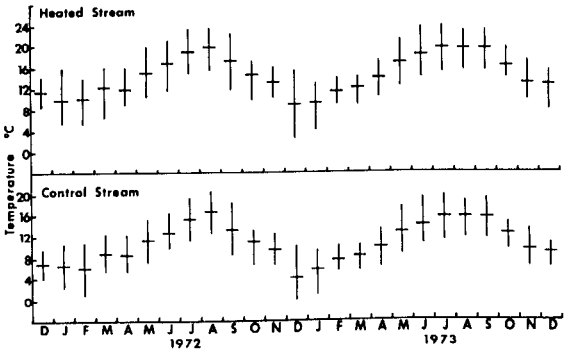

FIGURE 2.–Temperature conditions in the model streams. Horizontal and vertical lines represent monthly means and ranges, respectively.

glass observation windows in the control stream to break; as a result, the entire riffle substrate was exposed for several days while new windows were being installed and some losses of periphyton and invertebrates occurred. One window was also replaced in the heated stream at this time, necessitating exposure of one riffle.

Associated Flora

Vegetation surrounding the streams included red alder, *Alnus rubra*, and apple, *Malus* sp. These trees contributed leaves, catkins, and flowers as well as a variety of terrestrial invertebrates.

Periphytic algae composed the bulk of living plant material within the streams. The same plant species were found in both heated and control streams, although differences in biomass and temporal succession occurred. The dominant species from late spring to fall was *Cladophora glomerata*, a filamentous green alga that attached to large particles in the riffles and often trailed into pool areas. Various diatoms also made up a significant proportion of the flora. Two species exhibited especially heavy seasonal blooms. In early spring, filaments of a colonial diatom, *Melosira varians*, covered both riffles and pools; this species was noticeably more common in the control than in the heated stream. In summer and fall *Synedra ulna* became the dominant diatom, occurring both in the water mass and among living and dead algae on the bottom. Blue-green algae were generally found in late spring and summer. *Calothrix* and *Nostoc* were more abundant and appeared earlier in the heated stream than in the control. An unidentified dense moss colonized some of the large cobbles in the riffles. Diatoms and desmids, in addition to plant materials from terrestrial sources, were common in the drift. The desmid *Closterium lunula* was abundant in spring and early summer and was found to be an important food resource for filter-feeding invertebrates.

Benthos and Drift

Benthic plants and animals were sampled triweekly. Wire mesh baskets 20 × 20 × 6 cm painted with nontoxic paint and having wood bottoms were filled with substrate and placed against supporting blocks in the riffles. The mesh size (2 cm) was small enough to retain most of the particles and large enough to allow movement of invertebrates into and out of the baskets. Each riffle in the streams contained four baskets placed about 1 m apart from upstream to downstream end. One basket was selected from a different location in each riffle, the contents emptied into a bucket, and all large particles cleaned with a plastic scrub brush. The combined samples from four baskets (0.16 m^2 total) were then collected in a 200-μm mesh bag. One sample was taken from a pool in each channel, and collected material was combined and preserved in 10% Formalin.

Drifting organisms were collected triweekly by means of 333-μm mesh drift nets (Anderson 1967) that were suspended at the downstream end of the riffles. Two nets were fished in each stream (one per channel) for a 24-h period. Samples were removed and preserved at approximately sunrise and sunset so that diel differences in drift rates could be measured. Current velocity was measured at each sampling position and the amount of water passing through the nets during an interval was determined by multiplying this velocity by the cross sectional area of the water (330 cm^2) at the mouth of the net. During periods when considerable masses of leaves or algae were present in the drift, usually late summer and fall, some clogging took place and the volume of water entering the nets was overestimated.

All samples were allowed to remain in Formalin for 1 or 2 days, after which they were washed briefly with water. Drift samples were transferred directly to 70% ethanol prior to enumeration, while bottom samples were first sorted to remove invertebrates larger than 4 mm, and then subsampled (10% by volume) and preserved in ethanol. All organisms were measured to the nearest millimeter by means of a metric grid placed on the stage of the microscope. We assumed that no

length changes occurred during preservation. The number of individuals for each species in each size interval was recorded for every sample.

The remaining 90% of a bottom sample—that not sorted under magnification—was dried at 70°C for 4 days and then ashed at 600°C. Ten percent of its organic weight was arbitrarily assumed to have been lost during preservation. Subtracting the estimated biomass of small (<4 mm) invertebrates within this subsample from the total loss of ignition yielded the ash-free dry weight of filamentous algae, some diatoms, detritus, and organisms too small to be seen during the sorting process. Conversion to energy units (kcal) was accomplished by multiplying the plant-detritus biomass by 4.05, the mean of five samples combusted in an oxygen bomb calorimeter.

Computations of invertebrate biomasses were based on live specimens collected from a nearby stream, grouped according to size and species, and weighed after drying 4 days at 70°C. Their average dry weights were converted to calories by values obtained from Cummins and Wuycheck (1971) or determined directly by calorimetry. When no representatives of a certain size were available, a value for that interval was estimated by interpolation. Very similar forms were assumed to have identical values. For bottom samples, the biomass (kcal/m^2) of each size class of each taxon was taken as the product of the number of individuals in that class, the estimated caloric value for individuals of that size, and the appropriate area conversion factor. The product of the number of individuals and the caloric value was divided by the total amount of water passing through the nets to give biomass estimates per unit volume (cal/m^3) for the drift samples. Summing the values of all size intervals gave the total caloric content for each taxon.

Fish

Fertilized chinook salmon eggs were obtained from the Marion Forks Salmon Hatchery of the Oregon Department of Fish and Wildlife. Eggs for the 1972 experiment, taken 3 October 1971, were from a single pair mating. Eggs used in the 1973 experiment, taken 1 October 1972, were obtained by crossing three females with four males. This was done in order to increase genetic heterogeneity among fish in the 1973 experiment. Following fertilization, the eggs were transported immediately to holding facilities where they were incubated at 12°C.

In 1971, eggs were introduced into the streams when they reached the eyed stage. They were hatched in floating baskets and the fry were released shortly before yolk absorption was completed. Owing to accelerated development in warmer water, fish in the heated stream were released sooner than those in the control, although the initial number of individuals placed in the two streams was identical (425). A 10-wk recolonization period following repairs delayed introduction of salmon until mid-March 1973, when 200 fry were released simultaneously into each stream.

When the fish had reached approximately 0.4 g wet weight, they were all removed from the streams for measurement of individual length and weight every 3 wk until an experiment was terminated. From 5 to 20 fish were randomly drawn from the populations for stomach analyses. A blunted 22-gauge needle on a 5-ml syringe was inserted through the esophagus of an anesthetized fish into the anterior limb of the stomach. Several milliliters of water were gently injected into the stomach, forcing the contents out through the mouth into a collecting beaker. The combined whole food organisms and identified fragments of each taxon were weighed to the nearest 0.1 mg, and each taxon was assigned a percentage of the diet based on its fraction of the total wet weight of the sample.

Direct effects of the model stream temperature regimes on chinook salmon growth rates at different levels of food availability were studied in concurrent experiments. Fish of the same parentage and size as those in the model streams were placed in insulated streamside troughs, where they were fed live *Tubifex* at rations ranging from near maintenance to near repletion. The troughs received water directly from the model streams, and temperature differences between the troughs and streams were never greater than 0.3°C. Ten-day growth experiments were carried out once each season during 1973. Each experiment was preceded by a 10-day period of acclimation to temperature and ration size. Numbers of individuals tested at each ration level ranged from 10 to 20 depending upon fish size.

Average relative growth rates (Warren 1971) of the salmon were calculated as:

$$ARG = \frac{\bar{W}_2 - \bar{W}_1}{0.5\,(\bar{W}_1 + \bar{W}_2)\cdot t}$$

where ARG represented growth, $\bar{W}_1$ and $\bar{W}_2$

represented the mean weights of the fish at the beginning and end of the sampling interval, and t was the sampling interval in days. Growth was assumed to be linear over the relatively short 3-wk period. Relative growth rates, which were essentially the same as instantaneous growth rates, were considered more appropriate for comparison with relative food consumption rates.

Average biomass ($\bar{B}$) was calculated as:

$$\bar{B} = \frac{B_1 + B_2}{2}$$

where B_1 and B_2 represented the total weights of the fish at the beginning and end of the sampling interval.

Production during each sampling interval was calculated as the product of average relative growth rate (ARG) and average biomass ($\bar{B}$).

The conversion of wet weights to calories was accomplished by relating caloric content of tissue to condition factors of the fish, where condition factor was taken as 100 times a fish's weight (g) divided by the cube of its fork length (cm). Figure 9 of Warren et al. (1964:630), describing this relationship for cutthroat trout, *Salmo clarki*, was used for graphical estimates of calories per gram of wet weight for juvenile chinook salmon.

RESULTS

Temporal Changes in Production

Total production of chinook salmon in the heated stream was less than half that of the control in 1972 (Table 1). During the following year, production in the control stream was approximately 30% higher than in the heated stream. Mortality was greatest immediately after release into the streams, with populations attaining fairly stable levels by late summer. Population biomasses rose during winter and spring, were highest during late spring, and gradually declined through summer and fall. The mean annual biomass in the

TABLE 1.–Mean production statistics of experimental chinook salmon populations. H = heated stream, C = control stream.

Time interval	Individual size (kcal)		Population size (no.)		Mortality rate (%/day)		Biomass (kcal/m²)		Growth rate (cal·kcal/day)		Production (kcal/m²)	
	H	C	H	C	H	C	H	C	H	C	H	C
1972:												
20 Dec. -24 Jan.	0.31		302		1.61		4.12		1.85		0.27	
25 Jan. -14 Feb.	0.49		169		0.46		3.09		21.48		1.39	
15 Feb. - 7 Mar.	0.84	0.48	140	358	1.22	0.62	4.20	7.24	26.50	3.08	2.23	1.14
8 Mar. -27 Mar.	1.18	0.92	112	271	0.74	0.81	5.14	8.62	16.00	33.03	1.73	5.42
28 Mar. -15 Apr.	1.41	1.32	91	233	1.23	0.73	5.38	11.91	9.31	19.21	0.95	4.26
16 Apr. - 6 May	2.18	2.01	65	184	1.63	1.39	5.32	14.04	23.80	47.42	2.27	5.89
7 May -27 May	2.77	2.79	47	145	0.92	0.50	5.29	15.82	11.35	15.48	1.26	5.14
28 May -16 June	3.61	3.36	40	125	0.48	0.84	5.80	17.61	13.17	9.27	1.53	3.27
17 June - 7 July	4.36	3.75	34	105	0.88	0.75	6.25	16.97	8.96	5.22	1.18	1.86
8 July -28 July	4.53	4.32	31	92	0.01	0.35	6.26	16.97	1.82	6.73	0.24	2.40
29 July -22 Aug.	4.82	4.35	26	85	1.24	0.34	5.26	16.65	2.48	0.28	0.34	0.12
23 Aug. - 8 Sept.	5.68	4.74	19	67	0.84	2.03	4.65	13.84	9.64	5.05	0.76	1.19
9 Sept.- 3 Oct.	5.79	5.01	17	52	0.22	0.15	4.56	11.52	0.77	2.22	0.09	0.64
4 Oct. -19 Oct.	5.61	5.76	16	48	0.74	0.61	4.15	11.87	−1.44	9.29	−0.13	1.65
20 Oct. - 7 Nov.	6.15	5.73	14	46	0.35	0.01	3.88	12.01	4.83	−0.27	0.36	−0.06
8 Nov. -30 Nov.	6.45	5.50	14	45	0.00	0.01	4.01	11.49	2.07	−1.78	0.19	−0.47
Total											14.66	32.45
Mean							4.84	13.33				
1973:												
16 Mar. - 7 Apr.	0.98	1.02	187	185	0.57	0.66	7.14	7.48	14.49	12.70	2.38	2.19
8 Apr. -26 Apr.	1.57	1.48	154	168	1.23	0.15	8.93	9.55	24.36	19.37	4.13	3.51
27 Apr. -18 May	3.33	2.75	109	150	1.74	0.89	12.14	14.42	32.65	27.30	8.72	8.66
19 May - 7 June	4.69	3.63	65	106	2.42	2.26	11.85	15.37	17.85	14.52	4.02	4.24
8 June -27 June	6.92	4.98	41	63	1.09	1.75	10.82	12.33	19.31	15.68	4.16	3.87
28 June -19 July	7.31	5.99	34	45	0.42	0.90	11.00	11.22	2.49	8.37	0.60	2.07
20 July - 9 Aug.	6.87	6.96	32	41	0.30	0.01	10.31	12.07	−2.96	7.13	−0.64	1.81
10 Aug. -30 Aug.	7.00	7.10	30	40	0.15	0.12	9.46	12.78	0.89	0.95	0.18	0.25
31 Aug. -19 Sept.	6.76	7.89	29	37	0.17	0.75	9.07	12.61	−1.66	5.02	−0.32	1.33
20 Sept.-10 Oct.	6.48	8.23	29	33	0.00	0.28	8.73	12.09	−2.01	2.01	−0.37	0.51
11 Oct. -31 Oct.	6.35	9.00	26	29	0.86	0.78	7.58	11.36	−0.97	4.26	−0.15	1.02
1 Nov. -21 Nov.	6.65	8.71	22	25	0.59	0.53	6.50	10.06	2.18	−1.56	0.30	−0.33
22 Nov. -12 Dec.	6.07	8.66	19	23	0.91	0.20	5.49	9.08	−4.34	−0.27	−0.50	−0.05
Total											22.51	29.08
Mean							9.16	11.57				

heated stream was about twice as high in 1973 as in 1972, while average biomasses were slightly reduced following repairs in the control stream. Peak production in both streams occurred from April to June (Table 1, Figure 3), this being related to the high growth rates that took place during spring. Differences in production between the streams, however, were related primarily to higher population biomasses maintained in the control stream than in the heated stream, rather than to differences in growth rate.

Production of salmon in the heated stream during the spring, 1973, was higher than in the spring 1972 (Figure 3). The fish were stocked as fry in 1973, whereas in 1972 they were introduced as eyed eggs. The low average growth rate and survival (Table 1) of fish reared in the heated stream from the egg stage suggest that production was influenced by conditions during early development. Some individuals grew very rapidly during their first few weeks of residence; others apparently did not make the transition to feeding in the heated stream and died from the effects of starvation. Negative production occurred during fall months, when many fish had stopped growing and some were losing weight.

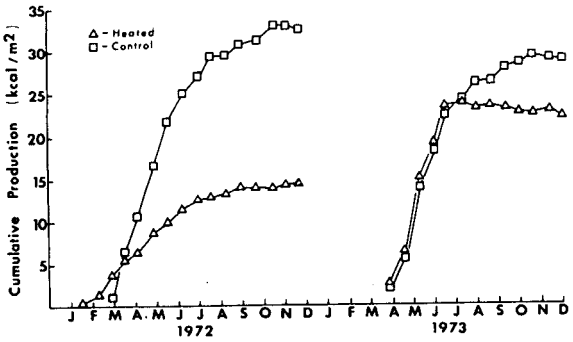

FIGURE 3.—Cumulative production of juvenile chinook salmon during 1972 and 1973.

Direct Temperature Effects on Growth

Relationships between average relative growth rate and food consumption rate of juvenile chinook salmon held in water from the model stream (Figure 4) showed that differences between fish held in heated and unheated water were greatest at low rations and least at high rations. At low rations, control individuals were most efficient; at high levels, there was no appreciable difference except during spring when the elevated temperature facilitated increased food consumption and growth efficiency. The highest rations were close to the maximum amount of food that the young salmon would eat at one feeding in a day, and the graphs for summer and fall indicate that maximum consumption declined as individuals' size increased.

The relationships observed in the experiments between temperature, ration level, and fish size were consistent with the results of laboratory studies of sockeye salmon, *O. nerka* (Brett et al. 1969; Brett and Shelbourn 1975); coho salmon (Averett 1969); and steelhead trout, *Salmo gairdneri*, (Wurtsbaugh 1973). At low levels of food availability, increased metabolic requirements associated with elevated temperature resulted in reduced growth rates; at high levels of food availability, growth rates were not appreciably altered by thermal increases. If responses of juvenile chinook to the range of ration levels in the aquarium growth experiments approximated growth of fish in the model streams at differing consumption rates (Carline and Hall 1973), the growth rate data of Table 1 suggest that during most of the year the fish were feeding well below their maximum possible consumption. Only during certain periods in late winter and spring did growth rates approximate the maximum rates shown in Figure 4. From this we concluded that,

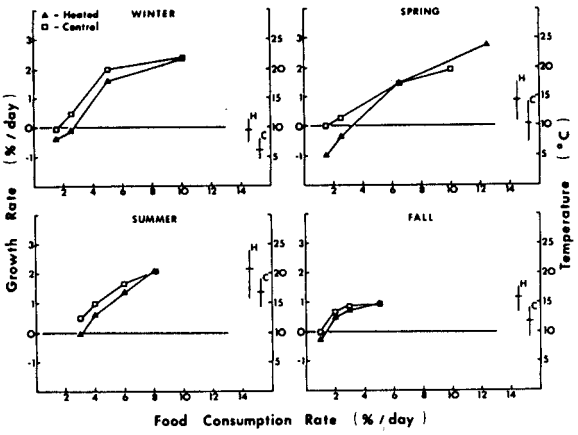

FIGURE 4.—Seasonal changes in the growth rates of juvenile chinook salmon. Experiments continued for 10 days and were preceded by 10 days of acclimation to temperature and ration size. Plotted values of growth rate at each feeding level were based upon the following numbers of fish: winter - 20; spring - 20; summer - 12; and fall - 10. Mean caloric contents (kcal) of the fish at the beginning of each experiment were: winter - 0.59; spring - 1.26; and summer - 7.05; and fall - 8.37.

during most of the year, the experimentally elevated temperature contributed directly to the reduced growth and production of the fish.

Disease

An unexpected indirect effect of elevated temperature was apparent protection from infestation by an intermediate stage of the trematode *Nanophyetus salmincola*, which was present in the streams from late spring through fall. Infective cercaria emerged from the snail *Oxytrema silicula* to encyst in the skin and tissues of juvenile chinook as metacercaria. The distinction between heavy vs. light infestation was made visually and was somewhat arbitrary (Figure 5): conspicuous bumps at the base of the caudal peduncle, darkening of fins, and papules on the body surface were considered symptoms of heavy infestation. While the parasite was obviously present in 1972, it was not until after its appearance in 1973 that attempts were made to quantify its effects.

Infestation rates in the heated stream remained low through summer and early fall and increased until termination of the experiment. Heavy infestations were present in most of the control fish soon after cercaria had begun emerging from the snails. In addition, a greater difference existed between the mean weights of heavily and lightly infested individuals in the control stream than in the heated stream. The impact of this parasite thus appeared to be more severe in the control than in the heated stream.

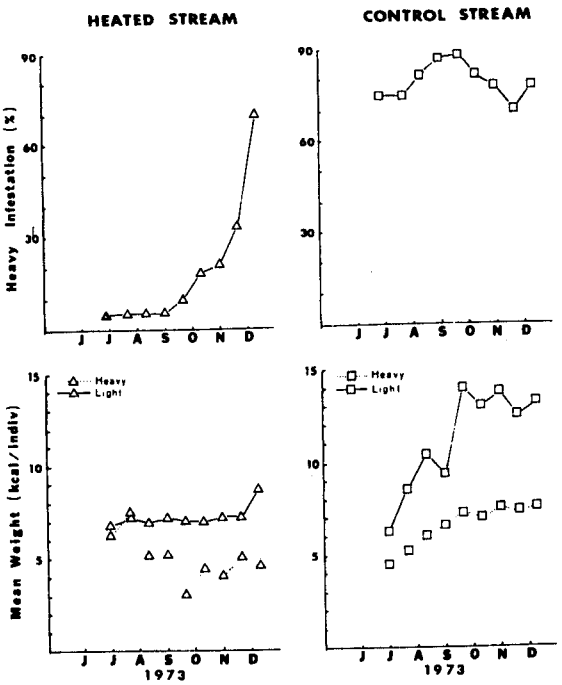

FIGURE 5.–Infestation rates and weight differences of juvenile chinook salmon infested by metacercaria of *Nanophyetus salmincola*.

Food Availability

An understanding of changes in food availability required: 1) that preferred food items be identified, 2) that it be determined when they were available for consumption, and 3) that their relative abundance was estimated under comparable circumstances. In this study, the second requirement was met through observation; food organisms became available only when they entered the drift and then mainly during daylight. Unlike many other salmonids, juvenile spring chinook salmon placed in the model streams were never seen feeding on invertebrates in the benthos. The extent of feeding during darkness was not determined, but was believed to be small. Identical sampling procedures were assumed to fulfill the third requirement, although differential consumption of food before it entered the drift nets could have caused some error.

Oligochaetes were almost completely excluded from the diet of large fish even though they composed an important fraction of the drift (Table 2). Mollusca (exclusively *Gyraulus* sp.) and Trichoptera were comparatively large food items and were consumed more readily by large fish than by small fish. Ostracod *Herpetocypris chevreuxi* was taken throughout the year in proportion to its relative abundance, while Ephemeroptera and Chironomidae–generally small organisms that were usually numerous in the drift–were preferred by smaller fish although these groups were always major components of the diet. In general, differences in food habits between populations in the streams were related to differences in the relative abundance of various food groups. One exception was the greater consumption of terrestrial forms (primarily aphids and spiders) by fish in the heated stream, despite approximately equal input of these invertebrates into both streams.

Measurements of food organisms drifting during daylight hours (Figure 6) were not well correlated with measurements of the biomass of those organisms in the riffle benthos (Figure 7).

TABLE 2.—Average percentages of different taxa (by weight) in the food of juvenile chinook salmon compared with percentages of those organisms in the day drift (in parentheses). H = heated stream, C = control stream.

	Oligochaeta		Mollusca		Ostracoda		Collembola		Ephemeroptera	
Season	H	C	H	C	H	C	H	C	H	C
1972:										
Winter	0(45)	<1(24)	1(4)	0(5)	5(4)	0(0)	1(<1)	0(4)	2(4)	30(2)
Spring	0(43)	0(37)	0(13)	0(4)	18(7)	4(2)	<1(<1)	<1(<1)	11(3)	45(24)
Summer	1(34)	<1(56)	0(5)	0(2)	32(28)	3(3)	<1(1)	0(<1)	10(<1)	10(8)
Fall	<1(7)	0(13)	2(18)	0(4)	7(4)	4(5)	7(1)	4(1)	12(15)	4(6)
1973:										
Spring	13(14)	15(43)	0(6)	<1(<1)	4(7)	1(<1)	<1(<1)	0(<1)	22(11)	25(6)
Summer	6(3)	1(8)	11(7)	1(2)	12(8)	4(11)	<1(<1)	<1(<1)	10(8)	30(18)
Fall	<1(6)	<1(1)	54(33)	4(5)	4(4)	<1(1)	6(2)	4(2)	4(3)	18(19)

	Plecoptera		Trichoptera		Chironomidae		Terrestrials		Miscellaneous	
Season	H	C	H	C	H	C	H	C	H	C
1972:										
Winter	25(9)	52(42)	0(0)	0(0)	51(26)	16(3)	14(10)	2(14)	<1(<1)	<1(<1)
Spring	12(7)	6(3)	3(<1)	5(21)	27(24)	36(6)	27(2)	7(2)	2(<1)	1(<1)
Summer	1(1)	4(<1)	<1(<1)	9(1)	49(65)	67(36)	2(2)	5(8)	2(5)	2(1)
Fall	2(1)	33(13)	21(1)	25(4)	33(39)	27(33)	14(10)	1(18)	<1(4)	1(1)
1973:										
Spring	<1(<1)	1(<1)	9(<1)	3(<1)	44(30)	49(32)	5(23)	2(16)	2(8)	3(1)
Summer	<1(3)	11(2)	11(1)	12(6)	38(65)	26(36)	8(2)	11(16)	2(3)	4(2)
Fall	<1(1)	9(5)	1(4)	33(10)	11(35)	25(55)	20(6)	7(2)	1(6)	1(1)

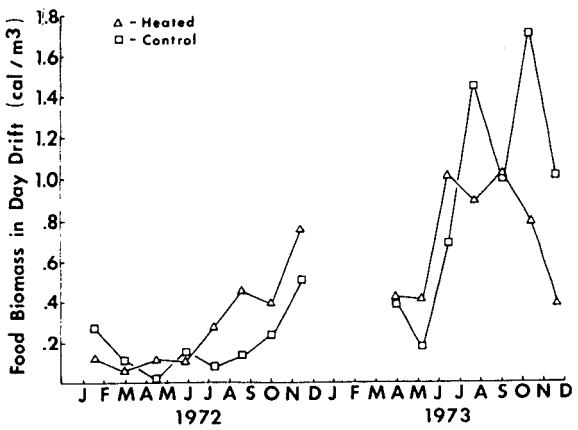

FIGURE 6.—Seasonal changes in the biomass of food organisms present in the day drift. Each point is the mean of two triweekly samples.

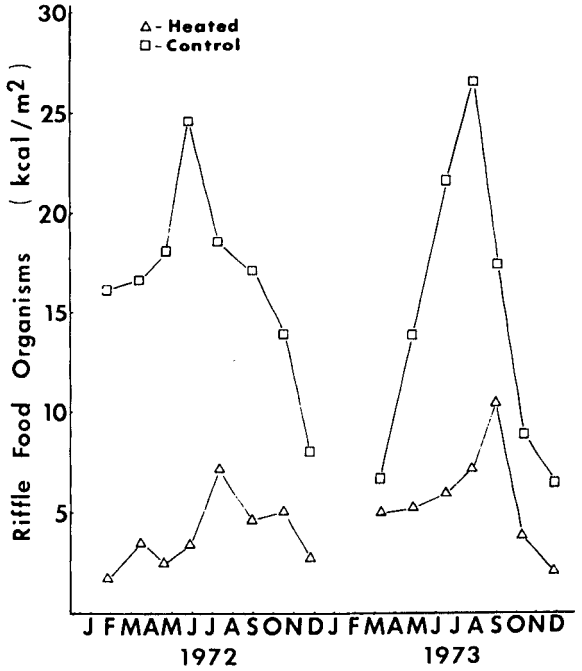

FIGURE 7.—Seasonal changes in the biomass of food organisms present in the riffle benthos. Each point is the mean of two triweekly samples.

Moreover, seasonal patterns in drift differed greatly between 1972 and 1973, with both streams exhibiting higher drift biomasses during the second year than during the first. Although benthic biomasses were significantly greater in the control than in the heated stream, ($P<0.001$, paired t-test), these differences were often not translated into drift; in fact, during the latter part of 1972 and spring 1973, more food was available in the heated stream. No explanation was found for increased drift in 1973 relative to 1972, but it appeared that increased food availability in 1973 resulted in more growth, higher biomasses, and increased production of fish in the heated stream. Why production in the control stream population did not reflect the greater abundance of food is not

TABLE 3.—Annual average biomasses (cal/m^2), drift rates (cal/m^3), and drift ratios of selected aquatic taxa, excluding winged adults. Drift ratios were calculated according to the formula (day drift/riffle biomass) × 10^5. Asterisks denote values for the heated stream that were significantly different (P<0.05, single classification analysis of variance) from the control.

	1972						1973					
	Heated			Control			Heated			Control		
Taxon	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio
Oligochaeta	6,532	0.117	1.74	10,698	0.106	1.43	4,112	0.036	1.26	4,034	0.043	1.56
Mollusca[1]	778	0.031	2.71	127	0.008	6.98	906	0.104	13.18	132	0.029	29.08
Ostracoda	703	0.055	23.63	177	0.010	8.87	273	0.036	29.23	218	0.030	28.40
Ephemeroptera	308	0.024	12.14*	7,812	0.011	0.23	430	0.031	8.46	4,150	0.102	3.12
Plecoptera	378	0.009	7.95*	5,966	0.033	0.59	173	0.002	20.37*	3,717	0.035	1.32
Trichoptera	516	0.001	0.22	1,643	0.018	0.36	570	0.010	5.86	1,569	0.039	2.48
Chironomidae	1,202	0.021	3.26*	1.661	0.011	0.95	2,549	0.052	2.20	1,979	0.045	3.67

[1]*Gyraulus* sp.

known, although severity of infestation by *Nanophyetus* was not compared over the 2 yr and may have been more serious in 1973.

In 1972, drift ratios (the ratio of drift to biomass) of several invertebrate taxa were higher in the heated stream than in the control (Table 3). The next year some of the drift ratios increased, and although many were higher in the control stream, the differences were not statistically significant. Of taxa showing increased drift ratios in the heated stream, Ephemeroptera and Plecoptera were most consistently influenced by elevated temperature. In 1972, Chironomidae also exhibited a significantly greater tendency to drift in the heated stream than in the control. These three groups were important components of both the day drift and the diet of juvenile salmon and often contributed to the greater availability of food in the heated stream than in the control during certain periods.

Fewer macroinvertebrate taxa were present in the heated stream than in the control. Paired t-tests indicated that number of taxa were significantly different in both riffles (treatment mean = 21, control mean = 34; P<0.001) and pools (treatment mean = 16, control mean = 19, P<0.01). Most of those taxa that were unique to one stream or the other were very rare and contributed little to fish production. Major biomass differences arose because many taxa had greater population densities in the control while only a few fared better in the heated stream. The several taxa that did exhibit higher biomass in the heated stream were very abundant and tended to dominate the bottom fauna to a greater extent than did common taxa in the control. The two most abundant invertebrates in the heated stream were *Oxytrema silicula* in the riffles and *Limnodrilus* sp. in the pools. Neither of these two species was consumed in significant quantities by the young salmon; thus, increased dominance in the heated stream did not give rise to greater food availability.

Periphyton Biomass and Sedimentation

Plants and detritus were significantly more abundant in the heated stream (P<0.001, paired t-test) than in the control (Figure 8). The greater amounts of plants and detritus in the heated

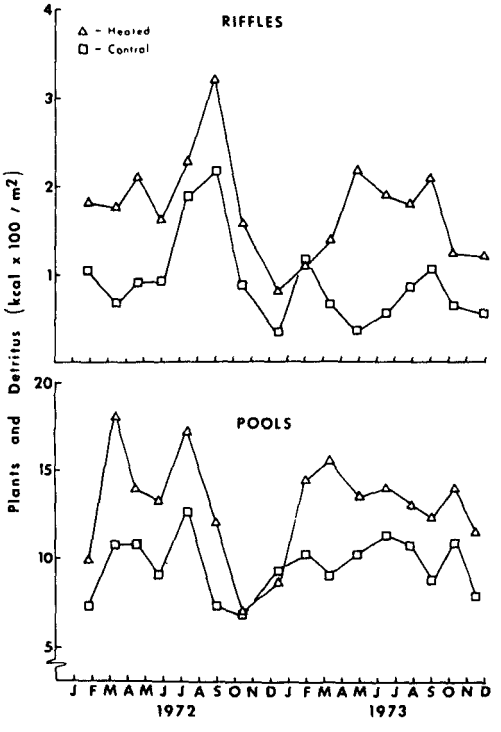

FIGURE 8.—Biomasses of plants and detritus in riffles and pools of the model streams. Each point is the mean of two triweekly samples.

stream than in the control were due to the high densities of filamentous algae in the riffles and the considerable accumulation of organic detritus in the pools. Increased primary production associated with elevated temperature in laboratory streams has been measured by Kevern and Ball (1965) and Phinney and McIntire (1965). The dominant algal species in our model streams, *Cladophora glomerata*, grows rapidly at high temperatures (Whitton 1971; Adams and Stone 1973).

Heavy growths of algae on the riffles apparently accelerated sedimentation rates in the heated stream (Table 4) by acting as filters to trap and consolidate fine particles introduced with exchange water. In the pools, where filamentous algae did not grow, fine sediment levels in both streams were similar. By indirectly enhancing sediment accumulation, elevated temperature probably had an important effect on the numbers of food organisms available to salmon in the heated stream. Hynes (1960) described how siltation alters the habitat of many invertebrates, with the result usually being a reduction in benthic biomass (Cordone and Kelly 1961). Greatly reduced mean annual biomasses of Ephemeroptera, Plecoptera, and Trichoptera in the heated stream (Table 3) compared with the control suggest that these groups were influenced by the amount of fine sediments in the substrate, and these insects were often preferred food items of the fish (Table 2).

TABLE 4.–Levels of fine sediments, expressed as grams dry weight per square meter, in the model streams during May 1974. The figures in parentheses refer to the amount of time that had elapsed since a major disturbance to the riffles.

Item	Particle size (mm)		
	0.175-1	0.088-0.175	0.088
Riffles:			
Control (17 mo)	41	19	169
Heated (17 mo)	147	37	943
Heated (31 mo)	167	91	1,443
Pools:			
Control	94	1,219	1,746
Heated	86	1,064	1,728

DISCUSSION

Our study was designed to examine the effects of elevated temperature on the production of juvenile chinook salmon. The constantly elevated temperature was not meant to simulate a particular type of thermal increase, but was within the range of temperature elevations caused by heated discharges into running waters (Wilber 1969, Parker and Krenkel 1970), irrigation runoff (Eldridge 1963), and removal of streamside vegetation (Brown and Krygier 1970). It was also within the limits of temperature increase legally allowed by some regulations (Burd 1969).

Both direct and indirect temperature effects influenced chinook salmon production, but the magnitude of these effects varied seasonally. Production was high in spring because temperature was in a range that was favorable to growth, parasitism had not yet become an important factor, and the small fish were able to efficiently exploit available food. Summer was generally a period of declining production because high temperatures resulted in an increase in maintenance requirements and, for the control stream, because parasites had attacked the majority of the population. Low production during late summer and fall was associated with high levels of infestation and the ineffectiveness of large fish in exploiting small organisms that were abundant in the drift.

The lack of correlation that existed between growth rates (Table 1) and food availability (Figure 6) may have been related to the species composition of drifting invertebrates. A high percentage of summer and fall drift was composed of very small forms such as oligochaetes (*Nais communis*) and chironomids (Table 2). During those seasons, tiny organisms were not preferred food items of the young salmon, which were larger and less numerous than during the spring. High growth rates exhibited by fish during winter and spring when drift rates were comparatively low suggest that smaller, more abundant fish were able to utilize the entire range of sizes of invertebrate species that left the substrate. It was impossible to determine whether food size preference affected fish in the two streams identically, but based on overall invertebrate composition (Table 3), taxa containing species of large size (Ephemeroptera, Plecoptera, Trichoptera) were more abundant in the control than in the heated stream. This was reflected in higher growth rates of salmon in the control than in the heated stream during summer and fall. Clearly, more intensive examination of the relationship between prey size and prey selection by salmonids is needed.

Low benthic invertebrate biomasses in the heated stream were associated with increased sedimentation rates and reduced numbers of taxa. Iverson (1972) suggested that the poor success of certain invertebrates in the heated stream was

due to their being cold-adapted species. No large scale mortality of larvae or pupae was detected in the heated stream, even during summer months. However, very early developmental stages and life history patterns may have been altered (Macan 1961a, b; Hynes 1970).

The tendency of certain invertebrates in the heated stream to enter the drift in greater proportion to their benthic biomasses (Table 3) was probably related both to elevated temperature and to fine sediment levels. Increased drift associated with increasing temperature was described for certain invertebrates by Müller (1963), Waters (1968), and Pearson and Franklin (1968). In other studies, significant positive correlations between drift and temperature have not been detected (Bishop and Hynes 1969; Wojtalik and Waters 1970; Müller 1970; Reisen and Prins 1972). Experimental additions of sediments to a stream were found by Rosenberg and Weins (1975) to significantly increase the drift of some invertebrate taxa and to have inconsistent effects on others.

Although the influence of elevated temperature on the production of juvenile chinook salmon was complex, we were able to identify both beneficial and harmful effects. The fish benefited in several ways. First, the temperature increase may have stimulated higher consumption rates when suitable food was very abundant, although this condition was rarely achieved. Second, higher temperatures afforded protection from infestation by a trematode parasite, which heavily infested the majority of individuals in the control stream. Third, certain invertebrates may have been stimulated to enter the drift and thus became more available as food. Fish were harmed in at least two ways. First, growth efficiencies were lowered at all but the highest consumption levels. Second, despite high drift ratios of some taxa, food availability was generally reduced because preferred food organisms were much less abundant in the substrate of the heated stream than in the control. The net result was that salmon production in the heated stream was about 50% less in 1972 and 25% less in 1973 compared with the unheated stream.

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LITERATURE CITED

ADAMS, M. S., AND W. STONE.
1973. Field studies on photosynthesis of *Cladophora glomerata* (Chlorophyta) in Green Bay, Lake Michigan. Ecology 54:853-862.

ANDERSON, N. H.
1967. Biology and downstream drift of some Oregon Trichoptera. Can. Entomol. 99:507-521.

AVERETT, R. C.
1969. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. Thesis, Oregon State Univ., Corvallis, 75 p.

BISHOP, J. E., AND H. B. N. HYNES.
1969. Downstream drift of the invertebrate fauna in a stream ecosystem. Arch Hydrobiol. 66:56-90.

BRETT, J. R., AND J. E. SHELBOURN.
1975. Growth rate of young sockeye salmon, *Oncorhynchus nerka*, in relation to fish size and ration level. J. Fish. Res. Board Can. 32:2103-2110.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP.
1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

BROWN, G. W., AND J. T. KRYGIER.
1970. Effects of clear-cutting on stream temperature. Water Resour. Res. 6:1133-1139.

BURD, R. S.
1969. Water quality standards for temperature. *In* F. L. Parker and P. A. Krenkel (editor), Engineering aspects of thermal pollution, p. 72-77. Vanderbilt Univ. Press, Nashville.

CARLINE, R. F., AND J. D. HALL.
1973. Evaluation of a method for estimating food consumption rates of fish. J. Fish. Res. Board Can. 30:623-629.

CORDONE, A. J., AND D. W. KELLEY.
1961. The influences of inorganic sediment on the aquatic life of streams. Calif. Fish Game 47:189-228.

CUMMINS, K. W.
1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Am. Midl. Nat. 67:477-504.

CUMMINS, K. W., AND J. C. WUYCHECK.
1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. 18:1-158.

ELDRIDGE, E. F.
1963. Irrigation as a source of water pollution. J. Water Pollut. Control. Fed. 35:614-625.

HYNES, H. B. N.
1960. The biology of polluted waters. Liverpool Univ. Press, Liverpool, 202 p.
1970. The ecology of running waters. Univ. Toronto Press, Toronto, 555 p.

IVERSON, R. A.
1972. Effects of elevated temperature on juvenile coho salmon and benthic invertebrates in model stream communities. Ph.D. Thesis, Oregon State Univ., Corvallis, 98 p.

KEVERN, N. R., AND R. C. BALL.
1965. Primary productivity and energy relationships in artificial streams. Limnol. Oceanogr. 10:74-87.

MACAN, T. T.
1961a. Factors that limit the range of freshwater animals. Biol. Rev. (Camb.) 36:151-198.
1961b. A review of running water studies. Int. Ver. Theor. Angew. Limnol. Verh. 14:587-602.

MÜLLER, K.
1963. Diurnal rhythm in organic drift of *Gammarus pulex*. Nature (Lond.) 198:806-807.
1970. Die Drift von Insektenlarven in Nord - und Mitteleuropa. Österr. Fisch. 23:111-117.

PARKER, F. L., AND P. A. KRENKEL.
1970. Physical and engineering aspects of thermal pollution. CRC Press, Cleveland, 100 p.

PEARSON, W. D., AND D. R. FRANKLIN.
1968. Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. Ecology 49:75-81.

PHINNEY, H. K., AND C. D. MCINTIRE.
1965. Effect of temperature on metabolism of periphyton communities developed in laboratory streams. Limnol. Oceanogr. 10:341-344.

REISEN, W. K., AND R. PRINS.
1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. Ecology 53:876-884.

ROSENBERG, D. M., AND A. P. WEINS.
1975. Experimental sediment addition studies on the Harris River, N.W.T., Canada: the effect on macro-invertebrate drift. Int. Ver. Theor. Angew. Limnol. Verh. 19:1568-1574.

WARREN, C. E.
1971. Biology and water pollution control. W. B. Saunders Co., Phila., 434 p.

WARREN, C. E., J. H. WALES, G. E. DAVIS, AND P. DOUDOROFF.
1964. Trout production in an experimental stream enriched with sucrose. J. Wildl. Manage. 28:617-660.

WATERS, T. F.
1968. Diurnal periodicity in the drift of a day-active stream invertebrate. Ecology 49:152-153.

WHITTON, B. A.
1971. Terrestrial and freshwater algae of Aldabra. Philos. Trans. R. Soc. Lond., Ser. B., Biol. Sci. 260:249-255.

WILBER, C. G.
1969. The biological aspects of water pollution. Charles C. Thomas, Springfield, Ill., 296 p.

WOJTALIK, T. A., AND T. F. WATERS.
1970. Some effects of heated water on the drift of two species of stream invertebrates. Trans. Am. Fish. Soc. 99:782-788.

WURTSBAUGH, W. A.
1973. Effects of temperature, ration, and size on the growth of juvenile steelhead trout, *Salmo gairdneri*. M.S. Thesis, Oregon State Univ., Corvallis, 69 p.

REPRODUCTIVE CYCLE, FECUNDITY, AND SEX RATIOS OF THE RED PORGY, *PAGRUS PAGRUS* (PISCES: SPARIDAE) IN NORTH CAROLINA

CHARLES S. MANOOCH, III[1]

ABSTRACT

Macroscopic examination of gonads and gonad indices demonstrated that March and April were the peak spawning months in Raleigh and Onslow bays, N.C. Ripe fish were collected over irregular bottom from January to April in water ranging from 21 to 100 m in depth. Bottom temperatures during the spawning period ranged from 16.4° to 21.5°C. Three predictors of fecundity, total length, weight, and age were evaluated and regression equations derived. Fish weight proved to be the most precise predictor of fecundity: ln fecundity = 1.7369 + 1.5178 (ln weight of the fish) where fecundity is the total number of eggs in both ovaries. Fecundity estimates ranged from 48,660 for a 304-mm (390-g) red porgy to 488,600 for a 516-mm (1,783-g) fish. Although some individuals reached sexual maturity at age II, most spawn for the first time at age III. Chi-square tests revealed a significant departure from the expected 1:1 sex ratio when data were stratified by month, year, and size. Females were encountered more frequently each month for all 3 yr, and in the smaller size intervals.

The red porgy, *Pagrus pagrus* Linnaeus, is one of the most important demersal marine fishes taken by recreational anglers fishing from headboats[2] between Cape Hatteras, N.C., and Charleston, S.C. In 1972 and 1973, 513,700 red porgy weighing 1.3 million pounds were taken by this sport fishery (Sekavec and Huntsman 1972; Huntsman 1976). In spite of the importance of the species, published information on the red porgy in the western Atlantic is scarce. Dias et al. (1972) described the length-weight relationship for *Pagrus* collected off South Carolina; Ciechomski and Weiss (1973) reported on egg, embryo, and larval development of red porgy from the Argentine Sea; and Manooch et al. (in press); Manooch (in press), discussed the taxonomic status and the food habits of *P. pagrus*, respectively.

This study investigated reproduction of red porgy in North Carolina to determine: 1) spawning season, 2) size and age of females at sexual maturity, 3) prediction equations for estimating fecundity, 4) sex ratios by month and size, 5) spawning ecology, and 6) a description of the eggs and young. This research is part of a National Marine Fisheries Service project which is studying the bottom fishes of the outer continental shelf of the Carolinas.

MATERIALS AND METHODS

Length, weight, sex, stage of gonad development, and gonad length and weight were recorded for fish sampled from North Carolina headboats and by experimental fishing aboard the RV *Onslow Bay* from 1972 to 1974. Gonads were preserved in 10% Formalin[3] and macroscopically examined to determine maturity using modified criteria from Orange (1961): Stage 1-S: infantile, gonads small and ribbonlike (sex determination by gross examination not possible); Stage 1: immature, gonads elongated, slender, but sex discernible by gross examination; Stage 2: early maturing, gonads slightly enlarged, individual ova not visible to naked eye; Stage 3: late maturing, gonads enlarged, individual ova visible to naked eye; Stage 4: ripe, ovary greatly enlarged, many ova translucent and easily dislodged from follicles or loose in lumen of ovary; and Stage 5: spawned, includes recently spawned fish with mature ova occurring as remnants in various stages of reabsorption.

Time of spawning based on 243 females was determined by using: 1) the gonad index (G.I.) of Schaefer and Orange (1956), and 2) the index: 100G.W./F.W., where G.W. is the fresh gonad weight to the nearest 0.01 g and F.W. is the body weight of the fish to the nearest 1.0 g. Mean values

[1]Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[2]Headboats are those that charge for a day's fishing on a per person basis.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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of these indices were plotted monthly, to thus indicate duration and peak of spawning, and age and size at sexual maturity. The linear regressions fecundity on length, weight, and age were calculated based on mature (Stage 4) ovaries from 50 females (ages II-IX, 304 to 520 mm TL) collected from January through March for the years 1973 and 1974. One ovary randomly selected from each pair was blotted dry and weighed to the nearest 0.01 g. The selected ovary was crumbled and all ovarian tissue removed. The eggs were then filtered, blotted dry, and weighed. One sample from each ovary of 0.2-0.4 g was weighed to the nearest 0.001 g and placed in a 6 × 6 counting grid and all ova were counted. The formula:

$$Y = \frac{(W)(W_i')}{(W_i)(w)} \quad y$$

was used to estimate the number of eggs in the ovaries, where Y = total number of eggs in both ovaries, W = weight of both ovaries, W_i = weight of selected ovary, W_i' = weight of ovary after removal of ovarian tissue, w = weight of sample, and y = number of eggs in the sample (Lassiter 1962).

RESULTS AND DISCUSSION

Sexual Maturity

Ovary condition progressed from ripe, Stage 4, dominant from January through March, to spawned, Stage 5, dominant from May through June, indicating that peak spawning occurred in March and April (Figure 1). Ovaries collected in April and May were flaccid and showed resorption of eggs. By June all of the fish were early maturing. The ovaries gradually became more firm after resorption in early summer and little change in gonad condition was noted in late summer and early fall. Maturation of ovaries occurred between October and January. Stratification of the sexual maturity data by month supported the hypothesis of late winter to early spring spawning. Approximately 23% of the fish examined in January were late maturing and 77% were ripe. By February, 12.5% were classified as late maturing, and 87.5% were ripe. The first spawned (Stage 5) fish were collected in March and their frequency of occurrence increased to 60.5% in April (Figure 2). Walker (1950) reported ripe *P. pagrus* in January and February off North Carolina, and Ranzi (1969) found that they were sexually mature from April to June in the Mediterranean Sea off Algeria.

Early maturing and ripe stages of males were easily discernible by gross examination of the testes, but the late maturing and ripe classes were difficult to separate. Milt could be pressed from the

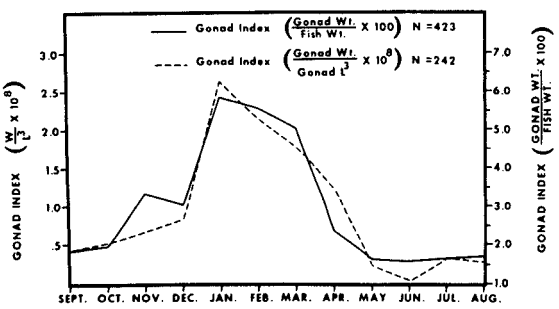

FIGURE 1.–Mean monthly gonad indices for female *Pagrus pagrus* collected from Onslow Bay, N.C., 1972 to 1974.

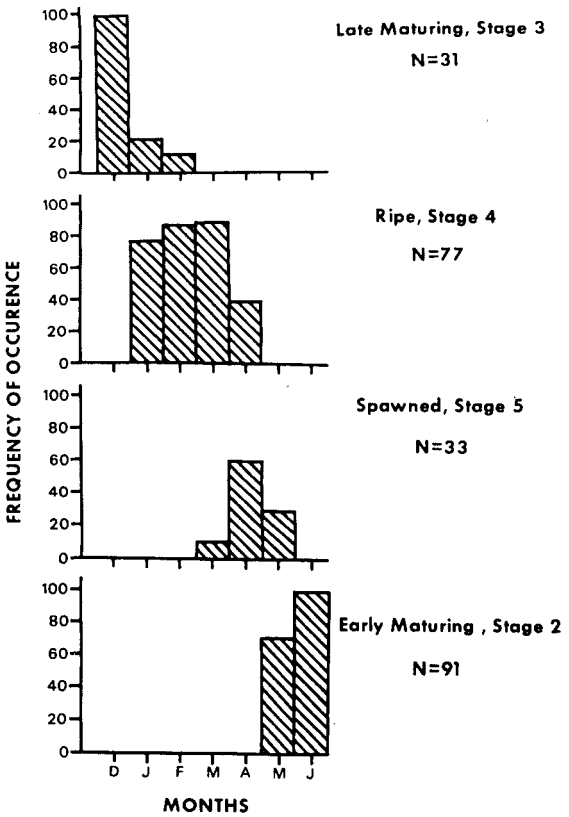

FIGURE 2.–Percentage of female red porgy at various stages of sexual maturity, collected in Onslow and Raleigh bays, N.C., by month.

central canal of testes from January through April.

Female red porgy were separated into two maturity classes: Immature fish, and mature (maturing, ripe, and spawned). No individuals less than 260 mm and all fish greater than 360 mm were sexually mature (Table 1). The linear regression of percent maturity (Y) on total length (X):

$$Y = -211.2946 + 0.8576X, r = 0.94,$$

was significant at $\alpha = 0.01$. Half the females were mature at 304 mm. By inserting age data (Manooch 1975) to the graph, age at sexual maturity was determined. Regression of age with length suggests that none of the age I fish, 37% of the age II, 81% of the age III, and 100% of the age IV fish were mature. Some age II and III females apparently showed the characteristic, seasonal maturation of ovaries but did not spawn the first year, because several specimens had ovaries containing absorbed ova during the peak spawning period.

TABLE 1.—Number and percentage of female red porgy, grouped into 20-mm size categories, staged as immature and mature (maturing, ripe, and spawned) off North Carolina 1972-74.

Total length (mm)	Immature (no.)	Mature (no.)	Mature (%)
<220	22	0	0.0
220-239	1	0	0.0
240-259	4	0	0.0
260-279	8	4	33.3
280-299	11	2	15.4
300-319	5	7	58.3
320-339	4	29	87.9
340-359	5	34	87.2
360-379	0	57	100.0
380-399	0	80	100.0
400-419	0	75	100.0
420-600	0	214	100.0
Total	60	502	

Fecundity

Regression analyses indicated total length, weight, or age could be used to predict fecundity of red porgy, but weight proved to be the best predictor of fecundity ($r^2 = 0.70$) and had the lowest error mean square. Combinations of two independent variables, weight and length, improved predictability only slightly, therefore, separate equations were derived by using weight on fecundity, and length on fecundity. The equations describing the relationships (Figure 3) and coefficients of determination (r^2) are:

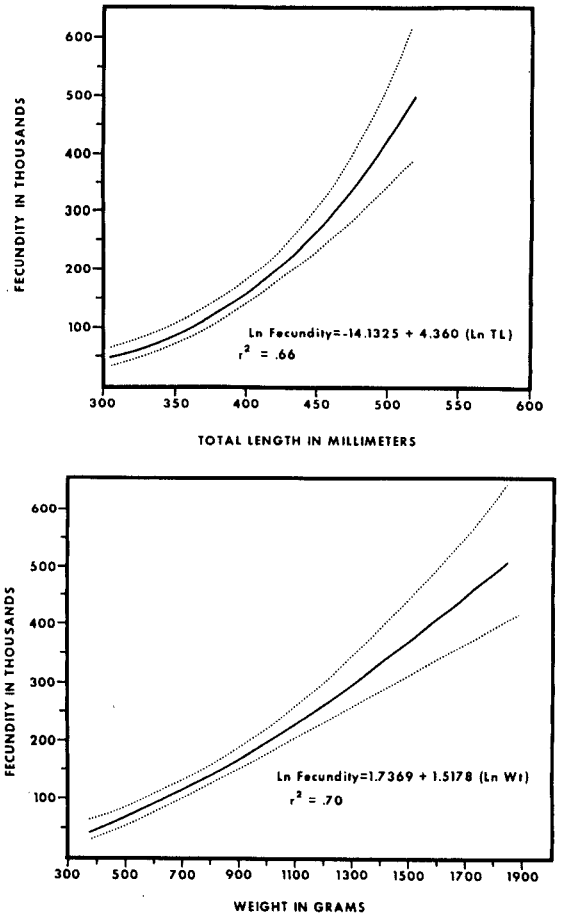

FIGURE 3.—Relationship between fecundity and two predictors: (top) length and (bottom) weight of 50 red porgy collected in Onslow Bay, N.C.

$$\ln \text{Fecundity} = 1.7369 + 1.5178(\ln \text{Wt}),\quad r^2 = 0.70 \text{ and}$$

$$\ln \text{Fecundity} = -14.1325 + 4.3598(\ln \text{TL}),\quad r^2 = 0.66.$$

The 95% confidence limits have also been calculated. Predicted fecundity ranges from 48,660 eggs for fish 304 mm TL and 390 g in weight to 488,600 ova for fish 516 mm TL and 1,783 g. Theoretically, a 600-mm red porgy which is not uncommon in the sport catch, could produce approximately 943,000 eggs if maximum ova production is not obtained at a smaller size.

Sex Ratios and Hermaphroditism

Sex of 736 red porgy collected in 1972, 1973, and 1974 was grouped by year and month, and data

revealed females to be more abundant in the catch than males (Table 2). The sex ratio was not 1:1 males to females as hypothesized but actually 1:2.1 when the years were combined. Data for each year analyzed separately also provided significant deviations from expected. The sex ratio for each year was 1:2.1, 1:1.9, and 1:3.3 for 1972, 1973, and 1974, respectively (Table 2). The overall, higher deviation from 1:1 for 1974 is because most of the fish were collected in late winter and spring of that year, months which reflected the greatest deviation from 1:1. Of all months examined, only August, September, and November were nonsignificant, revealing equal number of males and females. The ratio for October could not be tested because of insufficient data. During the spawning season, chi-square values were very high and perhaps reflect monosexual schooling.

Sex ratios for males and females grouped into 50-mm length intervals had significant departures from the expected 1:1 ratio for most size categories (Table 3). In general, females predominated in the smaller size classes, whereas males predominated in the larger size classes. The nonsignificant value for the smallest size interval is probably unrealistic since the sample is very small and the sequential intervals are highly significant in favor of females.

Both protandrous and protogynous hermaphroditism are relatively common among the sparids (D'Ancona 1950, 1956). *Pagrus pagrus* collected from the west coast of Florida appear to display protogynous hermaphroditism although data available are insufficient for quantitative description (D. S. Beaumariage pers. commun.).

TABLE 2.–Number of male and female red porgy collected by month during 1972, 1973, and 1974 with chi-square values obtained from testing a 1:1 sex ratio in each month (a), and each year (b).

Month	Year 1972	1973	1974	Total[a]	df	X^2
May	9:12	17:41	0:5	26:58	2	12.08**
June	16:22	26:45	—	42:67	1	5.74*
July	9:27	27:44	—	36:71	1	11.44**
Aug.	11:15	30:33	—	41:48	1	.55
Sept.	3:9	21:26	—	24:35	1	2.04
Oct.	1:9	—	—	1:9		
Nov.	2:3	12:15	—	14:18	1	.50
Dec.	5:15	3:11	—	8:26	1	9.52**
Jan.	—	0:2	9:22	9:24	1	6.82**
Feb.	—	5:12	8:32	13:44	1	16.86**
Mar.	—	5:26	4:32	9:58	1	17.92**
Apr.	—	6:29	10:10	16:39	1	9.62**
Total[b]	56:112	152:284	31:101	239:497		
df	7	10	4	11		
X^2	18.6**	39.96**	37.12**	90.44**		

* = $P<0.05$.
** = $P<0.01$.

TABLE 3.–Number of male and female red porgy grouped into 50-mm size categories with chi-square values assuming a 1:1 sex ratio.

Length	Male	Female	Total	X^2
<300	1	6	7	3.57
300-350	2	53	55	47.28**
351-400	10	157	167	129.40**
401-450	48	161	209	61.10**
451-500	124	83	207	8.12**
501-550	51	27	78	7.38**
551-600	3	10	13	3.76
>600	1	0	1	—
Totals	240	497	737	

* = $P<0.05$.
** = $P<0.01$.

The predominance of females at smaller size intervals in this study and discovery of individuals with both ovarian and testicular tissue supports the theory of protogyny. Although hermaphroditic red porgy were found by macroscopic examination, only 16 specimens of the 752 examined (2%) contained both male and female gonadal tissues. Hermaphroditic red porgy ranged in size from 325 mm to 424 mm TL ($\bar{x}$ = 400 mm); possibly the length range over which sexual transition takes place. In each fish the ovaries were dominant with only redundant testicular tissue present. From preliminary studies with red porgy in the Gulf, M. A. Moe (pers. commun.) reported that the male portion of the gonad develops in the muscular tunica of the gonad wall and eventually completely takes over the gonad.

Spawning

Ripe red porgy were collected over irregular bottom from January through April in water depth ranging from 21 to 100 m and bottom temperatures of 16.4° to 21.5°C (Figure 4). *Pagrus pagrus* spawns from December through January in the Argentine Sea when water temperature is approximately 20° to 21°C (Ciechomski and Weiss 1973).

The relationship of the gonad index to photoperiod and bottom temperature were plotted monthly (Figure 4). By inspecting this figure one could conclude that photoperiod is more directly correlated to gonad maturation and spawning. Similarly, gonad maturation of red grouper, *Epinephelus morio*, another demersal reef species, was unrelated to bottom temperature (Moe 1969). Harrington (1956) demonstrated the importance of photoperiod to gonad maturation and spawning

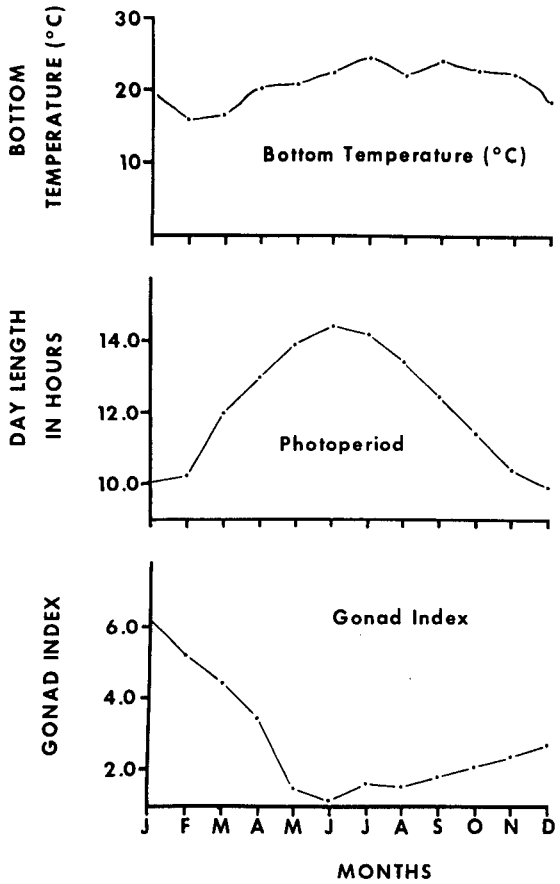

FIGURE 4.—Mean gonad indices for female *Pagrus pagrus* for each month compared with photoperiod and bottom temperatures.

for the banded sunfish, *Enneacanthus obesus*. *Pagrus pagrus* spawns between January and April, when photoperiod increases rapidly, but when bottom temperatures fluctuate irregularly. Gonads were in spent and resting stages during maximum photoperiod, May to August, and began developing as photoperiod decreased. The graphs suggest that seasonal increase in photoperiod in late winter and early spring initiates final maturation of ovaries and ultimately, the spawning of *P. pagrus*.

Eggs and Young

Red porgy eggs are pelagic, spherical, without appendages and contain a single oil droplet. Preserved eggs were generally yellow to orange in color, they measured 0.31 to 0.94 mm in diameter and the oil droplet was 0.20 to 0.32 mm in diameter. This size description is similar to the unfertilized eggs of another sparid, *Stenotomus chrysops*, which were 0.66 to 0.95 mm and had an oil droplet 0.17 to 0.40 mm in diameter (Finkelstein 1969). I induced three females (355-560 mm TL) to release ova in aquaria in March 1975. These eggs appeared transparent and were noticeably larger than those described above. Since I considered these eggs to be most representative of mature, unfertilized eggs, I recorded size for 10 eggs from each fish. Their mean size was 0.88 mm in diameter and ranged from 0.64 to 0.92 mm; the oil droplet averaged 0.25 mm in diameter. Very little difference was found in egg size for each fish.

Prejuvenile red porgy were collected in April off South Carolina. An 18-mm specimen had minute spines along the dorsal and ventral outlines of the body, and five to six vertical pigment bands (Figure 5). These bars appeared red on stressed adults. Ranzi (1969) described young *P. pagrus* from the Bay of Naples and referred to the vertical bands in specimens 13 mm and larger.

Forty-four juvenile *P. pagrus* ranging in length from 42 to 59 mm ($\bar{X}$ = 51 mm) were collected by trawl off Charleston in relatively shallow water (9-20 m); bottom temperatures ranged from 17.5° to 18.5°C. The fish were also collected in April, indicating spawning may occur slightly earlier in that area compared with Onslow Bay and Raleigh Bay, N.C.

SUMMARY AND CONCLUSIONS

Red porgy spawn in North Carolina waters from January through April with a peak in spawning activity between March and April. Maturation of gonads and spawning appear to be correlated with increased photoperiod. Spawning fish were collected over irregular bottom ranging from 21 to 100 m in depth. Bottom temperatures at these depths ranged from 16.4° to 21.5°C. Collection of relatively large juveniles off Charleston in April indicates that spawning may occur earlier there.

Some female *P. pagrus* attain sexual maturity as 2-yr-old fish; however, the majority mature at 3 yr. All of the fish examined had reached sexual maturity by the fourth year. Approximately 50% of the females were mature at 304 mm TL, and 75% were mature at 334 mm. All fish 364 mm or more in length were sexually mature. Evidently, some of the age II and III fish experience regular, seasonal maturation of gonads but do not spawn that first year. This conclusion is based upon several fish I

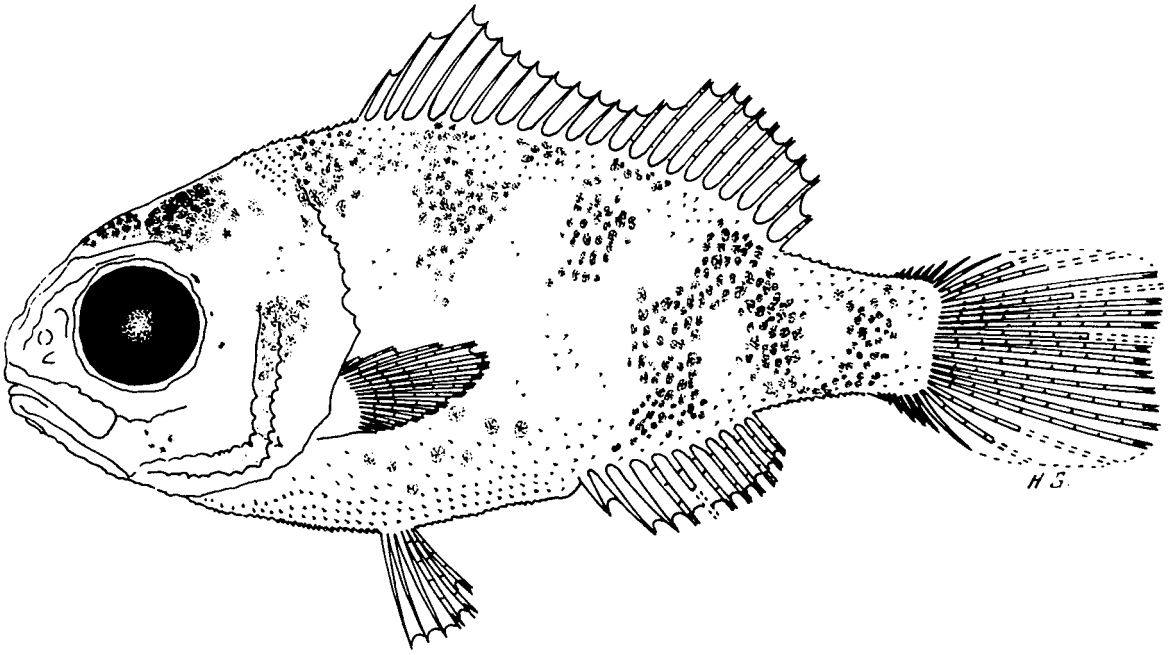

FIGURE 5.–Young red porgy, 18 mm total length, collected by trawl off Charleston, S.C., in April 1974 (drawing by Herbert Gordy, National Marine Fisheries Service, NOAA).

observed which had ovaries containing absorbed ova during the peak spawning period.

Fecundity estimation for red porgy ranged from 48,656 eggs for a 304-mm female to 488,600 ova for a 516-mm fish. Larger fish (>600 mm TL), which occasionally appear in the sport fishery, may produce over 900,000 eggs. Eggs removed from ripe females ranged in size from 0.31 to 0.94 mm in diameter. The developed *P. pagrus* eggs averaged 0.88 mm in diameter and contained a single oil droplet averaging 0.25 mm in diameter. While fecundity was correlated to three predictors; length, weight, and age, weight was the most accurate predictor of fecundity. Although age was not as satisfactory a predictor of fecundity as weight and length, it should not be overlooked, because the age-fecundity relation can have useful application in population modeling. High variability in fecundity estimates for age-groups is expected due to range in size and variation in gonad size among fish of the same size (Bagenal 1967).

Sex ratios for red porgy were usually unbalanced in favor of females. Analyzing data by month, year, and size, I observed a domination by females. The overall sex ratio observed was 1:2. The occurrence of females was higher during the spawning season. This predominance may be attributed to difference in feeding behavior of ripe fish, or to true population differences in the areas sampled. I do not believe gear selectivity influenced sex ratios. The dominance of females for the smaller size classes and actual documentation of hermaphroditic red porgy in the study lends some support to the theory of protogynous hermaphroditism reported for the species in the Gulf of Mexico (Beaumariage pers. commun.). Both protandrous and protogynous hermaphroditism are relatively common among the sparids (D'Ancona 1950, 1956). Although only 2% of the fish examined were obviously hermaphroditic, a complete histological study of gonadal development is needed to determine if the species displays sex reversal. Protogynous hermaphroditism may have selective advantages as Atz (1964:224) mentioned providing an endocrinologically better balanced fish, assuring presence of both sexes in isolated, insular areas, or a mechanism of population control. For the latter purpose, certain population pressures presumably stimulate sexual transition. Probably more applicable to red porgy hermaphroditism is the "size advantage model" proposed by Ghiselin (1969). The theory explains sequential hermaphroditism as occurring when an organism reproduces more efficiently as one sex when small and the opposite sex when larger. A male's poten-

tial, theoretically, is higher than a female's at larger sizes, and conversely, a female's reproductive potential is higher than a male's at smaller sizes. The female reproductive capabilities could continue to increase with age. Perhaps males function more efficiently at larger sizes because they can mate with numerous females. Evolutionary factors which favor protogyny are those which tend to depress male reproductive potential at early ages, such as inexperience, territoriality, or female mate selection (Warner 1975). Without additional information on the spawning behavior of *Pagrus*, it would be difficult to eliminate any of these factors.

ACKNOWLEDGMENTS

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LITERATURE CITED

ATZ, J. W.
1964. Intersexuality in fishes. *In* C. N. Armstrong and A. J. Marshall (editors), Intersexuality in vertebrates including man, p. 145-232. Academic Press, N.Y.

BAGENAL, T. B.
1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. Wiley, N.Y.

CIECHOMSKI, J. D. DE, AND G. WEISS.
1973. Desove y desarollo embrionario y larval de besugo, *Pagrus pagrus* (Linné) en el Mar Argentina (Pisces, Sparidae). Physis Rev. Asoc. Argent. Cienc. Nat., Secc. A 32:481-487.

D'ANCONA, U.
1950. Détermination e différenciation du sexe chez les poissons. Arch. Anat. Microsc. Morphol. Exp. 39:274-294.
1956. Inversion spontanées et expérimentales dans les gonades des Téléostéens. Annee Biol., Sér. 3, 32:89-99.

DIAS, R. K., J. K. DIAS, AND W. D. ANDERSON, JR.
1972. Relationships of lengths (standard, fork and total) and lengths to weight in the red porgy, *Pagrus sedecim* (Perciformes, Sparidae), caught off South Carolina. Trans. Am. Fish. Soc. 101:503-506.

FINKELSTEIN, S. L.
1969. Age at maturity of scup from New York waters. N.Y. Fish Game J. 16:224-237.

GHISELIN, M. T.
1969. The evolution of hermaphroditism among animals. Q. Rev. Biol. 44:189-208.

HARRINGTON, R. W., JR.
1956. An experiment on the effects of contrasting daily photoperiods on gametogenesis and reproduction in the centrarchid fish, *Enneacanthus obesus* (Girard). J. Exp. Zool. 131:203-223.

HUNTSMAN, G. R.
1976. Offshore headboat fishing in North Carolina and South Carolina. Mar. Fish. Rev. 38(3):13-23.

LASSITER, R. R.
1962. Life history aspects of the bluefish, *Pomatomus salatrix* (Linnaeus), from the coast of North Carolina. M.S. Thesis, North Carolina State Univ., Raleigh, 68 p.

MANOOCH, C. S.
1975. A study of the taxonomy, exploitation, life history, ecology and tagging of the red porgy, *Pagrus pagrus* Linnaeus off the Carolinas. Ph.D. Thesis, North Carolina State Univ., Raleigh, 275 p.
In press. Food habits of the red porgy, *Pagrus pagrus* Linnaeus (Pisces: Sparidae) off North Carolina and South Carolina, U.S.A. Bull. Mar. Sci.

MANOOCH, C. S., G. R. HUNTSMAN, B. SULLIVAN, AND J. ELLIOTT.
In press. Conspecific status of the sparid fishes *Pagrus sedecim* Ginsberg and *Pagrus pagrus* Linnaeus. Copeia.

MOE, M. A., JR.
1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes), from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour., Mar. Res. Lab., Prof. Pap. Ser. 10, 95 p.

ORANGE, C. J.
1961. Spawning of yellowfin tuna and skipjack in the eastern tropical Pacific, as inferred from studies on gonad development. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 5:457-526.

RANZI, S.
1969. Sparidae. *In* S. Lo Bianco, Eggs, larvae, and juvenile stages of Teleostei, Parts I and II, p. 330-375. Fauna and flora of the Bay of Naples, Monograph No. 38. (Translated from Ital., TT68-50346.)

SCHAEFER, M. B., AND C. J. ORANGE.
1956. Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the eastern Pacific Ocean, by examination of gonads. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull 1:281-349.

SEKAVEC, G. B., AND G. R. HUNTSMAN.
1972. Reef fishing on the Carolina Continental Shelf. Proc. 15th Annu. Int. Game Fish Res. Conf., p. 76-86.

WALKER, E. T.
1950. Spawning records of fishes seldom reported from North Carolina waters. Copeia 1950:319.

WARNER, R. R.
1975. The adaptive significance of sequential hermaphroditism in animals. Am. Nat. 109:61-82.

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MERCURY IN FISH AND SHELLFISH OF THE NORTHEAST PACIFIC. I. PACIFIC HALIBUT, *HIPPOGLOSSUS STENOLEPIS*

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ABSTRACT

A total of 1,227 Pacific halibut, *Hippoglossus stenolepis*, were analyzed for mercury content in the edible muscle tissue. These fish were obtained from five geographical areas within the species range: the Bering Sea, Gulf of Alaska, southeast Alaska, British Columbia, and Washington-Oregon. Mercury was found to be uniformly distributed from nape to tail in the edible muscle tissue. Within each geographical area the mercury concentration increased as the size of the fish increased. The mercury concentration also increased in fish of the same size from the northern to the southern part of the species range.

In the past few years, numerous investigators have examined the distribution and levels of mercury in food, including aquatic food animals, because of the potential health hazards involved. The U.S. Food and Drug Administration established an administrative guideline of 0.50 ppm mercury in fish and shellfish in 1969. Since that time, the guideline has been the subject of several reviews and recently has been proposed as a formal action level (Schmidt 1974).

Since 1970, the Pacific Utilization Research Center (PURC) and the Southeast Utilization Research Center (SEURC) at College Park, Md., have been conducting extensive studies of fish and shellfish taken from marine and inland waters of the United States to determine the extent to which mercury exceeds the guideline in our aquatic resources. This paper reports our findings on mercury in the edible tissue of the Pacific halibut, *Hippoglossus stenolepis* Schmidt.

EXPERIMENTAL PROCEDURE AND METHODS

Halibut were obtained from commercial fishing vessels, fish processing companies, and research vessels of the International Pacific Halibut Commission (IPHC). Data were obtained on area and date of catch, and weight or length of each fish analyzed. Data were also obtained on age and sex when possible.

The five areas of catch were: Washington-Oregon, British Columbia, southeast Alaska, Gulf of Alaska, and the Bering Sea (Figure 1). Commercial halibut are eviscerated at sea, landed as a heads-on eviscerated product, and then beheaded for marketing as fresh or frozen fish. Weights reported here are in pounds for heads-off eviscerated fish because this is the standard practice of the halibut industry. For convenience of some readers who do not normally use our measurement system, approximate metric equivalents in kilograms are given in the tables and figures. When actual weights were impractical to obtain, the lengths of the heads-on fish were used, and heads-off eviscerated weights were estimated using length-weight conversion tables of the IPHC. Age was determined, as described by Hardman and Southward (1965), from otoliths collected at the landing site when circumstances permitted and on all halibut taken by IPHC research vessels.

Before setting up sampling procedures, experiments were carried out to determine the uniformity of distribution of mercury in the muscle of individual fish. No significant differences in concentration of mercury (deviation did not exceed ± 0.03 ppm) were noted in muscle tissue taken from nape, midbody, or tail sections.

Analytical samples consisted of skinned and deboned edible muscle tissue that was normally taken from the nape section just behind the head. Some samples, however, were in the form of steaks and a few consisted of the entire fillets of small fish. Portions, usually about 400 g, taken from the

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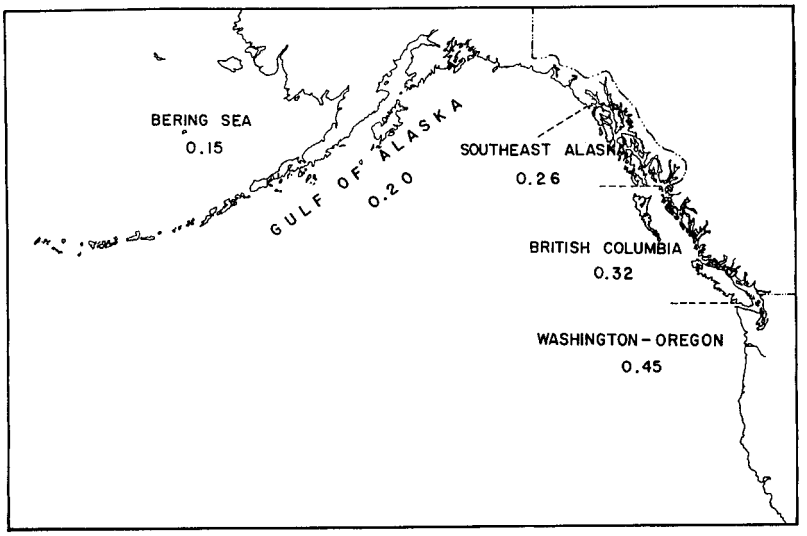

FIGURE 1.–Mean mercury levels in Pacific halibut by area of catch.

nape section were ground in a Hobart grinder[3] equipped with a ⅛-inch (3.2-mm) hole stainless steel plate. Larger steaks and fillets were ground in a Hobart Silent Food Cutter (Model 84181). The comminuted flesh was mixed thoroughly before subsampling for analysis. Because samples were often collected more rapidly than they could be analyzed, they were stored at -29°C until analysis. No change in mercury content was observed in halibut that were analyzed immediately or that had been held in frozen storage in either glass vials or aluminum containers if dehydration was prevented. A halibut sample stored in the above manner and used as an analytical control showed a mean mercury content of 0.88 ± 0.02 ppm over a 2-yr period. This control was analyzed routinely to verify both accuracy and precision of the method.

Total mercury was determined at the PURC by either the method of Munns and Holland (1971) or Malaiyandi and Barrette (1970) as modified by Munns (1972). The former method uses sulfuric, nitric, and perchloric acids for digestion with sodium molybdate as a catalyst, while the Munns' modification utilizes nitric and sulfuric acids for digestion and vanadium pentoxide as a catalyst. Some samples were analyzed at the SEURC by the method of Hatch and Ott (1968) as modified by Uthe et al. (1970). This method uses sulfuric acid for digestion and potassium permanganate as an oxidizing agent.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Final quantitation was by flameless spectroscopy using a Perkin-Elmer Model 403 Atomic Absorption Spectrophotometer at the PURC and by a Varian Techtron Model AA5 at the SEURC. In a collaborative study, the mean deviation between laboratories and methods did not exceed ± 0.02 ppm Hg. All samples were analyzed in duplicate or triplicate, depending upon the method of analysis used. We consider ± 0.05 ppm a significant deviation; therefore, when differences between replicates exceeded this level the samples were reanalyzed. Results are stated in parts per million wet weight.

RESULTS AND DISCUSSION

A total of 1,227 halibut were analyzed for mercury content. Results indicated a relationship between mercury levels and area of catch, age, and size of fish. The results are broken down by the previously described catch areas (Figure 1). The fish taken from each area were separated by weight classes that approximate those used in the halibut industry; the low, high, and mean mercury values for each weight class are given with a frequency distribution of the fish by increasing mercury concentration (Tables 1 through 5). Because we thought that large fish would be more likely to exhibit higher concentrations of mercury, we attempted to obtain as many large fish as was practicable. For this reason our sampling contains a greater percentage of large fish than do the commercial catches from most of the areas dis-

cussed here. Therefore, these data cannot be interpreted to indicate the approximate percentage of the commercial catch that is likely to contain mercury in concentrations over the guideline.

In 152 halibut taken from the Bering Sea, the mercury level in the muscle of 7 fish (5% of the sample) was over the guideline (Table 1). The incidence (percentage over the guideline of the total number of fish within a weight range) was highest among fish weighing more than 80 pounds.

Most of our samples, 761 fish, were taken from the Gulf of Alaska. We found that mercury in the muscle of 38 fish (5% of the sample) exceeded the guideline (Table 2). The highest incidence occurred in fish weighing more than 80 pounds. The weight ranges contributing most to the incidence were those of 126 to 150 pounds and those of more than 150 pounds. These two weight ranges contribute 21% and 32%, respectively, in contrast with only 3% in each of the weight ranges 81 to 100 pounds and 101 to 125 pounds.

The analytical data on 70 fish taken from southeast Alaska area showed that mercury in the muscle of 9 fish (13% of the sample) was 0.50 ppm or higher (Table 3). The small number of fish in the larger weight ranges makes it impossible to be definitive, but it is reasonably clear that in this group, too, the incidence of mercury levels over the guideline was greatest among the largest fish.

Analyses on 163 fish from the British Columbia area showed that 44 of these (27% of the sample) were over the guideline (Table 4). In addition to this relatively high incidence, we saw for the first time the presence of significant numbers of high-mercury-level fish in all weight groups, i.e., 10% of the fish were over the guideline in the 5- to 60-pound range, 75% in the 61- to 80-pound range, 73% in the 81- to 100-pound range, 100% in the 101- to 125-pound range, and 67% in the 126- to 150-pound range. We also saw that the concentration of mercury tended to increase with an increase in the incidence of fish that were over the guideline.

The analytical results on 81 fish taken from the Washington-Oregon area, the most southerly area of the range of the Pacific halibut, showed 29 fish

TABLE 1.–Mercury concentration in heads-off eviscerated Pacific halibut from the Bering Sea.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue											
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	88	0.02	0.78	0.11	82	0	2	2	1	1	0	0	0
61-80 (28-36)	33	0.06	0.42	0.15	30	2	1	0	0	0	0	0	0
81-100 (37-45)	16	0.09	0.55	0.19	13	1	1	1	0	0	0	0	0
101-125 (46-57)	10	0.08	1.00	0.32	7	0	1	1	0	0	0	0	1
126-150 (57-68)	5	0.22	0.35	0.27	2	3	0	0	0	0	0	0	0
Total	152	0.02	1.00	0.15	134	6	5	4	1	1	0	0	1

TABLE 2.–Mercury concentration in heads-off eviscerated Pacific halibut from the Gulf of Alaska.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue											
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	378	0.01	0.50	0.11	371	4	2	1	0	0	0	0	0
61-80 (28-36)	92	0.05	0.47	0.18	77	13	2	0	0	0	0	0	0
81-100 (37-45)	76	0.05	1.10	0.25	49	15	10	1	0	0	0	0	1
101-125 (46-57)	92	0.03	0.74	0.29	37	36	16	2	0	1	0	0	0
126-150 (57-68)	67	0.12	1.28	0.38	19	23	11	6	3	3	0	1	1
Over 151 (68)	56	0.14	1.05	0.45	8	16	14	6	5	4	2	0	1
Total	761	0.01	1.28	0.20	561	107	55	16	8	8	2	1	3

TABLE 3.–Mercury concentration in heads-off eviscerated Pacific halibut from southeast Alaska.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue											
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	33	0.04	0.34	0.12	30	3	0	0	0	0	0	0	0
61-80 (28-36)	10	0.09	1.30	0.33	7	1	1	0	0	0	0	0	1
81-100 (37-45)	9	0.09	0.59	0.28	4	4	0	1	0	0	0	0	0
101-125 (46-57)	13	0.22	0.95	0.46	1	6	1	3	0	0	1	1	0
126-150 (57-68)	3	0.26	0.36	0.31	0	3	0	0	0	0	0	0	0
Over 151 (68)	2	0.50	1.10	0.80	0	0	0	1	0	0	0	0	1
Total	70	0.04	1.30	0.26	42	17	2	5	0	0	1	1	2

TABLE 4.–Mercury concentration in heads-off eviscerated Pacific halibut from British Columbia.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue											
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	122	0.04	1.04	0.19	99	7	4	5	3	2	0	1	1
61-80 (28-36)	20	0.12	1.23	0.69	2	2	1	1	4	3	2	3	2
81-100 (37-45)	11	0.10	1.22	0.66	1	2	0	1	2	2	0	0	3
101-125 (46-57)	7	0.50	1.46	0.96	0	0	0	2	0	1	0	1	3
126-150 (57-68)	3	0.25	0.77	0.52	0	1	0	1	0	1	0	0	0
Total	163	0.04	1.46	0.32	102	12	5	10	9	9	2	5	9

TABLE 5.–Mercury concentration in heads-off eviscerated Pacific halibut from Washington-Oregon.

Weight range Pounds. (kg)	No. of fish	Mercury (ppm) in edible muscle tissue											
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	75	0.10	1.43	0.42	23	20	9	5	8	3	4	0	3
61-80 (28-36)	6	0.70	1.13	0.88	0	0	0	0	0	2	2	0	2
Total	81	0.10	1.43	0.45	23	20	9	5	8	5	6	0	5

(36% of the sample) were over the guideline (Table 5). None of these fish weighed more than 80 pounds, and only six weighed more than 60 pounds; 31% of the 5- to 60-pound fish and all of the 61- to 80-pound fish were over the guideline. In fish from this area, as in those from British Columbia, the concentrations of mercury increased with the incidence of fish over the guideline.

It is apparent that the mean level of mercury in the edible tissue and the incidence of fish over the guideline increases from the northern to the southern part of the range of the Pacific halibut (Figure 1, Table 6). There is also a relationship between the size of fish and the level of mercury in the muscle. Because of the sex-size relationship of halibut, i.e., males rarely exceed 80 pounds regardless of age, the correlation of mercury to age should be closer than that of mercury to size. However, age data were collected on only 76% of the total sampling, whereas weight was obtained on all samples. For this reason, and as a guide to industry, we have worked mostly with the mercury-size relationship. Evaluation of the data by regression analyses showed that the data are well described by the exponential function ($y = ax^b$). Comparisons of the weights of halibut against

TABLE 6.–Summary of mercury concentration in Pacific halibut.

Area of catch	Number of fish	Mean weight lb	Mean weight kg	Mercury (ppm) Low	Mercury (ppm) High	Mercury (ppm) Mean	Percent of samples exceeding 0.50 ppm
Bering Sea	152	54.6	24.8	0.02	1.00	0.15	4.6
Gulf of Alaska	761	71.8	32.6	0.01	1.28	0.20	5.0
Southeast Alaska	70	67.6	30.7	0.04	1.30	0.26	12.8
British Columbia	163	39.3	17.8	0.04	1.46	0.32	27.0
Washington-Oregon	81	30.3	13.8	0.10	1.43	0.45	35.8

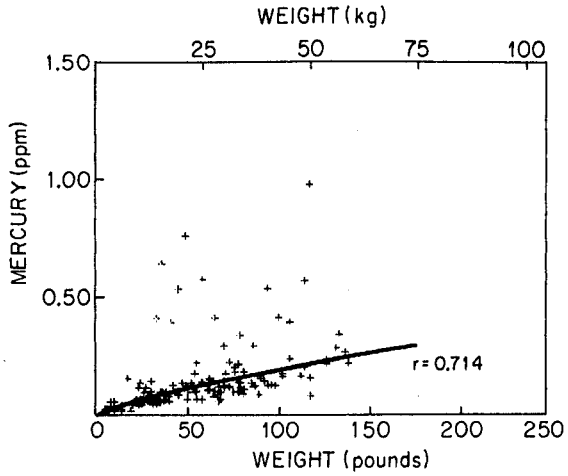

FIGURE 2.–Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from the Bering Sea.

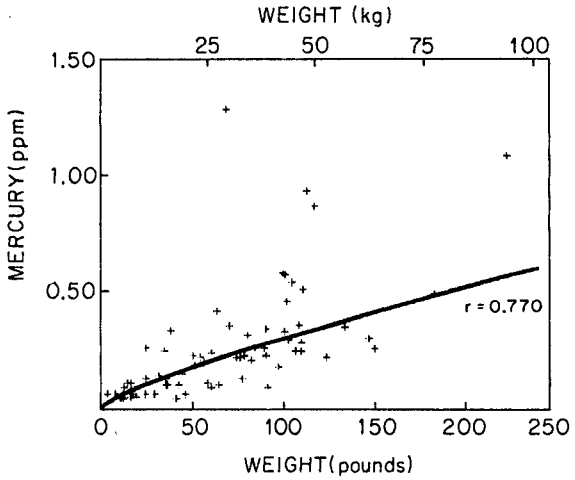

FIGURE 4.–Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from southeast Alaska.

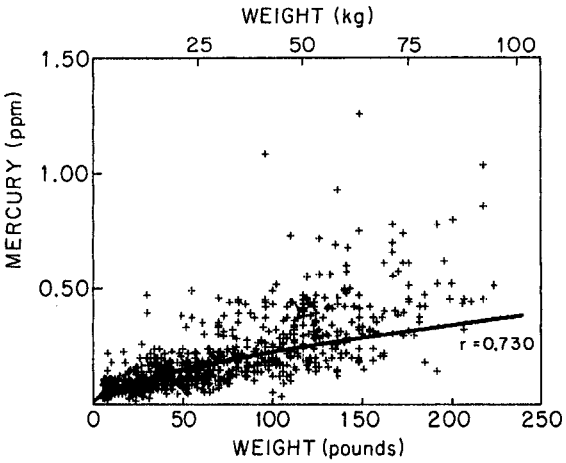

FIGURE 3.–Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from the Gulf of Alaska.

mercury concentrations in the edible tissue for each area are shown in Figures 2 through 6. Correlation coefficients (r values) are shown on each plot and are significant at the 0.1% level. Correlation coefficients between length and mercury were also significant at the 0.1% level within each area and were essentially identical to the correlation coefficients between weight and mercury. This would be expected from the weight-length relationship. Correlation between age and mercury was higher than between weight or length and mercury for fish from the Bering Sea, the Gulf of Alaska, and southeast Alaska; the same for fish from British Columbia; and lower for fish from Washington-Oregon. These correlation coefficients between age and mercury were also significant at the 0.1% level in all areas.

In evaluating the data, areas were used that are either the same as the fishery management areas defined by the International Pacific Halibut Commission (1974) or subdivisions of a management area. This was both logical and practical for the purpose of providing useful information to the halibut industry. The plots of mercury concentration in the edible muscle against weight of fish taken from both the Bering Sea and the Gulf of

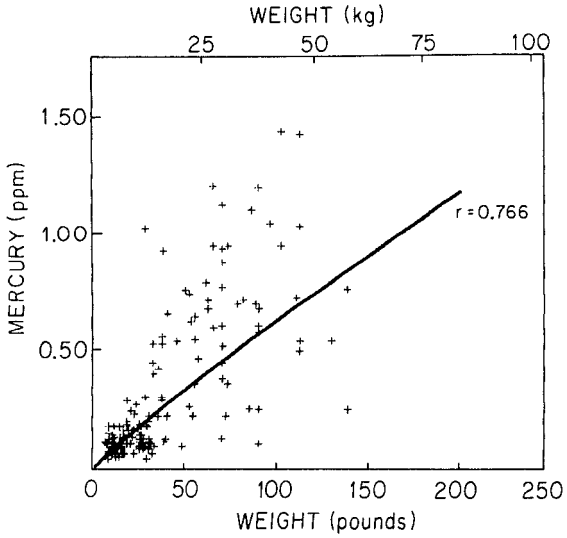

FIGURE 5.—Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from British Columbia.

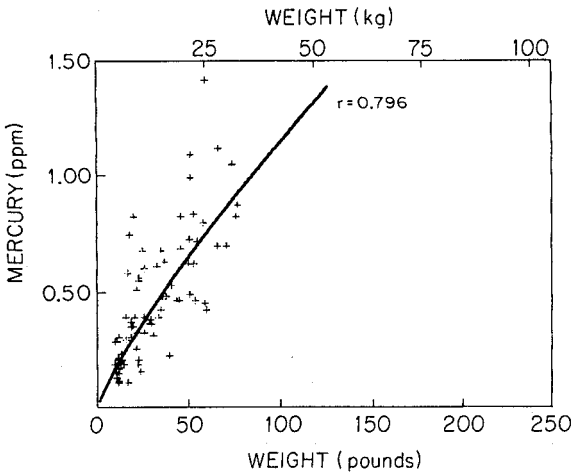

FIGURE 6.—Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from Washington-Oregon.

Alaska (Figures 2, 3) are so similar as to suggest that the environmental and biological factors that determine the rate and extent of deposition of mercury in the muscle are the same in both areas. In any case, the mean level of mercury and the incidence of fish exceeding the guideline increases, while the size of the fish decreases, from north to south.

Increasing concentrations of mercury have been noted in other marine animals as one moves south from the Bering Sea. Anas (1974) pointed out that the harbor seal, *Phoca vitulina richardi*, which is a nonmigratory, inshore carnivore that feeds principally on fish, provides geographical information on local concentrations of contaminants. The livers of harbor seals taken from the Bering Sea contained lower levels of mercury than did those from Washington and Oregon, and those from southern California contained the highest levels. Sablefish, *Anoplopoma fimbria* (Pallas), also shows a similar pattern and will be the subject of another paper in this series.

These observations suggest that the total mercury contamination in the ocean environment (natural plus man-made) increases in a north-to-south direction. Unfortunately, conclusive data to substantiate this hypothesis are not available. Eggerman and Mar (1972), in a review of the research that has been conducted on the various aspects of mercury transport, state that there is a paucity of available data, especially on the biological transport of mercury in marine waters.

ACKNOWLEDGMENTS

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LITERATURE CITED

ANAS, R. E.
1974. Heavy metals in the northern fur seal, *Callorhinus ursinus*, and the harbor seal, *Phoca vitulina richardi*. Fish. Bull., U.S. 72:133-137.

EGGERMAN, T., AND B. MAR.
1972. Mercury in the North Pacific-NORFISH NF01. Cent. Quant. Sci., Univ. Wash., Seattle, 15 p.

HARDMAN, W. H., AND G. M. SOUTHWARD.
1965. Sampling the commercial catch and use of calculated lengths in stock composition studies of Pacific halibut. Int. Pac. Halibut Comm. Rep. 37, 32 p.

HATCH, W. R., AND W. L. OTT.
1968. Determination of sub-microgram quantities of mercury by atomic absorption spectrophotometry. Anal. Chem. 40:2085-2087.

INTERNATIONAL PACIFIC HALIBUT COMMISSION.
1974. Pacific Halibut Fishery Regulations 1974. Int. Pac. Halibut Comm., Seattle, Wash., 5 p.

MALAIYANDI, M., AND J. P. BARRETTE.
1970. Determination of submicro quantities of mercury in biological materials. Anal. Lett. 3:579-584.

MUNNS, R. K.
1972. Mercury in fish by cold vapor AA using sulfuric-nitric acid/V_2O_5 digestion. FDA (Food Drug Admin.) Lab. Inf. Bull. 1500, 8 p.

MUNNS, R. K. AND D. C. HOLLAND.
1971. Determination of mercury in fish by flameless atomic absorption: A collaborative study. J. Assoc. Off. Anal. Chem. 54:202-205.

SCHMIDT, A. M.
1974. Action level for mercury in fish and shellfish. Fed. Regist., 39 (236) Part II: 42738-42740.

UTHE, J. F., F. A. J. ARNSTRONG, AND M. P. STAINTON.
1970. Mercury determination in fish samples by wet digestion and flameless atomic absorption spectrophotometry. J. Fish. Res. Board Can. 27:805-811.

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MERCURY IN FISH AND SHELLFISH OF THE NORTHEAST PACIFIC. II. SABLEFISH, *ANOPLOPOMA FIMBRIA*

ALICE S. HALL, FUAD M. TEENY, AND ERICH J. GAUGLITZ, JR.[1]

ABSTRACT

Sablefish, *Anoplopoma fimbria*, collected from several locations in Alaska, Washington, Oregon, and California were analyzed for their mercury content. Mean mercury level in this species varied with the geographical location of catch, showing a gradual increase in magnitude from north to south; the average size of the specimens decreased in the same pattern, north to south. Of the 692 specimens analyzed in this study, approximately 30% exceeded the U.S. Food and Drug Administration action level of 0.50 ppm mercury. Significant relationships between the size of the fish and mercury content were observed.

Following the Canadian disclosure in March 1970 of high mercury levels in fish caught in Lake St. Clair (Hearnden 1970), the National Marine Fisheries Service (NMFS) initiated studies to determine the distribution and level of mercury in our marine resources. Since that time, the Pacific Utilization Research Center, NMFS, has been conducting extensive screening studies of fish and shellfish of the northeast Pacific in order to evluate the mercury problem as it relates to those species taken by both commercial and sport fisheries. The main objectives were to determine which species contained mercury in excess of the Food and Drug Administration (FDA) action level of 0.50 ppm (Schmidt 1974) and the severity of the problem.

During our preliminary screening of Pacific species, we found that the edible muscle tissue of a number of sablefish contained mercury in excess of the FDA action level. This species ranges from southern California to the Bering Sea (Clemens and Wilby 1961:240). Domestic landings in 1971 were about 6 million pounds (2.7×10^6 kg) (Thompson 1971) but its high value as a smoked product and the availability to the fishermen of additional supplies of this species suggests that landings will increase.

This paper is the second in a series and reports our findings on mercury in the edible muscle tissue of sablefish, *Anoplopoma fimbria* (Pallas). The first paper in the series is on the Pacific halibut, *Hippoglossus stenolepis* Schmidt (Hall et al. 1976).

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EXPERIMENTAL PROCEDURE AND METHODS

Most of the sablefish used in this study were obtained by NMFS personnel aboard National Oceanic and Atmospheric Administration (NOAA) research vessels. Some samples were obtained from commercial lots through the cooperation of fish processors in order to cover the range of this species. Samples were obtained from the waters off Alaska, Washington, Oregon, and California. Date and location of catch were recorded for all specimens.

Weights and lengths are reported for heads-off eviscerated fish because this is the standard practice for landing sablefish. Round weights and lengths were converted to the heads-off eviscerated values using conversion tables. Where possible, sex was determined by physical examination when the specimens were eviscerated. Age was determined from the otoliths which were removed at the same time.

Analytical samples consisted of the entire fillets of each fish. The edible muscle tissue was ground in a Hobart grinder[2] equipped with a stainless steel plate perforated with holes ⅛ inch (3.2 mm) in diameter. The comminuted flesh was mixed thoroughly; subsamples were removed, packaged, and stored at -29°C until analysis.

Total mercury was determined by either the FDA method of Munns and Holland (1971) or Malaiyandi and Barrette (1970) as modified by

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Munns (1972). Final quantitation was by flameless spectroscopy using a Perkin-Elmer Model 403 Atomic Absorption Spectrophotometer.

Results are stated in parts per million wet weight. All samples were analyzed in duplicate and where the deviation for replicates exceeded ±0.05 ppm, the analyses were repeated. Control samples of known value were analyzed routinely to verify both accuracy and precision of the method.

RESULTS AND DISCUSSION

A total of 692 sablefish taken from the Bering Sea and coastal waters of the Pacific Ocean from Kodiak Island, Alaska, to San Diego, Calif., were analyzed for individual mercury content. The specific locations of catch and the mean mercury levels by area are shown in Figure 1. The mean mercury levels show a general increase from north to south, as does the percentage of fish that exceed the FDA action level of 0.50 ppm (Table 1).

TABLE 1.–Summary of mercury concentration in sablefish.

Area of catch	No. of fish	Mean weight Pounds (kg)	Mercury (ppm) Low	High	Mean	% samples over 0.50 ppm
Bering Sea-Kodiak Island	30	2.02 (0.92)	0.02	0.11	0.04	0
Southeast Alaska	120	5.22 (2.37)	0.06	0.77	0.28	5
Washington	121	5.27 (2.39)	0.06	1.28	0.37	23
Oregon	174	4.33 (1.96)	0.06	1.23	0.40	29
Northern California	98	3.14 (1.42)	0.03	0.95	0.26	21
Central California	30	5.68 (2.58)	0.08	0.79	0.47	43
Southern California	119	2.93 (1.33)	0.04	2.11	0.60	72

Effect of the Geographical Location

The fish caught in the Bering Sea and in the vicinity of Kodiak Island were all small (less than 3 pounds [1.4 kg]) and contained very low levels of

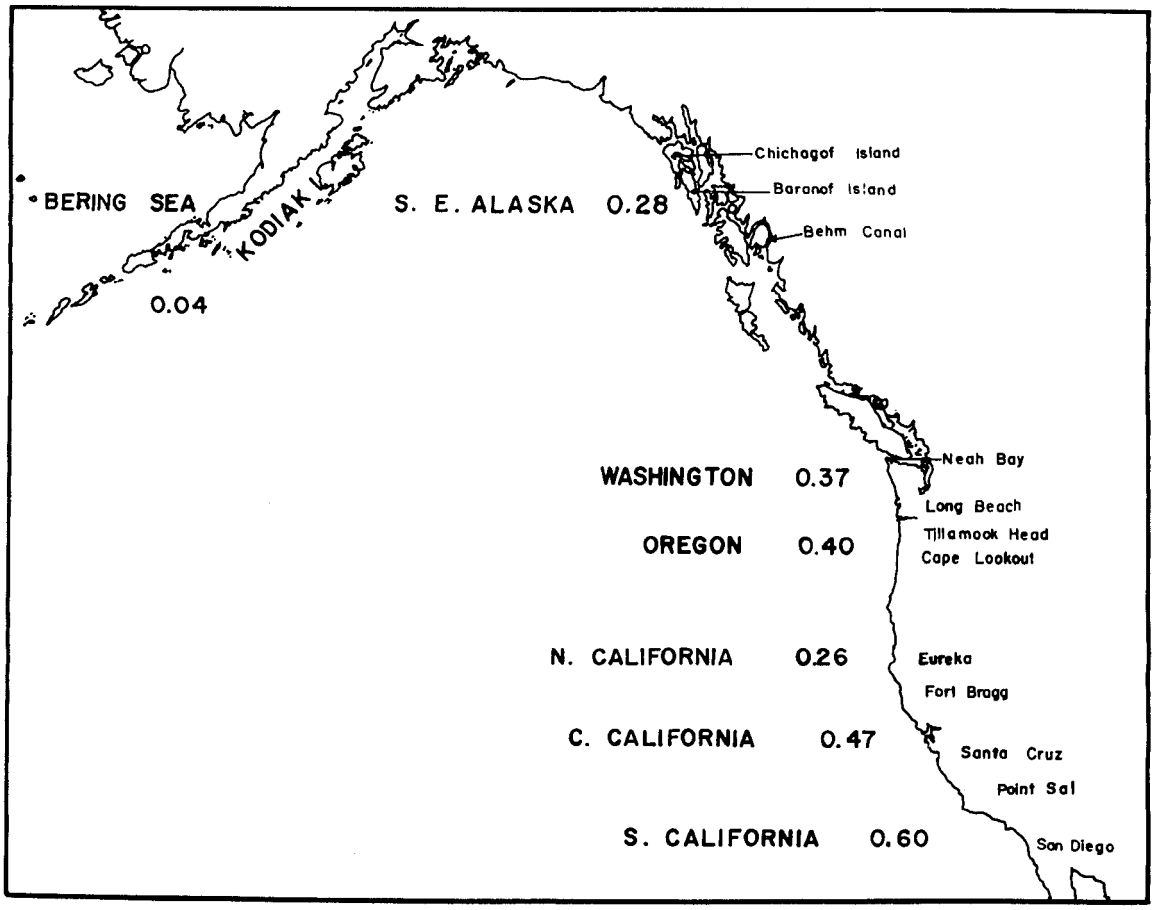

FIGURE 1.–Mean mercury levels (parts per million) in sablefish by area and the specific locations of the catches.

mercury (0.02-0.11, $\bar{x}$ 0.04 ppm). The data for the specimens from these two areas were combined since the samples were relatively few in number, and there was no evidence of any significant differences based on area (Table 1).

A much better weight distribution is seen in the 120 fish from southeast Alaska (Table 2). The fish taken from several locations around Baranof and Chichagof islands (45 specimens) contained a significantly lower mean level of mercury (0.19 ppm) than did the 75 fish taken from the Behm Canal area (0.34 ppm). The only fish (5% of the total sample) from southeast Alaska that exceeded 0.50 ppm mercury were caught off Betton Island, which is in the north arm of Behm Canal. This would indicate a higher level of mercury contamination in the inland waters than in the offshore waters around the outer islands.

Analyses of 121 fish from Washington showed that 23% (28 fish) of the sample exceeded the action level (Table 2). The fish taken from the northern coast off Neah Bay and those taken from the southern coast off Long Beach showed little difference in mercury content.

Of the 174 fish from Oregon, 51 or 29% exceeded the action level (Table 2), which is an increase over that observed in previously discussed areas. A significant part of the total sample (39%) consisted of fish weighing less than 3 pounds (1.4 kg) and of these small fish we observed an increase in the percentage that exceeded 0.50 ppm mercury.

The sampling from northern California (Table 3) consisted of 98 fish of which 62% (61 fish) weighed less than 3 pounds (1.4 kg) and contained low levels of mercury. Only one of these small fish exceeded 0.50 ppm mercury. Of the remaining 37 larger fish, the mercury level of 20 fish exceeded 0.50 ppm. The mean mercury level of the total lot of 98 fish was 0.26 ppm, and 21 fish or 21% exceeded the action level. Considering that this lot represented an atypical weight distribution, it seems likely that both the mean and the percentage of fish exceeding the action level would be higher in a sampling where the number of fish are more uniformly distributed over the weight range.

The 30 fish collected in central California were well distributed over the weight range (Table 3) and 43% of these fish exceeded the action level.

Analytical data on 119 fish from the southern California area showed that 72% (86 fish) exceeded the action level (Table 3). Of this group, 47% weighed less than 3 pounds (1.4 kg). Here, as in Oregon, we saw that smaller fish contained high levels of mercury in comparison to other areas. The weight range of the fish from southern California was small (from 0.5 to 5.5 pounds [0.2-2.5 kg]), but the mercury levels were higher than were observed in any other area.

Effect of Size of Fish

The observations on mercury levels and size of

TABLE 2.—Mercury concentration in heads-off eviscerated sablefish from southeast Alaska, Washington, and Oregon.

Weight range	Southeast Alaska					Washington					Oregon				
	Fish		Mercury (ppm)			Fish		Mercury (ppm)			Fish		Mercury (ppm)		
Pounds (kg)	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean
0.5-2.99 (0.23-1.36)	31	0	0.06	0.23	0.12	23	4	0.07	0.52	0.27	68	7	0.06	0.69	0.25
3.0-3.99 (1.36-1.81)	17	0	0.07	0.48	0.29	21	14	0.12	0.82	0.35	29	24	0.20	0.63	0.43
4.0-4.99 (1.82-2.26)	15	0	0.12	0.40	0.27	22	4	0.06	0.52	0.29	14	43	0.22	0.71	0.48
5.0-5.99 (2.27-2.72)	17	0	0.19	0.46	0.33	14	29	0.26	0.61	0.41	14	21	0.18	0.72	0.45
6.0-6.99 (2.72-3.17)	9	11	0.23	0.61	0.39	11	18	0.12	0.62	0.33	20	55	0.06	1.23	0.51
7.0-7.99 (3.18-3.63)	13	15	0.18	0.66	0.36	14	36	0.08	0.72	0.41	11	64	0.33	0.84	0.55
8.0-8.99 (3.63-4.09)	8	0	0.20	0.47	0.35	3	67	0.48	0.65	0.58	12	58	0.33	0.72	0.52
9.0-9.99 (4.09-4.54)	4	0	0.24	0.48	0.37	7	57	0.15	1.28	0.61	5	80	0.44	1.02	0.68
10.0-10.99 (4.54-4.99)	3	67	0.46	0.77	0.61	3	100	0.52	0.90	0.72	0	—	—	—	—
11.0-11.99 (4.99-5.44)	1	100	0.56	0.56	0.56	3	100	0.50	0.67	0.58	1	100	1.15	1.15	1.15
12.0-12.99 (5.45-5.90)	2	0	0.38	0.48	0.43	—	—	—	—	—	—	—	—	—	—

TABLE 3.—Mercury concentration in heads-off eviscerated sablefish from California.

Weight range	Northern California					Central California					Southern California				
	Fish		Mercury (ppm)			Fish		Mercury (ppm)			Fish		Mercury (ppm)		
Pounds (kg)	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean
0.5-2.99 (0.23-1.36)	61	2	0.03	0.65	0.12	4	0	0.08	0.18	0.13	68	59	0.04	1.74	0.50
3.0-3.99 (1.36-1.81)	8	50	0.20	0.85	0.45	5	40	0.36	0.54	0.46	35	86	0.38	2.11	0.73
4.0-4.99 (1.82-2.26)	14	50	0.22	0.73	0.47	7	29	0.42	0.79	0.53	12	100	0.53	0.88	0.72
5.0-5.99 (2.27-2.72)	9	44	0.22	0.75	0.49	4	25	0.13	0.57	0.40	4	100	0.54	0.83	0.71
6.0-6.99 (2.72-3.17)	2	100	0.70	0.75	0.73	2	0	0.31	0.44	0.37	—	—	—	—	—
7.0-7.99 (3.18-3.63)	2	50	0.32	0.89	0.61	1	100	0.58	0.58	0.58	—	—	—	—	—
8.0-8.99 (3.63-4.09)	1	100	0.95	0.95	0.95	3	100	0.62	0.69	0.66	—	—	—	—	—
9.0-9.99 (4.09-4.54)	1	100	0.53	0.53	0.53	2	100	0.61	0.68	0.64	—	—	—	—	—
12.0-12.99 (5.45-5.90)	—	—	—	—	—	1	100	0.71	0.71	0.71	—	—	—	—	—
13.0-13.99 (5.90-6.35)	—	—	—	—	—	1	100	0.61	0.61	0.61	—	—	—	—	—

sablefish are analogous to what was found in Pacific halibut (Hall et al. 1976); i.e., mercury levels increased from north to south until at the southern part of the range even small fish exhibited high mercury levels. Anas (1974) observed a similar pattern in the harbor seal, *Phoca vitulina richardi*.

There appears to be a direct relationship between the size of the sablefish and the mercury level found in the muscle. Comparisons between weight and mercury level for fish from each area are given in Figures 2-8. The exponential function, $y = ax^b$, was used for the statistical evaluation of the data. Length-to-mercury relationships are very similar to those for weight-to-mercury and are not shown for this reason. Correlation coefficients (r values) are shown on each plot, and the relationship between weight and mercury was highly significant (0.1% level) in all areas except in the Bering Sea-Kodiak Island area where the relationship was not significant.

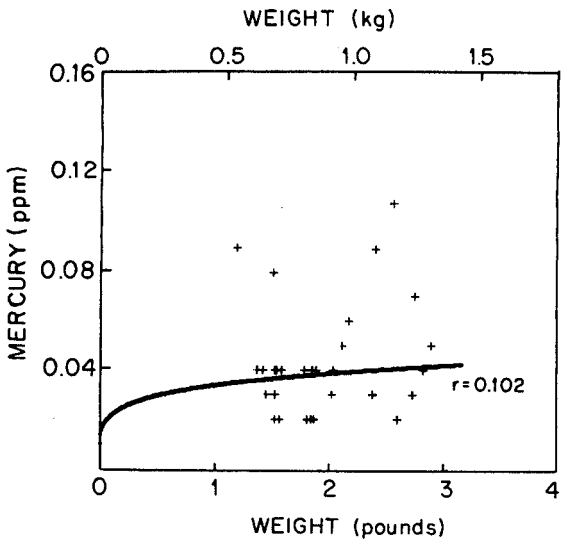

FIGURE 2.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from the Bering Sea-Kodiak Island, Alaska.

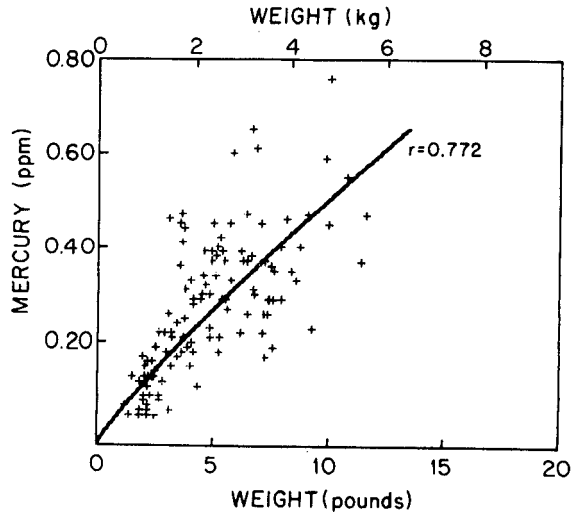

FIGURE 3.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from southeast Alaska.

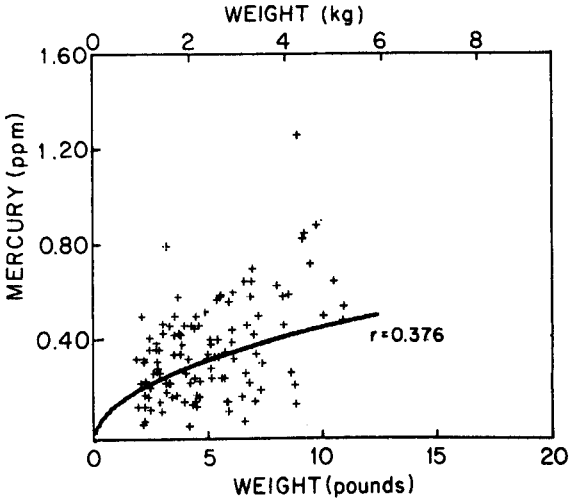

FIGURE 4.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from Washington.

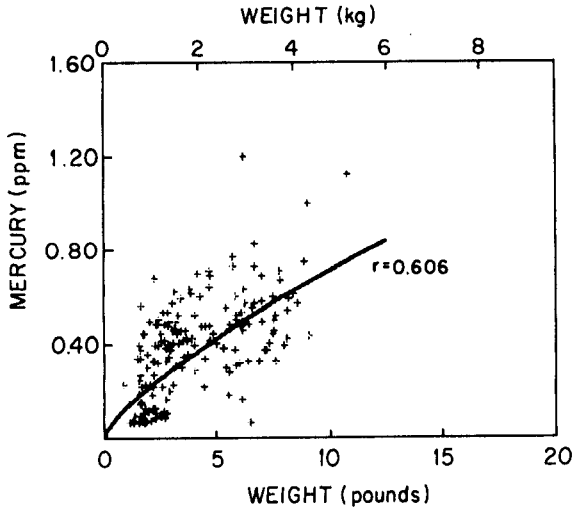

FIGURE 5.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from Oregon.

Effect of Age

Since the female sablefish grows faster and attains a larger size than the male (Clemens and Wilby 1961), it would seem logical to assume that the correlation between age and mercury level might be better than that of weight and mercury level. However, higher correlation coefficients exist between weight and mercury than between age and mercury in all areas except Oregon.

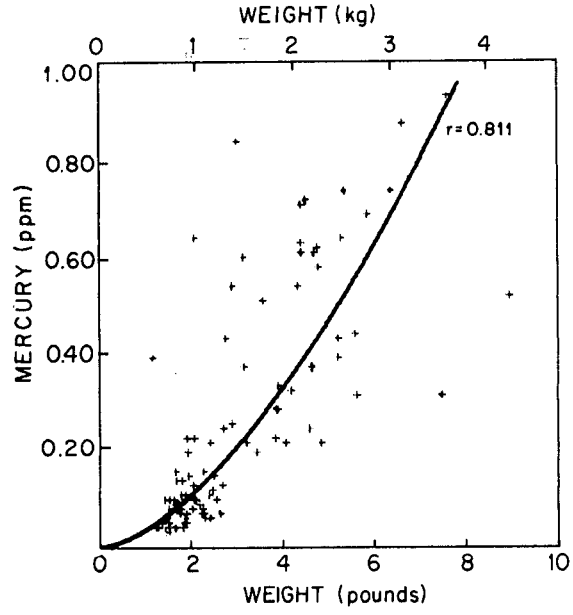

FIGURE 6.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from northern California.

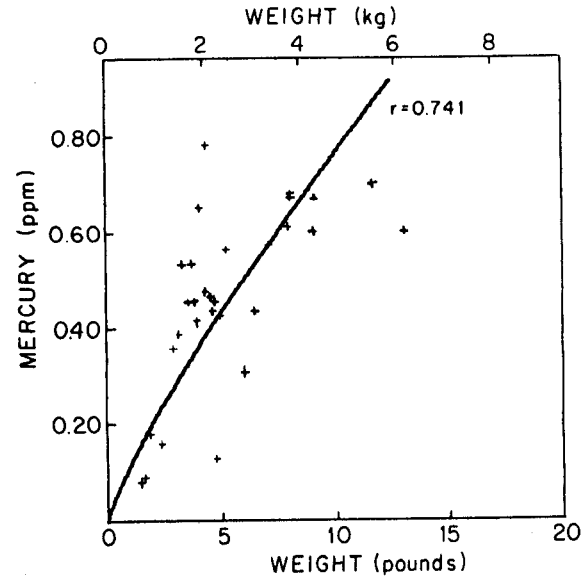

FIGURE 7.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from central California.

Relationships between age and mercury are significant in all areas except Washington (Table 4). Age was not obtained on fish from the Bering Sea-Kodiak Island area.

TABLE 4.–Correlation coefficients for relationship of mercury level in the edible flesh to weight, age, and sex of sablefish.[1]

Area of catch	Number of fish	Weight to mercury	Number of fish	Age to mercury	Number of females	Weight to mercury	Number of males	Weight to mercury
Bering Sea-Kodiak Island	30	[2]0.102	—	—	—	—	—	—
Southeast Alaska	120	0.772	103	0.684	71	0.868	43	0.762
Washington	121	0.376	38	[2]0.179	30	0.731	10	[2]0.349
Oregon	174	0.606	80	0.693	116	0.657	53	0.480
Northern California	98	0.811	63	0.558	—	—	—	—
Central California	30	0.741	28	[3]0.430	17	[4]0.630	12	[4]0.758
Southern California	119	0.748	97	0.439	30	0.661	11	[2]0.203

[1]Correlation coefficients significant at the 0.1% level unless otherwise indicated.
[2]Not significant.
[3]Significant at 5% level.
[4]Significant at 1% level.

