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Fishery Bulletin

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CREPUSCULAR AND NOCTURNAL ACTIVITIES OF CALIFORNIAN NEARSHORE FISHES, WITH CONSIDERATION OF THEIR SCOTOPIC VISUAL PIGMENTS AND THE PHOTIC ENVIRONMENT[1]

EDMUND S. HOBSON,[2] WILLIAM N. MCFARLAND,[3] AND JAMES R. CHESS[2]

ABSTRACT

Activities in 27 of the major southern Californian nearshore fish species, with emphasis on trophic relationships, were studied between 1972 and 1975 at Santa Catalina Island. Because these fishes orient primarily by vision, they are strongly influenced by the underwater photic environment, which we define with representative spectra. We center on crepuscular and nocturnal events, but also describe daytime events for comparison.

The species that feed mostly by day include *Atherinops affinis*, *Paralabrax clathratus*, *Girella nigricans*, *Medialuna californiensis*, *Brachyistius frenatus*, *Cymatogaster aggregata*, *Damalichthys vacca*, *Embiotoca jacksoni*, *Chromis punctipinnis*, *Hypsypops rubicunda*, *Halichoeres semicinctus*, *Oxyjulis californica*, *Semicossyphus pulcher*, *Alloclinus holderi*, *Gibbonsia elegans*, *Heterostichus rostratus*, and *Coryphopterus nicholsi*. Those that feed mostly at night include *Scorpaena guttata*, *Sebastes atrovirens*, *S. serranoides* (subadult), *S. serriceps*, *Xenistius californiensis*, *Seriphus politus*, *Umbrina roncador*, and *Hyperprosopon argenteum*. Those that show no clear diurnal or nocturnal mode include *Leiocottus hirundo* and *Pleuronichthys coenosus*.

Activity patterns tend to be defined less clearly in the warm-temperate fish communities of California than in fish communities of tropical reefs. Included are the twilight patterns of transition between diurnal and nocturnal modes, which are considered to be defined by predation pressures. The lesser definition of twilight patterns in California could mean reduced crepuscular predation there, but we believe that Californian fishes, too, have evolved under severe threats from crepuscular and nocturnal predators. We suggest this is evidenced in the spectral sensitivities of their scotopic visual pigments, which cluster around 500 nm—the best position for vision during twilight and at night in Californian coastal waters.

Although the scotopic system dominates vision in dim light, the spectral sensitivities of the scotopic pigments are poorly matched to the major forms of incident light at night—moonlight and starlight. Rather, they match twilight and bioluminescence, which favor similar spectral sensitivities. We believe this benefits these fishes most on defense. The match with twilight, when the low levels of incident light shift briefly to shorter wavelengths, enhances vision during the crepuscular periods of intensified threats from predators. And the match with bioluminescence permits fishes to react to threatening moves in nocturnal predators by responding to luminescing plankton that fire in the turbulence generated by these moves.

Most fishes that live in southern Californian coastal waters orient by vision, and so are strongly influenced by the characteristics of underwater light at different times of the diel cycle. Knowing that these variations in light are accompanied by differing behavior patterns in the fishes (Hobson and Chess 1976; Ebeling and Bray 1976), we consider here circumstances during twilight and at night, when light is reduced and the fishes' scotopic (dim-light sensitive) visual systems are operating (McFarland and Munz 1975c). A later report will consider circumstances during daylight. We relate the crepuscular and nocturnal activities of the fishes and their scotopic visual pigments to the spectral composition of light in their warm-temperate habitat, and compare these relationships with the similar ties among activities, visual pigments, and light among fishes in tropical waters.

We stress trophic relationships, because we consider these the major forces shaping activity patterns and related sensory systems in these fishes. The species studied are among the more numerous and readily observed in the nearshore warm-temperate eastern Pacific Ocean. Our accounts of

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their activities cover observations over 15 yr in southern California—from San Diego north to Point Conception—but our more detailed observations, along with the light measurements and analysis of visual pigments, refer to Santa Catalina Island (lat. 33°28′N, long. 118°29′W), 35 km from the mainland (Figure 1). Here the water is consistently warmer and more transparent than on the adjacent mainland; during our study surface temperatures ranged between about 11° and 20° C, and underwater visibility generally exceeded 10 m. Thus, when related to comparable data collected earlier in the tropics (Hobson 1968a, 1972, 1974; Munz and McFarland 1973; McFarland and Munz 1975a), these results offer a conservative measure of differences between warm-temperate and tropical habitats.

METHODS

Determining the Spectral Composition of Submarine Sunlight

The spectral distribution of submarine light was measured with a Gamma 3000R spectroradiometer[4] mounted in an underwater housing (Munz and McFarland 1973). The instrument, fitted with a cosine receptor head and calibrated in photons per square centimeter per nanometer per second, draws a quantal irradiance spectrum. Radiance of the backlighting along a particular line of sight was measured by restricting the angle of view of the receptor head to a narrow cone (ca. 0.008 steradians). Usually radiance was determined along the zenith, horizontal, and nadir lines of sight.

Because we were interested in comparing the spectral distribution of submarine light for different water conditions and along different lines of sight, results have been normalized and are presented in terms of relative number of photons. The light levels that occur at twilight were beyond the spectroradiometer's sensitivity for measurement of spectral radiance. At twilight, therefore, spectral irradiance and not spectral radiance was measured. Irradiance data are reported in terms of absolute numbers of photons.

To facilitate comparisons, several of the spectral curves were indexed by calculating their λP_{50} values (Munz and McFarland 1973; McFarland and Munz 1975a). The λP_{50} value represents the wavelength within the visible spectrum (400-700 nm) that halves the total number of photons under a spectral curve. Because underwater light is usually homochromatic and fairly symmetrical in distribution, λP_{50} provides a useful single index to a spectrum.

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

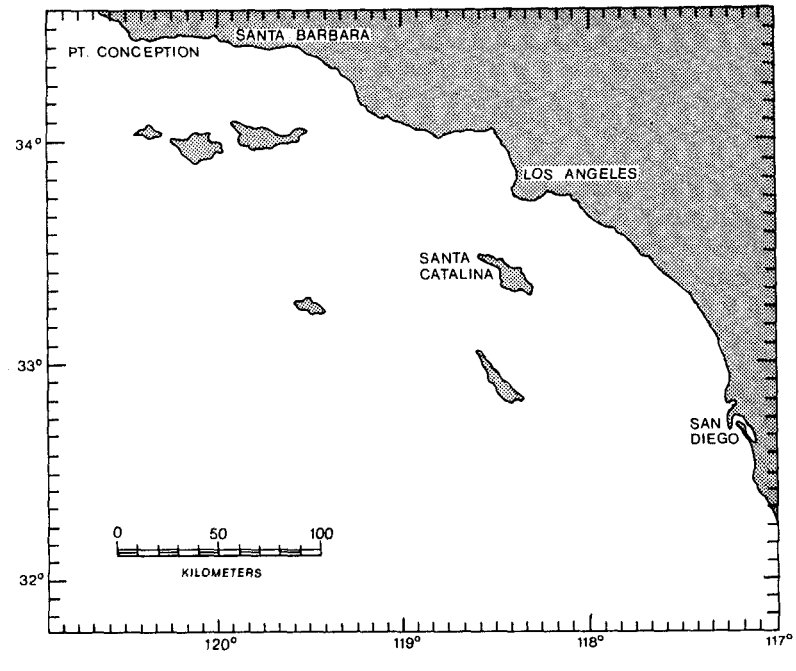

FIGURE 1.—The study area in southern California. Santa Catalina Island was the site of detailed observations, including light measurements and analysis of visual pigments in fishes.

Determining Activity Patterns in Fishes

Our accounts of activity patterns in the fishes stem from direct underwater observations and from study of gut contents. The underwater observations were made using scuba and by snorkeling during all hours of day and night. The gut contents were from fishes speared at all hours of day and night, but primarily during late afternoon and within 2 h before first morning light—times which best distinguish diurnal and nocturnal habits. To study the gut contents, the digestive tract of each fish specimen was removed immediately after collection and preserved in a 10% formaldehyde solution. Analysis under a binocular dissecting scope was performed later in the laboratory. We note in this report only major food items that we believe might add insight to our accounts of diel activity patterns. More detailed accounts of the food habits are given elsewhere (Hobson and Chess 1976; in prep.). All measurements of fish size are of standard length (SL). Although our accounts center on crepuscular and nocturnal events, we describe enough of what happens in daylight to consider these events in the context of diel patterns.

Determining Spectral Photosensitivity of Fishes

Two techniques were used to obtain both fresh, and dark-adapted retinae from the fishes. Some of the specimens were captured alive and dark-adapted under laboratory conditions, whereas others were speared at night and immediately placed in dark containers before being returned to the laboratory for additional treatment. Spectral absorbance characteristics of the visual pigments from these retinae were determined by standard procedures. After each fish was dark-adapted, its eyes were enucleated, the retinae were removed under deep red light (Wratten #2 filter), and then frozen in 4% alum. Later the retinae were thawed, washed in triplicate, centrifuged, and the pellet extracted in 2% digitonin. Sonication of the pellet at 0° C for 1 min assisted solubilization of the visual pigment. After centrifugation, 10% by volume of saturated sodium borate and 10% by volume of 0.2 M hydroxylamine were added to the supernatant and the spectral absorbance of the extracted visual pigment recorded with a Cary 14 spectrophotometer. The method of partial bleaching (Dartnall 1952) was applied to test whether each retinal extract was homogeneous or contained more than one visual pigment. Pigment analysis was assisted by a computer program (Munz and Allen 1968) designed to test for homogeneity and also to characterize each visual pigment by estimation of the wavelength of peak absorbance (λ_{max}). Generally, the major photolabile component in a vertebrate retinal extract is the rod visual pigment, and the minor component(s) is the cone visual pigment(s) (Munz and McFarland 1975; McFarland and Munz 1975b). Thus, in each retinal extract from the Catalina samples the dominant pigment is considered the scotopic (or rod) visual pigment.

UNDERWATER PHOTIC ENVIRONMENT

Coastal waters characteristically absorb light of shorter wavelengths than do oceanic waters because they contain more dissolved organic matter. They also scatter more light due to higher concentrations of suspended particulate matter. As a result, they transmit light of longer wavelengths, and, therefore, under a midday sun appear blue-green, rather than blue like the open sea (see Jerlov 1968 for classification of water types). Starting with these well-established facts, we attempted to characterize the underwater photic environment at Santa Catalina Island.

Submarine Daylight

Midday Spectra

Essentially all submarine daylight meaningful to fishes is produced by the sun. Although photic conditions during midday are not our concern in this paper (they will be considered in a later report), midday spectra effectively illustrate some fundamental aspects of the photic environment that are needed to understand scotopic vision in fishes. In particular, midday spectra can be used to define the spectral transmission characteristics of a given water mass, and so provide means to compare the photic environment in Californian coastal waters with the photic conditions elsewhere, including comparisons of crepuscular and nocturnal circumstances between different habitats.

Californian coastal waters vary greatly in the way they transmit light, and while some of this variation is seasonal, much is shorter term and irregular. At times during our study at Santa Catalina very little suspended material was pres-

ent, and underwater visibility exceeded 20 m, but at other times heavy phytoplankton blooms reduced visibility to <3 m. (We define underwater visibility as the horizontal distance over which we could see major environmental features in daylight.) Most of the time, however, conditions were intermediate between these extremes. Although our irregular observations of visibility do not permit a precise figure, we estimate that at least 70% of the time horizontal visibility in daylight was between 8 and 12 m. The images that we saw in these more typical conditions were relatively sharp—more like images seen in clear water than the relatively fuzzy images seen in turbid water.

So in characterizing the photic environment in the surface waters, we recognize three sets of conditions: 1) clear—when visibility exceeded about 15 m amid relatively small amounts of visible suspended or dissolved materials, 2) bloom—when visibility was less than about 5 m owing to dense phytoplankton, and 3) typical—the more usual condition, when circumstances were intermediate to the above. Thus, when visibility was about 20 m in July 1976, the spectral radiance showed the essential blue-greenness of the water (Figure 2: clear curve), whereas when visibility was about 3 m during a phytoplankton bloom in May 1974, the spectra showed a shift toward the yellow-green

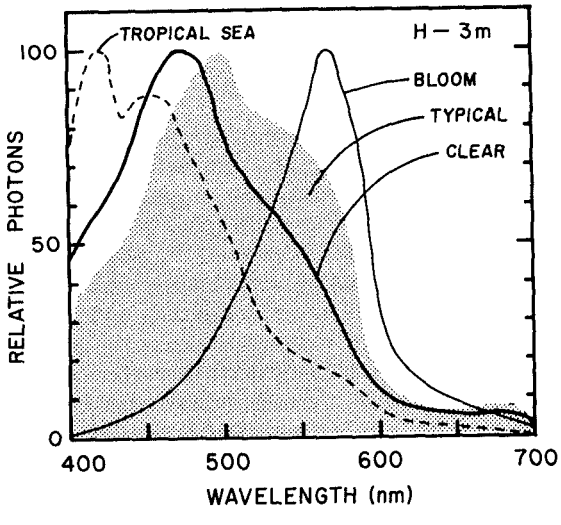

FIGURE 2.—Horizontal spectral radiance in warm-temperate coastal waters (Santa Catalina Island) under typical, bloom, and clear conditions, and in a tropical sea (Enewetak Atoll) under clear conditions. Cosine detector was 3 m below surface oriented horizontally (90° from the zenith). All values normalized, with typical condition at Santa Catalina stippled for emphasis.

wavelengths (with >50% of the photons in the visible spectrum located between 500 and 600 nm; Figure 2: bloom curve). Under bloom conditions, therefore, the radiance was similar to that of lakes rich in plants (McFarland and Munz 1975c). The more usual intermediate condition, however, was closer to the clear than to the bloom condition (Figure 2: typical curve). Nevertheless, even under the clearest conditions encountered at Santa Catalina, the water was greener than it was under similar circumstances in a tropical lagoon (Figure 2: tropical-sea curve).

The spectra depicted in Figure 2 represent a horizontal view, which effectively measures the background spacelight (or horizontal backlighting) against which the fishes studied here see most objects. At the same time we also measured downwelling and upwelling spectra, but they add nothing to the topics considered in this paper that is not illustrated by the horizontal readings. So they will be included in our later paper on photic conditions during midday.

Twilight Spectra

The broad spectrum of downwelling light in near-surface waters at Santa Catalina shifted toward the blue during twilight (Figures 3, 4), even though skylight acquires relatively more red photons at this time. Fading daylight characteristically loses photons between 550 and 700 nm more rapidly than it loses photons below 550 nm, so that as twilight progresses the proportion of photons at the shorter wavelengths steadily increases (McFarland and Munz 1975c; McFarland et al. 1979). The pattern varies in response to changing local conditions, however. For example, on 21 November 1974, events at day's end proceeded typically under a clear sky until shortly after sunset (Figure 3, top and middle panels). At this time, the sky suddenly was covered by a layer of cirrostratus clouds and immediately acquired a red-orange hue (through refraction of the sun's rays). Although we did not record atmospheric spectra at this time, an underwater spectrum recorded 10 min after sunset (Figure 3, bottom panel) was essentially flattened across the visible wavelengths. Other variations in the twilight shift to shorter wavelengths occur under differing water conditions, as exemplified by a weakening of the phenomenon during phytoplankton blooms (Figure 4). The extent of the blue shift during underwater twilight can be measured by the

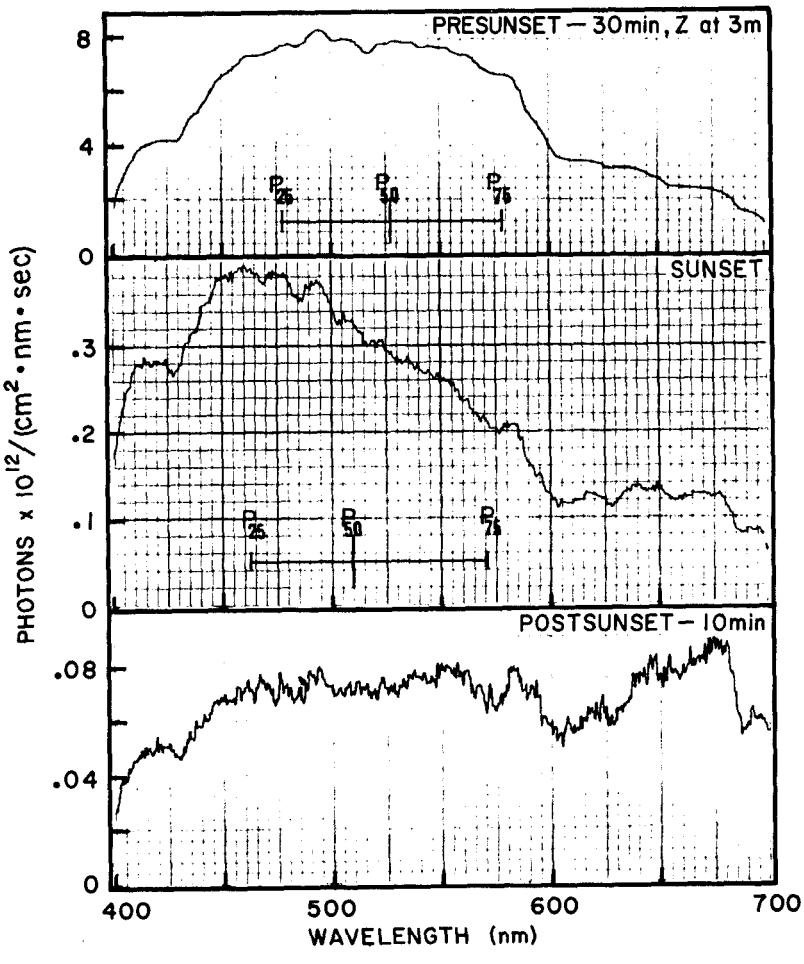

FIGURE 3.—Changes in downwelling submarine spectral irradiance through sunset near the surface at Santa Catalina Island under typical conditions. The shift toward the shorter wavelengths typical of surface waters at sunset (McFarland and Munz 1975c) is apparent in the upper and center graphs, where those wavelengths that divide the number of visible photons into equal quarters are identified by P_{25}, P_{50}, and P_{75}. The bottom graph represents the underwater spectrum when a thin layer of clouds moved over the sky at about 300 m altitude and demonstrates some of the variability that can stem from meteorological events.

changes in λP_{50}. Thus, during our observations under typical conditions, λP_{50} shifted from a pre-sunset value of 527 to 509 nm (Figure 3), and during bloom conditions from 540 to 528 nm (Figure 4). Presumably the λP_{50} would have been closer to 500 nm had we made comparable measurements during twilight when the water was exceptionally clear.

Submarine Nightlight

Moonlight, starlight, and bioluminescence are the major forms of submarine nightlight meaningful to fishes. We did not measure these during the present study, but data available in the literature permit a comparison of the spectra each would be expected to produce in water like that typical of Santa Catalina (Figure 5). The influence of moonlight and starlight on activities in fishes and other aquatic predators has been discussed (e.g., Hobson 1965, 1966). This report considers the role of bioluminescent emissions of epipelagic plankton in predator-prey relationships.

Epipelagic bioluminescent plankton, especially dinoflagellates, are widespread in most neritic and oceanic seas (Tett and Kelley 1973). Sailing narratives and logbooks of open water mariners are replete with descriptions of the "phosphorescent

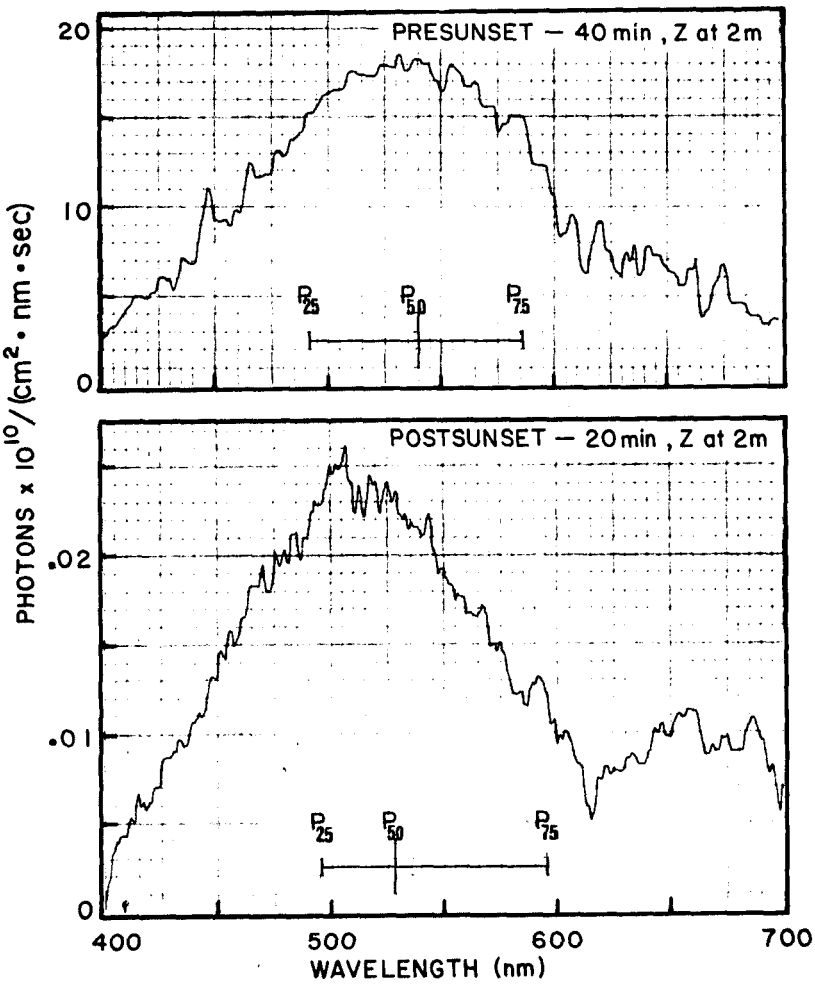

FIGURE 4.—Changes in downwelling submarine light through sunset near the surface at Santa Catalina Island during a phytoplankton bloom. Although there is relatively less blue light under these conditions, a blue shift at and following sunset is nonetheless evident when compared with daylight under bloom conditions (Figure 2). P_{25}, P_{50}, and P_{75} identify those wavelengths that divide the number of visible photons into equal quarters.

fire" of the ship's wake, the luminescent shroud about porpoises running before the bow, and the showers of sparks that trail fishes dashing below the hull. At Santa Catalina Island, bioluminescence from plankton was visible in the water at all times of the year, more so at some times than at others.

Most marine bioluminescent plankton emit light in the blue region of the spectrum (Tett and Kelley 1973). For example, light from *Gonyaulax polyedra* and *Noctiluca miliaris* (which is representative of most dinoflagellates) peaks near 475 nm, and more than half of the photons are emitted below 500 nm (Hastings and Sweeney 1957; Nicol 1958). Because of the skewed emission spectra from these organisms (Figure 6), however, fishes close to the luminescent source would absorb more photons with visual pigments that have λ_{max} values nearer 490 nm than 475 nm.

In any event, the spectral quality of bioluminescence received by the fishes is modified by two variables—distance the fishes are from the light's source, and clarity of the intervening water. Because the water more effectively absorbs the longer than the shorter wavelengths, a fish farther from a target in clear water will receive relatively more photons at the shorter wavelengths (Figure 6, upper panel). Water clarity, however, has an

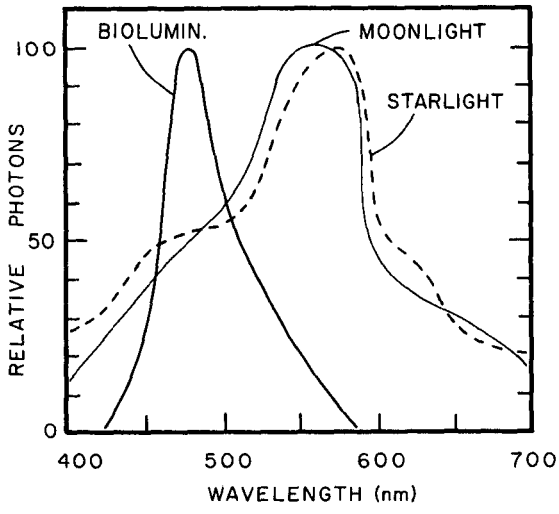

FIGURE 5.—Underwater spectral distributions of moonlight, starlight, and bioluminescence. Values for bioluminescence are for *Noctiluca miliaris*, as given by Nicol (1958), at zero range. Values for moonlight and starlight, based on measurements in Munz and McFarland (1977), are for downwelling light at zero range from a flat spectral reflector at a depth of 3 m in water equivalent to typical conditions at Santa Catalina Island (Jerlov 1968, Coastal Type 1).

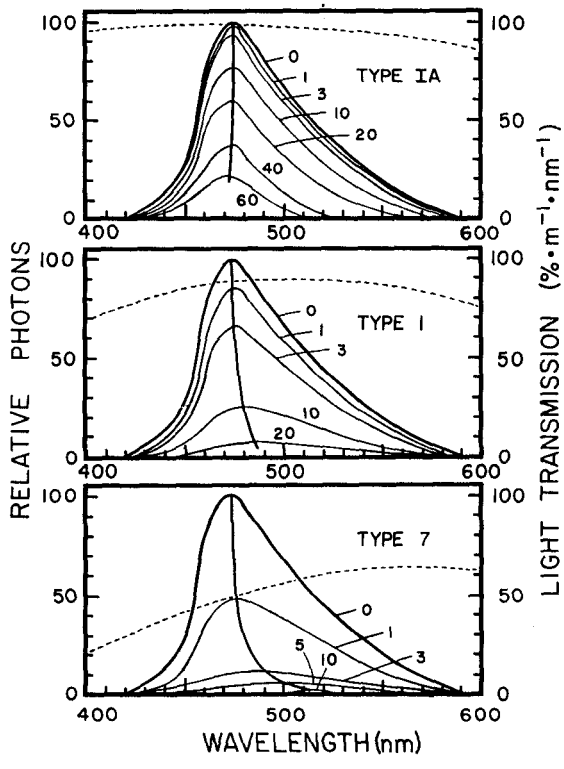

FIGURE 6.—Attenuation and spectral distribution of light emitted by *Noctiluca miliaris* over distance in water of differing clarities. The three panels of the figure each represent a different water type (clarity), as defined by Jerlov (1968): Type 1A (upper) is equivalent to clear tropical seas; Coastal Type 1 (middle) is equivalent to typical conditions at Santa Catalina Island; and Coastal Type 7 (lower) is equivalent to conditions of heavy phytoplankton bloom at Santa Catalina. The heavy outer curve in each panel represents the light emitted by *N. miliaris* (left axes) at zero range, and so is the same in each water type. The inner curves in each panel represent relative attenuation of light at distances (in meters) indicated by the accompanying numbers. The broken line in each panel represents the transmission values/meter (right axes) for that water type, as given by Jerlov (1968).

even greater effect than distance on the attenuation and spectral modification of submarine light. In the typical water we encountered at Santa Catalina, for example, there was a fairly high transmission of light between 425 and 575 nm. As light travels from a source like *N. miliaris* under these conditions its radiance attenuates slowly and its spectrum shifts only slightly (Figure 6, middle panel). On the other hand, as the same light travels through water heavily loaded with phytoplankton it attenuates rapidly and there is a marked and continuous spectral shift toward the green (Figure 6, lower panel).

ACTIVITY PATTERNS AND VISUAL PIGMENTS IN FISHES

Because the photic environment contrasts sharply between day and night, those visually orienting fishes that are adapted to diurnal conditions should be less suited to feed after dark, while those adapted to nocturnal conditions should be less suited to feed by day. This expectation has been supported in studies of temperate species, both marine (Hobson and Chess 1976; Ebeling and Bray 1976) and freshwater (Emery 1973; Helfman 1979), just as it has in studies of marine fishes in the tropics (Hobson 1965, 1968a, 1972, 1974, 1975; Starck and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972; Vivien 1973). Thus, in considering the impact of diel variations in the photic environment it is meaningful to distinguish diurnal and nocturnal species, even though some nearshore fishes feed at all hours—many by changing their food or tactics between day and night, e.g., the serranids *Epinephelus labriformis* in the Gulf of California (Hobson 1968a) and *E. merra* in the Indian Ocean (Harmelin-Vivien and Bouchon 1976) and the mullid *Parupeneus bifasciatus* in Hawaii (Hobson 1974).

We consider 27 of the most abundant fish species in the nearshore waters at Santa Catalina Island, describing what each does during twilight and at night, and noting the wavelengths of light to which the scotopic system of each is most sensitive (λ_{max}). In examining the retinae from the fishes, we noted whether the visual pigments were homogeneous. Significantly, there were no secondary pigments in 12 species and only a trace in 5. Secondary pigments, which presumably are cone pigments (Munz and McFarland 1975), were present in 10 species and abundant in only 3. The data are given below, grouped according to that segment of the diel cycle when the species obtains most of its food. It is important that we observed only slight variation in the λ_{max} of any one species.

TABLE 1.—Some southern Californian marine fishes that feed primarily by day, with the spectral absorbance maximum (λ_{max}) of pigments extracted from their retinae.

Family and species	λ_{max} ±95% C.I.	N	Other pigments[1]
Atherinidae:			
Atherinops affinis[2]	505.8	2	0
Serranidae:			
Paralabrax clathratus[2]	498.8±2.0	4	+
Kyphosidae:			
Girella nigricans	498.3±1.0	3	0
Medialuna californiensis	496.9	2	+
Embiotocidae:			
Brachyistius frenatus	500.9±0.5	3	0
Cymatogaster aggregata	500.4±4.0	3	+
Damalichthys vacca	500.9	2	+
Embiotoca jacksoni[2]	500.8	2	+
Pomacentridae:			
Chromis punctipinnis[2]	496.1	1	+
Hypsypops rubicunda	496.3±0.1	3	0
Labridae:			
Halichoeres semicinctus[3]	513.2±7.4	3	++
Oxyjulis californica[3]	511.8	1	++
Semicossyphus pulcher[2]	496.7±3.5	3	++
Clinidae:			
Alloclinus holderi	496.5	2	0
Gibbonsia elegans	499.7±8.9	3	+
Heterostichus rostratus	499.7±2.0	4	T
Gobiidae:			
Coryphopterus nicholsi[2]	497.9	1	0
Mean[4]	499.1		
Range[4]	496.1-505.8		

[1]Other than the primary pigment: 0 = none; T = trace; + = <10%; ++ = >10%.
[2]Visual pigments for these species were also studied by Munz (1957, 1958b, c, 1964). He reported similar λ_{max} values for all but *E. jacksoni*, which he listed (Munz 1958b) as 506 nm. The difference can be attributed to varying amounts of secondary pigments in his extracts, which can bias the λ_{max} estimates if not taken into account.
[3]Visual pigments in these species are porphyropsins, which are based on the aldehyde of Vitamin A_2. Pigments in all other species are rhodopsins, which are based on the aldehyde of Vitamin A_1.
[4]*Halichoeres semicinctus* and *O. californica* excluded owing to basic differences in their pigments (see footnote 3, above).

Fishes That Feed Primarily by Day

Some of the fishes that feed primarily by day are known to be inactive at night, but evidence of nocturnal inactivity remains lacking for others, and still others are known to feed routinely after dark. The predominantly diurnal Californian fishes considered in this paper, along with certain of their visual characteristics, are listed in Table 1. The following accounts of diel activities emphasize crepuscular and nocturnal habits.

Atherinidae: *Atherinops affinis*

The topsmelt aggregates by day in the surface waters close to kelp forests, but at night most larger individuals move away from the kelp and disperse close beneath the water's surface over adjacent deeper water. At first we suspected these larger individuals might feed after dark. Their movements are similar to those of tropical Pacific atherinids of the genus *Pranesus*, which are known to be nocturnal feeders (Hobson and Chess 1973; Hobson 1974; Major 1977), and nocturnal habits are widespread in other planktivorous atherinids, including *Allanetta harringtonensis* in the tropical Atlantic Ocean (Starck and Davis 1966). Furthermore, we have often seen *Atherinops affinis* feed at night next to illuminated piers, although we consider this an artificial situation.

Despite the evidence of nocturnal feeding in other atherinids, however, our suspicions concerning *A. affinis* were contradicted by examination of gut contents. Of 22 individuals (129-219 mm SL, $\bar{x}$ = 168.8) collected at dawn as they reassembled in schools along the outer edge of kelp forests, 19 were empty, 2 contained just a few fish scales, and 1 contained calanoids and cyphonautes larvae that appeared recently ingested—probably since sunrise that morning. At least some of the smaller *A. affinis* remain close to the kelp at night, but there is little evidence that they feed during that period. Of 10 (82-160 mm SL, $\bar{x}$ = 102.4) collected close to kelp during the hour before dawn, 9 were empty. The one with food, however, contained three gammarids and one isopod that obviously had been taken at night. In contrast, there is ample evidence that *A. affinis* feeds intensively during the day. We routinely observed this species feeding in the surface waters during all daylight hours, and only 1 of 10 (126-190 mm SL, $\bar{x}$ = 158.6) collected from a large aggregation during midafternoon lacked food in its gut; the other 9 contained $\bar{x}$ = 1,325 prey items, mostly cladocerans and copepods.

Serranidae: *Paralabrax clathratus*

The kelp bass progresses through three major ontogenetic phases based on trophic relationships. The first phase includes juveniles up to about 65 mm SL that feed primarily on zooplankton during the day and pass the night sheltered amid vegetation. The third phase includes the largest individuals—those exceeding about 165 mm SL—which are increasingly piscivorous with growth and may be primarily crepuscular (although limitations in our data leave the feeding chronology at this larger size in question).

In this paper we consider individuals representing the second phase—subadult fish between 65 and 165 mm SL. Individuals of this size feed mostly on crustaceans that live on or close to a substrate by day and swim in the water column after dark, including certain gammarid and caprellid amphipods, isopods, cumaceans, mysids, and carideans. The subadult *P. clathratus* capture these crustaceans mainly by day close to benthic cover. Most subadult *P. clathratus* do not feed at night. Only 42% (13 of 31, 72-163 mm SL, $\bar{x}$ = 110.3) of those collected during the hour before sunrise contained prey, whereas there was prey in 96% (51 of 53, 68-153 mm SL, $\bar{x}$ = 107.9) of those collected during the afternoon.

Whether or not the subadult *P. clathratus* feeds at night, however, seems related to their location. Most of them are amid rocks and vegetation at night, just as during the day, and here they seem to feed little, if at all. Of 16 (95-146 mm SL, $\bar{x}$ = 108.6) collected in these surroundings during the hour before dawn, only 1 (6%) had food in its stomach (a moderately digested caridean). Nocturnal feeding in subadult *P. clathratus* seems to occur mostly in those individuals that move after dark out over open sand (Figure 7)—a habitat only infrequently occupied by them during the day. Of the 16 (72-148 mm SL, $\bar{x}$ = 97.4) collected in such places during the hour before dawn 12 (75%) contained food, much of it fresh. Major prey were the cumacean *Cyclaspis nubila* (4 mm), the gammarids *Ampelisca cristata* (3-4 mm) and *Amphideutopus oculatus* (2-3 mm), and the caprellid *Caprella californica* (6-8 mm)—all species that are active on or close above the sand at night. Clearly, the nocturnal move over the sand is a well established feeding pattern in subadult *P. clathratus*. Nevertheless, even under these special circumstances predatory success after dark seems limited. Among specimens from open sand at night the stomachs containing food averaged only 30% full, compared with 66% full for specimens from a wide range of diurnal circumstances.

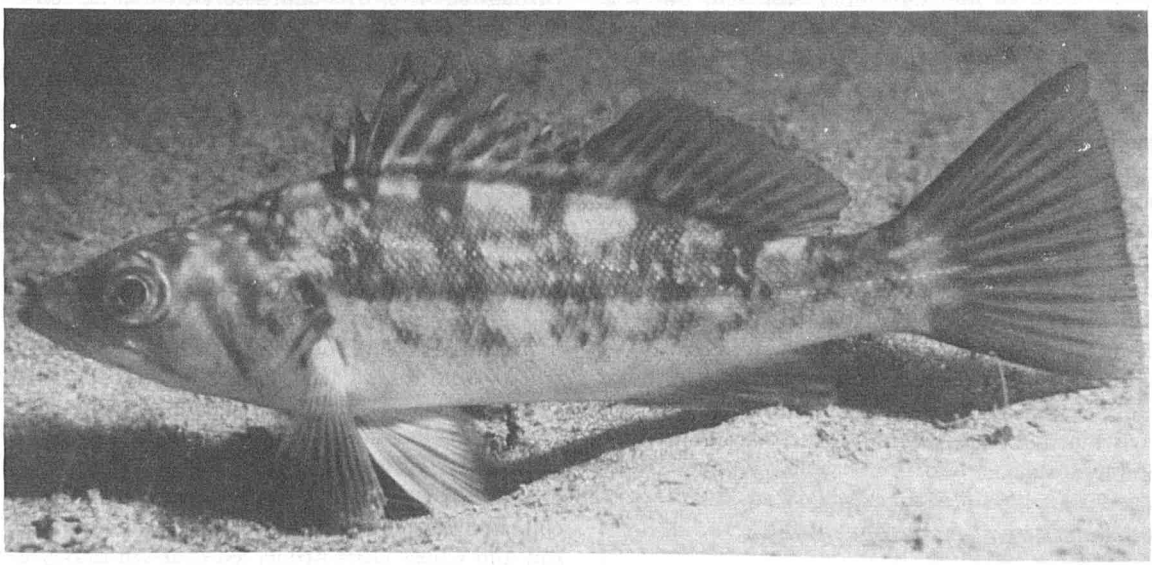

FIGURE 7.—A subadult *Paralabrax clathratus*, about 150 mm SL, alert on open sand at night. Some individuals of this size feed under these circumstances even while larger and smaller conspecifics are inactive close to rocks and algae. Apparently the sand reflects enough moonlight and starlight to permit some predominantly diurnal fishes to feed in these surroundings at night.

Kyphosidae: *Girella nigricans*

The opaleye does not seem to feed extensively at night, although our limited observations on this point are somewhat ambiguous. This rather tenuous opinion rests heavily on two points. First, the species feeds largely on algae, and various organisms that live on algae—a diet generally indicative of diurnal feeding (Hobson 1965, 1974; Vivien 1973). Second, kyphosids generally have been found to feed by day (e.g., Randall 1967). On the other hand, observations of kyphosids at night have indicated a variable condition. *Kyphosus incisor* reportedly rests "...in sheltered, though not confined, locations on the reef-top" in the Florida Keys (Starck and Davis 1966), and *K. elegans* has been noted to behave similarly in the Gulf of California (E. S. Hobson unpubl. obs.). But *K. elegans*, at least, is alert in these shelters, and *K. cinerascens* in Hawaii not only swims above the reef at night, but may feed at this time as well (Hobson 1974). The presence of *G. nigricans* "...in holes or on the bottom..." at night led Ebeling and Bray (1976) to consider it diurnal. We agree with them even though we frequently saw this species swimming in the water column after dark, especially in the kelp forest.

Limited study of gut contents suggest reduced feeding in some *G. nigricans* at night. One (201 mm) sampled among the rocks during the hour before sunrise had an empty stomach, but the stomach of another (264 mm) that was swimming above the bottom at this time was 20% full. Sixty-seven percent of the gut contents in this second individual consisted of motile animals, including gammarids, caprellids, carideans, and the gastropod *Tricolia* sp., whereas only 10% consisted of algae. This material, much of it fresh, differed sharply from that in gut contents of individuals that had been feeding by day. Benthic algae constituted 81% of the material in all 11 individuals (173-255 mm SL, $\bar{x}$ = 206) that were collected during the afternoon, and whose stomachs averaged 75% full; essentially all other items in these individuals were sessile organisms that encrust, or live attached to, algae—principally bryozoans and hydroids.

Kyphosidae: *Medialuna californiensis*

We consider the halfmoon primarily diurnal for essentially the same tenuous reasons that led us to this conclusion for *G. nigricans*: many of its close relatives reportedly are diurnal, as documented above, and it feeds heavily on plants (Limbaugh 1955; Quast 1968), a diet widely associated with diurnal foraging. Furthermore, we saw *M. californiensis*, like *G. nigricans*, in the water column in far fewer numbers at night than during the day. But although we saw *G. nigricans* in larger numbers close to rocky substrata at night, we saw *M. californiensis*, which was exceptionally numerous in the kelp forests by day, only in sharply reduced numbers there after dark. Reporting a similar situation in a kelp forest at Santa Barbara, Ebeling and Bray (1976) observed about half as many *M. californiensis* on their transect line at night as during the day. They summarized their nocturnal observations by stating that this species "...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." Leading to much the same position, our study of gut contents from 14 specimens (146-243 mm SL, $\bar{x}$ = 196) collected during the afternoon (Hobson and Chess in prep.) shows that this largely herbivorous species unquestionably feeds by day, but leaves unanswered whether or not it also feeds at night.

Embiotocidae: *Brachyistius frenatus*

Although the kelp perch is basically diurnal throughout life, this characteristic can be somewhat variable. When less than about 100 mm SL it feeds primarily on zooplankters in the water column, and as it grows larger it increasingly turns to tiny prey—mostly crustaceans—that it picks from vegetation (Hobson and Chess 1976). At night it occurs in most of the same places that it occupies by day, but is more numerous in midwater aggregations fully exposed along the outer edges of the kelp forests (Hobson and Chess 1976). Describing the nocturnal condition of this species, Bray and Ebeling (1975) noticed that it "...tended to hang motionlessly along the kelp stipes or even in open water" and added that it was "...quiescent at night and easily caught with a small hand net...." They concluded that *B. frenatus* feeds "...mostly, if not exclusively, during the day"—an opinion based on study of gut contents from specimens collected every 2 h throughout the night. But Hobson and Chess (1976) reported that while *B. frenatus* is primarily diurnal, larger individuals also feed to a limited extent at night. In addition to the data presented in that paper, all of which involved

specimens <100 mm long, 6 of 14 (102-114 mm SL, $\bar{x}$ = 106.8) collected during the hour before dawn contained prey, many of them fresh. The major nocturnal prey, which included the gammarid *Batea transversa* (2-4 mm), the caprellid *Caprella californica* (8-14 mm), and the isopod *Paracercies cordata* (1-6 mm), were organisms that rise into the water column at night. We believe these prey were captured in the water column because most were in fish that had been aggregated in midwater outside the seaward edge of a kelp forest. Perhaps Bray and Ebeling (1975) found no evidence of nocturnal feeding because their sample comprised mostly smaller fish. Significantly, the major organisms apparently taken in the water column at night include the same species picked from the surface of algae by day.

Embiotocidae: *Cymatogaster aggregata*

The shiner perch, which is even more variable in its diel behavior than *Brachyistius frenatus*, has two basic feeding modes: it captures zooplankton, mostly crustaceans, in the water column, and it captures organisms, again mostly crustaceans, that are in, on, or close above a sandy bottom. The planktivorous habit predominates among individuals smaller than about 65 mm SL and continues to be important throughout life, whereas feeding on sand-dwelling forms becomes increasingly important to individuals >65 mm SL until it predominates among the largest individuals. The planktivorous habit is diurnal, whereas feeding on or close to a sandy bottom occurs during both day and night, but mostly at night.

Thus, the small juveniles are primarily day feeders: of 23 (53-64 mm SL, $\bar{x}$ = 58.2) collected during the afternoon, 12 (53%) contained food, the major items being zooplankters (mostly copepods). Only two (12%) also included prey that may have been taken from the seafloor (gammarid fragments). In comparison, only 2 of 17 (37-64 mm SL, $\bar{x}$ = 46.5) collected during the hour before dawn contained food: one (58 mm) contained just a few cumacean fragments, but the other (54 mm) contained a variety of sand-dwelling crustaceans, some fresh, including the cumacean *Cyclaspis nubila* (2-4 mm), the gammarid *Acuminodeutopus heteruropus* (1-2 mm), and the tanaid *Leptochelia dubia* (2-4 mm), along with sand.

The changes in food habits that appear among individuals >65 mm SL were similarly defined. Of 34 (67-110 mm SL, $\bar{x}$ = 91.8) collected during the afternoon, 27 (79%) contained food presumably taken by day: 19 (70%) of these had fed exclusively on zooplankton (primarily calanoid and cyclopoid copepods and cladocerans), 4 (15%) had taken only sand-dwellers (primarily tanaids and gammarids), and 4 (15%) had fed on both zooplankton and sand-dwellers in large numbers (combinations of the above forms, with the two types sharply separated in the guts). In comparison, of 46 (66-120 mm SL, $\bar{x}$ = 85.9) collected during the hour before dawn, 37 (80%) contained prey, many fresh, that appeared for the most part to have been taken at night. Significantly, all these prey were sand-dwellers, the major forms being the cumacean *Cyclaspis nubila* (2-4 mm), the gammarids *Acuminodeutopus heteruropus* (1-2 mm) and *Ampelisca christata* (2-4 mm), the tanaid *Leptochelia dubia* (3-4 mm), and the ostracod *Euphilomedes carcharondonta* (1-2 mm), along with sand.

Embiotocidae: *Damalichthys vacca* and *Embiotoca jacksoni*

Damalichthys vacca, the pile perch, and *E. jacksoni*, the black perch, both appear to be strictly diurnal feeders. During daytime, adults of *D. vacca* feed primarily on mollusks and other heavily shelled prey, whereas adults of *E. jacksoni* take an exceptionally wide variety of benthic organisms, including polychaetes, mollusks, gammarids, caprellids, isopods, and mysids (Limbaugh 1955; Quast 1968). At night we observed both species hovering close to the seafloor, generally in exposed positions. On the other hand, Ebeling and Bray (1976) reported *D. vacca* "... scattered in the water column at night." That neither species feeds after dark is evidenced by the absence of fresh food in their guts at that time (Ebeling and Bray 1976).

Pomacentridae: *Hypsypops rubicunda* and *Chromis punctipinnis*

Although the Californian pomacentrids—*H. rubicunda*, the garibaldi, and *C. punctipinnis*, the blacksmith—are strictly diurnal fishes that remain relatively inactive in their nocturnal shelters, they nevertheless remain alert throughout the night. *Hypsypops rubicunda*, in fact, often appears restless as it moves in its shelter place. This species is solitary during both day and night, and its nocturnal shelter is a specific hole or crevice in the well-defined territory that also includes its

diurnal foraging area (Clarke 1970). In contrast, *C. punctipinnis* is highly gregarious during both day and night, and often individuals crowd nocturnal shelters among the rocks. When its nocturnal resting places are far from its diurnal feeding grounds, *C. punctipinnis* migrates between the two locations during twilight in prominent processions (Hobson and Chess 1976). These migrations tend to be better defined in the evening than in the morning. At times evening migrations began up to 30 min or more before sunset, while at other times they were not evident until about sunset. Generally, however, the migrations peaked from shortly before sunset until about 15 min after, and then continued at greatly reduced levels for another 10 min or so before ending.

Chromis punctipinnis is among the most numerous species on many nearshore reefs in southern California (Limbaugh 1955; Quast 1968), and in some places apparently there is insufficient rocky shelter to accommodate at night the vast numbers that forage in the water column by day. In such places excess individuals sometimes cluster after dark in dense numbers on the sand next to the reef. Occasionally *C. punctipinnis* is in the water column at night, but does not seem to feed at this time. This is attested by the empty stomachs of all 11 specimens examined from predawn collections by Hobson and Chess (1976).

Labridae: *Oxyjulis californica*, *Halichoeres semicinctus*, and *Semicossyphus pulcher*

The Californian labrids are so obviously quiescent at night that we have no doubt that, like tropical labrids (Hobson 1965, 1974), they do not feed at this time. Also, like their tropical relatives, they follow precise patterns when shifting between diurnal and nocturnal modes (Hobson 1972; Domm and Domm 1973). *Oxyjulis californica*, the señorita, buries in the sand at nightfall (Herald 1961), a habit also attributed to *H. semicinctus*, the rock wrasse, by Limbaugh (1955), who noted that this species "sleeps buried with head protruding." Feder et al. (1974) repeated this statement, as did Fitch and Lavenberg (1975), who reported that it also "burrows between or under rocks to escape predators or to sleep." We found that *H. semicinctus* consistently took nocturnal shelter amid low benthic algae (from which it often was unintentionally flushed by our nocturnal activities). Both *O. californica* and *H. semicinctus* were consistent in timing their descent to shelter in the evening, and their rise into the water the next morning. Data on the timing of these events were collected during 1973 and 1974 at Fisherman's Cove, Santa Catalina Island, in a sand-bottomed habitat dominated by the low brown alga *Dictyopteris zonaroides*. The last *O. californica* seen entering the sand on four evenings at this site slipped from view 11-22, $\bar{x}$ = 16.8, min after sunset, which agrees with Bray and Ebeling (1975), who on three occasions observed this species entering sand and rubble "About 15 min after sunset...." The first *O. californica* seen here on 11 mornings appeared 11-22, $\bar{x}$ = 15.8, min before sunrise. During the same period at this site the last *H. semicinctus* seen taking cover on six evenings disappeared 20-24, $\bar{x}$ = 22.0, min after sunset, and the first to appear on 10 mornings emerged 18-25, $\bar{x}$ = 22.8, min before sunrise. It may be significant that *H. semicinctus*, which grows to a larger size, tended to be active later in the evening and earlier in the morning. Among diurnal fishes on tropical reefs, the larger individuals tend to retire later and rise earlier (Hobson 1972). Comparable data are lacking for *S. pulcher*, the sheephead (the largest of the three Californian labrids), even though this species was numerous at the observation site during the day. *Semicossyphus pulcher* shelters among rocks at night (Hobson 1968b), and probably because the observation site lacked rocks, this species left the area sometime before going under cover. On 4 evenings the last *S. pulcher* departed the observation site 10-21, $\bar{x}$ = 18.0, min after sunset, and on 11 mornings the first to return arrived 11-24, $\bar{x}$ = 17.0, min before sunrise. On just one evening, in a nearby rocky area where the species found shelter, the last active *S. pulcher* was seen 30 min after sunset.

Because *S. pulcher* rested in distinctive shelters and was visible throughout the night (Figure 8), it offered the best opportunity to investigate consistency in resting places among individuals. Reportedly, at least some tropical wrasses return each evening to specific resting sites (Winn and Bardach 1960; Starck and Davis 1966; Hobson 1972). So the resting places of nine *S. pulcher* were located at midnight during November 1973, and then revisited at the same hour once each week for 3 wk. On the first return only two of the nine positions were occupied, No. 3 and No. 5—both by what appeared to be the same individuals that had been there before. On the second return, again only two positions were occupied: No. 5 seemed to

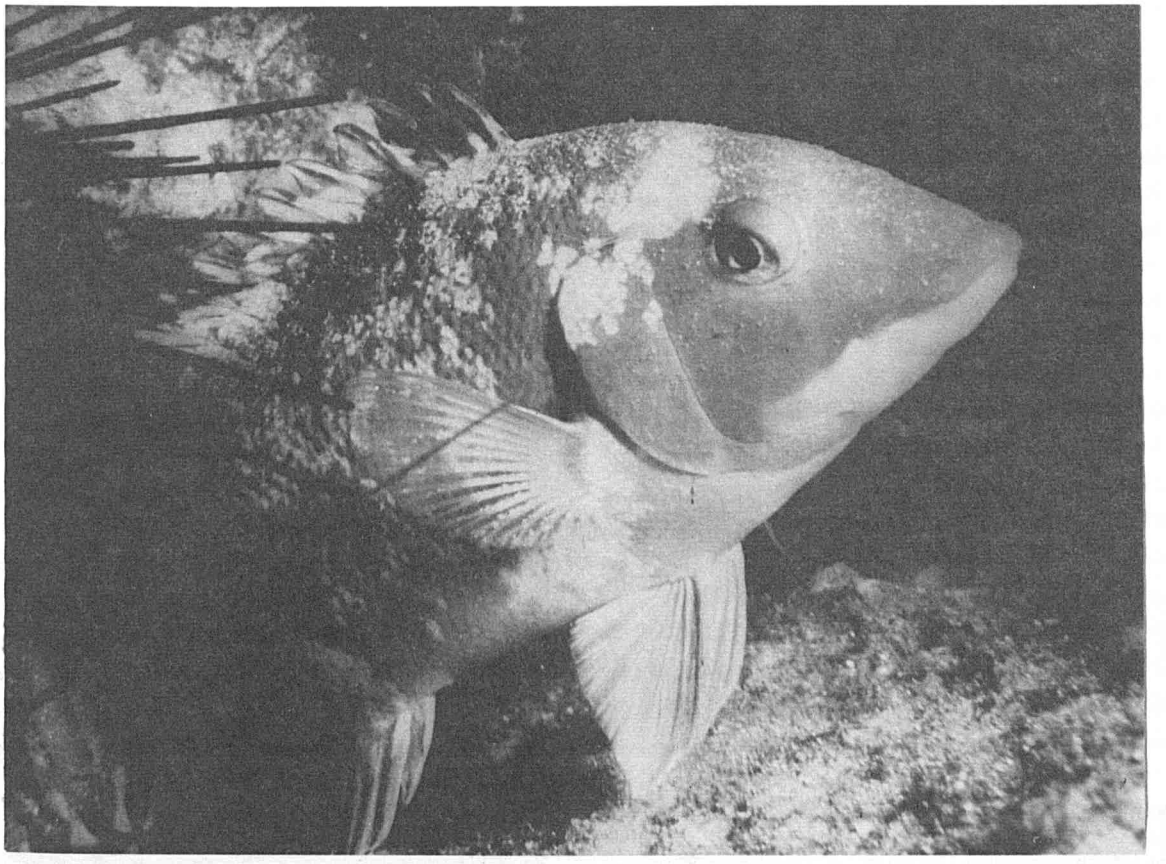

FIGURE 8.—A female *Semicossyphus pulcher* at rest on the seafloor at night, showing the typical pattern of its nocturnal hues. Its exposed position is common in this and many other nocturnally resting diurnal fishes in California.

harbor the same fish as before, but this time position No. 1 contained a small individual not seen before. On the final return, position No. 5 once more was occupied by what seemed to be the same fish. Again, just one other position was filled—No. 6, which harbored the fish seen in position No. 9 on the first night (recognized by a notch in its dorsal fin), but which had gone unseen since then. Thus, only one position, No. 5, sheltered a fish each time. And contrary to what one might expect, of the nine positions, No. 5 offered the least cover. It was simply a shallow depression on the reeftop where the resting fish was largely exposed, and certainly would not seem an effective shelter.

Clinidae: *Alloclinus holderi*, *Gibbonsia elegans*, and *Heterostichus rostratus*

The three Californian clinids studied here—*A. holderi*, the island kelpfish; *G. elegans*, the spotted kelpfish; and *H. rostratus*, the giant kelpfish—are known to feed regularly by day, based on fresh food in specimens collected during the afternoon (Hobson and Chess in prep.). But it is difficult to determine relative activity in these highly cryptic fishes because they move so infrequently and, therefore, often go unnoticed even when fully exposed. Both *A. holderi*, which sits on rocks, and *G. elegans*, which sits amid benthic algae, retire to shelter at nightfall, as do various tropical clinids (Starck and Davis 1966; Smith and Tyler 1972). *Heterostichus rostratus*, on the other hand, often hovers among columns of giant kelp during both day and night (Figure 9). Our data comparing relative feeding activity in *H. rostratus* between day and night are limited, but indicate that daytime feeding predominates. The one individual (184 mm) collected during the hour before sunrise

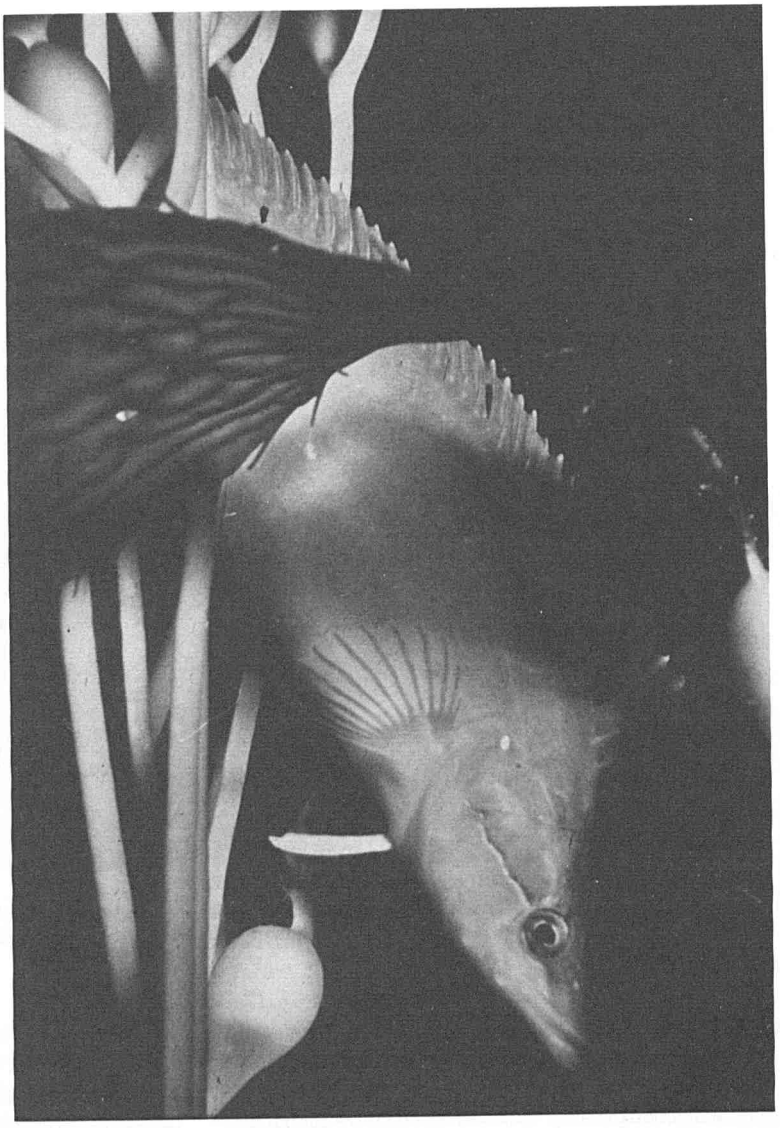

FIGURE 9.—While most of its smaller blennioid relatives go under cover at nightfall, the large clinid *Heterostichus rostratus*, here amid rising kelp stipes at night, shows a similar attitude at all hours, even though it seems to feed primarily by day.

was empty, and the two (163 and 207 mm) collected at midnight contained only well digested fragments. In comparison, among eight individuals (234-385 mm SL, $\bar{x}$ = 280) collected during midafternoon, four contained fresh food, one contained only well digested fragments, and three were empty.

Gobiidae: *Coryphopterus nicholsi*

Large numbers of the blackeye goby rested in exposed positions on sand bottoms in and around rocks throughout the day, when intermittently, they darted forward, or a short distance into the water column, and snapped at tiny prey. Few, however, were visible at night. Presumably most sheltered in the reef after dark—a pattern reportedly followed by four species of *Coryphopterus* in the tropical Atlantic Ocean (Smith and Tyler 1972). Gut contents indicate this species feeds little, if at all, after dark. Among the few individuals seen at night, seven (43-83 mm SL, $\bar{x}$ = 59.3) were collected during the hour before the first morning light; the gut of one was empty, and the other six contained only well digested items. In comparison, all 69 specimens (36-90 mm SL, $\bar{x}$ = 64.1) collected

during the afternoon had food in their guts, with 31 of these (88%) containing recently ingested material.

Fishes That Feed Primarily at Night

The fishes that feed primarily at night clearly are specialized to detect and capture prey in the dark; nevertheless, under appropriate circumstances some also take prey during the day. The predominantly nocturnal species considered in this paper, with certain of their visual characteristics, are listed in Table 2. The following accounts of diel activities highlights major features of their crepuscular and nocturnal habits.

TABLE 2.—Some southern Californian fishes that feed primarily at night, with the spectral absorbance maximum (λ_{max}) of pigments extracted from their retinae.

Family and species	$\lambda_{max} \pm 95\%$ C.I.	N	Other pigments[1]
Scorpaenidae:			
Scorpaena guttata[2]	496.7	2	0
Sebastes atrovirens	497.5	2	+
S. serranoides (subadult)	501.3	2	+
S. serriceps	496.4±1.0	3	0
Haemulidae:			
Xenistius californiensis	501.8±0.4	2	T
Sciaenidae:			
Seriphus politus[2]	502.2±1.5	3	0
Umbrina roncador	503.1±0.4	3	0
Embiotocidae:			
Hyperprosopon argenteum[2]	505.1±0.9	7	0
Mean	501.0		
Range	496.4-505.1		

[1]See Table 1, footnote 1.
[2]See Table 1, footnote 2.

Scorpaenidae: *Scorpaena guttata*

The sculpin rests immobile among rocks during the day (Figure 10) and generally is difficult to discern owing to its cryptic features. Although Limbaugh (1955) noted *S. guttata* on open sandy bottoms in deeper (to 60 m) water during the day, at our study sites it generally occurred among rocks. This fish seems well suited by its cryptic and immobile attitude to ambush prey that have come

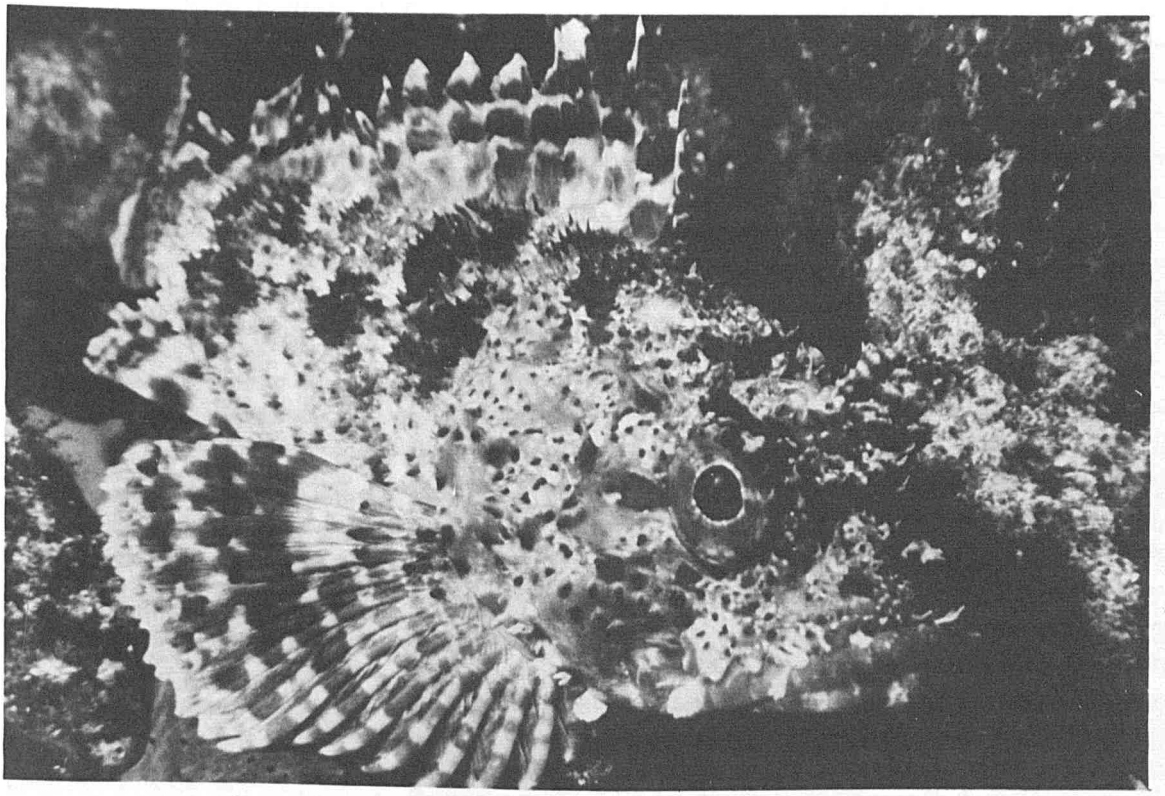

FIGURE 10.—The morphology, coloration, and sedentary behavior of *Scorpaena guttata* render it virtually invisible on the seafloor. Although many tropical scorpaenids use these features to advantage in ambushing prey during the day, *S. guttata* is primarily nocturnal.

within range of a short, explosive rush—a tactic used during the day by the Hawaiian scorpaenid, *Scorpaenopsis cacopsis*, which is similarly cryptic (Hobson 1974). Based on gut contents, however, *Scorpaena guttata* seems to capture most of its prey at night. All seven specimens (140-270 mm SL, $\bar{x}$ = 213) collected during the hour before dawn contained prey, many of them fresh. Major items were the crab *Podochelia* sp. (7 mm), the shrimps *Lysmata californica* (50 mm) and *Spirontocaris* sp. (15 mm), and the squid *Loligo opalescens* (120-190 mm), a species that was spawning in the area at the time. One *Scorpaena guttata* had captured a 108 mm *Chromis punctipinnis*, a species that shelters among the rocks at night (see above). In comparison, of seven individuals (164-237 mm SL, $\bar{x}$ = 208.3) collected among the rocks during mid-afternoon, the stomachs of four were empty, two contained only well digested octopuses, and one contained recently ingested prey (a crab, *Paraxanthias taylori*, 17 mm wide, and a shrimp, *Alpheus clamator*, 20 mm long). Crabs, shrimps, octopuses, squids, and fishes are recognized prey of this species (Limbaugh 1955; Quast 1968).

Scorpaenidae: *Sebastes atrovirens*

The kelp rockfish feeds at night while hovering solitarily in the water column close among the giant kelp plants (Figure 11). It is relatively inactive by day—often at rest on rocky substrata or hanging motionless close beneath the kelp canopy. This was the conclusion of Hobson and Chess (1976), who presented details of its diel feeding habits. Of 23 individuals (89-225 mm SL, $\bar{x}$ = 177.5) collected at night, more than 4 h after sunset, 20 (87%) contained prey, many recently ingested. Major prey were mysids (*Siriella pacifica*, 4-10 mm, and *Acanthomysis sculpta*, 4-10 mm), carideans (*Hippolyte clarki*, 7-14 mm, and *Eualus herdmani*, 5-10 mm), a gammarid (*Batea transversa*, 3-4 mm), and an isopod (*Paracercies crodata*, 2-9 mm).

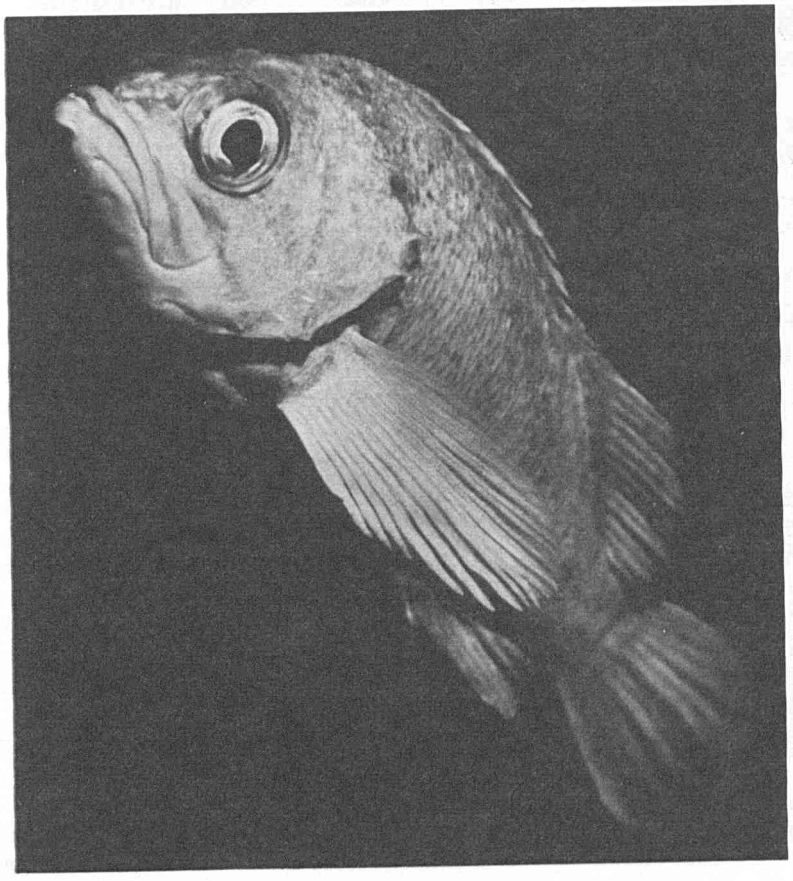

FIGURE 11.—In hovering tail-down close beneath the canopy of a kelp forest, this *Sebastes atrovirens* illustrates an attitude typical of many nocturnal predators that hunt in the water column. From this position they may use the relatively light water's surface as a contrasting background against which prey are visible.

Scorpaenidae: *Sebastes serranoides*

The olive rockfish progresses through stages characterized by distinctive trophic relationships (as described by Hobson and Chess 1976). These stages parallel those described above for the serranid *Paralabrax clathratus*, although the nocturnal element in the subadults is much stronger in *S. serranoides*.

Juveniles appear inshore when they are about 30 mm SL, and feed by day on zooplankton until they have grown to about 55-65 mm. When about 55 mm SL they begin to feed at night, a transition most of them complete by the time they are 65 mm SL. These nocturnal feeders, which are our major concern here, have assumed a pattern of activity that will characterize them until they are about 120-150 mm SL. By day they hover in relatively inactive schools, often at the edge of kelp forests, and during evening twilight they disperse over the surrounding area, where they forage in the water column. Many of them move away from the sheltering kelp to hover solitarily in open water. On the five evenings that the event was noted, the first one seen in a nocturnal mode away from cover was noted 16-30, $\bar{x}$ = 25.8, min after sunset. They remain 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.