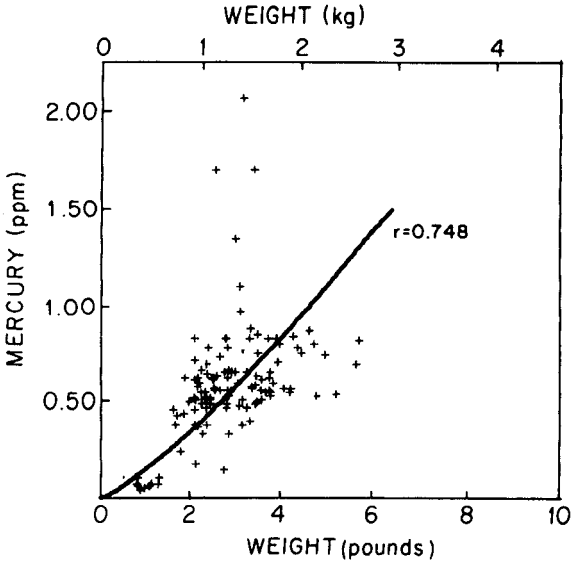

FIGURE 8.–Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from southern California.

Effect of Sex

The females show better correlation between weight and mercury than do the males, and correlation coefficients are significant for females from all areas (Table 4). Correlation coefficients for weight to mercury are also significant for males in all areas except Washington and southern California. Sex was not obtained on fish from the Bering Sea-Kodiak Island or northern California.

Effect on Utilization of Sablefish

It is apparent that sablefish can accumulate mercury in amounts that exceed the maximum level permitted in fish by the FDA. Spinelli et al. (1973) noted that fish withheld from food use due to high mercury levels constitute a significant loss to the industry and showed that such losses could be reduced by using a cysteine treatment to lower the mercury content of the fish during processing. Teeny et al. (1974) conducted a similar study on the reduction of mercury in sablefish, and found that up to 80% of the mercury present in the edible tissue could be removed. Processing techniques of this type could result in all sablefish being acceptable for human consumption.

ACKNOWLEDGMENTS

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LITERATURE CITED

ANAS, R. E.
1974. Heavy metals in the northern fur seal, *Callorhinus ursinus* and harbor seal, *Phoca vitulina richardi*. Fish. Bull., U.S., 72:133-137.

CLEMENS, W. A., AND G. V. WILBY.
1961. Fishes of the Pacific Coast of Canada. 2d ed. Fish. Res. Board Can., Bull. 68, 443 p.

HALL, A. S., F. M. TEENY, L. G. LEWIS, W. H. HARDMAN, AND E. J. GAUGLITZ, JR.
1976. Mercury in fish and shellfish of the northeast Pacific. I. Pacific halibut, *Hippoglossus stenolepis*. Fish. Bull., U.S. 74:783-789.

HEARNDEN, E. H.
1970. Mercury pollution Fisheries Department acts quickly to safeguard public health. Fish. Can. 22(10):3-6.

MALAIYANDI, M., AND J. P. BARRETTE.
1970. Determination of submicro quantities of mercury in biological materials. Anal. Lett. 3:579-584.

MUNNS, R. K.
1972. Mercury in fish by cold vapor AA using sulfuric-nitric acid/V_2O_5 digestion. FDA (Food Drug Admin.) Lab. Inf. Bull. 1500, 8 p.

MUNNS, R. K., AND D. C. HOLLAND.
1971. Determination of mercury in fish by flameless atomic absorption: A collaborative study. J. Assoc. Off. Anal. Chem. 54:202-205.

SCHMIDT, A. M.
1974. Action level for mercury in fish and shellfish. Fed. Regist. 39(236) Part II:42738-42740.

SPINELLI, J., M. A. STEINBERG, R. MILLER, A. HALL, AND L. LEHMAN.
1973. Reduction of mercury with cystein in comminuted halibut and hake fish protein concentrate. J. Agric. Food Chem. 21:264-268.

TEENY, F. M., A. S. HALL, AND E. J. GAUGLITZ, JR.
1974. Reduction of mercury in sablefish (*Anoplopoma fimbria*) and the use of the treated flesh in smoked products. Mar. Fish. Rev. 36(5):15-19.

THOMPSON, B. G.
1971. Fishery Statistics of the United States. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Stat. Dig. 65, 424 p.

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ECOLOGY OF HAWAIIAN SERGESTID SHRIMPS (PENAEIDEA: SERGESTIDAE)

JOHN F. WALTERS[1]

ABSTRACT

This paper describes the vertical distribution and migration, population size, seasonal size-frequency distribution, and diet of 20 species of sergestid shrimps collected between 1970 and 1973 in the vicinity of Oahu, Hawaii.

During the daytime, half-red sergestids live between 450 and 725 m, while all-red sergestids range from 650 to at least 1,200 m. At night all but two species migrate into the 0- to 300-m region, half-red and all-red groups mixing together. One nighttime group lives above 100 m, another lives between 125 and 300 m. Moonlight depresses the shallow group below 150 m; it has little effect on the deep group. In addition, some species stop migrating around full moon, remaining at their daytime depths.

All species examined eat zooplanktonic crustacea in the 1- to 3-mm size range. Some species can also utilize smaller zooplankton around 0.4-0.6 mm. This ability is unrelated to the enlarged maxillipeds found in some species.

Most species appear to spawn mostly during the spring, although ovigerous females can be found at any time of the year. Life span appears to be 1 yr for all species except *Sergia bisulcata*, which lives 2 yr. One species does not reproduce in Hawaiian waters.

Hawaiian sergestids are specialized by size, morphology, and vertical distribution. The most closely related species pairs are always separated by size. The Hawaiian sergestid assemblage is very similar to assemblages reported from two areas of the tropical Atlantic.

Shrimps of the family Sergestidae (Decapoda, Penaeidea) are one of the most characteristic groups of micronekton over much of the open ocean. They dominate the crustacean micronekton over large areas of the North Pacific, where they form sound-scattering layers (Barham 1957) and feed baleen whales (Omori et al. 1972). Two speciose sergestid assemblages have been described from the subtropical Atlantic by Foxton (1970) and Donaldson (1973, 1975). This paper examines the sergestid assemblage from the central Pacific near the Hawaiian Islands, reporting vertical distribution and migration, abundance, growth and reproduction, and diet.

MATERIALS AND METHODS

Sampling Area

All the sergestids examined in this study were collected off the leeward (west) coast of Oahu, Hawaii at about lat. 21°30′N, long. 158°20′W. Most trawling was done 10-25 km offshore in water 1,500-4,000 m deep. Physical and chemical data for this area, as well as the nearby Gollum Station (lat. 22°10′N, long. 158°00′W), have been reported by Gundersen et al. (1972) and Gordon (1970). The mixed layer is 50-80 m thick with a temperature of 23°-26°C. The annual variation in temperature of the mixed layer is only about 3°C (Gordon 1970). A broad thermocline extends to approximately 500 m, where the temperature is 5°-7°C. Salinity varies from 34.0 ‰ at 400-500 m to 35.2 ‰ at 100 m; oxygen varies from 7 mg/liter at 100 m to 1 mg/liter at 700-900 m. The water is very clear. In situ measurements of irradiance to 500 m at lat. 28°29′N, long. 155°14′W in August 1972 gave an extinction coefficient of 0.029 m^{-1} at a wavelength of 471 nm for depths below 200 m; surface irradiance at 471 nm was 7×10^2 $\mu W/cm^2$ per nm, decreasing to 1×10^{-4} $\mu W/cm^2$ per nm at 500 m (E. M. Kampa, pers. commun.). Annual net primary productivity has been estimated at 50 g C/m^2 (S. A. Cattell in T. A. Clarke 1973:431). Nakamura (1967) found an annual mean standing crop of zooplankton of 2.6 g/m^2 in the upper 200 m.

The sampling area was chosen as the deep water nearest to Honolulu. It has the further advantage of being in the lee of Oahu under normal tradewind conditions, an important practical consideration when working from RV *Teritu*. In

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spite of its proximity to land, the area appears to be representative of the open waters of the central North Pacific. Meroplankton is sometimes abundant, particularly larval stomatopods, but never dominates the zooplankton. The light regime at night may be affected by light from the urbanized areas of Oahu, although direct light from Honolulu is shielded by mountains. Doty and Oguri (1956) found enhanced values of primary productivity near the Hawaiian Islands (the "island mass effect"), but Gilmartin and Revelante (1974) found this effect only within about 1 km of land. The advantages of nearness to port and convenience of study greatly outweigh the potential disadvantages of being affected by nearshore processes.

Vertical Distribution: Teuthis Sampling Program

Most of the material studied was collected during the "Teuthis" program, a series of 23 cruises during 1971-73 by the University of Hawaii's RV *Teritu*. The primary objective of the program was to determine the vertical distributions of the various species of micronekton during the daytime and at night. For this purpose an extensive series of horizontal tows was made using a modified Tucker trawl (MT) with a mouth 3 m wide. The trawl can be opened and closed at the desired sampling depth, avoiding contamination of the sample by organisms from shallower depths during setting and retrieval. It is lined with knotless nylon mesh, with apertures about 7 mm in diameter. The cod end is a 1-m plankton net of 303-μm Nitex.[2] Mounted on the trawl is a time-depth recorder (Benthos 1170) which provides a record of the depths sampled by the trawl.

This basic configuration was extensively modified during the course of the sampling program to obtain more reliable operation and better data. The original acoustic-controlled opening-closing system (Inter-Ocean) was replaced by a more reliable messenger-operated double-trip mechanism (modified General Oceanics No. 4020). A digital flowmeter (General Oceanics No. 2030) was added at the beginning of 1972, giving a more accurate estimate of the volume of water sampled by the trawl. An acoustic telemeter (AMF No. 1024) allowed real-time monitoring of trawl depth beginning in November 1972; earlier tows wandered vertically over 10-20% of their maximum depth.

The limitations of time and unreliability of sampling gear forced abandonment of plans for a uniform series of standard tows. Each cruise attempted instead to sample depths not yet sampled or to answer questions raised by previous sampling. Informal as this protocol was, the actual depths sampled often differed greatly from the plan. Before a telemeter was available, the sampling depth was set by the amount of wire paid out; two tows with the same amount of wire out often showed a twofold variation in modal depth. Over the course of the program the upper 1,200 m was sampled rather thoroughly, with a few deeper tows down to 2,300 m.

A typical cruise lasted 4 days. On each day two tows were made during the daytime and two at night, avoiding the twilight periods when many mid-water animals are migrating. Tows sampled for 3 h at a towing speed of about 4 knots. The catch was immediately placed in chilled seawater, and live specimens were removed to an aquarium for observation. The rest of the catch was sorted and preserved in buffered 5% Formalin seawater. The inside of the net was picked clean of animals after each tow to prevent contamination of subsequent tows. Physical conditions recorded included ship's position at the beginning and end of sampling, weather conditions and sea state, time of sunrise and sunset, and lunar phase. Bathythermograph casts were made during the early cruises, later replaced with expendable bathythermograph casts; at least one was taken per cruise (Maynard et al. 1975). The 1973 cruises also recorded biological sound scattering at 25 kHz and surface light irradiance (Walters in prep.). In the laboratory, the sergestids were sorted to species, sexed, and counted, and the carapace length (CL) from the base of the rostrum to the posterior margin of the carapace at the dorsal midline was measured to the nearest 0.1 mm with an eyepiece micrometer in a dissecting microscope.

Between February 1971 and June 1973, 16 cruises produced 160 horizontal tows (Table 1). Daytime (DAY) tows were lumped together, but nighttime tows were divided into tows during the dark of the moon or with the moon obscured by clouds (NIGHT) and tows made under substantial amounts of moonlight (MOON). Total trawling time for each 25-m interval of the water column to 1,500 m for the entire series was calculated from time-depth records (Table 2).

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.–Summary of sampling, 1970-73.

Cruise	Dates	Samples	Remarks
70-12	8-10, 13-17 Dec. 1970	31	3-m IKMT[1] horizontal open tows
Teuthis IV	19-21 Feb. 1971	8	3-m MT[2] horizontal opening-closing tows
Teuthis V	15-19 Mar. 1971	14	
Teuthis VI	22-26 Apr. 1971	12	
Teuthis VII	24-26 May 1971	7	
Teuthis VIII	21-25 June 1971	12	
Teuthis IX	30 July-1 Aug. 1971	8	
Teuthis X	22-24 Sept. 1971	1	
Teuthis XI	28 Jan.-1 Feb. 1972	8	
Teuthis XII	25-29 Feb. 1972	6	
Teuthis XIII	25-29 Mar. 1972	11	
Teuthis XV	23-27 May 1972	11	
Teuthis XVI	29 June-2 July 1972	12	
Teuthis XVII	1-5 Aug. 1972	10	
Teuthis XIX	3-7 Nov. 1972	12	
Teuthis XXI	4-7 May 1973	13	
Teuthis XXIII	13-17 June 1973	15	
Teuthis XVIII	30 Sept.-4 Oct. 1972	25	3-m IKMT shallow and deep oblique open tows
Teuthis XXII	23-27 May 1972	15	
DSB III	2-3 Feb. 1973	14	3-m MT horizontal and oblique open tows
Echo IV	5-11 Dec. 1973	25	3-m IKMT stratified oblique open tows

[1]IKMT = Isaacs-Kidd midwater trawl.
[2]MT = modified Tucker trawl.

Oblique Series: Teuthis XVIII and XXII

Teuthis XVIII, 30 September to 4 October 1972, represented a departure from our normal sampling program. It consisted of a series of oblique tows with a 3-m Isaacs-Kidd midwater trawl (IKMT) designed to assess the relative importance in numbers and biomass of the various groups of micronekton, and also to determine the proportion of the mid-water community undergoing diurnal vertical migration (Table 1). Two series of oblique tows were taken: "deep" tows from the surface to 1,200 m, and "shallow" tows from the surface to 400 m. The catches were preserved unsorted in 5% Formalin seawater and returned to the laboratory, where they were sorted into the major taxa, blotted dry, counted, and weighed. Further details of sampling methods and results can be found in Maynard et al. (1975). The sergestids were divided into half-red and all-red types, counted, and weighed. They were later separated by species, counted, and sexed, and the carapace length measured.

Teuthis XXII, 23-27 May 1973, followed the same sampling protocol as Teuthis XVIII, with series of shallow and deep oblique tows. Sergestids from this cruise were separated by species, counted, and sexed, and the carapace length measured.

Effects of Moon: 70-12 and Echo IV

The Teuthis cruises were unevenly spaced in time, making it difficult to use the data for studying growth rates and other aspects of population dynamics. In particular there were no cruises at all between early November and late January. To fill this gap in the seasonal coverage, I examined the sergestids from the December 1970 cruise of T. A. Clarke (70-12). This cruise used a 3-m IKMT for an extensive series of 2- and 3-h horizontal open tows in the upper 1,250 m of the water column (Table 1). Further details of sampling can be found in T. A. Clarke (1973). While the material from this cruise helped balance the seasonal data, it raised new questions about the vertical distribution of sergestids. Many of the species in the 70-12 samples showed abnormal vertical distributions. Since the cruise took place near full moon, it appeared that the abnormalities, in particular the absence of normal vertical migration patterns in some species until the final two nights of the cruise, were related to lunar phase. Unfortunately, shallow and deep tows were not taken on the same night, so it was unclear whether entire populations were affected and on which night normal behavior resumed.

The sampling program of Echo IV attempted to clarify these problems. We planned to make shallow and deep oblique tows with a 3-m IKMT from first quarter to full moon in an attempt to find when vertical migration ceased. Mechanical difficulties postponed the cruise until three nights before full moon; migration had already ceased by this time. The sampling protocol called for a shallow tow, either 0-200 m or 200-400 m; an

TABLE 2.–Number of tows and total towing time for each depth interval, 0-1,500 m, Teuthis sampling program.

Depth (m)	DAY			NIGHT			MOON		
	No. of tows	No. of tows >10 min	Total min	No. of tows	No. of tows >10 min	Total min	No. of tows	No. of tows >10 min	Total min
	3	0	6	7	3	433	13	0	38
	3	0	6	7	4	425	14	4	514
	3	0	8	7	5	313	13	5	350
	3	0	9	8	5	385	12	5	604
100 –				–			–		
	3	1	124	6	6	381	8	2	124
	4	2	95	6	3	336	8	2	51
	3	1	91	6	6	486	8	5	530
	3	1	106	5	5	306	6	4	324
200 –				–			–		
	4	2	121	1	0	2	5	4	204
	4	2	83	2	1	131	3	2	335
	3	2	105	4	4	337	2	1	180
	2	2	116	5	3	149	3	3	208
300 –				–			–		
	3	3	122	3	2	118	4	3	199
	4	4	115	3	3	61	2	2	162
	4	4	150	3	3	48	1	0	9
	4	3	302	4	4	123	0	0	—
400 –				–			–		
	6	4	160	5	5	266	2	1	42
	8	6	291	4	2	135	2	2	211
	13	9	609	3	3	241	2	2	95
	14	11	406	5	2	94	2	2	49
500 –				–			–		
	10	7	508	3	2	86	2	2	236
	9	8	260	4	2	140	1	1	14
	12	9	370	4	1	23	1	0	5
	14	11	492	4	1	75	2	0	11
600 –				–			–		
	15	14	559	6	4	216	3	2	71
	10	7	225	6	4	147	4	4	293
	8	5	274	7	3	82	6	5	205
	12	7	371	5	3	172	5	4	210
700 –				–			–		
	13	8	388	4	3	249	5	5	115
	14	10	459	3	1	40	3	3	143
	12	9	341	3	2	88	2	1	35
	13	11	449	2	1	51	2	2	114
800 –				–			–		
	11	7	379	4	2	91	3	2	74
	9	7	206	4	2	119	3	2	62
	7	6	190	4	1	29	3	2	69
	9	6	165	3	2	62	2	1	13
900 –				–			–		
	10	6	185	3	1	57	2	1	24
	10	7	179	2	1	44	1	0	2
	9	4	197	2	2	29	1	0	4
	8	4	148	1	1	17	1	0	5
1,000 –				–			–		
	5	3	166	1	0	6	1	0	4
	5	2	209	1	0	7	1	0	4
	5	2	62	1	0	7	1	0	8
	4	1	26	1	1	15	1	1	12
1,100 –				–			–		
	3	2	47	1	1	85	1	0	8
	3	2	126	1	0	2	1	1	48
	2	1	14	0	0	—	1	1	12
	2	2	42	0	0	—	0	0	—
1,200 –				–			–		
	2	2	89	0	0	—	0	0	—
	3	2	39	0	0	—	0	0	—
	3	1	62	0	0	—	0	0	—
	3	2	71	0	0	—	0	0	—
1,300 –				–			–		
	3	3	53	1	1	10	0	0	—
	3	3	104	1	1	20	0	0	—
	3	2	59	1	1	45	0	0	—
	2	1	18	1	1	23	0	0	—
1,400 –				–			–		
	2	1	18	1	0	7	0	0	—
	2	2	27	2	2	80	0	0	—
	1	0	6	2	0	10	0	0	—
	1	1	16	2	0	8	0	0	—
1,500 –				–			–		

intermediate tow of 400-600 m; and a deep tow of 400-1,200 m, each night of the cruise. Daytime trawling investigated possible moon-related changes in the daytime distribution of sergestids and included a 400- to 800-m tow and a 600- to 1,000-m tow each day. The actual depths sampled by the trawl deviated somewhat from the protocol, as we used no telemetry on the trawl. The last daytime tow was an all-day affair sampling from 1,100 to 1,900 m. The sergestids from this cruise were identified to species and counted, but not sexed or measured.

Feeding Study: DSB III

An important problem in any study of feeding in mid-water animals is the effect of the sampling gear on feeding behavior. A mid-water trawl concentrates animals in the cod end to unnaturally high densities. Often the trawl lumps together animals from different depth zones. A predator feeding on the contents of the cod end is likely to eat prey it would not normally take in the natural state, either because predator and prey do not occur at the same depth or because the prey can normally escape the predator. Examination of sergestid stomach contents from the Teuthis series suggested that many shrimp had been feeding in the trawl. A modification of the trawl became necessary to get reliable feeding data.

The DSB III cruise of 2-3 February 1973 was designed to investigate the feeding behavior of mid-water animals. The MT was modified by tieing off the cod end ahead of the plankton net, allowing zooplankton to escape through the meshes. The trawl mouth was tied open. Daytime and nighttime oblique and horizontal tows were taken, the main objective being to obtain as large and varied a collection of mid-water animals as possible without much concern for their depth of capture (Table 1). The samples were preserved in 5% Formalin seawater and returned to the laboratory, where the sergestids were sorted out and their stomach contents identified.

Using the MT in this fashion produced one unexpected bonus. In addition to flushing out prey-sized zooplankton, the water current forced the catch and the inner lining of the net through the coarse outer net in pockets. Within each pocket the animals were firmly held by the force of the water, preventing movement and feeding. Future feeding studies might profit from deliberately designing this effect into the sampling gear.

Analysis of Vertical Distribution Data: The Contamination Problem

Most previous studies of vertical distribution (e.g., Foxton 1970, T. A. Clarke 1973, Donaldson 1975) have assumed that all the animals captured in a horizontal tow were taken at a single depth. While such an assumption simplifies the presentation and interpretation of the data, it can produce a misleading picture of the vertical structure of the mid-water community if the tows actually fish over a substantial depth range. Open trawls like the IKMT are the most susceptible to contamination of the catch by animals from other depths, since they fish during setting and retrieval. In this case, contamination usually takes the form of shallow-living animals appearing to have been captured below their normal depth. Rapid setting and retrieval can minimize but not eliminate the problem (T.A. Clarke 1973). Foxton (1970) and Donaldson (1975) have shown that animals from other depths can contaminate IKMT samples even when the trawl is fitted with opening-closing cod end buckets. Some animals become temporarily entangled in the net early in the tow. When they break free later on, the trawl may be fishing at a different depth, resulting in a sample that mixes shallow and deep animals in an unknown proportion.

Even an opening-closing trawl like the MT can give misleading results if it is allowed to wander vertically while open. In such a case, assigning the entire catch to the modal depth broadens out the apparent vertical range in both directions. Our experience has shown that towing the MT deeper than 200 m results in substantial vertical wandering unless its depth is constantly monitored and adjusted. Since a working telemeter was available only during the latter part of our program, most of our "horizontal" tows actually have a vertical range of 50-100 m. The problem increases with depth; tows below 800 m commonly wander 200 m or more. Assigning the catch to a modal depth would produce a misleading vertical distribution pattern.

The vertical distribution diagrams presented in this paper allow for vertical wandering of the trawl and for unequal sampling time with depth. Only horizontal tows are considered. The water column is divided into 25-m zones, and the amount of time each tow spent in each zone is determined from the various depth zones in proportion to the time towed in each zone. Let c_i be the number of

shrimp captured by the ith tow and $t_{i,j}$ be the amount of time tow i spent in the jth depth zone. Then the proportional catch $c_{i,j}$ from the ith tow in the jth depth zone is

$$c_{i,j} = \frac{c_i}{t_{i,j}} . \quad (1)$$

For each depth zone j, summing proportional catches from all tows and dividing by total trawling time in the zone gives the catch rate r_j:

$$r_j = \frac{\sum_i c_{i,j}}{\sum_i t_{i,j}} . \quad (2)$$

Ideally, the catch rate is proportional to the population density, so that dividing the catch rate by trawl filtering rate gives an estimated population density; i.e.,

$$D_j = \frac{r_j}{M_e \cdot f \cdot v} , \quad (3)$$

where D_j is the estimated population density in the jth zone, M_e is the effective mouth area of the trawl (because of the design of the trawl, this quantity decreases with increasing towing speed), f is the filtering efficiency of the trawl, and v is the towing speed.

Proportional allotment of the catch by this method assumes that a particular shrimp is equally likely to have been captured at any instant during the tow. This assumption is clearly false for tows that spend only part of their time in the shrimp's actual depth range. However, spurious catch rates outside the actual depth range are minimized by additional tows in these zones that do not enter the actual depth range and do not catch shrimp; these tows increase the denominator of Equation (2) without increasing the numerator. It follows that this method of estimating vertical distributions works best when each depth zone is sampled many times.

Table 2 shows that during the daytime all depth zones between 400 and 1,075 m were sampled at least five times and that at least five tows spent more than 10 min in all zones between 425 and 950 m. Nighttime sampling was less thorough because tows were split into two groups on the basis of moonlight. In both groups all zones in the upper 200 m were sampled at least five times, as was the 600- to 700-m range (NIGHT) and 650- to 725-m range (MOON). NIGHT tows in the 200- to 225-m zone sampled only 2 min; estimated population densities for this zone, while generally plausible-looking, should be regarded cautiously. The 0- to 25-m zone for MOON tows were sampled many times for brief periods by open tows that spent nearly all their time at depths of 50-150 m, but was never sampled extensively by any tow. Many species show spuriously high estimated population densities in this zone. There were no NIGHT tows between 1,150 and 1,300 m, and no MOON tows between 375 and 400 m or below 1,175 m. Nighttime sampling was generally sparse below 800 m, and the estimated population densities for this region are very crude.

A second major assumption of this method of presenting vertical distribution data is that the vertical distribution remains constant throughout the sampling period, allowing data from many different cruises to be summed together. The resulting estimated population densities represent an average over the entire sampling period. The actual vertical structure on any given cruise may vary considerably from this average. The separation of nighttime tows into NIGHT and MOON tows is the only systematic attempt to show variations in vertical distribution; other variations are discussed in the species accounts.

Presentation of Results

A brief explanation will aid in interpreting the vertical distribution figures that follow (e.g., Figure 1). Catch rates were converted to estimated population densities in numbers per 10^5 m^3 by assuming an average trawling speed of 2 m/s, effective trawl mouth area of 5.1 m^2 (at 2 m/s), and filtering efficiency of 90%. DAY, NIGHT, and MOON (see above) distributions are shown for the entire population as histograms on the right side of the figure. The number to the right of each histogram is the sample size. In addition, the catches were divided into size classes, and population densities were estimated by the same method for each size class. Species with a maximum carapace length less than 17.0 mm were divided into 0.5-mm classes, while larger species were divided into 1.0-mm classes. The result was an array of estimated population densities as a function of size and depth. Interpolation produced a series of contours of equal population density. The lowest contour level represents 0.2 shrimp per 10^5 m^3 per mm CL; each successive contour level

represents a tenfold increase over the previous one.

The oblique tows of September 1972 (Teuthis XVIII) and May 1973 (Teuthis XXII) provided data that yield two estimates of the population densities of the various species, using the method of Maynard et al. (1975). Summing over the entire water column the depth-specific population densities obtained from the horizontal tows provides a third estimate of population densities. The results of these estimates are reported as numbers per 100 m^2 of ocean surface in Table 3. Sample sizes and standard deviations are given for the mean values of the oblique series. Because of the nature of the calculations for the horizontal tows, no standard deviations can be figured, but the variation is probably of the same order as those of the oblique series, since horizontal tows sampled each depth interval about the same number of times and for roughly the same total amount of time as the oblique tows.

The Teuthis data are poorly suited for investigating growth and reproduction of sergestids. The sampling program was designed primarily to investigate the vertical distribution of mid-water animals. Depth coverage varied widely from cruise to cruise, and the cruises were spaced irregularly throughout the year. In order to smooth the irregularities as much as possible, the data are lumped into 3-mo periods. The cruises invoved are:

Jan. - Mar.	T4, T5, T11, T12, T13
Apr. - June	T6, T7, T8, T15, T16, T21, T23
July - Sept.	T9, T10, T17, T18
Oct. - Dec.	T19, 70-12.

Histograms show the size-frequency distribution of males and females for each species. For *Sergestes pectinatus* only, data from the oblique series of May 1973 (Teuthis XXII) are added into the second quarter histogram.

Because of the problem of feeding in the trawl (discussed above), only the stomach content data from DSB III (February 1973) are presented. Table 4 shows the average condition of the stomach contents for each tow. The two indices reported represent the quantity of food present and its state of digestion. Both are based on an arbitrary scale of 1 to 5:

Contents	*Digestion*
1. Packed full, distended.	Whole animal, with little evidence of digestion.
2. More than half full.	Body still mostly intact, appendages separated, some digestion of soft parts.
3. 25-50% full.	All soft parts digested, cuticle remaining, usually disarticulated.
4. Less than 25% full.	Cuticle broken into small fragments.
5. Empty.	Empty.

Stomach contents with a digestion state of 1 were seldom found in the DSB III samples but were rather common in the Teuthis material, probably because of feeding in the trawl.

Table 5 shows the kind and number of food items found in the stomachs of each species. Often the stomach contents were too well digested for identification. Food items were not identified beyond the general categories presented except for the calanoid copepod genus *Pleuromamma*, which has a prominent shiny knob on the side of the metasome that is highly resistant to digestion.

RESULTS

Sergestid species occurring in Hawaiian waters are listed in Table 6, along with the total number caught. *Sergestes* and *Sergia* until recently were considered to be subgenera of genus *Sergestes* s.l.; however, Omori (1974) has rightly elevated the subgenera to full genera. This paper follows his usage but gives feminine endings to species of *Sergia*. A paper presenting systematic descriptions of Hawaiian species is in preparation.

Sergestes atlanticus Milne Edwards 1830

Vertical Distribution (Figure 1)

The normal daytime range of *S. atlanticus* was 550 to 725 m. Small individuals had a more restricted range than the larger ones; shrimp less than 5.5 mm CL stayed between 550 and 650 m. *Sergestes atlanticus* was occasionally taken at 800 m or below. The small concentrations between 800 and 1,050 m in Figure 1 all resulted from the June 1973 cruise. In addition, the December 1970 cruise took seven shrimp in an 800-m tow. At night *S. atlanticus* occurred over a wide range from the surface to about 300 m. The large concentration in the upper 25 m resulted from a single large capture in May 1973. This depth interval was extensively sampled by only three tows, so it is unclear

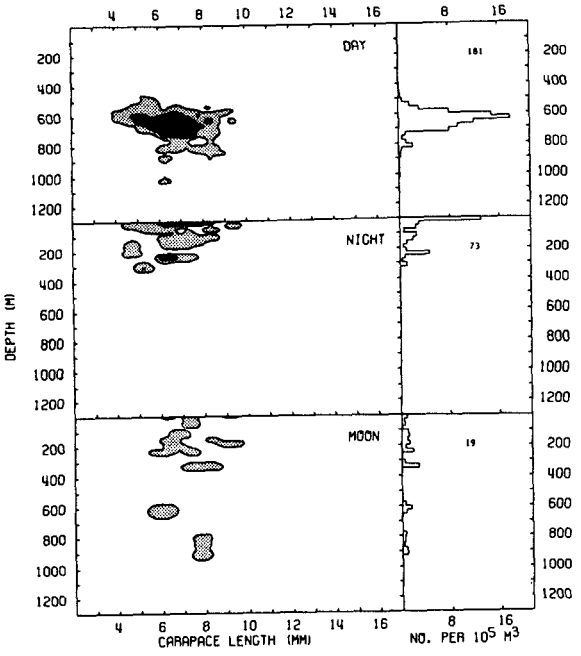


FIGURE 1.—Vertical distribution of *Sergestes atlanticus*.

whether the bulk of the population normally occurs so shallow. A number of night tows in the 75- to 150-m range took small numbers of *S. atlanticus*, and one tow at about 250 m captured five individuals. There appeared to be no significant variation of depth with size. Tows on moonlit nights took small numbers of *S. atlanticus* from the surface to about 350 m, with a possible concentration around 150-175 m. Several captures were made between 600 and 925 m, suggesting that at least part of the population did not always migrate. The December 1970 cruise took substantial numbers (up to seven) near full moon between 250 and 300 m, and also between 550 and 800 m, indicating that only part of the population was migrating. Later in the cruise when the moon was waning, tows between 30 and 100 m took *S. atlanticus* in moderate numbers (four to six).

Population Size, Growth, and Reproduction (Figure 2)

Sergestes atlanticus was moderately abundant, turning up regularly in tows at the appropriate

TABLE 3.—Estimated population sizes of Hawaiian sergestids from all horizontal tows and two series of oblique tows (no. per 100 m²).

Species	Teuthis XVIII (1)	$\bar{x}$	s	n	Teuthis XXII (1)	$\bar{x}$	s	n	Horizontal (1)	$\bar{x}$	n
Sergestes atlanticus	DD	4.36	3.66	28	DD	1.17	1.67	9	D	2.10	180
	DN	2.66	1.31	19	DN	1.10	1.47	6	N	0.84	68
	SN	4.28	3.09	47	SN	0.28	0.56	2	M	0.46	19
		3.79	2.75	94		0.88	1.33	17		1.31	267
Sergestes erectus	DD	7.22	3.06	45	DD	1.79	1.25	13	D	5.55	542
	DN	5.30	3.83	39	DN	1.91	1.00	10	N	2.02	156
	SN	5.46	2.61	59	SN	2.28	0.80	16	M	2.83	151
		5.85	3.03	143		1.97	1.01	39		3.81	849
Sergestes armatus	DD	12.37	14.47	73	DD	1.18	1.85	8	D	2.48	251
	DN	12.16	7.69	84	DN	1.46	1.70	8	N	2.63	141
	SN	7.61	3.61	83	SN	0.87	0.80	6	M	1.83	41
		10.22	8.28	250		1.15	1.45	22		2.35	433
Sergestes vigilax	DD	3.33	2.52	20	DD	0.76	0.96	6	D	0.52	57
	DN	2.30	1.55	17	DN	0.72	0.81	4	N	0.28	30
	SN	4.63	1.42	50	SN	0.99	0.83	2	M	0.15	13
		3.58	1.95	87		0.61	0.75	12		0.35	100
Sergestes orientalis	DD	5.54	4.12	34	DD	0.65	0.92	5	D	1.61	160
	DN	5.11	2.00	38	DN	0.18	0.31	1	N	1.39	130
	SN	12.45	5.03	130	SN	0.99	0.83	7	M	0.75	42
		8.43	5.29	202		0.64	0.80	13		1.32	332
Sergestes consobrinus	DD	6.72	3.70	42	DD	2.48	1.42	18	D	0.72	81
	DN	3.30	1.28	24	DN	2.10	1.96	11	N	1.99	231
	SN	5.82	4.13	63	SN	1.45	1.03	10	M	0.57	13
		5.26	3.46	129		2.08	1.40	39		1.05	325
Sergestes sargassi	DD	10.37	7.85	68	DD	1.55	1.41	11	D	0.64	71
	DN	3.53	1.40	25	DN	1.68	0.95	9	N	1.07	77
	SN	4.91	2.16	52	SN	2.06	1.60	15	M	0.40	26
		5.84	4.73	145		1.74	1.29	35		0.70	174
Sergestes pectinatus	DD	23.24	17.36	141	DD	6.95	4.04	51	D	2.01	245
	DN	24.14	14.13	178	DN	2.58	1.34	14	N	1.54	136
	SN	30.44	20.86	330	SN	2.89	2.04	21	M	1.40	86
		26.67	17.30	649		4.70	3.59	86		1.71	467

TABLE 3.—Continued.

Species	Teuthis XVIII (1)	$\bar{x}$	s	n	Teuthis XXII (1)	$\bar{x}$	s	n	Horizontal (1)	$\bar{x}$	n
Sergia fulgens	DD	0.35	0.69	2	DD	24.15	19.01	186	D	1.55	185
	DN	0.29	0.40	2	DN	8.63	4.17	46	N	2.21	237
	SN	0.63	0.60	12	SN	9.15	5.08	64	M	3.57	134
		0.45	0.55	16		15.95	14.91	296		2.26	556
Sergia scintillans	DD	9.86	8.55	40	DD	5.12	4.41	39	D	3.69	355
	DN	6.80	5.17	51	DN	0.72	0.81	4	N	3.59	329
	SN	12.14	6.95	130	SN	3.80	2.17	27	M	2.35	151
		9.90	6.83	221		1.90	2.25	70		3.31	835
Sergia gardineri	DD	8.80	2.13	55	DD	5.12	4.41	17	D	11.22	964
	DN	11.74	9.23	88	DN	0.72	0.81	15	N	9.95	793
	SN	9.44	3.88	100	SN	0.56	0.45	4	M	2.67	51
		10.00	5.58	243		1.90	2.25	36		8.65	1,808
Sergia bigemmea	DD	2.50	2.04	16	DD	0.29	0.45	2	D	0.37	27
	DN	3.19	2.57	23	DN	0.76	0.84	4	N	1.48	116
	SN	1.67	0.95	18	SN	0.00	0.00	0	M	0.19	2
		2.35	1.85	57		0.31	0.53	6		0.64	145
Sergia inequalis	DD	2.01	1.76	12	DD	0.38	0.63	3	D	0.63	16
	DN	0.61	1.37	5	DN	0.57	0.56	3	N	0.76	50
	SN	0.57	0.60	6	SN	0.00	0.00	0	M	0.19	10
		0.94	1.29	23		0.31	0.52	6		0.55	76
Sergia bisulcata	DD	1.15	1.09	7	DD	1.03	1.19	8	D	1.04	91
	DN	1.31	1.76	9	DN	0.37	0.64	2	N	1.32	68
	SN	1.12	0.48	12	SN	0.82	0.90	6	M	1.96	38
		1.19	1.08	28		0.82	0.96	16		1.35	197
Sergia tenuiremis	DD	0.43	0.52	3	DD	0.77	0.97	6	D	0.93	39
	DN	0.86	1.17	6	DN	0.55	0.96	3	N	0.99	25
		0.67	0.91	9		0.70	0.91	9	M	0.73	14
										0.89	78
Petalidium suspirlosum	DD	1.09	0.73	7	DD	1.50	2.29	10	D	1.94	53
	DN	1.30	1.09	9	DN	0.93	0.58	5	N	0.82	13
		1.21	0.90	16		1.31	1.85	15	M	2.84	22
										1.84	88

[1]DD—Deep Day tows (0-1,200 m): T18 four tows, T22 six tows.
DN—Deep Night tows (0-1,200 m): T18 five tows, T22 three tows.
SN—Shallow Night tows (0-400 m): T18 seven tows, T22 five tows.
D—DAY Horizontal tows.
N—NIGHT Horizontal tows.
M—MOON Horizontal tows.

TABLE 4.—Feeding chronology of sergestids from DSB III.

Species	DAY (Tow no. 1-3, 12) Number examined	Empty (%)	Content[1]	Digestion[1]	NIGHT (Tow no. 5-10) Number examined	Empty (%)	Content[1]	Digestion[1]
Sergestes atlanticus	0	—	—	—	2	0	1.5	3.5
Sergestes erectus	12	17	3.7	3.9	38	26	3.3	3.8
Sergestes armatus	11	82	4.8	4.7	20	65	3.7	4.3
Sergestes vigilax	0	—	—	—	1	100	5.0	5.0
Sergestes orientalis	1	100	5.0	5.0	1	0	3.0	4.0
Sergestes sargassi	0	—	—	—	10	30	3.5	4.0
Sergestes pectinatus	0	—	—	—	9	22	2.7	3.6
Sergia fulgens	2	50	4.0	4.5	6	67	4.1	4.2
Sergia scintillans	0	—	—	—	28	18	2.8	3.8
Sergia gardineri	3	67	3.7	4.1	8	37	3.2	4.2
Sergia bigemmea	2	0	3.0	4.0	76	11	3.0	3.6
Sergia inequalis	0	—	—	—	1	0	4.0	3.5
Sergia bisulcata	2	0	3.2	4.0	5	20	3.0	3.6
Sergia tenuiremis	1	100	5.0	5.0	0	—	—	—
Total sample	34	62	4.1	4.2	205	22	3.1	3.7

[1]See text.

depths, but seldom in numbers greater than five or six for a 3-h tow. The average population density estimated from all horizontal tows was 1.31 per 100 m^2. Daytime tows caught larger numbers than nighttime tows, the population density from daytime horizontal tows being 2.10 per 100 m^2. The

TABLE 5.–Diet of sergestids from DSB III.

Number of shrimp containing	*Sergestes atlanticus*	*Sergestes erectus*	*Sergestes armatus*	*Sergestes vigilax*	*Sergestes orientalis*	*Sergestes sargassi*	*Sergestes pectinatus*	*Sergia fulgens*	*Sergia scintillans*	*Sergia gardineri*	*Sergia bigemmea*	*Sergia inequalis*	*Sergia bisulcata*	*Sergia tenuiremis*
Calanoid copepods	1	27	6			3	7	1	7	2	23	1		
Pleuromamma[1]	1	8	1			1	5		2		3			
Cyclopoid copepods									3		6			
Amphipods	1	3	3					1	3		6		1	
Ostracods					1			1	1	1	15		2	
Euphausiids		1	1			1							1	
Decapod larvae			1						1	1	1		1	
Bivalve larvae	1							1	18	1	16		1	
Foraminifera								3	10	2	4		1	
Chaetognath spines											3			
Unidentified crustacea		19	1			3	3	1	17	3	33		3	
Fibrous matter									5		2		1	
Other[2]	1	1						1	5	1	4			
Empty		17	29	1	1	3	2	2	5	13	11		1	3
Total number examined	3	62	41	1	2	10	12	9	35	19	88	1	8	3

[1]Included with calanoid copepods.
[2]Including gastropod larvae, radiolarians, pteropods, fish eggs, and fish scales.

TABLE 6.–Numbers of Hawaiian sergestids captured, 1970-73.

Half-red species	
Sergestes atlanticus Milne-Edwards	546
Sergestes cornutus Krøyer	17
Sergestes erectus Burkenroad	1,371
Sergestes armatus Krøyer	1,113
Sergestes vigilax Stimpson	271
Sergestes orientalis Hansen	1,030
Sergestes tantillus Burkenroad	21
Sergestes consobrinus Milne	647
Sergestes sargassi Ortmann	497
Sergestes pectinatus Sund	1,541
Sergia fulgens (Hansen)	1,118
Sergia scintillans (Burkenroad)	1,610
All-red species	
Sergia gardineri (Kemp)	3,096
Sergia bigemmea (Burkenroad)	398
Sergia inequalis (Burkenroad)	149
Sergia bisulcata (Wood-Mason)	350
Sergia maxima (Burkenroad)	2
Sergia tenuiremis (Krøyer)	147
Petalidium suspiriosum Burkenroad	170

September 1972 oblique series gave a figure of 3.79 per 100 m^2, and the May 1973 oblique series yielded 0.88 per 100 m^2; these figures are probably close to the maximum and minimum population density.

Recruitment was highest during the third quarter (July-September), the only time of year when immature shrimp less than 4 mm CL were taken. The largest shrimp were most abundant during the second quarter (April-June).

Diet (Table 5)

Only three individuals examined had recognizable stomach contents: a calanoid copepod (*Pleuromamma*), an amphipod, and fragments of larval bivalve shells.

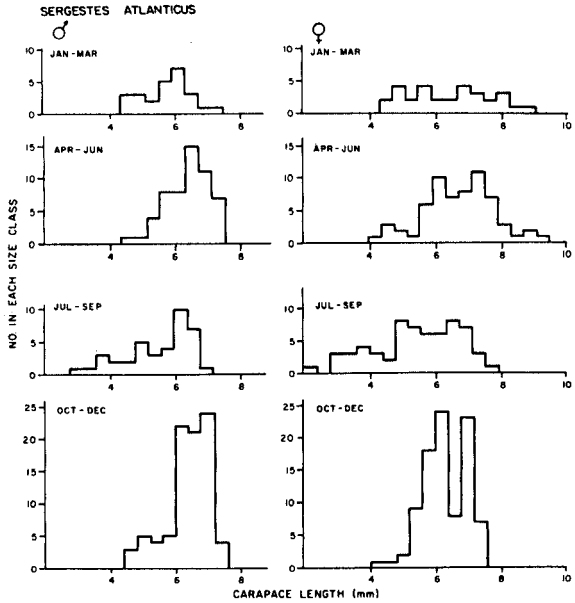


FIGURE 2.–Quarterly size-frequency distribution of *Sergestes atlanticus*.

Sergestes cornutus Krøyer 1855

Vertical Distribution

Only four individuals were captured in horizon-

tal closing tows; these were all daytime tows between 450 and 550 m. Several were captured in 0- to 400-m oblique night tows, indicating that *S. cornutus* is a vertical migrator. Donaldson (1975) found *S. cornutus* mostly in the upper 50 m at night.

Population structure and diet were not studied because of the small sample size.

Sergestes erectus Burkenroad 1940

Vertical Distribution (Figure 3)

Sergestes erectus was abundant in our collection, but nearly half of the shrimp came from daytime tows of the November 1972 cruise. The daytime vertical range was about 550 to 800 m, with maximum catches between 625 and 750 m. Immature shrimp did not occur below 750 m. The nighttime range varied with size. Small immature shrimp less than 12 mm CL occurred between the surface and 200 m, mostly below 125 m. Intermediate-sized shrimp between 12 and 16 mm CL, including immature and newly mature shrimp, ranged between 150 and 250 m. Adult shrimp larger than 16 mm CL were found between 250 and 325 m. Moonlight depressed the vertical range of adults very little, although there were some captures in the 350- to 475-m range; immatures were found between 175 and 250 m. The peak in the upper 25 m is a sampling artifact. There was no positive evidence of full moon nonmigration in the horizontal samples, but the December 1970 cruise took a dozen shrimp in the 575- to 700-m range, suggesting that about 20-30% of the population was not migrating.

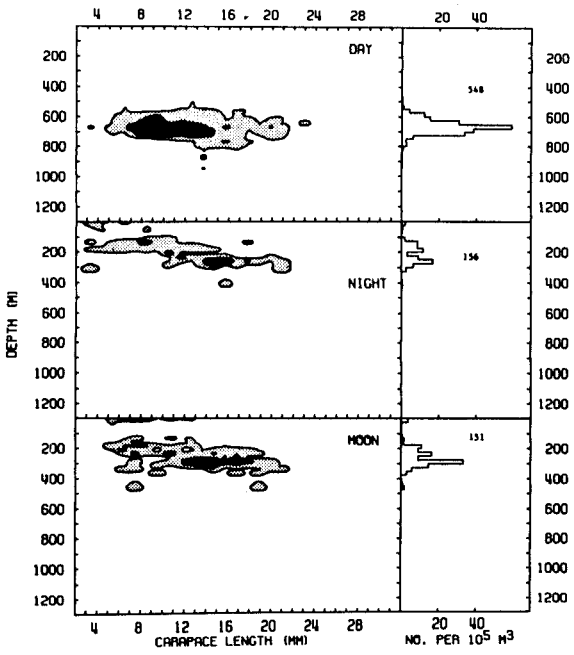


FIGURE 3.—Vertical distribution of *Sergestes erectus*.

Population Size, Growth, and Reproduction (Figure 4)

Sergestes erectus was the second most abundant species in the horizontal series, the average population density estimated from all horizontal tows amounting to 3.81 per 100 m^2. Like *S. atlanticus*, it was taken in larger numbers during the daytime than at night, the population density estimated from daytime horizontal tows amounting to 5.55 per 100 m^2. These numbers reflect its extreme abundance during the November 1972 cruise, when as many as 157 were taken in a single 3-h tow. The oblique series of September 1972 and

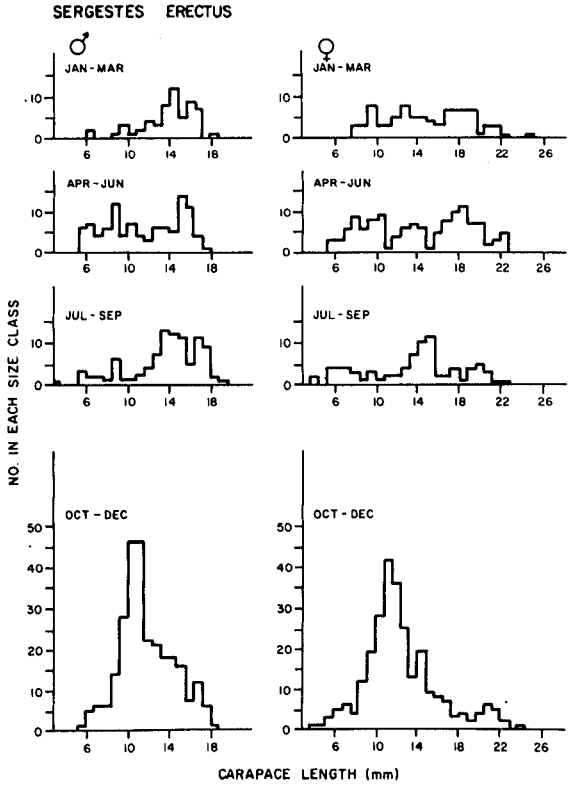


FIGURE 4.—Quarterly size-frequency distribution of *Sergestes erectus*.

May 1973 yielded figures of 5.85 and 1.97 per 100 m^2, respectively.

Recruitment was not noticeably high during any particular quarter. However, medium-sized shrimp in the 10- to 14-mm CL range were significantly more abundant during the fourth quarter (October-December) than at other times of the year (Kolmogorov-Smirnov test, $P<0.05$).

Diet (Table 5)

Calanoid copepods made up the bulk of the stomach contents of the *S. erectus* from DSB III. A few amphipods and a single euphausiid were also found. One individual had some material very tentatively identified as a small fish, the only one found in the DSB III collection. No food items in the 0.4- to 0.6-mm size range were found.

Sergestes armatus Krøyer 1855

Vertical Distribution (Figure 5)

The daytime vertical distribution of *S. armatus* varied somewhat with size. Immature shrimp ranged between 450 and 600 m; adults were generally between 550 and 650 m, but sometimes as shallow as 450 m. One tow in November 1972 took 13 shrimp at about 675 m. The December 1970 cruise took nine shrimp in open tows below 800 m; most of these were probably contaminants. The nighttime range also varied with size; shrimp smaller than 8 mm CL usually occurred between 100 and 200 m, while adults were found mostly between 150 and 300 m, with occasional captures as deep as 450 m. Moonlight did not depress the vertical distribution of *S. armatus*. The peak in the upper 25 m is a sampling artifact. The open tows of the December 1970 and December 1973 cruises took small to moderate numbers of *S. armatus* at the daytime depth. If these shrimp were not contaminants, they suggest that about 5-20% of the December 1973 population was not migrating.

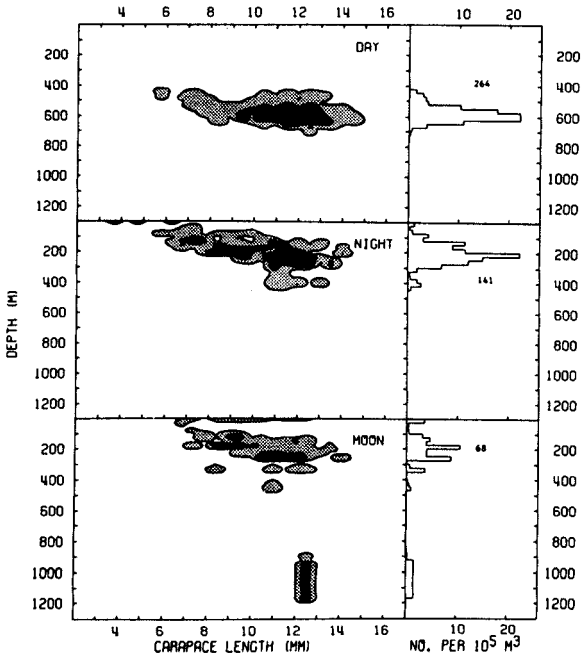


FIGURE 5.—Vertical distribution of *Sergestes armatus*.

Population Size, Growth, and Reproduction (Figure 6)

Sergestes armatus was abundant in the horizontal series, the average population density of 2.35 per 100 m^2 estimated from all horizontal tows making it the fourth most abundant sergestid. The catch was even greater during the September 1972 oblique series, which yielded a figure of 10.22 per 100 m^2, second only to *S. pectinatus*. The May 1973 oblique series took much smaller numbers, amounting to only 1.51 per 100 m^2.

Recruitment was much higher during the second quarter (April-June) than during the rest of the year. Large individuals were most abundant during the fourth quarter (October-December).

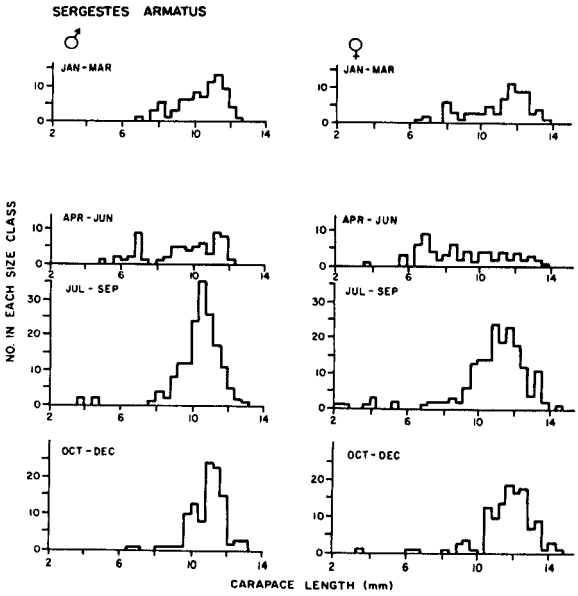


FIGURE 6.—Quarterly size-frequency distribution of *Sergestes armatus*.

Diet (Table 5)

DSB III took over 40 *S. armatus*, but two-thirds had empty stomachs. Food items included calanoid copepods, amphipods, an euphausiid, and an unidentified decapod larva. Prey in the 0.4- to 0.6-mm size range, such as foraminifera or bivalve larvae, were not found.

Sergestes vigilax Stimpson 1860

Vertical Distribution (Figure 7)

The daytime vertical range of *S. vigilax* was about 550 to 725 m, with a concentration at about 675 m. Nighttime captures were all in the 0- to 200-m depth range, peaking at about 50-75 m. Moonlight depressed the peak to 150-200 m, but some individuals remained shallower. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 8)

Sergestes vigilax was not abundant in Hawaiian waters. The average population density estimated from all horizontal tows was only 0.35 per 100 m^2. Daytime catches were larger than night catches, the population estimate from the day tows being 0.52 per 100 m^2. The oblique series of September 1972 and May 1973 took larger numbers, yielding estimates of 3.57 and 0.61 per 100 m^2, respectively. These larger population sizes may indicate that the finer mesh of the IKMT sampled *S. vigilax*, a relatively small species, more efficiently than did the MT used for the horizontal tows.

The seasonal size-frequency histograms are not significantly different from one another. Shrimp less than 5 mm CL were most abundant in the third quarter (July-September).

Diet (Table 5)

Only a single individual was examined; it had an empty stomach.

Sergestes orientalis Hansen 1919

Vertical Distribution (Figure 9)

The daytime vertical distribution of *S. orientalis* varied with size; small shrimp less than 6.5 mm CL were taken from 450 to 575 m, while larger ones were found between 500 and 625 m, mostly between 550 and 600 m. The nighttime range was from the surface to 125 m, with largest numbers in the 25- to 50-m and 75- to 100-m zones. Small shrimp less than 6 mm CL stayed above 75 m. Moonlight depressed most of the nighttime

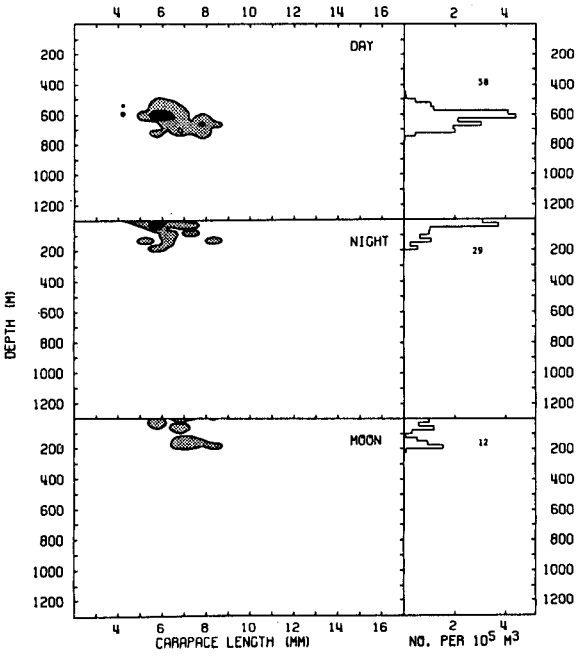


FIGURE 7.—Vertical distribution of *Sergestes vigilax*.

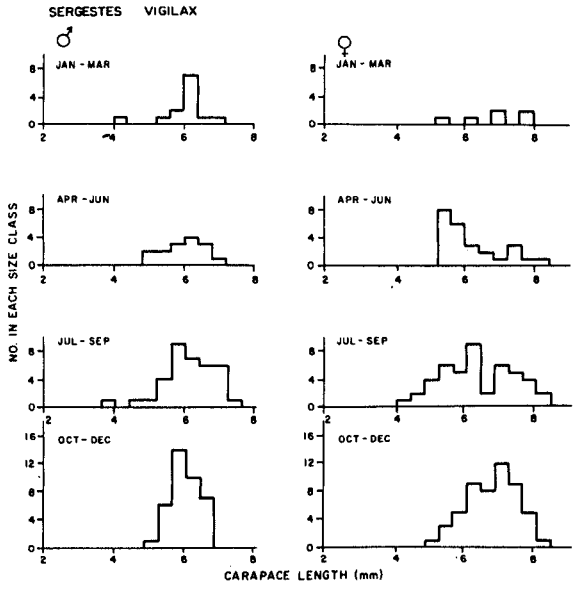


FIGURE 8.—Quarterly size-frequency distribution of *Sergestes vigilax*.

population into the 100- to 200-m range, although some remained shallower. A few nighttime captures were made in the daytime depth range. The December 1970 cruise took large numbers near full moon at 550-600 m (up to 40), and also at 150-200 m (up to 21). Apparently at least 50% of the population was not migrating. Later in the cruise, when the moon was waning, large numbers of *S. orientalis* were taken in tows between 30 and 120 m (up to 70). There was no evidence of full moon nonmigration during the December 1973 cruise.

Population Size, Growth, and Reproduction (Figure 10)

Sergestes orientalis was moderately abundant in Hawaiian waters. The average population density estimated by all the horizontal tows was 1.32 per 100 m^2, daytime and night tows giving similar figures. The oblique series of September 1972 yielded a higher figure of 8.43 per 100 m^2, *S. orientalis* being the second most abundant species in the shallow night tows. On the other hand, it was much scarcer during the oblique series of May 1973, which gave a population density of only 0.64 per 100 m^2. *Sergestes orientalis* was particularly abundant during the December 1970 cruise, when as many as 70 were taken in a single 3-h IKMT tow.

The seasonal size-frequency histograms are all very similar to one another. Shrimp smaller than 6 mm CL were proportionally most abundant during the first quarter (January-March), but the difference was not statistically significant (Kolmogorov-Smirnov test, $P > 0.05$).

Diet (Table 5)

Only two individuals from DSB III were examined. One had an empty stomach; the other had eaten an ostracod.

Sergestes tantillus Burkenroad 1940

Vertical Distribution

Because of the rarity of *S. tantillus*, little can be inferred about its vertical distribution. Single shrimp were taken in daytime tows between 410 and 915 m. The largest night catch was at 50 m (four shrimp), with individual captures to about 200 m. A tow between 635 and 715 m on a moonlit night took six shrimp.

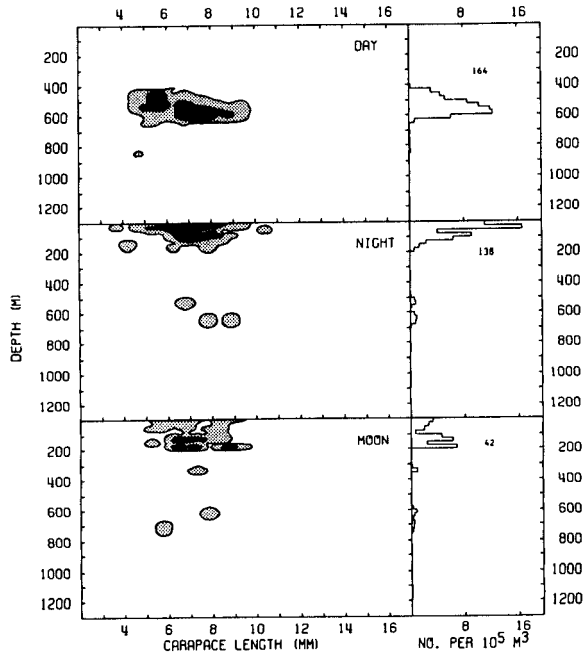


FIGURE 9.—Vertical distribution of *Sergestes orientalis*.

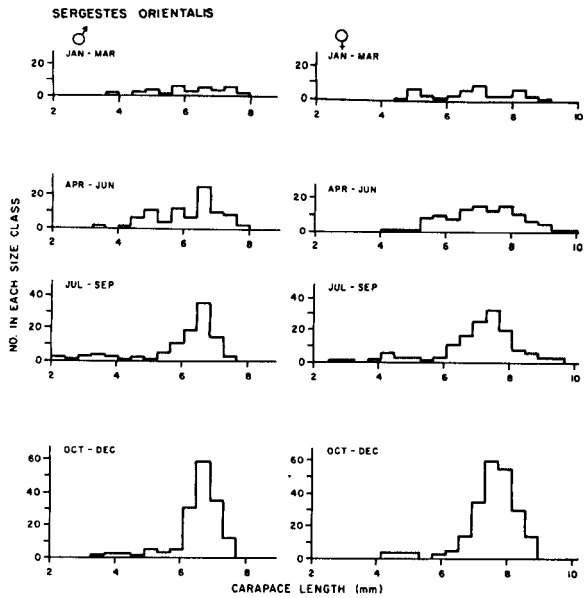


FIGURE 10.—Quarterly size-frequency distribution of *Sergestes orientalis*.

Growth, reproduction, and diet were not studied because of the small sample size.

Sergestes consobrinus Milne 1968

Vertical Distribution (Figure 11)

Nearly two-thirds of the captures during the Teuthis series were from shallow night tows during the May 1973 cruise (Teuthis XXI); it was also fairly abundant in the oblique series of September 1972 and May 1973 (Teuthis XXII).

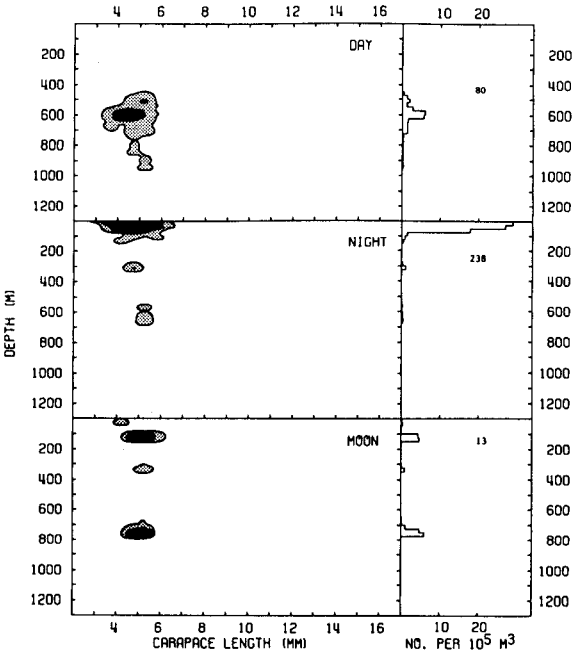


FIGURE 11.–Vertical distribution of *Sergestes consobrinus*.

Sergestes consobrinus was broadly distributed during the daytime, from 450 to 725 m. The population maximum appeared to be around 600 m, but most daytime catches were small. A few captures were made between 800 and 950 m; these may have been contaminants. The nighttime distribution showed a broad peak from the surface to 75 m, with lesser numbers to 125 m. These numbers were strongly influenced by the May 1973 captures. Moonlight depressed most of the population to 100-150 m, with a substantial number remaining at the daytime depth. The December 1970 cruise took *S. consobrinus* near full moon in tows between 140 and 180 m, and also in a 700- to 800-m tow. Later catches when the moon was waning were in the upper 120 m, with a large catch at 30 m.

Population Size, Growth, and Reproduction (Figure 12)

Like *S. vigilax*, *S. consobrinus* appears to have been undersampled by the MT. The average population size estimated by all horizontal tows was 1.05 per 100 m^2. The figure for only the night tows was 1.99 per 100 m^2, reflecting the large night catches of the May 1973 cruise (Teuthis XXI)–up to 76 in a single 3-h tow. The oblique IKMT series of September 1972 and May 1973 (Teuthis XXII) yielded higher figures of 5.42 and 2.08 per 100 m^2, respectively, presumably because the finer mesh of the IKMT retained more of the small shrimp.

The seasonal size-frequency histograms show a maximum proportion of small individuals in the third quarter (July-September). The largest shrimp were taken in the first and second quarters, although first quarter catches were small.

Diet was not examined, since none were taken during DSB III.

Sergestes sargassi Ortmann 1893

Vertical Distribution (Figure 13)

With the possible exception of *S. cornutus*,

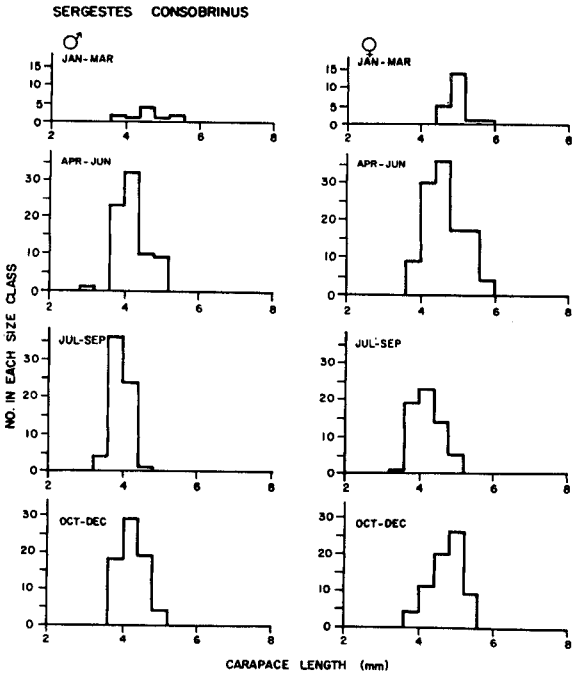


FIGURE 12.–Quarterly size-frequency distribution of *Sergestes consobrinus*.

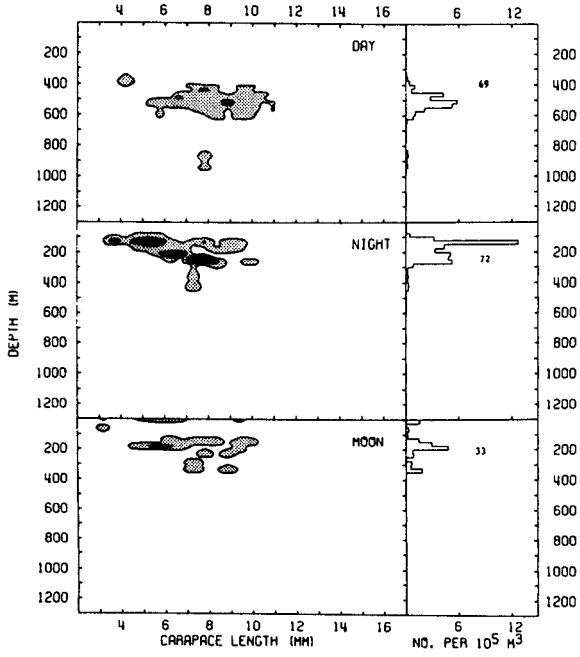


FIGURE 13.—Vertical distribution of *Sergestes sargassi*.

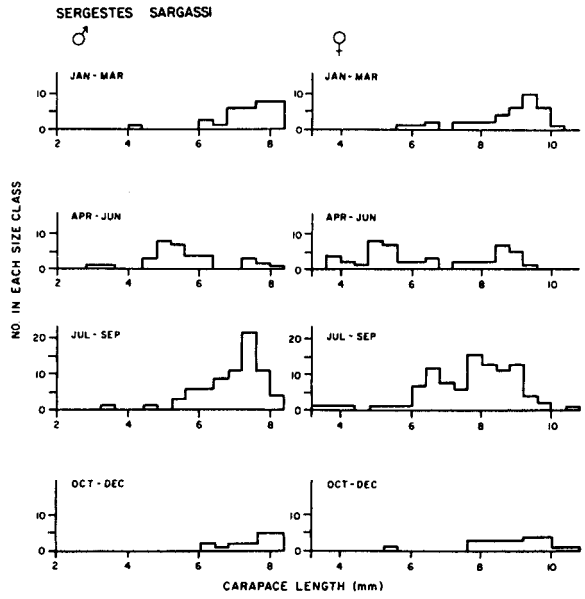


FIGURE 14.—Quarterly size-frequency distribution of *Sergestes sargassi*.

which is very rare in Hawaiian waters, *S. sargassi* had the shallowest daytime range of the local species: 450-575 m, with a maximum around 475 m. No significant variation of depth with size was noted, perhaps because of the small number caught. One immature shrimp was captured between 340 and 425 m, and oblique tows from the surface to about 350 m took a few immature specimens in September 1972. There was a pronounced variation of size with depth at night. Immature individuals less than 6 mm CL occurred between 100 and 200 m, mostly in the 125- to 150-m range. Larger shrimp were found from 125 to 300 m, mostly from 225 to 275 m. Most of the adults captured at night were males; the few females were mostly taken between 125 and 175 m. This apparent segregation by sex was probably a sampling artifact, since the December 1970 cruise took both males and females in tows from 250 to 300 m. Moonlight had little effect on the depth range of adults; immature individuals were depressed to about 150-200 m. The peak in the upper 25 m is a sampling artifact. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 14)

Sergestes sargassi was not very abundant in the horizontal collections, the estimated average population density being only 0.70 per 100 m^2. The night tows gave a higher total than the daytime tows, 1.07 and 0.64 per 100 m^2, respectively. The two IKMT oblique series of September 1972 and May 1973 produced higher estimates, 5.84 and 1.74 per 100 m^2, respectively; the daytime figure of 10.37 per 100 m^2 in September was the third highest such total for that cruise. These higher figures for the IKMT tows were not the result of more efficient filtering, as appears to be the case for the smaller species, since *S. sargassi* is a moderately large species, about the same size as *Sergia scintillans* and *Sergia gardineri*, neither of which showed any signs of significant undersampling by the MT.

Recruitment was highest during the second quarter (April-June), when nearly 70% of the population was immature. Growth during the summer was about 1.0-1.3 mm CL per month, slowing during the third and fourth quarters to 0.2-0.5 mm CL per month. Maximum sizes were attained in December and the first quarter (January-March).

Diet (Table 5)

DSB III took 10 *S. sargassi*. Three had empty stomachs. The rest had eaten zooplanktonic

crustacea, including calanoid copepods and a euphausiid.

Sergestes pectinatus Sund 1920

Vertical Distribution (Figure 15)

The daytime range of *S. pectinatus* was broad, extending from 425 to 725 m. The peak at 425-450 m came from a single tow in the June 1971 cruise, and the peak at 650-675 m was also from a single tow in the November 1972 cruise. Most large catches centered around 575 to 625 m. There was a poorly defined size-depth trend. Small shrimp less than 4 mm CL seldom occurred below 600 m, while the very large females seldom occurred above 550 m. At night the size-depth trend was pronounced. Males less than 3.5 mm CL were found in the upper 100 m, mostly between 25 and 75 m. From 4 to 5 mm CL, maximum catches were in the 75- to 250-m range, peaking around 150 m. The largest males were taken in the 200- to 275-m range. Females showed a similar trend; maximum catches of shrimp less than 4.5 mm CL occurred around 50 m, increasing to 150 m for shrimp between 4.5 and 6 mm CL, and 200 m for shrimp larger than 6 mm CL. A few shrimp were taken below 300 m; these may have been contaminants. The moon depressed most of the population to about 150-250 m. The peak in the upper 25 m is a sampling artifact. None of the Teuthis samples showed any indications of full moon nonmigration. The December 1970 cruise took 14 specimens in three open tows between 400 and 600 m, probably representing less than 10% of the population.

Population Size, Growth and Reproduction (Figure 16)

Sergestes pectinatus appeared to be significantly undersampled by the MT. The average population density estimated by all horizontal tows was 1.71 per 100 m^2. The IKMT with its finer mesh captured many more shrimp than the MT. *Sergestes pectinatus* was the most abundant sergestid in the September 1972 oblique series, which yielded a population density estimate of 26.67 per 100 m^2. The shrimp from this cruise composed nearly 40% of the entire catch of *S. pectinatus*. The May 1973 series gave a figure of 4.70 per 100 m^2, second only to *S. fulgens*. In both cases, the average size of an individual was considerably smaller than in a typical MT tow. Interpretation of the size-frequency histograms is complicated by the undersampling problem. For *S. pectinatus* only, data from the May 1973 oblique series were added to the second quarter horizontal data. This means

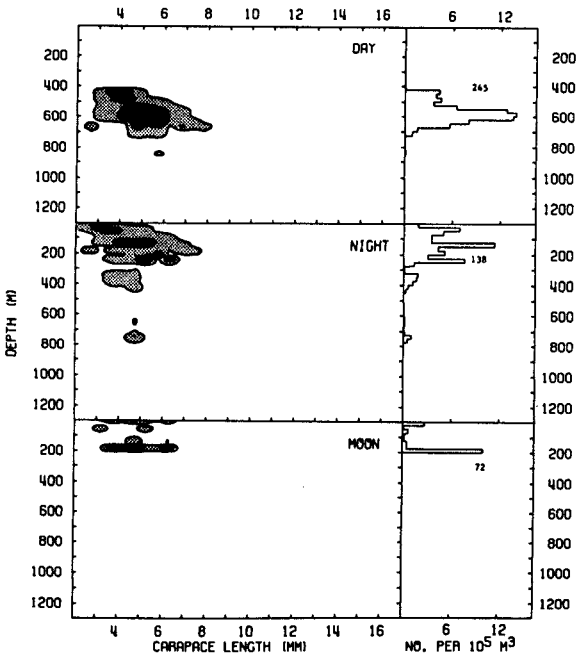


FIGURE 15.—Vertical distribution of *Sergestes pectinatus*.

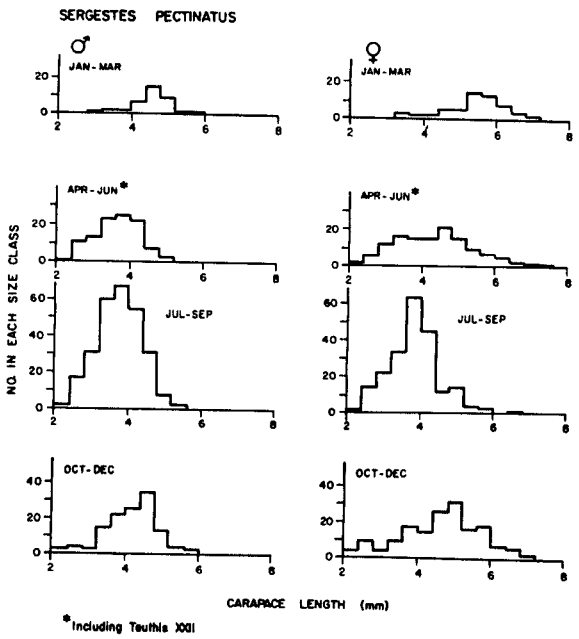


FIGURE 16.—Quarterly size-frequency distribution of *Sergestes pectinatus*. April-June quarter includes data from Teuthis XXII.

that IKMT data were included in three of the four quarters, only the first quarter (January-March) lacking IKMT data. Small shrimp were proportionately most abundant during the third quarter (July-September), and large shrimp were most abundant during the first quarter, although lack of IKMT data probably affected the shape of the first quarter histogram.

Diet (Table 5)

Seven of the twelve shrimp from DSB III had eaten calanoid copepods, mostly *Pleuromamma* spp.

Sergia fulgens (Hansen 1919)

Vertical Distribution (Figure 17)

Because of the peculiar fluctuations in abundance during the course of the sampling program, the vertical distribution patterns of *S. fulgens* derived from the data should be regarded strictly as estimates. All the daytime captures lay between 550 and 625 m; there was no variation in depth with increasing size. The open tows of the December 1970 cruise took nine specimens between 525 and 630 m. Most nighttime captures lay between 75 and 125 m for immature shrimp less than 8 mm CL, with some as shallow as 25-50 m. Nearly all the adults came from a single tow at 150-200 m; a few captures came as shallow as 75 m. Almost all of the captures near full moon came during the June 1973 cruise, which took immature shrimp between 250 and 475 m; there were three captures of adults between 150 and 325 m. The peak in the upper 25 m is a sampling artifact. The December 1970 cruise took nine adults in open tows between 160 and 300 m and one adult at 400 m. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 18)

Sergia fulgens fluctuated drastically in abundance during the sampling program. The first 13 cruises of the Teuthis series (Teuthis IV-XVII, February 1971-August 1972) caught a total of 13 specimens. After the September 1972 cruise it turned up in many tows, often in very large numbers. Nearly all the specimens were immature shrimp less than 10 mm CL. However, one horizontal night tow in May 1973 took 89 adults. In addition, the December 1970 cruise caught a total of 21 *S. fulgens*; 19 of these were adults. Combining the very low numbers from the first 13 horizontal series with the very high numbers from the last 3 horizontal series gives an average population

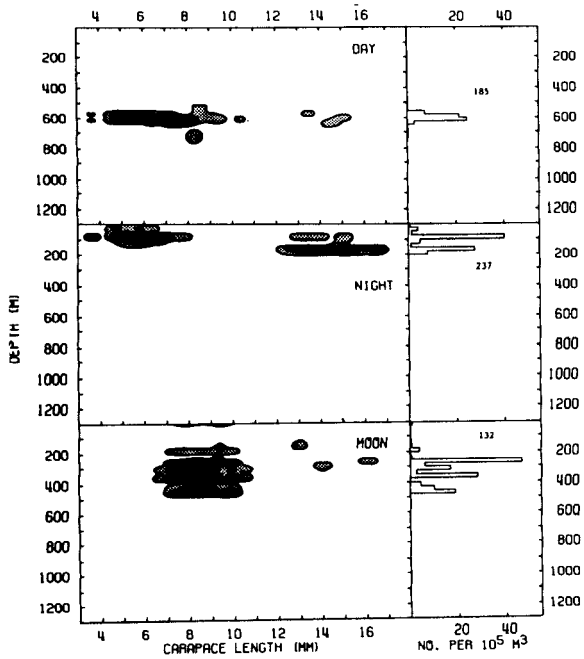


FIGURE 17.–Vertical distribution of *Sergia fulgens*.

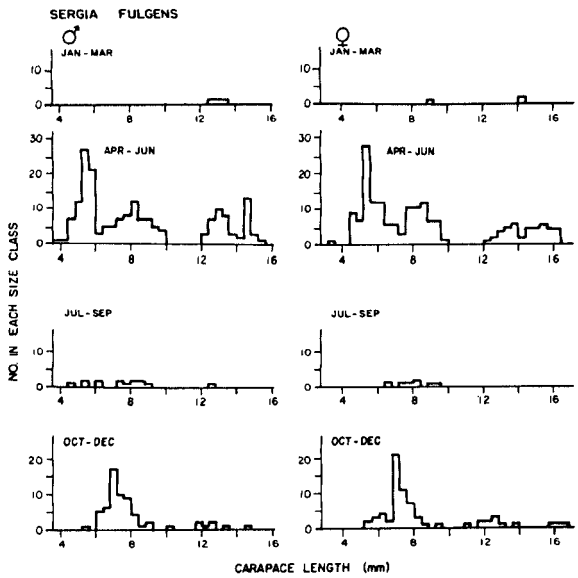


FIGURE 18.–Quarterly size-frequency distribution of *Sergia fulgens*.

density of 2.26 per 100 m^2, an estimate of doubtful meaning. The two oblique series produced very different estimates. The September 1972 cruise gave a figure of only 0.43 per 100 m^2, making *S. fulgens* the least abundant of the 16 regularly occurring species. On the other hand, the May 1973 cruise gave a figure of 15.95 per 100 m^2, more than 3 times greater than any other species, and 37 times the September figure.

The seasonal size-frequency histograms reflect the fact that nearly all *S. fulgens* were caught in the second and third quarters. The second quarter (April-June) histogram is trimodal. The peaks at 5.5 and 8 mm CL represent the same cohort as sampled in May and June (the Teuthis XXII oblique series of late May took 6.5-mm shrimp), giving a growth rate of 2.1-2.2 mm CL per month for immature shrimp in this size range. The assumption that the peak at 13-15 mm in May is the same cohort as the peak at 7.5 mm from the preceding November yields a growth rate of 1.0-1.2 mm CL per month, reflecting a slowing of the growth rate as the shrimp approach maturity. The presence of large numbers of immature shrimp in the second and fourth quarters implies that *S. fulgens* either has a very broad spawning period or has two widely separated spawning peaks.

Diet (Table 5)

DSB III took nine *S. fulgens*. Seven of these had food in their stomachs, including a calanoid copepod, an amphipod, and an ostracod, plus smaller prey including larval bivalve and foraminifera.

Sergia scintillans (Burkenroad 1940)

Vertical Distribution (Figure 19)

The vertical distribution of *S. scintillans* showed a slight tendency for smaller shrimp to live deeper than larger ones, both day and night. Daytime ranges were about 575 to 700 m for individuals less than 7 mm CL and 525 to 650 m for those larger than 7 mm CL, with maximum catches between 575 and 625 m. The small peak at 325-350 m resulted from two shrimp taken in a tow that dipped as deep as 480 m; they were probably captured at the deep end of the tow. At night the adults were mostly between 25 and 125 m, but immature shrimp less than 6 mm CL ranged

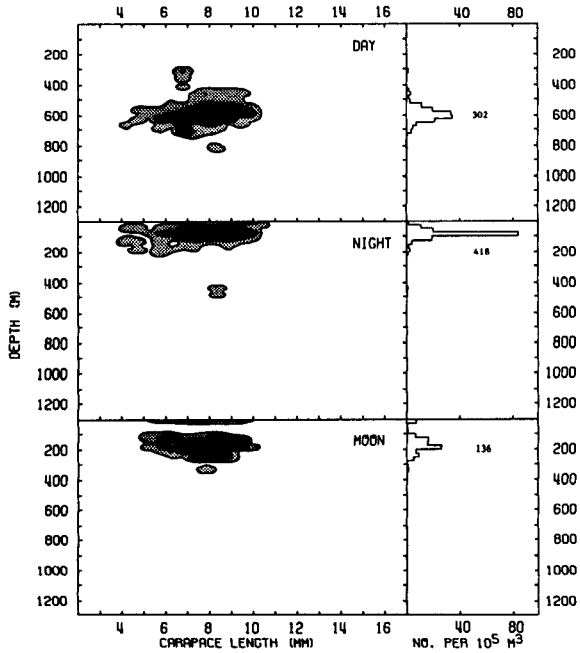


FIGURE 19.—Vertical distribution of *Sergia scintillans*.

between 50 and 225 m. Although the population was centered at 100-125 m for both sexes, few males occurred shallower than 50 m. Three shallow tows from the May 1973 cruise that caught 40 females and 12 males are primarily responsible for this difference. Moonlight depressed the depth of most of the population to 100-275 m, peaking around 200 m. The peak in the upper 25 m is a sampling artifact. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 20)

Sergia scintillans was one of the most abundant sergestids in Hawaiian waters. The average population density estimated by all horizontal tows was 3.31 per 100 m^2, the daytime and nighttime figures being similar. It was particularly abundant in the shallow night tows of the May 1973 cruise (Teuthis XXI), one 3-h tow taking 179 shrimp. The oblique series of September 1972 and May 1973 (Teuthis XXII) produced figures of 9.90 and 3.70 per 100 m^2, respectively.

Small shrimp were proportionally most abundant in the third quarter (July-September). First and second quarter populations were similar in size-frequency, although the larger females occurred in the second quarter (April-June).

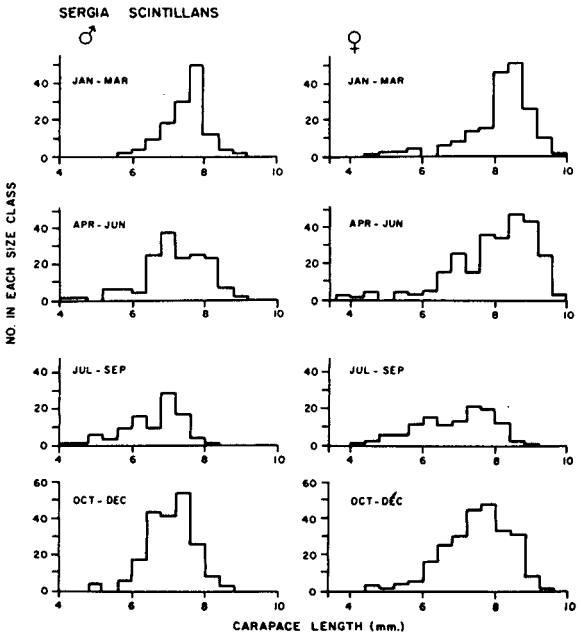


FIGURE 20.—Quarterly size-frequency distribution of *Sergia scintillans*.

Diet (Table 5)

The DSB III material showed that *S. scintillans* ate the usual variety of zooplanktonic crustacea, including calanoid copepods, amphipods, and an ostracod. The 0.4- to 0.6-mm size fraction was also taken; bivalve larvae, foraminifera, and cyclopoid copepods were found in many individuals. Other food items included the large cyclopoid copepod *Sapphirina*, a larval decapod, and masses of an unidentified greenish, fibrous material.

Sergia gardineri (Kemp 1913)

Vertical Distribution (Figure 21)

Sergia gardineri was usually found between 650 and 775 m during the daytime, although shrimp smaller than 5 mm CL seldom occurred below 700 m. The extremely high values in this range were largely due to the catches of the November 1972 cruise. On certain occasions the population seemed to extend downward to at least 1,200 m. The June 1973 cruise took 59 specimens in three tows between 850 and 1,050 m, and only 8 specimens in four tows between 650 and 850 m. The December 1970 cruise caught only nine specimens in an open tow at 650-680 m, but tows below 800 m caught large numbers, including 77 in a tow from 1,150 to 1,250 m. On the other hand, all four daytime tows on the May 1972 cruise between 650 and 950 m took only one shrimp.

The nighttime distribution was strongly influenced by large catches from the May 1973 cruise. It showed a concentration in the upper 150 m, with shrimp less than 6 mm CL restricted to 25-100 m. All large shrimp in the upper 25 m were females, the result of a single tow in May 1973 that fished between 15 and 45 m, taking 36 adult females and 1 very small male. A tow at 20 m on the same cruise took no *S. gardineri*, indicating that this species probably does not reach the surface. There were a few captures below the normal range on moonless nights, notably a 250-m tow in September 1971 that took four, and a 480- to 550-m tow in November 1972 that took five.

Most captures of *S. gardineri* on nights with much moonlight were at the daytime depth, except for the March 1971 cruise, which took 16 shrimp at 320-340 m and 20 shrimp at 100-150 m, although a tow at 170-200 m did not take any. Three open tows near full moon on the December 1970 cruise took 207 *S. gardineri* between 700 and 1,000 m, while a 550- to 600-m tow took 9. Later in the cruise when the moon was waning, they were captured at 80 and 30 m (but not at 100-110 or 50 m!). The

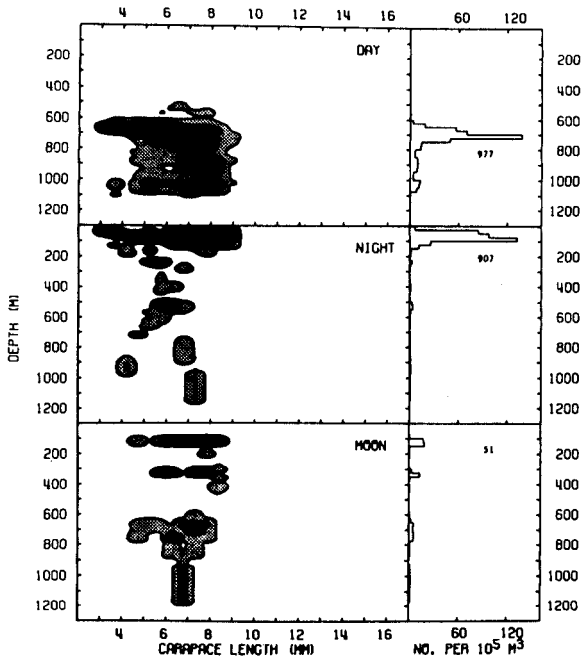


FIGURE 21.—Vertical distribution of *Sergia gardineri*.

December 1973 cruise took only two immature specimens at night in 10 oblique tows less than 650-m maximum depth. Six oblique tows from 400 to 1,200 m took a total of 62 shrimp, although high seas resulted in some catch spillage in two cases. *Sergia gardineri* clearly does not migrate near full moon.

Population Size, Growth, and Reproduction (Figure 22)

Sergia gardineri was by far the most numerous sergestid in the Teuthis collections, the average population density of 8.65 per 100 m^2 estimated from all horizontal tows being more than twice as high as the next most abundant species. Horizontal tows taking more than 100 shrimp occurred in February 1971 (night), June 1971 (day and night), November 1972 (day), and May 1973 (night). In addition, the open tows of the December 1970 cruise took large numbers, including 129 in a night tow. *Sergia gardineri* appeared to have been much less abundant during the first half of 1972, although most of these cruises occurred near full moon, when the normal vertical distribution patterns seem to be disrupted. The estimate from night tows affected by moonlight, 2.66 per 100 m^2, was much lower than the daytime or moonless night estimates. The oblique series of September 1972 and May 1973 gave figures of 10.00 and 1.90 per 100 m^2, respectively.

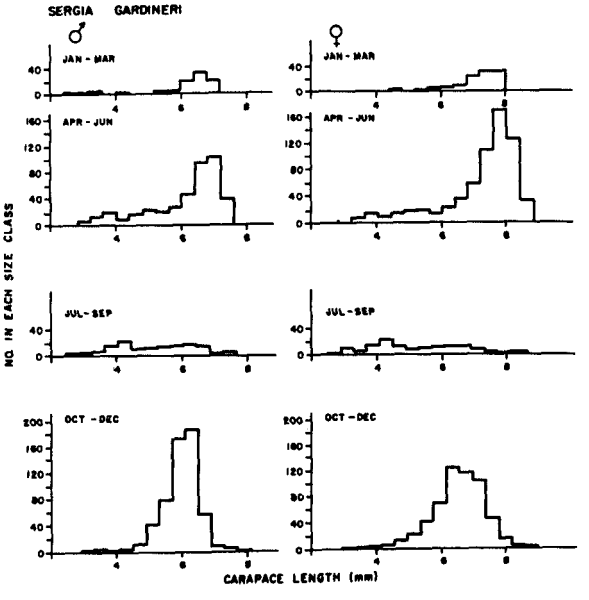


FIGURE 22.–Quarterly size-frequency distribution of *Sergia gardineri*.

Recruitment was highest during the third quarter (July-September), although small shrimp began to enter the population in June. The median carapace length increased from 4.9 mm to 6.4 mm between the September 1972 and November 1972 cruises, giving a growth rate of about 1.2 mm CL per month. From November to May the growth rate was much lower, about 0.25 mm CL per month. The average size of females was largest in May, although a few very large females were still present in June. *Sergia gardineri* has a total life span of about 1 yr.

Diet (Table 5)

Thirteen of the nineteen specimens of *S. gardineri* taken during DSB III had empty stomachs. The others contained calanoid copepods, an ostracod, a larval decapod, bivalve larvae, foraminifera, and greenish fibrous matter.

Sergia bigemmea (Burkenroad 1940)

Vertical Distribution (Figure 23)

Most of the few daytime captures of *S. bigemmea* during the Teuthis series were of immature shrimp less than 8 mm CL. A tow between 610 and 690 m took 15 in July 1971; 5 were caught in November 1972 in a tow probably around 750 m. The peak around 1,100 m resulted from two tows that fished as shallow as 820 m. Two of the three daytime captures of adults during the Teuthis series were between 1,000 and 1,100 m; the other was around 750-850 m. The December 1970 cruise took 20 adults in open tows between 800 and 1,200 m. The nighttime distribution varied with size; shrimp smaller than 10 mm CL generally occurred between 50 and 225 m, while the adults ranged between 125 and 250 m. The February 1973 cruise (DSB III) took several large hauls of *S. bigemmea*, including 49 specimens in a 1-h tow at 150-175 m. Only a few were caught under moonlit conditions; most of these were between 250 and 350 m. The December 1970 cruise took 5 *S. bigemmea* at 250 m and 11 at 750 m, indicating that much of the population was not migrating.

The vertical distribution patterns of *S. bigemmea* appeared to be affected by avoidance. While the females of most sergestid species grow considerably larger than the males, in *S. bigemmea*

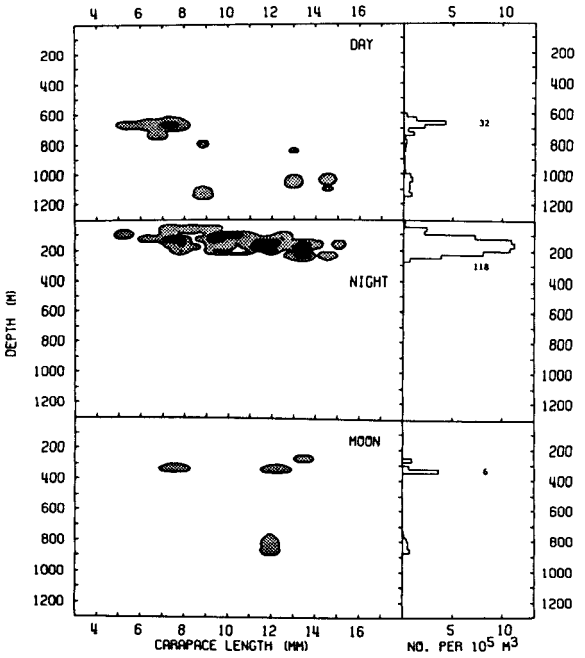


FIGURE 23.—Vertical distribution of *Sergia bigemmea*.

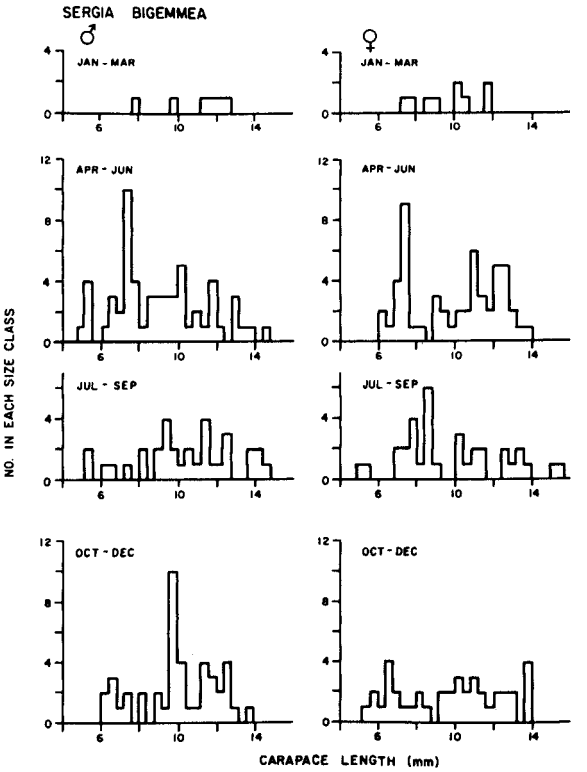


FIGURE 24.—Quarterly size-frequency distribution of *Sergia bigemmea*.

the maximum size was the same in both sexes, suggesting that the largest shrimp were escaping capture. Daytime catches were much smaller than nighttime catches, indicating that avoidance was more effective during the day. However, the maximum size captured was the same during the daytime as at night. It is curious that neither *Sergestes erectus* nor *Sergia fulgens* showed any signs of avoidance, though those caught are larger than *S. bigemmea*; perhaps *S. bigemmea* is particularly fast for its size or better at sensing the approach of the trawl.

Population Size, Growth, and Reproduction (Figure 24)

Sergia bigemmea was one of the less common sergestids in our collection; the average population density estimated from all horizontal tows was only 0.64 per 100 m^2. Most catches occurred at night, the figure for nighttime tows being 1.48 per 100 m^2. Very few *S. bigemmea* were captured during the first half of 1972, when most sampling was done near full moon. The oblique series of September 1972 took moderate numbers, producing a population density figure of 2.35 per 100 m^2, higher than any other all-red sergestid except *S. gardineri*. It was also moderately abundant during the December 1970 cruise, which had the only large daytime catch: 23 in an 800- to 900-m open IKMT tow. The largest catches of *S. bigemmea* occurred during the February 1973 cruise (DSB III) when it was the most abundant species taken, with 49 in a 1-h open tow. The May 1973 oblique series took only a handful, giving a population density estimate of 0.31 per 100 m^2.

None of the seasonal size-frequency histograms are significantly different from the others (Kolmogorov-Smirnov test: $P>0.05$). Females larger than 12 mm CL were proportionately most abundant in the third quarter (July-September).

Diet (Table 5)

The surprisingly large catch of *S. bigemmea* during DSB III produced a more detailed picture of its diet than for the other species. Only 11 of the 88 shrimp had empty stomachs. *Sergia bigemmea* ate crustacean zooplankton, including calanoid copepods, amphipods, and ostracods; ostracods appeared to be a more important prey item than in the other species. Smaller prey were also

eaten—larval bivalves, small cyclopoid copepods, and foraminifera commonly occurring in the diet. *Sergia bigemmea* was the only species in which chaetognath spines were found. Other food items included the large cyclopoid copepod *Sapphirina*, a single larval decapod, and unidentified fibrous matter.

Sergia inequalis (Burkenroad 1940)

Vertical Distribution (Figure 25)

As with *S. bigemmea*, *S. inequalis* may have avoided the trawl. The few daytime captures were nearly all below 750 m; the peak near 550 m resulted from a tow in June 1971 that dipped to 760 m. Maximum daytime depth appeared to be 1,100-1,200 m. The December 1970 cruise took *S. inequalis* in open tows between 800 and 1,250 m—seven in a 950- to 1,000-m tow and four in a 1,150- to 1,250-m tow. The nighttime distribution varied with size. Small shrimp less than 12 mm CL were found in the upper 100 m; larger shrimp occurred between 100 and 250 m. Moonlight did not significantly affect the adults; there were no captures of small shrimp under these conditions. The Teuthis series showed no evidence of full moon nonmigration, but the December 1970 cruise took five specimens at night between 550 and 800 m.

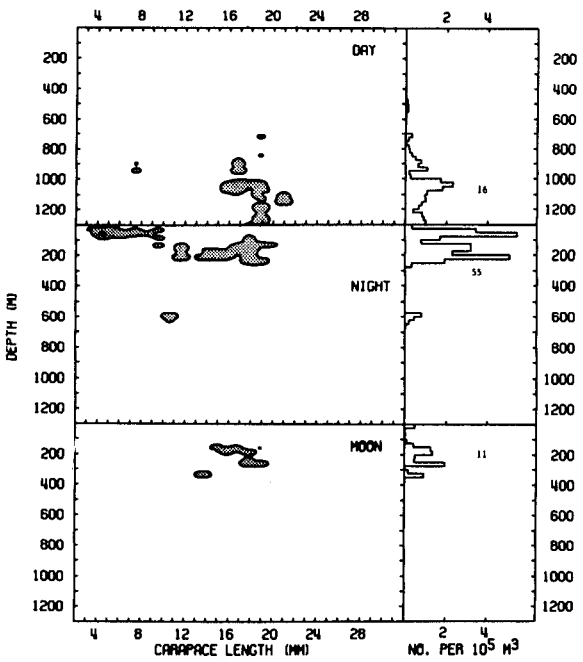


FIGURE 25.—Vertical distribution of *Sergia inequalis*.

Population Size, Growth, and Reproduction (Figure 26)

Sergia inequalis was not abundant in Hawaiian waters; the average population density estimated from all horizontal tows was only 0.55 per 100 m^2, less than any other regularly occurring all-red sergestid. The largest catch of adults was only seven, from an open tow in December 1970. The oblique series of September 1972 and May 1973 gave estimates of 0.94 and 0.31 per 100 m^2, respectively.

In spite of its relative rarity, *S. inequalis* showed a clear seasonal cycle of growth, although because of the small sample size, the differences among histograms are only marginally significant statistically (Kolmogorov-Smirnov test, II different from III, $0.10 > P > 0.05$). Recruitment was greatest in the second quarter (April-June), and

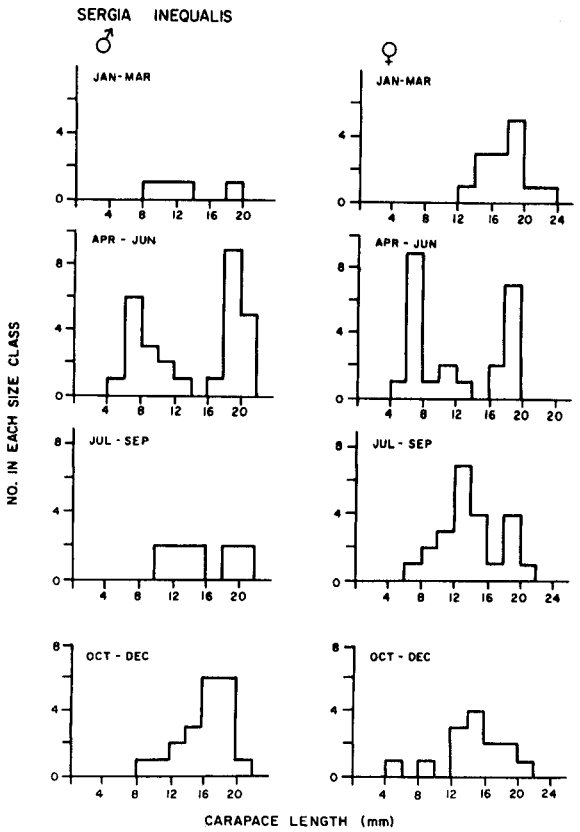


FIGURE 26.—Quarterly size-frequency distribution of *Sergia inequalis*.

the population increased in average size of individuals in succeeding quarters, the largest females being proportionately most abundant in the first quarter (January-March).

Diet (Table 5)

The single *S. inequalis* taken by DSB III had a calanoid copepod in its stomach.

Sergia bisulcata (Wood-Mason 1891)

Vertical Distribution (Figure 27)

As with *S. bigemmea*, equality in size of the sexes and small daytime catches indicate that *S. bisulcata* was avoiding the trawl. Immature shrimp were mostly taken between 675 and 750 m during the daytime, adults mostly from 700 to 900 m, with a few catches as deep as 1,100 m. The December 1970 cruise took 19 individuals, including both immatures and adults, in an open tow from 650 to 680 m, with much smaller catches down to 1,200 m. At night, immature shrimp occurred between 175 and 300 m, adults mostly from 225 to 350 m, with occasional captures as deep as 450 m. Moonlight depressed the population below 300 m; two tows at 450 m during the June 1973 cruise took 10 and 8 individuals, respectively. There was no evidence of full moon nonmigration.

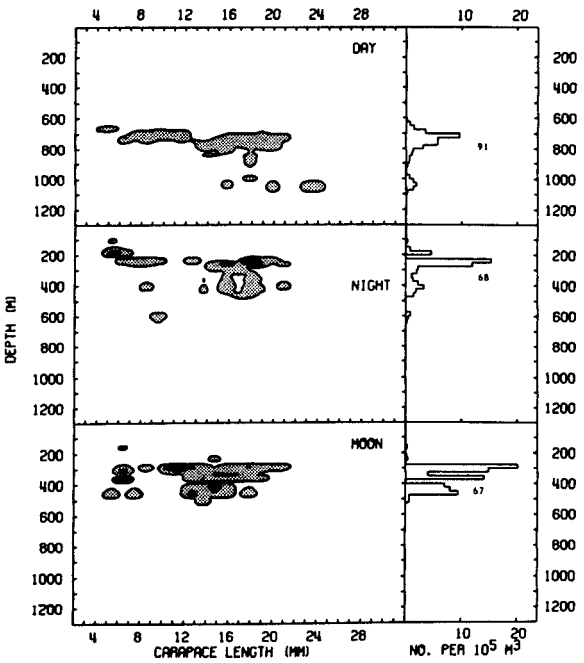


FIGURE 27.–Vertical distribution of *Sergia bisulcata*.

Population Size, Growth, and Reproduction (Figure 28)

Sergia bisulcata was the second most abundant all-red sergestid in the Teuthis collection, though far below *S. gardineri* in numbers. The average population density figure from all horizontal tows was 1.35 per 100 m^2. The figure for tows on moonlit nights was higher, 1.96 per 100 m^2, probably a sampling artifact. The two oblique series produced similar numbers; September 1972 gave 1.19 and May 1973 gave 0.82 per 100 m^2.

While quarterly variations in the size-frequency distributions of most Hawaiian sergestids suggest that they live about 1 yr, only in *S. bisulcata* is there evidence for a longer life span. Small immature shrimp around 7-9 mm CL were recruited in the second quarter (April-June) and grew to sexual maturity at about 14-18 mm CL in 1 yr. They continued to grow at a rate of approximately

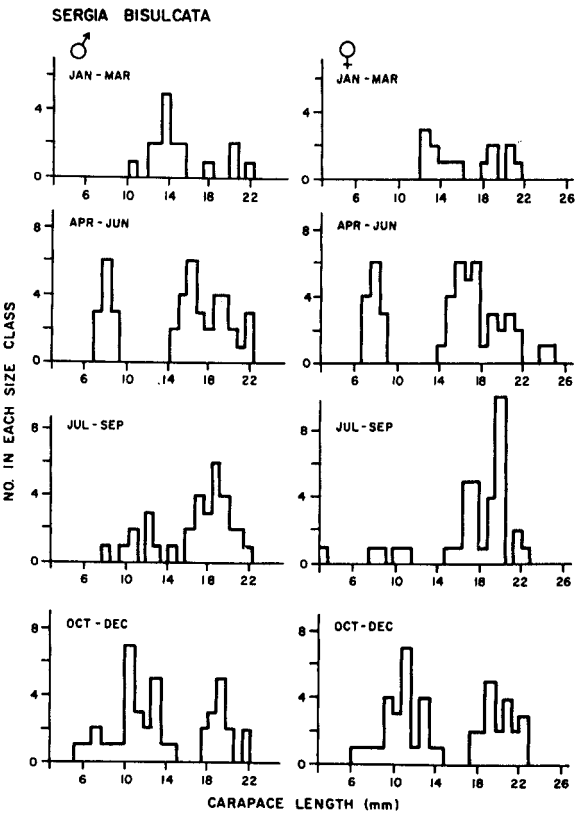


FIGURE 28.–Quarterly size-frequency distribution of *Sergia bisulcata*.

0.6 mm CL per month for up to one additional year. Few males appeared to live beyond 18 mo, but a few large females greater than 22 mm CL were probably a full 2 yr old. The pattern of growth appears clear cut, but the small sample size means that the data should be treated cautiously. The Kolmogorov-Smirnov test showed that only the third and fourth quarter size-frequency curves for the females were significantly different from each other ($0.05 > P > 0.01$).

Diet (Table 5)

Seven of the eight *S. bisulcata* taken by DSB III had food in their stomachs. Food items included ostracods, an amphipod, foraminifera, bivalve larva, and crustacean remains probably including a euphausiid and a larval decapod. No copepods were found, probably because of the small sample size.

Sergia maxima (Burkenroad 1940)

Only two individuals of this species were captured, one on the March 1972 cruise in a 480- to 615-m daytime tow and the other on the December 1973 cruise in an open tow between 400 and 550 m. Both individuals were immature males.

Sergia tenuiremis (Kröyer 1855)

Vertical Distribution (Figure 29)

During the daytime most of the population was below 800 m, although shrimp were sometimes taken as shallow as 700-750 m. A single immature individual was taken in June 1971 between 610 and 690 m. The deepest capture was in a tow between 1,220 and 1,500 m in August 1972. Tows below 1,500 m did not capture *S. tenuiremis*, but total trawling time in this region was rather small. Immature shrimp less than 15 mm CL were vertical migrators, moving up to 300-500 m at night. The adult population did not migrate as a whole, but part spread upward at night as shallow at 550-600 m. Moonlight had no effect on the nighttime vertical distribution of *S. tenuiremis*.

Population Size, Growth, and Reproduction (Figure 30)

Sergia tenuiremis is not abundant in Hawaiian waters. The average population density estimated by all horizontal tows was 0.89 per 100 m^2, day and night values being similar. The two oblique series produced slightly smaller values, 0.67 per 100 m^2 in September 1972 and 0.70 in May 1973. Since these

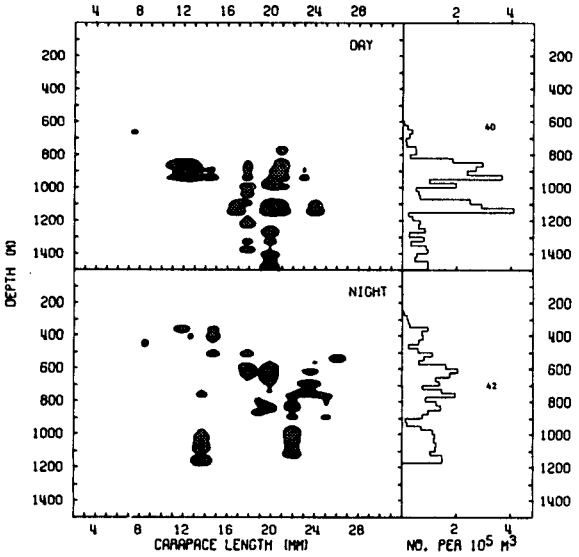


FIGURE 29.—Vertical distribution of *Sergia tenuiremis*. NIGHT and MOON data combined.

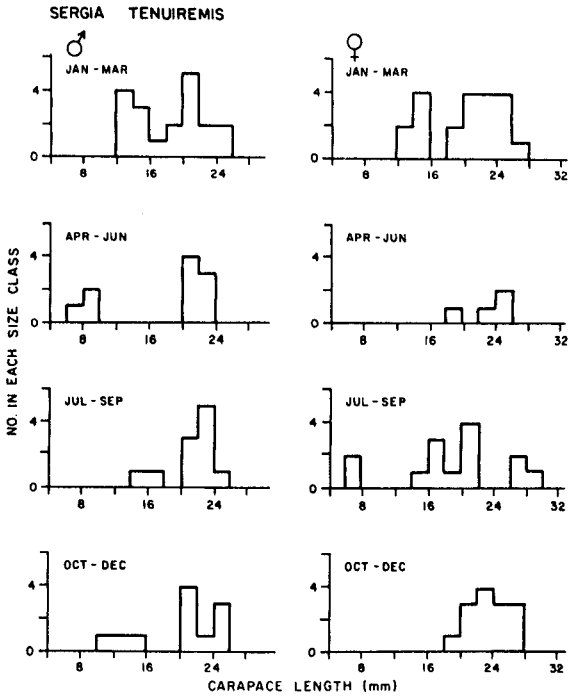


FIGURE 30.—Quarterly size-frequency distribution of *Sergia tenuiremis*.

series sampled only to 1,200 m, they may have missed the deeper portion of the population.

The seasonal size-frequency histograms are not significantly different from one another.

Diet (Table 5)

DSB III took only three specimens, all with empty stomachs.

Sergia laminata (Burkenroad 1940)

Vertical Distribution

Only four individuals were captured in closing tows, all in daytime tows during the November 1972 cruise. A tow at 650-725 m took three shrimp, and a tow at about 750-800 m took one shrimp. At night oblique tows in the upper 400 m took single shrimp during the September 1972 and May 1973 cruises, suggesting that *S. laminata* may be a vertical migrator. On the other hand, the December 1970 cruise captured one shrimp in an open horizontal tow at 550-600 m at night, suggesting that *S. laminata* may not migrate near full moon.

The small sample size did not allow studies of growth, reproduction, or diet.

Petalidium suspiriosum Burkenroad 1937

Vertical Distribution (Figure 31)

A deep-living nonmigrator, *P. suspiriosum* generally stayed below 800 m day and night. The shallowest captures came during the June 1972 cruise, which took six in a 750- to 800-m day tow and five in two night tows between 630 and 720 m. Maximum depth appeared to be at least 1,500 m; as with *S. tenuiremis*, limited trawling below 1,500 m did not catch any *P. suspiriosum*.

Population Size, Growth, and Reproduction (Figure 32)

Petalidium suspiriosum is more abundant than its small numbers in our collection would seem to indicate, since the depths below 800 m where it lives were not as thoroughly sampled as the shallower waters. The average population density estimated from all horizontal tows was 1.84 per 100 m^2, making it the second most abundant all-red sergestid. Like *S. tenuiremis*, the oblique series

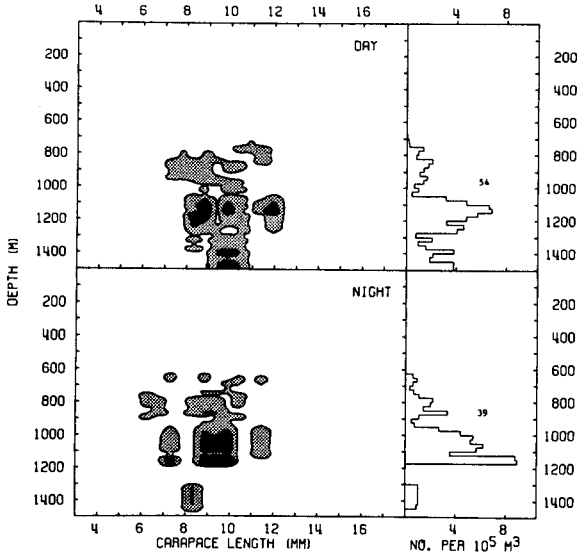


FIGURE 31.—Vertical distribution of *Petalidium suspiriosum*. NIGHT and MOON data combined.

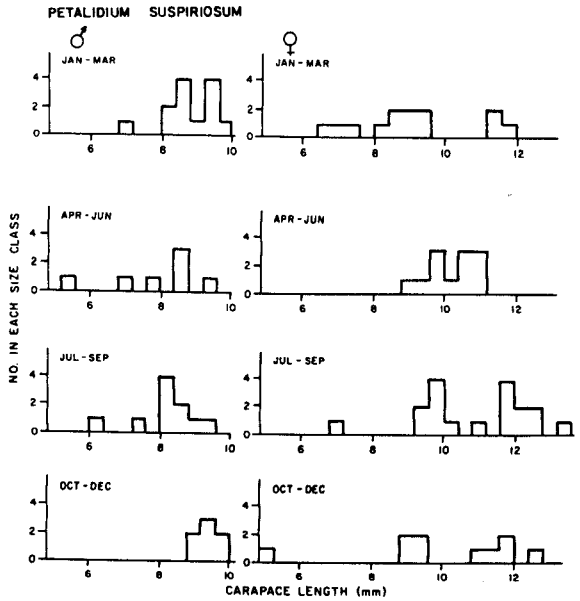


FIGURE 32.—Quarterly size-frequency distribution of *Petalidium suspiriosum*.

gave lower numbers, 1.21 per 100 m^2 in September 1972 and 1.31 in May 1973, probably because some of the population was below the 1,200 m maximum of the oblique tows.

Because of its susceptibility to damage, it was possible to make accurate measurements of carapace length on only about two-thirds of the specimens in the collection. There was no

significant seasonal trend in the size-frequency distributions of *P. suspiriosum*.

DSB III did not take *P. suspiriosum*, so its diet was not examined.

DISCUSSION

Color Pattern and Daytime Vertical Distribution: Role of Countershading

Sergestids display two basic color patterns. One group, including *Sergestes* and species of *Sergia* in Yaldwyn's (1957) "*S. challengeri*" species group, is "half-red," that is, its members are semitransparent except for the eyes and viscera, with red, stellate, subcuticular chromatophores scattered over the body and appendages, most concentrated on the cephalothorax. All half-red sergestids have well-developed photophores; *Sergestes* species have internal photophores, the organs of Pesta, and the half-red *Sergia* species have external cuticular lensed photophores. The other group, including the remaining species of *Sergia* and *Petalidium*, is "all-red," that is, its members are covered with a relatively uniform red cuticular pigment. All-red sergestids have simple lensless cuticular photophores or else lack photophores altogether.

Foxton (1970) showed that most mid-water decapods in the Fuerteventura area (Canary Islands) are either half-red or all-red. He found that half-red shrimps generally live shallower than 700 m during the daytime, while all-red shrimps generally live below 700 m. He concluded that the half-red color pattern and complex photophores are adaptations for concealment by countershading to match the light intensity of the surrounding waters when viewed from any angle, the photophores producing a ventrally directed beam of light to fill in the shadow of the animal. He suggested that the half-red pattern gives way to the all-red pattern at the depth where bioluminescent light becomes more important than penetrating surface light. Although many all-red decapods have simple photophores, he concluded that their function does not involve daytime countershading. Donaldson (1975) did not discuss this phenomenon, but an examination of his vertical distribution data for the Bermuda area shows the same daytime pattern of shallower half-red sergestids and deeper all-red sergestids, the dividing line again being approximately 700 m.