When these fish shift to nocturnal foraging they also change their diet. From the copepods and other small zooplankton (about 1-2 mm long) they had taken during their earlier diurnal phase, they now capture larger organisms that swim in the nearshore water column only after dark (Hobson and Chess 1976). These nocturnal food habits were defined by study of gut contents. Of 72 individuals (65-157 mm SL, $\bar{x}$ = 85) collected more than 4 h after sunset, 70 (97%) were full of prey, many of them fresh. Major prey were the gammarid *Batea transversa* (2-5 mm), the mysid *Siriella pacifica* (3-9 mm), the cumacean *Cyclaspis nubila* (4-6 mm), the caprellid *Caprella pilidigita* (5-11 mm), and the isopod *Paracercies cordata* (3-6 mm).

Scorpaenidae: *Sebastes serriceps*

The treefish rests in rocky crevices at all hours of day and night, and evidence of specific feeding times is limited; nevertheless, it appears to be predominantly nocturnal or crepuscular. Of six individuals (138-227 mm SL, $\bar{x}$ = 189.5) collected during the hour before dawn, all contained relatively large crustaceans, including the shrimps *Lysmata californica* (12-70 mm), *Alpheus bellimanus* (60 mm), and *Spirontocaris* sp. (25 mm). Greatly reduced feeding during the day was evidenced by 22 individuals (122-330 mm SL, $\bar{x}$ = 276.1) collected during the afternoon from among rocks; of these, the guts of 13 (59%) were empty, and the other 9 contained material that was for the most part extensively digested—seven had each taken a single *Chromis punctipinnis* (68-135 mm SL), while other prey were the crab *Paraxanthias taylori* (16-38 mm wide), and the carideans *Lysmata californica* (38-45 mm) and *Herbstia parvifrons* (10 mm). Most of these prey had been in the guts for some time: only the two crabs appeared recently ingested. We suspect that all but the two crabs were captured during the previous night or morning twilight. We would expect the crustaceans to have been more accessible after dark, when we have seen the species in exposed locations. Further, the major prey in these collections, *C. punctipinnis*, generally swims high in the water column during the day, and would seem ill-suited then as prey of this bottom-dwelling rockfish. *Chromis punctipinnis* would be more vulnerable at night, when it settles to shelter on the seafloor (see account of *C. punctipinnis* above). However, the absence of *C. punctipinnis* in the guts of *Sebastes serriceps* taken before dawn indicates that the prey in these samples may have been captured during morning twilight, perhaps as they left cover for their ascent into the midwaters.

Haemulidae: *Xenistius californiensis*

The salema assembles in relatively inactive schools during the day, then disperses at nightfall and forages in the water column at night (Hobson and Chess 1976). This diel activity pattern is widespread among the many species of haemulids in tropical waters (Starck and Davis 1966, in the tropical Atlantic, and Hobson 1968a, in the Gulf of California). Frequently *X. californiensis* schools in the upper levels of the water column within the kelp forests, and during twilight, moves considerable distances to nocturnal feeding grounds. One location at Santa Catalina Island, known to be a nocturnal feeding ground for this species, was >400 m from the nearest point where the species had been seen during the day (Hobson and Chess 1976). On four evenings we noted when the first salema arrived on this feeding ground, and this

proved to be between 34 and 40, $\bar{x}$ = 37.3, min after sunset. Once there, its behavior was much like that described above for nocturnally feeding olive rockfish. Its diet, too, proved similar to that of the rockfish. All 13 individuals (163-170 mm SL, $\bar{x}$ = 173.7) collected more than 3 h after sunset were full of food, much of it fresh. Prey were organisms that are in the nearshore water column only at night, with major forms being the gammarids *Batea transversa* (2-4 mm) and *Ampelisca cristata* (3-8 mm), the caprellid *Caprella pilidigita* (6-12 mm), the cumacean *Cyclaspis nubila* (2-4 mm), the mysid *Siriella pacifica* (4-10 mm), and epitokous nereid polychaetes (15 mm).

Sciaenidae: *Seriphus politus*

The queenfish schools in relatively inactive assemblages near shore during the day and disperses to feed in the water column at night after moving away from its daytime schooling sites (Hobson and Chess 1976). Thus, its diel activity pattern is similar to that of subadult *Sebastes serranoides* and *X. californiensis*, described above. The first *Seriphus politus* appeared at a nocturnal feeding site on four occasions at 38-60, $\bar{x}$ = 44, min after sunset. Food and feeding behavior of *S. politus* also are similar to the other two species. All 31 individuals (114-193 mm SL, $\bar{x}$ = 151) sampled later than 3 h after sunset contained prey, much of it fresh. All were larger zooplankton that are in the water column only at night, with major forms being mysids (*Siriella pacifica*, 3-11 mm, and *Acanthomysis sculpta*, 6-11 mm), a gammarid (*Batea transversa*, 2-4 mm), and an isopod (*Paracercies* sp., 2-7 mm).

Sciaenidae: *Umbrina roncador*

The yellowfin croaker schools close to sandy beaches during the day, and at nightfall disperses here and also to the regions immediately offshore. It feeds on organisms in the sediment, often probing with its snout to make the capture. Most of its foraging seems to occur at night. Of 20 individuals (191-255 mm SL, $\bar{x}$ = 210.8) collected more than 3 h after sunset, all but 1 contained prey, much of it fresh. Major items were sand-dwelling polychaetes, many of them tubicolous, with *Onuphis* sp. (15-40 mm) and *Nothria stigmaeus* (10-20 mm) predominating; other important prey were sand-dwelling gammarids, especially *Ampelisca cristata* (2-12 mm), *Acuminodeutopus heteruropus* (2-3 mm), and *Paraphoxus heterocuspidatus* (2-3 mm). Only limited feeding occurs by day, as attested by eight individuals (210-239 mm SL, $\bar{x}$ = 222.5) collected during the afternoon. Of these, only two contained fresh material (sand-dwelling amphipods, most of them *Ampelisca cristata*). These same two, and two others, also contained extensively digested polychaetes that obviously had been in the guts for some time; the other four (50% of the sample) were empty.

Embiotocidae: *Hyperprosopon argenteum*

The walleye surfperch is the only predominantly nocturnal species among the five embiotocids considered in this paper. It schools inactively by day, often close to shore, then disperses at nightfall and moves to feeding grounds some distance away (Hobson and Chess 1976; Ebeling and Bray 1976). It forages in the water column, where it takes the larger zooplankton that are numerous there only after dark. Thus, *H. argenteum* has habits similar to those of the other nocturnal planktivores described above. Although it usually forages lower in the water column than these others, its diet and feeding behavior also are similar: of 29 individuals (100-157 mm SL, $\bar{x}$ = 126) collected over nocturnal feeding grounds at night, or from recently formed schools before sunrise, 28 (97%) contained food, much of it fresh. Major prey items were the gammarids *Batea transversa* (2-4 mm), *Ampelisca cristata* (3-4 mm), and *Ampithoe* sp. (4-6 mm); the cumacean *Cyclaspis nubila* (2-4 mm); the isopod *Paracercies* sp. (2-5 mm); and the caprellid *Caprella pilidigita* (4-10 mm).

Fishes That Feed Day and Night

Only two of the species studied resist classification as being either primarily diurnal or primarily nocturnal in their feeding activities. Both seem equipped to exploit circumstances that permit effective feeding during all hours of day and night. They are listed in Table 3, along with certain of their visual characteristics. The following accounts of their diel foraging activities puts their diurnal and nocturnal habits in perspective.

Cottidae: *Leiocottus hirundo*

The lavender sculpin rests immobile in exposed locations on sandy substrata, usually near rocks and algae, at all hours of day and night. On the

TABLE 3.—Some southern Californian fishes that feed day and night, with the spectral absorbance maximum (λ_{max}) of pigments extracted from their retinae.

Family and species	λ_{max} ±95% C.I.	N	Other pigments[1]
Cottidae:			
Leiocottus hirundo	500.0	2	0
Pleuronectidae:			
Pleuronichthys coenosus	500.9±0.5	3	T
Mean	500.5		

[1]See Table 1, footnote 1.

rare occasions that feeding was observed, this fish moved only a few centimeters to snatch an object in the sand. Eight specimens (130-196 mm SL, $\bar{x}$ = 177) were collected from a variety of habitats during the afternoon. Six (75%) contained food in their stomachs, with the predominant prey being the polychaetes *Glycera capitata* (30-85 mm), *Lumberineris* sp. (20-90 mm), and terrebellid tentacles. One had taken the gammarid *Ampelisca cristata* (12 mm), and one a holothurian (17 mm). Comparable data on nocturnal feeding was obtained from eight specimens (66-194 mm SL, $\bar{x}$ = 136) collected during the hour before dawn. Again, six (75%) contained food in their stomachs, with polychaetes—*Glycera* sp. (35 mm), *Nothria stigmatis* (8 mm), and a terrebellid (30 mm)—the major prey, though less so than during the day. Gammarids, especially *Ampelisca cristata* (2-6 mm) were important to these nocturnal individuals, as was the clam *Solemya valvus* (8-10 mm). But these differences in prey selection between day and night may relate to fish size rather than to time of feeding: two *Leiocottus hirundo* collected during the night were smaller (66 and 84 mm) than any taken by day, and it was these that had preyed mostly on gammarids. Aside from these minor differences in food composition, feeding habits appear similar day and night: stomachs of the day feeders averaged 75% full, and contained $\bar{x}$ = 4.2 items, compared with an average of 69% full and $\bar{x}$ = 4.8 items for the night feeders.

Pleuronectidae: *Pleuronichthys coenosus*

The C-O turbot rests immobile on sandy substrata at all hours of day and night—usually exposed but sometimes under a thin layer of sediment. Often it occurs in the same habitat as *L. hirundo*, but more so than the cottid it ranges into regions of open sand, where its highly variable coloration often matches the surroundings. We have observed feeding only in daylight, when typically this species rests motionless, with body somewhat elevated on dorsal and anal fins and head poised above the substratum (Figure 12). Its mobile, closely set eyes are oriented vertically on a bony ridge, and function almost as if set in a turret. This arrangement permits the fish to scan the seafloor close at hand, probably for moving sediments or other signs of prey that are just below the surface. Occasionally we have seen individuals that had been immobile in one spot for some time move a meter or so across the seafloor, pause for a moment, and then drive their heads into the sediment. Usually we were unable to see what they had taken, but daytime quarry were identified in the 11 specimens that contained food out of 14 (161-212 mm SL, $\bar{x}$ = 186) collected from sandy substrata during the afternoon (stomachs averaged 47% full). The major prey were polychaetes, especially terrebellid tentacles. Although we did not observe feeding at night, prey were identified in all 11 specimens (159-220 mm SL, $\bar{x}$ = 183.5) collected during the hour before dawn (stomachs averaged 72% full). Again, polychaetes, especially terrebellid tentacles, predominated. Clearly its trophic relationships are similar to those of *L. hirundo*, except that it may be more able to feed at night.

DISCUSSION

Events during twilight and at night in Californian marine habitats can be compared with equivalents on tropical reefs. Tropical activity patterns have been described (Hobson 1965, 1968a, 1972, 1974; Starck and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972; Vivien 1973), as has scotopic vision in tropical fishes (Munz and McFarland 1973). Below we relate our findings with Californian coastal fishes to these and other studies made elsewhere. First we consider crepuscular and nocturnal activity patterns and then scotopic spectral sensitivity, first in relation to ambient light, and then to bioluminescence.

Activity Patterns

In relating diel activity patterns of fishes in Californian waters near Santa Barbara to fishes on tropical reefs, Ebeling and Bray (1976) referred to the Californian species as "kelp-bed" fishes. We assume they implied a broad concept of this term that includes fishes sometimes in kelp forests, but more characteristic of other habitats. This is because the tropical side of their comparison (which

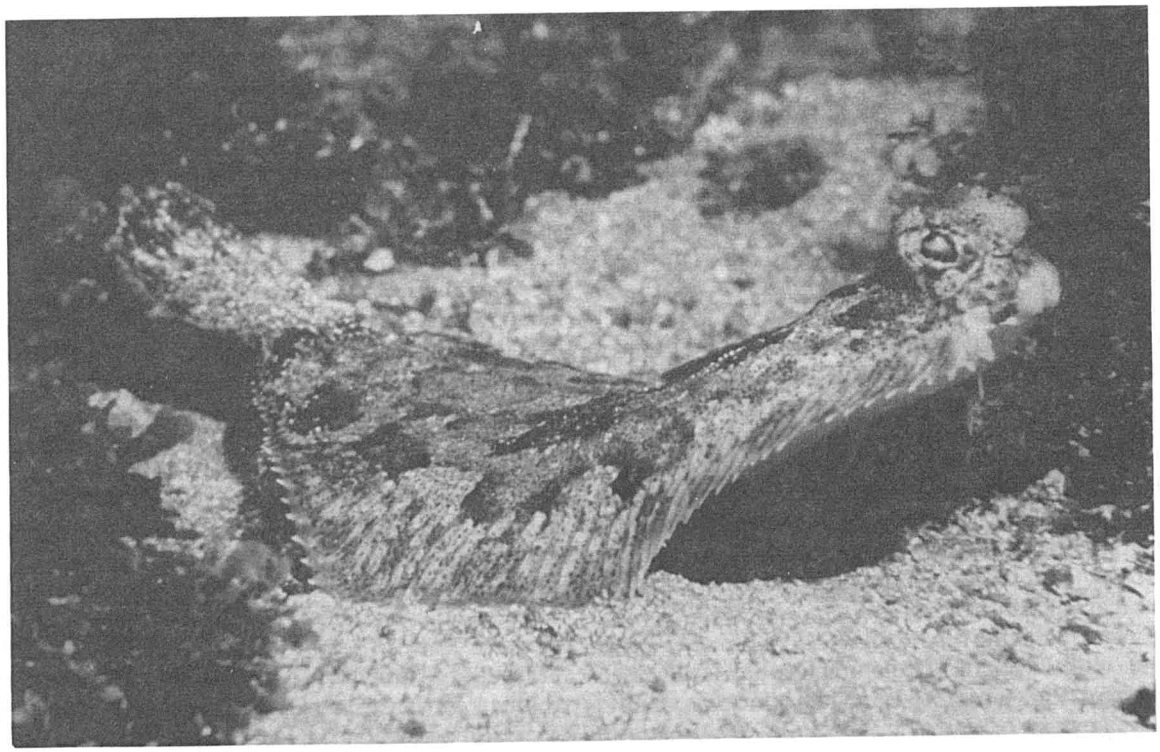

FIGURE 12.—*Pleuronichthys coenosus*, which feeds day and night, largely on sand-dwelling polychaetes, has eyes on either side of a bony ridge set almost as if in a turret. This arrangement increases its ability to scan the surrounding seafloor for prey and threatening predators.

is based on observations by Hobson 1965, 1968a, 1974; Starck and Davis 1966; and others) involves species (often referred to as coral-reef fishes) from a variety of contiguous habitats. A comparison of diurnal and nocturnal behavior requires a multihabitat view because so many fishes move from one habitat to another between day and night.

The general scene in Californian nearshore habitats differs dramatically between day and night. A major aspect of this difference is the sharp drop in observed activity among fishes on reefs after dark. Describing an "aura of desolation..." in the "notably lackluster night life,..." Ebeling and Bray (1976) considered this feature of kelp forests to be in contrast to tropical reefs. But on tropical reefs, too, one notes less activity at night than during the day (e.g., Starck and Schroeder 1965). Nevertheless, there may be an especially pronounced difference where Ebeling and Bray studied, because the relative dearth of nocturnal activities there led them to conclude: "...in kelp beds there is no broad replacement for the 'day shift' of fishes at night." In particular, they reported an absence of fishes that move from daytime assemblages on reefs to nocturnal feeding grounds on adjacent sand, and also to there being relatively few nocturnal planktivores. But the situation they described is unlike that which prevails in the more southerly waters around Santa Catalina, where many species are most active at night. Following a pattern widespread in the tropics, for example, *Xenistius californiensis*, *Umbrina roncador*, *Seriphus politus*, and *Hyperprosopon argenteum* (to mention species considered in this report) are relatively inactive in schools near shore, reefs, or kelp forests by day, and disperse over feeding grounds elsewhere at night. It may be significant, however, that with the exception of *H. argenteum*, these are species with close tropical affinities (Table 4). In contrasting the relative absence of nocturnal planktivores at their Santa Barbara study site, with the many such forms at Santa Catalina (as reported by Hobson and Chess 1976), Ebeling and Bray suggested

TABLE 4.—Geographic affinities[1] of the fishes studied.

I.	Warm-temperate representatives of basically tropical families or genera; species that do not range into the colder waters northward from central California. Twelve species:	
	Scorpaena guttata	*Girella nigricans*
	Paralabrax clathratus	*Chromis punctipinnis*
	Xenistius californiensis	*Hypsypops rubicunda*
	Seriphus politus	*Halichoeres semicinctus*
	Umbrina roncador	*Oxyjulis californica*
	Medialuna californiensis	*Semicossyphus pulcher*
II.	Temperate representatives of basically tropical families; species that range widely into the colder waters northward from central California. Two species:	
	Atherinops affinis	*Coryphopterus nicholsi*
III.	Warm-temperate representatives of temperate families or genera; species that do not range northward from central California. Five species:	
	Sebastes atrovirens	*Alloclinus holderi*
	S. serriceps	*Gibbonsia elegans*
	Leiocottus hirundo	
IV.	Representatives of temperate families or genera; species that range widely northward from central California. Eight species:	
	Sebastes serranoides	*Embiotoca jacksoni*
	Brachyistius frenatus	*Hyperprosopon argenteum*
	Cymatogaster aggregata	*Heterostichus rostratus*
	Damalichthys vacca	*Pleuronichthys coenosus*

[1]Based on ranges given in Miller and Lea (1972).

that the difference may reflect the proximity of Santa Barbara to Point Conception, the northern boundary of the warm-temperate zoogeographic region (Hubbs 1960; Quast 1968; Briggs 1974).

Certainly there is a strong tropical influence in many of the more clearly defined crepuscular and nocturnal activity patterns among southern Californian fishes. Species with the most distinctive patterns tend to be warm-temperate representatives of what basically are tropical families. The three Californian labrids, for example, seek and leave nocturnal shelter at precise times relative to sunset and sunrise, just as their tropical relatives do. And the two Californian pomacentrids shelter under reef cover at night in the same manner as tropical pomacentrids. Similarly, of the species listed above that school inactively by day and disperse to feed at night, most represent the predominantly tropical families Haemulidae and Sciaenidae. Clearly these behavior patterns are rooted deeply in their tropical ancestry, and are as characteristic of their kind as the more generally recognized morphological features that define their families. Ebeling and Bray recognized the strong influence that ancestral relationships exert on activity patterns, and distinguished "temperate derivatives" from "tropical derivatives." (Unaccountably, however, they considered *Paralabrax clathratus* and *Coryphopterus nicholsi* to be of temperate stock, even though the affinities of both are predominantly tropical.) These relationships, then, are insightful in understanding how activity patterns are integrated in southern Californian nearshore fish communities. The geographical affinities of the various species (Table 4) are helpful in gaining an overview of these relationships.

Because nearshore communities in warm-temperate southern California mix fishes of temperate and tropical affinities, it is tempting to interpret behaviors in terms of interactions between these two lineages. Such comparisons are risky. For example, Ebeling and Bray (1976) stated: "It is paradoxical that the 'tropical derivatives'...persist in their complex...shelter-seeking while many primarily temperate fishes remain exposed." We see no paradox here. On tropical reefs, too, many diurnal fishes remain exposed at night, while others seek cover. Size often influences which strategy is used. For example, while smaller acanthurids (surgeonfishes) and chaetodontids (butterflyfishes) generally are sheltered, larger members of their families often rest exposed (Hobson 1972, 1974). Ebeling and Bray went on to suggest: "... the 'tropical derivatives' may...compete more successfully against primarily temperate species such as surfperches for shelter on the reef." This speculation, too, is unsupported by our observations. Most of the temperate species involved here are widespread northward (see Table 4, Group IV), well beyond the ranges of the tropical derivatives, and there too they are exposed at night (E. S. Hobson pers. obs.).

We doubt that nocturnal shelter sites are in short supply on California reefs except under exceptional circumstances. The places we identified as resting sites of *Semicossyphus pulcher* were just sporadically occupied, which seems an unlikely circumstance if there is strong competition for these sites. But clearly there is a shortage of shelter sites where the diurnal planktivore *Chromis punctipinnis* is so numerous that at night resting individuals overflow from the rocks and actually pile up on the adjacent sand. Apparently this exceptional situation exists where the zooplankters on which this fish feeds are abundant by day, but appropriate nocturnal shelter is limited. Significantly, however, the competition for this shelter appears to be intraspecific.

A casual appraisal of southern Californian fishes agrees with Ebeling and Bray (1976) that activities among fishes of the kelp-bed community are "... more loosely 'programmed'" than among fishes in tropical reef communities. A similar condition has been described for temperate lake fishes

(Helfman 1979). This position is strengthened by the more clearly defined behavior in the Californian representatives of tropical families. But at least two considerations complicate this comparison. First, activity patterns, no matter how highly structured, will be less evident in temperate fish communities because a greater proportion of the species there are sedentary. As stated for tropical fishes (Hobson 1972), relative activity in sedentary species is difficult to quantify. Second, and perhaps more important, because there are far fewer species in the temperate habitats, community activity patterns will be less distinct if only because they are defined by fewer forms. It need not follow that activities of each species are less structured. Despite these cautions, however, it is generally accepted that organisms tend to have less specialized habits where species are fewer, and this circumstance should produce more loosely structured activities.

Whether or not activities of individual species are less structured in California than in the tropics, certainly the overall community patterns in California are less clearly defined. In examining the changeovers between diurnal and nocturnal modes, for example, we found little evidence of the detailed community transition-patterns that typically characterize these phenomena on tropical reefs (Hobson 1972; Collette and Talbot 1972; Domm and Domm 1973; McFarland et al. 1979). In particular, we were unable to clearly define a "quiet period," that 15-20 min segment of twilight on many tropical reefs when smaller fishes—both diurnal and nocturnal—have vacated the water column. Based on studies in the tropics (Hobson 1968a, 1972; Munz and McFarland 1973), the quiet periods are considered times of increased danger from predators when smaller fishes find it adaptive to avoid exposed positions. So if the quiet periods are less evident in California, it could indicate reduced crepuscular predation there.

When the sequence of twilight events identified at Santa Catalina Island is related to the timing of the quiet period at Kona, Hawaii (Figure 13), there might appear to be more overlap between the diurnal and nocturnal modes in California. For instance, as the nocturnal juveniles of *Sebastes serranoides* move into exposed locations (Figure 13, event 5), they sometimes pass above active labrids (Figure 13, events 2, 3, and 4) and close to the

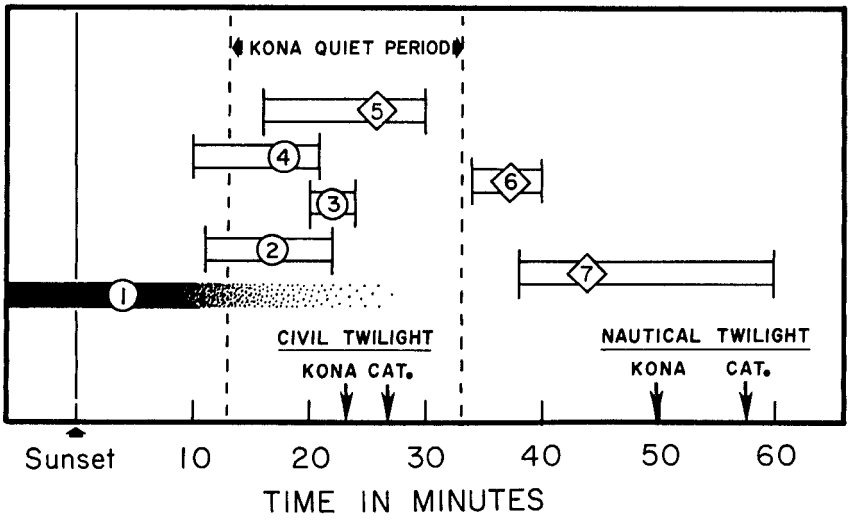

FIGURE 13.—Events during the evening changeover between day and night at one southern Californian site from August to November 1973, relative to timing of the quiet period at Kona, Hawaii (Hobson 1972). (The Californian site is illustrated in Hobson and Chess 1976: fig. 2, 3.) Circles represent diurnal species, diamonds represent nocturnal species. Event 1 is based on estimates, events 2-7 on counts, with bars encompassing range, and numbers located at mean. 1. Migration of *Chromis punctipinnis* to nocturnal resting area: progressive disintegration of bar represents decreasing numbers of individuals in migrating groups (n = 6). 2. Time last *Oxyjulis californica* was seen active (n = 4). 3. Time last *Halichoeres semicinctus* was seen active (n = 6). 4. Time last *Semicossyphus pulcher* departed observation site for nocturnal resting places elsewhere (n = 4). 5. Time first *Sebastes serranoides* appeared at open water feeding ground (n = 5). 6. Time first *Xenistius californiensis* arrived on feeding ground (n = 4). 7. Time first *Seriphus politus* arrived on feeding ground (n = 4). Times of civil and nautical twilight are from Nautical Almanac (U.S. Naval Observatory, Washington, D.C.) and are means of times on dates observations were made.

last migrating *Chromis punctipinnis* (Figure 13, event 1). But this apparent overlap can be explained without evoking a more relaxed regime. Although the three species of Californian labrids retire relatively late (even considering the longer twilight at temperate latitudes), they grow larger than most of their tropical relatives, and it is generally true that among diurnal fishes larger individuals retire later (Hobson 1972). Similarly, there are tropical equivalents to the relatively early shift made by juvenile *S. serranoides* to its nocturnal mode. In the western tropical Pacific Ocean, for example, the largely transparent nocturnal juveniles of some apogonids move away from shelter long before their larger adults. Some of them—many <30 mm long—move out as early as 10 min after sunset (E. S. Hobson unpubl. obs.). This entry into exposed locations at a time when many piscivorous predators hunt most effectively might seem in conflict with the quiet-period concept. But in the dim twilight we are not surprised that these inconspicuous little fishes seem to go unseen by the visual hunters that so seriously threaten the more visible adults. Certainly these juveniles go unseen by human eyes at this time, except upon close inspection with a diving light, and so fail to detract from the aura of inactivity that characterizes the quiet period.

So what might appear to be a more loosely structured sequence of events during twilight in California may instead reflect the lesser number of species that define the transition pattern there. At least some semblance of a quiet period is evident. On the occasions depicted in Figure 13, the numbers of migrating *C. punctipinnis* declined sharply about 10 min before the juvenile *S. serranoides* first appeared, and after that only scattered small groups passed that way. Considering the tremendous numbers of *C. punctipinnis* in that area (we have never seen a single species so dominant on coral reefs), numerous exceptions from the norm should be expected. Furthermore, major species that occupy the water column at night—*Xenistius californiensis* and *Seriphus politus*—did not arrive until about 20 min after the vast majority of *C. punctipinnis* had passed through. So although crisp definition is lacking, there is evidence of a quiet period in Californian waters from about 15 to 35 min after sunset.

It remains uncertain whether the dangers smaller fishes face during twilight in southern Californian coastal waters are as intense as those faced on tropical reefs. Limited data from gut contents indicate that such major predators as *Paralabrax clathratus* and *Sebastes serriceps* are primarily crepuscular when capturing smaller fishes. Unfortunately, we can no longer directly observe much of the predation that has influenced the evolution of coastal fishes in southern California. This is because during recent decades populations of the larger predators involved—including the giant seabass, *Stereolepis gigas*, and the white seabass, *Cynoscion nobilis*—have been decimated by fishermen. Nevertheless, as we discuss next, the possibility that Californian fishes have faced intensified selection pressures during twilight is also indicated by the nature of their scotopic visual pigments. Significantly, despite the varied forms and habits of these fishes, the maximum absorptions (λ_{max}) of their scotopic pigments cluster about 500 nm, which indicates strong selection for enhanced photosensitivity over this segment of the spectrum.

Scotopic Spectral Sensitivity and Ambient Light

Tropical reef fishes have scotopic pigments that cluster about wavelengths that spectrally match twilight, which underwater is bluer than the light of day or night (Munz and McFarland 1973). In developing their Twilight Hypothesis, Munz and McFarland pointed out that because dawn and dusk are the most dangerous times for fishes on tropical reefs (Hobson 1972), even slightly increased photosensitivity during twilight may be crucial.

The Twilight Hypothesis is a variation of the Sensitivity Hypothesis (Lythgoe 1966), which declares that visual sensitivity is improved when absorption of photo pigments matches ambient light. The scotopic pigments of both aquatic and terrestrial vertebrates are known to cluster about narrow wave bands, but at different regions of the spectrum (for review, see McFarland and Munz 1975b). Among fishes, the scotopic pigments broadly match the spectral transmission of the water in which the fishes live (Lythgoe 1972). Deep sea fishes, for example, have scotopic pigments that tend to be even more blue sensitive (λ_{max} from 478 to 490 nm: Denton and Warren 1956; Munz 1957), than tropical marine fishes (λ_{max} from 489 to 500 nm: Munz and McFarland 1973), and the pigments of freshwater fishes are green sensitive (λ_{max} from 503 to 540 nm: McFarland and Munz

1975b). The present study shows that fishes associated with Californian kelp forests have pigments that are most sensitive to blue-green light (λ_{max} from 496 to 506 nm).

If the adaptive advantage of matching ambient light lies in heightened photosensitivity, then the match should be to light that prevails when selection for improved vision is most intense. We are not surprised, therefore, that the λ_{max} values for fishes in a given habitat match not the light of day or night, but rather the bluer twilight, and thus the fishes are equipped to meet an intensified threat from crepuscular predators. In clear tropical waters, for example, the λ_{max} values of the scotopic pigments in reef fishes cluster about 492 nm, which in that habitat matches twilight, rather than the greener light of day or night (Munz and McFarland 1977). Of course, the spectral position of this match is influenced by the light transmission characteristics of water in that particular habitat. For example, in most fresh waters the match is made above 520 nm, but this position nevertheless approximates the λP_{50} of twilight in these very green waters and is in fact toward the blue from light that prevails there during day and night (McFarland and Munz 1975c).

As could have been predicted from the Sensitivity Hypothesis, the scotopic pigments of fishes in the blue-green coastal water of California cluster at wavelengths intermediate between those of fishes on coral reefs and those of fishes in freshwater, at about 500 nm (Tables 1-3). The match with twilight, however, is less clear in Californian waters than in the other two environments because, we believe, photic conditions in Californian waters are more variable. Nevertheless, the tight clustering of scotopic pigments around 500 nm in the Californian fishes better matches ambient light during twilight than at night. Both moonlight and starlight are richer in red light than daylight or twilight (Munz and McFarland 1977), and for all water conditions we encountered at Santa Catalina Island downwelling light at night would have λP_{50} values well above 520 nm (Figure 5). Only during twilight does ambient light underwater shift far enough toward the blue-green region of the spectrum (Figures 3, 4) to produce a close match with the visual pigment λ_{max}.

In evaluating the impact of crepuscular predators on the spectral position of scotopic pigments, however, we must not forget that other selection pressures are operating. We would expect scotopic pigments in fishes to be particularly responsive to such alternate pressures at night, which is especially "short of light" (Dartnell 1975). Certainly fishes must be sensitive to the emissions of bioluminescent organisms, because few visual cues could be more apparent than a flash of light in the dark.

Scotopic Spectral Sensitivity and Bioluminescence

Bioluminescence often signifies underwater movement. According to Hobson (1966), "In many areas of the sea at night, a moving object is readily observed due to the luminescence of many minute planktonic organisms, mostly protozoans, which light up when disturbed. These organisms are often so numerous that while making observations underwater I have been able to identify, to species, fishes that swam actively among them. This was not because the fish itself was illuminated, but rather because there were so many minute luminescent organisms about the fish that its form was essentially traced out in tiny flecks of light." If such cues are evident to human eyes, adapted to a diurnal, terrestrial existence, the capacity to sense and to orient by them must be highly refined in animals like fishes that have evolved in this environment.

Bioluminescence offers an especially effective way to detect predators or prey because predator-prey interactions generally involve movement, and luminescence by plankton is greatly increased in the turbulent water around moving objects. We believe, as did Burkenroad (1943), that this fact has had enormous impact on the nocturnal tactics of both predators and prey. The motionless attitude that characterizes nocturnal planktivorous fishes when they hunt probably is enforced by the need to minimize turbulence in the water about them. By minimizing turbulence they minimize the firing of luminescent organisms that would betray their presence, and so hover unseen in the dark, ready to strike when nearby prey advertise their positions by disturbing the plankton. This tactic is in essence an ambush and probably is effective only at short range. Reasons for this limitation are two. First, an attack, once launched, is immediately identified by flashing plankton, thus giving prey more than a short distance away time for evasive maneuvers. Second, a long-range attack directed at plankton luminescing around a particular prey may be led to the prey's wake, because the targets that elicited the attack are left behind when the prey darts away. Probably pred-

ators can be led by luminescent plankton to prey over some distance (Nichol 1962), but we suggest the approach must be made with great stealth to avoid turbulence and resulting luminescence. Surely such limitations preclude many kinds of predatory activities after dark, especially when the prey are as agile as most small fishes. In fact, the diminished threat from predators that smaller reef fishes enjoy at night (Hobson 1973, 1975, 1979) may stem largely from the difficulties predators have at this time moving undetected to within striking range.

If fishes use luminescent plankton to detect predators and prey, undoubtedly they have experienced strong selection pressures to enhance this detection. An obvious adaptive response to such pressures would be a match of the scotopic visual pigments to the emission spectra of the luminescent plankton. Certain vertebrates living at great depths, or in the open ocean, reportedly have scotopic pigments that match the luminescent emissions of organisms with which they interact, socially or as predator or prey (Clarke 1936; Munz 1958a; Lythgoe and Dartnall 1970; McFarland 1971; Locket 1977). These animals, however, interact directly with the luminescent organisms, whereas we stress indirect interactions. Of course, the principle is the same either way—detection is enhanced by matching visual pigment absorption to a luminescent emission.

The emission spectra of most luminescent plankton, as exemplified by *Noctiluca miliaris* and *Gonyaulax polyedra* (Figure 5), indicate that fishes would sense the emitted photons best with blue-sensitive visual pigments that have λ_{max} values near 490 nm. But this holds only before the light has passed through water. As noted above, the spectrum of light changes as it travels through water, with the degree of change sharply affected by the water's clarity. Clearly any such change will favor a different λ_{max} value in visual pigments.

The relative effectiveness of visual pigments with differing λ_{max} values in waters of differing clarities can be estimated with some simple calculations. Given the relative attenuation of light at each wavelength, which is a function of water type, we can compare the relative photoabsorption of different visual pigments at increasing distances from the luminescent source. Let us consider, for example, how a series of pigments with λ_{max} values at 10 nm intervals between 450 and 550 nm, each at 0.4 absorbance units, would absorb the light emitted by *Noctiluca* as this light passes through differing clarities of seawater, as defined by Jerlov (1968). The relative photoabsorption of each pigment at a given distance from the source can be estimated by multiplying that pigment's percentage absorption at each wavelength by the relative amount of light available at that wavelength and then integrating the products over all wavelengths (Figure 14). Thus, to see

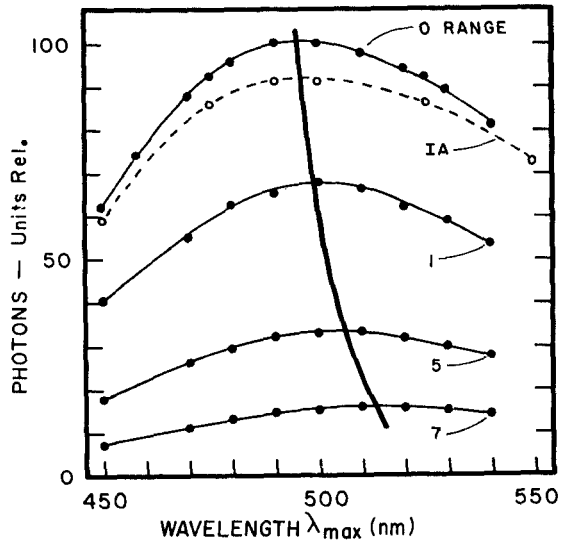

FIGURE 14.—Expected relative effectiveness of visual pigments with differing λ_{max} values (positioned at wavelengths indicated by circles) in sensing luminescent emissions of *Noctiluca miliaris* under varying circumstances. Top curve, for reference, represents effectiveness at zero range (no alteration of emission spectrum by intervening water); dashed curve (with open circles), for comparison, represents effectiveness at distance of 3 m in clear tropical water (water type 1A of Jerlov 1968); three lower curves represent relative effectiveness in waters of decreasing clarity (water types 1, 5, and 7 of Jerlov 1968). Vertical line crosses each curve at the optimal λ_{max} position. Method of calculation in text.

luminations from an organism like *N. miliaris* at a distance of 3 m in coastal waters (as at Santa Catalina), fishes would best have visual pigments with λ_{max} values between 500 and 510 nm. And as range increases, and water clarity decreases, photodetection of this luminant source would be improved by shifting the λ_{max} position slightly, but continuously, toward the greener wavelengths (Figure 15).

In reality, of course, the reduced visibility in turbid water sharply limits the practical extent of such a shift. During heavy phytoplankton blooms, for example, even large objects in full daylight are

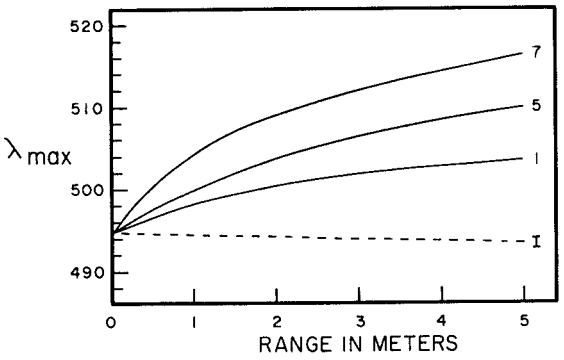

FIGURE 15.—Calculated optimum λ_{max} position for absorption of luminescent emissions of *Noctiluca miliaris* at increasing range in waters of differing clarity. Water types I, 1, 5, and 7 of Jerlov (1968). Solid lines = coastal waters of increasing turbidity; dashed line = clear tropical water.

invisible beyond 2-3 m. Obviously under such conditions bioluminescence, too, would be invisible at these distances. Probably most meaningful interactions involving fishes and the bioluminescent emissions of plankton occur over distances of just a few meters or less, and to see bioluminescence at these ranges in the waters of varying visibility that surround Santa Catalina fishes probably would best have visual pigments with λ_{max} values at a little above 500 nm (Figure 15).

One might expect diurnal fishes to be less sensitive than nocturnal or crepuscular fishes to selection pressures on scotopic pigments because they are less active under low light. But among species studied at Santa Catalina the λ_{max} values scarcely differ between the two groups (diurnal feeders: $\bar{x}$ = 499.1 nm, range = 496.1-505.8—Table 1; nocturnal feeders: $\bar{x}$ = 501 nm, range = 496.1-505.1—Table 2). Perhaps there is little difference here because many of these diurnal feeders are exposed at night and need means to detect threatening predators. In fact, if the fishes are grouped according to their relative exposure after dark, rather than by how active they are at this time, their λ_{max} values show a clear pattern (Table 5). Those fishes that are exposed at night, compared with those that are sheltered, tend to have scotopic pigments with spectral sensitivities closer to what we consider optimum for detecting bioluminescence in Californian coastal waters. This would mean that, despite their apparent quiescence, at least many diurnal fishes remain visually alert for potential threats during the night.

So the similar λ_{max} values in the diurnally feeding *Atherinops affinis* (505.8 nm) and the nocturnally feeding *Hyperprosopon argenteum* (505.1 nm) may answer the similar threats both face while exposed in the water column at night. We assume the increased sensitivity to bioluminescence would also benefit *H. argenteum* in feeding, but suspect this advantage would be less forceful. The need to evade predators should be sharper than the need to capture prey. Both needs are critical, but there is less tolerance for error on defense than on offense. A fish as prey is likely to be eliminated the first time it errs in responding defensively to an attack, but the same fish as an attacker may err many times without serious consequences.

Bioluminescence, triggered by movement, represents a well-defined indicator of immediate danger that can effectively focus selection pressures on a narrowly defined adaptive response. Moonlight and starlight would seem less suited for this because neither so effectively identifies specific threats and because the impact of both

TABLE 5.—Relative exposure at night, and λ_{max} position of scotopic visual pigments in certain southern Californian marine fishes.[1]

Relative exposure at night	Species		λ_{max} mean	λ_{max} range
I. Fully exposed in water column	*Atherinops affinis*	*Brachyistius frenatus*	502.1	500.4-505.8
	Sebastes serranoides	*Cymatogaster aggregata*		
	Xenistius californiensis	*Hyperprosopon argenteum*		
	Seriphus politus			
II. Fully exposed on or near seafloor, often on open sand	*Umbrina roncador*	*Leiocottus hirundo*	501.1	500.0-503.1
	Damalichthys vacca	*Pleuronichthys coenosus*		
	Embiotoca jacksoni			
III. Partially or fully sheltered by rocks or algae	*Scorpaena guttata*	*Hypsypops rubicunda*	497.3	496.1-499.7
	Sebastes atrovirens[2]	*Semicossyphus pulcher*		
	S. serriceps	*Alloclinus holderi*		
	Paralabrax clathratus	*Heterostichus rostratus*		
	Girella nigricans	*Coryphopterus nicholsi*		
	Chromis punctipinnis			

[1]Of species studied, *Medialuna californiensis* is excluded because its nocturnal habits remain uncertain (see text), and *Halichoeres semicinctus* and *Oxyjulis californica* are excluded because they have a different type of visual pigment (see Table 1, footnote 3).
[2]Even though *S. atrovirens* feeds in the water column at night, these activities occur close to rising kelp stipes or just beneath the surface canopy.

tends to be diffused over a greater range of visual circumstances. Bioluminescence is more constant: the spectral compositions of moonlight and starlight change with water depth and atmospheric conditions, but the spectral composition of bioluminescence is independent of these variables. And, of course, there is less light from moon or stars with increased water depth, which, again, is untrue of a bioluminescent emission. So it is not surprising that the narrow range of λ_{max} positions in visual pigments of Californian fishes more closely matches bioluminescence than it does moonlight or starlight (Figure 16).

Undoubtedly moonlight and starlight have strong influences on nocturnal relationships among predators and prey. But probably both help fishes more on offense than on defense. Predators can position themselves, and time their attacks, to play both types of light to their advantage, and to the prey's disadvantage. By charging at prey from below, for example, predators view their targets against the water's relatively light surface, while their own movements are masked by the surrounding gloom (Hobson 1966). Certainly attacks that so often spring from the shadows would greatly dilute a defensive advantage prey might gain with spectral sensitivities that match moonlight or starlight. Under these circumstances prey face a broad range of threats that calls for a more generalized response. So we can understand why many smaller reef fishes that habitually range into the water column at night stay closer to shelter under moonlight (Hobson 1968a).

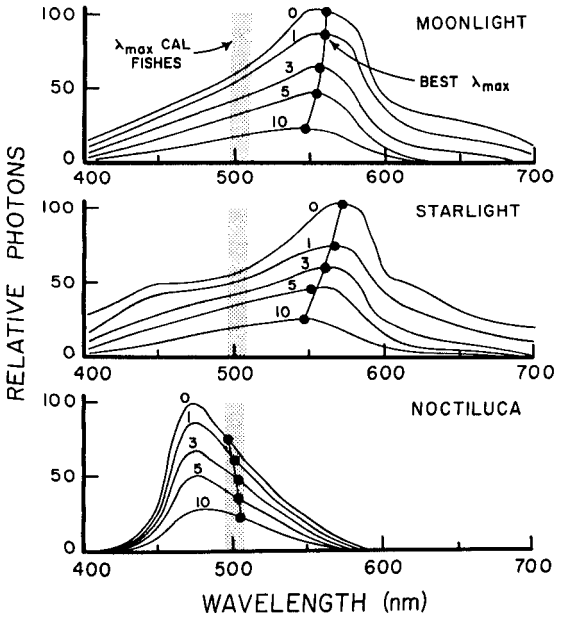

FIGURE 16.—Relationships between the spectral distributions of moonlight, starlight, and bioluminescence (as produced by *Noctiluca miliaris*) in seawater typical of southern California and the spectral sensitivities of fishes that live there. The five curves for each type of light represent the spectral distribution expected to reach a fish at the distance (in meters) indicated by the number that accompanies each curve. The curves depict moonlight and starlight off a flat reflector at a depth of 3 m (using values from Munz and McFarland 1977), and the luminescence of *N. miliaris* (using values from Nicol 1958), in water equivalent to typical conditions at Santa Catalina Island (Coastal Type 1 of Jerlov 1968). The solid circle on each spectral curve identifies the wavelength to best match with a visual pigment for maximum photosensitivity, and the stippled column represents the spectral range of maximum photosensitivity in scotopic pigments of Californian fishes (λ_{max}). Note that these coincide only with bioluminescence.

Despite the offensive advantage that certain predators likely gain from moonlight (or starlight), their scotopic visual pigments tend to be better matched to bioluminescence (or twilight), probably because this answers a more pressing need on defense. So it would seem that even those species that have special tactics to use moonlight or starlight to better see their prey must compromise with visual pigments less than optimal for this task. Included are those nocturnal planktivores, like subadult *Sebastes serranoides*, that characteristically hover tail-down in the water column, where apparently prey are visible to them against moonlight or starlight from above. Included, too, are those predominantly diurnal fishes, like *Paralabrax clathratus* and *Cymatogaster aggregata*, that apparently are able to hunt at night close to sand where light levels are elevated by reflected moonlight and starlight. We suggest not that their visual pigments are unsuited to see prey by moonlight or starlight, but rather that these pigments simply could have better spectral sensitivities for this particular job (Figure 16).

These arguments, favoring bioluminescence over moonlight and starlight as a selective force in determining λ_{max} position, would also favor bioluminescence over twilight. But there is an important difference in this last comparison. Moonlight and starlight would select for spectral positions different from that selected for by bioluminescence, and so a conflict would exist. Twilight, on the other hand, would select for essentially the same spectral position as bioluminescence, so that the two would act in concert (see below).

If scotopic visual pigments with spectral positions slightly above 500 nm are optimally located to detect bioluminescence in Californian coastal waters, one can see why such pigments occur there in fishes exposed to nocturnal predators. But questions remain concerning why fishes apparently less threatened are consistent in having scotopic pigments positioned slightly under 500 nm. Why are these pigments not loosely positioned above, as well as below, the optimum location? The answer to this question might lie in ancestral relationships. In grouping the Californian fishes according to whether their geographical affinities are tropical or temperate (Table 4), our concern was with current relationships. In fact, all these fishes belong to groups that stem from tropical origins (Berg 1940). The radiation of acanthopterygian[5] fishes from a relatively few ancestral forms early in the Cenozoic (Patterson 1964; Romer 1966) has been related (by Hobson 1974) to the concurrent development of modern coral reef communities (Newell 1971). And we have seen that conditions under which coral reefs flourish, compared with conditions in temperate Californian waters, favor in fishes' scotopic visual pigments that are more sensitive to slightly shorter wavelengths. The mean λ_{max} of 492 nm that Munz and McFarland (1973) found in the scotopic pigments of coral-reef fishes, compared with the values around 500 nm that characterize Californian fishes, is consistent with the fact that water around coral reefs is generally clearer and more transparent to blue light than water around Santa Catalina (Figure 2). The extent that λ_{max} values of scotopic pigments in Californian coastal fishes have shifted toward the green from what may have been ancestral positions near 490 nm, and, especially, have become located slightly above 500 nm (the optimal position in California), may roughly measure the relative strength of nocturnal or crepuscular predation pressures on each species in these greener waters.

The argument that scotopic pigments may be positioned to detect bioluminescence can be extended to coral reef fishes. Our calculations show that visual pigments with different λ_{max} values would trap percentages of the light from *Noctiluca miliaris* as follows: P450 nm = 62%, P475 nm = 94%, P490 nm = 100%, P500 nm = 99%, P525 nm = 93.5%, P550 nm = 79%. Although the peak is broad, the central wavelength for maximum absorption at zero range would be near 495 nm (Figure 14), which is close to the λ_{max} of 492 nm in the scotopic pigments of coral-reef fishes. And as distance from the source increases the match becomes even better (Figure 15).

Twilight or Bioluminescence?

Whether the clustering and spectral position of visual pigments in warm-temperate and tropical reef fishes is the result of natural selection, or is simply fortuitous, is a complex question. If, as we believe, these features have been refined by intense selection pressures from predators, it remains problematical whether the advantage lies in detecting bioluminescence, or in enhancing photoabsorption during twilight—as suggested by the Twilight Hypothesis. Indeed, both may be important. The scotopic pigments have spectral positions that would be effective in both functions, and the benefits of one would complement the other. Unquestionably, there has been ample time to influence evolution. Bioluminescent plankton have existed since before the first fishes (Seliger 1975), and so has twilight's unique spectrum. Because fishes have experienced these features throughout their history, the slightest favorable adjustment could have been adaptive. Although a 5-10 nm shift in λ_{max} position would improve photoabsorption by no more than a few percentage units, even this could have been meaningful. And if selection pressures to detect bioluminescence have, in fact, acted in concert with those to enhance crepuscular vision, which to us seems likely, then their combined impact certainly would have been a powerful evolutionary force.

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[5]All fishes considered in this paper have been included among the acanthopterygians, or spiny-finned teleosts, although one, *Atherinops affinis*, would be relegated by some systematists (e.g., Greenwood et al. 1966) to another group.

(NMFS), NOAA, typed the manuscript, and Susan Smith, Southwest Fisheries Center Tiburon Laboratory, NMFS, NOAA, drew Figure 1. Portions of this study were supported by N.I.H. Research Grant EY-00323 from the National Eye Institute.

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RESPIRATION RATES AND LOW-OXYGEN TOLERANCE LIMITS IN SKIPJACK TUNA, *KATSUWONUS PELAMIS*

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ABSTRACT

Oxygen-uptake rates and swimming speeds of voluntarily active skipjack tuna, *Katsuwonus pelamis*, at 23°-24° C were measured in the laboratory from captivity-habituated fish (0.6-3.8 kg) and at sea from just-caught fish (1.8-2.2 kg). In the shipboard tests, skipjack tuna swam 2-5 lengths/s (length = fork length) and consumed 0.9-2.5 (median = 1.3) mg O_2/g per h during their first 2.2 h of captivity. In laboratory tests, skipjack tuna swam at a mean speed of 1.4 lengths/s and consumed oxygen at a mean rate of 0.52 mg O_2/g per h. For the laboratory fish, routine swimming speed (S, in lengths/second) was inversely related to fish weight (W, in grams)—$S = 3.12 - 0.53 \log_{10} W$; oxygen-uptake rate ($\dot{V}_{O_2}$, in milligrams O_2/gram per hour) was directly related to both weight and speed (i.e., speed independent of weight effects)—$\log_{10}\dot{V}_{O_2} = -1.20 + 0.19/\log_{10} W + 0.21\ S$. However, laboratory fish swimming at their characteristic (weight dependent) speeds respired at rates independent of weight. Calculations based on the above interrelations among metabolic rate, swimming speed, and body weight indicated that skipjack tuna of all sizes may have an optimum swimming speed (for maximum distance per unit energy expenditure) near 2.1 lengths/s.

Captivity-habituated skipjack tuna (0.8-3.4 kg) also were subjected to a step decrease in concentration of dissolved oxygen (O_2) at 23°-24° C to determine their responses to acute hypoxia. At levels of O_2 below 4 mg/l, voluntary swimming speed increased as O_2 declined, reaching 3.9 lengths/s at the lowest test value of O_2, 1.4 mg/l. The 4-h median tolerance limit for low O_2 proved similar to the O_2 level critical for change in swimming speed, about 4 mg/l.

Experimental results are analyzed and compared with those from other fishes to arrive at the following conclusions: 1) The skipjack tuna's "standard" metabolic rate is two to five times that of typical fishes of similar size; 2) the weight exponent for "standard" metabolic rate of skipjack tuna is a positive value near 0.2, as opposed to the −0.2 value typical of fishes; 3) but, because the characteristic swimming speed of routinely active skipjack tuna is inversely related to weight, routine metabolic rate is virtually independent of fish weight; 4) highly active skipjack tuna can consume oxygen from air-saturated seawater at rates exceeding those known from any other fish of similar size; and 5) the skipjack tuna is relatively inefficient in its use of oxygen and food-energy for swimming (at least at low speeds) and it dies at O_2 levels still well above those lethal for other fishes.

Until the mid-1960's the environmental requirements of commercially important tunas (Scombridae) were known mainly from correlations between fishery catch rates and oceanographic conditions (see discussions by Robins 1952; Laevastu and Rosa 1963; Broadhead and Barrett 1964; Blackburn 1965; Williams 1970; Blackburn and Williams 1975; Matsumoto 1975). With the advent of techniques for studying tunas in captivity (Magnuson 1965; Nakamura 1972), many unresolved issues of tuna biology could be explored such as feeding and gut-evacuation rates (Magnuson 1969), auditory perception (Iversen 1967), visual perception (Nakamura 1968; Tamura et al. 1972), thermoperception (Dizon et al. 1974, 1976; Steffel et al. 1976), nerve-muscle physiology (Rayner and Keenan 1967), tissue metabolism (Gordon 1968), respiratory physiology (Stevens 1972), body temperature and thermal inertia (Stevens and Fry 1971; Neill et al. 1976), lethal temperatures (Dizon et al. 1977), swimming mechanics (Magnuson 1970), and swimming speed as a function of water temperature (Stevens and Fry 1971; Dizon et al. 1977), dissolved oxygen (O_2) concentration, and salinity (Dizon 1977). In addition, several works of a more integrative nature (Magnuson 1973; Barkley et al. 1978; Kitchell et al. 1978; Stevens and Neill 1978) have drawn heavily on these and unpublished laboratory studies. Among the latter are the experiments documented in this paper on oxygen-uptake rates and limits of tolerance to low oxygen in skipjack tuna, *Katsuwonus pelamis*.

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Respiration research on tunas is still quite limited. Besides the present work, there are only four published studies—three involving tuna metabolism (Gordon 1968; Stevens 1972; Brill 1979) and one involving tunas' lower tolerance limits for O_2 (Anonymous 1965). Gordon (1968), using volumetric microrespirometers, determined rates of oxygen uptake in minced preparations of muscle from skipjack tuna and bigeye tuna, *Thunnus obesus*. Stevens (1972) measured the oxygen concentration of water entering and leaving the gills of restrained, perfused skipjack tuna; from these data he computed oxygen-uptake rate and utilization. Brill (1979), using a similar technique, estimated the relation between standard metabolism and body weight of skipjack tuna. Stevens (1972) also measured oxygen utilization in free-swimming skipjack tuna by sampling exhaled water collected via opercular cannulation. Experiments conducted with skipjack tuna at the Kewalo Research Facility provided the earliest estimate of the lower lethal-oxygen limit for a tuna (Anonymous 1965).

Our purposes in this work were 1) to determine the magnitude of oxygen-uptake rate in routinely active skipjack tuna, 2) to establish the relation among oxygen-uptake rate, swimming speed, and body weight in skipjack tuna, and 3) to estimate the lowest concentration of O_2 that skipjack tuna can withstand for 4 h. The results already have contributed importantly to the development of models of skipjack tuna distribution (Barkley et al. 1978) and bioenergetics (Kitchell et al. 1978).

MATERIALS AND METHODS

Source and Preexperimental Treatment of Fish for Laboratory Experiments

Skipjack tuna were caught by angling in Hawaiian waters at sea-surface temperatures between 23° and 24° C. The fish were transported in 2,400 l shipboard tanks that were supplied with flowing seawater and supplemental oxygen. Upon arrival at the National Marine Fisheries Service's Kewalo Research Facility in Honolulu, the skipjack tuna were transferred into either 40,000 or 700,000 l outdoor holding tanks. Nakamura (1972) described in greater detail the techniques that have been developed at the Kewalo Research Facility for transporting and maintaining live tunas.

The seawater in the holding tanks had 23°-24° C temperatures, pH 7.4-7.6, 32-33‰ salinity, and 6.4-6.7 mg/l O_2. The seawater well that supplied water to the holding tanks was also the source of water for the experimental tanks. At night the holding tanks were illuminated at a low level.

Experiments were conducted with fish that had been in captivity 7-26 d. Once the skipjack tuna started feeding (usually within 3-5 d after capture), they were fed to satiation on thawed northern anchovies, *Engraulis mordax*, or smelt, *Allosmerus* sp., once a day. Prior to experiments, the fish were fasted for periods ranging from 24 to 27 h, which is more than sufficient time for gut evacuation in skipjack tuna (Magnuson 1969). However, our method of moving fish from the holding to the experimental tanks involved some food ingestion. Two to four hours before data collection, the fish were removed from a holding tank by angling with a baited, barbless hook. Although a small piece of food (1-2 g) was usually swallowed, this transfer technique did select healthy and actively feeding fish.

Oxygen-Uptake Experiments in Laboratory

Apparatus

Two unstirred, sealed respirometers of different sizes were used. Circulation of water during experiments was provided only by movements of the fish.

The larger respirometer was used only during the first of the 10 series of experiments (Table 1). The circular chamber was a vinyl-lined plywood tank, 4.57 m in diameter and 1 m deep, with a cover made of transparent vinyl film bonded to an inflatable tube, 18 cm in cross section, that encircled the tank's inner perimeter just below the rim. After the tube was in place and any trapped air had been removed with an electric pump, the clear plastic cover lay over the entire water surface, forming an effective seal. We initially had intended to run all of the experiments with this respirometer. However, it proved to be difficult to operate and visibility of fish within the chamber was poor. Most importantly, a tank of its volume (16,000 l) required a large biomass of fish in each experiment to effect oxygen reduction in a reasonably short period of time. Skipjack tuna are difficult and expensive to capture and maintain; so, to use fish as economically as pos-

sible, we built a smaller respirometer for the nine subsequent series of experiments.

The smaller respirometer consisted of a fiber glass tank, elliptical in the horizontal plane; it held 2,400 l of water and was 2.44 m long by 1.83 m wide by 0.61 m deep (Figure 1). The top edge of the tank had a 5.0 cm wide lip to which was cemented a 0.9 cm thick sponge-neoprene gasket; on this gasketed lip, there was seated, and firmly clamped, a rigid cover made of 0.4 cm thick transparent acrylic plastic strengthened by three 10 cm wide strips of 6.5 cm thick marine plywood cemented to its outer surface. A short length of 5 cm PVC pipe, which served as a vent and access port, was tapped vertically through the plastic and plywood in the center of the cover. Glued flush with the inside surface of the acrylic, the pipe extended about 8 cm above the water level.

An inlet and drain allowed fresh seawater to flow through the chamber at rates up to 190 l/min. Both inlet and drain were valved. By slightly overfilling the chamber before closing the inlet valve, we caused the acrylic cover to bulge upward 4 cm at the center. The domed conformation permitted the easy removal of bubbles from the chamber through the vent pipe. A sponge rubber ball, fitted snugly into the pipe during experiments, completed the seal.

Both respirometers were illuminated with overhead fluorescent lights. Indirect natural light coming through windows and doors was not excluded. Visibility of fish in the smaller respirometer was excellent, permitting detailed observation of fish speed and behavior during an experiment.

Dissolved oxygen measurements in both respirometers were made with a YSI[3] model 51A oxygen-temperature meter coupled with a YSI model 5418 oxygen-temperature probe. For measurements in the larger respirometer, water was electrically pumped between the tank and a small acrylic chamber in which the probe was mounted. In experiments involving the smaller respirometer, the oxygen-temperature probe was placed inside the tank through the vent pipe in the cover. The probe was vigorously jiggled for about 15 s before each reading of the meter; during the intervals between readings, a sponge rubber ball

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA, or by Texas A&M University.

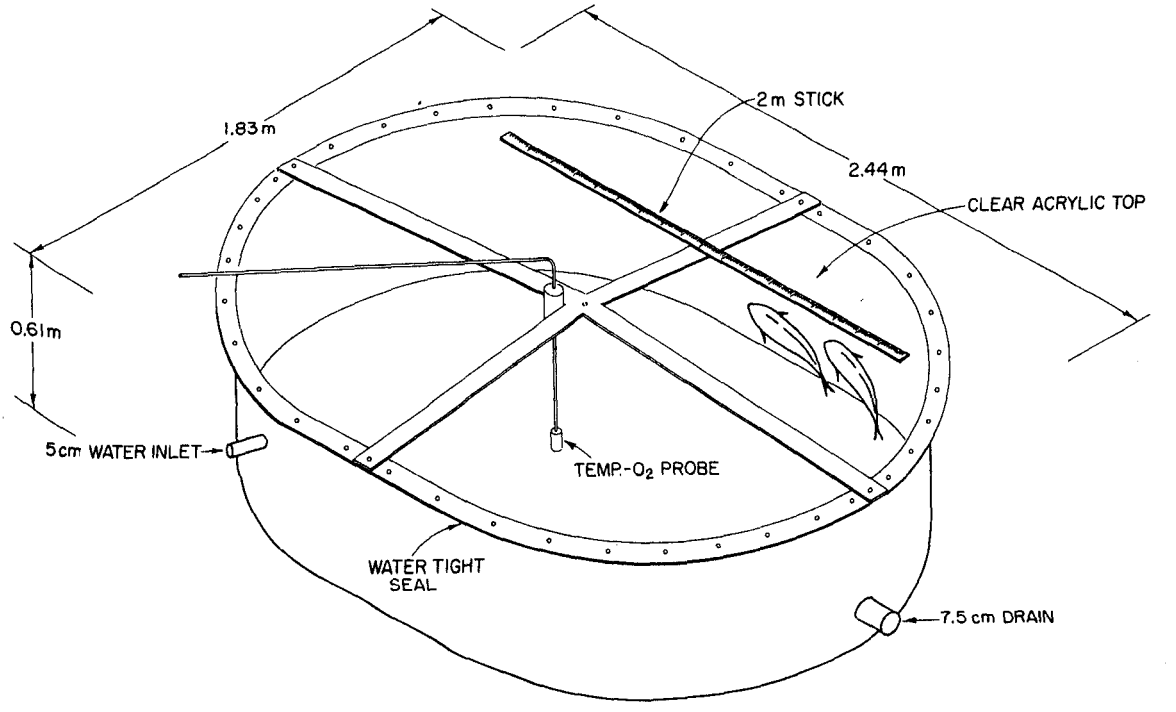

FIGURE 1.—The small sized respirometer used in oxygen-uptake experiments 2-10 on skipjack tuna.

was seated tightly against the cable connecting probe and meter. Calibration of the O_2 meter was checked against air-saturated seawater at the start, midpoint, and end of each experimental run; and the temperature readings were frequently verified with a mercury thermometer. As an additional check on the O_2 meter's accuracy, readings were twice compared with Winkler determinations. The instrument gave stable and reliable readings with accuracy ± 0.2 mg O_2/l.

Oxygen was supplied from standard 6,800 l cylinders through fine (800 grit) 15 cm aluminum oxide grinding stones (Baldwin 1970) to produce minute bubbles.

Preliminary and Control Experiments

Preliminary experiments conducted in each respirometer and subsequent work by Dizon (1977) indicated that skipjack tuna demonstrate no overt behavioral manifestations of stress as long as O_2 levels are maintained above 4.5 mg O_2/l. We thus assumed that the fish under our experimental conditions would exhibit respiratory independence between 7.0 and 5.0 mg O_2/l. All subsequent oxygen-uptake experiments were conducted within that range.

The preliminary experiments indicated that 1.5-2.0 g of fish per liter of water consumed oxygen at a rate that would limit a run to <3 h, which we rather arbitrarily set as about the maximum time an experiment should last.

Experimental Procedure

The 10 series of 4 experiments each were made with groups of 2-8 fish (Table 1). The basic procedures for a series of experimental runs were essentially the same for both respirometers. The detailed procedures, herein described, are for experiments with the small respirometer.

Each series of experimental runs started between 0900 and 1100 h and continued through the day and night, into the early hours of the follow-

TABLE 1.—Respiration rate experiments with laboratory held skipjack tuna. Length measure is fork length.

Fish lot	Number of fish	Mean weight and range (g)	Mean length and range (cm)	Experiment	Respiration rate (mg O_2/g per h)	Mean respiration rate of fish lot	Swimming speed (L/s)	Mean swimming speed
1	8	3,834 (3,114-5,222)	58.6 (53.2-68.0)	1	0.561	0.499	1.2	1.1
				2	0.485		1.1	
				3	0.408		0.9	
				4	0.542		1.1	
2	6	671 (530-844)	36.1 (33.3-39.0)	1	0.488	0.551	1.7	1.7
				2	0.590		1.8	
				3	0.532		1.8	
				4	0.600		1.7	
3	5	632 (475-805)	35.5 (31.5-38.1)	1	0.581	0.506	2.2	1.8
				2	0.542		1.9	
				3	0.462		1.7	
				4	0.439		1.5	
4	2	1,719 (1,412-2,026)	44.8 (42.4-47.2)	1	0.525	0.522	1.5	1.4
				2	0.560		1.3	
				3	0.476		1.5	
				4	0.529		1.2	
5	2	2,539 (2,411-2,667)	52.8 (52.7-52.8)	1	0.456	0.382	1.2	1.2
				2	0.364		1.2	
				3	0.360		1.2	
				4	0.350		1.3	
6	2	1,703 (1,496-1,910)	45.1 (43.5-46.7)	1	0.578	0.555	1.8	1.6
				2	0.561		1.6	
				3	0.520		1.5	
				4	0.564		1.6	
7	2	2,178 (1,890-2,467)	49.3 (47.1-51.5)	1	0.574	0.577	1.2	1.4
				2	0.576		1.6	
				3	0.577		1.6	
				4	0.581		1.3	
8	2	2,790 (2,523-3,057)	51.6 (49.8-53.3)	1	0.778	0.658	1.7	1.4
				2	0.624		1.1	
				3	0.624		1.3	
				4	0.608		1.3	
9	2	1,349 (1,161-1,537)	44.6 (42.4-46.7)	1	0.395	0.395	1.2	1.3
				2	0.346		1.1	
				3	0.404		1.9	
				4	0.434		1.1	
10	2	2,200 (2,132-2,268)	50.2 (48.3-52.1)	1	0.580	0.575	1.3	1.3
				2	0.565		1.3	
				3	0.563		1.2	
				4	0.593		1.4	
Overall means		1,962	46.9		0.522			1.4

ing morning. The skipjack tuna were transferred from the holding tank to the respiration tank through which water was flowing at about 130 l/min. The fish were observed for 30 min and any that showed unusual behavior was replaced with another fish from the holding tank. Then the cover of the respirometer was installed and the water flow, now supplemented with oxygen, was continued. The animals were allowed to habituate until they were schooling and swimming slowly around the chamber at about 1.5 fork lengths/s (L/s) with no overt signs of stress. During this period (1-3 h) O_2 concentration in the chamber was maintained at air saturation, 6.9-7.0 mg O_2/l. The outlet water valve was then closed, the oxygen shut off, and the inflowing water was reduced to about 10 l/min. The chamber was slowly filled with water until the acrylic cover domed; then the inflow of water was stopped. When all bubbles were excluded, the sponge rubber ball was positioned to seal the vent pipe and the first experimental run was begun. At the start of a run, O_2 concentration in the respirometer was between 6.9 and 7.0 mg O_2/l. Oxygen concentration, temperature, swimming speed, and general behavior of the fish were monitored and recorded every 15 min. Swimming speed was estimated by measuring the mean time for three passes by the fish over a straight line distance of 1-2 m. (A comparison of values obtained from this technique with mean speeds during complete circuits of fish in the respirometer showed that speed was essentially constant and that the technique yielded an accurate measure of mean speed during a given circuit.) When the O_2 level in the respirometer had been reduced to 5.0 ± 0.1 mg O_2/l, final observations were recorded and the run terminated.

A water flow of about 130 l/min and oxygenation were then resumed, which quickly brought the O_2 in the respirometer up to about 7.0 mg O_2/l where it was maintained for from 1 to 1.5 h until the start of the next run. Following the same procedure, three more runs were made with each group of fish. In all of the experiments, the fish appeared to be in as good condition at the end of a four-run series as they had been at the beginning.

Oxygen Consumption by Just-Caught Skipjack Tuna

Rates of oxygen uptake were measured in 11 tank-lots of skipjack tuna while they were in shipboard transit between the fishing grounds and the shoreside research facility in Honolulu. These observations were made during three separate fishing trips during December 1972 (*Charles H. Gilbert* cruise 129). Sea-surface temperature was uniformly 24° C.

Apparatus

The five transport tanks served as respirometers. Except for the type of cover and differences in plumbing, these tanks were almost identical to the smaller laboratory respirometer described above. The cover of each transport tank consisted of an elliptical fiber glass plate with an open hatchway in its center (see fig. 15 in Nakamura 1972). The hatchway was an 80 by 48 cm oval in cross section and extended, chimneylike, 20 cm above the plane of the tank cover. Each cover was tightly bolted to the gasketed rim of its tank.

Seawater was pumped through each tank at a nearly constant rate between 150 and 250 l/min. Water entered a tank near the bottom at one end and exited at the top through an outlet in the hatchway wall. Oxygenation equipment like that described for the laboratory experiments was used in each tank to supplement O_2, which was measured with the same type of meter used in laboratory experiments.

Experimental Procedures

The transport tanks were made ready before fishing began by establishing a flow of seawater and 200-300% supersaturation of oxygen. Each fish caught was lowered on the fishing line through a tank's hatch and allowed to escape the barbless hook. On each day, the entire complement of fish was taken from a frenzy-feeding school (Strasburg and Yuen 1960) within a period of about 10 min. A tank-lot ranged from 7 to 12 fish, averaging 1.83-2.22 kg; estimated mean weight of captive fish was the actual mean weight of 20 other fish caught from the same school. Such an estimate is quite accurate because the size of individual fish within a skipjack tuna school is remarkably uniform (Brock 1954).

Within 2 h of capture, oxygen-uptake rate ($\dot{V}_{O_2}$) was measured for each of the 11 tank-lots of fish. In each tank the flow of oxygen was stopped and the time was measured for O_2 to decline from the saturation level (6.9 mg O_2/l) to a

second level between 6.2 and 5.6 mg O_2/l. For three tank-lots of fish, a second measurement of $\dot{V}_{O_2}$ was made after resaturation of the tank with oxygen. Because the flow of water through the tanks was maintained throughout the 3- to 15-min period of O_2 measurement, calculation of $\dot{V}_{O_2}$ accounted for O_2 both supplied to and removed from the tank in the flow of water:

$$\frac{d[O_2]_c}{dt} \cdot C = ([O_2]_I - [O_2]_c)\dot{Q} - N \cdot \overline{W} \cdot \dot{V}_{O_2}$$

which gives, upon integration and solution for $\dot{V}_{O_2}$,

$$\dot{V}_{O_2} = \frac{([O_2]_I - [O_2]_c) \cdot \dot{Q}}{N \cdot \overline{W} \cdot (1 - \exp(-\dot{Q} \cdot C^{-1} \cdot t))}$$

where $\dot{V}_{O_2}$ = oxygen-uptake rate (milligrams O_2/gram per hour),
$[O_2]_I$ = concentration of O_2 in incurrent water (milligrams O_2/liter),
$[O_2]_c$ = concentration of O_2 in tank and in excurrent water (milligrams O_2/liter),
$\dot{Q}$ = water exchange rate (liters/hour),
N = number of fish in tank,
$\overline{W}$ = estimated mean weight of fish (grams),
C = operating volume of tank (liters),
t = time (hours) for oxygen concentration in tank to decline from $[O_2]_I$ to $[O_2]_c$.

Low-Oxygen Tolerance Experiments

Apparatus

The tank used for the low-oxygen tolerance experiments was identical to the smaller respirometer tank but was uncovered and was supplied with unaerated water (0.5 mg O_2/l) directly from the seawater well. During the time it took to fill the tank, the water took up atmospheric oxygen and O_2 increased to 1.4 mg O_2/l.

Experimental Procedure

Twelve experiments were made, using 21 skipjack tuna (Table 2). The fish for six of the experiments were the same pair that had been used for a preceding series of oxygen-uptake experiments. For the other six experiments, skipjack tuna were taken directly from a holding tank. The fish were rested in the uncovered respiration tank at air-saturated O_2 levels (6.8-7.0 mg O_2/l) for about 2 h prior to being transferred to an immediately adjacent low-oxygen test tank. Because of a fish shortage, we were forced to use single rather than paired animals for the last three experiments.

TABLE 2.—Swimming speed and resistance time to low oxygen of skipjack tuna at various oxygen concentrations. Those fish which continued swimming for 240 min were considered to have survived. Length measure is fork length.

Experiment	Oxygen level (mg/l)	Weight of fish (g)	Resistance time (min)	Swimming speed range (L/s)
1	3.0	1,496	74	1.8-2.0
		1,910	115	
2	2.0	2,467	10	1.8-3.7
		1,890	20	
3	2.5	3,057	57	1.8-2.7
		3,523	60	
4	1.4	1,537	9	2.8-5.0
		1,161	10	
5	3.0	1,545	55	1.5-2.8
		1,887	70	
6	3.5	3,430	65	1.5-2.0
		1,616	155	
7	3.5	890	91	1.1-2.0
		902	Survived	
8	3.5	812	53	1.2-2.5
		791	65	
9	4.0	830	Survived	1.0-1.5
		1,020	Survived	
10	3.0	2,132	106	1.5-2.6
11	2.0	1,765	7	2.0-4.0
12	2.5	1,353	28	1.7-2.2

The experiments were done with O_2 ranging from 1.4 to 4.0 mg O_2/l and temperatures between 23° and 24° C. When O_2 in the low-oxygen tank reached the required levels, the fish were netted from the resting tank into the test tank. Each transfer took <5 s, and two fish were transferred within 30 s.

The O_2 and the behavior and swimming speeds of the fish were observed continuously. During an experiment, the water took up atmospheric oxygen at a rate dependent on the air-water pressure gradient. However, at all of the experimental O_2 levels there would have been a decrease of O_2 concentration due to the fish's respiration had we not gradually introduced oxygen as it was depleted by the fish; by so doing we continuously maintained O_2 concentration within ± 0.2 mg/l of the nominal experimental level.

A fish's resistance time was the period from introduction into the low-oxygen tank until the animal lost equilibrium and settled to the bottom. A fish was considered to have survived if it was still swimming after 240 min, at which time the experiment was terminated. At the conclusion of each experiment, weight and fork length of each fish were measured.

RESULTS

Oxygen-Uptake Experiments in Laboratory

Condition Factor

It has been our experience that skipjack tuna do not do well in captivity for extended periods. Obviously, valid behavioral and physiological data require that the experimental animals be in good health. As mentioned above, our fish were actively feeding and had been captive for less than a month. Some additional evidence relative to their general condition is provided by comparing the length-weight relationship of the experimental fish with the relationship obtained by Nakamura and Uchiyama (1966) for freshly caught skipjack tuna. For our captive fish, $\log W$ (grams) $= -2.657 + 3.532 / \log L$ (centimeters); for wild skipjack tuna, $\log W$ (grams) $= -2.317 + 3.368 / \log L$ (centimeters) ($\log = \log_{10}$). This comparison indicates that our experimental fish were, on average, about 14% lighter at a given length than wild fish of the same mean length (ca. 48 cm), the difference in weight-at-length decreased with increasing fork length. Part of the weight discrepancy resulted from the near emptiness of the guts of the experimental fish. Raju (1964) reported that pole-and-line caught skipjack tuna weighing about 1.4 kg had stomach contents comprising about 1.5% of body weight on the average and 6.3% of body weight at maximum.

General Behavior

The behavior of a group or pair of fish over the four experimental runs changed very little, and behavioral variation among the 10 series of experiments was slight.

The fish, usually in close company, continuously circled the respirometer 20-30 cm from the sides. Their course in the smaller respirometer was usually elongate but quite frequently shifted to a circle with a radius of 60-70 cm. Direction reversal and figure of eight patterns were not unusual. Rarely one fish would break away and swim separately, sometimes in a direction opposite the other fish, but such divergent patterns never persisted for long.

Swimming Speed

Swimming speed of skipjack tuna, averaged over all experiments, was 1.4 L/s. Speed was independent of O_2 over the experimental range (5.0-7.0 mg O_2/l), but stepwise multiple regression indicated significant ($P \leq 0.05$) effects of fish weight, length of time the fish had been in the respirometer, and the time-order of experimental series:

$$S = 3.55 - 0.53 / \log \overline{W} - 0.02t - 0.04 \cdot k$$

where S = swimming speed (lengths/second),
$\overline{W}$ = mean fish weight (grams),
t = time (hours) the fish had been in the respirometer,
k = time-order (1, ..., 10) of the experimental series.

Thus, length-specific swimming speed decreased with increasing fish size and with increasing values of both time-related variables. Solution of the regression equation at mean values of t (9.28 h) and k (5.5) yielded $S = 3.14 - 0.53 / \log \overline{W}$ (Figure 2).

Respiration Rate

Mean respiration rate over all experiments was 0.52 mg O_2/g per h (Table 1). The data suggested

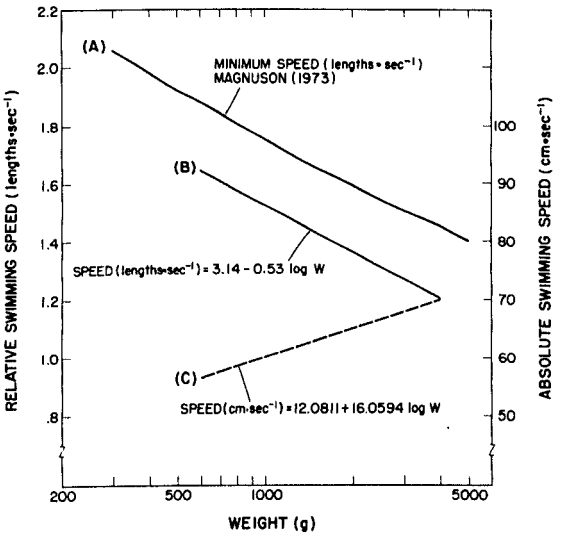

FIGURE 2.—Relation between voluntary swimming speed and body weight in skipjack tuna. Line A connects point-solutions from Magnuson's minimum speed function (Magnuson 1973). Line B is the relation between relative swimming speed and weight observed in the present study. Line C is the relation between absolute speed and weight observed in the present study. Length measure is fork length.

a slight but statistically nonsignificant decrease in respiration rate with decreasing oxygen concentration. Thus, our assumption of respiratory independence at oxygen concentrations down to 5.0 mg O_2/l seems valid; however, our experimental design did not permit proper analysis of the relation between respiration rate and O_2.

Of the other variables included in a stepwise regression analysis (fish weight, swimming speed, total time in respirometer, time of day, experimental order), only fish weight and swimming speed significantly ($P \leq 0.05$) affected respiration rate:

$$\log \dot{V}_{O_2} = -1.20 + 0.19 \log \overline{W} + 0.21 S$$

where $\dot{V}_{O_2}$ = oxygen-uptake rate (milligrams O_2/gram per hour),
$\overline{W}$ = mean fish weight (grams),
S = swimming speed (lengths/second).

We hasten to point out an irregularity in the relation just presented. While we offer the equation as a best available predictor of independent weight and speed effects on oxygen uptake in skipjack tuna, we recognize that $\overline{W}$ and S in our fish were not independent. As indicated in the last section, the fish tended to swim at a characteristic speed inversely proportional to the logarithm of body weight (Figure 2): $S = 3.14 - 0.53 / \log \overline{W}$. When this and the previous equation are combined to express the relation between oxygen-uptake rate and body weight for skipjack tuna swimming at their characteristic speeds, we are left with $\log \dot{V}_{O_2} = -0.54 + 0.08 / \log \overline{W}$. Thus, the speed-inclusive effect of $\overline{W}$ on oxygen-uptake rate actually observed in our experiments was quite small (Figure 3). A multiple regression analysis with speed deleted from the independent-variable list yielded no significant relation between $\dot{V}_{O_2}$ and $\overline{W}$ ($P > 0.05$). In contrast, the weight-inclusive effect of speed on $\dot{V}_{O_2}$ was readily apparent in a simple plot of log $\dot{V}_{O_2}$ versus S (means) for all experiments (Figure 4).

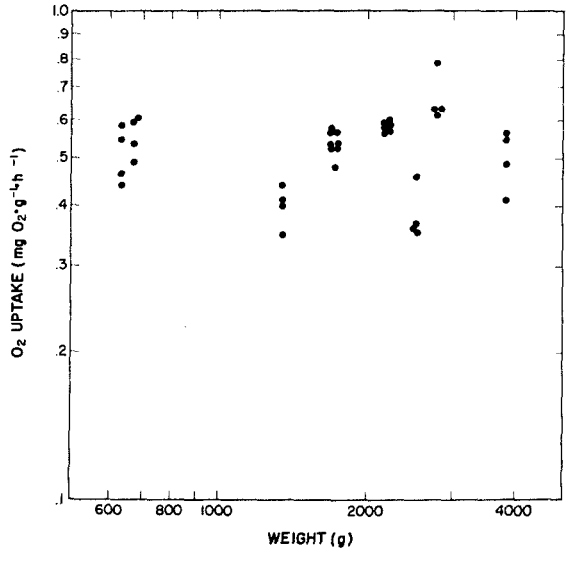

FIGURE 3.—Lack of significant relation between oxygen-uptake rate and weight of skipjack tuna swimming at voluntary speeds. Weights are means for the fish in each experimental series.

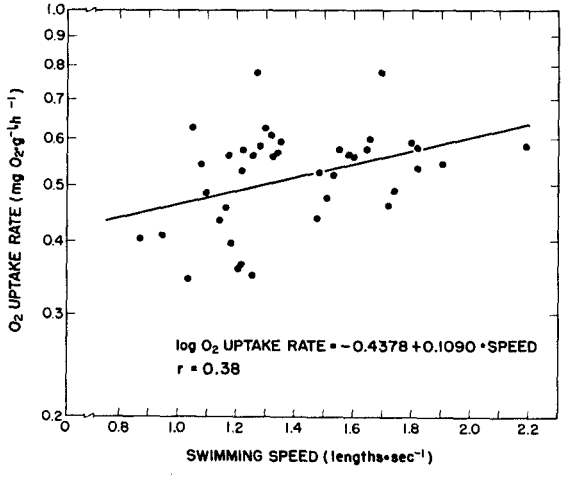

FIGURE 4.—Relation between oxygen-uptake rate and relative swimming speed of skipjack tuna (ranging from 60 to 4,000 g). Data are means for each experiment. Length measure is fork length.

Oxygen Consumption and Activity of Just-Caught Skipjack Tuna

Skipjack tuna, during their first 2.2 h of captivity, consumed oxygen at rates between 0.9 and 2.5 mg O_2/g per h, the median for the 14 determinations being 1.3 mg O_2/g per h at 75 min (Figure 5). Swimming speeds were correspondingly great—between 2 and 5 L/s.

Rate of oxygen consumption was not significantly correlated with time since capture (Kendall's $\hat{\tau} = -0.20$, $P \approx 0.18$; Siegel 1956) when all 14 rate determinations were considered as random observations from the same bivariate distribution. However, some features of the experiment suggested a decline in the rates of both oxygen con-

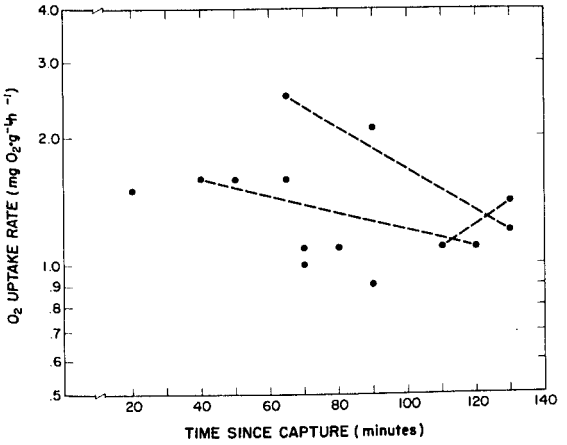

FIGURE 5.—Relation between the rate of oxygen uptake and the time elapsed after capture of skipjack tuna. Dashed lines connect paired determinations of oxygen-uptake rate for the same tank-lot of fish.

sumption and activity during the 2-h interval following capture. An initial period of frantic swimming, lasting 10-15 min, had already ended before we were able to collect our earliest respiration data. Still, the first five determinations of oxygen-consumption rate (within about 1 h of fish capture) were 1.5 mg O_2/g per h or more. In two cases, a tank-lot of fish respired at a much reduced rate during the second of two sampling intervals separated by about 1 h. (In a third set of such paired observations, oxygen uptake during the second was 0.3 mg O_2/g per h more than during the first, but these determinations were separated by only 20 min.) In conclusion, we believe the oxygen-uptake rate of our fish immediately after their capture was underestimated by the overall median value of 1.3 mg O_2/g per h and, in fact, may have exceeded 2.0 mg O_2/g per h.

Low-Oxygen Tolerance Experiments

General Behavior

Comparative behavioral responses of the fish in low-oxygen (≤3.5 mg/l) water were quite consistent. However, the sequence of behavior was more accelerated and the fish's reactions were often more violent at the lower oxygen concentrations.

At the two lowest O_2's (1.4 and 2.0 mg/l) the fish showed symptoms of considerable stress within about 30 s of introduction. Stress was manifested as very fast swimming (2.6 *L*/s), wide mouth-gape, and little or no attempt to school. During the last few minutes before the skipjack tuna died, they assumed a steep angle of attack with their snouts out of the water and swam jerkily, with intermittent bursts of speed up to 6 *L*/s. Complete collapse came abruptly; the fish simply ceased swimming and settled to the bottom. At 2.5 and 3.0 mg O_2/l, the initial stress reactions were milder and the fish started schooling within a few minutes after introduction. Swimming speeds were still relatively high (1.7-2.8 *L*/s), and the sequence and types of behavior were similar to those at the lowest O_2. At 4.0 mg O_2/l, both skipjack tuna swam and otherwise behaved as if they were in oxygen-saturated water.

Resistance Time and Swimming Speed

There was a marked, direct relation between the logarithms of resistance time and oxygen concentration at oxygen levels up to 3.5 mg O_2/l (Table 2, Figure 6). At 3.5 mg O_2/l, four of the experimental fish had resistance times in the same range as the fish exposed to 3.0 mg O_2/l, but one fish survived for the 240-min duration of the experiment. The survivor showed few overt signs of stress but did swim faster than the fish in oxygen-saturated water. At 4.0 mg O_2/l, both experimental fish survived 240 min.

The 21 skipjack tuna used in the 12 experiments ranged in weight from 791 to 3,523 g (Table 2). There was no significant correlation between weight and resistance time to low-oxygen levels.

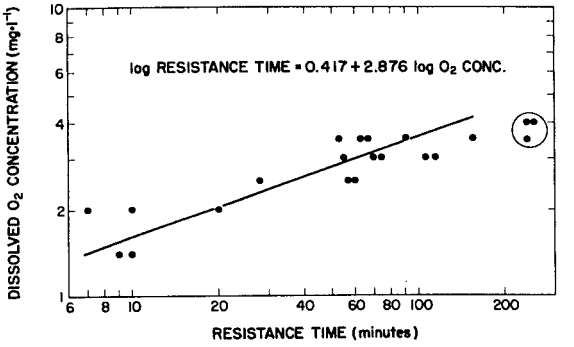

FIGURE 6.—Relation between resistance time to low-oxygen concentration and dissolved oxygen concentration. Resistance time was the period from the fish's introduction into the low-oxygen tank until it stopped swimming and settled to the bottom. Circled points indicate three fish that were still swimming after 240 min. The regression line was fitted to the points for fish that died.

Mean swimming speed increased as O_2 decreased (Figure 7), reaching 3.9 *L*/s at the lowest O_2, 1.4 mg O_2/l. Mean speed at 4.0 mg O_2/l was slightly less than at higher O_2 values (oxygen-uptake experiments); therefore, the critical O_2 for an increase in swimming speed appeared to lie between 4.0 and 3.5 mg O_2/l.

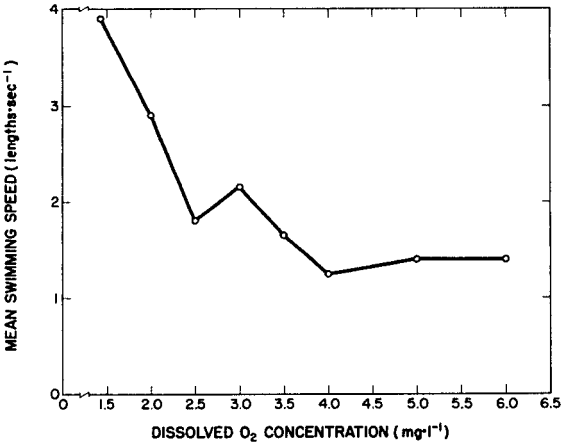

FIGURE 7.—Relation between mean swimming speed and dissolved oxygen concentration. The data for O_2 of 6.0 and 5.0 mg · l^{-1} are from the oxygen-uptake experiments. Those at lower concentrations are derived from the low-oxygen tolerance experiments. Length measure is fork length.

DISCUSSION

Terminology Relevant to Tuna Metabolism

In this paper we have strived to quantify the activity and respiration levels of our fish. The question of terminology remains. Doudoroff and Shumway (1970) have emphasized that "different meanings have been attached by different authors to the same term or different terms have been used in the same sense...." The question of terminology is further complicated in tunas because they, unlike typical fishes, must maintain some minimum forward motion for hydrodynamic lift (Magnuson 1973) and for gill perfusion (Brown and Muir 1970; Stevens 1972); a stationary tuna both sinks and suffocates. Thus, the notion of "resting" metabolic rate (Doudoroff and Shumway 1970) is not applicable to tunas.

What we have collected in our laboratory experiments were data on "routine" (Fry 1957, 1971) activity and metabolism. Fry (1971) defined routine metabolic rate as "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 protected from outside stimuli." Our fish were in a postabsorptive state (except for bits of food they may have eaten during the transfer process) and were as quiescent as tunas are ever likely to be when confined in a small tank. Perhaps, our laboratory data reflect minimum metabolism for skipjack tuna in that the fish were swimming at speeds actually below the hydrodynamic minima calculated by Magnuson (1973) for skipjack tuna (Figure 2). On first consideration, it would seem unlikely that tunas—which lack ventilatory pumps and are, therefore, obligate ram-ventilators (Brown and Muir 1970)—could achieve minimum swimming speed without also achieving minimum rate of oxygen uptake. However, Stevens (1972) has shown that skipjack tuna have the capability for doubling the amount of oxygen they extract per unit flow of water irrigating the gills (utilization efficiency, 0.4-0.8) with only a 17% reduction in ventilation rate (from 3.0 to 2.5 l H_2O/kg per min). Thus, it is conceivable that a skipjack tuna could decrease swimming speed and simultaneously increase oxygen uptake. We must, therefore, recognize the possibility that "excitement" (Fry 1971) associated with the alien and confining environment of our respirometers resulted in heightened rates of oxygen uptake compared with those that might obtain in wild, unexcited skipjack tuna swimming in the sea at the same speeds. However, the data we collected do not permit an objective evaluation of this possibility. For purposes of further discussion, we assume that our laboratory measurements of oxygen-uptake rate contained no component of "excitement" metabolism independent of swimming speed. Lack of change in respiration rate among sequential experiments indicates that any activity-independent excitement component of metabolism that may have been present was habituation-time invariate. This has encouraged us to go so far in the following section as to estimate the hypothetical "standard" (= "basal"—see Fry 1971; Brett 1972) metabolism of skipjack tuna from our respiration data; this we did, as Fry (1971) recommends, by simply extrapolating to zero speed the regression equation relating respiration rate and swimming speed.

Rates of oxygen uptake measured in the "just-caught" fish can scarcely be considered "routine"

but still may have underestimated the skipjack tuna's maximum or "active" (Fry 1971; Brett 1972) rate of oxygen consumption. Wild skipjack tuna similar in size to our experimental fish can swim at sustained speeds probably exceeding 10 *L*/s (Yuen 1970); our just-caught fish swam at speeds ≤ 5 *L*/s during the intervals when oxygen-uptake rates were measured. However, the experimental fish may have been repaying an oxygen debt incurred during the feeding frenzy preceding capture or during the early minutes of captivity; recovery from oxygen debt could have heightened oxygen-uptake rates to levels above those commensurate with sustained swimming at the observed speeds (Brett 1972).

"Standard" Metabolism

Even though tunas never lie stationary in the water, it is of interest from the bioenergetic and comparative standpoints to separate the routine metabolic rate into standard and activity-related components. From the equation on p. 38, with swimming speed set equal to 0.0,

$$\log \dot{V}_{O_2} = -1.20 + 0.19 \log \overline{W},$$

where $\dot{V}_{O_2}$ = oxygen-uptake rate (milligrams O_2/gram per hour),
$\overline{W}$ = mean fish weight (grams).

Solutions of this equation at our experimental extremes for $\overline{W}$ are $\dot{V}_{O_2} = 0.21$ mg O_2/g per h at $\overline{W} = 632$ g and $\dot{V}_{O_2} = 0.30$ mg O_2/g per h at $\overline{W} = 3{,}834$ g. These values are extraordinary for two reasons: 1) They are at the extreme upper limit for nontuna (cf. fig. 4 of Brett 1972), a fact that becomes even more remarkable when one considers that other teleost values are almost all for small (10-100 g) individuals, and 2) the weight exponent is a positive 0.19, not a negative value in the neighborhood of -0.2 characteristic of typical fishes (Fry 1957, 1971; Winberg 1960). While weight exponents for active metabolic rate in salmonids may frequently approach 0.0 (Job 1955; Brett 1965; Rao 1968), we know of no data to suggest weight exponents as large as $+0.2$ for metabolic rate in nonscombrid fishes. The validity of a large, positive value for the weight exponent of "standard" metabolic rate in skipjack tuna is supported by independent data, via direct calorimetry, on heat production rates; the red muscle of sedated skipjack tuna (maintained by gill perfusion) metabolized at a rate proportional to $W^{0.13}$ (Neill et al. 1976).

In marked contrast with our estimate of skipjack tuna's weight exponent for standard metabolism is that reported by Brill (1979)—negative 0.44, a value at the other extreme for fishes. Considering that Brill's and our groups of fish were similar in size range and preexperimental history, we must deduce that the large discrepancy between estimates relates principally to the difference in experimental methodologies: Brill took, as the standard metabolic rate, the stabilized minimum $\dot{V}_{O_2}$ of perfused skipjack tuna that had been first injected with the neuromuscular blocking agent gallamine triethiodide, then spinalectomized.

Activity-Related Metabolism

Our respiration experiments estimated only rates of oxygen uptake, not rates of instantaneous metabolic demand for oxygen. Neill et al. (1976) estimated that the oxygen demand of red muscle in highly active (chased) skipjack tuna can reach 7 mg O_2/g per h for periods on the order of 1-2 min. For even shorter periods, involving only true burst swimming, the rate of oxygen demand must be even higher. Brett (1972) has estimated that burst-swimming fishes' instantaneous rate of oxygen demand (on a whole-body basis) exceeds the maximum rate of supply by a factor of 10. Any excess of demand over supply accumulates as an oxygen debt that ultimately must be repaid.

Our observations on just-caught fish provided (probably conservative) estimates of the maximum rate at which skipjack tuna can supply oxygen to meet their metabolic demands. Like the skipjack tuna's "standard" metabolic rate, its maximum (active) rate of oxygen uptake must be substantially beyond that typical of fishes. Just-caught skipjack tuna respired at a median rate of 1.3 mg O_2/g per h; the highest five values (those obtained during the fish's first hour of captivity) were between 1.5 and 2.5 mg O_2/g per h. Brett (1972), in reviewing his own and others' work, reported that fishes' maximum rates of oxygen consumption reach a "probable ceiling" near 1.0 ± 0.2 mg O_2/g per h.

The activity-respiration relationship obtained at sea for just-caught skipjack tuna was reasonably consistent with that extrapolated from the laboratory experiments (Figure 8). However, data of the two kinds may have agreed less well had

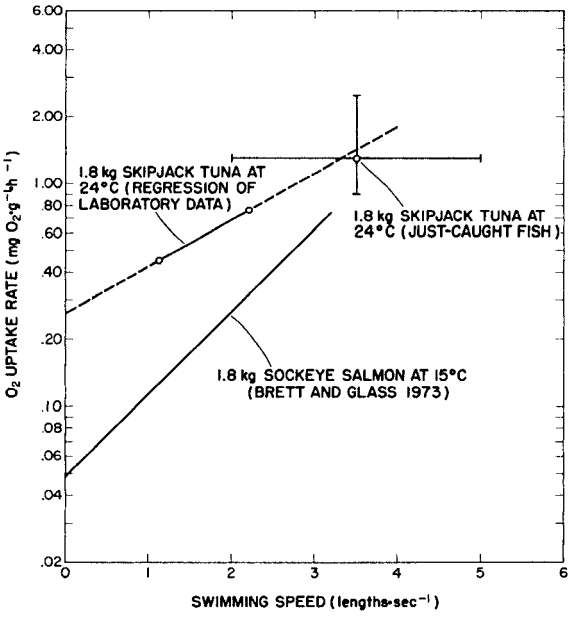

FIGURE 8.—Comparison between respiration-speed relations for 1.8 kg skipjack tuna calculated from the present study and for 1.8 kg sockeye salmon computed from equations given by Brett and Glass (1973). Ranges of observed values are indicated by the lines extending from the median value for just-caught skipjack tuna. Length measures are fork length.

we been able to accurately measure swimming speeds in just-caught fish. The basis for our cautious appraisal of such apparently good "fit" is suspicion that the linear model, log $\dot{V}_{O_2} = a + b \cdot$ speed, which seems adequate for many fishes (Brett 1972; Brett and Glass 1973; Webb 1975), cannot hold for skipjack tuna over the entire range of swimming speeds that they can sustain. Personal observations on these fish and Yuen's (1970) report of a school of skipjack tuna (ca. 44 cm fish) that traveled 28 km in 107 min (average minimum speed = 4.4 m/s) convince us that 40-50 cm skipjack tuna can swim for at least an hour at speeds near 10 *L*/s. If that is so, our linear model predicts oxygen uptake in 1.8 kg skipjack tuna (median size of just-caught fish) at a maximum sustained rate of at least 33.0 mg O_2/g per h. Active metabolic rate of skipjack tuna may substantially exceed Brett's (1972) predicted maximum for fishes, but we are confident it does not do so by a factor of nearly 30. The most logical interpretation of this conundrum is nonlinearity in the relation between log $\dot{V}_{O_2}$ and speed; as skipjack tuna swim faster, they must become more efficient in their use of oxygen and energy. The same is probably true for other fast-swimming fishes, such as Peterson's (1976) striped mullet, *Mugil cephalus*. Even in the relatively sluggish goldfish, *Carassius auratus*, oxygen-uptake rate actually declines as the fish pass from spontaneous activity at low apparent speeds to induced swimming (against currents) at higher speeds (Smit 1965).

There is, of course, an alternative explanation: Our laboratory experiments overestimated the true coefficient for speed. In fact, taking the lower 95% confidence limit on the speed coefficient—0.11—yields a comparatively modest 3.31 mg O_2/g per h for predicted $\dot{V}_{O_2}$ at 10 *L*/s. But a true speed coefficient as low as 0.11 is not only inconsistent with the comparable coefficient in other fishes (Fry 1971; Brett 1972) but also with other, independent data (Chang et al.[4]) on metabolism-speed relations in skipjack tuna. The speed coefficient estimated from that study was 0.22, a value remarkably similar to our mean estimate.

To close our consideration of activity-related metabolism in skipjack tuna, we offer a comparison between respiration-speed relations of a 1.8 kg skipjack tuna at 24° C and a 1.8 kg sockeye salmon, *Oncorhynchus nerka*, at 15° C (Figure 8). We chose the sockeye salmon because its active metabolic rate "is one of the highest [for fishes] on record, exceeding that determined for other salmonids by 30% to 40%" (Brett and Glass 1973). The sockeye salmon respiration-speed relation was computed from equations given by Brett and Glass (1973); 15° C-values were used because this is near the sockeye salmon's thermal optimum for fast swimming and several other vital functions (Brett 1971). Skipjack tuna seem to swim and metabolize at rates nearly independent of temperature (Dizon et al. 1977; Chang et al. footnote 4).

At all speeds common to the two fishes, skipjack tuna have the higher metabolic rate—3.7 times higher at 1.1 *L*/s (the skipjack tuna's minimum speed) decreasing to 1.7 times higher at 3.2 *L*/s (the sockeye salmon's maximum sustained speed). If the basis of comparison is the energy cost of swimming (oxygen-uptake rate associated with any particular speed minus standard uptake), the difference between these fishes is lessened but the qualitative relation is unchanged: at

[4]Chang, R. K. C., B. M. Ito, and W. H. Neill. Manuscr. in prep. Temperature independence of metabolism and activity in skipjack tuna, *Katsuwonus pelamis*. Southwest Fish. Cent., Natl. Mar. Fish. Serv., Honolulu, HI 96812.

1.1 and 3.2 L/s, the cost for skipjack tuna are, respectively, 2.5 and 1.4 times those for sockeye salmon. We can only conclude that 1.8 kg skipjack tuna swim at intermediate speeds less efficiently than 1.8 kg sockeye salmon—this despite the fact that, among fishes, the skipjack tuna represents the apex of evolutionary engineering for speed (Magnuson 1973; Stevens and Neill 1978). Presumably, the evolution of skipjack tuna (like that of fast cars) has involved sacrifice of energetic efficiency at low speeds in favor of increased efficiency at high speeds, permitting a dramatic increase in maximum attainable speed.

Interrelation of Metabolic Rate, Swimming Speed, and Body Weight

Voluntary speeds (S, lengths/second) of skipjack tuna swimming in our laboratory respirometers were inversely related to fish weight by the relation $S = 3.14 - 0.53 / \log W$. Magnuson (1973), working from basic hydrodynamic relations, predicted minimum speed for steady-state swimming in various tunas; his model for skipjack tuna yielded a speed versus fish-weight relation very similar in slope to that we observed (Figure 2). The difference in means may be attributable to differences in condition factor and/or body-water content (Kitchell et al. 1977) between our captive fish and the wild skipjack tuna on which Magnuson's calculations were based.

Oxygen-uptake rates ($\dot{V}O_2$, milligrams O_2/grams per hour) of our laboratory fish were influenced not only by swimming speed but also by fish weight independent of speed: $\log \dot{V}O_2 = -1.20 + 0.19 \log W + 0.21S$. We have concluded above that 1) the intercept value ("standard" rate at any weight) is unusually large for fishes; 2) the weight coefficient is opposite in sign from that typical of fishes (and of organisms, generally); and 3) the interdependency of $\log \dot{V}O_2$ and S on weight is compensatory, resulting in no statistically demonstrable difference among oxygen-uptake rates for skipjack tuna of various weights (600-4,000 g) swimming at their characteristic speeds.

Conclusion (3) led us to explore the relation between oxygen-uptake rate per unit distance ($\dot{V}\acute{O}_2$, milligrams O_2/gram per kilometer) and swimming speed for skipjack tuna of different sizes. Exponentiating the linear regression equation relating $\dot{V}O_2$ in milligrams O_2/gram per hour to W and S, $\dot{V}O_2 = 0.063 \cdot W^{0.19} \cdot 10^{0.21S} = 0.063 \cdot W^{0.19} \cdot e^{0.48S}$. Multiplying the last equation by $27.78 \cdot \text{km}^{-1} \cdot S^{-1} \cdot L^{-1}$ generated an equivalent expression for $\dot{V}\acute{O}_2$ in milligrams O_2/gram per kilometer:

$$\dot{V}\acute{O}_2 = 1.75 \cdot L^{-1} \cdot S^{-1} \cdot W^{0.19} \cdot e^{0.48S}.$$

Finally, we used the exponentiated length-weight relationship for experimental fish: $\log W = -2.657 + 3.532 \log L$; thus, $W = 0.0022L^{3.532}$ to eliminate W:

$$\dot{V}\acute{O}_2 = 0.55 \cdot L^{-0.33} \cdot S^{-1} \cdot e^{0.48S}.$$

Solutions of this equation for $\dot{V}\acute{O}_2$ at various values of L and S are shown graphically in Figure 9. Small fish are less efficient (higher $\dot{V}\acute{O}_2$) at any particular speed than are larger fish, but fish of all sizes reach their particular minimum $\dot{V}\acute{O}_2$ at the same relative speed—about 2.1 L/s. The relation between this, the optimum speed (S_{opt}) for covering distance, and the value of the coefficient, 0.48, for the exponential term in S is simple—each is the reciprocal of the other:

$$\frac{d\dot{V}O_2}{ds} = 0.55 \cdot L^{-0.33} \text{ per } \frac{0.48S \cdot e^{0.48S} - e^{0.48S}}{S^2};$$

$$\text{at } \frac{d\dot{V}\acute{O}_2}{ds} = 0,\ 0.48S \cdot e^{0.48S} = e^{0.48S};$$

$$\text{therefore, } S_{opt} = \frac{1}{0.48} \approx 2.08.$$

For skipjack tuna between 30 and 60 cm length, the characteristic speeds and $S_{opt} = 2.08$ correspond with $\dot{V}\acute{O}_2$ rates that are maximally (for 60 cm fish) different by only 13% of min $\dot{V}\acute{O}_2$ (Figure 9). The question arises as to whether the observed characteristic speeds, rather than "S_{opt}," might be the (evolutionary) "design" speeds that minimize $\dot{V}\acute{O}_2$. The characteristic speeds agree remarkably well (better than does "S_{opt}") with the optimum speed predicted by Weihs' (1973b) model; Weihs, reasoning from thrust and drag relations for fishes, argued that speed is optimized (energy expended per unit distance is minimized) when "the rate of energy expenditure required for propulsion [and associated physiological work?] is equal to the standard (resting) metabolic rate." For our skipjack tuna, S at $\dot{V}O_2$ equivalent to twice the hypothetical standard rate was 1.43 L/s, a value that falls midway in the range of speeds

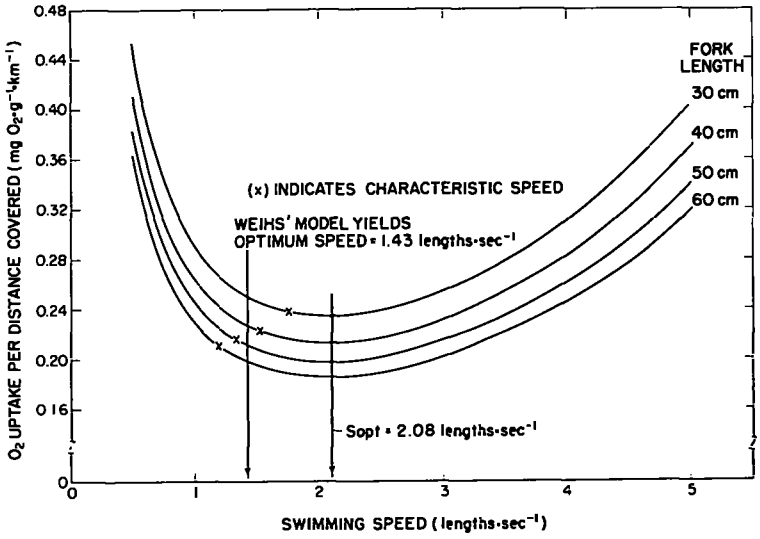

FIGURE 9.—Relation of rate of oxygen uptake per unit distance ($\dot{V}O_2$) swam to swimming speed for skipjack tuna of various lengths. The x's indicate characteristic swimming speeds of fish in the present study. S_{opt} is the optimum speed for covering distance in terms of minimum $\dot{V}O_2$. The arrow at 1.43 lengths · sec^{-1} is the optimum speed predicted by Weihs' (1973b) model.

characteristic of fish between 30 and 60 cm length (Figure 10).

In a subsequent paper, Weihs (1977) showed that fishes' optimum swimming speeds on an absolute basis ought to be proportional to $L^{0.43}$. The characteristic speeds of our tuna, when computed in centimeters per second and treated as a power function of fish length, are proportional to

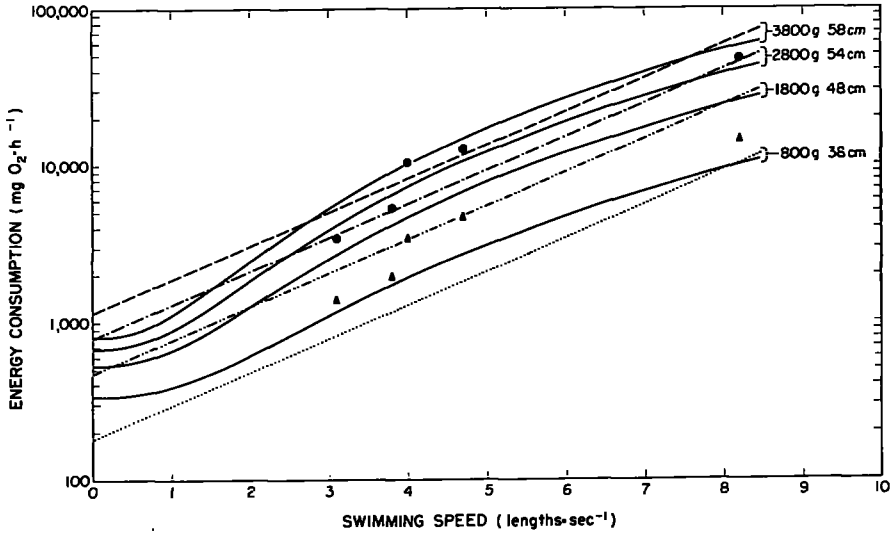

FIGURE 10.—Comparison between the measured oxygen uptake relationship extrapolated between 0 and 8.5 lengths sec^{-1} (broken lines) and the theoretically expected power consumption (solid lines) for four skipjack tuna. Triangles (▲) are the theoretical power consumption based on a detailed analysis of drag forces for a 40 cm, 1,003 g skipjack tuna (Magnuson 1978). Points (•) are based upon a detailed analysis of thrust forces (Magnuson 1978). Length measures are fork length.

$L^{0.45}$ and, thus, fit Weihs' model almost perfectly.

We conclude by noting that our discussion of optimum swimming speeds for covering distance relates only to skipjack tuna swimming at constant depth (as those in our respirometers were required to do). Weihs (1973a) has calculated that negatively buoyant fishes like the skipjack tuna could achieve an energy savings of 20% (compared with swimming at constant depth) by alternately gliding downward at an angle of about 11° (to the horizontal), then actively swimming upward at an angle near 37°.

Resistance to Low Oxygen

In areas of the world ocean with surface waters not stressfully warm for skipjack tuna there is always available air-saturated water that overlies oxygen-depleted strata (Barkley et al. 1978). Therefore, the 4-h exposure period we adopted in this study would seem to include all intervals of low-oxygen exposure that skipjack tuna ever need endure at sea.

The data suggest for skipjack tuna a threshold of response to hypoxic stress at about 4.0 mg O_2/l (Figure 7); this value is at or below that representative of fishes (Davis 1975). In our experiments, the skipjack tuna's response to low oxygen was an increase in swimming speed; this would seem adaptive in that increased swimming speed initiated by hypoxic stress would facilitate return of fish from deep, oxygen-depleted water to air-saturated surface water.

The 4-h median tolerance limit to low oxygen was also near 4.0 mg O_2/l (Figure 6). This value, in keeping with the skipjack tuna's exceptionally high metabolic rate, is apparently higher than that of any other fish yet investigated (Doudoroff and Shumway 1970).

Angular Acceleration and Excess Body Temperature

Compared with other studies of fish metabolism, our experiments with skipjack tuna involved two unusual elements: 1) The fish were forced, by the relatively small size of the tanks, to swim a curved path, and 2) they probably had core temperatures up to several degrees higher than the temperature of the surrounding water.

Weihs (1981) has suggested that our continuously turning fish expended more propulsive energy than they would in swimming a straight path at the same speed. A turning tuna must counter centrifugal forces by "banking" with its pectoral fins to produce a component of lift directed inwards along the turning radius. Therefore, our results may overestimate the oxygen-uptake rates and perhaps also the lower lethal oxygen concentration for skipjack tuna at sea. However, we doubt that the magnitude of the overestimate can be very great, for fish in the large and small respirometers (with radii of typical swimming paths about 2 and 0.8 m) respired at similar rates (Table 1). Furthermore, metabolic rates of fish in our experiments were consistent with those inferred from weight and energy "loss" rates of starved skipjack tuna living in tanks 7.3 m in diameter (Kitchell et al. 1978).

Oxygen-uptake rates of our test fish also compare well with theoretical estimates of the amount of energy consumed by similarly sized fish swimming a straight course at the same speeds (Figure 10). The observed oxygen-uptake relationship (milligrams O_2/hour) was extrapolated from 0 to 8.5 L/s for four skipjack tuna ranging in weight from 800 to 3,800 g (dashed lines). (Recall that mean speeds of our fish were between only 0.9 and 2.2 L/s.) Superimposed on the empirical relationship are theoretical projections of energy consumption based on estimates of drag force. Theoretical energy uptake—in keeping with the reasoning of Webb (1975), Sharp and Francis (1976), Sharp and Vlymen (1978), and Dizon and Brill (1979)—was computed according to the following rationale:

1. Total power required is the sum of the power required for nonswimming processes (P_2) plus power required for thrust (P_1), the latter divided by an estimate of total aerobic efficiency $\equiv 0.2$ (Webb 1975).
2. Power required for nonswimming metabolic processes (the standard metabolic rate of a fasted fish from Brill (1979)),

$$P_2 = 1.53 \cdot W^{0.563}$$

where P_2 = power (watts),
W = weight (kilograms).

Brill's (1979) relation is used despite some doubts about the validity of the exponent because it provides for skipjack tuna the only estimate of P_2 independent of our data.

3. Thrust power must be equal to drag force multiplied by velocity

$$P_1 = 0.5 \cdot \rho \cdot S \cdot U^3 \cdot C_d \cdot 10^{-7}$$

where P_1 = power (watts),
ρ = water density (1.0234),
S = surface area ($0.4\ L^2$) where L = length (centimeters),
U = velocity (centimeters/second),
C_d = drag coefficient.

4. The drag coefficient is estimated using Webb's (1975) formula, as

$$C_d = 10 \cdot \left(\frac{\rho L U}{\mu}\right)^{-0.5}$$

where μ = water viscosity (0.0096).

5. Assuming an oxycaloric equivalent of 3.4 cal/mg O_2, power in watts can be converted into oxygen uptake in milligrams O_2/hour by multiplying watts by 253.

The simple model of energy consumption presented here makes no pretention of precision because no attempt was made to accurately determine either the coefficient of drag or the surface area of the fish. Magnuson and Weininger (1978) and Magnuson (1978) did do that. We have included their estimates for power consumption of a 40 cm, 1,003 g skipjack tuna in Figure 10. The five triangles are estimates of power consumption based on Magnuson's (1978) determination of drag forces, the points based upon Lighthill's (1969) model of thrust forces (data from Magnuson 1978: table XI). Whether a sophisticated estimate of power consumption or a simple one is employed, the correspondence between the theoretically expected and the empirically derived power consumption is good. We take this as additional evidence that our experimental values are reasonable estimates of oxygen uptake of skipjack tuna swimming straight courses at sea.

Skipjack and other tunas are warm bodied, owing to their high metabolic rates coupled with large thermal inertia (Neill et al. 1976; Stevens and Neill 1978). Thus, our fish undoubtedly were warmer than the water in which they swam. Skipjack tuna used in the laboratory experiments probably had core-temperature excesses on the order of 2°-4° C (cf. Stevens and Fry 1971; Neill et al. 1976); the just-caught fish, being more active, may have had core temperatures as much as 10° C above ambient water temperature (cf. Stevens and Fry 1971). Interpretation of our results has not been complicated by consideration of the difference between tissue and environmental temperatures, because metabolism of skipjack tuna has been shown to be virtually independent of temperature (Gordon 1968; Chang et al. footnote 4).

CONCLUSION

Our findings emphasize the unique evolutionary position of the skipjack tuna (and, by extension, other tunas) among fishes. The skipjack tuna epitomizes what Stevens and Neill (1978) have termed "energy speculators": forms that "operate to maximize energy gain by gambling large energy expenditures...on the expectation of proportionately large energy returns." The skipjack tuna's "standard" metabolic rate is two to five times that of typical fishes of similar size. Moreover, the skipjack tuna is relatively inefficient in its use of oxygen and food-energy for swimming (at least at low speeds) and it dies at O_2 levels still well above those lethal to other fishes. Clearly, the skipjack tuna's ability to sustain high levels of activity has not been achieved without substantial physiological cost.

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AN ANALYSIS OF CATCH AND EFFORT DATA FROM THE U.S. RECREATIONAL FISHERY FOR BILLFISHES (ISTIOPHORIDAE) IN THE WESTERN NORTH ATLANTIC OCEAN AND GULF OF MEXICO, 1971-78[1]

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ABSTRACT

Catch and effort data from the United States recreational fishery for billfishes in the Atlantic Ocean and Gulf of Mexico were examined to evaluate their usefulness in determining trends in abundance. In the Gulf of Mexico, data were recorded from both organized fishing tournaments and from noncompetitive fishing. A fishing power model was developed and comparisons made between catch per unit effort from tournament data, nontournament data, and Japanese longline data. The results indicate that catch and effort statistics for white marlin, *Tetrapturus albidus*, and sailfish, *Istiophorus platypterus*, in the Gulf of Mexico appear to be reliable and can be aggregated to provide a means of indexing relative abundance of these species. The model did not appear to be appropriate for blue marlin, *Makaira nigricans*, however. The general trend in catch per unit effort from 1972 to 1978 for sailfish and white marlin in the Gulf of Mexico appears to be downward.

Based on catch per unit effort from all fishing areas, there appears to be a single stock of white marlin in the western North Atlantic and Gulf of Mexico.

In 1971, the National Marine Fisheries Service's Southeast Fisheries Center initiated research on the billfish stocks of the western North Atlantic Ocean and Gulf of Mexico. The purpose of this research was to develop and evaluate a method of determining changes in relative abundance of billfish stocks using catch and effort data from the recreational fishery. This report has been prepared to present a description of this research, evaluate the reliability of the sampling techniques, and make a preliminary determination of the validity of catch and effort data from the recreational fishery as an indicator of changes in relative abundance of billfish populations.

THE RECREATIONAL FISHERY

The development of the U.S. recreational fishery for billfishes (families Istiophoridae and Xiphiidae) has been reviewed in detail by de Sylva (1974). The first sailfish caught by rod and reel in the Atlantic was probably taken off Miami, Fla., around the turn of the century. After World War II, increased leisure time and affluence coupled with newer and better fishing gear, vessels, and angling techniques spurred a dramatic expansion of the fishery geographically as well as to a broader segment of the population. In the Atlantic, anglers now fish for billfishes from almost every state along the eastern coast of the United States as well as from the U.S. Virgin Islands, Puerto Rico, and numerous foreign ports.

Species

The billfish species in the Atlantic recreational fishery are the sailfish, *Istiophorus platypterus*, the white marlin, *Tetrapturus albidus*, the blue marlin, *Makaira nigricans*, and to a much lesser extent the swordfish, *Xiphias gladius*, and the longbill spearfish, *Tetrapturus pfluegeri*. Sailfish, the most commonly occurring species in the catch, is more coastal in its habitat than any of the other species and consequently is available to a greater number of anglers. It is also the smallest in average size, with the possible exception of the longbill spearfish, and generally requires less expensive and sophisticated fishing tackle than is commonly used in fishing for marlins. The two marlins are most abundant in oceanic waters, generally far from the coast of the United States, and fishing for marlins usually requires relatively large vessels and expensive fishing gear. Prior to 1976, recreational fishing for swordfish was a specialized type of fishing where the fish was usually sighted before the fishing lines were placed in the water.

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Fishing was done in a fairly restricted area off the northeastern United States. In 1976, however, a new method of fishing for swordfish was developed off the southeast Florida coast. This method involved drifting baited lines at various depths at night. Fishing success using this technique has been substantially higher than by the earlier method, and swordfish are now available to fishermen all along the Gulf of Mexico and Atlantic coasts of the United States, whereas previously the fishery was confined to a relatively small geographical area.

Longbill spearfish are rare in the recreational catch. They are believed to be primarily an open ocean species and generally are not common in the areas where recreational fishing takes place.

Because of the nature of the fishery for swordfish and the scarcity of longbill spearfish in the recreational catch, our study involves only the sailfish and the two marlins, and the following discussions deal only with these species.

Fishing Techniques

Fishing, using rod and reel, is conducted primarily by trolling dead or artificial baits at speeds ranging from 3 to 15 kn. The baits are fished mainly at the surface, although sometimes baits are rigged to troll down to a meter or more beneath the surface. Generally, three to four lines are fished simultaneously, although as many as eight are occasionally used. In some areas the use of live bait has become increasingly popular. Our study does not include catch and effort data involving the use of live bait.

Once a billfish is hooked, the boat operator usually maneuvers the boat so that the effort required by the angler is reduced. Once the fish is brought to the boat it is either gaffed and brought onboard or released alive. More and more frequently, anglers and crews are tagging their fish before releasing them in cooperation with the National Marine Fisheries Service Cooperative Game Fish Tagging Program (formerly the National Marine Fisheries Service-Woods Hole Oceanographic Institution Cooperative Game Fish Tagging Program).

Billfishes are not highly desirable as food in the continental United States, although they are utilized to some extent as a smoked product. However, many fishermen are learning that fresh marlin, in particular, is an excellent food fish. In Puerto Rico and the Virgin Islands there is a great demand for fresh marlin which commands a high price on the local fresh fish markets.

THE LONGLINE FISHERY

The high seas longline fishery for tunas was begun in the Atlantic by the Japanese in 1956. Fishing effort increased rapidly, peaking in 1965 when almost 100 million hooks were set and the fishery included almost all waters between lat. 40° N and 40° S. Effort fell off rapidly, however, in response to declining catch rates and increasing costs, and by the early 1970's the Japanese were averaging only about 40 million hooks annually. In the mid-1960's, Taiwan and South Korea entered the fishery and by the 1970's theirs were the dominant fleets in the Atlantic. An excellent review of the development of the fishery is available in Ueyanagi (1974).

The longline fishery in the Atlantic is directed primarily at tunas, and billfishes are incidental catches, although large numbers are caught. From 1956 through 1976, for example, almost 140,000 t of white marlin, blue marlin, and sailfish/spearfish were caught by longliners in the Atlantic (Table 1). There is some evidence that stocks of white and blue marlin in the North Atlantic and South Atlantic are discrete groups (Mather et al. 1972; Wise and Davis 1973). Longline catch per unit effort (CPUE) values for white and blue marlins within these two areas in the 1970's are for the most part considerably below those in the 1960's (Figure 1).

TABLE 1.—Estimated landings, in metric tons, of blue marlin, white marlin, and sailfish/spearfish by the tuna longline fishery in the Atlantic Ocean, 1956-76. Data from Conser and Beardsley,[1] tables 1 and 4, for blue marlin and white marlin, and Conser,[2] table 1, for sailfish/spearfish.

Year	Blue marlin	White marlin	Sailfish/ spearfish	Year	Blue marlin	White marlin	Sailfish/ spearfish
1956	6	—	1	1967	2,316	1,421	1,421
1957	92	15	39	1968	3,572	2,458	2,281
1958	722	25	50	1969	3,727	2,538	1,586
1959	847	123	72	1970	4,939	2,916	2,758
1960	1,517	206	160	1971	4,316	2,999	1,710
1961	4,004	713	383	1972	3,047	2,452	1,551
1962	7,414	1,984	602	1973	2,925	2,461	1,298
1963	9,034	2,526	841	1974	2,761	2,958	1,413
1964	7,847	3,634	1,240	1975	3,000	1,987	1,122
1965	6,019	4,847	2,587	1976	1,076	2,062	750
1966	3,713	3,296	2,032				

[1]Conser, R. J., and G. L. Beardsley. 1979. An assessment of the status of stocks of blue marlin, *Makaira nigricans*, and white marlin, *Tetrapturus albidus*, in the Atlantic Ocean. Collect. Vol. Sci. Pap. 8(2):461-489. Int. Comm. Conserv. Atl. Tunas, General Mola 17, Madrid, Spain.

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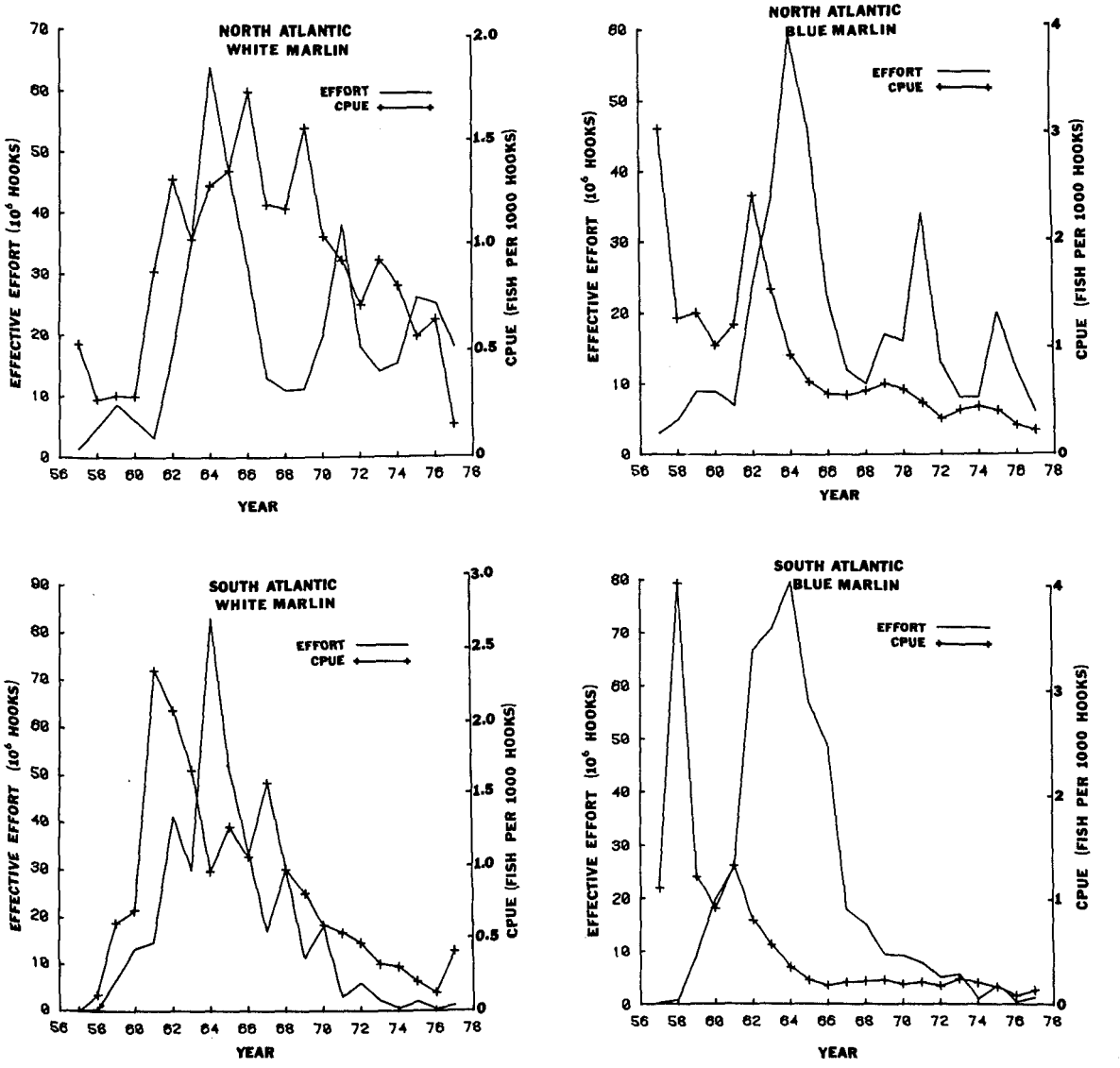

FIGURE 1.—Effective effort in millions of hooks and catch per unit effort (CPUE) in numbers of fish caught per 1,000 hooks for blue marlin and white marlin in the North and South Atlantic Oceans, 1956-77. Data on the Japanese longline fishery are reported by the Fisheries Agency of Japan, Annual report of effort and catch statistics by area on Japanese tuna longline fisheries, 1962-77.

THE SAMPLING PROGRAM

Prior to 1970 almost no data are available from the U.S. recreational fishery for billfishes on fishing effort, although a considerable amount of information exists on catch. Because of the large number of big-game fishing tournaments taking place throughout much of the range of the billfishes, and the fairly continuous and often intensive fishing effort at various fishing centers along the U.S. coast, it seemed feasible that catch and effort from the recreational fishery could be used to detect changes in relative abundance from year to year as well as short-term changes in availability. As a consequence, the Oceanic Game Fish Investigations Program was organized at the Southeast Fisheries Center Miami Laboratory in 1972 to develop an effective system for the collection of billfish catch and effort data in the Gulf of Mexico, Caribbean Sea, and western North Atlantic

Ocean, and to analyze these data to provide information on temporal and spatial changes in relative abundance.

The program is directed primarily at sailfish, white marlin, and blue marlin, although data on recreational catches of yellowfin and bluefin tunas are also recorded. Swordfish and longbill spearfish are rare in the recreational catch, but some data have been obtained.

Much preliminary work had already been accomplished in the Gulf of Mexico by the Southeast Fisheries Center Panama City Laboratory, NMFS, NOAA, in cooperation with various big-game fishing clubs and charterboat associations along the coast. Sampling sites were established and coverage of fishing effort during the fishing season in the gulf was estimated to be as high as 90% (Nakamura and Rivas 1974).

Initial contact with big-game fishing clubs, tournament managers, and others associated with big-game fishing tournaments produced a list of about 40-50 tournaments scheduled throughout the Bahamas, Caribbean, Gulf of Mexico, and along the eastern coast of the United States. Contact with various state marine research agencies provided cooperative sampling agreements for tournaments within their states. In addition to tournament sampling, port samplers were stationed in the Gulf of Mexico to maintain day-to-day coverage of nontournament fishing activity at major fishing areas along the coast. At present, coverage includes Port Aransas, Tex.; Grand Isle and South Pass, La.; Orange Beach, Ala.; and Pensacola, Destin, and Panama City, Fla. The fishing season in the Gulf of Mexico usually runs from April through October.

Data Acquisition

Sampling procedures at tournaments are reasonably uniform regardless of locality or season. At the end of each fishing day, program samplers interview the angler or a member of the crew of each boat participating in the tournament. Information on environmental conditions, number and species of fish hooked, and other activities are recorded. At most tournaments all of the participating boats are located at a single marina, and sampling coverage is usually 100%. Tournament sampling is further simplified in that most tournaments have rigidly controlled fishing hours, and all boats in the tournament fish the same amount of time. After the statistical information is collected, the sampler obtains biological data from each billfish landed.

Daily port sampling is more difficult than tournament sampling. Fishing frequently takes place from a variety of locations, the boats return to the dock at different times, and fishing effort is frequently not as consistent as during tournaments. Much of the success of daily sampling is attributable to the samplers' knowledge of the area and their persistence and resourcefulness in obtaining the data.

Sampling Problems

There are numerous sampling problems that appear to be unique to the recreational fishery for billfishes. The first is the determination of what constitutes the catch portion of the CPUE ratio. When trolling for billfishes there are three distinct levels of activity that feasibly could be associated with effort and provide an estimate of relative abundance. The first is commonly known as a fish "raised." This term refers to the visual observation of a billfish behind the trolling baits whether it ultimately strikes the baits or not. The inherent problem in using this measure is species identification. In addition, it is apparently not uncommon for a single billfish to be raised more than once during a given day's fishing, occasionally by the same boat. There is also the possibility that two or more billfishes are raised in rapid succession, but the observer may interpret this as a single fish. The second level of activity, and the one used in this study, is fish "hooked." Disadvantages of this criterion are differences in the skills of anglers in hooking fish, and the fewer data obtained since many fish that are raised are not hooked. Its advantages are that identification reliability is considerably increased since billfishes almost always jump when hooked and positive identification is usually possible. The third level of activity is a billfish "boated" (or caught and released). The biggest difficulty with this measure of catch is that different tournaments use different categories of line-test; comparing CPUE on 9 kg test line with CPUE on 36 kg test line is not reasonable. Another drawback is that the number of data points available from "boated" fish decreases significantly. The value of this measure is that species identification is no longer a problem. We decided to use fish hooked as our measure of catch, and all subsequent references to CPUE in the recreational

fishery refer to number of billfishes hooked per hour of trolling.

Another problem was the determination of which tournaments were suitable for use in the analysis of any given species. Billfish tournaments may be classified as "all billfish" or restricted to a single species or combination of species. In examining CPUE of white marlin in the Bahamas, for example, it is unreasonable to include data from tournaments that are exclusively blue marlin tournaments, because when fishing for blue marlin many boats troll large baits, and white marlin, considerably smaller in average size than blue marlin, either refuse to strike at such baits or are unusually difficult to hook. Accordingly, any analysis of a given species used only data from tournaments that were specifically directed at that species or that were designated as "all billfish."

An additional sampling problem, encountered in almost any kind of fisheries survey, is reliability of recall. We believe that, in general, the respondents are able to recall accurately their fishing activity during the day; however, it may occasionally be difficult for the angler or crew to recall each species of billfish hooked if fishing was good and several billfishes were hooked during the day. When possible, more than one member of the fishing party was consulted if there was some doubt expressed in the original interview. Tournament and port samplers have received excellent cooperation at every level, and most of the anglers and crew members make every effort to assist our data collection activities. Consequently, we do not believe that errors in recall significantly affect the results of our analyses.

Sampling Coverage

Tournament sampling extends along the east and gulf coasts of the United States from Long Island, N.Y., to Port Isabel, Tex. (Figure 2). Additional tournament sampling has been or is being conducted in the Bahamas, Jamaica, Mexico, Puerto Rico, and the Virgin Islands. Tournaments are scheduled throughout the year to coincide with the presence of seasonal concentrations of billfishes. In the Bahamas, for example, the tournament season extends from March through July. In southeast Florida, most tournaments are scheduled from November through January. Most of the tournaments sampled are annual events and occur at approximately the same time each year. Tournament scheduling is also arranged so that

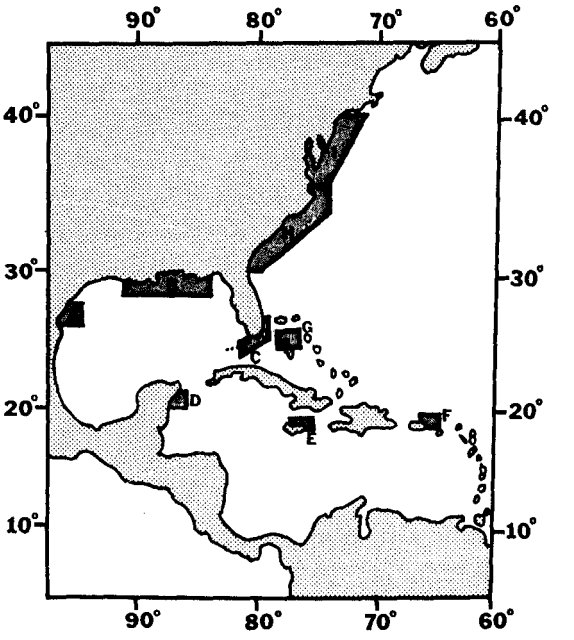

FIGURE 2.—Areas in the western North Atlantic Ocean, Caribbean Sea, and Gulf of Mexico where the recreational fishery for billfishes is sampled. Primary species available by area are: A—blue marlin, sailfish; B—blue marlin, white marlin, sailfish; C—sailfish; D—sailfish; E—blue marlin; F—blue marlin; G—blue marlin, white marlin, sailfish; H—blue marlin; I—white marlin.

there are few instances where two or more tournaments are held at the same time in the same area.

Seasonal port sampling on a daily basis is conducted in the gulf beginning in April and extending through October. The amount of effort measured and the recorded number of fish hooked from daily dock sampling from 1971 through 1978 and from tournament sampling, 1972 through 1978, are shown in Table 2.

DATA ANALYSIS—GULF OF MEXICO

Methodology

There are several areas along the Atlantic and Gulf of Mexico coasts of the United States where recreational and commercial fishermen compete for billfishes. This interaction occurs most frequently in the northern Gulf of Mexico where intensive recreational fishing for billfishes takes place from a number of ports from Florida to Texas during April through October. During the same

TABLE 2.—Data on effort and catch for billfishes recorded by tournament and dock sampling, 1971-78, in the western North Atlantic and Gulf of Mexico.

Year	Hours fished	No. fish hooked		
		Blue marlin	White marlin	Sailfish
	Tournaments			
1972	23,090.4	365	170	399
1973	17,864.0	512	233	684
1974	18,473.6	537	368	768
1975	26,858.4	684	1,088	1,664
1976	27,368.4	655	750	1,062
1977	35,333.9	772	781	1,989
1978	40,601.0	801	992	1,752
	Dock sampling			
1971	11,609.9	266	491	482
1972	13,298.2	306	517	528
1973	7,859.5	176	414	140
1974	10,462.8	290	487	197
1975	8,852.5	196	684	434
1976	8,174.5	177	434	577
1977	8,575.0	225	398	232
1978	12,522.7	251	402	200

period of the year, Japanese longliners fish in the same area for yellowfin and bluefin tunas but frequently catch billfishes as well. Detailed and consistent catch and effort data are available from both the recreational and longline fisheries in this area over the period 1971-78. These attributes make the northern Gulf of Mexico fishery unique when compared with other billfish fisheries in that more than one type of gear is operating at significant effort levels in the same time and place, and consistent catch and effort statistics are available from both types of fishing operations for a reasonably long time series. In this analysis we attempt to: 1) determine the utility and consistency of catch and effort data from the recreational and longline fisheries for indexing changes in abundance of billfish populations, 2) obtain species- and area-specific indices of abundance that incorporate both recreational and longline data, and 3) gain a better understanding of the dynamics of the fishery by modeling the general characteristics of recreational and longline fishing for billfishes.