Other mid-water animals show similar depth-related changes in color patterns during the daytime. Badcock (1970) noted that mesopelagic fishes in the Fuerteventura area tend to be silvery above 650-700 m and dark below that depth. Amesbury (1975) found the same pattern in Hawaiian mesopelagic fishes, several independent analyses of community structure locating a major faunal boundary at 675-700 m between mostly silvery shallow mesopelagic fishes and mostly dark deep mesopelagic fishes.

Figure 33 shows how half-red and all-red sergestids differ in depth during the daytime in Hawaiian waters. The half-red species range from 425 to 725 m, with maximum abundance in the 600- to 625-m interval. The all-red species range from 625 to 1,500 m, with maximum abundance at 700-725 m.

Rather surprisingly, the depths of maximum abundance for the two types are only 100 m apart, and there is a large amount of overlap in their ranges, particularly in the zone between 650 and 725 m. Nearly half of the half-red sergestids below 650 m are *Sergestes erectus*, a species often taken in large numbers in tows that also take large

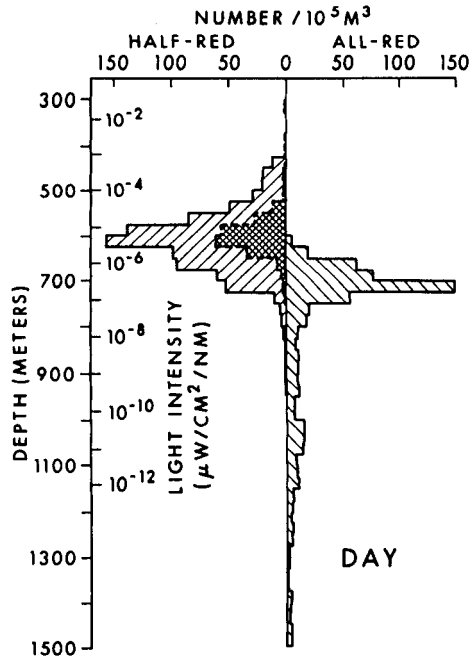


FIGURE 33.—Daytime vertical distribution of half-red and all-red Hawaiian sergestids. Half-red species are on the left (half-red *Sergia* spp. crosshatched), all-red species on the right. Scale of light intensity is from unpublished data of E. M. Kampa, at lat. 28°N.

numbers of *Sergia gardineri*, the most abundant all-red sergestid. To see if this overlap is real and not an artifact produced by vertical excursions of the trawl or seasonal variations in the position of a sharper transition depth, Teuthis XIX extensively sampled the 600- to 800-m zone in November 1972, using depth telemtery to try and maintain the trawl within a 25- to 50-m depth range. One tow between 630 and 680 m took 139 *Sergestes erectus* and 31 *Sergia gardineri*, another from 650 to 730 m took 157 *Sergestes erectus* and 289 *Sergia gardineri*, and a third from 700 to 740 m took 19 *Sergestes erectus* and 312 *Sergia gardineri*. On this occasion, at least, substantial numbers of both color patterns were living between 650 and 725 m.

Other investigators have found similar transition zones. In Hawaii, Riggs (pers. commun.) has found that the all-red species *Gennadas propinquus* (Penaeidae, Benthesicymae) lives as shallow as 600 m, with maximum numbers at 650-675 m. Ziemann (1975) obtained similar results for another all-red shrimp, *Systellaspis debilis* (Caridea, Oplophoridae), 75% of the adult population being found above 650 m on one occasion. In the Atlantic, Foxton's (1970) data show the half-red *Sergestes corniculum* (closely related to *S. erectus*) extending to at least 800 m, overlapping the ranges of the all-red species *Sergia robusta* and *Systellaspis debilis* (although most of the catch of the latter species were lighly pigmented juveniles). Donaldson's (1975) data show a transition zone from 650 to 800 m occupied by the half-red *Sergestes atlanticus* and *S. corniculum* and the all-red *Sergia grandis*. In view of this extensive overlap in the distribution of half-red and all-red decapods, it is necessary to review the conditions under which countershading is an effective concealment strategy and, in particular, Foxton's conclusion that only half-red decapods countershade.

The angular distribution of light in the mesopelagic environment is independent of solar elevation and depth (Denton and Nicol 1965). At any given point, the background light intensity is highest directly overhead, falling off rapidly to the sides, with a very low light intensity of backscattered light from below. The intensity of the background light 90° from the vertical is only 3-4% of the zenith value, decreasing to 0.3-0.5% at 180° from the zenith (Tyler and Preisendorfer 1962). Changes in surface irradiance or depth change the intensity but not its angular distribution. Countershading mechanisms match the animal to this background pattern; thus mid-water fishes use a dark dorsal surface, silvery sides, and ventral photophores for countershading (W. D. Clarke 1963; Nicol 1967; Badcock 1970). Foxton (1970) concluded that the half-red coloration of shallow mesopelagic decapods is a countershading mechanism using transparency rather than reflectors for lateral countershading. I propose that some deep mesopelagic all-red decapods also countershade ventrally and that ventral countershading can be effective below the transition zone from half-red to all-red decapods.

As depth increases and the intensity of the penetrating light dwindles, bioluminescence becomes relatively more and more important as a source of light in the mesopelagic environment. Bioluminescent light has a much different temporal and spatial distribution from the penetrating surface light. The bioluminescent light field is the sum of glows and flashes from many point sources whose angular distribution is more or less random. Countershading is an ineffective concealment strategy against bioluminescence; the silvery sides which camouflage a mid-water fish against the penetrating sunlight may in deeper water reflect a bioluminescent flash and reveal the fish against a black background. The best strategy of concealment in an environment lit only by random flashes is to be as nonreflective as possible. The dark brown or black fishes and all-red crustacea of the deep mesopelagic zone reflect blue light poorly (Nicol 1958), presumably indicating their use of this strategy.

Another effect of increasing depth is that the penetrating light eventually becomes too dim to be seen. The absolute visual threshold for deepsea fishes has been estimated as about $3 \times 10^{-20}\ \mu W / cm^2$ by Clarke and Denton (1962), a figure that undoubtedly varies in other groups of animals correlated with the degree of development of the eye. A slightly higher intensity is required before countershading becomes necessary. The maximum depth of effective countershading depends on the angular distribution of the penetrating light; thus in Hawaiian waters the threshold of lateral countershading is reached 110-120 m higher in the water column than the threshold for ventral countershading. Between these two depths lateral countershading is not needed but ventral countershading can still be effective.

The all-red sergestids with photophores appear to combine an antibioluminescent color pattern

with a ventral array of simple photophores for low-intensity ventral countershading. This interpretation implies that the transition from half-red to all-red sergestids at 650-725 m marks the upper limit of bioluminescence as an important source of ambient light. The lower limit of all-red sergestids with photophores should then mark the threshold of ventral countershading. Unfortunately, this study produced good daytime vertical distribution data for only one such species, *Sergia gardineri*. If its lower limit under normal conditions is typical of the other species, then the threshold of ventral countershading should lie at approximately 775 m. This depth is also the approximate upper limit of the two sergestids, *Sergia tenuiremis* and *Petalidium suspiriosum*, that lack photophores (Figures 29, 31). If 775 m is the threshold of ventral countershading, then the threshold for lateral countershading should be 110-120 m higher or about 660 m, approximately the depth of the transition from half-red to all-red sergestids.

It thus appears that the transition from half-red to all-red sergestids does not mark the absolute lower limit of countershading, but is related to the depth at which lateral countershading becomes ineffective and bioluminescent light forces a change in concealment strategy. Although the all-red color pattern hides the shrimp from bioluminescent flashes, enough of the penetrating light remains directly overhead that ventral countershading continues to be effective more than 100 m below the transition zone. The simple lensless photophores of the all-red sergestids presumably produce low levels of light in this dimly lit region. Other mid-water animals that lack lateral countershading mechanisms but have ventral arrays of photophores, such as many of the black stomiatoid fishes, may have evolved the same kind of camouflage.

Nighttime Vertical Distribution and Migration

The structure of the sergestid assemblage changes drastically as day gives way to night. All Hawaiian sergestid species except *Sergia tenuiremis* and *Petalidium suspiriosum* migrate into the upper 300 m of the water column. As figure 34 shows, the division into a shallow half-red and a deep all-red mesopelagic sergestid assemblage disappears on moonless nights. The species fall with little overlap into a shallow and a deep migratory group, adults of the shallow group

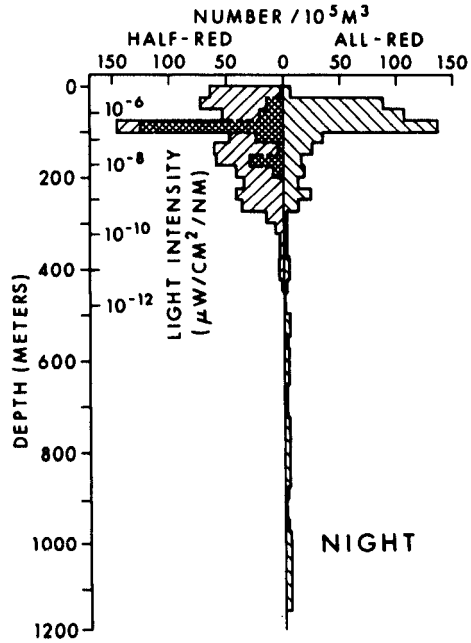


FIGURE 34.—Nighttime vertical distribution of half-red and all-red Hawaiian sergestids (moonless conditions). Hachure, etc., as in Figure 33. Light intensity estimated from unpublished daytime data of E. M. Kampa at lat. 28°N, using G. L. Clarke's (1968) values for relative intensity of day vs. night.

living in the upper 100 m, adults of the deep group living from 125 to 300 m. The shallow group includes *Sergestes vigilax*, *S. consobrinus*, *Sergia scintillans*, and *S. gardineri*. The deep group includes *Sergestes erectus*, *S. armatus*, *S. sargassi*, *Sergia bigemmea*, *S. inequalis*, and *S. bisulcata*. The single large nighttime capture of adult *Sergia fulgens* is at about 175 m, probably placing this species also in the deep group. In addition, *Sergestes pectinatus* is broadly distributed from 25 to 250 m, and *S. atlanticus* may likewise be broadly distributed if the single large catch in the upper 25 m is not representative of its normal distribution. T. A. Clarke (1973) found a similar pattern in the nighttime distribution of Hawaiian myctophid fishes, with a shallow group down to 125 m, a deep group at 150-250 m, and a few species broadly distributed in the upper 250 m. Closely related pairs of myctophid species separate into a shallow species and a deep species. Most sergestid species pairs are found at the same nighttime depths, except for *Sergestes armatus* and *S. vigilax*, and probably *Sergia scintillans* and *S. fulgens*.

The division of the nighttime sergestid assemblage at 100-125 m may possibly be related to

the penetrating surface light. The scale at the left of Figure 34 is an estimate, derived by assuming the value of light intensity at the surface on a moonless night to be 10^7 times fainter than during the day, a figure used by G. L. Clarke (1968), and applying this correction to the daytime light curve of E. M. Kampa (unpubl. data) used in Figure 33. The lower limit of daytime ventral countershading, estimated above as approximately 775 m, is equivalent to a nighttime depth of approximately 125-150 m, suggesting that the shallow group, but not the deep group may countershade at night. The lower limit of daytime lateral countershading, estimated as about 660 m, is equivalent to about 50 m at night, the approximate upper limit of *S. gardineri*, the shallowest all-red sergestid at night. Although these figures admittedly pile estimate on estimate, they suggest that light may influence the vertical distribution of sergestids at night as well as during the daytime.

W. D. Clarke (in Barham 1970:118) and Foxton (1970) have suggested that countershading may occur primarily at night in some mid-water animals. While nighttime ventral countershading appears feasible for some species of Hawaiian sergestids, these species all may need to countershade during the daytime also (Table 7). A number of species maintain approximately constant illumination day and night. Some species live in much brighter waters during the daytime than at night. No species, however, lives in brighter waters at night than during the daytime, as would be expected if countershading were occurring only at night.

Only two species of Hawaiian sergestids definitely do not migrate. *Sergia tenuiremis* appears to migrate to 300-400 m when less than 15 mm CL. The adult population spreads upward from an upper limit of 750-800 m during the day to about 600 m at night, although many shrimp remain in the daytime depth range. *Petalidium suspiriosum* remains below 750-800 m both day and night. Few Hawaiian sergestids occupy the depths between 300 and 600 m at night, in contrast to the Atlantic, where Donaldson (1973) found *Sergestes corniculum* and *Sergia grandis* and Foxton (1970) found *Sergestes corniculum* and *Sergia robusta* in this depth range. The reasons for this difference are unknown.

TABLE 7.—Estimated light intensities for daytime and dark night habitats of Hawaiian sergestids. Numbers are negative logarithms of light intensity (smaller numbers mean brighter light).

Species	Daytime habitat	Night habitat	
Sergestes atlanticus	5.0- 6.7	5.5- 6.0	D ~ N
Sergestes erectus	5.5- 6.7	9.0-10.0	D >>N
Sergestes armatus	4.7- 6.0	8.2- 9.7	D >>N
Sergestes vigilax	5.0- 6.7	5.5- 7.7	D ~ N
Sergestes orientalis	4.0- 5.2	5.5- 7.2	D > N
Sergestes consobrinus	4.7- 5.2	5.5- 6.2	D > N
Sergestes sargassi	3.5- 5.0	7.7- 9.5	D >>N
Sergestes pectinatus	4.2- 6.2	7.5- 9.0	D > N
Sergia fulgens	4.7- 5.5 ?	7.7- 8.2 ?	D > N ?
Sergia scintillans	4.2- 6.5	5.7- 7.2	D ~ N
Sergia gardineri	4.7- 7.2	5.7- 7.2	D ~ N
Sergia bigemmea	(7.0-11.0)	7.7- 9.0	D ~ N
Sergia inequalis	(7.0-11.0)	7.7- 9.0	D ~ N
Sergia bisulcata	6.5- 8.7	8.7-10.2	D > N

Although considerable evidence links diurnal vertical migration to the diurnal light cycle (e.g., Marshall 1954), the exact relation of light to vertical migration is complex and poorly understood. The simplest scheme, merely maintaining a constant light intensity around the clock, is not used by all Hawaiian sergestids, as Table 7 shows. The daytime sergestid assemblage cannot shift en masse to equivalent light levels at night, because the light intensity at the surface on a moonless night is approximately equivalent to that at 600 m during the daytime. Instead, we find species with similar daytime ranges but different nighttime ranges, such as *Sergestes armatus* and *S. consobrinus*; species with similar nighttime ranges but different daytime ranges, such as *Sergia scintillans* and *S. gardineri*; and species that exchange relative positions, such as *Sergestes sargassi* and *Sergia gardineri*. Vertical migration is a more complicated behavior than merely maintaining a constant light level.

A further complication of the vertical migration mechanism involves the response of sergestids to moonlight. When the moon increases the nighttime surface irradiance, the two groups of migrators react in different ways. The deep group remains relatively unaffected by moonlight, the young often moving downward to the depth of the adults. Moonlight drastically affects the shallow group, depressing most of the species below 150 m. The two assemblages, which separate by depth on dark nights, mix together on moonlit nights.

In addition to the normal response of sergestids to moonlight, there appears to be a period of about a week around full moon when some species stop migrating entirely, remaining at their daytime depths. This behavior is poorly shown by the results of the Teuthis cruises, showing up better in the supplementary data from 70-12 and Echo IV. Not all species react the same way to the full moon period. *Sergia gardineri* and probably *Sergestes*

atlanticus appear to stop migrating altogether. During cruise 70-12 part of the populations of *Sergestes orientalis* and *S. consobrinus* migrated, while the rest of the populations remained at their daytime ranges; during Echo IV both species appeared to migrate normally. Other species, such as *Sergestes vigilax* and *Sergia scintillans*, have shown no indications of nonmigratory behavior. Species showing the best evidence of nonmigration are all members of the shallow migratory group, but sampling was inadequate to determine definitely whether any species in the deep group are also nonmigrators. The data from cruise 70-12 and the June 1973 Teuthis cruise further suggest that when a species is not migrating its daytime depth can also be abnormal. *Sergia gardineri*, normally found between 650 and 775 m during the daytime, was taken as deep as 1,200 m on these cruises, and *Sergestes atlanticus*, normally found between 600 and 725 m, was taken down to 800 m.

The nonmigration of some sergestids around full moon is a separate behavior from the moonlight depression below 150 m. Nonmigration is not a direct effect of increased light levels. During Echo IV the moon was often heavily obscured by cloud, yet the nonmigratory species remained deep. During Cruise 70-12, nonmigratory species remained deep until the next-to-last night, when normal migration resumed, although light intensity in the surface waters could not have been radically different than on the previous night. Nonmigratory behavior has been observed in December and June, suggesting that it occurs during most seasons of the year.

Studies of seasonal variation in vertical migration can be complicated by moon effects. For example, Donaldson (1973) found abnormally deep distributions day and night for *Sergia splendens* during a February 1972 cruise. He also cited data from the same cruise showing that sergestid numbers were strongly influenced by moonlight in the upper 100 m, both at the quarter and at full. Knowing only that the moon was in various phases during the February 1972 cruise, it is impossible to separate seasonal effects from moonlight effects for *S. splendens*. Other mid-water groups show nonmigratory behavior not tied to lunar phase. Riggs (pers. commun.) found that species of the penaeid shrimp *Gennadas* did not migrate during our November 1972 cruise, which sampled near new moon when sergestids appeared to be migrating normally, and concluded that a seasonal factor was involved. In summary, the depth structure of the mesopelagic community changes in a bewilderingly complex manner under the influence of ambient light, lunar phase, season, and probably other undiscovered effects.

Feeding Chronology and Diet

In studies of the diets of mesopelagic animals, the time of day when feeding takes place is as interesting a datum as the kinds of prey eaten. The most widely accepted theory of the function of vertical migration holds that mesopelagic animals move into the food-rich shallow water at night to feed in the dark and retreat into deeper water at sunrise to escape the efficient visual predators of the epipelagic zone (Marshall 1954). If this theory is correct, an examination of the feeding chronology of vertical migrators should reveal that the majority, at least, of feeding occurs at night.

Table 4 compares the stomach contents of day-caught with night-caught sergestids from the DSB III cruise of February 1973. The night samples as a whole had a lower percentage of empty stomachs, a greater amount of food in the stomachs, and a lesser degree of digestion than the day samples, indicating that most feeding occurred at night. Unfortunately, only two species were abundant both day and night. *Sergestes armatus* fed more at night than during the daytime, although most specimens had empty stomachs regardless of time of day. *Sergestes erectus* actually had a lower percentage of empty stomachs during the daytime than at night, but the night specimens on the average were fuller than the day specimens. Other studies of feeding chronology in sergestids, notably those of Omori (1969) on *Sergia lucens*, Judkins and Fleminger (1972) on *Sergestes similis*, and Foxton and Roe (1974) on a variety of Atlantic species, also indicated that most feeding occurs at night. However, the DSB III day samples contained a number of individuals with appreciable amounts of food in their stomachs, showing that a certain amount of feeding occurs during the daytime. Donaldson (1973) found that *Sergestes sargassi*, *S. pectinatus*, and *Sergia japonica* appeared to feed around the clock. The first two species also live in Hawaiian waters; unfortunately, they only occurred in the night samples of DSB III, so this study could not test his observations.

If Hawaiian sergestid species have specialized by dietary preference, they might be expected to exhibit specialized structures for catching prey.

One important systematic character, the third maxilliped, appears directly related to feeding. Many species of *Sergestes* have greatly enlarged third maxillipeds, armed with stout spines and varying in length and development among the different species. *Sergestes pectinatus* in particular has highly modified third maxillipeds, with a series of short, comblike setae between the longer spines. The division of Hawaiian sergestids into a long-maxilliped group and a short-maxilliped group would seem logically to indicate a difference in diet between the two groups.

The results of the DSB III study (Table 5) are rather unexpected. All the species captured fed largely on zooplankton-sized crustacea in the 1- to 3-mm size range, chiefly calanoid copepods, myodocopid ostracods, and hyperiid amphipods. Some species also ate smaller zooplankton in the 0.4- to 0.6-mm size range, chiefly larval bivalves, foraminifera, and cyclopoid copepods. Ability to utilize prey in the small size range appeared to depend not on the length of the third maxillipeds but on the degree of setation of the first three pairs of pereiopods and (when not enlarged) the third maxillipeds. Species feeding on small zooplankton all have long setae spaced about 0.3-0.4 mm apart. All well-sampled species in the short-maxilliped group except *Sergestes erectus* fed on the small zooplankton. Within the long-maxilliped group, there is a gradation in degree of setation of the pereiopods from *S. armatus*, which has very short, sparse setae, through the *S. orientalis* group, which have somewhat longer, more numerous, but still rather sparse setae, to *S. sargassi* and *S. pectinatus*, which have rather long setae spaced about 0.5-0.6 mm apart. Of this group only *S. armatus* was captured in quantity during DSB III; its diet definitely lacked small zooplankton. A few specimens of *S. sargassi* and *S. pectinatus* were captured; none contained small zooplankton, but with the small sample size their status remains in doubt.

The dietary specializations of Hawaiian sergestids thus appear more related to size than to type of prey. The variety of copepods, amphipods, and ostracods that compose the large zooplankton fraction all seem to be equally acceptable as prey. The various modifications of the third maxilliped may reflect specialized methods of capturing prey rather than a specialized diet. In particular, the diet of *S. pectinatus* lacks any distinctive characteristics which can be associated with its unusual maxillipeds. While large zooplankters are probably seized individually, the small zooplankton appear to be sieved from the water onto the long setae, spaced so as to retain zooplankton and pass water, a process akin to filter feeding.

The small zooplankton probably represent a supplementary rather than a primary resource for sergestids. Larval bivalves, as meroplankton, are unlikely to be abundant all year around (they were abundant in the zooplankton during the December 1973 cruise; I have not examined other zooplankton samples) and are unlikely to be abundant far from land. Many of the individuals containing small zooplankton also contain masses of an unidentified greenish, fibrous material. Judkins and Fleminger (1972) reported similar material in *Sergestes similis*, and Foxton and Roe (1974) reported similar material in a number of Atlantic species. If this material is detritus and not the digested remains of some unidentified organism, it would represent another resource available to sieving sergestids, potentially very important when small zooplankton is sparse. The inefficient-looking sieving mechanism of the Hawaiian sergestids are a reminder that none of these species feed solely, or even primarily, on the small zooplankton. Any modifications for increased sieving ability must not hamper the animal's ability to seize large zooplankton.

The results from DSB III are quite different from those reported by Donaldson (1975). He found a much larger proportion of large prey, such as euphausiids and fishes, and also many more chaetognaths. Part of the difference is due to his much larger sample, where infrequently eaten prey are more likely to turn up. Large sergestids captured in very small numbers during the DSB III cruise, particularly *Sergia bisulcata*, *S. inequalis*, and perhaps *S. tenuiremis*, are likely to eat larger prey than is reported here. However, some of the difference between Donaldson's results and the DSB III results may be due to a higher degree of feeding in the trawl during Donaldson's study. The abnormal conditions in the cod end of a mid-water trawl are apt to lead to abnormal feeding. Judkins and Fleminger found a much lower proportion of euphausiids in the stomachs of sergestids caught by albacore than in trawl-caught shrimp. They also found fish scales only in trawl-caught shrimp, an unlikely food item under natural conditions. These results emphasize the need for future feeding studies to take whatever steps are necessary to minimize or eliminate feeding in the trawl.

Reproduction and Growth

It is diffcult to determine when sergestids spawn. Copulation occurs long before spawning; female *Sergia gardineri* whose ovaries have not started to mature often bear spermatophores. Eggs are spawned directly into the water rather than being carried on the appendages as in the carideans. Some spawning probably occurs year around, as sexually mature females can be captured at any time of the year. In *Sergestes*, the anterior lobes of the ovary vary greatly in size, filling much of the carapace at maximum development. However, there is no correlation of ovary development with carapace length in adult females. One possible explanation is that a female may spawn several batches of eggs over a period of several months, the ovaries regressing in size between batches.

Recruitment to a catchable size can be determined from the quarterly size-frequency histograms. Omori (1969) found that *Sergia lucens* required about 2 mo from spawning to recruitment; assuming the time is similar for Hawaiian species, a maximum in recruitment implies a maximum in spawning about one quarter earlier. Most Hawaiian sergestids showed peak recruitment in either the second (April-June) or third (July-September) quarter. Species with maximum recruitment in the second quarter included *Sergestes armatus*, *S. sargassi*, *Sergia inequalis*, and *S. bisulcata*. Species with maximum recruitment in the third quarter included *Sergestes atlanticus*, *S. consobrinus*, *S. pectinatus*, *Sergia scintillans*, and *S. gardineri*. Some species showed no significant difference from one quarter to the next; these included *Sergestes orientalis*, *Sergia bigemmea*, and probably *S. tenuiremis* and *Petalidium suspiriosum*. *Sergestes vigilax* had somewhat higher recruitment in quarters two and three than during the rest of the year. *Sergestes erectus* showed no particular recruitment maximum, but intermediate-sized shrimp were most abundant in the fourth quarter. *Sergia fulgens* is a peculiar case, to be discussed later.

Size-frequency data indicate that most Hawaiian sergestids appear to live about 1 yr, in agreement with most other studies (Pearcy and Forss 1969; Omori 1969; Donaldson 1973). The size-frequency histograms of *Sergia bisculcata* indicate that this species has a 2-yr life span, though the conclusion is based on a small sample. Donaldson concluded that *S. robusta* may also live 2 yr. Genthe (1969) arrived at a 2-yr life span for *Sergestes similis* off California, though Pearcy and Forss found a 1-yr life span for the same species off Oregon. Genthe asserted that juveniles less than 5 mm CL are 9 to 11 mo old, which seems too old. His data support a 1-yr life span if a 2- to 3-mo larval development time is assumed. Probably only a few large all-red species live more than a single year.

Sergia fulgens differed from all other Hawaiian species by showing an extremely modal size-frequency distribution and varying drastically in abundance from one month to the next (Figure 18). This behavior can best be explained by assuming that *S. fulgens* is an expatriate species occasionally moving into Hawaiian waters from elsewhere. Adult females from the December 1970 cruise and the May 1973 cruise (Teuthis XXI) had small ovaries with eggs about 150 μm in diameter. Mature females of the closely related but smaller species *S. scintillans* had proportionately larger ovaries with eggs about 260 μm in diameter. Omari (1969) reported an average diameter of 255 μm for another closely related species, *S. lucens*. It thus appears that the large female *S. fulgens* are not ripe. While it is possible that female *S. fulgens* continue to grow to 18 or 20 mm CL before spawning and that ripe females have never been captured, it seems more likely that *S. fulgens* do not reproduce in Hawaiian waters and that the local population is carried in by currents from its normal breeding range. Unfortunately, the geographic range of *S. fulgens* is almost totally unknown; in addition, it is very similar or identical to *S. talismani* in the Atlantic. Influxes of *S. fulgens* did not coincide with captures of *Sergestes tantillus*, an equatorial species occasionally found in Hawaiian waters, but little more can be inferred about the source of the local population of *S. fulgens*.

Interspecific Relationships

The 20 species of Hawaiian sergestids exhibit a variety of specializations in morphology and habit that appear to minimize interspecific competition and allow them to coexist as a stable assemblage. Most obvious is the division into half-red and all-red species, related to shallow and deep daytime depth ranges and the different concealment strategies required. The all-red sergestids are subdivided by size and nighttime vertical distribution, as are the half-red sergestids, which are also further subdivided by photophore type and

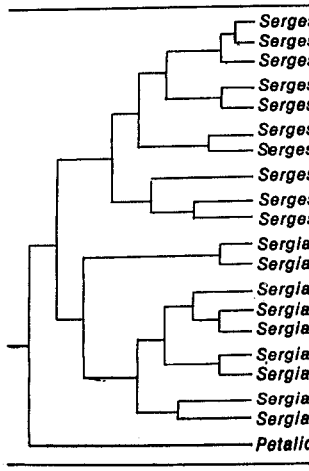
length of third maxillipeds. Finally, nearly all species cooccur with at least one other species that is much more closely related than any of the other Hawaiian sergestids. Interspecific competition should be strongest between members of a species pair; the ways in which two closely related sergestids divide up the mid-water environment should suggest the kinds of competition that occur in the mid-water environment and how competition is minimized.

Table 8 shows some observed parameters of Hawaiian sergestids. The dendrogramlike pattern at the left is a subjective representation of the affinities among the species, based on morphological features. Some differences will be noted in the vertical distribution patterns of the species pairs; for example, *Sergestes vigilax* is more broadly distributed than *S. armatus* and tends to live shallower at night. However, most species pairs are commonly found together over much of their vertical ranges. The most striking difference among closely related species is adult size. In every case the most closely related species show little or no overlap in the adult size range. For example, *Sergia scintillans* appears nearly identical to *S. fulgens*, differing chiefly in the number of photophores on the antennal scale and exopod of the uropod. However, adult *S. scintillans* vary from 5.5 to 10.5 mm CL, while adult *S. fulgens* vary from 11 to 16.5 mm CL. The only exception to this rule, the species triplet *Sergestes orientalis-S. tantillus-S. consobrinus*, is a revealing case. *Sergestes orientalis* is well separated in size from *S. consobrinus*, the largest females of *S. consobrinus* overlapping only slightly with the smallest males of *S. orientalis*. However, *S. tantillus*, while somewhat smaller in average size than *S. orientalis*, still overlaps considerably in size with the larger species. In this case it turns out that *S. tantillus* is primarily an equatorial species (Judkins 1972), occurring only rarely in Hawaiian waters. MacArthur (1972) has shown on theoretical grounds that when three similar species differ in only one parameter, such as body size, the competition pressures are strongest on the middle species. One of the factors determining the northern limit of *S. tantillus* may be this competition from both a larger and a smaller species.

Specialization solely by adult size could still result in competition if adults of the small species cooccur with similar-sized juveniles of the large species. In this case, other specializations appear to become important. When the species have similar vertical ranges, the juveniles may live shallower than the adults. For example, adult *Sergia bigemmea* and adult *S. inequalis* both occur at about 150 to 225 m at night. Juvenile *S. inequalis* in the 10- to 13-mm CL range, the size of adult *S. bigemmea*, are mostly found between 50 and 150 m, so that similar-sized individuals of the two species seldom occur together.

Competition could occur if the large species lives somewhat deeper than the small species, so that juveniles of the large species live at about the

TABLE 8.—Characteristics of Hawaiian sergestid species. Dendrogram shows estimated phylogenetic affinities among species.



Species	Adult size (CL, mm)	Day depth (m)	Night depth (m)	Population size (no./100 m²)
Sergestes orientalis	5.5-10	500- 625	0- 125	1.32
Sergestes tantillus	5.5- 8	450- 650?	0- 100?	<0.10
Sergestes consobrinus	3.8- 6	450- 725	0- 75	1.05
Sergestes armatus	9 -14.5	550- 650	150- 300	2.35
Sergestes vigilax	6 - 8.5	550- 725	0- 200	0.35
Sergestes atlanticus	5 - 9	550- 725	0- 300	1.31
Sergestes cornutus	3.5- 5	450- 550?	(0- 50)?	<0.10
Sergestes erectus	13 -24.5	550- 800	250- 325	3.81
Sergestes sargassi	7 -10.5	450- 575	125- 300	0.70
Sergestes pectinatus	3.2- 7.5	450- 725	75- 275	1.71
Sergia fulgens	11 -16.5	550- 625?	75- 200?	2.26
Sergia scintillans	5.5-10.5	525- 700	25- 125	3.31
Sergia gardineri	4.5- 9	650- 775	25- 150	8.65
Sergia bigemmea	9.5-14.5	750-1,100?	125- 250	0.64
Sergia inequalis	13.5-22	750-1,100?	100- 250	0.55
Sergia bisulcata	16.5-23	700- 900	225- 350	1.35
Sergia maxima	(41.5)	?	?	<0.10
Sergia tenuiremis	18.5-29	750-1,300+	550-1,200+	0.89
Sergia laminata	7 -10	700- 800?	?	<0.10
Petalidium suspiriosum	8.5-12	800-1,300+	800-1,200+	1.84

same depth as adults of the small species. The clearest example of this type in Hawaiian waters is *Sergestes vigilax* and *S. armatus*, where most juvenile *S. armatus* in the 6- to 8.5-mm CL range live around 100 to 150 m at night, overlapping somewhat with adult *S. vigilax* in the same size range (most *S. vigilax* live above 100 m, but adults often occur somewhat deeper). However, it appears that adult *S. vigilax* are most abundant from October to March, while juvenile *S. armatus* in the same size range are most abundant from April to June (Figures 6, 8). Thus the actual overlap at any one time is probably small.

The Hawaiian sergestid assemblage can thus be described by size, morphology, and vertical distribution. Consider the half-red species first. Those with short maxillipeds are divided into a pair of species with lensed cuticular photophores and three species with organs of Pesta. The pair with cuticular photophores includes a large species, *Sergia fulgens*, and a small species, *S. scintillans*; these species may also live at different depths at night. Of the three species with organs of Pesta, *Sergestes erectus* is very large, distantly related to the other two, and lives deeper at night; *S. atlanticus* is larger than *S. cornutus* and may live deeper during the daytime. Long third maxillipeds appear to have evolved at least twice, possibly three times, in *Sergestes* (Burkenroad 1937; Foxton 1972). The *S. sargassi-S. pectinatus* pair is distinct from the others; again, *S. sargassi* is large and *S. pectinatus* is small, with specialized maxillipeds and broader vertical distributions day and night. The other two groups are more closely related, but the *S. armatus-S. vigilax* pair has longer maxillipeds than the *S. orientalis-S. tantillus-S. consobrinus* triad. *Sergestes armatus* is larger than *S. vigilax* and lives deeper at night; the other group has been discussed above.

Among the all-red Hawaiian sergestids, a similar organization prevails. The *Sergia inequalis-S. bigemmea-S. gardineri* group are respectively large, medium-sized, and small; in addition, *S. gardineri* lives shallower than the other two at night, and perhaps during the daytime. The *S. bisulcata-S. maxima* pair is related to the above triad, but *S. bisulcata* is somewhat larger than *S. inequalis* and lives deeper at night, while the rare *S. maxima* is extremely large. Two species without photophores are nonmigrators; *S. tenuiremis* is much larger than *Petalidium suspiriosum*. The rare *S. laminata*, while related to *S. tenuiremis*, is smaller, has photophores (Walters 1975), and appears to migrate.

Studies of sergestid assemblages in the subtropical Atlantic by Foxton (1970) near Fuerteventura (Canary Islands) and Donaldson (1975) near Bermuda showed interesting parallels to the present study in the subtropical Pacific (Table 9). The two Atlantic areas were very similar to one

TABLE 9.—Atlantic and Hawaiian sergestid assemblages.

Hawaii	Bermuda[1]	Fuerteventura[2]
Sergestes consobrinus	*(Sergestes edwardsii)*	n.e.[3]
Sergestes orientalis / *(Sergestes tantillus)*	n.e.	n.e.
Sergestes armatus	*Sergestes armatus*	*Sergestes armatus*
Sergestes vigilax	*Sergestes vigilax*	*Sergestes vigilax*
Sergestes atlanticus	*Sergestes atlanticus*	*(Sergestes atlanticus)*
(Sergestes cornutus)	*Sergestes cornutus*	n.e.
Sergestes erectus	*"Sergestes corniculum"*[4]	*"Sergestes corniculum"*[4]
Sergestes sargassi	*Sergestes sargassi*	*Sergestes sargassi*
Sergestes pectinatus	*Sergestes pectinatus*	*Sergestes pectinatus*
Sergia fulgens	*(Sergia talismani)*	n.e.
Sergia scintillans	n.e.	n.e.
Sergia gardineri / *Sergia bigemmea*	*Sergia splendens*	*Sergia splendens*
Serga inequalis	*Sergia robusta*	*Sergia robusta*
Sergia bisulcata / *Sergia maxima*	*Sergia grandis*	n.e.
(Sergia laminata)	*(Sergia tilicta)*	n.e.
Sergia tenuiremis	*Sergia tenuiremis*	*Sergia tenuiremis*
n.e.	*Sergia japonica*	*Sergia japonica*
Petalidium suspiriosum	—	—

[1]From Donaldson (1975).
[2]From Foxton (1970).
[3]n.e. — no equivalent.
[4]See text.

another except for the abundance of *Sergestes atlanticus* and *Sergia grandis* (Sund 1920) in Bermuda relative to Fuerteventura (the Fuerteventura material all came from a single cruise and may have lacked some of the less-abundant species). More surprising, the Atlantic sergestids were very similar to the Hawaiian species, particularly the half-red types. "*Sergestes corniculum* Krøyer 1855"[3] replaced its close relative, *S. erectus* in the Atlantic, and two rare Bermuda species, *S. edwardsii* Krøyer 1855 and *Sergia talismani* (Barnard 1947), had close relatives, *Sergestes consobrinus* and *Sergia fulgens*, in Hawaiian waters; otherwise, all the half-red species in the two Atlantic studies also occurred in the present study. There were some differences in abundance and vertical distribution, partly real and partly due to differences in sampling. *Sergestes vigilax* was more abundant than *S. armatus* in the Atlantic studies, and *S. sargassi* was more abundant than *S. pectinatus*; the opposite was true in Hawaiian waters. *S. atlanticus* was more abundant near Bermuda and less abundant near Fuerteventura than near Hawaii. *Sergestes corniculum* was more broadly distributed at night than its Hawaiian counterpart, *S. erectus*. The biggest differences were the rarity or absence in the Atlantic collections of the *S. orientalis* types and the half-red *Sergia* species, both of which were abundant in Hawaiian waters. Still, the similarities between the subtropical Atlantic and Pacific were considerable: one or more large species with short third maxillipeds and with fairly deep nighttime distributions, one or two smaller species with short maxillipeds and living shallower at night (in Bermuda), and a variety of species with long maxillipeds occurring in closely related groups of large and small species.

The all-red sergestids also showed similarities between the subtropical Atlantic and Pacific, although the parallelism was not as striking as in the half-red types. *Sergia tenuiremis* was found in all three areas. The role of *S. gardineri* was filled in the Atlantic by the closely related *S. splendens* (Sund 1920). It was somewhat larger than *S. gardineri*, exceeding 11 mm CL, but had no potential competition in the 10- to 15-mm CL size range like the Hawaiian *S. bigemmea*. The nearest Atlantic equivalents of *S. inequalis* and *S. bisulcata*, respectively *S. robusta* (Smith 1882) and *S. grandis*, lived much deeper at night, in the 400- to 600-m zone, which was nearly devoid of sergestids around Hawaii. *Sergia filicta* (Burkenroad 1940) may be the Atlantic counterpart of *S. laminata*, but very little is known about either species. *Sergia japonica* (Bate 1881) had no Hawaiian equivalent, and *S. maxima* had no Atlantic equivalent. Neither Atlantic study mentioned *Petalidium*, so it is unclear whether there is an Atlantic counterpart to the Hawaiian *Petalidium suspiriosum* (*P. foliaceum* Bate 1881 occurs in the South Atlantic (Kensley 1971)). Both oceans thus contain an all-red assemblage consisting of one or more nonmigrators, a small, abundant species with a shallow nighttime range, and several larger species living deeper at night. In general, the Hawaiian area appears to have more half-red and fewer all-red sergestid species than the subtropical Atlantic.

While the parameters of Table 8 indicate that Hawaiian sergestids have partitioned the midwater environment, this study has left unclear the ecological significance of most of the parameters. Differences in size, length of third maxilliped, and nighttime vertical range are presumably related to diet, but the data on feeding show little dietary specialization other than the ability of some species to eat submillimeter-sized zooplankton. A more elaborate study may reveal more subtle variations in diet, perhaps related to vertical distribution of prey or differences in hunting strategies. Daytime vertical distribution and color pattern seem most likely related to predation. Virtually nothing is known about predation on Hawaiian sergestids. The division of half-red sergestids into species with organs of Pesta and species with lensed cuticular photophores has an unknown ecological significance. Cuticular photophores are fixed in position, but I have observed sergestids with organs of Pesta rotating them through nearly 180°, maintaining a vertical orientation of the photophores regardless of the attitude of the animal (see also Omori 1974). Studies of live sergestids may reveal differences in behavior between the two groups related to the need for ventral countershading. Hawaiian sergestids appear to occupy distinct niches, but the niches cannot be defined yet in an ecologically meaningful way.

[3]Crosnier and Forest (1973) have reviewed the systematics of Atlantic species of Yaldwin's "*Sergestes corniculum*" species group. They replaced *S. corniculum* Krøyer with *S. henseni* (Ortmann 1893) and three new species–*S. paraseminudus*, *S. pediformis*, and *S. curvatus*. Donaldson's figure of *S. corniculum* corresponded to *S. curvatus*. Foxton gave no drawings of *S. corniculum*, but a later study in the same area, Foxton and Roe (1974) found *S. henseni* and *S. curvatus*.

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LITERATURE CITED

AMESBURY, S. S.
1975. The vertical structure of the micronektonic fish community off leeward Oahu. Ph.D. Thesis, Univ. Hawaii, Honolulu, 176 p.

BADCOCK, J.
1970. The vertical distribution of mesopelagic fishes collected on the Sond Cruise. J. Mar. Biol. Assoc. U.K. 50:1001-1044.

BARHAM, E. G.
1957. The ecology of sonic scattering layers in the Monterey Bay area. Stanford Univ., Hopkins Mar. Stn. Tech. Rep. 1, 182 p.
1970. Deep-sea fishes: Lethargy and vertical orientation. *In* G. B. Farquar (editor), Proceedings of an International Symposium on Biological Sound Scattering in the Ocean, p. 100-118. Maury Cent. Ocean Sci. Rep. 005.

BURKENROAD, M. D.
1937. The Templeton Crocker Expedition. XII. Sergestidae (Crustacea Decapoda) from the Lower Californian region, with descriptions of two new species and some remarks on the organs of Pesta in *Sergestes*. Zoologica (N.Y.) 22:315-329.

CLARKE, G. L.
1968. Light measurements. BioScience 18:965-966.

CLARKE, G. L., AND E. J. DENTON.
1962. Light and animal life. *In* M. N. Hill (editor), The sea, Vol. 1, p. 456-468. Interscience, N.Y.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.

CLARKE, W. D.
1963. Function of bioluminescence in mesopelagic organisms. Nature (Lond.) 198:1244-1246.

CROSNIER, A., AND J. FOREST.
1973. Les crevettes profondes de l'Atlantique oriental tropical. Faune Tropicale, Tome XIX. ORSTOM (Off. Rech. Sci. Tech. Outre-Mer), Paris, 409 p.

DENTON, E. J., AND J. A. C. NICOL.
1965. Reflexion of light by external surfaces of the herring, *Clupea harengus*. J. Mar. Biol. Assoc. U.K. 45:711-738.

DONALDSON, H. A.
1973. Ecology of the Genus *Sergestes* (Decapoda, Natantia) in an area near Bermuda. Ph.D. Thesis, Univ. Rhode Island.
1975. Vertical distribution and feeding of sergestid shrimps (Decapoda: Natantia) collected near Bermuda. Mar. Biol. (Berl.) 31:37-50.

DOTY, M. S., AND M. OGURI.
1956. The island mass effect. J. Cons. 22:33-37.

FOXTON, P.
1970. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the Sond Cruise 1965. II. The Penaeidea and general discussion. J. Mar. Biol. Assoc. U.K. 50:961-1000.
1972. Further evidence of the taxonomic importance of the organs of Pesta in the genus *Sergestes* (Natantia, Penaeidea). Crustaceana 22:181-189.

FOXTON, P., AND H. S. J. ROE.
1974. Observations on the nocturnal feeding of some mesopelagic decapod crustacea. Mar. Biol. (Berl.) 28:37-49.

GENTHE, H. C., JR.
1969. The reproductive biology of *Sergestes similis* (Decapoda, Natantia). Mar. Biol. (Berl.) 2:203-217.

GILMARTIN, M., AND N. REVELANTE.
1974. The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. J. Exp. Mar. Biol. Ecol. 16:181-204.

GORDON, D. C., JR.
1970. Chemical and biological observations at station Gollum, an Oceanic Station near Hawaii, January 1969 to June 1970. Hawaii Inst. Geophys., Tech. Rep. HIG-70-22, 44 p.

GUNDERSON, K., C. W. MOUNTAIN, D. TAYLOR, R. OHYE, AND J. SHEN.
1972. Some chemical and microbiological observations in the Pacific Ocean off the Hawaiian Islands. Limnol. Oceanogr. 17:524-531.

JUDKINS, D. C.
1972. A revision of the decapod crustacean genus *Sergestes* (Natantia, Penaeidea) *sensu lato*, with emphasis on the systematics and geographical distribution of *Neosergestes*, new genus. Ph.D. Thesis, Univ. California, San Diego, 289 p.

JUDKINS, D. C., AND A. FLEMINGER.
1972. Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. Fish. Bull., U.S. 70:217-223.

KENSLEY, B. F.
1971. The family Sergestidae in the waters around Southern Africa (Crustacea, Decapoda, Natantia). Ann. S.-Afr. Mus. 57:215-264.

MACARTHUR, R. H.
1972. Geographical ecology: Patterns in the distribution of species. Harper & Row, Publishers, Inc., N.Y., 269 p.

MARSHALL, N. B.
1954. Aspects of deep sea biology. Philosophical Library, N.Y., 380 p.

MAYNARD, S. D., F. V. RIGGS, AND J. F. WALTERS.
1975. Mesopelagic micronekton in Hawaiian waters: Faunal composition, standing stock, and diel vertical migration. Fish Bull., U.S. 73:726-736.

NAKAMURA, E. L.
1967. Abundance and distribution of zooplankton in Hawaiian waters 1955-56. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 544, 37 p.

NICOL, J. A. C.
1958. Observations on luminescence in pelagic animals. J. Mar. Biol. Assoc. U.K. 37:705-752.
1967. The luminescence of fishes. Symp. Zool. Soc. Lond. 19:27-55.

OMORI, M.
1969. The biology of a sergestid shrimp, *Sergestes lucens* Hansen. Univ. Tokyo, Bull. Ocean Res. Inst. 4, 83 p.
1974. The biology of pelagic shrimps in the ocean. Adv. Mar. Biol. 12:233-324.

OMORI, M., A. KAWAMURA, AND Y. AIZAWA.
1972. *Sergestes similis* Hansen, its distribution and importance as food of fin and sei whales in the North Pacific Ocean. *In* A. Takenouti (editor), Biological oceanography of the northern North Pacific Ocean, p. 373-391. Idemitsu Shoten, Tokyo.

PEARCY, W. G., AND C. A. FORSS.
1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. Limnol. Oceanogr. 14:755-765.

TYLER, J. E., AND R. W. PREISENDORFER.
1962. Transmission of energy within the sea. *In* M. N. Hill (editor), The sea, Vol. 1, p. 397-451. Interscience, N.Y.

WALTERS, J. F.
1975. Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae). Ph.D. Thesis, Univ. Hawaii, 227 p.

YALDWYN, J. C.
1957. Deep-water crustacea of the genus *Sergestes* (Decapoda, Natantia) from Cook Strait, New Zealand. Zool. Publ., Victoria Univ., Wellington (N.Z.) 22:1-27.

ZIEMANN, D. A.
1975. Patterns of vertical distribution, vertical migration, and reproduction in the Hawaiian mesopelagic shrimp of the family Oplophoridae. Ph.D. Thesis, Univ. Hawaii, 112 p.

DECISION THEORY APPLIED TO THE SIMULATED DATA ACQUISITION AND MANAGEMENT OF A SALMON FISHERY[1]

GARY E. LORD[2]

ABSTRACT

A salmon fishery management model utilizing statistical decision theory has been constructed. The model provides for the successive acquisition of data that can be used to formulate and maintain an optimum management strategy. The Bayes risk is defined as the expected economic loss resulting from a set of fishery management decisions and the criterion of optimality is taken to be the strategy that minimizes the Bayes risk. Specific functional forms are assumed where necessary in order to obtain a closed form expression for the Bayes risk. The Bayes risk, in units of numbers of fish, can then be computed for any particular sequence of fishery management decisions.

This paper represents a continuation of an earlier effort (Lord 1973) in which statistical decision theory was applied to the data acquisition and management of a salmon fishery. The crucial feature was not that the species considered was salmon but that the assumed fishery was both dynamic and subject to errors in the population estimation. The population is assumed to be subject to continuing assessment, however, so that as the season progresses it is possible to make repeatedly more refined estimates of the true state of nature. The management strategy may thus be modified successively to reflect the additional data as they become available.

The development was quite abstract and presented only the basic theory in a relatively general way. The present paper represents an intermediate situation in which the theory is applied to a specific model constructed to represent such a fishery. The principal features of this model are: 1) a Ricker spawner-return relationship, 2) simulated sampling for population estimation purposes, and 3) an economic loss function based on maximum substained yield (MSY).

A limitation of the present model is that it is constructed in such a manner that a closed analytic form is obtained without recourse to Monte Carlo or other approximate methods of analysis. In other words, the Bayes risk may be computed exactly upon the specification of well defined sets of parameters. The imposition of such analytical requirements constrains the choice of functions to those that are mathematically tractable. Anticipating the final results, Equations (18) and (20), I feel that about the maximum degree of generality has been retained consistent with analytical tractability. It is likely that models possessing a greater degree of fidelity to the actual fishery situations will require the use of Monte Carlo methods as Mathews (1966) used in his simulation of the cannery portion of the Bristol Bay fishery.

ANALYSIS

The notation used in Lord (1973), with only minor changes, will be retained here. In this section I will discuss the Bayes risk for a particular fisheries model based on the Ricker spawner-return relation. The criterion of optimality will be taken as MSY. Economic losses will accrue as the actual management strategies depart from the optimum. Generally these losses will be reflected in either a decreased present catch or in diminished future returns due to prior overfishing.

A loss function proportional to the difference between the optimum catch and the actual catch, on an MSY basis, will be assumed. This is a simple and intuitively reasonable concept but, nonetheless, a unique formulation of the loss function from this criterion is no simple task. The difficulty arises from the use of a spawner-return relation which reflects the biological fact that the present state of the system is necessarily the result of past actions and, similarly, that future conditions will depend on present actions. In the case of sockeye salmon,

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an added complication is provided by the fact that the run in any year represents the progeny of several spawning groups.

The Ricker spawner-return relation, for a single spawning group, is given by

$$R_n = aE_{n-k}e^{-bE_{n-k}} \tag{1}$$

where R_n is the return in year n resulting from an escapement E_{n-k} k years prior, e is the base of natural logarithms, and a and b are parameters assumed unique for any river system or spawning group. We may generalize Equation (1) to the case of multiple spawning groups to give

$$R_n = \sum_{k=1}^{K} a_k E_{n-k} e^{-bE_{n-k}} \tag{2}$$

where the relevant spawning occurs over the years $(n - 1)$ through $(n - K)$. In Equation (2) the coefficients $\{a_k\}$ now reflect not only the magnitude of the run, as in Equation (1), but the proportion of the run arising from each spawning group. Specifically we can write $a_k = ap_k$ where a is the parameter in Equation (1) and p_k is proportion of the run in year n arising from spawners in year $(n - k)$. We have the condition $\sum_{k=1}^{K} p_k = 1$ from which it follows that $\sum_{k=1}^{K} a_k = a$.

The return as given by Equation (1) or Equation (2) is a deterministic function of the parameters. In actual practice, however, the return, from the biologist's point of view, is a random variable in which case some additive or multiplicative error term must be appended to Equation (1). Thus, at an appropriate point in the analysis, the return will be assumed to be a random variable whose expected value is given by Equation (1).

Let X_n be the catch in year n. Then

$$X_n = a \sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}} - E_n .$$

Let X_{tot} be the total catch over some fixed but otherwise arbitrary number, say n^*, of fishing seasons. Then

$$X_{tot} = \sum_{n=1}^{n^*} \left[\sum_{k=1}^{K} a_k E_{n-k} e^{-bE_{n-k}} - E_n \right]. \tag{3}$$

If we attempt to maximize X_{tot} with respect to the yearly escapements $E_1, E_2, \ldots E_{n^*}$, it turns out that as $n^* \to \infty$: a) a steady state solution exists and b) the optimum steady state escapement, E_0, is that which maximizes the function $(aEe^{-bE} - E)$.

Let L_n denote the economic loss in any year n and define L_n as the difference between the optimum catch, X_{opt}, and the actual catch X_{act}, i.e., $L_n = X_{opt} - X_{act}$. From Equation (3) we obtain

$$L_n = (aE_0e^{-bE_0} - E_0) - \left(a \sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}} - E_n\right). \tag{4}$$

E_0 is fixed and all of the escapements $\{E_{n-k}\}(k = 1 \ldots K)$ have already occurred thus leaving only E_n at our disposal. L_n is clearly minimized by setting $E_n = 0$ but since this would eliminate a portion of the run in future years the subsequent loss would be high indeed. Consider now the combined loss for two successive years n and $(n + 1)$. Proceeding along the same lines that led to Equation (4) we obtain

$$L_n + L_{n+1} = 2(aE_0e^{-bE_0} - E_0) - \left(a \sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}} - E_n\right) - \left(a \sum_{k=1}^{K} p_k E_{n+1-k} e^{-bE_{n+1-k}} - E_{n+1}\right).$$

If this is treated as a function of the single variable E_n, an optimum value can be obtained. However, this loss also depends on E_{n+1} which has not yet occurred. Let us extend this process through year $(n + K)$, which is a convenient stopping point since it represents the completion of a cycle starting at year n. The total loss over this period is given by

$$L_{n,n+K} = (K + 1)(aE_0e^{-bE_0} - E_0) - \sum_{j=n}^{n+K} \left[a \sum_{k=1}^{K} p_k E_{j-k} e^{-bE_{j-k}} - E_j \right]. \tag{5}$$

The loss given by Equation (5) depends not only on past and present escapements but on the future values $E_{n+1}, E_{n+2}, \ldots E_{n+K}$ as well. Thus, when formulating a policy for any particular year one must take into account future policies also. From a mathematical point of view what we have emerging here is another dynamic program, i.e., the optimum year-to-year allocation as well as the within-year allocation is in the form of a dynamic program. This is too great an anlytical burden to

bear. However, we can invoke the "Principle of Optimality" (Bellman 1957:83) to specify that $E_{n+j} = E_0$ for all $j \geq 1$, i.e., all future escapements are assumed to be the optimum MSY escapement. This is a reasonable assumption since the principle of optimality states that an optimal policy is one which, given the present state of the system, establishes and maintains an optimal policy for all future time periods. Since E_0 represents such an optimum steady state escapement it follows that $E_{n+j} = E_0$ for future optimality. In this case Equation (5) takes the form

$$L_{n,n+K} = L(E_n) = (K+1)(aE_0e^{-bE_0} - E_0) - (aE_ne^{-bE_n} - E_n) + \text{(terms depending on } E_0 \text{ and past escapements only)}. \quad (6)$$

From Equation (6) it appears that the optimization will be over a total of $(K + 1)$ seasons. This is not actually the case since, as noted above, the constraint $E_{n+j} = E_0$ has been imposed and the analytical procedures used in year n will be applicable in year $(n + 1)$, etc. Note also the intuitively reasonable result that the loss given by Equation (6) is minimized by setting $E_n = E_0$, the optimum MSY escapement.

The analysis thus far has assumed that all quantities are deterministic. Random variables will now be introduced to simulate the situation actually existing in salmon fishery assessment and management. Let N_n denote the run size resulting from the (known) escapements $\{E_{n-j}\}(j = 1, \ldots K)$ and let N_n be a random variable which, for definiteness, will be assumed to have the two-parameter gamma density

$$f_1(N_n \mid y_0) = \frac{\beta_0^{\alpha_0}}{\Gamma(\alpha_0)} N_n^{\alpha_0 - 1} e^{-\beta_0 N_n} \quad (7)$$

where Γ denotes a gamma function. The parameters (α_0, β_0) are subscripted to denote that they are applicable prior to the start of the run and f is subscripted by one to denote that it is applicable to the first fishing period. The quantity y_0 is a symbolic conditioning variable denoting the preseason information that is available for the specification of (α_0, β_0). Anticipating the dynamic nature of the fishery and its management the probability density of N_n will be conditioned successively to reflect the data obtained after the start of the run.

We assume now that the expected value, shown as $E[N_n]$ is that given by the Ricker relation, i.e.,

$$R_n = E[N_n] = a \sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}}. \quad (8)$$

The variance of N_n may be estimated from historical data, e.g., smolt outmigrations, high seas catches, etc. Knowledge of the mean and variance is sufficient to determine the parameters (α_0, β_0).

At this point it might be well to justify, or at least explain, the assumption of a gamma density for N_n. Clearly, one cannot obtain Equation (7) on the basis of biological arguments. On the other hand, a gamma density does not do particular violence to one's intuition concerning the distribution of population sizes. In particular, Equation (7) confines N_n to positive values with scale and location specified by (α_0, β_0). In salmon population estimation, it is rare that parameters beyond mean and variance are available from whatever source. It is in this spirit that Equation (7) is introduced. Further, the gamma distribution, not coincidentally, has the added virtue that it is an analytically convenient function. Similar arguments will be used to justify some of the functions to be introduced subsequently.

For the remainder of the analysis, only events in year n will be considered so that the subscript may be omitted from N_n. The fishing season is assumed to consist of m nonoverlapping time periods during each of which a management decision, δ, must be made. Let $\{\delta_i\}$ $(i = 1, \ldots m)$ be an arbitrary sequence of decisions where each of the δ_i is a member of some finite set of possible management decisions.[3] Assume now that during the ith period a fraction ρ_i of the total run enters the fishery. The set $\{\rho_i\}(i = 1, \ldots m)$, which is assumed to be known, may be obtained from such sources as the almanac prepared by Royce (1965). The $\{\rho_i\}$ must obviously satisfy the condition

$$\sum_{i=1}^{m} \rho_i = 1.$$

Corresponding to any actual realization of the run, N, there exists some unique set of optimum catch-escapement allocations $\{\eta_i\}$ $(i = 1, \ldots m)$. Rothschild and Balsiger (1971) used linear pro-

[3]A typical set of management decisions consists of such actions as opening or closing the fishery, the imposition of gear limitations, waiting periods, etc.

gramming to determine an optimum set of such allocations. Such fine-scale is not practical here so that the individual η_i are irrelevant here except that they must satisfy the condition

$$N \sum_{i=1}^{m} \rho_i \eta_i = E_0.$$

Let $\{\hat{\eta}_i\}$ $(i = 1, \ldots m)$ be the actual allocations where each $\hat{\eta}_i$ will be assumed to be a random function of the management decision δ_i taken during the ith period. It will be assumed that the $\{\hat{\eta}_i\}$ $(i = 1, \ldots m)$ have independent beta distributions where the beta parameters (ν_i, μ_i) are uniquely determined by the management decision δ_i that is taken during period i. Thus we have

$$g(\hat{\eta}_1, \hat{\eta}_2 \ldots \hat{\eta}_m \mid \delta_1, \delta_2, \ldots \delta_m) = \prod_{i=1}^{m} g_i(\hat{\eta}_i \mid \delta_i) \quad (9a)$$

where

$$g_i(\hat{\eta}_i \mid \delta_i) = \frac{\Gamma(\nu_i + \mu_i)}{\Gamma(\nu_i)\,\Gamma(\mu_i)} \hat{\eta}_i^{\nu_i - 1} (1 - \hat{\eta}_i)^{\mu_i - 1}. \quad (9b)$$

This is a reasonable probability density to assume since it confines $\hat{\eta}_i$ to the interval (0,1) and the parameter choice permits, within appropriate limits, the specification of the mean and variance[4] of $\hat{\eta}_i$.

Return now to the central feature of the analysis which is to take into account the dynamics of the fishery. Equation (7) is the probability density of N appropriate for the first period of the fishery during which only preseason conditioning information, denoted symbolically by y_0, is available. Assume now that, during the first and subsequent time periods, additional population data, $y_1, y_2, \ldots$ become successively available. This data may then be used to condition the probability density of N, hopefully in such a manner that our knowledge of the true value of N, as measured by its variance, improves as more data are gathered. At each stage of the fishing season we compute the Bayes risk with respect to the then current probability density of N and adopt a strategy that takes into account all available data and all previous management decision. This will be formalized analytically upon the specification of an appropriate sampling distribution for the $\{y_i\}$ $(i = 1, 2, \ldots m - 1)$. y_m is irrelevant since it is obtained after the final decision δ_m will have been made.

Assume that during each stage of the run some fixed fraction ϵ of the total number of fish entering the fishery is vulnerable to sampling. For example, if the sampling is done by gill nets ϵ may be determined from knowledge of the length, the time of soak, and the efficiency of the net. With such a sampling scheme, it is reasonable to assume that the samples $y_1, y_2, \ldots y_{k-1}$ will have independent Poisson densities with parameters $\lambda_1, \lambda_2, \ldots \lambda_{k-1}$ where $\lambda_i = \epsilon\rho_i N$, i.e., $\epsilon\rho_i N$ is the expected sample size for the ith period and

$$P(Y_i = y_i \mid N) = e^{-\epsilon\rho_i N} \frac{(\epsilon\rho_i N)^{y_i}}{y_i!} \quad (10)$$

where $y_i = 0, 1, \ldots$. Equation (10) and Bayes theorem may be utilized to modify or update Equation (7) to reflect the additional information that is assumed to have become available. Assume that the system is now at the start of the second stage and that the sample y_1 is now available. Bayes theorem gives

$$f_2(N \mid y_0, y_1) = \frac{P(Y_1 = y_1 \mid N) f_1(N \mid y_0)}{\int_0^\infty P(Y_1 = y_1 \mid N') f_1(N' \mid y_0) dN'}. \quad (11)$$

Substituting Equations (7) and (10) in Equation (11) gives, after dividing common factors,

$$f_2(N \mid y_0, y_1) = \frac{N^{\alpha_0 + y_1 - 1} e^{-(\beta_0 + \epsilon\rho_1)N}}{\int_0^\infty N^{\alpha_0 + y_1 - 1} e^{-(\beta_0 + \epsilon\rho_1)N} dN}. \quad (12)$$

The integral in the denominator of Equation (12) is a standard form expressible in terms of gamma functions which gives

$$f_2(N \mid y_0, y_1) = \frac{\beta_1^{\alpha_1}}{\Gamma(\alpha_1)} N^{\alpha_1 - 1} e^{-\beta_1 N} \quad (13)$$

where $\alpha_1 = \alpha_0 + y_1$ and $\beta_1 = \beta_0 + \epsilon\rho_1$. The updated probability density for N given by Equation (13) is, like the prior density given by Equation (7), a gamma density but with modified parameters α_1 and β_1. The process by which Equation (13) was obtained may be repeated indefinitely to give

$$f_k(N \mid y_0, y_1, \ldots y_{k-1}) = \frac{(\beta_{k-1})^{\alpha_{k-1}}}{\Gamma(\alpha_{k-1})} N^{\alpha_{k-1} - 1} e^{-\beta_{k-1} N} \quad (14)$$

[4]The conditioning of $\hat{\eta}$ by δ only is probably an oversimplification. There is evidence to indicate that $\hat{\eta}$ also depends on the number of fish that enter the fishery during any fishing period.

as the posterior density for N at the start of the kth fishing period. The parameters are given by $\alpha_{k-1} = \alpha_0 + y_1 + y_2 + \ldots + y_{k-1}$ and $\beta_{k-1} = \beta_0 + \epsilon(\rho_2 + \rho_2 + \ldots + \rho_{k-1})$. At this point it is appropriate to observe that, as time progresses and additional population data are obtained, the distribution of N, as specified by the parameters α_{k-1} and β_{k-1}, will more and more reflect the in-season sampling data with a corresponding decrease in the relevance of the preseason information implied by α_0 and β_0.

The probability densities given by Equations (7), (10), and (14) enjoy a peculiar relationship in which the posterior density of N, given by Equation (14), is from the same family as the prior density, Equation (7), for the particular sampling distribution given by Equation (10). Such pairs of densities are called conjugate pairs (DeGroot 1970:159-166). It is obvious that one cannot, in general, be so fortunate as to have parameter and sampling distributions that form a conjugate pair as in the model assumed here. However, DeGroot does outline some somewhat ad hoc procedures for constructing reasonable posterior probability densities.

All of the quantities and distributions necessary to compute the average or expected loss, i.e., the Bayes risk, are now available. The expression for the Bayes risk, to be evaluated at the start of the kth fishing period, may be written formally as

$$R_k(\delta_1, \delta_2, \ldots \delta_m \mid y_0, y_1, \ldots y_{k-1}) = \int_0^\infty f_k(N \mid y_0, y_1, \ldots y_{k-1}) dN \int_0^1 d\hat{\eta}_1 \ldots \int_0^1 d\hat{\eta}_m L(E_n) \prod_{i=1}^{m} g_i(\hat{\eta}_i \mid \delta_i) \tag{15}$$

where g_i, $L(E_n)$, and f_k are given by Equations (9), (6), and (14) respectively. Notice that the Bayes risk as given by Equation (15) is a function not only of the decisions already made, $\delta_1, \delta_2, \ldots \delta_{k-1}$ and the decision about to be made, δ_k, but of all future decisions $\delta_{k+1}, \ldots \delta_m$ as well. This dependence on all decisions, past, present, and future, reflects the assumption that the loss is a function primarily of the final state of the system, i.e., to a first approximation one cannot ascribe values to individual units of escapement during the season but only to the final total escapement. This presents no particular analytical difficulties since any particular sequence of optimum future decisions $\delta_{k+1}, \ldots \delta_m$ is certainly subject to revision as time passes and additional information becomes available.

Substituting Equations (6), (9), and (14) in Equation (15) gives

$$R_k(\delta_1, \delta_2, \ldots \delta_m \mid y_0, y_1, \ldots y_{k-1}) = \frac{(\beta_{k-1})^{\alpha_{k-1}}}{\Gamma(\alpha_{k-1})} \int_0^\infty N^{\alpha_{k-1}-1} e^{-\beta_{k-1}N} dN \int_0^1 d\hat{\eta}_1 \ldots \int_0^1 d\hat{\eta}_m \left\{ L'(E_0, E_{n-1}, \ldots E_{n-K}) - (aE_n e^{-bE_n} - E_n) \right\} \prod_{j=1}^{m} \frac{\Gamma(\nu_j + \mu_j)}{\Gamma(\nu_j)\Gamma(\mu_j)} \hat{\eta}_j^{\nu_j - 1} (1 - \hat{\eta}_j)^{\mu_j - 1} \tag{16}$$

where $L'(E_0, E_{n-1}, E_{n-2}, \ldots E_{n-K})$ denotes that portion of the loss function that does not depend on E_n. Thus L' is a fixed quantity and may be removed from the integral signs. This leaves only probability densities, which must integrate out to unity, so that

$$R_k(\delta_1, \delta_2, \ldots \delta_m \mid y_0, y_1, \ldots y_{k-1}) = L'(E_0, E_{n-1}, \ldots E_{n-K}) - \frac{(\beta_{k-1})^{\alpha_{k-1}}}{\Gamma(\alpha_{k-1})} \int_0^\infty N^{\alpha_{k-1}-1} e^{-\beta_{k-1}N} dN \int_0^1 d\hat{\eta}_1 \ldots \int_0^1 d\hat{\eta}_m (a e^{-bN \sum_{i=1}^{m} \rho_i \hat{\eta}_i} - 1) N \sum_{i=1}^{m} \rho_i \hat{\eta}_i \cdot \prod_{j=1}^{m} \frac{\Gamma(\nu_j + \mu_j)}{\Gamma(\nu_j)\Gamma(\mu_j)} \hat{\eta}_j^{\nu_j - 1} (1 - \hat{\eta}_j)^{\mu_j - 1} \tag{17}$$

where the escapement E_n has been expressed as

$$E_n = N \sum_{i=1}^{m} \rho_i \hat{\eta}_i .$$

The integrations in Equation (17) cannot be performed as expressed. If the order of the integrations is reversed, the integration with respect to N may be performed but the remaining integrations over $\hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_m$ will be virtually impossible. However, if the exponential term $\exp\left(-bN \sum_{i=1}^{m} \rho_i \hat{\eta}_i\right)$ is expanded in its Maclaurin series and if the resulting multinomials of the form $\frac{1}{n!}\left(-bN \sum_{i=1}^{m} \rho_i \hat{\eta}_i\right)^n$ $(n = 0, 1, \ldots)$ are expanded according to the multinomial theorem, the integrand in Equation (17) will be in a completely factored form. As a result of this factorization, the integrals take the form of various moments about

the origin. These integrals are all standard forms (c.f., Bierens de Haan 1939). The reader will be spared the details of this reduction and the ensuing integrations. The final expression for the Bayes risk is

$$R_k\,(\delta_1,\delta_2,\ldots\delta_m\,|y_0,y_1,\ldots y_{k-1})$$

$$= L'(E_0,E_{n-1},\ldots E_{n-K}) + \frac{\alpha_{k-1}}{\beta_{k-1}}\sum_{i=1}^{m}\frac{\rho_i\nu_i}{\nu_i+\mu_i}$$

$$-\frac{a}{\beta_{k-1}}\sum_{n=0}^{\infty}\left(-\frac{b}{\beta_{k-1}}\right)^n\frac{\Gamma(\alpha_{k-1}+n-1)}{n!\,\Gamma(\alpha_{k-1})}$$

$$\sum_{\substack{k_i=0\\ \Sigma k_i=n}}^{n}\binom{n}{k_1k_2\ldots k_m}\sum_{i=1}^{m}\frac{\rho_i(\nu_i+k_i)}{\nu_i+\mu_i+k_i}$$

$$\cdot\prod_{j=1}^{m}\frac{\Gamma(\nu_j+\mu_j)\,\Gamma(\nu_j+k_j)}{\Gamma(\nu_j)\,\Gamma(\nu_j+\mu_j+k_j)}\,\rho_j^{\,k_j} \qquad (18)$$

where $\binom{n}{k_1k_2\ldots k_m}$ denotes a multinomial coefficient.

A slightly different form for the risk may be obtained under an alternate set of assumptions. Considerable emphasis has heretofore been placed on the conjugacy of the gamma-Poisson families of distributions. The gamma-Poisson assumption is a reasonable one and the resulting conjugacy lends a certain elegance. However, this line of analysis results in posterior gamma parameters (α_k, β_k) that, among other things, depend on the run fractions $\{\rho_i\}$ $(i = 1, \ldots k)$. This parameter dependence on the run fractions virtually precludes treating the set $\{\rho_i\}$ $(i = 1, \ldots k)$ as anything but fixed quantities; i.e., once a variable becomes the argument of a gamma function one has usually arrived at an analytical dead end. In actual practice, however, the quantities $\{\rho_i\}$ $(i = 1, \ldots m)$ are random variables since there may be considerable year-to-year variation in the time profile of the run. Such temporal variation may be of considerable importance in Bristol Bay because of the large magnitude of the run and its short duration.

It has been suggested (O. A. Mathisen, pers. commun. and others) that the probability density of N is most appropriately conditional upon the catch-per-unit-effort (CPUE) observed during the course of the run. In so doing one can remove the explicit dependence of (α_k, β_k) on $\{\rho_i\}$ $(i = 1, \ldots k)$. An implicit dependence remains, however, since the CPUE will be a function of the run fractions. One can formally bypass this dependence, however, by relating the density of N directly to the CPUE. In so doing one can then introduce temporal variability in the set $\{\rho_i\}$ $(i = 1, \ldots m)$ and in evaluating the Bayes risk an additional expectation with respect to the density of these random variables must be taken.

An almost ideal probability density to describe the run fractions is the Dirichlet density defined by

$$h(\rho_1,\rho_2,\ldots\rho_m) = \frac{\Gamma(\gamma_1+\gamma_2+\ldots+\gamma_m)}{\Gamma(\gamma_1)\Gamma(\gamma_2)\ldots\Gamma(\gamma_m)}\,\rho_1^{\gamma_1-1}\,\rho_2^{\gamma_2-1}\ldots\rho_m^{\gamma_m-1} \qquad (19)$$

where $\rho_i \geq 0$ for all i. As written this density is singular since the variates must satisfy the side condition $\sum_{i=1}^{m}\rho_i = 1$. The choice of the parameters $(\gamma_1, \gamma_2, \ldots \gamma_m)$ then permits the specification of any m of the means, variances, and covariances of the $\{\rho_i\}$ $(i = 1, \ldots m)$. If Equation (19) is substituted in Equation (16) the integrations with respect to N and $(\hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_m)$ may be done as before. The remaining integrals over $(\rho_1, \rho_2, \ldots \rho_m)$ are all Dirichlet integrals (Wilks 1962:177, et seq.) for which the values are readily determined. The resulting Bayes risk for this case may then be shown to be given by

$$R_k(\delta_1,\delta_2,\ldots\delta_m\,|\,\text{CPUE})$$

$$= L'(E_0,E_{n-1},\ldots E_{n-K}) + \frac{a\alpha_{k-1}}{G\beta_{k-1}}\sum_{i=1}^{m}\frac{\nu_i\gamma_i}{\nu_i+\mu_i}$$

$$-\frac{a}{\beta_{k-1}}\sum_{n=0}^{\infty}\left(-\frac{b}{\beta_{k-1}}\right)^n\frac{\Gamma(\alpha_{k-1}+n+1)}{\Gamma(\alpha_{k-1})\,\Gamma(G+n+1)}$$

$$\sum_{\substack{k_i=0\\ \Sigma k_i=n}}^{n}\binom{n}{k_1k_2\ldots k_m}$$

$$\cdot\prod_{i=1}^{m}\frac{\Gamma(\nu_i+k_i)\,\Gamma(\nu_i+\mu_i)\,\Gamma(\gamma_i+k_i)}{\Gamma(\nu_i)\,\Gamma(\nu_i+\mu_i+k_i)\,\Gamma(\gamma_i)}$$

$$\sum_{j=1}^{m}\frac{(\gamma_j+k_j)(\nu_j+k_j)}{\nu_j+\mu_j+k_j} \qquad (20)$$

where $G = \sum_{i=1}^{m}\gamma_i$.

Equations (18) and (20) are somewhat intimidating, particularly if one were to attempt to infer the qualitative behavior of the system as the parameters descriptive of the fishery and its management are varied. Indeed, Equations (18) and (20) are virtually useless for this purpose with the exception of the determination of certain

limiting behavior as the appropriate parameters assume their extreme values. However, Equations (18) and (20) do have the virtue that, in closed form, the most crucial features of the fishery dynamics and statistics are accommodated in a quantitative and, hopefully, reasonably accurate fashion.

A NUMERICAL EXAMPLE

The foregoing mathematical model was applied to the simulated management of the Wood River system of Bristol Bay. It should be emphasized at the outset, however, that the assumptions, methods, and results presented here should in no way be construed as representing a management scheme preferable to those currently in use. The Wood River was chosen simply because, based on Mathews' (1966) data, it seemed to follow the Ricker spawner-return curve reasonably well.

In the example considered here, the model was limited to a fishing season of five time periods during each of which a choice of two management decisions was possible. This limitation was necessary to avoid inordinately lengthy calculations. Ricker parameter values of $a = 4.077$ and $b = 0.8 \times 10^{-6}$, which were used by Mathews, were used here. The return was assumed to consist of only the progeny of a single spawning group K years prior where K is arbitrary, i.e.,

$$p_i = \begin{cases} 1 & i = K \\ 0 & i \neq K \end{cases}.$$

All prior escapements were assumed to be the optimum escapement E_0 so that the loss function given by Equation (5) becomes

$$L_n = (aE_0e^{-bE_0} - E_0) - (aE_ne^{-bE_n} - E_n).$$

For the above values of the Ricker parameters, the MSY escapement is given by $E_0 = 709{,}000$. The expected value and standard deviation of a $\Gamma(\alpha_0, \beta_0)$ variate are given by α_0/β_0 and $\alpha_0^{1/2}/\beta_0$, respectively. In terms of the Ricker parameters, the expected run size is given by $aE_0 \exp(-bE_0)$ which determines the ratio $\alpha_0/\beta_0 = 1.64 \times 10^6$. An initial (i.e., preseason) standard deviation of one-half the expected run size was assumed. In terms of the gamma parameters this gives $\alpha_0^{1/2}/\beta_0 = \alpha_0/2\beta_0$ or $\alpha_0 = 4.0$ and $\beta_0 = 2.44 \times 10^{-6}$. The two management strategies assumed were complete closure (option 2) and one level of opening (option 1). In terms of the beta parameters, closure is simulated merely by setting $\mu_2 = 0$ with an arbitrary positive value for ν_2. During fishery opening it was assumed that an average of 80% of the available fish are caught with a standard deviation of 0.25. This gives $(\nu_1, \mu_1) = (0.312, 1.248)$ as the appropriate beta parameters. The set of run fractions $\{\rho_i\}$ $(i = 1, \ldots 5)$ was determined from the time profile proposed by Royce (1965). Values of 0.156, 0.282, 0.348, 0.160, and 0.054, using five equal length time intervals, were obtained. No attempt was made to treat the run fractions as random variables. All of the parameter values were chosen to reflect reasonably well the known behavior of the system.

The fishery dynamics were treated by two distinct methods. The first method utilized the gamma prior density for N with a Poisson sampling density thus, through conjugacy, giving a gamma posterior density. A gamma posterior distribution was also assumed in the second method but the posterior gamma parameters were back-calculated after introducing prescribed stage-to-stage trends in the population mean and standard deviation.

The Bayes risk at each stage was computed for each of the $2^5 = 32$ total possible sequences of decisions, past, present, and future; i.e., no attempt was made to formulate and solve the functional equation associated with dynamic programming.[5] While relatively unsophisticated, this approach does permit one to use hindsight to determine, ex post facto, what an optimum previous strategy would have been, given the information currently available. In real life, of course, "what might have been" is irrelevant in the management of a dynamic system—one must optimize the system as it exists in real time in accordance with the principal of optimality, the relevant homily for which might well be "what's past is prologue."

The numerical results are summarized in Tables 1 to 3. Tables 1 and 2 give the optimum strategies and corresponding minimum Bayes risks for a gamma prior run size distribution with simulated

[5]Subsequent to the submission of this paper, C. J. Walters (1975) published a paper in which the ideas of dynamic programming were applied to the optimum year to year management of a salmon fishery. His work is of considerable interest, particularly since he managed to impose the principle of optimality and carry out the backward recursive scheme proposed by Bellman (1957). It remains to be seen if this method can be applied to the decision theoretic model presented here, but I am no longer as pessimistic as I formerly was.

TABLE 1.—Optimum strategies and minimum Bayes risks for a five-period, two-decision fishery with a sampling fraction $\epsilon = 1 \times 10^{-3}$.

Time period (i)	1	2	3	4	5
Run fraction (ρ_i)	0.156	0.282	0.348	0.160	0.054
Poisson parameter (λ_i)	256	462	570	262	—
$y_i = \lambda_i$					
Simulated samples (y_i)	256	462	570	262	—
Optimum strategy	open	open	close	open	open
Minimum Bayes risk	1.80×10^5	3.49×10^4	3.33×10^4	3.29×10^4	3.28×10^4
$y_i = 2\lambda_i$					
Simulated samples (y_i)	512	924	1,140	564	—
Optimum strategy	open	open	open	open	close
Minimum Bayes risk	1.80×10^5	1.89×10^5	1.70×10^5	1.90×10^5	1.90×10^5
$y_i = \frac{1}{2}\lambda_i$					
Simulated samples (y_i)	128	231	285	131	—
Optimum strategy	open	close	close	close	close
Minimum Bayes risk	1.80×10^5	6.90×10^3	3.35×10^3	2.48×10^3	2.29×10^3

TABLE 2.—Optimum strategies and minimum Bayes risks for a five-period, two-decision fishery with a sampling fraction $\epsilon = 1 \times 10^{-4}$.

Time period (i)	1	2	3	4	5
Run fraction (ρ_i)	0.156	0.282	0.348	0.160	0.054
Poisson parameter (λ_i)	26	46	57	26	—
$y_i = \lambda_i$					
Simulated samples (y_i)	26	46	57	26	—
Optimum strategy	open	close	open	open	open
Minimum Bayes risk	1.80×10^5	5.86×10^4	4.55×10^4	4.19×10^4	4.11×10^4
$y_i = 2\lambda_i$					
Simulated samples (y_i)	52	92	114	52	—
Optimum strategy	open	open	open	open	close
Minimum Bayes risk	1.80×10^5	1.86×10^5	1.87×10^5	1.89×10^5	1.88×10^5
$y_i = \frac{1}{2}\lambda_i$					
Simulated samples (y_i)	13	23	29	13	—
Optimum strategy	open	close	close	close	open
Minimum Bayes risk	1.80×10^5	4.14×10^4	1.85×10^4	1.12×10^4	9.65×10^3

TABLE 3.—Optimum strategies and minimum Bayes risks for a five-period, two-decision fishery with linear stage-to-stage trends in the expected run size and the run size standard deviation with preseason parameters $\alpha_0 = 4.0$ and $\beta_0 = 2.44 \times 10^{-6}$.

Time period (i)	1	2	3	4	5
Run fraction (ρ_i)	0.156	0.282	0.348	0.160	0.054
Constant expected run size:					
$\alpha_{i-1} / \beta_{i-1}$	1.64×10^6	1.64×10^6	1.64×10^6	1.64×10^6	1.64×10^6
$\sqrt{\alpha_{i-1}} / \beta_{i-1}$	8.20×10^5	6.89×10^5	5.57×10^5	4.26×10^5	2.95×10^5
Optimum strategy	open	close	open	open	open
Minimum Bayes risk	1.80×10^5	1.41×10^5	1.07×10^5	7.87×10^4	5.74×10^4
Increasing expected run size:					
$\alpha_{i-1} / \beta_{i-1}$	1.64×10^6	1.97×10^7	2.30×10^6	2.63×10^6	2.95×10^6
$\sqrt{\alpha_{i-1}} / \beta_{i-1}$	8.20×10^5	6.89×10^5	5.57×10^5	4.26×10^5	2.95×10^5
Optimum strategy	open	open	open	close	open
Minimum Bayes risk	1.80×10^5	1.40×10^5	1.26×10^5	1.43×10^5	1.90×10^5
Decreasing expected run size:					
$\alpha_{i-1} / \beta_{i-1}$	1.64×10^6	1.48×10^6	1.31×10^6	1.15×10^6	9.84×10^5
$\sqrt{\alpha_{i-1}} / \beta_{i-1}$	8.20×10^5	6.89×10^5	5.57×10^5	4.26×10^5	2.95×10^5
Optimum strategy	open	open	close	close	close
Minimum Bayes risk	1.80×10^5	1.52×10^5	1.25×10^5	9.57×10^4	6.68×10^4

Poisson sampling. The sampling was intended to simulate actual run sizes equal to, greater than, or less than the preseason estimate of the run size, α_0/β_0. The Poisson sampling was done by brute force in which sample values exactly equal to the desired expected values were chosen. For example, to simulate an actual run size twice that based on the preseason parameters we choose $y_i = 2\lambda_i$ where $\lambda_i = \epsilon\rho_i\ \alpha_0/\beta_0$ is the Poisson parameter for the ith period obtained from the preseason parameters. The deterministic samples (which is really a contradiction in terms) permit one to elicit the response of the system to specified input stimuli.

The Bayes risks are all in units of numbers of fish. The optimum strategy is that strategy which

minimizes the Bayes risk given that all prior decisions were optimum for the time periods in which they were made. In other words, the "hindsight" feature was not utilized to "improve" a past decision—once made any decision is retained through all subsequent stages.

The mathematical machinery developed generally gives intuitively reasonable results. Specifically, the tendency toward larger or smaller run sizes results in optimum strategies that tend successively toward more or fewer open periods respectively. The Bayes risk generally, but not always, decreases as the season progresses, largely reflecting the decreasing variances in the estimates of the run size. Increases in the Bayes risk can usually be attributed to past decisions that, in the light of subsequent sampling, are no longer optimum thus requiring corrective action.

CONCLUSIONS

The mathematical models assumed and developed here for the objective management of a typical salmon fishery, as previously noted, are based on quite specific functional forms and thus represent somewhat of an idealized situation. However, these functions were chosen to reflect the behavior of the system insofar as the knowledge of such behavior is available. Indeed, the acquisition of such detailed knowledge is an important area of current research and subsequent refinements of the statistics will be possible as more data are gathered.

Of more concern than the accuracy of the fine-scale mathematical behavior of the system is the appropriateness of the basic mathematical theory upon which the models are built. I feel that statistical decision theory is a most natural framework on which to base an objective management model. The nomenclature lends support to this view. For example, the equivalence of a management decision and a statistical decision is obvious.[6] The term risk, in the economic if not the strict Bayesian sense, is frequently used in discussions of fishery management. Finally, Bayes theorem provides a convenient and theoretically appropriate method for accommodating the combined data acquisition and dynamics of the fishery.

[6]This equivalence is not always evident even within decision theory itself. For example, it requires a slight mental contortion to treat statistical estimation as an application of decision theory as the statisticians have done.

Advantage has been taken of some powerful analytical tools to characterize salmon fishery management. However, any enthusiasm for these quite contemporary methods should be tempered somewhat by consideration of some of the specific practical difficulties likely to be encountered. One of these, mentioned in Lord (1973), is the difficulty associated with multistage dynamic processes. While the fishery management problem under discussion falls very naturally into a class of stochastic dynamic programs it is not yet obvious whether the functional equation arising from the imposition of the principal of optimality can be formulated or solved in a useful fashion. The calculations done here were more of the brute force variety in which all strategy combinations, optimal or not, were considered. In other words, the backward recurrence scheme central to dynamic programming was not used to reduce the total number of possible strategies to be considered. In so doing, the "Curse of Dimensionality," about which Bellman (1957:6) so aptly warned, proved to be a limiting condition. To evaluate completely the five-stage, two-decision fishery considered here required from 10 to 15 min of Control Data Corporation[7] 6400 central processor time for each set of input parameters. This is not a trivial numerical effort and should give one pause when considering more elaborate models.

In conclusion I feel that advantage should be taken of the appropriate analytical tools as they are made available by the mathematicians or, at the very least, such tools should be investigated. However, the availability of such methods in no way indicates their eventual practicality for any specific problem. For this careful additional investigation is necessary.

LITERATURE CITED

BELLMAN, R.
1957. Dynamic programming. Princeton Univ. Press, 340 p.

BIERENS DE HAAN, D.
1939. Nouvelles tables d'intégrules définies. G. E. Stechert & Co., 716 p.

DEGROOT, M. H.
1970. Optimal statistical decisions. McGraw-Hill Book Co., Inc., 489 p.

LORD, G. E.
1973. Characterization of the optimum data acquisition and management of a salmon fishery as a stochastic dynamic program. Fish. Bull., U.S. 71:1029-1037.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

MATHEWS, S. B.
1966. The economic consequences of forecasting sockeye salmon (*Oncorhynchus nerka*, Walbaum) runs to Bristol Bay, Alaska: A computer simulation study of the potential benefits to a salmon canning industry from accurate forecasts of the runs. Ph.D. Thesis, Univ. Washington, Seattle, 238 p.

ROTHSCHILD, B. J., AND J. W. BALSIGER.
1971. A linear-programming solution to salmon management. Fish. Bull., U.S. 69:117-140.

ROYCE, W. F.
1965. Almanac of Bristol Bay sockeye salmon. Univ. Wash. Fish. Res. Inst. Circ. 235, 48 p.

WALTERS, C. J.
1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. J. Fish. Res. Board Can. 32:1777-1784.

WILKS, S. S.
1962. Mathematical statistics. John Wiley & Sons, Inc., N.Y., 644 p.

DIEL CHANGES IN SWIM BLADDER INFLATION OF THE LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

Laboratory and field studies demonstrated that larval anchovy 10 mm standard length and larger inflate their swim bladders each night and deflate them in the day. Maximum night levels of inflation were attained 2 h after the onset of dark and typical day levels occurred about 2 h after the onset of light. Laboratory experiments indicated that larvae fill their bladders at night by swallowing air at the water surface and the vertical distribution of sea-caught larvae suggested that they migrate to the surface each night to fill their swim bladders. Gas is released by passing bubbles through the pneumatic duct into the alimentary canal. The diel rhythm of inflation was viewed as an energy sparing mechanism. Measurements of sinking speed of larvae with and without inflated bladders suggested that the energy saved at night by inflation of the swim bladder would exceed the cost of vertical migration to the surface and that the migratory range over which energy savings are possible would be greater as larvae increased in length.

Northern anchovy, *Engraulis mordax* Girard, are more vulnerable to starvation in the larval stage than at any other time of life, consequently, energy sparing mechanisms may be critical to their survival. In a recent paper Uotani (1973) showed that the larvae of several clupeoid fishes, *Engraulis japonicus* (Houttuyn), *Sardinops melanosticta* (Temminck and Schlegel), and *Etrumeus teres* (DeKay) have expanded swim bladders when captured at night in the sea and deflated ones when captured during the day. Energy conservation is certainly one of the possible adaptive advantages of such behavior, but the energy saved must be evaluated in terms of the energy cost of daily filling the bladder. This requires that the mechanism of filling be known. The object of the present study was to determine if the larvae of the northern anchovy display a similar rhythm and to evaluate this behavior as a possible energy sparing mechanism.

The swim bladder in adult northern anchovy is a tubular vesicle that extends the length of the body cavity. It is connected to the alimentary canal by a pneumatic duct which originates from the dorsal wall of the cardiac stomach; no anal duct exists as it does in some clupeoids (O'Connell 1955). Two tubules on each side of the body extend from the anterior end of the bladder into the cranium where they expand into two pairs of capsules, termed prootic and pterotic bullae (O'Connell 1955). The swim bladder of the larva is basically similar to that of the adult. At the time of initial filling of the swim bladder, the pneumatic duct is functional and the bullae become filled with gas. No histological evidence exists for gas secretion in adult *E. mordax* nor for the larvae (O'Connell 1955, and pers. commun.).

The swim bladder is deflated by passing gas bubbles through the pneumatic duct into the alimentary canal and out the anus. On a number of occasions we have observed this process while examining a live anchovy larva under a dissection microscope. We have also captured larvae with deflated swim bladders that had gas bubbles in the alimentary canal.

METHODS

Fertilized anchovy eggs were obtained from a captive population of adults maintained in spawning condition in the laboratory (Leong 1971) and the larvae were reared using the techniques, foods, and tanks described by Hunter (1976). The larvae were reared at temperatures of 16.5° ± 0.2°C and 16.9° ± 0.9°C. A 12-h photoperiod was used without a dawn or dusk transition in light intensity. Incident light at the surface was about 2,000 lx in the day and at night no light was provided in the closed room which contained the rearing tanks.

Larvae reared in the laboratory were sampled at

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various times of day commencing at age 1 day to determine if a daily rhythm of inflation existed and to determine the larval length at which the swim bladder was inflated. Samples of preserved specimens from California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collections were also examined to determine if differences existed in swim bladder inflation in sea-caught specimens.

The standard length was measured to the nearest 0.1 mm and the maximum width and length of the swim bladder to the nearest 0.02 mm. The volume of the swim bladder was calculated by using the equation for a prolate spheroid, $V = 4/3\pi ab^2$, where a is half the maximum bladder length and b is half the maximum width. For larvae 16 mm and larger, the calculated swim bladder volume may be converted to actual gas volume by multiplying it by the coefficient 0.82 (Figure 1). This conversion is based on data obtained while measuring the composition of swim bladder gas. The larvae used in that experiment were larger (mean length 15.6 to 29.6 mm) than most of the larvae in the rest of the experiments. For this reason we have used the calculated swim bladder volume in all computations.

We also sampled larvae reared in the laboratory to determine the effect of swim bladder development and swim bladder inflation on sinking rate. The method of Blaxter and Ehrlich (1974) was used to measure sinking rates of larvae. Larvae anesthetized in MS 222[2] were measured and added to a 1-liter graduated cylinder without contact with the air. The larvae were allowed to sink a few centimeters, then the rate of descent was timed with a stopwatch for a distance of 7 to 35 cm. Only one measurement was made per larva and larvae were reexamined after the test to determine if they were still alive (dead larvae sank faster than live ones) and if any gas had been lost from their bladders. Fresh seawater was used in the graduated cylinder for each day's run and the specific gravity and temperature of the seawater were measured before each larva was tested. The specific gravity averaged 1.0262 and ranged from 1.0259 to 1.0266. The graduated cylinder was immersed in a temperature-controlled water bath which was maintained within 1°C of the rearing temperature. One rearing group was tested at 15.9° ± 0.2°C and another at 18.0° ± 0.1°C. In the Results section we have combined the data from these two rearing groups because covariance analysis indicated that the differences in sinking speed when adjusted for swim bladder volume and larval length were not significant.

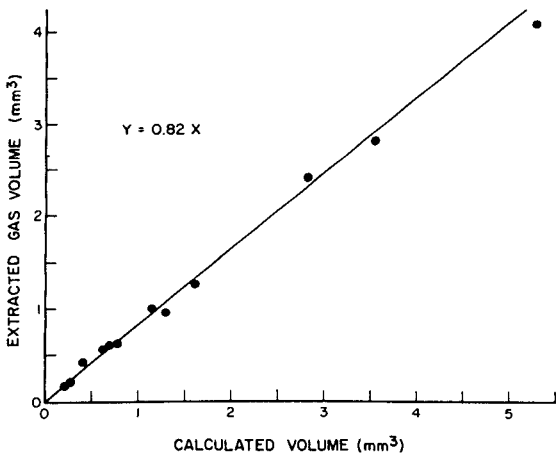

FIGURE 1.—Relation between the volume of the swim bladder calculated from the equation $V = 4/3\,\pi\,ab^2$ and the actual volume of gas extracted from the swim bladder for northern anchovy larvae of mean length 15.6 to 29.6 mm. Each point is the mean volume of the swim bladder calculated for a sample of two to eight larvae taken at night and the average volume of gas extracted from that sample. Sample means were weighted by their variances to calculate the regression line; intercept for line did not differ from 0; and the standard error of line was 0.0428.

To determine if anchovy larvae filled the swim bladder by gulping air at the water surface, the following experiment was performed. Commencing 4 h after the onset of dark, larvae in a 400-liter rearing tank were sampled and the lengths and dimensions of the swim bladder of each larva in the sample measured. Just before the onset of dark on the following day, the surface of the tank was sealed with a 0.5-cm layer of mineral oil. A second sample was taken commencing at 2400 h, 4 h after the onset of dark and ending just before the beginning of light at 0800. A third sampling was taken of larvae in the sealed tank during the day beginning at 1000 h, 2 h after the onset of light, and ending at 1400.

The gas content of the swim bladders of laboratory-reared larvae captured in the dark was analyzed using the micro gasometric method and apparatus described by Scholander et al. (1955). Swim bladders were dissected from the larvae in acid citrate solution, removed with a Pasteur pipette, and injected into an acid citrate filled capillary tube sealed at one end. After two to eight

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

swim bladders had been collected, they were macerated in the tube and the gas withdrawn with a Pasteur pipette and inserted into the syringe gas analyzer (Scholander et al. 1955). In the analyzer, the carbon dioxide was absorbed with alkaline citrate, oxygen by pyrogallol, and the volume of gas determined before and after each treatment. The remaining gas was considered to be nitrogen. The volume of gas was read under a dissecting microscope using an optical micrometer. Reading error was about ±0.09 μl or from 1 to 2% depending on the volume of the sample.

RESULTS

Diel Rhythm in Swim Bladder Inflation

The volume of the swim bladder of larvae captured at night in the sea was greater than that of larvae collected in the day (Table 1). Similarly, the volume of the swim bladder of larvae reared in the laboratory was greater at night than in the day. To illustrate these daily changes for laboratory-reared larvae, the mean volume of the swim bladder for 2-h intervals was calculated for each of three length classes (10.0 to 11.9 mm, N = 121; 12.0 to 13.9 mm, N = 202; 14.0 to 15.9 mm, N = 129). No evidence existed for anticipation of the onset of dark at 2200 h nor for the onset of light at 1000 h (Figure 2). In all three length classes the mean volume did not return to the daytime level until about 2 h after the onset of light nor did they reach the maximum at night until about 2 h after the onset of dark.

The swim bladder of larvae at night was frequently so inflated that it constricted the gut (see fig. 8 in Uotani 1973). Larvae in the dark with filled swim bladders were motionless or slowly sinking. The body was oriented head down at an oblique angle to the water surface. After sinking a short distance, the larvae swam back to the water surface, a behavior closely resembling that of yolk-sac larvae (Hunter 1972).

TABLE 1.–Swim bladder volume (mm³) of preserved northern anchovy larvae from standard CalCOFI oblique plankton tows taken at night and in the day in southern California inshore waters.

Length class (mm)	Night samples N	Night samples Swim bladder vol (mean ± 2 SE)	Day samples N	Day samples Swim bladder vol (mean ± 2 SE)
11.0-11.9	23	0.044 ± 0.007	28	0.018 ± 0.008
12.0-12.9	20	0.073 ± 0.015	30	0.015 ± 0.004
13.0-13.9	24	0.124 ± 0.011	17	0.030 ± 0.016
14.0-14.9	14	0.128 ± 0.011	6	0.029 ± 0.003

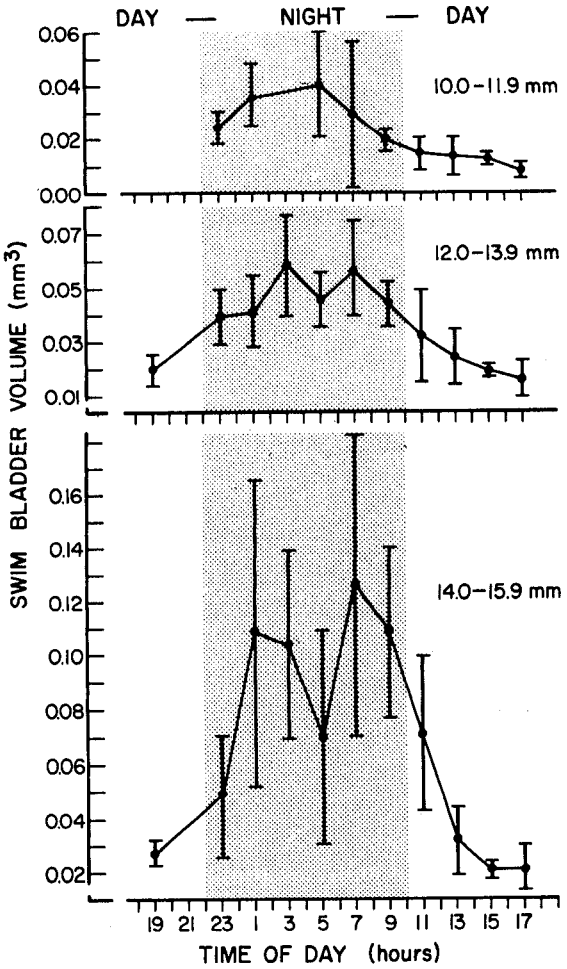

FIGURE 2.–Mean swim bladder volume ± 2 SE of mean for 2-h class intervals plotted at midpoint of each 2-h class. Data shown for three length classes of laboratory-reared northern anchovy larvae; the onset of dark was at 2200 h and onset of light at 1000 h. No transitional level of illumination existed between night and day.

Specimens with obviously inflated swim bladders occurred occasionally in day samples from the sea and laboratory but these were only a few percent of the larvae examined if the first 2 h after the onset of light are excluded. On the other hand, the occurrence of larvae with deflated bladders at night was more common. About 10% of the wild larvae and 20% of the laboratory-reared (12.0 to 12.9 mm) larvae had swim bladder volumes at night comparable to those in the day (Figure 3). The proportion of larvae with deflated bladders at night decreased with larval length.

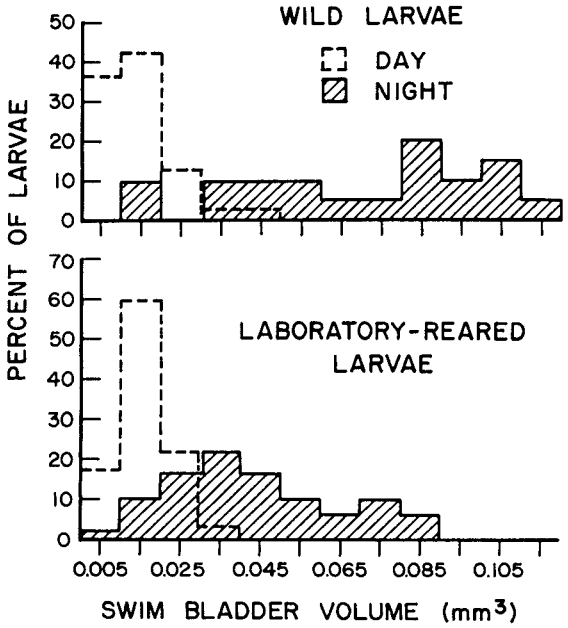

FIGURE 3.–Percent of northern anchovy larvae, 11.9 to 12.0 mm, at night (solid bars) and in day (dashed bars) having swim bladder volumes in various 0.01-mm³ classes; numbers on abscissa are midpoints of swim bladder volume classes. Upper panel, larvae from CalCOFI ichthyoplankton collections (preserved specimen length), $N = 20$ for night, and $N = 30$ for day. Lower panel, larvae reared in laboratory (live specimen length), $N = 49$ for night, and $N = 29$ for day. Data from 2-h after onset of dark and 2-h after onset of light were excluded in laboratory-reared larvae.

The mean swim bladder volume at night was greater for wild than for laboratory-reared larvae of the same length. The effect of preservation on larval length for larvae of this size is not known but a shrinkage of about 10% in length in the Formalin-preserved ichthyoplankton specimens would account for this difference. The effect of preservation on swim bladder volume is also unknown. In some of the preserved specimens, we noticed the bladder was filled with fluid but we did not routinely make an examination of the bladder contents.

Swim Bladder Inflation and Larval Length

The swim bladder was fully formed when larvae reached 8 to 9 mm but it usually was not inflated. To determine the larval size at which nightly inflation commenced, night and day samples from the laboratory were grouped into 1-mm length classes (9.0 to 9.9 mm, 10.0 to 10.9 mm, etc.), and the mean volume for day and night samples for each class calculated, and compared using the t test. The first 2 h after the onset of dark and the onset of light were excluded from the classes.

Some of the 9.0 to 9.9 mm larvae appeared to have inflated swim bladders at night but the night-day difference in swim bladder volume was not significant ($0.2>P>0.1$). Mean volumes for day and night samples were different in larvae 10.0 to 10.9 mm as were those for larvae in all succeeding length classes ($P<0.001$). Thus, the threshold larval length for nightly inflation of the swim bladder occurred at about 10 mm, the point at which the means for day and night volumes diverge (Figure 4).[3] From this point, mean volume of night samples increased exponentially with length whereas that for day samples increased linearly.

Relation Between Sinking Speed, Swim Bladder Volume, and Larval Length

We observed that larvae with inflated bladders sank more slowly than those with uninflated

[3]Swim bladder inflation is reported to occur at 7 mm in *E. japonicus* (Uotani 1973). Comparison of his illustrations to those of Uchida et al. (1958) suggests Uotani's reported lengths are in error and that *E. japonicus* also inflates the bladder at about 10 mm.

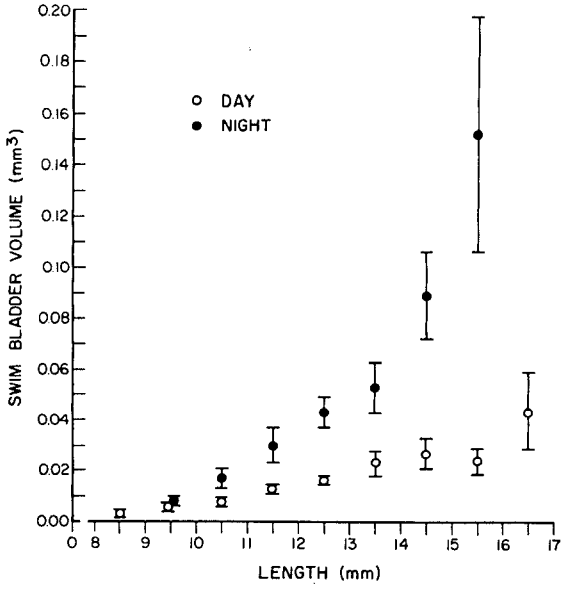

FIGURE 4.–Mean swim bladder volume ± 2 SE for laboratory-reared northern anchovy larvae for 1-mm classes of length plotted at the midpoint of each class. Solid circles are night (first 2-h after onset of dark omitted) and open circles day (first 2-h after onset of light omitted).

bladders. At night, larvae were occasionally neutrally buoyant but most were slightly negatively buoyant.

To develop an equation for expressing sinking speed in terms of larval length and swim bladder volume, the data on sinking speeds were grouped into four classes of larval length: 10.0 to 11.9 mm, $N = 30$; 12.0 to 13.9 mm, $N = 41$; 14.0 to 15.9 mm, $N = 54$; and 16.0 to 17.9 mm, $N = 14$. A regression of sinking speed on swim bladder volume for each length class yielded the following slopes and standard errors for the regression lines: -3.040, SE = 2.339; -4.001, SE = 1.297; -4.8796, SE = 0.616; and -5.070, SE = 1.680, respectively. Covariance analysis of these data indicated that the slopes were not different whereas the intercepts for the regression lines were statistically different ($P = 0.01$). Since no difference existed in the slopes among the four groups, the common slope from the covariance analysis, -4.769, SE = 0.487, was used to express the relation between sinking rate and swim bladder volume for each length class (Figure 5, lower panel). When adjusted for the common slope, the sinking rate intercepts of the four regression lines showed a precise linear relationship when plotted against the midpoints of their respective length classes (Figure 5, upper panel). The equation for the intercept-length relationship was $y = 0.18L - 1.51$ where L is larval length (the midpoints of the larval length classes) and y is the intercept for the regression of sinking rate on swim bladder volume (the sinking rate at $V = 0$ in Figure 5). This equation was combined with the common slope to provide the equation given below:

$$S = 0.18L - 1.51 - 4.77V$$

where S = sinking speed in centimeters per second
L = larval length in millimeters
V = swim bladder volume (outside dimensions) in cubic millimeters.

We examined the changes in sinking speed of larvae from the time of hatching through the development of the swim bladder. These changes are of interest because they illustrate the timing of swim bladder development, its effect on buoyancy, and the advantage of a nightly inflation cycle. Data for sinking rates for larvae 4.0 to 9.9 mm were grouped into 1-mm classes and the means plotted at the midpoints of the class intervals except for the yolk-sac larvae (3.7 mm) which were all about the same length. For larvae 10.0 mm or larger, we calculated sinking speeds from the mean swim bladder volume given in Figure 4 using the equation given in the preceding paragraph.

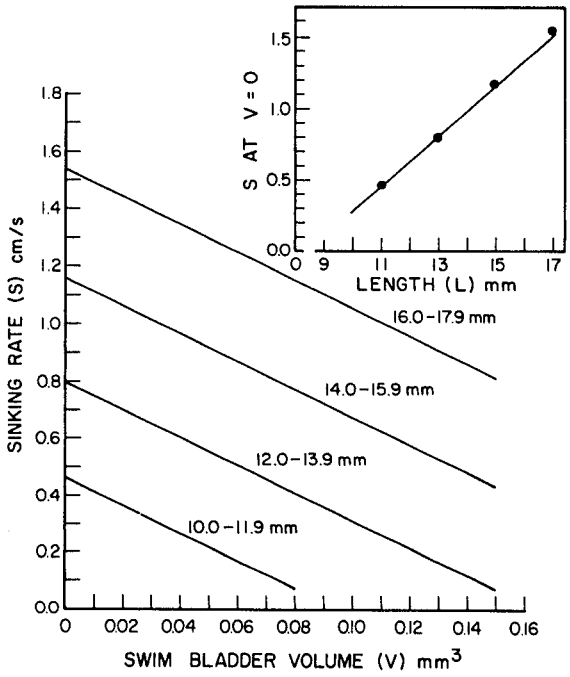

FIGURE 5.—The relation in larval northern anchovy between sinking speed (S), swim bladder volume (V), and larval length (L). Lower panel, regression lines show relation between sinking speed and swim bladder volume for the four classes of larval length indicated in the figure, when a common slope of -4.769 is used (see text). Upper panel, the regression of the y intercepts (S at $V = 0$) of the four regression lines on larval length (midpoints of the four length classes); equation for intercept line was $y = 0.18L - 1.51$. Final equation is $S = 0.18L - 1.51 - 4.77V$.

Sinking speed increased exponentially with length, when larvae sampled at night are excluded (Figure 6). The increase is roughly proportional to the cube of the length (curved line in Figure 6). This might be expected since sinking speed is dependent upon buoyancy which varies with the volume (L^3) and the difference in specific gravity between the fish and its medium. For estimating mean sinking speed for larvae with swim bladders in the day, or for those without swim bladders the equation $S = 0.094 + 0.000264L^3$ where L is length in millimeters and S is sinking speed in centimeters per second, gives a good fit to the data.

The length threshold for filling the swim bladder (about 10 mm) coincides with a rapid acceleration

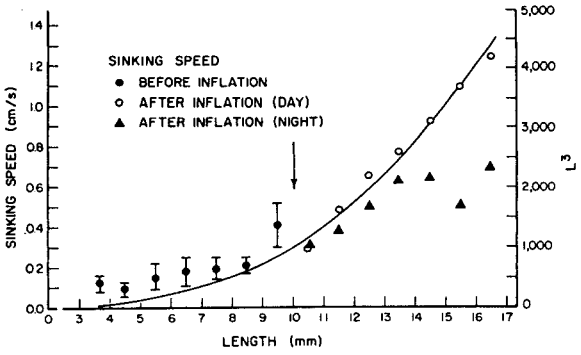

FIGURE 6.—Change in sinking speed from hatching through threshold of the initial inflation of swim bladder (arrow) of northern anchovy larvae. For larvae <10 mm, mean sinking speed ± 2 SE were plotted against the midpoint of 1-mm length classes, except for the first point which was for yolk-sac larvae and is plotted at average length for the class. For larvae >10 mm, sinking rates are estimated from the mean swim bladder volume given in Figure 3 using the general equation for sinking speed given in Figure 5. Open circles are estimates for the day and solid triangles for the night. Line is the cube of the length (L^3) plotted against length.

in the volume of the larva and its sinking speed. Thus, the timing of the swim bladder inflation may be related to these events.

The effect of night inflation of the swim bladder is also illustrated in Figure 6. For larvae 12 mm and larger, the average sinking speed at night appears to be relatively constant at about 0.6 ± 0.1 cm/s (22 m/h) while the sinking speed in the day increased exponentially with length. A larva 16.5 mm long had a sinking speed at night nearly half that of the day. Swimming speeds of larval anchovy while searching for food in the day, range from about 0.6 to 1.0 body length/s (Hunter in press). If a larva did not inflate the swim bladder at night, the swimming required just to maintain a position in the water would be equivalent to that used in the search for food in the day. Since larvae do not feed at night, filling the swim bladder would clearly be advantageous as an energy conserving mechanism.

Mechanism of Swim Bladder Inflation

It was not possible to determine if larvae in the tank sealed with mineral oil swam just below the layer of oil or into it because our view was from above rather than from the side. However, the mean swim bladder volume for larvae sampled at night in the sealed tank was less than that for larvae sampled on the previous night when the tank was not sealed (*t* test, $P = 0.001$, Table 2). The mean volumes of the swim bladders for larvae in the day and at night in the sealed tank were not different. This experiment suggests that anchovy larvae in the laboratory fill their swim bladders by swallowing air at the surface.

TABLE 2.—Mean swim bladder volume and mean length of northern anchovy larvae in sealed and unsealed containers.

Treatment	*N*	Mean length of larvae (mm ± 2 SE)	Mean swim bladder vol (mm³ ± 2 SE)
Unsealed tank:			
Night	12	13.9 ± 0.37	0.094 ± 0.037
Sealed tank:			
Night	18	14.1 ± 0.41	0.035 ± 0.008
Day	17	13.8 ± 0.86	0.026 ± 0.019

An analysis of the oxygen content of the swim bladder could suggest whether or not the gas in the swim bladder was secreted or taken from the air. Newly secreted gas would be expected to be oxygen (Wittenberg 1958), but if larvae were swallowing air the concentration should be about 21% oxygen. Our analysis did not agree with either pattern even though some measurements were made 30 min after the onset of dark. Samples averaged about 11% oxygen, consistently less than the atmospheric concentration (Table 3). Carbon dioxide levels (0.9 to 2.2%) were higher than atmospheric levels but little can be concluded because our experimental reading error was 1 to 2% owing to the small volumes used. It is probable that oxygen was lower than atmospheric concentration because it was absorbed from the bladder by the larva. Except for the first two observations in Table 3, oxygen concentration tended to decrease with time from the onset of dark. It should be noted that preferential removal of oxygen from swim bladder gases is not unique to anchovy larvae but is found in most fishes which have been studied (Wittenberg 1958).

The rate at which the swim bladder was filled also suggests that the filling is accomplished by gulping air. Larvae with filled swim bladders were captured 20 to 30 min after the onset of dark and the means were at a maximum by 2 h after dark. Uotani (1973) reported for *E. japonicus* that filling was completed by 1 h in the sea. Fishes that fill the swim bladder by secretion require much more time to fill the bladder, for example, *Stenotomus versicolor* (Mitchill) requires 10 to 12 h; *Anguilla rostrata* (LeSueur), 12 to 24 h; *Opsanus tau* (Linnaeus), *Prionotus carolinus* (Linnaeus), and *P. evolans* (Linnaeus), 24 h; and *Tautoga onitis*

TABLE 3.—Percent composition of swim bladder gas of laboratory-reared northern anchovy larvae sampled at night, listed in order of time of sampling.

Elapsed time after onset of darkness (h)	(min)	Number of larvae	Mean larval length (mm)	Composition of swim bladder gas (%) CO_2	O_2	N_2	Sample volume (μl)	Oxygen in tank (ml/liter)
0	30	2	27.1	1.2	9.6	89.2	5.54	5.4
0	30	2	29.6	1.6	8.2	90.2	8.12	—
0	50	4	22.1	1.3	14.2	84.5	4.99	5.7
3	15	5	21.0	1.8	13.1	85.0	6.08	5.0
4	20	3	25.3	2.2	11.1	86.7	7.18	5.1
6	25	8	19.3	0.9	12.7	86.4	4.85	4.6
6	25	7	18.9	0.6	12.6	86.9	4.05	5.0
7	35	6	22.1	1.4	9.1	89.5	6.06	4.9
8	10	6	20.1	0.6	9.5	89.9	3.70	4.8

Linnaeus, about 24 h (Wittenberg 1958). Considering the evidence presented here, and the apparent lack of gas secretion in clupeoid fishes in general (Brawn 1962), the most tenable hypothesis is that swim bladder inflation is accomplished in larval anchovy by taking in air at the water surface.

Vertical Migration

If anchovy larvae fill their swim bladders each night by swallowing air, they must either remain near the surface throughout the day and night or migrate to the surface at dusk.

We reexamined the original data collected by Ahlstrom (1959) to determine if any evidence existed for vertical movements in northern anchovy larvae. Ahlstrom (1959) made extensive horizontal tows for fish larvae with opening and closing nets and presented the average number of larvae of all lengths at various depths. We separated his original length data into two length classes: larvae <11.75 mm (preserved standard length) and larvae ≥11.75 mm for night and day collections; we omitted those collections occurring near dawn and dusk. Unfortunately, only 14 larvae ≥11.75 mm were taken in the day while 279 were taken at night but the depth pattern in the day collections was relatively consistent. Larvae <11.75 mm were more abundant: N = 6,456, night; and N = 331, day.

At night, over 50% of the larvae ≥11.75 mm were taken in the upper 10 m whereas in the day the upper 10 m contained less than 10% of the larger larvae (Figure 7). About 50% of the larvae <11.75 mm occurred in the upper 10 m, but no obvious difference between day and night samples existed. These results are in general agreement with those of Ida (1972) who studied the vertical distribution of the Japanese anchovy, *E. japonicus*, a closely related species that also has a diel rhythm in swim bladder inflation (Uotani 1973). Ida (1972) found a striking diel change in the vertical distribution of *E. japonicus* with the maximum numbers occurring at the surface at night and at 20 to 30 m during the day with the movement to the surface occurring at twilight. Examination of the size frequency histograms from some of the collections

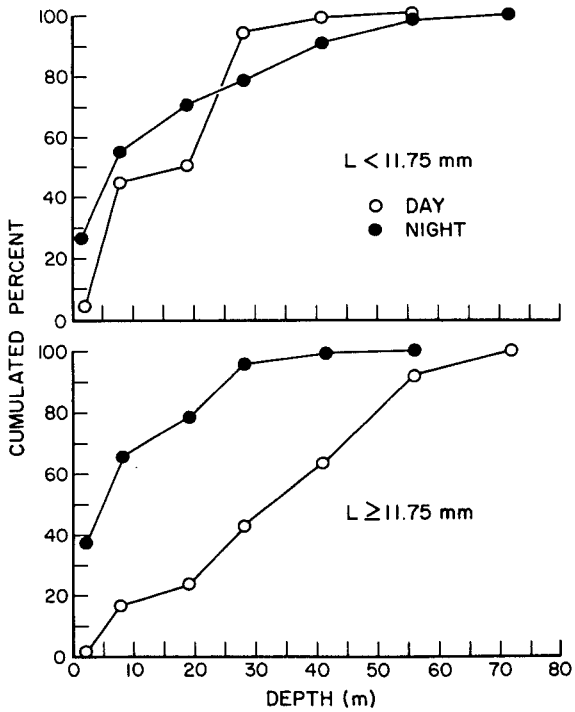

FIGURE 7.—The vertical distribution in the sea of northern larvae at night and in the day for two length classes; length <11.5 mm, upper panel, and length ≥11.5 mm, lower panel (lengths for preserved specimens). Numbers of larvae taken at each depth were cumulated starting at the shallowest tow (5 m) and expressed as the cumulated percent of the total larvae taken. Data are from Ahlstrom (1959).

led Ida to conclude that the diurnal change was caused by the vertical migration of the larger larvae (10 to 15 mm).