The northern Gulf of Mexico was divided into three areas based on the general distribution of recreational fishing (shaded areas in Figure 3). The easternmost, Panhandle, groups fishing effort from Panama City, Destin, and Pensacola, Fla., and Orange Beach and Mobile, Ala. The center, New Orleans, combines effort from South Pass and Grand Isle, La., and the westernmost, Texas, encompasses all fishing from Texas. Recreational catch and effort data are acquired in each of these areas by sampling both daily, noncompetitive recreational fishing as well as fishing conducted during organized big-game fishing tournaments. From 1971 through 1978 over 136,000 h of tournament and nontournament fishing for billfishes in these three areas were recorded (Table 3). Tournament and dock data were processed and monthly total catch and total effort were compiled by species, area, and type of fishing. CPUE was computed for those months in which 60 h or more of fishing effort had been sampled. The 60-h minimum effort criterion was chosen by making two series of calculations of the variance of monthly CPUE using various minimum effort criteria, and then subjectively selecting a minimum effort level which provided a balance between the variance and sample size considerations. Using the 60-h minimum effort criterion produced more reliable statistics without causing the sample size to become unacceptably small. It represents approxi-

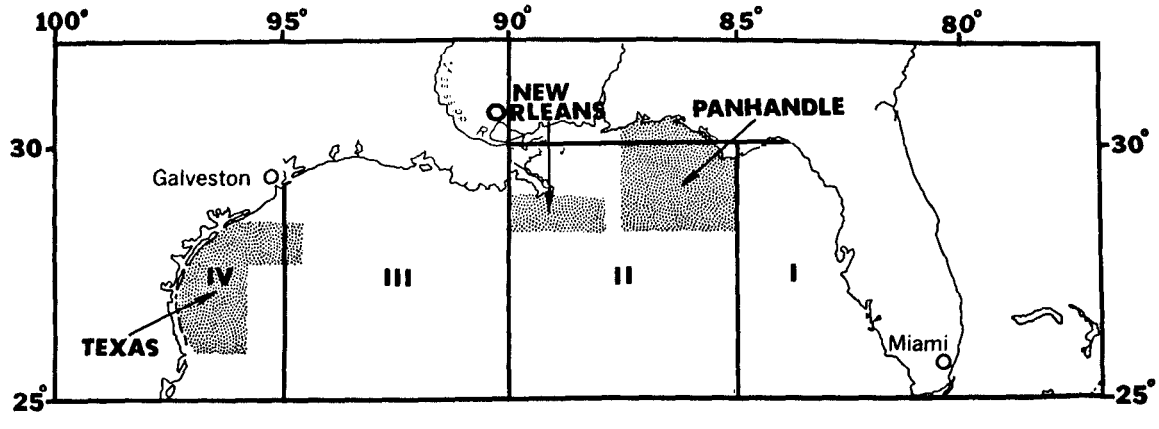

FIGURE 3.—The shaded areas, Panhandle, New Orleans, and Texas, are major recreational fishing areas for billfishes. The larger areas, I, II, III, and IV, are 5° squares from which Japanese longline catch and effort data are available.

TABLE 3.—Number of fishing hours recorded from tournament (tourn.) and dock sampling at three major fishing areas for billfishes in the Gulf of Mexico, 1971-78. See Figure 3 for location of areas.

Year	Panhandle		New Orleans		Texas	
	Tourn.	Dock	Tourn.	Dock	Tourn.	Dock
1971	—	8,287.7	—	3,322.2	—	—
1972	143.5	4,225.2	355.2	3,380.0	462.0	254.3
1973	703.6	8,605.2	—	3,730.0	52.7	963.0
1974	584.2	5,618.1	—	3,395.0	—	1,449.7
1975	2,020.0	5,587.1	2,441.3	2,034.3	1,767.8	1,230.1
1976	4,279.7	4,619.3	3,552.3	1,762.4	2,314.3	1,792.8
1977	6,088.3	5,516.2	5,981.0	2,412.6	4,496.0	646.2
1978	6,983.4	7,410.8	7,576.1	3,966.2	4,999.4	1,145.7

mately 10 boat-days of fishing and occurs in a region of the effort distribution where moderate changes in the minimum effort criterion would have little effect on the number of months used. The resulting CPUE values by area and type of fishing are displayed in Figure 4 for blue marlin, Figure 5 for white marlin, and Figure 6 for sailfish.

Monthly catch and effort statistics by 5° area for the Japanese longline fleet are reported by the Fisheries Agency of Japan in the *Annual Report of Effort and Catch Statistics by Area on Japanese Tuna Longline Fisheries* for the period 1962-77. Japanese longliners fish all four of the 5° areas that compose the northern Gulf of Mexico (Areas I through IV, Figure 3). However, 52% of their fishing effort in the northern gulf during 1971-77 occurred in area II and 39% in area III. Only 1% occurred in area I and 8% in area IV. Since nearly all recreational fishing for billfishes in the northern gulf occurs in areas II and IV, only longline data from these two areas were used in this comparative analysis. Although no data on the distribution of longline effort within 5° areas are given in the Japanese annual reports, data supplied by Honma[3] on the distribution of catch and effort during 1971-75 show that most longline effort in areas II and IV occurred in the more coastal regions which coincides fairly well with the location of recreational fishing grounds as displayed in Figure 3. Catch and effort statistics by species for areas II and IV were compiled from the Japanese annual reports for 1971-77 (Table 4). Comparable statistics for 1978 were compiled from the quarterly reports submitted to the Southeast Fisheries Center by Japanese longliners fishing in the U.S. Fishery Conservation Zone. CPUE was then computed for those months in which 2,000 hooks or more of fishing effort occurred. As with

[3]Misao Honma, Far Seas Fisheries Research Laboratory, Shimizu, Japan, pers. commun. July 1977.

TABLE 4.—Japanese catch (in numbers of fish) and effort (in numbers of hooks) from the two 5° areas (longline areas II and IV in Figure 3) in the northern Gulf of Mexico which coincide with recreational fishing areas, 1971-78. BM = blue marlin, WM = white marlin, and SF = sailfish.

Year	Area II				Area IV			
	Effort (hooks)	Catch			Effort (hooks)	Catch		
		BM	WM	SF		BM	WM	SF
1971	413,941	220	1,273	853	227,552	114	2,627	1,402
1972	664,295	181	2,280	571	—	—	—	—
1973	237,092	93	998	204	64,787	28	533	797
1974	53,632	34	213	42	104,298	120	635	505
1975	712,659	149	546	313	220,337	140	1,174	878
1976	2,999,552	269	3,100	850	309,118	97	622	937
1977	2,206,500	181	993	272	54,407	8	64	87
1978	1,454,447	100	719	62	36,355	6	90	29

the recreational data, using a minimum effort criterion produced more reliable statistics and the number of months accepted was not sensitive to moderate changes in the threshold level. The Japanese longline CPUE values by species and comparable recreational fishing area are also shown in Figures 4-6.

Murphy (1960), Rothschild (1977), and others have discussed some of the important aspects involved in using longline statistics to estimate changes in abundance. One of the demonstrated functional relationships, which may be pertinent in this analysis, is that the average amount of effective effort per hook is a function of the amount of "soaking time" the gear is in the water. Although the Japanese annual reports do not provide time in the water data, NMFS observers aboard Japanese vessels in the northern gulf report a consistency in the time the gear is in the water during recent years (Lopez et al. 1979). Although no data are available from earlier years of the analysis period, soaking times tend to remain more or less constant in most tuna longline fisheries and consequently, fishing time can be measured by the number of hooks set (Food and Agriculture Organization 1976). The lack of data on time in the water should, therefore, not contribute significantly to any bias in the estimates of relative abundance. Another aspect of the longline data which is also pertinent to this analysis is that sailfish and spearfish catches are combined in the Japanese annual reports. This problem may be minimal in coastal areas, however, since Ueyanagi et al. (1970) demonstrated that sailfish are found primarily in coastal areas and spearfish tend to inhabit more oceanic waters. In this analysis all catches from areas II and IV that were reported as sailfish/spearfish in the annual reports were assumed to be sailfish.

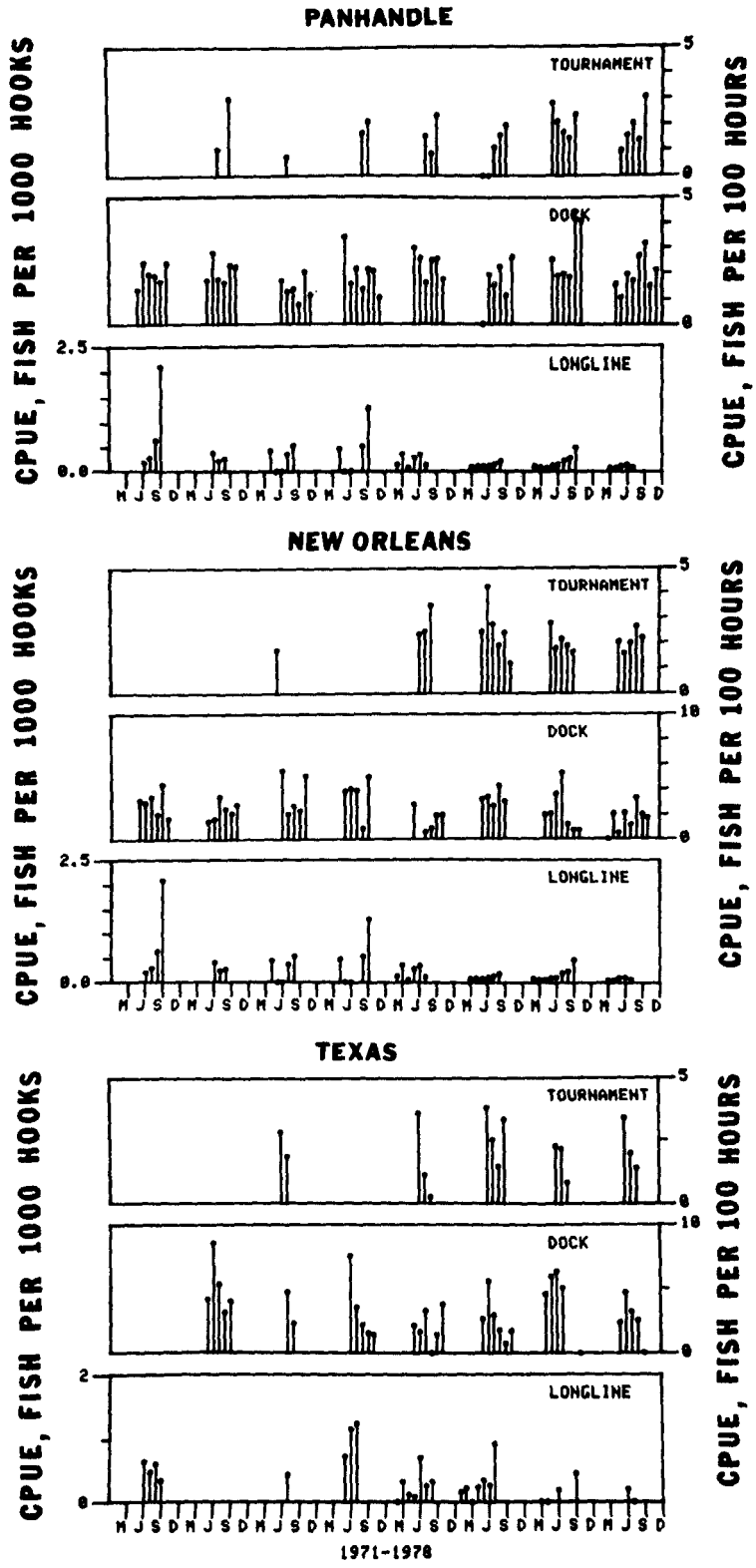

FIGURE 4.—Monthly CPUE for blue marlin from the longline fishery and the recreational fishery in the three major fishing areas in the northern Gulf of Mexico, 1971-78. Longline CPUE depicted for Panhandle and New Orleans were derived from data taken from the 5° square labeled II in Figure 3. CPUE for Texas was taken from the 5° square labeled IV in Figure 3. The first month depicted on the abscissa is March (M) 1971. CPUE is in numbers of fish caught per 1,000 hooks in the longline fishery and numbers of fish hooked per 100 hours fished in the recreational fishery. The Tournament panel displays CPUE calculated from billfish fishing tournaments while the panel labeled Dock shows CPUE derived from noncompetitive fishing.

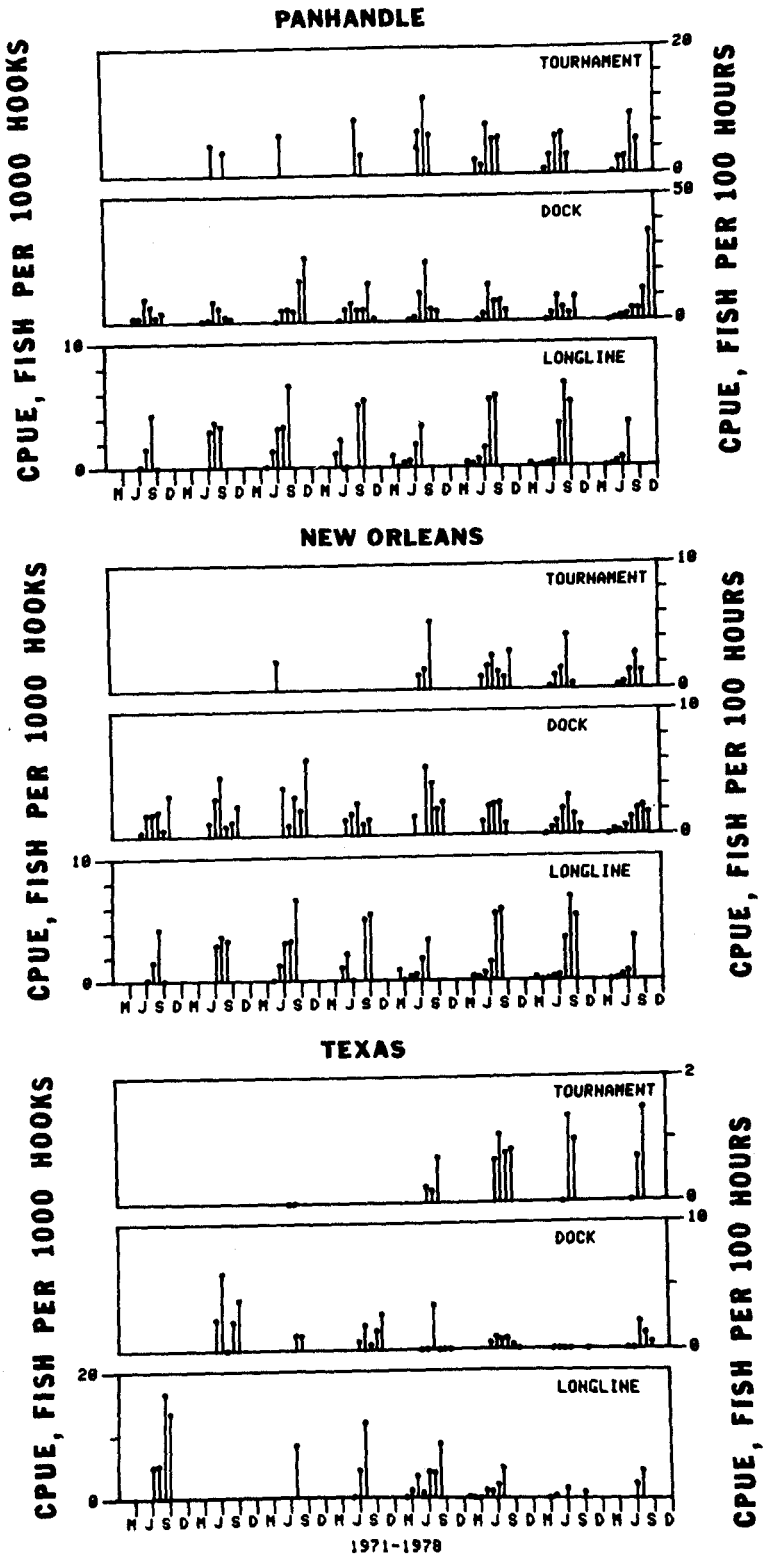

FIGURE 5.—Monthly CPUE for white marlin from the longline fishery and the recreational fishery in the three major fishing areas in the northern Gulf of Mexico, 1971-78. Longline CPUE depicted for Panhandle and New Orleans were derived from data taken from the 5° square labeled II in Figure 3. CPUE for Texas was taken from the 5° labeled IV in Figure 3. The first month depicted on the abscissa is March (M) 1971. CPUE is in numbers of fish caught per 1,000 hooks in the longline fishery and numbers of fish hooked per 100 hours fished in the recreational fishery. The Tournament panel displays CPUE calculated from billfish fishing tournaments while the panel labeled Dock shows CPUE derived from noncompetitive fishing.

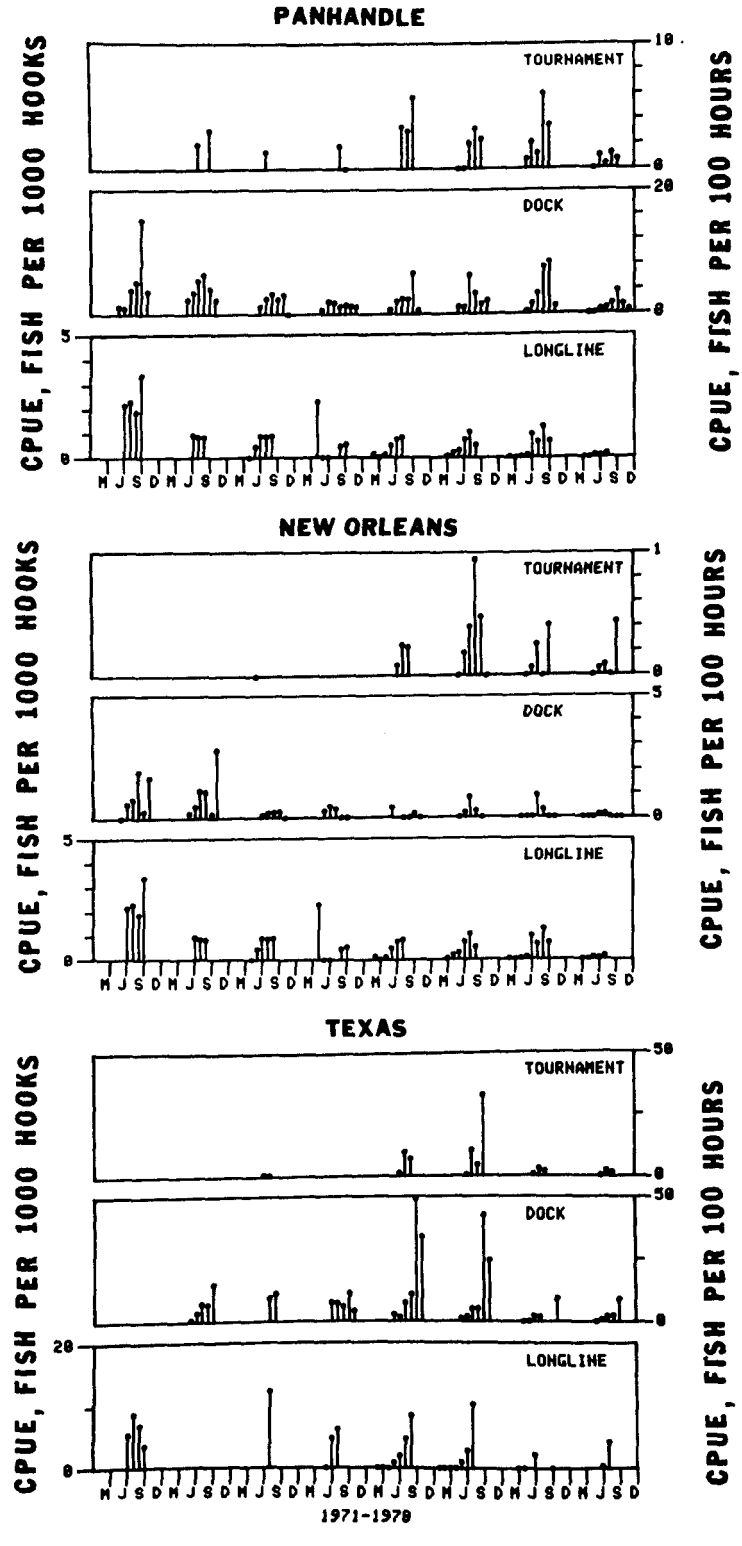

FIGURE 6.—Monthly CPUE for sailfish from the longline fishery and recreational fishery in the three major fishing areas in the northern Gulf of Mexico, 1971-78. Longline CPUE depicted for Panhandle and New Orleans were derived from data taken from the 5° square labeled II in Figure 3. CPUE for Texas was taken from the 5° square labeled IV in Figure 3. The first month depicted on the abscissa is March (M) 1971. CPUE is in numbers of fish caught per 1,000 hooks in the longline fishery. The Tournament panel displays CPUE calculated from billfish fishing tournaments while the panel labeled Dock shows CPUE derived from noncompetitive fishing.

Catch Model

A basic catch model was used for dock, tournament, and longline fishing in the northern Gulf of Mexico:

$$C_{ijk} = q_{ik} f_{ij} \bar{N}_{jk} \epsilon_{ijk} \quad (1)$$

where C_{ijk} is the catch of species k from the ith type of fishing during month j, q_{ik} is the catchability coefficient of the ith type of fishing on species k, f_{ij} is the amount of fishing effort expended by the ith type of fishing during month j, $\bar{N}_{jk}$ is the average population size of species k in month j, and ϵ_{ijk} is a log-normally distributed error term. Note that no k index appears on the f_{ij} since effort is not generally directed at any particular billfish species in the recreational fishery in the northern Gulf of Mexico. This basic catch model has been used by many authors to study fisheries in which more than one type of fishing was employed (Gulland 1956; Beverton and Holt 1957; Robson 1966). Equation (1) can be written as a linear, two factor analysis of variance (ANOVA) model by dividing through by f_{ij}, taking natural logarithms, and obtaining

$$Y_{ijk} = \alpha_{ik} + \beta_{jk} + \epsilon'_{ijk} \quad (2)$$

where $Y_{ijk} = \ln (C_{ijk}/f_{ij})$,
$\alpha_{ik} = \ln q_{ik}$,
$\beta_{jk} = \ln \bar{N}_{jk}$, and
$\epsilon'_{ijk} = \ln \epsilon_{ijk}$.

The ANOVA can be used to test for significant differences in the catchability of various types of fishing and in population density over time. The ANOVA model cannot, however, be used to estimate catchability or population densities, but it can be reparameterized to obtain estimates of relative catchability (P_{ik}) and relative population density (D_{jk}), where

$$P_{ik} = q_{ik}/q_{sk} \quad (3)$$

$$D_{jk} = \bar{N}_{jk}/\bar{N}_{sk} \quad (4)$$

in which s refers to the type of fishing and month designated as standard. After reparameterization, Equation (2) becomes

$$Y_{ijk} = u_k + \alpha'_{ik} + \beta'_{jk} + \epsilon'_{ijk} \quad (5)$$

where $u_k = \alpha_{sk} + \beta_{sk}$,
$\alpha' = (\alpha_{ik} - \alpha_{sk})$, and
$\beta'_{jk} = (\beta_{jk} - \beta_{sk})$.

The parameters u_k, α'_{ik}, and β'_{jk} can be estimated by solving the usual normal equations and estimates of relative fishing power and relative population density can be obtained from [$P_{ik} = \exp(\hat{\alpha}_{ik})$ and $\hat{D}_{jk} = \exp(\hat{\beta}'_{jk})$].

To apply the basic catch model to the billfish fishery in the northern gulf, it is necessary to assume that for each type of fishing (i.e., dock, tournament, and longline) catchability is constant throughout the analysis period, there is no interaction between catchability and density, and units of effort operate independently. The first two assumptions may be tenuous for this fishery and will be investigated in the analysis. The third assumption appears to be reasonable.

The basic catch model was used initially to determine what relationship existed between catch and effort data from dock and tournament data. Figure 7 presents a flow diagram for the determi-

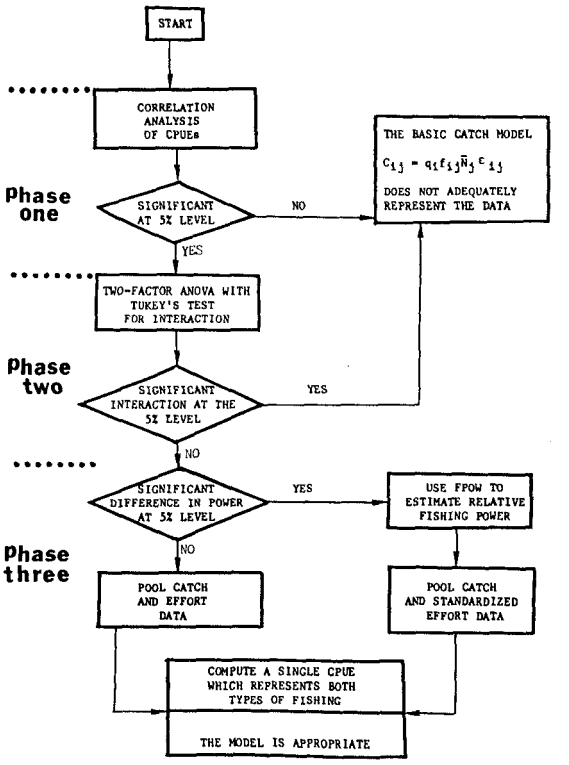

FIGURE 7.—Flow diagram for determining the appropriateness of using the basic catch model to represent data from the two different kinds of fishing methods.

nation of the appropriateness of the basic catch model for a single species-area case. Separate analyses were performed for blue marlin, white marlin, and sailfish in each of the three recreational areas.

Since the model assumes that the catchability coefficients of dock and tournament fishing are proportional [Equation (3)], correlation analysis was performed on the dock and tournament CPUE values (Phase 1, Figure 7) and the model was considered appropriate for estimating fishing power only when the CPUE's were significantly correlated at the 5% level. Data used in the correlation analysis were from all months in which dock and tournament fishing met the minimum effort threshold concurrently.

The two factor ANOVA model [Equation (2)] was then used to test for significant differences in fishing power and density, and Tukey's (1949) test was used to test for significant interaction. The data used in the ANOVA were from all months in the 1971-78 period for which dock and tournament sampling met the minimum effort threshold concurrently and for which CPUE's were >0 for both types of fishing. The positive CPUE constraint was necessary because of the log transformation used in obtaining Equation (2). Because the model requires that there be no interaction between power and density, the model was not considered appropriate when interaction was significant at the 5% level.

For all cases in which the model was deemed appropriate and the ANOVA test for difference in power was not significant at the 5% level, the catch and effort data were pooled and a single recreational CPUE was calculated for those species-area combinations. Where the model was appropriate and the power was significantly different, dock sampling was designated as the standard and the relative fishing power of tournament fishing was estimated from Equation (5). The computer program FPOW (Berude and Abramson 1972) was used to estimate the relative fishing power. FPOW solves the normal equations like Equation (5) and corrects for the logarithmic bias using a Taylor series expansion of the estimate about its true value (Laurent 1963). The FPOW program was modified to perform the usual F-test for the significance of the overall regression and to compute the coefficient of determination. As in the ANOVA test, the data used in the fishing power estimation were from all months for which dock and tournament fishing met the minimum effort threshold concurrently, and for which both CPUE's were >0. For those species-area combinations in which the model adequately represented the recreational data, the entire procedure was then repeated in an analogous manner to compare the recreational and longline data.

Results

The results of the correlation, ANOVA, and regression analyses for blue marlin, white marlin, and sailfish from the Panhandle, New Orleans, and Texas areas are summarized in Table 5.

Blue Marlin

In the Panhandle area, dock and tournament CPUE data are fairly consistent and it appears that fishing power is greater for dock data than for tournament data. When the dock and tournament data were pooled and compared with the longline data, no correlation was found and interaction between power and density was apparent. In the New Orleans and Texas areas, no significant difference in the power of dock and tournament data was found, but the CPUE's were not correlated and interaction was significant in the New Orleans data.

The blue marlin results generally indicate that the basic catch model does not adequately represent the blue marlin data in the northern Gulf of Mexico. While it may be possible to obtain adequate indices of abundance from recreational or longline data, the two types of fishing appear to be providing very different indices in the same local areas, and it cannot be determined which, if either, provides a valid measure of relative abundance. It appears that until the dynamics of the blue marlin fishery are better understood, the use of nominal catch and effort data to index relative abundance may produce inconsistent and misleading results.

White Marlin

In the Panhandle and New Orleans areas, the CPUE's were well correlated, no significant difference in the power of dock and tournament data was found, and no interaction was apparent. When dock and tournament data were pooled and compared with longline data, the CPUE's were well correlated, and a significant difference in power was found, but significant interaction was found in

TABLE 5.—Summary of the results from the correlation, ANOVA, and regression analyses for blue marlin, white marlin, and sailfish from the Panhandle, New Orleans, and Texas areas. See text for use of these test statistics in determining the appropriateness of the basic catch model.

Species	Area	Standard fishing	Other fishing	Correlation	Two Factor ANOVA with Tukey's Test[1]			Regression (FPOW)[2]			
					Power	Density	Interaction	Significance	Degree of fit	Estimate of power	95% C.I.
Blue marlin	Panhandle	Dock	Tournament	$r_{21} = 0.58^{**}$	$F_{1,20} = 5.19^{*}$	$F_{20,20} = 2.98^{**}$	$F_{1,19} = 0.90$	$F_{21,20} = 3.09^{**}$	$R^2 = 0.76$	0.82	0.70-0.97
		Longline	Recreational	$r_{28} = 0.01$	$F_{1,24} = 1.527^{***}$	$F_{25,24} = 2.83^{**}$	$F_{1,24} = 39^{***}$	—	—	—	
	New Orleans	Dock	Tournament	$r_{15} = 0.07$	$F_{1,15} = 2.35$	$F_{16,15} = 2.59^{*}$	$F_{1,15} = 21^{***}$	—	—	—	
	Texas	Dock	Tournament	$r_{11} = 0.32$	$F_{1,11} = 1.78$	$F_{11,11} = 0.88$	$F_{1,10} = 2.23$	—	—	—	
White marlin	Panhandle	Dock	Tournament	$r_{21} = 0.78^{***}$	$F_{1,22} = 0.04$	$F_{22,22} = 9.32^{***}$	$F_{1,21} = 1.85$	—	—	1.00	
		Longline	Recreational	$r_{28} = 0.55^{**}$	$F_{1,26} = 132^{***}$	$F_{26,26} = 2.92^{**}$	$F_{1,25} = 0.005$	$F_{21,26} = 7.77^{***}$	$R^2 = 0.89$	13.01	8.6-20.7
	New Orleans	Dock	Tournament	$r_{15} = 0.66^{**}$	$F_{1,16} = 3.59$	$F_{16,16} = 9.31^{***}$	$F_{1,15} = 0.76$	—	—	1.00	
		Longline	Recreational	$r_{31} = 0.54^{**}$	$F_{1,27} = 155^{***}$	$F_{28,27} = 4.37^{***}$	$F_{1,27} = 11.49^{**}$	$F_{29,28} = 7.06^{***}$	$R^2 = 0.88$	7.74	5.4-11.5
	Texas	Dock	Tournament	$r_{11} = -0.07$	$F_{1,6} = 0.83$	$F_{6,6} = 0.23$	$F_{1,5} = 0.14$	—	—	—	
Sailfish	Panhandle	Dock	Tournament	$r_{21} = 0.74^{***}$	$F_{1,18} = 2.71$	$F_{18,18} = 4.91^{***}$	$F_{1,17} = 1.62$	—	—	1.00	
		Longline	Recreational	$r_{28} = 0.76^{***}$	$F_{1,25} = 674^{***}$	$F_{25,25} = 6.14^{***}$	$F_{1,24} = 0.22$	$F_{26,25} = 31.6^{***}$	$R^2 = 0.97$	31.76	24.6-41.7
	New Orleans	Dock	Tournament	$r_{15} = 0.22$	$F_{1,5} = 1.00$	$F_{5,5} = 3.75$	$F_{1,4} = 0.17$	—	—	—	
		Longline	Dock	$r_{29} = 0.44^{*}$	$F_{1,17} = 57^{***}$	$F_{17,17} = 2.92^{*}$	$F_{1,16} = 0.18$	$F_{18,17} = 5.90^{***}$	$R^2 = 0.86$	4.89	3.3-7.6
	Texas	Dock	Tournament	$r_{11} = 0.94^{***}$	$F_{1,12} = 3.11$	$F_{12,12} = 5.39^{**}$	$F_{1,11} = 1.86$	—	—	1.00	
		Longline	Recreational	$r_{12} = 0.65^{*}$	$F_{1,12} = 113^{***}$	$F_{12,12} = 7.27^{***}$	$F_{1,11} = .09$	$F_{13,12} = 15.4^{***}$	$R^2 = 0.94$	8.64	5.9-13.2

$^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$.
[1]Tukey's test for interaction was used in the ANOVA. When interaction was not significant, the interaction sum of squares was pooled into the error sum of squares and the test statistics shown for power and density were calculated using the pooled error term.
[2]FPOW was used to estimate relative fishing power only when the ANOVA showed a significant difference in power and the CPUE's were significantly correlated.

the New Orleans area. The interaction implies that a better model exists for representing the data, probably one with a cross product term, but since the data were well correlated, we believe a reasonable power estimate could be obtained using the simpler basic catch model. The degree of fit of the regression model used to estimate power is good in both areas, accounting for nearly 90% of the variation in the data, and despite the interaction found in the New Orleans area the power estimates appear to be reasonable. So few white marlin are caught in the Texas area that sample size was not adequate to make similar determinations. The correlation and ANOVA analyses produced nonsignificant results.

The results generally indicate that the basic catch model adequately represents the white marlin data in the northern Gulf of Mexico. It appears that any one of the data types (dock, tournament, and longline) can be used to index relative abundance for local areas but more reliable indices will result if all three are aggregated as was done here and displayed in Figure 8.

Sailfish

No significant differences were found in the fishing power of dock and tournament data and no interactions were apparent in any of the three areas. CPUE's were significantly correlated in the Panhandle and Texas areas but not in the New Orleans area. Relatively few sailfish are caught in the New Orleans area, especially in tournament fishing during the early years, and sample size was inadequate for comparison of dock and tournament data. Sample size was better from dock data, so dock and longline data were compared in the New Orleans area while dock and tournament data were pooled and compared with longline data in the Panhandle and Texas areas. In all three areas, the CPUE's were significantly correlated, significant differences in power were found between recreational and longline fishing, and no interactions were apparent. The regression model used for estimating power is highly significant, and the degree of fit is good in all three areas, but the recreational fishing power estimate may be somewhat inflated in the Panhandle area because

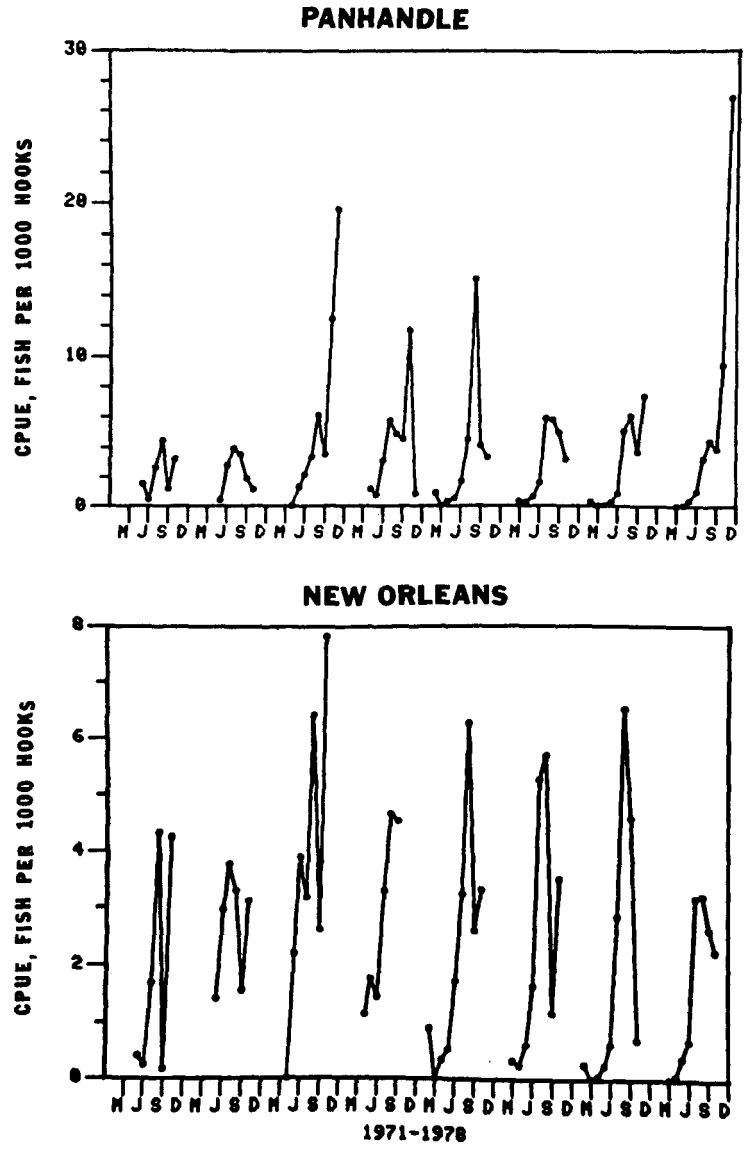

FIGURE 8.—Monthly CPUE for white marlin from the Panhandle and New Orleans areas, 1971-78. CPUE is derived from standardized recreational (both dock and tournament fishing) and longline effort. The first month depicted on the abscissa is March (M) 1971.

part of the comparable longline effort probably occurred in the western portion of area II where few sailfish are caught. Recreational and longline data were pooled, and the aggregate indices of abundance are shown in Figure 9. The results indicate that the basic catch model is adequate for representing the sailfish data in the northern Gulf of Mexico.

In view of these results, it then seems appropriate to examine white marlin and sailfish catch data from the Gulf of Mexico to see if any trends in relative abundance are apparent. Figure 8 presents CPUE for white marlin from the Panhandle and New Orleans areas and suggests that a general decline in white marlin abundance has taken place since 1973. There was a peak in 1975 in both areas (also seen in the yearly average of CPUE shown below) and two good months in 1978 in the Panhandle area, but the overall trend would appear to be downward.

Figure 9 presents similar data for sailfish from all three gulf areas. For this species, too, the general trend in relative abundance, at least in the Panhandle and New Orleans areas, appears to be

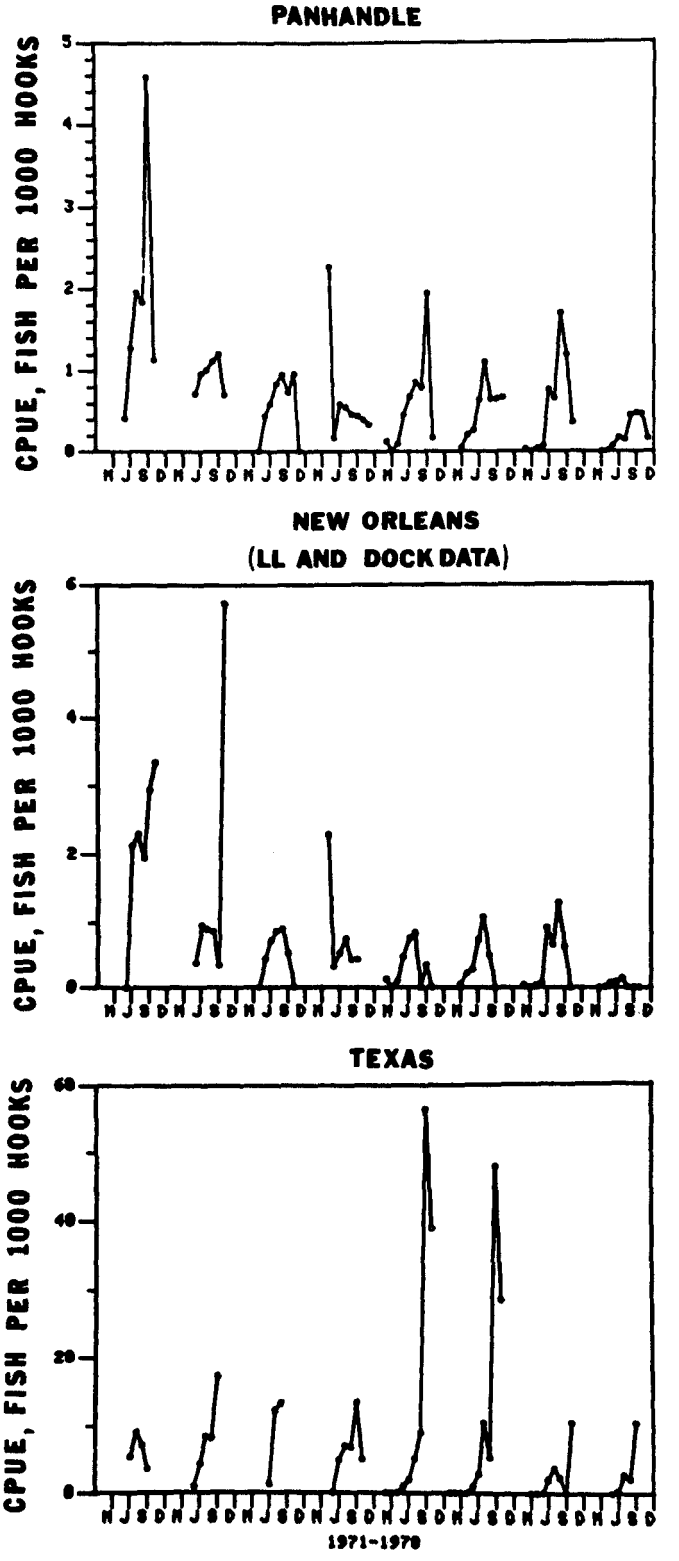

FIGURE 9.—Monthly CPUE for sailfish from the Panhandle, New Orleans, and Texas areas, 1971-78. CPUE is derived from standardized recreational (both dock and tournament except for New Orleans) and longline effort. The first month depicted on the abscissa is March (M) 1971.

clearly downward. In the Texas area, 1975 and 1976 were years when CPUE was unusually high, but in 1977 and 1978 CPUE dropped back to levels more consistent with earlier years.

DATA ANALYSIS—ALL AREAS

Only tournament data are available from the recreational fishery in areas other than the Gulf of Mexico, hence a fishing power analysis similar to the one conducted for the gulf is not presented. It is informative, nevertheless, to examine CPUE data from all sources throughout the western Atlantic and Gulf of Mexico in view of the results of the analysis presented for the gulf.

Blue Marlin

Data on blue marlin were divided into two areas: the Gulf of Mexico and the Atlantic and Caribbean (Figure 10). Both tournament and dock sampling were combined for the gulf. This division does not necessarily mean we support a separate stock theory for these areas, but merely that the geographical separation of fishing effort indicates that this is a logical division for comparative purposes. If, however, trends in CPUE from the two areas are similar, one might conclude that there is at least prima facie evidence of a single stock. Figure 10 shows that trends between the two areas are similar only from 1973 to 1976, which is obviously inconclusive. It should also be noted that there is little fluctuation in CPUE over the time series presented, particularly when compared with white marlin (Figure 11) and sailfish (discussed below). Normally one would expect CPUE for a long-lived species with numerous age groups contributing to the fishery to fluctuate much less than that for a species with a relatively short life span where the impact of a large or small incoming year class would be much greater on the fishery. Although no reliable age and growth data are available on blue and white marlins, the Atlantic blue marlin grows to a much larger size than either the white marlin or the sailfish, occasionally reaching weights of over 580 kg (International Game Fish Association 1979) and would therefore appear to be the longest lived of the three species. The trends in CPUE for the three species appear to conform to the general pattern one might expect based on their presumed relative life span and the length of time they would be expected to contribute to the recreational fishery.

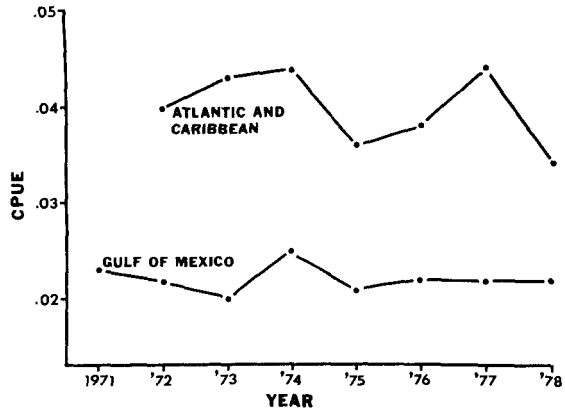

FIGURE 10.—CPUE, in number of fish hooked per hour of fishing, from the recreational fishery for blue marlin in the two major fishing areas, 1971-78.

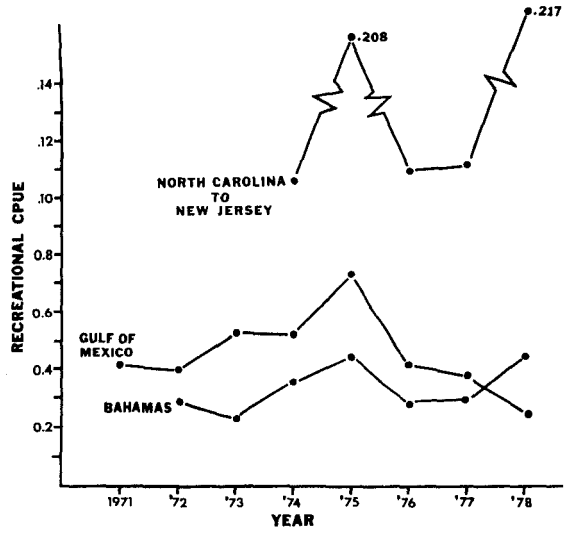

FIGURE 11.—CPUE, in number of fish hooked per hour of fishing, from the recreational fishery for white marlin in three major fishing areas, 1971-78.

White Marlin

Data on catch and effort for white marlin were divided into three areas (Figure 11). Mather et al. (1972) hypothesized that the gulf and Atlantic stocks of white marlin were separate based on tag return data and the distribution of CPUE in the Japanese longline fishery. More recent tag return data, however, indicate that there may be considerable mixing of white marlin between the Gulf of Mexico and the Atlantic Ocean.[4] There is rather

[4]Chester C. Buchanan, U.S. Fish and Wildlife Service, Anchorage, AK 99503, pers. commun. June 1977.

clear evidence (Mather et al. 1972) that the group of white marlin available to the recreational fishery in the Florida Straits and Bahamas in late winter and early spring (labeled Bahamas in Figure 11) is the same group that concentrates off the northeastern coast of the United States in late summer and early fall (labeled North Carolina to New Jersey in Figure 11). If CPUE from the recreational fishery is adequately measuring the relative abundance of white marlin stocks, one would expect a high degree of correlation between CPUE from a single stock from three widely separated areas assuming a constant percentage of the total stock was available in each area, each year. By inspection, it is clear that for the time series available a close relationship appears to exist between CPUE from the three areas sampled. It is also interesting to note that 1975 was a good year in all three areas. Although availability obviously plays an important role in affecting CPUE, it seems unlikely that it is the dominant factor in this case since the three fishing areas are widely separated geographically, and conditions affecting availability would not likely be optimal in all three areas in the same year. Correlation coefficients were calculated for all three areas (5 yr) and for the Gulf of Mexico and the Bahamas (7 yr). The multiple correlation coefficient for all three areas was significant at the 95% level ($R = 0.925$) and the simple correlation coefficient for the Bahamas and the Gulf of Mexico was significant at the 99% level ($r = 0.865$). If we are indeed measuring relative abundance, then the similarities in all three sets of data support the hypothesis that the three general fishing areas harbor a single stock of white marlin.

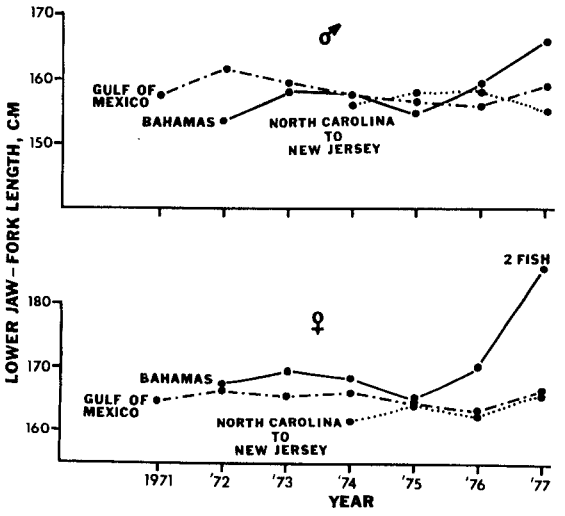

FIGURE 12.—Length frequencies of white marlin from three major fishing areas, 1971-77.

Size data from 1971 through 1977 separated by sex do not reveal any substantial differences among fish in the three areas (Figure 12). Average size has remained fairly stable over the period with females averaging larger than males for all areas. Earlier size data from the recreational fishery, not differentiated by sex, and with the Atlantic and gulf areas combined, suggest that a moderate reduction in average size has occurred since the late 1950's and early 1960's (Figure 13), but that size may have stabilized since 1970.

Sailfish

CPUE data for sailfish were separated into three areas (Figure 14). These are the major fish-

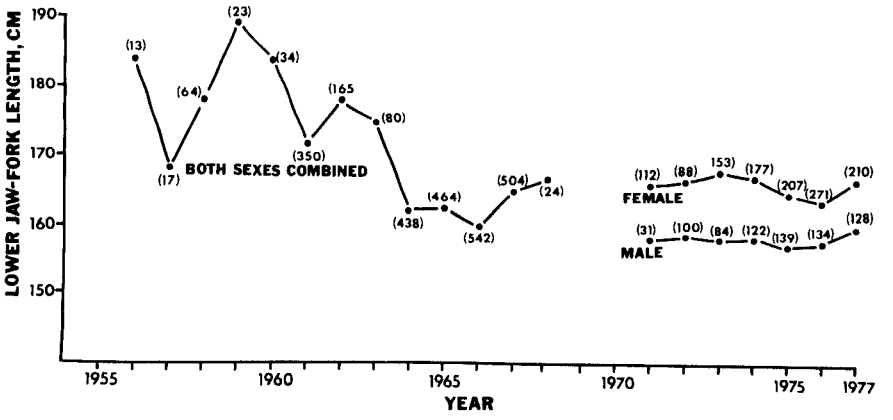

FIGURE 13.—Length frequencies of white marlin from the recreational fishery in the western North Atlantic and Gulf of Mexico. The number of specimens measured is shown in parentheses.

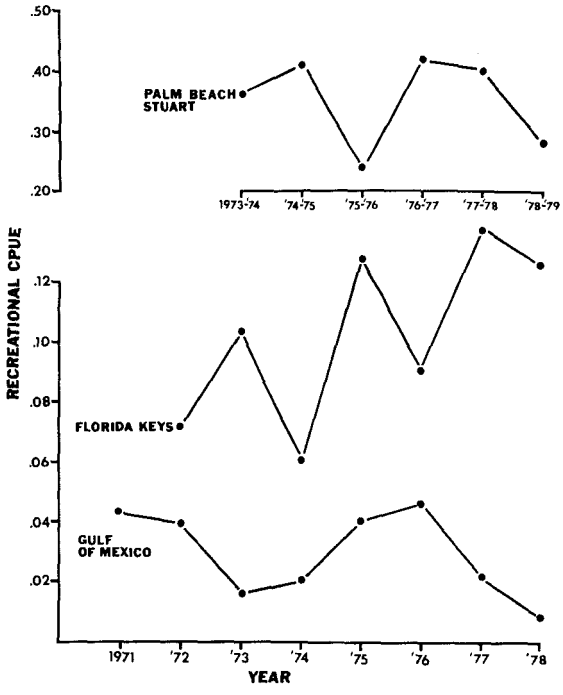

FIGURE 14.—CPUE, in number of fish hooked per hour of fishing, from the recreational fishery for sailfish, 1971-78. The panel labeled Palm Beach-Stuart is an area along the southeast Florida coast about 40 nautical miles long and fishing is concentrated at the end of one year and the beginning of the next.

ing areas for sailfish in the continental United States. Although fishing effort for sailfish is fairly intensive all year long along the southeast Florida coast, we divided the area into two specific locations: the Florida Keys and the Palm Beach-Stuart area. Our sampling at these two areas was concentrated into two separate time periods and we believe that different groups of fish are exploited in each area.

CPUE fluctuates widely in all three areas. One might expect this from a relatively short-lived species where the effect of year-class strength on the fishery is pronounced. In addition, the sailfish is more coastal in its habitat than the marlins and availability may be more strongly influenced by environmental conditions (Jolley 1979). CPUE fell sharply in the gulf in 1977 and again in 1978. This overall decline was strongly influenced by a large decline off the coast of Texas where fishing for sailfish is usually better than in any other area of the gulf (Figure 15). CPUE in 1977 and 1978 was the lowest since we began sampling and 80% below the average of the previous 3 yr. There was also a sharp decline in the northern gulf in 1978 when CPUE fell to the lowest level of the 8-yr time series.

By inspection of Figure 14, it can be seen that there is an inverse relationship between CPUE in the Florida Keys and the Palm Beach-Stuart area except for the 1978 Keys point and the 1978-79 Palm Beach-Stuart point. It is also interesting to note that if we shift the CPUE data from the Florida Keys forward by 1 yr, we obtain a strong positive correlation, significant at the 99% level, between the two areas. Our sampling in the Keys occurred in November and early December and much of the catch consists of very small sailfish, often averaging only 4-7 kg. Our sampling in the Palm Beach-Stuart area was in late December and January and the average size of sailfish in this area during those months was about 14-18 kg. Jolley (1977) concluded as a result of his studies of growth by analysis of dorsal spines that age-2 sailfish averaged about 7 kg and age-3 sailfish about 14 kg. This approximates the difference in size of sailfish caught at the two areas. We believe that tournament sampling in the Keys is providing a measure of the strength of the incoming year class (age 2) and that this strength is reflected in CPUE from the Palm Beach-Stuart area (mostly age-3 fish) some 12-14 mo later.

DISCUSSION

Catch and effort statistics for white marlin and sailfish from the northern Gulf of Mexico appear to be reliable. With the exception of cases where sample size was inadequate, the data from three nearly independent sources, i.e., dock, tournament, and longline fishing, were consistent over an 8-yr period. It seems likely that if significant biases were present in the data sources, they would have behaved differently over the time series and inconsistencies would have resulted. This consistency over time provides greater confidence in each of the individual data sources and enables the pooling of data to form reliable indices of abundance. Although only tournament data are available from areas outside the gulf, a comparison of these data for white marlin indicates a consistency in trends among areas and suggests that catch and effort statistics are providing a reliable means of indexing abundance. We also believe that they provide some evidence that a single stock of white marlin exists throughout the sampling area.

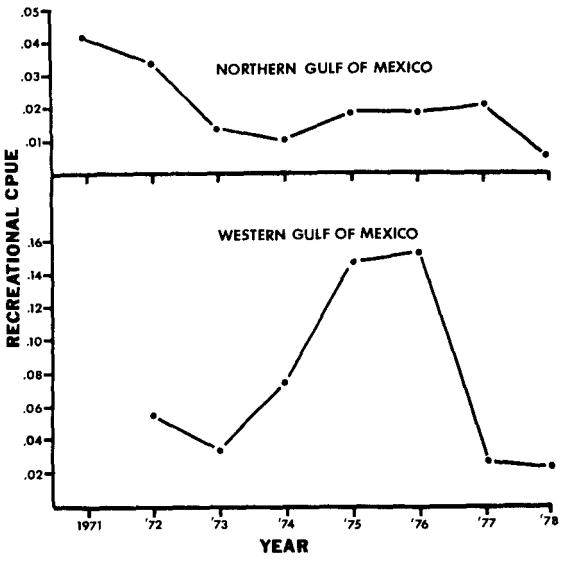

FIGURE 15.—CPUE, in number of fish hooked per hour of fishing, from the recreational fishery for sailfish in the northern and western Gulf of Mexico, 1971-78.

Although trends in CPUE for blue marlin in the Gulf of Mexico and in the Atlantic are similar for some years, the detailed analysis of data from the gulf indicates that caution should be exercised in interpreting catch and effort statistics for blue marlin. In the gulf, little agreement or consistency could be found among the three data sources, and it appears that the basic catch model is not appropriate. Some of the competition effect models discussed by Rothschild (1977), in which catchability decreases as effort increases, may be more appropriate for these data. Rothschild et al. (1970) also demonstrated that the fishing power of various gear types, relative to one another, can change as a function of stock abundance. Declining blue marlin abundance during the analysis period (Conser and Beardsley[5]; Kikawa and Honma[6]) may have caused this situation to occur in the northern gulf. It must be pointed out, however, that white marlin abundance was declining during the same period, but this change in relative fishing power did not occur.

In the analysis of Gulf of Mexico data, the proportionality of catchability over time for the various data sets was examined using correlation analysis of the CPUE's, but the available data did not allow testing the constancy of catchability over time. The results show that the catchability was proportional for all data sets with white marlin and sailfish. Therefore, if any change in catchability occurred, it would have been in the same direction for all data sets. This appears unlikely, however, since any change in catchability for the recreational fishery would probably have been an increase due to improvements in gear and equipment, but an increase in catchability for the longline fishery is unlikely because the fishery has been targeting more on bluefin tuna in recent years, and joint occurrences of billfishes and the tropical tunas tend to be more frequent than joint occurrences of billfishes and the temperate tunas, i.e., bluefin (Fox[7]). It appears reasonable, therefore, to assume that catchability has been constant for white marlin and sailfish, but this assumption would be tenuous for blue marlin in the northern Gulf of Mexico.

ACKNOWLEDGMENTS

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[5]Conser, R. J., and G. L. Beardsley. 1979. An assessment of the status of stocks of blue marlin, *Makaira nigricans*, and white marlin, *Tetrapturus albidus*, in the Atlantic Ocean. Collect. Vol. Sci. Pap. 8(2):461-489. Int. Comm. Conserv. Atl. Tunas, General Mola 17, Madrid, Spain.

[6]Kikawa, S., and M. Honma. 1979. Status of white and blue marlins caught by the longline fisheries in the North Atlantic Ocean. Collect. Vol. Sci. Pap. 8(2):513-515. Int. Comm. Conserv. Atl. Tunas, General Mola 17, Madrid, Spain.

[7]Fox, W. W. 1971. Temporal-spatial relationships among tunas and billfishes based on the Japanese longline fishery in the Atlantic Ocean, 1956-65. Univ. Miami Sea Grant Program, Sea Grant Tech. Bull. 12, 78 p.

ported by a number of staff members over the years. We particularly acknowledge Paul Pristas of the Southeast Fisheries Center Panama City Laboratory; Chester Buchanan, presently with the U.S. Fish and Wildlife Service in Anchorage, Alaska; Perry Thompson with the Southeast Fisheries Center Pascagoula Laboratory; and Allyn Lopez, Luis Rivas, and Edwin Scott of the Southeast Fisheries Center Miami Laboratory. Edward Houde, William Lenarz, Eugene Nakamura, and Gary Sakagawa reviewed the manuscript and we are grateful for their careful and thoughtful comments. Grady Reinert prepared all the charts and graphs.

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WESTERN ATLANTIC HAGFISHES OF THE GENUS *EPTATRETUS* (MYXINIDAE) WITH DESCRIPTION OF TWO NEW SPECIES

BO FERNHOLM[1] AND CARL L. HUBBS[2]

ABSTRACT

Recent trawl collections from the continental slopes of the western North Atlantic have yielded three species of the hagfish genus *Eptatretus* (treated herein) as well as two or three undescribed species of *Myxine*.

Eptatretus is accepted as the generic name for most of the multibranchiate myxinids including all the Atlantic species; *Paramyxine* Dean 1904, is restricted to western Pacific species.

The documentary material of *Paramyxine springeri* Bigelow and Schroeder 1952, contains two species, one of which is here described and named *Eptatretus minor*, new species. The two species are sympatric on the continental slope of the northeastern Gulf of Mexico, but appear to occupy relatively narrow, nonoverlapping depth ranges. *Eptatretus multidens*, new species, is described from the Caribbean Sea and Atlantic Ocean off French Guiana.

The value of tooth counts and the numbers of slime pores is stressed in systematic studies within *Eptatretus*.

Bigelow and Schroeder (1952) described *Paramyxine springeri* from three specimens caught in 1951 in the Gulf of Mexico. The only recognized species of *Paramyxine* at that time was *P. atami* Dean 1904 (now known to be a composite of two Japanese species, Fernholm unpubl. data). Other species of *Paramyxine*, later described from Taiwan (Teng 1958; Shen and Tao 1975) have strengthened the distinctiveness of that genus by having the generic character of crowded gill (or branchial) apertures even more pronounced than in the type-species.

We redescribe *P. springeri* and refer it to the genus *Eptatretus*. We also describe two new species of *Eptatretus* and point out the likely occurrence of at least two additional species of this genus from the midwestern Atlantic. We use the name *Eptatretus* for the Atlantic hagfishes with several gill apertures to stress that we believe they represent a phyletic line which is independent of, although similar to, that of the Asian hagfishes of the genus *Paramyxine*. It is more likely that *Eptatretus* from the Atlantic represents an offshoot from the western American *Eptatretus* group than that they are directly related to the Asian *Paramyxine*. That the western Atlantic species of *Eptatretus* seem to be restricted to Central American and adjacent waters indicates that they may have crossed between the American continents from the Pacific prior to the appearance of the isthmus. In the western Atlantic there are no records of *Eptatretus* outside those shown in Figure 1. On the European and African side of the ocean the only reported captures are those of *E. profundus*, *E. hexatrema*, and *E. octatrema*, all from South African waters (Barnard 1923, 1950).

All specimens treated herein were taken by bottom trawl, a method which usually produces few hagfishes. No doubt an expedition with baited traps would provide vastly more material that could fill in some of the gaps in the material we have at our disposal. However, the U.S. government research vessels (Springer and Bullis 1956; Bullis and Thompson 1965; Bayer 1969) that have secured most of our material give us data which are relatively homogeneous and complete, and thus yield some information on the hagfish habitats.

We show that *P. springeri* Bigelow and Schroeder includes two species, and describe some new forms of *Eptatretus*. We also mention here that hagfishes of the genus *Myxine* have been found in the western Atlantic (Hubbs unpubl. data). They are not yet systematically analyzed, but it is expected that they compose two new species. It thus seems likely that the hagfish fauna

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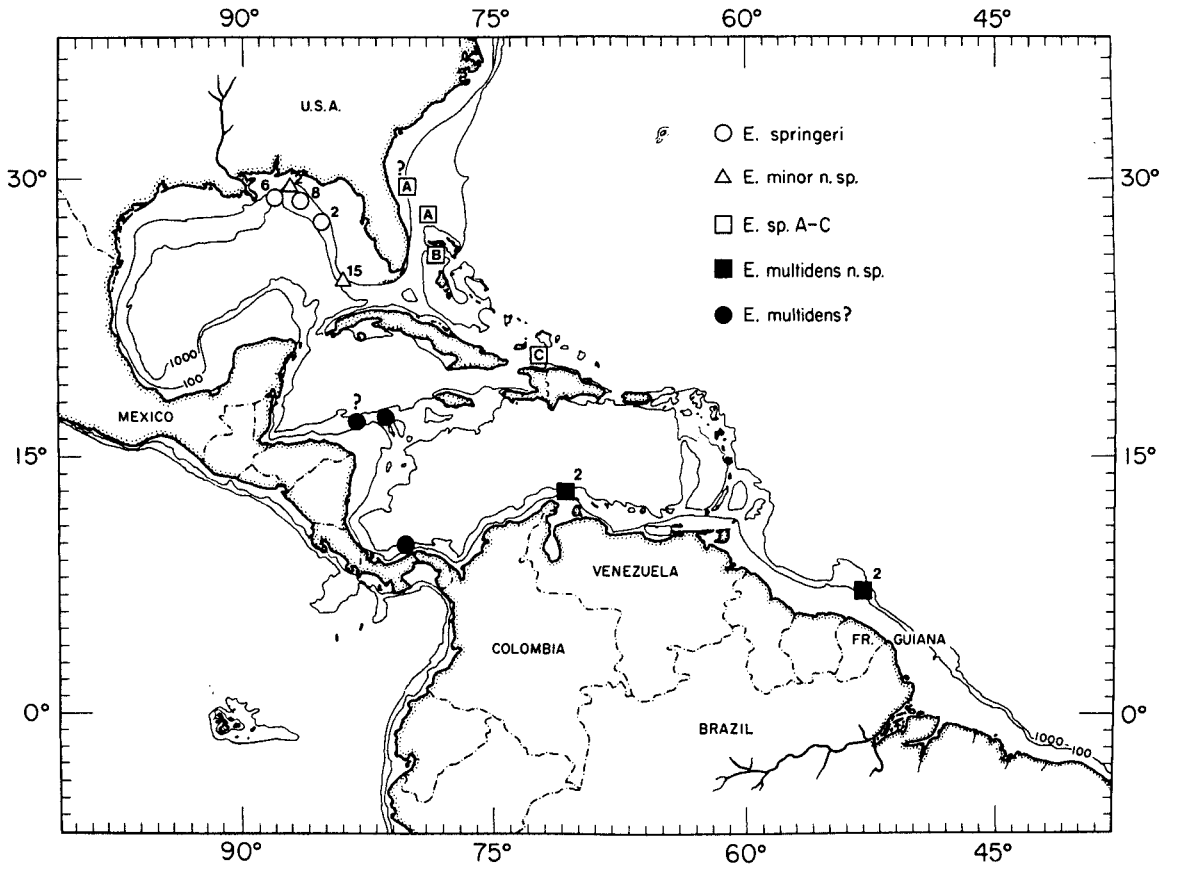


FIGURE 1.—Distribution of *Eptatretus* species in the western Atlantic Ocean. Numbers indicate more than one specimen taken. Two inferential records are indicated with question marks. Isobaths in meters.

of the western Atlantic is about as rich as it is in Japanese waters (cf. Dean 1904).

Anticipating more material of *Eptatretus* from this area, we have chosen to name only those forms that are represented by four or more specimens in the available material. Many hagfish species have been described from one or a very few specimens and this has caused much confusion, especially since subsequent investigators have not been aware of what may be regarded as normal intraspecific variation of characters in different genera of hagfishes.

MATERIALS AND METHODS

We have examined material from the following repositories: FMNH—Field Museum of Natural History, Chicago; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge; SIO—Scripps Institution of Oceanography, La Jolla, Calif.; UMML—Rosenstiel School of Marine and Atmospheric Sciences, Miami; USNM—National Museum of Natural History, Washington, D.C. Details of the studied material are given under each species.

Weight for each preserved specimen was recorded in grams.

The following measurements have been taken on the left side of the specimen:

Total length (TL): from extreme tip of snout at midpoint, excluding barbels, to rear margin of fin around tip of tail; moderate stretching may be needed to approximate normal form. This process has been used for other measurements.

Trunk length: from front of pharyngocutaneous aperture to front of cloacal slit.

Tail length: from front of cloacal slit to tip of tail fin.

Prebranchial length: from tip of snout to front of anteriormost gill aperture.

Branchial length: from front of anteriormost gill aperture to front of pharyngo-cutaneous aperture.

Preocular length: from tip of snout to center of clear area marking ocular region.

Body width: maximum, with body molded into seemingly natural conformation.

Body depth: maximum overall, near middle of body, including ventral fin fold (if applicable).

Body depth excluding fin fold: same region as in body depth, but excluding fin fold.

Body depth over cloaca: over front of cloacal slit.

Tail depth: maximum, taken at right angle to local axis, including fins.

Length of each of the three barbels: from crease at outer-anterior base.

The following counts have been taken:

Cusps on multicuspids (Figure 2): outer/inner row of teeth on both sides. Usually the head is cut open ventrally to count the teeth.

Unicuspids, outer row (including smaller cusps).

Unicuspids, inner row (including smaller cusps).

Total sum of all cusps.

Prebranchial (tip of snout to front of anteriormost gill aperture) slime pores (left side).

Branchial slime pores (left side).

Trunk slime pores (left side).

Tail slime pores (left side).

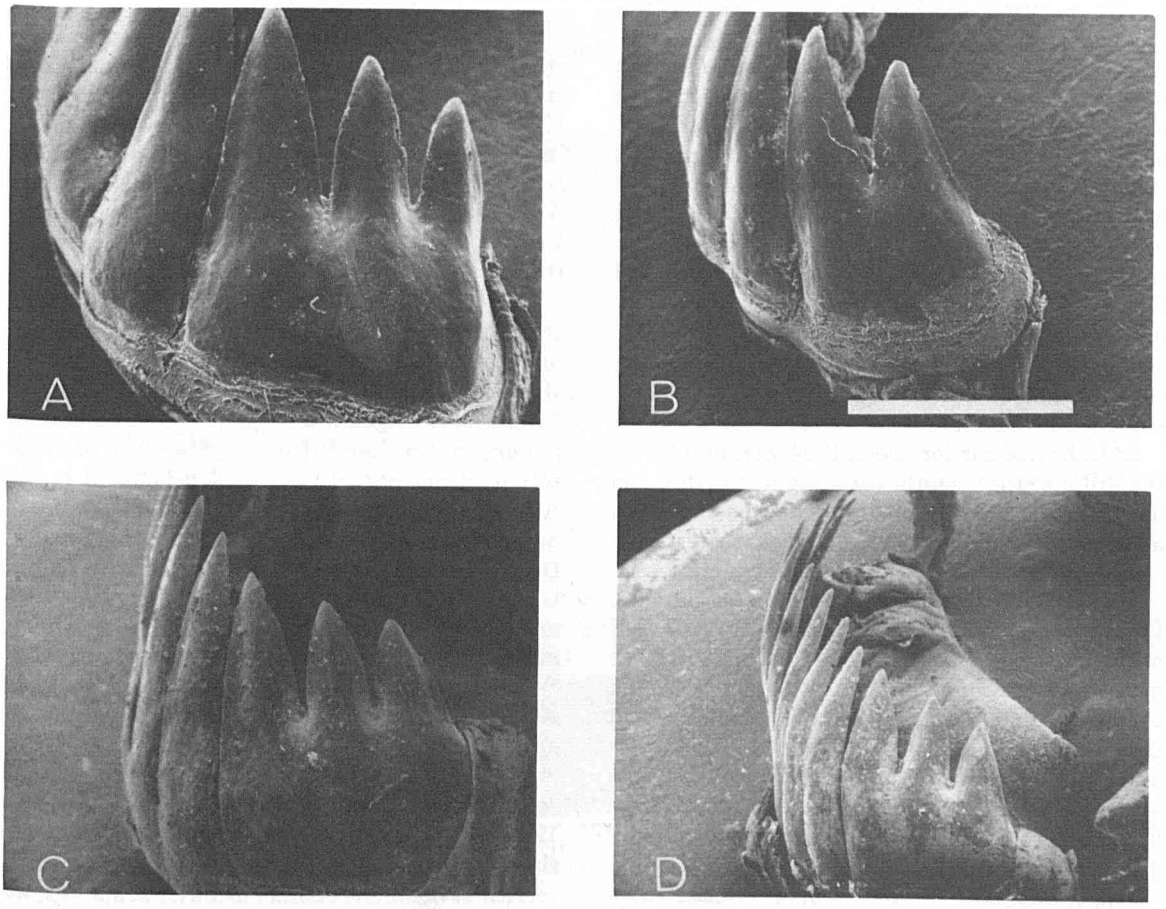


FIGURE 2.—Multicusps of *Eptatretus springeri* by scanning electron microscopy. A—right outer tooth row, B—right inner tooth row to show pattern of fused teeth 3/2 (see text). Multicusps of *E. minor*. C—right outer tooth row, D—right inner tooth row to show pattern of fused teeth 3/3. Scale indicated in B is 2 mm for all figures.

Total sum of slime pores on left side.

Total sum of gill apertures (not counting the pharyngo-cutaneous aperture if the left posteriormost gill aperture opens separately).

Many specimens were cut open to determine the number of gill pouches and their position relative to the tongue muscle and branching of aorta.

Sex was determined by examining the gonad through a cut in the lateral right side body wall anterior to the cloaca.

The usefulness of different counts and measurements for systematic studies in *Paramyxine* and *Eptatretus* have been discussed (Dean 1904; Bigelow and Schroeder 1952; Strahan 1975). We agree with Dean's (1904) statement that "... in the case of myxinoids it is peculiarly necessary to base specific determinations upon the average characters of as great a number of individuals as practicable." Dean (1904) and Strahan (1975) stressed the importance of the relative position of the gill apertures and body proportions, which we also find useful. Dean (1904) tended to disregard the number of slime pores as a systematic character, but we stress the value of that count and point out that both Bigelow and Schroeder (1952) and Strahan (1975) arrived at ranges for this character which are far too broad because they include two composite species (*P. springeri* Bigelow and Schroeder and *P. atami* Dean). This inclusion of an undescribed species (*E. minor*, see below) in *P. springeri* also led to the erroneous conclusion (Bigelow and Schroeder 1952) that the number of slime pores increased with length of the animal.

As indicated earlier (Dean 1904; Strahan 1975), the gill aperture counts vary slightly within the five- to seven-gilled species of *Eptatretus*, but when a larger sample is available, the character is, of course, quite valuable and is easily examined.

Tooth counts were considered of little value by Dean (1904) and Strahan (1975). We find, however, as had Regan (1912) in his admirable yet terse synopsis of the multibranchiate myxinids, that this is a very useful character. Especially we find the pattern of fused cusps (Figure 2) in the inner and outer row of teeth to be constant within species in all of the hundreds of specimens of *Eptatretus* and *Paramyxine* we have studied (unpubl. data).

The movements of the rasping lingual tooth plates are rather elaborate in hagfishes and complicate the terminology used to express positional relationships. In agreement with some previous authors (Dean 1904; Strahan 1975), we have chosen to call the row of teeth with larger teeth the outer row and the other row the inner. The fused tooth or multicusp we regard as the anterior in each row, and to designate the pattern of fused cusps or teeth in the multicusps of the outer/inner row we write 3/2 or 3/3, which are the two patterns found in the Atlantic species of *Eptatretus*.

The shape of the gill apertures, as well as extension and shape of the relatively low ventral fin fold, have been used as systematic characters, but we find it difficult to assess these characters in preserved specimens.

The pattern of fused teeth (3/2 or 3/3), supplemented with counts of gill apertures and slime pores, appears to suffice to distinguish the western Atlantic species of *Eptatretus*.

GENERIC ALLOCATION

The generic allocation of the polybranchiate species of hagfishes has been considerably discussed (for summary, see Holly 1933 and Strahan 1975). To us it is obvious that the name with priority, *Eptatretus* Cloquet, 1819, should be used. As stressed earlier (Bigelow and Schroeder 1948; Adam and Strahan 1963; Hubbs 1963; Strahan 1975), there is no obvious advantage in dividing the genus into subgenera.

It has been argued that *Paramyxine* as a genus should be treated as a junior synonym of *Eptatretus* (Strahan 1975). It is true that tendencies to shortening of the gill aperture area can be found in *E. springeri* (Bigelow and Schroeder 1952) and in *E. burgeri* (Strahan 1975), but we believe this represents a convergent trend of development in the Atlantic and Pacific Oceans. We retain the generic name *Paramyxine* for the western Pacific species. Dean (1904) defined the genus *Paramyxine* on the basis of a single specimen of *P. atami*. Now that much more material is available, it is somewhat a matter of choice whether one wants to retain *Paramyxine* for the Asian species. We choose to do so for the following reasons: 1) Dean's concept of crowdedness of gill apertures has been strengthened by the description of Taiwanese species of *Paramyxine* (Teng 1958; Shen and Tao 1975), which are more extreme in this character than is the type-species; 2) as a further characteristic of the many Asian *Paramyxine* species, we point to the absence of slime pores in the branchial area (with the exception that in *P. atami* Dean and *P. cheni* Shen and Tao, there may be a single pair of

slime pores in the branchial area); 3) *Paramyxine* defined in this way is a geographically, and we believe phylogenetically, distinct group limited to the waters of southeastern Asia.

Key to the Western Atlantic Species of *Eptatretus*

1a. Three anterior teeth in outer row and two anterior teeth in inner row fused at bases 2
1b. Three anterior teeth in each row fused at bases 4
2a. Gill apertures 6 or 7. Body and head stout (Figures 3, 4) 3
2b. Gill apertures 5. Body thin. Head narrow. One specimen, 308 mm (Figure 5). South of Bahama Islands ..... sp. B
3a. Slime pores 84-92. Maximum known length 590 mm. Northeastern Gulf of Mexico .. *E. springeri*
3b. Slime pores 78. One specimen, 433 mm. North of Bahama Islands ..... sp. A
4a. Gill apertures 7 ..... *E. multidens*?
4b. Gill apertures 6 (rarely 5) 5
5a. A thin whitish middorsal stripe. Total cusp count of teeth 46-54. Maximum known size 395 mm. Northeastern Gulf of Mexico. ..... *E. minor*
5b. No whitish middorsal stripe. Total cusp count of teeth 52-58. Caribbean Sea and Atlantic Ocean off French Guiana and Haiti 6
6a. Slime pores 75. Total cusp count of teeth 58. One specimen 380 mm. North of Haiti ..... sp. C
6b. Slime pores 87-91. Total cusp count of teeth 52-57. Maximum known length 655 mm. Caribbean Sea and Atlantic Ocean off French Guiana ..... *E. multidens*

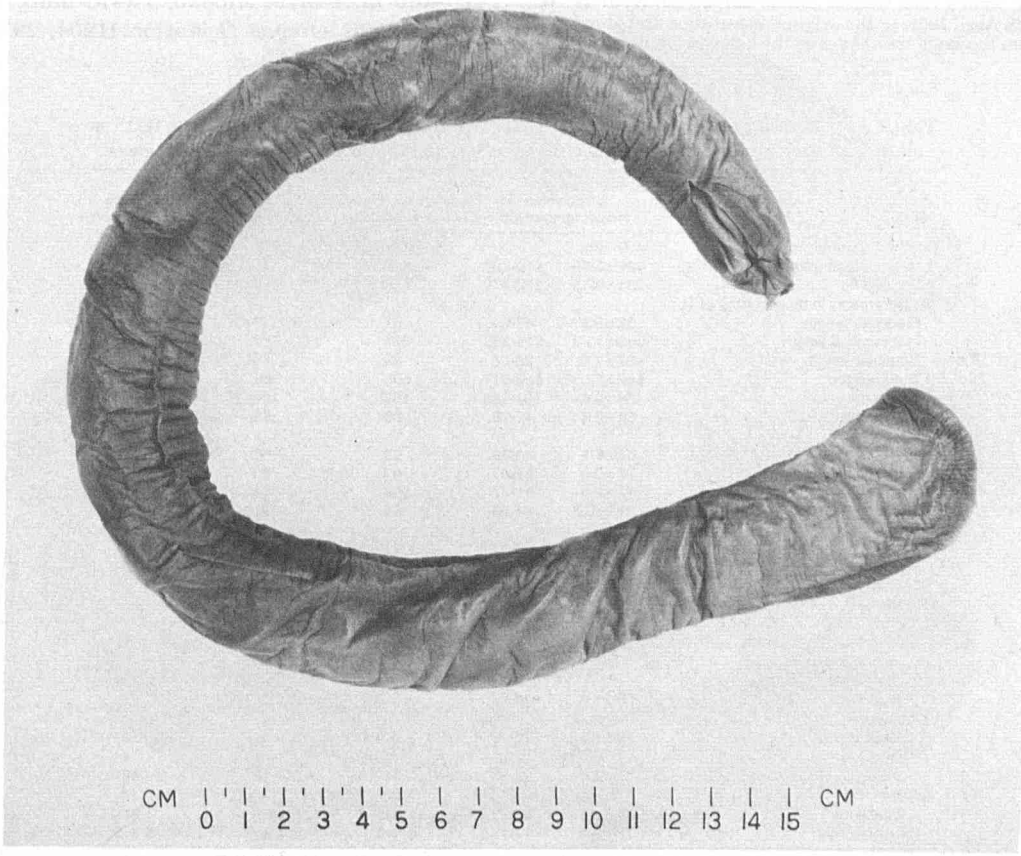


FIGURE 3.—*Eptatretus springeri* (MCZ 39939).

DESCRIPTION OF SPECIES

Eptatretus springeri (Bigelow and Schroeder) Figure 3, Table 1

Paramyxine springeri Bigelow and Schroeder 1952:1-10 (in part; original description; holotype, 590 mm, and an additional specimen, 505 mm; comparison with *P. atami*; includes, as do the following references, one 338 mm specimen of *E. minor*). Teng 1958:5-6 (comparison with other species referred to *Paramyxine*). Lindberg and Legeza 1959:23-24 (gill apertures). Strahan and Honma 1961:323-341 (comparison with *P. atami* and *P. yangi*). Adam and Strahan 1963:7 (characters; size; Gulf of Mexico). Lindberg and Legeza 1959:19, 21 (gill apertures). Rass 1971:18 (Gulf of Mexico).

Material.—MCZ 37399,[3] 1 (505 mm), 29 September 1951, 1340-1540 h, *Oregon* station 489, 27°44′ N, 85°09′ W, depth 465 m, bottom temperature 10.3° C, bottom type blue mud; MCZ 39939, 3 (500, 509, 576 mm), 13 March 1955, 0835-1305 h, *Oregon* station 1282, 29°10′ N, 88°03′ W, depth 475 m, bottom temperature 10° C, bottom type gray mud; MCZ 42423, 3 (410, 433, 450 mm), 12 March 1962, *Oregon* station 4076, 28°33′ N, 86°27′ W, depth 460 m; SIO 76-248 (formerly UMML 4405), 1 (542 mm), 18 February 1956, 0805-0835 h, *Oregon* station 1450, 29°17′ N, 87°41′ W, depth 440 m; USNM 161512 (holotype), 1 (590 mm), 29 September 1951, 1340-1540 h, *Oregon* station 489, 27°44′ N, 85°09′ W, depth 465 m, bottom temperature 10.3° C, bottom type blue mud; USNM 188210, 1 (522 mm), 23 October 1962, *Oregon* station 4005, 29°07.5′ N, 88°09′ W, depth 550 m; USNM 218396, 2 (513, 526 mm), 4 February 1970, *Oregon II* station 10899, depth 550 m; USNM 218397, 2 (500, 540 mm), 5 February 1970, *Oregon II* station 10900, 28°50.2′ N, 86°59′ W, depth 730 m; USNM 218394, 1 (417 mm), 29 August 1970, *Oregon II* station 11192, 29°19′ N, 86°45′ W, depth 420-460 m; USNM 218395, 1 (418 mm), 1 September 1970, *Oregon II* station 11204, 29°12′ N, 87°55′ W, depth 550 m.

[3]"Additional material" of Bigelow and Schroeder (1952). Labelled as coming from *Oregon* station 321; 29°27′ N, 87°19′ W, 400 m, 28 April 1951. In the original description stated to have come from the same trawl haul as the holotype and so regarded here.

TABLE 1.—Characters of western Atlantic species of *Eptatretus* with 3/2 cusps (see text) on multicuspids of outer/inner row of teeth. Mean ± SD and range given for multiple specimens.

Item	*E. springeri* 16 specimens including holotype		Holotype	*E.* sp. A 1 specimen	*E.* sp. B 1 specimen
Depth of capture (m)	420-730		465	950	590
Total length, TL (mm)	496±53.9	410-590	590	433	308
Weight (g)	231±97.3	102-479	479	182	40
Measurements in thousandths of TL:					
Preocular length	53±5.6	47-64	61	53	—
Prebranchial length	243±13.3	215-268	243	215	250
Branchial length	37±7.9	25-56	39	79	39
Trunk length	568±17.5	529-611	563	550	568
Tail length	156±9.8	134-168	155	157	146
Body width	52±6.8	42-70	70	55	37
Body depth:					
Including fin fold	81±8.1	66-99	99	88	67
Excluding fin fold	77±9.4	62-97	97	85	62
Over cloaca	67±7.5	51-77	69	74	48
Tail depth	81±10.3	64-93	85	81	67
Barbel length:					
First	9±1.4	7-11	11	15	10
Second	10±1.8	7-14	7	16	12
Third	15±2.8	10-20	10	16	15
Counts:					
Teeth:					
Cusps on multicuspids	3/2		3/2	3/2	3/2
Unicuspids, outer row[1]		10-11	11 + 11	10 + 11	10 + 10
Unicuspids, inner row[1]		9-11	10 + 10	10 + 10	10 + 11
Total sum of cusps	50±1.4	48-52	52	51	51
Slime pores, left side:					
Prebranchial	18±1.1	16-19	19	14	18
Branchial	3.2±0.9	2-5	4	4	4
Trunk	54±1.8	52-57	55	48	48
Tail	11±1.1	9-13	13	13	11
Total sum	87±2.6	84-92	91	79	81
Gill apertures[1]	12±0.4	12-13	6 + 6	7 + 7	5 + 5

[1]Left + right count for single specimen.

Diagnosis.—An *Eptatretus* with six (rarely seven) gill apertures. Total cusp count 48-52, with three teeth fused in outer and two in inner row of teeth (Figure 2). Slime pores 84-92.

Description.—*E. springeri* is a large hagfish; the 16 available specimens range from 410 to 590 mm with the mean about 500 mm. The five sexually mature females were 500 mm or longer. Eggs in the most mature female, 526 mm, are about 10 × 36 mm.

Only 1 of our 16 specimens had the sixth left gill aperture opening separately in front of the pharyngo-cutaneous aperture (cf. *E. burgeri* with 10% of the animals showing this condition according to Dean 1904). Two animals had an extra gill aperture on the right side and one an extra on the left side. Of these three, two had an extra seventh gill pouch on the right side and one had an extra seventh pouch on each side; the extra pouches were all more or less reduced in size.

The tongue muscle typically overlies gill pouches 1-3, and the aorta divides between gill pouches 4 and 5.

The color of our specimens is dark brownish purplish to very light brown; the eyespots are not plainly visible.

Distribution.—*Eptatretus springeri* has been found only in the northeastern part of the Gulf of Mexico (Figure 1) at depths between 410 and 576 m, but it must be realized, of course, that incidental capture (by trawling) is hardly adequate for our distributional map. The southernmost record is that of the holotype (USNM 161512).

Habitat and biology.—Specimens were collected by bottom trawl in March (475 m) and September (465 m) where the habitat temperature was about 10° C. It could not be determined whether the animals were in or above the substrate, which seemed to be composed of blue or gray mud. At least six of the specimens were caught during daytime. Some females contained ripe eggs (21-41

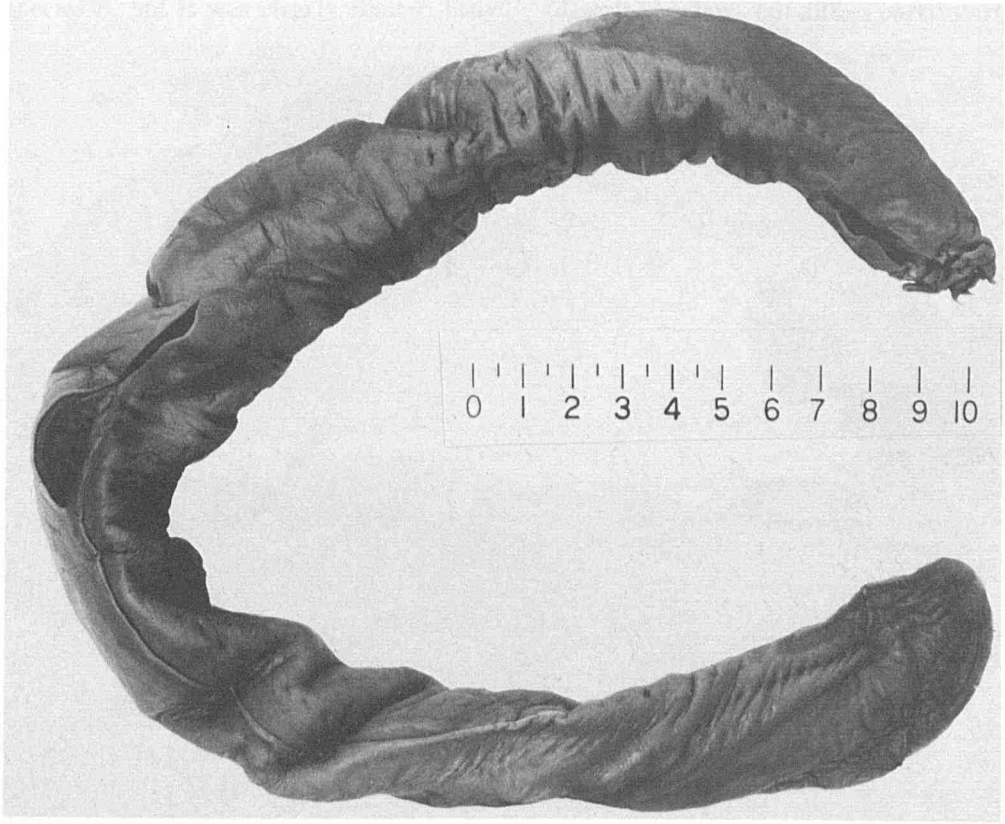


FIGURE 4.—*Eptatretus* sp. A (MCZ 40370). Scale in centimeters.

mm) in February, March, and September; thus the population presumably spawned throughout the year.

Eptatretus species A and B
Figures 4 and 5, Table 1

Material.—Species A, MCZ 40370, 1 (433 mm), 9 June 1958, 1925-2225 h, *Silver Bay* station 445, 28°03′ N, 78°44′ W, depth 910-950 m, bottom type coral and sand; Species A (inferential; the specimen cannot be located), 21 June 1958, 0730-1030 h, *Silver Bay* station 490, 29°49′ N, 80°11′ W, 330 m, bottom type green mud. Species B, SIO 76-252 (formerly UMML 31521), 1 (308 mm), 27 September 1973, RV *Columbus Iselin* station 137, 26°07′ N, 78°34.1-36.6′ W, depth 590-560 m.

Two specimens of *Eptatretus* (herein provisionally designated A and B) have been taken at depths of 950 and 590 m, respectively, in the vicinity of Grand Bahama Island (Figure 1). The pattern of fused teeth is 3/2 in these specimens and the total number of cusps is essentially the same. They exhibit differences large enough that they cannot be convincingly included in *E. springeri*. There are differences in the numbers of gill pouches and apertures, the relative branchial length, and number of prebranchial, trunk, and total slime pores (Table 1). Although there is variability in the number of gill pouches, and specimens having one more or less pouch are found among the six-gilled species of *Eptatretus*, it seems unlikely that our five- and seven-gilled specimens from south and north of Grand Bahama Island represent a single species with normally six gill pouches. The body width, the relative depth over the cloaca, and counts of prebranchial slime pores (Table 1) also indicate specific distinction for these two Atlantic *Eptatretus* specimens.

Species A, a mature male, is considerably stouter than the thin specimen designated as species B and is about as stout as *E. springeri*. The tail is less flaring and more pointed than that of *E. springeri*. The skin is light brown overall with the ventral fin fold whitish. Patches of transparent skin overlie the eyes. Trunk and total slime pore counts are outside the range of *E. springeri* in this seven-gilled specimen (Table 1), but the internal

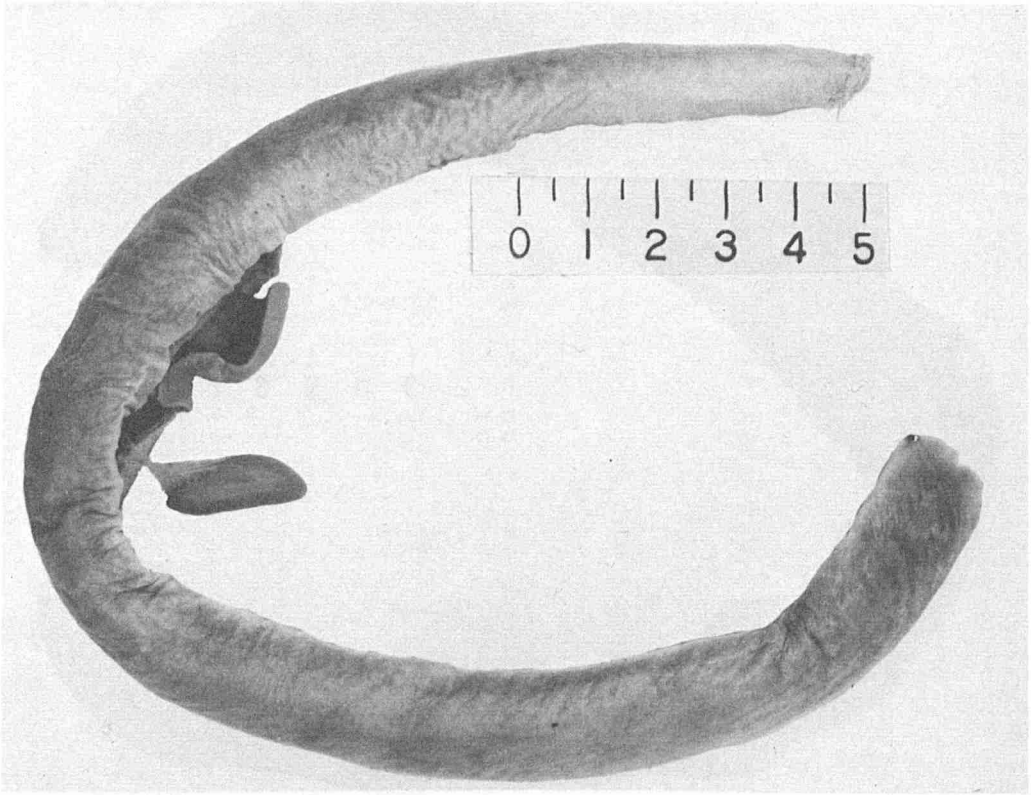


FIGURE 5.—*Eptatretus* sp. B (SIO 76-252). Object dependent from slit is an egg. Scale in centimeters.

anatomy is similar: the tongue muscle overlies gill pouches 1-3, and the aorta divides between gill pouches 5 and 6.

Species B is represented by a five-gilled female having a slender body and narrow head. The skin is light pinkish tan, with the ventral side only slightly lighter; no eyespots are visible. The thin ventral fin fold is white, and extends forward from the cloaca, reaching its maximum height at about the middle of the body, and gradually tapers off toward the posterior part of the branchial region. Several small depressions in the skin, about 0.4 mm in diameter, located mostly in the head region, may be traces of ectoparasitic trematodes. Species B differs from *E. springeri* in internal anatomy, having a tongue muscle overlying only the first gill pouch and an aorta bifurcating between the second and third gill pouch. *Eptatretus profundus* (Barnard 1923) is the only described species of *Eptatretus* having five gill apertures. Unfortunately, only the holotype is extant. It was measured by Hubbs (figures in parentheses, below) in the South African Museum (no. 13035) and was found not to differ much in length proportions from species B, but it was clearly stouter: body width (thousandths of total length), 37 (63); body depth including fin fold, 67 (94); body depth excluding fin fold, 62 (91); body depth over cloaca, 48 (68). The South African species yielded a lower total tooth count, 51 (42), but a similar number of slime pores, 81 (84). The difference in tooth count and stoutness indicate that the two specimens probably are not conspecific.

Eptatretus species C Figure 6, Table 2

Material.—USNM 218400, 1 (380 mm), 13 October 1963, *Silver Bay* station 5146, 19°55.5′ N, 72°00′ W, depth 860-910 m.

This six-gilled specimen, from off Haiti, is a female with eggs 2-3 mm long, apparently in quite early stages of development. The pattern of fused cusps, 3/3, and several other characters indicate relationship to *E. minor* (described below). It differs from that species, however, in having a longer tail, shorter branchial length, greater body depth, slightly higher tooth count, and a lower prebranchial slime-pore count. It is similar to *E. multidens* (described below), but differs particularly in hav-

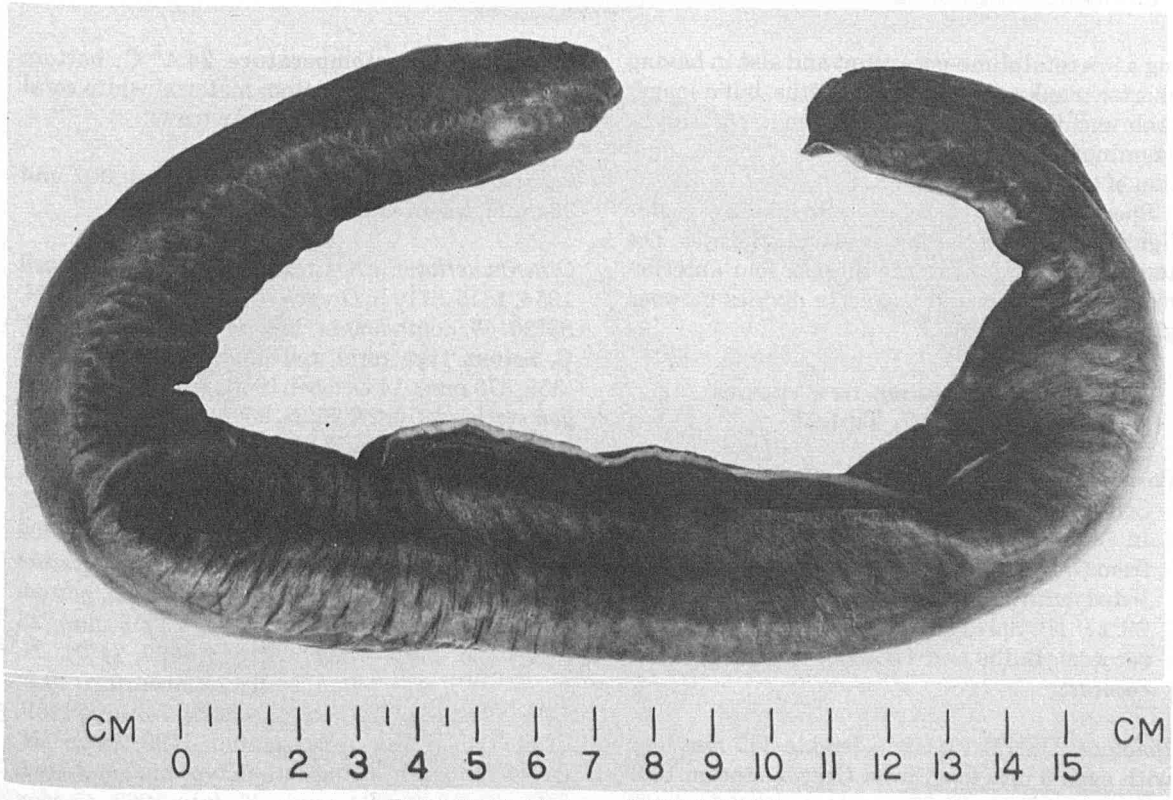


FIGURE 6.—*Eptatretus* sp. C (USNM 218400).

TABLE 2.—Characters of western Atlantic species of *Eptatretus* with 3/3 cusps (see text) of multicuspids of outer/inner row of teeth. Mean ± SD and range given for multiple specimens.

Item	*E. minor* n. sp. 17 specimens including holotype		Holo-type	*E. multidens* n. sp. 4 specimens including holotype		Holo-type	*E. multidens*? MCZ 40409	USNM 218405	*E.* sp. C
Depth of capture (m)	300-400		370	510-770		510	500	365	910
Total length, TL (mm)	330±47.8	223-395	359	526±125.3	377-655	600	331	364	380
Weight (g)	85±33.5	22-138	107	494±302.1	164-757	561	84	128	154
Measurements in thousandths of TL:									
Preocular length	55±8.8	31-62	59	46±3.1	43-49	43	—	61	59
Prebranchial length	243±14.3	201-259	245	200±8.4	188-207	202	214	236	237
Branchial length	59±7.6	51-72	71	65±4.0	61-69	62	73	78	47
Trunk length	529±15.1	506-559	522	560±8.0	552-571	560	517	504	526
Tail length	165±14.1	139-183	162	179±8.0	169-188	182	196	181	190
Body width	61±10.6	48-78	62	45±5.7	39-50	39	48	77	57
Body depth									
Including fin fold	94±12.3	71-114	92	104±16.0	80-115	109	97	114	100
Excluding fin fold	89±10.5	71-108	88	102±16.0	78-113	107	—	105	99
Over cloaca	69±9.1	52-79	74	72±8.8	60-81	81	69	82	84
Tail depth	82±14.8	53-116	84	76±8.7	66-86	79	97	107	79
Barbel length:									
First	17±2.8	13-23	16	12±3.4	8-15	15	14	16	13
Second	18±3.3	13-25	22	14±0.6	13-14	13	19	17	14
Third	25±4.7	14-32	30	18±2.3	15-20	18	21	24	21
Counts:									
Teeth:									
Cusps on multicuspids	3/3		3/3	3/3		3/3	3/3	3/3	3/3
Unicuspids, outer row[1]		8-11	9 + 8		11-12	12 + 11	11 + 12	12 + 13	12 + 12
Unicuspids, inner row[1]		8-10	9 + 9		9-11	11 + 11	10 + 11	10 + 11	11 + 11
Total sum of cusps	50±2.7	46-54	47	55±2.4	52-57	57	56	58	58
Slime pores, left side:									
Prebranchial	16±1.0	15-18	15	15±1.0	14-16	16	13	15	13
Branchial	5.0±0.4	4-6	5	5.5±0.6	5-6	5	6	6	4
Trunk	45±2.1	41-48	48	54±1.5	52-55	55	50	47	44
Tail	12.4±0.7	11-14	12	15±0.0	15	15	12	11	14
Total sum	78±2.6	74-82	80	89±1.8	87-91	91	81	79	75
Gill apertures[1]	11.9±0.5	10-12	6 + 6	12±0.0	12	6 + 6	7 + 7	7 + 7	6 + 6

[1]Left + right count for single specimen.

ing a low total slime-pore count and also in having shorter trunk and branchial lengths, but a longer prebranchial length. Until more material can be examined, it seems desirable to delay the designation of this specimen as a new species.

Species C is light brown with plainly visible lighter patches on the skin overlying the eyes. The tongue muscle overlies the three or four anteriormost gill pouches and the aorta divides between gill pouches 5 and 6.

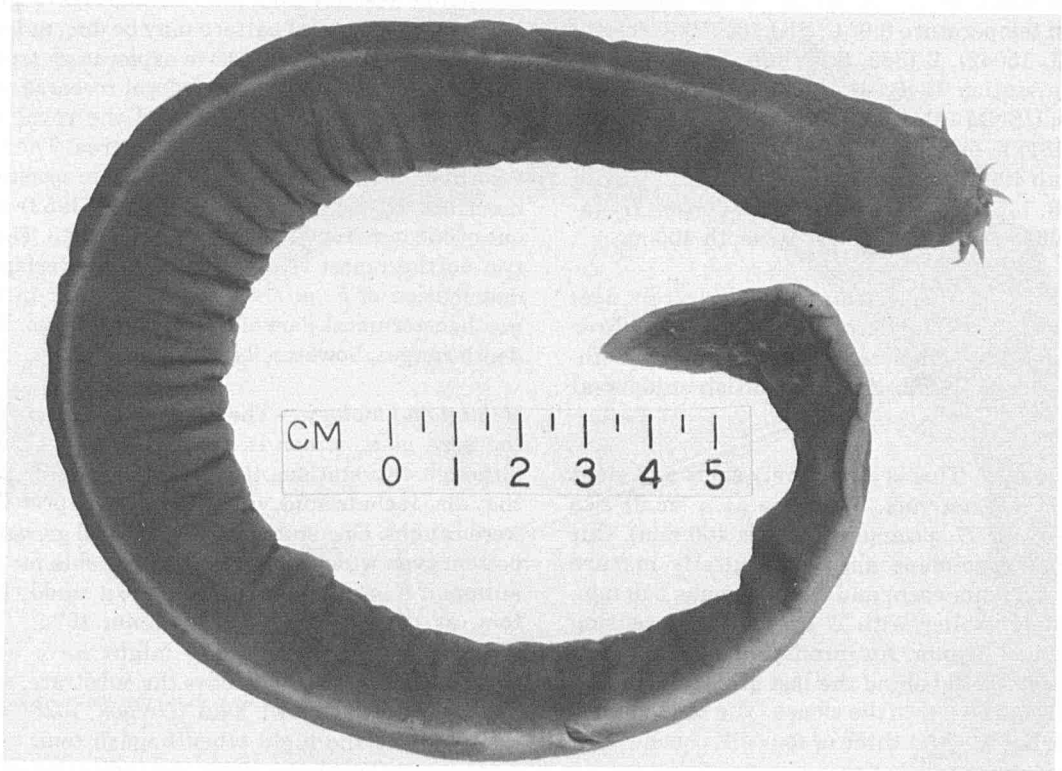
Eptatretus minor, new species
Figure 7, Table 2

Paramyxine springeri (in part).—Bigelow and Schroeder 1952:1-10 (the 338 mm long specimen in "additional material" stated to have come from *Oregon* station 321, which was erroneously listed with lat. 27°27′ N; correct latitude is 29°27′ N). Springer and Bullis 1956:40 (survey records). Bullis and Thompson 1965:17 (survey records).

Holotype: USNM 164119, a female 359 mm long, with eggs 9 mm long, from *Oregon* station 1009, 24°34′ N, 83°34′ W, 370 m, 14 April 1954, 0450-0730 h; surface temperature 24.4° C, bottom temperature 11.7° C; bottom material white coral and mud; in 12 m (40-ft) shrimp trawl.

Paratypes: USNM 218399, two females, 307 and 334 mm, taken with the holotype.

Other material: FMNH 59959, 1 (340 mm), 13 April 1954, 1815-2110 h, *Oregon* station 1006, 24°20′ N, 83°20′ W, depth 350 m, bottom temperature 10.6° C, bottom type coral and mud; FMNH 65817, 2 (355, 370 mm), 14 October 1959, 1805-2150 h, *Oregon* station 2670, 24°26′ N, 83°24′ W, depth 390 m, bottom type mud; MCZ 38707, 1 (313 mm), 19 April 1954, 2115-2300 h, *Oregon* station 1026, 25°08′ N, 84°19′ W, depth 300 m, bottom temperature 10° C, bottom type sand and gravel; MCZ 40679, 1 (306 mm), 7 June 1959, 1940-2140 h, *Silver Bay* station 1189, 24°20.5′ N, 83°25′ W, depth 300 m, bottom type mud and sand; MCZ 51084, 1 (355 mm), 23 November 1963, *Oregon* station 4529, 24°31′ N, 83°26′ W, depth 390 m, bottom temperature 10.2° C; SIO 76-251, 3 (223, 223, 310 mm), 7-8 June 1959, 2245-0045 h, *Silver Bay* station 1190, 24°28′ N, 83°34′ W, depth 330 m, bottom type mud and sand; SIO 76-249, 1 (341 mm), 26 July 1963, *Oregon*



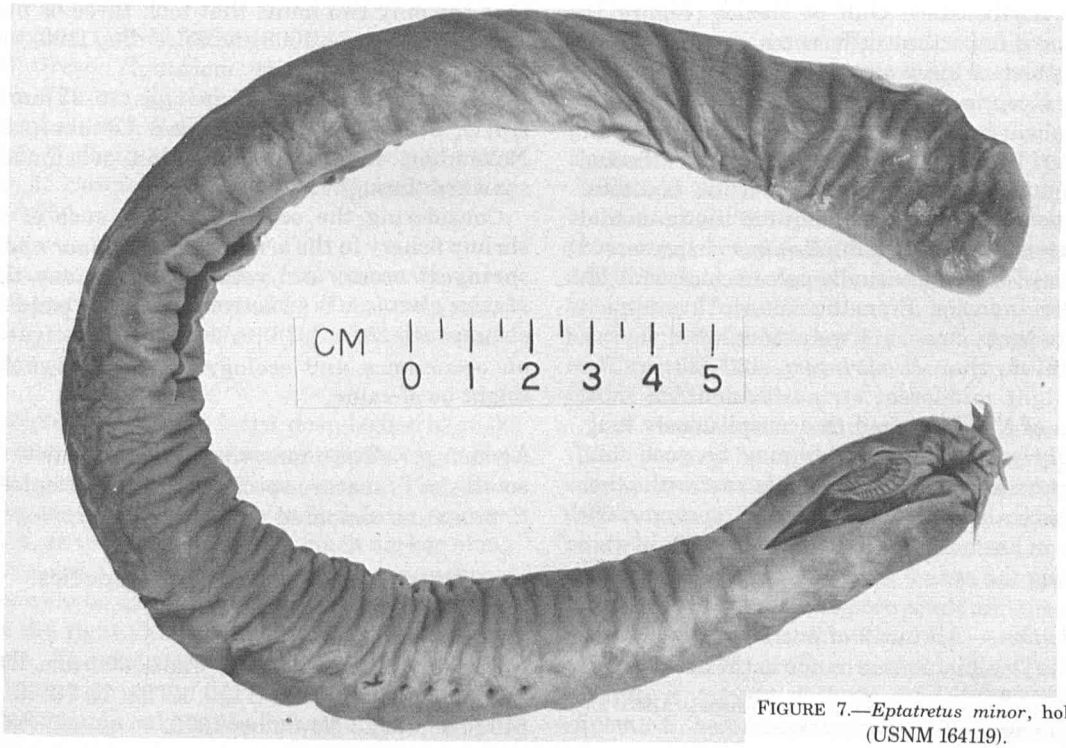


FIGURE 7.—*Eptatretus minor*, holotype (USNM 164119).

station 4338, 24°18′ N, 83°18′ W, depth 380 m, bottom temperature 8.9° C; SIO 76-250 (formerly UMML 15042), 2 (385, 395 mm), 29 July 1963, *Oregon* station 4346, 24°28′ N, 83°29′ W, depth 380 m; USNM 161513,[4] 1 (332 mm), 28 April 1951, 1630-1817 h, *Oregon* station 321, 29°27′ N, 87°19′ W, depth 400 m, bottom temperature 10° C; USNM 218398, 1 (358 mm), 23 June 1969, *Oregon II* station 10643, 29°30′ N, 87°09′ W, depth 400 m.

Diagnosis.—An *Eptatretus* with six (rarely five) gill apertures. Total cusp count 46-54, with three teeth fused in both outer and inner rows of teeth. Slime pores 74-82. A thin whitish middorsal stripe.

Description.—This is a relatively short and stout species of *Eptatretus*, maturing at a small size (none of our 17 specimens exceeds 400 mm). Our shortest specimens are two sexually mature males, 223 mm each, and a ripe female, 310 mm, extremely swollen with 12 eggs, each measuring about 10 × 31 mm. An inconspicuous ventral fin fold begins well behind the last gill aperture and extends backward to the cloaca. The tongue muscle overlies the first three or four gill pouches and the aorta branches between pouches 5 and 6.

Eptatretus minor and *E. springeri* are sympatric in the northeastern Gulf of Mexico (Figure 1). There are important differences between them. The pattern of fused teeth is 3/3 in *E. minor* and 3/2 in *E. springeri* (Figure 2). There may be a difference in the relative trunk lengths, *E. springeri* being longer. This difference is reflected in the nonoverlapping counts of trunk and total slime pores. The relative length of the branchial region tends to be greater in *E. minor*. In preserved material *E. minor* is usually pale in color, while *E. springeri* is darker. From the material available it appears that *E. minor* lives at shallower depths, 300-400 m, than *E. springeri*, 420-730 m. The thin, light middorsal stripe, evident on most species of *E. minor*, and the conspicuously long, laterally protruding barbels may be good field characters for that species. In contrast with other field species of *Eptatretus*, neither *E. springeri* nor *E. minor* has a conspicuous lighter patch of skin overlying the eye.

Distribution.—All but 2 of our 17 specimens are from the Dry Tortugas grounds in the archipelago extending westerly from the Florida Keys (Figure 1). The distributional pattern may be due, at least to some extent, to the massive exploratory trawling activities carried out by federal research vessels to monitor the population of the royal red shrimp, *Pleoticus robustus*, in that area. The two records outside this area are the 338 mm specimen described by Bigelow and Schroeder (1952) and one of 358 mm from *Oregon II* station 10643. These two northernmost records indicate an overlap in distribution of *E. minor* and *E. springeri* in the northeasternmost part of the Gulf of Mexico. The depth ranges, however, do not overlap.

Habitat and biology.—The bottom temperature in the area of *E. minor* is about 8.9°-11.5° C, and although two stations list coral as bottom type, they also include mud, where the hagfish probably were caught. One station lists sand and gravel as bottom type which would be less suitable for the animal if *E. minor* usually digs into a muddy bottom, as does *E. burgeri* (Fernholm 1974). The specimen from that station might have been caught when swimming above the substrate, as is likely, since the trawl haul (*Oregon* 1026) was taken during the night when hagfish tend to be most active (Fernholm 1974). An indication of increased night activity may also be found in the fact that the only two hauls that took three or more specimens (*Oregon* 1009 and *Silver Bay* 1190) were taken at night or in early morning.

Some females contained ripe eggs (25-33 mm) in April, June, July, September, October, and November; thus the population presumably spawned throughout the year.

Considering the economic importance of the shrimp fishery in the areas where *E. minor* and *E. springeri* occur, and recent suggestions that *Myxine glutinosa* is an active predator on pandalid shrimps (Shelton 1978), a detailed investigation on occurrence and ecology of these hagfishes might be of value.

Etymology.—The name *minor*, small, refers to the small size of mature specimens in our samples of *E. minor*, as compared with those of *E. springeri*.

Eptatretus multidens, new species
Figure 8, Table 2

Holotype: USNM 218401, a male, 600 mm long, from *Oregon II* station 11299, 12°52′ N, 70°43′ W, 510 m depth, 23 November 1970.

[4]"Additional material" of Bigelow and Schroeder (1952) and labelled paratype of *Paramyxine springeri*.

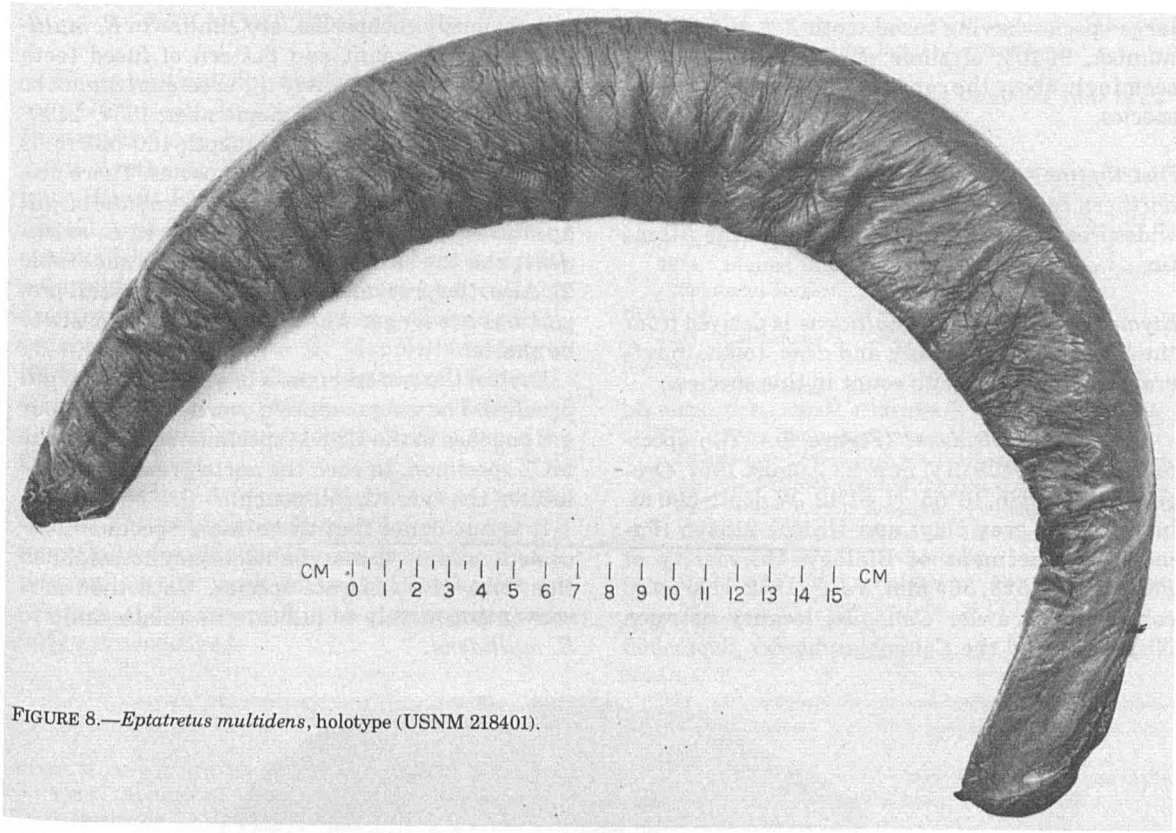


FIGURE 8.—*Eptatretus multidens*, holotype (USNM 218401).

Paratypes: USNM 218404, 1 (655 mm), 12 May 1969, *Oregon II* station 10611, 7°13′ N, 52°52′ W, depth 770 m; USNM 218403, 1 (473 mm), 19 November 1969, *Oregon II* station 10804, 7°18′ N, 52°56′ W, depth 710-630 m; USNM 218402, 1 (377 mm), 23 November 1970, *Oregon II* station 11300, depth 550 m.

Diagnosis.—A six-gilled *Eptatretus* with three fused teeth in each row (3/3). Total cusp count 52-57. Slime pores 87-91. No middorsal light stripe.

Description.—This is a large, deep-bodied hagfish. The color of the four preserved specimens varies from pale brown to medium brown. The paler specimens may have been bleached during preservation, as the wrinkled tail is much darker along the creases. On the paler specimens the eyespots can barely be discerned, while on the darker animals the light skin overlying the eyes is clearly visible. The holotype appears bleached on the right anterior part of the body which renders the eyespot visible only on the left side. A small ventral fin fold of noncontrasting brownish color is evident from the middle of the body to the cloaca.

The tongue muscle overlies the first two or three gill pouches, and the aorta branches at the level of the sixth posteriormost gill pouch.

When *E. multidens* is compared with *E. springeri*, noticeable differences in addition to the important pattern of fused teeth are the longer tail and branchial area but shorter prebranchial of *E. multidens*. These differences in body proportions are reflected in the higher slime-pore counts in tail and branchial areas and the lower prebranchial counts of *E. multidens*.

If *E. multidens* is compared with *E. minor*, to which it may be closely related by having the common pattern of fused teeth, it is found that the differences in body proportions are not pronounced. The best definitive characters to separate these two species seem to be the nonoverlapping trunk or total slime-pore count and the more noticeable eyespot in *E. multidens*.

Other than *E. springeri* and *E. minor*, the only Atlantic *Eptatretus* with six gills is the probably endemic *E. hexatrema* from South Africa. This is a

large species having fused teeth 3/2 and a high number, 91-105, of slime pores (Strahan 1975), seemingly above the range of the western Atlantic species.

Distribution.—Records of this species along the northern coast of South America indicate it to be widespread in both the Caribbean and the Atlantic.

Etymology.—The name *multidens* is derived from the Latin *mult(us)*, many, and *dens*, tooth, in reference to the high tooth count in this species.

Eptatretus multidens? (Figure 9).—Two specimens, MCZ 40409 (331 mm, 23 August 1957, *Oregon* station 1886, 16°55′ N, 81°12′ W, depth 500 m, bottom type gray clay) and USNM 218405 (formerly Department of Biology, University of Panama, no. 523, 364 mm, 5 July 1972, chartered commercial trawler *Canopus*, locality between Nicaragua and the Colombian border, depth 365 m), obviously conspecific, are similar to *E. multidens* in tooth count and pattern of fused teeth (3/3). A third record where the specimen cannot be located (MCZ 40218, 16 September 1957, 2100-2200 h, *Oregon* station 1945, depth 460-550 m) is inferred to belong to the same species. There are, however, important differences in counts of gill apertures, 7 + 7, instead of 6 + 6 as in *E. multidens*, and the slime pores seem to be fewer (Table 2). Also, the prebranchial, branchial, and tail proportions are longer whereas the trunk appears to be shorter.

Each of the two specimens has seven pairs of gill pouches. The tongue muscle overlies three or four gill pouches in the USNM specimen and five in the MCZ specimen. In each the aorta branches at the level of the seventh gill pouch.

It is our belief that when more specimens become available it may be necessary to establish this form as a separate species. Until then it is convenient merely to indicate its relationship to *E. multidens*.

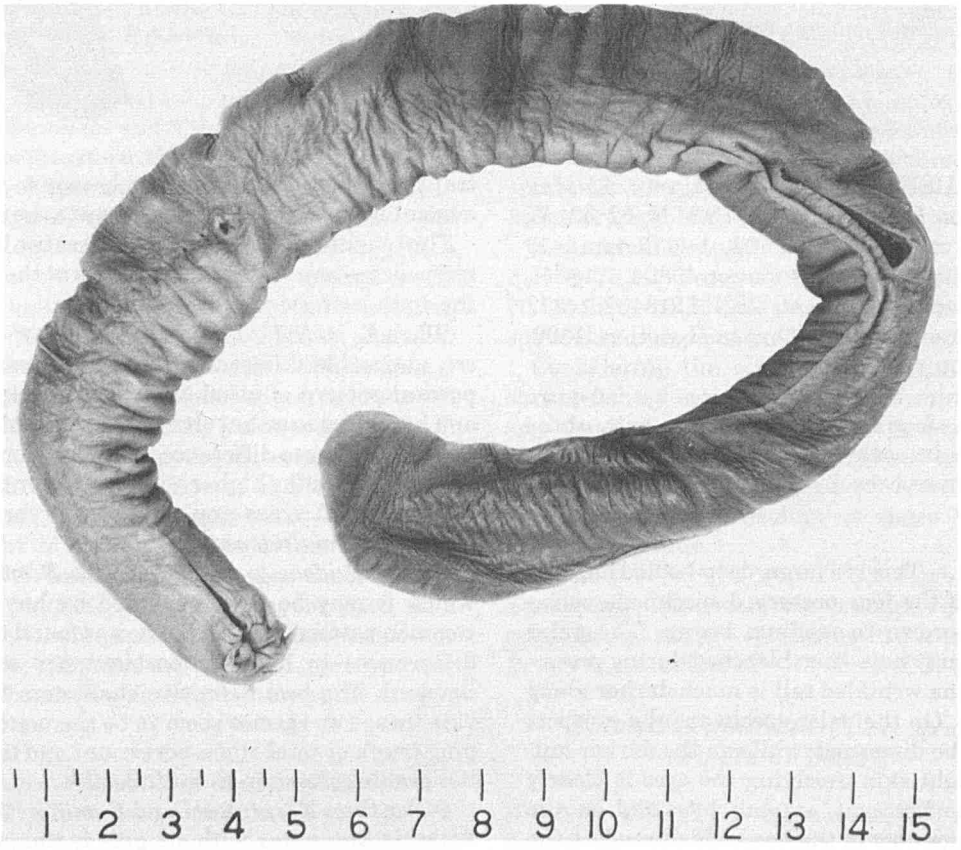


FIGURE 9.—*Eptatretus multidens*? (MCZ 40409). Scale in centimeters.

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OBSERVATIONS ON DISTRIBUTION AND LIFE HISTORY OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, IN AUSTRALIAN WATERS

MAURICE BLACKBURN[1] AND D. L. SERVENTY[2]

ABSTRACT

Skipjack tuna occur in many areas around Australia, but have been little fished or investigated there because of low commercial demand. Their distribution in Australian coastal waters is not continuous, although suitable temperatures occur in all areas. Abundance in coastal waters is probably highest in the southeast. The southern limit of skipjack tuna range varies seasonally with the 15° C surface isotherm, and that temperature appears to be limiting. Length-frequency polygons for skipjack tuna of southeastern Australia show modes at about 37, 46, 53, and 59 cm fork length in the southern summer. The regression of weight W (grams) upon length L (millimeters) for east coast skipjack tuna is $W = 0.000000839\ L^{3.5202}$. Gonads of coastal skipjack tuna are all immature. The euphausiid *Nyctiphanes australis* is the principal food in east Australian waters south of latitude 34° S. Small fish such as clupeoids are eaten in some of those areas and are the principal food elsewhere.

The skipjack tuna, *Katsuwonus pelamis* (Linnaeus), occurs in tropical and warm temperate waters of all oceans. It supports large fisheries in many areas and is considered to have much potential for further exploitation (Gulland 1971). The scientific literature on the species is large (Klawe and Miyake 1967) and growing. Australian contributions to that literature have been few, although the organized collection of data on Australian skipjack tuna began in 1938. One reason is that the Australian tuna industry has shown little interest in skipjack tuna. It operates principally upon southern bluefin tuna, *Thunnus maccoyii*.

The purpose of this paper is to present unpublished biological information on skipjack tuna in Australian waters and relate it to what has been published from the region. Many of the observations were made by us. We do not discuss fishing operations or prospects, except to note briefly here that skipjack tuna have been caught in Australian coastal waters by live-bait fishing, purse seining, mesh netting, and trolling. Most of those catches were incidental to fishing for southern bluefin tuna. In the year 1974-75 the Australian tuna catch was 11,288 t, of which 2,375 t was skipjack tuna and the rest southern bluefin tuna (Anonymous 1975, 1976). It is our opinion, admittedly subjective, that the biomass of skipjack tuna in Australian coastal waters is at least as high as that of southern bluefin tuna. It was much higher than the biomass of southern bluefin tuna off eastern Tasmania in 1965, according to estimates from aerial surveys (Hynd and Robins 1967).

One of us originally proposed the name "striped tuna" for this species in Australia, instead of "skipjack" which is the usual English vernacular elsewhere (Serventy 1941). The intention was to avoid confusion with another pelagic fish which is sometimes called "skipjack" in Australia, namely *Pomatomus saltator*. "Striped tuna" has not gained acceptance as an English vernacular outside Australia, however, and both names are now used in Australia. Therefore we now refer to *Katsuwonus pelamis* as skipjack.

METHODS

Our summaries of biological data are based on skipjack tuna taken from 1938 to 1965. All were obtained by hook fishing at the sea surface, except for some Victorian samples which may have been caught near the surface in nets. Thus our biological observations essentially refer to surface fish. The same applies to other specimens mentioned in literature cited, except those noted to be from Japanese longliners.

Length was measured from the tip of the snout to the caudal fin fork (FL), sometimes in millime-

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ters and sometimes to the nearest centimeter. Other authors whom we quote measured in the same way. Weight of fish was measured ungutted, usually at sea, in pounds and ounces. These weights were converted to grams and rounded to the nearest 50 g. Gonads were weighed fresh to the nearest gram, usually at sea.

Statements about mean positions of isotherms are based on charts by Vaux (1970) and Gorshkov (1974).

SPATIAL DISTRIBUTION

Skipjack tuna have an extensive distribution in the Australian region (Figure 1), but prior to 1938 they had been recorded only off New South Wales. It is now known that they have a continuous range in east Australian coastal waters from Lady Elliott Island to Storm Bay, although the limits may vary seasonally as discussed later. The RV *Warreen* and RV *Stanley Fowler* of the Commonwealth Scientific and Industrial Research Organization (CSIRO) established this distribution from trolling surveys between 1938 and 1951. Most specimens were taken on the continental shelf, many of them close inshore.

East coast inshore waters north of Lady Elliott Island lie within the Great Barrier Reef. Skipjack tuna are unknown there, although most of the area is well fished by sports and commercial fishermen (Marshall 1964; Hynd 1968). The *Warreen* and *Stanley Fowler* prospected by trolling in northern Australian waters from July to October 1949, traversing much of the coast from Torres Strait to Broome. Skipjack tuna were found on banks near the edge of the Australian continental shelf to the south of Timor, but nowhere else, and no other records exist from northern coastal waters. Thus the distribution appears to be quite limited in coastal waters around northeast and northern Australia (Figure 1). This is not true of the adjacent oceanic waters, however. Japanese longline vessels began to fish for tuna in the area of Figure 1 about 1950. They did not seek skipjack tuna but took them incidentally. Figure 1 shows the general areas in which those vessels took any skipjack tuna in the years 1964-67, as established by Matsumoto (1975). Evidently skipjack tuna occur to some extent almost everywhere in ocean waters east, north, and west of the Australian mainland and New Guinea. Skipjack tuna were first recorded in Papua New Guinea waters between 1948 and 1950 by the Australian RV *Fairwind*, in localities shown in Figure 1 (Munro 1958). Japanese longlining began there at about the same time. About 1969 vessels of the Japanese live-bait fishery began taking skipjack tuna north and northeast of New Guinea, and a similar fishery was later established by nationals of Papua New Guinea within the same area (Kasahara 1977; Lewis and Smith 1977). Figure 1 shows the general area of the Japanese live-bait fishery in 1973, as reported by Kasahara (1977).

Skipjack tuna were first recorded off the west coast of Australia in 1945. By 1951 an apparently continuous range from Onslow to Albany had been established, mostly by trolling surveys of the *Warreen*. Later surveys, made by the Department of Fisheries and Wildlife of Western Australia, extended this range to Broome (Robins 1975). Skipjack tuna in Western Australia appear to be less abundant than in southeastern Australia, at least on the continental shelf. Most were taken on the outer part of the shelf or just beyond the shelf edge.

On the southern coast of Australia east of Albany, skipjack tuna were first found by the CSIRO RV *Derwent Hunter* in 1953, near the edge of the shelf in the eastern part of the Great Australian Bight. Soviet workers extended the known range to the western part of the Bight, again in waters near the shelf edge (Shuntov 1969). In 1978 the CSIRO RV *Courageous* found skipjack tuna between the western end of the Bight and Albany (Maxwell[3]). East of the Bight, skipjack tuna have been taken by South Australian tuna fishermen almost to Kangaroo Island, from the shelf edge to near the coast (Olsen[4]; Williams[5]). Thus there is probably a continuous distribution along the southern coast of Australia to Kangaroo Island (Figure 1).

We know of no certain skipjack tuna occurrences between Kangaroo Island and Australian east coast waters. The most westerly of the east coast records are Lakes Entrance in eastern Victoria, the mouth of the Tamar River in northeast Tasmania (Scott 1975) and Storm Bay in southeast Tasmania (Figure 1). The apparent gap in skipjack tuna distribution to the west of those places is not readily explained. The skipjack tuna food or-

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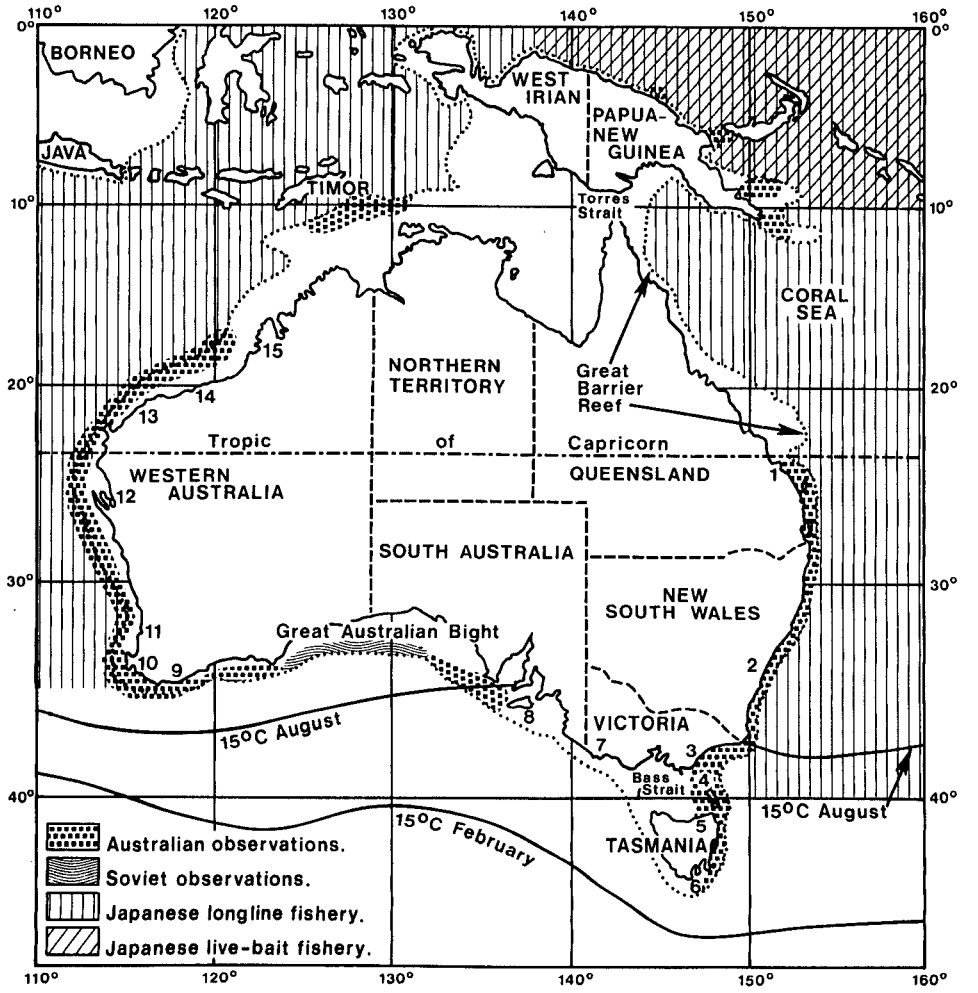

FIGURE 1.—Australia and vicinity, showing areas of skipjack investigations and fisheries, edge of continental shelf (dotted line), mean February and August positions of the 15° C surface isotherm, and the following localities mentioned in the text: 1—Lady Elliott Island, 2—Sydney, 3—Lakes Entrance, 4—Furneaux Group, 5—Tamar River, 6—Storm Bay, 7—Portland, 8—Kangaroo Island, 9—Albany, 10—Cape Leeuwin, 11—Fremantle, 12—Shark Bay, 13—Onslow, 14—Port Hedland, 15—Broome.

ganism *Nyctiphanes australis*, mentioned later, is abundant. Skipjack tuna can tolerate temperatures down to 15° C as shown below, and all waters in the area of no skipjack records have mean surface temperatures over 15° C in some months in most years. Aerial sightings of presumed skipjack tuna have been made near Portland and off western Tasmania (Williams footnote 5). Nevertheless, we think the gap is real, at least in central and western Bass Strait. We and our colleagues have done much trolling in those areas in various seasons and years without catching any skipjack tuna. Southern bluefin tuna are likewise absent or very rare in central and western Bass Strait, although quite plentiful east and west of that region (Serventy 1956). Hynd and Robins (1967) showed that surface temperatures in the western approaches to Bass Strait are under 15° C in parts of the summer because of upwelling, and perhaps as cold as that all summer in some years. This might restrict the distribution of skipjack tuna in waters east of Kangaroo Island. Hynd and Robins (1967) discussed the possibility of a similar effect upon southern bluefin tuna. Another possibility is that Bass Strait is too turbid for skipjack tuna, since it is shallow, receives several rivers, and is well mixed by waves and tides. Very little is known about effects of turbidity on tunas, however.

SEASONAL DISTRIBUTION

The range of skipjack tuna in eastern coastal waters is subject to seasonal variation. Table 1 shows where specimens have been taken in those waters in each month, in investigations made by or in cooperation with CSIRO, with data of all years combined. The southern limit of the range is farthest south in February-March and farthest north in July-August, and this variation is explicable. All positions of the limit lie in the well-surveyed waters south of Sydney (approximately lat. 34° S), and they generally agree with positions of limiting sea surface isotherms as was shown by Robins (1952). Figure 1 shows the mean February and August positions of the 15° C surface isotherm, the one closest to the lowest temperature at which any skipjack tuna have been caught (14.7° C, by Robins). The isotherm positions agree fairly well with the observed limits of skipjack tuna range in the same months, considering that no observations were made south of lat. 44° S. The lower limiting temperature for skipjack in abundance is about 16° C according to Robins (1952). The mean positions of that surface isotherm (about 2° of latitude north of the 15° C surface isotherm in each month) agree almost exactly with the skipjack tuna range limits in Table 1. From 1938 to 1942 skipjack tuna were hardly ever found south of lat. 43° S and seldom found south of lat. 42° S. They were fairly numerous between lat. 43° and 44° S in 1951, when temperatures were unusually high (Robins 1952). Hynd and Robins (1967) reported aerial sightings of a few schools of presumed skipjack tuna off the southern tip of Tasmania where surface temperatures were probably about 13° C. Neither the species nor the temperature was confirmed, however.

TABLE 1.—Records of captured skipjack tuna (X) and sightings of skipjack tuna (S) in Australian east coast waters by months. Sources are Robins (1952), Hynd (1968), and unpublished data from the Commonwealth Scientific and Industrial Research Organization for the period 1938-78. Waters between lat. 33° and 24° S were completely covered only in May, July, and September, and not covered at all in November and December. Waters between lat. 33° and 44° S were completely covered in all months.

Lat. S	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
24°-25°		X	S			X						
25°-26°										S		
26°-27°												
27°-28°					X		S					
28°-29°												
29°-30°					X			X				
30°-31°	X			X				X	X	X		
31°-32°				X	X	X			X	X		
32°-33°		X	X	X		X	X	X	X	X		
33°-34°	X	X		X		X	X	X	X	X	X	
34°-35°	X	X	X	X	X	X	X	X	X	X	X	X
35°-36°	X	X	X	X	X		X	X	X	X	X	X
36°-37°	X	X	X	X	X				X	X	X	X
37°-38°	X	X	X	X	X	X					X	X
38°-39°					X	X						
39°-40°	X	X	X	X	X							X
40°-41°		X	X	X	X							
41°-42°		X	X	X	X							
42°-43°		X	X	X	X							
43°-44°		X	X									

It is difficult to recognize or hypothesize any seasonal change in the northern limit of skipjack tuna range in eastern coastal waters, especially in view of the incomplete vessel coverage north of Sydney (Table 1). The northern limit of any occurrence (excluding offshore data from Japanese longliners) is between lat. 24° and 25° S, and skipjack tuna were found there in February and June. If data from sightings are accepted there is evidence of skipjack tuna between lat. 24° and 26° S in various months from February to October. It would not be surprising if skipjack tuna occurred in those waters to some extent in all months. Mean monthly surface temperatures are maximal between 27° and 28° C, whereas skipjack tuna can tolerate 30° to 32° C (Williams 1970; Dizon et al. 1977).

The occurrence of skipjack tuna at temperatures down to 15° C is of special interest, because the species has not been found in such cool waters in other parts of the world. It has been recorded at temperatures down to 17° C in the eastern Pacific (Williams 1970) and 18° C near Japan (Uda 1957). Dizon et al. (1977) exposed four captive Hawaiian skipjack tuna to gradually decreasing water temperatures with the following results. Three fish stopped feeding at 17° C and died at 16° C; corresponding temperatures for the fourth fish were 15° and 14° C.