The diel vertical movements that appear in larval anchovy at the time of swim bladder inflation probably persist into adult life. The adults, however, are quite variable in their behavior which changes with size of school and season (Mais 1974). Vertical migration is most noticeable in large schools which are deep during the day (119 to 220 m) and rise to the surface and disappear as sonar targets at dusk. These schools reform and descend at first light in the morning (Mais 1974).

Possible Adaptive Advantages

Inflation of the swim bladder reduces the energy required for maintaining a position in the water column. This reduction in sinking speed could represent an important energy savings for larval anchovy because they do not feed at night and swimming can not be used in the search for food. The major energy cost of a diel rhythm of swim bladder inflation is the required vertical migration to the surface. Laboratory work suggests that anchovy larvae, by modification of swimming speed and direction of turning, are able to find and remain in area of high food density (Hunter and Thomas 1974). Thus, it is possible that a larva could follow an upward and downward movement of food at dusk and dawn. In this case the added cost for vertical movements would be slight since the energy spent in swimming could be used in searching for food. It is unlikely, however, that this condition could always be met. Thus, the energy saved at night by inflation of the swim bladder should exceed that used in vertical migration. Assuming the energy used per centimeter swum is the same for vertical migration as for maintaining a position in the water at night, the energy used in a round trip vertical migration of 100 m would be equivalent to that used to maintain a position for 10 h at night when the sinking speed was 0.28 cm/s. Thus, the difference between day and night sinking speeds would have to exceed 0.28 cm/s before a 100-m round trip could be considered an energy sparing mechanism. The difference in sinking rates exceeds 0.28 cm/s for larvae 13.5 mm and larger (Figure 6). This difference increases with larval length suggesting that the vertical range of migration over which energy savings are possible increases with length. In addition, the difference between day and night sinking speeds may be underestimated because sinking speeds were measured at the surface. If larvae descend during the day the gases in the swim bladder would be compressed, increasing body density and thereby increasing the sinking speed for larvae in the day.

These calculations are, of course, a great oversimplification, but they do illustrate that the energy saved by inflation of the swim bladder at night could exceed the cost of a vertical migration and that the possible range of migration could be greater for larger larvae.

The energy costs of maintaining a position in the water column for fish with and without swim bladders have been calculated by Alexander (1972). His calculations are not appropriate for anchovy larvae at night because he considered fish without a bladder to be continuously swimming and gaining lift from the pectoral fins. The behavior of an anchovy at night that failed to inflate the swim bladder would probably resemble one with an inflated bladder. It would sink motionless at an oblique angle to the water surface and interrupt sinking by bursts of near vertical swimming. To maintain a position, these bursts of swimming would have to be of longer duration or of greater frequency than if the swim bladder were filled.

In addition to an energy sparing mechanism, a nightly pattern of swim bladder inflation could possibly reduce predation. Some predators of larval fishes, for example chaetognaths and medusae, use the movement or turbulence produced by prey for detection and attack (Horridge 1966; Newbury 1972). Thus, the reduction of activity produced by slower sinking speeds could reduce predation. The vertical migration of the larvae could also result in exposure to different and possibly less hazardous predators at night. It would also serve to aggregate larvae, thus facilitating social contacts necessary for the development of schooling which begins at about 15 mm.

ACKNOWLEDGMENTS

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

ALEXANDER, R. McN.
1972. The energetics of vertical migration by fishes. Symp. Soc. Exp. Biol. 26:273-294.

BLAXTER, J. H. S., AND K. F. EHRLICH.
1974. Changes in behaviour during starvation of herring and plaice larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 575-588. Springer-Verlag, Berl.

BRAWN, V. M.
1962. Physical properties and hydrostatic function of the swim-bladder of herring (*Clupea harengus* L.) J. Fish. Res. Board Can. 19:635-656.

HORRIDGE, G. A.
1966. Some recently discovered underwater vibration receptors in invertebrates. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 345-405. George Allen & Unwin Ltd., Lond.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
In press. Behavior and survival of northern anchovy *Engraulis mordax* larvae. Symposium on Fishery Science Cienca Marinas, Spec. Suppl.

HUNTER, J. R., AND G. L. THOMAS.
1974. Effect of prey distribution and density on the searching and feeding behaviour of larval anchovy *Engraulis mordax* Girard. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 559-574. Springer-Verlag, N.Y.

IDA, H.
1972. Some ecological aspects of larval fishes in waters off central Japan. Bull. Jap. Soc. Sci. Fish. 38:981-994.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game, Fish Bull. 162, 79 p.

NEWBURY, T. K.
1972. Vibration perception by chaetognaths. Nature (Lond.) 236:459-460.

O'CONNELL, C. P.
1955. The gas bladder and its relation to the inner ear in *Sardinops caerulea* and *Engraulis mordax*. U.S. Fish Wildl. Serv., Fish. Bull. 56:505-533.

SCHOLANDER, P. F., L. VAN DAM, C. L. CLAFF, AND J. W. KANWISHER.
1955. Micro gasometric determination of dissolved oxygen and nitrogen. Biol. Bull. (Woods Hole) 109:328-334.

UCHIDA, K., S. IMAI, S. MITO, S. FUJITA, M. UENO, Y. SHÔJIMA, T. SENTA, M. TAHUKU, AND Y. DÔTU.
1958. Studies on the eggs, larvae and juveniles of Japanese fishes. [In Jap.] Kyushu Univ., Fac. Agric., Fish. Dep., 2d Lab. Fish. Biol., Ser. 1, 89 p.

UOTANI, I.
1973. Diurnal changes of gas bladder and behavior of postlarval anchovy and other related species. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 39:867-876.

WITTENBERG, J. B.
1958. The secretion of inert gas into the swim-bladder of fish. J. Gen. Physiol. 41:783-804.

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CERIANTHARIA, ZOANTHIDEA, CORALLIMORPHARIA, AND ACTINIARIA FROM THE CONTINENTAL SHELF AND SLOPE OFF THE EASTERN COAST OF THE UNITED STATES

BERNT WIDERSTEN[1]

ABSTRACT

Specimens were examined from 95 stations located between lat. 37°49′N, long. 75°25′W and lat. 44°41′N, long. 66°14′W and from depths between 9 and 366 m. The material was collected by the Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Mass., in the years 1955-68. The collection, which will be deposited in the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, comprises two ceriantharian species, *Cerianthus borealis* and *Ceriantheopsis americanus*; one zoanthid species, *Epizoanthus incrustatus*; one species of *Corallimorpharia*, *Corynactis delawarei* n. sp., and 19 species of Actiniaria, *Edwardsia sulcata*, *Halcampa duodecimcirrata*, *Haloclava producta*, *Peachia parasitica*, *Bolcera tuediae*, *Tealia crassicornis*, *Actinostola callosa*, *Stomphia coccinea*, *Paranthus rapiformis*, *Antholoba perdix*, *Metridium senile fimbriatum*, *Haliplanella luciae*, *Sagartiogeton verrilli*, *Hormathia nodosa*, *Actinauge verrilli*, *Phelliactis americana* n. sp., *Amphianthus nitidus*, *Stephenauge nexilis*, and *Stephenauge* (?) *spongicola*.

The following description of the anthozoan species from the western North Atlantic is based on material collected by the Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Mass., during 1955-68. The collection will be deposited in the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole.

Besides the morphological descriptions of different species, much importance has been attributed to the cnidom of the studied specimens. The sizes of the nematocyst capsules mentioned in the description refer to unexploded capsules.

While the fixation and preserving of the material in Formalin[2] and alcohol had only slightly affected the sizes of the nematocysts, the measurements of the column, tentacles, pedal disc, and other organs are, naturally, not directly comparable with those in living specimens.

The terminology used in this paper follows that by Stephenson (1935) and Carlgren (1949). The nomenclature of the nematocysts is the classical one, founded by Weill (1934) and amplified by Carlgren (1940a, 1945, 1949).

The sectioned mterial was stained with Heidenhain's azan or iron hematoxylin-eosin.

All nematocyst measurements are given in microns.

A list of the stations with names of the species collected at each station and with ADP (automatic data processing) codes for latitude and longitude; time, day, month, year, and number of collection; vessel; cruise; station number; gear; water depth; water temperature; and sediment type is on file at the Northeast Fisheries Center, Woods Hole.

DESCRIPTIONS

Ceriantharia
Cerianthidae

Cerianthus borealis Verrill 1873

OCCURRENCE.–40°10′N, 71°00′W, 146 m, silty sand, 1 specimen; 41°00′N, 70°48′W, ? m, 1 specimen; 41°50′N, 67°56′W, 51 m, sand, 2 specimens; 42°41′N, 70°05′W, 114 m, gravel, 2 specimens.

GENERAL CHARACTERISTICS.–The specimens were strongly damaged in their proximal parts. The morphology of the distal part of the body as well as the composition of the cnidom and the sizes of the nematocysts were typical of the species (cf. Carlgren 1940a). While the specimens from the two southernmost localities were young (diameter of the distal part of the body 4-8 mm), the other individuals were older, the largest of them being equipped with 150 labial as well as marginal tentacles.

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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NEMATOCYSTS (those of the southernmost specimen within parentheses).–*Marginal tentacles*: microbasic *b*-mastigophors 21 × 3.2-3.8 - 26 × 3.8, 36 × 4.4 - 41 × 4.9, 54.5 × 9.2 - 61 × 7.1 (25.3 × 3.8 - 28.3 × 4.4); atrichs 33 × 4.4 - 36 × 5.5 (9.8 × 1.6 - 27.5 × 2.7); spirocysts 20 × 3.3 - 56 × 6.5 (22 × 3.8 - 28 × 3.8-4.9). *Labial tentacles*: microbasic *b*-mastigophors (axial filament short and thin, less than half the length of the capsule) 37 × 3.8-4.4 - 45 × 5.5 (ca. 18.5 × 2.7); microbasic *b*-mastigophors (axial filament = about half the length of the capsule 20.7-35.4 × 3.8 (19.1 × 3.3 - 30.5 × 4.9); microbasic *b*-mastigophors (axial filament tall and coarse; more than half the length of the capsule) 57 × 8.3 - 63.7 × 7.1 (23.4-30 × 4.9-6); atrichs (not common) 55 × 9.8 - 63.7 × 28.3 (ca. 18 × 3.3); spirocysts 18 × 3.3 - 54 × 6 (14.7-16.8 × 2.7-3.3) μm. Holotrichs were very rare (in the distal part of the column = 22.3 × 14.7 - 43.6 × 17.4, and in the telocraspedon = 61 × 13.6 μm).

Ceriantheopsis americanus (Verrill 1864)

OCCURRENCE.–42°04′N, 67°30′W, 40 m, gravelly sand, 1 specimen; 42°25′N, 70°56′W, 13 m, 1 specimen.

GENERAL CHARACTERISTICS.–The proximal parts of the two studied specimens were missing. The individuals were young; the only specimen, being preserved with a 12-mm-long column part, had a diameter of 6 mm. The marginal tentacles were equipped with stout basal parts and acute apices. The labial tentacles were about 70 (69 in one specimen).

NEMATOCYSTS.–*Column* (distal part): microbasic *b*-mastigophors (not common) 19.6 × 3.8 - 32.7 × 5.5; atrichs (very common) 26 × 6.5 - 50 × 10.9-16.4. *Marginal tentacles*: microbasic *b*-mastigophors 16.3 × 3.8-4.4 - 19 × 4.9; atrichs (?) ca. 12 × 2.7, 8.7-12.5 × 4.9; spirocysts 12 × 2.7 - 27.3 × 4.9. *Labial tentacles*: microbasic *b*-mastigophors 16.3 × 3.8 - 32.7 × 6.5; spirocysts 13.6 × 2.7 - 27.3 × 4.9. *Actinopharynx*: microbasic *b*-mastigophors (axial filament more than half the length of the capsule) 21 × 4.9 - 32 × 6; microbasic *b*-mastigophors (axial filament less than half the length of the capsule) 13.6 × 2.7 - 18 × 3.3, 20.7 × 3.8 - 23 × 4.4. *Filaments* (orthocraspedon): microbasic *b*-mastigophors 19-21 × 3.3, 26 × 5.4 - 33 × 6.5; spirocysts (very rare) ca. 21 × 3.8 μm.

Zoanthidea
Epizoanthidae

Epizoanthus incrustatus Düben and Koren 1847

OCCURRENCE.–40°03′N, 71°16′W, 183 m, 4 specimens; 42°10′N, 65°37′W, 238 m, two colonies with 10 and 19 specimens respectively, and one solitary specimen, on a shell fragment.

GENERAL CHARACTERISTICS.–The color of the column and the coenenchyme is greyish brown; both are strongly encrusted with sand grains. The polyps were in the contracted state about 5 mm tall, with the column diameter about 4 mm. Most of the 17 capitular ridges as well as the insertions of the 36 mesenteries were indistinct (because it is heavily encrusted with sand). The tentacles numbered about 36.

NEMATOCYSTS.–*Column:* holotrichs 22 × 7 - 24 × 8.2; spirocysts 22 × 4.4 - 31 × 5.4. *Tentacles*: microbasic *p*-mastigophors 22-33 × 3.3 (35 × 6); microbasic *b*(?)-mastigophors 22-23.4 × 4.4; holotrichs 22-24 × 7.6-8.2 (common), 34 × 15.3 - 40 × 17.4 (not common); spirocysts (very common) 10 × 3.8 - 32 × 4.9. *Actinopharynx*: microbasic *p*-mastigophors (not common) ca. 22 × 6; holotrichs 21-25 × 7.6, 38 × 14.2 - 41 × 14.7. *Filaments*: microbasic *p*-mastigophors 20 × 5.4 - 28 × 6.5; microbasic *b*(?)-mastigophors 11 × 4.9 - 21 × 6; holotrichs 23 × 7.6 - 26 × 8.3 μm.

Corallimorpharia
Corallimorphidae

Corynactis delawarei n. sp.

HOLOTYPE.–Deposited as a series of sections in the Zoological Institute, Uppsala. Syntypes deposited in the U.S. National Museum, catalog number USNM 54322. Thirty-two specimens aggregated on a tube fragment of an onuphid polychaete, collected by the vessel *Delaware* from the type-locality on 14 June 1962, with a 1-m Naturalist dredge, in station number 9.

TYPE-LOCALITY.–39°56′N, 69°45′W, 201 m,

sandy bottom, on a tube fragment of an onuphid polychaete.

DIAGNOSIS.–Column rather firm, smooth, 15 mm tall, bright red (sometimes whitish) to reddish brown in color. Tentacles rather short, with well-limited acrospheres; two or three per endocoele, the total number being 90. Sphincter long, entodermal to ento-mesogloeal. Maximum number of mesenteries 60. At least six pairs of mesenteries perfect. Retractors diffuse. Cnidom: *column*–holotrichs and spirocysts; *tentacles* (acrospheres)–holotrichs and microbasic *b*- and *p*-mastigophors; *tentacles* (peduncles)– microbasic *b*- and *p*-mastigophors, atrichs (?), and spirocysts; *actinopharynx*–holotrichs, atrichs, microbasic *p*-mastigophors, and spirocysts; *filaments*–holotrichs, microbasic *p*-mastigophors, atrichs (?), and spirocysts.

GENERAL CHARACTERISTICS.–The column is smooth and rather firm. In the contracted state there are distally a number of transverse as well as a few longitudinal furrows. The shape of the column is proximally dependent on the shape of the substrate. The color of the column and the pedal disc is bright red to reddish brown. (There are also, however, some whitish individuals in the collection, with red mesenterial insertions shimmering through the ectoderm.) The longitudinal muscle sheet of the ectoderm forms a thin, but distinct layer in the column. The tentacles are rather short, with cylindrical peduncles and well-limited, white acrospheres. The entodermal as well as the ectodermal muscle sheets of the peduncles are well developed. The inner tentacles are shorter than the outer ones; the exocoelic tentacles are the largest. The stichodactyline arrangement of the tentacles is rather indistinct in the often strongly contracted specimens of the collection. There are, however, two or three tentacles per endocoele, the total number being 90. The sphincter is long, entodermal to entomesogloeal (Figure 1A), and is only occasionally capable of covering all the tentacles. The actinopharynx is short, in the contracted state, with longitudinal as well as transverse folds. There is only one indistinct siphonoglyph. The retractors of the maximum 60 mesenteries are diffuse, forming an insignificant sheet over the edge of the mesentery (Figure 1B). At least six pairs (including the directive pair) of the mesenteries are perfect. Reproduction is probably asexual by longitudinal fission. The size of the normally cylindrical column is of a maximum 15 mm, with a proximal diameter of 8 mm.

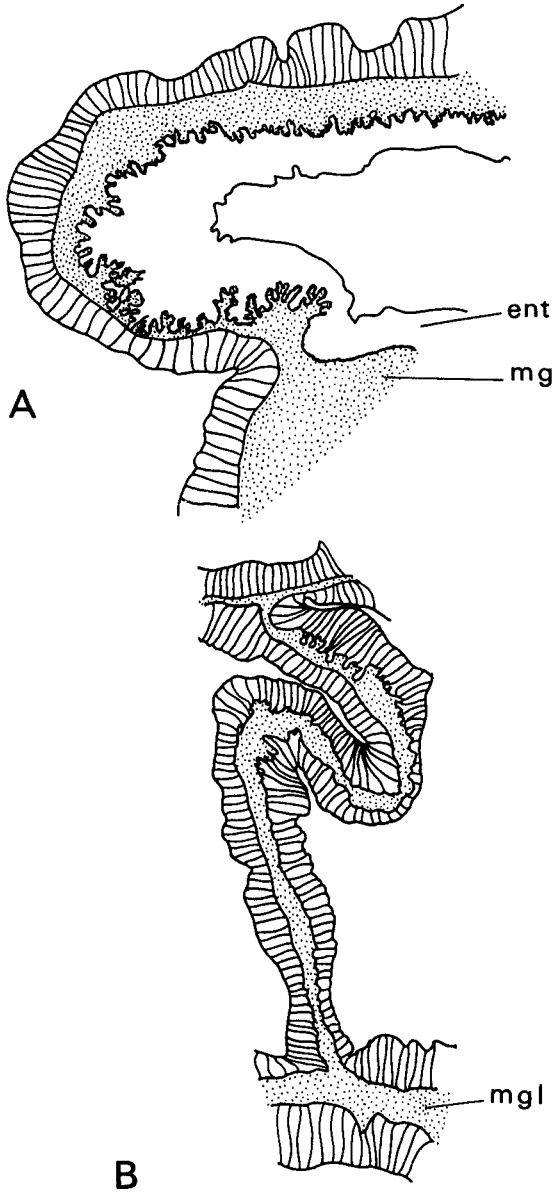


FIGURE 1.–*Corynactis delawarei* n. sp. A. Section through the sphincter region of the column. B. Cross section of a perfect mesentery. ent–entoderm, mgl–mesogloea.

NEMATOCYSTS.–*Column*: holotrichs 38 × 8.7 - 53.4 × 10.9; spirocysts 18.5 × 3.3 - 27 × 4.4. *Tentacles* (acrospheres): holotrichs 69 × 21.8 - 85 × 10.9-16.4; hoplotelous microbasic *p*-mastigophors 33 × 5.5 - 82 × 8.8-9.7; hoplotelous

microbasic *b*-mastigophors 31-34 × 4.4-4.9; 69-72 × 5.5 *Tentacles* (peduncles): microbasic *b*-mastigophors 19-24 × 3.8-4.9; microbasic *p*-mastigophors (very rare) ca. 36 × 7.6; atrichs (?) ca. 15 × 5.5; spirocysts 19 × 3.8 - 38 × 5.5. *Actinopharynx*: holotrichs 28 × 5.5 - 46 × 12; atrichs (rare) ca. 12 × 4.9; microbasic *p*-mastigophors (rare) ca. 22 × 6; spirocysts 17-23 × 3.8-4.4. *Filaments*: holotrichs 37 × 12 - 78 × 32.7; hoplotelous microbasic *p*-mastigophors 24 × 5.5 - 44 × 10.9-12; atrichs (?) 34 × 3.8-35 × 4.4; spirocysts (rare) ca. 31 × 3.8 μm.

The three individuals in the collection having a whitish color of the column (see above) deviate from the combination of the cnidom and the frequency of the nematocysts in some organs. *Tentacles* (acrospheres): holotrichs 49 × 16.4 - 65.4 × 35.4; atrichs (?) 22 × 5.5 - 41 × 10.4; microbasic *p*-mastigophors 19 × 4.9 - 46 × 6.5. *Tentacles* (peduncles): holotrichs ca. 66.5 × 19.6; hoplotelous microbasic *p*-mastigophors 37 × 7.1 - 64 × 8.7; microbasic *b*(?)-mastigophors 61 × 6.5 - 88 × 8.7; spirocysts 23 × 2.7 - 52 × 4.4 μm.

It is probable that the nematocysts characterized as atrichs in the tentacles of the whitish variety actually are holotrichs, the structure of which was made unobservable by the fixing agent. Difficulties in distinguishing between the two nematocyst types has been pointed out by Carlgren (1945) with concern to corallimorpharians.

Until studies on vital material of the whitish color form have been undertaken, which will possibly confirm the presence of atrichs in the acrospheres, I am inclined to consider it as a member of the species *Corynactis delawarei*. [In *Corynactis annulata* (Swedish Museum of Natural History, reference number 1244) collected off Tristan da Cunha, there is, however, a nematocyst equipment in the acrospheres suggestive of that described in the whitish color variety: holotrichs 46 × 12.5 - 60 × 9.3; microbasic *p*-mastigophors (rare) ca. 20 × 4.9; atrichs (?) 19 × 5.4 - 25 × 6.5 μm; microbasic *b*-mastigophors were not found in the specimen studied by me.]

Actiniaria
Edwardsiidae

Edwardsia sulcata (Verrill 1864)

OCCURRENCE.–44°00′N, 68°15′W, 110 m, silt-clay, 6 specimens, collected from three dredges.

GENERAL CHARACTERISTICS.–The physa is well developed. The scapus is divided into longitudinal compartments separated by the mesenterial insertions of the macrocnemes. The color of the scapus is yellowish grey. The nemathybomes are numerous and often closely aggregated (Figure 2A). The periderm is strong, but easily falls off; its color is yellowish brown. The scapulus is provided with high, longitudinally oriented ridges in the strongly contracted material. The maximum length of the scapus and scapulus is 40 mm, whilst the largest diameter is 4 mm. The 16 tentacles are conical, without ridges or nematocyst concentrations. The yellowish-white actinopharynx has one distinct siphonoglyph. The retractors of the eight macrocnemes are circumscribed and more or less reniform (Figure 2B). The parietal muscles are strongly developed with 10-12 partly branched muscle (lamellae on each side of the lamella of the septum (Figure 2C, D). The mesogloea of the mesentery is much thinner in the vicinity of the retractor portion than was described by Carlgren (1931) in *Edwardsia elegans* (Figure 2B).

NEMATOCYSTS.–*Scapus* (nemathybomes): microbasic *b*-mastigophors 90 × 5.4 - 110 × 6, 49 × 3.8 - 71 × 4.4 (the smaller nematocyst type has reached a considerable less degree of specialization than the larger type, the axial filament of which shows great conformity with that in *b*-mastigophors of *Edwardsia longicornis* Carlgren (cf. Carlgren 1940a). *Scapulus*: basitrichs 14 × 1.6 - 16 × 2.2. *Tentacles*: basitrichs 19-26 × 2.2-2.7; spirocysts 10 × 2.7 - 25 × 3.8. *Actinopharynx*: basitrichs 16-26 × 2.2; microbasic *p*-mastigophors (rare) ca. 24 × 4.4. *Filaments*: basitrichs 19 × 2.2 - 24 × 2.7; microbasic *p*-mastigophors (often with somewhat bent capsules; axial filament = one third to half the length of the capsule) 21-33 × 3.8-4.4; microbasic *p*-mastigophors (axial filament remarkably thin, and about three-fourths of the length of the capsule) 23-32 × 4.4-4.8 μm.

There are many morphological similarities between *E. sulcata* and *E. sipunculoides*. The *b*-mastigophors in the nemathybomes of the latter species are, however, always much smaller (in one specimen from the U.S. east coast, studied by me, they were 62 × 4.9 - 72.5 × 5.5, 42-44 × 4.4 μm; cf. also Carlgren 1931).

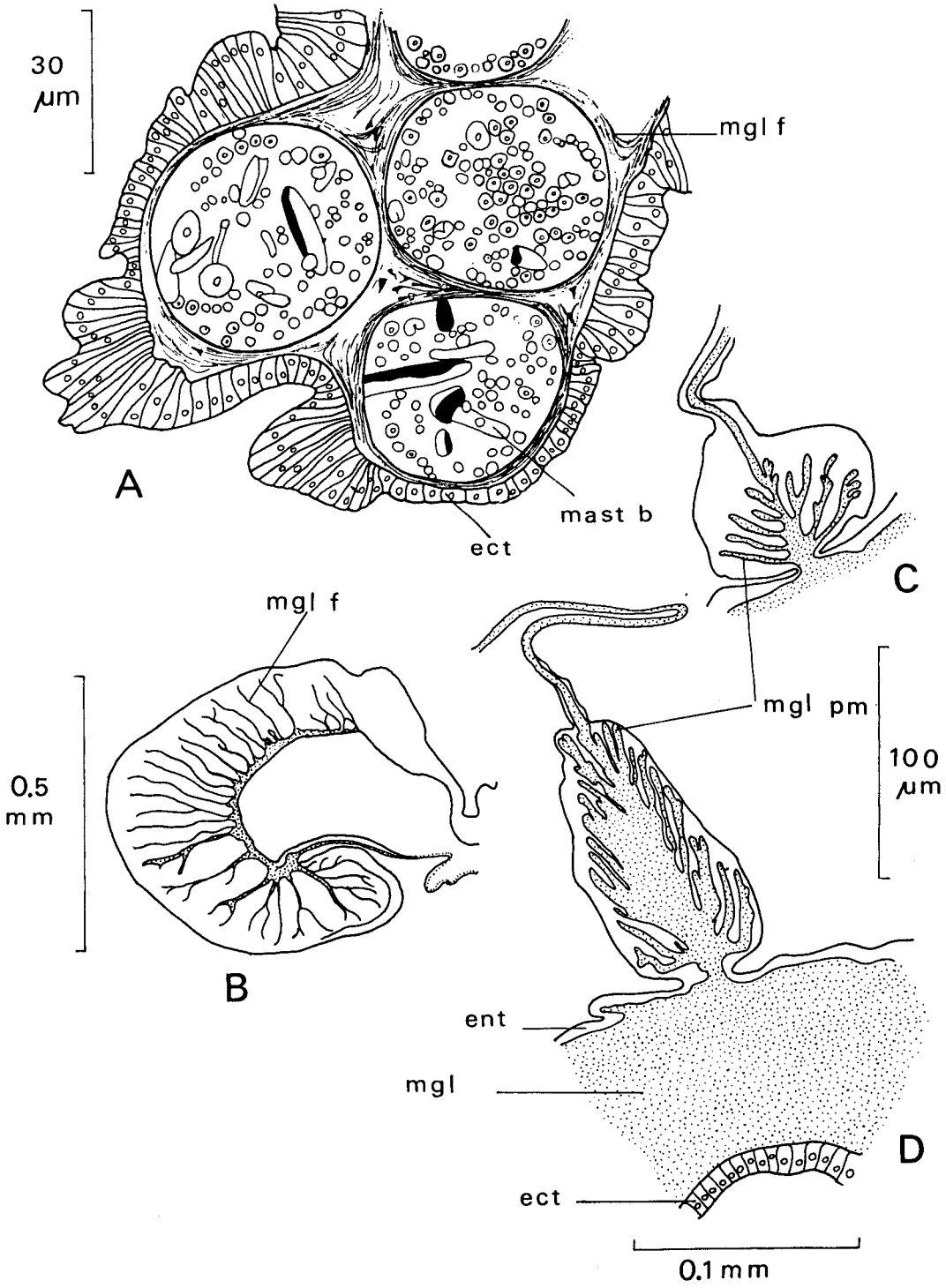


FIGURE 2.–*Edwardsia sulcata.* A. Section through three nemathybomes. B. Cross section through a retractor. C, D. Sections through two parietal muscles. ect–ectoderm, ent–entoderm, mast b–sectioned parts of microbasic *b*-mastigophors, mgl–mesogloea, mgl f–mesogloeal fibril, mgl pm–mesogloeal tract of parietal muscle.

Halcampa duodecimcirrata M. Sars 1851

OCCURRENCE.–43°10′N, 70°25′W, 64 m, till, 1 specimen.

GENERAL CHARACTERISTICS.–They agree with earlier descriptions of the species (cf. Carlgren 1893). The reddish scapus is provided with tenaculi and distinct mesenterial insertions shimmering through the ectoderm. The six pairs of macrocnemes (Figure 3A) (including two pairs of directives) have strongly developed, circumscribed, and reniform retractors (Figure 3B). The parietal muscles are provided with a rather small

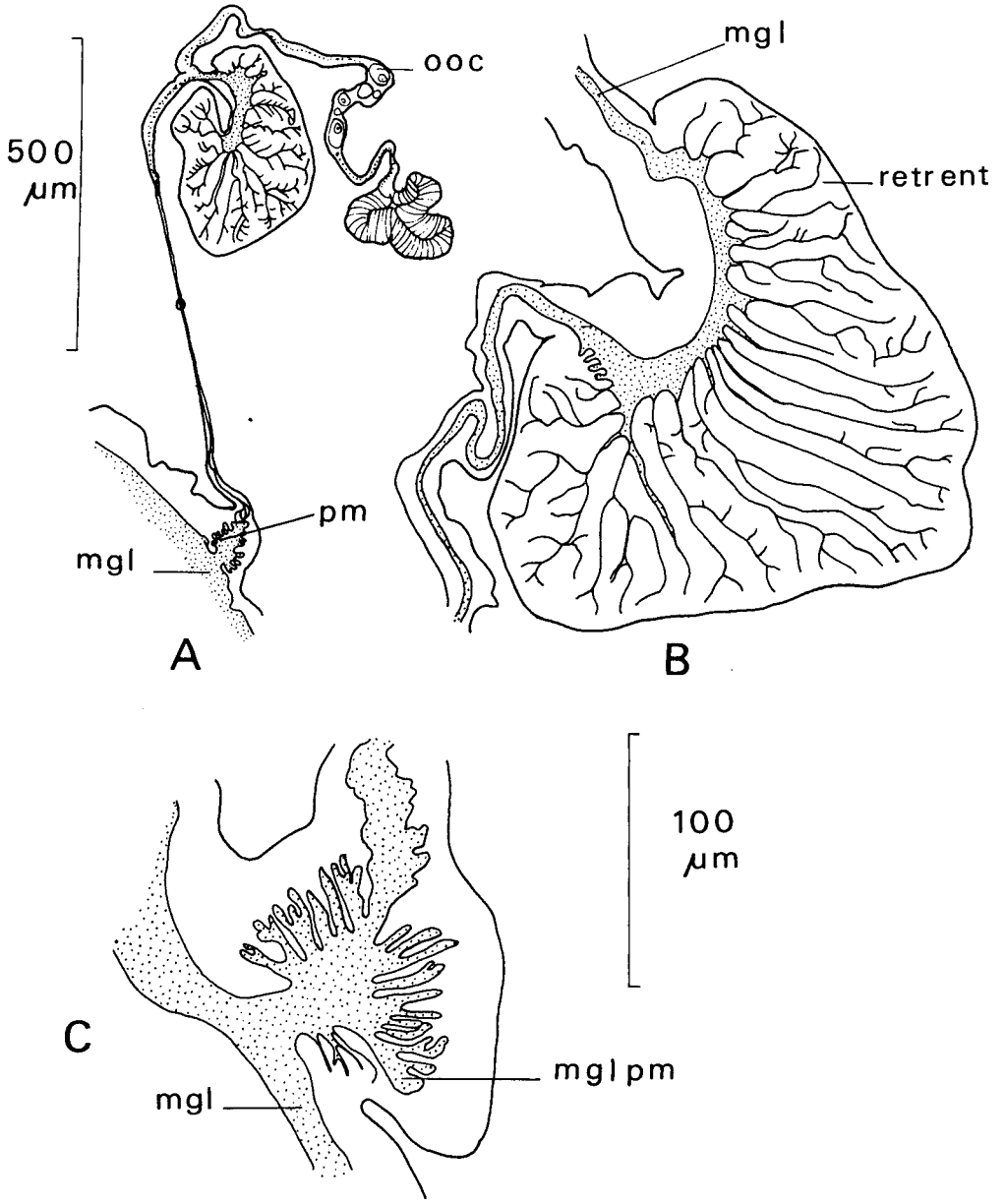


FIGURE 3.–*Halcampa duodecimcirrata*. A. Section through a macrocneme. B. Cross section of a retractor. C. Section through the peripheral part of a mesentery (the ectoderm is omitted in the figure). mgl–mesogloea, mgl pm–mesogloeal lamella of parietal muscle, ooc–oocyte, pm–parietal muscle, retr ent–entoderm of retractor muscle.

number of muscle lamellae (Figure 3C). The short, conical tentacles were 10 (12?) in number.

NEMATOCYSTS.–*Scapus*: basitrichs (rare) ca. 22 × 3.3, spirocysts (rare) ca. 28 × 3.8. *Scapulus*: spirocysts 25 × 3.8 - 49 × 4.4; basitrichs were not found in the very damaged scapular ectoderm. *Tentacles*: basitrichs (rare) 11.5 × 1.6-2.2 - 20 × 2.7; spirocysts 14 × 2.7 - 25 × 3.3. *Actinopharynx*: microbasic *p*-mastigophors 24-32 × 3.5; spirocysts 17 × 2.2 - 25 × 4.9. *Filaments*: microbasic *p*-mastigophors 22-23 × 4.4-4.9; basitrichs (?) 12-13.6 × 3.8 μm.

The alleged differences as to the form of the tentacles between *H. duodecimcirrata* and *H. chrysanthellum* would argue against my decision to refer the specimen to the former species. Considering the extensive contraction of the specimen, this characteristic must, however, be regarded as of minor importance. Of greater importance here is the conformity with *H. duodecimcirrata* of the sizes of the nematocysts in different organs (cf. Carlgren 1940a). The number of fertile mesenteries (eight in the studied specimen) is another argument for the individual being placed in *H. duodecimcirrata.*

Haloclavidae

Haloclava producta (Stimpson 1856)

OCCURRENCE.–39°00′N, 74°45′W, 15 m, sandy bottom, 1 specimen.

GENERAL CHARACTERISTICS.–The column of the strongly contracted and partly damaged specimen is fusiform with the ectoderm in closely lying, transverse folds. The color is grey. The scapus has a few sand grains attached to the ectoderm. The length of the column is 16 mm, with the greatest diameter (at the middle of the body) about 8 mm. The retractors of the protomesenteries are very strong, circumscribed, and reniform (Figure 4A). The four pairs of metamesenteries are weaker than the protomesenteries. The parietal muscles are rather strong (Figure 4B). There is no sphincter. The actinopharynx is rather short with a very deep siphonoglyph. The number of tentacles was impossible to confirm; as there were only mesogloeal fragments left of the tentacles, neither the nematocyst types nor their sizes can be treated. The location of the fragments of the tentacles favors the belief that there are 20 tentacles in the living animal.

NEMATOCYSTS.–*Column*: basitrichs 20 × 2.7 - 24.5 × 3.3. *Actinopharynx*: basitrichs 14 × 2.2 - 17.4 × 2.7, 38-57 × 4.4-4.9; spirocysts (only one found) 43.1 × 3.8. *Filaments*: basitrichs 14 × 2.7 - 25 × 3.3, 70-83 × 4.4-5.5, 54.5 × 7 - 75 × 6.5-7.1 μm.

Peachia parasitica (Agassiz 1859)

OCCURRENCE.–44°16′N, 67°38′W, 91 m, silt-clay, 1 specimen.

GENERAL CHARACTERISTICS.–The column of the specimen is strongly contracted, with the length 24 mm and the largest diameter (at the middle of the body) 15 mm. The proximal diameter of the column is 8 mm. The exact arrangement of the extended lobes of the conchula was not possible to observe in the specimen. There is no sphincter. The only siphonoglyph is thick-walled and of the typical *Peachia* appearance. The number of mesenteries are 20, six pairs being perfect, and supplied with strong, diffuse retractors with rather high muscle lamellae. The four pairs of imperfect mesenteries are equipped with rather small, diffuse retractors and are laterally and ventrolaterally located. The 10 conical tentacles have broad bases.

NEMATOCYSTS.–*Column*: basitrichs 27-34 × 3.8-4.4. *Tentacles*: basitrichs 27-39 × 3.8-4.4; spirocysts ca. 23 × 3.3 *Actinopharynx*: basitrichs 40-46 × 5.5; spirocysts 19-23 × 2.2-2.7. *Filaments*: basitrichs 27 × 3.8 - 38 × 4.4; basitrichs (?) 39 × 6 - 45 × 7.6; microbasic *p*-mastigophors (rare) ca. 28 × 3.8 μm.

The filamental nematocysts named "basitrichs (?)" (above) might be *p*-mastigophors. As I have had no chance of observing the exploded capsules and as the axial filament does not show the typical *p*-mastigophor structure in the unexploded capsules, I am not now inclined to consider these nematocysts, which are probably homologous to the "penicilli-like mastigophors" found by Carlgren (1940b), as microbasic *p*-mastigophors.

Actiniidae

Bolocera tuediae (Johnston 1832)

OCCURRENCE.–41°27′N, 69°02′W, 146 m, 1 specimen; 41°50′N, 69°26′W, 165 m, 1 specimen; 42°15.5′N, 69°59.5′W, ? m, 1 specimen; 42°25′N,

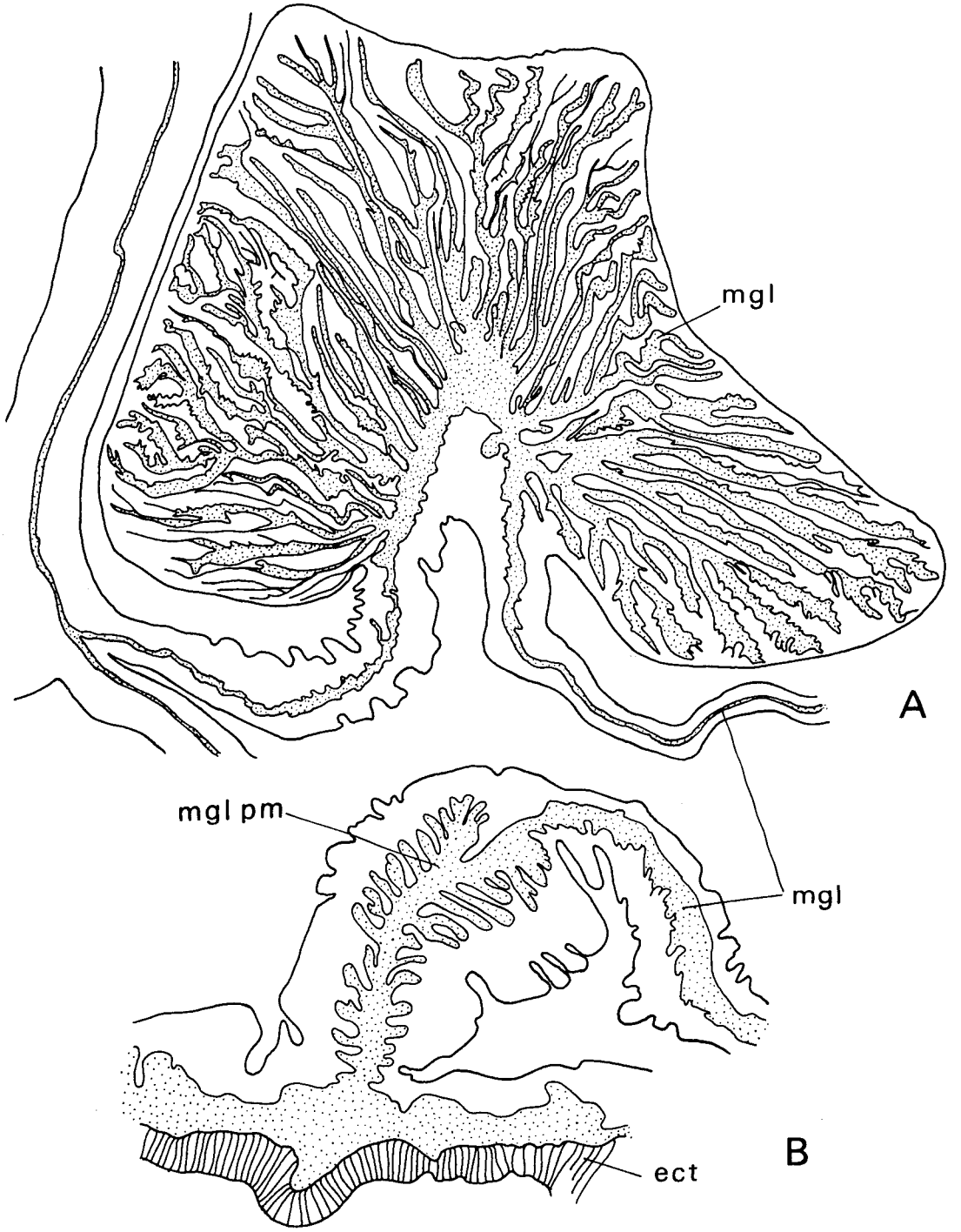


FIGURE 4.–*Haloclava producta*. A. Section through a retractor muscle. B. Section through the peripheral part of a mesentery and adjacent parts of the body wall. ect–ectoderm, mgl–mesogloea, mgl pm–mesogloeal tract of parietal muscle.

67°06′W, 366 m, 3 specimens; 42°48′N, 69°39′W, 183 m, 1 specimen; 43°17′N, 70°24′W, 46 m, 1 specimen; 43°19′N, 67°16′W, 201 m, 1 specimen; 43°20′N, 68°45′W, 119 m, 1 specimen.

GENERAL CHARACTERISTICS.–The structure of the specimens agrees with earlier descriptions of the species (cf. Carlgren 1891:242, 1893:50; Stephenson 1935:130; Verrill 1922:G 115).

NEMATOCYSTS.–*Column*: basitrichs 16 × 2.2 - 21 × 2.7, 33 × 3.3 - 41 × 3.8 (-63 × 5.5). *Tentacles*: basitrichs 21 × 2.7 - 36.5 × 3.3-3.8, 52 × 3.8 - 87 × 4.9-6.5 (most often 60-70 × 4.5-6); spirocysts 31-74 × 3.3-5.5; *Actinopharynx*: basitrichs 50 × 4.4 - 79 × 5.5; microbasic *p*-mastigophors 23-33 × 5.5 *Filaments*: basitrichs 20-22 × 2.7-3.8, 50 × 3.8 - 74 × 4.4-5.5; microbasic *p*-mastigophors 19.6 × 4.9 - 35.4 × 5.5 μm.

Tealia crassicornis (Müller 1776)

OCCURRENCE.–41°02′N, 69°00′W, 80 m, gravelly sand, 1 specimen; 41°13′N, 68°58′W, 102 m, gravelly sand, 3 specimens; 41°33′N, 69°47′W, 27 m, gravelly sand, 1 specimen; 41°50′N, 67°56′W, 51 m, sand, 3 specimens; 42°11′N, 65°56′W, 229 m, gravel, 1 specimen; 42°25′N, 66°05′W, 249 m, gravel, 1 specimen; 42°26′N, 67°02′W, 366 m, 2 specimens; 43°11′N, 66°31′W, 92 m, gravel, 3 specimens; 43°11′N, 67°05′W, 181 m, 1 specimen; 43°12′N, 65°33′W, 73 m, shelly sand, 1 specimen; 43°33′N, 69°35′W, 159 m, 1 specimen; 43°37′N, 68°12′W, 198 m, 1 specimen; 43°49′N, 68°31′W, 95 m, 2 specimens; 43°52′N, 66°42′W, 102 m, 2 specimens; 43°53′N, 68°38′W, 91 m, 1 specimen; 44°26′N, 67°28′W, 73 m, till, 1 specimen; 44°30′N, 66°30′W, 157 m, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of the studied specimens agrees with earlier descriptions of the species (cf. Verrill 1867; Carlgren 1893). The pedal disc is wide, circular (diameter = 16-114 mm) or oval (16 × 22 - 47 × 63 mm). The rather firm column is in the contracted state, cylindrical to semispherical, 14-38 mm high. In those cases where the column is provided with verrucae, these are chiefly spread over the distal parts of the column. In some specimens there is a distinct annulus with 48 marginal verrucae. The number of mesenteries is somewhat larger proximally than distally (in a specimen with 68 mesenteries only four were limited to the proximal part of the column). The two outer of the four to five mesenterial cycles are often not quite completed. With the exception of the youngest, proximally located cycle, and the 10 oldest perfect pairs, the mesenteries are fertile. In the specimens coming from 43°11′N, 66°31′W, the entodermal and circumscribed sphincter is obviously asymmetric, with one half of it considerably more strongly developed than the other.

Many of the specimens in the collection are viviparous with larvae and young stages equipped with tentacles lying in the proximal part of the gastrocoele.

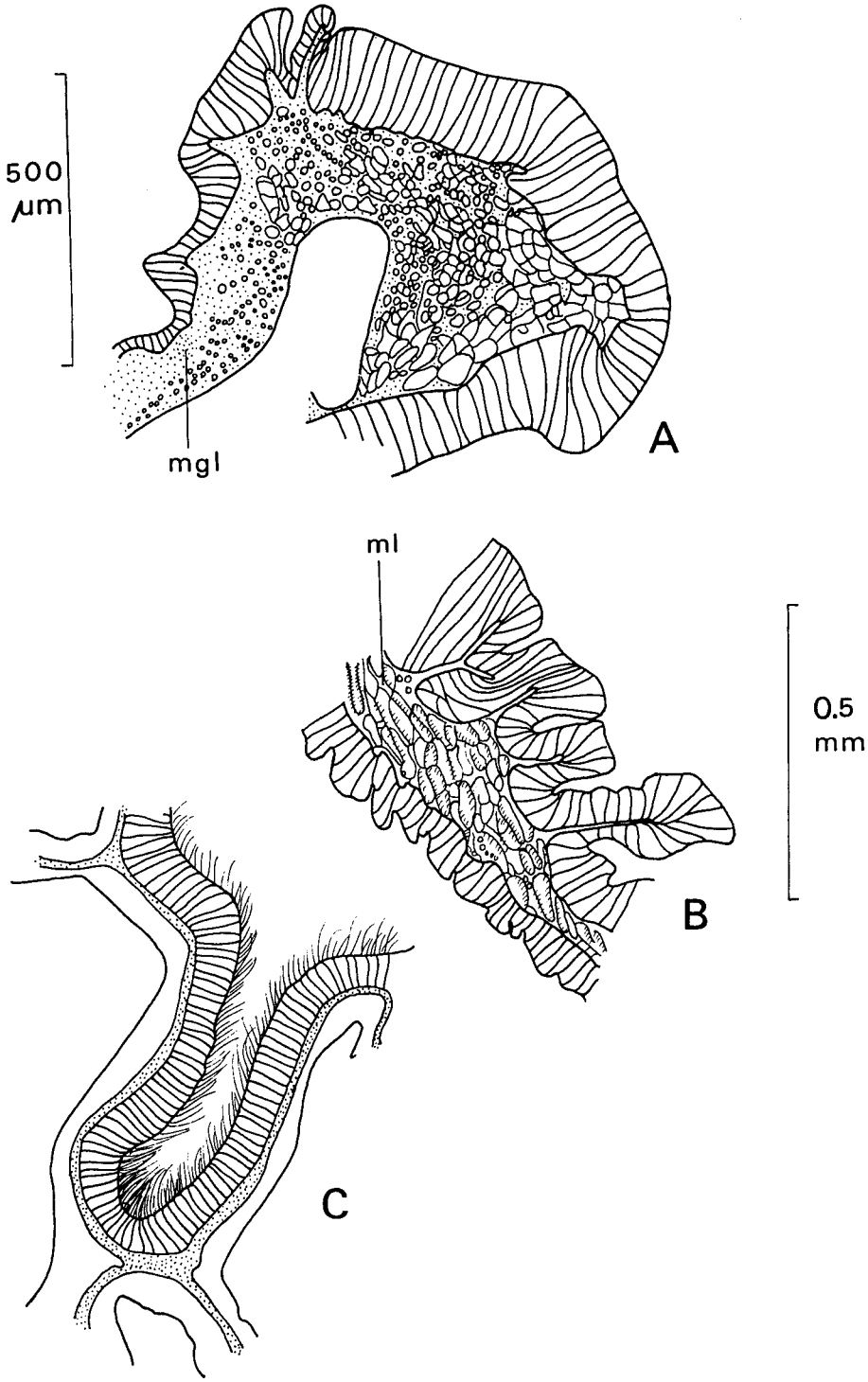
NEMATOCYSTS.–*Column*: basitrichs 5.5 × 1.1 - 9 × 2.7, 18 × 2.2 - 27 × 2.7-3.3; in larger specimens found in the deeper localities: 12.5-14 × 2.7, 23-37 × 3.8, 79 × 5.5 - 83.4 × 8.2; spirocysts 22 × 2.7 - 69 × 4.4. *Tentacles*: basitrichs 10-14 × 2.2-2.7, 20 × 1.6 - 36.5 × 2.7-3.8; spirocysts 17.4 × 2.7 - 71 × 4.9-5.5. *Actinopharnyx*: basitrichs 49 × 5.5-6 - 91 × 6-7.1, 12 × 1.6 - 26 × 2.7; microbasic *p*-mastigophors 23 × 4.9 - 30 × 5.5-6.5; spirocysts (rare) 28-41 × 3.8. *Filaments*: basitrichs 11 × 2.2 - 34 × 2.7, 49 × 5.5-6 - 68 × 7.1; microbasic *p*-mastigophors 20 × 4.9 - 41 × 6.5 μm.

Actinostolidae

Actinostola callosa (Verrill 1882)

OCCURRENCE.–42°10′N, 69°57′W, 142 m, 1 specimen; 42°11′N, 68°16′W, 198 m, 1 specimen; 42°21′N, 68°02′W, 190 m, 3 specimens; 42°26′N, 66°35′W, 302 m, 1 specimen; 42°27′N, 66°08′W, 247 m, gravel, 1 specimen; 42°51′N, 65°12′W, 159 m, 1 specimen; 42°54′N, 69°35′W, 159 m, 2 specimens; 43°21′N, 69°57′W, 155 m, 1 specimen; 44°41′N, 66°14′W, 134 m, till, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of this species has been carefully described by Carlgren (1893:71). The length of the column varies between 13 and 196 mm, and the diameter of the pedal disc is 13-48 mm. The tentacles are arranged in six cycles (6+6+12+24+48+96). The mesenteries (in five or six cycles) are arranged according to the *Actinostola* rule. Twenty-four pairs of mesenteries are perfect, those of the two inner cycles (including the two directive pairs) being sterile, as well as those of the outer cycle.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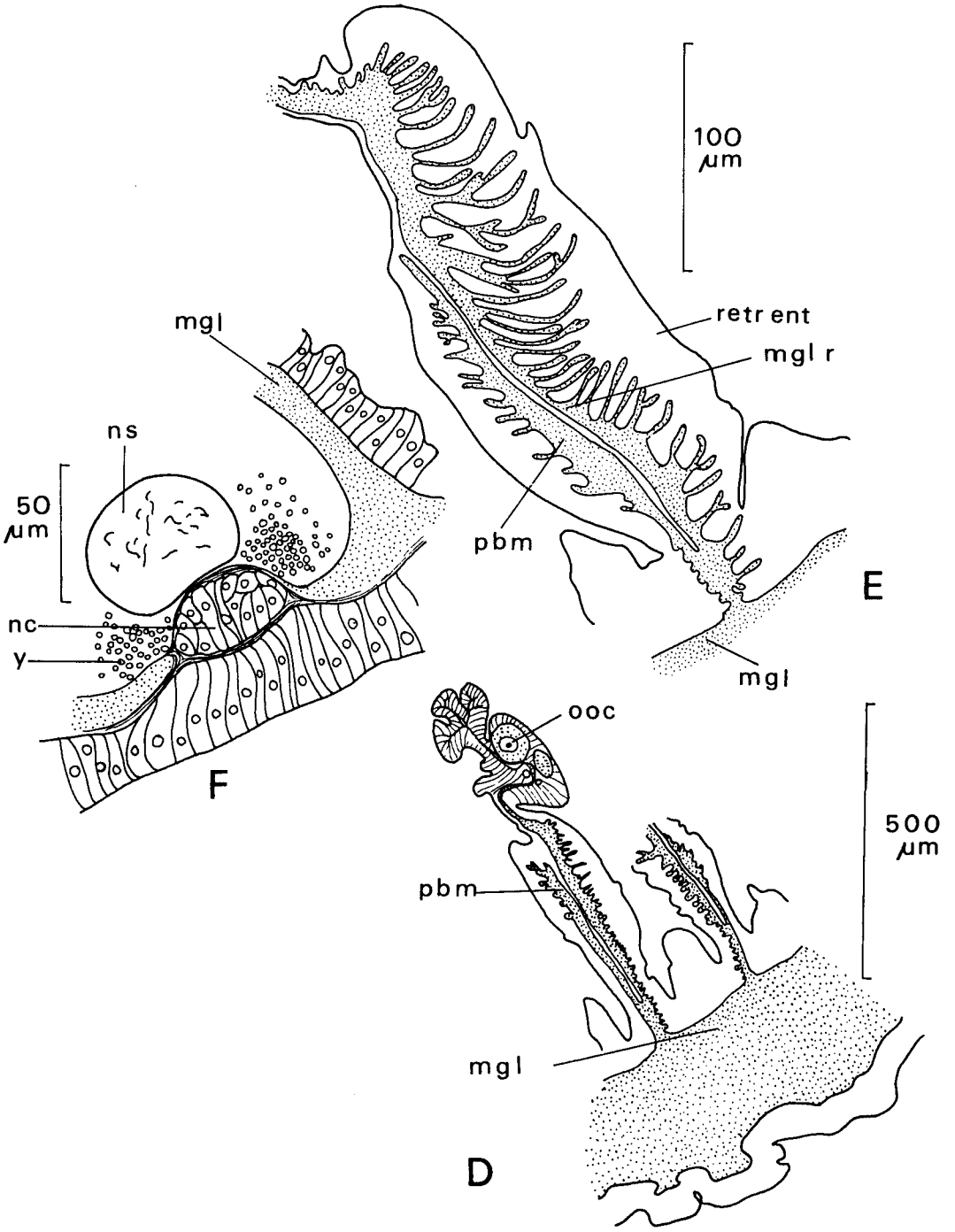


FIGURE 5.—*Stomphia coccinea*. A. Cross section of the sphincter in a young specimen. B. Section through part of a tentacle showing the arrangement of the muscle fibrils (ml) in a young specimen. C. Section through a siphonoglyph. D. Section through a mesentery in a young specimen. E. Section through a retractor and parietobasilar muscle of a young specimen. F. Section of an oocyte and nurse cells. mgl–mesogloea, mgl r–mesogloea of retractor, nc–nurse cell, ns–nucleus, ooc–oocyte, pbm–parietobasilar muscle, retr ent–entoderm of retractor muscle, y–yolk.

NEMATOCYSTS.–*Column*: basitrichs 19 × 2.7 - 35.4 × 2.7-3.3; spirocysts 24.5 × 3.3 - 57 × 5.5-6. *Tentacles*: basitrichs 26 × 2.2 - 41 × 2.7 (most often 30-35 × 2.7); microbasic *b*-mastigophors (in the apex) 42.5 × 7.1 - 56 × 7.1-8.2; spirocysts 27 × 2.7 - 64 × 7.6. *Actinopharynx*: basitrichs 21-32 × 2.7; microbasic *p*-mastigophors 22-28 × 4.9. *Filaments*: microbasic *p*-mastigophors 21-28 × 4.4, 20-29 × 5.5 μm. The cnidom in specimens from the eastern North Atlantic was described by Carlgren (1940a).

Stomphia coccinea (Müller 1776)

OCCURRENCE.–41°20′N, 69°22′W, 49 m, 3 specimens; 41°37′N, 66°16′W, 91 m, sand, 4 specimens; 42°18′N, 65°28′W, 113 m, sandy gravel, 1 specimen; 42°32′N, 65°39′W, 95 m, gravel, 1 specimen; 42°40′N, 65°56′W, 91 m, sandy gravel, 4 specimens; 43°10′N, 66°04′W, 92 m, gravel, 1 specimen; 43°21′N, 66°22′W, 60 m, shelly gravel, 2 specimens; 44°12′N, 66°36′W, 91 m, gravel, 1 specimen; 44°16′N, 66°28′W, 201 m, gravel, 1 specimen; 44°24′N, 67°14′W, 90 m, till, 1 specimen; 44°25′N, 66°25′W, 188 m, till, 3 specimens; 44°26′N, 66°19′W, 174 m, till, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of the studied specimens agrees with earlier descriptions made of the species (e.g., Carlgren 1893). The height of the contracted column is 3-28 mm. The pedal disc is wide with a distinct limbus. The relations between the length of the column and the diameter of the pedal disc is in the contracted state 14/23-7/17. The mesogloeal, diffuse sphincter is distally very strong (Figure 5A). The tentacles, conical and longitudinally furrowed with an apical pore, are arranged in four (sometimes five ?) cycles. The tentacular muscles are mesogloeal (Figure 5B). The number of mesenteries varies (in one of the larger specimens it is equal to 120 in the proximal part of the body). Most often (with the exception of the southernmost specimens) there are 16 pairs of perfect and sterile mesenteries. (In the specimens from 41°20′N, the number of perfect and sterile mesenteries is approximately 24-29, with an organization reminiscent of that in, e.g., *Parasicyonis*.) The long, folded actinopharynx is equipped with two siphonoglyphs (Figure 5C). All the imperfect mesenteries excluding those of the last cycle are often fertile (Figure 5D), the oocytes being provided with well-developed nurse cells (Figure 5F) during oogenesis. The parietobasilar muscles form even in very young individuals their own lobes high up in the column (Figure 5D, E).

NEMATOCYSTS.–*Column*: basitrichs 12-20 × 2.2-2.7, 30.5-38 × 4.4-5.5. *Tentacles*: basitrichs 14 × 2.2 - 24.5 × 3.3; microbasic *b*-mastigophors (30.5 × 6.5 -) 39-53 × 6.5-7.1; spirocysts 19 × 3.3 - 50 × 4.4-5.5 (in the young specimen from 44°24′N, the column of which was 3 mm high and the number of tentacles equal to 36, there was a somewhat different size for the tentacular nematocysts: basitrichs 15 × 2.2 - 22 × 2.7, microbasic *b*-mastigophors 28 × 5.3 - 33 × 7.1, spirocysts 14-22 × 2.7-3.8 μm). *Actinopharynx*: basitrichs 14 × 2.2 - 23 × 3.8; microbasic *p*-mastigophors 18 × 3.3 - 27 × 4.9; spirocysts 22 × 3.8 - 57 × 4.9-5.5. *Filaments*: basitrichs 9.5 × 2.2 - 22 × 2.7; microbasic *p*-mastigophors (17 × 3.8 -) 19 × 4.9 - 29 × 5.5, 24 × 3.3 - 29 × 3.3-4.4 μm.

My placing of the three specimens from the southernmost station within *S. coccinea* may be discussed. In some morphological characteristics, they resemble *Anthosactis* as well as *Parasicyonis*; apart from the development of the perfect mesenteries, the morphological differences between these, obviously young individuals, and the adult, typical *S. coccinea* are, however, not so comprehensive as to require description of a new subspecies.

Paranthus rapiformis (Lesueur 1817)

OCCURRENCE.–37°49′N, 75°25′W, 12 m, sand-silt-clay, 1 specimen.

GENERAL CHARACTERISTICS.–The column is smooth, much wider distally than proximally, and with a reddish brown color. The length of the column is 26 mm, with the proximal diameter 8 mm; the distal is 23 mm. The numerous tentacles are arranged in five (six ?) cycles. They are imperfectly retractile and acuminate. The sphincter is mesogloeal, of diffuse type, and weak. The yellowish, longitudinally folded actinopharynx is provided with two siphonoglyphs. The mesenteries are proximally fewer than distally, where they are arranged in four cycles (6+6+12+24 pairs). Twelve pairs of mesenteries (including the two pairs of directives) are perfect. The mesenterial retractors are of diffuse-restricted type. The parietobasilar muscles are only

slightly developed. The pedal disc is well defined and excavated. The individual studied was sterile.

NEMATOCYSTS.–*Column* (distally): basitrichs 17 × 1.6; microbasic *p*-mastigophors (?) ca. 16 × 3.3; spirocysts 33-60 × 3.8. *Column* (proximally): basitrichs 21-26 × 2.2, 16 × 2.7 - 26 × 3.8; microbasic *p*-mastigophors (rare) ca. 33 × 5.5; spirocysts 14 × 2.7 - 53 × 3.3. *Tentacles:* basitrichs 22 × 2.2 - 24.5 × 2.7; microbasic *p*-mastigophors 22 × 3.8 - 27 × 4.4; spirocysts 15 × 2.2 - 26 × 3.3. *Actinopharynx*: basitrichs 25 × 2.7 - 30 × 3.3; microbasic *p*-mastigophors 18.5 × 4.9 - 24.5 × 6; microbasic *p*(?)-mastigophors 27 × 4.9 - 30 × 5.5. *Filaments*: basitrichs 22 × 3.3 - 32 × 3.8-4.9; microbasic *p*-mastigophors (axial filament = about half the length of the capsule) 20 × 4.4 - 26 × 5.4; microbasic *p*-mastigophors (axial filament = almost the length of the capsule) 12.5 × 4.4 - 15 × 4.9; spirocysts 49-57 × 3.8-5.5 μm.

The most obvious difference between the above-mentioned specimen and the earlier description of the species (cf. Carlgren and Hedgpeth 1952:159), besides the different color of the column and the occurrence of 12 pairs of perfect mesenteries, is the size of the filamental basitrichs. While the filaments in material from Port Aransas and Port Isabel are provided with basitrichs ranging in size from 12.7 to 14 × 2.2 μm, the above-described specimen has much larger nematocysts of the corresponding type: 22 × 3.3 - 32 × 4.9 μm. The same tendency can be seen also with regards to the basitrichs of the column.

Antholoba perdix (Verrill 1882)

OCCURRENCE.–40°06′N, 71°00′W, 179 m, 1 specimen; 40°10′N, 70°00′W, 114 m, silty sand, 1 specimen; 40°10′N, 71°15′W, 110 m, silty sand, 1 specimen.

GENERAL CHARACTERISTICS.–The column is smooth and, in the material studied, tranversely wrinkled. The smaller specimens are olive-shaped; the larger specimen is cup-shaped with an expanded distal part. The color is greyish, with scattered, irregularly shaped, brownish spots. The oral disc of the larger specimen is greyish yellow with faintly marked, brown, and radially directed streaks. An outer lip-shaped fold is here provided on its outside with a zone, reddish brown in color. Two parallel ribbons of the same color divide this fold and the central part of the oral disc into two halves. The excavated pedal disc is faintly set off from the column. The length of the column is 12-21 mm, and its diameter is 16-44 mm. The pedal disc is maximally 23 mm in diameter. The tentacles are numerous (in the largest specimen about 600), short and conical, greyish in color. They are longitudinally furrowed and provided with an apical pore; in the smaller specimens they are sometimes equipped with small, papillar processes. The tentacles are arranged in five cycles, those of the outer cycles being much smaller than the inner ones (even in the largest specimen the outer tentacles are papillary). The fifth cycle of mesenteries is not complete. The number of perfect mesenteries in the larger specimen is 48. There are more mesenteries distally than proximally. The sphincter is alveolar (Figure 6). The retractors are diffuse and extended in length. The entoderm of the tentacles and the oral disc is reddish brown. All the specimens were sterile.

NEMATOCYSTS.–*Column*: basitrichs 20-28 × 2.7-3.3. *Tentacles*: basitrichs 15-16 × 1.6-2.2, 23 × 2.2 - 36 × 3.3-3.8; spirocysts (very numerous)

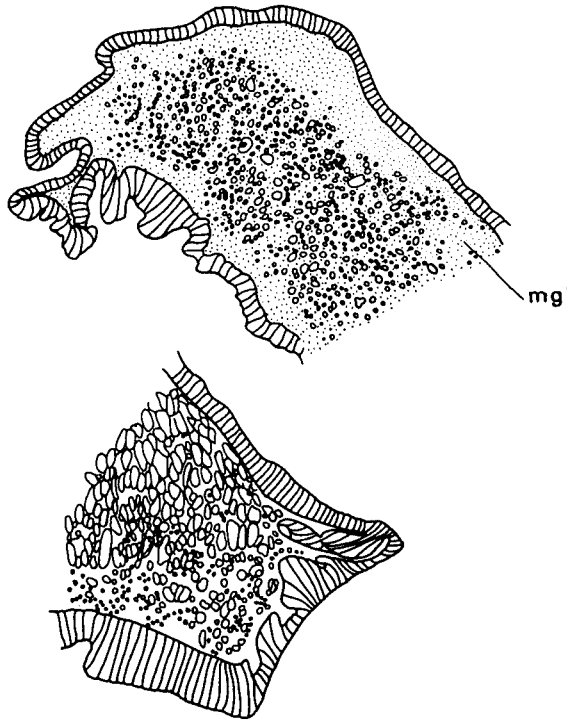


FIGURE 6.–*Antholoba perdix*. Sections through the distal parts of the sphincter in young specimens. mgl–mesogloeal layer.

19 × 3.3 - 46 × 3.8. *Actinopharynx*: basitrichs 14 × 1.6 - 16 × 2.2 (- 27 × 2.7); microbasic *p*-mastigophors 15 × 3.3 - 31 × 4.9. *Filaments*: basitrichs 14 × 1.6 - 28 × 2.7; microbasic *p*-mastigophors (very numerous) 14 × 4.4 - 31× 4.9-5.5 μm.

Metridiidae

Metridium senile fimbriatum (Verrill 1865)

OCCURRENCE.–40°35′N, 67°59′W, 84 m, gravel, 5 specimens; 40°40′N, 68°01′W, 84 m, sand, 1 specimen; 40°51′N, 68°55′W, 66 m, sand, 4 specimens; 41°04′N, 71°24′W, 42 m, 1 specimen; 42°00′N, 69°56′W, 48 m, gravelly sand, 1 specimen; 42°15′N, 70°12′W, 26 m, 3 specimens; 42°22′N, 70°18′W, 33 m, 2 specimens; 42°42′N, 65°18′W, 91 m, 1 specimen; 42°42′N, 65°40′W, 90 m, 3 specimens; 42°47′N, 66°25′W, 99 m, 1 specimen; 42°54′N, 66°14′W, 166 m, 2 specimens; 43°07′N, 65°57′W, 97 m, 1 specimen; 43°17′N, 65°35′W, 40 m, gravel, 1 specimen; 43°36′N, 68°50′W, 115 m, 2 specimens; 43°43′N, 66°30′W, 84 m, 1 specimen; 43°44′N, 66°28′W, 75 m, 1 specimen.

GENERAL CHARACTERISTICS.–They agree with earlier descriptions of the species (cf., e.g., Carlgren 1893:102). The height of the column varies between 5 and 35 mm, and the diameter of the pedal disc is 7-47 mm. The color is yellow to yellowish brown in the preserved state. The specimens from 40°51′N were all very young, the youngest being equipped with only 12 tentacles.

NEMATOCYSTS (sizes of the above-mentioned, small specimens in parentheses).–*Column*: basitrichs 15 × 2.7 - 19 × 3.3 (10 × 1.6 - 12 × 2.2); microbasic amastigophors 26-28 × 3.8-4.4 (16 × 3.3 - 21 × 3.8-4.4); microbasic *p*(?)-mastigophors 23-31 × 3.8-4.4; spirocysts 22-27 × 3.3-3.8. *Tentacles*: basitrichs (11.5 × 1.6 -) 18 × 2.2 - 28 × 2.7-3.3 (17-21 × 2.7-3.3); microbasic amastigophors 13 × 2.7 - 15 × 3.3; spirocysts 21 × 3.3 - 31 × 4.9 (11 × 2.7 - 17 × 4.4). *Actinopharynx*: basitrichs 26-39 × 3.8 (17 × 2.2 - 27 × 2.7-3.3); microbasic *p*-mastigophors 22-23 × 3.8 (17-23 × 3.3-3.8); microbasic amastigophors (rare) ca. 31 × 4.4. *Filaments*: basitrichs (very rare) ca. 14 × 3.8 (12 × 2.7); microbasic *p*-mastigophors 16-25 × 4.4, 24-32 × 3.8-4.4 (12-14 × 4.4, 21-23 × 3.8-4.4). *Acontia*: microbasic *b*-mastigophors 51-67 × 3.2-4.9 (40 × 3.8 - 57 × 4.4); microbasic amastigophors (28 × 3.8 -) 49-64 × 4.9-5.5 (36 × 4.4 - 55 × 5.5) μm.

Aiptasiomorphidae

Haliplanella luciae (Verrill 1898)

OCCURRENCE.–39°00′N, 76°22′W, 16 m, silty clay, 10 specimens.

GENERAL CHARACTERISTICS.–They agree with earlier descriptions (Stephenson 1925:888, 1935:197; Field 1949:10). The sizes of the nematocyst capsules deviate, however, in some respects from what has been described earlier (cf. Carlgren 1940a).

NEMATOCYSTS.–*Column*: basitrichs 10-11 × 1.6, 19 × 3.3 - 23 × 3.8; microbasic *p*- or amastigophors 19 × 3.8 - 21 × 4.4. *Tentacles*: basitrichs 15 × 1.6 - 20 × 2.2; microbasic *p*-mastigophors 18 × 3.8 - 25 × 4.9; spirocysts ca. 16 × 4.4-4.9. *Actinopharynx*: basitrichs (?) (the capsules are slightly bent) 30-32 × 2.7-3.3; microbasic *p*-mastigophors 23-27 × 3.8; microbasic *p*- or amastigophors 21-23 × 2.7-3.3. *Filaments*: basitrichs 14 × 1.6 - 19 × 2.2; microbasic *p*-mastigophors 22-28 × 3.8; microbasic a(?)-mastigophors 17 × 3.3 - 28 × 3.8; spirocysts 12.5 × 2.7 - 17 × 5.4. *Acontia*: basitrichs 15-18 × 1.6; microbasic *p*-mastigophors 43 × 5.5 - 56 × 6.5 μm. It was not possible to determine if there are any microbasic amastigophors present in the acontia, as all the mastigophor capsules were unexploded.

The only difference in the cnidom of the above-mentioned specimens and earlier descriptions of the species (cf. Carlgren 1945; Field 1949) besides the unsettled presence of microbasic amastigophors in the acontia (cf. Hand 1955) are the occurrence in this sample, of basitrichs in the actinopharynx, in agreement with the conditions in *Aiptasiomorpha texaensis* (cf. Carlgren and Hedgpeth 1952).

Sagartiidae

Sagartiogeton verrilli Carlgren 1942

OCCURRENCE.–40°32′N, 67°05′W, 338 m, 3 specimens, on fragments of mussel shell; 42°25′N, 66°21′W, 256 m, gravel, 1 specimen.

GENERAL CHARACTERISTICS.–The length

of the column varies between 8 and 18 mm, whilst the diameter of the pedal disc is 12-20 mm. The column is greyish, salmon-colored and divisible into scapus and scapulus. The scapus is provided with distinct mesenterial insertions shimmering through the ectoderm and has small tenaculi. The tentacles of the studied specimens are about 9 mm long, conical and acute. They are hexamerously arranged; in the largest specimen there are five cycles (6+6+12+24+40). The reddish-brown actinopharynx is strongly folded and provided with two siphonoglyphs. The color of the tentacles is greyish white, the largest specimen with reddish-brown pigmentation. The pairs of mesenteries are arranged in four to five cycles (proximally there are 90-100 mesenteries–distally only half the number are developed). The number of perfect mesenteries tends to vary. In one of the studied specimens there are 17 pairs (including the two directive pairs). The first cycle of mesenteries is sterile. The retractors of the first cycle of mesenteries are strong, of a circumscribed diffuse type (Figure 7A); in the other mesenteries they are diffuse. The parietobasilar muscles are rather weak (Figure 7B). The acontia are numerous and whitish in color. The mesogloeal, diffuse spincter is rather long.

NEMATOCYSTS.–*Scapus*: basitrichs 9-11.5 × 1.6, 16-17 × 2.2-3.3; microbasic amastigophors 30.5-35 × 4.4, ca. 15 × 3.8 (rare). *Tentacles*: basitrichs 13 × 2.2 - 27 × 2.7; microbasic amastigophors (16 × 3.8 -) 26 × 4.4 - 44 × 6.5; spirocysts 22 × 3.8 - 36 × 6. *Actinopharynx*: basitrichs 27-32 × 3.3; microbasic *p*-mastigophors ca. 23 × 4.4, 27-31 × 4.4-4.9. *Filaments*: basitrichs (rare) ca. 27 × 3.8; microbasic *p*-mastigophors 26-31 × 4.4-4.9; spirocysts 22 × 4.9 - 34 × 6. *Acontia*: basitrichs 36.5 × 3.8 - 43 × 4.4-4.9; microbasic amastigophors 57 × 6 - 64 × 7.1 μm.

Hormathiidae

Hormathia nodosa (Fabricius 1780)

OCCURRENCE.–40°54′N, 66°35′W, 265 m, 4 specimens; 41°30′N, 69°00′W, 146 m, till, 1 specimen; 42°14′N, 69°57′W, 102 m, 1 specimen; 42°26′N, 66°28′W, 265 m, gravel, 8 specimens.

GENERAL CHARACTERISTICS.–The 9-28 mm high scapus is provided with white tubercles arranged in longitudinally oriented rows. The

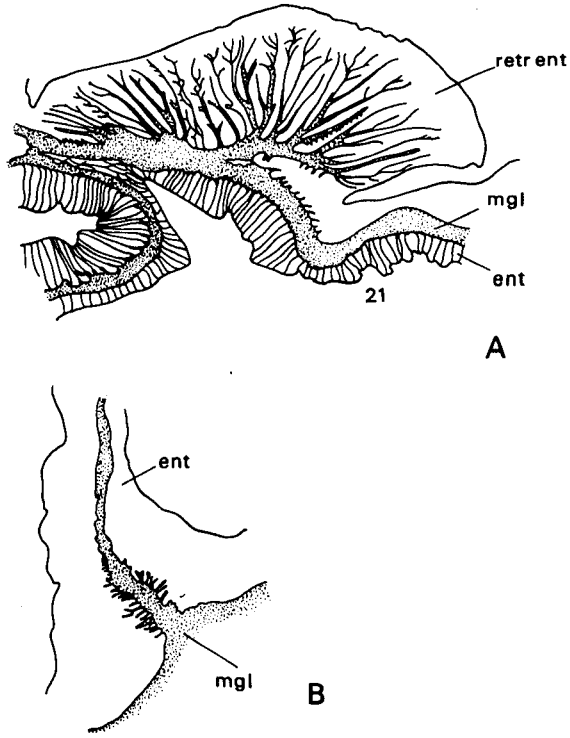


FIGURE 7.–*Sagartiogeton verrilli*. A. Section of the retractor of a perfect mesentery with adjacent parts of the actinopharynx. B. Section of the peripheral part of a mesentery (from the distal part of the scapus). ent–entoderm, mgl–mesogloea, retr ent–entoderm of retractor muscle.

scapular ridges are white and are 12 in number. The scapus is covered by a thin, greyish-white to greyish-brown periderm and is equipped with shallow longitudinal as well as transverse furrows; on the edge of the scapulus only radiating furrows are seen. The diameter of the column is 12-33 mm (diameter of scapus: diameter of the pedal disc = ca. 3:4). The tentacles are conical, reddish brown, and in older specimens longitudinally furrowed. They are 96 in number. The mesenteries have a maximum of 48 pairs (6+6+12+24), 6 of which (including the 2 pairs of directives) are perfect and sterile. The anatomical characters agree with earlier descriptions (cf. Carlgren 1893, 1933; Verrill 1922).

NEMATOCYSTS.–*Scapus*: basitrichs 8 × 1.1 - 11 × 1.6, 21-24 × 3.3-3.8; spirocysts 17 × 3.8 - 25 × 4.4. *Tentacles*: basitrichs 17 × 2.2 - 34 × 3.8; spirocysts 23 × 3.3-4.4 - 44 (56) × 5.4-7.6. *Actinopharynx*: basitrichs 16 × 1.6 - 35 × 3.3-3.8; microbasic *p*-mastigophors 23-33 × 3.8. *Fila-*

ments: basitrichs 14 × 1.1 - 16.4 × 1.6, 28 × 3.3 - 31 × 3.8-4.4; microbasic *p*-mastigophors 21 × 3.3 - 23 × 3.8. *Acontia*: basitrichs 32-40 × 3.8-4.4 μm.

Hormathia nodosa (?) (Fabricius 1780)

OCCURRENCE.–41°34′N, 68°40′W, 128 m, sandy silt, 1 specimen.

GENERAL CHARACTERISTICS.–The column is divisible into scapus and scapulus, the former being provided with a thin periderm and rather large, acuminated tubercles spread over the surface. The color of the scapus is proximally dark greyish brown, distally brown. Bordering upon the scapulus there are 12 large marginal tubercles. The pedal disc is not excavated; there are traces of mussel shell. The tentacles lack bulbous swellings on the abaxial side. They are arranged in four cycles. The actinopharynx and the sphincter agree with those in *H. nodosa* (cf. Carlgren 1893). The number of mesenteries is 96 (6+6+12+24 pairs), the perfect ones being 24 pairs in the distal part of the column. Immediately above the margin of the actinopharynx there are 20 pairs of perfect mesenteries. Only the six pairs of protomesenteries are sterile. The morphology of the retractors, parietobasilar, and basilar muscles agrees with that in typical *H. nodosa*. The length of the preserved specimen is: scapus 16 mm and scapulus 7 mm. The size of the pedal disc is 36 × 49 mm. The sizes of the different nematocyst types differ only slightly from those described in *H. nodosa* (see above). The large number of perfect mesenteries is, however, remarkable.

In view of the many morphological similarities between this specimen and typical *H. nodosa*, I consider it as an aberrant specimen of this species.

Actinauge verrilli McMurrich 1893

OCCURRENCE.–42°11′N, 65°56′W, 229 m, gravel, 1 specimen; 42°20′N, 67°28′W, 289 m, sandy gravel, 1 specimen; 42°50′N, 69°00′W, 187 m, sand-silt-clay, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of these specimens agrees with earlier descriptions of the species (cf. McMurrich 1893; Carlgren 1933). The scapus is equipped with a greyish-brown or brown periderm; it has a reticular appearance, arising from transverse as well as longitudinal, rather low, furrows. Distally there are 12 coronary tubercles. The firm wall of the scapulus is often whitish and is provided with 24, white, scapular ridges, proximally fusing two by two into 12. The scapus is cylindrical or dome-shaped, with the length 29-30 mm. The diameter of the scapus is proximally 17-30 mm and distally 19-20 mm. The length of the scapulus is 14 mm. The pedal disc is strongly excavated, often embracing sand grains. The long and tapering tentacles are arranged in four to five cycles. The outer tentacles are basally provided with abaxial swellings, which give rise to distinct processes. There are four cycles of mesenteries. Six pairs (including the two directive pairs) are perfect and sterile.

NEMATOCYSTS.–*Scapus*: basitrichs 8 × 1.6 - 23 × 4.4. *Tentacles*: basitrichs 12 × 2.2 - 27 × 2.7-3.3, ca. 40 × 3.8 (rare); microbasic *p*-mastigophors 24.5 × 3.8-5.2 - 38 × 8.2; spirocysts 19 × 3.3 - 37 × 4.4-6; 46-56 × 5.5-7. *Actinopharnyx*: basitrichs 13 × 1.6 - 17 × 2.2, 28-50 × 3.3; microbasic *p*-mastigophors 22 × 3.8 - 29 × 4.4. *Filaments*: basitrichs 11 × 1.1 - 17 × 2.2; 28-30.5 × 3.3, microbasic *p*-mastigophors 19 × 3.8-4.9 - 35 × 4.4. *Acontia*: basitrichs (14 × 2.2 -) 26 × 3.3 - 36.5 × 3.8-4.4 μm.

Phelliactis americana n. sp.

HOLOTYPE.–Specimen collected by the vessel *Delaware* from the type-locality (station number 27) on 19 February 1963 with an otter trawl. Deposited in the U.S. National Museum, catalog number USNM 54323.

TYPE-LOCALITY.–42°48′N, 63°42′W, 366 m, temperature +1.7°C.

PARATYPE.–Specimen collected by the vessel *Albatross IV* from station number 73 (42°17′N, 65°55′W, 238 m, gravel) on 15 August 1968 with a 1-m Naturalist dredge. Deposited in Northeast Fisheries Center, Woods Hole.

DIAGNOSIS OF HOLOTYPE.–Column firm, divisible into scapus and scapulus; somewhat asymmetric. Scapus distally with 48 rows of large, sometimes acute, tubercles. Scapular ridges about 70. Sphincter mesogloeal, and alveolar, very strong. Tentacles about 190, conical, and longitudinally furrowed with basal, abaxial swellings. Mesenteries in five cycles, 12 pairs being perfect

and sterile. Retractors of diffuse, restricted type. Parietobasilar muscles weak. Cnidom: *scapus* basitrichs; *tentacles* basitrichs and spirocysts; *actinopharynx* basitrichs and microbasic *p*-mastigophors; *filaments* basitrichs and microbasic *p*-mastigophors; *acontia* basitrichs.

GENERAL CHARACTERISTICS.–The column is firm and divisible into scapus and scapulus. It has a somewhat asymmetric appearance, one half of the body being larger than the other. The scapus (18 mm long) is cylindrical in the contracted state and has a reticular appearance with low tubercles formed by longitudinally as well as transversely oriented, low furrows; distally the scapus is provided with 48 rows of larger, sometimes acute, tubercles. The color of the remaining traces of periderm is brownish. The proximal part of the body is pillarlike, with the diameter 30 mm. About 70 scapular ridges are continued in the basilar swellings of the outer tentacles. The sphincter is rather short, but very strong, especially orally; it is alveolar and vertically stratified (Figure 8B). The actinopharynx is equipped with 12 longitudinal folds on each side of the two symmetrically arranged siphonoglyphs. The tentacles number about 190; they are rather short, conical, and longitudinally furrowed and are basally provided with abaxial swellings. The mesenteries are arranged in five cycles (6+6+12+25+50 pairs), 12 pairs (including the 2 pairs of directive mesenteries) being perfect and sterile. The retractors are of diffuse type, rather strong, and with their, in some perfect mesenteries, rather restricted pennons near to the actinopharyngeal wall (Figure 8C, D). The parietobasilar muscles are weak. The column, being somewhat wider distally than proximally, lacks cinclides. The whitish acontia are numerous and often very long. The mesogloeal layer is very thick in the whole column as well as in the mesenteries.

In the *paratype* the distal part of the column is in some parts severely damaged; the oral part is also introverted, giving rise to an oral slit, 58 mm long. The length of the scapus in this specimen is 40-30 mm; it is provided with low tubercles spread out over the column; distally there are 24 tubercles bordering the scapular ridges. The tentacles are arranged in four cycles (there are about 70 in the outer cycle) and are provided with abaxial swellings (Figure 8A). The mesenteries are hexamerously arranged in five cycles (the last cycle is, however, not complete in this specimen); proximally there are 75 pairs in total. The number of perfect and sterile mesenteries was impossible to determine in the paratype, but there are probably less than 12 pairs (probably 8). The wide and peripherally almost membraneous pedal disc is, to a small extent, excavated; its diameter measures 90 mm.

NEMATOCYSTS.–*Scapus*: basitrichs ca. 14 × 1.6-2.2, 24.5-44 × 3.3; spirocysts (not found in the paratype) 27 × 4.4 - 60 × 5.5. *Tentacles*: basitrichs 17-21 × 2.2 (not common), 34-43 × 3.3-3.8; spirocysts 38 × 4.4-4.9 - 75 × 8.7. *Actinopharynx*: basitrichs 16 × 2.2 (rare), 37 × 3.3 - 42 × 3.8; microbasic *p*-mastigophors 30 × 4.4 - 39 × 4.9. *Filaments*: basitrichs 12 × 1.6 - 22 × 2.2, 33 × 2.7 - 48 × 3.3; microbasic *p*-mastigophors 28 × 4.4 - 34 × 4.9. *Acontia*: basitrichs 16 × 2.2 - 23 ×2.5, 32 × 3.3 - 52 × 3.8 μm.

There are some morphological similarities between the above described specimens and *Phelliactis hertwigii* Simon as well as *Ph. incerta* Carlgren. The retractors of the perfect mesenteries are, however, stronger in *Ph. americana*, and the number of perfect mesenteries is larger (in the holotype 12 pairs).

Amphianthus nitidus (Verrill 1899)

OCCURRENCE.–41°27′N, 66°06′W, 128 m, 1 specimen; 41°39′N, 65°50′W, 183 m, 6 specimens; 42°10′N, 65°29′W, 163 m, 1 specimen.

GENERAL CHARACTERISTICS.–The column is firm, in the contracted state semispherical, and 9-16 mm high. The color is greyish white with a blue luster. The scapus is, in one of the studied specimens, equipped with eight low, extended tubercles. The diameter of the pedal disc is 12-16 mm. There is a distinct limbus. The tentacles are hexamerously arranged in four to five cycles (6+6+12+24+ a seldom completed fifth cycle), rather short, conical, and sometimes provided with an apical pore. The inner tentacles are larger than the outer ones. There are four to five cycles (57 pairs at most) of hexamerously arranged mesenteries, eight to nine pairs of which (including the two directive pairs) are perfect. All the mesenteries, except those of the last cycle and at least one of the directive pairs, are fertile. The number of mesenteries is larger proximally than distally. The acontia are numerous and yellow. The distally very strong, mesogloeal sphincter, the actinopharynx,

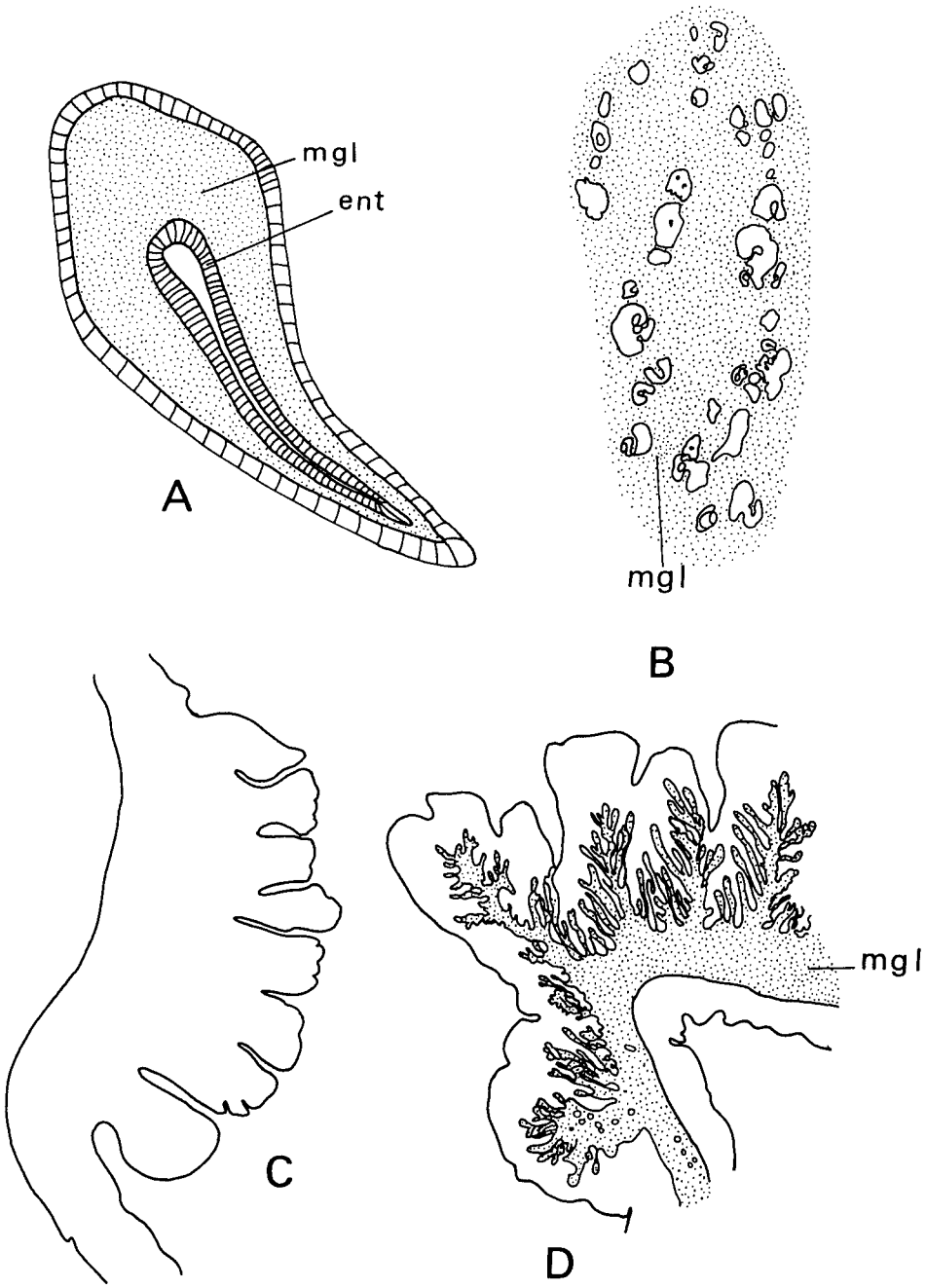


FIGURE 8.–*Phelliactis americana*. n. sp. A. Section through the basal part of a tentacle. B. Section through a part of the sphincter, showing the alveolar arrangement of the muscle fibrils (the fibrils are omitted in the figure). C. Section through a retractor from the third cycle of mesenteries. D. Cross section of a part of a retractor of one of the directive mesenteries. ent–entoderm, mgl–mesogloea.

and musculature of the specimens agree with earlier descriptions (cf. Carlgren 1934).

NEMATOCYSTS.–*Column*: basitrichs 8 × 1.6 - 12.5 × 2.7, 29-35 × 2.7; microbasic *p*-mastigophors 17 × 4.9 - 27 × 6; spirocysts 29 × 3.3 - 61 × 6. *Tentacles*: basitrichs 18.5 × 3.8 - 30 × 6; microbasic *p*(?)-mastigophors 18.5 × 4.4 - 29 × 4.4-5.5; spirocysts 19 × 3.3 - 47 × 7.6. *Actinopharynx*: basitrichs 24-25 × 3.3; microbasic *p*-mastigophors 23 × 4.4 - 26 × 5.5 (axial filament = about half the length of the capsule); ca. 27 × 4.9 (axial filament almost as long as the capsule). *Filaments*: basitrichs ca. 9 × 2.2; microbasic *p*-mastigophors 22 × 4.4 - 28 × 4.9. *Acontia*: basitrichs ca. 14 × 2.2; 42 × 6 - 57 × 6.5 μm.

Stephanauge nexilis (Verrill 1883)

OCCURRENCE.–41°54′N, 65°44′W, 366 m, 2 specimens; on the denuded axis of an octocoral.

GENERAL CHARACTERISTICS.–The yellowish, firm column is strongly elongated in the sagittal plane. The dimensions of the scapus is proximally 22 × 4 mm, the height of the column being 7 mm. In one of the specimens, the scapus is provided with 26 low, circularly arranged tubercles bordering 28 vague, radiating scapular ridges. The mesenterial insertions into the body wall are distinct. The number of the yellow, short, basally wide tentacles is not greater than that of the mesenteries (72 and 78). The sphincter is alveolar and strong, slowly diminishing in thickness towards the proximal part of the scapus. The wide actinopharynx is brownish yellow. It is equipped with two siphonoglyphs. The mesenteries are hexamerously arranged, more than six pairs (including the two pairs of directives) being perfect. At least some of the perfect mesenteries are equipped with genital organs. The retractors are diffuse and rather weak. The strong parietobasilar muscles produce distinct muscular lobes high up in the scapus, approximately at the middle of the mesenteries. The number of mesenteries is not greater proximally than distally. No acontia were found in these specimens (they might have been few and hidden by the strongly developed filaments), but basitrichs of probably acontian origin were measured in one of the specimens. No cinclides could be found.

NEMATOCYSTS.–*Scapus*: basitrichs (rare) ca. 12 × 2.2; microbasic *p*-mastigophors 12 × 4.4-5.5 - 19 × 5.5. *Tentacles*: basitrichs 9 × 1.7 - 20 × 2.7; microbasic *p*-mastigophors (axial filament almost as long as the capsule; diameter = 1.5 μm) 21 × 5.5 - 23 × 7.1; spirocysts 25 × 3.8 - 49 × 4.4. *Actinopharynx*: basitrichs 15-18 × 3.3; microbasic *p*-mastigophors 17 × 4.4 - 22 × 5.4-6. *Filaments*: basitrichs 14-16 × 2.7-3.3 (-28 × 2.7); microbasic *p*-mastigophors 16 × 3.8 (-6) - 27 × 5.5. *Acontia*(?): basitrichs 30.5-36.5 × 3.8 μm.

Hormathiidae (?)

Stephanauge (?) spongicola (Verrill 1883)

OCCURRENCE.–39°56′N, 69°45′W, 201 m, 3 specimens; 40°00′N, 69°30′W, 128 m, 3 specimens; 40°02′N, 70°47′W, 161 m, 6 specimens; 40°03′N, 71°16′W, 183 m, 16 specimens. At all the localities the specimens were found on the outside of the parchmentlike tubes of onuphid polychaetes.

GENERAL CHARACTERISTICS.–The column is often smooth but sometimes provided with a few adhesive warts; it is divisible into scapus and scapulus. The scapus was reddish brown to greyish brown in the preserved material, its length being 4-12 mm. The largest diameter is 10-11 mm. The scapulus is whitish to pale red. The periderm of the scapus is thin and easily falls off. The tentacles are conical, acute, and yellowish. They are hexamerously arranged in four to six cycles, those of the inner cycles being distinctly longer than the outer ones. The sphincter is short, mesogloeal, and agrees in its structure with that described by Carlgren (1950). It is not capable of covering all the tentacles. The actinopharynx is about three-quarters the length of the column, wide, and equipped with 18-20 deep, closely lying longitudinal folds (Figure 9A); it is yellowish in color. One (?) to four siphonoglyphs are present. In a specimen with two siphonoglyphs there was an eccentric position for them. There are (5-) 8-12 pairs of perfect mesenteries, the imperfect ones being 8-16 (-22) pairs. The structure of the retractors of the perfect mesenteries was in agreement with that described by Carlgren (1950) and in many ways reminiscent of those in *Phellia gausapata*. The number of directive pairs varies, being two, three, or four. The retractors of the perfect

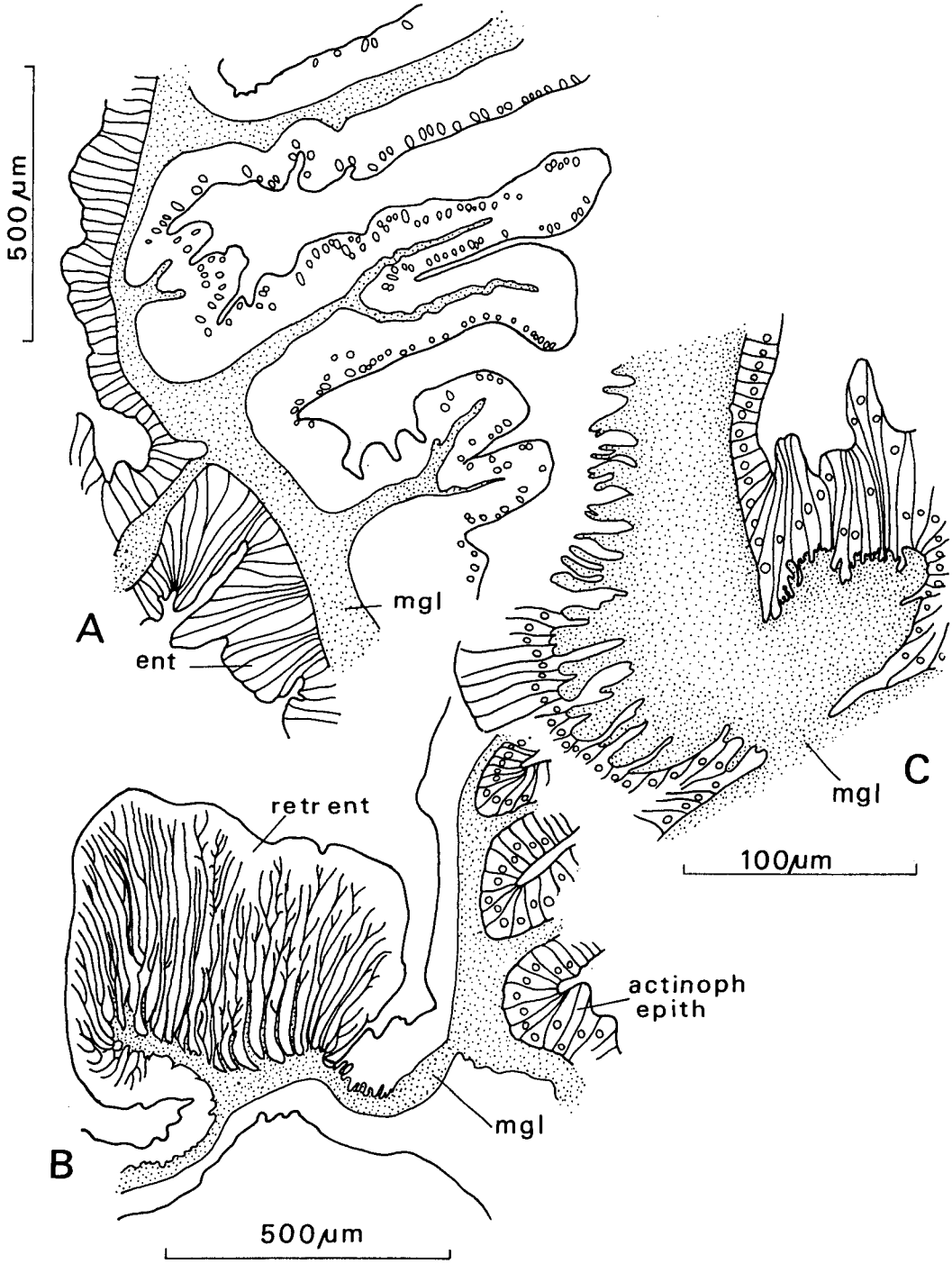
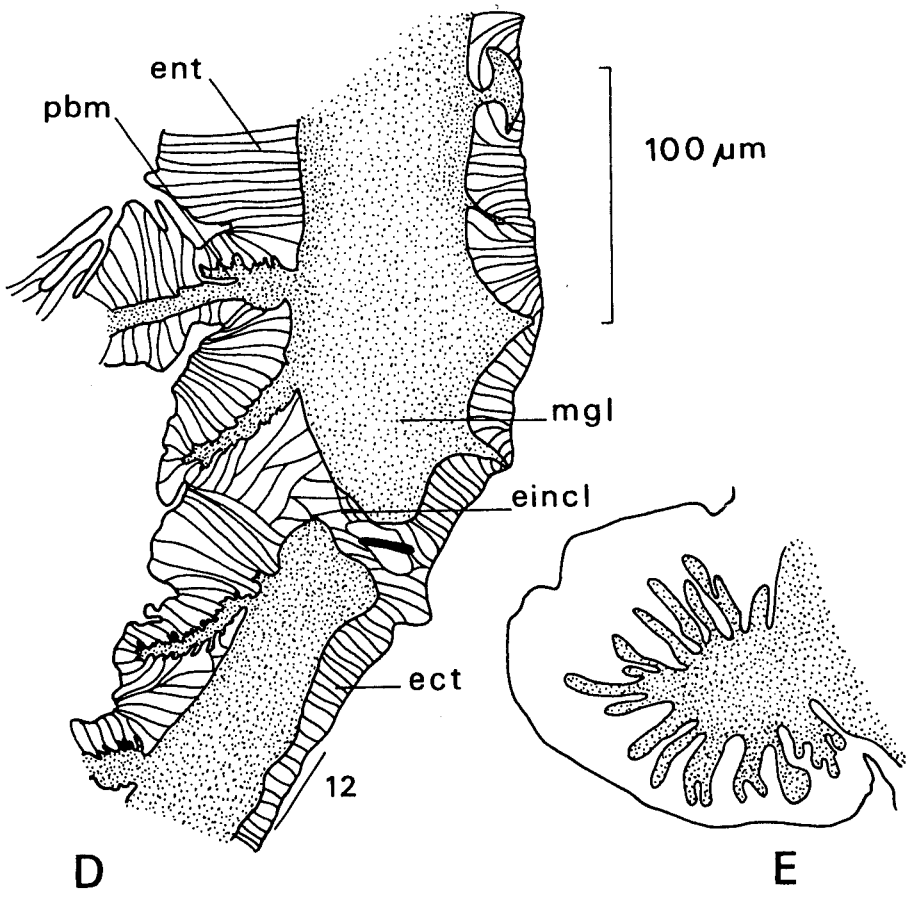


FIGURE 9.—*Stephanauge(?) spongicola.* A. Section through part of the actinopharynx. B. Cross section of a retractor of one of the protomesenteries. C. Cross section of the peripheral part of a perfect mesentery (the section is from the distal part of the column). D. Section through a part of the body wall. E. Section through a mesentery of the last cycle. actinoph epith—epithelium of actinopharynx, ect—ectoderm, eincl—ectodermal invagination forming an imperforate cinclis, ent—entoderm, mgl—mesogloea, pbm—parietobasilar muscle, retr ent—entoderm of retractor muscle.



mesenteries are strong, five to eight pairs being circumscribed, and sometimes reniform (Figure 9B), those of the other perfect mesenteries being diffuse but with a tendency to become restricted. The parietobasilar muscles are rather strong, forming distinct lamellae on the peripheral parts of the mesenteries (Figure 9C). The imperfect mesenteries lack retractors as well as filaments (always ?) (Figure 9E). In those specimens where genital organs were found, these were always developed in perfect mesenteries. The acontia are numerous and provided with basitrichs. Only one imperforate cinclis (Figure 9D) was found in the sections of the species. Probably the species reproduces asexually by laceration. The proximal part of the column and the often wide pedal disc are often asymmetrical.

NEMATOCYSTS.–*Column*: basitrichs (21 × 2.7 -) 23-27 × 3.3-3.8, 31-39 × 4.4; atrichs 19-20 × 4.4-4.9, 39-45 × 12.5-14.7. *Tentacles*: basitrichs 11 × 1.6-2.2 - 33 × 3.3-3.8; atrichs (not common; in many tentacles completely missing) 39 × 13.1 - 49 × 5.5, spirocysts (very numerous, and in some of the studied specimens with a very small variation in size) 17 × 2.2 - 34 × 3.8-4.9. *Actinopharynx*: basitrichs 14 × 2.2 - 32 × 3.8; microbasic *p*-mastigophors 17-26 × 3.8-4.4. *Filaments*: basitrichs 12-15 × 2.2; microbasic *p*-mastigophors 13 × 3.3 - 26 × 4.3-5.5. *Acontia*: basitrichs 13-16 × 2.2-2.7, 33 × 3.3 - 45 × 3.8 µm.

In specimens from 40°03′N, there were also found atrichs in the filaments (12 × 6, 18 × 4.9 - 24 × 5 µm) as well as holotrichs (22 × 4.9 - 24 × 5 µm). Both these nematocyst types are probably residues of intaken food–the specimens in question were found together with some individuals of *Epizoanthus incrustatus*.

This species, first described by Verrill (1883) as *Sagartia spongicola*, has been the object of later investigations by, e.g., McMurrich (1898) and Carlgren (1950). Carlgren (1950) (on the basis of acontian armament with basitrichs ?) described the species as a hormathiid and a member of the

genus *Stephanauge*, being aware of the existing anatomical differences in the development of the sphincter, the retractors, and the number of perfect mesenteries, siphonoglyphs, and directive mesenteries. To these differences should be added the occurrence of atrichous haplonemes, not only in the column ectoderm, but also in, at least, some of the inner tentacles. The arrangement of the mesenteries into filament-equipped perfect and into imperfect ones devoid of filaments as well as retractors should also be taken into consideration.

The morphology of this species shows so many differences from other species of the genus *Stephanauge* that I consider it very doubtful to place the species in this genus, or, taking into consideration the occurrence of atrichs in the studied specimens, in any other hormathiid genus.

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LITERATURE CITED

CARLGREN, O.

1891. Beiträge zur Kenntnis der Actinien-Gattung *Bolocera* Gosse. Öfvers. K. Vetenskaspakad. Förh. 48:241-250.

1893. Studien über Nordische Aktinien I. K. Sven. Vetenskaspakad. Handl. 25:1-148.

1931. Zur Kenntnis der Actiniaria Abasilaria. Ark. Zool. 23A(3), 48 p.

1933. The Godthaab Ezpedition 1928. Zoantharia and Actiniaria. Medd. Grønland 79(8), 55 p.

1934. Zur Revision der Actiniarien. Ark. Zool. 26A(18), 36 p.

1940a. A contribution to the knowledge of the structure and distribution of the cnidom in the Anthozoa. K. Fysiogr. Sällsk. Handl. Lund, N.F. 51:1-62.

1940b. Actiniaria from Alaska and Arctic waters. J. Wash. Acad. Sci. 30:21-27.

1945. Further contributions to the knowledge of the cnidom in the Anthozoa, especially in the Actiniaria. Lunds Univ. Arsskr., Ny Fobijl 41(9):1-24.

1949. A survey of the Ptychodactiaria, Corallimorpharia, and Actiniaria. K. Sven. Vetenskapsakad. Handl. 4(1): 1-121.

1950. A revision of some Actiniaria described by A. E. Verrill. J. Wash. Acad. Sci. 40:22-28.

CARLGREN, O., AND J. W. HEDGPETH.

1952. Actiniaria, Zoantharia and Ceriantharia from shallow water in the northwestern Gulf of Mexico. Publ. Inst. Mar. Sci. 2(2):141-172.

FIELD, L. R.

1949. Sea anemones and corals of Beaufort, North Carolina. Duke Univ. Mar. Stn. Bull. 5:1-39.

HAND, C.

1955. The sea anemones of central California. Part III. The Acontiarian anemones. Wasmann J. Biol. 13:189-251.

MCMURRICH, J. P.

1893. Report on the Actiniae collected by the United States Fish Commission steamer Albatross during the winter of 1887-1888. Proc. U.S. Natl. Mus. 16:119-216.

1898. Report on the Actiniaria collected by the Bahama Expedition of the State University of Iowa, 1893. Bull. Lab. Nat. Hist., State Univ. Iowa 4:225-249.

STEPHENSON, T. A.

1925. On a new British sea anemone. J. Mar. Biol. Assoc. U.K. 13:880-890.

1935. The British sea anemones. Vol. II. Ray Soc. (Lond.), Publ. 121, 426 p.

VERRILL, A. E.

1864. Revision of the *Polypi* of the eastern coast of the United States. Mem. Boston Soc. Nat. Hist. 1:1-45.

1867. Notes on the Radiata in the Museum of Yale College, with descriptions of new genera and species. Trans. Conn. Acad. Arts Sci. 1:247-596.

1883. Report on the results of dredging, under the supervision of *Alexander Agassiz*, on the east coast of the United States, during the summer of *1880*, by the U.S. Coast Survey steamer "*Blake*," *Commander J. R. Bartlett, U.S.N., commanding. XXI.* Report on the Anthozoa, and on some additional species dredged by the "Blake" in *1877-79*, and by the U.S. Fish Commission Steamer "Fish Hawk" in *1880-82*. Bull. Mus. Comp. Zool. 11(1):1-72.

1922. The Actiniaria of the Canadian Arctic Expeditions, with notes on interesting species from Hudson Bay and other Canadian localities. *In* A. E. Verrill (editor), Alcyonaria and Actinaria, p. 89-164. Rep. Can. Arctic Exped. 1913-18 8(G).

WEILL, R.

1934. Contribution à l'étude des cnidaires et de leurs nématocystes I-II. Trav. Stn. Zool. Wimereux 10-11:1-701.

DUAL STRUCTURAL EQUILIBRIUM IN THE FLORIDA SHRIMP PROCESSING INDUSTRY

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ABSTRACT

Stability, entry, exit, and mobility patterns for six size categories of firms in Florida shrimp processing industry for the 1959-71 period were studied by utilizing Markov Chain analysis. Forecasts over time predict that a structural equilibrium in the industry will be achieved by 1985. The forecasted changes in firm distribution suggest that Florida shrimp industry sales will become increasingly concentrated due to expansion in number of both small and large firms. A dual equilibrium, resulting in fewer medium-sized firms and more small- and large-sized firms, can be explained by the tendency for small firms to develop a specialty product and/or services in order to differentiate their markets from those of the very large firms. Medium-sized firms, then, tend to expand in size, or decline and either move to specialty products and services or exit from the industry.

Structural characteristics and patterns of Florida shrimp processing firms over the 1959-71 period, and the forecasts reveal several important structural characteristics of the industry. Entry into the Florida shrimp processing industry is relatively easy for small firms and more difficult for large firms. All firms are likely to move up in size by one only step or size category per time period. Exit from the industry in one time period is less probable for small and large firms than for medium-sized firms. Large firms are most likely to maintain their size between any two time periods and also experience less probability of declining in size than do medium- and small-sized firms.

Shrimp are the most important seafood processed in Florida. Total value of the shrimp processed in Florida in 1972 was slightly over $88 million. Processed shrimp products account for approximately 69% of Florida's total volume of nonindustrial seafood products and 70% of the value of seafood processed. In 1972, Florida's share of processed shrimp production in the southeast region was 28% (the southeast region representing about 75% of U.S. production). The growth of this industry was substantial during the last decade; both Florida's production and share of the U.S. market increased (Alvarez 1974).

Despite the growth in processing experienced by this industry, shrimp landings in the State declined significantly during the 1960-73 period. In 1960, 51 million pounds (23 million kg) of shrimp were landed; however, by 1973, landings declined to only 20 million pounds (13 million kg). Currently, the volume of shrimp processed in the State is three times as large as the volume of landings in the State, with the deficit being met by imports and non-Florida U.S. landings (Alvarez 1974). These comparisons indicate the basis of concern for the growth potential and nature of competition within the Florida shrimp processing industry. In a recent study addressing this concern (Alvarez 1974), emphasis was placed on processor sales concentration since there was evidence of "market power" in raw product purchases. The present study corroborates the findings of that study and further explains the results.

Predictions regarding future economic relationships are important to this industry for current managerial and investment decisions by firms and for long-run planning in optimizing firm size, scale economies, and product lines. Knowledge of the estimated number and size distribution of firms in the future will also help predict the character and intensity of competition within the market. Markov Chain analysis, employed in this study, is a useful tool for making such predictions. The analysis is a discrete-time stochastic process for which the state of the process at any time k depends only on the state of the process at the immediately previous time $k - 1$. A Markov Chain is described by listing the states of the chain, the initial probabilities of being in various states, and the probabilities of transition from one state to another (Bishir and Drewes 1970).

The purpose of this paper is to analyze by size category the entry and exit patterns of firms in the Florida shrimp processing industry during the

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1959-71 period. The prevailing entry and exit patterns during the 1959-71 period are then used to forecast firm distribution over time and predict the equilibrium state of firms within the market. Results from a 1973 survey (Alvarez 1974) of the Florida shrimp processing industry are utilized in discussing the economic and managerial implications of entry and exit patterns identified in this analysis.

This study only considers shrimp processing firms and not handlers who deal exclusively with raw headless shrimp. Shrimp processors cook, peel and devein, and bread or prepare specialty shrimp products.

THEORETICAL CONSIDERATIONS

That market structure of an industry, according to Bain (1968), embodies the framework or conditioning environment within which specific enterprise behavioral characteristics evolve. This behavior encompasses both the market conduct and the market performance of firms. These conditions in turn influence the type of structural equilibrium achieved within an industry. The following brief paragraph discusses the market structure theory relevant to this paper.

Market structure is defined as "... those characteristics of the organization of a market which seem to influence strategically the nature of competition and pricing within the market" (Bain 1968). The number and size distribution of sellers, the conditions of entry, exit, and mobility within the industry are important aspects of market structure to be considered. The number of sellers specifies how many firms are competing for the buyer's dollar. Generally, an increase in the number of competing firms is indicative of a movement toward freer competition (Ward and Smoleny 1973). The size distribution of firms is generally measured by volume of sales or by the proportion of total output of the industry supplied by a firm or a group of firms. Conditions of entry are defined as the relative easy or difficulty with which new firms may enter the market, determined generally by the advantage or control which established firms exercise over potential entrants (Bain 1968). Mobility gives an indication of the ability for firms within an industry to make adjustments in their size and, therefore, is an indicator of the degree of structural rigidity within an industry (Ward and Smoleny 1973). Structural equilibrium is that point where net changes are no longer shown in the market structure. The number and distribution of firms remain fixed. Firm entry and exit occur at offsetting rates (Ward and Smoleny 1973).

ENTRY AND EXIT PATTERNS DURING THE 1959-71 PERIOD

Lack of time series data for total sales by individual firms necessitated use of employment data during the 1959-71 period as a measure of firm size (Florida State Chamber of Commerce 1959-71). A comprehensive research project based on a 1973 survey conducted by the authors showed that firm size measured by employment compared favorably with sales or volume as a measure of firm size (Alvarez 1974). Productivity per worker for firms with similar product lines (95% of industry sales) is quite similar to further corroborate this conclusion. Thus, employment is a good proxy for firm size in the shrimp industry.

The Florida shrimp processing industry is composed of several firms, each of a given size. The measurement of size as well as size categories (states of nature) are defined in this study as follows:

State	*Size of firm (employees)*	*Sales classification, 1972*	
1	0	–	–
2	1- 10	small	<$2 million
3	11- 30	small	<$2 million
4	31-100	medium	$2-12 million
5	101-300	medium	$2-12 million
6	>300	large	>$20 million

Thirty-one firms processed shrimp in Florida during the 1959-71 period. These firms and their respective states of nature throughout the entire period are presented in matrix form (Table 1) in 2-yr intervals because the data are only reported biannually. Rows in the matrix specify the different states of nature for each firm during the period under consideration. Firm number 2, e.g., with state 1 in 1959 and 1961 was not in business, then in 1963 entered the industry in state 6 (firm size of over 300 employees), maintained that size in 1965 and 1967, and exited from the industry in 1969. From the data contained in the matrix of Table 1, the transition matrix presented in Table 2 was calculated.

The probabilities on the transition matrix illustrate the stability (diagonal), entry (row one), exit (column one), and mobility (off diagonal) patterns

TABLE 1.–Total number of Florida shrimp processing firms and their respective states of nature[1] during the 1959-71 period.

Firm no.	1959	1961	1963	1965	1967	1969	1971
1	4	4	4	2	2	3	3
2	1	1	6	6	6	1	1
3	4	4	4	5	5	5	5
4	4	1	1	1	1	1	1
5	1	1	1	4	1	1	1
6	1	1	1	1	1	3	1
7	1	1	1	1	1	2	1
8	3	3	3	3	3	1	1
9	1	1	3	3	3	1	1
10	1	1	1	2	2	2	2
11	1	1	1	1	2	2	2
12	1	2	2	2	2	2	2
13	5	5	1	1	1	1	1
14	4	3	3	3	3	4	4
15	1	1	1	3	3	3	3
16	5	5	5	6	6	6	6
17	5	5	5	1	1	1	1
18	1	1	1	3	3	3	3
19	1	1	1	2	1	1	1
20	3	3	1	1	1	1	1
21	4	4	4	1	1	1	1
22	3	3	3	4	3	3	3
23	6	6	6	5	5	6	6
24	5	5	1	1	1	1	1
25	1	1	1	5	5	5	5
26	1	1	1	6	6	6	6
27	1	1	3	3	3	1	1
28	1	1	1	1	4	3	3
29	1	1	1	1	4	4	4
30	2	2	2	2	2	3	3
31	3	3	3	3	3	4	3

[1]For a definition of state of nature utilized in this study see text.