On the other hand, the northern limit of the range of skipjack tuna in abundance could be south of the limit of total range and could vary with season, as Robins (1952) claimed. He put the northern limit of the main area of occurrence at about lat. 30° S in August-September and lat. 38° S in February, corresponding to the positions of the 19° C surface isotherm in those months. Robins considered that temperatures about 19° C were limiting for the main occurrence of skipjack tuna, 18° C limiting for occurrence in abundance, and 20.5° C limiting for any occurrence, at the warm end of the distribution along the east coast. The

data in Table 1 are insufficient to support or deny Robins' conclusions as far as the actual skipjack tuna distribution is concerned. We note however that skipjack tuna are often abundant in other parts of the world at temperatures much above those mentioned (Blackburn 1965; Williams 1970). They have been found plentifully at 24° C off New South Wales (Williams footnote 5). Of course, abundance may reflect other conditions, as well as the distributions of temperature most suitable for adults. The occurrence of skipjack tuna in coastal waters north of Sydney, and its possible connections with offshore distributions to the east and northeast, should be further investigated.

Our knowledge of seasonal distribution in other coastal waters of Australia is incomplete. Off Western Australia skipjack tuna have been taken as follows, including records by Robins (1975): Broome to Port Hedland, July, August, and October; Port Hedland to Shark Bay, January, April-June, August, September, and November; Shark Bay to Cape Leeuwin, February, March, and June-August; off Albany, May-July. Our records for the area south of Timor are for September and October. Australian and Soviet records between Albany and Kangaroo Island are all for the period December-May. All the areas just mentioned and others in northern Australia where no skipjack tuna have been found are warm enough for some skipjack tuna to occur all year (i.e., over 15° C at the sea surface, Figure 1).

In the Japanese longline fishing area east of Queensland there may be some seasonal change in abundance of skipjack (Matsumoto 1975), but the pattern is not clear. In the similar area west of Western Australia the abundance appears to be low at all seasons. In surface waters of Papua New Guinea, according to Lewis and Smith (1977), there is no obvious seasonal change.

LENGTH AND WEIGHT

Length measurements of about 4,500 east coast skipjack tuna were made in CSIRO investigations to the end of 1965. The observed range was 30-65 cm FL north of Sydney, 35-66 cm FL in mainland waters south of Sydney, and 35-66 cm FL off Tasmania. We have no length data for Great Australian Bight or South Australian fish except those of Shuntov (1969), which were 48-52 cm FL. Larger skipjack tuna to about 80 cm have been taken off New South Wales and South Australia in recent years (Williams footnote 5). Robins (1975) measured about 300 skipjack tuna from Western Australia, which were 29-78 cm FL. Our earlier measurements from the same area fall in that range. For Papua New Guinea a range of 35-62 cm FL was reported by Kearney et al. (1972). All these skipjack tuna were taken very near the sea surface. Barkley et al. (1978) hypothesized that large skipjack tuna require lower temperatures than small skipjack tuna and are therefore more abundant in the upper thermocline than at the sea surface, in the tropical Pacific.

Figure 2 summarizes most of the east coast data in length-frequency polygons for various periods. Most of these sets of measurements are rather small in number, even when combined for certain months and years as in some of the polygons. Data for the Southern Hemisphere winter (polygons A, H, and M) show modes at about 34, 44, and 51 cm. Polygons for the southern summer (C, E, F, G, and J) have modes at about 37, 46, 53, and 59 cm. The first three modes for the summer are close to the three for the winter and are shown as I, II, and III, respectively, for each season. Modes at similar sizes in other polygons are labelled in the same way. This labelling does not imply that the modes represent successive age-groups a year apart, or that the absolute age is known for any mode, because such conclusions could not be drawn with confidence from these scattered data. If the modes do represent successive age-groups, the mean growth rate of east coast skipjack tuna must be about 6-10 cm/yr for fish between 35 and 60 cm. Most published estimates of skipjack tuna growth rate in that range of length are higher, as discussed by Shomura (1966), Joseph and Calkins (1969), and Chi and Yang (1973) for Hawaii, Japan, the eastern Pacific, and Taiwan. The range of annual growth increment in those studies was 11-27 cm, with many values near 15 cm, and some of those estimates were obtained from tagging. On the other hand, Batts (1972) estimated 8-9 cm/yr for skipjack tuna >40 cm from North Carolina, from annuli in cross sections of dorsal spines. Kearney[6] referred to an estimate of 7 cm/yr for Papua New Guinea skipjack tuna, based on tagging, but gave no details.

Skipjack tuna of modal group I were obtained only from 1938 to 1941 in east coast waters. They may have been particularly abundant then, or there may have been some difference in trolling

[6]Kearney, R. E. 1978. Some hypotheses on skipjack (*Katsuwonus pelamis*) in the Pacific Ocean. South Pac. Comm., Noumea, New Caledonia, Occas. Pap. 7, 23 p.

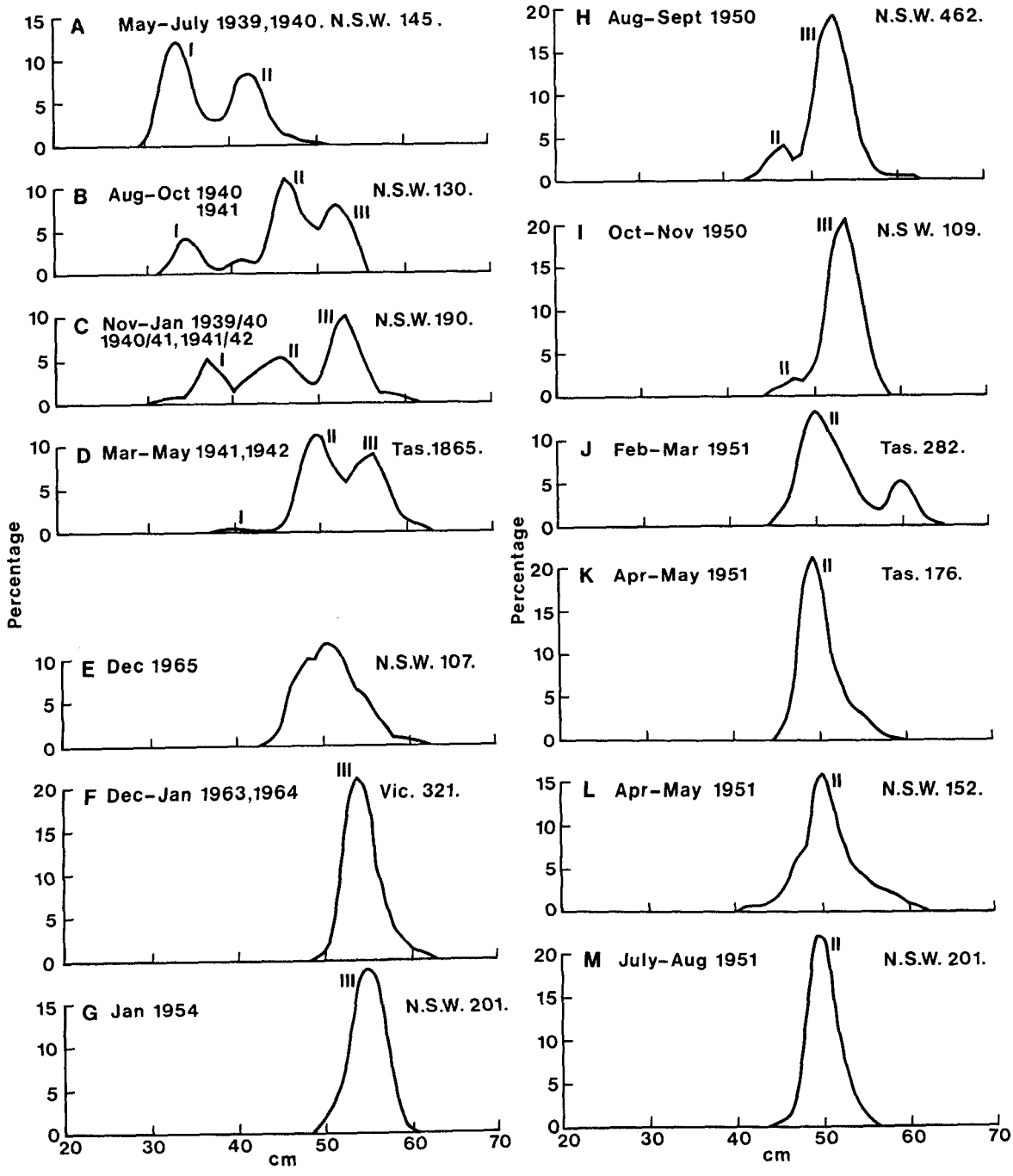

FIGURE 2.—Percentage fork length (centimeters) frequency polygons of skipjack from New South Wales (mostly south of Sydney), Victoria (Lakes Entrance), and Tasmania (Furneaux Group to Storm Bay). The data are smoothed by a moving average of three. The number of specimens is given after the locality abbreviation in each polygon. Polygons A to D, E to G, and H to M show data for 1939-42, 1954-65, and 1950-51, respectively. The order of the polygons in each of those groups is based on the month or months in which the data were taken. Roman numerals are for identification of modes, and do not necessarily indicate ages.

method (e.g., speed, lure type, lure size) between that period and later. Robins (1975) took similar fish in the period April-June off Western Australia, mostly by purse seining but occasionally by trolling.

Weight as well as length was measured for 607 east coast skipjack tuna. The following significant linear regression was found between the common logarithms of the variables:

$$\log W = -6.0762 + 3.5202 (\log L)$$

where W is weight (grams) and L is fork length (millimeters). The coefficient of determination, R^2, is 0.856. Standard errors of the first and second constants in the equation are 0.1595 and 0.0586, respectively. The equation is equivalent to:

$$W = 0.000000839\, L^{3.5202}.$$

The range of L in the data used is 410-645 mm. The heaviest fish weighed 5.67 kg.

The 95% confidence limits of the regression coefficient are 3.4048 and 3.6356, calculated from the standard error. Other published regressions of skipjack tuna weight on length for large samples (>200) indicate regression coefficients from 3.2164 to 3.67. Those samples were taken in the eastern, central, and northwestern Pacific (Nakamura and Uchiyama 1966, and references there) and off North Carolina (Batts 1972). Standard errors of the coefficients were not published in most cases. The standard error can be calculated from data of Hennemuth (1959), for a regression coefficient of weight on length for 1,280 skipjack tuna from the eastern Pacific (combined areas). The coefficient was 3.336, with 95% confidence limits 3.296 and 3.376. Thus the east Australian and eastern Pacific regressions are significantly different at the 5% level of probability. The meaning of this difference is not clear. The two groups of skipjack tuna probably belong to different populations (Fujino 1972; Sharp 1978). However, Hennemuth (1959) found regression coefficients from 3.144 to 3.555 in different areas of the eastern Pacific north of the Equator, a region considered to contain only one skipjack tuna population (Fujino 1972; Sharp 1978), and some of those coefficients were significantly different.

SEXUAL CONDITION

The gonads of 418 east coast skipjack tuna were weighed. Ovary weights ranged from 4 to 30 g. Most ovaries were white to pink. Discrete small ova were visible to the naked eye in some ovaries, but large yolked ova were not observed. Ovaries of a reddish flaccid appearance, which might have been spent, were seen occasionally from April to August in New South Wales and Tasmanian waters. Testes were small, weighing mostly 1-2 g with a maximum of 13 g. Milt could sometimes be expressed from them by pressing. Similar observations were made on a small number of skipjack tuna from the west and northwest coasts of Australia, except that no gonads were weighed. A specimen taken off Fremantle in July was possibly spent. No gonad data are available from South Australia.

Orange (1961) compared ovaries of skipjack and yellowfin tunas by means of a "gonad index" equal to

$$(\text{gonad weight}) / (\text{fish length}^3)\, 10^8$$

with gonad weight in grams and fish length (fork length) in millimeters. This is a ratio between gonad weight and an estimate of fish weight. The estimate is not accurate for skipjack tuna, since weight increases with fork length to some power slightly higher than 3 in that species, as noted earlier. However Orange also compared gonad indices with the appearance of the ovaries and ova, and found that only indices over 30 indicated approaching sexual maturity in skipjack tuna. Naganuma (1979) made similar comparisons which indicated that spawning skipjack tuna have gonad indices of 80 or higher, measured on Orange's scale. Thus calibrated, the index has some utility, and it has been employed by other skipjack tuna investigators. None of the gonad indices in our east Australian material reached 30 (Table 2); only 2, out of 224, were slightly over 20. Thus no females appeared to be mature on the basis of gonad index, confirming the observations on the gonads themselves. Yet virtually all these skipjack tuna were at or over the size at which first sexual maturity has been found in other Pacific waters, i.e., about 45 cm (Kearney et al. 1972; Blackburn and Williams 1975; Naganuma 1979).

It is clear from these observations that skipjack tuna do not spawn to any significant extent in east Australian coastal waters, and there is no evidence that they spawn in any Australian coastal waters; nevertheless, they do spawn in the

TABLE 2.—Length range, sex ratio, and female gonad indices (see text) for three groups of Australian east coast skipjack tuna.

Area	Period	Fork length (cm)	Sex ratio (F/M)	Gonad index	
				Range	Mean
New South Wales, south of Sydney	Nov.-Dec. 1941	44-57	47/30	5.6-20.7	12.3
Tasmania	Mar.-May 1942	47-61	166/154	3.4-17.8	10.1
New South Wales, north of Sydney, and southern Queensland	June 1941, 1942	51-65	11/10	8.6-21.5	10.7

offshore tropical waters. Ueyanagi (1970) showed that skipjack tuna larvae occur between November and February in the Coral Sea east of tropical Queensland, north and east of New Guinea, and in ocean waters west of northwest Australia. From May to August the larvae are scarcer in Coral Sea and New Guinea waters than in the preceding period, and possibly so off northwest Australia. Gonad indices are higher in Coral Sea and New Guinea waters in the southern summer than in winter (Naganuma 1979). Thus the skipjack tuna spawning season in waters near Australia is probably the southern summer, and the principal spawning areas seem to be in offshore waters northeast and northwest of the continent.

FOOD

Observations were made on stomach contents of 660 skipjack tuna from east coast waters and 30 from west and northwest coast waters (Table 3). Euphausiids were mostly *Nyctiphanes australis* although *Thysanoessa gregaria* was occasionally observed. Also included with euphausiids were several stomachs which contained a red liquid. This liquid was often found together with euphausiids, never with any other food, and was certainly a product of the digestion of euphausiids.

The main point of interest in Table 3 is the proportion of stomachs with euphausiids. Evidently euphausiids are almost the sole food of skipjack tuna in Tasmania and the principal food in southern New South Wales, but a small component of diet in the other sampled areas. Small pelagic fish are a large food item in all areas except Tasmania. Cephalopods are a minor item in all areas. Table 3 does not include data on east coast skipjack tuna from Robins (1952) because they are nonquantitative, but his findings were similar, as follows. Euphausiids were the principal food in Tasmania and New South Wales waters south of Sydney. North of Sydney the principal food was fish, especially the young of pilchard, *Sardinops neopilchardus*, and anchovy, *Engraulis australis*. Park and Williams[7] found the following in stomachs of skipjack tuna taken near Sydney: fish larvae, mainly pilchard; *N. australis*; brachyuran and decapod larvae; copepods; and squid.

These changes in diet by area appear to reflect the kinds of small nekton and large zooplankton that are available to skipjack tuna in coastal waters. *Nyctiphanes australis* is the principal coastal euphausiid in the southeast Australian region. Its range along the east coast is from lat. 31° S to the southern end of Tasmania (Sheard 1953). It is abundant off Victoria and Tasmania (including all of Bass Strait) and also off southern New South Wales, but not common in waters north of Sydney (Blackburn 1980). The species is unrecorded off Western Australia, although it occurs in South Australian waters. Off eastern Tas-

[7]Park, J. S., and K. Williams. 1977. A study of the relationship between the composition of food organisms of skipjack tuna *Katsuwonus pelamis* and the abundance and species composition of the plankton in the waters adjacent to Cronulla, New South Wales, Australia. Unpubl. manuscr. Commonwealth Scientific and Industrial Research Organization, Division of Fisheries and Oceanography, Cronulla, 2230, Aust.

TABLE 3.—Foods of skipjack tuna collected in Australian coastal waters, by numbers of stomachs in which they occurred. Nil means empty stomachs.

Area	Nil	Euphausiids	Fish remains	Pilchard[1]	Mackerel[2]	Other fish	Squid	Mixed	Other[3]	Total
New South Wales, north of Sydney	16	1	7	12	1		1		6	44
New South Wales, Sydney and south	104	[4]77	10	2	4	[5]1	1	[6]5		204
Tasmania	82	322	1					[7]1	6	412
Western and northwestern Australia	14		6			[8]3	1	[9]6		30

[1]*Sardinops neopilchardus*.
[2]*Scomber australasicus*.
[3]Yellow liquid, except for two stomachs from Tasmania which contained salps.
[4]Including three stomachs which also contained hyperiid amphipods.
[5]Bellows fish (Macrorhamphosidae).
[6]Euphausiids plus fish or squid. Fish included *Scomberesox forsteri*, *Trachurus* sp. and Macrorhamphosidae.
[7]Euphausiids plus squid.
[8]Flying fish (Exocoetidae), juvenile *Gonorhynchus greyi*, *Harengula* sp. and anchovy (probably *Engraulis australis*).
[9]Fish plus crustaceans or cephalopods or pteropods. Fish included Myctophidae. Cephalopods included squid and paper nautilus.

mania, where skipjack tuna occur only in summer and autumn, *N. australis* is probably the only abundant food organism available to them. Pilchards are not common in that area (Blackburn 1950b). Mackerel, *Scomber australasicus*, have been recorded from Tasmania, but were not found there by us and are probably rare. Anchovies are common in Tasmania, but their occurrence in summer and autumn is mostly in inlets which skipjack tuna do not enter (Blackburn 1950a). Jack mackerel, *Trachurus declivis*, are also abundant, but mostly occur closer inshore than skipjack tuna (Hynd and Robins 1967).

DISCUSSION

The need for further information of various kinds on Australian skipjack tuna has been shown. It would be particularly interesting to know if the apparent discontinuities in distribution are real, and if so, what causes them. The probable determinants of skipjack tuna distribution in surface waters are temperature, food, and turbidity (Blackburn 1965, 1969). Dissolved oxygen concentration can be an additional limiting environmental property in the vertical plane, since skipjack tuna are stressed at concentrations below about 2.8 ml/l (Dizon 1977; Sharp 1978). Concentrations at 100 m in waters near Australia are higher than 3.0 ml/l, however, except in an area off the west coast of West Irian (Reid et al. 1978). Temperatures required by skipjack tuna larvae may be higher than those preferred by adults, causing spawning adults to seek warmer waters than those not spawning (Blackburn and Williams 1975). It has been shown that all surface waters around Australia are warm enough (>15° C) for adult skipjack tuna in the warm season, and most waters warm enough at all seasons. The absence or rarity of skipjack tuna in some of those areas probably indicates that suitable food organisms are scarce, that the waters are too turbid for the fish to find food, or that the vertical distribution of temperature is not such as to force the fish to the surface.

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A METHOD FOR GROWTH CURVE COMPARISONS

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ABSTRACT

Suppose one has a sample of pairs of age and length measurements from each of two or more populations of fish. The mathematical forms of the growth curves associated with the populations are assumed to be specified but each form contains at least one unknown parameter. Presented in this paper is a data analytic approach to the problem of deciding which, if any, of the populations have essentially the same growth curve and which have different ones.

A common problem in fisheries research is that of comparing two or more growth curves. This problem arises whenever investigators gather data for the purpose of trying to determine whether or not different species or the sexes of a given species of fish grow at different rates, or for the purpose of assessing growth variation of a species from environment to environment, area to area, or stratum to stratum in which it is found.

Since the models generally used for the age-length relationships (e.g., von Bertalanffy, Laird-Gompertz, logistic, etc.) are most often nonlinear in the unknown parameters and cannot be linearized by transformations of the variates, the usual techniques for comparing regression equations are not applicable. Up to this point little has been done in the way of development of quantitative methods for determining whether or not unknown growth curves do in fact differ. Thus the investigator can often do little more than visually examine plots of age-length data for samples from the various populations being compared and arrive at some rather subjective conclusions.

An exception is a paper by Allen (1976) which treats the special case where each of the growth curves being compared belongs to the von Bertalanffy family. There are, of course, numerous instances where the von Bertalanffy model is not appropriate and the Allen procedure does not apply if it is not. Further, even if this model is appropriate, some severe assumptions need to be made in order to apply the analysis. These include: 1) the equality of the scale parameters for all curves being compared, 2) the true value of the common scale parameter being exactly equal to its estimated value, and 3) the usual normality, independence, and equality of variance assumptions for the error term. The first assumption quite clearly biases the procedure in favor of the null hypothesis of equality of the growth curves, while validity of the second seems to be too much to hope for.

Gallucci and Quinn (1979) also discuss the growth curve comparison problem for the von Bertalanffy case. They essentially reparameterize the model and test the hypothesis of equality of one of the new parameters for all curves being compared, assuming, apparently, that the other two have the same value for all of the curves. The comments in the preceding paragraph also apply to these authors' work.

The purpose of this paper is to point out how some predictive sample reuse techniques, described in a recent paper by Geisser and Eddy (1979), can be adapted and applied to a growth curve comparison problem where two or more populations are being studied, the growth curves associated with each of the populations are unknown and are to be compared, and a sample of age-length data is available from each population. The problem then is to use the data to decide which, if any, of the population growth curves are the same and which are different.

We will assume that the growth curves associated with each of the populations are specified except for the values of unknown parameters. These specifications often would be made by plotting the sets of age-length data, fitting various possible models suggested by the data plots, and selecting the models which best fit the data. The growth curves can, but need not, belong to the von Bertalanffy family. In fact, they can belong to any family. Thus, in essence, we are

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considering a much more general and widely applicable problem than that discussed by Allen (1976) and by Gallucci and Quinn (1979). For the technique presented here, the only assumption that is made is that the forms of the population growth curves can be specified. No parameters are assumed to be known or equal, and no distributional assumptions are made.

The solution, described in the following sections, of our growth curve comparison problem is not obtained via a classical statistical hypothesis testing approach. That is, we do not formulate an appropriate null hypothesis and derive a criterion which dictates when and only when it should be rejected. Instead, in the spirit of Geisser and Eddy (1979), we formulate various possible models and give a data analytic approach to selecting the one model preferred by the data.

A difficulty, which plagues classical hypothesis testing, does not exist for the approach described here. It is the necessity of specifying a significance level. Historically, significance levels such as 0.10, 0.05, and 0.01 have routinely been used for tests without objective justification. Yet the choice of a significance level affects the conclusions arrived at. For example, it is quite possible to find that a hypothesis can be rejected at the 0.05 level, but not at the 0.01 level. Further, the choice of a significance level affects the probability of rejecting a false hypothesis. Lowering the significance level usually lowers the probability of rejecting a false hypothesis. Requiring one to specify a significance level presumes that one has a sound basis for controlling the probability of rejecting one of two possible hypotheses when it is true, that one can objectively assign a significance level which controls this probability, and that controlling this probability is more crucial than controlling the probability of not rejecting the hypothesis when it is false. The contention here is that for many, if not most, scientific investigations, the consequences of rejecting one hypothesis when it is true are no more serious than rejecting the other when it is true. That is, often an investigator has no reason to favor either hypothesis, but merely wants to know which one is more reasonable, given the data that has been collected.

THE TWO POPULATIONS CASE

Suppose that two populations of fish are being studied. For example, the first population might consist of all fish of a given species inhabiting one area while the second might consist of all fish of this species inhabiting a different area. Suppose we are interested in comparing the growth curves associated with the two populations.

We consider two possible models, say M_1 and M_2. The model M_1 specifies that the growth curves are the same, while under M_2 the two growth curves differ.

Let x and y represent, respectively, the age and length of a fish. Then we rewrite M_1 and M_2 as

M_1: $y = f(x;\theta) + \epsilon$ (1)
no matter which of the two populations fish belongs to.

M_2: $y = f_1(x;\theta_1) + \epsilon$ (2)
if the fish belongs to the first population.

$y = f_2(x;\theta_2) + \epsilon$ (3)
if the fish belongs to the second population.

Here $f(x;\ \theta)$, $f_1(x;\ \theta_1)$, and $f_2(x;\ \theta_2)$ are each functions of x. θ, θ_1, and θ_2 are each vectors of unknown parameters and f, f_1, and f_2 are specified except for the values of elements of θ, θ_1, and θ_2. Essentially, f, f_1, and f_2 represent three different growth curves which are specified except for the values of unknown parameters present in each. The function f represents the expected length of a fish whose age is x, assuming equal growth curves for the two populations, while f_1 and f_2 are, respectively, the expected lengths for fish of age x from the first and second populations, assuming the growth curves differ. As usual, ϵ represents the unknown, random error term.

We now give a data analytic approach for selecting one of the two possible models M_1 or M_2. The data used to make the selection are pairs of age-length measurements for samples of fish from each of the two populations.

Let (x_{11}, y_{11}), $(x_{12}, y_{12}),\ldots,(x_{1n}, y_{1n})$ represent a sample of n pairs of observations of x and y from the first population and (x_{21}, y_{21}), $(x_{22}, y_{22}),\ldots,$ (x_{2m}, y_{2m}) represent a sample of m pairs of observations of x and y from the second population. These $n + m$ pairs of observations are the data gathered by the investigator and we want to use these data to select either M_1 or M_2.

Assume, for the moment, that M_2 is correct. For $j = 1, 2,\ldots,n$, let $\hat{\theta}_{1(j)}$ represent the vector of

(least squares, say) estimates of the elements of θ_1 found by taking the relationship between x and y to be given by Equation (2) and using the data $(x_{11}, y_{11}), (x_{12}, y_{12}),\ldots,(x_{1(j-1)}, y_{1(j-1)}), (x_{1(j+1)}, y_{1(j+1)}),\ldots,(x_{1n}, y_{1n})$, that is, all of the n pairs of observations of x and y from the first population except for the jth pair. Set

$$D_{21} = \sum_{j=1}^{n} [y_{1j} - f_1(x_{1j}; \hat{\theta}_{1(j)})]^2.$$

Note that the second term inside the brackets is the predicted length for the jth fish in the sample from the first population, assuming M_2 is correct. The observed length of this fish is the first term inside the brackets. Thus D_{21} is the sum of the squares of the differences between the observed and predicted fish lengths for the fish in the first population sample, for model M_2.

Similarly, for $j = 1, 2,\ldots,m$, let $\hat{\theta}_{2(j)}$ represent the vector of (least squares, say) estimates of the elements of θ_2 found by taking the relationship between x and y to be given by Equation (3) and using the data $(x_{21}, y_{21}), (x_{22}, y_{22}),\ldots,(x_{2(j-1)}, y_{2(j-1)}), (x_{2(j+1)}, y_{2(j+1)}),\ldots,(x_{2m}, y_{2m})$, i.e., all of the m pairs of observations of x and y from the second population except for the jth pair. Set

$$D_{22} = \sum_{j=1}^{n} [y_{2j} - f_2(x_{2j}; \hat{\theta}_{2(j)})]^2$$

and $D_2 = D_{21} + D_{22}$.

The quantity D_{22} has an interpretation similar to that given to D_{21}. Putting these two together, we see that D_2 represents the sum of the squares of the differences between the observed fish lengths and the predicted fish lengths for all $n + m$ fish in the samples, under model M_2.

Next, assume that M_1 is correct, pool the data, and consider the $n + m$ pairs $(x_{11}, y_{11}), (x_{12}, y_{12}),\ldots, (x_{1n}, y_{1n}), (x_{21}, y_{21}), (x_{22}, y_{22}),\ldots, (x_{2m}, y_{2m})$. Let (x_j, y_j) represent the jth of these $n + m$ pairs, for $j = 1,\ldots,n + m$. Further, for $j = 1, 2,\ldots, n + m$, let $\hat{\theta}_{(j)}$, represent the vector of (least squares, say) estimates of the elements of θ obtained by taking the relationship between x and y to be given by Equation (1) and using the data $(x_1,y_1), (x_2,y_2),\ldots,(x_{j-1},y_{j-1}), (x_{j+1},y_{j+1}),\ldots, (x_{n+m}, y_{n+m})$, that is, all $n + m$ pairs of observations of x and y from the first and second populations except for the jth pair. The sum of the squares of the differences between the observed and predicted fish lengths for all $n + m$ fish in the samples, under M_1, is

$$D_1 = \sum_{j=1}^{n+m} [y_j - f(x_j; \hat{\theta}_{(j)})]^2.$$

Our rule for selecting either of M_1 or M_2 can be simply stated as follows. Select M_1 if $D_1 \leq D_2$, otherwise select M_2. This rule is a very natural and objective one. It is based on whether the data (i.e., the observed fish lengths) are better predicted by one growth curve or two. If the sum of squares of the differences between observed and predicted lengths under M_1 does not exceed the sum of squares of the differences between observed and predicted lengths under M_2 (i.e., $D_1 \leq D_2$), the data are better predicted by one growth curve than by two and M_1 should be selected. Otherwise, they are better predicted by two distinct growth curves and M_2 should be selected.

AN EXAMPLE

To illustrate the procedure described in the previous section, we consider an example. The numbers given in the first two columns of Table 1 are the ages and corresponding lengths of 15 fish taken from the first of two populations, while the numbers in the first two columns of Table 2 are the ages and corresponding lengths of 14 fish taken from the second population. These data are hypothetical. In fact they were generated by a computer.

We want to use these two sets of data to decide which of two models, M_1 or M_2, is preferred, where under M_1 the growth curves for the two populations are the same, and under M_2 the two populations have different growth curves.

Among several growth curves, including the von Bertalanffy, Laird-Gompertz, and logistic ones, the best fit, for both data sets as well as the combined data set, was provided by the logistic. The average length of a fish whose age is x, for a logistic growth curve, is

$$f(x;a,b,c) = \frac{a}{1 + e^{-(bx + c)}} \qquad (4)$$

where a, b, and c are unknown parameters.

Thus, we take M_1 to specify that the average length of a fish whose age is x is Equation (4) no

TABLE 1.—Ages, lengths, parameter estimates, and predicted lengths, under models M_1 and M_2, for 15 Population I fish.

Age	Length	Least squares estimates of a_1, b_1, c_1 under M_2	Predicted length under M_2	Least squares estimates of a, b, c under M_1	Predicted length under M_1
1	4.0	55.27, 0.36, −2.70	4.9	55.67, 0.35, −2.62	5.2
2	8.3	54.76, 0.38, −2.80	6.2	55.44, 0.36, −2.66	6.9
3	5.6	55.86, 0.34, −2.56	9.9	55.91, 0.34, −2.56	10.0
5	16.0	55.11, 0.37, −2.73	15.9	55.57, 0.35, −2.63	16.5
6	20.9	55.13, 0.37, −2.74	20.3	55.56, 0.35, −2.64	20.8
7	27.7	55.40, 0.36, −2.77	24.8	55.70, 0.35, −2.65	25.4
8	31.9	55.43, 0.36, −2.73	29.9	55.70, 0.35, −2.64	30.4
9	32.9	54.62, 0.38, −2.76	35.7	55.28, 0.36, −2.65	35.6
10	40.2	55.24, 0.36, −2.71	39.4	55.62, 0.35, −2.63	39.5
11	39.9	54.88, 0.38, −2.81	44.0	55.37, 0.36, −2.67	43.7
12	45.6	55.15, 0.37, −2.74	46.4	55.56, 0.36, −2.64	46.4
13	49.6	54.96, 0.36, −2.72	48.6	55.51, 0.35, −2.63	48.7
14	53.0	54.32, 0.37, −2.71	50.0	55.26, 0.35, −2.63	50.4
16	54.2	54.23, 0.37, −2.74	52.2	55.27, 0.36, −2.64	52.8
17	51.5	56.97, 0.35, −2.68	54.8	56.25, 0.35, −2.62	54.2

TABLE 2.—Ages, lengths, parameter estimates, and predicted lengths, under models M_1 and M_2, for 14 Population II fish.

Age	Length	Least squares estimates of a_2, b_2, c_2 under M_2	Predicted length under M_2	Least squares estimates of a, b, c under M_1	Predicted length under M_1
1	6.5	55.65, 0.35, −2.60	5.3	55.43, 0.36, −2.66	5.0
2	6.4	56.09, 0.34, −2.52	7.7	55.62, 0.35, −2.62	7.1
3	8.0	56.24, 0.33, −2.48	10.4	55.69, 0.35, −2.60	9.7
4	14.1	55.74, 0.35, −2.60	12.9	55.47, 0.36, −2.66	12.5
5	17.6	55.84, 0.35, −2.59	16.8	55.53, 0.36, −2.66	16.3
6	21.8	55.90, 0.35, −2.58	21.1	55.58, 0.36, −2.65	20.7
8	31.4	56.05, 0.34, −2.56	30.6	55.65, 0.35, −2.64	30.4
9	34.4	55.48, 0.35, −2.59	35.9	55.46, 0.36, −2.64	35.4
11	43.0	55.78, 0.35, −2.57	43.5	55.54, 0.36, −2.64	43.3
13	49.1	55.83, 0.34, −2.56	48.8	55.54, 0.35, −2.63	48.7
14	50.4	55.92, 0.35, −2.57	50.7	55.58, 0.35, −2.64	50.6
15	52.3	55.78, 0.35, −2.56	52.0	55.50, 0.35, −2.64	52.0
16	54.3	55.25, 0.35, −2.57	52.7	55.24, 0.36, −2.64	52.8
17	53.0	56.53, 0.34, −2.55	54.4	55.78, 0.35, −2.63	53.9

matter which population it belongs to. On the other hand, we take M_2 to specify that the average length of a fish whose age is x is Equation (4) with a, b, and c replaced, respectively, by a_i, b_i, and c_i, if the fish belongs to population i, for $i = 1, 2$. Note that in the notation of the previous section θ is the vector whose elements are a, b, and c, while θ_i is the vector whose elements are a_i, b_i, and c_i, for $i = 1, 2$. Also $n = 15$ and $m = 14$, for this example.

The ith row, or threesome, for $i = 1,\ldots,15$, of the third column of Table 1 is the set of least squares estimates of a_1, b_1, and c_1 obtained by assuming M_2 to be correct and using all of the age-length data pairs in Table 1, except for the ith pair, to estimate a_1, b_1, and c_1. For example, when the data point (8, 31.9) is ignored, the least squares estimates of a_1, b_1, and c_1 are, respectively, 55.43, 0.36, and −2.73. The fourth column of Table 1 gives the predicted lengths for each of the first population fish, assuming M_2 is correct. That is, the ith element in this column is

$$\frac{\hat{a}_{1(i)}}{1 + e^{-(\hat{b}_{1(i)}x_i + \hat{c}_{1(i)})}} \tag{5}$$

where x_i is the ith element of the first column and $\hat{a}_{1(i)}$, $\hat{b}_{1(i)}$, and $\hat{c}_{1(i)}$ represent the ith threesome of the third column.

The ith row, or threesome, for $i = 1,\ldots,15$, of the fifth column of Table 1 is the set of least squares estimates of a, b, and c obtained by assuming M_1 to be correct and using all of the age-length data pairs in Tables 1 and 2, except for the ith pair in Table 1, to estimate a, b, and c. The last column of Table 1 gives the predicted lengths for each of the first population fish, assuming M_1 is correct. The ith element of this column is (5) after $\hat{a}_{1(i)}$, $\hat{b}_{1(i)}$, and $\hat{c}_{1(i)}$ have been replaced by $\hat{a}_{(i)}$, $\hat{b}_{(i)}$, and $\hat{c}_{(i)}$, where the latter threesome is the ith row of column five.

The discussion of columns three, four, five, and six of Table 2 is completely analagous to that given in the preceding two paragraphs for these

columns of Table 1. Thus, essentially, the fourth and sixth columns of Table 2 give the predicted lengths of the second population sampled fish for models M_2 and M_1, respectively.

In the notation of the previous section, D_{21} is the sum of the squares of the differences between the corresponding elements of columns two and four of Table 1. We find that $D_{21} = 87.31$, for this example. Similarly, D_{22} is the sum of the squares of the differences between the corresponding elements of columns two and four of Table 2 and we find that $D_{22} = 19.39$. Further, $D_2 = D_{21} + D_{22} = 106.70$. Finally, D_1 is the sum of the squares of the differences between the corresponding elements of columns two and six of Tables 1 and 2. We find that $D_1 = 86.77$ and since $D_1 < D_2$, the model, M_1, of equal growth curves for the two populations is the one best supported by the data.

For this example, the length of the jth fish from population i was taken to be

$$Y_{ij} = \frac{a}{1 + e^{-(bx_{ij} + c)}} + \epsilon_{ij}$$

for $i = 1, 2$, where x_{ij} is the age of the jth fish from population i, $a = 55$, $b = 0.35$, $c = -2.55$ and the ϵ_{ij}'s were each normal random variates with mean zero and standard deviation equal to two. The normal variates were generated using the algorithm of Box and Muller (1958). Thus, in essence, we generated both data sets using the same growth curve and the procedure described in the previous section made the correct selection.

MORE THAN TWO POPULATIONS

The procedure used to compare the growth curves for two populations is easily extended to the case where the growth curves for three or more populations are to be compared. As before, we begin by formulating all possible or plausible models. The number of possible models increases considerably as the number of populations being studied increases. For example, if there are three populations, there are five possible models, say $M_1, \ldots, M_5$. Here M_1 specifies that all three growth curves are the same. M_2 specifies that the growth curves for the first two populations are the same but they differ from that for the third population. M_3 specifies that the first and third populations have the same growth curve but the second population's growth curve is different. M_4 specifies that the first population's growth curve differs from those for the second and third populations but the latter two are the same. Finally, M_5 specifies that all three growth curves differ. Once again we assume that the forms of the common and distinct growth curves are specified for each model, but each contains one or more unknown parameters.

Once the models have been formulated, the problem is to use data to select one of them as being most plausible. The data consist of samples of pairs of age-length measurements from the populations being studied. For each model, we compute the sum of the squares of the differences between observed and predicted lengths for all of the fish in the samples, where the predicted lengths are computed by assuming the model is correct. The model selected as most appropriate, by the data, is the one that corresponds to the smallest sum of squares.

In order to compute the sums of squares, we must calculate a predicted length for each fish in the samples, under each model. For a given fish and a given model, the fish's predicted length is calculated by noting the population from which it came and grouping together all data points from this population and the populations, if any, whose growth curves are asserted, by the given model, to be equal to the growth curve for the fish's population. The fish's age and length measurements are then eliminated from the group of data points and the remaining data points in the group are used to estimate the unknown parameters in the asserted common growth curve. Once these estimates are obtained, unknown parameters in the asserted common growth curve are replaced by their estimates, and the fish's age is substituted into the result to obtain the fish's predicted length.

As an example, consider the data given in Table 3. These data represent the ages and corresponding lengths of 20 fish taken from each of three populations. Once again, the data have been generated by a computer. Our goal is to use the data to select one of five possible models, $M_1, \ldots, M_5$, where the M_i's are delineated in the first paragraph of this section.

For this example, a growth curve of the form

$$y = a(1 - e^{-be^{cx}}) + \epsilon \qquad (6)$$

fits each data set better than the von Bertalanffy, Laird-Gompertz, and logistic growth curves. The first term on the right hand side of Equation (6) is

essentially a constant times an extreme value for minima distribution function. This growth curve does not appear to have been used in the literature as yet. But it probably should be considered as a possible model whenever the other three are tried, as I have found cases where it fits real data better than the others.

TABLE 3.—Ages and lengths of 20 fish from each of the three populations.

Age	Population I length	Population II length	Population III length
1	4.7	5.0	5.3
2	5.4	7.5	6.1
3	10.0	14.2	10.8
4	12.6	11.0	13.5
5	19.0	17.8	20.0
6	16.0	17.5	17.2
7	19.0	19.2	20.1
8	22.3	27.9	23.5
9	28.1	27.7	29.2
10	27.2	34.1	28.2
11	38.0	32.7	38.8
12	41.5	40.8	41.8
13	42.1	48.1	41.7
14	49.9	51.5	48.9
15	53.3	53.3	51.4
16	57.0	56.3	54.3
17	56.3	55.9	52.8
18	58.3	57.9	54.1
19	59.6	60.2	55.0
20	59.9	57.9	55.1

Because Equation (6) fits each data set so well, one takes each of the common and distinct growth curves for each model to be in the form of Equation (6). Then for each model one calculates a predicted length for each of the 60 fish in the samples and a sum of squares of the differences between observed and predicted lengths. For the models $M_1,\ldots,M_5$, these sums of squares, are respectively, 334.27, 298.58, 346.45, 331.58, and 312.94. Since the second of these is the smallest, the model, M_2, which asserts that the growth curves for the first two populations are the same but that for the third population is different is the selected one.

Each of the fish lengths for this example was calculated using Equation (6), where y represents length and x represents age. Once again, ϵ was taken to be a normal random variate with mean zero and a standard deviation of 2. For each of the fish in the first two of the three samples, $a = 60$, $b = 0.10$, and $c = 0.20$. For the 20 fish in the third sample, $a = 55$, $b = 0.12$, and $c = 0.20$. Thus the first two data sets were generated using the same growth curve, but the third data set was generated using a different growth curve. Our procedure made the correct selection.

SOME CONCLUDING REMARKS

It is, in general, not feasible to attempt to carry out the calculations required for our growth curve comparison procedure by hand or with a desk calculator. This is because nonlinear regression analyses are usually required and there are many of them. However, the computations are easily programmed for a computer.

For many growth studies, rather massive amounts of data are gathered. If the amount of data available is excessively large, computer time and costs may become prohibitive. It is natural to ask whether the number of computations required can be reduced by doing away with the process of eliminating a data point from a data set before estimating parameters. Indeed, if this could be done, the number of least squares analyses needed would be drastically reduced. Unfortunately, however, it cannot be done. For it can be shown that if it is done, the selected model will always be the one which asserts different growth curves for all populations.

Often though, when there is a large amount of data, each age in the samples is common to many fish. In this case, a possible procedure is to work with the data points consisting of ages and average lengths, thus reducing the number of data points considerably. However, if the numbers of lengths used to calculate the average lengths vary widely from age to age, then it seems sensible to use weighted sums of squares of differences between observed and predicted lengths, and weighted least squares estimates of parameters, with the weights, in each case, being the numbers of lengths used to calculate the average lengths. The idea is that the larger the number of observations used to calculate an average, the closer the average should be to the true growth curve ordinate and, thus, the more weight that should be assigned to it. This modification of the present procedure was used in Boehlert and Kappenman (1980).

The dangers of extrapolation, after regression analyses, are well known. Thus, the practice of obtaining a predicted value for the dependent variable for a subject whose independent variable value lies outside the range of independent variable values used to carry out the regression analysis, is generally discouraged. There may be instances where extrapolation will bias our comparison procedure away from one or more models. The easiest way of checking to see if it does, in

any given situation, is to examine the observed and predicted length differences for each model. Differences, corresponding to youngest or oldest fish, being excessively large for one or more models might be an indication that extrapolation is biasing the procedure. This difficulty did not appear in the examples used in this paper, but it is possible to imagine rare cases where it could be a problem. If this problem does arise, it is easily remedied. One can always eliminate from a sum of squares of differences between observed and predicted lengths those differences whose predicted lengths are obtained by extrapolation. If this is done, the sums of squares in the model selection criterion should be replaced by averages of squares of differences.

For each of the examples given in this paper, all of the specified growth curves were taken to be of the same form. This is not necessary. Any growth curve can be given any form. For example, in the two population case, the common growth curve, for the model of equality of growth curves, can have a mathematical form which is different from the forms of the growth curves specified under the model of different growth curves. And, in fact, the latter two forms can be different from each other. Thus it is possible to handle the case where M_1 specifies equal growth curves and the common growth curve belongs to, say, the logistic family, while M_2 specifies different growth curves and the curves belong to, say, the Laird-Gompertz family or one belongs to the Laird-Gompertz family and the other belongs to the generalized extreme value for minima family.

Finally, it should be pointed out that although this paper has been concerned solely with growth curve comparisons, the procedure described here can be applied to the general problem of comparing regression equations. The regression equations of interest can be either linear or nonlinear functions of the unknown parameters. Where they are nonlinear is of particular interest since such comparisons have apparently not been discussed in the literature.

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CURRENT KNOWLEDGE OF LARVAE OF SCULPINS (PISCES: COTTIDAE AND ALLIES) IN NORTHEAST PACIFIC GENERA WITH NOTES ON INTERGENERIC RELATIONSHIPS[1]

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ABSTRACT

Current knowledge of cottid larvae in northeast Pacific genera is summarized. Larvae are known for representatives of 25 of the 40 genera reported from Baja California to the Aleutian Islands although two genera, *Gymnocanthus* and *Icelus*, are represented only by species which live in other areas as adults. Included are illustrations of larvae of 29 species representing the 25 genera plus one potentially new northeast Pacific genus, identified only as "Cottoid Type A."

The larvae exhibit a wide diversity of form. Based on shared larval characters, including spine patterns, body shape, and pigmentation, 6 phenetically derived groups of genera are apparent within the 25 genera for which representatives are considered: 1) *Artedius*, *Clinocottus*, *Oligocottus*, *Orthonopias*; 2) *Paricelinus*, *Triglops*, *Icelus*, *Chitonotus*, *Icelinus*; 3) *Dasycottus*, *Psychrolutes*, *Gilbertidia*, ?*Malacocottus*, "Cottoid Type A"; 4) *Scorpaenichthys*, *Hemilepidotus*; 5) *Blepsias*, *Nautichthys*; 6) *Leptocottus*, *Cottus*. Six genera do not fit with any group: *Enophrys*, *Gymnocanthus*, *Myoxocephalus*, *Radulinus*, *Rhamphocottus*, *Hemitripterus*.

If these preliminary larval groupings reflect relationship, as evidence indicates, they tend to support a number of previously implied relationships within the cottids, but there are some important differences. These include the distinctiveness of the *Artedius* (Group 1) line; the separation of *Artedius* and *Icelus*, once considered closely related; the relationship of *Paricelinus*, generally considered a primitive and rather distinct form, with other members of Group 2; the apparent relationship of *Icelus* to other genera in Group 2 and its questionable placement in a separate family; the distinctiveness of *Radulinus*, previously considered to be related to *Chitonotus* and *Icelinus*.

The Cottidae, which in this paper are considered broadly to include sculpinlike fishes of Cottidae, Icelidae, Cottocomephoridae, Comephoridae, Normanichthyidae, Cottunculidae, and Psychrolutidae of the suborder Cottoidei of Greenwood et al. (1966), comprises a diverse group of temperate and boreal fishes. Nelson (1976) estimated that the group may contain over 350 species, three-fourths marine, in about 86 genera. They are generally coastal fishes inhabiting all oceans but the Indian. Greatest species diversity occurs in the North Pacific. The systematics of the group are not well understood (Quast 1965; Nelson 1976).

Until recently, larvae of relatively few cottids had been described. They were a difficult group to identify in ichthyoplankton collections, particularly in the northeast Pacific where 40 genera are reported to occur between Baja California and the Aleutian Islands (Table 1). With the recent work by Richardson and Washington (1980), larvae are now known for representatives of 25 of these 40 cottid genera, although two genera, *Icelus* and *Gymnocanthus*, are represented only by larvae of species that live in other areas as adults.

The purpose of this paper is twofold. It presents for the first time a summary of important cottid larval characters (those characters occurring only during the larval period and most useful in identifying and distinguishing species) based on the larvae of these 25 northeast Pacific genera. (Larvae of these genera that are known for species inhabiting other areas as adults are also considered.) This knowledge, which is a necessary prerequisite for systematic studies using larvae, is presented to provide a foundation to which future work on cottid larvae can be compared and upon which it can be expanded as more larvae become known. The paper also presents a preliminary examination of generic groupings within these northeast Pacific cottid genera based on shared larval characters, i.e., similarity. These phenetic groupings, even though preliminary, are helpful

[1]This paper was presented at the Second International Symposium on The Early Life History of Fish (sponsored by ICES, IAO, ICNAF, IAOB, SCOR) held at Woods Hole, Mass., 2-5 April 1979. An abstract of the paper appeared in the symposium publication.

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TABLE 1.—List of cottid genera occuring in the northeast Pacific Ocean between Baja California and the Aleutian Islands based on Howe and Richardson (text footnote 3) with a summary of illustrations (accessible to author) of larvae known for those genera worldwide. Lengths (millimeters) of larvae are reported as they appeared in the literature: NL = notochord length; SL = standard length; TL = total length; mm = no length definition was given.

Genus and species	Reference	Sizes illustrated
Artediellus —	—	—
Artedius harringtoni	Richardson and Washington 1980	3.0, 4.7, 6.9 mm NL, 7.3, 9.3, 13.6 mm SL
A. lateralis	Budd 1940	4.1 mm SL
	Marliave 1975	4, 8, 11, 14 mm TL
Artedius Type 2	Richardson and Washington 1980	3.0, 4.7, 6.0 mm NL, 7.2, 9.9, 11.8 mm SL
Ascelichthys —	—	—
Asemichthys —	—	—
Blepsias cirrhosus	Blackburn 1973	12.2 mm SL
	Marliave 1975	10, 14, 19, 15.5 mm TL
Chitonotus pugetensis	Richardson and Washington 1980	3.0, 6.3 mm NL, 8.5, 11.5, 15.4, 16.6 mm SL
	Misitano 1980	3.0, 4.8 mm SL
Clinocottus acuticeps	Richardson and Washington 1980	3.7, 3.9, 6.9 mm NL, 7.6, 10.4, 13.8, 16.5 mm SL
C. analis	Eigenmann 1892	ca. 4 mm
	Budd 1940	ca. 4 mm
C. recalvus	Morris 1951	4.6, 5.0, 7.6, 8.3, 9.9, 10.8, 18.0, 24.3 mm TL
Cottus asper	Stein 1972	5.5, 9.0, 10.8 mm TL
	Richardson and Washington 1980	5.2 mm NL, 8.2, 9.9 mm SL
Dasycottus setiger	Blackburn 1973	7.4 mm SL
Enophrys bison	Blackburn 1973	7.5 mm SL
	Marliave 1975	10 mm TL
	Misitano 1978	5.0, 5.4, 5.8, 6.7, 7.1, 7.6 mm SL
	Richardson and Washington 1980	4.8, 7.0 mm NL, 9.1 mm SL
E. bubalis[1]	Cunningham 1891[2]	5.7 mm
	McIntosh and Masterman 1897[2]	Larva (size not given)
	Ehrenbaum 1904[2]	5.8, 10, 11 mm
	Ehrenbaum 1905-9	5.8, 10, 11 mm
	Russell 1976[3]	4.5, 5.7, 6.4, 9.5 mm
E. lilljeborgi[1]	Bruun 1925[4]	5.6, 6.8, 8.7 mm TL
	Rass 1949[5]	6.8 mm
	Russell 1976[6]	4.08, 4.2, 5.7, 7.0 mm
Eurymen —	—	—
Gilbertidia sigalutes	Blackburn 1973	7.9, 9.5 mm SL
	Marliave 1975	7, 13, 15, 25, 34 mm TL
Gymnocanthus herzensteini[1]	Kyushin 1970	5.79, 6.59, 7.55 mm
G. tricuspis[1]	Koefoed 1907	10.7, 12.7, 15.5 mm
	Rass 1949	9 mm
	Khan 1972	12.2, 13.9, 15.9 mm TL
G. ventralis[1]	Ehrenbaum 1905-9	15, 18 mm
Hemilepidotus gilberti[1]	Gorbunova 1964	7.5, 11.4, 17.5 mm
	Hattori 1964	7.1, 11.6, 19.2, 24.8, 32.5 mm
H. hemilepidotus	Gorbunova 1964	7.25, 10.5 mm
	Peden 1978	ca. 20 mm SL
	Richardson and Washington 1980	5.8, 5.9, 9.1 mm NL, 10.7, 11.5, 19.0 mm SL
H. jordani	Gorbunova 1964	6.4, 10.7, 13.0 mm
	Peden 1978	ca. 20 mm SL
H. papilio	Gorbunova 1964	10.7, 13.7 mm
H. spinosus	Follett 1952	12, 21 mm SL
	Peden 1978	ca. 20 mm SL
	Richardson and Washington 1980	5.0, 6.6, 8.9 mm NL, 11.0, 11.8, 19.0 mm SL
H. zapus	Peden 1978	ca. 20 mm SL
Hemitripterus americanus[1]	Warfel and Merriman 1944	ca. 12 mm
	Khan 1972	11.7,[7] 14.5, 18.8 mm TL
	Fuiman 1976	12.6, 15.5, 20 mm TL
H. villosus[8]	Kyushin 1968	14.78, 15.57, 16.52 mm SL
	Okiyama and Sando 1976	11.6, 14.4, 17.4, 20.0 mm
Icelinus spp.[9]	Richardson and Washington 1980	3.3, 8.6 mm NL, 10.9, 13.8, 15.2, 16.5, 12.5, 16.6 mm SL
Icelus bicornis[1]	Ehrenbaum 1905-9[10]	25 mm
	Rass 1949	12.3 mm
Jordania —	—	—
Leiocottus —	—	—
Leptocottus armatus	Jones 1962	ca. 4 mm
	Blackburn 1973	7.6, 8.3, 12.0 mm SL
	Marliave 1975	8, 12, 13 mm TL
	White 1977	4.9 mm NL
	Richardson and Washington 1980	5.1, 8.1 mm NL, 11.1 mm SL
Malacocottus ?M. zonurus Type 1	Richardson and Bond[11]	7.0, 9.8, 14.2, 24.0 mm SL
	Richardson unpubl. data	6.6, 7.0, 8.8, 9.8, 10.4, 14.2, 24.0 mm SL
Myoxocephalus aenaeus[1]	Perlmutter 1939	6 mm
	Khan 1972	5.0, 7.1, 9.7, 11.8 mm TL
	Lund and Marcy 1975	5.4, 6.1, 6.8, 7.5, 8.5, 9.2 mm TL
M. octodecemspinosus[1]	Colton and Marak 1969	6.8, 8.5, 10.5, 15.2 mm TL
	Khan 1972	7.0, 9.5, 10.7, 12.5, 14.5 mm TL
M. polyacanthocephalus	Blackburn 1973	7.7, 10.7 mm SL
M. quadricornis[1] (marine form)	Zvjagina 1963	12.3, 12.8, 13.6, 14.5, 16.2, 32 mm
	Khan 1972	12.8, 14.5, 17.0 mm TL
	Khan and Faber 1974	12.8, 14.4, 17.0 mm TL

TABLE 1.—*Continued.*

Genus and species	Reference	Sizes illustrated
M. scorpius[1]	McIntosh and Prince 1890[12]	Larva (size not given)
	McIntosh and Masterman 1897[12]	Larva (size not given)
	Ehrenbaum 1904[12]	8.24, 8.16, 10, 18 mm
	Ehrenbaum 1905-9	8.2, 10, 18 mm
	Koefoed 1907	9.5 mm
	Rass 1949	7.9, 9.3 mm
	Bigelow and Schroeder 1953	8.2, 10, 18 mm
	Khan 1972	7.6, 8.5, 10.4, 14.0, 17.4 mm TL
	Russell 1976	7.5, 9.5, 10, 14 mm
Nautichthys oculofasciatus	Blackburn 1973	7.5, 13 mm SL
	Marliave 1975	9.5, 13, 17, 26 mm TL
	Richardson and Washington 1980	11.7 mm NL, 16.6 mm SL
Oligocottus maculosus	Stein 1972	4.6-5.2, 6.0, 6.6, 9.2 mm TL
	Stein 1973	4.6-5.2, 6.0, 6.6, 9.2 mm TL
O. snyderi	Stein 1972	4.5-4.75, 5.5 mm TL
Orthonopias triacis	Bolin 1941	ca. 3-4 mm SL
Paricelinus hopliticus	Richardson and Washington 1980	5.6, 6.2 mm NL, 13.8, 18.6, 25.6 mm SL
Phallocottus —	—	—
Porocottus —	—	—
Psychrolutes paradoxus	Blackburn 1973	10.3 mm SL
	Marliave 1975	10.5, 13, 14, 13 mm TL
Radulinus asprellus	Richardson and Washington 1980	4.7, 7.9, 9.6, 10.9 mm NL, 12.6, 14.4 mm SL
R. boleoides	Richardson and Washington 1980	8.7 mm NL
Rhamphocottus richardsoni	Blackburn 1973	6.7, 10 mm SL
	Marliave 1975	10, 11.5, 15 mm TL
	Richardson and Washington 1980	8.4 mm NL, 10.6, 11.7 mm SL
Scorpaenichthys marmoratus	O'Connell 1953	5.85, 6.26, 10, 17, 30, 48 mm
	Richardson and Washington 1980	5.3, 7.5, 8.6 mm NL, 8.7, 10.4, 13.8 mm SL
Sigmistes —	—	—
Stelgistrum —	—	—
Sternias —	—	—
Stegicottus —	—	—
Synchirus —	—	—
Thyrisicus —	—	—
Triglops murrayi[1]	Khan 1972	8.4, 11.6, 18.9, 23.4 mm TL
T. pingeli[8]	Ehrenbaum 1905-9	18 mm
	Koefoed 1907	13, 16.5, 22 mm
	Rass 1949	10 mm
Triglops sp.	Blackburn 1973	8.3, 12 mm SL
	Richardson and Washington 1980	6.9 mm NL, 15.4 mm SL
Zesticelus —	—	—

[1]Not northeast Pacific species.
[2]As *Cottus bubalis*.
[3]As *Taurulus bubalis*.
[4]As *Cottus lilljeborgi*.
[5]As *Acanthocottus lilljeborgi*.
[6]As *Taurulus lilljeborgi*.
[7]Probably *Myoxocephalus scorpius* (Laroche text footnote 6).
[8]Species occurs in northeast Pacific but larvae described from other areas.
[9]Not identified below genus level.
[10]As *Centridermichthys hamatus*.
[11]Text footnote 5.
[12]As *Cottus scorpius*.

in reducing taxonomic problems. The potential usefulness of the larval groups in providing insights into systematic relationships and evolutionary trends within this difficult group of fishes is also discussed. The use of larval forms of fishes to elucidate systematic relationships has been demonstrated in a number of groups, e.g., ceratioids (Bertlesen 1941), myctophids (Moser and Ahlstrom 1970, 1972, 1974), gonostomatids (Ahlstrom 1974), scombroids (Okiyama and Ueyanagi 1978), and serranids (Kendall 1979).

LARVAL CHARACTERS OF COTTIDS

This is a summary of important larval characters in cottids, i.e., those characters occurring only during the larval period which can be of most use in distinguishing species. These characters include preopercular spine pattern, body shape, and pigmentation. Although meristic characters may be of prime utility in identifying cottid larvae, they persist in adults and are not considered truly larval. Meristic characters for northeast Pacific cottids have been discussed by Richardson and Washington (1980) and Howe and Richardson.[3] The purpose of this summary is to point out the kinds of larval characters that are useful for identification and the spectrum in which those characters may be exhibited since cottid larvae manifest a wide diversity of form.

This summary is based on only the representatives of northeast Pacific cottid genera listed in

[3]Howe, K. D., and S. L. Richardson. 1978. Taxonomic review and meristic variation in marine sculpins (Osteichthys: Cottidae) of the northeast Pacific Ocean. Final rep., NOAA NMFS Contract No. 03-78-MO2-120, 1 January 1978 to 30 September 1978, 142 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

Table 1. Species from areas outside the northeast Pacific are included when larvae are known because of the taxonomic information their larvae may provide. Generic level designations are used throughout the text for continuity and emphasis although larvae of all species (number of species based on the taxonomic status summary by Howe and Richardson footnote 3) in a genus may not be known. In some cases the genera are monotypic (*Chitonotus*, *Dasycottus*, *Gilbertidia*, *Leptocottus*, *Orthonopias*, *Paricelinus*, *Rhamphocottus*, *Scorpaenichthys*) and thus larval characters of the genus may readily be defined. At least some developmental stages are known for all six species of *Hemilepidotus*, providing good generic level definition. In some cases larvae of a few, but not all species within a genus are known [*Artedius* (3 species out of 7); *Gymnocanthus* (3 of 6); *Hemitripterus* (2 of 2 or 3); *Myoxocephalus* (5 of 18); *Oligocottus* (2 of 4); *Radulinus* (2 of 5); *Triglops* (3 of 9)]. In those instances, constancy of larval characters among species provides good indications of generic level definition. Larvae of *Icelinus* spp. have only been described at the generic level as none of the eight species have yet been distinguished. For some genera, larvae are known for only one of a few species: *Blepsias* (1 of 2), *Cottus* (1 of 2 brackish water species), *Icelus* (1 of 13), *Malacocottus* (1 of 5), *Nautichthys* (1 of 3), *Psychrolutes* (1 of 2). In those, generic level definition may not be as precise; however, larvae of all species appear rather distinctive and thus may be good representatives of their genera. In the following summary those genera which provide the best examples of patterns are listed in parentheses.

Principal preopercular spines typically (18 of 25 genera) number 4 (*Scorpaenichthys*, *Icelinus*, *Leptocottus*, *Enophrys*) and may vary in degree of development. Modifications of this basic pattern may occur (*Myoxocephalus*, ?*Malacocottus*) in which four main spines are present with one or two auxiliary spines. Another pattern consists of multiple preopercular spines, usually small, numbering up to ca. 25 (*Artedius*, *Clinocottus*). Sometimes only one spine is present (*Rhamphocottus*) or none (*Psychrolutes*, *Gilbertidia*). Spines in other regions of the head (particularly parietal-nuchal, postocular, posttemporal-supracleithral, opercular) may also be important.

General body shape can range from rather stubby and deep (*Artedius*, *Enophrys*) to moderately slender and elongate (*Icelinus*, *Triglops*) to globose (?*Malacocottus*). The snout can be quite rounded (*Scorpaenichthys*, *Hemilepidotus*) or pointed (*Icelinus*, *Chitonotus*). Snout to anus length can be rather short, <40% SL (standard length) (*Dasycottus*), to moderately long, >60% SL (*Rhamphocottus*), although this can change with development. The gut may appear tightly compacted (*Dasycottus*) or be distinctively coiled (*Cottus*). The hindgut may trail somewhat below the body (*Artedius*, *Clinocottus*). Unusual gut diverticula may be present (*Artedius*, *Clinocottus*). Pectoral fins may be noticeably elongated (*Nautichthys*) or fanlike early in development (*Myoxocephalus*).

Melanistic pigment patterns range from relatively unpigmented to heavily pigmented. Pigment may be variously present or absent over the head, snout, cheek, jaws, cleithral base, throat. Pigment over the dorsolateral surface of the gut may vary in intensity, ventrolateral extent, and pattern (e.g., bars, *Leptocottus*; distinct round melanophores, *Enophrys*). In some species the entire gut region is pigmented (*Paricelinus*). The ventral midline of the gut may have a distinct line of melanophores (*Cottus*, some *Myoxocephalus*) or be unpigmented (*Scorpaenichthys*). The nape may be distinctively pigmented (*Artedius*, *Enophrys*). The lateral body surface above the gut may be unpigmented (*Chitonotus*), have dorsolateral pigment not extending to the gut (*Radulinus*) or be entirely pigmented (*Scorpaenichthys*). In the tail region posterior to the anus, pigment may be absent (some *Triglops*, *Dasycottus*), present along only the ventral midline (*Artedius*, *Chitonotus*), present along only the ventral and dorsal midlines [*Gymnocanthus*, small (<8 mm) *Hemilepidotus*], or present on the lateral body surface, sometimes in combination with a ventral midline series (*Scorpaenichthys*, *Radulinus*, *Blepsias*). Number, spacing, position, and shape of ventral midline melanophores are important as is the posterior extent of lateral pigment. Melanophores may variously appear along the caudal fin base (*Paricelinus*, *Chitonotus*). Pectoral fins are generally unpigmented, but some species have heavily pigmented fins (*Psychrolutes*, *Gilbertidia*) or a pigment band along the fin margin (*Nautichthys*).

LARVAL COTTID GROUPS

Within the 25 cottid genera considered, 6 groups of genera are apparent based on shared larval characters, i.e., similarity , and 6 genera do not fit into any group (Table 2). Characters within each

TABLE 2.—Groupings of 25 cottid genera reported to occur in the northeast Pacific Ocean between Baja California and the Aleutian Islands based on shared larval characters. Group characteristics were based on representative species for which larvae are known, as listed in Table 1. Also included in the groupings is an unidentified larval type, "Cottoid Type A" of Richardson and Washington (1980) which may represent a new genus.

Group	General characteristics	Genera
1	Multiple preopercular spines, rounded snout, stubby shape, slightly trailing gut, sometimes with gut protrusions or diverticula	*Artedius*, *Clinocottus*, *Oligocottus*, *Orthonopias*
2	Four preopercular spines, pointed snout, moderately slender, postanal pigment when present usually restricted to ventral midline	*Paricelinus*, *Triglops*, *Icelus*, *Chitonotus*, *Icelinus*
3	Four principal preopercular spines or none, rounded snout, often globose shape with loose skin, pigmented pectoral fins	*Dasycottus*, *Psychrolutes*, *Gilbertidia*, *?Malacocottus*, Cottoid Type A (new genus?)
4	Four preopercular spines, rounded snout, relatively deep bodied, ca. 4-5 mm NL at hatching, postanal pigment dorsally, ventrally, and laterally	*Scorpaenichthys*, *Hemilepidotus*
5	Four preopercular spines not pronounced, rounded snout, relatively slender, postanal pigment dorsally, ventrally, laterally, probably >7 mm NL at hatching, pectoral fins unpigmented or with pigment band near margin	*Blepsias*, *Nautichthys*
6	Four preopercular spines, rounded snout, relatively slender, no additional head spines, postanal pigment restricted to ventral midline	*Leptocottus*, *Cottus*
Ungrouped genera	*Enophrys*, *Gymnocanthus*, *Myoxocephalus*, *Radulinus*, *Rhamphocottus*, *Hemitripterus*	

group and of each ungrouped genus are summarized to facilitate recognition and minimize taxonomic and identification problems involving cottid larvae. These groupings are based on complete developmental series to the extent available, but only representative figures illustrating one point on a developmental continuum are presented (Figures 1-9). The groupings are necessarily preliminary because not all species in all genera are known as larvae. The groups described below are not arranged in any particular order. Generic designations are used as discussed in the previous section.

Group 1

This is the tightest group among the 25 genera. Included are *Artedius*, *Clinocottus*, *Oligocottus*, and tentatively *Orthonopias* (Figures 1, 2). The unique multiple preopercular spine pattern distinguishes it from all other groups or genera. [Although a complete series of *Orthonopias* has not been described and the spine pattern is unknown, small larvae (Figure 2) are very similar to *Artedius* in form and pigment characteristics and are tentatively included in this group.] The stubby body shape, rounded snout, and somewhat trailing gut are remarkably consistent within the group. Presently, identification to genus based on larval characters is still difficult and in need of better definition. Characters used to distinguish species (besides fin ray counts) include: number, spacing, and shape of ventral midline melanophores; intensity of gut pigmentation; presence of unusual gut diverticula; total number of preopercular spines and position of largest spines; number of spines (e.g., none, two, cluster) in the parietal and posttemporal-supracleithral regions; presence or absence of pigment on the nape or head.

Although the multiple preopercular spine pattern persists through the larval period, adults have four preopercular spines with the lower three reduced and the upper variously modified. Remnants of the larval serrations have been observed only in adult *A. notospilotus* (Howe[4]). It is unclear which four spines of the larvae persist in adults.

Group 2

This is also a rather cohesive group (Figure 3) consisting of slender forms with pointed snouts and four prominent preopercular spines [*Paricelinus*, *Triglops*, *Icelus* (tentatively), *Chitonotus*, *Icelinus*]. This general body shape is remarkably similar among genera and is not found in any other genera considered. All have a relatively short snout to anus distance. Postanal ventral midline pigment is usually present (absent in one species of *Triglops*) with some additional melanophores along the caudal fin base. Dorsal midline pigment is usually absent except for a few spots in some *Icelinus* and possibly a row in some late stage *Triglops*. Generic differences include degree of gut pigmentation (e.g., darkest in *Paricelinus* and some *Triglops*), number and position of ventral midline melanophores, and degree of head spination (e.g., postocular spines in *Paricelinus* and *Triglops*).

[4]K. D. Howe, Ph.D. candidate, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, pers. commun. September 1978.