TABLE 2.–Transition matrix of the Florida shrimp processing industry.

Employees (number)		States of nature 1	2	3	4	5	6
0	1	0.8025	0.0617	0.0617	0.0370	0.0123	0.0247
1- 10	2	.1053	.7895	.1053	—	—	—
11- 30	3	.1351	—	.7838	.0811	—	—
31-100	4	.1667	.0556	.2222	.5000	.0556	—
101-300	5	.1667	—	—	—	.7222	.1111
>300	6	.0769	—	—	—	.0769	.8462

to delineate the structure of the Florida shrimp processing industry during the 1959-71 period. Each entry (P_{ij}) in Table 2 represents the probability of a firm moving from state i (row) to state j (column); e.g., P_{34} (0.0811) is the probability of a firm increasing in size from state 3 to state 4 in the next time period, and P_{42} (0.0556) is the probability of a firm decreasing in size from state 4 to state 2 in the following time period.

Industry stability, the probability of a firm maintaining the same size between any two successive time periods, is represented by numbers on the diagonal. The highest probabilities in the transition matrix are for shrimp processing firms to maintain the same size between any two time periods, suggesting that the industry is fairly stable. Firms of the largest size (state 6) are most likely to maintain their size. Medium-sized firms in state 4 are least stable, illustrated by an equal probability of remaining in the same size category or changing between any two periods.

Firm entry, specified in row one, is most probable for the smaller sizes (0.0167 for sizes 2 and 3) while the probabilities decrease for larger sizes.

Firm exit probabilities, shown in column one, are lowest for the largest and smallest firms.

Firm mobility, measured by increases or decreases in firm size, is shown by the off-diagonal numbers in the transition matrix. Shrimp processing firms of any size have at least some probability of moving one state upward at a time but almost zero probability of increasing in size by more than one state at a time. Moving downward in size scale is somewhat different. The largest firms (state 6) have a small probability of going from state 6 to 5, and zero of moving more than one state at a time. The second largest firms (state 5) have zero probability of moving down possibly because state 4 is not stable for various economic reasons. There are probabilities of declines by one or two states for firms of size 4 but a zero probability of decline from state 3 to state 2.

CHARACTERISTICS OF THE DUAL EQUILIBRIUM

Several important implications for the structure of the Florida shrimp processing industry can be drawn from the above description of the transition matrix, for the 1959-71 period. A dual equilibrium, created by instability of medium-sized firms and greater stability of small and large firms, is evident in the industry. Medium-sized firms are least stable as shown by the highest probabilities for either exiting from the industry or increasing or decreasing in size, and the highest probabilities for moving down more than two states in any time period. The dual equilibrium, with most stability for firms with less than 30 and for firms with 300 or more employees, is the result of a special characteristic of the Florida shrimp processing industry.

The largest firms may be able to exert some "market power" for a number of reasons. To be competitive, firms desiring to sell a general line of shrimp products must be sufficiently large to achieve the economies of scale in purchasing and processing presently experienced by large firms. Even though entry into the largest size is difficult, exit from that size in one time period is very unlikely. Size characteristics along with the high

probability of remaining in the largest state for a long period of time permit large firms to be more secure and ultimately more stable than small firms. Thus, large firms develop greater access to raw supply sources which are currently scarce, and greater knowledge of the national market accompanied by stability in supplying their customers.

Small firms, being able to enter with relative ease, find it very difficult to advance in size but remain in their state without too much difficulty. These firms are more likely to succeed if they produce specialty products, sell in isolated markets, or develop forward integration from shrimp fishing operations.

Firms of medium size, neither displaying the characteristics of large nor small firms, either exit from the industry or make adjustments in their size and/or product lines. Medium-sized firms tend to be unstable initially because they apparently are not organized to successfully enter shrimp specialty markets yet are too small to compete in the national major line shrimp markets.

FORECASTING FIRM DISTRIBUTION AND PREDICTING A STRUCTUAL EQUILIBRIUM

A forecast[2] for the 1961-71 period of the number of shrimp processing firms in each state of nature was conducted and compared with the actual number of firms appearing in the data during the same period (Table 3). The purpose of this procedure was to evaluate the appropriateness of the transition matrix for forecasting firm distribution within the industry.[3] When comparing actual firm numbers to predicted numbers in states 2 through 6 for 1961 through 1971, 17 of the 30 predictions were accurate and in state 4, which is least stable, 5 of the 6 predictions were accurate, giving confidence that the dual equilibrium structure remains intact with the predicted numbers.

[2]To forecast firm distribution in the Florida shrimp processing industry over time requires that the transition matrix be stationary; that is, the probabilities in the transition matrix do not change over time. Although, the chi-square "goodness-of-fit" test was conducted and the results show the transition matrix to be stationary, predictions should be considered tentative due to the small number of observations per cell caused by the low number of firms in the industry. Forecasted distribution, however, being very close to that found in the past, indicates that the transition matrix remains useful for prediction.

[3]Some of the differences may be due to the small number of observations or to rounding procedures.

Forecasting Firm Distribution Over Time

The biannual forecasted distribution of firm size for the Florida shrimp processing industry from 1973 to equilibrium appears in Table 3. Few changes in the number of firms in each state are observed. The smallest sizes (states 2 and 3) experienced an increase of one firm each while the remainder (states 4, 5, and 6) show no change. Thus, there is an increase of two in the total number of active firms. The number and size of firms in the industry will attain a structural equilibrium in a relatively short period of time.

Equilibrium State Within the Market

The equilibrium matrix for the Florida shrimp processing industry was calculated to show the final distribution of firms within the industry under the assumption of a stationary transition matrix (Derman et al. 1973). In equilibrium, firms may still enter and exit but neither the number of firms in each state of nature nor the total number of firms in the industry changes once the equilibrium is reached.

The distribution of firms in the equilibrium state compared with the distribution of firms

TABLE 3.—Actual number[1] of firms in each state of nature in the Florida shrimp processing industry, compared with the corresponding predicted numbers[2] using the transition matrix, 1959-71 and forecasting to 1985 and equilibrium.

Year		States of nature 1	2	3	4	5	6	Total no. active firms
1959		16	1	4	5	4	1	15
1961	a	16	2	5	3	4	1	15
	b	15	2	5	3	3	2	15
1963	a	16	2	6	3	2	2	15
	b	15	3	6	3	3	2	17
1965	a	11	5	7	2	3	3	20
	b	15	3	7	2	2	2	16
1967	a	10	5	8	2	3	3	21
	b	11	5	7	2	3	3	20
1969	a	12	4	7	3	2	3	19
	b	11	5	8	2	3	3	21
1971	a	14	3	7	2	2	3	17
	b	12	4	7	2	2	3	18
1973	b	13	3	7	2	2	3	17
1975	b	13	4	7	2	2	3	18
1977	b	13	4	7	2	2	3	18
1979	b	12	4	7	2	2	3	18
1981	b	12	4	7	2	2	3	18
1983	b	12	4	7	2	2	3	18
1985	b	12	4	8	2	2	3	19
Equilibrium[3]		12	4	8	2	2	3	19

[1]Data from source (Florida State Chamber of Commerce).
[2]Computed using the transition matrix.
[3]The equilibrium probabilities of transition in column order for the six states of nature were one (0.3881), two (0.1319), three (0.2454), four (0.0685), five (0.0603), and six (0.1058) for each of the six respective columns.

during the 1959-71 period (Table 3) shows that firms of the smaller sizes (states 2 and 3) increase in number as the industry reaches the structural equilibrium, while firms in states 4 and 5 decrease and firms in the largest size increase in number. This is a consequence of the industry dual equilibrium conditions of entry and exit identified in the 1959-71 period.

At the structural equilibrium, and in support of the dual equilibrium, the probabilities for firm entry are highest for firms with less than 30 employees and for those with more than 300 employees. Thus, the least amount of entry activity will occur within the medium-sized firms.

Mean Lifetime for Each Size Category

Mean lifetime values for each size category were calculated (Table 4) and further support the prevalence of a dual equilibrium in the Florida shrimp industry. Mean lifetime represents the number of years a firm tends to stay in a given state of nature. The largest firms tend to maintain their size for a greater number of years (13) than firms in any other size category. Firms of sizes 2 and 3 have mean lifetime values of 9 yr, while firms of size 4 and size 5 tend to remain for an average of 4 and 7 yr in their respective states. These findings are the result of the firms' probabilities of maintaining their size between any two time periods. Column 2 of Table 4 represents the number of years spent in each size for an equilibrium distribution (perfectly mobile industry); the values are very similar. The data in Column 3 indicate state rigidity where the smaller the ratio, the more rigid the state. State 6 is the most rigid state in the industry, followed by states 2, 3, 5, and 4, respectively.

TABLE 4.—Mean lifetime in years for each size category for the Florida shrimp processing industry[1]

States of nature[2]	Column 1 Average[3] (yr)	Column 2 Perfect[4] (yr)	Column 3 Ratio[5]
2	9.500	2.304	0.243
3	9.250	2.650	.286
4	4.000	2.418	.604
5	7.200	2.128	.296
6	13.000	2.236	.172

[1]Mean lifetime represents the number of years a firm tends to stay in a given size category. In this case, results were multiplied by 2 since each time period equals 2 (yr) in the data.

[2]State 1 is not included because it is an absorbing state.

[3]Calculated from the transition matrix with the formula $(1/1 - P_{ii})$.

[4]Time spent in each state for a perfectly mobile industry as calculated from the equilibrium size distribution.

[5]Column 2 ÷ Column 1.

LITERATURE CITED

ALVAREZ, J.
1974. The Florida shrimp processing industry: Economic structure and marketing channels. M.S. Thesis, Univ. Florida, Gainesville, 168 p.

BAIN, J. S.
1968. Industrial organization. John Wiley and Sons, Inc., N.Y., 678 p.

BISHIR, J. W., AND D. W. DREWES.
1970. Mathematics in the behavioral and social sciences. Harcourt, Brace & World, Inc., N.Y., 714 p.

DERMAN, C., J. G. LEON, AND O. INGRAM.
1973. A guide to probability and application. Holt, Rinehart, and Winston, Inc., N.Y., 750 p.

FLORIDA STATE CHAMBER OF COMMERCE.
1959-71. Directory of Florida industries. Florida State Chamber of Commerce, Jacksonville, Biannual Issues.

WARD, R. W., AND C. SMOLENY.
1973. The market structure of Florida fresh grapefruit packers: An application of Markov Chain analyses. Econ. Res. Dep. 73-1, Fla. Dep. Citrus and Univ. Fla, Gainesville, 91 p.

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DISTRIBUTION AND ECOLOGY OF PELAGIC FISHES STUDIED FROM EGGS AND LARVAE IN AN UPWELLING AREA OFF SPANISH SAHARA

MAURICE BLACKBURN[1] AND WALTER NELLEN[2]

ABSTRACT

Fish eggs and larvae were taken in vertical zooplankton hauls in a small upwelling area off Spanish Sahara. Series of hauls were made repetitively from March to May 1974, sometimes with accompanying hydrocasts. About 58% of the eggs and 72% of the larvae belonged to the following pelagic species: *Sardina pilchardus*, *Engraulis encrasicholus*, *Trachurus* spp., and *Maurolicus* sp. It was estimated from contemporaneous current meter data and other information that the eggs of those species were spawned very close in time and space to where they were collected. Thus adult *Sardina* and *Engraulis* appeared to occur typically on the continental shelf, adult *Trachurus* at the edge of the shelf, and adult *Maurolicus* over the continental slope. These distributions were verified for *Sardina* and *Trachurus* from fishing results of Polish vessels. Acoustically detected concentrations of fish were identified by species according to those results.

The area of abundance of *Sardina* was characterized by maxima of phytoplankton and small zooplankton. Abundance of *Sardina* eggs changed with time, because of variations in the size of the adult population in the area (acoustically estimated) and in its production of eggs. The major change in population size coincided with a similar change in the amount of food, especially phytoplankton, available. Variations in egg production may have been associated with the mean temperature in the water column, since eggs were scarce when the mean was below 16.5°C even when adults were abundant.

A multidisciplinary group of U.S. scientists made an oceanographic study off Spanish Sahara from March through May 1974. The program is called Coastal Upwelling Ecosystems Analysis (CUEA) and is part of the International Decade of Ocean Exploration (IDOE). The operation off Spanish Sahara (Figure 1) was called JOINT-I. It made observations of many kinds over an upwelling area which was small enough to be studied synoptically in great detail repetitively under various conditions such as changes in the wind field. Most of the work was done from the coast to long. 18°00′W, between lat. 21°30′ and 21°50′N. The continental shelf in this area is bounded by the 100-m isobath, beyond which there is a steep slope (Figures 2-4).

Pelagic fish are a major component of the animal biomass in the area. They support large fisheries conducted by several nations. It was the task of a small group of CUEA investigators to estimate biomass of pelagic fishes by species and, if possible, by trophic levels during JOINT-I; to show the distributions of these biomasses in space and time;

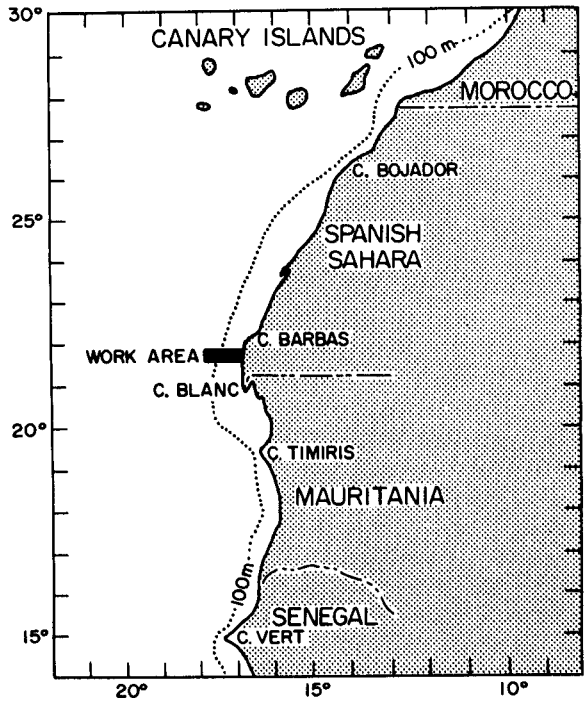

FIGURE 1.—Part of northwest Africa showing the principal area of JOINT-I work.

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and to explain the distributions in terms of environmental parameters. Biomass of total pelagic fish was estimated acoustically (Thorne et al. in press). Partitioning it by species was to be based on the following: contemporaneous catches by fishing or fishery research vessels, samples of fish taken by the CUEA ships, fish eggs and larvae from the zooplankton catches of the CUEA ships, and the literature. In the outcome, only the fish eggs and larvae (ichthyoplankton) were useful during the cruise. Good information on fish catches by other vessels was not received until many months later, sampling from the CUEA ships was unproductive for adults of epipelagic species, and the literature did not resolve all questions. The ichthyoplankton results and the fish catches agreed as to the principal species present in different parts of the area. Acoustically detected concentrations of fish (Thorne et al. in press) were identified accordingly.

This paper gives the principal results of work on the eggs and larvae. It then uses the egg distributions to estimate contemporaneous distributions of adults of some species and compares those with data from contemporaneous fish catches and the literature. Finally the paper attempts to explain the distributions of an abundant species, *Sardina pilchardus* (Walbaum), according to environmental data collected at the same time as the eggs.

MATERIAL AND METHODS

Zooplankton

The fish eggs and larvae were sorted from the zooplankton catches made during JOINT-I and partly identified by Blackburn. Most of the identifications were made later by Nellen. The zooplankton catches were made and processed, apart from the ichthyoplankton, by R. I. Clutter. Some observations on the zooplankton in general are relevant in this study. A more complete report on JOINT-I zooplankton will appear elsewhere.

The net hauls for zooplankton were made vertically from 200 m or the bottom, whichever was less, to the sea surface. Two cylindro-conical, nonclosing Bongo plankton nets mounted side by side were used. Each net had a mouth diameter of 60 cm and a uniform mesh size of 102 μm. Nets were lowered at 40 m/min and hauled up at 60 m/min. A calibrated digital flowmeter was mounted in the mouth of each net. Volume of water filtered by the two nets ranged from 12 to 158 m^3, depending mainly upon the haul length. Only one net was used in series 1 and 2 (Table 1).

Processing was as follows, with exceptions shown in footnotes to Table 1. The catches from the two nets were immediately combined and suspended in water. The suspension was shaken and four ¼-aliquots were decanted. Each of two aliquots was filtered through a series of sieves (mesh sizes 1,050, 505, 223, and 102 μm) until no more water dripped. This procedure yielded subsamples of zooplankton in four size ranges, approximately 100 to 200, 200 to 500, 500 to 1,000, and > 1,000 μm. The subsamples from one aliquot were scraped from the filters, blotted on paper towels until no more water appeared, and weighed. The subsamples from the other aliquot were washed off the filters and preserved in Formalin.[3] The fish eggs and larvae were sorted from the preserved 500- to 1,000- and >1,000-μm samples and combined. The four wet weights per haul were standardized in grams under 1 m^2 of sea surface. Allowance was made trigonometrically for effects

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

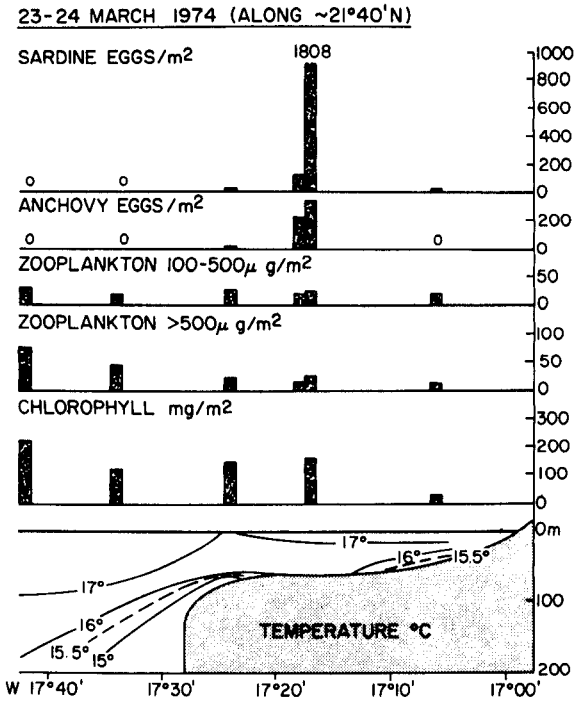

FIGURE 2.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40'N on 23-24 March 1974 (series 5 in Table 1).

TABLE 1.—Means of variables for the water column at stations from long. 17°08′ to 17°25′W, in series of stations along lat. 21°40′N together with indications of relative abundance of adult sardines explained in Discussion.

Series	Date 1974	No. of stations	Sardine eggs/m²	Anchovy eggs/m²	Temp. °C	Chlorophyll (mg/m²)	Small zooplankton (g/m²)	Abundance of adult sardines
1	8- 9 Mar.	[1]4	10	1	16.5	115	[2]85	Low
2	10-11 Mar.	[3]4	4	0	16.5	30	[2]90	Low
3	15-17 Mar.	[4]4	0	0	16.0	193	[5]78	([6])
4	18 Mar.	3	5	30	16.0	71	[5]27	([6])
5	23-24 Mar.	3	648	195	16.5	164	20	High
6	1- 2 Apr.	2	0	57	16.5	52	19	Low
7	5 Apr.	3	8	5	15.5	187	24	Medium
8	12-13 Apr.	[7]3	54	36	17.0	147	32	Medium
9	22-23 Apr.	3	7	19	16.0	192	28	Medium
10	9-10 May	4	431	2	16.5	323	53	High

[1]Three stations for eggs and zooplankton.
[2]Estimated from settled volumes at 1 ml = 0.8 g. Not corrected for phytoplankton contamination.
[3]One station for chlorophyll.
[4]Two stations for eggs and zooplankton.
[5]Estimated according to mean ratio of small to total zooplankton at same longitudes in other series, namely 67%. Not corrected for phytoplankton contamination.
[6]Unknown.
[7]Two stations for chlorophyll.

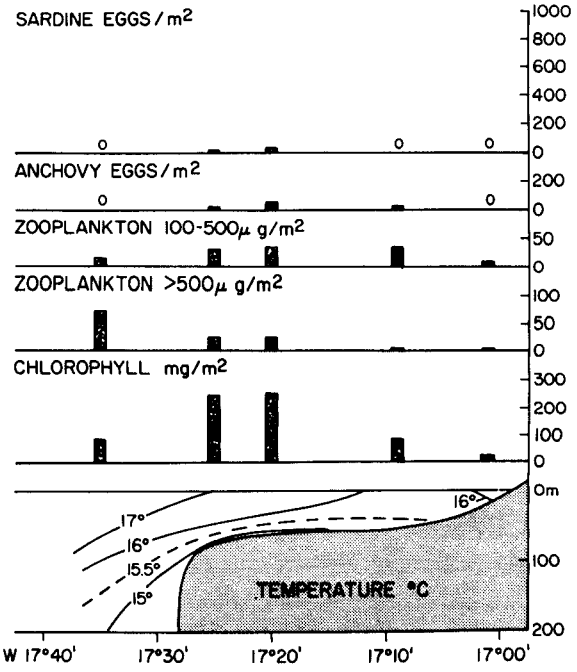

FIGURE 3.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40′N on 22-23 April 1974 (series 9 in Table 1).

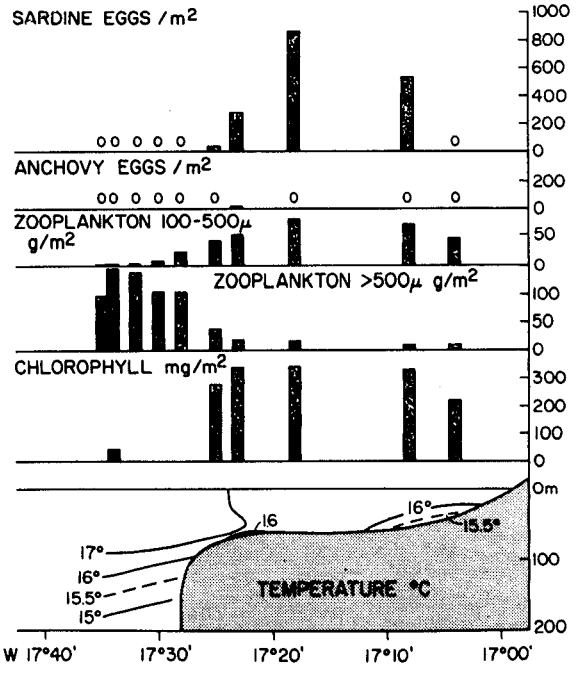

FIGURE 4.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40′N on 9-10 May 1974 (series 10 in Table 1).

of nonzero wire angles on distance covered by the net. To determine effects of clogging, the expected flow of water through the net was compared with that indicated by the flowmeter revolutions. Counts of various kinds of fish eggs and larvae from each haul were standardized in numbers under 1 m² of sea surface.

In general the spatial distribution of zooplankton biomass was similar for the 100- to 200- and 200- to 500-μm fractions. The two fractions of larger-sized plankton were also distributed similarly, but not like the smaller-sized fractions. Thus we distinguish only zooplankton at 100 to 500 μm and at >500 μm (Figures 2-4). Most of the

biomasses given here, but not all (see Table 1), have been corrected for contamination by phytoplankton. The correction was made as follows. The amount of chlorophyll *a* was determined in a ¼-aliquot by SCOR methods (UNESCO 1966) and partitioned among the four subsamples according to inspection of the preserved samples. The inspection indicated approximate relative amounts of phytoplankton in the samples. The chlorophyll weight for each subsample was converted to carbon following Lorenzen (1968) and then to wet weight according to Cushing et al. (1958). The correction generally reduced the original biomass by less than 10% but occasionally up to 30%. All biomasses shown in Figures 2 to 4 have been corrected.

The preserved samples of zooplankton <500 μm were not examined for ichthyoplankton, because few specimens (except some newly hatched larvae) were expected to pass through a 500-μm sieve. For eggs of Engraulidae, which are oval and measured from 500 to 580 μm (mean 570 μm) in transverse diameter in our material, our numbers per haul could have been slightly too low because of losses through the 500-μm sieve. It is unlikely that these losses were high. During a later cruise (AUFTRIEB 1975) in the same area, we counted engraulid eggs in the catches of two Bongo nets of uniform mesh sizes, 300 and 500 μm, but otherwise identical and hauled side by side in the same net assembly. Egg numbers were 122 and 145, so the 300-μm net retained no more than the 500-μm net.

Temperature and Chlorophyll *a*

These properties were measured from hydrographic casts which used plastic 5-liter Niskin bottles with reversing thermometers. Sampling depths in the upper 200 m were usually 0, 3, 10, 20, 30, 50, 75, 100, 150, and 200 m, depending on the bathymetry. Concentrations of chlorophyll *a* were determined by SCOR methods (UNESCO 1966) and integrated in milligrams per square meter. The integration program summed the area of each depth integral using the area formula of a trapezoid. Samples for chlorophyll *a* were generally not taken below 75 or 100 m, because results of other casts showed little chlorophyll below those depths.

Area and Periods of Study

Almost all the zooplankton hauls and hydrographic casts of JOINT-I were made in the area shown in Figures 1 and 5. They were generally made along an east-west line at about lat. 21°40′N, where series of hauls and casts (not always together) were frequently repeated. Figure 5A shows the positions of all zooplankton hauls made in the area. Nine other hauls were scattered in space and time in adjacent areas, and are not used in this paper. No distinction is made here between day and night hauls. Hauls on the shelf were made mostly by day and those on the slope mostly at night. Eggs are of more interest than larvae in this study as explained above and should have been equally available by day and night. Larvae might have avoided the nets more by day than by night.

The total period of JOINT-I in which zooplankton hauls were made was 8 March to 10 May 1974. It was divided by port calls into three parts, Legs 1, 2, and 3 (Table 2). The periods of these legs (first to last zooplankton haul) were 8 to 24 March, 1 to 14 April, and 22 April to 10 May.

Ten series of hauls were made together with hydrographic casts along lat. 21°40′N, each series occupying 1 to 3 days. Figures 2 to 4 show data for some of the series and Table 1 summarizes data for all of them.

TABLE 2.—Principal categories of fish eggs and larvae taken on JOINT-I in the area of Figure 5, showing numbers per square meter averaged for hauls on each leg of the cruise and summed for the cruise.

Category	Leg 1 (41 hauls)	Leg 2 (22 hauls)	Leg 3 (38 hauls)	Cruise total	
				No.	%
Eggs:					
Sardina	77.7	10.9	75.9	6,308	35.1
Engraulis	19.0	16.1	14.8	1,695	9.4
Maurolicus	6.2	29.3	15.4	1,487	8.3
Soleidae	9.9	15.0	8.8	1,071	6.0
Carangidae	4.8	0.7	18.1	897	5.0
Others	55.3	56.1	79.8	6,531	36.2
Larvae:					
Clupeoidei	60.5	82.9	84.7	7,522	69.7
Heterosomata	24.1	16.5	5.0	1,541	14.3
Sparidae	6.6	22.6	9.3	1,120	10.4
Maurolicus	1.2	1.3	2.8	185	1.7
Myctophidae	0.9	0.7	1.3	102	0.9
Carangidae	0.4	2.1	0.4	78	0.7
Others	3.5	2.3	1.5	251	2.3

IDENTIFICATION AND ENUMERATION OF EGGS AND LARVAE

The eggs and larvae from all stations in Figure 5A were identifiable in the categories shown in Table 2. Most of the identifications were made at the Institut für Meereskunde from the large collections, literature, and experience of northwest

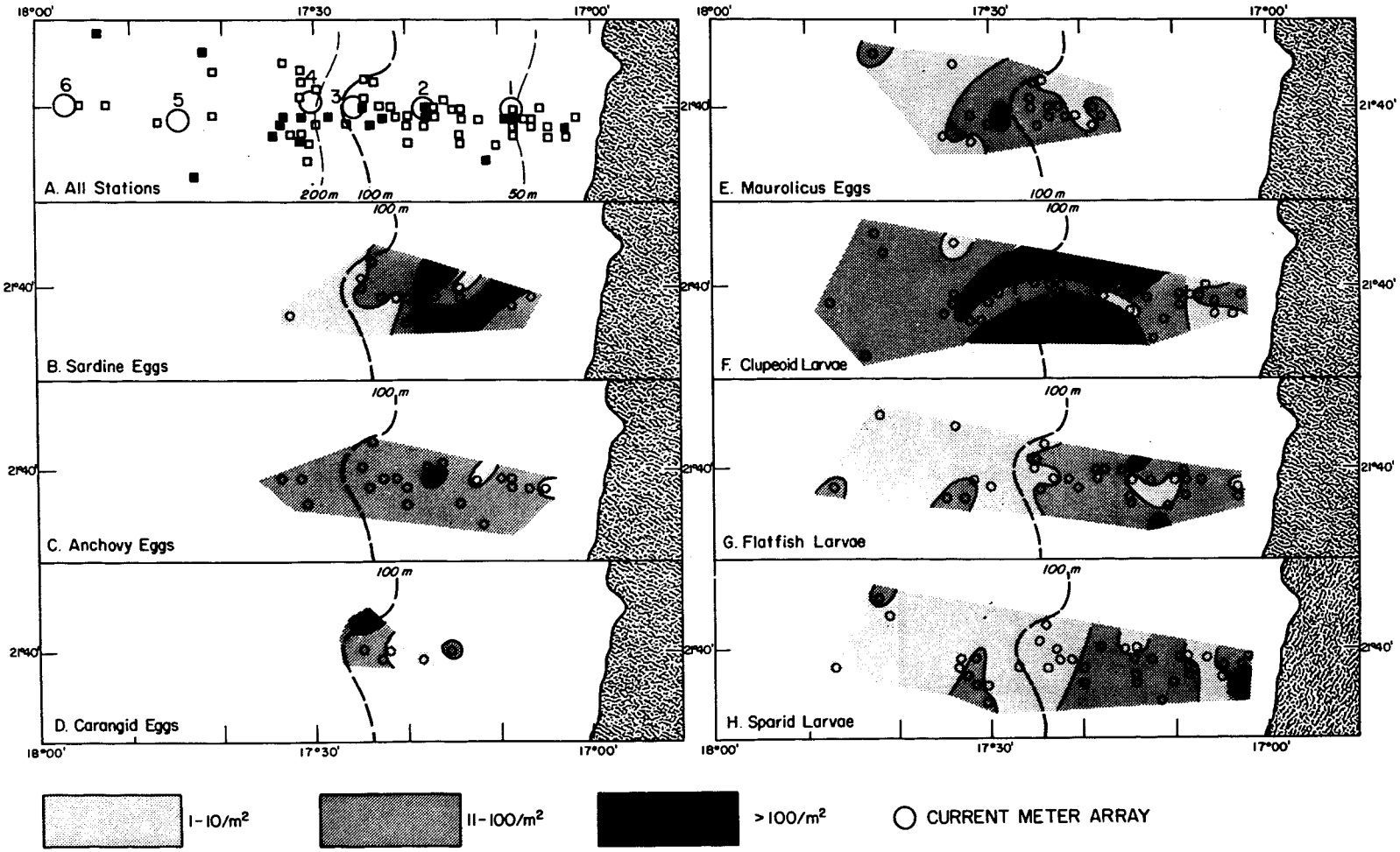

FIGURE 5.—Distributions of fish eggs and larvae from the zooplankton of JOINT-I, between lat. 21°30′ and 21°50′N. A. Positions of all zooplankton hauls. Solid squares show where hauls were repeated. Circles show current meter arrays. B to H. Positions of positive hauls for kinds of eggs and larvae stated, contoured in numbers per square meter.

African ichthyoplankton available there. Identifications of larvae were more complete than those of eggs, as is usual in work of this kind.

Among the eggs the following kinds, which are well known in literature because of conspicuous characters, were easily identified: *Sardina, Engraulis, Maurolicus*, and Soleidae.

The eggs of *Sardina* and *Sardinops* are alike but the only species of either genus recorded off northwest Africa is *Sardina pilchardus* (Walbaum). *Sardina pilchardus* occurs off southwestern Europe, in the Mediterranean, and on the coast of northwest Africa as far south as lat. 20°N (de Buen 1937; Larrañeta 1960; Maurin 1968; Furnestin and Furnestin 1970). We identify the eggs as that species, which we later call "sardine." Egg diameters in our material range from 1.33 to 1.50 mm (mean 1.46 mm), slightly lower than those of the same species in the Mediterranean (1.40 to 1.70 mm; Larrañeta 1960). However they are considerably larger than those of *Sardinella*, the other clupeid genus that might occur, whose eggs measure 1.1 to 1.3 mm off west Africa (Marchal 1967).

Engraulid eggs were easily recognizable by their oval shape. Two species of Engraulidae have been reported off southern Spanish Sahara, *Engraulis encrasicholus* (Linnaeus) and *Anchoa guineensis* (Rossignol and Blache) (Lozano Cabo 1970; Bravo de Laguna Cabrera and Santaella Alvarez 1973). No adults were obtained during JOINT-I, so identification has been made from the eggs. Eggs of *E. encrasicholus* range from 0.90 to 1.9 mm in length and 0.42 to 1.2 mm in maximum breadth (Demir 1963); corresponding ranges for *A. guineensis* are 1.05 to 1.23 and 0.54 to 0.58 mm, respectively (Marchal 1966), and for our material 1.33 to 1.50 and 0.50 to 0.58 mm, respectively. Our eggs could belong to either species as far as breadth is concerned, but only to *E. encrasicholus* on the basis of length. We refer to this species later as "anchovy." It occurs off western Europe and in the Mediterranean and Black seas, as well as off northwest Africa, where its southern limit is not exactly known (de Buen 1931 and references above).

The eggs of *Maurolicus* (family Gonostomatidae) are those of *M. muelleri* (Gmelin), which has been recorded off southern Morocco and northern Mauritania (Maurin et al. 1970). The eggs of Soleidae could belong to several species recorded off Spanish Sahara (Maurin et al. 1970; Lozano Cabo 1970).

The carangid eggs were identified with help from E. H. Ahlstrom, who noted that some of them resembled *Trachurus*. They measured about 0.9 to 1.0 mm, in the size range reported for *T. trachurus* (Linnaeus) off northwest Africa (Kiliachenkova 1970). Three other species of *Trachurus* have been recorded off northwest Africa, namely *T. picturatus* (Bowdich), *T. trecae* Cadenat, and *T. mediterraneus* Steindachner. *Trachurus picturatus* is not common and *T. mediterraneus* may be a subspecies of *T. trachurus* (Letaconnoux 1951; Maurin et al. 1970; Witzell 1973). The three most common carangids in the area of Figure 1 are *T. trachurus*, *T. trecae*, and *Caranx rhonchus* Geoffroy St. Hilaire. The first two spawn off Spanish Sahara from about November to April, and *C. rhonchus* from about May to August (Boely et al. 1973). Aboussouan (1967) and Conand and Franqueville (1973) described larvae of these species. The distinctions between larvae of *Trachurus* and *C. rhonchus* are slight and the larvae of the two *Trachurus* species cannot be distinguished. Most of our carangid eggs are probably *Trachurus* ("horse mackerel"), which was abundant along the coast of Spanish Sahara between March and June 1974. The most likely species is *T. trachurus*. All specimens of *Trachurus* taken in research trawling during JOINT-I were that species. We took 22 post-larval and juvenile *Trachurus* up to 6 cm long in various hauls of a micronekton net during JOINT-I. All specimens large enough to be identified were *T. trachurus*. We identified carangid eggs conservatively and so may have failed to count some.

The remaining eggs, 36% of the total, were of several kinds not readily identifiable by us. Probably few of them were eggs of pelagic species, except possibly some carangids as suggested above. They lacked segmented yolks and thus were probably not Isospondyli. *Scomber japonicus* Houttuyn is a pelagic species that spawns mostly from December to February in the vicinity of Cap Blanc (references in Blackburn 1975). If *Scomber* eggs occurred in our collections, they were probably not abundant. We found no *Scomber* larvae. Other abundant pelagic species of the JOINT-I area spawn principally in summer (Blackburn 1975). Thus unidentified eggs probably were mostly demersal species, as were 25% of larvae, i.e., Heterosomata and Sparidae, as shown in Table 2. Spatial distribution of unidentified eggs resembled that of the demersal larvae (Figure 5G, H).

All larvae were identified to some taxon. Closer

identifications could have been made in some cases but were not needed for this study. Clupeoids predominated. Many clupeoids were small (about 5 to 10 mm) and had lost part of the intestine, probably because of the repeated filtering of the zooplankton. Clupeidae and Engraulidae were not separately counted, but both families were well represented. Preanal myomeres were counted in randomly selected good clupeid specimens. These counts ranged from 41 to 43, which agree with *Sardina pilchardus* (Saville 1964). Comparable ranges in two other west African clupeids, *Sardinella aurita* Valenciennes and *Sardinella eba* (Valenciennes), are respectively 38 to 41 and 35 to 38 (Conand and Fagetti 1971). These species were looked for because Maigret (1972) found *Sardinella* larvae near the area of JOINT-I in May. Evidently they were absent or scarce in our material. They were absent or scarce in the 1974 fish catches reported to us. We conclude that our clupeoid larvae were *Sardina pilchardus* and *Engraulis encrasicholus*, like the clupeoid eggs. Carangid larvae were scarce. Larvae in the last line of Table 2 ("Others") were *Merluccius*, *Callionymus*, Paralepididae, and Anguilliformes (leptocephali).

Table 2 shows that *Sardina* dominated the egg samples. It shows also that abundance of *Sardina* eggs varied greatly during JOINT-I, which is discussed later.

SPATIAL DISTRIBUTION OF EGGS AND LARVAE

Figure 5B-H shows distribution and abundance of the principal kinds of eggs and larvae identified, during the whole period of cruise JOINT-I. All positive hauls for each kind were charted and the observed numbers per square meter were contoured without averaging. The purpose of Figure 5 is to show where maxima and minima occurred, although some of them were more prominent at those locations on some legs of the cruise than on others. For example the midshelf maximum of *Sardina* eggs was not prominent on Leg 2, when eggs were scarce everywhere (cf. Tables 1, 2). We were most interested in the pelagic species and especially in their eggs, whose distributions should be close to those of the adults. Furthermore, the methods employed were more suitable for eggs than larvae. Some larvae could have avoided the nets, especially in daytime.

Sardine and anchovy eggs were absent close inshore, most abundant on the continental shelf between the 50- and 100-m isobaths, and occasionally found just beyond the shelf edge (Figure 5B, C). These eggs occur most abundantly in the uppermost 25 m of the water column (Furnestin and Furnestin 1959; Larrañeta 1960; Demir 1963), where temperatures on JOINT-I were about 16° to 17°C (Figures 2-4). The eggs take about 3 days to hatch at such temperatures (Larrañeta 1960; Demir 1963), so their average age should be about 1.5 days.

Six vertical arrays of current meters were moored during JOINT-I (Figure 5A). No ichthyoplankton were collected near array number 6. The other arrays operated for periods of about 20 days (number 3) to 60 days (number 2). Means of the meridional and zonal components of water movement, v and u, are available for each current meter during the period of operation (Pillsbury et al. 1974). The top meter in each array was about 20 m below the surface. At this depth, mean v was about 20 cm/s on the continental shelf (arrays 1 and 2) and 10 cm/s on the edge and slope (arrays 3, 4, and 5), towards the south. Mean u was about 2 cm/s towards the west, except at array 3 where it had the same velocity towards the east. Thus, from where it was spawned by the parent, a sardine or anchovy egg of average age on the continental shelf could have drifted about 14 nautical miles to the south and 1.4 miles to the west. The movement to the west is negligible for our purpose. The coastline and isobaths run generally north and south along this section of the coast, as do isopleths of surface temperature and surface nitrate concentration (Voituriez et al. 1974; D. W. Stuart and J. J. Walsh, pers. commun.). Thus the parent fish probably occurred over the same bathymetry and under the same environmental conditions as the eggs did, but slightly farther north.

Carangid eggs (Figure 5D) were found on the outer half of the shelf, especially at the edge. Kiliachenkova (1970) found eggs of *Trachurus trachurus* distributed in exactly the same way in the same area in November, December, and May. The literature does not clearly show the vertical distribution of the eggs of *T. trachurus*. Kiliachenkova (1970) found them abundant at the surface. The eggs of the related *T. symmetricus* in the California Current are most common at the surface but fairly abundant down to 30 m, with smaller numbers occurring deeper (Ahlstrom 1959). We, therefore, assume our eggs came mostly from the top 30 m. *Trachurus trachurus* eggs

hatch 3 or 4 days after being spawned at temperatures from 15° to 19°C (Letaconnoux 1951), so average age in our material should be 1.5 to 2 days. Then, taking mean v as 10 cm/s we estimate that a *Trachurus* egg collected near the shelf edge was probably spawned near the edge about 7 to 10 miles farther north.

Maurolicus eggs (Figure 5E) were most abundant just outside the shelf edge. Adults are mesopelagic fish of the continental slope (Maurin et al. 1970; Hureau and Tortonese 1973) and presumably spawn there. We frequently found eggs on the outer one-third of the shelf as well as on the slope, which suggests some eastward transport. The current meter data from arrays 3 and 4 show a mean u about 10 cm/s to the east at 60 m. This could account for the observed distribution if *Maurolicus* eggs occur at that depth and hatch in a few days. Eggs of *M. japonicus* off Japan are most abundant at 50 to 60 m (Nishimura 1957). This species is considered synonymous with *M. muelleri* (Hureau and Tortonese 1973).

Clupeoid larvae (Figure 5F) were abundant at midshelf, on the outer shelf, and over the slope. In general their distribution extended about 10 to 15 miles west of the eggs. Their average age probably was 10 to 20 days more than that of the eggs. Larvae of *Sardina pilchardus* and *Engraulis encrasicholus* occur most commonly in the upper 25 m (Fage 1920). Thus the movement of 20-m shelf water towards the west at about 0.9 nautical mile/day generally explains the observed larval distribution. This water movement is presumably the Ekman transport, which provides a mechanism for the coastal upwelling.

Larvae of demersal fish (flatfish and sparids) occurred mostly on the shelf as expected, but occasionally on the slope. They were most common in inshore waters where eggs and larvae of pelagic species were scarce (Figure 5G, H).

VERIFICATION FROM COMMERCIAL FISH CATCHES

From egg and larval evidence, the adult pelagic fishes in the area and period of JOINT-I should have been predominantly *S. pilchardus* and *E. encrasicholus*, especially the former, on the shelf; *Trachurus*, probably *T. trachurus*, at the shelf edge; and the mesopelagic *M. muelleri*, on the continental slope. Differences in fecundity between species could affect these findings, however, and other species could have been present but not spawning. Commercial fish catches provide a useful check on the results of the studies with eggs and larvae. Some useful information of that type was kindly provided by the Sea Fisheries Institute of Gdynia, Poland.

Polish pelagic (mid-water) trawlers of the Odra Deep Sea Fishing Company fished just south of the JOINT-I area at the end of March 1974. They operated from lat. 20°40′ to 21°00′N, between the coast and shelf edge. Reported catches (tons/day) of pelagic species were about 3.3 *Trachurus* spp., 6.5 *Caranx rhonchus*, and 0.2 *Scomber japonicus*. *Caranx rhonchus* was the principal species within the 50-m isobath, *Trachurus* the principal fish in more offshore waters. During April, the trawlers were located far north of the JOINT-I area between lat. 23° and 27° N, where their catches were predominantly *Sardina pilchardus*.

The Polish research vessel *Professor Siedlecki*, equipped for large-scale pelagic trawling, made 77 hauls between 13 May and 24 June, starting just after JOINT-I. The hauls were made between lat. 20°16′ and 25°01′N which includes the area of JOINT-I. Hauls north of lat. 21°00′ were all on the continental shelf between the 35- and 70-m isobaths and caught almost exclusively *Sardina*. Hauls south of lat. 21°00′ were made at the shelf edge (100-m isobath) and caught almost exclusively *Trachurus* or *Sardina*, usually *Trachurus*.

Klimaj (1971, 1973) summarized results of commercial Polish trawling from 1965 to 1971 in a small area (his area 22) which includes the area of JOINT-I. The principal pelagic fishes taken from March to May were *Trachurus* spp., *Caranx rhonchus*, *Scomber japonicus*, and *Pomatomus saltatrix*. *Caranx rhonchus* was common only in March and *P. saltatrix* only in May. The other two were important in all months, with *Trachurus* generally much more abundant than *Scomber*. The *Trachurus* would have been either *T. trachurus* or *T. trecae*, which are not distinguished in the Polish fishery.

It was noted earlier that the principal spawning seasons of *Caranx* and *Scomber* are respectively later and earlier than the period of JOINT-I. The spawning season of *Pomatomus* is also later (references in Blackburn 1975). Thus these forms could have occurred in the area and period of JOINT-I although we did not recognize them in the ichthyoplankton. *Caranx rhonchus* probably did occur in March, especially inshore, and *S. japonicus* may have occurred, although not in great abundance.

The Polish data support our conclusion that *Trachurus* was the principal pelagic fish at the edge of the shelf. Our conclusion that *Sardina pilchardus* was an important species on the shelf is supported by the results of the *Professor Siedlecki* hauls, but not by those from the commercial vessels. Commercial fishing for that species is concentrated farther north, especially between lat. 24° and 26°N (Chabanne and Elwertowski 1973; Ödra Company results given above). Sardine catches of the *Professor Siedlecki* were much higher between lat. 22° and 25°N (mean of 62 hauls, 2.37 tons/h) than between lat. 20° and 22°N (mean of 15 hauls, 0.17 ton/h). There appears to be no commercial fishing for *Engraulis* off Spanish Sahara.

SPATIAL AND TEMPORAL DISTRIBUTION OF SARDINE AND ANCHOVY EGGS

In this section we characterize the area in which sardine and anchovy eggs occurred on JOINT-I, and note temporal changes in their abundance. The findings on areal distribution would apply also to adult fish in reproductive condition. We have assembled data on temperature, chlorophyll *a*, small zooplankton (<500 μm), large zooplankton (>500 μm), sardine eggs, and anchovy eggs for the 10 series along lat. 21°40′N. Figures 2 to 4 show the data for three series, including the two series in which sardine eggs were most abundant. Anchovy eggs were most abundant in the 23-24 March series (Figure 2).

Vertical distributions of temperature and density varied as shown by Barton (1974) and L. A. Codispoti (pers. commun.), and are not discussed in detail. Figure 3 shows typical coastal upwelling and Figure 4 a relaxation of upwelling conditions. Figure 2 shows weak coastal upwelling and upwelling at the shelf edge. Other series showed similar variations. It is doubtful if upwelling ever occurred only at the edge.

Chlorophyll *a* in the water column always showed a primary or secondary maximum on the middle or outer part of the shelf, and sometimes another maximum over the slope. The maximum over the slope was found when upwelling occurred at the edge, as in Figure 2, and was probably a result of it. Maxima of small zooplankton were distributed like those of chlorophyll. Both chlorophyll and small zooplankton were relatively low, close inshore in all series, and also beyond the shelf edge in series where second maxima did not occur. Large zooplankton were relatively scarce on the shelf in each series. Their biomass increased sharply at the edge, and generally continued high as far offshore as we sampled.

Sardine and anchovy eggs were virtually confined to the middle and outer parts of the shelf on all series, regardless of their abundance. Their mean abundance there is given in Table 1, together with means of temperature, chlorophyll, and small zooplankton for the water column in the same area, for each series. Temperature means are approximate.

DISCUSSION

Sardine eggs were most abundant on the middle and outer continental shelf during haul series 5 and 10, moderately abundant during series 8, and scarce on other series (Table 1). Figures 2 to 4 show the abundance on series 5, 9, and 10. Low numbers of eggs indicate either a small population of adults in the vicinity, or one that is spawning little. Mean biomass of adult fish was estimated acoustically for the same part of the shelf on the same sampling line, at various dates commencing 31 March (Thorne et al. in press). This biomass showed an irregular increase with time. It was about 8 g/m^2 on 31 March, 40 g/m^2 on 6 to 9 April and 22 to 26 April, and 80 g/m^2 on 1 to 6 May. These four periods were close in time to series 6, 7, 9, and 10, respectively. The predominant species was probably sardine as stated earlier. The egg numbers show that adult sardines were probably abundant on series 5 and moderately so on series 8, but we have no acoustic estimates of biomass for those series or for series 1 to 4.

The low mean egg number on series 6 probably reflected a very small adult population, but it is unlikely that the low numbers on series 7 and 9 did so, in view of the biomass estimates just given. It is more probable that sardine spawning was inhibited during series 7 and 9. The low mean temperatures in the water column during those series, namely, 15.5° and 16.0°C (Table 1), could have been responsible. Furnestin and Furnestin (1959, 1970) stated that spawning of *Sardina* is absent or feeble below 15.5°C and optimal from 16.0° to 18.0°C, especially over 16.5°C, in Moroccan waters. Spawning might, therefore, be low at 15.5° to 16.0°C in waters off Spanish Sahara. The limiting effect of temperature appears to be not on the spawned eggs, which can develop at 10°C

(Larrañeta 1960), but on the adults, as to whether or not they release eggs. The adults occur in most parts of the water column (Furnestin and Furnestin 1970; Thorne et al. in press), which is the reason for considering mean water temperature here. Furnestin and Furnestin (1970) make it clear that spawning depends on the temperatures over most of the water column, not necessarily on those in the upper 25 m where most eggs are found. Thick layers of water below 15.5°C make an area unsuitable for sardine spawning even if there is warm water at the surface, according to those authors. Figure 3 shows such a situation for series 9. From the criteria of Furnestin and Furnestin and the vertical distributions of temperature in our 10 series (examples given in Figures 2-4), it can be said that temperature conditions on series 3, 4, 7, and 9 were unsuitable for sardine spawning on the middle and outer shelf. Conditions on the other series were relatively suitable with mean temperatures for the water column at 16.5° or 17.0°C. It can then be deduced that adult sardines were scarce on series 1 and 2, because few eggs were found. We have no information about relative abundance of adults on series 3 and 4; they could have been present but not spawning. Relative abundance of adult sardines on the other series is given as low, medium, or high in Table 1, according to indications discussed above.

This succession of changes in abundance of adults is too irregular to be attributed to growth of individuals in a stationary population. It must be due largely to movements into and out of the small area studied. In the last major change, the biomass approximately doubled in about 2 wk between series 9 and 10. No pelagic fish species has such a high growth rate for adult individuals. It was noted during April and May that fish on the continental shelf were more abundant north of the sampling line (as far as lat. 22°20′N, which was the limit of the acoustic surveys) than along the sampling line (Thorne et al. in press). The fishing results of the *Professor Siedlecki* also indicated that sardines were more abundant to the north of our area than within it. It is therefore very probable that the biomass increase between series 9 and 10 represented a movement of sardines into the study area from the north.

It is of interest to consider possible causes of the sardine movements. A population of sardines living off the southern part of the coast of Spanish Sahara would be likely to move into a particular area, like our study area, when conditions were suitable to them and move out of the area when conditions became unsuitable. The principal determinants of distribution of pelagic fish are believed to be temperature and food supply. Temperature conditions in the study area were suitable for adult sardines during the whole period of JOINT-I, since they occur in waters from 14° to 18°C off Morocco (Furnestin and Furnestin 1970). Changes in abundance of food might however have caused movements of sardines into and out of the study area. No studies of the diet of *Sardina pilchardus* have been made off Spanish Sahara except for two fish mentioned later. Elsewhere in its range, including waters off Morocco, it feeds on phytoplankton and small zooplankton (Larrañeta 1960; Furnestin and Furnestin 1970). The distribution of sardines along the sampling line was like that of phytoplankton and small zooplankton as shown earlier: all three having maxima on the middle and outer parts of the continental shelf. This suggests that relative abundance of one or both of those kinds of food determines sardine distribution in a spatial sense and might do so in a temporal sense.

Comparison of means of zooplankton concentration with data on sardine abundance (Table 1) shows no relation between them. If means of chlorophyll concentration are used, there is the following relation: sardine abundance is low when chlorophyll values are 115 mg/m^2 or less, and medium or high when chlorophyll values are 147 mg/m^2 or more. This suggests that sardines entered the study area in order to feed on phytoplankton when it was relatively abundant and left the area when phytoplankton was relatively scarce.

No adult sardines were obtained during JOINT-I. On cruise AUFTRIEB 1975 we caught two sardines in the same area in February. M. Elbrächter kindly identified the contents of their stomachs: one contained no organisms except foraminifera, and the other contained phytoplankton in good condition, including 15 species of diatoms, and 2 species of dinoflagellates, and 2 copepods. Thus *S. pilchardus* feeds on phytoplankton and zooplankton off Spanish Sahara, as it does off Morocco and in other parts of its range. Phytoplankton might be an important part of the diet of the Sahara sardine, sufficiently to cause the sardine to move in relation to changes in phytoplankton abundance as suggested by our data, but we cannot be certain. More work on the diet of the sardine off Spanish Sahara is needed. Mauritanian

sardines have more gillrakers than Moroccan sardines of the same size (Furnestin 1955). This could signify that the mean size of organisms in the diet of sardines decreases from north to south along the African coast.

Table 1 shows that abundance of anchovy (*Engraulis*) eggs does not run parallel in time with that of sardine eggs. There is a large difference between the ratio of the mean numbers of the two kinds of eggs on series 5 and 10, for instance, although temperatures were about the same (Figures 2, 4). We are unable to draw any conclusions about changes in anchovy abundance and their causes, even in the tentative ways attempted here for the sardine.

The concentration of *Trachurus* at the shelf edge may indicate a feeding aggregation on large zooplankton, such as euphausiids and large copepods, which are more abundant there than on the shelf (Figures 2-4). The high abundance of large zooplankton sometimes extends farther offshore than *Trachurus*, however. Some other factor must help to determine abundance of *Trachurus*. The diet of *T. trachurus* and *T. trecae* off northwest Africa is about 80% euphausiids, 10% copepods, and 10% small fish such as anchovy (Boely et al. 1973). Phytoplankton is sometimes a minor constituent of *Trachurus* stomach contents, however (Letaconnoux 1951; Overko 1964; S. Schulz pers. commun.).

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LITERATURE CITED

ABOUSSOUAN, A.
1967. Oeufs et larves de teleosteens de l'ouest africain. 5. *Caranx rhonchus* Geoffr. St.-Hil. (Carangidae). Affinites avec *Trachurus trecae* Cadenat. Bull. Inst. Fondam. Afr. Noire, Ser. A, Sci. Nat. 29:1039-1050.

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

BARTON, D.
1974. Upwelling events during JOINT I. CUEA (Coastal Upwelling Ecosystems Anal.) Newsl. 3(5):21-27.

BLACKBURN, M.
1975. Summary of existing information on nekton of Spanish Sahara and adjacent regions, northwest Africa. CUEA (Coastal Upwelling Ecosystem Anal.) Tech. Rep. 8, 49 p.

BOELY, T., A. WYSOKINSKI, AND J. ELWERTOWSKI.
1973. Les chinchards des côtes sénégalaises et mauritaniennes. Doc. Sci. Provis., O.R.S.T.O.M., Dakar, 46, 47 p.

BRAVO DE LAGUNA CABRERA, J., AND E. SANTAELLA Alvarez.
1973. Observaciones biológico-pesqueras en el banco pesquero sahariano. Bol. Inst. Esp. Oceanogr. 171, 79 p.

CHABANNE, J., AND J. ELWERTOWSKI.
1973. Cartes des rendements de la pêche des poissons pélagiques sur le plateau continental nord-ouest africain de 11°à 26°N. Doc. Sci. Provis., O.R.S.T.O.M., Dakar, 49, 8 p.

CONAND, F., AND E. FAGETTI.
1971. Description et distribution saisonièrre des larves de sardinelles des côtes du Sénégal et de la Gambie en 1968 et 1969. Cah. O.R.S.T.O.M., Sér. Océanogr. 9:293-318.

CONAND, F., AND C. FRANQUEVILLE.
1973. Identification et distribution saisonièrre de larves de carangidés au large du Sénégal et de la Gambie. Bull. Inst. Fondam. Afr. Noire 35, Ser. A, Sci. Nat. 4:951-978.

CUSHING, D. H., G. F. HUMPHREY, K. BANSE, AND T. LAEVASTU.
1958. Report of the committee on terms and equivalents. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 144:15-16.

DE BUEN, F.
1931. Clupéidés et leur pêche (4e rapport). Rapp. P.-V. Réun. Comm. Int. Explor. Mer Méditerr. 6:289-336.
1937. Clupéidés et leur pêche (7e rapport). Rapp. P.-V. Réun. Comm. Int. Explor. Mer Méditerr. 10:317-419.

DEMIR, N.
1963. Synopsis of biological data on anchovy *Engraulis encrasicolus* (Linnaeus) 1758 (Mediterranean and adjacent seas). FAO Fish. Synop. 26, 44 p.

FAGE, L.
1920. Engraulidae, Clupeidae. Rep. Dan. Oceanogr. Exped. 1908-1910, Mediterr. 2, Biol. A9, 140 p.

FURNESTIN, J.
1955. Remarques sur quelques caractères de la sardine de Mauritanie (*Sardina pilchardus* Walbaum). Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 137:24-25.

FURNESTIN, J., AND M. L. FURNESTIN.
1959. La reproduction de la sardine et de l'anchois des côtes atlantiques du Maroc (Saisons et aires de ponte). Rev. Trav. Inst. Pêches Marit. 23:79-104.
1970. La sardine marocaine et sa pêche. Migrations trophiques et génétiques en relation avec l'hydrologie et le plancton. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:165-175.

HUREAU, J. C., AND E. TORTONESE.
1973. Carangidae. *In* J. C. Hureau and Th. Monod (editors), Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, Clofnam I, p. 373-384. Unesco, Paris.

KILIACHENKOVA, V. A.
1970. Development and distribution of eggs and larvae of *Trachurus trachurus* L. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:194-198.

KLIMAJ, A.
1971. Atlas rybacki (Fishery atlas) szelfu Afryki Polnocno-zachodniej. Tom. 1. Morsk. Inst. Rybacki, Gdynia, 129 p.
1973. Atlas rybacki (Fishery atlas) szelfu Afryki Polnocno-zachodniej. Tom. 2. Polowy Pelagiczne. Morsk. Inst. Rybacki, Gdynia, 128 p.

LARRAÑETA, M. G.
1960. Synopsis of biological data on *Sardina pilchardus* of the Mediterranean and adjacent seas. *In* H. Rosa, Jr. and G. Murphy (editors), Proc. World Scientific Meeting on the Biology of Sardines and Related Species, p. 137-173. Food Agric. Organ. U.N., Rome.

LETACONNOUX, R.
1951. Contribution à l'étude des espèces du genre *Trachurus* et spécialement du *Trachurus trachurus* (Linné 1758). Mém. Off. Sci. Tech. Pêches Marit. 15, 67 p.

LORENZEN, C. J.
1968. Carbon/chlorophyll relationships in an upwelling area. Limnol. Oceanogr. 13:202-204.

LOZANO CABO, F.
1970. Caractéristiques zoogéographiques de la faune ichthyologique des côtes des îles Canaries, du Maroc, du Sahara espagnol et de la Mauritanie avec une étude speciale des poissons côtiers. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:152-164.

MAIGRET, J.
1972. Campagne experimentale de pêche des sardinelles et autres espèces pélagiques, Juillet 1970-Octobre 1971. Tome 1. Observations concernant l'océanographie et la biologie des espèces. S.C.E.T.-International, 148 p.

MARCHAL, E. G.
1966. Oeufs, larves et post-larves de l'anchois de Golfe de Guinee, *Anchoviella guineensis* (Blache et Rossignol). Doc. Sci. Provis., O.R.S.T.O.M., Abidjan 5, 15 p.
1967. Cle provisoire de determination des oeufs et larves des clupeides et engraulides ouest-africains. Doc. Sci. Provis., O.R.S.T.O.M., Abidjan 14, 10 p.

MAURIN, C.
1968. Ecologie ichthyologique des fonds chalutables atlantiques (de la baie ibéro-marocaine a la Mauritanie) et de la Méditerranée occidentale. Rev. Trav. Inst. Pêches. Marit. 32:1-147.

MAURIN, C., F. LOZANO CABO, AND M. BONNET.
1970. Inventaire faunistique des principales espèces ichthyologiques frequentant les cotes nord-ouest africaines. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:15-21.

NISHIMURA, S.
1957. Vertical distribution of the floating eggs of *Maurolicus japonicus* Ishikawa, a gonostomatid fish, in the sea. Rep. Jap. Sea Reg. Fish. Res. Lab. 3:13-22.

OVERKO, S. M.
1964. Biology and fishing of scad near the northwestern shores of Africa. [In Russ.] Tr. Atl. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 11:45-64.

PILLSBURY, R. D., J. S. BOTTERO, R. E. STILL, AND E. MITTELSTAEDT.
1974. A compilation of observations from moored current meters. Vol. VIII. Wind, currents and temperature off northwest Africa along 21°40'N during JOINT-I, February-April 1974. Sch. Oceanogr. Oreg. State Univ., Data Rep. 62, Ref. 74-20, 143 p.

SAVILLE, A.
1964. Clupeoidae. Cons. Perm. Int. Explor. Mer, Fiches Identification Oeux Larves Poissons 1, 5 p.

THORNE, R. E., O. A. MATHISEN, R. J. TRUMBLE, AND M. BLACKBURN.
In press. Distribution and abundance of pelagic fish off Spanish Sahara during CUEA Expedition JOINT-I. Deep-Sea Res.

UNESCO.
1966. Determination of photosynthetic pigments in seawater. Monogr. Oceanogr. Methodol. 1, 69 p.

VOITURIEZ, B., P. DUFOUR, AND R. LE BORGNE.
1974. Preliminary results on R. V. *CAPRICORNE* 7402 Cruise in Cape Blanc. CUEA (Coastal Upwelling Ecosystem Anal.) Newsl. 3(5):1-7.

WITZELL, W. N.
1973. Gonostomatidae. *In* J. C. Hureau and Th. Monod (editors), Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, Clofnam I, p. 144-122. Unesco, Paris.

LIFE HISTORY OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN SASHIN CREEK, SOUTHEASTERN ALASKA

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ABSTRACT

The freshwater life of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska, was studied from the fall of 1963 through the summer of 1968. Additional information on age composition and fecundity of adults returning to Sashin Creek and a nearby stream was collected through the fall of 1972. Some pre-1963 data on coho salmon entering and leaving Sashin Creek were used. Weir counts and estimates of numbers of adult salmon determined from spawning ground counts and mean redd life were poor measures of the total escapement of coho salmon in Sashin Creek; an estimate made from tagging a portion of the escapement and subsequently determining tagged-to-untagged ratios of spawners on the riffles proved to be a more reliable measure. The number of spawning coho salmon varied for the years 1963 through 1967 from 162 to 916; the dominant age group was 4_3. The salinity of the surface water of the estuary of Sashin Creek usually is less than 10-15‰; bioassays of salinity tolerance indicated that coho salmon fry can survive in these salinities. In 1964, 44,000 coho salmon fry migrated to the estuary soon after emergence, although none of the scales collected from returning spawners in subsequent years showed less than 1 yr of freshwater residence. Survival curves constructed from periodic estimates of the stream populations of juvenile coho salmon for the years 1964-67 showed that mortality was highest in midsummer of the first year of life, when 62% to 78% of the juveniles were lost in a 1-mo period. Most coho salmon smolts migrated from Sashin Creek in late May or early June. In the spring of 1968, 1,440 smolts left Sashin Creek—37% were yearlings, 59% were 2-yr-olds, and 4% were 3-yr-olds. The average fork lengths were 83 mm for yearlings, 105 mm for 2-yr-olds, and 104 mm for 3-yr-olds.

Coho salmon, *Oncorhynchus kisutch* (Walbaum), occur over a broad geographic range in the North Pacific Ocean and Bering Sea. They spawn in coastal streams from northern California to northwestern Alaska and from northern Hokkaido, Japan, to the Anadyr River, USSR (Figure 1). The young usually remain in fresh water for 1 to 3 yr before migrating to sea as smolts; they are sexually mature after about 14 to 18 mo in the sea. In some systems some fry emigrate to salt water in their first spring or summer of life, but they apparently do not contribute significantly to the adult return (Chamberlain 1907; Gilbert 1913; Pritchard 1940; Wickett 1951; Foerster 1955).

Among the numerous populations of coho salmon, there are differences in freshwater life history that appear to be related to latitude. In the southern one-third of their range, coho salmon typically remain in fresh water about 1 yr before they migrate to sea in their second year of life—15 to 18 mo from egg deposition (Pritchard 1940; Briggs 1953; Smoker 1953). Farther north, in Alaska, coho salmon remain 1, 2, or 3 yr (occasionally 4) in fresh water after they emerge from the gravel (International North Pacific Fisheries Commission 1962; Godfrey 1965; Drucker 1972). In some of the Alaska streams and in Kamchatka, USSR, coho salmon that remain in fresh water for 2 yr may represent a larger percentage of the population than those that remain for 1 yr (Gilbert 1922; Semko 1954; Andrews 1962; Logan 1963; Engel 1966; Kubik 1967; Redick 1968; Armstrong 1970; Drucker 1972).

Most studies of coho salmon behavior and survival in fresh water have been conducted in the southern and central parts of the range: California, Oregon, Washington, and British Columbia in the eastern Pacific (Neave 1948; Wickett 1951; Briggs 1953; Smoker 1953; Shapovalov and Taft 1954; Foerster 1955; Salo and Bayliff 1958; Chapman 1962, 1965; Koski 1966); and Kamchatka in the western Pacific (Kuznetsov 1928; Gribanov 1948; Semko 1954). Information on more northerly stocks is much less detailed.

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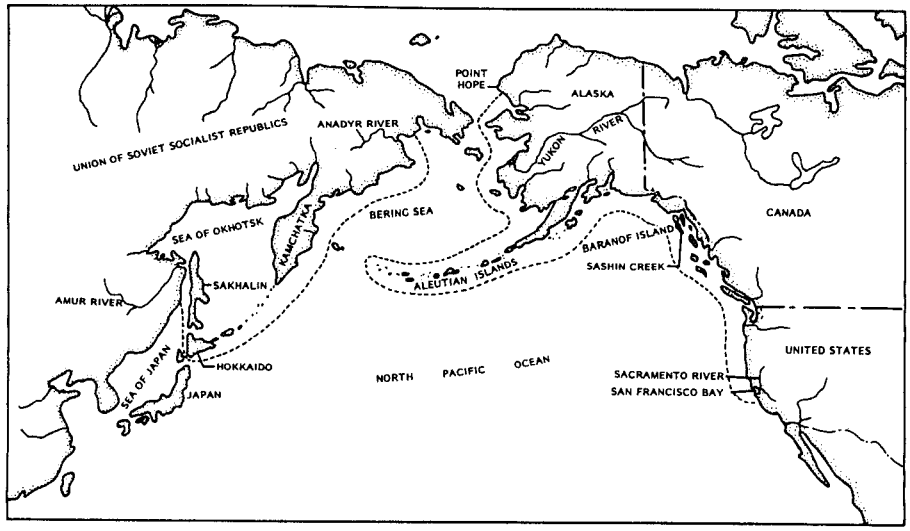

FIGURE 1.—Geographic range of coho salmon in North Pacific Ocean and Bering Sea. Dashed line indicates coastline where coho salmon enter streams for spawning.

In our studies at Sashin Creek, southeastern Alaska, we have attempted to determine important aspects of the life histories of populations of the coho salmon near the center of its range (southeastern Alaska). We have compared our findings with life histories of populations in other parts of the range and have emphasized 1) characteristics of adult spawners (including time of stream entry and time of spawning, longevity on the spawning grounds, age structure, and fecundity), 2) survival of eggs and alevins in the gravel, and 3) survival and growth of juveniles up to the time of seaward migration.

STUDY AREAS

Sashin Creek empties into Chatham Strait in the inner bay of Little Port Walter on the southeastern shore of Baranof Island (Figure 2). The stream originates in Sashin Lake about 3 km from tidewater and drains about 10 km^2 of forested watershed—mostly western hemlock. *Tsuga heterophylla*, and Sitka spruce, *Picea sitchensis* (U.S. Geological Survey 1972).

The discharge pattern of Sashin Creek is governed by seasonal rainfall and the rate of melting of accumulated snow. For the 10-yr period 1963-72, annual precipitation at Little Port Walter averaged about 587 cm (231 inches).[3] Although Sashin Lake intercepts part of the runoff and tends to even out flows in Sashin Creek, discharge varies from less than 0.3 m^3/s in midwinter to as much as 34 m^3/s after heavy rains in September and October.

Salmon have access to the 1,100 m of stream between the weir at the upper limits of salt water and a high waterfall upstream. Coho salmon rarely spawn in the 160 m of stream immediately below the waterfall or in the intertidal stream channel; both areas have a steep gradient and coarse bottom material.

The spawning ground is divided into three areas (upper, middle, and lower) which have different physical characteristics but in total contain about 13,000 m^2 of spawning gravels (Table 1). The upper area contains about 25% of the stream's suitable spawning gravels and is characterized by a steep gradient (relative to the other sections) and coarse bottom materials. The middle area has about 30% of the spawning gravel and an intermediate gradient with a higher proportion of smaller gravel and fines. The lower area is the largest and contains about 45% of the spawning gravel; it has a low gradient and a high proportion of fines in the bottom materials.

Rearing areas of juvenile coho salmon include the three spawning areas plus pools, backwaters, and to a limited extent, the 160-m section of stream in the canyon immediately downstream from the waterfall. In our investigation of juvenile coho salmon, the three ecologically distinct study areas were maintained. An additional 3,473 m^2 were included in the study areas to incorporate

[3]This average was computed from data from volumes 49-58 of the U.S. Weather Bureau's "Climatological Data, Alaska, Annual Summary." However, because precipitation for August 1967 (vol. 53) was reported incorrectly as 6.99 inches, we used the figure from the original records at Little Port Walter of 19.08 inches for August 1967 in computing the 10-yr average precipitation.

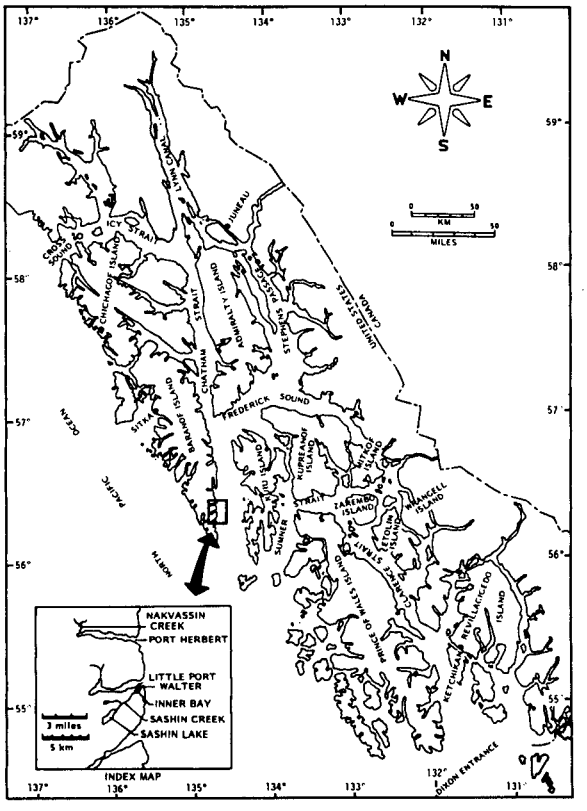

FIGURE 2.–Southeastern Alaska and Little Port Walter region, site of coho salmon study.

pools and backwaters, for a total of 16,557 m^2 (Table 1).

In 1965-67, part of Funny Creek, a small tributary of Sashin Creek near tidewater, was added to the study area. Funny Creek is about 1.5 m wide on the average and slow flowing; the bottom is mostly mud and detritus but has a few gravel areas that are used by coho salmon for spawning. The Funny Creek study area included 441 m^2 of stream from its junction with Sashin Creek upstream 290 m; the first 215 m flows through a muskeg meadow and the most upstream 75 m flows through forest.

The fish fauna of Sashin Creek consists of pink salmon, *O. gorbuscha*; coho salmon; chum salmon, *O. keta*; rainbow trout, *Salmo gairdneri*; Dolly Varden, *Salvelinus malma*; and coastrange sculpin, *Cottus aleuticus*. A few adult sockeye salmon, *O. nerka*, occasionally stray into the stream.

ADULT COHO SALMON STUDIES

In our studies of adult coho salmon we determined: 1) size of escapement, i.e., the number of coho salmon spawners that returned to Sashin Creek; 2) average redd life of females; 3) distribution and density of spawners in each study section; 4) interspecific competition between coho and pink salmon; 5) age structure of spawners; 6) fecundity of females; and 7) egg retention of spent females. In addition, for comparison with data from Sashin Creek, we obtained data on the age and fecundity of adult coho salmon from Nakvassin Creek in Port Herbert, a 7-km-long fiord about 5 km north of Little Port Walter (Figure 2). Nakvassin Creek, about 0.4 km long, is the outlet stream from 30-hectare Nakvassin Lake. Coho and sockeye salmon, Dolly Varden, rainbow trout, coastrange sculpin, and threespine stickleback, *Gasterosteus aculeatus*, inhabit the lake. These species plus pink and chum salmon inhabit Nakvassin Creek.

Size of Escapement

Adult coho salmon generally enter Sashin Creek from early August to early November, but the greatest numbers enter from late August to mid-October. Spawning usually begins early in October and ends in mid-November.

Adult salmon have been counted in Sashin Creek since 1934 through a weir at the head of tidewater. From 1934 to 1969, counts of coho salmon at the

TABLE 1.–Surface area, average gradient, and size composition of bottom materials less than 15.2 cm in diameter in three study areas of Sashin Creek.[1]

Study area	Spawning area (m^2)	Total area[2] (m^2)	Average gradient (%)	Percentage of spawning area composed of: Cobbles (> 12.7 mm)	Pebbles and granules (1.68-12.7 mm)	Sands and silts (< 1.68 mm)
Upper	2,945	4,049	0.7	81	16	3
Middle	4,067	4,441	0.3	61	26	13
Lower	6,072	8,067	0.1	47	36	17
Total	13,084	16,557	0.3	—	—	—

[1]Table adapted from McNeil (1966).
[2]This area includes pools and backwaters.

weir ranged from 0 to 567 (Table 2). The weir counts are not accurate measures of the number of coho salmon in the escapements, however, because the weir was maintained primarily to count pink salmon and the panels were usually removed at the end of the pink salmon run near the end of September. Moreover, coho salmon can jump over the weir panels and many did so each year and were therefore not counted.

Because of the problems with weir counts, an effort was made to obtain accurate estimates of the coho salmon escapements in 1963-65 and 1967 on the basis of repeated observations of the number and distribution of salmon in the three study areas (Table 3). Adults on the spawning riffles were counted by periodic visual censuses, and the counts were recorded separately for each area. In 1963 and 1964, salmon were counted only when water conditions were most favorable for observing fish; spawners were not recorded separately by sex. In 1965 and 1967, visual surveys were conducted daily, except for 6 days in 1965 when the water was too high to make observations; males and females were recorded separately. Funny Creek was included in the surveys in 1965 and 1967.

Spawners on the riffle areas were usually counted between 1000 and 1400 h, when light conditions were most favorable for observing fish. The observer (wearing polarizing glasses to reduce glare at the water surface) began counting at the upstream end of the spawning area and continued downstream. In 1965 and 1967, the observer recorded the location of individual females with reference to section markers spaced at 30.5-m intervals and a baseline running longitudinally between markers in the stream. The number of

TABLE 2.–Number of adult coho salmon counted into Sashin Creek at the weir by 2-wk intervals, 1934-69.[1]

	Two-week period							
Year	1-14 Aug.	15-28 Aug.	29 Aug.-11 Sept.	12-25 Sept.	26 Sept.-9 Oct.	10-23 Oct.	24 Oct.-7 Nov.	Total
1934	—	—	—	[2]1	—	—	—	1
1935	—	—	—	([2])	—	—	—	0
1936	—	2	2	[2]36	—	—	—	40
1937	—	3	[2]5	—	—	—	—	8
1938	—	—	1	([2])	—	—	—	1
1939	—	16	94	12	([2])	—	—	122
1940	—	—	—	[2]1	—	—	—	1
1941	—	—	—	[2]1	—	—	—	1
1942	—	—	—	[2]2	—	—	—	2
1943	—	5	2	9	[2]12	—	—	28
1944	—	6	1	10	249	[2]62	—	328
1945	—	—	18	98	219	[2]232	—	567
1946	—	—	1	82	6	[2]22	—	111
1947	—	—	21	40	[2]50	—	—	111
1948	—	9	36	19	138	[2]6	—	208
1949	—	—	27	170	[2]5	—	—	202
1950	—	19	7	37	[2]3	—	—	66
1951	1	21	50	10	[2]53	—	—	135
1952	—	20	24	138	30	([2])	—	212
1953	4	3	65	8	[2]35	—	—	115
1954	—	—	46	108	([2])	—	—	154
1955	4	6	74	74	[2]10	—	—	168
1956	—	—	12	73	3	([2])	—	88
1957	—	6	28	—	[2]36	—	—	70
1958	—	16	79	65	[2]19	—	—	179
1959	5	5	33	37	58	[2]133	—	271
1960	—	27	57	19	5	1	([2])	109
1961	51	27	11	5	4	([2])	—	98
1962	—	2	3	29	3	([2])	—	37
1963	—	2	202	[2]107	—	—	—	311
1964	—	10	13	—	([2])	—	—	23
1965	—	—	100	1	[2]23	—	—	124
1966	—	—	82	[2]8	—	—	—	90
1967	—	30	49	[2]4	—	—	—	83
1968	—	14	100	[2]70	—	—	—	184
1969	4	—	3	([2])	—	—	—	7
Total	69	249	1,246	1,274	961	456	—	4,255
Percent of all fish counted	1.6	5.9	29.3	29.9	22.6	10.7	—	—

[1]Daily counts for 1934-63 from Olson and McNeil (1967).
[2]Weir discontinued during this period.

males near each female and the number of males on the riffles but not with females also were recorded.

The estimates of the total number of spawners based on the periodic counts on the spawning riffles were obtained in the following manner. The counts of both sexes were plotted against time (Figure 3). In the figure each point for 1965 and 1967 represents the average of three successive daily counts of spawners, and each point for 1963 and 1964 represents a daily count. A curve was drawn by eye through each set of points, and the resulting area under the curve represents the spawning effort in fish-days (see Table 3 and section on Redd Life). The estimates of the total number of spawners were then derived by dividing the total number of fish-days by the average redd life (the number of days a female spends on the spawning site or redd). The method was modified from McNeil (1966). The average of the mean redd life computed for coho salmon females in 1965 and 1967 was used to calculate total number of spawners in 1963 and 1964.

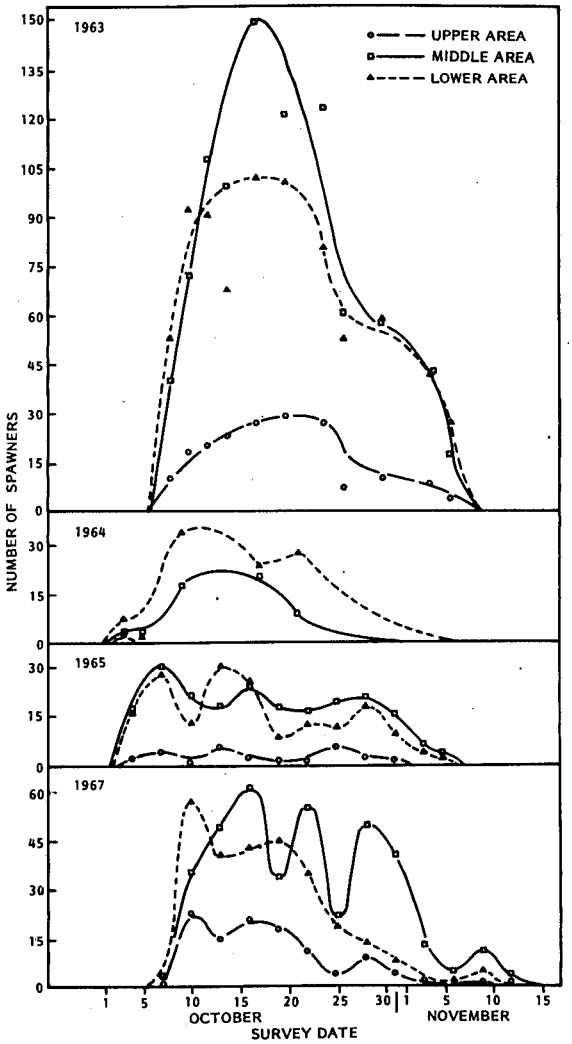

FIGURE 3.–Stream survey estimates of numbers of spawning coho salmon in Sashin Creek, based on periodic counts on spawning riffles, 1963-65 and 1967. Area under each curve is spawning effort, expressed in fish-days.

As indicated in the following tabulation, estimates of the total number of spawners derived from the stream survey data were much higher than the counts at the weir, except for 1965.

Year	*Counted at weir*	*Derived from stream survey (spawning effort-redd life)*
1963	311	458
1964	23	81
1965	124	94
1967	83	209

We also estimated the size of the escapement in 1965 and 1967 by conducting a mark-recapture experiment using the Bailey modification of the Petersen formula as given by Ricker (1958). In 1965, 46 adult coho salmon (32 females and 14 males) were tagged before spawning; in 1967, 73 unspawned coho salmon (28 females and 45 males) were tagged. The tags used were plastic Petersen disks. Marked-to-unmarked ratios were obtained from observations made during the visual censuses and these were used to estimate the populations. Based on the marked-to-unmarked ratios, the estimated number of coho salmon spawners (both sexes) in Sashin Creek was 221 in 1965 and 370 in 1967 (Table 4).

The estimates of escapement size in 1965 and 1967 based on marked-to-unmarked ratios were much higher than either the counts at the weir or the estimates based on spawning effort and redd life (Table 4). Several possible sources of error existed in estimating numbers of spawners from spawning effort and redd life: 1) The levels of spawning activity were lower at low streamflows, when visibility was good, and higher at high streamflows (Figure 4), when visibility was restricted. (In other words, the least accurate counts of spawners occurred when the greatest numbers were spawning.) 2) Some redds were occupied only at night (indicated from our limited observations). 3) The assumption that the mean spawning life of females was equal to that of males could be invalid.

TABLE 3.—Distribution and density of spawning coho salmon in three areas of Sashin Creek in 1963-65 and 1967.

	Distribution							Density of spawning (fish-days per square meter)			
	% of total salmon observed			Spawning effort (fish-days)							
Brood year	Upper area	Middle area	Lower area	Upper area	Middle area	Lower area	Total	Upper area	Middle area	Lower area	Total
1963[1]	10	48	42	553	2,652	2,289	5,494	0.19	0.65	0.38	0.42
1964	1	35	64	5	297	674	976	<0.01	0.07	0.11	0.07
1965	6	51	43	74	607	543	1,224	0.03	0.15	0.09	0.09
1967	14	50	36	320	1,151	828	2,299	0.11	0.28	0.14	0.18

[1]W. J. McNeil, unpublished notes on 1963 coho studies. On file at Auke Bay Fisheries Laboratory, Auke Bay, AK 99821.

TABLE 4.—Estimates of coho salmon escapements to Sashin Creek, 1963-65 and 1967, based on three methods of estimation.

	Number of coho salmon each year			
Method of estimation	1963	1964	1965	1967
Weir count	311	23	124	83
Spawning effort and redd life	458	81	94	209
Marked to unmarked ratios	—	—	221	370
(95% confidence interval)	—	—	197-250	342-403
Spawner escapement assumed in this report	[1]916	[1]162	221	370

[1]Based on observations in 1965 and 1967 that spawning ground counts and redd life estimates were about one-half the estimates based on marked-to-unmarked ratios of spawners.

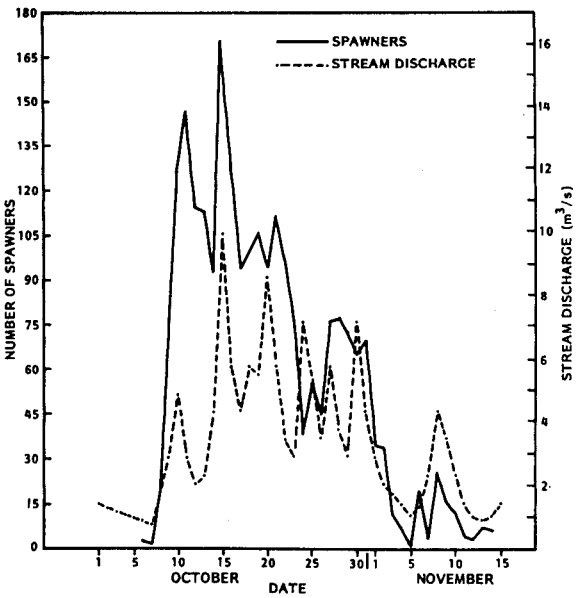

FIGURE 4.—Spawning ground counts of coho salmon in relation to stream discharge, Sashin Creek, 1967.

We believe that the best estimates of abundance of spawners are those based on tagging and observing marked-to-unmarked ratios, but such estimates are not available for 1963 and 1964. Therefore, because the estimates derived from spawning effort and redd life in 1965 and 1967 were approximately one-half the estimate from marked-to-unmarked ratios, the assumption was made that in 1963 and 1964, only 50% of the spawners in Sashin Creek were estimated from spawning effort and redd life. Our best estimates of the numbers of coho salmon spawners are 916 in 1963, 162 in 1964, 221 in 1965, and 370 in 1967 (Table 4). These values are used in the remainder of this report.

The population estimates of coho salmon spawners in Sashin Creek do not include jack coho salmon (precocious males of various freshwater ages but only one summer of marine life) because none were tagged; without tags, their presence on the spawning riffles would have been difficult to detect. Apparently, only a few jack coho salmon enter Sashin Creek; none were seen during the 1965 surveys of the spawning grounds, and only five were seen during underwater observations in 1967.

Redd Life

The estimates of mean redd life used in our calculations of escapement size were based on experiments with marked females in Sashin Creek in 1965 and 1967. Many untagged females that could be identified from natural markings, such as wounds, fungused areas, color, and size, were used along with the tagged females. A female had to be observed at the same location on two consecutive days before she was considered to have selected a permanent spawning site. One day was added to the observed redd life for females, on the assumption that they began to construct a redd an average of one-half day before first being observed and remained on the redd for an average of one-half day after last being observed.

The mean redd life of female coho salmon varied between tagged and untagged (identified from natural markings) females in both 1965 and 1967. In 1965 the mean redd life for 56 females (18

tagged and 38 untagged) was 13 days (range of 6 to 21 days). In 1967, 151 females (21 tagged and 130 untagged) remained an average of 11 days on the spawning riffles (range of 3 to 24 days). Tagged females had shorter mean redd lives than untagged females—12 versus 13 days in 1965 and 9 versus 11 days in 1967. The difference between tagged and untagged fish may have been due to difficulty in positively identifying untagged females with short redd lives, thus biasing the mean toward a greater value. Also, handling and tagging might have resulted in a shorter mean redd life for tagged females.

Tagged male coho salmon in Sashin Creek and both sexes in Funny Creek had shorter spawning lives than tagged females in Sashin Creek. Because males in Sashin Creek in 1965 were all tagged with the same color and could not be recognized individually on the spawning grounds as they moved from female to female, their spawning life could not be calculated. In 1967, however, the males in Sashin Creek had a mean spawning life of 9 days. The spawning life of coho salmon (males and females combined) was from 3 to 7 days in Funny Creek in 1965 and 1967. Rapidly rising and falling water levels, which caused some spawners to leave the area at low flows, and predation by brown bears, *Ursus arctos*, probably contributed to the shorter spawning life in Funny Creek.

In Sashin Creek, stream life and spawning life are not the same length because many coho salmon enter the stream and mature in pools for a month or more before they spawn. In Oregon, the mean length of time that female coho salmon spent in a tributary of Wilson River, Spring Creek, before death was 11 days (Willis 1954). Adults migrating into Spring Creek frequently begin spawning as soon as they enter the tributary; apparently they stay in the larger Wilson River until they are ripe (Willis 1954). Koski (1966) reported mean stream lives of 13.7 and 13.1 days for coho salmon that spawned in two tributaries to Drift Creek, Oreg.

Distribution and Density of Spawners

The distribution and density of spawners on the Sashin Creek spawning grounds were observed in 1963, 1964, 1965, and 1967 (Table 3). Distribution in each study area is expressed as the percentage of the total number of salmon observed spawning and as total spawning effort (fish-days) observed in each area. Density is the observed spawning effort divided by the square meters of spawning area.

In each of the 4 yr, the density of spawning coho salmon was higher in the middle and lower study areas than in the upper. In 1963, 1965, and 1967, the middle area had the highest density of spawners; in 1964 the lower area had the highest.

In Funny Creek a few coho salmon were seen spawning in 1965 and 1967. In those 2 yr about 4% of the estimated escapement of coho salmon to Sashin Creek spawned in Funny Creek.

The distribution and escapement of pink and coho salmon in Sashin Creek are shown in Table 5. Pink salmon usually were distributed more evenly throughout the creek than coho salmon. Merrell (1962) and McNeil (1966) reported that spawning pink salmon used the upper area extensively only in years when spawning escapements were large; when pink salmon escapements were small, spawning was concentrated in the lower area. The fact that relatively few coho salmon used Sashin Creek may explain why such a small proportion spawned in the upper area. In addition, ecological features of that area such as steep gradient and coarse bottom materials may limit its usefulness for spawning.

TABLE 5.—Distribution and escapement of spawning coho and pink salmon in three study areas of Sashin Creek, 1963-67.

Year and species of salmon	Escapement	Percentage of total salmon observed		
		Upper area	Middle area	Lower area
1963				
Coho	916	10	48	42
Pink	16,757	19	41	40
1964				
Coho	162	1	35	64
Pink	2,193	3	30	67
1965				
Coho	221	6	51	43
Pink	14,813	24	39	37
1966				
Coho	(1)	—	—	—
Pink	5,761	4	41	54
1967				
Coho	370	14	50	36
Pink	38,067	27	35	38

[1]The weir count of coho salmon was 90 when the weir gates were removed in md-September.

Interspecific Competition

Pink salmon are the most abundant fish in Sashin Creek—the number of adult pink salmon ranged from about 2,000 to 72,000, and their progeny ranged from about 0.3 to 3.6 million for the years of this study, 1963-72.

Because pink salmon complete their spawning

in Sashin Creek before coho salmon spawning begins, spawning by coho salmon could be detrimental to pink salmon embryos. In 1965, we tried in each of the three study areas to assess the effect of coho salmon superimposing their redds on those of pink salmon. The densities of live pink salmon embryos, which were estimated from routine sampling of the spawning riffles with a hydraulic sampler prior to coho salmon spawning (McNeil 1964), were used in conjunction with the average size of a coho salmon redd to estimate the total number of pink salmon embryos that could have been destroyed in gravel disturbed by spawning coho salmon. At 13 redds throughout the stream the average area of gravel disturbed by spawning coho salmon was 2.6 m^2 per redd.

The possible effect of coho salmon spawning on pink salmon embryos in October 1965 is shown in Table 6. The estimated spawning population of 110 female coho salmon would have disturbed a total of 286 m^2 of spawning gravel. Hydraulic sampling of the spawning grounds in late September before the coho salmon spawned indicated an average density of 680 live pink salmon embryos per square meter (see footnote 1, Table 6). About 200,000 live pink salmon embryos resided in areas disturbed by coho salmon spawners.

In years when the numbers of coho and pink salmon spawners are similar to those of 1965, it is doubtful that coho salmon spawning has a significant detrimental effect on the survival of pink salmon embryos. Even assuming complete mortality of pink salmon embryos in gravels utilized by spawning coho salmon, the impact on survival of pink salmon in 1965 would have been slight—about 2% of the viable pink salmon embryos present. Mortality of pink salmon eggs from redd superimposition by coho salmon could be significant if the number of coho salmon spawners were to greatly increase by natural or artificial processes.

Age Determination

We determined the age structure of samples of adult coho salmon in Sashin Creek in 1965-67 and 1969 and in Nakvassin Creek in 1966-72 by scale analysis (Table 7). Most of the salmon had spent two summers and two winters in fresh water after emergence from the gravel, had migrated to sea in the beginning of their third year, and had then spent two summers and one winter in the ocean (designated in the Gilbert-Rich system as age 4_3). A smaller portion of those sampled had spent 1 yr in fresh water after emergence, had entered the sea at the beginning of their second year, and had then remained two summers in the ocean (age 3_2). Adults that had migrated to sea at the beginning of their fourth year of life and spent two summers in salt water (age 5_4) usually constituted the smallest fraction of each year's run.

The presence of a large and dominant brood year of coho salmon in Nakvassin Creek is indicated by the percentage age distribution of returning adults. In 1967, 40% of the adults sampled for scales were age 3_2—1964 brood coho salmon that had spent 1 yr in fresh water before migrating as smolts; in 1968, 94% of the adults

TABLE 7.—Age structure as determined from samples of scales of adult coho salmon from Sashin Creek, 1965-67 and 1969, and Nakvassin Creek, 1966-72.

Source and year of sample	No. of fish sampled	Percentage age distribution		
		3_2	4_3	5_4
Sashin Creek:				
1965	27	18	78	4
1966	17	29	59	12
1967	76	25	64	11
1969	16	37	62	0
Nakvassin Creek:				
1966	25	28	68	4
1967	20	40	55	5
1968	16	6	94	0
1969	28	11	61	29
1970	46	15	76	9
1971	78	8	88	4
1972	92	9	71	21

TABLE 6.—Possible effect of coho salmon spawning on pink salmon embryos in Sashin Creek steambed in October 1965.

Area	Percentage of observed coho salmon spawning effort	Estimated coho salmon females	Area of gravel disturbed by coho salmon (m^2)	Live pink salmon embryos/m^2 before coho salmon spawned[1]	Estimated viable pink salmon embryos disturbed by coho salmon	Estimated viable pink salmon embryos in study areas	Percentage of total pink salmon embryos disturbed by coho salmon
Upper	6	7	18	750	14,000	2,209,000	0.6
Middle	51	56	146	1,200	175,000	4,880,000	3.6
Lower	43	47	122	300	37,000	1,822,000	2.0
Total	100	110	286	[2]680	226,000	8,911,000	[3]2.2

[1]W. J. McNeil, Auke Bay Fisheries Laboratory, (pers. commun.).
[2]Mean density, weighted according to area size.
[3]Mean percentage, weighted according to area size.

were 4_3–1964 brood coho salmon that had spent 2 yr in fresh water; and in 1969, 29% of the adults were 5_4–1964 brood coho salmon that had spent 3 yr in fresh water. Another large brood year indicated by the ages of returning adults is the 1967 brood. No similar patterns of a strong brood year are evident in the 4 yr of data from Sashin Creek coho salmon (Table 7).

Direct comparison of the many studies on age composition of coho salmon must be done with caution because of year-to-year variations and different sampling techniques, but a general clinal change in freshwater and total age with latitude is suggested—southerly populations are predominantly age 3_2 and northerly populations predominantly age 4_3. In British Columbia, Washington, Oregon, and California, coho salmon (exclusive of jacks) are almost all age 3_2 (Pritchard 1940; Marr 1943; Smoker 1953; Shapovalov and Taft 1954; International North Pacific Fisheries Commission 1962). Gilbert (1922) reported that about 60% of the coho salmon of the Yukon River were age 4_3; the remainder were age 3_2. Coho salmon populations in most streams studied in the Cook Inlet-Kenai Peninsula area of Alaska are composed of 60% to 95% age 4_3 fish (Andrews 1962; Logan 1963; Engel 1966; Kubik 1967; Redick 1968). In the Karluk River system on Kodiak Island, Alaska, age 4_3 fish also are dominant but age 5_4 fish, rather than age 3_2, are the second most abundant (Drucker 1972). Semko (1954) listed age composition of coho salmon from the Bolshaya River, Kamchatka, for 8 yr; in two of the years (1946 and 1947) age 4_3 adults outnumbered age 3_2. The highest percentage of age 4_3 fish reported by Semko (1954) was 64.7%. The age composition of coho salmon from the commercial fisheries of the Taku and Stikine rivers in southeastern Alaska in 1955 was 68.0% age 3_2 and 28.2% age 4_3 (International North Pacific Fisheries Commission 1962). A later report on Stikine River coho salmon caught in 1955 gives age composition as 45.2% age 3_2 and 51.9% age 4_3 (Godfrey 1965). Of several thousand coho salmon represented by scales collected from the commercial fisheries in southeastern Alaska, about half spent one winter in fresh water (age 3_2) and half spent two winters in fresh water (age 4_3) (Smoker 1956). Nearly equal numbers of ages 3_2 and 4_3 also were reported for coho salmon at Hood Bay Creek in southeastern Alaska (Armstrong 1970).

Fecundity

We determined the fecundity of female coho salmon from Sashin Creek in 1966, 1970, and 1971 and, for comparison, from nearby Nakvassin Creek in 1966-72 (Table 8). Most of the females from Sashin Creek were collected at the weir and the rest were collected with sport fishing gear in the estuary (a total of 3 to 22 each year). All samples from Nakvassin Creek were collected with sport fishing gear in the estuary (6 to 45 females each year). Ovaries from individual females were placed in containers of water and boiled until the eggs hardened and separated from the ovarian tissues. The mean of the annual fecundity samples from Sashin Creek was 3,186 eggs per female (33 fish); the fish from Nakvassin Creek were slightly smaller and the mean of the samples was 2,326 eggs (116 fish).

The relation between number of eggs and fork length for Sashin Creek and Nakvassin Creek coho salmon was calculated by the method of least squares regression. The regressions for Sashin Creek and Nakvassin Creek are $\hat{Y} = -441.48 + 51.633X$ ($r = 0.31$) and $\hat{Y} = -824.59 + 47.686X$ ($r = 0.37$), respectively. $\hat{Y}$ is the estimated number of eggs and X is the fork length in centimeters of females. Log transformations of number of eggs and fork length did not increase the values of r significantly.

Average fecundities of coho salmon reported for other streams range between 1,983 and 5,343 (Table 9). Although these values were derived in many different ways and therefore are not strictly comparable, a general trend of increasing fecundity from south to north and east to west does appear.

TABLE 8.—Mean and range of fecundity and length of female coho salmon from Sashin Creek in 1966, 1970, and 1971 (3 to 22 fish) and Nakvassin Creek in 1966-72 (6 to 45 fish).

Creek and year	No. of females sampled	Number of eggs		Fork length (cm)	
		Mean	Range	Mean	Range
Sashin Creek:					
1966	8	2,868	1,195-4,418	70.5	64.8-73.7
1970	3	3,472	3,277-3,581	65.6	64.3-68.2
1971	22	3,217	2,537-4,665	69.6	63.1-79.8
Nakvassin Creek:					
1966	7	2,463	1,853-2,931	67.8	64.8-70.0
1967	8	2,143	1,737-2,565	65.6	61.3-70.8
1968	6	2,545	2,086-3,301	66.3	60.0-68.6
1969	15	2,228	1,664-3,120	66.4	56.0-69.5
1970	22	2,294	1,259-3,127	64.1	57.0-67.5
1971	13	2,414	2,000-2,816	66.7	63.5-69.9
1972	45	2,194	1,182-3,574	63.9	56.0-71.0

Retained Eggs

In 1965 and 1967, dying and dead spent female coho salmon were examined for retained eggs

TABLE 9.—Summary of available data on fecundity of coho salmon throughout most of the geographic range.[1] The data are not strictly comparable among the various published and unpublished sources because of differences in methodology. Localities arranged in counterclockwise order from California to Sakhalin Island, USSR.

Area	Average no. of eggs	No. of fish in sample	Average fork length (cm)	Source of data
California:				
Scott Creek	[2]2,616	65	[3]66.3	Shapovalov and Taft (1954)
Oregon:				
Fall Creek, Alsea River	1,983	92	[2]66.2	Koski (1966)
Big Creek	3,030	74	70.2	James R. Graybill (pers. commun. 31 May, 1973)
Washington:				
Minter Creek	2,500	1,120	—	Salo and Bayliff (1958)
University of Washington, Seattle	3,100	63	63	Allen (1958)
British Columbia:				
Cowichan River, Vancouver Island	2,329	—	—	Neave (1948)
Oliver Creek (tributary to Cowichan River)	2,267	—	—	Foerster (1944)
Beadnell Creek (tributary to Cowichan River)	2,789	—	—	Foerster (1944)
Sweltzer Creek	2,300	—	—	Foerster and Ricker (1953)
Fraser River	3,152	48	[4]65.3	Foerster and Pritchard (1936)
Nile Creek	2,310	([5])	—	Wickett (1951)
Namu Cannery	3,002	21	[4]69.8	Foerster and Pritchard (1936)
Port John Creek	2,313	3	—	Hunter (1948)
Alaska:				
Sashin Creek, southeastern	3,186	33	68.6	Present study
Nakvassin Creek, southeastern	2,326	116	65.8	Present study
Bear Creek, Cook Inlet	4,115	193	—	Lawler (1963, 1964)
Bear Creek, Cook Inlet	[6]3,595	179	66.9	Logan (1968)
Dairy Creek, Cook Inlet	4,177	155	72.8	Lawler (1963), Engel (1965) combined
Cottonwood Creek, Cook Inlet	2,346	220	55.1	Andrews (1961), McGinnis (1966) combined
Fish Creek, Cook Inlet	2,426	112	—	Calculated from Andrews (1962)
Swanson River, Cook Inlet	3,448	1,019	62.3	Calculated from Engel (1967)
Lake Rose Tead, Kodiak Island	4,201	—	—	Marriott (1968), Van Hulle (1970) combined
Lake Miam, Kodiak Island	4,209	277	—	Van Hulle (1971)
Karluk River, Kodiak Island	4,706	49	[7]62.1	Drucker (1972)
Union of Soviet Socialist Republics:				
Kamchatka River, Kamchatka	4,883	—	[8]60.4	Kuznetsov (1928)
Bolyshaya River, Kamchatka	4,300-5,343	—	[8]56.5	Semko (1954)
Paratunka River, Kamchatka	4,350	—	[8]59.1	Gribanov (1948)
Tymi River, Sakhalin Island	4,570	—	—	Smirnov (1960)

[1]Table adapted from Rounsefell (1957) and Allen (1958).
[2]Value calculated from regression curve.
[3]Mean length determined from 338 females.
[4]Total length.
[5]Three to eight specimens per year.
[6]After introduction of Swanson River coho salmon stocks into Bear Lake.
[7]Mideye to fork length.
[8]Lengths given by Gribanov (1948), not from females sampled for fecundity.

during daily stream surveys. Only seven spent females were examined each year because high water washed most dying spawners from the stream. The number of eggs ranged from 0 to 64 and averaged 8 per female for the two seasons. Koski (1966) examined 30 spent female coho salmon in an Oregon stream and found an average of four eggs per female. In streams of Kamchatka, Semko (1954) found that coho salmon retained 0.3% of the actual fecundity (about 7 to 16 eggs per female).

JUVENILE COHO SALMON STUDIES

With anadromous salmon, the result of freshwater production is a juvenile migrating to the ocean—a smolt or fry physiologically adapted to enter salt water, where most growth takes place. Our studies were designed to measure the yield of coho salmon smolts and to determine some of the factors that bear on this yield. We counted and sampled the juvenile coho salmon at a weir as they left Sashin Creek and entered the estuary, and also sampled juveniles in the stream with seines. In addition, after determining that many fry of unknown physiological capabilities entered salt water, we performed experiments to determine the ability of these fry to survive the salinities existing in the estuary. For studies in the stream coho salmon juveniles were considered as two groups—fry (age 0) and fingerlings (age I and older).

Specific topics considered here are: 1) the numbers of coho salmon smolts and fry entering

the estuary from Sashin Creek each year, 1956-68; 2) the migration of fry to the estuary and their ability to survive in salt water; 3) age and growth of juveniles in the stream; 4) survival through various life stages (potential egg deposition to fry emergence and as juveniles in the stream); and 5) mortality in fresh water.

Juveniles Entering the Estuary

In Sashin Creek the emergence of coho salmon fry from the gravel usually begins in April and is completed by the end of May, although in especially cold years emergence may not start until June or July. Juvenile coho salmon usually live in Sashin Creek for 1 to 3 yr before migrating to salt water as smolts, but some migrate to the estuary during their first spring or summer as fry. The migration of fry to salt water soon after they emerge has been reported in several other streams (Chamberlain 1907; Gilbert 1913; Pritchard 1940; Wickett 1951; Foerster 1955), but none of these authors reported a substantial return of adult salmon from such early-migrating fry. All of the scale samples from adult coho salmon at Sashin Creek indicated that the fish had spent at least 1 yr in fresh water. The absence of adults originating from early-migrating fry suggests very poor survival of fry entering the estuary at a small size (usually <35 mm from Sashin Creek), which could be the result of heavy predation or some failure to adapt physiologically to the marine environment. We have assumed that we can identify adults derived from early-migrating fry on the basis of the pattern of circuli on their scales. However, if fry surviving in the estuary developed scale patterns indistinguishable from those of fry spending a year or more in fresh water, our assumption that age 0 emigrants did not contribute to the adult run could be incorrect.

Numbers of Fry and Smolts

Counts and estimates of the numbers of juvenile coho salmon migrating from Sashin Creek ranged from 218 to 44,023 fry and 928 to 2,865 smolts between 1956 and 1968 (Table 10). In 1964, 44,023 fry left the stream between 19 April and 28 August, and most migrated in a 2-wk period in mid-June—the greatest migration was 3,528 fry on 15 June. The smolt migration in Sashin Creek varied about threefold from 1956 through 1968 (excluding 1965-66—Table 10). The relatively low counts of smolts in 1964 probably resulted from a change in the trapping procedures at the weir. Before 1964, all fish migrating from Sashin Creek were captured. The procedures used in 1964 were designed to capture a portion of the emigrating fry and did not retain smolts well. Because of high water and ice damage to the weir, complete counts of emigrating fry and smolts were not made for 1965-67. In 1965 and 1967, estimates of fry and smolts were based on catches in fyke nets that sampled the migrants at the weir site. No estimates were obtained in 1966.

A comparison of the time of smolt migration from Sashin Creek with the time of migration from streams and lakes along the eastern Pacific coast from south-central Alaska to central coastal California indicates that there is a tendency

TABLE 10.—Numbers and times of migration of coho salmon fry and smolts past the Sashin Creek weir and yield of smolts, 1956-68.[1]

Year	Number counted at weir[2]		Counting period	Date of largest migration		Date last fish was observed to emigrate		Yield of smolts per 100 m² of rearing area
	Fry	Smolts		Fry	Smolts	Fry	Smolts	
1956	—	928	16 Apr.-30 June	—	15 June	—	20 June	5.5
1957	373	1,961	10 Apr.-29 June	17 June	24 May	27 June	27 June	11.5
1958	2,854	1,015	7 Mar.-3 June	4 May	20 May	31 May	2 June	6.0
1959	218	1,587	1 Apr.-21 July	14 July	27 May	15 July	3 July	9.3
1960	9,923	1,258	17 Mar.-2 July	12 June	10 June	30 June	30 June	7.4
1961	2,699	2,489	22 Mar.-19 June	21 May	28 May	17 June	17 June	14.6
1962	1,209	2,865	11 Mar.-4 July	14 June	27 May	4 July	3 July	16.9
1963	1,236	1,599	11 Mar.-8 July	30 May	24 May	1 July	3 July	9.4
1964	44,023	[3]334	15 Mar.-28 Aug.	15 June	24 May	28 Aug.	6 July	—
1965[4]	12,000	—	11 Apr.-30 July	24 June	—	15 July	—	—
1967[4]	10,000	1,400	10 Apr.-8 Aug.	28 June	25 May	8 Aug.	5 July	8.2
1968	1,665	1,440	26 Mar.-3 Aug.	5 June	24 May	3 Aug.	5 July	8.5

[1]The year 1966 is not included because the weir was damaged and substitute sampling was not conducted.
[2]Daily counts for 1956-64, available from Olson and McNeil (1967).
[3]Counting procedure changed from total to partial counts; holding facilities were inadequate for retaining all smolts captured.
[4]Weir not functional; fyke net(s) fished to sample a portion of the spring emigration. Numbers of fry and smolts presented are estimates made from fyke net catches.

toward earlier migration in the southern part of the range (Table 11).

To compare yields of coho salmon smolts between streams, we express yield in numbers per unit area. Estimates of the annual yield of coho salmon smolts from Sashin Creek for the period 1956-68 (except 1964-66) ranged from 5.5 to 16.9/100m^2 of rearing area (Table 10). The yield of smolts for a 5-yr period in three streams tributary to Drift Creek ranged from 18 to 67/100 m^2 (Chapman 1965). The much lower yield of smolts from Sashin Creek probably reflects increased mortality accompanying the additional 12 mo of freshwater residence for most smolts from Sashin Creek. The number of nonmigrant yearling coho salmon in Sashin Creek in early summer (determined from population studies) approximates the yield of smolts from Drift Creek tributaries more closely than does the yield of smolts (all ages) from Sashin Creek.

Early Emigration and Salinity Tolerance of Fry

The number of fry entering the estuary is great enough (Table 10) that the question of their fate in salt water is important. Many factors such as predation, failure to find adequate food, failure to adjust physiologically to salt water, and disease may act alone or in combination to determine the survival of fry entering marine waters. We had opportunity to explore adjustment to salt water as a factor in survival of migrating fry.

Early-migrating coho salmon fry might have reentered Sashin Creek undetected, although they could not have done so while the fry and smolt weir was in operation. In addition, a low waterfall immediately downstream from the weir is a barrier to upstream migration of coho salmon fry except for several days each year when above-average high tides inundate the falls. Our popula-

TABLE 11.—Timing of seaward migration of coho salmon smolts from streams and lakes in Alaska, British Columbia, Washington, Oregon, and California.

Location	Migration period	Peak of migration	Source of data
South-central Alaska:			
Fire Lake (lat. 61°21′N)	Mid May-early July	Late May-early June	Wallis (1967, 1968)
Bear Lake (lat. 60°12′N)	Late May-early Aug.	Early June	Logan (1963)
Little Kitoi Lake, Afognak Island (lat. 58°12′N)	Late May-late July	Mid June	Parker and Vincent (1956)
Karluk Lake, Kodiak Island (lat. 57°27′N)	Mid May-early July	Late May-early June	Drucker (1972)
Lake Margaret (lat. 57°46′N)	Mid Mar.-early July	Late May-early June	Van Hulle (1971)
Lake Genivieve (lat. 57°46′N)	Mid May[1]-mid July	Late May-early June	Van Hulle (1971)
Souhteastern Alaska:			
Taku River (lat. 58°33′N)	Mid Apr.-mid June[2]	Mid May-early June	Meehan and Siniff (1962)
Eva Lake (lat. 57°24′N)	Mid May-mid June	Late May	Armstrong (1970)
Hood Bay Creek (lat. 57°20′N)	Early May-late June	Mid May-early June	Armstrong (1970)
Sashin Creek (lat. 56°23′N)	Apr.-early July	Late May-early June	Table 10, this report
Central coastal British Columbia:			
Port John (Hooknose Creek) (lat. 52°08′N)	Mid Apr.-early June	May	Hunter (1948, 1949)
Southern British Columbia:			
Cultus Lake (lat. 49°03′N)	Apr.-June	Late May-early June	Foerster and Ricker (1953)
West-central Washington:			
Minter Creek (lat. 47°22′N)	Feb.-early June	May	Salo and Bayliff (1958)
Northwestern Oregon:			
Gnat Creek (lat. 46°12′N)	Apr.-early June	May	Willis[3]
Northern coastal Oregon:			
Spring Creek (lat. 45°36′N)	Late Feb.-May	Late Mar.-early May	Willis et al.[4]
Central coastal Oregon:			
Drift Creek tributaries: Deer, Flynn, and Needle Branch Creeks (lat. 44°32′N)	Feb.-May	Late Mar.-early Apr.	Chapman (1962, 1965)
Crooked Creek (lat. 44°25′N)	Feb.-early June	Apr.-May	Harry H. Wagner (pers. commun. 9 July 1973)
Southern coastal Oregon:			
Sixes River (lat. 42°51′N)	Mar.-June	Apr.-May	Reimers[5]
Central coastal California:			
Waddell Creek (lat. 37°06′N)	Apr.-early June	Late Apr.-May	Shapovalov and Taft (1954)

[1]Trapping facilities were completed after the beginning of the migration.
[2]Period when a sampling trap was operated.
[3]Willis, R. A. 1962. Gnat Creek weir studies. Final Rep., BCF Contract 14-17-0001-469, Fish Comm. Oreg., Res. Div., 71 p.
[4]Willis, R. A., R. N. Breuser, A. L. Oakley, and R. W. Hasselman. 1959. Coastal Rivers Investigations Prog. Rep., August 1957-June 1958, Fish Comm. Oreg., 24 p.
[5]Reimers, P. E. 1971. The movement of yearling coho salmon through Sixes River estuary. Coastal Rivers Investigations Prog. Rep. 71-2, Fish Comm. Oreg., 15 p.

tion studies of juvenile coho salmon in Sashin Creek suggest that no large-scale reentry of coho salmon fry occurs.

Coho salmon fry from an Oregon coast stream adjusted to water of moderately high salinities in laboratory tests (Conte et al. 1966). Our field observations, live-box experiments, and bioassays at Little Port Walter confirm that ability for fry from Sashin Creek. In July 1964, after about 44,000 coho salmon fry had migrated from Sashin Creek, schools of fry were seen near the surface of the inner bay. Most of them appeared to be in water of low salinity above a density interface about 30 cm deep, but they retreated to deeper more saline waters when disturbed.

To study the ability of coho salmon fry to adjust to the saline conditions in the Little Port Walter estuary, some fry were confined in live-boxes in the inner bay during the summer of 1964. Two sizes of live-boxes were used: six small boxes (86 by 86 by 122 cm deep) were arranged so that the water depth in the box was 81 cm, and two large boxes (122 by 122 by 244 cm deep) were suspended from a floating frame so that water depth was 235 cm. The small boxes were arranged in three sets of two boxes each, and 60 fry were placed in each box; the fry were from the weir trap, the inner bay, and Sashin Creek. Twenty-five fry from the inner bay were placed in each of the large boxes.

Initially, the Sashin Creek and weir trap fry in the live-boxes entered high-salinity water for short periods only, whereas some inner bay fry remained in the high-salinity water for long periods. Most of the fry stayed at or near the density interface close to the top of the box where the salinity was 14‰ or less; but some, especially those from the inner bay, swam for extended periods near the bottom of the box where salinity was 28 to 29‰.

Survival and growth of the fry seemed to be related more to the size of the live-box and the resulting competition for food than to the fry's ability to adjust to the saline water of the bay. In the small live-boxes, during the first 5 days 3% of the fry died and in 30 days 26% had died; in the large live-boxes in 35 days only 8% of the fry died (Table 12). The general comparison is true both for the entire small-box group versus the large-box group and for the small-box group of fish from the inner bay versus the large-box group (also from the inner bay). No supplemental food was provided, and the fry in the small boxes grew very little or not at all, whereas those in the large boxes grew about 5 mm (Table 12).

Tests were conducted in July 1964 to measure the ability of coho salmon fry to survive abrupt transfer to higher salinity waters. Salinities were determined with hydrometers. Plastic buckets were used as test containers, and as in the live-box studies, coho salmon fry were taken from Sashin Creek, the weir trap, and the inner bay. For each test, 10 fish were abruptly transferred from their source water to the test water. The fry from all three sources survived 48 h in salinities up to 23.5‰ (Table 13). In 29‰ water, the fry from the inner bay lived for 48 h, but none of those from the weir trap and only 50% of those from Sashin Creek survived 48 h. Of seven fry from the weir trap that survived 96 h in 17.6‰ salinity, three were transferred to 31‰ for 48 h, and one survived; four were transferred to 23.5‰ and three survived for 48 h. Seven fry that survived 96 h in 23.5‰ salinity were transferred to 31‰—four of these fry were still alive 48 h later when the experiment was

TABLE 12.—Mortality and growth of coho salmon fry held in live-boxes in the inner bay of Little Port Walter in the summer of 1964.

Size of live-box and no. of fish	Source of fish	Total mortality after			Average initial fork length of fry (mm)	Average fork length at end of experiment (mm)
		5 days	30 days	35 days		
Small:						
60	Weir trap	2	13	(1)	36.8	35.9
60	Inner bay	2	15	(1)	38.6	38.6
60	Weir trap	6	24	(1)	36.8	35.7
60	Sashin Creek	1	18	(1)	36.8	36.8
60	Inner bay	0	13	(1)	38.6	38.9
60	Sashin Creek	0	11	(1)	36.8	36.4
Large:						
25	Inner bay	(2)	(2)	1	40.0	44.7
25	Inner bay	(2)	(2)	3	40.0	45.4

[1]Experiment terminated after 30 days.
[2]No observations until day 35.

TABLE 13.–Cumulative deaths of coho salmon fry taken from the inner bay of Little Port Walter, the weir trap at the mouth of Sashin Creek, and Sashin Creek and held in waters of various salinities, July 1964.

Salinity (‰)	Number of fish	Source of fish	Size range (fork length, mm)	Cumulative deaths at 24 h	48 h	72 h	96 h	144 h
0	10	Weir trap	32-38	0	0	0	0	0
0	10	Inner Bay	37-45	0	0	(1)	—	—
0	10	Weir trap	35-39	0	0	(1)	—	—
0	10	Sashin Creek	35-41	0	0	0	—	—
2.2	10	Inner Bay	36-47	0	0	(1)	—	—
12.5	10	Inner Bay	35-40	0	0	(1)	—	—
12.5	10	Weir trap	35-42	0	0	0	—	—
12.5	10	Sashin Creek	38-45	0	0	0	—	—
17.6	10	Weir trap	33-39	0	0	1	3	2 6
19.3	10	Weir trap	34-39	0	0	0	—	—
19.3	10	Sashin Creek	34-63	0	0	0	—	—
23.5	10	Weir trap	33-40	0	0	0	0	0
23.5	10	Weir trap	32-40	0	0	3	3	3 6
29	10	Inner Bay	31-42	0	0	2	—	—
29	10	Weir trap	29-35	8	10	—	—	—
29	10	Sashin Creek	33-52	1	5	(1)	—	—
31	20	Weir trap	31-42	18	20	—	—	—

[1]Accidentally discontinued before 72 h.
[2]Of seven survivors in 17.6‰ at 96 h, three were transferred to 31‰ for 48 h, and one survived; four were transferred to 23.5‰, and three survived for 48 h.
[3]Period from 96 to 144 h at 31‰ salinity.

ended (Table 13). Otto (1971) found that salinity tolerance of juvenile coho salmon was increased by a 35-day exposure to water of lower salinity.

The inner bay has horizontal and vertical salinity gradients (Powers 1963), which are excellent for acclimation of young salmon to salt water. Much of the surface of the inner bay is usually less than 10-15‰ salinity. Our bioassays show that fry able to survive 48 h in 23‰ salinity should be able to acclimate fully to salinities encountered in the inner bay if they have access to the low salinity refuge. Our observation of coho salmon fry in live-boxes confirms this ability.

Juveniles in the Stream

Age Determination

Because length frequencies of different age-groups can overlap broadly at some times of the year (Figures 5-7), scales of juvenile coho salmon were analyzed to assign age-groups. Analysis of scale samples indicated that an average of 11% of all fingerlings (age I and older) collected from the stream were age II. Sizes of the various age-groups sampled by month for 1964-67 are shown in Figure 5.

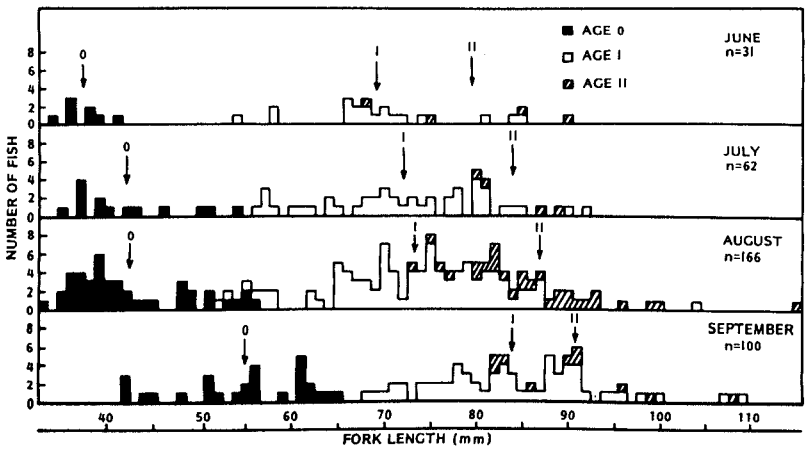

FIGURE 5.–Length frequencies and ages of coho salmon juveniles from Sashin Creek grouped by month of collection, June to September 1964-67. Ages were determined by analysis of scale samples, and lengths were measured on preserved fish. Arrows indicate location of mean lengths for each age class.

Most coho salmon fry (age 0) collected in June were under 40 mm in fork length and had not formed scales. Gribanov (1948) found that the scale covering usually appeared on young coho salmon from Kamchatka at 40 mm long.

Growth and Age Characteristics

Growth of juvenile coho salmon in Sashin Creek was determined from fork lengths (measured to the nearest millimeter) of samples of fry and fingerlings. Fry were collected periodically during summer 1964, and fry and fingerlings were captured during each of several population estimates of juveniles in Sashin Creek during 1965-67. An additional 50 fry from each of the three study areas of Sashin Creek were measured in mid-July 1966 and mid-August 1967. Samples of fingerlings from the three study areas were measured in early July, early August, and mid-September 1968.

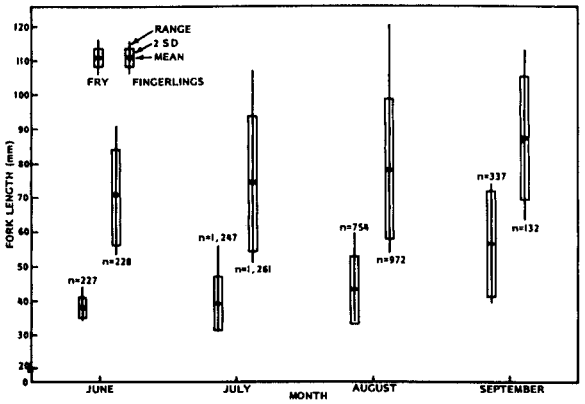

FIGURE 6.—Mean and range of fork lengths of fry (age 0) and fingerling (ages I and II) coho salmon, Sashin Creek, 1964-68. Lengths were measured from live fish.

There was no consistent difference in the mean fork lengths of corresponding age groups of juvenile coho salmon captured in the upper, middle, or lower areas in any sampling period (Table 14). Juveniles from Funny Creek were usually slightly smaller than those from Sashin Creek during a corresponding period.

The length data for juvenile coho salmon sampled in Sashin Creek for 1964-68 have been combined by month for fry and fingerlings (Figure 6). The difference between the fork length of fry and fingerlings was pronounced in early summer, but by July the lengths of fast-growing fry and slow-growing fingerlings overlapped (Figure 6). Occasionally it was difficult to assign the proper age-group to juveniles in the overlapping sizes, although they could usually be separated by the brightly colored and proportionally longer fins and smaller eyes of the fry.

The average fork length of coho salmon fry in Sashin Creek in October is about 60 mm. The average length of those that do not become smolts the following spring but remain in the stream a second year is usually 65-75 mm by July. In the 1968 migration, age I smolts averaged 83 mm, age II smolts 105 mm, and age III smolts 104 mm (Figure 7). In comparison, in 1968 coho salmon from Hood Bay Creek in southeastern Alaska averaged 83 mm fork length as age I smolts and 96 mm as age II smolts; in 1969 age I smolts averaged 79 mm and age II smolts 91 mm (Armstrong 1970). For the years 1956, 1965, and 1968, coho salmon smolts migrating from Karluk Lake, Kodiak Island, Alaska, averaged 111 mm as age I smolts, 139

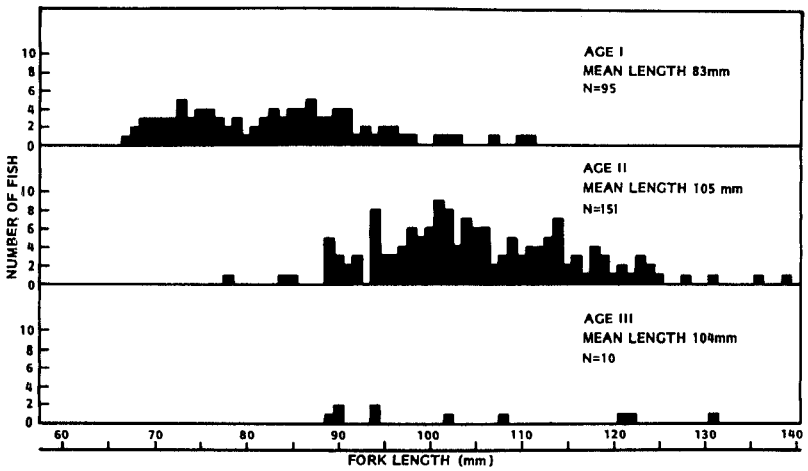

FIGURE 7.—Length frequencies of ages I, II, and III coho salmon smolts, Sashin Creek, 1968. Total sample was 256 fish, of which 37% were age I, 56% age II, and 4% age III. Ages were determined by analysis of scale samples, and lengths were measured on live fish.

TABLE 14.—Fork length (mm) of coho salmon fry and fingerlings captured in three study areas of Sashin Creek and Funny Creek, 1964-68.

Date[1] and type of sample	Sashin Creek												Funny Creek		
	Upper area			Middle area			Lower area			Total					
	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.
1964:															
7 July:															
Fry	—	—	—	—	—	—	—	—	—	31-46	36.8	43	—	—	—
15 July:															
Fry	—	—	—	—	—	—	—	—	—	33-49	39.8	92	—	—	—
21 July:															
Fry	—	—	—	—	—	—	—	—	—	32-46	37.0	34	—	—	—
28 July:															
Fry	—	—	—	—	—	—	—	—	—	34-50	39.2	91	—	—	—
31 July:															
Fry	—	—	—	—	—	—	—	—	—	33-52	38.9	39	—	—	—
18 Aug.															
Fry	—	—	—	—	—	—	—	—	—	37-59	45.1	56	—	—	—
1965:															
17 July:															
Fry	34-44	38.5	37	34-44	38.0	43	35-45	38.1	103	34-45	38.2	183	—	—	—
Fingerlings	55-80	67.7	71	53-90	68.8	99	51-86	69.7	147	51-90	69.0	317	—	—	—
1 Aug.:															
Fry	—	—	—	—	—	—	—	—	—	—	—	—	37-43	39.1	29
Fingerlings	—	—	—	—	—	—	—	—	—	—	—	—	47-80	62.1	28
11 Aug.:															
Fry	39-47	41.9	17	37-46	40.5	12	35-49	40.3	99	35-49	40.5	128	35-46	39.1	84
Fingerlings	56-84	73.4	24	56-90	70.6	96	54-91	70.2	102	54-91	70.7	222	49-91	63.8	43
30 Sept.:															
Fry	45-74	62.2	73	59-69	64.3	7	49-69	60.4	7	45-74	62.2	87	39-70	53.4	61
Fingerlings	76-104	88.0	11	84	84	1	75-97	86.0	2	75-104	87.4	14	71-105	85.8	44
1966:															
27 June:															
Fry	35-40	37.0	34	34-43	37.4	133	35-44	39.3	60	34-44	37.9	227	34-39	36.6	61
Fingerlings	60-89	71.9	24	53-85	67.6	69	56-91	71.8	135	53-91	70.6	228	50-98	72.1	78
8 July:															
Fry	35-43	37.7	24	33-47	37.7	95	34-50	40.3	101	33-50	39.0	220	34-50	38.0	102
Fingerlings	62-93	77.9	48	58-95	75.4	45	56-104	77.5	56	56-104	77.0	149	50-102	70.6	105
14 July:															
Fry	34-44	37.8	50	33-46	38.9	50	36-47	39.5	50	33-47	38.7	150	36-47	39.9	50
29 July:															
Fry	34-56	46.4	50	36-53	42.4	53	36-55	43.0	51	34-56	43.9	154	33-56	40.8	54
Fingerlings	55-98	76.3	63	65-105	79.1	58	68-102	81.6	45	55-105	78.7	166	61-105	75.5	50
14 Aug.:															
Fry	38-58	48.1	100	36-59	46.2	100	37-60	46.2	100	36-60	46.8	300	32-63	44.7	100
Fingerlings	60-102	82.0	89	63-107	84.2	100	65-106	84.6	100	60-107	83.7	289	56-119	81.1	100
8 Sept.:															
Fry	44-68	57.3	50	39-67	49.6	100	46-68	58.0	100	39-68	54.5	250	40-68	52.1	100
Fingerlings	67-102	86.7	50	63-95	81.5	10	69-113	87.8	36	63-113	86.6	96	61-108	85.3	100
1967:															
23 July:															
Fry	33-41	36.5	50	34-45	37.9	71	33-52	38.8	120	33-52	38.0	241	36-42	37.9	50
Fingerlings	52-104	70.8	100	53-93	69.5	105	53-92	72.8	112	52-104	71.1	317	52-103	77.1	107
4 Aug.:															
Fry	—	—	—	—	—	—	34-49	38.6	116	34-49	38.6	116	35-50	40.2	75
Fingerlings	—	—	—	—	—	—	57-104	76.2	228	57-104	76.2	228	55-104	74.3	50
17 Aug.:															
Fry	36-46	40.7	50	35-50	40.9	54	37-55	41.1	50	35-55	40.9	154	—	—	—
5 Sept.:															
Fry	—	—	—	—	—	—	—	—	—	—	—	—	38-64	46.3	38
Fingerlings	—	—	—	—	—	—	—	—	—	—	—	—	72-90	81.0	3
17 Oct.:															
Fry	—	—	—	—	—	—	—	—	—	—	—	—	45-69	59.5	159
Fingerlings	—	—	—	—	—	—	—	—	—	—	—	—	70-97	79.8	27
1968:															
2 July:															
Fingerlings	56-96	74.6	110	59-103	80.0	98	59-107	83.2	104	56-107	79.2	312	57-103	77.9	74
1 Aug.:															
Fingerlings	59-101	76.9	68	57-104	82.2	80	66-120	81.3	85	57-120	80.3	233	59-107	82.4	62
20 Sept.:															
Fingerlings	79-100	88.7	22	—	—	—	—	—	—	79-100	88.7	22	—	—	—

[1]Dates given for 1965, 1966, 1967, and 1968 measurements are middates of the measuring period.

mm as age II smolts, 151 mm as age III smolts, and 175 mm as age IV smolts (Drucker 1972). Kamchatka streams at about the same latitude as Sashin Creek produce 40- to 70-mm coho salmon fry by September (Gribanov 1948), 85-mm age I smolts, and 130-mm age II smolts (Semko 1954). In

California (Shapovalov and Taft 1954) and British Columbia (Foerster and Ricker 1953), the mean lengths of coho salmon smolts (mostly age I) usually ranged from 110 to 120 mm.

In coho salmon, attaining the smolt stage is apparently more a function of size than age. Data on lengths and numbers of juvenile coho salmon in Sashin Creek during September and early summer suggest that most require two summers of freshwater residence to reach smolt size. Coho salmon can grow much faster; some juveniles in a brackish pond in Oregon grew from about 40 mm (890 to the pound) to about 120 mm and became smolts in only 3 mo instead of the usual 1 yr (Garrison 1965).

The growth of juvenile coho salmon in Sashin Creek varies from year to year. During summer 1966, for instance, fry were larger than in 1964, 1965, and 1967 (Figure 8). In the summers of 1966 and 1968, fingerlings (mainly age I) were larger than in 1965 and 1967 (mainly age I). The number of fingerlings in 1966 and 1968[4] (≈3,000 on 1 July) was less than in either 1965 (≈5,000 on 1 July) or 1967 (≈3,500 on 1 July), and less competition for food would be expected and could account for the larger size of the fingerlings in 1966. Also, the presence of fewer fingerlings in summer 1966 may have allowed the fry to reach a larger size because of less competition for food or space. Food abundance, controlled by factors other than coho salmon population size, may have an important influence on coho salmon growth in Sashin Creek. We have no information on possible year-to-year differences in food supply independent of fish populations which could result in differences in growth of juvenile coho salmon.

[4]An estimate of 2,960 fingerlings in Sashin Creek was made on 2 July 1968.

Survival from Potential Egg Deposition to Emergence

The estimated potential egg depositions for brood years 1963, 1964, and 1965 were determined by multiplying the mean fecundity (determined from 1966, 1970, and 1971 samples) by the estimated number of females (one-half of the estimated population of spawners). These estimates are considered to be only rough approximations: 1,460,000 for 1963; 260,000 for 1964; and 350,000 for 1965.

Estimates of the numbers of preemerged salmon alevins in the streambed were obtained in the early spring by hydraulic streambed sampling (McNeil 1964). In Sashin Creek this sampling is done to estimate the number of pink salmon alevins, but after relatively large escapements of coho salmon reliable estimates of the number of coho salmon alevins in the streambed also can be made. No coho salmon alevins were found during the hydraulic streambed sampling in the spring of 1966, so the estimate of the alevin population was zero. Because many age 0 fry were in the stream in the summer of 1966, we have estimated the number of alevins that were in the gravel that spring by interpolation of the survivorship curves.

The numbers of preemerged coho salmon alevins for 1964-66 estimated from the results of hydraulic sampling or interpolation of survivorship curves are: 214,000 in spring 1964 (1963 brood year), 58,000 in spring 1965 (1964 brood year), and 100,000 in spring 1966 (1965 brood year). From these figures and estimates of potential egg deposition, we calculated survival from potential egg deposition to just before fry emergence to be 15%, 22%, and 26% for the 1963, 1964, and 1965 brood years, respectively.

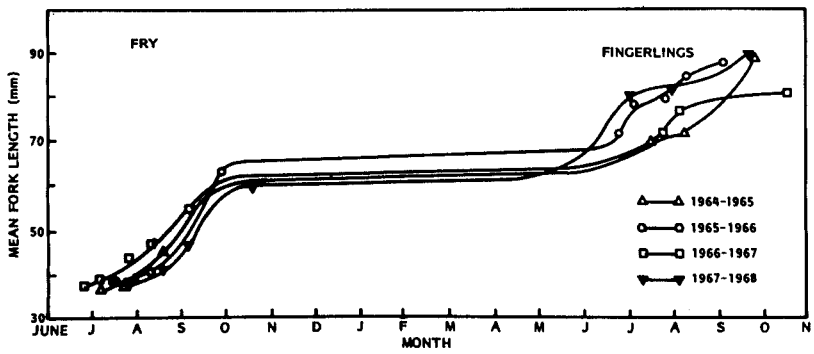

FIGURE 8.—Mean fork lengths of coho salmon fry measured several times each summer, 1964-67, and resulting fingerlings (≈90% age I and 10% age II) the next summer, 1965-68, Sashin Creek.

Survival of Juveniles in Sashin Creek

We estimated the population periodically during the summers from 1964 through 1967 to establish curves depicting changes in the number of juvenile coho salmon by brood year during their freshwater life. In 1964 the numbers of fry were estimated in July and August. In 1965 the numbers of fingerlings (predominantly age I, the balance age II) and fry were estimated in July and August. In 1966 the numbers of fingerlings and fry were estimated in June, July, and September. In 1967 estimates were made of coho salmon fingerlings and fry in Sashin Creek in July and in Funny Creek in July and August.

Juvenile salmon in the stream were captured by a combination of baiting and seining. A homogenized mixture of salmon eggs, ovarian tissue, and water was prepared with an electric blender and injected into the stream at the seining site (Figure 9). Underwater observations indicated that several squirts of the egg solution from a plastic squeeze bottle were adequate to attract rainbow trout, Dolly Varden, coastrange sculpins, and coho salmon fingerlings and large fry from at least 30 m downstream. The downstream sides of gravel bars, logs, and rocks were chosen as collecting sites because these obstructions formed slow-water areas in which the bait would linger for several minutes. In some instances it was necessary to construct a rock barrier to divert the current and create a suitable site. During early summer, when coho salmon fry are quite small, they congregate along the shallow edges of the stream and in backwaters. These small fry will not travel far in response to bait, and we often had to seine for them along the stream edges and backwaters near the baiting site.

Captured fish were anesthetized with MS-222 Sandoz[5] and marked by removing part of one fin. A different fin clip was used for each marking date within a summer. When they recovered from the anesthetic, the marked fish were released at the collection site.

To allow the marked juveniles to become redistributed, we did not begin to recapture them until several days after they were marked. To reduce bias in the population estimate, we selected random points as seining sites during the recapture portion of the experiment. Random numbers between 0 and 99 were chosen from a table of random numbers (Snedecor 1956) for each of the 30.5-m (100-foot) sections of stream. The numbers chosen represented the distance in feet downstream from the origin of each section to the sites that would be baited. These distances were paced off, and one or several places across the width of the stream at the site were baited. A site was repeatedly baited and seined until only a few fish could be taken in each seine haul. All fish captured at a site were anesthetized and examined for marks. When they recovered from the anesthetic, the fish were released. The numbers of unmarked and marked coho salmon juveniles were recorded for each site.

The Bailey-Petersen mark-and-recapture method (Ricker 1958) was used to make all population estimates, except in August 1964 when a Schnable multiple mark-and-recapture method (Ricker 1958) was used for fry. In 1966 and 1967 the numbers of juveniles to be marked and recaptured were predetermined to obtain preassigned levels of accuracy and precision of population estimates (Robson and Regier 1964). We tried to mark and recapture enough fish to be 95% certain that the error in estimating the population was not more than 10% (Table 15). Confidence limits to population estimates were obtained by methods given by Ricker (1958) and Robson and Regier (1968).

The number of coho salmon fry decreased greatly between the first and second estimate (Tables 15, 16). In the month between estimates, the population dropped by 71% in 1964, 78% in 1965, and 62% in 1966. Weir counts of emigrant coho salmon fry, which were continued until mid-August in 1964, showed that only about 2,000 fry (4% of the first population estimate) left Sashin Creek between mid-July and mid-August population estimates. Fyke net catches indicated that even fewer fry migrated from the stream in 1965 and 1966 than in 1964. Therefore, we attribute the large decrease in number of fry each year to mortality rather than emigration. Observation of the activities of fish and avian predators led us to believe that predation probably accounted for the major portion of the mortality. The number of fingerling coho salmon also decreased as the summer progressed, although not as rapidly as the number of fry (Table 17).

The fry population was greater in 1964 than in 1965, 1966, or 1967 as a result of the large number of spawners entering Sashin Creek in the fall of 1963. The population of fingerlings in 1965 was also greater than in 1966 or 1967; the fingerlings in 1965

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

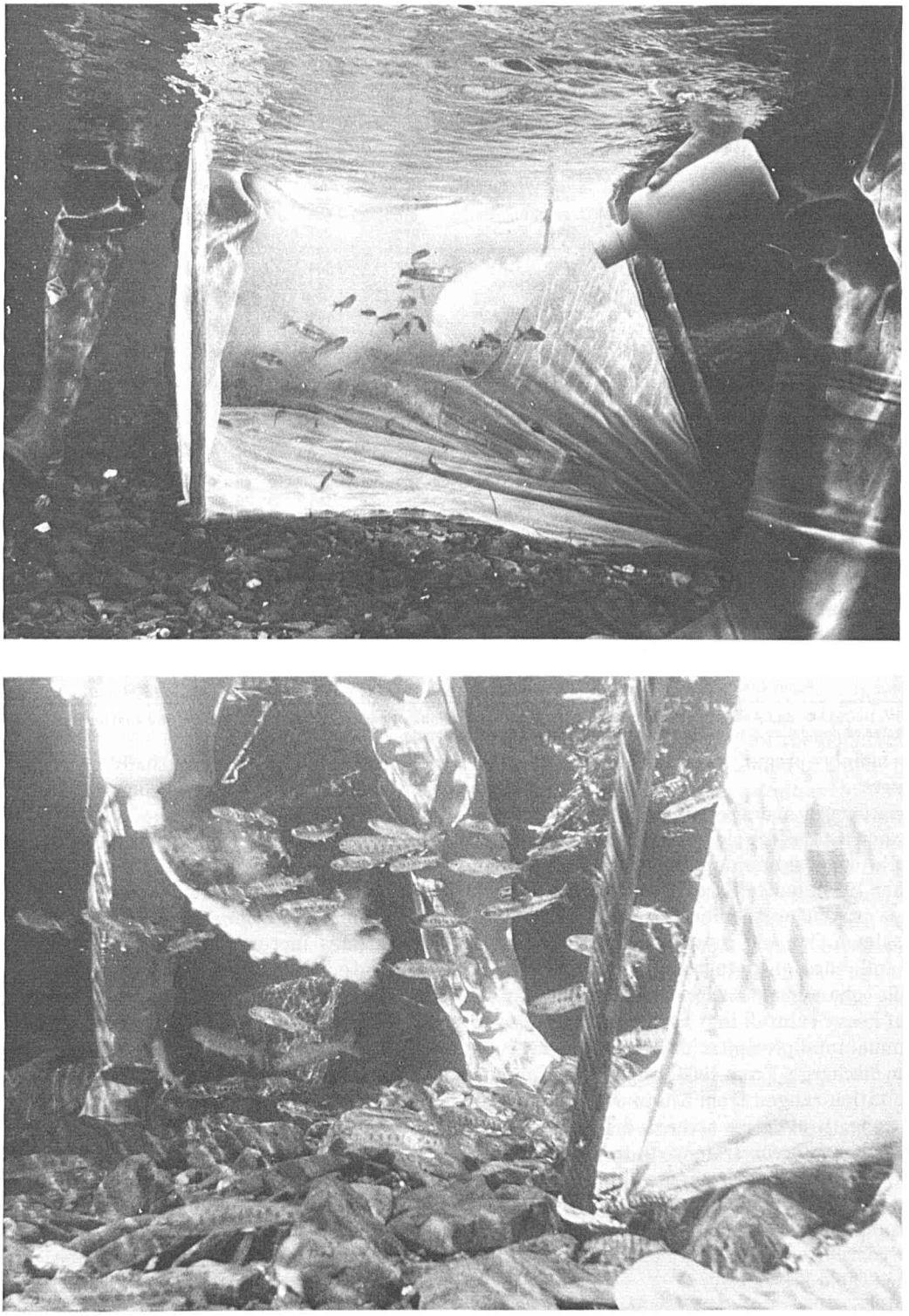

FIGURE 9.–Underwater views of technique used to capture juvenile coho salmon, Sashin Creek. Bait is a blended mixture of salmon eggs, ovarian tissue, and water.

TABLE 15.—Population estimates of juvenile coho salmon from mark-and-recapture experiments in Sashin Creek and Funny Creek, 1964-67.

Middate of estimate	Location	Fin clip used[1]	Age-group	Number marked	Census sample size	Number of marked fish recaptured	Population estimate	95% confidence interval
1964:								
12 July	Sashin Creek	LV&RV	Fry	1,454	4,421	123	51,852	43,939-62,216
12 Aug.	Sashin Creek	ULC	Fry	1,475	1,929	174	15,185	12,530-17,840
1965:								
17 July	Sashin Creek	RV	Fry	1,801	485	42	20,355	14,849-28,039
17 July	Sashin Creek	RV	Fingerlings	510	520	57	4,581	3,659- 5,960
1 Aug.	Funny Creek	LLC	Fry	276	221	50	1,201	900- 1,601
1 Aug.	Funny Creek	LLC	Fingerlings	213	107	26	852	565- 1,283
11 Aug.	Sashin Creek	LV	Fry	847	804	149	4,546	3,965- 5,294
11 Aug.	Sashin Creek	LV	Fingerlings	949	581	143	3,836	3,356- 4,459
11 Aug.	Funny Creek	LV	Fry	221	244	54	984	762- 1,300
11 Aug.	Funny Creek	LV	Fingerlings	106	141	26	557	370- 841
1966:								
27 June	Sashin Creek	ULC	Fry	2,263	2,541	163	35,077	30,436-40,951
27 June	Sashin Creek	ULC	Fingerlings	332	520	59	2,883	2,312- 3,731
27 June	Funny Creek	ULC	Fry	716	509	225	1,616	1,474- 1,793
27 June	Funny Creek	ULC	Fingerlings	78	160	49	251	187- 328
29 July	Sashin Creek	LLC	Fry	3,002	2,957	660	13,434	12,584-14,394
29 July	Sashin Creek	LLC	Fingerlings	816	817	420	1,585	1,488- 1,701
29 July	Funny Creek	LLC	Fry	208	338	67	1,037	816- 1,300
29 July	Funny Creek	LLC	Fingerlings	223	257	147	389	354- 442
8 Sept.	Area U[2]	Anal	Fry	227	378	93	915	757- 1,081
8 Sept.	Area U[2]	Anal	Fingerlings	63	155	20	468	293- 755
8 Sept.	Funny Creek	Anal	Fry	287	314	146	615	552- 700
8 Sept.	Funny Creek	Anal	Fingerlings	110	100	34	317	221- 451
1967:								
23 July	Sashin Creek	ULC	Fry	1,604	1,015	131	12,346	10,616-14,604
23 July	Sashin Creek	RV	Fingerlings	1,431	890	418	3,043	2,848- 3,274
23 July	Funny Creek	ULC	Fry	202	213	53	801	622- 1,092
23 July	Funny Creek	RV	Fingerlings	289	359	206	503	459- 551
17 Aug.	Sashin Creek	Anal	Fry	996	—	—	—	—
17 Aug.	Sashin Creek	Anal	Fingerlings	807	—	—	—	—
17 Aug.	Funny Creek	Anal	Fry	249	158	18	2,084	1,383- 3,381
17 Aug.	Funny Creek	Anal	Fingerlings	354	27	7	1,239	745- 3,218

[1]LV, RV, ULC, LLC, and Anal refer to left pelvic, right pelvic, upper lobe of caudal, lower lobe of caudal, and anal fin clips, respectively.
[2]Estimates of population size in the whole of Sashin Creek were not made.

were mainly progeny of the abundant 1963 spawners.

Variations in average annual streamflow have been shown to affect significantly the number of juvenile coho salmon in Washington streams (Smoker 1953), but in Sashin Creek, other factors such as parent escapement, original number of coho salmon fry, and competition probably have more influence on determining the number of juvenile coho salmon. Sashin Creek is located in an area of heavy rainfall that has small variations in the annual total precipitation and annual average stream discharge. From 1964 through 1967, annual precipitation ranged from 546 to 643 cm. Greater variations in average stream discharge for a specific month occur from year to year. Annual variations in stream discharge during the 1-mo period in midsummer when populations of juvenile coho salmon decreased most rapidly do not appear to be correlated with the rates of population decline (Table 17).

In 1965, 1966, and 1967, when estimates of juvenile coho salmon populations were made in each study area, the highest densities of coho salmon in Sashin Creek usually occurred in the lower study area, which is characterized by slow water. Densities of coho salmon fry and fingerlings were even higher in Funny Creek, another slow-water habitat (Table 18).

Funny Creek was unique in our study areas in that the populations of juvenile coho salmon sometimes increased during the summer. The estimated number of coho salmon fingerlings increased from 251 to 389 between late June and late July in 1966 (1964 brood year) and from 503 to 1,239 between mid-July and mid-August in 1967 (1965 brood year); the number of fry increased from 801 to 2,084 between mid-July and mid-August in 1967 (1966 brood year) (Table 16). The 95% confidence interval estimates (Table 15) indicate that the populations did increase, and the additional coho salmon juveniles must have immigrated to this area from Sashin Creek. On all other occasions, in both streams the populations of fry and fingerlings decreased between estimates. The movement of juvenile coho salmon from Sashin Creek into Funny Creek during midsummer suggests the use of this small tributary stream as a

TABLE 16.—Population estimates of juvenile coho salmon of brood years 1963-66[1] in Sashin Creek and Funny Creek in the summers of 1964-67. Separate estimates are included for three areas of Sashin Creek.

Brood year and area	Number of fish (by brood year) on									
	12 July 1964	12 Aug. 1964	17 July 1965	1 Aug. 1965	11 Aug. 1965	27 June 1966	29 July 1966	8 Sept. 1966	23 July 1967	17 Aug. 1967
1963:										
Sashin Creek:										
Upper	—	—	668	—	593					
Middle	—	—	1,216	—	1,115					
Lower	—	—	2,533	—	2,079					
Stream estimate	51,852	15,185	4,581	—	3,836					
Funny Creek	—	—	—	852	557					
1964:										
Sashin Creek:										
Upper			2,979	—	254	402	509	468		
Middle			2,195	—	951	690	555	—		
Lower			14,738	—	3,477	1,562	555	—		
Stream estimate			20,355	—	4,546	2,883	1,585	[2]1,350		
Funny Creek			—	1,201	984	251	389	317		
1965:										
Sashin Creek:										
Upper						1,192	1,497	915	810	—
Middle						7,759	5,091	—	801	—
Lower						26,662	7,851	—	1,453	—
Stream estimate						35,077	13,434	[2]8,000	3,043	—
Funny Creek						1,616	1,037	615	503	1,239
1966:										
Sashin Creek:										
Upper									1,828	—
Middle									1,862	—
Lower									8,627	—
Stream estimate									12,346	—
Funny Creek									801	2,084

[1]The estimated populations of fish of a brood year at age I (second summer of life) include an average of 11% age II fish from the preceding brood year.
[2]Estimate of population from expansion of estimated populations in upper area and Funny Creek.

TABLE 17.—Mean stream discharge and percentage decrease in numbers of juvenile coho salmon between a first estimate (late June to late July) and a second estimate (mid-July to mid-August) in Sashin Creek, 1964-67.

Year	Mean stream discharge (m^3/s)	Decrease in population size	
		Fry	Fingerlings
1964	[1]1.70	71% (51,852 to 15,185)	([2])
1965	0.99	78% (20,355 to 4,546)	16% (4,581 to 3,836)
1966	0.82	62% (35,077 to 13,434)	45% (2,883 to 1,585)
1967	1.42	([3]) (12,346)	([3]) (3,043)

[1]Stream discharge data for August 1964 not measured. An estimate of mean stream discharge for the period was calculated from July 1964 stream discharge and rainfall data in conjunction with the August 1964 rainfall pattern.
[2]Size of fingerling population not estimated in 1964.
[3]First population estimate; second population estimate was not completed.

feeding area or refuge from undesirable conditions in Sashin Creek, such as competition or predation. Fall migration of juvenile coho salmon into small tributary streams in Oregon has been reported (Skeesick 1970).

Estimates of the number of coho salmon fry and fingerlings were used to construct curves depicting the changes in the sizes of the populations of three of the brood years studied (Figures 10, 11). Estimates of the total number of fry and fingerlings in Sashin Creek in early September 1966 are projected from estimates of population size obtained in the upper area and in Funny Creek. In these two study areas in early September the number of fry averaged 60% and the number of fingerlings 85% of their populations in late July. We assumed that these percentages pertained also to the lower and middle areas of Sashin Creek.

Survival and Instantaneous Mortality Rates

We compared survival and instantaneous mortality rates of juvenile coho salmon of three brood years by dividing their freshwater lives into the following five periods between the time of egg deposition and late in the second summer of life:

Period	*Time covered*
1	Egg deposition to just before emergence (mid-October to late March or early April).

TABLE 18.–Densities of juvenile coho salmon by brood year (1963-66)[1] on dates of population estimates in Sashin Creek and Funny Creek. Separate estimates are included for three areas of Sashin Creek.

Brood year and area	Density of fish (per square meter) on									
	12 July 1964	12 Aug. 1964	17 July 1965	1 Aug. 1965	11 Aug. 1965	27 June 1966	29 July 1966	8 Sept. 1966	23 July 1967	17 Aug. 1967
1963:										
Sashin Creek:										
Upper	—	—	0.16	—	0.15					
Middle	—	—	0.27	—	0.25					
Lower	—	—	0.31	—	0.26					
Stream estimate	3.13	0.92	0.28	—	0.23					
Funny Creek	—	—	—	1.93	1.26					
1964:										
Sashin Creek:										
Upper			0.74	—	0.06	0.10	0.13	0.12		
Middle			0.49	—	0.21	0.16	0.12	—		
Lower			1.83	—	0.43	0.19	0.07	—		
Stream estimate			1.23	—	0.27	0.17	0.10	[2]0.08		
Funny Creek			—	2.72	2.23	0.57	0.88	0.72		
1965:										
Sashin Creek:										
Upper						0.29	0.37	0.23	0.20	—
Middle						1.75	1.15	—	0.18	—
Lower						3.31	0.97	—	0.18	—
Stream estimate						2.12	0.81	[2]0.48	0.18	—
Funny Creek						3.66	2.35	1.39	1.14	2.81
1966:										
Sashin Creek:										
Upper									0.45	—
Middle									0.42	—
Lower									1.07	—
Stream estimate									0.75	—
Funny Creek									1.82	4.73

[1]The estimated populations of fish of a brood year at age I (second summer of life) include an average of 11% age II fish from the preceding brood year.
[2]Estimate of density calculated from population obtained from expansion of estimated populations in upper area and Funny Creek.

2 Just before emergence to first estimate of fry population (end of period 1 to late June or mid-July).
3 First to second estimate of fry population during first summer (end of period 2 to late July or mid-August).
4 Second estimate of fry population to first estimate of population as yearlings (end of period 3 to late June or mid-July of the following year).
5 First to second estimate of yearling population (end of period 4 to late July or mid-August).

Although the lengths of the corresponding periods for the three brood years are similar, they varied according to when the population estimates were made.

We compared the estimates of the population at the end of each of the five periods with the original population (potential egg deposition) to obtain percentage survival during nearly 2 yr of their freshwater life for the brood years 1963-65 (Table 19). Survival from potential egg deposition to just before fry emergence (period 1) was estimated to be 15%, 22%, and 26% (mean of 21%) for the 1963, 1964, and 1965 broods, respectively. Other investigators have found similar survival to emergence for coho salmon. A range in survival to emergence in terms of counted fry of 11.8% to 40.0% (mean of 21.0% and 26.5%) is reported for two tributaries of the Cowichan River, British Columbia (Pritchard 1947). Koski (1966) obtained survival values to fry emergence of 0% to 78% (mean of 27.1%) for individual redds of coho salmon in three streams tributary to Drift Creek. For Karymaisky Spring on Kamchatka, Semko (1954) reports survival to emergence of 0.8% to 21.4% (mean 10.6%).

TABLE 19.–Survival through five periods[1] in the freshwater life of three brood years of coho salmon in Sashin Creek, expressed as a percentage of potential egg deposition.

Brood year	Percentage survival through period				
	1	2	3	4	5
1963	14.66	3.55	1.04	0.28	0.23
1964	22.31	7.83	1.75	0.99	0.54
1965	25.71	10.02	3.84	0.77	—

[1]See text for explanation of time covered in each period.

Because the lengths of the five periods were not equal and a specific period was not the same length

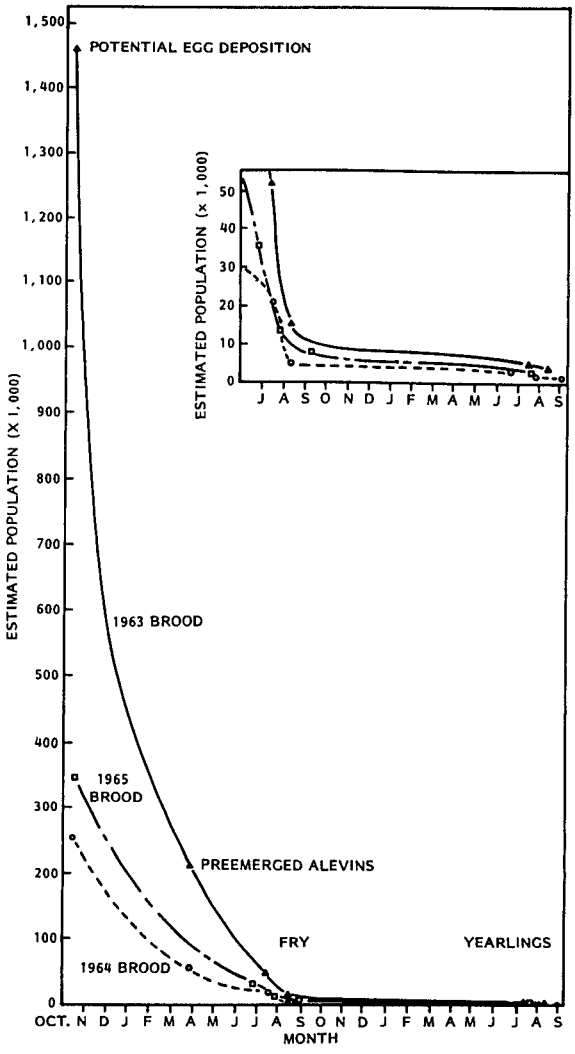

FIGURE 10.–Estimated populations of juvenile coho salmon of three brood years, Sashin Creek, from potential egg deposition to late summer of second year. (Arithmetic plot.)

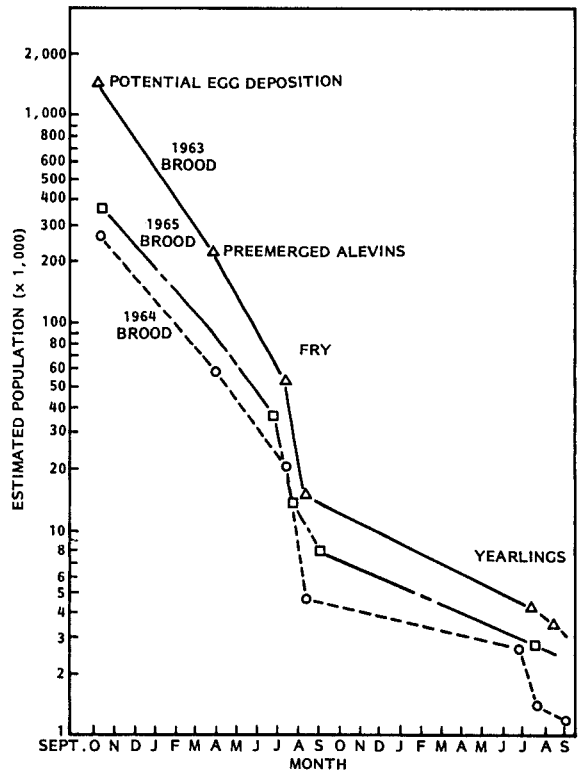

FIGURE 11.–Estimated populations of juvenile coho salmon of three brood years, Sashin Creek, from potential egg deposition to late summer of second year. (Semilogarithmic plot to indicate mortality rate.)

TABLE 20.–Instantaneous mortality coefficients during five periods[1] in the freshwater life of three brood years of coho salmon in Sashin Creek.

Brood year	Instantaneous mortality coefficient in period				
	1	2	3	4	5
1963	0.37	0.38	1.23	0.12	0.25
1964	0.27	0.30	1.88	0.05	0.55
1965	0.25	0.32	0.87	0.14	—

[1]See text for explanation of time covered in each period.

for each of the three brood years, instantaneous mortality coefficients (Ricker 1958) were computed to compare mortality for the periods and years (Table 20). The equation for determining the instantaneous mortality coefficient,

$$M_{jn} = \frac{-\ln (S_{jn})}{t},$$

follows the notation of McNeil (1966), where t, the interval of time, is in months (one unit is equal to 1 mo); the symbol ln represents the natural logarithm; j is the brood year; and n is the study period. S_n is the survival within the nth period and is calculated from the formula,

$$S_1 \cdot S_2 \cdot \ldots \cdot S_n = S,$$

or

$$S_n = \frac{S}{S_1 \cdot S_2 \cdot \ldots \cdot S_{(n-1)}},$$

where S is survival through n study periods expressed as a percentage of potential egg deposition (Table 19).

Instantaneous mortality was higher through

periods 1 and 2 for the 1963 brood than for the 1964 and 1965 broods. We estimated that eggs of the 1963 brood were over four times as abundant as those of the 1965 brood and over five times as abundant as those of the 1964 brood. Resulting density-dependent factors such as superimposition of redds, selection of inferior redd sites, and emigration of fry from the stream because of lack of living space could be the cause of the higher initial mortality of the 1963 brood.

For all three broods the highest instantaneous mortality occurred in period 3—between the first and second population estimates of the first summer of life—during July and the first half of August (Table 20). Predation from fishes (both intraspecific and interspecific) is thought to be a major cause of this high mortality. In period 2 the fry live in the backwater and shallow edges of the stream where larger piscivorous fish do not regularly occur. During period 3 the fry move into deeper parts of the main channel where current is still relatively slow, but here larger fish occur and the fry may be more subject to predation.

Instantaneous mortality during the winter (period 4) was much less than that of the first summer. Predation probably was less during this period for two reasons: 1) in winter the feeding rate of cold-blooded predators is slowed, and 2) restricted access because of ice and snow and lowered activity and availability of the juvenile coho salmon combine to lessen the hunting success of warm-blooded predators.

Mortality increased during the second summer (period 5) but only to a third or less of the corresponding part of the first summer (period 3).

Some of the estimated mortality of fry and fingerlings might have been due to undetected emigration from the creek. When the fry weir or fyke nets were fished in summer (periods 3 and 5), however, only a few fry and fingerlings emigrated and the low mortality rate in period 4 also suggests that only a few fry emigrated in fall and winter. Some age I smolts probably migrated from the stream in the spring of period 4 in each of the 3 yr studied. The drop in population of a brood year due to age I smolt emigration is included as part of period 4 mortality. Age composition of smolts in 1965, 1966, and 1967 was not determined. The age composition of returning adults in 1966 and 1967 (25% and 29% age 3_2, respectively) indicates that some age I smolts emigrated in the spring of 1965 and 1966. In 1968 the smolts were sampled for age composition; about 500 yearling smolts migrated. Scale samples for age analysis were not collected from adults in 1968.

SUMMARY

The number of adult coho salmon that enter Sashin Creek varies from year to year. Coho salmon have been counted at the weir as they enter Sashin Creek each year since 1934, but this count has usually been incomplete.

Several methods were used to estimate coho salmon escapements to Sashin Creek for the years 1963-65 and 1967. These included weir counts, adults on spawning riffles, mean redd life, and marked-to-unmarked ratios of spawners. The last system produced the most accurate estimates, resulting in 916, 162, 221, and 370 salmon for the respective study years.

In the 4 yr that spawning ground studies were made, the density of coho salmon on the spawning grounds in Sashin Creek tended to be greater in the middle and lower study areas than in the upper area.

The effect of coho salmon spawning on the survival of pink salmon embryos was insignificant in 1965 relative to the population ratios of coho and pink salmon present. Significant numbers of pink salmon embryos might be killed if relatively large numbers of coho salmon utilized Sashin Creek for spawning.

The 4_3 age-group of coho salmon made up 78%, 59%, 64%, and 62% of the adults that returned to Sashin Creek in 1965, 1966, 1967, and 1969—higher percentages of this age group than reported for most other streams. In California, Oregon, Washington, and southern British Columbia, adult coho salmon are almost exclusively age 3_2. Studies of growth and scales of fry, fingerlings, and smolts and estimates of the population sizes of juveniles indicate that most coho salmon remain in Sashin Creek for two summers and winters.

In some years, substantial numbers of coho salmon fry enter the estuary of Sashin Creek shortly after emergence. These fry were tested and found to be able to survive in salinities encountered in the inner bay of the Little Port Walter estuary. However, analysis of scales of adult coho salmon returning to Sashin Creek revealed none that had migrated to the estuary at the fry stage, suggesting no fry (or at best very few) that migrate to the ocean survive to return as adults. This agrees with studies of other stocks of coho salmon.

Estimates of populations of fry in the early summer for the 4 yr studied ranged from about 12,000 to 52,000, and apparently varied directly with potential egg deposition of the brood year. However, by early in the second summer of freshwater life, the three broods studied had been reduced to a relatively narrow range of 3,000 to 4,500. Weir counts indicate 1,000 to 3,000 coho salmon smolts migrate from Sashin Creek each year.

The survival of coho salmon from potential egg deposition to just before the emergence of fry in Sashin Creek averaged 21%; this percentage is similar to survival reported for stocks from other areas in the eastern Pacific. Mortality of embryos and alevins was highest for the large 1963 brood, which suggests that some of the mortality before emergence was due to compensatory factors such as selection of inferior redd sites and superimposition of redds.

Highest mortality during the freshwater life of coho salmon from Sashin Creek occurred in July and early August of the first summer in all three broods studied. The lowest mortality occurred over winter.

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LITERATURE CITED

ALLEN, G. H.
1958. Notes on the fecundity of silver salmon (*Oncorhynchus kisutch*). Prog. Fish-Cult. 20:163-169.

ANDREWS, R. E.
1961. Inventory and cataloging of the sport fish waters in the Cook Inlet and Copper River drainages. Alaska Dep. Fish Game, Sport Fish Div., 1960-61 Dingell-Johnson Proj. Rep. 2:47-55.
1962. Inventory and cataloging of sport fish and sport fish waters of the Cook Inlet drainages. Alaska Dep. Fish Game, Sport Fish Div., 1961-62 Dingell-Johnson Proj. Rep. 3:221-225.

ARMSTRONG, R. H.
1970. Age, food, and migration of Dolly Varden smolts in southeastern Alaska. J. Fish. Res. Board Can. 27:991-1004.

BRIGGS, J. C.
1953. The behavior and reproduction of salmonid fishes in a small coastal stream. Calif. Dep. Fish Game, Fish Bull. 94, 62 p.

CHAMBERLAIN, F. M.
1907. Some observations on salmon and trout in Alaska. [U.S.] Bur. Fish., Rep. Comm. Fish. 1906. Doc. 627, 112 p.

CHAPMAN, D. W.
1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. 19:1047-1080.
1965. Net production of juvenile coho salmon in three Oregon streams. Trans. Am. Fish. Soc. 94:40-52.

CONTE, F. P., H. H. WAGNER, J. FESSLER, AND C. GNOSE.
1966. Development of osmotic and ionic regulation in juvenile coho salmon *Oncorhynchus kisutch*. Comp. Biochem. Physiol. 18:1-15.

DRUCKER, B.
1972. Some life history characteristics of coho salmon of the Karluk River system, Kodiak Island, Alaska. Fish. Bull., U.S. 70:79-94.

ENGEL, L. J.
1965. Egg take investigations in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., 1964-65 Dingell-Johnson Proj. Rep. 6:155-163.
1966. Egg-take investigation in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1965-66 Prog. Rep. 7:109-116.
1967. Egg take investigation in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1966-67 Prog. Rep. 8:111-116.

FOERSTER, R. E.
1944. Appendix IV. Report for 1943 of the Pacific Biological Station, Nanaimo, B.C. Annu. Rep. Fish. Res. Board Can. 1943:22-26.
1955. The Pacific salmon (genus *Oncorhynchus*) of the Canadian Pacific coast, with particular reference to their occurrence in or near fresh water. Int. North Pac. Fish. Comm., Bull. 1:1-56.

FOERSTER, R. E., AND A. L. PRITCHARD.
1936. The egg content of Pacific salmon. Biol. Board Can., Prog. Rep. Pac. Biol. Stn. Pac. Fish. Exper. Stn. 28:3-5.

FOERSTER, R. E., AND W. E. RICKER.
1953. The coho salmon of Cultus Lake and Sweltzer Creek. J. Fish. Res. Board Can. 10:293-319.

GARRISON, R. L.
1965. Coho salmon smolts in ninety days. Prog. Fish-Cult. 27:219-220.

GILBERT, C. H.
1913. Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus*. Bull. [U.S.] Bur. Fish. 32:1-22. (Doc. 767.)
1922. The salmon of the Yukon River. Bull. [U.S.] Bur. Fish. 38:317-332. (Doc. 928.)

GODFREY, H.
1965. Salmon of the North Pacific Ocean—Part IX, Coho, chinook and masu salmon in offshore waters. 1. Coho salmon in offshore waters. Int. North Pac. Fish. Comm., Bull. 16:1-39.

GRIBANOV, V. I.
1948. The coho salmon (*Oncorhynchus kisutch* Walbaum)—a biological sketch. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 28:43-101. (Fish. Res. Board Can. Transl. Ser. 370, 83 p.)

HUNTER, J. G.
1948. Natural propagation of salmon in the central coastal

area of British Columbia. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 77:105-106.

1949. Natural propagation of salmon in the central coastal area of British Columbia. II. The 1948 run. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 79:33-34.

INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION.

1962. The exploitation, scientific investigation and management of salmon (genus *Oncorhynchus*) stocks on the Pacific coast of the United States in relation to the abstention provisions of the North Pacific Fisheries Convention. Int. North Pac. Fish. Comm., Bull. 10, 160 p.

KOSKI, K V.

1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. M.S. Thesis, Oregon State Univ., Corvallis, 84 p.

KUBIK, S.

1967. Population studies of anadromous species with emphasis on upper Cook Inlet drainage. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1966-67 Prog. Rep. 8:117-128.

KUZNETSOV, I. I.

1928. Some observations on spawning of the Amur and Kamchatka salmons. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 2. (Fish. Res. Board Can. Transl. Ser. 22, 9 p.)

LAWLER, R. E.

1963. Silver salmon egg taking investigations in Cook Inlet drainage. Alaska Dep. Fish Game, Sport Fish. Div., 1962-63 Dingell-Johnson Proj. Rep. 4:161-173.

1964. Egg take investigation in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., 1963-64 Dingell-Johnson Proj. Rep. 5:123-132.

LOGAN, S. M.

1963. Silver salmon studies in the Resurrection Bay area. Alaska Dep. Fish Game, Sport Fish Div., 1962-63 Dingell-Johnson Proj. Rep. 4:175-194.

1968. Silver salmon studies in the Resurrection Bay area. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:117-134.

MARR, J. C.

1943. Age, length, and weight studies of three species of Columbia River salmon (*Oncorhynchus keta*, *O. gorbuscha*, *O. kisutch*). Stanford Ichthyol. Bull. 2:157-197.

MARRIOTT, R. A.

1968. Inventory and cataloging of the sport fish and sport fish waters in southwest Alaska. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:81-93.

MCGINNIS, D.

1966. Inventory, cataloging and population sampling of the sport fish and sport fish waters of the Cook Inlet drainage. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1965-66 Prog. Rep. 7:155-169.

MCNEILL, W. J.

1964. A method of measuring mortality of pink salmon eggs and larvae. U.S. Fish. Wildl. Serv., Fish. Bull. 63:575-588.

1966. Distribution of spawning pink salmon in Sashin Creek, southeastern Alaska, and survival of their progeny. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 538, 12 p.

MEEHAN, W. R., AND D. B. SINIFF.

1962. A study of the downstream migrations of anadromous fishes in the Taku River, Alaska. Trans. Am. Fish. Soc. 91:399-407.

MERRELL, T. R., JR.

1962. Freshwater survival of pink salmon at Sashin Creek, Alaska. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 59-72. Univ. B.C., H. R. MacMillan Lect. Fish., Vancouver.

NEAVE, F.

1948. Fecundity and mortality in Pacific salmon. Trans. R. Soc. Can., Ser. 3, Sect. 5, 42:97-105.

OLSON, J. M., AND W. J. MCNEIL.

1967. Research on pink salmon at Little Port Walter, Alaska, 1934-64. U.S. Fish Wildl. Serv., Data Rep. 17, 301 p. on 5 microfiche.

OTTO, R. G.

1971. Effects of salinity on the survival and growth of pre-smolt coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 28:343-349.

PARKER, R. R., AND R. E. VINCENT.

[1956]. Progress report on research studies at the Kitoi Bay Research Station. Alaska Fish. Board and Alaska Dep. Fish. 1955 Annu Rep. 1957:25-67.

POWERS, C. F.

1963. Some aspects of the oceanography of Little Port Walter estuary, Baranof Island, Alaska. U.S. Fish Wildl. Serv., Fish. Bull. 63:143-164.

PRITCHARD, A. L.

1940. Studies on the age of the coho salmon (*Oncorhynchus kisutch*) and the spring salmon (*Oncorhynchus tshawytscha*) in British Columbia. Trans. R. Soc. Can., Ser. 3, Sec. 5, 34:99-120.

1947. Efficiency of natural propagation of Pacific salmon. Can. Fish Cult. 1:22-26.

REDICK, R. R.

1968. Population studies of anadromous fish populations—southwestern Kenai Peninsula and Kachemak Bay. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:135-155.

RICKER, W. E.

1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.

ROBSON, D. S., AND H. A. REGIER.

1964. Sample size in Petersen mark-recapture experiments. Trans. Am. Fish. Soc. 93:215-226.

1968. Estimation of population number and mortality rates. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 124-158. IBP (Int. Biol. Programme)., Handb. 3.

ROUNSEFELL, G. A.

1957. Fecundity of North American Salmonidae. U.S. Fish Wildl. Serv., Fish. Bull. 57:451-468.

SALO, E. O., AND W. H. BAYLIFF.

1958. Artificial and natural production of silver salmon, *Oncorhynchus kisutch*, at Minter Creek, Washington. Wash. Dep. Fish., Res. Bull. 4, 76 p.

SEMKO, R. S.

1954. The stocks of west Kamchatka salmon and their commercial utilization. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 41:3-109. (Fish. Res. Board Can. Transl. Ser. 288, 131 p.)

SHAPOVALOV, L., AND A. C. TAFT.

1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dep. Fish Game, Fish Bull. 98, 375 p.

SKEESICK, D. G.
1970. The fall immigration of juvenile coho salmon into a small tributary. Oreg. Fish Comm. Res. Rep. 2:90-95.

SMIRNOV, A. I.
1960. The characteristics of the biology of reproduction and development of the coho *Oncorhynchus kisutch* (Walbaum). Vestn. Mosk. Univ., Ser. VI, Biol. Pochv. 1960(1):9-19. (Fish. Res. Board Can. Transl. Ser. 287.)

SMOKER, W. A.
1953. Stream flow and silver salmon production in western Washington. Wash. Dep. Fish. Fish. Res. Pap. 1(1):5-12.
[1957.] Silver salmon research. Alaska Fish. Board and Alaska Dep. Fish. 1956 Annu. Rep. 8:42-46.

SNEDECOR, G. W.
1956. Statistical methods. 5th ed. Iowa State Univ. Press, Ames, 534 p.

U.S. GEOLOGICAL SURVEY.
1972. Water resources data for Alaska, 1968. Part 1. Surface water records. U.S. Dep. Inter. Geol. Surv., Water Res. Div., 155 p.

VAN HULLE, F. D.
1970. Inventory and cataloging of the sport fish and sport fish waters in southwest Alaska. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1969-70 Prog. Rep. 11:47-63.
1971. Inventory and cataloging of the sport fish and sport fish waters in southwest Alaska. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1970-71 Prog. Rep. 12:29-51.

WALLIS, J.
1967. Salmonid rearing and migration study—Fire Lake system and Fort Richardson cooling pond. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1966-67 Prog. Rep. 8:129-152.
1968. Salmonid rearing and migration study—Fire Lake system and Ft. Richardson and Elmendorf rearing ponds. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:173-191.

WICKETT, W. P.
1951. The coho salmon population of Nile Creek. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 89:88-89.

WILLIS, R. A.
1954. The length of time that silver salmon spent before death on the spawning grounds at Spring Creek, Wilson River, in 1951-52. Oreg. Fish Comm. Res. Briefs 5:27-31.

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VERTICAL DISTRIBUTION AND DIEL MIGRATION OF EUPHAUSIIDS IN THE CENTRAL REGION OF THE CALIFORNIA CURRENT

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ABSTRACT

The density, vertical range, and diel movement of total zooplankton and euphausiid populations in the central region of the California Current were determined during a period of coastal upwelling, July-August 1970. Collections were made along four transects with opening-closing Bongo nets towed through 50- to 100-m intervals in the upper 800 m. Four- to nine-depth intervals at 13 day-night stations were sampled. Twenty euphausiid species from seven genera were identified from 124 hauls.

Zooplankton assemblages in the nearshore regions differed from those farther offshore in having a larger biomass as well as a smaller number and higher density of several species. Diel vertical movement among euphausiid populations, particularly *Euphausia pacifica*, tended to be more pronounced in offshore waters. This behavior suggests that, although assemblages of zooplankton are strongly structured by physical factors, some species alter their vertical distribution and diel migration, presumably in response to the prevailing food supply.

Since 1949 an intensive plankton sampling program has been conducted in the California Current under the auspices of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). These surveys, concentrating on the distribution and density of pelagic organisms in the upper 150 m, have revealed abundance and dispersion patterns of zooplankton which are related to annual and seasonal changes in hydrographic conditions (Brinton 1960, 1962a; Thrailkill 1963; Fleminger 1964, 1967; Alvariño 1965; McGowan 1967; Berner 1967; Isaacs et al. 1969). Within a given year, varying proportions of zooplankton assemblages typical of any one of several water masses are likely to be present (Berner 1957; Bieri 1959; Brinton 1962b; Johnson and Brinton 1963; Cushing 1971). Seasonal hydrographic fluctuations near the coastal boundary of the current act to further transform the numbers and types of pelagic species that develop. For example, the eutrophic environment produced by coastal upwelling during the spring and summer months is characterized by a much higher biomass and lower species diversity than the more oligotrophic, offshore portion of the current (Frolander 1962; Hebard 1966; Laurs 1967; Longhurst 1967; Pieper 1967).

Considerably less attention has been given to the vertical distribution of zooplankton in this current principally because it is difficult, time consuming, and costly to repeatedly sample discrete depths. The scope of this study was to describe the vertical distribution and diel migration of zooplankton, particularly euphausiids, in nearshore and offshore oceanic regions of the central California Current during a period when coastal upwelling was well developed. The samples were collected in the summer of 1970 on two cruises, Stanford Oceanographic Expedition (SOE) cruise 22 and CalCOFI cruise 7008.

DESCRIPTION OF THE ENVIRONMENT

The California Current is a blend of water masses (Subarctic, North Pacific Drift, Central, and Equatorial) and is therefore an extremely variable environment (Reid et al. 1958; McGowan 1971). It flows southward throughout the year with an average velocity of less than 0.5 knot. The boundaries of this transitional water are between lat. 48° and 23°N and extend to 700 km (long. 130°W) from the coast. Between depths of 200 and 400 m, a subsurface countercurrent flows northward at about 0.5 knot from Baja California to Cape Mendocino (Kin'dyushov 1970).

Near the coast, hydrographic fluctuations in this current have been separated into seasonal periods of divergence (upwelling), relaxation (oceanic), and convergence (downwelling) (Bolin and Abbott

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1963; Dodimead et al. 1963). From March to August, the force of the prevailing northerly winds and the earth's rotation cause the southerly flowing surface waters, within 100 km of the shore, to move away from the coast (Yoshida 1955). This displaced water is replaced by cooler, more saline, nutrient-rich water upwelled from deeper regions, providing favorable conditions for high rates of primary production. In the central part of this current, the upwelling period is considered to begin and end with the shifting of the 9°C isotherm above and below the 100-m level (Barham 1957).

The northerly winds subside from September to November and surface water temperatures increase, resulting in the formation of a strong thermocline in the upper 50 m. During this surface-warmed period, in the absence of upwelling, tongues of offshore, oceanic water of the California Current may reach the coast. Where this occurs there is probably considerable mixing of oceanic and neritic planktonic communities (e.g., see Longhurst 1967).

When southerly winds prevail, in the period from December to February, a northerly flowing, coastal countercurrent (Davidson Current) may develop. Surface water converges toward the coast and disrupts the stratification characteristic of the surface-warmed water period. Vertical eddy circulation results, promoting the overturn, mixing, and downwelling of warm, lower salinity, nutrient-poor surface waters. This mixed water period can be characterized by a temperature gradient of less than 1°C in the upper 50 m.

The environments sampled at the shoreward and seaward stations in the summer of 1970 differed in several ways. Physical and chemical features relating to phytoplankton studies during the SOE cruise are presented in Malone (1971). These and other hydrographic features in the upper 800 m at each station are tabulated and discussed in Youngbluth (1973). By way of summary, it was clear from the low temperatures and high salinities and the shoreward elevation of nitrate isopleths that upwelling conditions prevailed near the coast. Chlorophyll-*a* values in the upper 150 m decreased with increasing distances from shore, 2.1-0.5 mg/m^3. The photic zone was usually deeper at the seaward stations, ranging from 55 m in coastal regions to 105 m at the western edge of the transects. The depth of the thermocline was shallower nearshore and deeper offshore, ranging from 5 to 40 m, respectively. The largest temperature difference between the thermocline and 150 m was about 4°C. At depths below 150 m, temperatures differed by 2°C or less among stations.

Temperature-salinity (T-S) curves from each station were compared to two different schemes (Youngbluth 1973). First, the data, when plotted with T-S relationships that characterize the percent mixing between waters near the northern and southern limits of the California Current (Okutani and McGowan 1969), indicated that between 150 and 800 m 70-100% northern water was present. The small percentage of southern water was most noticeable at the intermediate and nearshore stations of the southern transect. Second, the data, when contrasted with T-S curves that distinguish water masses, revealed that samples below 250 m were collected in North Pacific Intermediate water.

MATERIALS AND METHODS

Zooplankton samples were collected with opening-closing Bongo nets of 0.333-mm mesh and cod ends with 0.222-mm mesh (McGowan and Brown 1966). At nearly all stations, shallow and mid-water casts were made, within 3 h of midday and midnight at nearly the same location (Table 1). Shallow tows were taken with a single frame (SOE) or with four frames (CalCOFI) in the upper 150-200 m. Three (SOE) or four (CalCOFI) frames were used on mid-water hauls between 200 and 600

TABLE 1.—The date and position of Bongo net tows.

Cruise	Date 1970	Station	Position Lat. N	Position Long. W
SOE 22	27 July 28 July	9	37°09′	124°24′
	29 July 30 July	16	37°15′	128°45′
	31 July 1 Aug.	25	36°39′	130°53′
	3 Aug. 4 Aug.	39	39°54′	129°58′
	5 Aug. 6 Aug.	47	39°53′	127°48′
	7 Aug. 8 Aug.	56	39°53′	125°48′
	16 Aug. 18 Aug.	68	43°49′	125°49′
	19 Aug.	74	43°55′	128°03′
	20 Aug.	81	43°32′	129°58′
CalCOFI 7008	27 Aug. 28 Aug.	70.75	35°23′	123°27′
	20 Aug. 21 Aug.	50.80	38°40′	126°21′
	18 Aug. 19 Aug.	50.110	37°40′	128°33′
	16 Aug. 17 Aug.	50.140	36°40′	130°44′

m. Depth intervals of about 100 m were sampled. A single frame (CalCOFI) was employed at depths from 600 to 800 m. The nets were hauled along a single oblique path (all CalCOFI and shallow SOE casts) or undulated obliquely through the depth intervals sampled (all mid-water SOE casts). Each point on the graphs representing these data is the middepth of the water column sampled.

The strata sampled were recorded with a Benthos depth-time device attached a few meters below the bottom frame. Vessel speed during the tows ranged between 2 and 2.5 knots (3.7 and 4.6 km/h) and was regulated to maintain a wire angle of approximately 50°. Mean volumes of 619 m^3 (SOE shallow tows), 957 m^3 (SOE mid-water tows), and 546 m^3 (all CalCOFI tows) were filtered. All data were standardized to a volume of 1,000 m^3, assuming 100% filtration efficiency. Clogging of net apertures was observed only in the uppermost nets at the nearshore stations on the CalCOFI cruise.

The samples were preserved in 5% Formalin[2] solution buffered to pH 7.6. All organisms longer than 2 cm were removed from the sample and wet weights were determined after draining the remaining portion on a 0.222-mm mesh screen and blotting it on absorbent paper for 20 min. Duplicate estimates varied by an average of 6%.

The larvae (furcilia), juveniles (postlarvae and immatures), and adults (sexually mature) of all euphausiid species were studied. All individuals of the less abundant species were identified and counted. The densities of the more numerous species were determined from subsamples made with a modified Folsom Plankton Splitter. The average number of specimens examined in the subsamples was about 300. Duplicate counts were compared with each other by calculating a Percent Similarity Index (Whittaker 1952).

If the index indicated at least 80% agreement between the first two replicates, no other counts were made. Occasionally a third count was necessary.

The taxonomy of adult euphausiids follows Boden et al. (1955). Identification of certain difficult groups, e.g., *Nematoscelis* spp., *Thysanoessa* spp., and all larvae were verified by E. Brinton, T. Antezana, and K. Gopalakrishnan at the Scripps Institution of Oceanography. When specimens lacked some of the usual key characters, general body form and eye size, shape, and color were used to distinguish the species.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Sampling Variability Between Cruises

Samples were collected along four transects. The stations ranged from 130 to 693 km off the coast (Figure 1). During the CalCOFI cruise, a smaller average volume of water was filtered by each net. Presumably this smaller volume could have introduced some bias by reducing species diversity and abundance estimates. Comparisons of the results from each cruise indicate that, except for three rarely caught species: 1) the number of euphausiid species collected was identical and 2) the order of species abundances was quite similar on each cruise. Biomass values of total zooplankton tended to be larger at the seaward stations during the CalCOFI cruise. This difference is most likely related to the greater number and narrower, vertical width of the tows taken during this cruise, and, to some extent, growth and development of each life stage as well

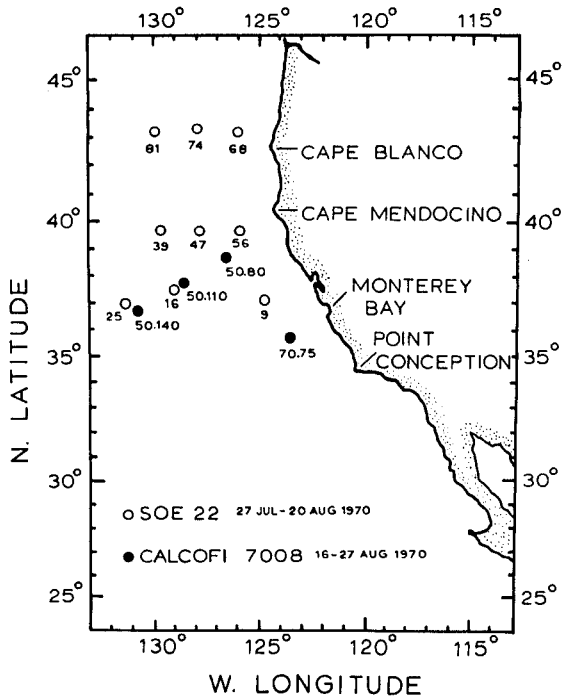

FIGURE 1.–Positions of the day-night stations in the central portion of the California Current.

as offshore transport of the more numerous species observed in nearshore waters.

Distribution of Zooplankton Biomass

The standing stock of zooplankton was highest at the nearshore stations and decreased with distances seaward. The largest and smallest biomass values occurred along the southern transect and corresponded with high and low phytoplankton stocks, respectively (Malone 1971).

Zooplankton were concentrated in the upper 100-150 m at most stations, particularly in the mixed layer (ca. 0-40 m). Densities ranged from 10 to 580 g wet wt/1,000 m^3 (Figure 2). Below 100-150 m, the amount of zooplankton at approximately 100-m intervals was generally between 25 and 150 g wet wt/1,000 m^3. Diel fluctuations in biomass were greatest in the surface water (0-150 m) increasing at night by factors of 1.2-8. At two nearshore stations, CalCOFI 50.80 and 70.75, large quantities of phytoplankton clogged net meshes in the upper 50 m and prevented any quantitative comparison of day and night catches. Below 150 m, a small but consistent increase in biomass was usually observed at night ($P = 0.20$, Sign Test). During the day, at some intervals between 250 and 400 m, biomass was equal to or slightly greater than concentrations in the upper 150 m.

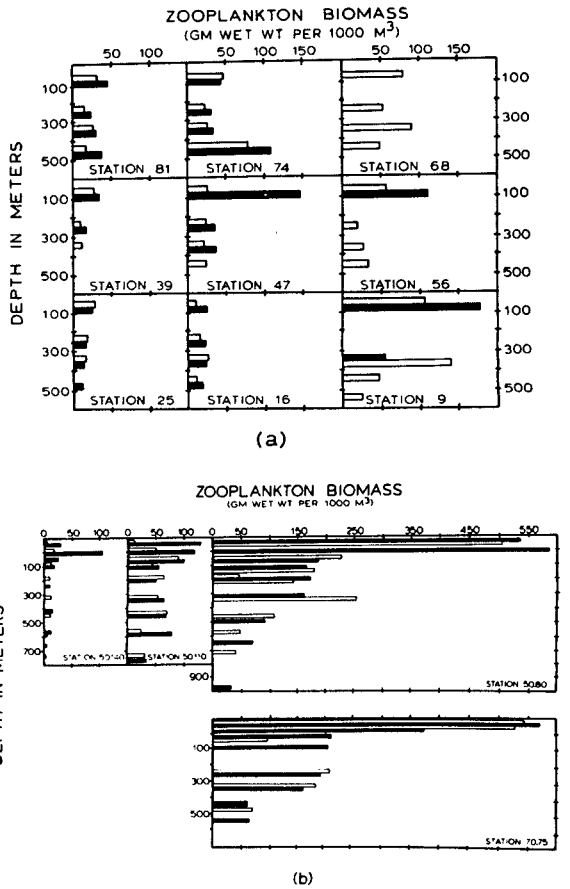

FIGURE 2.–The vertical distribution of zooplankton biomass. Clear bars indicate day samples; dark bars designate night samples. (a) SOE cruise 22 and (b) CalCOFI cruise 7008.

Diversity, Density, and Distribution of Euphausiid Species

Twenty species of euphausiids distributed among seven genera were identified. Thirteen species occurred frequently enough and in sufficient numbers to allow descriptions of their vertical distribution. In the upper 150 m, 8 species formed 50% of the total abundance and 12 made up 90%. Nine species were found at more than half the stations. In the total water column sampled (ca. 0-700 m), 6 and 11 species composed 50 and 90% of the total species abundance. At most stations one or two species were numerically dominant.

The distributions of euphausiids at midday and midnight are discussed in the following paragraphs. Only examples of a few species are illustrated to represent the major patterns observed since a large number of profiles were derived from the data for all the species collected at each station (Youngbluth 1973). In many cases, diurnal changes in vertical distributions were obscured either by patchiness or avoidance or incomplete sampling due to gear failure or foul weather. This account is thus a composite description of the data from all stations.

Euphausia

Four species of *Euphausia* were taken–*E. pacifica*, *E. recurva*, *E. gibboides*, and *E. mutica*. With the exception of *E. pacifica*, these species were only abundant at the offshore stations along the southern transects (SOE 16, 25; CalCOFI 50.110). In this region densities of each species usually ranged between 10 and 200/1,000 m^3. Juveniles and larvae were often more than twice as numerous as adults. The daytime habitat of *E. mutica* larvae was between 100 and 400 m. Juveniles of this species were found only in one haul which sampled from 400 to 500 m (SOE 16). *Euphausia gibboides* and *E. recurva* were collected

somewhat deeper, 250-350 m and 400-600 m, respectively. At night all stages of these species migrated into the upper 100 m. *Euphausia mutica* and *E. recurva* appeared in the upper 50 m, whereas *E. gibboides* was more widely distributed with most of the population between 50 and 250 m (e.g., CalCOFI 50.140).

The relative abundance, vertical distribution, and diel migration of *E. pacifica* varied with distance from the coast (Figure 3). Data from all stations are illustrated to show the number of patterns exhibited by this species. Larvae and juveniles tended to occupy a much wider vertical range in nearshore waters. The bulk of the larvae was usually found in the upper 150 m day and night. The single exception to this pattern was observed at CalCOFI 70.75 where the larvae were abundant at 250 m throughout the day and in very large numbers in the upper 100 m at night. Juveniles were numerous in the surface waters as well as at depths to 450 m. The adult phase was frequently most abundant between 200 and 400 m during the daytime. Offshore, during the day, densities of this species were reduced, adults were rarely collected, and populations occurred at deeper, narrower intervals. At night, both nearshore and offshore, only some members of each stage migrated to the surface waters from depths of 250-450 m. The general features of the geographical distribution of this species in the central regions of the California Current agree with observations by Brinton (1962b, 1967); the vertical dimensions are more detailed.

Tessarabrachion

The only species of this genus, *T. oculatus* was frequently found in small numbers, i.e., 10-20/1,000 m^3. Juveniles and adults of this characteristic subarctic species were common and occurred between 70 and 500 m. Somewhat greater numbers were collected at night. The larvae tended to remain closer to the surface, i.e., from 70 to 200 m (SOE 74; CalCOFI 50:110), than juveniles and adults which were usually found between 200 and 400 m. Thus, this species inhabits a wide depth interval below the thermocline regardless of the time of day.

Thysanopoda

Three species of *Thysanopoda* were collected—*T. aequalis*, *T. acutifrons*, and *T. egregia*. Very few specimens of these species were taken. Larvae of *T. aequalis*, a species typical of central water masses, were found in the upper 200 m at the offshore stations of the southernmost transect. Adults, found only at night at the same stations, were collected above 300 m. Larvae of *T. acutifrons* were not observed. One juvenile and one adult were taken during the day between 400 and 500 m at different offshore stations. At night a total of 11 adults and 2 juveniles were caught between 200 and 500 m (SOE 16, 74; CalCOFI 50.110, 50.140). One to four larvae of *T. egregia* were collected between 50 and 450 m at nearly all but the most northern stations.

Thysanoessa

Three species of *Thysanoessa* were found—*T. spinifera*, *T. gregaria*, and *T. longipes*. *Thysanoessa spinifera* was only collected near the coast, most frequently in the upper 150 m. Small densities of juveniles, the most abundant stage, were present in tows from 150 to 350 m (CalCOFI 50.80, 70.75). Adults were not collected. The preponderance of *T. spinifera* in the neritic environment has been noticed previously (Brinton 1962a; Hebard 1966). Diel changes in the vertical distribution of juveniles indicate that perhaps some members of this phase migrated into the upper 100 m at night (Figure 4a). These data support other studies that have suggested this species is a diel migrant (Regan 1968; Day 1971; Alton and Blackburn 1972).

Thysanoessa gregaria occurred at all but one location (SOE 68). This species was found most often in the upper 150 m, although it ranged to 300 m. Juvenile phases dominated the catches during the SOE cruise. All stages were abundant among the CalCOFI samples gathered 2 wk later. Densities were greater along the southern transects. From 50 to 500 individuals/1,000 m^3 were recorded within depth intervals where the largest concentrations occurred. Larvae usually resided in the upper 50 m. Juveniles and adults were numerous between 50 and 200 m and often 3-10 times more numerous in the night tows. These data suggest that the older stages probably avoided the sampling gear during the day. At one station (CalCOFI 70.75), all stages of *T. gregaria* were observed only in the upper 20 m during the day. At night this species ranged to 400 m with the largest densities occurring between 60 and 100 m and no specimens were collected in the upper 30 m. These

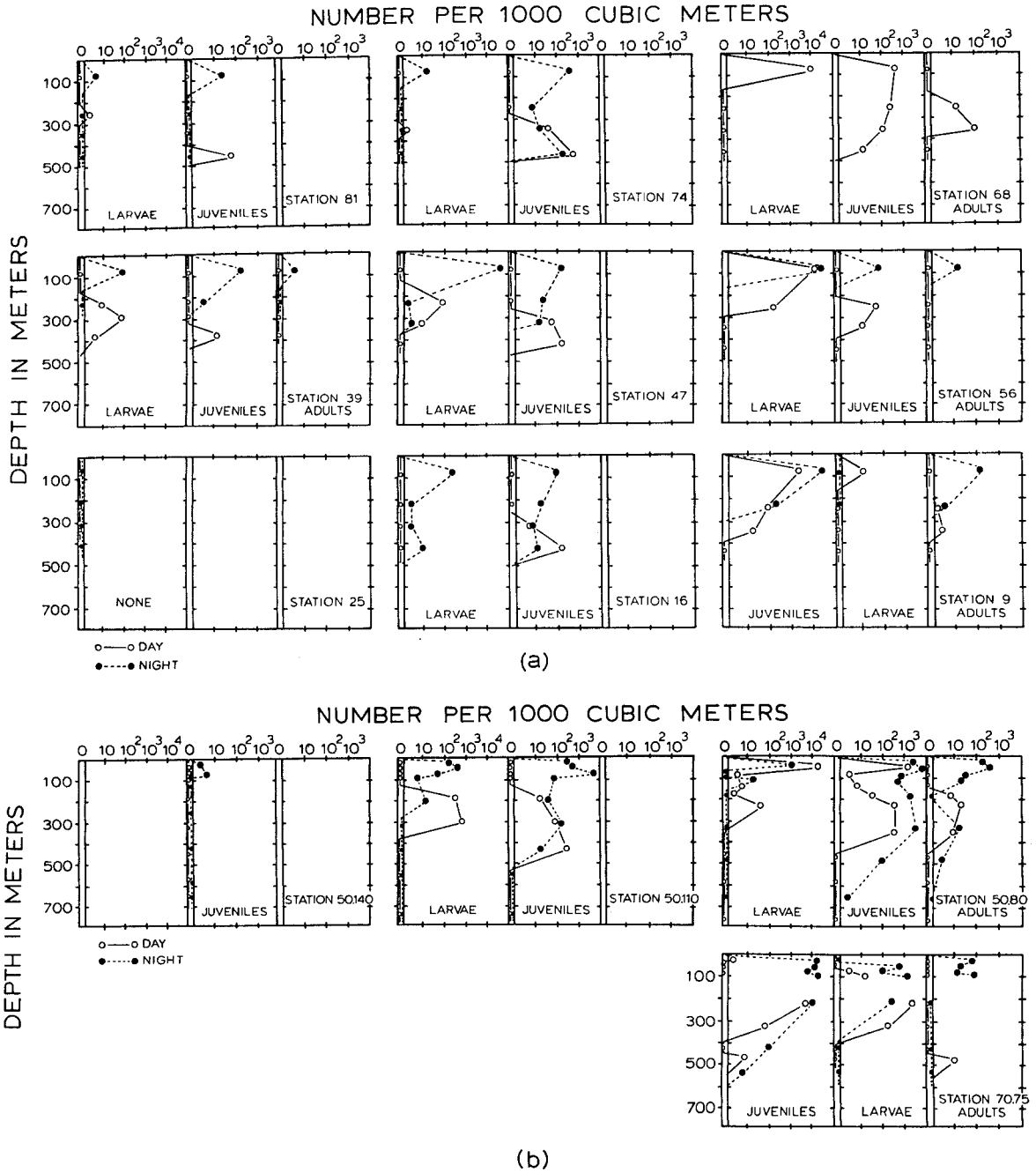

FIGURE 3.—The vertical distribution of *Euphausia pacifica* according to stage of development. (a) SOE cruise 22 and (b) CalCOFI cruise 7008.

observations indicate this species can be contagiously dispersed.

All phases of *T. longipes* (unspined form) were collected in the upper 150 m. Juveniles and adults were also abundant between 200 and 800 m. Portions of these older populations appeared to migrate toward the surface at night at several stations (SOE 9, 74, 81; CalCOFI 50.80, 50.110) (Figure 4b). The vertical range of this species agrees with observations by Brinton (1962b) and

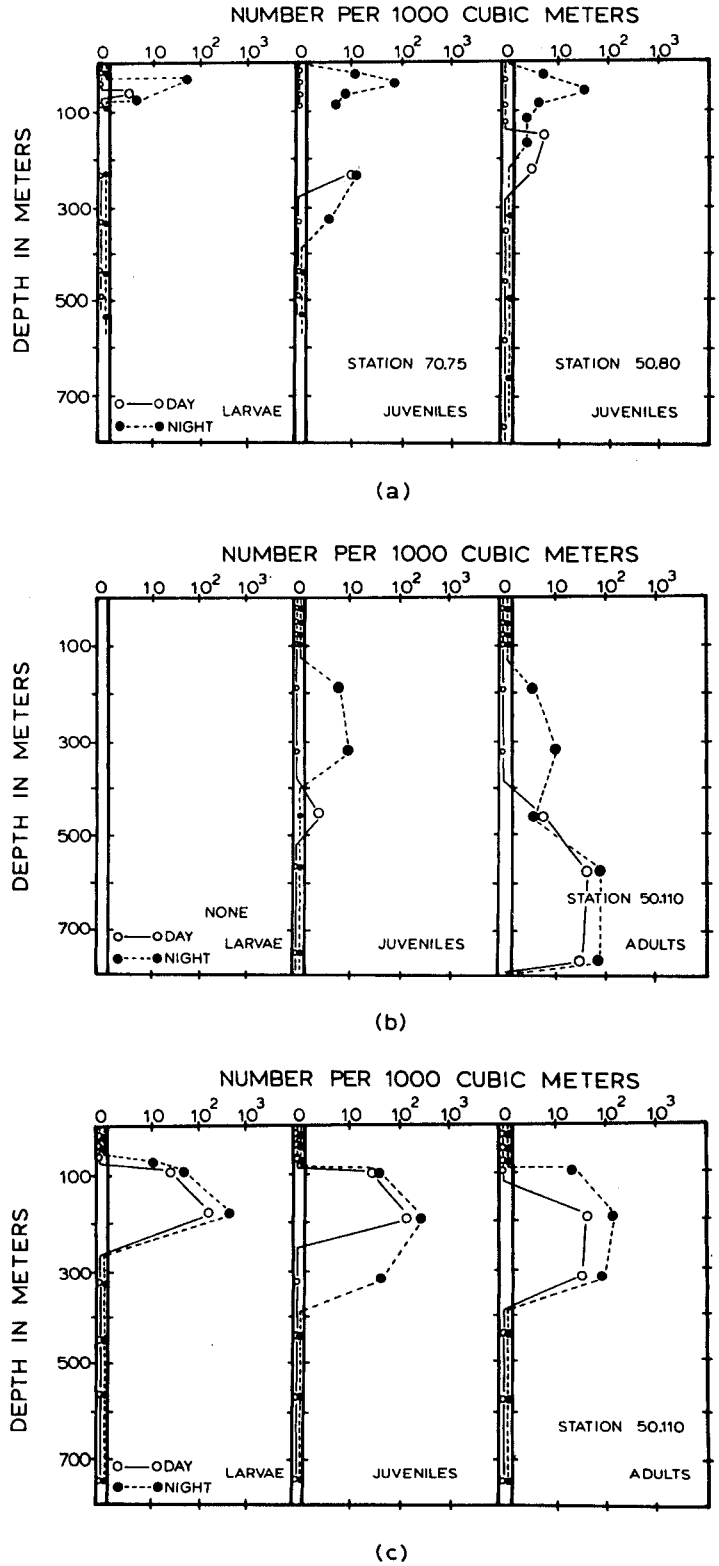

FIGURE 4.—Examples for the vertical distribution of (a) *Thysanoessa spinifera*, (b) *Thysanoessa longipes*, and (c) *Stylocheiron longicorne* according to stage of development.

Ponomareva (1963). The abundance in subsurface waters and the possible migratory behavior of this unspined form have not been documented previously.

Nematoscelis

Two species of *Nematoscelis* were taken—*N. tenella* and *N. difficilis*. *Nematoscelis tenella* was collected at only one day-night station (SOE 16). The few adults and juveniles caught, 2-13/1,000 m^3, were found between 400 and 500 m during the day and 0 and 250 m at night. *Nematoscelis difficilis* occurred between the surface and 450 m at all but one station (SOE 25). This species was more abundant near the coast along the CalCOFI transect. Densities ranging in the hundreds per 1,000 m^3 at nearshore stations were an order of magnitude larger than concentrations among samples from waters farther offshore. Larvae and most juveniles were taken only in the upper 100 m. Adults were more abundant between 100 and 300 m, particularly at night.

Stylocheiron

Five species of this genus were found—*S. affine*, *S. longicorne*, *S. maximum*, *S. elegatum*, and *S. abbreviatum*. These species occupied similar depth intervals day and night although each species tended to inhabit a separate portion of the water column. *Stylocheiron affine* occurred only along the southern transect. All stages were collected between 40 and 135 m and primarily at the most offshore stations where densities of 60-150/1,000 m^3 were recorded (SOE 25; CalCOFI 50.140). Each stage was often more abundant in the night samples. *Stylocheiron longicorne*, the most abundant species of this genus, ranged between 70 and 350 m, but the bulk of the populations were within the 150- to 250-m interval (Figure 4c). More specimens were usually caught at night. *Stylocheiron maximum* occurred in low densities at every station, i.e., 5-40/1,000 m^3. Larvae and juveniles of this species were found most often between 70 and 200 m. Adults were generally deeper, ranging from 200 to 400 m. Differences between day and night distributions indicate that this species migrated less than 100 m, if at all. Very small densities of *S. elongatum*, 1-27/1,000 m^3, were observed at the offshore stations between 200 and 600 m. A few adults of *S. abbreviatum* were found along the southern transect of the SOE cruise. Four individuals were collected in the upper 150 m at stations well offshore (SOE 25, 39) and one between 300 and 400 m nearshore (SOE 9).

Nematobrachion

Two species of *Nematobrachion* were found—*N. boopis* and *N. flexipes*. One to two individuals of *N. boopis*, mostly juveniles, were taken between 300 and 500 m and only during the day at a few, southern stations (SOE 9; CalCOFI 70.75, 50.140). *Nematobrachion flexipes* occurred at all but one station (SOE 68). Small concentrations, usually 1-30/1,000 m^3 but ranging up to 69/1,000 m^3, were found regardless of the time of day. Juveniles were often the most numerous stage. This species was frequently encountered at 200-500 m during the day. At night specimens were collected from 450 m to the surface with most of a population in the upper 150 m.

PATTERNS OF ABUNDANCE, VERTICAL DISTRIBUTION, AND DIEL MIGRATION

The abundance and vertical distribution of the more numerous euphausiid species in the upper 500-700 m differed in relation to distance from shore, longitudinal position in the area sampled, and vertical ranges occupied during a given day. The largest densities of euphausiids occurred near the coast (Table 2). Among the nearshore stations (ca. 100-150 km from the coast) *E. pacifica* was the numerically dominant euphausiid day and night, composing 75-90% of all species observed. At intermediate distances from the coast (ca. 300 km), *E. pacifica* was less abundant, making up 36-60% of the species collected, but still ranked first except in the north (SOE 74) where *Thysanoessa longipes* formed 69% of the day catch. Other euphausiid species constituting 15-30% of the total number included *S. longicorne*, *E. gibboides*, *T. gregaria*, and *T. longipes*. At stations farthest offshore (ca. 600-700 km) along the southern transects, *T. gregaria* and *S. longicorne* were the most abundant species, forming 75% of the total during the day. At night, larger numbers of *E. gibboides*, *E. mutica*, and *E. recurva* were collected such that these populations also ranked among 75% of the euphausiids collected. To the north, *T. longipes* and *S. longicorne* were the abundant species, composing 70-80% of all euphausiids. These changes in species composition and dominance represent the

TABLE 2.–The smallest and largest densities of all euphausiid phases among the depth intervals sampled. Data from night tows unless marked with a plus (+) sign which indicates densities are from day tows.

	SOE transects									CalCOFI transect			
	Northern stations			Central stations			Southern stations						
Species	81	74	68	39	47	56	25	16	9	50.140	50.110	50.80	70.75
Euphausia pacifica	[1]27	9-540	72-10,783+	3-188	22-32,748	29,847	—	10-296	224-13,793	2-3	17-7,340	2-8,220	10-14,098
E. recurva	1	—	—	3	5+	1+	33	103	—	178-224	62	—	4+
E. gibboides	—	—	—	10	1-4+	—	198	9-207	2	2-82	6-26	2-9	4-24
E. mutica	—	—	—	—	—	—	—	7+	—	142-181	59-85	—	—
Tessarabrachion oculatus	1-3	11-31	2-34+	49	2-10	2	2+	1-11	9-54	2	2-16	5-20	2-8
Thysanopoda aequalis	—	—	—	—	—	—	4	7	—	4-44	—	—	—
T. acutifrons	—	1	—	—	—	—	1-2	1	—	2	2-2	—	—
T. egregia	—	—	—	—	—	—	4	2	1	3	2+	2	2+
Thysanoessa spinifera	—	—	14+	—	—	10	—	—	1-4	—	—	2-37	4-118
T. gregaria	25	2	—	33-34	81	29	1-173	3-71	6-142	4-646	2-481	3-223	7-768
T. longipes	8-109	27-197	4-134+	321	17-303	33	—	3	59-141	2	9-89	6-94	6-12
Nematoscelis tenella	—	—	—	—	—	—	—	3-4	—	—	—	—	—
N. difficilis	8	1-9	4-4+	9-9	2-7	3-3	—	33-43	89-109	15	8-26	8-512	12-189
Stylocheiron affine	—	—	—	—	—	—	62	1-18	—	2-151	2	6	11-18
S. longicorne	2-55	3-4	2+	34-52	2-53	11	1-295	17-73	26-229	8-130	2-900	2-248	4-68
S. maximum	1-5	2-2	1+	8	2-7	2	1-16	2-6	3-19	2-20	4-16	6-20	2-48
S. elongatum	—	—	—	1	1+	—	—	1-4	—	—	—	—	—
S. abbreviatum	—	—	—	2+	—	—	—	—	1+	—	—	—	—
Nematobrachion boopis	—	—	—	—	—	—	—	—	1+	2+	—	—	2-2+
N. flexipes	1-15	1-5	—	51	1-3	2	16	1-37	1-4	10-37	2-28	2-24	2-13
Number of depth intervals sampled	4	4	4	2	3	1	4	4	2	9	9	9	8

[1]A single density indicates a species was captured within only one depth interval.

complex interaction of: 1) the recruitment and mixing of species characteristic of the water masses that compose the California Current, 2) the daily vertical movements of euphausiids, 3) the ability of most species to avoid the sampling gear, and, to some extent, 4) their contagious dispersion. Consequently only the more obvious patterns have been noted.

The vertical distributions of adults and juveniles in the upper 500-700 m are summarized in Table 3 and compared with data from the southern part of the California Current. As previously mentioned, 7 of the 20 species collected appear to be diel migrants. Distances of 300 m or more were traversed by four species of *Euphausia*. Portions of other populations such as *Nematobrachion flexipes*, *T. longipes*, and *T. spinifera* may migrate up to 200 m.

The larval phases of most species live in the upper 150 m. *Tessarabrachion oculatus* and *Stylocheiron* spp. larvae were found more often below the thermocline. The young of *Euphausia* spp. tended to occupy and migrate through the same depths as the older stages. In nearly all instances, differences in density between day and night catches of larvae were small.

The nonmigrating species included *Thysanoessa gregaria*, *Tessarabrachion oculatus*, *S. maximum*, *S. affine*, and *S. longicorne*. The first three species were usually scattered throughout a broad vertical range. The other two species, *S. affine* and *S. longicorne*, were vertically segregated and occurred within much narrower depth intervals. The different strata occupied by these two nonmigrating species was also observed in other regions by Brinton (1967), Baker (1970), and Youngbluth (1975).

DISCUSSION

Differences in the distribution patterns of many species of zooplankton have been associated with their response to environmental gradients, particularly temperature and illumination (Harris 1953; Lewis 1954; Banse 1964; Boden and Kampa 1967). In this study, the causative factors influencing vertical and horizontal distributions are difficult to elucidate. It is clear, however, that the thermocline was an upper distribution boundary for several species, e.g., *T. oculatus*, *E. gibboides*, *S. affine*, *S. longicorne*, and *S. maximum*. In the southern part of the California Current, the upper range of these species was also restricted by the thermocline (Brinton 1967). Studies on the tolerance of *E. pacifica* to changes in temperature and salinity suggest that other unknown factors probably regulate its distribution in the California Current (Gilfillan 1972a, b).

Recently Isaacs et al. (1974) have proposed that "by responding to light intensity, most vertically migrating marine creatures are directed to food. ... In areas of low standing crops of phytoplank-

TABLE 3.—Comparisons of diel changes in the vertical distributions of adult and juvenile euphausiids. Depth ranges (m) are 10% and 90% levels.

Species	Central California Current		Southern California Current (Brinton 1967)	
	Day	Night	Day	Night
Euphausia pacifica	20-500	0-450	150-425	0-150
E. recurva	300-600	0-50	180-550	0-150
E. gibboides	300-600	10-150	[1]300-500	40-120
E. mutica	[2]370-470	0-150	—	—
Tessarabrachion oculatus	70-450	70-450	—	—
Thysanoessa spinifera	125-300	0-150	—	—
T. gregaria	0-200	0-350	20-180	0-250
T. longipes	0-800	0-800	—	—
Nematoscelis difficilis	0-400	0-400	[2]50-200	0-275
Stylicheiron affine	40-100	35-100	[3]50-200	15-250
S. longicorne	100-350	100-350	125-300	125-300
S. maximum	70-450	70-450	[4]130-200	[4]130-200
Nematobrachion flexipes	200-500	0-130	100-450	100-350
Sampling range (m)	0-800		0-600	
Sampling interval	50-150		25-100	
Gear employed	Bongo nets		Leavitt nets	
Mesh opening	0.333 mm		0.550 mm	

[1]Adults only.
[2]Based on seven specimens from one station.
[3]Mostly juveniles.
[4]Maximum concentration of juveniles.

ton, daylight penetrates further into the ocean causing the migrating animals to descend deeper. In the turbid water associated with high standing crop, the migrating forms remain closer to the surface." Observations on the vertical distribution and daily movements of one euphausiid species in this study lend support to this hypothesis. In more turbid, upwelled water near the coast where standing stocks of phytoplankton were greater (e.g., CalCOFI 50.80), populations of juvenile *E. pacifica* were larger and extended over wider vertical ranges but their diel vertical migrations were not pronounced. In clearer, more oligotrophic waters farther offshore (e.g., CalCOFI 50.110; SOE 16, 47, 74), populations were reduced in size, occupied deeper, usually narrower depth intervals, and daily vertical movements were more obvious. From these few observations it appears that density levels and migration intensities of this species may be coupled with the standing stock of phytoplankton in surface waters.

The persistence of nonmigrating forms, e.g., *Stylocheiron* spp., within the same, relatively narrow depths day and night in waters of varying origin and the recurrence of the finding in this and other studies (Brinton 1967; Youngbluth 1975) that only a portion of a population categorized as a migrating form, e.g., *Euphausia* spp., may actually make daily vertical movements to surface waters, suggest that factors in addition to temperature and light act to regulate the distributions recorded. These observations indicate that more attention should be directed toward sampling those horizons where zooplankton populations are concentrated to determine how distributional and behavioral patterns are structured by the physical and biological fluctuations within their preferred habitats.

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LITERATURE CITED

ALTON, M. S., AND C. J. BLACKBURN.
1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen in coastal waters of Washington. Calif. Fish Game 58:179-190.

ALVARIÑO, A.
1965. Distributional atlas of Chaetognatha in the California Current region. Calif. Coop. Oceanic Fish. Invest., Atlas 3, 291 p.

BAKER, A. DE C.
1970. The vertical distribution of euphausiids near Fuerteventura, Canary Islands ('Discovery' SOND Cruise, 1965). J. Mar. Biol. Assoc. U.K. 50:301-342.

BANSE, K.
1964. On the vertical distribution of zooplankton in the sea. Prog. Oceanogr. 2:53-125.

BARHAM, E. G.
1957. The ecology of sonic scattering layers in the Monterey Bay area. Stanford Univ., Hopkins Mar. Stn. Tech. Rep. 1, 182 p.

BERNER, L. D., JR.
1957. Studies on the Thaliacea of the temperate northeast Pacific Ocean. Ph.D Thesis, Scripps Inst. Oceanogr., Univ. Calif., San Diego, 144 p.
1967. Distributional atlas of Thaliacea in the California Current region. Calif. Coop. Oceanic Fish. Invest., Atlas 8, 322 p.

BIERI, R.
1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnol. Oceanogr. 4:1-28.

BODEN, B. P., M. W. JOHNSON, AND E. BRINTON.
1955. The Euphausiacea (Crustacea) of the North Pacific. Bull. Scripps Inst. Oceanogr., Univ. Calif. 6:287-400.

BODEN, B. P. AND E. M. KAMPA.
1967. The influence of natural light on the vertical migrations of an animal community in the sea. Symp. Zool. Soc. Lond. 19:15-26.

BOLIN, R. L. AND D. P. ABBOTT.
1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Oceanic Fish. Invest., Rep. 9:23-45.

BRINTON, E.
1960. Changes in the distribution of euphausiid crustaceans in the region of the California Current. Calif. Coop. Oceanic Fish. Invest., Rep. 7:137-146.
1962a. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8:51-269.
1962b. Variable factors affecting the apparent range and estimated concentration of euphausiids in the North Pacific. Pac. Sci. 16:374-408.
1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

CUSHING, D. H.
1971. Upwelling and the production of fish. Adv. Mar. Biol. 9:255-334.

DAY, D. S.
1971. Macrozooplankton and small nekton in the coastal waters off Vancouver Island (Canada) and Washington,

spring and fall of 1963. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 619, 94 p.

DODIMEAD, A. J., F. FAVORITE, AND T. HIRANO.
1963. Salmon of the North Pacific Ocean. Part II. Review of the oceanography of the subarctic Pacific region. Int. North Pac. Fish. Comm. Bull. 13, 195 p.

FLEMINGER, A.
1964. Distributional atlas of calanoid copepods in the California Current region, part I. Calif. Coop. Oceanic Fish. Invest., Atlas 2, 313 p.
1967. Distributional atlas of calanoid copepods in the California Current region, part II. Calif. Coop. Oceanic Fish. Invest., Atlas 7, 213 p.

FROLANDER, H. F.
1962. Quantitative estimations of temporal variations of zooplankton off the coast of Washington and British Columbia. J. Fish. Res. Board Can. 19:657-675.

GILFILLAN, E.
1972a. Seasonal and latitudinal effects on the responses of *Euphausia pacifica* Hansen (Crustacea) to experimental changes of temperature and salinity. *In* A. Y. Takenouti (editor), Biological oceanography of the northern North Pacific Ocean, p. 443-463. Idemitsu Shoten, Tokyo, Jap.
1972b. Reactions of *Euphausia pacifica* Hansen (Crustacea) from oceanic, mixed oceanic-coastal and coastal waters of British Columbia to experimental changes in temperature and salinity. J. Exp. Mar. Biol. Ecol. 10:29-40.

HARRIS, J. E.
1953. Physical factors involved in vertical migration of plankton. Q. J. Microsc. Sci. 94:537-550.

HEBARD, J. F.
1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanographic conditions. Ph.D. Thesis, Oregon State Univ., Corvallis, 94 p.

ISAACS, J. D., A. FLEMINGER, AND J. K. MILLER.
1969. Distributional atlas of zooplankton biomass in the California Current region: Spring and fall 1955-1959. Calif. Coop. Oceanic Fish. Invest., Atlas 10, 252 p.

ISSACS, J. D., S. A. TONT, AND G. L. WICK.
1974. Deep Scattering Layers: vertical migration as a tactic for finding food. Deep-Sea Res. 21:651-656.

JOHNSON, M. W., AND E. BRINTON.
1963. Biological species, water-masses and currents. *In* M. N. Hill (editor), The Sea, Vol. 2, p. 381-414. Interscience, N.Y.

KIN'DYUSHOV, V. I.
1970. Seasonal changes of water masses in the California region of the Pacific Ocean. [In Russ., Eng. summ.] Okeanologia. 10:596-606.

LAURS, R. M.
1967. Coastal upwelling and the ecology of lower trophic levels. Ph.D. Thesis, Oregon State Univ., Corvallis, 121 p.

LEWIS, J. B.
1954. The occurrence and vertical distribution of the Euphausiacea of the Florida Current. Bull. Mar. Sci. Gulf Caribb. 4:265-301.

LONGHURST, A. R.
1967. Diversity and trophic structure of zooplankton communities in the California Current. Deep-Sea Res. 14:393-408.

MCGOWAN, J. A.
1967. Distributional atlas of pelagic molluscs in the California Current region. Calif. Coop. Oceanic Fish. Invest., Atlas 6, 218 p.
1971. Oceanic biogeography of the Pacific. *In* B. M. Funnell and W. R. Riedel (editors), The micropaleontology of oceans, p. 3-74. Camb. Univ. Press., Lond.

MCGOWAN, J. A. AND D. M. BROWN.
1966. A new opening-closing paired zooplankton net. Scripps Inst. Oceanogr. Ref. 66-23, 56 p.

MALONE, T. C.
1971. The relative importance of nannoplankton and netplankton as primary producers in the California Current system. Fish. Bull., U.S. 69:799-820.

OKUTANI, T. AND J. A. MCGOWAN.
1969. Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California Current, April, 1954–March, 1957. Bull. Scripps Inst. Oceanogr., Univ. Calif. 14, 90 p.

PIEPER, R. E.
1967. Mesopelagic faunal discontinuities in the eastern North Pacific. AC Electronic-Def. Res. Lab. Rep. TR67-19, 38 p.

PONOMAREVA, L. A.
1963. Euphausiids of the North Pacific, their distribution and ecology. Akad. Nauk SSSR Inst. Okeanol. (Translated by Israel Program Sci. Transl., Jerusalem 1966, IPST cat. no. 1368, 154 p.)

REGAN, L.
1968. *Euphausia pacifica* and other euphausiids in the coastal waters of British Columbia: Relationships to temperature, salinity and other properties in the field and laboratory. Ph.D. Thesis, Univ. British Columbia, Vancouver, 235 p.

REID, J. L., JR., G. L. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest., Prog. Rep., 1 July to 1 Jan. 1958, p. 27-57.

THRAILKILL, J. R.
1963. Zooplankton volumes off the Pacific Coast, 1959. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 414, 77 p.

WHITTAKER, R. H.
1952. A study of summer foliage insect communities in the Great Smokey mountains. Ecol. Monogr. 22:1-44.

YOSHIDA, K.
1955. Coastal upwelling off the California coast. Rec. Oceanogr. Works Jap., New Ser. 2(2):8-20.

YOUNGBLUTH, M. J.
1973. The vertical distribution, diel migration, and community structure of euphausiids. Ph.D. Thesis, Stanford Univ., Palo Alto, Calif., 298 p.
1975. The vertical distribution and diel migrations of euphausiids in the central waters of the eastern South Pacific. Deep-Sea Res. 22:519-536.

THE APPLICATION OF SYSTEMATIC SAMPLING TO A STUDY OF INFAUNA VARIATION IN A SOFT SUBSTRATE ENVIRONMENT[1]

STEPHEN SCHERBA, JR.[2] AND VINCENT F. GALLUCCI[3]

ABSTRACT

Stratified systematic sampling was applied to an intertidal macrofauna sediment study. A stratified systematic sampling plan retains the advantages of the more common fixed level transect sample, and possesses additional advantages which recommend it for use in some intertidal studies. The field data collected in this study demonstrated the effectiveness of stratified systematic sampling for quantifying both sediment and population characteristics along a sediment gradient, and for the testing of biological hypotheses.

Intraarea, interarea, and interseason hypotheses about sediment composition were tested in terms of particle size distributions. Populations of bivalves and polychaetes were simultaneously sampled and hypotheses concerning spatial and seasonal variations in an intertidal mud flat were tested. Experimental results using stratified systematic sampling suggest that Newell's hypothesis can be extended to encompass temporal variation. Fine sediment grades (silty areas) may act to insulate infauna against the extremes of seasonal stresses.

Sediment composition, as measured by the average percentage composition by weight of various grain sizes, was not sufficient to predict macrofaunal presence.

The study of the complex relationship existing between macrofauna (e.g., bivalves and polychaetes) and their soft substrate environment is of wide interest in marine biology. Soft sediments are both a shelter from predators and a food source for deposit feeders. The particle size distribution of the sediment influences such factors as food availability, the depth of the aerobic layer, water content, pH differentials, and growth rates. Detrital content and particle size distribution of the sediment are largely determined by the hydrodynamics of currents. However, Rhoads (1967) demonstrated that macrofauna modify sediment stability, composition, and water content by activities such as building tubes, ingesting sediment and detritus (to remove bacteria from sediment particles), depositing feces, etc. The particle size distribution of the sediment is, therefore, one measure of certain types of biological activity (Newell 1965).

Studies in soft substrate environments usually involve sediment samples which contain large numbers of macrofaunal species in different densities as well as different particle size distributions. Then, it may be necessary to make comparisons between samples which may call for the use of statistical methods as found in standard textbooks (e.g., Sokal and Rolf 1969). The validity of tests of comparisons, however, must rest upon the application of valid sampling plans in the field, but most valid sampling plans do not meet the needs of the ecologist. This paper reports on the use of stratified systematic sampling which, to our knowledge, is heretofore unused in the marine literature. Stratified systematic sampling seems to meet the needs of most studies that would have used transecting methods which, generally, are statistically unacceptable. The sampling method is applied to a study of animal and sediment gradients in a basically marine embayment subject to seasonal variation in density of animals and algae. Hypotheses comparing areas of different sediment composition in the winter, spring, and summer are tested using animal-presence and sediment-particle-size data collected using a stratified systematic sampling plan. The bay is shown to contain a sediment gradient from fine silt to coarse sand, with an associated polychaete distribution expressed by both the number of animals per species and by the number of species found.

A variety of sampling methods are described in the literature. For example, the works of Skellam (1958) and Sen et al. (1974) presented different

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types of transect methods, and Saila and Gaucher (1966), Russell (1972), and Loesch (1974) described subtidal stratified random sampling methods.

Transecting methods used in the soft substrate of the intertidal zone usually involve the choice of a narrow belt of one or two sampling units in width, placed perpendicular to the water line. Samples are collected at fixed and predetermined tidal levels (e.g., every 10 m) to correspond to changes in such things as algal and sediment composition (Matthiessen 1960; Vassallo 1969; Warme 1971; Bloom et al. 1972). This method will be referred to as fixed level transect sampling (FLTS). A common denominator in this type of work is that no probability model is used in selecting the location of the sampling units. An alternative to FLTS is simple or stratified random sampling where the discrete uniform probability distribution underlies the selection of sample sites. The disadvantage of random sampling is that there is no guarantee that sample sites will be in those areas where experimental interest is focused. However, without an underlying probability model, valid statistics may not be estimated (Cochran 1963) because the sample sites may not be independently located and subsequent statistical tests may be invalid. These points are often overlooked.

Stratified systematic sampling (SSS) is proposed as an alternative to the FLTS method currently popular in intertidal fieldwork. The usefulness of SSS is demonstrated by applying it to a study of spatial and temporal variation in a macrofauna-sediment relationship. This field study was conducted at Garrison Bay (Figure 1), a small embayment on San Juan Island, Wash. (lat. 48°35′N, long. 128°08′W).

MATERIALS AND METHODS

Applications of systematic sampling are found in the forestry literature (Osborne 1942; Finney 1948; Matern 1960; Faber 1972). Mathematical details are found in sampling texts such as Cochran (1963), Raj (1968), or Sukhatme and Sukhatme (1970) and in many theoretical papers.[4] Systematic sampling assumes that the sampling units in the area to be studied are numbered consecutively. The attractiveness of the method is increased by the relatively sessile nature of many intertidal organisms. From N sampling units numbered 1, 2, . . ., N; n sampling units are selected, all evenly spaced at a distance of K sampling units apart. Thus, $N = nK$. The location of the first unit to actually be sampled is randomly chosen by selecting a number between 1 and K from a table of random numbers. Hence, systematic sampling is based upon a uniform probability distribution (Raj 1968). SSS is a variation in which the region is divided into strata, e.g., at the locations of the fixed levels where samples would have been collected using FLTS. Each stratum is independently sampled in the manner described above.

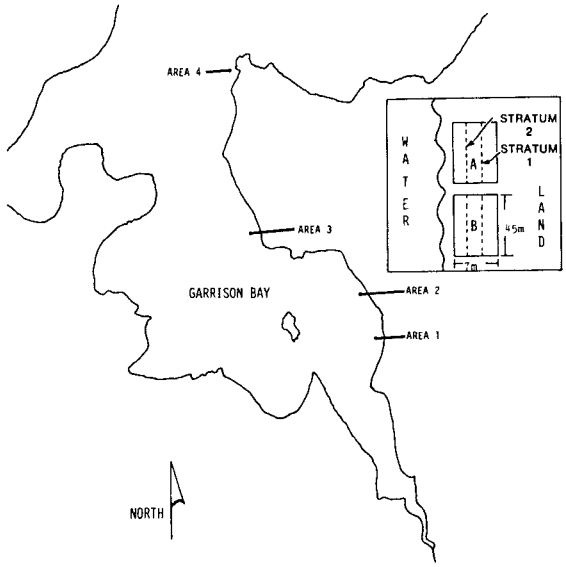

FIGURE 1.–Shoreline of Garrison Bay showing the location of the four study areas. Insert shows the representative arrangement of the subareas (A and B) and the strata (1 and 2) in these areas.

Four regions with different sediment compositions were a priori defined in the intertidal area of Garrison Bay (Figure 1). Representative areas within these regions were sampled in the winter (January and February), spring (May and June), and summer (July and August) 1974. A north-south sediment gradient exists because fine sediment is deposited at the closed end of the bay where the water is less turbulent. Thus, the south (closed) end of the bay consists principally of fine grades of sediment, while the north (open) end consists mainly of coarser grades. Visual examination indicates that perpendicular to the water, there is a sediment gradient as well as a zonation of intertidal animals. However, the statistical comparisons of the data from strata, which were

[4]Scherba, S., Jr., and V. F. Gallucci. 1976. Quantification of species-presence gradients by stratified systematic sampling and the autocovariance function. Unpubl. manuscr., 15 p.

placed parallel to the water, do not show the gradient. This is probably a consequence of the short distance between strata.

Field Procedures

Within each region (Figure 1), a rectangular study area was defined, measuring 95 m in length parallel to the waterline, and approximately 7 m wide, perpendicular to the waterline. Two parallel strata, approximately 2.5 m apart, were placed within each area, parallel to the waterline. The stratum at the highest tidal level was designated stratum 1 while the lower stratum was designated stratum 2. Stratum 1 within the areas was located at -1.4, -1.2, -1.1, and -1.2 feet in areas 1, 2, 3, and 4 respectively; while stratum 2 in those same areas was at -1.5, -1.7, -1.5, and -1.6 feet.[5] The study areas were numbered one (1) to four (4) (south to north) and defined by stakes marked with fluorescent tape for night identification.

It is necessary to test the homogeneity of sediment composition within a region if the areas are to be considered representative. This test was accomplished by dividing each area into two subareas,[6] separated by 5 m, and denoted as A (for the northmost subarea) and B (for the southmost). Each subarea contained about 448 sampling units. Two samples were then collected on each stratum, from each subarea, using a systematic sampling plan.

Each subarea was considered to contain separate populations, and the two population Kolmogorov-Smirnov procedure with $n = 4$ (Conover 1971) was applied to the data collected. This use of both subareas was carried out only for the winter sampling. Winter sampling of the subareas was done on: 8 January 1974 (1A, 1B), 9 January 1974 (3A, 3B), 2 February 1975 (2A, 2B), and 3 February 1974 (4A, 4B).

Spring and summer sampling was conducted only in subareas 1B, 2A, 3A, and 4A as follows: 24 May 1974 (1B, 3A), 21 June 1974 (2A, 4A), 19 July 1974 (1B, 4A), and 16 August 1974 (2A, 3A). Each stratum in these four subareas was independently sampled during these two seasons with $n = 4$ on each stratum.

All samples were collected using a thick-walled, cylindrical corer made of polyvinyl chloride pipe, 10 cm inside diameter and 18 cm long. The corer was pressed into the sediment to 18 cm, and its contents removed by hand, placed in a labeled plastic bag, and taken to the laboratory. Each sample was passed through a 1-mm sieve, and the contents retained by the sieve were sorted twice by eye to remove all bivalves and polychaetes (the only members of the macrofauna identified). These organisms were placed in 80% ethanol and 8% formaldehyde, respectively, for later identification. Only the common bivalves and polychaetes were identified to genus and species. The sediment portion of each sample was dried at 100°C for approximately 4 h. The method used to quantify the particulate properties of the sediment was the percentage composition by weight of selected sediment grain sizes. A mechanical shaker was used to pass the sediment portion of each sample through a series of Wentworth sieves (1.981, 0.495, 0.246, 0.124, 0.063 mm). The contents of each sieve were weighed and recorded as percentage of the total weight of that sample.

Statistical Procedures

Estimates of the variances of the sample means, obtained from SSS were approximated by the estimate of the variance of the sample mean from a simple random sample (see Cochran 1963), i.e., by using

$$\mathrm{var}\,(\bar{y}) = \left(\frac{N-n}{N}\right)\left(\left(\sum_{j=1}^{n}(y_j - \bar{y})^2\right)/n(n-1)\right)$$

where $$\bar{y} = \left(\sum_{j=1}^{n} y_j\right)/n.$$

The rational for this approximation is discussed later.

Two statistical tests were used to quantify the sampling results. The K sample Kolmogorov-Smirnov (K-S) test with $\alpha = 0.10$, using the T_3 test statistic (Birnbaum and Hall 1960; Conover 1971), was used to test hypotheses about variation in sediment composition. The chi-square test for several multinomials with $\alpha = 0.05$ (Conover 1971) was used to test hypotheses about variation in bivalve and polychaete community structure.

In the within-area sediment homogeneity test empirical distribution functions were constructed for each subarea. The K-S test ($\alpha = 0.10$) was then used to test the null hypothesis (H_0) of equality of

[5]Tidal heights are reported in feet to conform with U.S. Coast and Geodetic Survey Tide Tables.

[6]We thank A. R. Sen for this suggestion.

these distribution functions. Using winter samples only, the test failed to reject H_0; thus, the data from each A and B subarea pair were combined and considered to be one subarea for comparison to the subareas sampled in the spring and summer. Hence, all data were analyzed as if they had been collected from four equal sized subareas, of dimensions 45 m by 7 m, during each season, using a sample of size four on each stratum.