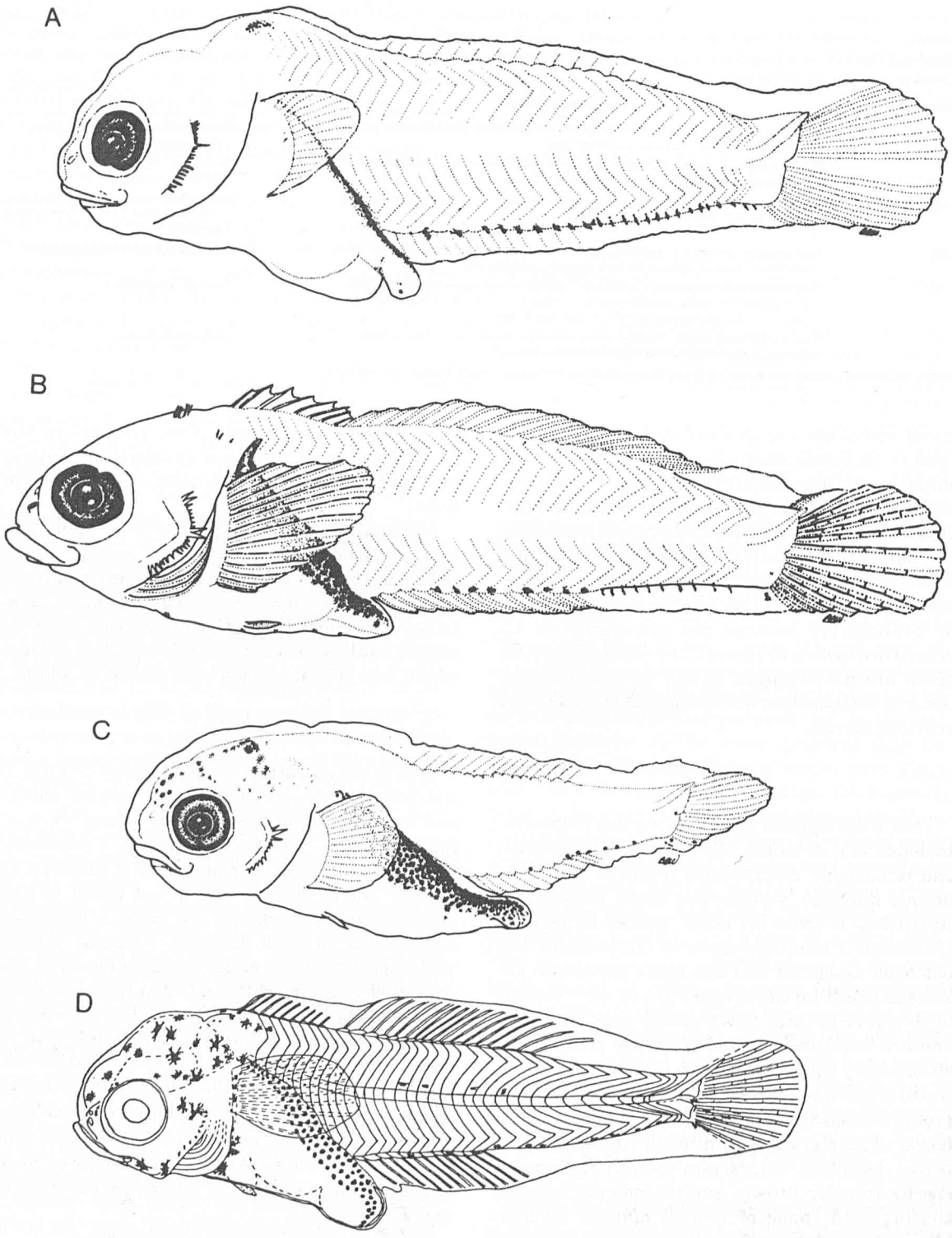

FIGURE 1.—Larvae of A) *Artedius harringtoni* (7.3 mm SL), B) *Artedius* Type 2 (9.9 mm SL), C) *Clinocottus acuticeps* (7.6 mm SL), D) *Oligocottus maculosus* (9.2 mm TL) (A-C, Richardson and Washington 1980; D, Stein 1973).

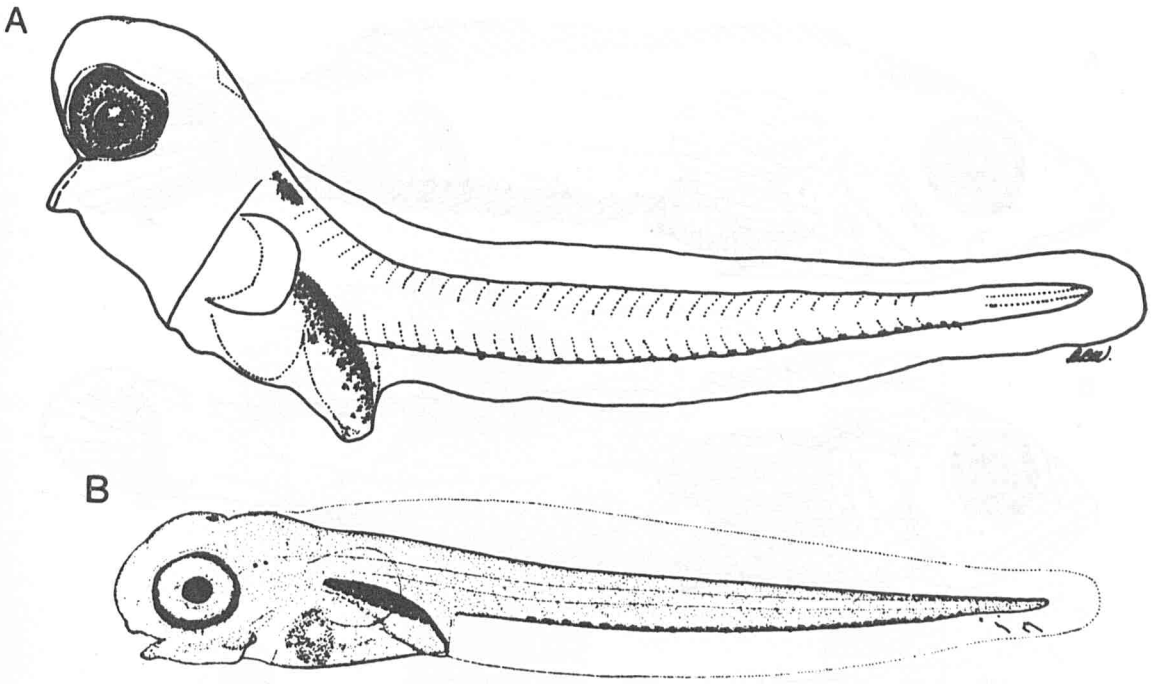

FIGURE 2.—Larvae of A) *Artedius harringtoni* (3.0 mm NL) and B) *Orthonopias triacis* (≈4 mm) (A, Richardson and Washington 1980; B, Bolin 1941).

The tentative placement of *Icelus* with this group is of interest as it has been considered to constitute a distinct family, the Icelidae (Jordan 1923; Greenwood et al. 1966) based on the presence of scales in adults. Although larvae of *Icelus* are known to the author only from descriptions in the literature (Table 1), they strongly resemble other members of this group in form and preopercular spine pattern. Inclusion of *Paricelinus* is also of interest as it has been considered to be a rather distinct and primitive form (Bolin 1947). It possesses five pelvic soft rays, the ancestral condition, whereas the number of soft rays is reduced to three or two in other members of the group.

Group 3

Group 3 (Figure 4) consists of the "psychrolutid" cottids [*Dasycottus*, *Psychrolutes*, *Gilbertidia*, ?*Malacocottus*,[5] "Cottoid Type A" (new genus?)] often considered a separate family (Nelson 1976). ["Cottoid Type A" may possibly be *Psychrolutes phrictus* but positive identification awaits additional specimens—see Discussion by Richardson and Washington (1980). If it is *P. phrictus*, larval evidence indicates that the species is incorrectly placed and that a new northeast Pacific genus of cottid is in need of description.] This group is not as cohesive as the two previous groups. The most distinctive character of Group 3 is the pattern of pigmentation of the pectoral fin, a pattern not found in any of the other genera considered. In all, at least the basal portion of the fin develops pigment with the entire fin pigmented in *Psychrolutes*, *Gilbertidia*, and small (<9 mm SL) ?*Malacocottus*. Pigment on small (<8 mm SL) *Dasycottus* is restricted to the inside surface of the pectoral fin base but later it develops distally on the outer surface. (The pigment band near the margin of the elongated pectoral fin of *Nautichthys* is a very different pattern.) Only *Dasycottus* and ?*Malacocottus* develop four preopercular spines, the latter genus with an accessory spine at the base of the second spine. All but the more slender *Dasycottus* have relatively rounded snouts and deep bodies. Both ?*Malacocottus* and "Cottoid Type A"

[5]Identification of larvae is tentative pending resolution of taxonomic problems of adults at the generic level [see Howe and Richardson footnote 3 and also Richardson, S. L., and C. E. Bond. 1978. Two unusual cottoid fishes from the northeast Pacific. Unpubl. manuscr., 6 p. + 25 figs. (Available from senior author.) (Paper presented at the American Society of Ichthyologists and Herpetologists, 1978.)]

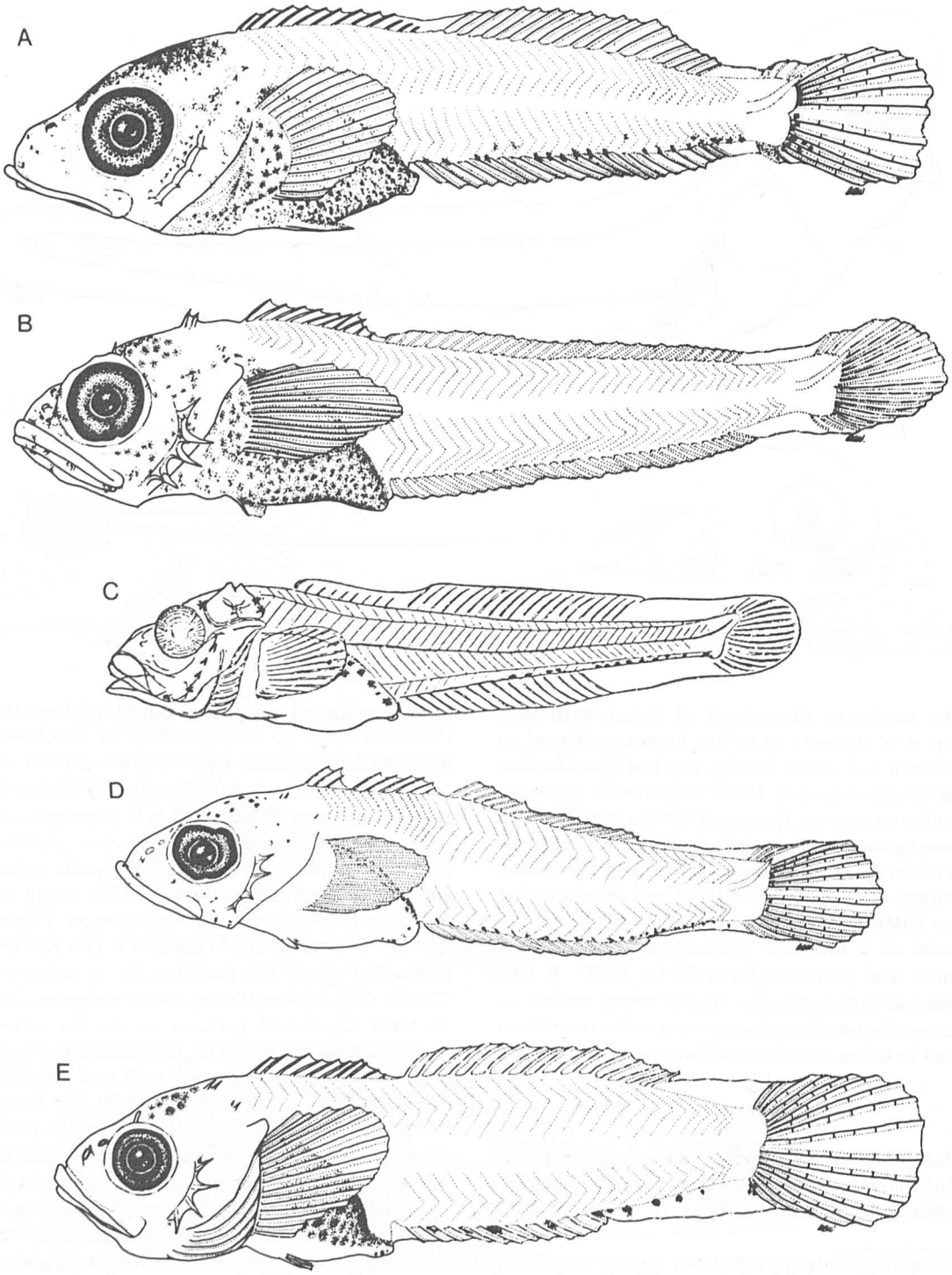

FIGURE 3.—Larvae of A) *Paricelinus hopliticus* (13.8 mm SL), B) *Triglops* sp. (15.4 mm SL), C) *Icelus bicornis* (25 mm), D) *Chitonotus pugetensis* (11.5 mm SL), E) *Icelinus* sp. (13.8 mm SL) (A, B, D, E, Richardson and Washington 1980; C, Ehrenbaum 1905-9).

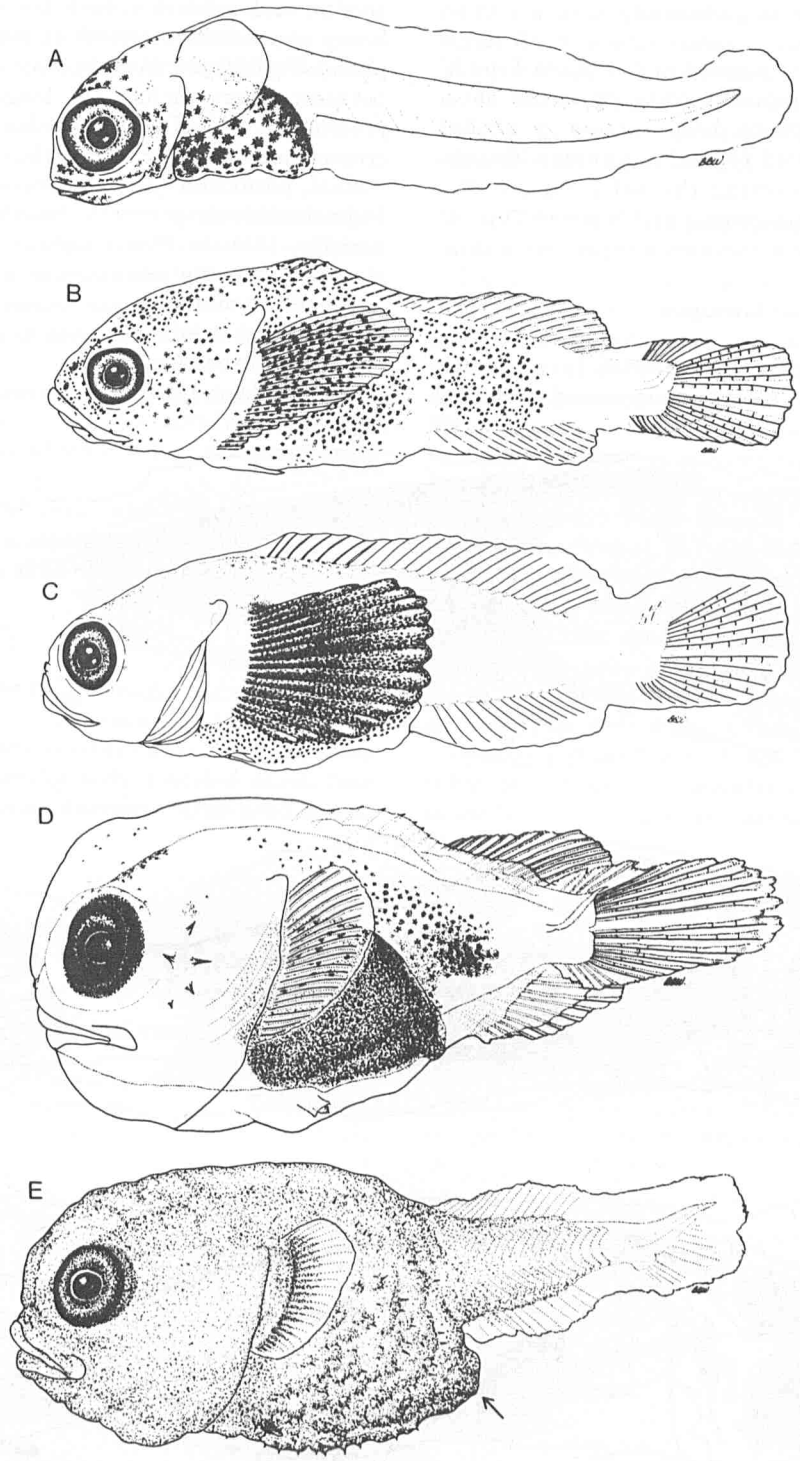

FIGURE 4.—Larvae of A) *Dasycottus setiger* (8 mm NL), B) *Psychrolutes paradoxus* (transforming, 13 mm SL), C) *Gilbertidia sigalutes* (13 mm SL), D) ?*Malacocottus zonurus* (10.4 mm SL), E) Cottoid Type A (9.8 mm SL) (A-D, original illustrations; E, Richardson and Washington 1980).

develop a pronounced globose appearance with an outer bubble of skin. Small larvae of all forms have head and gut pigment and "Cottoid Type A" also has lateral pigment posterior to the anus. Some lateral pigment develops later in all but *Dasycottus*. "Cottoid Type A" has unique "thumbtack" prickles covering the belly region. The pelvic fins of ?*Malacocottus* and "Cottoid Type A" often appear to be withdrawn into pockets of skin.

Group 4

Group 4 (Figure 5) includes larvae with four preopercular spines, conspicuously rounded snouts, and relatively deep bodies with rather heavy pigmentation, except at the smallest sizes (*Scorpaenichthys*, *Hemilepidotus*). Differences between genera include the longer gut and the preanal fin fold of *Scorpaenichthys* and the increased head spination of *Hemilepidotus* (parietal, nuchal, postocular, posttemporal-supracleithral). Pigmentation is generally heavier in *Scorpaenichthys* than in *Hemilepidotus* of comparable size. It is initially concentrated along the dorsal and ventral midlines, particularly in *Hemilepidotus*, filling in laterally with development. Larvae of both are neustonic.

The two genera in this group are certainly more

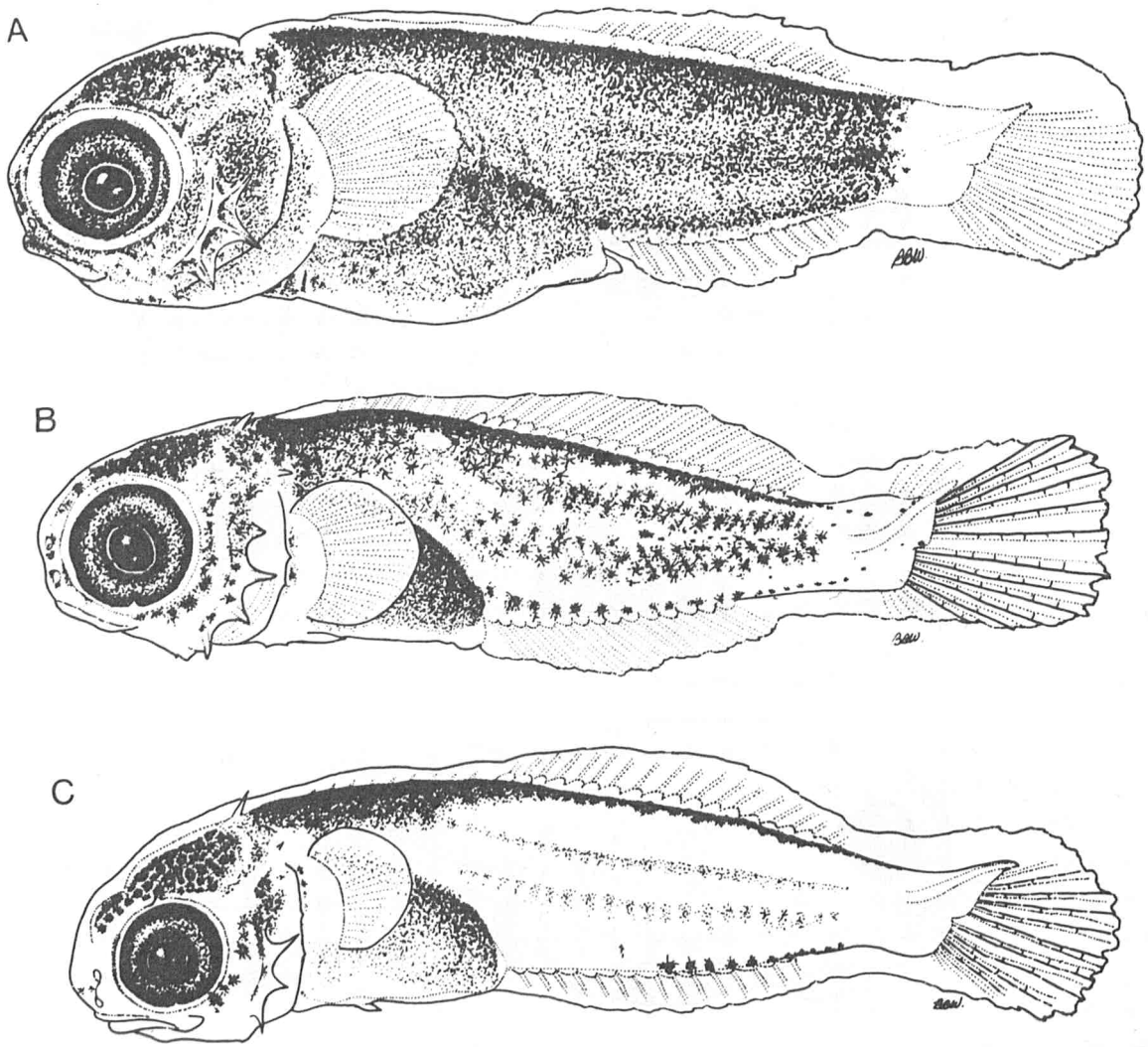

FIGURE 5.—Larvae of A) *Scorpaenichthys marmoratus* (8.7 mm SL), B) *Hemilepidotus spinosus* (11.0 mm SL), C) *H. hemilepidotus* (10.7 mm SL) (A-C, Richardson and Washington 1980).

similar to each other than to any other cottids considered, although *Scorpaenichthys* was given familial status in the past (Jordan 1923; Tarenets 1941).

Group 5

This group consists of two elongated, slender-bodied genera, *Blepsias* and *Nautichthys* (Figure 6). Both hatch at a relatively large size, >7 mm NL (notochord length). Both have rounded snouts, relatively heavy pigmentation, and four preopercular spines that never become pronounced and sharp. *Nautichthys* (at least *N. oculofasciatus*) develops greatly elongated pectoral fins soon after hatching, each of which develops a pigment band near its distal margin.

The genera *Blepsias* and *Nautichthys* have been placed in a separate family, Blepsiidae, in the past (Jordan 1923).

Group 6

Group 6 (Figure 7) contains *Leptocottus* and *Cottus* (as based on the brackish water species *C. asper*). They share several characters, including the relatively slender body, rounded snout, four preopercular spines, absence of other head spines, ventral midline pigment along gut, and postanal pigment restricted to ventral midline. Both hatch and transform at similar sizes, ca. 3-4 mm NL and ca. 10-12 mm SL, respectively. *Leptocottus* has a unique gut pigment pattern of bars, and *Cottus* has a distinctively coiled gut.

Ungrouped Genera

Enophrys (Figure 8) has four pronounced preopercular spines, rounded snout, deep stubby shape, pigmented nape, and postanal pigment only along the ventral midline. It has a postocular spine and opercular spines, and a preanal fin fold. Melanophores over the gut are distinctively round in shape and densely concentrated. This suite of larval characters is not shared by any other genus. *Enophrys* bears some resemblance to Group 6 (*Leptocottus-Cottus*) but differs too much to be part of it. The deep body, bulging gut, and pigmented nape somewhat resemble Group 1 (*Artedius* et al.) but spine patterns differ drastically. Larvae of *E. bubalis* and *E. lilljeborgi* from the North Atlantic (Table 1) are extremely similar to *E. bison* from the northeast Pacific.

Gymnocanthus (Figure 8) apparently never develops pronounced preopercular spines, according to the literature (Table 1). Larvae of *G. tricuspis*

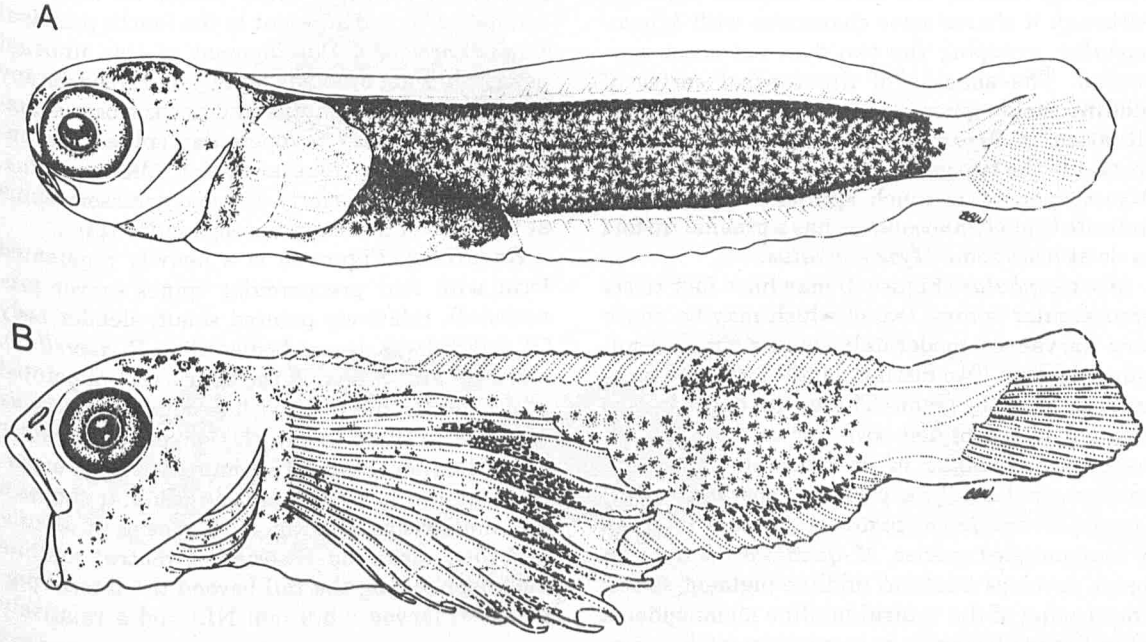

FIGURE 6.—Larvae of A) *Blepsias cirrhosus* (11 mm NL) and B) *Nautichthys oculofasciatus* (11.7 mm NL) (A, original illustration; B, Richardson and Washington 1980).

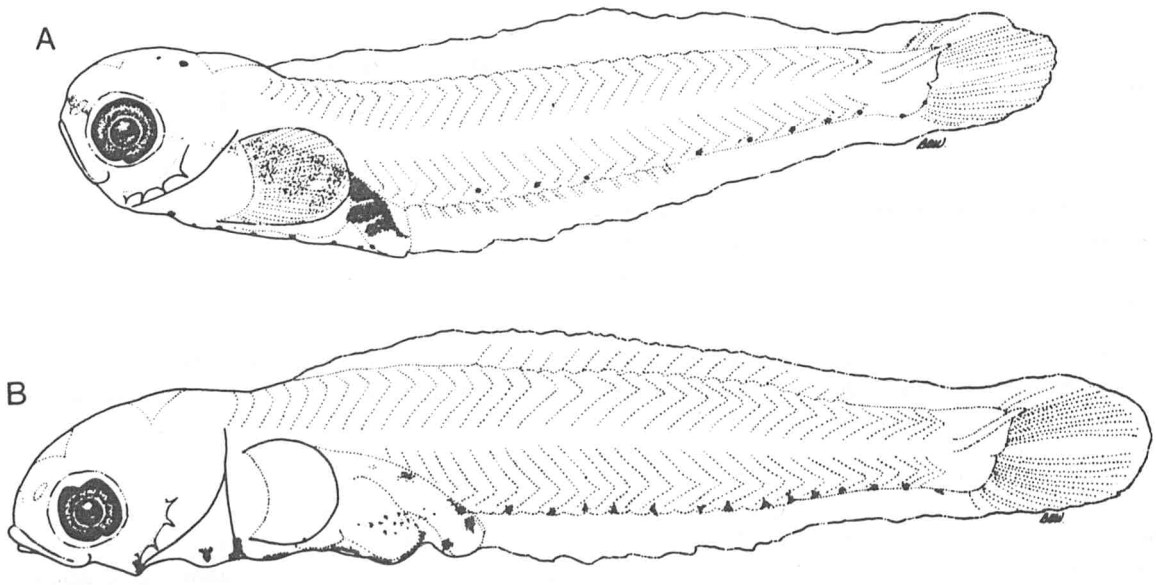

FIGURE 7.—Larvae of A) *Leptocottus armatus* (8.1 mm NL) and B) *Cottus asper* (8.2 mm SL) (A, B, Richardson and Washington 1980).

develop three very small preopercular spines, visible only on stained specimens, and the spines of 14-15 mm *G. ventralis* are barely perceptible. *Gymnocanthus* is relatively slender with a semi-pointed snout; it develops dorsal (at least *G. tricuspis*), ventral, and lateral midline pigment. Although it shares some characters with *Myoxocephalus*, grouping the two does not seem warranted. The spacing of the ventral series of midline melanophores somewhat resembles the situation in *Myoxocephalus*. General shape of species of the two genera is also similar although *Myoxocephalus* is much spinier. Some figures indicate that *Gymnocanthus* has a preanal fin fold as do at least some *Myoxocephalus*.

Myoxocephalus (Figure 8) may have four to six preopercular spines, two of which may be auxiliary. Larvae are moderately slender with a semi-pointed snout. Two distinct larval forms (subgenera?) occur in the genus. Those with dense lateral pigment in the region posterior to the anus (*M. polyacanthocephalus*, *M. scorpius*) and those with only ventral midline pigment postanally (*M. aeneus*, *M. octodecemspinosus*). Another relatively unpigmented species, *M. quadricornis* (marine form), develops a lateral midline pigment series. The spacing of the ventral midline melanophores is similar in all species as is gut pigment. The fan-shaped pectoral fin is obvious early in development (at least in some species) and a preanal fin fold is present (in some or maybe all species). The pattern of preopercular spination is unusual. All species apparently have four principal spines but some may have one or two posteriorly directed auxiliary spines anterior to and near the base of the second principal spine and/or an auxiliary spine ventral and adjacent to the fourth principal spine (Laroche[6]). Development of this unusual pattern has not been adequately described for any species of *Myoxocephalus* and needs closer examination. Auxiliary preopercular spines are unknown in other genera except ?*Malacocottus*, which has an anteriorly directed accessory spine at the base of the second preopercular spine.

Radulinus (Figure 9) is a heavily pigmented form with four preopercular spines (never pronounced), relatively pointed snout, slender body (*R. boleoides* is deeper bodied than *R. asprellus*), and long gut. It shares the characters of pointed snout and slender body with Group 2 (*Paricelinus* et al.) but differs too much (longer gut, heavier pigmentation, reduced prominence of preopercular spines) to be part of that group. It shares a few similarities with the dark species of *Myoxocephalus*, including a series of ventral midline melanophores on the tail beyond the lateral pigment (in larvae <8-9 mm NL) and a relatively

[6]J. L. Laroche, Research Assistant, Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564, pers. commun. September 1978.

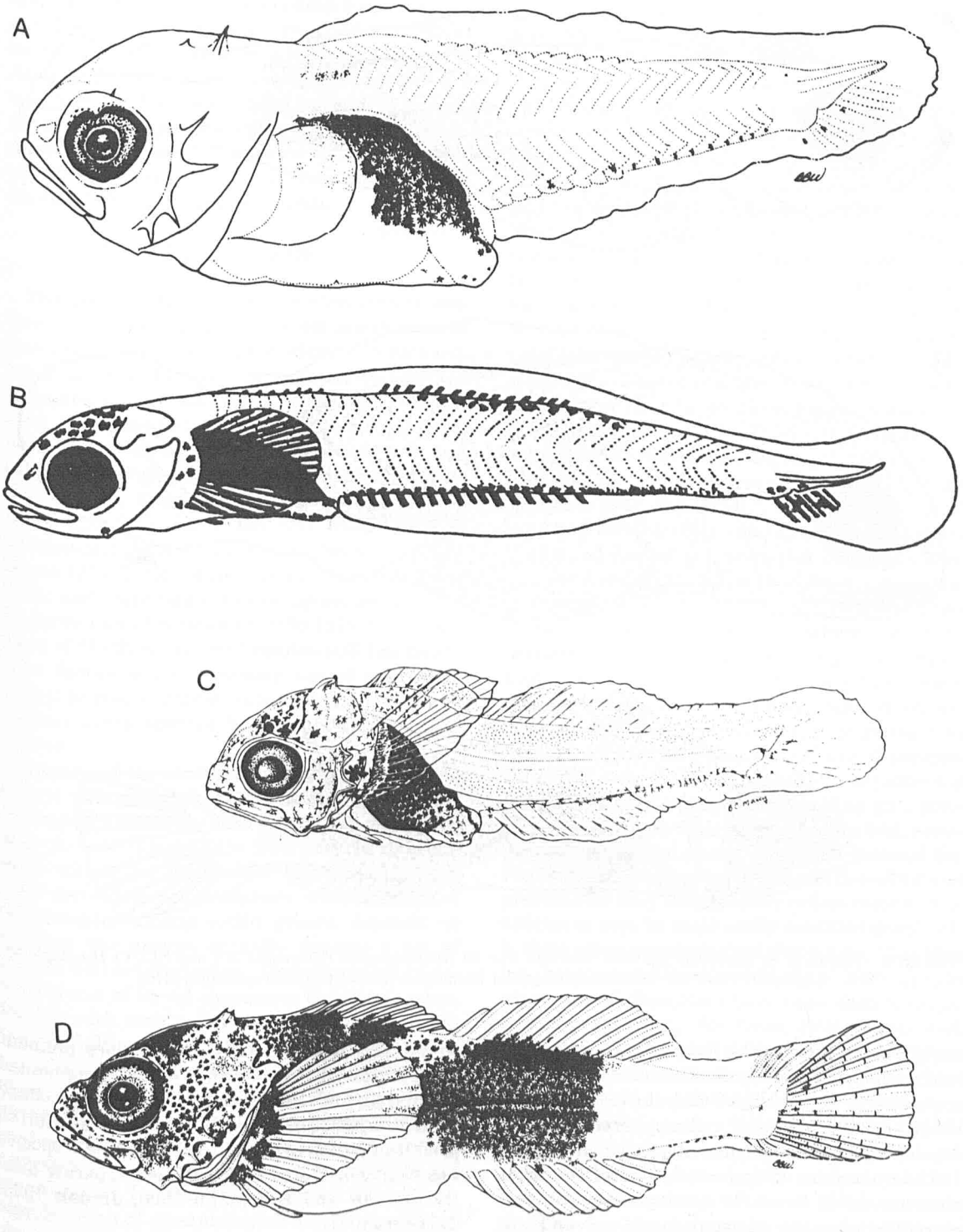

FIGURE 8.—Larvae of A) *Enophrys bison* (7.0 mm NL), B) *Gymnocanthus tricuspis* (13.9 mm), C) *Myoxocephalus aeneas* (8.5 mm TL), D) *M. polyacanthocephalus* (12 mm SL) (A, Richardson and Washington 1980; B, Khan 1972; C, Lund and Marcy 1975; D, original illustration).

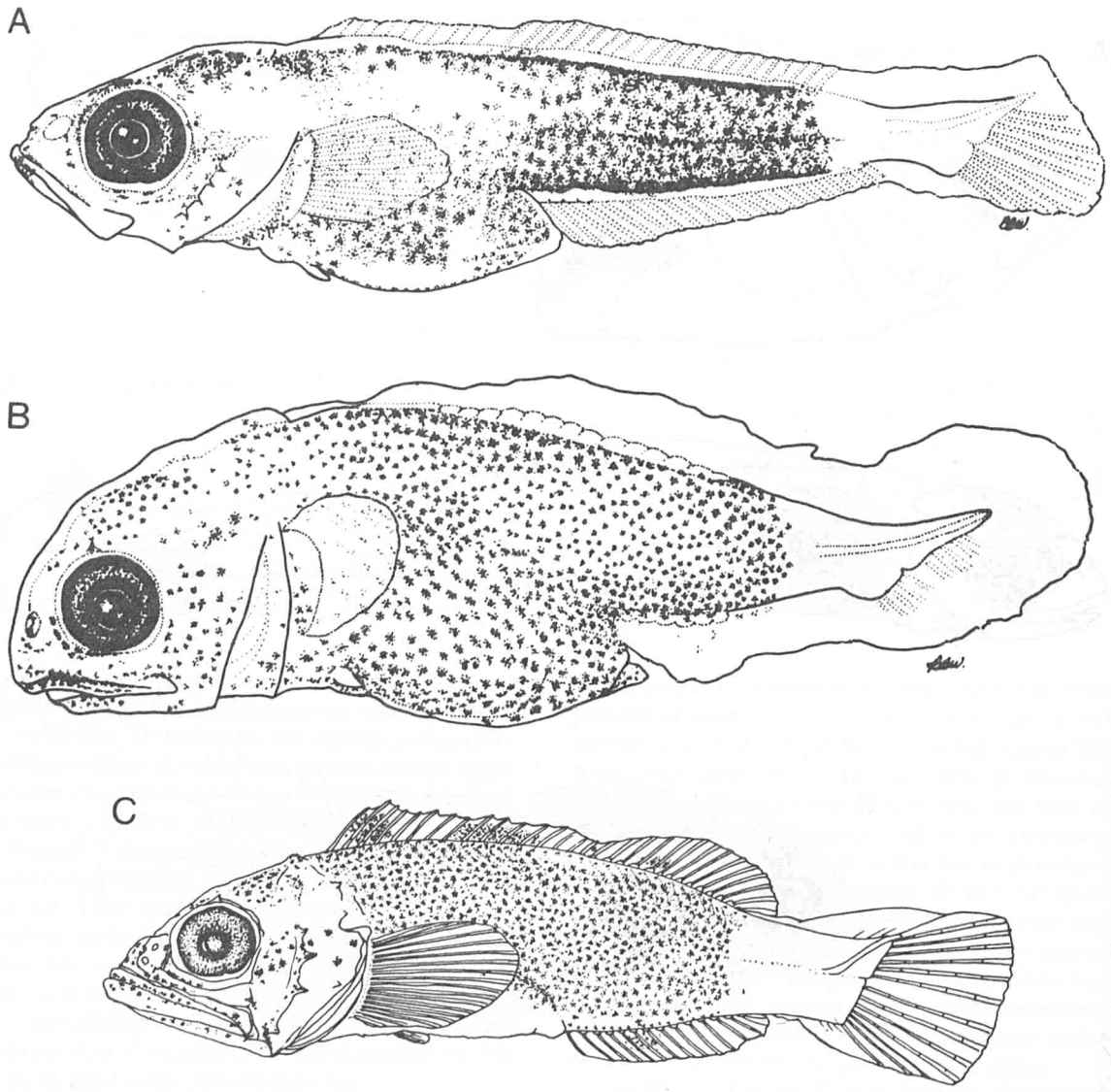

FIGURE 9.—Larvae of A) *Radulinus asprellus* (10.9 mm NL), B) *Rhamphocottus richardsoni* (8.4 mm NL), C) *Hemitripterus villosus* (17.4 mm SL) (A, B, Richardson and Washington 1980; C, Okiyama and Sando 1976).

unpigmented area on the body above the abdominal cavity. Small larvae also resemble *Scorpaenichthys* except that they have a distinct lateral midline series of melanophores and soon develop a pointed snout and more slender body.

Rhamphocottus (Figure 9) is one of the most aberrant cottid forms. It develops only one preopercular spine, an unusual snout, a deep body, heavy pigmentation, and a preanal fin fold. At small sizes, ca. 6-7 mm NL, it bears some resemblance to *Scorpaenichthys* in pigmentation and shape, but it has a longer gut, more pigment ventrally along the head and gut, and a pigmented preanal fin fold. By 8-9 mm SL, the distinct shape of *Rhamphocottus* is obvious and spinelike prickles develop over the body. The single species has been considered to represent a separate family (Jordan and Evermann 1898; Jordan 1923; Taranets 1941).

Hemitripterus (Figure 9) is also a heavily pigmented and distinct form. Based on the literature (Table 1), it has four preopercular spines, a moder-

ately pointed snout, relatively deep body, and long gut. Larvae are quite large, ca. 12-14 mm NL, at hatching. The larvae of *H. americanus* from the Atlantic and *H. villosus* from Japan (Table 1) are very similar. The heavy body pigment is a character shared with a number of apparently unrelated cottid genera. The genus was considered to constitute a separate family, Hemitripteridae, by Jordan (1923) and Taranets (1941).

DISCUSSION

The present state of cottid systematics is confused and the group and its allies are in need of intensive study (Nelson 1976; Howe and Richardson footnote 3). Family limits are not well defined (compare, e.g., Jordan 1923; Berg 1940; Taranets 1941; Greenwood et al. 1966; Bailey et al. 1970; Nelson 1976). Some genera still need revision and potential new species remain to be described (e.g., Nelson 1977; Richardson and Washington 1980; Howe and Richardson footnote 3). Studies of intergeneric relationships have been few (e.g., Regan 1913; Taranets 1941; Bolin 1947; Watanabe 1960) and these had many disagreements (Table 3). Jordan and Evermann's (1898:1879-1800) comment of North American Cottidae still has merit, "The family is an extremely varied one which cannot be readily thrown into subordinate groups. Almost every species has an individuality of its own...."

Because of the confused state of cottid systematics it seems reasonable to consider whether this preliminary summary of 25 genera of cottid larvae may provide insight into intergeneric relationships within the group. Whether these phenetically derived larval groupings are indicative of relationships among cottid genera depends on whether the groups actually possess a set of shared, derived characters. Determination of derived states of larval characters is difficult when dealing with such a diverse group as the cottids and their allies because the larvae of many species are still unknown and complete developmental series have not been described for many other species. Such determinations are further hindered by the confused state of adult cottid systematics. Although an in depth analysis of derived character states is beyond the scope of this study, consideration of several factors allows discussion of the potential significance of, and possible relationships within, at least some of the larval cottid groups described here. Larval characters such as spine patterns, relative body form, and pigmentation have been used to demonstrate or clarify systematic relationships in other groups of fishes, e.g., scorpelarchids (Johnson 1974), gonostomatids (Ahlstrom 1974), myctophids (Moser and Ahlstrom 1974), myctophiforms (Okiyama 1974), marine teleosts in general (Ahlstrom and Moser 1976), bothids (Futch 1977), scombroids (Okiyama and Ueyanagi 1978), serranids (Kendall 1979). In these studies, similarity of larval form has been in remarkable agreement with relationships implied from adult characters. Although larval characters have not been used previously as indicators of relationship (i.e., based on synapomorphies) among cottids, it seems highly probable that at least some of these characters would be as useful in cottids as in other groups of fishes. In addition, if the cottids were derived from an ancestral stock related to the Scorpaenidae, the most generalized group in the Order Scorpaeniformes (Gill 1889; Taranets 1941; Bolin 1947) and if Bolin's (1947) ancestral cottid form is valid and *Scorpaenichthys* closely resembles the primitive condition, then primitive or derived states of at least some larval characters of cottids can be postulated. Primitive states of larval characters may include four strong preopercular spines, relatively deep but compact body, compact gut, lack of gut diverticula, possession of a preanal fin fold, rounded snout, relatively short pectoral fin. Derived character states may include reduced size and/or numbers of preopercular spines or modification of the basic pattern of four, slender or globose body, trailing gut, presence of gut diverticula, no preanal fin fold, semipointed or pointed snout, elongated pectoral fin. Pigment patterns are more difficult to evaluate as presumably they may possibly reflect responses to habitat or may be more easily modified geneticaly than other morphological characters. This idea has been generally discredited in other groups where larval characters have been used to imply relationships (e.g., Ahlstrom 1974; Moser and Ahlstrom 1974; Kendall 1979) as pigment patterns have substantiated findings based on other characters. Recent experiments on larvae of the zebrafish, *Brachydanio rerio*, (Milos and Dingle 1978) have demonstrated constancy in numerical regulation of melanophores which indicates larval pigment patterns may not be as plastic as once thought. Among the cottids, *Scorpaenichthys* is heavily pigmented but *Enophrys*, also considered to be a relatively primitive form (Sandercock and Wilimovsky 1968), is not. Heavy pigmentation

seems to be related to a neustonic habitat in some (e.g., *Scorpaenichthys*, *Hemilepidotus*) but not others (e.g., *Radulinus*). Relative constancy of pigment pattern (such as presence or absence of lateral pigment posterior to the anus) within a group used in conjunction with other characters, however, may provide additional evidence for within-group relationships.

If this line of reasoning and these assumptions are valid, then certain trends seem apparent which may be indicative of relationships. Group 1 (*Artedius* et al.) appears to be a natural group sharing a number of derived characters not present in any other group or genus (i.e., multiple preopercular spines, somewhat trailing gut, unusual gut diverticula, or at least bulging guts). A preanal fin fold is apparently absent and pigment pattern is relatively constant. The grouping agrees with findings of Taranets (1941), in part, and Bolin (1947), who considered the genera to be closely related (Table 3). It seems to be a rather specialized group as Bolin (1947) implied, and, based on the distinctiveness of larval characters, may warrant consideration at possibly the subfamilial level.

Group 2 (*Paricelinus* et al.) shares the derived slender body form with pointed snout, and also possesses relative constancy of pigmentation, i.e., no lateral pigment. Relationships among at least some of the genera in this group have been implied previously (Table 3). The distinctiveness of larval form within this group suggests a separate lineage; this group may warrant possible subfamilial status.

In Group 3, all but *Dasycottus* share a highly modified larval form tending in degrees toward globose. The constancy of the pigmented pectoral fin is unique among all groups or genera considered. With the possible exception of *Dasycottus*, the genera appear to bear at least some relationship to each other.

Group 4 is the most generalized in that a number of primitive character states are exhibited and relationships cannot be assessed on given present

TABLE 3.—Intergeneric relationships of cottids as interpreted by A = Regan (1913), B = Taranets (1941), C = Bolin (1947), and D = Watanabe (1960). Included are only those 25 northeast Pacific genera for which larvae are known and discussed in this paper. Parentheses indicate a more distant relationship.

Genus	*Artedius*	*Blepsias*[1]	*Chitonotus*	*Clinocottus*	*Cottus*	*Dasycottus*	*Enophrys*	*Gilbertidia*[4]	*Gymnocanthus*[5]	*Hemilepidotus*[6]	*Hemitripterus*[6]	*Icelinus*	*Icelus*	*Leptocottus*	*Malacocottus*	*Myoxocephalus*	*Nautichthys*	*Oligocottus*	*Orthonopias*	*Paricelinus*	*Psychrolutes*	*Radulinus*	*Rhamphocottus*[7]	*Scorpaenichthys*[8]	*Triglops*[9]
Artedius	***																								
Blepsias[1]		***																							
Chitonotus	B,[2](C)		***																						
Clinocottus	B,[3]C			***																					
Cottus					***																				
Dasycottus						***																			
Enophrys					A		***																		
Gilbertidia[4]						B		***																	
Gymnocanthus[5]									***																
Hemilepidotus	(C)		(C)							***															
Hemitripterus[6]		(A),D									***														
Icelinus	B,[2](C)		B,C							(C)		***													
Icelus	B[2]		B							D		A,B	***												
Leptocottus					B		C							***											
Malacocottus						B,D		B							***										
Myoxocephalus							B									***									
Nautichthys		A,C,D									(A),D						***								
Oligocottus	B,[3]C			B,C	A		A											***							
Orthonopias	B,[3]C			B,C														B,C	***						
Paricelinus																				***					
Psychrolutes						B		B							B						***				
Radulinus	(C)		C							(C)		C										***			
Rhamphocottus[7]												A	A										***		
Scorpaenichthys[8]										A										(C)				***	
Triglops[9]												A	A										A		***

[1]Considered in family Blepsiidae by Taranets (1941).
[2]*Artedius* as *Ruscarius*, *Ruscariops* of Taranets (1941).
[3]*Artedius* including *Aryias*, *Allartedius*, *Astrolytes*, *Parastrolytes* of Taranets (1941).
[4]Considered in subfamily Gilbertinae by Watanabe (1960).
[5]Considered in subfamily Gymnocanthinae by Watanabe (1960).
[6]Considered in family Hemitripteridae by Taranets (1941).
[7]Considered in family Rhamphocottidae by Taranets (1941).
[8]Considered in order Notothenliformes by Taranets (1941).
[9]Considered in subfamily Triglopsinae by Watanabe (1960).

knowledge. Group 5 shares derived character states of a very elongate, slender body form and reduced prominence of preopercular spines; it also exhibits relative constancy in pigment pattern suggesting relationships between the genera. The relatively large hatching size (>7 mm NL) of larvae in Group 6 represents another specialization indicative of relationship; such a large size is not known in any of the other genera except *Hemitripterus* whose larvae are ca. 12-14 mm NL at hatching. Group 6 genera share a somewhat elongate form and constancy of pigmentation, i.e., lack of lateral pigment, although these characters alone do not provide strong evidence of relationship. That the six ungrouped genera did not share a set of derived characters suggests that they bear no close relationship with one another.

In summary, this preliminary examination of larval characters within 25 genera of cottids has provided some new insights into cottid systematics. Larval evidence seems to support current concepts of generic limits in most instances (e.g., *Enophrys*, *Hemitripterus*, *Hemilepidotus*) and has indicated a potentially new northeast Pacific genus represented by "Cottoid Type A." Larval characters offer support for the distinctiveness of some genera (e.g., *Rhamphocottus*) and strong relationships among others (e.g., the *Artedius* group). Some of the larval groupings discussed here tend to support previously implied relationships within the cottids (compare Tables 2 and 3) but some important differences seem apparent [e.g., the distinctiveness of Group 1 demonstrated herein; the separation of *Artedius* and *Icelus*, once considered closely related (Jordan 1923); the relationship of *Paricelinus*, generally considered a primitive and rather distinct form (Bolin 1947; Sandercock and Wilimovsky 1968), with other members of Group 2; the apparent relationship of *Icelus* to other genera in Group 2 and its questionable placement in a separate family (Jordan 1923; Greenwood et al. 1966); the distinctiveness of *Radulinus*, previously considered related to *Chitonotus* and *Icelinus* (Bolin 1947)]. Because of the wide diversity of form among cottid larvae, they offer great potential for helping to clarify relationships and evolutionary trends within this difficult group of fishes. However, larvae of many species remain to be described (rearing may be the best approach), generic limits of larval characters must be defined, and developmental sequences including osteology need to be examined before that potential can be fully realized.

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GROWTH AND AGE STRUCTURE OF LARVAL ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*, IN THE SHEEPSCOT RIVER ESTUARY, MAINE, AS DETERMINED BY DAILY GROWTH INCREMENTS IN OTOLITHS[1]

DAVID W. TOWNSEND[2] AND JOSEPH J. GRAHAM[3]

ABSTRACT

Larval Atlantic herring, *Clupea harengus harengus*, were sampled in the Sheepscot River estuary, Maine, using both towed, and buoyed and anchored plankton nets from October 1978 to March 1979, to determine growth rates and age structure. Larval densities and length-frequency distributions, determined from the buoyed and anchored net samples, and the ages of larvae captured in the towed nets, as determined by daily growth increments in the otoliths, showed that there were at least two normally distributed age-groups of larvae which entered the estuary in November and December. The two groups hatched during early October and late November, and each appeared in the estuary when about 4 weeks old. Each of the two age-groups of larvae experienced a reduction in growth rate during the latter half of January and early February. The older of the two groups grew approximately 2.1 mm per week from October to early January and from late February to early March. These older larvae grew little if any, during the midwinter period. The younger of the two groups of larvae showed a similar reduction in growth rate during midwinter and grew about 2.0 mm per week before and about 1.5 mm per week after this period.

Research on larval Atlantic herring, *Clupea harengus harengus* Linnaeus, has been conducted extensively in the western North Atlantic in recent years. This has resulted in numerous accounts of the abundance and distribution of the larvae, as well as estimates of the generalized growth rates. The growth of Atlantic herring larvae in the Gulf of Maine-Bay of Fundy areas has been reported by Tibbo et al. (1958), Tibbo and Legaré (1960), Das (1968, 1972), Sameoto (1972), Graham et al. (1972), and Boyar et al. (1973). These workers used the length-frequency method to determine average growth rates of the larvae. Various studies on the seasonal abundance and size distribution of Atlantic herring larvae have shown that in some years there may be more than one mode in the length-frequency distribution for a particular time and geographical area (Tibbo et al. 1958; Tibbo and Legaré 1960; Das 1968, 1972; Graham et al. 1972; Boyar et al. 1973; Graham in press), indicating multiple spawnings. These polymodal length-frequency distributions of Atlantic herring larvae complicate growth rate estimates since an individual sample may not represent a single homogeneous group of larvae.

A relatively new technique for studying the growth of larval fishes was introduced by Pannella (1971, 1974). He observed daily growth increments in the otoliths of some tropical and low-temperature adult fishes. Brothers et al. (1976) and Struhsaker and Uchiyama (1976) verified the daily nature of these growth increments in several species of larval fishes. Subsequently, others applied this technique to age and growth studies (Ralston 1976; Taubert and Coble 1977; Barkman 1978). Rosenberg and Lough[4] used otoliths to age larval Atlantic herring from Georges Bank. The purpose of our study was to use the otolith aging technique to investigate the growth of Atlantic herring larvae in the Sheepscot River estuary of Maine and to examine the age structure of the larvae entering the estuary.

METHODS

Larval herring were sampled in the Sheepscot River estuary of Maine using both towed, and

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[4]Rosenberg, A. S., and R. G. Lough. 1977. A preliminary report on the age and growth of larval herring (*Clupea harengus* L.) from daily growth increments in otoliths. ICES C.M. 1977/L:26.

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buoyed and anchored plankton nets. Shaw[5] has shown that when used at night there is a little, if any, difference between these gear with regard to catch rates or larval fish avoidance. Only the samples collected by the towed nets were used for otolith analysis. These towed net samples were collected at night on seven occasions from 24 October 1978 to 6 March 1979 using a 1 m, 0.75 mm mesh plankton net. One daytime sample (10 January) was taken with a 61 cm bongo net with 0.505 mm mesh nets on each side. Buoyed and anchored net samples were collected from 5 October 1978 to 27 February 1979 as part of the regular larval Atlantic herring monitoring program conducted by the Maine Department of Marine Resources. The buoyed and anchored nets consisted of six lines of nets fished at four stations in the estuarine channel. Each line had four 0.5 m, 0.75 mm mesh nets, with a digital flowmeter mounted in each net. The nets were set at dusk and retrieved at dawn each sampling date, and fished approximately one semidiurnal tidal cycle. The buoyed and anchored net samples were preserved in 5% Formalin[6] and length-frequency distributions and catch rates for larval Atlantic herring determined. The characteristics and performance of the buoyed and anchored nets were reported by Graham and Venno (1968), Graham and Davis (1971), and Graham (1972).

The larvae from the towed samples were not preserved, but were sorted within 2 h of collection, placed in plastic Petri dishes, and frozen fresh at −18° C for future otolith analysis. The samples were later thawed and each fish measured to the nearest 0.5 mm. Figure 1 shows that the frozen larvae shrink an average of about 1-2 mm more than Formalin preserved larvae. The sagittae, or largest otoliths, from both sides of the head were teased onto a microscope slide under a binocular microscope. The otoliths were mounted in Permount and covered with a glass coverslip. The numbers of daily growth increments in one of each pair of sagittae were counted under a compound microscope at 1,000 × magnification. The increments were counted twice and their mean number computed. Only those otoliths in which there was a difference between counts of 5% or less were used in the analysis. These data were used to estimate daily growth rates and age composition of the larvae. The daily growth increments in larval Atlantic herring otoliths show up very clearly, and only 17 of the 317 larvae examined had otoliths with increments too faint to be counted accurately.

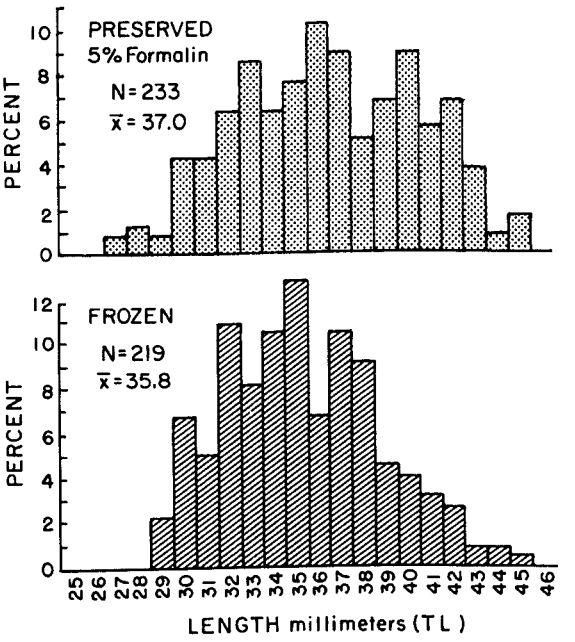

FIGURE 1.—Length-frequency comparison of 5% Formalin preserved versus frozen Atlantic herring larvae captured with 61 cm bongo nets on 4 April 1980 in the Damariscotta River estuary, Maine. Larvae from the starboard net were preserved in Formalin and larvae from the port net were frozen. Measurements were performed 2 mo later. A modified t-test (Snedecor and Cochran 1967) showed that the two means were significantly different ($P < 0.01$).

RESULTS

Larval Age Structure

Changes in modal lengths of larvae during autumn and winter indicate that groups of larvae entered the estuary and subsequently lost their identities through differential mortality and growth, since the larvae are not known to depart the estuary once established there (Graham et al. 1972). Length-frequency data from the buoyed and anchored net samples (Figure 2) showed a trimodal length distribution (range 6-30 mm) for larvae present in the Sheepscot River estuary on 19 October. A large group of smaller larvae entered on 2 November when only a trace of the

[5]Richard F. Shaw, Ph.D. candidate, Department of Oceanography, University of Maine at Orono, Ira C. Darling Center, Walpole, ME 04573, pers. commun. May 1980.

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

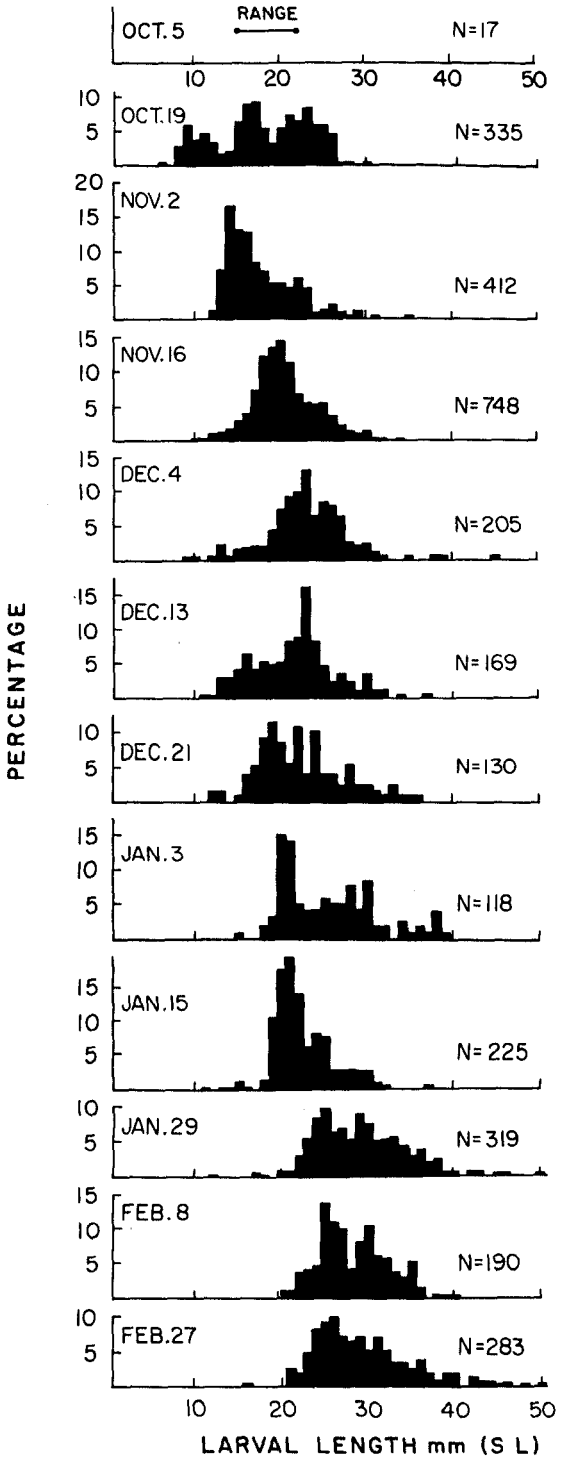

FIGURE 2.—Length-frequencies of Atlantic herring larvae captured at night in the buoyed and anchored nets in the Sheepscot River estuary, Maine, 5 October 1978 to 27 February 1979.

larger larvae from the 19 October population remained. By 16 November there was only one major size mode of larvae in the estuary. During December a second size mode of smaller larvae began to appear and in late December and early January at least two modes were present. By 27 February the two modes were no longer distinguishable. The appearance of the larval group in December was also evidenced by a leveling off of the decline in larval catch rate for that month (Figure 3). The catch rates then increased in January as the second group became established in the estuary.

Assuming the otolith growth increments are deposited with a daily periodicity, increment counts can be used to estimate larval age and growth rates. Figure 4 shows the age structure of the Atlantic herring larvae captured with the towed net in the estuary. The larger and presumably older larvae represented in the 19 October sample of the buoyed and anchored nets (Figure 2) were not detected in the towed net samples; there appeared to be only one major age-group of larvae occupying the estuary through November. The addition of the second age-group of larvae was readily apparent by 10 January and resulted in a shift of the age-frequencies to the reader's right. This second and younger group of larvae was present until the last sampling date (6 March), when the remnant larvae from the first group were detected as a negative skewness in the age-frequency histogram.

The bottom panel of Figure 4 shows the bimodal

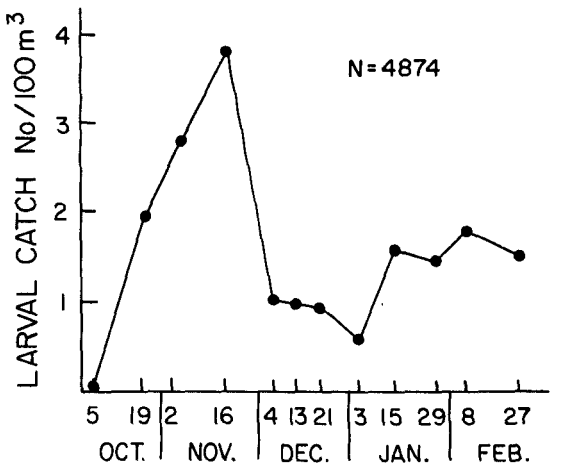

FIGURE 3.—Catch rates of Atlantic herring larvae for the buoyed and anchored nets in the Sheepscot River estuary, Maine, based on flowmeter readings.

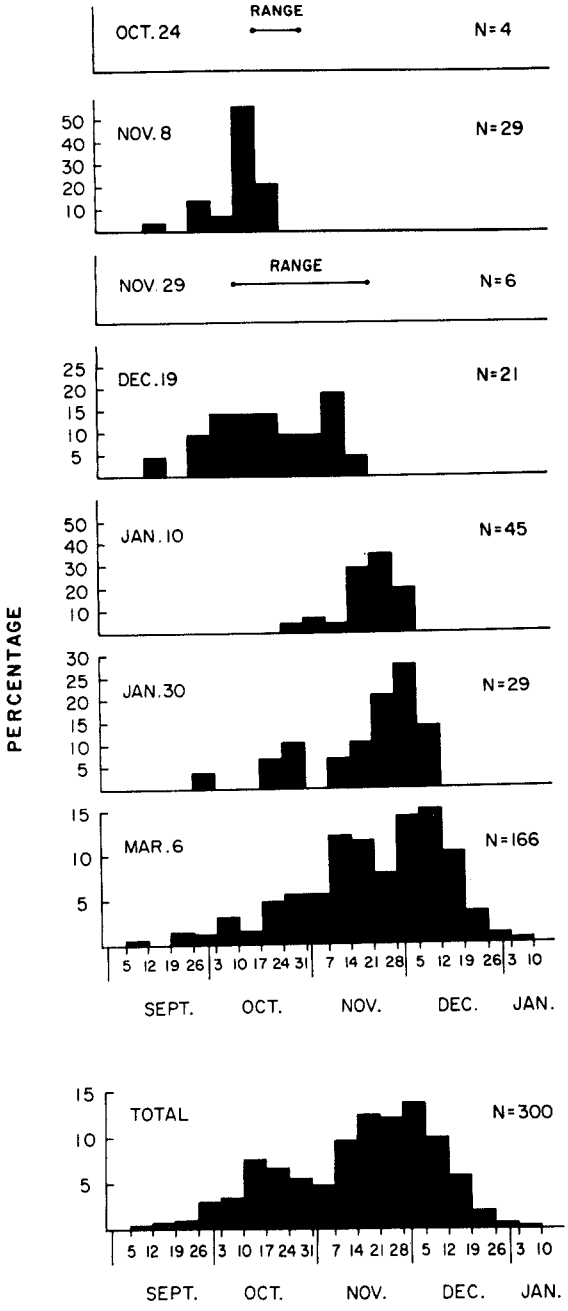

FIGURE 4.—Age distributions of Atlantic herring larvae caught in the towed nets as determined by daily growth increments in the otoliths. The ages are represented as the times of first daily growth increment formation. The distributions for the individual sample dates and the total for all the sample dates are given. The dates on the abscissa correspond to the time of formation of the first otolith daily growth increment. These dates are determined by subtracting the number of days, represented by the number of otolith increments, from the date of capture. Two modes are apparent in the total histogram.

age distribution of larvae from all the towed samples. This bimodal age-frequency distribution was analyzed graphically by the method of Harding (1949) (Figure 5). The total age-frequencies were plotted on probability paper as cumulative percentages, and were found to fall on a sigmoidal curve having a point of inflection on the 32% vertical. The fitted line EF in Figure 5 is the resultant of the two straight lines AB and CD which were found by assuming the data to be bimodally distributed (see Harding 1949 for a more complete discussion). Line AB represents those larvae (about 32% of the total) in which the first otolith growth increment was deposited before 30 October. This date is approximately the point of inflection of the plotted data. Line CD represents the second, younger group of larvae (about 68% of the total). The two straight lines, AB and CD, indicate that the two groups of Atlantic herring larvae which entered the estuary were normally distributed with respect to age. The mean dates on which the first otolith growth increments were laid down for each age-group were determined by the intersection of lines AB and CD with the vertical at 50%. The standard deviations of these dates were estimated from the points where the two lines intersect the verticals at 15.87% and 84.13%, the standard deviation being half this distance on the *Y*-axis. The mean dates on which the first daily growth increments were laid down were approxi-

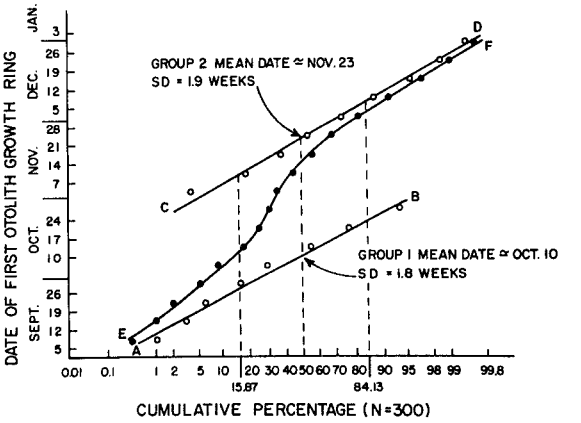

FIGURE 5.—Probability plot of the total bimodal age distribution of Atlantic herring larvae depicted in Figure 4. The dots are the dates on which the first otolith daily growth increment was formed in each larva and are plotted as cumulative percentages. The circles are the cumulative percentages for each of the 2 age-groups using the inflection point of the sigmoidal curve as a dividing point for the two groups. See text for explanation.

mately 10 October for the first group of larvae and 23 November for the second. This analysis indicates, along with the length-frequency data (Figure 2) and the larval catch rates (Figure 3), that there were at least two peaks in spawning effort along the Maine coast, separated by about 6 wk, and that the two groups of larvae entered the estuary at separate times. The times of hatching for each group of larvae can be approximated by assuming that the first otolith daily growth increment is formed at the time of yolk-sac absorption (Rosenberg and Lough footnote 4) and allowing about 5 d for yolk-sac absorption at 10° C (Blaxter and Hempel 1966). The two broods of larvae which entered the estuary in November and December were probably hatched, therefore, in early October and mid-November, and were probably spawned in late September and early November.

Larval Growth Rates

Growth of the larvae was examined separately for each of the two major age-groups which entered the estuary. The first group included those in which the first otolith daily growth increment was laid down before 30 October, which is the dividing point between the two age distributions discussed above. The second group of larvae included those in which the first daily growth increment was laid down on or after 30 October.

Both age-groups of larvae experienced approximately a 2-3 wk period of retarded growth. The changes in growth rate appeared as breaks in the plotted data in Figures 6 and 7. Figure 2 showed also that modal lengths increased only slightly, if at all, from 29 January to 27 February. The first major group of larvae to enter the estuary showed retarded growth (Figure 6) beginning at a length of about 35 mm and about 80-100 d after 10 October, the mean date on which the first otolith daily growth ring was formed (Figure 5). Thus, this period of retarded growth began during the latter half of January and continued until early February. The second major group to enter the estuary showed retarded growth (Figure 7) beginning at a length of about 26 mm, and 50-60 d after 23 November, the mean date of the first otolith daily growth ring for group 2 (Figure 5). This period of retarded growth also began during the latter half of January and continued until early February. It appears, then, that these two groups of larvae, which differed in age by about 6 wk and in length by about 9 mm, experienced similar reductions in their growth rates during the same period in late January and early February. Apparently the environment at this time was not conducive to their growth.