The empirical cumulative distribution functions were constructed from the data by defining a random variable X as the sum of the percent of the total sediment weights retained in the sieve sizes <0.063, 0.063, and 0.124 mm. The random variable X takes a value of each sample, in each subarea, on each stratum. Thus, the empirical distribution functions constructed from this data characterized the sum of the weights of three finest sediment grades (and by subtraction from 100%, the three coarsest grades as well) for each stratum in each subarea. These three sieve sizes were grouped together because they constitute what may be called the finer grades of sediment and they probably have the greatest biological impact (Newell 1965). If the grain size which is of principal importance to the organisms is known, then the random variable could be chosen accordingly. There is much evidence that grain size is important to the organisms (e.g., see Loosanoff and Tommers 1948; Sanders 1958; Wieser 1959; Gray 1974). Subject to this limitation of comparing only the finer sediment groups, the sediment data may be statistically compared stratum to stratum in any one subarea, between subareas, or in combinations of these, both within or between seasons.

In each case, the null hypothesis for the K-S test on sediment was

$$H_0: F_1(x) = F_2(x) = \ldots = F_k(x) \qquad (1)$$

and the alternative

H_a: there is at least one inequality where $F_j(x)$ is the cumulative distribution function of the random variable X corresponding to area j.

The statistical analysis of the distribution of animal populations was based upon standard chi-square procedures (Conover 1971). Let the random variable Z have a multinomial distribution where the number of classes corresponds to the number of species types used, and the number of trials is the total number of individuals of all species. The chi-square test was applied to those species types with entries in the expected value table which were either greater than unity, or at least, not far below unity. All species identified are listed, but, in certain cases, some species were grouped into families for the analysis; these are noted in the tables of data. Grouping of data is often advisable on statistical or biological grounds depending upon the objectives of the study. When data were grouped in this study, the grouping was dictated by sample sizes and was consistent with biological facts such as where the organisms occur in Garrison Bay, their modes of feeding, and their taxonomy.

The data were organized into contingency tables for a multinomial distribution. We denote the probability of a randomly selected value from the ith population as being classified in the jth class by P_{ij}. The columns of the table represent species (classes) while the rows represent populations, i.e., a particular stratum in a given subarea during a specific season. The null hypothesis may be stated as:

$$H_0: P_{1j} = P_{2j} = \ldots = P_{rj} \text{ for all } j; j = 1, 2, \ldots, c, \qquad (2)$$

and the alternative

H_a: there is at least one $P_{ij} \neq P_{kj}$ for some j and pair i, k where r equals the number of rows and c equals the number of columns. Under H_0,

$$P_{11} = P_{21} = \ldots = P_{r1} = P_1$$
$$\vdots$$
$$P_{1c} = P_{2c} = \ldots = P_{rc} = P_c$$

where $\hat{P}_j = C_j/N$; C_j = sum of observations in column j; N = total number of observations from all samples; and $\hat{P}_j$ estimates P_j. When a row or column of a particular contingency table equalled zero, it was not possible to reach a decision about the chi-square null hypothesis. To maintain consistent comparisons, no alteration of the contingency tables was made in such cases. The results of some of these tests of homogeneity are summarized in the next section.

RESULTS

The sampling data and the estimates of the variances of the sample means appear in Tables

1-3. It was necessary to pool the winter samples that were used to test for homogeneity (see Statistical Procedures) within each area. The samples in each area were considered to be from one subarea to correspond to the subareas used for the spring and summer sampling. The spring and summer samples were collected exclusively from subareas 1B, 2A, 3A, and 4A. The data in Tables 2 and 3 are for the species of bivalves and polychaetes which could be identified from the samples.

Sediment

The sediment data (Table 1) and statistical analyses confirm the existence of a particle size gradient from the closed (south) end to the open (north) end of the bay. Subareas 1B and 4A appear similar in Table 1, but subarea 1B is located in the closed end of Garrison Bay (Figure 1) which is much muddier with more fine grained particles and has poorer drainage than subarea 4A. Because the data suggest that subareas 1B and 4A contain approximately the same proportion of coarse grain particles (i.e., ≥1.981 mm), a qualitative description was used to supplement the quantitative analysis based on grain size composition by percentage weight: the 1.981-mm sieve in samples from subarea 1B contained large amounts of shell fragments, which will remain in suspension longer due to their flattened shape, while the same sieve size in subarea 4A contained mostly round pebbles, which settle more rapidly, and few shell fragments. Thus, despite their heavy weight, shell fragments were carried into the quiet part of the bay.

Samples from subarea 2A often had added weight in the 1.981-mm sieve in the form of rocks of about 5 cm across. This is probably the result of the activities of early settlers or of recent anthropoligical investigations.

The K-S procedures ($\alpha = 0.10$) confirmed the existence of a north-south sediment gradient between similarly numbered strata in all seasons between all four subareas. All six of the null hypotheses (1) of equality were rejected.

The sources of this gradient were located by using the K-S procedure ($\alpha = 0.10$) to compare all combinations of subarea pairs and seasons for similarly numbered strata. This resulted in the testing of 36 null hypotheses (1) of no difference, of which 25 were rejected and the remainder accepted. Thus, a gradient may be said to be the result of

TABLE 1.—Average percent of total weight of sediment in each of six particle size categories: W = Winter, Sp = Spring, Su = Summer. The numbers in parentheses are estimates of the variance of sample means.

Particle size (mm)	Subarea 1B						Subarea 2A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
<0.063	6.7(1.0)	10.7(0.28)	6.7(1.0)	4.3(0.64)	9.5(4.9)	6.9(0.31)	10.4(2.6)	6.8(0.99)	7.9(1.5)	9.2(4.2)	5.0(0.04)	5.4(0.22)
0.063	8.5(0.77)	11.2(1.3)	9.4(0.74)	5.6(1.4)	9.1(1.3)	9.4(0.43)	7.9(3.5)	7.1(1.2)	8.2(1.5)	8.0(1.7)	4.6(0.11)	5.9(0.10)
0.124	13.7(1.3)	20.9(7.8)	15.6(1.5)	11.9(6.0)	19.4(5.2)	16.7(2.7)	10.3(10)	11.3(0.71)	11.8(1.8)	10.6(1.9)	7.5(0.05)	11.2(0.02)
0.246	11.7(0.04)	15.5(4.8)	15.5(5.3)	10.9(3.0)	15.9(0.94)	16.5(6.5)	9.1(3.3)	11.5(0.33)	10.5(0.57)	9.2(0.35)	9.0(0.93)	12.4(0.15)
0.495	16.2(1.0)	15.3(3.4)	18.5(0.58)	15.0(2.7)	15.1(1.7)	16.9(4.2)	13.2(1.4)	14.8(1.2)	13.2(3.1)	12.7(0.80)	11.7(0.51)	13.3(0.20)
1.981	43.2(6.0)	26.2(21)	34.3(8.4)	52.3(59)	30.9(36)	33.5(48)	49.0(72)	48.8(11)	48.4(28)	50.2(20)	62.2(4.2)	51.8(2.1)

Particle size (mm)	Subarea 3A						Subarea 4A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
<0.063	6.0(2.1)	10.9(1.5)	7.1(1.8)	8.0(3.2)	11.9(0.11)	9.2(1.2)	3.4(0.07)	4.6(0.39)	4.5(0.19)	3.0(0.11)	3.8(0.26)	4.8(0.49)
0.063	14.6(7.4)	20.8(5.7)	16.9(4.6)	17.9(6.3)	22.0(2.6)	17.8(1.9)	9.9(0.80)	9.5(1.2)	9.2(1.6)	7.7(0.38)	9.8(1.4)	8.3(0.34)
0.124	37.0(29)	36.1(6.0)	35.9(32)	39.2(7.3)	26.0(1.1)	30.6(1.7)	16.2(2.8)	20.2(4.6)	19.6(17)	9.1(0.19)	22.3(12)	22.6(4.8)
0.246	12.5(1.7)	8.4(0.52)	11.8(9.1)	14.5(11)	10.6(0.13)	11.9(2.2)	3.4(0.27)	9.1(0.95)	6.6(0.83)	4.4(0.45)	10.4(5.5)	10.6(4.6)
0.495	13.2(12)	7.7(0.55)	12.6(5.8)	10.5(3.1)	12.5(0.11)	12.5(1.9)	15.0(2.3)	14.9(0.25)	15.3(0.58)	14.6(0.72)	19.3(0.85)	20.2(0.81)
1.981	16.7(33)	16.0(15)	15.6(37)	10.4(17)	16.9(5.5)	17.9(5.6)	52.2(8.8)	41.2(16)	44.8(37)	61.1(4.6)	34.6(39)	30.4(31)

different subareas being dissimilar in a season. In particular, it was found that: 1) in the spring, subareas 1B and 2A were significantly different on both strata, while only stratum 2 in those subareas was significantly different in the summer; 2) both strata in subareas 1B and 3A and subareas 3A and 4A were significantly different throughout all seasons; and 3) stratum 1 of subareas 2A and 4A were significantly different only in the spring, while stratum 2 in these subareas was different in each season.

The K-S procedure ($\alpha = 0.10$) was used to test sediment composition homogeneity both between the strata of a given subarea and among the three seasons for a single stratum. Over half of these null hypotheses were accepted. Therefore, sediment composition of the strata remained largely stable throughout the three seasons and apparently lacked a consistent zonation perpendicular to the water.

Polychaetes

Table 2 shows that the dominant polychaete species vary according to season and sediment type. These species were found to be: *Lumbrineris bicirrata*, *Dorvillea japonica*, *Scoloplos pugettensis*, *Cirratulus cirratus*, and *Capitella capitata*. In this study the dominant species is the species with the largest number of individuals.

Spatial and temporal dominance patterns may be seen. In subarea 2A, the dominant organism is generally *D. japonica* (in all seasons on stratum 2 and in the winter and spring on stratum 1). *Capitella capitata* is usually the dominant species in subarea 3A (*S. pugettensis* being dominant there only in the winter on stratum 1). The increase in this species during the summer, as compared to the spring, on both strata of subarea 3A may have been influenced by the presence of a dense algal mat of *Enteromorpha* sp. which covered large intertidal areas. Subarea 4A has the greatest fluctuation with respect to the dominant species. On stratum 2 of subarea 4A, *C. capitata* is dominant in the spring and summer, replacing *L. bicirrata*, the winter dominant. *Capitella capitata* is dominant only in the spring on stratum 1 of subarea 4A; *C. cirratus* is dominant in both winter and summer. Subarea 1B shows the smallest seasonal fluctuation of any subarea in both total polychaete assemblage and dominant species. *Cirratulus cirratus* is dominant on both strata in the spring and summer, replacing the winter dominants *S. pugettensis* (on stratum 1) and *L. bicirrata* (on stratum 2).

No simple seasonal pattern is discernible on the strata of the various subareas (see Table 2). Stratum 1 in both subareas 1B and 3A shows a steady increase in total number of individuals between spring and summer. In the cases of subarea 1B (stratum 2), subarea 2A (strata 1 and 2), and subarea 4A (stratum 2), the largest number of individuals is present in the spring. Subarea 3A (stratum 2) and subarea 4A (stratum 1) have the largest number of individuals in the winter, due to *Cirratulus capitata* and *Capitella cirratus*, respectively. However, there is insufficient data to conclude that stratum 2 is uniformly sustaining the greatest total numbers of individuals seasonally (perhaps due to the small horizontal distance separating the strata in each subarea).

Table 2 shows that it is possible to rank the subareas, in descending order, with regard to number of species present: subareas 1B, 4A, 2A, and 3A; as well as with respect to the total number of individuals: subareas 1B, 2A, 4A, and 3A. There are occasional seasonal reordering of these ranks.

Statistical analysis using the chi-square procedures ($\alpha = 0.05$, 33 df) confirmed the existence of a within season polychaete distribution (for the 12 groups used in the analysis) on identically numbered strata, between the four subareas in five of these six comparisons. The one exception was the comparison of stratum 1, between the four subareas, during the winter. In that instance, a "no decision" result was reached.

To investigate the sources of this difference in distribution, the polychaete assemblage on similarly numbered strata, all combinations of subarea pairs and season were examined using chi-square tests ($\alpha = 0.05$, 11 df). Eleven of these 36 null hypotheses (2) resulted in a "no decision" conclusion while the remaining 25 were rejected using this analysis. In the case of stratum 2, the null hypotheses comparing subareas 1B and 2A, 1B and 3A, 1B and 4A, 3A and 4A, and 2A and 4A were rejected in all seasons. The fluctuation of this biotic distribution in time (season) and space (sample area) is apparent.

The homogeneity (2) of the polychaete assemblage between the three seasons for a single stratum was examined using chi-square tests ($\alpha = 0.05$, 22 df). Of the eight null hypotheses of homogeneity (2), six were rejected (i.e., both strata 1 and 2 in both subareas 1B and 3A, and stratum 2 in both subareas 2A and 4A). The two remaining

TABLE 2.—Total number of individuals of the eighteen common polychaete species in four samples: W = Winter, Sp = Spring, Su = Summer. The numbers in parentheses are estimates of the variance of sample means.

	Subarea 1B						Subarea 2A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
Species - Number	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Harmothoe multisetosa - 1	2(0.08)	1(0.06)	0(0)	1(0.06)	1(0.06)	0(0)	1(0.06)	4(0.49)	4(0.17)	1(0.06)	3(0.06)	1(0.06)
Eulalia parvoseta - 2	0(0)	2(0.25)	0(0)	0(0)	4(0.49)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)
Gyptis brevipalpa[1] - 3	1(0.06)	4(0.49)	10(2.7)	2(0.08)	3(0.06)	3(0.23)	0(0)	0(0)	0(0)	1(0.06)	4(0.17)	2(0.08)
Ophiodromus pugettensis[1] - 4	1(0.06)	6(2.2)	10(2.4)	0(0)	7(0.39)	5(0.89)	0(0)	0(0)	1(0.06)	0(0)	4(0.99)	9(2.0)
Platynereis bicanaliculata - 5	2(0.08)	2(0.25)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)
Nephtys caeca - 6	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Glycera capitata[2] - 7	4(0.17)	3(0.56)	3(0.23)	1(0.06)	2(0.08)	1(0.06)	4(0.50)	1(0.06)	2(0.08)	0(0)	1(0.06)	0(0)
Diopatra ornata - 8	0(0)	0(0)	0(0)	0(0)	2(0.08)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)
Lumbrineris bicirrata[2] - 9	8(3.9)	31(4.9)	64(26.6)	36(3.7)	75(4.5)	72(5.1)	39(3.4)	55(39)	22(3.5)	20(1.5)	64(21)	45(18)
Dorvillea japonica[2] - 10	10(1.7)	50(22)	81(6.2)	15(1.1)	85(30)	36(13.7)	78(49)	96(36)	48(28)	35(11.6)	165(119)	56(61)
Scoloplos pugettensis[2] - 11	27(1.5)	26(8.8)	42(12.3)	6(1.4)	8(0.99)	4(0.49)	15(3.2)	43(25)	52(27)	9(1.1)	20(4.1)	1(0.06)
Naineris quadricuspida[2] - 12	0(0)	2(0.25)	7(2.0)	0(0)	5(0.06)	2(0.08)	25(9.3)	12(0.83)	14(1.4)	6(0.41)	39(38)	5(0.39)
Cirratulus cirratus[2] - 13	7(0.39)	124(183)	127(148)	17(3.5)	133(182)	110(56.2)	6(0.41)	24(4.5)	61(15)	2(0.08)	27(3.8)	21(2.7)
Armandia brevis[2] - 14	4(0.33)	6(0.74)	3(0.23)	1(0.06)	3(0.23)	1(0.06)	3(0.23)	16(5.1)	0(0)	1(0.06)	5(0.23)	0(0)
Capitella capitata[2] - 15	18(5.4)	94(135)	65(41)	10(0.41)	82(49)	66(12.6)	20(2.1)	36(11.6)	66(49)	3(0.23)	36(7.1)	13(0.23)
Axiothella rubrocinta[2] - 16	0(0)	0(0)	2(0.08)	7(1.4)	7(1.1)	5(1.5)	0(0)	0(0)	0(0)	1(0.06)	1(0.06)	2(0.25)
Owenia fusiformis[2] - 17	0(0)	2(0.08)	7(0.72)	8(1.2)	4(0.49)	9(1.1)	0(0)	1(0.06)	1(0.06)	0(0)	0(0)	1(0.06)
Thelepus crispus[2] - 18	8(2.8)	27(8.9)	34(13.3)	8(0.50)	19(3.4)	52(37.7)	4(0.33)	4(0.33)	5(0.39)	2(0.08)	18(2.7)	18(6.2)

	Subarea 3A						Subarea 4A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
Species - Number	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Harmothoe multisetosa - 1	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	4(0.99)	3(0.23)	3(0.23)	2(0.08)	1(0.06)
Eulalia parvoseta - 2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Gyptis brevipalpa[1] - 3	0(0)	1(0.06)	2(0.25)	3(0.06)	2(0.08)	0(0)	1(0.06)	5(0.89)	2(0.25)	3(0.55)	3(0.06)	3(0.06)
Ophiodromus pugettensis[1] - 4	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	2(0.25)	1(0.06)	2(0.25)	2(0.25)	0(0)	3(0.56)
Platynereis bicanaliculata - 5	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	13(1.1)	1(0.06)	0(0)	8(0.17)	5(0.23)
Nephtys caeca - 6	0(0)	0(0)	0(0)	2(0.08)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Glycera capitata[2] - 7	4(0.33)	4(0.33)	1(0.06)	2(0.08)	4(0.17)	1(0.06)	0(0)	2(0.08)	2(0.08)	2(0.08)	5(0.39)	1(0.06)
Diopatra ornata - 8	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Lumbrineris bicirrata[2] - 9	11(2.5)	6(0.91)	6(2.2)	0(0)	4(0.49)	6(0.91)	77(0.7)	8(1.9)	17(9.3)	40(3.8)	13(0.22)	15(2.7)
Dorvillea japonica[2] - 10	10(0.70)	13(0.54)	6(0.91)	5(0.88)	23(0.54)	15(3.2)	9(1.7)	17(2.9)	7(0.39)	14(2.7)	14(12)	5(0.56)
Scoloplos pugettensis[2] - 11	46(0.40)	18(0.41)	29(0.70)	55(4.5)	31(0.70)	19(2.4)	5(0.88)	5(0.39)	9(1.7)	6(1.4)	8(0.33)	2(0.25)
Naineris quadricuspida[2] - 12	2(0.25)	6(0.41)	4(0.17)	1(0.06)	5(0.23)	2(0.08)	40(0.48)	0(0)	3(0.56)	5(0.88)	1(0.06)	1(0.06)
Cirratulus cirratus[2] - 13	1(0.06)	19(2.2)	28(1.4)	4(0.99)	9(2.5)	2(0.25)	187(3.1)	16(1.2)	94(2.2)	6(0.74)	24(1.1)	24(0.66)
Armandia brevis[2] - 14	6(0.41)	2(0.08)	0(0)	8(0.08)	7(1.4)	0(0)	2(0.25)	21(0.06)	1(0.06)	4(0.33)	12(1.3)	8(1.8)
Capitella capitata[2] - 15	9(2.7)	81(0.54)	97(1.5)	104(1.4)	52(1.1)	85(1.9)	35(3.2)	59(4.1)	41(1.2)	28(4.1)	104(1.1)	43(0.22)
Axiothella rubrocinta[2] - 16	0(0)	0(0)	1(0.06)	0(0)	2(0.25)	3(0.23)	0(0)	24(1.6)	13(0.38)	17(2.4)	17(2.7)	9(1.2)
Owenia fusiformis[2] - 17	2(0.08)	2(0.25)	4(0.17)	4(0.49)	0(0)	3(0.23)	0(0)	0(0)	0(0)	2(0.25)	5(0.56)	0(0)
Thelepus crispus[2] - 18	0(0)	3(0.23)	0(0)	0(0)	5(0.56)	2(0.08)	1(0.06)	19(2.2)	5(0.39)	1(0.06)	0(0)	8(0.83)

[1]Treated as one group in the statistical analysis.
[2]Used in the statistical analysis.

null hypotheses resulted in no decision. The data from Table 2 indicate that the apparent variation does occur in these two cases (stratum 1 in both subareas 2A and 4A) as well.

The homogeneity (2) of the polychaete assemblage between strata, in a given subarea, in a given season was also examined using chi-square tests ($\alpha = 0.05$, 12 df). Five of the 12 null hypotheses were rejected (i.e., subarea 4A in the winter, subareas 1B, 2A, and 3A in the spring, and subarea 1B in the summer). A no decision result was reached in the remaining cases.

Bivalves

The sampling data collected on the bivalve populations in Garrison Bay are given in Table 3. The data are organized as follows: 1) *Protothaca staminea*, *Venerupis japonica*, and *Saxidomus giganteus* were grouped as one into the Veneridae; 2) *Macoma inconspicua*, *M. irus*, and *M. nasuta* were grouped as one into the Tellinidae; 3) *Transennella tantilla*, *Clinocardium nuttalli*, *Mya arenaria*, and *Mysella tumida* were considered individually; and 4) *Macoma secta* was considered apart from the Tellinidae because of its usual occurrence in clean sandy environments.

The size and the number of sampling units in this study were generally inadequate for sampling most mature bivalves. As a consequence, hypotheses for small bivalves, such as *T. tantilla* and *M. tumida*, are best represented by the data in this study. Indeed, large densities of *T. tantilla* were found in all four subareas, with the largest numbers in subarea 3A, and *M. tumida* was found in large numbers only in subarea 4A.

The north-south bivalve distribution, as constructed from these data, is somewhat different from that found in the polychaetes. The data in Table 3 show that the subareas may be ranked in descending order with respect to the total numbers of individuals as follows: subareas 3A and 1B and subareas 2A and 4A are about the same. However, occasional seasonal reorderings do occur. The high densities in subarea 3A are probably due to the presence of large numbers of *T. tantilla*. In terms of the number of species present, subarea 1B generally ranks highest and the remaining three subareas are almost indistinguishable.

Differences in the bivalve distributions within a season, on like-numbered strata, and between subareas were examined using chi-square tests

TABLE 3.—Total number of individuals of the seven groups of common bivalves in four samples: W = Winter, Sp = Spring, Su = Summer. Numbers in parentheses are estimates of the variance of sample means.

Species or family - Number	Subarea 1B						Subarea 2A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Veneridae[1] - 1	1(0.06)	6(0.41)	3(0.23)	3(0.06)	7(1.1)	4(0.33)	2(0.08)	2(0.25)	4(0.17)	2(0.25)	3(0.23)	2(0.08)
Tellinidae[1] - 2	10(2.4)	3(0.06)	3(0.23)	17(1.7)	3(0.06)	8(0.17)	8(1.2)	5(0.06)	2(0.08)	10(0.74)	3(0.23)	7(0.40)
Transennella tantilla[1] - 3	4(0.99)	13(3.2)	0(0)	8(0.83)	11(5.8)	6(0.08)	6(0.74)	16(1.5)	10(0.74)	9(1.7)	6(1.4)	2(0.08)
Macoma secta - 4	4(0.33)	1(0.06)	2(0.08)	2(0.08)	0(0)	1(0.06)	0(0)	1(0.06)	2(0.25)	0(0)	0(0)	0(0)
Clinocardium nuttalli - 5	1(0.06)	2(0.25)	0(0)	1(0.06)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mya arenaria - 6	0(0)	0(0)	1(0.06)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mysella tumida - 7	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)

Species or family - Number	Subarea 3A						Subarea 4A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Veneridae[1] - 1	3(0.06)	0(0)	1(0.06)	1(0.06)	2(0.08)	0(0)	6(0.08)	1(0.06)	6(0.41)	1(0.06)	4(0.50)	5(0.89)
Tellinidae[1] - 2	3(0.06)	10(0.41)	9(0.23)	13(0.72)	10(0.74)	10(0.41)	9(0.39)	12(0.83)	11(2.4)	11(0.06)	12(0.50)	7(0.72)
Transennella tantilla[1] - 3	23(6.0)	9(0.56)	69(128)	27(1.5)	3(0.23)	35(30)	5(0.88)	3(0.23)	2(0.08)	0(0)	1(0.06)	0(0)
Macoma secta - 4	1(0.06)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Clinocardium nuttalli - 5	0(0)	1(0.06)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mya arenaria - 6	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mysella tumida - 7	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	7(0.23)	4(0.17)	0(0)	12(1.1)	6(0.74)

[1]Used in the statistical analysis.

(α = 0.05, 6 df). All six of the null hypotheses (2) were rejected. Thus the bivalve distributions between subareas are different. To investigate the sources of this difference in distribution, the bivalve assemblage on similarly numbered strata, in all combinations of subarea pairs and season were examined using chi-square tests (α = 0.05, 2 df). Nineteen of these 36 null hypotheses of homogeneity (2) were rejected. Thus, the bivalve distribution is not consistent in either time (season) or space (sample subareas).

The homogeneity (2) of the bivalve assemblage between the three seasons for a single stratum was examined using chi-square tests (α = 0.05, 4 df). Four of the eight null hypotheses were rejected. The homogeneity (2) of the bivalve assemblage between strata, in a given subarea, in a given season was also examined using chi-square tests (α = 0.05, 2 df). Two of the 12 null hypotheses were rejected. Thus, a definitive statement about the dependence between bivalve presence and season cannot be made. Furthermore, the differences between the strata of a single subarea are apparently minimal.

DISCUSSION

The sediment and macrofauna data collected in the Garrison Bay study were analyzed under the assumption of intrasample independence within each subarea (i.e., the contents of one sampling unit neither predicts nor influences the contents of any other unit). The assumption is based upon the homogeneity of macrofauna and sediment composition within study subareas. Macrofaunal homogeneity is defined here as meaning that all members of a given species on a given stratum are described by the same spatial probability distribution. Although specific probability distributions were not fit to the data, chi-square and Kolmogorov-Smirnov tests are legitimately applied to the sample data.

There are K different systematic samples, each of size n, that could be chosen (recall $N = nK$); one of these is selected at random. The sample mean of the ith such systematic samples, $\bar{y}_i$, and the population mean, $\bar{Y}$, are defined respectively as:

$$\bar{y}_i = (\sum_{j=1}^{n} y_{ij})/n \text{ and}$$

$$\bar{Y} = (\sum_{i=1}^{K} \sum_{j=1}^{n} y_{ij})/nK$$

where y_{ij} is the attribute of interest in the sample (e.g., the number of individuals of a given species in the jth sample). Since systematic sampling is a probability sampling scheme, a valid expression for the variance of the sample mean is

$$\text{var}(\bar{y}_i) = (\sum_{i=1}^{K} (\bar{y}_i - \bar{Y})^2)/K \qquad \text{(Sukhatme and Sukhatme 1970).}$$

Alternative expressions of this quantity have been derived (Cochran 1963). No difficulties arise in using any of these forms of var ($\bar{y}_i$) in theoretical studies, but in applications of systematic sampling, no reliable estimate of var ($\bar{y}_i$) is known from taking only one sample of size n from an area. This is a disadvantage of SSS. In practice, approximations to var ($\bar{y}_i$) are used as estimators of this statistic. The texts by Cochran (1963:224-227) and Sukhatme and Sukhatme (1970:369-370) present several methods to approximate var ($\bar{y}_i$) from a single systematic sample. However, if m ($\geq$2) independent systematic samples (each of size n) are taken on the same stratum at the same time, an exact (as opposed to an approximate) estimate of var ($\bar{y}_i$) is possible. Letting $\bar{y}_i$ represent the sample mean from one of the m systematic samples, then

$$\text{var}(\bar{y}) = \sum_{i=1}^{n} (\bar{y}_i - \bar{y})^2/m(m-1)$$

$$\text{where } \bar{y} = (\sum_{i=1}^{m} \bar{y}_i)/m \qquad \text{(Sukhatme and Sukhatme 1970).}$$

In this study the estimate of the variance of the sample means was approximated by the variance calculated for a simple random sample (Cochran 1963). This is reasonable because of the within-area homogeneity of the sediment and macrofauna in each of the four study areas. Of course, it is preferable to take at least two independent systematic samples, each of size n.

Cochran (1963) discussed the difference in precision between random and systematic sampling based on the results of these methods upon certain types of population data. Special attention should be given to data which is either inherently periodic or subject to a periodic input, e.g., tidal forces. Under these circumstances, K must be carefully selected. Periodic variation in the north-south direction in Garrison Bay is considered to be unlikely.

The use of SSS allows strata to be placed at tidal heights where experimental interest is focused. Thus, samples may be taken at fixed tidal levels as

in FLTS and statistically valid estimates of means and variances on a stratum found. Furthermore, no greater physical effort is required in SSS than in FLTS. SSS also provides a method to quantify species-presence gradients. Hence, SSS is free of some of the disadvantages of FLTS while maintaining the advantages often ascribed to FLTS plans.

There is a sediment gradient in the bay in the sense of a gradual increase in coarseness (silt to sand) south to north over the four areas for all seasons. Over all seasons, subarea 1B generally contained the largest number of bivalve species and, were it not for the abundance of *Transennella tantilla* (which is discussed later), subarea 1B would have the largest number of bivalves also. In addition, in almost all seasons subarea 1B contained the largest number of individuals and species of polychaetes. Thus, there is a distribution in bivalve and polychaete presence, from high density and species numbers to low as the sediment becomes more coarse. The sediment composition, as measured by average percentage composition by weight of various grain sizes, is a necessary factor to consider in predicting macrofauna population dynamics, but it is not a sufficient predictor by itself. This viewpoint is based on the necessity of employing qualitative information concerning the types of material retained by the 1.981-mm sieve (see Results section), and the role we attribute to the algae *Enteromorpha* sp. in the population dynamics of *T. tantilla* (see later discussion).

Newell (1965) found a higher number of microorganisms in areas composed of finer grades of sediment and an associated higher number of the deposit feeders (*Hydrobia ulvae* and *Macoma balthica*). He concluded that the large number of microorganisms was a result of the greater surface area of fine sediment grades which is related to the amount of organic nitrogen (protein) available to deposit feeders. The polychaete data from Garrison Bay, and subsequent statistical analyses, suggest that Newell's (1965) hypothesis can be extended to incorporate a statement about the biological effects of different sediment compositions in the presence of temporal heterogeneity. Recall that the sediment data show that subarea 4A, the most exposed subarea, experiences greater interseason fluctuations than does subarea 1B, the most sheltered subarea. Furthermore, the polychaete assemblage in subarea 1B shows the smallest seasonal fluctuation with regard to both total numbers of individuals and species as compared with subarea 4A. Subareas 2A and 3A also show smaller seasonal variations in both polychaete assemblage and sediment composition than does subarea 4A. All of this suggests that mixed fine sediment grades (silty areas) may act as insulators for certain infauna against seasonal stresses. That is, fine sediments with their larger total surface area to volume ratio retain larger quantities of nutrients (organic nitrogen) and hold more interstitial water. If the areas composed chiefly of fine sediment grades occur in the cul de sac of an embayment, where wave action is minimal, then these areas are more likely to retain larger numbers of individuals and species than other areas within the embayment. Thus, despite the periodic fluctuations in many environmental parameters of the intertidal zone, a constant sediment particle composition contributes to a high degree of environmental predictability. Slobodkin and Sanders (1969), Levinton (1972), and Gray (1974) considered aspects of the consequences of temporal predictability for deposit and suspension feeders.

The bivalves and polychaetes listed in Tables 2 and 3 represent both suspension and deposit feeders. Rhoads and Young (1970) advanced the hypothesis that animals of one trophic level modify the environment and affect the dynamics of members of another trophic level, and called it trophic group amensalism. They found suspension feeders in the subtidal to be generally restricted to sandy or firm mud bottoms, and deposit feeders to be more numerous in soft silty substrates. The polychaete results generally support this hypothesis. An exception noted by Young and Rhoads (1971) was the case in which it was hypothesized that tube-building polychaetes (both suspension and deposit feeders) make it possible for higher densities of bivalve and polychaete suspension feeders to coexist with deposit feeders in silty sediments because of their ability to bind particles together and thereby stabilize sediments. This hypothesis may be useful in explaining why suspension feeders, e.g., the tube builder *Owenia fusiformis* and the members of the Veneridae, are so numerous in subarea 1B, as well as why the tube building terebellid *Thelepus cripus*, a surface level deposit feeder, reaches its maximum density in subarea 1B. The combination of tube building coupled with the feeding behavior of suspension feeders may provide these organisms a survival advantage in this otherwise soft

silty area. Further studies are being conducted to develop hypotheses for Garrison Bay.

Newell's (1965) hypothesis does not appear to explain the abundance and apparent sediment preferences of *T. tantilla*. Maurer (1969) found *T. tantilla* to be ubiquitous in a bay with a sediment gradient similar to that of Garrison Bay, while attaining its greatest numbers in a region composed principally of finer sediment particle sizes. Excluding subarea 3A, similar results follow for *T. tantilla* in Garrison Bay. The increased abundance of this bivalve in the summer on both strata of subarea 3A indicates that the principal response of *T. tantilla* may be to something other than just sediment composition. The extensive covering of subarea 3A by a dense algal mat of *Enteromorpha* sp. is probably involved in the population explosion. *Transennella tantilla* would gain protection from some physiological stresses such as elevated temperatures and increased water evaporation by the sun and wind. Similar dense mats of *Enteromorpha* sp. were not found in the other three areas at the sampling times.

The polychaete assemblage in Garrison Bay is described by a distribution which is apparently sediment and season dependent. The limited data on the distribution of bivalves does not have the same patterns. Preliminary analyses from an investigation (Gallucci)[7] involving the collection of large numbers of bivalves in Garrison Bay substantiates the lack of a simple gradient relationship for bivalves. Life in a calcium carbonate shell seems to allow for greater independence from environmental fluctuations than life near the sediment surface without such a shell.

Although the effects of seasonal and sediment type variations are often evident, causal links must be established by the examination of specific factors, e.g., competition, predation, food availability and selection, salinity, and temperature. Toward this end, Hylleberg and Gallucci (1975) and Gallucci and Hylleberg (1976) have examined the role of food availability and sediment composition upon the growth of the deposit feeder *Macoma nasuta* in Garrison Bay. Garrison Bay daylight summer surface water temperatures are about 1°C higher in the closed end than in the open end (Gallucci, unpubl. data), and short stretches of intertidal areas sustain a subsurface freshwater runoff.

In this paper we have developed an appropriate sampling method for marine studies and the statistical machinery for testing certain relevant hypotheses. We have applied these methods in an intertidal study. The biological results pertain to sediment and animal gradients under seasonal change. Conclusions are based upon statistical comparisons in which the null hypothesis was rejected, tempered by extensive biological studies.

The data and results of the Garrison Bay study have obvious significance for shellfish culture. Factors such as the selection of sediment type in which to establish seed beds, interspecies associations, the season in which to make population assessments, and the sampling techniques should all be considered if sound management decisions are to be made.

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LITERATURE CITED

BIRNBAUM, Z. W., AND R. A. HALL.
1960. Small sample distributions for multi-sample statistics of the Smirnov type. Ann. Math. Stat. 31:710-720.

BLOOM, S. A., J. L. SIMON, AND V. D. HUNTER.
1972. Animal-sediment relations and community analysis of a Florida estuary. Mar. Biol. 13:43-56.

COCHRAN, W. G.
1963. Sampling techniques. 2d ed. John Wiley & Sons, Inc., N.Y., 413 p.

CONOVER, W. J.
1971. Practical nonparametric statistics. John Wiley & Sons, N.Y., 462 p.

[7]Gallucci, V. F. 1976. Bivalve community relationships as determined from age composition and growth rates. Unpubl. manuscr., 30 p.

FABER, J. A. J.
1972. Precision of sampling by dots for proportions of land use classes. Inst. Stat. (Raleigh, N.C.), Mimeogr. Ser. 773, 153 p.

FINNEY, D. J.
1948. Random and systematic sampling in timber surveys. Forestry 22:64-99.

GALLUCCI, V. F., AND J. HYLLEBERG.
1976. A quantification of some aspects of growth in the bottom-feeding bivalve *Macoma nasuta*. Veliger 19:59-67.

GRAY, J. S.
1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Annu. Rev. 12:223-262.

HYLLEBERG, J., AND V. F. GALLUCCI.
1975. Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta*. Mar. Biol. (Berl.) 32:167-178.

LEVINTON, J.
1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. Am. Nat. 106:472-486.

LOESCH, J. G.
1974. A sequential sampling plan for hard clams in lower Chesapeake Bay. Chesapeake Sci. 15:134-139.

LOOSANOFF, V. L., AND F. D. TOMMERS.
1948. Effect of suspended silt and other substances on rate of feeding of oysters. Science (Wash., D.C.) 107:69-70.

MATERN, B.
1960. Spatial variation: Stochastic models and their application to some problems in forest surveys and other sampling investigations. Medd. Statens Skogsforkningsinst. 49:1-144.

MATTHIESSEN, G. C.
1960. Intertidal zonation in populations of *Mya arenaria*. Limnol. Oceanogr. 5:381-388.

MAURER, D.
1969. Pelecypod-sediment association in Tomales Bay, California. Veliger 11:243-249.

NEWELL, R.
1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc. Zool. Soc. Lond. 144:25-45.

OSBORNE, J. G.
1942. Sampling errors of systematic and random surveys of cover-type areas. JASA (J. Am. Stat. Assoc.) 37:256-264.

RAJ, D.
1968. Sampling theory. McGraw-Hill Book Co., N.Y., 302 p.

RHOADS, D. C.
1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. J. Geol. 75:461-476.

RHOADS, D. C., AND D. K. YOUNG.
1970. The influence of deposit feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150-178.

RUSSELL, H. J., JR.
1972. Use of a commercial dredge to estimate a hardshell clam population by stratified random sampling. J. Fish. Res. Board Can. 29:1731-1735.

SAILA, S. B., AND T. A. GAUCHER.
1966. Estimation of the sampling distribution and numerical abundance of some mollusks in a Rhode Island salt pond. Proc. Natl. Shellfish. Assoc. 56:73-80.

SANDERS, H. L.
1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3:245-258.

SEN, A. R., J. TOURIGNY, AND G. E. J. SMITH.
1974. On the line transect sampling method. Biometrics 30:329-340.

SKELLAM, J. G.
1958. The mathematical foundations underlying the use of line transects in animal ecology. Biometrics 14:358-400.

SLOBODKIN, L. B., AND H. L. SANDERS.
1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol. 22:82-95.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry: The principles and practice of statistics in biological research. W. H. Freeman & Co., San Franc., 776 p.

SUKHATME, P. V., AND V. B. SUKHATME.
1970. Sampling theory of surveys with applications. Iowa State Univ. Press, Ames, 452 p.

VASSALLO, M. T.
1969. The ecology of *Macoma inconspicua* (Broderip & Sowerby, 1829) in central San Francisco Bay. Part I. The vertical distribution of the *Macoma* community. Veliger 11:223-234.

WARME, J. E.
1971. Paleoecological aspects of a modern coastal lagoon. Univ. Calif. Publ. Geol. Sci. 87, 131 p.

WIESER, W.
1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. Limnol. Oceanogr. 4:181-194.

YOUNG, D. K., AND D. C. RHOADS.
1971. Animal-sediment relations in Cape Cod Bay, Mass. I. A transect study. Mar. Biol. (Berl.) 11:242-254.

SIZE COMPOSITION AND GROWTH OF YOUNG ROCK CRAB, *CANCER IRRORATUS*, ON A ROCKY BEACH IN MAINE[1]

JAY S KROUSE[2]

ABSTRACT

Monthly hand collections of small rock crab, *Cancer irroratus*, were made from an intertidal zone in East Boothbay, Maine, from June 1972 through April 1975. An analysis of size and sex frequencies indicated: 1) young-of-the-year crabs (≤5 mm carapace width) entered the intertidal area in late summer-early fall and remained there through the second fall with a resultant width range between 15 and 40 mm; 2) a deceleration and/or cessation of growth in winter; 3) an emigration of crabs >40 mm carapace width from the intertidal area associated with declining winter temperatures and/or behavioral changes; 4) sex ratios approximated a 1:1 relationship; and 5) small male and female rock crabs (<60 mm carapace width) had a common growth rate.

While searcing beneath the rocky substrate of an intertidal zone for juvenile American lobster, *Homarus americanus* Milne Edwards, whose early distribution and abundance is generally unknown, I discovered numerous small rock crab, *Cancer irroratus* Say, burrowed under the rubble. Because rock crab is a valuable commercial species as well as an important food source of lobsters (Ennis 1973), I believe it important to describe the distribution of young crabs in their natural environment along with other life history information (size structure, sex ratio, and growth).

METHODS

Rock crabs were carefully hand collected about once a month during extreme low slack tides from the intertidal zone of Grimes Cove, East Boothbay, Maine (Figure 1). The rocky substrate of this unsheltered seaward cove consists of rocks of assorted sizes intermingled amongst areas of bedrock, sand, and pulverized shells. By using large boulders as landmarks, it was possible to sample consistently the same general area near the low water mark. Unfortunately, for various reasons, samples could not be obtained for all months of the study.

After two biologists concurrently expended 1 h gathering crabs, their catches were immediately returned to the laboratory where sex and carapace width (distance between the two most posterior notches on the anterolateral border) to the nearest millimeter were recorded. The sex of crabs <10 mm carapace width (CW) was determined under a dissecting microscope.

Width-frequency histograms were compiled by 2-mm increments for rock crabs caught each month from June 1972 through April 1975.

RESULTS AND DISCUSSION

Size Composition and Seasonal Distribution

Since there were no discernible differences in size distribution between male and female crabs, the data for sexes were combined in monthly width-frequency histograms (Figure 2). This similarity in size composition of male and female crabs <60 mm CW suggested a common growth rate for both sexes up to this size, unlike the marked size disparity of larger male and female rock crabs (>60 mm CW) caught in commercial lobster traps which was primarily attributed to a decrease in the growth rate of females after the onset of sexual maturity (Krouse 1972).

Modal groups, which most likely represented one or, perhaps, more molt classes, were quite conspicuous in each of the monthly histograms. However, due to extensive overlapping of modes I was unable to quantitatively follow these modal groupings from month to month for purposes of estimating mortality rates.

Inspection of monthly histograms revealed that young-of-the-year crabs (recently metamorphosed from megalops to first crab, ≤5 mm CW) initially

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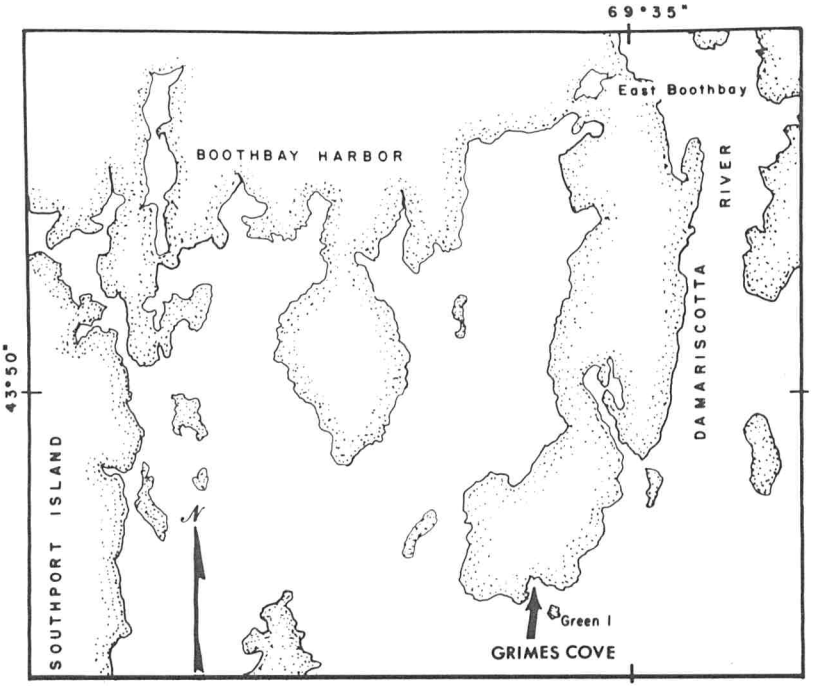

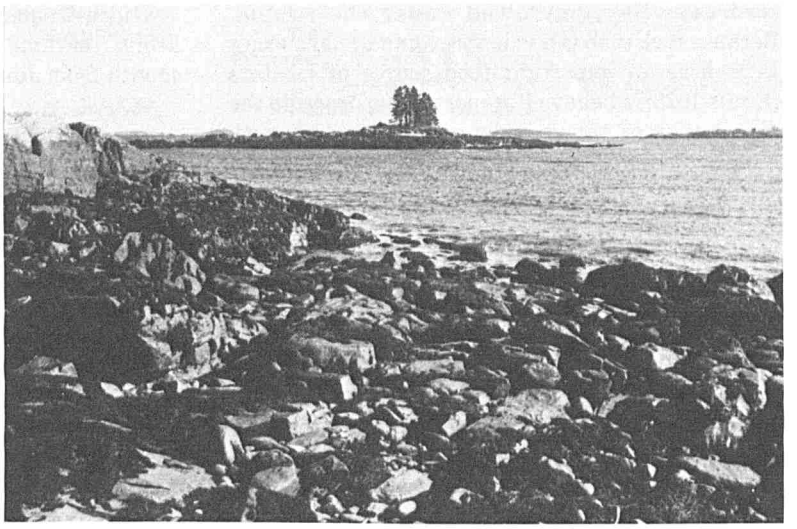

FIGURE 1.—Chart of Boothbay region with a seaward view at low tide of the intertidal beach of Grimes Cove, East Boothbay, Maine.

appeared during September 1972 and late August 1973 and 1974. This seasonal appearance of young crabs agreed with earlier observations of female rock crabs hatching their eggs in late spring and early summer in Maine waters (Krouse 1972) and the culture work of Sastry (1970) which demonstrated that 40 - 60 days are required for rock crabs to develop through the pelagic larval stages to the first crab stage at 15°C and a salinity of 30‰.

Histograms showed a gradual upward progression of the first modal grouping (comprised of young-of-the-year crabs, <10 mm CW) from August through December 1974, while distributions from January through April 1975 revealed relatively little change (Figure 2). This apparent cessation of growth was further supported by sighting very few, if any, cast exoskeletons and/or soft-shelled crabs while sampling during the winter. At other times of the year, when crabs were growing, numerous recently cast shells and/or shedders were readily observed. In spring when growth resumed, the percentages of in-

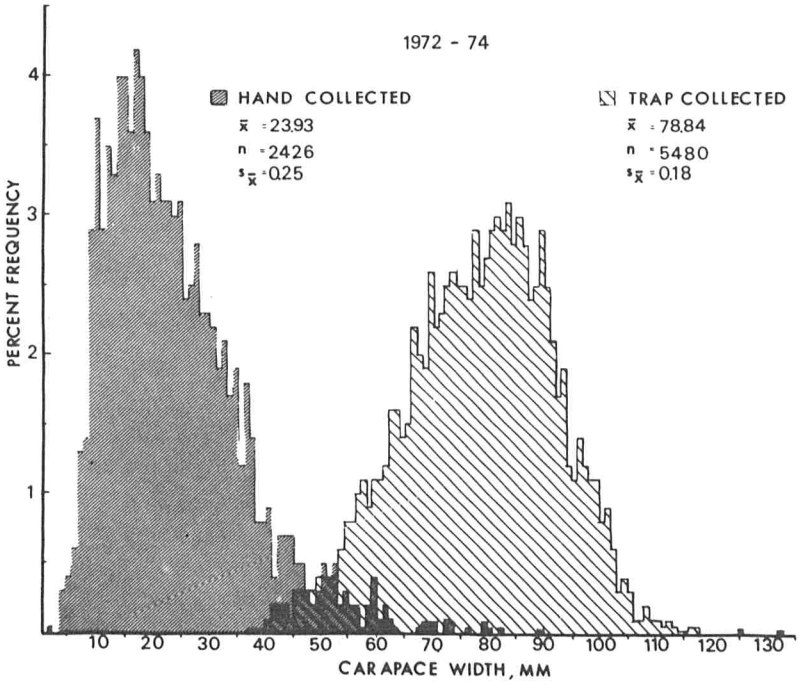

FIGURE 2.—Width-frequency distributions for rock crabs collected monthly by hand at an intertidal area in East Boothbay, Maine, 1972-75.

dividuals <10 mm CW began to diminish progressively until late summer when young-of-the-year crabs once again settled to the bottom (Table 1).

Rock crabs >40 mm CW were decidedly less abundant during the fall and winter (Table 1). In fact, not a single crab >50 mm CW was captured from January through April (Figure 2). This seasonal shift in size distribution suggested that crabs >40 mm CW moved seaward from the intertidal zone with declining temperatures. Jeffries (1966) reported that *C. irroratus* moved from Narragansett Bay, R.I., in winter to the deeper and warmer ocean waters. Conversely, in southern waters during the late fall and winter, rock crabs moved into Delaware Bay (Winget et al. 1974) and inshore waters of Virginia (Shotton 1973; Terretta 1973) as the water temperatures fell within a preferred range.

Aside from the apparent thermal effects and/or behavioral changes on the seasonal displacement of these large crabs from the intertidal zone, this movement may also be associated with the larger crabs' physical ability to emigrate with ease from an area of low temperature. In addition, the size of these crabs may inhibit their ability to find suitable burrows in the littoral zone necessary to afford protection from the often tempestuous winter sea. Jeffries (1966) stated that *C. irroratus* was not well suited for burrowing into coarse bottom.

TABLE 1.—Percentage of rock crabs of two carapace widths in monthly samples for 1972-75.

Month	≤10 mm (%)	≥40 mm (%)	Month	≤10 mm (%)	≥40 mm (%)
Jan.	39.6	0	Aug.	1.6	16.6
Mar.	47.4	2.6	Sept.	13.7	12.7
Apr.	34.8	2.7	Oct.	31.4	6.7
May	32.8	2.9	Nov.	40.9	8.0
June	7.8	8.5	Dec.	40.7	3.7
July	2.4	8.8			

Sex Ratio

Ratios of males to females for each of the monthly samples ranged from 0.60:1 to 1.57:1 (Table 2). The chi-square test revealed that only sex ratios of catches of July and August 1973 deviated significantly ($P = 0.05$) from a 1:1 relationship. Thus I concluded that sex ratios of the intertidal catches approximated a 1:1 relationship (1,353 males: 1,376 females); whereas, rock crabs larger than 50 mm CW collected in traps near Boothbay Harbor, Maine, showed disproportionate sex ratios which varied by season and locality (Krouse 1972). It appears that these disparate sex ratios were primarily a function of the onset of sexual maturity which subsequently altered the growth rate and seasonal distribution of male and female crabs.

TABLE 2.–Sex ratios of the monthly collections of rock crabs taken intertidally in East Boothbay, Maine, 1972-75. Sex ratios that deviated significantly ($P = 0.05$) from 1:1 are marked *.

Mo.	1972 M:F	1973 M:F	1974 M:F	1975 M:F	Mo.	1972 M:F	1973 M:F	1974 M:F	1975 M:F
Jan.	—	1.27:1	—	0.96:1	Sept.	0.89:1	—	1.57:1	—
Mar.	—	—	—	1.23:1		0.71:1			
Apr.	—	0.60:1	0.76:1	1.08:1	Oct.	0.68:1	—	1.23:1	—
May	—	1.07:1	1:1	—	Nov.	—	—	0.96:1	—
June	1.02:1	0.95:1	1.03:1	—	Dec.	—	—	0.93:1	—
July	1.25:1	1.55:1*	0.82:1	—	Total	0.98:1	0.99:1	0.95:1	1.08:1
Aug.	1.01:1	0.71:1*	0.86:1	—					
		0.87:1							

Growth

Carapace width prior to shedding was plotted against the new carapace width after shedding for 45 crabs that molted while captive in the laboratory. This relationship was fitted by the method of least squares using the simple linear equation $Y = a + bX$, where Y = postmolt CW, X = premolt CW, and a and b were constants. Analysis of covariance, which was used to test homogeneity of regression coefficients, revealed no statistical differences between growth increments of males and females, so all data were pooled. The calculated equation for crabs ranging from 9 to 48 mm CW was $Y = 0.566 + 1.247X$. This relation was similar to Cleaver's (1949) constants ($a = 0.57$; $b = 1.23$) calculated for Dungeness crab, *C. magister*, juveniles (5-91 mm CW).

Based on the relationship between premolt vs. postmolt and measurements of cultured post-larval crabs (stages I-V) obtained from Herbert C. Perkins, formerly of the National Marine Fisheries Service, West Boothbay Harbor, Maine, I estimated sizes for instars I-XIII (Table 3). Sizes for instars above XIII were not computed because of the inherent uncertainties of extrapolating beyond the data range. If we assume that Maine rock crabs begin to attain maturity about 60 mm CW (Krouse 1972; Scarratt and Lowe 1972) and if as suggested by Butler's (1961) work with *C. magister* the premolt vs. postmolt relationship changes with the onset of sexual maturity, then sizes for instars beyond XIII (53 mm CW) are inadequately described by the aforementioned regression.

Because the increments of growth (24.3-28.3%) for post-larval crabs (instars III-V) cultured in the laboratory were appreciably less than those growth increments (29.2 to 30.6%) for instars VI-VIII of the captive wild crabs, widths for instars II-XIII were estimated by the empirical value (2.6 mm CW) for stage I and then the subsequent stages were calculated with the linear regression (Table 3). Instar sizes calculated by this procedure were larger (about one instar size greater) than those sizes based on empirical data for stages I-V and predicted by regression for instars VI-XIII, e.g., instar V (estimated by regression) = 9.5 mm and instar VI (other method) = 9.6 mm. For purposes of this study, those instar sizes calculated with the empirical post-larval data were favored.

TABLE 3.–Comparison of instar sizes of rock crabs. For one group, instars I-V represent actual measurements and instars VI-XIII are calculated by the relationship $Y = 0.566 + 1.247X$; for the other group, instar I is an actual measurement and the remaining instars are estimated from the aforementioned equation.

Instar	I-V: Actual measurements VI-XIII: regression values		Regression values	
	Carapace width (mm)	Increase (%)	Carapace width (mm)	Increase (%)
I	2.6		2.6	
II	3.7	42.3	3.8	46.4
III	4.6	24.3	5.3	39.5
IV	5.9	28.3	7.2	35.3
V	7.4	25.4	9.5	32.5
VI	9.6	30.3	12.4	30.6
VII	12.5	30.6	16.1	29.2
VIII	16.2	29.2	20.6	28.2
IX	20.8	28.2	26.3	27.4
X	26.4	27.4	33.3	26.8
XI	33.5	26.8	42.1	26.4
XII	42.4	26.4	53.0	26.0
XIII	53.4	26.0	66.7	25.7

An attempt was made to objectively assign size with age by correlating instar size with the monthly width-frequencies (Figure 2). As mentioned previously, post-larval crabs (2-5 mm CW) first entered the sampling area in August or September after having hatched in late spring or summer and having developed through the larval stages during the remainder of the summer. Size distributions for April 1974 through April 1975 revealed first entry of young-of-the-year crabs in August followed by subsequent growth of young crabs until about January when growth ceased and this modal group stabilized at about 4-20 mm CW (instars III-IX). This wide size range is best explained by varying hatching and settling dates whereby some crabs entered the population perhaps 1 to 2 mo later than the rest. These crabs settled to the bottom when temperatures were likely to be declining; thus these individuals experienced little growth until the following spring.

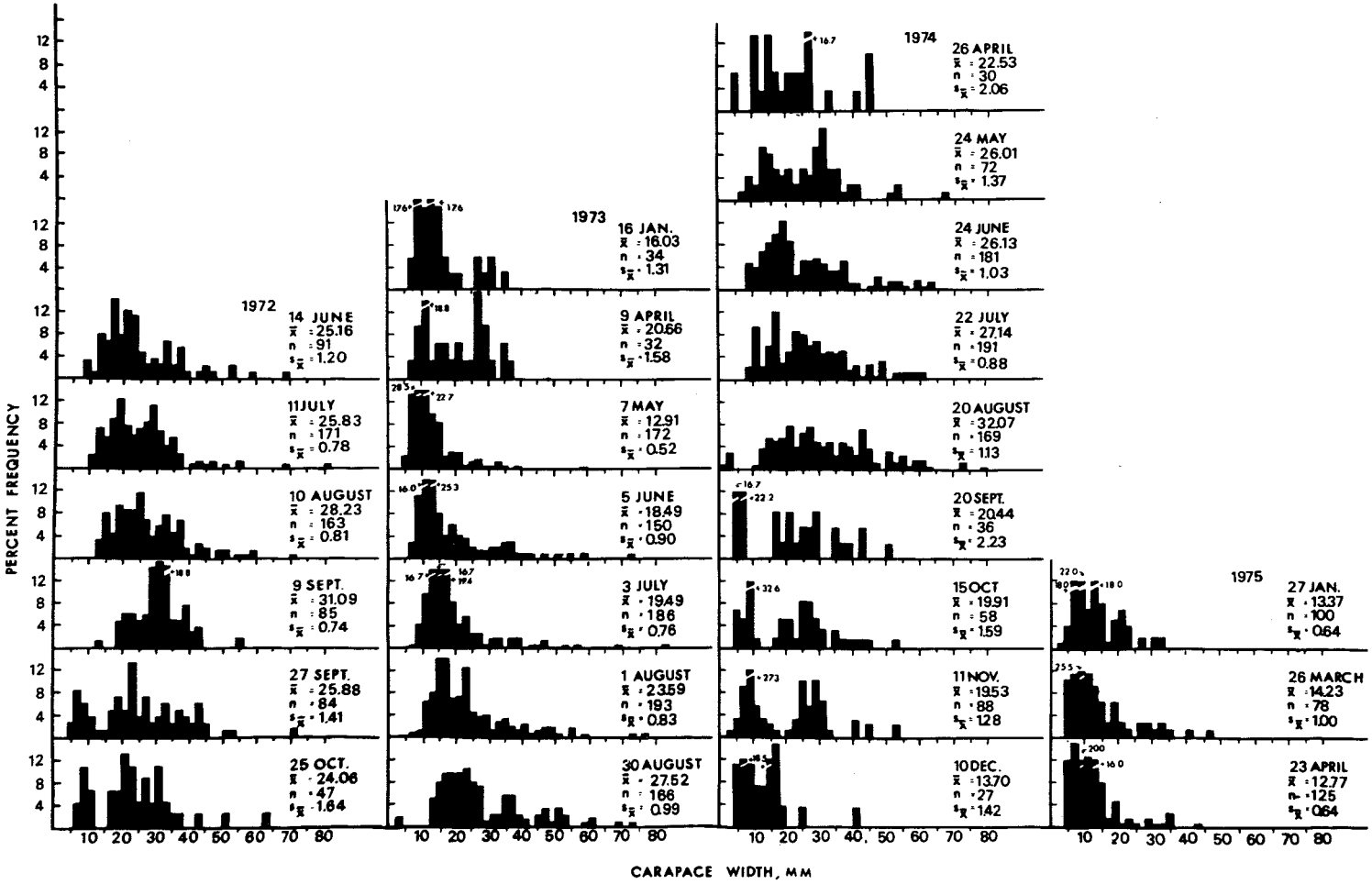

FIGURE 3.—Width-frequency distributions for rock crabs collected by hand in an intertidal area and by trap in the Boothbay region, 1972-74.

When growth resumed in late spring and summer, only a few juveniles (previous year's young-of-the-year) were <10 mm CW (stage VI). Unfortunately, the overlapping of modes prevented any objective determination of the upper limit of this second modal grouping that represented the juvenile crabs. Nevertheless, several of the monthly distributions (September-October 1972 and August 1973) exhibited an upper limit around 40 mm CW for this second modal grouping (Figure 2).

Although it was not possible to make precise determinations of age and growth from information of this study, the data suggest that young-of-the-year crabs ranged in size from about 4 to 20 mm CW (instars III-IX) and the juveniles in their second fall ranged from approximately 15 to 40 mm CW (instars VIII-XII).

Hand-Collected Vs. Trap-Caught Crabs

Prior to sampling small crabs in the intertidal zone, our rock crab work was based on incidental catches of crabs with wire lobster traps (25.4-×25.4-mm mesh) in the Boothbay Harbor area (Krouse 1972). Histograms plotted by 1-mm increments for 2,426 hand-collected and 5,480 trap-caught crabs (1972-74) graphically revealed marked differences in size composition of the catches for these two methods of capture (Figure 3). Average width for hand-collected crabs was 23.9 mm and 78.8 mm for trapped crabs. Even though these two complementary modes of capture sampled a broad range of sizes (2-133 mm CW), many crabs between 40 and 60 mm CW eluded either type of collection. This scarcity of crabs between 40 and 60 mm CW can be attributed to: 1) selectivity of traps against sizes <60 mm CW (based on Figure 3, crabs <70 mm CW were not fully vulnerable to the gear), and 2) movement of crabs >40 mm CW from the intertidal zone in association with low winter temperatures and possible behavioral changes with size. Scarratt and Lowe (1972) reported that small rock crabs (<65 mm CW) in the Northumberland Strait, Gulf of St. Lawrence, inhabited rocky areas, whereas larger crabs left the rocky substrate for sand and mud bottoms. Jeffries (1966) noted that *C. irroratus* dwelled chiefly on sand in the Narragansett Bay—the type of bottom this species is adapted to because of its well developed walking and burrowing abilities.

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LITERATURE CITED

BUTLER, T. H.
1961. Growth and age determination of the Pacific edible crab *Cancer magister* Dana. J. Fish. Res. Board Can. 18:873-891.

CLEAVER, F. C.
1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Wash. Dep. Fish., Biol. Rep. 49A:47-82.

ENNIS, G. P.
1973. Food, feeding, and condition of lobsters, *Homarus americanus*, throughout the seasonal cycle in Bonavista Bay, Newfoundland. J. Fish. Res. Board Can. 30:1905-1909.

JEFFRIES, H. P.
1966. Partitioning of the estuarine environment by two species of *Cancer*. Ecology 47:477-481.

KROUSE, J. S.
1972. Some life history aspects of the rock crab, *Cancer irroratus*, in the Gulf of Maine. J. Fish. Res. Board Can. 29:1479-1482.

SASTRY, A. N.
1970. Culture of brachyuran crab larvae using a re-circulating sea water system in the laboratory. Helgoländer wiss. Meeresunters. 20:406-416.

SCARRATT, D. J., AND R. LOWE.
1972. Biology of rock crab (*Cancer irroratus*) in Northumberland Strait. J. Fish. Res. Board Can. 29:161-166.

SHOTTON, L. R.
1973. Biology of the rock crab, *Cancer irroratus* Say, in the coastal waters of Virginia. M. A. Thesis, Univ. Virginia, Charlottesville, 72 p.

TERRETTA, R. T.
1973. Relative growth, reproduction and distribution of the rock crab, *Cancer irroratus*, in Chesapeake Bay during the winter. M.A. Thesis, College of William and Mary, Williamsburg, Va., 104 p.

WINGET, R. R., D. MAURER, AND H. SEYMOUR.
1974. Occurrence, size composition and sex ratio of the rock crab, *Cancer irroratus* Say and the spider crab, *Libinia emarginata* Leach in Delaware Bay. J. Nat. Hist. 8:199-205.

MINIMUM SWIMMING SPEED OF ALBACORE, *THUNNUS ALALUNGA*

RONALD C. DOTSON[1]

ABSTRACT

Measurements of density and pectoral lifting area of albacore, *Thunnus alalunga*, were made and compared with those previously described for yellowfin tuna, *Thunnus albacares*; bigeye tuna, *Thunnus obesus*; and skipjack tuna, *Katsuwonus pelamis*. Albacore have densities within the range of yellowfin tuna of similar size. The pectoral lifting area of albacore was always greater than skipjack tuna but similar to yellowfin tuna and bigeye tuna for fish less than 70 cm long. Larger albacore had increasingly larger fins than did the other species.

Minimum speed necessary for hydrostatic equilibrium of albacore was calculated and compared at 50 and 80 cm fork lengths to values calculated for the species above. Albacore minimum speeds were slower than those for skipjack tuna, similar to those of yellowfin tuna, and greater than those of bigeye tuna. Density variations of albacore, attributed to fat content and gas bladder volume, significantly affected estimates of minimum speed. Calculated speeds were slower than those estimated for albacore tracked at sea or estimated from tag returns.

Albacore tuna, *Thunnus alalunga* (Bonnaterre), being negatively buoyant in seawater, must swim continuously to maintain their position in the water column. The albacore's long pectoral fins help to compensate for their negative buoyancy by providing lift, thus lowering the swimming speed necessary to maintain hydrostatic equilibrium.

A model developed by Magnuson (1970) proposes that the minimum swimming speed of a scombrid fish is set by the necessity to maintain hydrostatic equilibrium rather than to provide adequate gill ventilation. When the lift provided by the pectoral fins necessary to compensate for the weight of the fish in water is estimated, the corresponding swimming speed can be considered the minimum necessary for the maintenance of hydrostatic equilibrium. This model was used by Magnuson (1973) to compare minimum speeds of several species of scombrid fishes that differed in pectoral lifting area, body shape, body density, and the presence or absence of a gas bladder.

The purpose of this paper is to 1) estimate the minimum swimming speed of albacore; 2) compare the minimum swimming speed of albacore with those for other scombrids; and 3) compare calculated minimum swimming speeds of albacore with swimming speeds estimated from sonic tracking of albacore at sea and from long distance tag returns.

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MATERIALS AND METHODS

To compute the minimum swimming speed with Magnuson's (1970) model, it is necessary to determine the mass of the fish, the lifting area, the density of the seawater, and the density of the fish. As the peduncle keels probably provide negligible lift (Magnuson 1973), they are excluded in the computation of minimum speeds.

To determine the mass of albacore, 477 specimens caught between long. 130° and 140°W and lat. 30° and 40°N during June 1974 were weighed to the nearest gram on a magnetically dampened pan balance and their fork lengths recorded to the nearest millimeter. Specimens were weighed and measured within 15 min after capture.

A regression $\ln M = \ln a + b(\ln L)$, where M is mass in grams and L is fork length in millimeters, was fitted to the length-mass data. The resultant equation was

$$M = 4.514 \times 10^{-5} L^{2.8746} \quad (1)$$

with 95% confidence limits on the exponent from 2.8245 to 2.9246.

The total pectoral lifting area (A) is equal to the projected surface area of the pectoral fins plus the projected body area between them, due to their analogy to wings in which the pressure distribution set up by the wings extends across the fuselage (Magnuson 1970). The pectoral lifting area was determined by tracing the outline of the

detached left pectoral fin on a piece of paper having a thickness of 0.25 mm. The outlined form was cut out and weighed to the nearest 0.01 g on a balance. Projected area was calculated from a ratio of the paper weights to a standard, and doubled to account for the other pectoral fin.

Thirty-three 100 cm^2 pieces of the paper were measured with a micrometer and weighed to determine the affect of variations in paper thickness and cutting accuracy on the calculations. The thickness of the paper varied less than 1% around the mean, and cutting accuracy varied by ±2%. The affect on calculations of pectoral lifting area was, therefore, assumed to be negligible.

The projected body area between the pectoral fins was determined by multiplying the body width at the pectorals by the width of the pectoral fin at its point of attachment to the body as measured on the fresh fish. Pectoral fin lifting areas were determined for 42 fish caught in the area described above and for 8 larger fish caught off Oregon in October 1974. The following relationship was established between the lifting area (A in square centimeters) and the fork length (L in millimeters):

$$A = 4.7351 \times 10^{-6} L^{2.6727}. \qquad (2)$$

Albacore observed cruising under the baitboat kept their pectoral fins extended continuously at a sweepback angle of approximately 45°. The tips of an albacore's fins are also not rigid, and the effect of this on the lifting capacity of the fin has been ignored.

A water density (D_c) of 1.025 g/ml was determined from temperature and salinity data from the offshore region described above. This also equalled the mean water density within the nearshore albacore fishery.

Fish densities were determined for three groups of fish: group 1—seven fish caught during June 1974 in the offshore region; group 2—14 fish caught 60 miles south of San Diego on 23 July 1975, presumably 2 wk after they appeared off the coast; and group 3—37 fish caught on 13 September 1975 in the same region as group 2 but assumed to have been near the coast for 2 mo.

The group 1 fish were frozen immediately after capture and, when returned to the laboratory, thawed and weighed on a spring balance while suspended in seawater to determine the density of the fish in seawater (D_f).

Fish from groups 2 and 3 were weighed in seawater on a pan balance immediately after capture and their densities in seawater determined.

VARIATIONS IN DENSITY

The density of group 1 fish (Figure 1) is well within the range of those determined for fresh fish of similar size indicating that freezing and thawing probably had negligible affect on density determinations. All specimens were caught on or near the surface by jigline or rod and reel, and there was no difference in density attributable to one method of capture over the other.

Rough estimates of the development of the gas bladders of 21 fish in group 3 were made immediately after other measurements were completed. In specimens less than 56 cm FL (fork length), the bladder was small (approximately 1 cm wide and 8 or 9 cm long) and contained little or no gas. In specimens 60 to 70 cm FL, the bladder was approximately 5 cm wide and 16 cm long and filled with gas to a depth of 4 or 5 cm. Fish over 80 cm FL had bladders approximately 30 cm long and 10 cm in diameter which occupied a large volume of

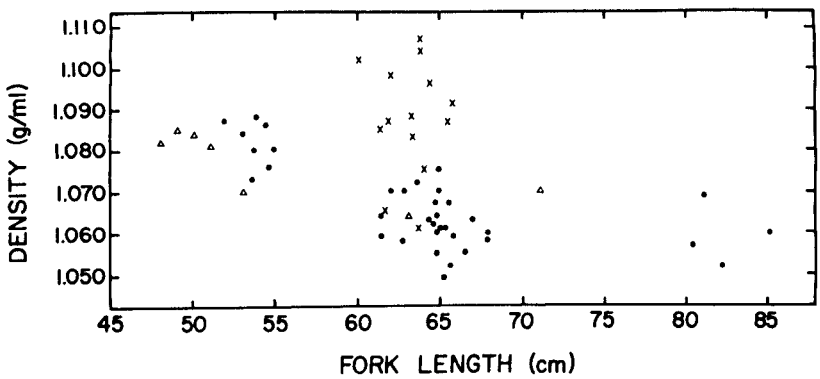

FIGURE 1.—Computed densities for three groups of albacore: group 1 (triangles); group 2 (crosses); and group 3 (dots). See text for explanation of groups.

the gut cavity. All developed gas bladders appeared full with two exceptions, and these may have been damaged during capture or dissection.

Seven albacore caught in September with fork lengths of 63 to 68 cm were examined to determine the effect of the gas bladder on density. Gas was removed from the bladder by a cannula (inside diameter = 1 mm) which was inserted through the ventral surface of the body while the fish was submerged in seawater, and the fish was then weighed while still submerged. The mean density increase with gas extraction was 0.007 g/ml (Table 1). Although this is probably a conservative estimate, the difference in density calculated before and after gas removal is used as the effect of the gas bladder on fish density. In an albacore less than 56 cm FL, the small gas bladder is not expected to affect density whereas the large and fully developed gas bladder of albacore greater than 80 cm FL should reduce density to a greater extent than was measured on the smaller fish above.

Densities of group 2 fish were considerably higher than those of similar size fish in groups 1 and 3 (Figure 1). Seasonal variations in density due to changes in fat content have been described for other pelagic species by Aleev (1963). Mass estimates were calculated from the length for each fish in all three groups using Equation (1), and compared with the observed values. The mean of the observed values for group 2 fell 403 g below the estimate from the regression line, ranging from 172 g greater to 999 g less. Because fish in group 2 had apparently just migrated into the area of capture, presumably from the central or western Pacific, the loss in mass was assumed to have been caused by the utilization of fat during migration. Group 1 would not yet have utilized this fat, and group 3 is assumed to have added fat by feeding in the rich coastal waters.

The densities in group 2 were recomputed on the assumption that the mass difference between the individuals and the regression curve is attributed to fat loss. An equation was developed by Magnuson (1970) relating the density (D_f) of a scombrid without a gas bladder to the percentage (P) of the total body weight that is fat. The equation

$$D_f = 1.100 - 0.0017\,P \qquad (3)$$

was used to recompute densities for the fish in group 2. The effect of the gas bladder on density was assumed to be 0.007 g/ml because fish in group 2 were in the same size range as the above fish for which gas bladder measurements were taken. This value was added to the observed density and the percentage body weight in fat calculated. The difference in mass (assumed to be fat loss) of each individual was then added and new densities determined with the increased percentage of body fat. The density effect of the bladder was subtracted from this value to yield a density adjusted for fat loss. When determining fat content in the fish, the density effect of the bladder was taken into account, except for those fish with measured densities greater than 1.100 g/ml, which is the level Magnuson (1970) chose as the density for a scombrid without a gas bladder. Fish with densities greater than 1.100 were assumed to have empty or damaged gas bladders, and the density difference due to the gas bladder was subtracted from the recomputed density.

Recomputed densities of group 2 are plotted in Figure 2 with the measured densities of groups 1 and 3. The close fit of the recomputed densities appears to support the assumption that fat content and gas bladder volume can account for the disparity in densities observed for group 2 in the original data. Density values are, therefore, expected to vary considerably depending on the development and condition of the gas bladder and the fat content of the fish when it is caught.

DETERMINATION OF MINIMUM SPEED

To estimate the minimum speed for hydrostatic equilibrium, it is necessary to calculate the amount of lift a fish must produce. The lift (L_f) required by a scombrid to attain hydrostatic equilibrium, expressed in dynes, is determined from the relation (Magnuson 1970)

$$L_f = M\left[\left(1 - \frac{D_e}{D_f}\right) 980\ \mathrm{cm/s^2}\right]. \qquad (4)$$

When the lift is assumed to be provided solely by the pectoral fins, and the coefficient of lift for the pectorals is assumed to be 1.0, then the equation for minimum swimming speed becomes (Magnuson 1970)

$$V = \left[\frac{L_f}{D_e/2(A)}\right]. \qquad (5)$$

Calculations of minimum swimming speed from

TABLE 1.–Density changes in albacore following gas bladder deflation and resultant effect on estimation of minimum speed.

Characteristic	Albacore no. 1	2	3	4	5	6	7	Mean
Fork length (mm)	627	643	646	648	653	679	679	654
Density with gas bladder (g/ml)	1.058	1.063	1.062	1.055	1.061	1.060	1.058	1.059
Density without gas bladder (g/ml)	1.063	1.069	1.068	1.058	1.067	1.067	1.071	1.066
Change in density due to gas bladder (g/ml)	0.005	0.006	0.006	0.003	0.006	0.007	0.013	0.007
Minimum speed with gas bladder (cm/s)	45.0	48.6	48.7	44.5	49.8	47.3	47.9	47.4
Minimum speed without gas bladder (cm/s)	47.9	52.2	52.4	46.5	53.9	51.7	56.3	51.6
Change in minimum speed due to gas bladder (cm/s)	2.9	3.6	3.7	2.0	4.1	4.4	8.4	4.2

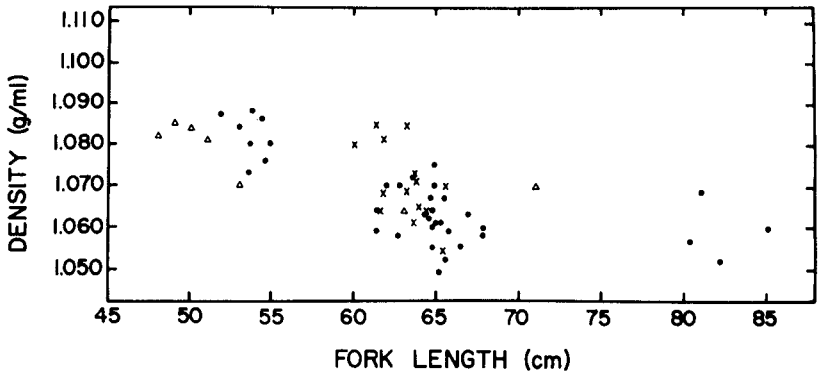

FIGURE 2.–Computed densities for three groups of albacore with group 2 densities (crosses) recomputed after correction for fat loss. Recomputation of group 2 densities is explained in the text.

this equation assume 100% extension of the pectoral fins.

The mass of the fish (M) and the lifting area (A) can be calculated using Equations (1) and (2), respectively. The density of the environment (D_e) is 1.025 g/ml. If we use M = 2,540 g, D_f = 1.082 g/ml, A = 77.4 cm^2 for a 50-cm fish, the calculated minimum speed V is 54 cm/s.

Density variations due to fat content and gas bladder volume can affect the minimum swimming speed necessary to maintain hydrostatic equilibrium. For a 65-cm albacore, a loss of 10% of its body weight in fat would result in a 10% increase in minimum speed. Loss or emptying of the gas bladder results in an 8% increase in minimum speed. Minimum speeds calculated from data on fish with full gas bladders and in good condition are therefore considered to be the minimum obtainable while retaining hydrostatic equilibrium.

COMPARISON OF MINIMUM SPEEDS OF FOUR SCOMBRIDS

Minimum speeds were calculated for albacore; yellowfin tuna, *Thunnus albacares*; bigeye tuna, *T. obesus*; and skipjack tuna, *Katsuwonus pelamis*, at fork lengths of 50 and 80 cm. The speeds are given in Table 2 with the density, mass, and pectoral lifting area used in the computations.

The minimum swimming speed of albacore decreases from 57 cm/s when they are 50 cm FL to 45 cm/s at 80 cm FL. The decrease is a direct result of the allometric growth of the pectoral fins (Yoshida 1968) and the gas bladder (Gibbs and Collette 1966). The gas bladder of albacore does not have significant development when the fish is less than 55 cm long, but has considerable volume at a fish length of 65 cm, and apparent complete development when the fish has reached 80 cm FL (data, this paper). Combined with the increasing length of the pectoral fins, the result is a relatively

TABLE 2.–Estimated minimum speeds of four species of scombrids at fork lengths of 50 and 80 cm. The mass of the fish (M), pectoral lifting area (A), and density of the fish (D_f) used in the computations are also given.

Species	Fork length (cm)	M (g)	A (cm^2)	D_f (g/ml)	V (cm/s)
Thunnus alalunga[1]	50	2,588	77.40	1.082	57
	80	9,992	271.04	1.056	45
Thunnus obesus[2]	50	2,429	96.63	1.047	32
	80	10,825	233.80	[3]1.030	21
Thunnus albacares[4]	50	2,501	91.56	1.087	55
	80	10,338	220.50	1.050	47
Katsuwonus pelamis[4]	50	2,539	47.88	1.090	78
	80	12,567	137.20	1.096	107

[1]Data from present paper.
[2]M, A, and D_f from Magnuson (1973).
[3]Extrapolated value.
[4]M calculated from Chatwin (1959), A and D_f from Magnuson (1973).

abrupt drop in minimum speed between 60 and 70 cm FL (Figure 3).

Albacore and yellowfin tuna have very similar densities (Table 2), but the pectoral fins of albacore are smaller in young fish (Gibbs and Collette 1966), increasing very rapidly in size as the fish mature (Figure 4). Thus, small albacore have a faster minimum swimming speed than small yellowfin tuna, and albacore over 65 cm have a slower minimum swimming speed than the same size yellowfin (Table 2, Figure 3) assuming similar fat content and gas bladder development.

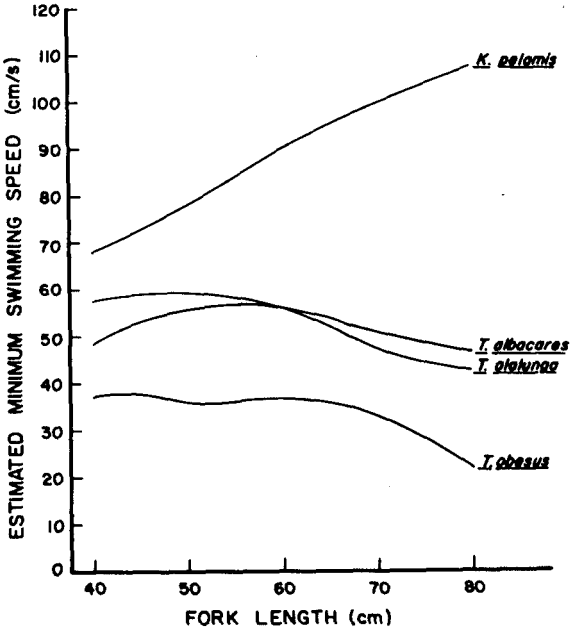

FIGURE 3.—The estimated minimum swimming speed of four scombrids using Magnuson's (1970) model for hydrostatic equilibrium.

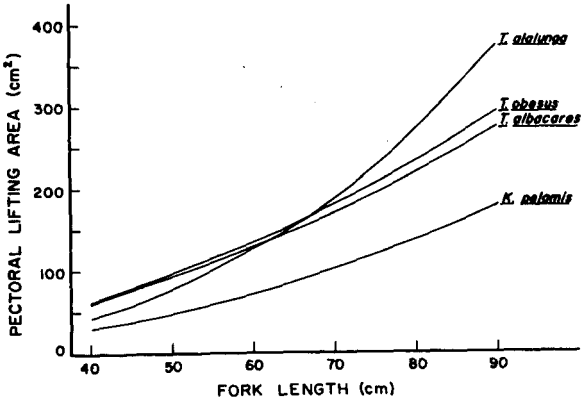

FIGURE 4.—Regression curves for pectoral lifting area (A) versus fork length. Curves for *Thunnus obesus*, *T. albacares*, and *Katsuwonus pelamis* are from Magnuson (1973). The curve for *T. alalunga* is from Equation (2) in the text.

Because bigeye tuna have a larger gas bladder than albacore and also have large pectoral fins, both of which grow allometrically (Gibbs and Collette 1966), their estimated minimum swimming speed is only half that of albacore at both 50 and 80 cm in length (Table 2).

The minimum swimming speed necessary for hydrostatic equilibrium of 50-cm albacore is 70% that of 50-cm skipjack and only 40% when each is 80 cm long (Table 2). Unlike albacore, skipjack have no gas bladder and always have small, short pectoral fins; therefore, skipjack tuna must swim faster as their mass increases in order to maintain hydrostatic equilibrium (Figure 3).

In Table 2 and Figure 3, density values for bigeye tuna were extrapolated beyond observed values and those of albacore were chosen from "fat" fish; therefore, actual values shown may not be exact, but the gross relationships among species are expected to hold true.

FIELD ESTIMATES OF ALBACORE SWIMMING SPEEDS

During August 1972, the National Marine Fisheries Service in cooperation with the American Fishermen's Research Foundation tagged six albacore with sonic tags and tracked their movements off the coast of Monterey Bay, Calif. (Laurs et al. 1972).[2]

Mean speeds observed during sonic tracking of three fish near 85 cm fork length were 95 cm/s during daylight hours and 62 cm/s during the night. These speeds are higher than the calculated minimum of 42 cm/s for a fish this size.

Each of two tagged albacore approximately 80 cm long, which were caught after a trans-Pacific migration, had a computed minimum or straight line speed (based on great circle route and time free) of 26 nautical miles/day or 55 cm/s (Japanese Fisheries Agency 1975). The calculated minimum speed of 45 cm/s is remarkably close to the estimated minimum migration speed of these two

[2]Laurs, R. M., H. S. H. Yuen, and J. H. Johnson. 1972. Study of the small-scale movements of albacore using ultrasonic tracking techniques. *In* Report of Joint National Marine Fisheries Service-American Fishermen's Research Foundation Albacore Studies Conducted during 1971 and 1972, p. 54-72. Unpubl. Rep. SWFC, NOAA, La Jolla.

fish but could be an artifact of many interacting processes and events.

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LITERATURE CITED

ALEEV, YU. G.
1963. Function and gross morphology in fish. Izd. Akad. Nauk SSSR, Mosc., 245 p. (Translated from Russian by the Israel Program Sci. Transl., 1969, 268 p.; available U.S. Dep. Commer, Natl. Tech. Inf. Serv., Springfield, Va., as TT 67-51391.)

CHATWIN, B. M.
1959. The relationships between length and weight of yellowfin tuna (*Neothunnus macropterus*) and skipjack tuna (*Katsuwonus pelamis*) from the Eastern Tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 3:305-352.

GIBBS, R. H., JR., AND B. B. COLLETTE.
1966. Comparative anatomy and systematics of the tunas, genus *Thunnus*. U.S. Fish. Wildl. Serv., Fish. Bull. 66:65-130.

JAPANESE FISHERIES AGENCY.
1975. Report of tuna tagging for 1974. [In Jap.] Pelagic Res. Sec., Far Seas Fish. Res. Lab., 18 p.

MAGNUSON, J. J.
1970. Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. Copeia 1970:56-85.
1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull., U.S. 71:337-356.

YOSHIDA, H. O.
1968. Pectoral fin length of juvenile albacore. Copeia 1968:625-626.

PRODUCTION OF FRY AND ADULTS OF THE 1972 BROOD OF PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, FROM GRAVEL INCUBATORS AND NATURAL SPAWNING AT AUKE CREEK, ALASKA

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ABSTRACT

Production of fry and adults of the 1972 brood of pink salmon, *Oncorhynchus gorbuscha*, at Auke Creek, Alaska, was compared between a gravel incubator hatchery and natural spawning. Natural production in the creek above the hatchery weir (estimated from hydraulic sampling) was 73,900 fry (SE: 32,800) from an estimated initial seeding of 934,065 eggs (SE: 42,811) for a survival rate of 0.079 (SE: 0.035). An estimated total of 579,000 unfed fry (SE: 25,296) were released from the hatchery for a comparable survival rate of 0.743 (SE: 0.047). Exactly 84,000 of the hatchery fry and 5,500 of the creek fry were released after being marked by clipping fins. All adults returning to the weir were examined for marks, and some additional marks were recovered from sport and commercial fishermen; 667 marked hatchery fish and 74 marked creek fish were recovered. Estimated survival of hatchery fry to returning adult was only 0.0079 (SE: 0.0003) equal to 0.59 (SE: 0.071) the corresponding estimate of 0.0135 (SE: 0.0016) for creek fry, which suggests that hatchery fry were inferior to creek fry in the marine environment; however, hatchery fry emigrated seaward 2 wk earlier than creek fry and may have encountered less favorable marine conditions. Survival from eggs to returning adult stage was 5.50 times (SE: 2.59) higher for hatchery fry than for creek fry because of much greater survival from egg to fry in the hatchery; the difference is not statistically significant. Hatchery fry were generally shorter but heavier than creek fry and emigrated seaward at a slightly earlier stage of development. No differences in size or time of return of adults could be traced to the incubation environment from which they came.

The level of harvest of pink salmon, *Oncorhynchus gorbuscha*, in Alaska in the 1970's (Seibel and Meacham 1975) has been about one-ninth the level of the 1930's (Kasahara 1963). This decline, in view of recent advances in salmon hatchery systems (Bams 1972), might be countered by large-scale artificial propagation of salmon fry to supplement natural spawning. As a first step toward developing systems for enhancing or rehabilitating the depleted stocks, the National Marine Fisheries Service, Northwest Fisheries Center Auke Bay Fisheries Laboratory and the Alaska Department of Fish and Game agreed in August 1971 to begin testing a gravel incubator hatchery on Auke Creek near Juneau in southeastern Alaska.

Auke Creek was selected because it is accessible and has a fish weir and a dependable water supply from nearby Auke Lake. Lake water is especially desirable for hatcheries in Alaska because the water temperature generally remains above freezing (3°-4°C). However, lake water has at least one disadvantage—it has a different seasonal temperature pattern than most of the streambed waters where pink salmon eggs normally incubate. Bams (1972) avoided the problem of temperature differences by collecting hatchery water from beneath the streambed, but this is not always feasible in Alaska because of the severe freezing conditions encountered at many potential hatchery sites. This report on the 1972 brood pink salmon at Auke Creek compares hatchery production and natural production in regard to 1) survival from eggs to emergent fry, fry to returning adults, and eggs to returning adults; 2) size, stage of development, and emergence timing of fry; and 3) size and time of return of adults returning to Auke Creek from hatchery and creek fry.

MATERIALS AND METHODS

A heated building (7.3 by 13.4 m) provided space for a water filter and ultraviolet purifier; incubators; instruments for measuring temperature and oxygen; equipment for censusing, sampling, and marking fry; and instruments for measuring and counting adult salmon. The building was located on Auke Creek near a fish-counting weir at the head of tide where eggs could be collected from

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returning adult salmon. The hatchery water supply came from nearby Auke Lake. The eggs were incubated to the eyed stage in Heath[2] incubators and then transferred to gravel incubators to complete development.

Water Filter and Purifier

The water filter and ultraviolet purifier system supplied treated water to one-half of the hatchery incubators; the rest were supplied with untreated water. The filter was rated to remove particles 10 μm in diameter or larger. The purifier was designed to give a minimum dosage of 35,000 $\mu W \cdot s/cm^2$ at 2,537 Å. The water treatment had no apparent beneficial effect.

Natural Spawning

From 4 August to 21 September 1972, 1,768 adult pink salmon entered the fish counting weir. About 55%, 459 females and 527 males, were released to spawn above the weir. The rest were kept for fecundity counts and hatchery spawn source. Ten females from which we obtained fecundity counts were treated as a simple random sample in later analysis, although no serious effort was made to assure randomness of selection. Average fecundity in this sample was 2,035 eggs/female (SE: 93.27). This estimate agreed closely with 2,023 eggs/female from an inventory of eggs obtained from the 386 females used as the hatchery spawn source after a rough correction for eggs retained. Most pink salmon released above the weir spawned in a 297-m section of stream between the weir and Auke Lake. Fewer than 20 adults spawned in Lake creek above Auke Lake. The alevin population of Auke Creek was estimated 20-21 March 1973 with a hydraulic pump census (McNeil 1964).

Collection and Eyeing of Eggs

Eggs for seeding incubators were obtained from the Auke Creek pink salmon run 8 August through 22 September 1972. These dates cover nearly the entire run, thereby assuring representation of all parts of the run in the next generation. Eggs were collected from 386 females (about 45% of the females in the spawning run) in the manner described by Bailey and Taylor (1974). Malachite green treatments, 15 ppm. for 1 h, were used at weekly intervals between 17 August and 19 October to control fungus growth until eyed eggs were removed from the Heath trays.

Raising Eyed Eggs to Fry Stage

The eyed eggs were raised to the fry stage in four gravel incubators (Bams 1970) designated A, B, C, D (Table 1). The incubators measured 1.2 by 1.2 by 1.2 m and used a system of perforated pipes and horizontal layers of graded gravel to achieve uniformity of upwelling flow through the eggs and gravel. Flow to A, B, and C was initially set at 75 liters/min and to D at 79 liters/min. Incubators A, B, and C were loaded with an estimated 150,000 eggs (SE: 1,030) each and incubator D with an estimated 158,000 eggs (SE: 1,085) (Table 1). Therefore each incubator initially contained 2,000 eggs per liter/min.

Iron bacteria sheaths and a flocculent iron precipitate accumulated in the incubators. The material seemed to accumulate as rapidly in incubators receiving filtered and irradiated water as in those receiving untreated water. The intended water flow through the incubators receiving treated water could not be maintained. Flow through incubator C had dropped from the desired 1.26 liters/s to 0.88 liter/s 18 December 1972, and flow through incubator B had dropped to 0.95 liter/s 3 January 1973. Flow through these incubators was maintained at 0.63-1.07 liters/s for the rest of the incubation period. The full 1.26 liters/s was maintained at all times in the two incubators receiving untreated water, probably because the hydraulic head on the untreated water supply was about twice the head on the treated water.

The estimates of numbers of eggs seeded in each incubator were determined by the method of Burrows (1951). Through an oversight, records of

TABLE 1.—Operating conditions in four gravel incubators seeded with eyed pink salmon eggs, Auke Creek, 1972. For each incubator the volume of substrate and eggs was 1.246 m^3.

Incubator	Number eggs	Water flow (liters/min)	Type of water treatment
A	150,000	75	Untreated
B	150,000	75	Filtered and ultraviolet treated
C	150,000	75	Filtered and ultraviolet treated
D	158,000	79	Untreated

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

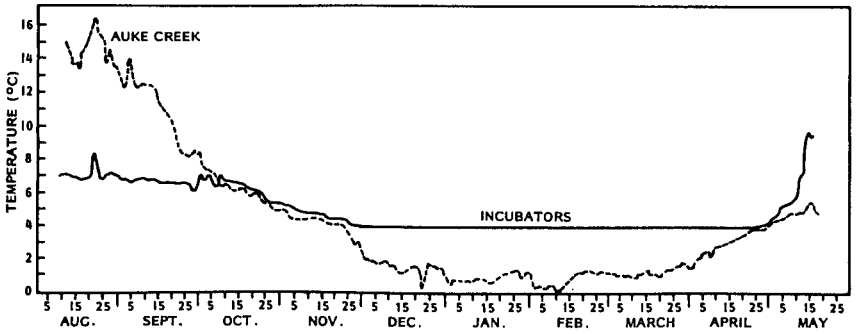

FIGURE 1.–Temperatures in gravel incubators and in surface water of Auke Creek, 8 August 1972 through 17 May 1973.

the procedure were of insufficient detail to estimate the precision of the initial seedings. Variances of these initial seedings were estimated from data obtained in recent years, 1974 and 1975. This source of error was determined to be negligible in later calculations.

Eggs were fertilized on the following schedule: incubator A, 4-31 August; B, 4 August to 8 September; C, 11-17 September; and D, 17-21 September.

Water Temperatures

We measured temperatures daily with a mercury thermometer (to the nearest 0.1°C) in Auke Creek and in the incubators from the time the first eggs were collected until the fry left the creek. While eggs were being collected (8 August to 22 September 1972), water in Auke Creek was warmer than water in the incubators (Figure 1). The creek water was cooler than the incubator water from 9 October throughout the rest of the incubation period, which ended when the fry emerged.

Oxygen Levels

Oxygen concentrations in the water supply to the hatchery and in effluents from the incubators were measured to the nearest 0.01 mg/liter by the Winkler method. Oxygen was measured at weekly intervals from shortly after eyed eggs were seeded (9 November 1972) until the fry began to emerge (23 March 1973). Oxygen content of the water supplied to the incubators decreased steadily–from 9.6 mg/liter (73% saturation) on 22 November 1972 to 7.8 mg/liter (59% saturation) on 23 March 1973 (Figure 2). Oxygen in effluents from gravel incubators decreased from 9.3 mg/liter (71% saturation) to 6.7 mg/liter (51% saturation) during the same period.

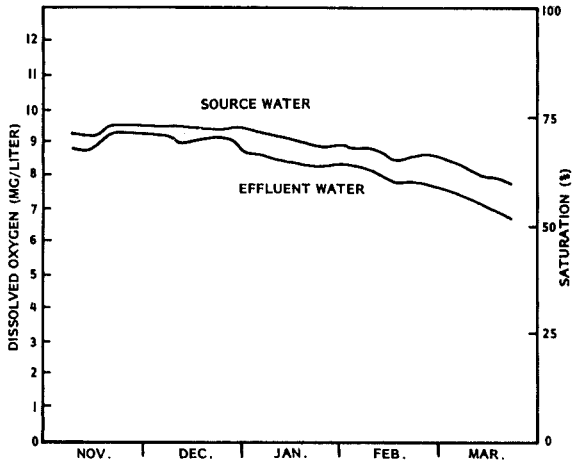

FIGURE 2.–Dissolved oxygen levels in source water and effluent water of gravel incubators at Auke Creek Hatchery, 9 November 1972 through 23 March 1973.

Counting and Processing Fry

We collected emigrating creek fry and hatchery fry to measure and mark, to determine time of migration, and to estimate abundance of hatchery fry. Two 0.91- by 0.91-m fyke nets with floating live-boxes were used to index the daily emigration of creek fry and to collect fry for a mark and recovery experiment. The daily counting of fry as they emerged from gravel incubators and the collection of fry for fin clipping and measuring was expedited by passing the incubator effluents over a cone-shaped sampling device[3] and then through a second sampling device consisting of a set of five parallel troughs. The first device provided small subsamples of fry from which total numbers emerging could be estimated; the second

[3]A blueprint for the cone-shaped fish sampler was supplied by the Washington Department of Fisheries.

device separated a larger subsample from the total numbers for marking.

We calibrated the cone device as a sampler with which to estimate total numbers of emerging fry from the incubators. Inspection of the relationship of total fry emigrating from an incubator (y) plotted against fry retained by the sampler (x) on 24 occasions indicated a constant ratio (straight line through the origin) with increasing variation at higher subsampler counts (Figure 3). Consequently, the average of the 24 ratios (y/x) available from the calibration study is taken as the slope estimate (Snedecor 1956: 153-156) and was calculated as 24.537 (SE: 1.072). The major portion of the fry passed the cone sampler and were then routed through the parallel troughs, one of which emptied into a holding tank and four of which emptied into the hatchery drain and then into Auke Creek. With these two devices we captured about one-fourth of the gravel incubator fry each day without impeding the seward migration of the other three-fourths.

Twice weekly, samples of 50 fry from each gravel incubator and the fyke nets were preserved in 5% Formalin. The preserved fry were allowed to stand for 6 wk before lengths were measured to the nearest millimeter and wet weights to the nearest milligram. An index to stage of development (Bams 1970) of the fry was computed from the formula

$$K_D = \frac{10\sqrt[3]{\text{weight in milligrams}}}{\text{length in millimeters}}.$$

This index is used only on unfed fry to indicate the relative yolk content. It is not a condition factor.

Weighted means and variances of pooled data were computed on the basis of the fraction of the migrant fry represented by each sample. Statistical comparisons were made of lengths, wet weights, and developmental index as follows:

$$\bar{Y}_W = \Sigma W_i \bar{Y}_i$$

where $\bar{Y}_W$ = weighted mean
$\bar{Y}_i$ = observed mean measurement in ith period
W_i = proportion of run leaving in ith period from index sampling, and

$$V(\bar{Y}_W) = \sum_{i=1}^{n} W_i^2 V(\bar{Y}_i)$$

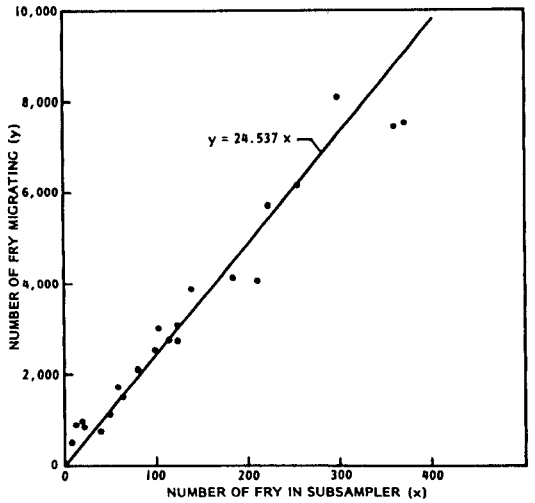

FIGURE 3.—Relation of number of fry migrating to number of fry in subsampler. Each point represents one sample.

where $V(\bar{Y}_W)$ = variance estimate of weighted mean
$V(\bar{Y}_i)$ = sample variance of estimated mean in ith period
n = number of periods sampled.

Technicians marked hatchery fry by clipping the adipose and left ventral fins and creek fry by clipping the adipose and right ventral fins. Before marking, the fry were anesthetized in a solution of 1:7,500 MS-222 (Tricaine methanesulfonate) buffered with sodium bicarbonate to pH 6.1-6.4; the solution was kept cool in a water table and recirculated to keep the oxygen content high. Surgical iris scissors were used to excise fins under a 3× magnifying lens. Technicians marked an average of about 200 fry/h on this study, whereas technicians marked about 400 fry/h on a similar study in Canada (R. A. Bams pers. commun.). Samples of fry from each technician were examined several times daily to ensure that the correct fins were excised as close to the body as possible. All marked fry were released at 1130 h the same day they were marked; most of the unmarked fry that had left the incubator or the stream at the same time had migrated seaward 24 h earlier. Dead fry remaining in the release tank were counted each morning. The immediate mortality from marking was less than 0.1% for both hatchery and creek fry. Totals of marked fry released were 84,000 from the hatchery and 5,500

from the creek. The daily numbers of marked fry released from the hatchery and the creek were roughly proportional to the respective migrations of fry from these two sources. There was a slight bias toward marking too few fry during the first half of the migration, but the bias was in the same direction and magnitude on both types of fry.

Less than 1% of the creek fry died in the fyke net and floating live-box, indicating slightly greater physical abuse for marked creek fry than marked hatchery fry.

Recovery of Marked Adults

Returning 1972 brood adults were counted at the weir in Auke Creek in the summer of 1974; some adult salmon were anesthetized and measured. Mideye-to-tail-fork lengths were measured to the nearest millimeter and weights to the nearest 0.01 kg.

Analysis of Survival

Survival probabilities from egg to fry and fry to returning adult are estimated from estimates of initial number of eggs, fry produced, and returning adults. Ratios of these survival estimates are used to compare survival of hatchery and creek salmon. Variances of survival and estimates of ratios of these survival estimates were approximated by the delta method (Deming 1943; Paulik and Robson 1969). Finite population correction factors were ignored in variance calculations; changes in variance estimates would have been insignificant.

Estimation of survival from marking requires special argument. The expected total unmarked returns from hatchery and creek fry combined is

$$T = Us + U's'$$

where U and U' are initial numbers of unmarked fry from the creek and hatchery respectively, and s and s' are the probabilities of survival of the two unmarked groups at sea. Marking increases mortality. If the probability of survival from marking is τ and identical for both groups, the probabilities of survival from both causes are $s\tau$ and $s'\tau$ for creek and hatchery fry respectively. The expected total return of the unmarked fry had they been marked, T', is

$$T' = Us\tau + U's'\tau.$$

The ratio of T' to T is τ. Therefore, we estimate survival from marking from estimates of T and T' as

$$\hat{\tau} = \hat{T}'/\hat{T}.$$

The expectation T is estimated by the total unmarked recoveries to the weir. The expectation T' is estimated from appropriate combinations of estimates of numbers of unmarked creek and hatchery fry and estimates of marine survival of marked fry of both groups.

Total variation among incubators in estimated survival from egg to fry is divided into three sources: 1) Underlying variation due to heterogeneity of genetic composition of pink salmon and environmental conditions among incubators, 2) binomial variation within incubators, and 3) sampling error in estimation of numbers of eggs and fry. We imagine an unobserved universe of survival probabilities s with mean $\bar{s}$ has been sampled randomly by our study; four members were drawn, each applying to one of our incubators. Actual survival within an incubator varies from its associated probability of survival due to binomial variation; instead of a fraction s surviving, the actual fraction is $\hat{s}$. This actual rate was not observed; rather, we estimated $\hat{s}$ by $\hat{\hat{s}}$, the ratio of estimated fry to estimated eggs.

Total variance of estimated survival among incubators, σ_t^2, is defined by

$$\sigma_t^2 = \underset{3}{E}(\hat{\hat{s}} - \bar{s})^2$$

where $\underset{3}{E}$ denotes the expectation operation over the three sources of variation.

This expression may be rewritten as

$$\sigma_t^2 = \underset{3}{E}[(\hat{\hat{s}} - \hat{s}) + (\hat{s} - s) + (s - \bar{s})]^2.$$

After completing the square and evaluating the expectations of the terms, we find

$$\sigma_t^2 = \sigma_1^2 + \sigma_2^2 + \sigma_3^2$$

where $\sigma_1^2 = \underset{1}{E}\,(s - \bar{s})^2$, the variance of underlying survival probabilities among incubators; $\sigma_2^2 = \underset{2}{E}\,(\hat{s} - s)^2$, the average binomial variance; $\sigma_3^2 = \underset{3}{E}\,(\hat{\hat{s}} - \hat{s})^2$, the average variance due to errors in estimates of fry and eggs; $\underset{1}{E}$ denotes the expectation operation over the first source of variation; and $\underset{2}{E}$ denotes the expectaton operation over the first two sources of variation.

Our experiment provides four unobserved selections from the underlying probabilities of survival, four estimates of binomial variation, and four estimates of variance in estimated survival due to errors in estimates of eggs and fry. Averages of the four estimates for the second and third sources are used to estimate σ_2^2 and σ_3^2. The sample variance of $\hat{s}$ is used to estimate σ_f^2. The estimate of σ_1^2 is obtained by subtraction.

RESULTS

First, we evaluate the effectiveness of the Auke Creek Hatchery by comparing survival of hatchery and creek fishes at different life stages: egg to emergent fry, fry to returning adult, and egg to returning adult. Next we estimate survival from marking. Then we compare size, stage of development, and emergence timing of hatchery fry with creek fry. Finally, we compare size and time of return of hatchery fish and creek fish as adults.

Survival from Egg to Fry

We estimated survival from potential egg deposition to fry for creek fry as the ratio of an estimate of the alevins in the spawning area of the creek above the weir in the spring of 1973 (just before emergence) to an estimate of the potential egg deposition. Because 459 females spawned in the stream above the weir, we estimate potential egg deposition as (459)(2,035) = 934,065 [SE: (459)(93.27) = 42,811 eggs].

On 20 and 21 March 1973, we determined the number of live alevins in each of 86 0.1-m^2 units of a simple random sample from the 8,600 such units making up the spawning area above the weir. The average number of alevins per unit was 8.593 (SE: 3.814). Hence, total live alevins in the spawning area was estimated to be (8,600)(8.593) = 73,900 alevins [SE: (8,600)(3.814) = 32,800 alevins].

Survival to time of sampling is estimated as the ratio of estimated total alevins to estimated potential egg deposition or 73,900/934,065 = 0.079 (SE: 0.035).

In the gravel incubators, estimated survival from live egg to fry was calculated as the ratio of estimated total emigrants to initial numbers of live eggs. The sums of the daily numbers of fry in subsamples from the four incubators were as follows: (A) 5,960; (B) 5,792; (C) 5,153; and (D) 6,692. Total emigrations from the incubators and corresponding standard errors were estimated using the calibration results: (A) (5,960)(24.537) = 146,240 fry [SE: (5,960)(1.072) = 6,389 fry]; (B) 142,118 (SE: 6,209); (C) 126,439 (SE: 5,524); and (D) 164,202 (SE: 7,174). The grand total of fry emigrating was 579,000 (SE: 25,296).

Estimates of survival from live eyed eggs to fry and the standard errors of these estimates were as follows: (A) 146,240/150,000 = 0.975 (SE: 0.043); (B) 0.947 (SE: 0.041); (C) 0.843 (SE: 0.037); and (D) 1.039 (SE: 0.045). The estimate for incubator D is not feasible, but since it lies within a standard error of the feasible range, we do not suspect errors in data recording or calculations. The mean of the survival estmates was 0.951, and the sample variance of the estimates was 0.00667.

This variance estimate is divided into three components—$\hat{\sigma}_1^2$, $\hat{\sigma}_2^2$, $\hat{\sigma}_3^2$—representing variation in underlying survival probabilities, binomial variation, and variation due to errors in estimating eggs and fry respectively. The estimates are as follows: $\hat{\sigma}_1^2 = 0.00493$, $\hat{\sigma}_2^2$ is negligible, and $\hat{\sigma}_3^2 = 0.00174$. Therefore, most of the total variance of survival estimates among the four incubators seems due to variation in underlying survival within the incubators rather than binomial variation or variation in egg or fry counts.

The incubator survival rates are from live eyed egg to fry. The creek survival rate is from potential egg deposition to fry. To make the survival rates comparable, we adjust the incubator survival to that from potential egg deposition to fry. The proportion of potential egg deposition which develops to the eyed stage in the hatchery is estimated as the ratio of total estimated eyed eggs obtained from the 386 females artificially spawned to estimated potential egg deposition by the females, or 614,000/785,510 = 0.782 (SE: 0.036). The adjusted incubator survival rate from potential egg deposition to fry is (0.782)(0.951) = 0.743 (SE: 0.047).

Survival from Fry to Returning Adult

Although most of the marked returning adults were recovered at the weir in Auke Creek below their point of origin, some were recovered from sport and commercial fishermen and from the intertidal spawning area of Auke Creek (Table 2). Total recoveries from all sources were used to estimate relative survival from fry to returning adult: 667 of the marked hatchery fish and 74 of the marked creek fish were recovered. Estimated survival of hatchery fry to returning adults is

667/84,000 = 0.0079 (SE: 0.0003). Estimated survival of creek fry for the same period is 74/5,500 = 0.0135 (SE: 0.0016). Therefore, our estimate of relative survival of hatchery fish as compared to creek fish is 0.0079/0.0135 = 0.59 (SE: 0.071).

TABLE 2.–Source of recoveries ofmarked pink salmon adults originating from fry marked at Auke Creek in 1973.

Source of recovery	Origin of marks	
	Hatchery	Creek
Commercial fishery	4	1
Sport fishery	8	0
Intertidal area of Auke Creek	11	2
Auke Creek weir	644	71
Total	667	74

Survival from Egg to Returning Adult

While hatchery fry suffered greater losses than creek fry in the marine environment, their increased survival under the artificial conditions during incubation was compensating. Overall relative survival from potential egg deposition to returning adult can be estimated as the ratio of the products of survival from potential egg deposition to alevin and from fry to returning adult for hatchery and creek fry. The survival of hatchery fish relative to creek fish is

$$(0.743)(0.0079)/(0.079)(0.0135) = 5.50 \text{ (SE: } 2.59).$$

Production of adults by the hatchery is estimated to be 5 to 6 times that of natural production, although the precision of that estimate is extremely low, as indicated by the standard error–a rough 95% confidence interval would include the possibility that survival from potential egg deposition to adult was smaller for hatchery operations than for natural spawning.

Survival from Marking Effects

Estimates of the initial numbers of unmarked creek and hatchery fry are 68,400 and 495,000, respectively. Unmarked recoveries to the weir totaled 5,545. Survival of marked fry to return at the weir is estimated by the ratios of marked recoveries at the weir (Table 2) to numbers of marked fry released, or 71/5,500 = 0.01291 for creek fry and 644/84,000 = 0.00767 for hatchery fry. Then survival from marking is estimated to be

$$[(68{,}400)(0.01291) + (495{,}000)(0.00767)]/5{,}545 = 0.84.$$

Determination of the precision of the marking mortality estimate was not attempted because of the apparent complexity of the problem.

Fry Size and Developmental Index

Most of the fry from gravel incubators were shorter (Figure 4) but heavier (Figure 5) than creek fry, although there were two exceptions: fry from incubator A had an average weight of 260.0 mg, which was not significantly different from the average weight for creek fry–260.2 mg (Table 3);

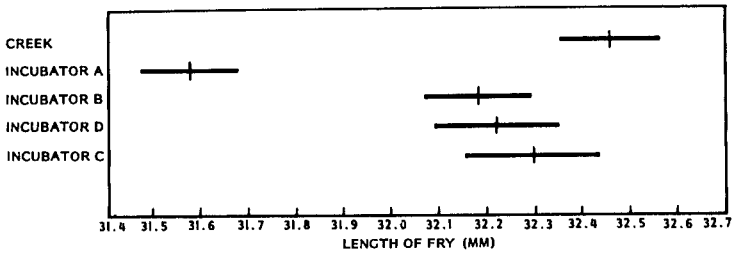

FIGURE 4.–Weighted means and 95% confidence intervals for these means of lengths of preserved fry from Auke Creek and four gravel incubators.

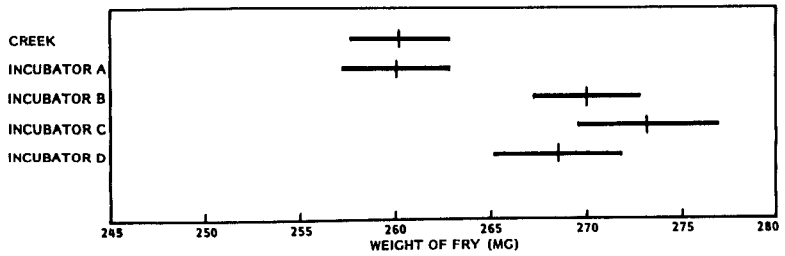

FIGURE 5.–Weighted means and 95% confidence intervals for these means of weights of preserved fry from Auke Creek and four gravel incubators.

TABLE 3.–Pooled means and variances of means for lengths, weights, and development index, K_D, of pink salmon fry (50 fry/sample) at Auke Creek in spring of 1973.

Source	Number of samples	Length (mm) Mean	Length (mm) Variance	Weight (mg) Mean	Weight (mg) Variance	K_D index Mean	K_D index Variance
Creek	13	32.45	0.00272	260.2	1.630	1.964	5.36×10^{-5}
Incubator:							
A	8	31.57	0.00252	260.0	1.917	2.008	5.50×10^{-5}
B	8	32.17	0.00276	269.9	1.856	2.009	5.54×10^{-5}
C	4	32.21	0.00412	273.2	3.352	2.012	9.61×10^{-5}
D	5	32.29	0.00483	268.6	2.714	1.987	9.92×10^{-5}

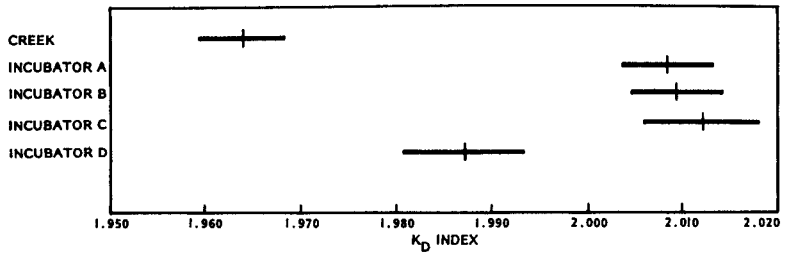

FIGURE 6.–Weighted means and 95% confidence intervals of these means of indices of development, K_D, of preserved fry from Auke Creek and four gravel incubators.

and fry from incubator D had an average length of 32.29 mm, which was not significantly different from the average length for creek fry–32.45 mm.

Indices of development were higher for fry from all the gravel incubators than for creek fry (Figure 6). The mean indices of development for gravel incubator fry ranged from 1.987 to 2.012, whereas the mean for creek fry was only 1.964 (Table 3). In an earlier test (Bailey and Taylor 1974) the average K_D index decreased about 0.005 unit/day in the final stages of alevin development. Since the average K_D index for incubator fry was 0.016 unit higher than the index for creek fry, incubator fry apparently emerged about 3 days earlier in their development.

Time of Emergence and Seaward Migration

Fry of the 1972 brood from the gravel incubators migrated voluntarily between 15 March and 23 May 1973; the median date was 14 April (Figure 7). Creek fry emigrated between 16 March and 15 May; the median date was 27 April (Figure 7).

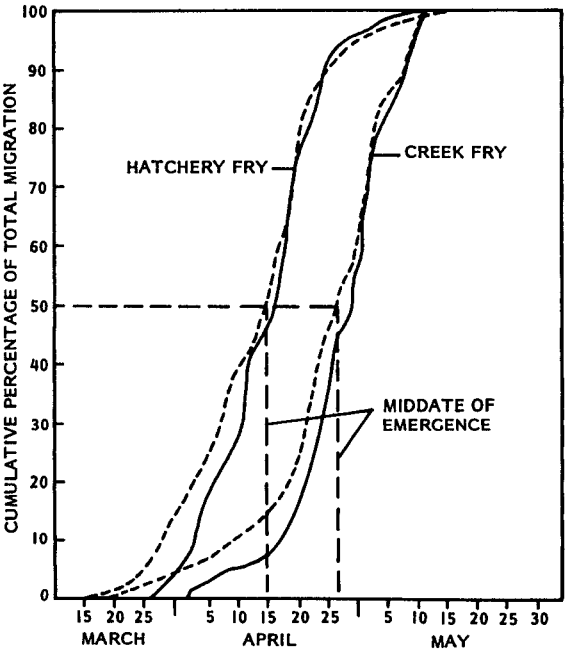

FIGURE 7.–Daily cumulative percentage of pink salmon fry migrations of creek fry and hatchery fry from Auke Creek in 1973; solid lines represent fin-marked fry and dashed lines represent total fry in the respective migrations.

Size of Returning Adults

Length measurements of adults from the 1972 brood that returned to the weir in 1974 are classified by sex, origin (whether creek or hatchery), and time of return (either early or late run). Mean lengths and sample sizes (Table 4) were used as basic observations with which to perform an analysis of variance (Scheffé 1959: 362-363) to search for differences in size among the classifications. Analyses were performed separately for each sex because underlying variances of hatchery fish differed significantly between sexes. Spawning males typically vary more in length than spawning females. The corresponding tests for creek fish did not indicate inequality of vari-

TABLE 4.–Average lengths of adult pink salmon returning to Auke Creek weir, early and late runs; the figures in parentheses represent the number of fish in the samples.

		Average lengths (mm)			
		Early run		Late run	
Mark	Origin	Male	Female	Male	Female
Unmarked	Hatchery and creek	493.1 (117)	495.2 (92)	512.4 (58)	500.8 (137)
Ad-LV[1]	Hatchery	500.2 (126)	499.6 (70)	510.0 (44)	495.6 (44)
Ad-RV[2]	Creek	505.6 (19)	515.9 (7)	515.7 (3)	497.3 (3)

[1]Ad-LV = adipose and left ventral fins.
[2]Ad-RV = adipose and right ventral fins.

ances, probably because of the small sample sizes.

Differences in length due to origin, time of return, or interaction were not detectable at the 95% level of testing for either sex (Table 5). Only time of return for females approached statistical significance (the test would have been significant at the 90% level). Mean lengths of samples of creek fish exceeded those of hatchery fish in all cases (Table 4). While our data suggest that creek fish were larger than hatchery fish upon return, the observed differences could be due to chance when samples were drawn. Larger samples would have been needed to resolve the issue.

TABLE 5.–Analysis of variance of size of returning adult male and female pink salmon classified by origin (creek or hatchery) and time of return (early or late).

Source	Degrees of freedom	Mean square	*F*
Males:			
Origin, A	1	30.8025	<1
Timing, B	1	99.0025	<1
AB	1	0.0225	<1
Error	188	161.543	—
Females:			
Origin, A	1	81.000	2.09
Timing, B	1	127.690	3.30
AB	1	53.290	1.38
Error	120	38.739	—

Timing of Adult Return

Marked hatchery fish entered the weir between 6 August and 25 September and marked creek fish entered between 16 August and 20 September (Figure 8). For 644 marked hatchery fish the median date of return was 13 September 1974; for 71 marked creek fish the median date was 10 September.

DISCUSSION

Gravel incubation of eggs and release of unfed fry increased the survival from potential egg deposition to returning adult an estimated 5 to 6 times over natural spawning for 1972 brood year pink salmon at Auke Creek. The estimate lacks precision, however, and a rough 95% confidence statement includes the possibility that egg-to-returning-adult survival was less for incubator fry than for naturally produced fry. Further, the estimate of relative survival is potentially biased unless marine mortality due to marking and fishing was similar for both groups of marked fry. The similarity of timing of adult returns from both groups gives no reason to suspect differential fishing mortality. The low mortality of creek fry in the fyke net and live-box suggests only slightly greater physical abuse occurred to marked creek fry than hatchery fry. The difference in survival from potential egg deposition to returning adult, if real, was accomplished in spite of certain deficiences in the quality of environment provided for eggs and alevins in the hatchery and in spite of

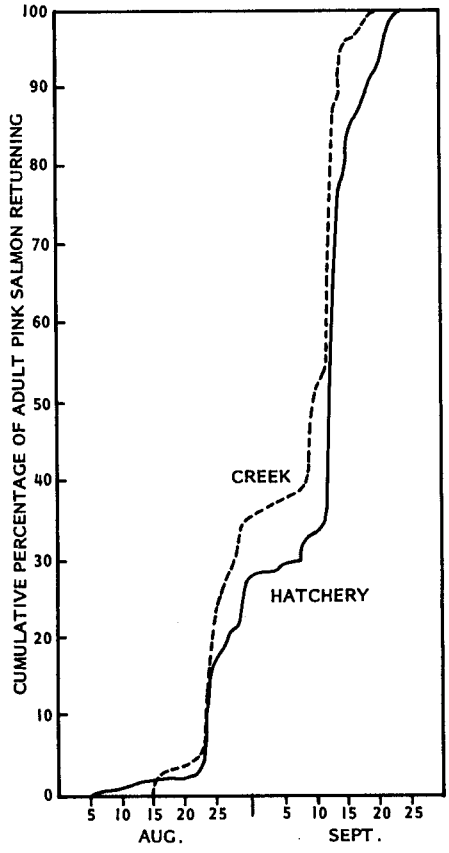

FIGURE 8.–Daily cumulative percentage recovery of marked adult pink salmon at Auke Creek weir, 1974.

a lower ocean survival for hatchery fry than for creek fry.

There is a notable difference in survival from marking in the tests at Auke Creek and the tests by Bams (1972, 1974) at Headquarters Creek, Vancouver Island. The estimate of survival from marking at Auke Creek, 84%, is much greater than the 17% and 36% survival we estimated from Bams' data on Headquarters Creek. Intertidal alevin production in Auke Creek below the weir was estimated by hydraulic pump survey to be 16% of that above the weir. Possible straying of these intertidal fish above the weir upon return would only bias our estimate below actual survival from marking. The slower rate at which our technicians clipped fins may be the cause of better survival from marking at Auke Creek.

Our estimates of fry releases and survivals imply that an increase in numbers of returning spawners at Auke Creek in 1974 was largely due to operation of the hatchery. If this is true, then hatcheries can be built on lake-water sources with a reasonable expectation of successfully enhancing salmon numbers. Projections of our data must be considered tentative because of the lack of precision. However, the magnitude of the Auke Creek escapement in relation to escapements to other streams in northern southeastern Alaska supports our conclusion that operation of the Auke Creek Hatchery did in fact enhance the return of adult salmon. For example, marked hatchery fry had a recovery rate of 0.767%. Survival from marking was 84%. The release of 579,000 hatchery fry would project to (579,000)(0.00767)/0.84 = 5,287 adults. The projected return of creek fry would be (84,000)(0.01291)/0.84 = 1,291 adults. In 1974, 6,260 adults returned to the Auke Creek weir from a parent escapement of 1,768 adults. This 3.5-fold increase occurred in the face of a general scarcity of pink salmon in this part of Alaska. According to Kingsbury (1975) the lowest escapement for pink salmon streams of northern southeastern Alaska since 1960 occurred in 1974.

The yolk content of fry when they leave the incubating bed, either natural or artificial, bears directly on the survival of the fry in the wild. Fry with a large amount of yolk have not attained their maximum potential size, are relatively poor swimmers, may not be able to osmoregulate in seawater, and are more vulnerable to predators. On the other hand, fry that have little or no yolk are losing weight and soon become weakened and emaciated and again are more vulnerable to predators. Naturally produced fry emerge volitionally from the stream gravel, presumably at the stage of development that ensures maximum survival. Our analysis of the developmental index showed our gravel incubator fry emerged prematurely in comparison to creek fry.

Earlier (in the temporal sense) emergence of fry produced in gravel incubators at Auke Creek also suggests that the Auke Creek Hatchery environment was inferior to the natural streambed environment. Hatchery fry emerged and migrated seaward 2 wk earlier than creek fry. This could place them in the estuary before the spring bloom of zooplankton on which they feed and before spring warming of estuarine surface water. The resulting slow growth rate could mean an excessively long period of high vulnerability to predators. Experiments by others (Levanidov 1964; Bams 1967; Kanid'yev et al. 1970; Parker 1971) show that small juvenile salmon suffer higher mortality from predation than large juvenile salmon.

The earlier time of migration and size of hatchery fry at Auke Creek were probably caused by one or more of the following: the higher average winter temperature of Auke Lake water (4°C) as compared to the temperature in natural redds in Auke Creek (0°-2°C); the low oxygen content of 60-70% saturation in lake water supplied to incubators; and the brown organic material from iron bacteria which accumulated in the gravel incubators and impeded the flow of water.

ACKNOWLEDGMENTS

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LITERATURE CITED

BAILEY, J. E., AND S. G. TAYLOR.
1974. Salmon fry production in a gravel incubator hatchery, Auke Creek, Alaska, 1971-72. U.S. Dep. Commer., NOAA Tech. Memo. NMFS ABFL-3, 13 p.

BAMS, R. A.
1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. 24:1117-1153.

1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish. Res. Board Can. 27:1429-1452.

1972. A quantitative evaluation of survival to the adult stage and other characteristics of pink salmon (*Oncorhynchus gorbuscha*) produced by a revised hatchery method which simulates optimal natural conditions. J. Fish. Res. Board Can. 29:1151-1167.

1974. Gravel incubators: a second evaluation on pink salmon, *Oncorhynchus gorbuscha*, including adult returns. J. Fish. Res. Board Can. 31:1379-1385.

BURROWS, R. E.

1951. Method for enumeration of salmon and trout eggs by displacement. Prog. Fish-Cult. 13:25-30.

DEMING, W. E.

1943. Statistical adjustment of data. John Wiley & Sons, Inc., N.Y., 261 p.

KANID'YEV, A. N., G. M. KOSTYUNIN, AND S. A. SALMIN.

1970. Hatchery propagation of the pink and chum salmons as a means of increasing the salmon stocks of Sakhalin. J. Ichthyol. 10:249-259.

KASAHARA, H.

1963. Catch statistics for North Pacific salmon. Int. North Pac. Fish. Comm., Bull. 12:7-82.

KINGSBURY, A. P.

1975. Salmon strategy, tight management for southeastern pinks. Alaska Fish Tales and Game Trails 9(6):1, 14-15.

LEVANIDOV, V. YA.

1964. O zavisimosti mezhdu razmerami mal'kov Amurskoi osennei kety *Oncorhynchus keta* infrasp. *autumnalis* Berg i ikh vyzhivaemost'yu. Vopr. Ikhtiol. 4:658-663.

MCNEIL, W. J.

1964. A method of measuring mortality of pink salmon eggs and larvae. U.S. Fish Wildl. Serv., Fish. Bull. 63:575-588.

PARKER, R. R.

1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28:1503-1510.

PAULIK, G. J., AND D. S. ROBSON.

1969. Statistical calculations for change-in-ratio estimators of population parameters. J. Wildl. Manage. 33:1-27.

SCHEFFÉ, H.

1959. The analysis of variance. John Wiley & Sons, Inc., N.Y., 477 p.

SEIBEL, M. C., AND C. P. MEACHAM (editors).

1975. A summary of preliminary 1975 forecasts for Alaskan salmon fisheries. Alaska Dep. Fish Game, Inform. Leafl. 167, 55 p.

SNEDECOR, G. W.

1956. Statistical methods applied to experiments in agriculture and biology. 5th ed. Iowa State Coll. Press, Ames, 534 p.

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COMPARISON OF THE MOST SUCCESSFUL AND LEAST SUCCESSFUL WEST COAST ALBACORE TROLL FISHERMEN

DONALD F. KEENE[1] AND WILLIAM G. PEARCY[2]

ABSTRACT

Catch data for albacore troll boats were collected from fishermen's logbooks and from dockside interviews during the 1968, 1969, and 1970 seasons. Fishing powers of these boats were calculated and used to determine the 10 most successful and 10 least successful fishermen (highliners and lowliners, respectively) who fished off Oregon and Washington. Characteristics of these two groups of fishermen were then compared. In general, highliners had longer boats and fished nearer the fleet center and along the offshore margin of the fleet. Lowliners tended to have smaller boats and fished along the trailing (south) inshore margin of the fleet. Both groups responded to changes in apparent albacore abundance by aggregating on days of high apparent abundance, although this response was less pronounced in 1969 and 1970. Highliners caught significantly smaller (but more) fish than the lowliners.

The west coast albacore troll-boat fleet consists of many types and sizes of vessels (Clemens 1955). Troll boats range in length from about 10.7 m (35 feet) to over 22.9 m (75 feet) with a displacement of about 15 tons. Part of this fleet begins fishing for albacore off the coast of Baja California in early summer. During the peak of the season (July, August, September) boats may be found from Mexico to the Gulf of Alaska. However, the most productive area usually lies between central Baja California and the Columbia River (Clemens 1961). Many boats, particularly those from Oregon and Washington, fish for other species (salmon, crab, shrimp) during part of the year (Roberts 1972) and occasionally during the albacore season when albacore fishing is slow.

Fishermen in the albacore fleet exhibit a large range of fishing success. Fishing success has been related to strictly physical parameters of the vessel, such as boat length (Fox[3]). Abramson (1963) suggested that fishing success is related to the skill and experience of the captain and crew, as well as the physical parameters of the boat. Little is known, however, about how fishing success is related to the activities of individual albacore fisherman and the activities of the surrounding fleet. (The fleet is considered to be an assemblage of fishing boats within an area of arbitrarily chosen size.) The objective of this paper is to describe and compare the characteristics and movements of the most successful with those of the least successful albacore fishermen during the 1968, 1969, and 1970 seasons.

METHODS

Sources and Treatment of Data

Information on number of fish caught per day by troll boats, location of the catch, boat length, and number of lines (1970 only) was collected from three sources for the 1968, 1969, and 1970 albacore seasons: 1) logbooks distributed by Oregon State University (1969 and 1970), 2) logbooks distributed by California Department of Fish and Game to fishermen who volunteered to submit daily information, and 3) interviews obtained by personnel of the Oregon Fish Commission at dockside during unloading of the albacore. Careful screening avoided duplication of logbook records since vessels often submitted records to more than one source. Only catch locations between lat. 42° and 49°N were used.

The number of reporting boats varied considerably between years. In 1968, 205 boats reported their daily catches and locations. In 1969 and 1970, 70 and 113 boats, respectively, reported. The total number of boats fishing during the 3 yr is unknown but is estimated to have been between 750 (Panshin 1971) and 1,000.

Data from the logbooks and interview sheets

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[3]Fox, W. W. "Fishing power of U.S. vessels participating in the Pacific coast albacore fishery 1961-1970." Paper presented at the 24th Tuna Conference, Lake Arrowhead, Calif., Oct. 1973.

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were punched on computer cards. Each card contained three pieces of information: the boat number, an area-data code (signifying the 1° latitude by 1° longitude rectangle and the calendar day), and the boat's catch of the day. There were approximately 3,300 observations in 1968, 1,500 in 1969, and 1,000 in 1970.

A particular boat was chosen to represent the standard unit of effort. Criteria for the standard boat choice included the following: it fished 1) during all three seasons; 2) in area-date strata concurrently with a majority of the fleet; 3) most of each season; and 4) consistently to provide a standard, nonvarying reference for the other boats.

Estimates of fishing power[4] of all boats in the fleet were initially determined relative to the standard boat. This was accomplished using a computer program called FPOW (Berude and Abramson 1972). FPOW utilizes Robson's (1966) linear two-factor analysis model for estimating the relative fishing power of fishing vessels. The estimates of fishing power derived from the model are logrithms. FPOW provides an approximate correction for this bias using a Taylor series expansion of the estimate about its true value. The method and assumptions used in FPOW are described in Robson (1966) and Abramson and Tomlinson (1972:1022-1023). The program's storage capacity was limited to 2,000 catch observations from a combined total of not more than 200 distinct boats and area-date strata. Data for each year were broken up into time segments short enough to satisfy this limitation. Ten segments were required in 1968, five in 1969, and three in 1970. Each segment was run independently and provided estimates of each boat's relative fishing power during the time segment.

Considerable within-season variation occurred in the average fishing power of the fleet (Table 1), suggesting that the standard boat fished inconsistently relative to the fleet. An examination of the logbooks showed that the standard boat occasionally experienced periods of very low catches (10 to 15 fish per day) while the majority of the fleet in the immediate area was catching 100 to 200 fish per boat. This was particularly obvious during segment 1 of the 1969 season.

As a result of the standard boat's inconsistent fishing, values of standardized catch per boat day were also inconsistent between data segments. For example, an average boat had fishing powers of 3.70 and 1.01 on 25 July and 26 July 1969, respectively (Table 1). If the average boat caught 100 fish on 25 July and 100 on 26 July 1969, values of standardized catch per boat day (100 fish/average fishing power) would be 27 and 99, respectively, for these 2 days. Therefore a serial examination of apparent abundance could not be performed without normalizing fishing power estimates of each boat in each data segment.

Fishing power estimates were normalized by subtracting the appropriate segment's average fishing power from each boat's fishing power and adding unity. (By definition the standard unit of effort is 1.0.) Each boat's fishing power estimate was now relative to the average fishing power of all boats fishing during the data segment. This procedure required the assumption that the fleet fished consistently relative to the standard boat throughout each season.

Daily standardized catch per boat within each area-date stratum was determined by summing the fish catches and dividing by the summation of fishing power in that area-data stratum. The standardized catch per boat day is an index of

TABLE 1.—Data segments for the 1968, 1969, and 1970 albacore seasons.

Segment	Dates	No. of obs.	No. of boats	No. of area-dates	Average fishing power
1968:					
1	6-16 July	242	60	47	0.69
2	17-21 July	320	85	34	1.14
3	21-31 July	410	74	76	0.99
4	1-4 Aug.	357	109	45	0.91
5	5-7 Aug.	290	108	33	0.70
6	8-11 Aug.	310	100	39	0.88
7	12-18 Aug.	420	88	78	0.82
8	19-24 Aug.	373	82	69	1.03
9	25-30 Aug.	235	72	46	0.53
10	31 Aug.-10 Sept.	385	70	113	0.99
1969:					
1	15-25 July	305	51	59	3.70
2	26 July-3 Aug.	374	66	60	1.01
3	4-11 Aug.	326	65	59	1.15
4	12-18 Aug.	212	56	63	1.47
5	19 Aug.-11 Sept.	296	40	111	1.16
1970:					
1	15-22 July	160	52	64	0.35
2	23-28 July	470	99	54	0.91
3	29 July-2 Sept.	262	65	86	0.67

[4]Fishing power is defined (Beverton and Holt 1957:172) as the ratio of the catch per unit of fishing time of a particular vessel to that of another vessel designated as the standard. It is assumed that both boats must have fished on the same density of fish during the same time interval and within the same fishing area when the ratio is determined. Fishing success, on the other hand, is related to fishing power but is more descriptive. It includes parameters difficult to quantify. For example, fishing success may include crew motivation, attitude, and access to useful information. Together with fishing power, these parameters are determinants of fishing success.

apparent abundance, the latter being a function of the accessibility of the albacore to the boats, the vulnerability of the fish to the lures (Marr 1951), and the true abundance of albacore.

The 10 most successful and 10 least successful fishermen (highliners and lowliners, respectively) of each season were selected according to their boats' average fishing power estimates throughout the entire season. Highliners and lowliners selected had fished for at least 15 days in 1968 and 1969 and 8 days in 1970. Thus fishermen who fished exceptionally well or poorly for only a few days in a season were not considered.

Area-Date Stratum of Apparent Abundance

Small-scale time and space information of catches and boat positions allowed a departure from the traditional time-area stratum of 1 mo and 1° latitude-longitude rectangle (Ayers and Meehan 1963; Clemens and Craig 1965). A mobile stratum was conceived to allow comparisons of apparent abundance and effort regardless of where the fleet moved, and without the problems of fixed geographic boundaries.

The new stratum was a circular area, the center being the daily medial location of the fleet. This medial point was determined such that the fleet was equally divided in the north-south and east-west planes. Criteria for the radius of the circular area were that it should be 1) as small as possible to include a homogeneous distribution of fish, but 2) large enough to accommodate a sufficient number of boats fishing on a given day so that catch and effort could be reliably estimated, and 3) large enough to give reasonable assurance that boats within the area remained in the area the entire day. Because of the lack of knowledge of small-scale albacore distributions, there was little basis for satisfying the first criterion.

Consecutively larger concentric circles were drawn around the medial point while noting the ratio of boats within each circle to the number of boats in the entire fleet. (Danils (1952) has presented theoretical considerations of sample point distributions within such circles.) During much of each season, over half the boats could be found within 25 miles of the fleet's center. Exceptions occurred in each season when the fleet was highly dispersed or split into two distinct groups. Two distinct groups of boats occurred on 2, 3, and 4 August 1968 and also 1, 2, and 8 August 1969. During these days the northernmost center was chosen to represent the fleet center because it always contained more boats.

The third criterion suggested a radius of at least 31 miles to insure that vessels remained within the area the entire day. This radius was determined on the basis of distances traveled daily by albacore boats. (This is reported later in this study.) A circle with a radius of 31 miles was therefore used as the area size. Figure 1 shows the percentage of boats that provided catch data within 31 miles of the fleet center each day during the 1968, 1969, and 1970 seasons. Only the time periods within the vertical lines in Figure 1 will be considered for this study. On days outside these periods few boats reported their catch, or the fleet was small and highly dispersed. The average daily percentage of those boats reporting within 31 miles of the fleet center was 46%, 57%, and 65% for the 1968, 1969, and 1970 seasons, respectively. The differences between the 1968 average and the 1969 and 1970 averages were highly significant (t-test, $P<0.01$), indicating that the 1968 fleet was more dispersed in general than the 1969 and 1970 fleets. (This was not a result of a greater number of boats reporting in 1968 because the number of boats reporting per day was often greater in 1969 and 1970 than in 1968.) There was a tendency in both 1968 and 1969

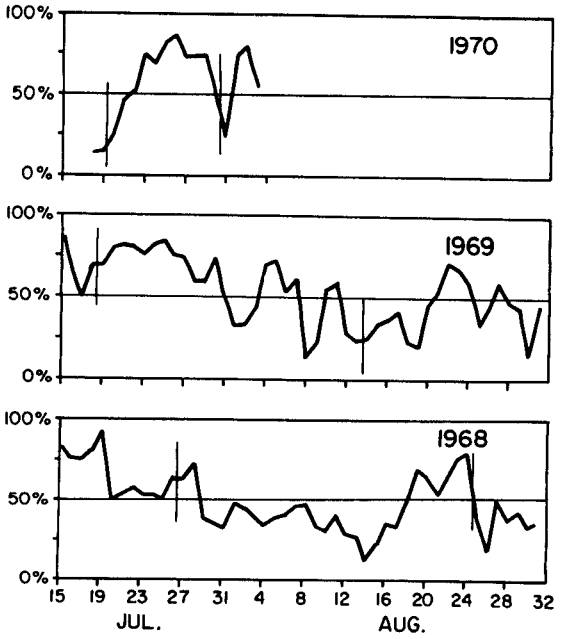

FIGURE 1.—Daily percentage of boats within 31 miles of the albacore fleet center; 1968, 1969, and 1970. Vertical lines on plots indicate the time periods considered in detail in this study.

for the fleet to become more dispersed as the season progressed.

Aggregation of the Boats

The index of aggregation used in this study was the mean separation distance of boats within a specified area. The index was determined by summing separation distances between all boats in the area and dividing this sum by the number of separation distances. This calculation required converting LORAN coordinates (given as the 2100 h PDT boat positions) to latitude-longitude coordinates. Accuracy of the iterative technique used to compute the coordinates has been estimated at 10 m (Thomas 1965:7-9, 38-52), although the absolute position accuracy varied considerably due to the precision of the LORAN operator and the distance from the LORAN transmitters. Boat positions reported at 2100 h within 200 miles of the coast are estimated to be within 3 miles of the absolute positions.

Hunter (1966) stated that mean separation distance is preferred for measuring relative changes in spacing, but for comparison of samples containing different numbers of individuals, mean distance to nearest neighbor (Clark and Evans 1954) should be used. We did not use mean distance to nearest neighbor because most fishermen fish together with one or more companion boats. Mean distance to nearest neighbor would thus represent the average distance separating the same groups of boats and would give little if any information on actual compactness of the fleet within a specified area.

RESULTS AND DISCUSSION

Fishing Power Versus Boat Length and Number of Lines

Sixty-six area-date strata (1° latitude by 1° longitude rectangles and 1-day periods) were selected to examine the relationship between the fishing power of a boat and its length and number of lines trolled. All strata had at least 20 boats reporting within them. (The new mobile stratum was not used here because the intent was to partition the fishery area into a number of equal quadrats, the size and location of the quadrat being of no consequence. Daily boat positions had been assigned to 1° longitude rectangles by FPOW, so this stratum was used for convenience.)

Fishing power estimates were then regressed on boat length and number of lines. (Data on number of lines were available only for the 1970 season.) In none of the strata, in any season, was a significant regression (F-test, $P < 0.05$) found. This indicated that no significant relationship existed between a vessel's fishing power and its length or reported number of lines trolled within a given 1° by 1° rectangle during any given day.

Because of the scatter of data for small-scale time and area strata, the above conclusion did not rule out the possibility of a significant relationship between fishing power and boat length or number of lines. Therefore, a larger stratum was chosen which included all data for each year. Fishing power estimates were again regressed on boat length (1968, 1969, 1970) and number of lines (1970). The results are shown in Table 2.

Boat length was significantly related ($P<0.05$) to fishing power of albacore boats in a time-area stratum of one season and the entire fishery, particularly in 1968. The significance of boat

TABLE 2.—Regression equations and analysis of variance data for boat length (in meters) and number of lines (1970) versus boat fishing power.

1968	Fishing power = 0.238 + 0.046 (boat length) FP (12.2-m boat) = 0.798 FP (18.3-m boat) = 1.078			
Source	df	Sum of squares	Mean square	F value
Total	810	185.459	0.229	
Regression	1	13.835	13.835	
Residual	809	171.624	0.212	65.23**
1969	Fishing power = 0.263 + 0.049 (boat length) FP (12.2-m boat) = 0.863 FP (18.3-m boat) = 1.163			
Source	df	Sum of squares	Mean square	F value
Total	271	165.265	0.610	
Regression	1	3.214	3.214	
Residual	270	162.051	0.600	5.35*
1970	Fishing power = 0.636 + 0.022 (boat length) FP (12.2-m boat) = 0.916 FP (18.3-m boat) = 1.056			
Source	df	Sum of squares	Mean square	F value
Total	200	24.777	0.129	
Regression	1	0.698	0.698	
Residual	199	24.079	0.121	5.76*
	Fishing power = 0.816 + 0.018 (number of lines) FP (8 lines) = 0.960 FP (12 lines) = 1.032			
Source	df	Sum of squares	Mean square	F value
Total	200	24.777	0.139	
Regression	1	0.110	0.110	
Residual	199	24.667	0.124	0.89 ns

** significant at the 0.01 level.
* significant at the 0.05 level.
ns nonsignificant.

length as it related to fishing power was considerably less in 1969 and 1970 than in 1968, although the 1968 and 1969 regression equations were nearly identical.

Fox (see footnote 3) reported that fishing power of albacore troll boats was related to boat length in a curvilinear manner for the 1961-70 period, with boats of the length class 12.2 to 14.9 m exhibiting the highest estimates of fishing power. There was no clear indication of a curvilinear relationship in 1968, 1969, or 1970, although several very long boats (>22.9 m) generally did not have as large fishing powers as the linear relationship predicted, thus supporting Fox's conclusions. The sample of boats used by Fox was considerably larger (10 yr) and therefore had many more observations of longer boats than used in this study.

Large boats, moreover, make up a minor portion of the albacore fleet. The average length (and standard deviation) of the sample of boats in 1968, 1969, and 1970 was 14.9 m (2.7), 14.9 m (2.1), and 15.2 m (2.7), respectively. Some fishermen feel that larger boats are more successful because of their increased seaworthiness and endurance, resulting in fewer trips to port and permitting more time on the fishing grounds. Fishermen also feel that larger boats fish the lures better in rough weather. Whereas smaller boats tend to jerk the lures as the waves hit the boats, larger boats push smoothly through the waves with less jerking of the lures.

The reported number of lines trolled in 1970 was not significantly related to fishing power. The number of lines reported varied from 6 to 14, with 10 being the mean and mode. The standard deviation was 1.0. The number of trolling lines reported on log sheets bears little resemblance to the number of lines used during varying periods of fishing activity, according to fishermen. When fishing activity increases, only two or possibly three lines are pulled by each man. During periods of intense activity, each man may only handle one line, although periods of intense activity are usually of very limited duration. When the catch rate increases, the longest lines are pulled on board first and only the short lines are fished. One fisherman stated that the number of lines used was determined primarily by the ability of the crew in avoiding tangling of lines. However, over 90% of the 1968 logbooks (in which crew size was recorded) indicated a crew size of two. It would appear that the possible increase in catch as a result of a larger crew size during the infrequent periods of intense fishing activity are offset by the increase in financial cost of a larger crew size. This is even more apparent considering that a daily catch of 180 fish (i.e., about 5 fish per hour per man for a two-man crew) is considered a very good catch by an albacore fisherman.

Comparison of Highliners and Lowliners

Some comparisons of highliner and lowliner boats are given in Table 3. Both groups fished approximately the same number of days and in the same period each season. The difference in boat length was highly significant in all years, particularly in 1968 when highliner boats averaged 4.9 m longer than lowliner boats. In 1969 and 1970 only 1.5 m separated the average length of highliner and lowliner boats. Seven of the 1968 highliner boats were over 15.5 m, whereas none of the 1969 and only one of the 1970 highliner boats were over 15.5 m. Essentially the same proportions of 15.5 m and longer boats made up the fleet samples in each season. Lowliner boat lengths were consistently short, between 14.0 and 15.2 m.

Lowliners often fished along the trailing margin of the fleet during all years as the fleet moved to the north. Highliners were more centrally located in the fleet and along the offshore or leading margin, as shown in Table 3. In 1968 lowliners were removed from the main body of the fleet, generally located far to the south and inshore of the fleet, whereas highliners tended to be slightly to the south but offshore of the main fleet center. In 1969 and 1970 both groups were located closer to the fleet center, although the lowliners were still three to four times farther away from the fleet center than were highliners. Lowliners fished consistently south of the center in all 3 yr.

A detailed description of the location of highliners and lowliners is presented in Figures 2-4.

TABLE 3.—Comparison of highliners with lowliners, west coast albacore trollers.

Item	1968	1969	1970
Average boat length (m):			
Highliners	19.2	15.5	16.2
Lowliners	14.3**	14.0**	14.6**
Average distance to fleet center (miles):			
Highliners	30 SW	5 W	8 N
Lowliners	104 SSE	22 SW	25 S
Average daily travel (miles):			
Highliners	21	26	27
Lowliners	31**	29 ns	28 ns
Average relative fishing power:			
Highliners	1.61	1.57	1.24
Lowliners	0.65	0.46	0.85

** significant at the 0.01 level, *t*-test.
ns nonsignificant.

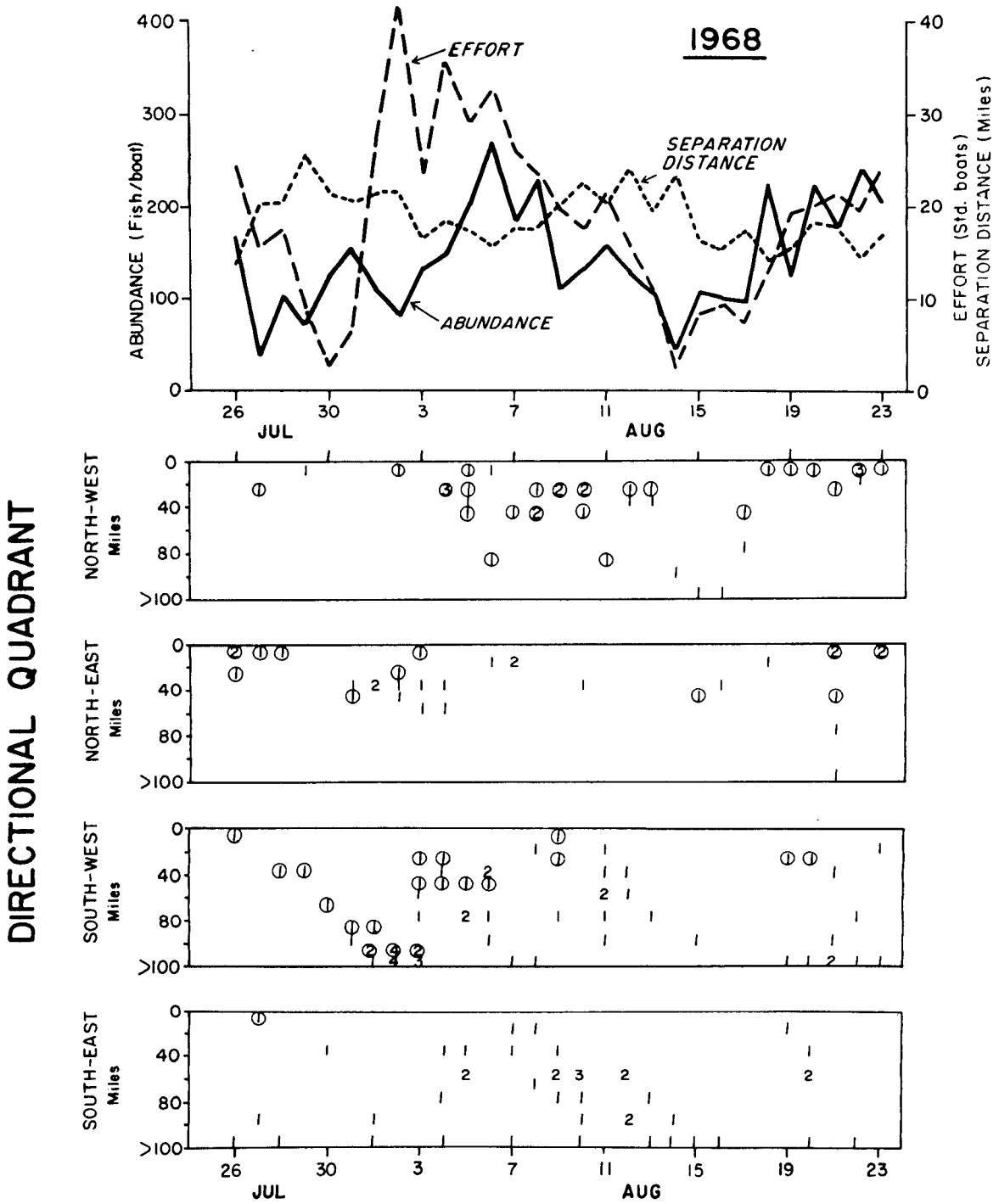

FIGURE 2.—Locations of 1968 highliners and lowliners relative to the center (medial) of the fleet. The top graph indicates the corresponding levels of apparent abundance of albacore, fishing effort, and boat separation distance within 31 miles of the fleet center. The lower four plots show the distance of highliners (circled numbers) and lowliners (noncircled numbers) from the medial fleet center.

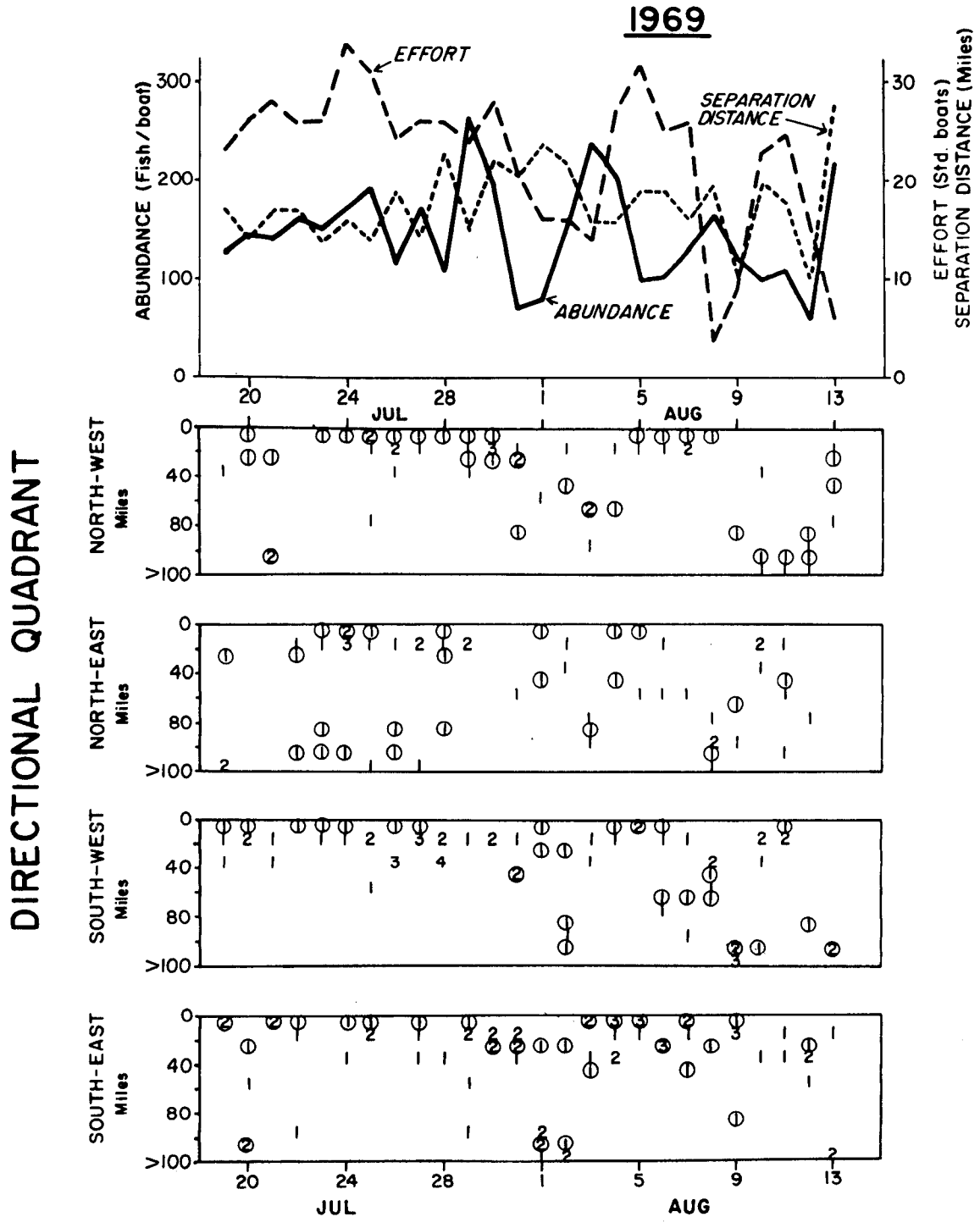

FIGURE 3.—Locations of 1969 highliners and lowliners relative to the center (medial) of the albacore fleet. See Figure 2 for explanation of plots.

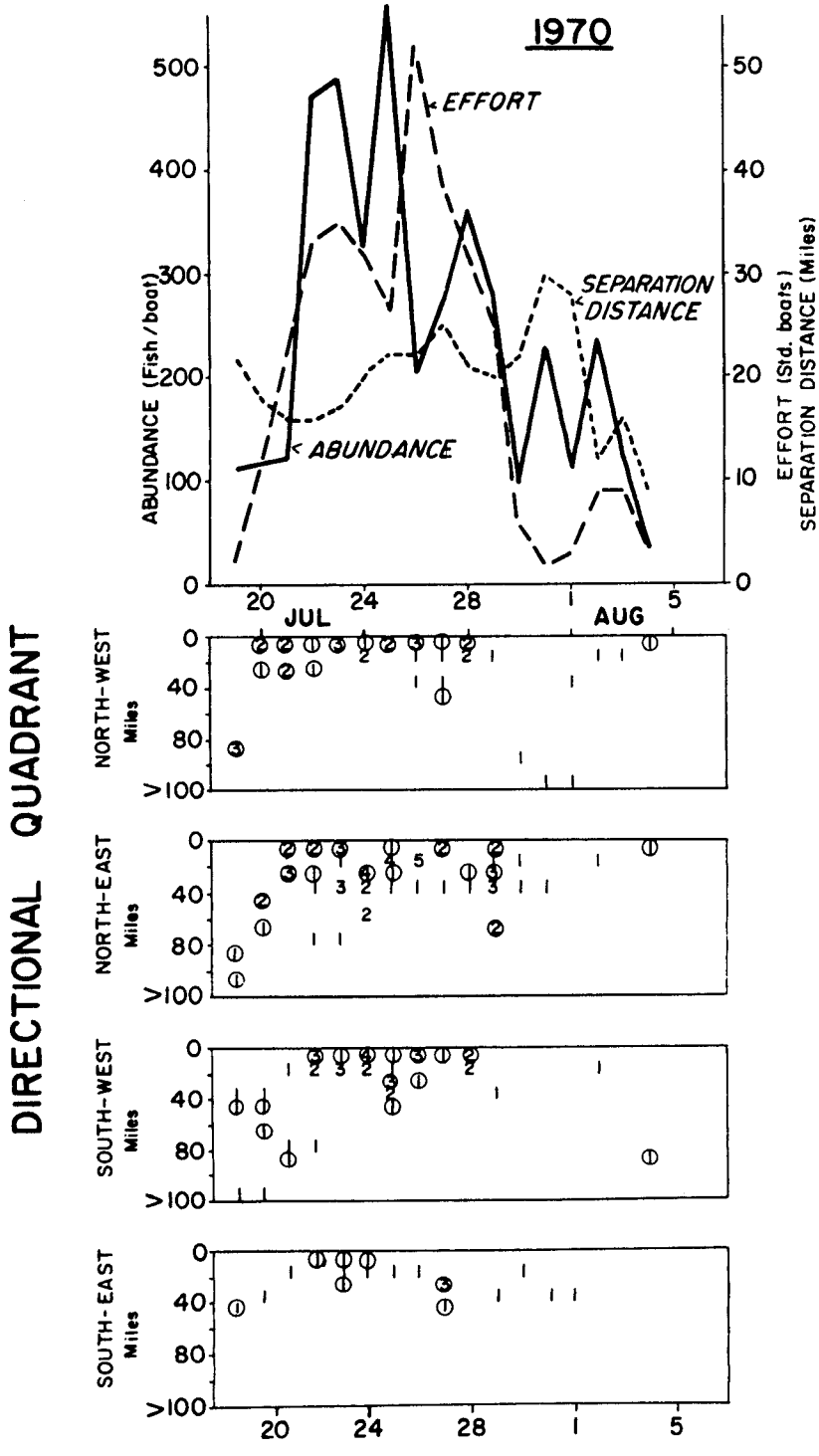

FIGURE 4.—Locations of 1970 highliners and lowliners relative to the center (medial) of the albacore fleet. See Figure 2 for explanation of plots.

The plots show where these two groups fished with respect to the fleet center during periods of variable levels of albacore abundance, fishing effort, and boat separation distance (shown at the top of the figures).

A very obvious separation of highliners and

lowliners occurred in 1968 (Figure 2). Highliners fished almost exclusively to the northwest and southwest of the fleet center. When abundance was low and effort high (26 July-3 August), highliners moved far from the fleet center, as seen in the southwest quadrant. During 5 and 6 August, when high catches coincided with high levels of effort, highliners were found close to the fleet center, but not as close as during periods of low effort. Lowliners fished mainly to the south and away from the fleet center during all levels of abundance. When abundance was high (5-8 August), lowliners in the southeast quadrant moved closer to the fleet center. Later as catches declined, the lowliners moved away from the center (southeast quadrant, 9-15 August).

There was no obvious separation of highliners and lowliners in 1969 (Figure 3) comparable to 1968. Highliners fished in all quadrants, as did lowliners. Some highliners fished away from the fleet center during periods of low abundance (31 July-2 August; 5-12 August), particularly in the northwest and southwest quadrants when effort was high (10-12 August). Lowliners again fished more in the southern quadrants than did highliners but not exclusively so and not as far from the fleet center as in 1968. In fact, most lowliners were located near the fleet center until all catches began decreasing after 5 August. Then, some lowliners moved away from the fleet (southwest, northeast; 10-11 August) but the majority remained near the fleet center.

The short 1970 season provided little information on the responses of highliners and lowliners (Figure 4). As the season began (19-21 July) highliners were fishing at some distance from the fleet center. During the period of very high catches (22-29 July) both highliners and lowliners fished within 40 miles of the fleet center. No boat reported a location farther than 80 miles from the center during this time. There was no indication that either group dispersed in response to the high levels of effort and aggregation of boats which occurred. On 22 July, when separation distance was lowest and on 26 July when effort was highest, most highliners were fishing within 20 miles of the fleet center.

Most highliners did not fish Oregon waters after 30 July, the day catches dropped precipitously. The lowliners that stayed were northwest of the fleet center. Catches never returned to their original high levels, and on 4 August the season was essentially over for the troll boats.

Some albacore fishermen believe that large numbers of small fish are located in the offshore fishing area and that highliners are able to exploit these fish to a greater degree because of their greater endurance and seaworthiness. To test this hypothesis, the average weight of each fish per trip reported by highliners during July and August was compared with the average fish weight per trip for lowliners. The results, given in Table 4, show that highliners caught significantly smaller fish than lowliners. This supports the fishermen's belief that smaller fish are found along the offshore margins of the fishery where highliners often fish, while larger fish are found along the inshore margins of the fishery where lowliners expend more effort.

The difference between average daily net travel of highliners and lowliners, based on 2100 h PDT positions, changed significantly within the 3 yr. Highliners in 1968 moved 10 miles less per day than did lowliners (Table 3). In 1969 and 1970 there was no statistical difference between the average distance traveled by the two groups. Travel distances in Table 3 can be compared with the daily travel of the fleet center (Figure 5). The fleet center moved an average of 14 miles per day in 1968, 29 miles per day in 1969, and 29 miles per day in 1970. Highliners moved in a much closer relationship with the fleet in 1968 than did lowliners. Lowliners in 1968 traveled twice as far as the general fleet, yet lagged behind the fleet's northerly movement. This was much less apparent in 1969 and 1970.

A comparison of average relative fishing powers showed that highliners of 1968 and 1969 were about three times more successful than lowliners in catching fish (Table 3). Lowliner fishing power decreased in 1969, even though lowliner and highliner boat lengths and daily distances traveled were similar. In 1970 lowliner and highliner characteristics were quite simlar to those of 1969, except for calculated fishing power. In 1970 fishing power of lowliners increased while that of highliners decreased. This was probably due to the

TABLE 4.—Average weight (kilograms) of individual albacore per trip taken by highliners and lowliners during July and August 1968, 1969, and 1970.

Year	Highliners	Lowliners
1968	5.7	6.2*
1969	6.0	6.4**
1970	6.1	6.8*

* significant at the 0.05 level.
** significant at the 0.01 level.

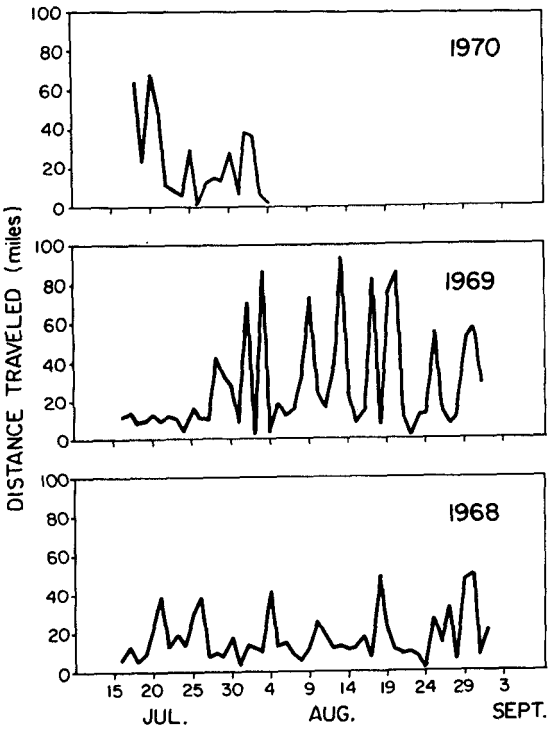

FIGURE 5.—Net daily movement of albacore fleet centers—1968, 1969, and 1970.

extremely short season on highly vulnerable fish, a situation which did not provide highliners the opportunity to utilize their capabilities and fully develop their tactics and strategies.

This study has shown that the most successful and least successful fishermen can be characterized by their activities as well as by the physical parameters of their vessels. Success is not assured by many years of experience, or by a large vessel, although these characteristics are often associated with the most successful fishermen. We agree with Abramson's (1963) suggestion that the fishing power of individual albacore boats is related to intrinsic factors of the captain and crew, in addition to the boat's physical parameters.

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LITERATURE CITED

ABRAMSON, N. J.
1963. A method for computing estimates and variances of relative log fishing powers of California albacore vessels. *In* H. Rosa, Jr. (editor), Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, p. 1209-1215. FAO Fish. Rep. 6.

ABRAMSON, N. J., AND P. K. TOMLINSON.
1972. An application of yield models to a California ocean shrimp population. Fish. Bull., U.S. 70:1021-1041.

AYERS, R. J., AND J. M. MEEHAN.
1963. Catch locality, fishing effort, and length frequency data for albacore tuna landed in Oregon, 1951-60. Oreg. Fish. Comm., Invest. Rep. 2, 180 p.

BERUDE, C. L., AND N. J. ABRAMSON.
1972. Relative fishing power, CDC 6600, FORTRAN IV. Trans. Am. Fish. Soc. 101:133.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 19, 533 p.

CLARK, P. J., AND F. C. EVANS.
1954. Distance to neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

CLEMENS, H. B.
1955. Catch localities for Pacific albacore (*Thunnus germo*) landed in California, 1951 through 1953. Calif. Dep. Fish Game, Fish Bull. 100, 28 p.
1961. The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951-1958. Calif. Dep. Fish Game, Fish Bull. 155, 128 p.

CLEMENS, H. B., AND W. L. CRAIG.
1965. An analysis of California's albacore fishery. Calif. Dep. Fish Game, Fish Bull. 128, 301 p.

DANIELS, H. E.
1952. The covering circle of a sample from a circular normal distribution. Biometrika 39:137-143.

HUNTER, J. R.
1966. Procedure for analysis of schooling behavior. J. Fish. Res. Board Can. 23:547-562.

MARR, J. C.
1951. On the use of the terms *abundance*, *availability* and *apparent abundance* in fishery biology. Copeia 1951:163-169.

PANSHIN, D. A.
1971. Albacore tuna catches in the northeast Pacific during summer 1969 as related to selected ocean conditions. Ph.D. Thesis., Oregon State Univ., Corvallis, 110 p.

ROBERTS, K.
1972. Diversity – characteristic of Oregon's year 'round fishery. Oreg. State Univ. Sea Grant, Ext. Mar. Advis. Program 15, 2 p.

ROBSON, D. S.
1966. Estimation of the relative fishing power of individual ships. Int. Comm. Northwest Atl. Fish., Res. Bull. 3:5-14.

THOMAS, P. D.
1965. Mathematical models for navigational systems. U.S. Nav. Oceanog. Off. Tech. Rep. TR-182, 151 p.

NOTES

SEASONAL SPAWNING CYCLES OF THE SCIAENID FISHES *GENYONEMUS LINEATUS* AND *SERIPHUS POLITUS*

The white croaker, *Genyonemus lineatus* (Ayres), and queenfish, *Seriphus politus* Ayres, are two of the common inshore fishes occurring along the southern California coast (Miller and Lea 1972). Detailed reproductive data are not available for these species. The purpose of this note is to provide information on their seasonal spawning cycles.

Materials and Methods

Monthly samples are from November 1974 to October 1975. Most specimens were collected by hook and line from the Santa Monica Pier, Los Angeles County, Calif. Remaining fishes were obtained about 4.2 km south of Santa Monica at the Scattergood Steam Plant, El Segundo, Los Angeles County. Scattergood fishes had been exposed to temperatures between 23° and 41°C. Histological comparisons of these fishes with freshly caught specimens showed the ovaries were not altered by this treatment. Specimens are deposited in the ichthyology collection of the Los Angeles County Museum of Natural History.

Fishes were immediately slit and placed in 10% Formalin.[1] Gonads were embedded in paraffin and histological sections cut at 8 μm. Slides were stained using iron hematoxylin followed by eosin counterstain. Seasonal occurrences of oocytes (Tables 1, 2) were calculated by randomly selecting areas of slides from each monthly representative and classifying oocytes as to their category (Type 1, 2, or 3). Areas of a slide were surveyed until at least 100 oocytes were classified.

Results and Discussion

Three classes of oocytes are present in the ovaries of *G. lineatus* (Table 1) and *S. politus* (Table 2). Type 1 is the most abundant class and varies from those recently derived from oogonia to those approaching Type 2 oocytes. Type 2 oocytes have diameters between 100 and 270 μm and differ from Type 1 oocytes in the presence of a zona pellucida and zona granulosa. Small quantities of yolk granules may be found on the periphery of larger representatives of this class. The diameter of yolk filled mature Type 3 oocytes is greater than 270 μm. The smallest fishes to contain Type 3 oocytes measured 143 mm standard length (SL) for *G. lineatus* and 148 mm SL for *S. politus*.

As shown in Tables 1 and 2 there are several differences in seasonal distribution of oocytes reflecting the spawning cycles of *G. lineatus* and *S. politus*. The major difference is in abundance of Type 3 oocytes indicating *G. lineatus* comes into spawning condition in October and spawns intermittently into April. *Seriphus politus* enters spawning condition in April and spawns into August. These data support the findings of Skogsberg (1939) who reported that *S. politus* spawns throughout summer and *G. lineatus* spawns from November through May off California.

TABLE 1.—Monthly distribution of *Genyonemus lineatus* oocytes with mean standard length (mm) ± standard error, November 1974-October 1975.

Month	*N*	Total oocytes	Type 1 (%)	Type 2 (%)	Type 3 (%)	$\overline{SL} \pm SE$
Nov.	11	1,369	60	13	27	203.3 ± 8.7
Dec.	13	1,579	65	11	24	228.8 ± 4.6
Jan.	11	1,316	60	12	28	217.3 ± 5.9
Feb.	12	1,478	64	12	24	202.1 ± 3.9
Mar.	14	1,717	69	11	20	200.7 ± 9.8
Apr.	13	1,631	77	10	13	204.2 ± 4.4
May	19	2,138	96	1	3	218.2 ± 4.7
June	10	1,251	90	5	5	218.0 ± 2.9
July	19	2,103	95	3	2	212.0 ± 4.0
Aug.	14	1,606	96	3	1	239.8 ± 3.5
Sept.	14	1,589	90	6	4	243.0 ± 3.8
Oct.	11	1,340	75	12	13	234.5 ± 6.2

TABLE 2.—Monthly distribution of *Seriphus politus* oocytes with mean standard length (mm) ± standard error, November 1974-October 1975.

Month	*N*	Total oocytes	Type 1 (%)	Type 2 (%)	Type 3 (%)	$\overline{SL} \pm SE$
Nov.	14	1,531	100	0	0	192.8 ± 2.6
Dec.	12	1,379	100	0	0	215.2 ± 4.6
Jan.	14	1,607	100	0	0	203.7 ± 2.4
Mar.	14	1,563	93	5	2	215.2 ± 5.1
Apr.	14	1,604	71	11	18	200.2 ± 5.5
May	15	1,729	77	9	14	214.6 ± 3.1
June	14	1,736	68	13	19	217.5 ± 3.9
July	14	1,864	72	8	20	225.8 ± 3.4
Aug.	14	1,536	78	9	13	202.9 ± 4.0
Sept.	14	1,499	97	2	1	212.9 ± 3.0
Oct.	14	1,574	98	0	2	207.6 ± 3.4

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

In both species oocyte maturation is a continuous process that occurs throughout the reproductive period (Tables 1, 2) with multiple spawnings occurring. Depleted ovaries containing mainly Type 1 oocytes were not observed until conclusion of the spawning season. The presence of various groups of developing oocytes as occurs in *G. lineatus* and *S. politus* was termed asynchronism by Yamamoto and Yamazaki (1961) who found this condition common in fishes with long breeding seasons and multiple spawnings.

Another difference (Table 1) was the persistence of small quantities of Types 2 and 3 oocytes in *G. lineatus* after the conclusion of spawning in April which persist throughout summer. It is more typical for remaining vitellogenic oocytes to undergo atresia at the end of the spawning season as occurs in *S. politus* whose inactive ovaries contained only Type 1 oocytes (Table 2) from November to January. These low frequencies of mature summer *G. lineatus* oocytes may suggest spawning continued at a reduced frequency during this period. A more plausible explanation might be that these oocytes will ovulate early in the next spawning season. It thus appears that some early ovulating *G. lineatus* oocytes initiated yolk deposition late in the previous spawning season and remained over summer. It may be energetically advantageous for these yolk filled eggs to remain over summer as opposed to resorbing them.

As *G. lineatus* ranges from Baja California to British Columbia and *S. politus* from Baja California to Oregon (Miller and Lea 1972), my data may be useful for subsequent investigations to determine geographic variation in reproduction for these species.

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Literature Cited

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

SKOGSBERG, T.
1939. The fishes of the family Sciaenidae (croakers) of California. Calif. Dep. Fish Game, Fish Bull. 54, 62 p.

YAMAMOTO, K., AND F. YAMAZAKI.
1961. Rhythm of development in the oocyte of the goldfish, *Carassius auratus*. Bull. Fac. Fish., Hokkaido Univ. 12:93-110.

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FOOD OF FIVE SPECIES OF COOCCURRING FLATFISHES ON OREGON'S CONTINENTAL SHELF

The purpose of this paper is to describe and to compare the food of five flatfish species that actually cooccurred at one specific time and place on the central Oregon continental shelf: English sole, *Parophrys vetulus* Girard; rex sole, *Glyptocephalus zachirus* Lockington; rock sole, *Lepidopsetta bilineata* (Ayres); petrale sole, *Eopsetta jordani* (Lockington); and Pacific sanddab, *Citharichthys sordidus* (Girard). These demersal fishes are common along the west coast of North America, their ranges overlapping between southern California and the Gulf of Alaska (Hart 1973). *Parophrys vetulus*, *C. sordidus*, and *L. bilineata* occur mainly on the inner continental shelf. *Eopsetta jordani* is fished commercially on its feeding grounds (73-128 m), and in deep water (311-457 m) where spawning occurs (Forrester 1969). *Glyptocephalus zachirus* has a broad bathymetric range—it is common off Oregon and Washington from 90 to 550 m (Alverson et al. 1964). Off Oregon it was the second most numerous member of a species association ranging from 119 to 199 m, on an average sediment type of 69% sand, 19% silt, and 12% clay (Day and Pearcy 1968). In that same study, *C. sordidus* and *P. vetulus* composed 80.3% of a species association of fishes in shallower water (42-73 m) on a sandy bottom. According to Alverson (1960), *L. bilineata* is common on sandy or gravel bottom. The five flatfish species attain maximum sizes ranging from 410 mm for *C. sordidus* to 700 mm for *E. jordani* (Hart 1973).

Pearcy and Vanderploeg (1973) listed major food items—combined from several locations, seasons, and years—for most of the above species. That

study provided generalized information on food habits, but little insight into possible intra- or interspecific differences in diets resulting from actual interaction among cooccurring fishes. Our study is based on a single collection minimizing temporal and spatial variations associated with sampling. Food items were identified to species whenever possible. Thus, a detailed comparison of food taxa is arrived at with minimal geographic and no seasonal effects.

A trawl haul of 75 min total duration was made beginning at 1345 h Pacific daylight time, on 13 April 1975 with an Atlantic-Western trawl (24-m footrope) from the *Betty-A*, a commercial dragger, at approximately lat. 44°42′N, long. 124°24′W. Depth of water was 95-106 m. The sediment was sand (Byrne and Panshin 1968). Stomachs of fishes were removed and preserved in Formalin[1] at sea (Table 1). Food items were identified and enumerated in laboratories ashore.

TABLE 1.—Fishes captured in an Atlantic-Western trawl on 13 April 1975.

Species	No. caught	Total length range (mm)	No. examined	No. with stomach contents
Citharichthys sordidus	181	90- 377	62	26
Parophrys vetulus	50	230- 450	50	37
Glyptocephalus zachirus	24	240- 360	22	21
Eopsetta jordani	22	240- 510	12	7
Lepidopsetta bilineata	19	247- 474	19	15
Raja binoculata	9	940-1,460	8	6
Raja rhina	2	800- 890	2	1
Raja kincaidi	2	560- 570	2	0
Pleuronichthys verticalis	2	251- 254	2	1
Ophiodon elongatus	1	850	1	0
Squalus acanthias	1	1,000	0	—

Forage Organisms

All the food items identified from five species of flatfishes are listed in Table 2, and the major food taxa (taxa having a frequency of occurrence of 10% or more) are listed for individual fish of three species of flounders in Table 3.

Parophrys vetulus had a diverse diet, feeding primarily on polychaetes and amphipods. Mollusks, ophiuroids, and crustacea were also represented. The amphipod *Ampelisca macrocephala*, the most numerous single prey species, occurred in 60% of fish. The diversity of the diet of *P. vetulus* is due to the many different types of food consumed by individual fish (represented by the vertical columns in Table 3) rather than by different fish feeding on different prey. *Parophrys vetulus* appears to be an opportunistic feeder. Forrester (1969) reported polychaetes, clams, and ophiuroids as primary food organisms of *P. vetulus*, with incidental occurrences of sandlance, crab, amphipods, shrimp, squid, and small fish. Pearcy and Vanderploeg (1973) found polychaetes, amphipods, and pelecypods were important prey of *P. vetulus* off Oregon.

Glyptocephalus zachirus fed primarily on four species of amphipods and secondarily on polychaetes. Amphipods occurred in all but one stomach, polychaetes in 71% of the stomachs with food. Nematodes were encountered in 38% of the stomachs but were probably parasitic (Robert Olson, pers. commun.). Pearcy and Vanderploeg (1973) also found polychaetes and amphipods to be the major food of *G. zachirus* off Oregon.

The principal food of *Lepidopsetta bilineata* was ophiuroids. All but one individual had been feeding on *Ophiura*, which constituted the bulk of the stomach contents. A few polychaetes and mollusks were also present. According to Shubnikov and Lisovenko (1964), the basic items of its diet are polychaetes, mollusks, shrimps, and other crustaceans. Fishes (sandlance) and echinoderms were occasionally found in stomachs. Food items reported for *L. bilineata* in Hecate Strait, British Columbia, by Forrester and Thomson (1969) were clams, polychaetes, crabs, shrimps, sandlance, herring, echinoderms, and amphipods.

Eopsetta jordani preyed on fishes and decapod crustaceans. Polychaetes and amphipods were not present in its diet. Ketchen and Forrester (1966) found euphausiids, herring, sandlance, and shrimp as major food items in stomachs of *E. jordani*. Pearcy and Vanderploeg (1973) reported shrimps, pelagic fishes, and euphausiids as major food items, indicating that this species feeds largely on pelagic prey.

Citharichthys sordidus had been feeding intensively on the northern anchovy, *Engraulis mordax*. Anchovy were noted in nearly all the sanddab when stomachs were removed, and all intact preserved stomachs contained them. Since anchovy were not caught in the otter trawl, feeding in the net is thought to be unlikely. According to Pearcy and Vanderploeg (1973), euphausiids, shrimps, amphipods, and crab larvae were common in *C. sordidus* stomachs.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Taxa identified from stomach contents of five species of Pacific Northwest flatfishes.[1]

Taxa	*Parophrys vetulus*	*Glyptocephalus zachirus*	*Lepidopsetta bilineata*	*Eopsetta jordani*	*Citharichthys sordidus*
POLYCHAETA	94.6	71.4	40.0		
Aphroditidae					
Aphrodita negligens			x		
Capitellidae					
[2] Capitellidae spp.	10.8				
Notomastus spp.	x				
Chaetopteridae spp.	x				
Cirratulidae					
Cirratulidae spp.	40.5				
Chaetozone setosa	x				
Chaetozone spp.	x				
Tharyx spp.	x				
Goniadidae					
Goniadidae spp.	x	x			
Glycinde picta (?)	13.5				
Lumbrineriidae					
Lumbrineris spp.	18.9				
Magelonidae					
Magelona spp.	x				
Maldanidae spp.	x				
Nephtyidae					
Nephtys caecoides	x				
Nephtys spp.	43.2				
Onuphidae					
Nothria geophiliformis (?)	x				
Nothria iridescens (?)	10.8	14.3	13.3		
Nothria spp.		19.0			
Opheliidae					
Opheliidae spp.		9.5			
Ammotrypane aulogaster	8.1				
Orbiniidae					
Haploscoloplos spp.	x				
Oweniidae					
Myriochele oculata	16.2				
Myriochele spp.	10.8				
Owenia spp.	16.2				
Paraonidae spp.	21.6				
Pectinariidae					
Pectinaria spp.	x	x	x		
Phyllodocidae					
Eteone longa	x				
Polynoidae spp.			13.3		
Sigalionidae					
Sigalionidae spp.	18.9				
Thalenessa spinosa	x				
Spionidae spp.	18.9				
Terebellidae					
Terebellidae spp.	35.1				
Polycirrus spp.	x				
Unidentified	x	x			
GASTROPODA	13.5				11.1
Cylichna attonsa	10.8				
Mitrella gouldii	x				
Mitrella spp. (?)					11.1
PELECYPODA	27.0	9.5	13.3		
Acila castrensis		x			
Axinopsida serricata	x				
Cardiomya oldroydi	x				
Nucula tenuis	16.2				
Macoma spp.	x				
Tellina carpenteri (?)	8.1		13.3		
Unidentified	x				
SCAPHOPODA	16.2	4.8			
Dentalium sp.	13.5				
Unidentified fragment	x				
Scaphopoda(?)		x			
CEPHALOPODA					11.1
Octopoda					11.1
Beak of *Loligo* spp. (?)					11.1
CRUSTACEA	91.9	100.0	6.7	28.6	33.3
Cypris larvae (?)	x				
Copepoda (calanoid)	10.8				
Mysidacea					
Neomysis spp.					11.1
Unidentified				14.3	
Ostracoda (?)	x				
Cumacea	10.8				
Tanaidacea	x				

TABLE 2.–Continued.

Taxa	*Parophrys vetulus*	*Glyptocephalus zachirus*	*Lepidopsetta bilineata*	*Eopsetta jordani*	*Citharichthys sordidus*
Euphausiacea					
Euphausia pacifica					22.2
Decapoda					
Natantia					
Crangon spp.					11.1
Nectocrangon spp.				14.3	
Unidentified shrimp					x
Reptantia					
Pagurus samuelis			x		
Mursia spp.				14.3	
Crab leg		x			
Amphipoda	83.8	95.2			
Ampeliscidae					
Ampelisca cristata		x			
Ampelisca macrocephala	59.5	33.3			
Ampelisca spp.	x				
Amphilochidae spp. (?)	x				
Aoridae					
Lembos spp.	x				
Argissidae					
Argissa hamatipes	x				
Isaeidae					
Photis brevipes	x	x			
Protomedeia spp.	x				
Lysianassidae					
Lysianassidae spp.	x				
Acidostoma spp.		x			
Anonyx anivae	x				
Hipomedon wecomus	18.9	28.6			
Oedicerotidae					
Monoculodes emarginatus	x				
Monoculodes sp. #1	x	x			
Synchelidium shoemakeri	x	x			
Westwoodilla caecula	x				
Phoxocephalidae					
Paraphoxus abronius	x				
Paraphoxus daboius (?)	x				
Paraphoxus epistomus (?)	21.6	33.3			
Paraphoxus fatigans	10.8	4.8			
Paraphoxus lucubrans	x				
Paraphoxus milleri		x			
Paraphoxus obtusidens	16.2	33.3			
Paraphoxus variatus	x				
Paraphoxus spp.	10.8				
Pleustidae					
Pleustidae spp.		x			
Pleusymtes coquilla		x			
OPHIUROIDEA	83.8		93.3		
Amphiodia periercta	10.8				
Amphiodia urtica	10.8				
Amphiuridae spp.	10.8				
Ophiura lutkeni	35.1		73.3		
Ophiura sarsii	x				
Ophiura spp.	8.1		20.0		
PISCES		9.5		100.0	100.0
Agonidae				14.3	
Engraulis mordax				14.3	100.0
Glyptocephalus zachirus				14.3	
Radulinus spp.				14.3	
Unidentified		x		x	
Fish scale	x	x			
NEMERTINEA	13.5				
NEMATODA	x	x			
SIPUNCULIDA	2.7		13.3		
ECHIURIDA		x			
ACANTHOCEPHALA		x			
Miscellaneous					
Gastropod egg case	x				
Egg mass	x				
Lenses					x
Unidentified remains	x	x			

[1]Frequency of occurrence is given as a percentage for food taxa whenever these taxa occur in 10% or greater of any of the five species of fishes. Opheliidae were significant on a weight basis in *G. zachirus*, and were combined with *Ammotrypane aulogaster* for calculation of similarity. An "x" denotes any other occurrence.

[2]Taxa enclosed within brackets were treated as a single group in Table 3.

TABLE 3.—Numbers of food items of major[1] taxa in contents of individual fish stomachs. Each vertical column represents one stomach.

Fish species and taxa	Number of food items																																	Total no.
Parophrys vetulus																																		
POLYCHAETA:																																		
Capitellidae						3															1	1									1				6
Cirratulidae	1			1		1	3	1	1			1			1	1		11	1			1		3							1	1			29
Glycinde picta (?)			1			1	1				1							1																	5
Lumbrineris spp.						*	*									2		3			1	*	1												10
Nephtys spp.	1		4			7	3					4				*	*	3				10	1	3		1		3				1	3	1	47
Nothria iridescens (?)				1			1		2													2													6
Myriochele oculata[2]																		3	1		1							1		1			1		8
Myriochele spp.							*						*	*			*																		4
Owenia spp.				1								*	1					2	1				*												7
Paraonidae						2	1		1	1	*							5													1	1			13
Sigalionidae			1						1		2	1						1					1									1			8
Spionidae						1	1					2						2			1	1									1				9
Terebellidae		*	2	1		1		1		1						1		5	2		4	1			*								2		23
AMPHIPODA:																																		
Ampelisca macrocephala			2	1	1	8	3	2				2		5	2	1	1	12		7	1	2		1		4		4	1	2		1		1	64
Hippomedon wecomus											1					1		1	1	2		1	1												8
Paraphoxus epistomus (?)																4		2	1	1		1		2				1			1				13
Paraphoxus fatigans	1																			1			1									1			4
Paraphoxus obtusidens						2	1				1				1	1	1																		7
Paraphoxus spp.[3]												*		1												*	1								4
GASTROPODA:																																		
Cylichna attonsa					1				2									1			1														5
PELECYPODA:																																		
Nucula tenuis			1				2											2				4		1		.							2		12
SCAPHOPODA:																																		
Dentalium sp.						3		1					2					1										1							8
COPEPODA (calanoid)						1	1	1				2																							5
CUMACEA					2										1							1												1	5
OPHIUROIDEA:																																		
Amphiodia periercta[2]						1								1											1	1									4
Amphiodia urtica												1				1							1				1								4
Amphiuridae							1						1																		1	1			4
Ophiura lutkeni		2			2	1				3	1	1				2		1					1	1		1						1	1		18
NEMERTINEA				1								1				*					*	*													5
Glyptocephalus zachirus																																		
POLYCHAETA:																																		
Nothria iridescens (?)									1						1								2												4
Nothria spp.[3]			*								*				3																1				6
Opheliidae											1						1																		2
AMPHIPODA:																																		
Ampelisca macrocephala			1																2		1		1				2		2				1		10
Hippomedon wecomus							1				1				3		1						1										1		8
Paraphoxus epistomus (?)			1		1										2								2		1		1						1		9
Paraphoxus obtusidens											1		2		3				2				1				1		3						13
Lepidopsetta bilineata																																		
POLYCHAETA:																																		
Polynoidae					*										*																				2
Nothria iridescens (?)																									1		3								4
SIPUNCULIDA (?)																	1										1								2
PELECYPODA:																																		
Tellina carpenteri (?)																	1		1																2
OPHIUROIDEA:																																		
Ophiura lutkeni			1						1		2		2		4		5		4		1		1		2		3								26
Ophiura spp.[3]					*		*																						*						3

[1]Taxa having a frequency of occurrence of at least 10%.
[2]Taxa within brackets were treated as a single group for calculation of similarity.
[3]Taxa not used to determine similarity.
*Fragment.

Discussion

The flatfishes examined in this study comprised two distinct feeding types based on the species composition of prey and the frequency of occurrence of major food items. *Parophrys vetulus*, *G. zachirus*, and *L. bilineata* were benthophagous, feeding on benthic infaunal and epifaunal invertebrates, mainly polychaetes, amphipods, and ophiuroids. *Eopsetta jordani* and *C. sordidus* were piscivorous and fed more on pelagic animals, consuming mainly fishes in addition to shrimp, mysids, euphausiids, and cephalopods. Fishes did not occur in the stomachs of the benthic invertebrate feeders, except for two fishes found in *G. zachirus*.

Differences were sometimes obvious in the food habits of fishes within each feeding type. The

similarity among the food habits of the three fishes that preyed on benthic invertebrates was calculated using commonly occurring prey (Table 3) and Horn's (1966) measure of niche overlap. The overlap was largest between *P. vetulus* and *G. zachirus* (C_λ = 0.40). This is because both fishes fed on the same species of amphipods and the polychaete *Nothria iridescens*. *Parophrys vetulus* preyed on a very diverse array of invertebrate taxa, while *G. zachirus* appeared to be more selective in its feeding.

The amount of food overlap among the other species pairs was low (0.19 between *P. vetulus* and *L. bilineata* and only 0.03 between *G. zachirus* and *L. bilineata*). These low values are explained by the high occurrence of *Ophiura lutkeni* only in *L. bilineata*. Also, *L. bilineata* fed on members of two scaleworm families, Aphroditidae and Polynoidae, neither of which is represented in the other flatfishes.

The food habits of the flatfishes that we found to be mainly piscivorous were also different. *Eopsetta jordani* preyed on various fishes, including benthic agonids, pleuronectids, and cottids, as well as a benthic shrimp and crab, whereas *C. sordidus* fed almost exclusively on the pelagic *Engraulis mordax*.

Partitioning of the food resources among the five flatfish species is obvious from our data—the different, syntopic species fed upon different organisms. According to MacArthur and Pianka (1966), a more productive environment should lead to a more restricted diet in terms of different species eaten, but in a patchy environment this does not apply to predators that spend most of their time searching. If the bottom occupied by *P. vetulus* is inhabited by patches of invertebrates, then this species might be such a scavenging "generalist" predator. Rae (1969) documented a food interaction similar to the one in this study between the lemon sole, *Microstomus kitt*, and witch, *Glyptocephalus cynoglossus*, off Scotland. The witch, restricted to muddy bottoms, fed on a more restricted fauna than the lemon sole, whose diet included the hard-bottom species typical of its habitat in addition to species from muddy-bottom types.

Differences in time of feeding could also account for differences in the species composition of prey. Diel changes in the habits of prey can serve to increase or decrease their exposure to predators, and hence their availability as food (Hobson 1965; Jones et al. 1973). More so than the other species, the stomach contents of *G. zachirus* were in a late stage of digestion, suggesting that they had fed a longer time before capture than other species.

The diet of fishes is related not only to their feeding behavior but also to their digestive morphology and mouth structure. The size of the mouth relative to body length correlated with the size of food organisms for bothid flounders in Georgia coastal waters (Stickney et al. 1974). Symmetry of the jaws plays an important role in the mode of feeding, as species with symmetrical jaws generally take free-swimming food, while those with asymmetrical jaws are mainly bottom feeders (Yazdani 1969). Flatfishes that feed on polychaetes and mollusks typically have smaller stomachs, larger intestines, and smaller gill rakers with fewer teeth than flatfishes that feed on other fishes (DeGroot 1971; Tyler 1973). The mouths of *P. vetulus*, *G. zachirus*, and *L. bilineata* are small,[2] the jaws and dentition are better developed on the blind side (i.e., asymmetrical), the teeth are incisorlike (bluntly conical in *L. bilineata*), and the gill rakers are without teeth. These morphological adaptations correlate with the preponderance of benthic invertebrates in their diets. The piscivores, *E. jordani* and *C. sordidus*, on the other hand, have larger mouths,[3] nearly symmetrical jaws with sharp teeth, and long gill rakers with teeth.

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Literature Cited

ALVERSON, D. L.
1960. A study of annual and seasonal bathymetric catch

[2]Length of maxillary into head on ocular side is 4¼-4⅗, 4½-5¼, and 3½-4⅕, respectively (Norman 1934); also see Norman for line drawings depicting the relative mouth size of flatfishes discussed in this paper.

[3]Length of maxillary into head is about 2⅗ and 2¾ (nearly 3), respectively (Norman 1934).

patterns for commercially important groundfishes of the Pacific Northwest coast of North America. Pac. Mar. Fish. Comm. Bull. 4:1-66.

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lectures in Fisheries, Inst. Fish., Univ. B.C., 190 p.

BYRNE, J. V., AND D. A. PANSHIN.
1968. Continental shelf sediments off Oregon. Oreg. State Univ. Sea Grant Ext. Mar. Advis. Program 8, 4 p.

DAY, D. S., AND W. G. PEARCY.
1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. J. Fish. Res. Board Can. 25:2665-2675.

DEGROOT, S. J.
1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5:121-196.

FORRESTER, C. R.
1969. Life history information on some groundfish species. Fish. Res. Board Can., Tech. Rep. 105, [17 p.]

FORRESTER, C. R., AND J. A. THOMSON.
1969. Population studies on the rock sole (*Lepidopsetta bilineata*) of northern Hecate Strait, British Columbia. Fish. Res. Board Can., Tech. Rep. 108, 104 p.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HOBSON, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.

HORN, H. S.
1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.

JONES, D. A., N. PEACOCK, AND O. F. M. PHILLIPS.
1973. Studies on the migration of *Tritaeta gibbosa*, a subtidal benthic amphipod. Neth. J. Sea Res. 7:135-149.

KETCHEN, K. S., AND C. R. FORRESTER.
1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in the waters of western Canada. Fish. Res. Board Can., Bull. 153, 195 p.

MACARTHUR, R. H., AND E. R. PIANKA.
1966. On optimal use of a patchy environment. Am. Nat. 100:603-609.

NORMAN, J. R.
1934. A systematic monograph of the flatfishes (Heterosomata). Vol. I. Psettodidae, Bothidae, Pleuronectidae. Br. Mus. (Nat. Hist.), Lond., 459 p.

PEARCY, W. G., AND H. A. VANDERPLOEG.
1973. Radioecology of benthic fishes off Oregon. *In* Radioactive contamination of the marine environment, p. 245-261. Int. At. Energy Agency, Vienna.

RAE, B. B.
1969. The food of the witch. Mar. Res. Dep. Agric. Fish. Scotl. 2, 23 p.

SHUBNIKOV, D. A., AND L. A. LISOVENKO.
1964. Data on the biology of rock sole of the southeastern Bering Sea. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 49 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 51): 209-214. (Transl. in Soviet Fisheries Investigations in the Northeast Pacific, Part II, p. 220-226, by Israel Program Sci. Transl., 1968, available Natl. Tech. Inf. Serv., Springfield, VA, as TT 67-51204.)

STICKNEY, R. R., G. L. TAYLOR, AND R. W. HEARD III.
1974. Food habits of Georgia estuarine fishes. I. Four species of flounders (Pleuronectiformes: Bothidae). Fish. Bull., U.S. 72:515-525.

TYLER, A. V.
1973. Alimentary tract morphology of selected North Atlantic fishes in relation to food habits. Fish. Res. Board Can., Tech. Rep. 361, 23 p.

YAZDANI, G. M.
1969. Adaptations in the jaws of flatfish (Pleuronectiformes). J. Zool. (Lond.) 159:181-222.

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AGE DETERMINATION OF A TROPICAL REEF BUTTERFLYFISH UTILIZING DAILY GROWTH RINGS OF OTOLITHS

The recent economic expansion of the aquarium fish industry in Hawaii has raised questions concerning the judicious exploitation of reef resources (Pellegrin 1973; Randall 1973; Reese 1973). However, appropriate management strategies cannot be implemented until sufficient biological data have been gathered, allowing a characterization of exploited populations of fishes. The relative paucity of such information concerning the vast majority of reef species underscores the need for future research.

Studies pertaining to the age and growth of fishes are especially useful in the analysis of exploited stocks. Unfortunately, efforts to age tropical fishes in the past have proved to be largely unsuccessful and/or involve considerable expenditures in time and effort (Pannella 1974). However, the recent studies of Pannella (1971, 1974) have initiated the development of a technique for determining the age of tropical fishes without having to resort to more elaborate approaches such as the Peterson method of ageing. Panella has provided evidence that many species of both temperate and tropical fishes deposit lamellae on their otoliths with a diel periodicity. These lamellae are visible as rings or circuli after the otolith has been properly prepared. In the absence of annuli, these rings may be used to age fish. A recent investigation by Struhsaker and Uchiyama (1976) using this technique was successful in ageing the Hawaiian

anchovy (*Stolephorus purpureus*) and in showing the daily nature of these lamellae.

This paper reports on studies of the age and growth of the Hawaiian endemic millet-seed butterflyfish, *Chaetodon miliaris* Quoy and Gaimard (Perciforms: Chaetodontidae), using this approach. Butterflyfishes are exceptionally attractive and are heavily exploited by the aquarium industry in Hawaii. This study was initiated in order to obtain information useful to state regulatory agencies in the management of reef fish stocks.

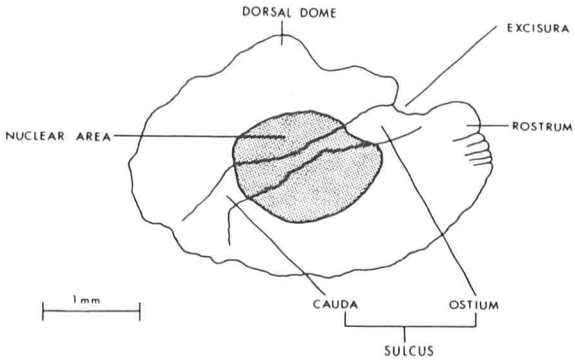

FIGURE 1.—Schematic representation of the left sagitta of a 94-mm *Chaetodon miliaris* viewed medially.

Methods

All fish were collected by spearing around the island of Oahu, Hawaii, during 1974 and were measured to the nearest millimeter standard length (SL) while still fresh. Next, the otoliths were extracted by means of a horizontal section through the cranium above the eyes. Of the three otoliths on each side, only the largest, the sagitta, was studied. Figure 1 depicts a left sagitta of a 94-mm *C. miliaris* viewed medially. After both sagittae were removed, all membranes and endolymph were carefully teased way under a dissecting microscope. The otoliths were then rinsed in water and placed in a 2% aqueous solution of HCl for several minutes of etching. They were then rinsed again, thoroughly dried, and finally mounted in depressions of glass slides where they were immersed in euparal (an aromatic oil which acts as a clearing agent) and covered with glass cover slips. After clearing for 2 wk, the otoliths were ready for reading. Otoliths were read from the nucleus outward along their long axis with a compound binocular microscope utilizing transmitted light at a magnification of 400× (Figure 2). The rings in each sagitta were counted twice, using a hand counter, and the average of the four readings obtained from each specimen was used to estimate the age of the fish in days.

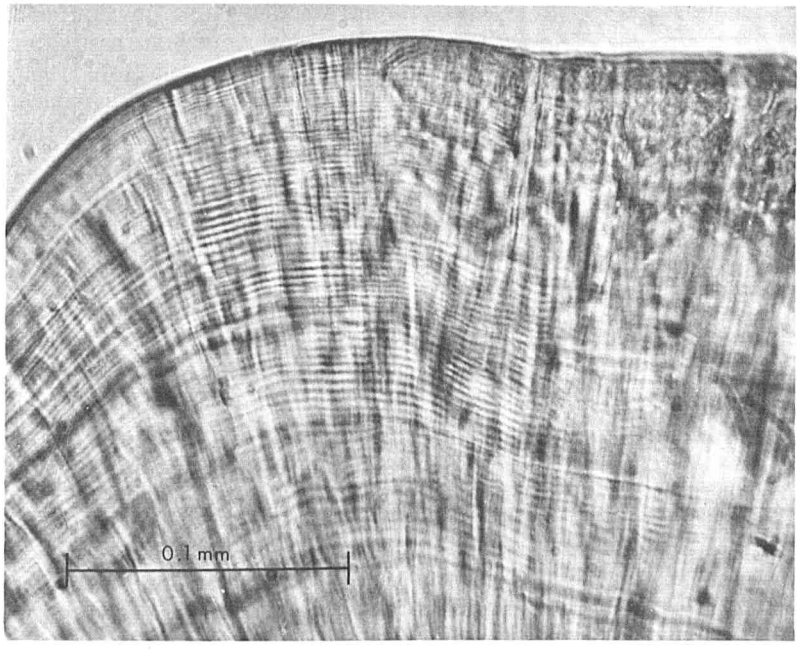

FIGURE 2.—Internal ring structure of the otolith of *Chaetodon miliaris* specimen number 11. Not all the rings are visible in this photograph.

Results

The counts of rings within otoliths are summarized in Table 1. The average number of rings for each fish has been rounded to the nearest integer.

On the assumption that one ring is equal to one day's growth (Pannella 1971, 1974; Struhsaker and Uchiyama 1976), the data were fitted to the von Bertalanffy growth equation employing the techniques of Allen (1966). This model states:

$$l_t = L_\infty (1 - e^{-K(t - t_0)}) \quad (1)$$

where l_t = length at time t
L_∞ = the average length of a group of fish grown for an infinite period of time
K = a growth parameter which describes the rate at which l_t is approaching L_∞
t_0 = the back calculated X intercept or the time at which size was zero.

The data are plotted along the calculated von Bertalanffy growth curve in Figure 3. The calculated growth equation for the data in this report is:

$$l_t = 127(1 - e^{-0.0031(t+30)}) \quad (2)$$

when size is expressed as SL in millimeters and time is expressed in days. Alternatively, when time is expressed in years, the equation becomes:

$$l_t = 127(1 - e^{-1.13(t+0.082)}). \quad (3)$$

The estimated asymptotic size of 127 mm SL is a reasonable figure. Of 345 *C. miliaris* examined in another study (Ralston 1975), 4 were larger than this size. Of those, three were 131 mm SL or less,

TABLE 1.–The number of rings counted in the otoliths of *Chaetodon miliaris* collected around Oahu, Hawaii, 1974.

Specimen	Date of capture	Standard length (mm)	Mean number of rings	Range of counts
1	7 June	27	35	32-38
2	18 June	29	71	65-74
3	7 June	32	51	48-52
4	11 July	35	108	99-115
5	11 July	42	133	124-138
6	1 Oct.	44	118	110-122
7	5 Oct.	50	115	107-121
8	1 Oct.	52	138	134-141
9	5 Oct.	56	147	141-153
10	5 Oct.	66	169	162-178
11	5 Oct.	70	227	215-238
12	5 Oct.	71	228	219-235
13	5 Oct.	71	221	216-227
14	1 Dec.	86	322	307-333
15	1 Dec.	87	375	362-391

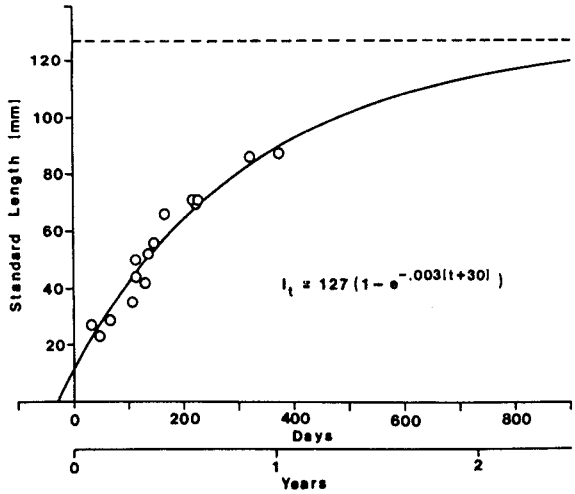

FIGURE 3.–The von Bertalanffy growth curve in length fitted to 15 individuals of *Chaetodon miliaris* aged by means of otoliths.

while the fourth was 137 mm SL. Because L_∞ can be thought of as an average, if sampling is intensive enough, one would expect to find individuals of a larger size. Of all the fish sampled in this earlier study, only 1.2% were larger than the estimated growth ceiling of the von Bertalanffy model as determined from the otoliths of the 15 individuals reported on here.

The growth of *C. miliaris* is very fast. The estimated growth parameter, K, of the von Bertalanffy equation describes how quickly growth proceeds. Large values of K are associated with rapid growth. Beverton and Holt (1959) presented values of K for 57 species of fishes and of those, only 6 species have K values exceeding that of *C. miliaris*.

It should also be noted that only fish which were less than 90 mm SL are reported on here. It was found that the otoliths of larger fish became increasingly difficult to read. Not only do the otoliths become thicker, but the peripheral ring increments become smaller with growth. For these reasons, larger fish could not be reliably aged in this study.

Discussion

On 2 August 1966, Wass (1967) defaunated a small patch reef in Kaneohe Bay, Hawaii, while studying the repopulation rates of various species of fishes. In so doing, he sampled 476 *C. miliaris* in 1 day. He gave a size-frequency distribution,

suitable for the Peterson method of ageing, which is reproduced in Figure 4.

The first mode centered on 7 cm total length (TL) could well represent a recently recruited cohort. A size of 70 mm TL corresponds to a length of 58 mm SL for *C. miliaris* (Ralston 1975). Spawning in this species is known to occur between December and April but peaks around the end of February or the beginning of March (Ralston 1975). Consequently, about 155 days elapsed between the time of peak spawning for this species and the date of capture of these 476 specimens. Assuming growth according to Figure 3, after 155 days of growth, juvenile *C. miliaris* are estimated to be 55 mm SL. This size corresponds closely with the first mode of Wass' size-frequency distribution (58 mm SL or 70 mm TL), thus corroborating Figure 3.

Further evidence in support of the von Bertalanffy growth curve and therefore, the interpretation of otolith ring patterns, comes from examining the size at which *C. miliaris* first reproduce. Ralston (in press) reported that both male and female *C. miliaris* reached reproductive maturity at a size of about 90 mm SL. Referring to Figure 3, fish of this size are about 1 yr old. If spawning is periodic, as it is in *C. miliaris* (Ralston 1975), one expects the onset of reproductive maturity to occur after some multiple of the interval between spawning periods has elapsed. One year is one such interval and *C. miliaris* becomes reproductive during the first spawning season after birth.

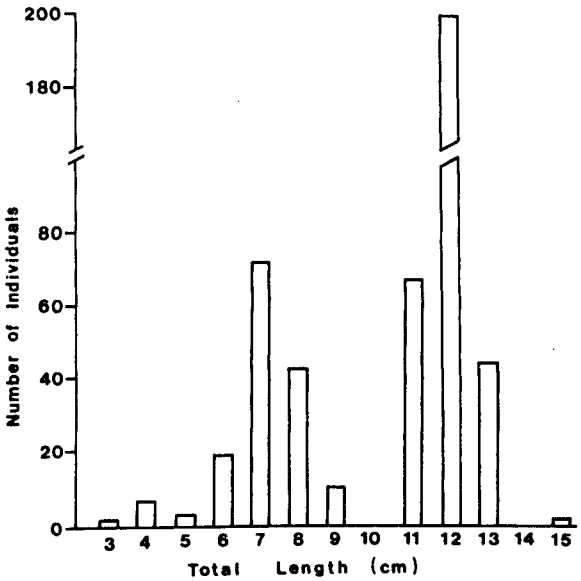

FIGURE 4.—Size-frequency distribution of *Chaetodon miliaris* collected by Wass (1967) in Kaneohe Bay. (Redrawn from his figure 7.)

Evidence presented here in the form of interpretation of the data of Wass (1967) and examination of age at maturity substantiate the growth of *C. miliaris* as described by the von Bertalanffy curve of Figure 3. These in turn confirm the accuracy and utility of employing the diel lamellae in the otoliths of fishes as growth chronometers. Although a new and as yet somewhat untried technique, Pannella's method of age determination offers the potential to age fishes in situations where this was not feasible in the past.

Acknowledgments

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Literature Cited

ALLEN, K. R.
1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board Can. 23:163-179.

BEVERTON, R. J. H., AND S. J. HOLT.
1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *In* G. E. W. Wolstenholme and M. O'Connor (editors), Ciba Foundation Colloquia on Ageing 5:142-177. J. & A. Churchill Ltd., Lond.

PANNELLA. G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (editor), Proceedings of an International Symposium on the Ageing of Fish, p. 28-39. Unwin Brothers Ltd., Surrey, Engl.

PELLEGRIN, D.
1973. Curbs urged in collecting tank fish. Honolulu Advertiser, Sept. 6.

RALSTON, S.
1975. Aspects of the age and growth, reproduction, and diet

of the millet-seed butterflyfish, *Chaetodon miliaris* (Pisces: Chaetodontidae), a Hawaiian endemic. M.S. Thesis, Univ. Hawaii, Honolulu.

In press. Anomalous growth and reproductive patterns in populations of *Chaetodon miliaris* (Pisces: Chaetodontidae) from Kaneohe Bay, Oahu. Pac. Sci.

RANDALL, J. E.
1973. Marine parks seen as key to reef beauty. Honolulu Advertiser, Sept. 5.

REESE, E.
1973. Collectors as a threat to reef fishes. Honolulu Star-Bulletin, May 15.

STRUHSAKER, P., AND J. H. UCHIYAMA.
1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae) from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

WASS, R.
1967. Removal and repopulation of the fishes on an isolated patch coral reef in Kaneohe Bay, Hawaii. M. S. Thesis, Univ. Hawaii, Honolulu.

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AN EPIBENTHIC SAMPLER USED TO STUDY THE ONTOGENY OF VERTICAL MIGRATION OF *PANDALUS JORDANI* (DECAPODA, CARIDEA)[1]

Pandalus jordani Rathbun, like many other species of pandalid shrimps, undergo regular diel changes in their vertical distribution (Tegelberg and Smith 1957; Alverson et al. 1960; Pearcy 1970, 1972; Robinson in press). Little is known, however, about the vertical distribution and diel migrations of larval and juvenile shrimp, or at what stage of the life history vertical migration and benthic existence are initiated.

Berkeley (1930) found that size or age of larval *P. danae* increased with increasing depth in a semienclosed embayment in British Columbia. Pearcy (1972) published the only information on day/night differences in benthic occurrence of juvenile *P. jordani*. Using a plankton net mounted on a beam trawl, he collected more juveniles (<7.0 mm in carapace length) near the bottom during day than night.

In order to sample the water column completely, it was necessary to supplement plankton tows with a discrete, quantitative sample on or just off the bottom. Various methods have been used for this purpose but we thought that all of them were inadequate for the present study. Many epibenthic samplers do not have an opening/closing device and therefore are subject to contamination from the water column above (Russell 1928; Frolander and Pratt 1962; Pearcy 1972; Beardsley 1973). Others are only capable of collecting small samples, in relatively shallow water (Clutter 1965; Macer 1967). In others the opening/closing device seems inefficient or overly complex (Bossanyi 1951; Wickstead 1953; Macer 1967; Hesthagen 1970). Design criteria for the sampler used in this study were: a simple, substrate activated, opening/closing device capable of quantitatively sampling in depths greater than 150 m and sampling at least 500 m^3 of water with no loss of filtration efficiency.

Epibenthic Sampler Design

The epibenthic sampler consists of a sled and a box, to which are attached a plankton net and a substrate-actuated opening/closing device (Figure 1). The frame of the sled was welded from flat steel strap (5.1 × 0.6 cm). The runners (23 × 0.6 cm mild steel plate) are joined across the front by a piece of the same steel bent to conform to the front of the sled. This serves to carry the sled over small obstructions on the seabed and further protect the door of the box when it is in the open position. A bumper bar (5.1 × 0.6 cm) was also fitted across the front of the sled to prevent large obstacles from entering the mouth of the sampler. Two brackets on either side of the sled serve as attachment points for the box. The six different positions allow the box to be positioned from 2.5 to 22.9 cm off the bottom. Two pieces of strap (5.1 × 0.6 cm) were welded along the top of the frame with nine holes to provide various attachment points for the towing bridle. In addition, four pairs of towing points were placed around the front of the frame.

The box (106.7 × 45.7 × 53.3 cm), made of 3.2-mm mild steel plate, is reinforced in front by steel strap (2.5 × 0.32 cm), forming a lip around the mouth of the box (Figure 1B). The box is further reinforced by L stock (2.5 × 0.32 cm) placed around the box 10 cm from the rear edge. Attach-

[1]This research was supported in part by Grant No. 04-5-158-2, Office of Sea Grant, National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

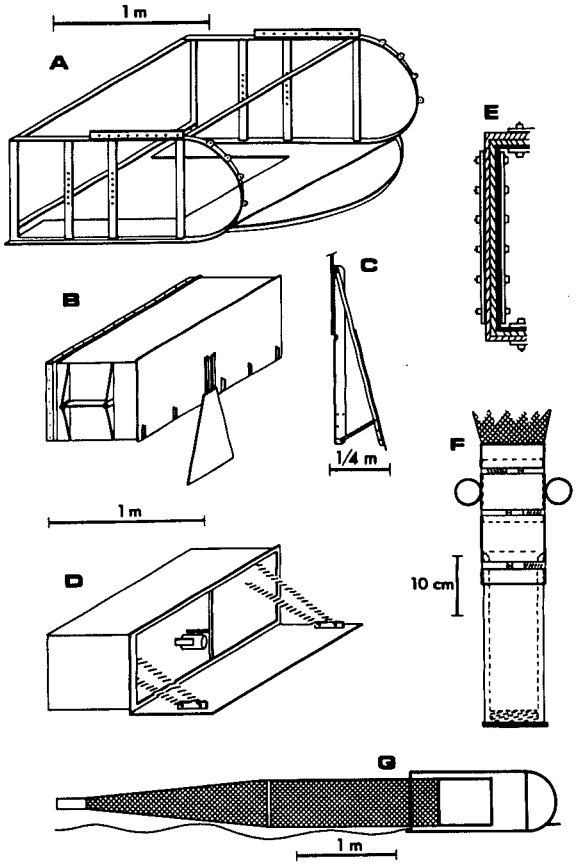

FIGURE 1.—Opening/closing epibenthic sampler: A) sled frame; B) box with door closed; C) detail, side view of shoe, hinge, and shoe adjustment device; D) box with door open showing flowmeter and springs for closing door; E) schematic net attachment, solid line is box wall, two cross hatched lines are collars of coarse mesh liner (inner) and plankton net (outer), open bars are stainless steel straps with bolts; F) safety collar insert with rings for cable attachment protruding through collar and PVC cod end with threaded teflon plug; G) schematic lateral view showing sled, box, net, and canvas chafing gear.

ment points for affixing the box to the sled were made from 3.8-cm round stock, tapped to 9.5 mm and reinforced with 5.1 × 0.48 cm flat stock. The box is fastened to the sled by four stainless steel bolts (0.95 × 3.8 cm).

The door of the box was made from mild steel plate (109.2 × 48.3 × 0.48 cm) and is hinged with a 6.4-mm stainless steel rod at five points along the bottom. The shoe which opens the door upon contact with the sea floor is triangular shaped (33.0 × 50.8 × 0.48 cm) and is hinged to allow adjustment, depending on the distance the box is set off the bottom (Figure 1C). Four large springs (5.1 × 22.9 cm), attached internally, pull the door shut when the sled leaves the sea floor (Figure 1D). The door-to-shoe surface area ratio is about 5:1, so that water pressure effectively holds the door shut on descent and ascent (Figure 1B). A TSK flowmeter[2] is mounted in the middle of the mouth by a brace (1.9 × 0.48 cm). The nets are attached to the rear of the box by sandwiching them between stainless steel straps (5.1 × 0.48 cm) bolted together at 7.6-cm intervals (Figure 1E). The inner strap has 6.4-mm stainless steel bolts welded to it, while the outer strap has holes drilled to correspond to the bolts in the inner strap, as well as the holes in the box and net collars. The entire sled, except for the springs and stainless steel fittings, was hot dipped galvanized.

The plankton net was made of 571-μm mesh nylon monofilament. The filtering area to mouth area ratio is 9:1. The "cylinder"/"cone" net had a total mesh area of 7.7 m^2, with 2.6 m^2 in the cone and 5.1 m^2 in the cylinder. The collars were made of plastic coated nylon webbing. The cod end is a 30.5-cm piece of 10.2 cm outside diameter schedule 80 polyvinyl chloride (PVC) pipe, with a threaded teflon plug for removing the sample. There is also a stainless steel insert above the cod end fitted with two rings protruding through slits in the collar, for attachment of safety wires from the sled frame to the cod end, in the event a large amount of sediment was retained (Figure 1F). Overall length of the net including collars and cod end is 5.1 m (Figure 1G). A small coarse mesh net 1 m deep (2.5-cm stretched mesh) was mounted inside the plankton net (see Figure 1E) to catch any large animals or objects and prevent them from damaging the plankton net or the sample in the cod end. A piece of heavy canvas (1.2 × 3.7 m, no. 4 duck) was attached to the rear of the sled by shackles, to protect the plankton net from chafing on the sea floor (Figure 1G).

Epibenthic Sampler Operation

Because of its size and weight (ca. 150 kg in air) the epibenthic sampler can only be used from a vessel with a suitable trawl winch; in the present study the 24.4-m RV *Cayuse* with a 9.5-mm diameter trawl wire was used. The sled was fastened to the trawl wire with a ball bearing swivel and a 3-m bridle of 9.5-mm wire attached to the

[2]Tsurumi-Seiki Kosakusho. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

second set of attachment points from the front of the sled. From these towing points the sled proved to be stable, never landing on the bottom upside down. It could be launched and recovered by two people in moderate-to-rough seas. The sled was launched while underway at 2 knots. A 20-min tow (bottom time) at 2 knots was calculated to be sufficient to filter 500 m^3 of water. Presence on the bottom was detected by the winch potentiometer.

Filtering efficiency of the sampler, based on the degree of clogging, was never markedly reduced over this time interval. However on soft muddy-sand bottoms, characteristic of *P. jordani* grounds, bottom times were reduced to 10 min because of the amount of fine sediment and meiofauna stirred up and retained in the cod end. Large organisms, including adult *P. jordani*, as well as the fragile urchin, *Allocentrotus fragilis*, and slender sole, *Lyopsetta exilis*, were effectively retained in the coarse mesh liner and prevented from reaching the sample in the cod end. Flowmeter readings indicated that at no time did the number of animals retained in the liner seriously occlude the mouth of the plankton net and affect its efficiency. On coarse sand bottoms, the samples were very clean, with little sediment and meiofauna retained, even when the net was only 5-8 cm off the bottom.

Though the sled was never observed firsthand while on the bottom, evidence from skid marks on the runners and shoe, behavior of the potentiometer while the sled was on the bottom, and the relationship between flowmeter readings and bottom time indicated that the epibenthic sampler was stable and not prone to dig in or bounce off the bottom while being towed.

Vertical Distribution of Larval *Pandalus jordani*

On 30 and 31 May 1972 the epibenthic sampler was used to sample near-bottom fauna and open bongo nets were used to obtain a series of quasi-vertically stratified plankton samples 10 nautical miles off Cascade Head, on the central Oregon coast (lat. 45°04.0′N, long. 124°15.1′W). The 0.7-m diameter bongo frames had paired cylinder/cone 571-μm Nitex nets, 5.1 m in length with an effective filtering area to mouth area ratio of 8:1. A scope to depth ratio of 2:1 was maintained by using a 40-kg multiplane kite otter as a wire depressor (Colton 1959). All nets contained TSK flowmeters. A time-depth recorder was fixed to the wire just above the bongo nets. Tows were made at four strata (0-10, 11-50, 51-100, 101-150 m) with the open bongo nets, and a bottom sample was taken with the epibenthic sampler at 160 m. Replicate tows were taken at each depth interval, both day (1200-1930 h) and night (2105-0400 h). Contamination in the open bongo net was minimized by lowering to the depth interval as fast as possible, doing a stepped oblique tow through the horizon, and then raising the net as quickly as possible. Towing time at depth was long enough to keep the period of contamination below 20% of the total sampling time for the deepest tows.

The vertical distribution of *P. jordani* larvae and juveniles is summarized in Figure 2. During

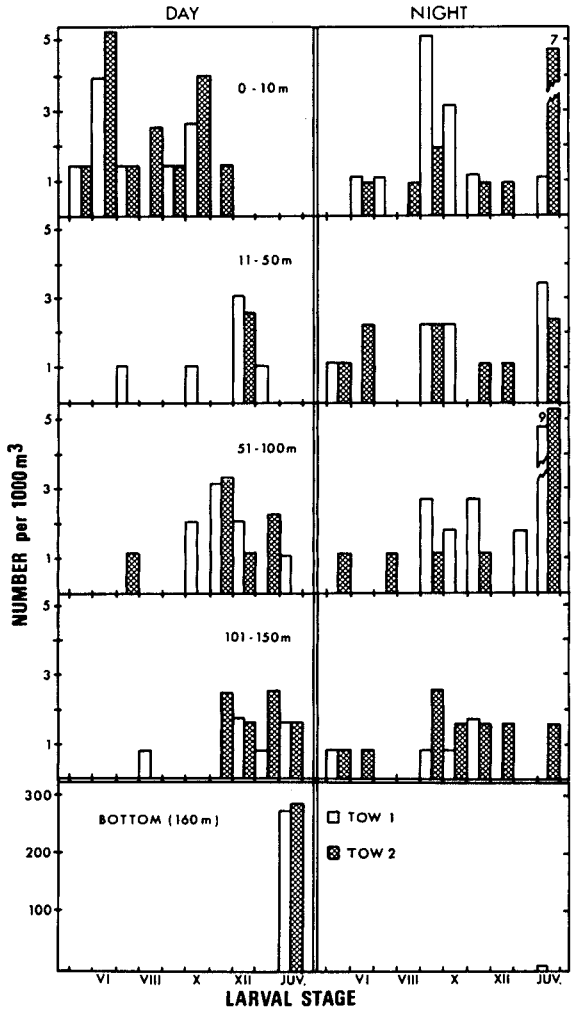

FIGURE 2.—Vertical distribution of larvae and early juvenile *Pandalus jordani*, during one day and one night period. All tows were replicated.

the day, larvae were distributed throughout the water column and were most abundant in the 0- to 10-m depth interval. A trend of increasing age with depth was evident. Early juveniles were present in low numbers in the 51- to 100-m and 101- to 150-m intervals. The sled tows revealed a very high concentration of early juveniles (284 and 290/1,000 m^3) on the bottom during midday.

At night larval shrimp were still distributed throughout the entire water column. The younger stages (V and VI), found in some abundance in the 0- to 10-m interval during the day, were not collected at night. Furthermore, an age gradient with depth was no longer present. This was due, in part, to the presence of late larvae at all depths in the water column. The most dramatic feature of the night distribution was the vertical migration of the early juveniles as indicated by their virtual absence on the bottom (0 and 4/1,000 m^3) in the sled samples. Juveniles were again present in the lower portion of the water column (101-150 m) and had migrated into the upper 100 m, including the top 10 m. There was no evidence that larvae younger than Stage XIII migrated to any extent. Vertical migratory behavior starts late in the larval phase, before the molt to juvenile and recruitment to the bottom.

Acknowledgments

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Literature Cited

ALVERSON, D. L., R. L. MCNEELY, AND H. C. JOHNSON.
1960. Results of exploratory shrimp fishing off Washington and Oregon (1958). Commer. Fish. Rev. 22(1):1-11.

BEARDSLEY, A. J.
1973. Design and evaluation of a sampler for measuring the near-bottom vertical distribution of pink shrimp, *Pandalus jordani*. Fish. Bull., U.S. 71:243-253.

BERKELEY, A. A.
1930. The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. 6:79-163.

BOSSANYI, J.
1951. An apparatus for the collection of plankton in the immediate vicinity of the sea-bottom. J. Mar. Biol. Assoc. U.K. 30:265-270.

CLUTTER, R. I.
1965. Self-closing device for sampling plankton near the sea bottom. Limnol. Oceanogr. 10:293-296.

COLTON, J. B., JR.
1959. The multiplane kite-otter as a depressor for high-speed plankton samples. J. Cons. 25:29-35.

FROLANDER, H. F., AND I. PRATT.
1962. A bottom skimmer. Limnol. Oceanogr. 7:104-106.

HESTHAGEN, I. H.
1970. On the near-bottom plankton and benthic invertebrate fauna of the Josephine Seamount and the Great Meteor Seamount. METEOR Forschungsergeb., Reihe D. 8:61-70.

MACER, C. T.
1967. A new bottom-plankton sampler. J. Cons. 31:158-163.

PEARCY, W. G.
1970. Vertical migration of the ocean pink shrimp *Pandalus jordani*: A feeding and dispersal mechanism. Calif. Fish Game 56:125-129.
1972. Distribution and diel changes in the behavior of pink shrimp, *Pandalus jordani*, off Oregon. Proc. Natl. Shellfish. Assoc. 62:15-20.

ROBINSON, J. G.
In press. The vertical distribution and diel migration of pink shrimp (*Pandalus jordani*) off Oregon. Oreg. Fish Comm. Invest. Rep.

RUSSELL, F. S.
1928. A net for catching plankton near the bottom. J. Mar. Biol. Assoc. U.K. 15:105-108.

TEGELBERG, H. C., AND J. M. SMITH.
1957. Observations on the distribution and biology of the pink shrimp (*Pandalus jordani*) off the Washington coast. Wash. Dep. Fish., Fish. Res. Pap. 2(1):25-35.

WICKSTEAD, J.
1953. A new apparatus for the collection of bottom plankton. J. Mar. Biol. Assoc. U.K. 32:347-355.

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HARNESS FOR ATTACHMENT OF AN ULTRASONIC TRANSMITTER TO THE RED DRUM, *SCIAENOPS OCELLATA*

The use of small ultrasonic transmitters for studying the movement and behavior of fish in the field is becoming very popular (Stasko 1971). As a result various methods have been devised for attaching transmitters to fish either externally or internally. These methods involve hooking into the dorsal musculature or insertion into the stomach (Henderson et al. 1966), surgical implantation into the peritoneal cavity (Hart and Summerfelt 1975), and others (Ohsumi 1969). The suitability of a procedure is dependent on the species of fish and on the particular objective of the study. For studies we are initiating on movements of the red drum, *Sciaenops ocellata*, none of the existent procedures were found to be entirely satisfactory.

This note describes a simple inelastic harness we have developed for the external attachment of an ultrasonic transmitter to the caudal peduncle. This attachment method is markedly superior to other methods we have tried with the red drum. We believe this procedure will be of immediate value to many workers involved in tracking studies and therefore we are describing it now rather than awaiting the completion of our investigation of migratory movements of the red drum.

Materials and Methods

The inelastic harness for attaching an ultrasonic transmitter to the caudal peduncle is shown in Figure 1. The components of the harness are as follows:

1. An inelastic plastic pull-tie (5 × 190 mm) of sufficient length to encircle the caudal peduncle;
2. Sections of soft Tygon[1] tubing (6-mm OD) and soft rubber tubing (12-mm OD, 1.5-mm wall thickness) threaded over the pull-tie to provide a soft flat cushion that minimizes abrasions and chafing to the fish when the pull-tie is attached and tightened;
3. Small plastic pull-ties to firmly affix the transmitter to the large pull-tie and tubing described above.

When attaching the harness, the large pull-tie is tightened just enough such that it fits snugly around the caudal peduncle and cannot slip over the tail (Figure 1 inset). Care must be taken not to tighten the tie so tightly that it compresses the peduncle. If the latter occurs, the tie must be cut off with scissors and replaced. These ties can only be tightened. The final position of the transmitter itself should be on the dorsal surface of the peduncle with the axis of the transmitter situated at a right angle to the longitudinal axis of the fish. After attachment the overlapping section of the pull-tie is cut off.

Harnesses are preconstructed prior to the time of use such that in the field the only modifications required are the addition or removal of small sections of Tygon and rubber tubing to provide a cushion of the exact size for a particular fish. A preconstructed harness can be attached to a red drum in less than 5 min. Plastic pull-ties of various lengths and widths are available at most hardware stores that stock materials used by electricians.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

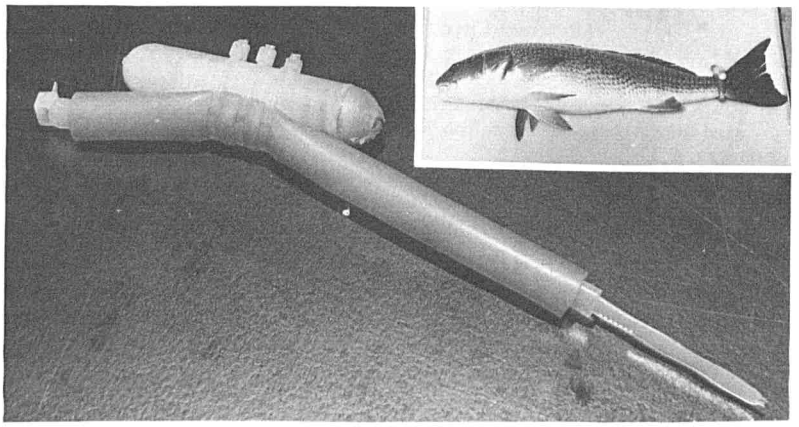

FIGURE 1.—Inelastic harness for attachment of ultrasonic transmitter to caudal peduncle of red drum. Transmitter = Smith Root SR 69. Total length of harness = 190 mm. Inset: Red drum (3.2 kg) with harness and transmitter attached.

The red drum used for testing the harness were caught in the Matanzas Inlet, Fla., by hook and line and maintained in captivity for approximately 2 mo prior to testing.

Results and Discussion

Observations of the suitability of the inelastic harness were conducted in a 3.3-m diameter fiber glass tank, in an enclosed half-acre pond (max depth 2.5 m), and in the Intracoastal Waterway near the Whitney Marine Laboratory. In the fiber glass tank, two red drum (2.5, 3.5 kg) with harnesses and "dummy" transmitters attached swam normally as soon as released and accepted food of shrimp and mullet within 30 min. A third red drum (ca. 3 kg) with harness and active transmitter (Smith Root SR 69) attached was released in the half-acre pond. During the 3-wk lifetime of the batteries in the transmitter, the movements of the fish were monitored almost daily with a receiver and hydrophone. The red drum moved actively about the pond, ate readily, and schooled with other fish. Mangrove roots, pilings, and other obstacles in the pond were not snagged by either the harness or the transmitter. More than 2 mo after the fish was initially released, the harness and inactive transmitter remained in place, and the fish continued to feed and behave normally.

A fourth red drum (3.2 kg) with harness and active transmitter attached was released into the Intracoastal Waterway on 12 January 1976 and tracked continuously for 7 h from a boat with a 74-kHz receiver and hydrophone. The position of the fish with respect to charted channel markers was recorded frequently to provide the summary described below. During the first 1.5 h after release, the fish moved approximately 1.6 km to the south of the release point. This movement was against the direction of the tidal flow. During the remaining time the fish moved 1.2 km to the north, again against the direction of the tidal flow. During this excursion, the fish entered the mouth of almost every creek encountered. At nightfall the fish had moved into a deep hole approximately 140 m up a small creek situated 400 m from the original release point. The fish was not located on the second day but on the third day was located at the edge of the main channel of the Intracoastal Waterway approximately 2 km to the south of the release point. Tracking of the fish had to be discontinued due to a malfunction in the receiver.

For the studies we are initiating on migratory movements of the red drum, the method selected for the attachment of the transmitter was extremely important, and we spent considerable time trying alternative methods. These methods included the hooking of saddles into either the dorsal or ventral musculature, surgical attachment to the pectoral girdle or to the lower jaw bone, surgical implantation into the peritoneal cavity, and insertion into the stomach. Utilization of the inelastic harness provided the following advantages over the other methods we tried.

1. The attachment procedure is simple and quick enough such that only a few minutes elapse between the time the fish is caught, tagged, and released.
2. The procedure results in no bleeding and causes minimal trauma, damage, or weakening of the fish.
3. The attachment is secure and assures that the transmitter remains attached to the red drum for the lifetime of the transmitters we are using (Smith Root SR 69 and SR 69A, lifetimes of 20 and 45 days).

Ichihara (1971) described a "saddle type" method for affixing a transmitter to a fish. This method employed an elastic strap of neoprene rubber that encircled the fish anterior to the dorsal fin. The author noted that fish with elastic harnesses of the saddle type died within 9 to 30 days. Regarding the above observations, we have also found that rubber elastic harnesses encircling the caudal peduncle are unsatisfactory because they constantly compress the peduncle and result in a progressive deterioration of the entire tail region. However, our inelastic harness causes no such deleterious effects. Although we have experimented with the inelastic harness on the red drum only, we are certain that it can be used with any large fish having a fairly rigid tail that is markedly broader than the caudal peduncle.

Acknowledgments

We are grateful to Jack R. Smith, Department of Electrical Engineering, University of Florida, for providing the hydrophone and 74-kHz receiver used in the current study. We also thank Marineland, Inc., for permitting us to use their saltwater pond and other facilities.

Literature Cited

HART, L. G., AND R. C. SUMMERFELT.
1975. Surgical procedures for implanting ultrasonic transmitters into flathead catfish (*Pylodictis olivaris*). Trans. Am. Fish. Soc. 104:56-59.

HENDERSON, H. F., A. D. HASLER, AND G. G. CHIPMAN.
1966. An ultrasonic transmitter for use in studies of movements of fishes. Trans. Am. Fish. Soc. 95:350-356.

ICHIHARA, T.
1971. Ultrasonic, radio tags and various problems in fixing them to marine animal body. Suisancho. Suisan Kenkyusho Gyogyo Shigen Kenkyu Kaigido. 12:29-44 (Translated by Transl. Bur., Foreign Lang. Div., Fish. Res. Board Can., St. Andrews, N.B., Transl. 1981, 38 p.)

OHSUMI, S.
1969. How to attach the telemetry equipment to marine life. Kaiyoseibutsu Telem. Kenkyu Kaiho 2:32-36. Translated by Transl. Bur., Foreign Lang. Div., Fish. Res. Board Can., St. Andrews, N.B., Transl. 1929, 11 p.)

STRASKO, A. B.
1971. Review of field studies on fish orientation. Ann. N.Y. Acad. Sci. 188:12-29.

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1) Page 563, left column, line 8, correct line to read:
   all 11 age-groups for females and using 12 and 11 (deleting oldest)

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