Assuming that growth was interrupted during late January and early February for each of the 2 age-groups of larvae, regression lines were calculated for those larvae caught before the interruption in growth and for those caught after. The larvae caught 30 January were therefore not included (Figures 6, 7). The slopes and elevations of the two regression lines for each age-group were compared using the t-test described by Zar (1974: 228-230). There was no significant difference between slopes for group 1 but the elevations differed significantly ($P<0.01$). The two regression lines for group 2 differed significantly in slope ($P<0.05$) and in elevation ($P<0.01$). Group 1 larvae, then, grew about 2.1 mm/wk before and after the interrupted growth period. Group 2 larvae grew approximately 2.0 mm/wk before this period and about 1.5 mm/wk after.

DISCUSSION

Previous workers have reported polymodal length-frequency distributions of Atlantic herring larvae in the Gulf of Maine-Bay of Fundy areas (Tibbo et al. 1958; Das 1968; Graham et al. 1972; Boyar et al. 1973). Graham et al. (1972) detected two broods of Atlantic herring larvae during September 1964 in the Boothbay area of the western Gulf of Maine, which includes the Sheepscot River estuary. The two broods were indicated by length-frequency modes of 9 and 13 mm. They reported that in 1965 only a single brood was detected in the area initially and that a second group of smaller larvae appeared in November. They suggested that the variations in lengths of the larvae might be attributed to the location of the Boothbay area within a coastal zone of transition in hatching times. Atlantic herring larvae hatch earlier in the eastern coastal Gulf of Maine than in the west, and may be carried westward and into the Boothbay area by coastal currents (Graham 1970; Graham et al. 1972). This may explain the variation in modal sizes on 19 October when the buoyed and anchored nets (Figure 2) captured larvae recently hatched (<10 mm) and others obviously older. The two groups of larvae captured in November and December (Figures 2, 4) perhaps also drifted along the coast before entering the estuary, since each group was about 4 wk old when first sampled.

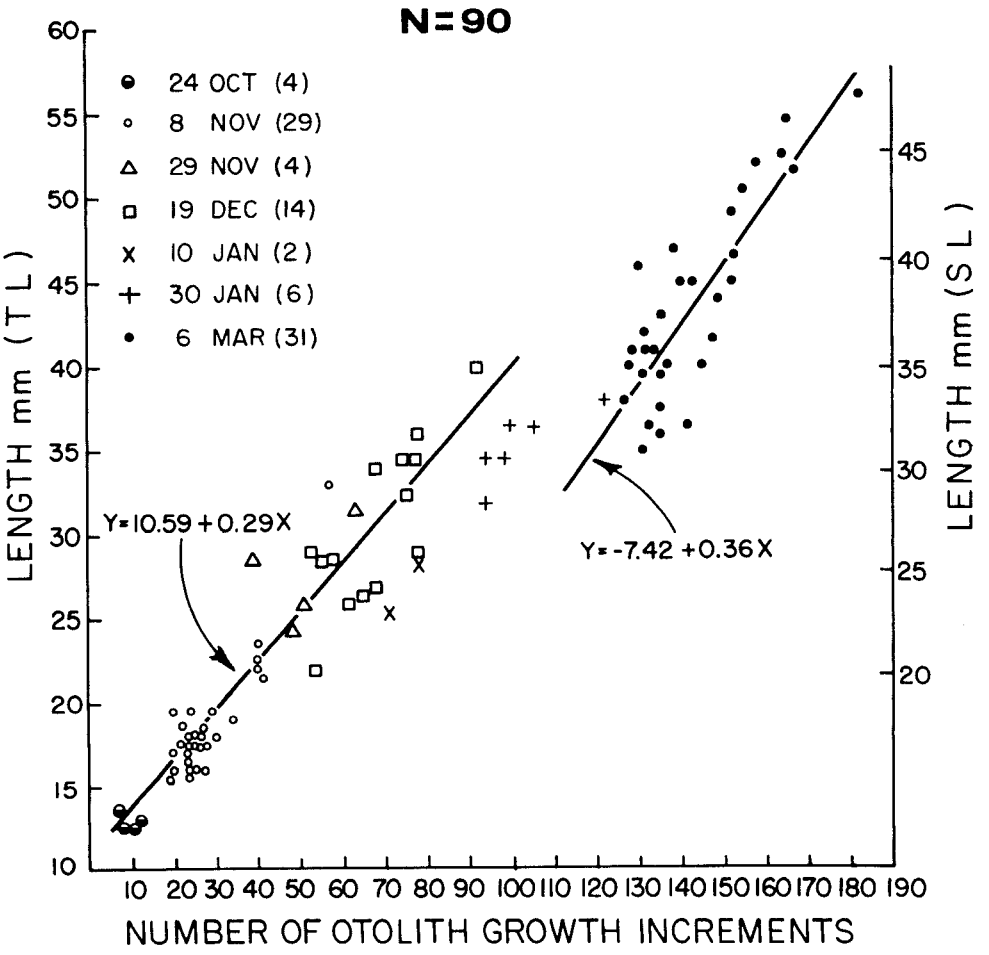

FIGURE 6.—Growth of the first group of Atlantic herring larvae which entered the Sheepscot River estuary, 1978-79. This includes all larvae from the towed net samples in which the first otolith daily growth increment was formed before 30 October. The plotted symbols indicate the collection date and the numbers in parentheses indicate sample size. Regression lines were calculated for the samples collected before and after the winter period of interrupted growth and the 30 January samples were therefore not included.

The growth rates of Atlantic herring larvae in the Sheepscot estuary as determined using daily growth increments in the otoliths were about 2 mm/wk, excluding the winter period of retarded growth. The growth rate of group 2 larvae, however, was lower after this period. Our estimates of larval growth rates, excluding the retarded growth period, are comparable with autumn and spring values reported by other workers (Table 1). Rosenberg and Lough (footnote 4) used daily growth increments in the otoliths to study the growth of Georges Bank herring larvae. The larvae were from a short sampling period (1-18 October 1976), but the authors estimated the growth rate to be about 2.4 mm/wk. This October growth rate estimate is greater than our fall and spring estimates, possibly the result of different water temperatures. The relatively wide range in esti-

TABLE 1.—Published growth rate estimates for fall spawned Atlantic herring larvae in the northwest Atlantic.

Growth rate (mm/wk)	Method used	Period studied	Source
1.7	Mean lengths	First 150 days	Tibbo et al. 1958
<1	Mean lengths	Oct.-June	Sameoto 1971, 1972
1-2	Mean lengths	Nov.-Mar.	Boyar et al. 1973
1.4-1.8	Mean lengths	Sept.-Dec.	Graham et al. 1972
2	Modal lengths	Sept. and Oct.	Das 1968, 1972
<1	Modal lengths	Winter	Das 1968, 1972
1.5	Modal lengths	April	Das 1968, 1972
2	Modal lengths	May	Das 1968, 1972
2.4	Larval otoliths	1-18 Oct.	Rosenberg and Lough 1977

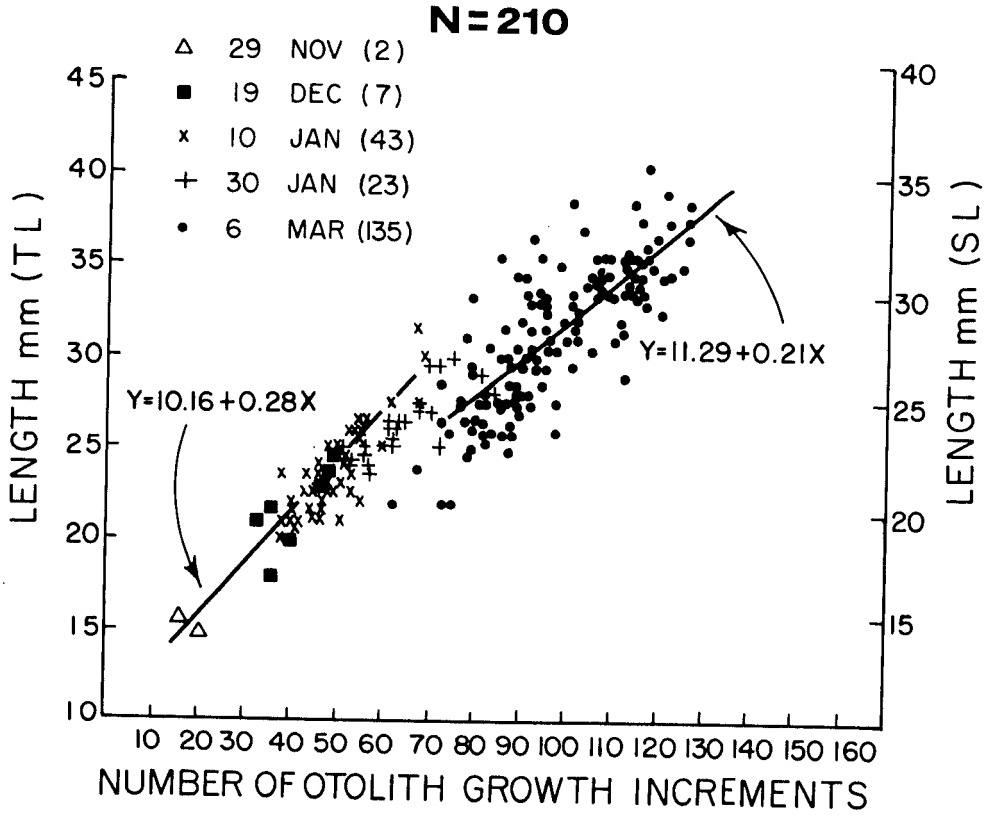

FIGURE 7.—Growth of the second group of Atlantic herring larvae which entered the Sheepscot River estuary, 1978-79. This includes all larvae from the towed net samples in which the first otolith daily growth increment was formed on or after 30 October. The plotted symbols indicate the collection date and the numbers in parentheses indicate sample size. Regression lines were calculated for the samples collected before and after the winter period of interrupted growth and the 30 January samples were therefore not included.

mates reported by others were perhaps developed from samples containing more than 1 age-group. Such combinations are difficult to distinguish in length-frequency data as pointed out by Das (1968, 1972) and Graham et al. (1972). Graham (in press) reported that from one to as many as four broods of larvae entered the Sheepscot estuary annually in recent years.

The winter retardation of larval growth rate observed in the Sheepscot estuary (Figures 6, 7) was more brief than the general slowing down of growth throughout the winter reported by others (Tibbo et al. 1958; Das 1968, 1972; Graham et al. 1972; Boyar et al. 1973). The duration of slowed growth lasted only 2 or 3 wk, from the latter half of January to early February, and occurred approximately when the second group of larvae was abundant in the estuary, but the exact cause of the retarded growth is not clear. Midwinter in general has been shown to be a period of stress for larval herring. Chenoweth (1970) showed that the relative condition of Atlantic herring larvae was poorest in February 1965, 1966, and 1967 and in January 1968 and that these periods of low condition factors coincided with the high mortalities reported by Graham and Davis (1971). Midwinter is a time when food densities are lowest (Sherman and Honey[7]), when water temperatures approach the lethal limit (Graham and Davis 1971) and when the feeding activity of the larvae is lowest (Sherman and Honey 1971). Any or all of these factors may have contributed to the period of retarded growth of larvae in our study.

In conclusion, it appears that the ages of larval herring determined by the otolith growth incre-

[7]Sherman, K., and K. Honey. 1970. Seasonal succession of the food of larval herring in a coastal nursery area. ICNAF Res. Doc. 70/72.

ments are in good agreement with the observed progression of length-frequencies with time, and that such precise age determinations hold much potential for further work on the dynamics of larval fishes. However, it would be advisable to investigate further, under controlled laboratory conditions, the factors controlling the growth of Atlantic herring larvae and otolith growth increment deposition.

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FEEDING SELECTIVITY OF SCHOOLS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Direct field measurements of the feeding of five schools of northern anchovy over four sets of conditions indicate consistent size-selective feeding on the dominant zooplankton taxa. At low-to-moderate prey concentrations (10-40 mg carbon per cubic meter), the schools consumed 35-50% of the total zooplankton biomass and >90% of the largest zooplankters present. The schools' feeding was a positive function of prey size primarily. The density of particular prey items did not significantly affect feeding selectivity. The northern anchovy fed preferentially upon a particular species in only one instance. No significant difference was found in the selectivity of two northern anchovy schools composed primarily of late 0-group and II-group fish, respectively, that were feeding under similar feeding conditions. At prey concentrations of 10-40 mg carbon per cubic meter, the degree of selectivity was inversely related to the size of the largest prey available. The prey size at which consumption is predicted to be 100% was proportional to the size of the largest prey.

Field studies have demonstrated that planktivorous fish can control zooplankton community structure in oligotrophic lakes and stocked fish ponds by selectively feeding upon the larger, more visible prey organisms (see Gliwicz and Prejs 1977 and Dodson 1979 for a critical discussion of this work). However, while highly productive regions in the world's oceans typically support large populations of schooling, planktivorous fish, the impact of these fish populations upon marine zooplankton communities is not known.

Taking as an example the estimated consumption of zooplankton by the northern anchovy, *Engraulis mordax*, in the Southern California Bight, it becomes clear that marine fish populations may have considerable impact on the zooplankton in the system. The prey consumption of the northern anchovy may be calculated based upon data for the biomass of the population, its annual reproduction and growth, and assumptions concerning its metabolic efficiency. The results of this calculation can then be compared with estimates of zooplankton production in the region.

In the Southern California Bight, the spawning biomass of the northern anchovy in the mid-1960's to early 1970's averaged between 1.32 and 2.35×10^6 t over a 40×10^3 km^2 area or 1.34-2.25 g C/m^2 (calculated from Smith 1972). *Engraulis mordax* spawns approximately 20 times annually and produces 389 eggs/g wet weight at each spawning (Hunter and Goldberg 1980). Averaged over the year, this is equivalent to a daily production rate of 0.43%, based upon a dry weight per egg of 0.030 mg (Hunter and Leong[2]) or 0.20 mg wet weight (assuming a 15% wet weight:dry weight conversion): $[(389 \times 20 \times 0.2 \times 10^{-3})/365] \times 100 = 0.43$.

The growth rate of the northern anchovy past the first year of life is negligible, approximately 0.08%/d from the end of the first year to the end of the third year (calculated from Sakagawa and Kimura 1976). The total daily production of the adult northern anchovy is thus approximately 0.43% + 0.08% = 0.51%. Assuming a 10-30% efficiency of food conversion (Paloheimo and Dickie 1966 and references therein; Jones and Hislop 1978; Lane et al. 1979), mature northern anchovy consume 1.7-5.1% of body weight daily: $0.51 \times 1/0.30 = 1.7$; $0.51 \times 1/0.10 = 5.1$. [The food consumption rate for 0-group northern anchovy is considerably greater since the daily growth rate during the first year is about 6.1% (calculated from Sakagawa and Kimura 1976).] The mature northern anchovy stock therefore consumes

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[2]Hunter, J. R., and R. Leong. The spawning energetics of female northern anchovy, *Engraulis mordax*. Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

0.02-0.11 g C/m^2 per d. Primary production in the Bight averages 0.5-1.0 g C/m^2 per d (Eppley et al. 1979). The northern anchovy feeds primarily upon zooplankton. Assuming a 20% conversion of primary to secondary production, the spawning population of *E. mordax* consumes 10 to >100% of secondary production in the Southern California Bight. This figure appears to give the right order of magnitude, since >80% of acoustic targets from pelagic surveys in this area are estimated to be northern anchovy schools (Mais 1974). It should be noted that the Southern California Bight appears to be an area of net zooplankton consumption, since zooplankton densities are typically greater in the California Current north of the Bight than in the Bight itself (Reid 1962). Presumably the zooplankton are being consumed as they are carried into the area. The northern anchovy also supplements its diet by filter feeding on phytoplankton.

If the feeding of the northern anchovy is size selective, its impact on the community of zooplankton could be considerable. Furthermore, the northern anchovy population is, relatively speaking, not all that large. The population of the Peruvian anchovetta, which is predominantly phytophagous but is a zooplankton feeder in certain areas and at certain stages of its life history (Rojas de Mendiola 1971), is estimated to have been an order of magnitude more densely concentrated (Walsh et al. 1980).

Most quantitative studies of the feeding selectivity of marine fish have been conducted in the laboratory with small groups of fish (Leong and O'Connell 1969; O'Connell 1972; Durbin and Durbin 1975). This permits only a crude approximation of their impact upon marine systems, where these fish populations are predominantly found in massive shoals. For example, approximately 90% of the biomass of the northern anchovy population is found in schools >25 t (calculated from Hewitt et al. 1976). While Eggers (1976) modelled the energetics of planktivorous fish schools using the extensive literature on the feeding of individual fish, there is no experimental data on the feeding of fish schools to test such models. Without better data on the feeding of schooling fish on the zooplankton, contemporary models of marine zooplankton community dynamics have perforce concentrated upon interactions among the lower trophic levels (Steele 1974; Steele and Frost 1977).

I report here the results of in situ measurements of the feeding selectivity of schools of *E. mordax* in the nearshore waters of the Southern California Bight. These represent the first direct quantitative field measurements of the feeding of schools of planktivorous fish.

METHODS

A vessel with side-scanning sonar and echo sounder was used to track and determine the dimensions of large (25-200 t), near-surface schools of northern anchovy. A school was considered appropriate for study when 1) the school was near the surface and of sufficient size (>50 m along the axis perpendicular to the school's movement) that plankton samples could unequivocally be taken in its wake, 2) the school did not show signs of being disturbed by the ship's presence, and 3) the school was either directly observed to be feeding (October 1976) or its general configuration and movement were consistent with feeding behavior. It was assumed that when feeding, a school would either form an amorphous "ball" (Radakov 1973) or that its long axis would be normal to its axis of motion (Weihs 1973), and that the school's velocity would not exceed several body lengths per second.

When a school was selected for study, a cruciform drogue with surface buoy was dropped into its center. The school's movements in relation to the drogue were monitored for 10-25 min, during which time the school usually moved 100 to several hundred meters from the drogue. A weighted buoy was then placed over the school. Thus a transect was established, over which the school had passed while presumably feeding. The school's physical dimensions and swimming speed relative to the water could be determined using the ship's sonar, echo sounder, and by timing the school's movement between the two buoys.

In general, the sampling regimen consisted of taking two replicate samples with zooplankton nets first in the wake of the school between the buoys and then in "control" areas either in front of or several hundred meters to the side of the school. The nets were lowered obliquely from the surface to the average depth of the school (as determined by echo sounder), towed at that depth for 2 min, and then hauled to the surface (total length of tow about 100 m). A 0.5 m diameter plankton net (102 μm mesh) with a TSK[3] flowmeter was towed in a harness with a 1.0 m

diameter (505 μm mesh) net with a digital meter. Zooplankton samples were obtained successfully on four cruises conducted in the spring, summer, and fall of 1975-76. All sampling was conducted in daylight hours. Samples of the northern anchovy from the schools were taken by a commercial purse seiner on all but one cruise (April 1976) for positive species identification, analysis of their size composition, and examination of gut contents.

The sampling scheme varied slightly on several of the cruises: 1) The data from April 1976 represent the results of four replicate tows taken in the wake of the school and three control tows, rather than the two replicates taken for each set of tows on other cruises. 2) On the last cruise of October 1976, the concentration of plankton was measured before and after a school passed through a single patch of water. The control tows were taken first, directly in front of the school; the second set was obtained after the school had passed through the same area. 3) On the first cruise of August 1975, the 0.5 m diameter net was used alone. However, no large zooplankters were found in the samples from this cruise, and those collected were well within the net's range of maximal efficiency, as determined by comparison of catches from this net and the larger, 1 m net on subsequent cruises.

Analysis of the plankton samples consisted primarily of determining the size-frequency composition of the zooplankton in the wake of the school as compared with its composition in control tows. I selected for analysis dominant species from the major taxa of zooplankton occurring in the samples (i.e., copepods, chaetognaths, cladocerans, and larvaceans (Table 1)). Species were also selected on the basis of size, so that representatives of the smallest and largest commonly occurring zooplankters in each set of samples were enumerated. Following Cassie (1968), aliquot size was determined to count 20-50 organisms/size category; size categories with actual counts <10 were lumped with the adjacent size category. Copepods were enumerated by life history stages, other organisms by body length. To facilitate comparison, results were converted whenever possible to micrograms carbon (μg C) using conversions obtained from the literature for *Calanus* (Mullin and Brooks 1976), microcopepods (Landry 1976, 1978; Bartram et al.[4]), and *Sagitta* (Reeve 1970; Sameoto 1971). The total zooplankton biomass in the plankton samples was determined from displacement volumes of the samples taken with the 0.5 m diameter net; these values were converted to milligrams carbon per cubic meter (mg C/m^3) (Wiebe et al. 1975).

TABLE 1.—Plankton biomass and genera enumerated from control samples of plankton tows taken around northern anchovy schools in the nearshore zone of the Southern California Bight.

Cruise	Biomass (mg C/m^3)	Genera enumerated	
		Microzooplankton	Macrozooplankton
Aug. 1975	[1]41	*Acartia* *Paracalanus* *Sagitta* (≤3 mm) *Oikopleura*	None
8 Mar. 1976	[2]663	*Evadne*	None
9 Mar.	[2]639	*Evadne*	None
Apr.	[1]33	*Acartia* *Sagitta* (0-3 mm)	*Calanus* *Sagitta* (≤12 mm)
Oct.	[3]10	*Acartia* Combined *Paracalanus-Clausocalanus-Ctenocalanus* Harpacticoids and cyclopoids	None

[1]Moderate.
[2]High.
[3]Low.

RESULTS

Characteristics of Northern Anchovy Schools

The estimated biomass of the five schools studied ranged from 25 to 200 t (Table 2). The length of the schools (the dimension normal to the school's motion) varied by a factor of 4 (55-200 m). The breadth of the schools (the dimension parallel to the school's axis of motion) was generally less than their length and varied by less than a factor of 2 (30-55 m). The breadth of a feeding school, as a function of the number of fish from front to back, is critical to the degree the school depletes the plankton. The lesser variability in the breadth of the schools may result from behavioral regulation of this parameter, which determines the relative difference in feeding conditions encountered from front to back of the school. However, these data are inadequate to

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

[4]Bartram, W. C., D. M. Checkley, and J. F. Heinbokel. 1976. Further use of a deep tank in the study of the planktonic food chain. IMR Rep., IMR Ref. 76-7, p. 157-166. Institute of Marine Resources A-018, University of California, San Diego, La Jolla, CA 92093.

TABLE 2.—Characteristics of northern anchovy schools examined for feeding selectivity: overall school biomass, physical dimensions, velocity and prey consumption, number measured, and mean and range of standard lengths of *Engraulis mordax* within the schools.

Cruise	a Biomass (t wet wt.)	b Dimensions (m) Length	c Front-back	d Vertical	e Velocity (m/s)	f Plankton consumption (mg C/m³)	g Body wt. consumed/h[1] (%)	*n*	Standard length (mm) $\bar{x}$ ±95% C.L.	Range
Aug. 1975	[2]42	200	30	6	—	20.5	—	20	115.20±5.02	96-139
8 Mar. 1976	[3]25	35	35	[4]26	—	—	—	55	122.84±29.17	83-148
9 Mar.	[3]50	55	[4]55	20	0.29	—	—	16	98.25±6.37	84-127
Apr.	[2]125	100	40	40	0.38	14.85	1.0	—	—	—
Oct.	[3]200	[5]200	[4]40	20	—	3.47	—	54	99.48±1.52	90-144

[1]Percentage body-weight consumed/h = [(volume swept clear/h)(food removed/unit volume)/(school biomass)] × 100
= [(π(0.5b)(0.5d)(e × 60²)(f × 10⁻³)/(a × 10⁶ × 0.05)] × 100.

[2]Estimated from physical dimensions, density of 1.5 kg/m³ (Hewitt et al. 1976), and assuming actual shape to be cylinder (August 1975) or oblate spheroid (April 1976).

[3]Fisherman's estimate based on purse seining of school.

[4]Back-calculated from tonnage, physical dimensions, and assumptions of average school density = 1.5 kg/m³ and of a cylindrical (October 1976) or oblate spheroidal (March 1976) school shape.

[5]Estimate.

evaluate relations between feeding conditions and school size and configuration.

Samples of the northern anchovy were obtained from four of the schools. Two of the schools were composed of northern anchovies that had completed approximately 1 year's growth (98-99 mm SL); the other schools were composed of predominantly I-group (115 mm SL) and II-group (123 mm SL) northern anchovies (Table 2; Sakagawa and Kimura 1976). Since the schools composed of the largest and smallest fish were sampled under the same feeding conditions (i.e., the spring diatom bloom dominated by cladocerans of March 1976; Tables 1, 3), the feeding selectivity of large and small northern anchovies can be compared.

TABLE 3.—Ivlev's Electivity Index (E) as computed from the frequency of size classes of *Evadne* spp. examined in northern anchovy stomach contents and plankton tows taken in vicinity of the two schools sampled on 8 and 9 March 1976.

Date	Body length (μm)	Stomach samples (n = 10) Total count	Proportion in ration (r)	Plankton tows Replicate sample counts	Proportion in tows (p)	$E = (r-p)/(r+p)$
8 Mar.	200-299	9	0.036	44; 30	0.10	−0.47
	300-399	75	.30	145; 101	.33	−.05
	400-499	42	.17	132; 59	.26	−.21
	500-599	70	.28	83; 53	.18	.22
	600-699	37	.15	57; 33	.12	.11
	700-899	15	.060	2; 2	.0054	.83
	Total	248		741		
9 Mar.	200-299	4	.03	15; 14	.14	−.64
	300-399	10	.08	19; 13	.16	−.35
	400-499	30	.23	24; 15	.19	.09
	500-599	35	.27	42; 24	.32	−.10
	600-699	33	.25	23; 11	.17	.20
	>700	19	.15	4; 0	.02	.76
	Total	131		204		

Feeding of Northern Anchovy Schools

The impact of the schools' feeding could be clearly determined from the plankton samples during all sampling periods except those of March 1976. In all 40 size categories of prey enumerated from August 1975 and April and October 1976 cruises, the median concentration was less in tows taken in the wake of the school than in control tows (Table 4). These data were analyzed as the fraction consumed [= 1 − (density of organisms in wake of school)/(density in controls)] as a function of the prey organisms' body size.

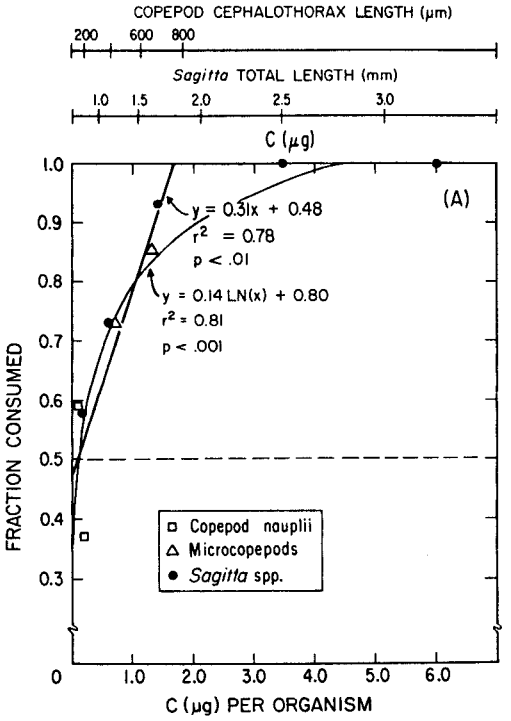
In computing regressions to analyze the feeding selectivity of the northern anchovy schools, it was often not clear either by eye, through analysis of residuals, or from the significance level of the regression whether a linear or curvilinear relationship best fit the data (Figure 1). In these instances, two regressions were performed: a linear regression and a regression in which the independent variable (i.e., prey body size) was $\log_e$-transformed. In computing the linear regressions (Figure 1), data points are excluded past the first size class at which the school has effectively consumed all the plankton (i.e., when consumption is >90%). An arcsine transformation was not performed, although it has been recommended for regressions performed on data expressed as fractions or percentages (Sokal and Rohlf 1969). The arcsine transformation did not significantly affect the form of the regressions presented below and only slightly enhanced their significance level. The data are therefore presented untransformed (Figure 1).

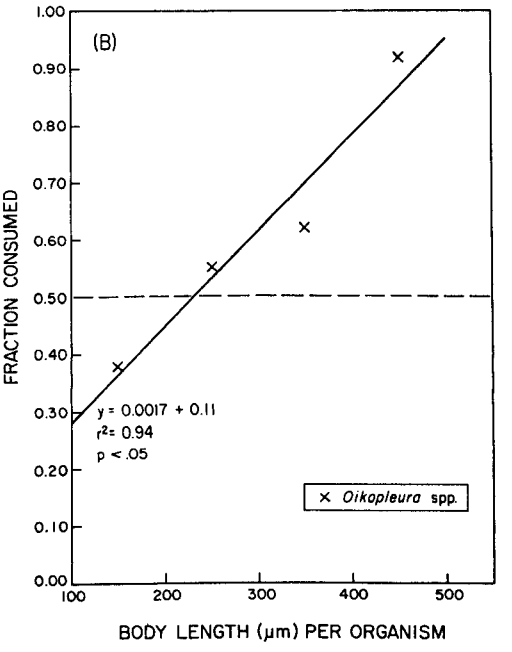
There was consistently a significant positive relationship between the fraction consumed and the size of the anchovy's prey on the cruises (Figure 1), despite the diversity of prey items within each cruise and the considerable differences in the composition and density of the zooplankton between cruises (Tables 1, 4). The fraction consumed ranged from 10-30% for the smallest organisms enumerated to 95-100% for

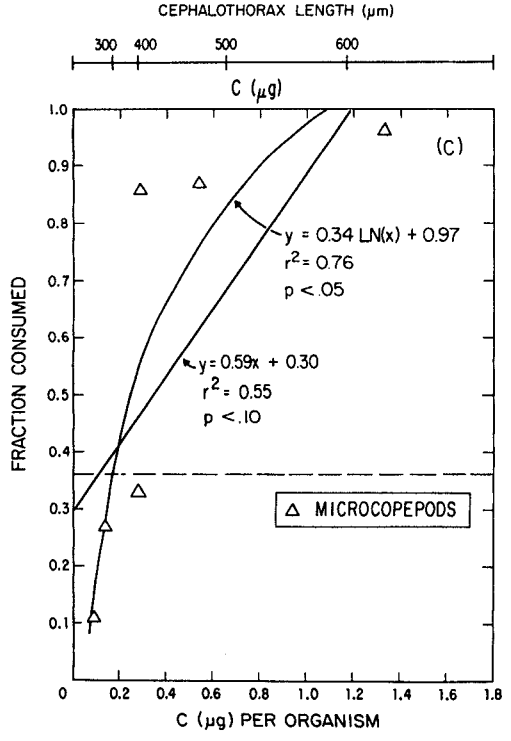
TABLE 4.—Sample counts, density (numbers and biomass per cubic meter), and fraction consumed of prey items examined from control plankton tows and tows taken in the wake of northern anchovy schools, August 1975 and April and October 1976.

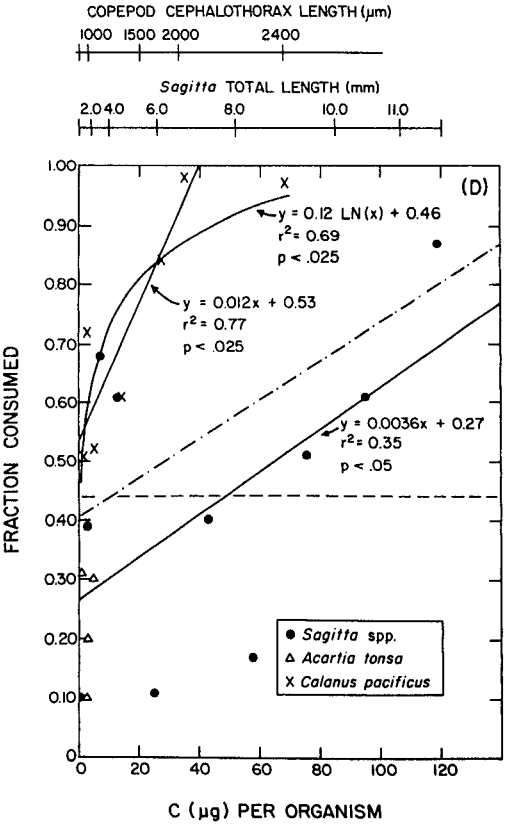
			Control tows				Behind-school tows				
Prey organisms	Size class	Body weight (μg C)	Replicate sample counts	Abundance (no./m³) Median	Abundance (no./m³) Range	Median biomass (μg C/m³)	Replicate sample counts	Abundance (no./m³) Median	Abundance (no./m³) Range	Median biomass (μg C/m³)	Fraction consumed
August:											
Euterpina acutifrons	Total Nauplii	0.10	128; 87	13,300	9,830-16,700	1,330	36; 45	5,430	5,370-5,500	543	0.59
Acartia tonsa	Total Nauplii	0.21	275; 302	35,000	34,100-35,900	7,360	135; 197	22,100	20,600-23,500	4,630	.37
Paracalanus parvus	CIII-VI	0.70	34; 53	209	178-240	165	9; 12	56.1	55.0-57.3	44.3	.73
A. tonsa	CIII-VI	1.35	136; 209	828	711-944	1,120	16; 31	122	97.7-148	166	.85
Sagitta spp.	500-999 μm	0.19	33; 11	111	49.7-172	21.1	12; 4	46.2	19.1-73.3	8.88	.58
	1,000-1,499 μm	0.62	264; 145	1,020	655-1,380	631	67; 31	279	148-409	173	.73
	1,500-1,999 μm	1.38	32; 20	129	90.4-167	178	2; 1	8.50	4.80-12.2	11.7	.93
	2,000-2,999 μm	3.42	14; 12	31.9	27.2-36.6	109	0; 0	0	.00-.00	0	1.00
	>3,000 μm	6.08	9; 12	50.6	47.0-54.2	308	0; 0	0	.00-.00	0	1.00
Oikopleura spp. (Trunk length)	<200 μm		64; 22	217	99.4-334		27; 22	135	105-165		.38
	200-299 μm		58; 51	267	230-303		25; 18	119	85.9-153		.55
	300-399 μm		15; 10	61.8	45.2-78.4		3; 6	23.5	18.3-28.6		.62
	>400 μm		6; 10	38.3	31.4-45.2		1; 0	3.10	.00-6.10		.92
April:											
A. tonsa	CI-IV	1.1	42; 38; 26	19.7	19.4-33.6	21.6	21; 15	13.6	13.1-14.1	15.0	.31
	CV	2.3	91; 34; 20	17.6	14.9-72.7	40.5	21; 20	15.8	14.1-17.5	36.4	.10
	CVI ♂	3.2	424; 279; 114	144	84.9-339	461	172; 130	115	114-116	368	.20
	CVI ♀	4.25	211; 294; 134	152	99.8-169	646	204; 85	106	74.5-137	451	.30
Calanus pacificus	CI	1.4	32; 203; 19	25.6	14.1-105	35.8	20; 13	12.4	11.4-13.4	17.4	.51
	CII	2.6	31; 173; 26	24.8	19.4-89.5	64.5	14; 5	6.89	4.38-9.40	17.9	.72
	CIII	4.9	44; 68; 30	35.2	22.3-35.2	172	31; 14	16.6	12.3-20.8	81.1	.52
	CIV[1]	14	481; 466; 297	30.9	27.8-46.6	433	137; 137; 164; 147	12.1	11.1-14.8	169	.61
	CV[1]	27	222; 136; 114	10.7	9.00-21.5	289	12; 16; 21; 34	1.69	.97-2.60	45.6	.84
	CVI ♂[1]	35	55; 35; 46	4.31	2.32-5.33	151	1; 0; 2; 1	.08	.00-0.16	2.80	.98
	CVI ♀[1]	68	45; 25; 27	2.53	1.66-4.36	172	1; 0; 1; 11	.08	.00-0.84	5.44	.97
Sagitta spp.	1.0-1.9 mm	0.96	29; 19; 54	23.2	9.8-40.2	22.3	16; 35	20.7	10.7-30.7	19.9	.11
	2.0-2.9 mm	3.22	43; 26; 40	29.8	13.4-34.4	96.0	31; 18	18.3	15.8-20.8	58.9	.39
	3.0-3.9 mm	7.13	33; 22; 23	17.1	11.4-26.4	122	7; 7	5.42	4.70-6.13	38.6	.68
	4.0-4.9 mm	12.9	16; 21; 9	12.8	6.70-10.9	165	11; 3	5.01	2.63-7.39	64.6	.61
	5.0-6.9 mm	25.5	16; 16; 9	8.28	6.70-12.8	211	9; 10	7.40	6.04-8.76	189	.11
	7.0-7.9 mm[1]	43	21; 19; 10	1.26	0.94-2.03	54.2	13; 10; 6; 2	.76	.15-1.08	32.7	.40
	8.0-8.9 mm[1]	58	30; 23; 10	1.52	0.94-2.91	88.2	15; 12; 13; 19	1.26	1.02-1.45	73.1	.17
	9.0-9.9 mm[1]	76	34; 47; 20	3.11	1.87-3.29	236	20; 12; 18; 34	1.52	1.30-2.60	116	.51
	10.0-10.9 mm[1]	95	47; 56; 35	3.71	3.28-4.55	352	25; 6; 14; 23	1.43	.65-2.03	136	.61
	≥11.0 mm[1]	119	35; 45; 21	2.98	1.97-3.39	355	9; 1; 3; 7	0.39	.11-0.73	46.4	.87
October:											
Harpacticoids and cyclopoids	100-299 μm	0.09	46; 34	585	476-694	52.6	70; 43	523	415-631	47.1	.11
	300-499 μm	0.28	12; 7	140	98.0-181	39.2	9; 11	93.6	81.1-106	26.2	.33
A. tonsa[2]	CI-II	0.29	92; 71; 62; 52	404	286-557	117	12; 16; 12; 21	57.4	45.1-81.0	16.6	.86
	CIII-VI	1.33	35; 23; 22; 12	135	66-211	180	0; 5; 0; 1	5.45	.00-18	7.25	.96
Paracalanus-Clausocalanus-Ctenocalanus[2]	CI-II	0.14	205; 184; 182; 259	1,190	1,003-1,424	167	262; 216; 260; 202	868	764-984	122	.27
	CIII-VI	0.54	48; 64; 92; 89	418	286-509	226	15; 21; 12; 12	55.6	45.4-75.7	30.0	.87

[1]Based on CalCOFI net tows.
[2]Sample counts for *A. tonsa* and combined *Paracalanus-Clausocalanus-Ctenocalanus* are presented in pairs, representing replicate counts from the same tows.


COPEPOD CEPHALOTHORAX LENGTH (μm)
200 600 800
Sagitta TOTAL LENGTH (mm)
1.0 1.5 2.0 2.5 3.0
C (μg)
(A)
y = 0.31x + 0.48
r² = 0.78
p < .01
y = 0.14 LN(x) + 0.80
r² = 0.81
p < .001
Copepod nauplii
Microcopepods
Sagitta spp.
FRACTION CONSUMED
C (μg) PER ORGANISM


(B)
y = 0.0017 + 0.11
r²= 0.94
p < .05
× Oikopleura spp.
FRACTION CONSUMED
BODY LENGTH (μm) PER ORGANISM


CEPHALOTHORAX LENGTH (μm)
300 400 500 600
C (μg)
(C)
y = 0.34 LN(x) + 0.97
r²= 0.76
p < .05
y = 0.59x + 0.30
r² = 0.55
p < .10
△ MICROCOPEPODS
FRACTION CONSUMED
C (μg) PER ORGANISM


COPEPOD CEPHALOTHORAX LENGTH (μm)
1000 1500 2000 2400
Sagitta TOTAL LENGTH (mm)
2.0 4.0 6.0 8.0 10.0 11.0
(D)
y = 0.12 LN(x) + 0.46
r²= 0.69
p < .025
y = 0.012x + 0.53
r²= 0.77
p < .025
y = 0.0036x + 0.27
r²= 0.35
p < .05
● Sagitta spp.
△ Acartia tonsa
X Calanus pacificus
FRACTION CONSUMED
C (μg) PER ORGANISM

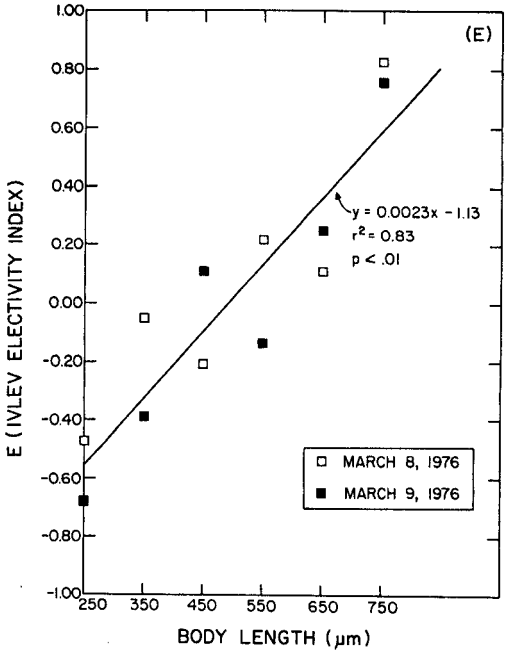


FIGURE 1.—Fraction consumed of zooplankton prey items by northern anchovy schools as a function of prey body size (A-D). Linear regressions were performed on all data sets, excluding from the regression data points past the first size class at which the school consumed >90% of prey. A curvilinear fit to the data based on a regression using a $\log_e$-transformation of values on the abscissa is shown where a curvilinear relationship provides as good or better fit. The regressions in Panels A-C include the data from each species found in the panel. In Panel D, the linear and curvilinear regressions in the upper left are based on data for *Calanus pacificus* alone; the solid lower regression is based upon data for *Sagitta* spp. and *Acartia tonsa*; the dashed oblique line is based upon the total data set for the sampling period. Dashed horizontal lines represent the fraction consumed of the total available zooplankton biomass. The significance level for each regression (which is also the significance level for each regression coefficient) is indicated. Panels: A and B—August 1975; C—October 1976; D—April 1976; E—March 1976: Ivlev's Electivity Index (E) as a function of the pigmented body length of *Evadne* spp.

the largest zooplankters (Table 4, Figure 1). Overall, the northern anchovy schools consumed 35-50% of the total available zooplankton in the areas sampled (Figure 1).

On the summer cruise (August 1975), a diverse assemblage of small plankton was present. Prey consumption appeared to be a function primarily of their size (expressed as their weight in micrograms carbon) (Figure 1A). A single regression, whether linear or curvilinear, adequately describes the northern anchovy's feeding selectivity for such morphologically dissimilar organisms as copepod nauplii, *Euterpina acutifrons* and *Paracalanus parvus*; small calanoid copepodites, *Acartia tonsa* and *P. parvus*; and small chaetognaths, *Sagitta* spp. There is no indication of species preference. Nor is there evidence that prey density significantly influenced the rate at which they were consumed. While the relative concentration of similar-sized prey items varied widely, they were consumed at equivalent rates [Table 4, compare the density and consumption of copepod nauplii and *Sagitta* spp. (0.5-1.0 mm), *P. parvus* CIII-VI and *Sagitta* spp. (1.0-1.5 mm), and *A. tonsa* CIII-VI and *Sagitta* spp. (1.5-2.0 mm)].

The data for the northern anchovy's feeding on the larvacean, *Oikopleura* spp., from the August cruise was not directly comparable to data for the other species sampled at this time because their body length cannot be converted to a carbon value for the whole organism (including "house"). However, the northern anchovy's feeding on *Oikopleura* appeared to be a linear function of prey size (Figure 1B).

The autumn cruise (October 1976) was characterized by a low density of zooplankton—the standing crop was a factor of 3-4 less than that encountered during the April 1976 and August 1975 cruises—entirely dominated by small zooplankton as in the August 1975 cruise (Tables 1, 4). Again the northern anchovy's feeding selectivity was positively related to prey size (Figure 1C). A curvilinear relationship here provides a better fit to the data.

Only on the cruise of April 1976 were both large and small zooplankton present; however, the zooplankton density was comparable to that found on the summer cruise (August 1975) (Table 1, compare the range of the prey sizes; Table 5, compare Figure 1D with Figure 1A, C). As in the summer

TABLE 5.—Maximum prey size and its density, prey size at 100% consumption by northern anchovy schools as predicted from linear regressions, and slope of linear regressions of the school's feeding selectivity of prey size.

Item	August 1975	April 1976		October 1976
		Calanus pacificus	*Sagitta* spp. and *Acartia tonsa*	
Maximum prey size (μg C)	6.08	68.00	119.00	1.33
Concentration of largest prey item (μg C/m³)	300	172	345	180
Predicted prey size (μg C) at 100% consumption	1.68	39.20	203.00	1.19
Slope of regression of feeding selectivity	0.31	0.012	0.0036	0.59

cruise (August 1975), the school's feeding on both the small copepods, *A. tonsa*, and the chaetognath, *Sagitta* spp., increased as a single function of prey weight (Figure 1D). However, the school appeared to select the larger copepod, *Calanus pacificus*, over the other prey examined from this cruise. To test for the differential feeding selectivity for *C. pacificus*, a single linear regression was performed through the pooled data for prey consumption from the sampling period (Figure 1D) (Quade 1967). All data points for *C. pacificus* and only 3 of 14 data points for the consumption of *Sagitta* spp. and *A. tonsa* lie above this regression line, indicating a significantly heterogeneous distribution of the data ($\chi^2 = 11.57$; $P < 0.01$).

For the two sets of samples collected from two different schools on consecutive days during the March 1976 cruise, no significant differences were found between the control tows and those taken in the wake of the school either in the displacement volumes or in the plankton's size-frequency composition. This cruise was undertaken during an intense spring diatom bloom; ambient plankton concentrations were a factor of 20 greater than during any other cruise. At these plankton densities, northern anchovies could fill their stomachs [ca. 5% of body weight (Rojas de Mendiola and Ochoa 1973) for *Engraulis ringens* or 0.05 g C] in approximately 40 min by simple filtration (filtering rate per individual northern anchovy = 2 l/min (Leong and O'Connell 1969)). Thus, the schools, or some part of them, may have ceased feeding. Furthermore, at these high densities of plankton, the schools would have to ingest far more material than on the previous cruises to consume a detectable fraction of the plankton. The fish stomachs examined from both schools were full, but the data on the dimensions and biomass of the schools indicate they were not significantly more densely packed. The schools had thus apparently been feeding, at least intermittently, but under these conditions, their feeding selectivity could not be determined from the plankton samples alone.

To analyze the northern anchovy's feeding during this cruise, I compared the size-frequency composition of prey in the stomach contents with that found in the zooplankton tows (Table 3). The data were analyzed using Ivlev's Electivity Index: $E = (r - p)/(r + p)$, where r = the proportion the prey item represents in the diet and p = the proportion the prey represents in the plankton samples (Ivlev 1961).

The feeding of the northern anchovy on the cladocerans (predominantly *Evadne nordmanni*), which dominated the plankton during the spring bloom was a linear function of prey size (Figure 1E). No significant difference was found between the electivity of the two schools sampled under similar conditions of food density and composition on this cruise, although northern anchovies from the school of 8 March 1976 were the largest and those sampled on the following day were the smallest encountered during the study. Their difference in mean length ($\bar{x}$ = 122.84 and 98.25, respectively) indicates the schools were composed predominantly of II-group and 0-group fish, respectively, with a difference in mean weight of approximately a factor of 2 (calculated from Sakagawa and Kimura 1976). But this difference in size apparently did not lead to a significant difference in their feeding selectivity under the sampling conditions.

Comparison of Feeding Selectivity Between Cruises

The three northern anchovy schools studied on the cruises of August 1975 and April and October 1976 each consumed approximately 100% of the largest prey available and a small fraction of the smaller prey. However, because the size distribution of available prey varied greatly between cruises, prey items that were almost entirely removed from the water when only small prey were available (e.g., the later copepodite stages of small copepods, such as *A. tonsa* or *P. parvus*, encountered during August 1975 or October 1976) were virtually ignored when larger prey were present (e.g., on the cruise of April 1976, compare Figure 1A, C with Figure 1D).

The prey size at which the northern anchovy school's consumption was approximately 100% on these three cruises (which may be defined as the intersection of the linear regressions with the line $y = 1$) varied by more than a factor of 100 (Table 5; Figure 1A, C, D). Furthermore, while the school's feeding selectivity was consistently a positive function of the prey's size, the slopes of the linear regressions from the cruises of August 1975 and April and October 1976 also varied by more than two orders of magnitude (Table 5). Both factors are related to the size range of prey available to the anchovy on these cruises, which varied to a similar degree.

There is a positive relation between the prey

size at which the anchovy school's consumption is about 100% and the size of the largest plankters enumerated (Figure 2A). The northern anchovy apparently adjusts its feeding so that it continues to select the largest prey over at least a hundred fold range in prey size. (It should perhaps be noted that the largest commonly occurring zooplankters were counted in all samples, and all were found in median concentrations of 172-345 μg C/m^3 (Table 5).) While less common, larger zooplankters may have occurred in the samples or at the sample sites, relatively rare individual prey items probably would not affect the feeding pattern of a planktivore, such as the northern anchovy.)

Similarly, the slope of the northern anchovy schools' feeding selectivity is a positive function of the inverse of the largest prey sizes occurring in the samples (Figure 2B), since $m = \Delta y/\Delta x \cong 1/x_L$, where m = the slope of the school's feeding selectivity; Δy = the difference between the fraction consumed of the largest and smallest prey ($\cong$ 1); Δx = the range (ω) in size of the prey organisms; and where the size of the largest prey, $x_L >> x_s$, the size of the smallest prey. For this limited set of observations, the relation between the slope of the schools' feeding selectivity (m), in fact, appears inversely proportional to the size of the largest prey available (x_L): the coefficient of the regression between m and $1/x_L$ is about 1 (Figure 2B). Stated another way, the northern anchovy schools' feeding selectivity over a range of conditions was related to the size of the largest prey available in significant quantity. The largest prey may be considered to be entirely consumed, and the consumption of smaller prey is approximately proportional to their size in relation to the largest prey.

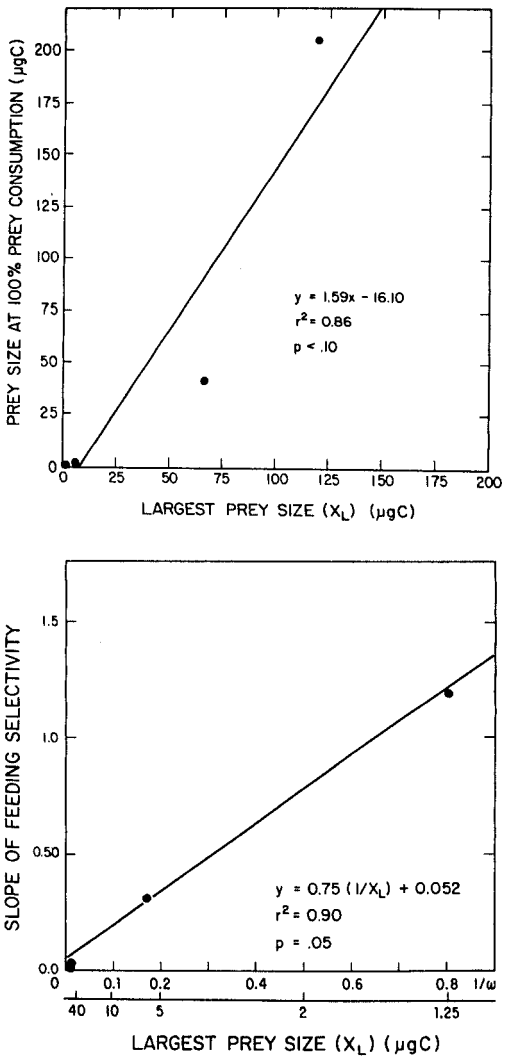


FIGURE 2.—(A) Predicted prey size at 100% prey consumption and (B) slope of feeding selectivity of northern anchovy schools (from Figure 1) as a function of, respectively, the largest prey size and the inverse of the largest prey size available in significant quantity. (See Table 4 and text for detailed explanation.)

DISCUSSION

Evaluation of the Field Method

There are several possible biasses to the field sampling method: 1) Its accuracy depends upon the choice of control samples. It is clearly preferable to sample a patch of water both before and after a school has passed through it. However, bias due to small-scale patchiness in selecting control samples on the sides of the school's path will probably lead to conservative estimates of prey consumption, since the school will presumably swim through the richest plankton patches. 2) The method would be biased to the extent that the disappearance of zooplankters in the wake of the school resulted from escape from the school rather than their consumption by it. However, this does not appear to be a significant problem, considering the large size of the fish schools sampled in this study. The range of swimming speeds of copepods is on the order of 5-50 body lengths/s (ca. 0.5-5.0 cm/s) (Enright 1977). The northern anchovy schools sampled were on the order of 50-200 m in length, 10-40 m in depth, and advanced at about 10-40 cm/s. Unless the zooplankters could detect

the school from a considerable distance, which seems unlikely, they could not escape it.

There are also advantages to the direct field sampling method: 1) It circumvents uncertainties attendant upon extrapolating from laboratory to field conditions. 2) It avoids the bias inherent in the use of fish stomachs, due to the differential digestibility of various prey organisms. This can significantly bias estimation of selective predation (e.g., see Gannon 1976). 3) It permits study of far larger aggregations than can be accommodated in the laboratory. In the Southern California Bight, approximately 90% of the biomass of the northern anchovy population is found in schools >25 t (calculated from Hewitt et al. 1976)—the size of the schools sampled in this study.

More generally, the feeding of planktivorous fish has hitherto been studied experimentally using individual or small groups of fish (Ivlev 1961; Beukema 1968; Leong and O'Connell 1969; O'Connell 1972; Ware 1972; Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976). Prey selectivity was analyzed as a complex function requiring understanding of the predator's metabolic state and the prey's size, density, and patchiness. It is an awesome, if not impossible, task to extrapolate this analysis to field situations involving 10^2-10^7 predators interacting within a school as they feed upon natural prey assemblages.

A field-oriented approach permits study of the feeding of fish schools from the perspective of a higher level of organization, as well as permitting a test of laboratory studies. Viewing the method in this context, it is important to note the close replication of results in the instance in which it was successfully repeated under a similar set of field conditions (March 1976, Figure 1E). The median significance level of the regressions (and the regression coefficients) in Figure 1 was also quite high ($P<0.025$), despite the relatively few data points on which the regressions are based and the nature of the data, which is derived from field sampling of zooplankton. The feeding of fish within large schools is sufficiently consistent that significant proportions of the variance in plankton distributions in the wake of the schools can be explained in terms of their impact.

Comparison with Other Studies

The results of the present study appear consistent in broad outline with the pattern of size-selective feeding noted in laboratory studies; i.e., prey selectivity proved a function of prey size rather than of their taxonomy (Ware 1972; O'Brien et al. 1976). This was found for a range of prey sizes and taxa (Figure 1, Table 4). Significantly enhanced consumption of a particular species was observed only once; i.e., for *Calanus* during the April 1976 cruise (Figure 1D). Since *Calanus* was encountered only on this cruise, it is not clear how much significance should be attached to this finding.

This study indicates it may be possible to predict the feeding selectivity of northern anchovy schools on the basis of data on the size of prey available to the school in significant quantity; i.e., both the slope of the northern anchovy's feeding selectivity and the size of the prey that will effectively be removed entirely from the water is a function of the largest available prey (Figure 2). This result is attractive, since data on the size distribution of the zooplankton can now be collected on a routine, continuous basis (Mackas and Boyd 1979; Herman and Dauphinee 1980).

However, experimental studies have often found that the concentrations of individual prey items significantly influence the feeding selectivity of fish (Ivlev 1961; Beukema 1968; O'Connell 1972; Ware 1972). This is presumably mediated through the varying degrees of experience the predator will have with prey at different densities. However, prey density did not appear to be a significant factor in determining the northern anchovy's prey selectivity in this study. On both the August 1975 and April 1976 cruises, small copepods and chaetognaths of equivalent body weight were consumed in approximately equal proportions (Figure 1A, D), although their relative densities frequently varied by a factor of 5 or greater (Table 4). Nor can prey density be invoked to explain the anchovy's heightened selectivity for *Calanus* (Figure 1D). The density of *Calanus* (April 1976) did not appear to differ significantly from the density of *Acartia* and *Sagitta* of similar size that were consumed to a lesser degree (Table 4).

This apparent difference between experimental and field results may arise from significant differences in the distribution of prey typically available in the two situations. In laboratory studies examining the influence of prey density on feeding selectivity, the fish are typically offered several prey items at varying densities (Ivlev 1961; Beukema 1968; O'Connell 1972; Ware 1972). Under

such conditions, the predator may form a "search image" for a particular prey item (Tinbergen 1960; also as discussed by Beukema 1968). However, planktivorous fish in marine systems typically have a wide variety of prey items available to them. Furthermore, the relative densities of different zooplankters available to the fish will vary constantly due to vertical and horizontal patchiness of the plankters' distribution, the movements of the school, and the very differences from front to back of the school created by its feeding. Thus, under most natural conditions, it may not be feasible for planktivorous marine fish to form "search images" and to select particular prey items based upon their relative abundance in the environment.

Further quantitative field studies on the feeding of marine schooling fish should enhance our understanding of the role of these planktivores in pelagic ecosystems. Particular questions to be addressed include 1) the role their feeding plays in regulating the structure of marine plankton communities, and 2) the degree to which fish populations themselves are regulated by inter- and intra-specific predation upon the early life stages. It should also be possible to study 3) the relation between planktonic conditions and the distribution and schooling behavior of planktivorous fish, which is no doubt linked to their availability to commercial fishing operations.

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BURST SWIMMING PERFORMANCE OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE

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ABSTRACT

Burst swimming performance was measured for northern anchovy larvae from 0.23 to 1.33 cm total length at a temperature of 17° C. Fast starts and burst swimming were initiated using a 3 V/cm direct current electric shock. Performance was measured from movie film recorded at 250 frames/s. Percentages of larvae responding to the stimulus increased from 9% 40 hours after eggs were spawned to a maximum of 95±4% after 125 hours. Distances traveled in a given time period increased linearly with length so that maximum speed (U_{max}) and mean speed ($\bar{U}$) similarly increased linearly with total length (L) according to $U_{max} = 20.8\,L + 1.95$; $\bar{U} = 8.18\,L + 4.89$. The maximum distance traveled per burst (S_{max}) was used as a measure of endurance and increased with length according to $S_{max} = 3.79\,L + 0.08$. These swimming speeds and endurance relationships can explain a large portion of size-dependent selectivity of towed plankton nets.

Larval swimming performance has been the focus of several studies (Blaxter 1969; Rosenthal and Hempel 1970; Hunter 1972). These have emphasized sustained swimming speeds which are considered an important factor affecting the volume of water searched by a larva, and hence food density requirements or the encounter frequency with food items. These low levels of activity apparently affect ration and at the same time are major contributors to routine energy expenditures (Vlymen 1974).

In contrast, very high activity levels (fast starts and steady burst swimming) are rare. While they are unlikely to constitute a large metabolic load, high speeds are essential to the act of capturing food items (Hunter 1972) and in escaping from predators. This aspect of larval performance has not been evaluated. Therefore, the purpose of this work was to determine the effect of size on burst swimming performance (acceleration and sprints) for northern anchovy, *Engraulis mordax*, larvae, and to evaluate the importance of such high levels of activity in prey capture and escape from predators, including nets.

METHODS

Northern anchovy larvae were reared from eggs as described by Hunter (1976). Eggs were spawned from five groups of parents taken from laboratory stocks on five separate occasions during the fall of 1979 (Table 1). Eggs were transferred to noncirculated filtered seawater in 400 l black fiber glass tanks. Food for the larvae was the dinoflagellate *Gymnodinium splendens* for 2- to 5-d-old larvae, and thereafter the rotifer *Brachionus plicatilis*. Water temperature was maintained at 17° C. Larvae were held under constant illumination from standard room fluorescent lights.

Experiments were performed on larvae of 11 different total lengths, ranging from 0.23 to 1.33 cm. Observations were concentrated on larvae in the first few days after hatching (Table 1) when greatest larval development occurs (O'Connell in press).

Groups of 5-50 larvae were observed using Schlieren optics. Details of this system are given in Holder and North (1963). Briefly, a vertical collimated light beam was produced by a high intensity monochromatic point source at the focus of a concave mirror attached to the ceiling. A second mirror on the floor focused the light on a black spot on a glass plate. The focal length of the mirrors was 140 cm.

A cylindrical tank, 17 cm in diameter and 5 cm deep, with parallel plate glass top and bottom, was introduced into the light beam. Discontinuities in

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TABLE 1.—Summary of spawning batches and dates of anchovy larvae of various total lengths used in experiments on burst swimming performance. Data for total length are $\bar{X} \pm 2$ SE.

Total length (cm)	Batch of eggs[1]	Date spawned (1979)	Number of larvae sampled
0.23±0.03	E	2 Dec.	10
0.27±0.03	B	1 Nov.	10
0.29±0.02	B	1 Nov.	10
0.34±0.05	E	2 Dec.	10
0.46±0.03	C	8 Nov.	10
0.51±0.05	C	8 Nov.	10
0.55±0.06	A	31 Oct.	10
0.65±0.06	A	31 Oct.	10
0.72±0.04	C	8 Nov.	5
1.14±0.08	C	8 Nov.	5
1.33±0.27	A	31 Oct.	5

[1]Batch D was infected by bacteria and therefore rejected.

the refractive index (e.g., larvae in water) deflected the light from the focus spot on the glass plate and were seen as bright spots against a dark background.

The stimulus initiating a maximum fast start and swimming burst was a 10 ms, 3 V/cm square wave electric shock delivered via two grids in the water bath. Responses were recorded on Kodak[3] Plus-X 16 mm movie film at a framing rate of 250 Hz. Experiments were performed at 17° C.

Movie film was analyzed frame by frame. The progression of the head was traced from frame to frame and the mean distance travelled was calculated as described by Hunter (1972) avoiding artifacts due to lateral oscillations of the head associated with propulsive movements. Speeds were calculated from the distances travelled and the elapsed time between measurements. Elapsed time was calculated from the product of number of frames between measurements divided by the framing rate.

RESULTS

The percentage of larvae responding to the nonspecific electric shock stimulus increased with age to a maximum of 88-100% (mean 95±4%; n = 7) after 125 h measured from the time of spawning (Figure 1). This corresponds to the age at which larvae raised under the same conditions begin intermittent swimming, i.e., periods of low speed swimming alternating with periods of rest (Hunter 1972).

The response to the stimulus was a fast start followed by a period of continuous high speed (sprint) swimming. Fast starts and sprint speeds

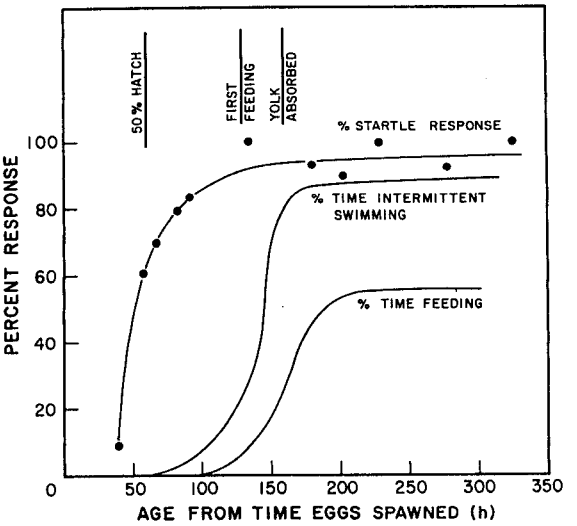

FIGURE 1.—Percentage responses (n = 20-50) to a 3 V/cm d.c. electric shock by northern anchovy larvae as a function of age, calculated from the time the eggs were spawned. The curve was fitted by eye. The curves for the time spent in intermittent swimming and in feeding are from Hunter (1972).

are defined as burst activities (see Webb 1975; Hoar and Randall 1978 for definitions). Therefore the response can be described as a burst of swimming activity.

Kinematics of larval fast starts and sprint swimming have been described in detail for zebra danio, *Brachydanio rerio*, (Eaton et al. 1977) and for northern anchovy (Hunter 1972). No differences were seen in the present experiments and therefore details are not repeated.

The most direct, and hence most accurate, measure of performance during a burst of swimming is the distance traveled in a known elapsed time for larvae accelerating from rest. The form of this relationship for the distance traveled by larvae of various total lengths is shown in Figure 2 for three representative time periods. Data were described by best fit linear regression equations without data transformation (Table 2). Similar linear relationships have been shown for larval cruising performance of plaice, *Pleuronectes platessa*, (Ryland 1963); herring, *Clupea harengus*, (Rosenthal 1968); walleye, *Stizostedion vitreum vitreum*, and yellow perch, *Perca flavescens* (Houde 1969). The total distance traveled per burst of swimming (S) also increased linearly with total length (L) according to

$$S = 0.08 + 3.79 \pm 0.76 L \quad (r^2 = 0.57;\ n = 85).$$

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

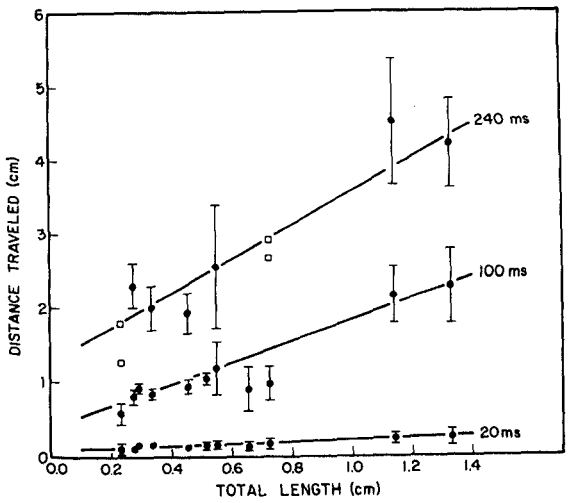

FIGURE 2.—Exemplary relationships between the distance traveled and total length of northern anchovy larvae after 20, 100, and 240 ms of burst swimming initiated by an electric shock stimulus. Vertical bars show ± 2 SE. Open squares show individual data points for individuals of groups of larvae when few swam for 240 ms.

TABLE 2.—Summary of relationships between distance traveled (S in centimeters) in various elapsed times as functions of total length (TL in centimeters) of northern anchovy larvae stimulated to maximum performance by an electric shock. 95% confidence intervals about the slope are shown.

Elapsed time from start of swimming (ms)	Best-fit equation relating distance traveled with total length	r^2	n
20	$S = 0.09 + 0.10 \pm 0.04$ TL	0.31	95
40	$S = 0.15 + 0.37 \pm 0.08$ TL	0.65	95
60	$S = 0.17 + 0.80 \pm 0.15$ TL	0.67	87
80	$S = 0.21 + 1.17 \pm 0.22$ TL	0.68	83
100	$S = 0.28 + 1.46 \pm 0.27$ TL	0.71	81
140	$S = 0.54 + 1.75 \pm 0.37$ TL	0.69	65
180	$S = 0.82 + 2.06 \pm 0.44$ TL	0.75	48
220	$S = 1.07 + 2.25 \pm 0.60$ TL	0.73	36
260	$S = 1.26 + 2.52 \pm 0.53$ TL	0.66	23

These distances were traveled by continuous swimming because gliding is limited for organisms the size of the larvae moving at low speeds (see Weihs 1980).

Although the relationships between distances traveled and total length were best described by linear regression equations, the coefficients of determination indicated that the relationship usually described only 65 to 75% of the variability. A major contributor to the variability was the apparent low performance of larvae with mean total lengths of 0.65 and 0.72 cm. For example, r^2 for the relationship between distance traveled in 100 ms and total length increased from 0.71 to 0.83 on deletion of the observations for larvae in these two groups. However, the larvae appeared healthy and there were no apparent reasons to assume these data were anomalous. The reason for their lower performance is unclear. Another factor contributing to variability in the data may have been the use of larvae from several spawnings at different times from different small sets of only 25-50 parents from laboratory stock. The very low r^2 for the distance-total length relationships at small elapsed times can also be attributed in part to greater measurement error. Larvae traveled small distances, of the order of 1 mm in 20 ms for small fish, and even with magnification of 2× these small distances were obviously subject to greater measurement error than larger distances.

Swimming speeds were not constant. Speed increased with time to reach the maximum burst speed after 80-100 ms and then speed declined for the remainder of the burst (Figure 3). The time to reach maximum burst speed was not affected by total length, but the decrease in speed from the maximum was greater for larger larvae, and extended over a longer period of time. The maximum burst speed increased linearly with total length (Figure 4), and since time to maximum speed was independent of length, mean acceleration rates will also be proportional to total length. Mean speeds during a burst of swimming ($\bar{U}$) also increased linearly with length (Figure 5), but at a lower rate than maximum burst speeds (U_{max}) where

$$\bar{U} = 4.89 + 8.18 \pm 1.1\,L \quad (r^2 = 0.861;\ n = 85)$$
$$U_{max} = 1.95 + 20.8 \pm 2.5\,L \quad (r^2 = 0.891;\ n = 85).$$

The difference between maximum and mean speeds increased with total length because variations in speed in a burst increased with total length (Figure 3). Maximum and mean speeds during a burst were consequently similar for the smallest larvae.

Figure 5 also shows other relationships between swimming speed and length reported in the literature for comparison. The mean speeds measured for anchovy larvae were greater than those measured for other larvae, exceeding the "... theoretical 10 body lengths/sec ..." (Blaxter 1969) maximum. Intermittent swimming speeds (Hunter 1972), the normal voluntary swimming pattern of larvae, and voluntary bursts were lower than the burst speeds measured here, presumably because of the absence of threatening stimuli.

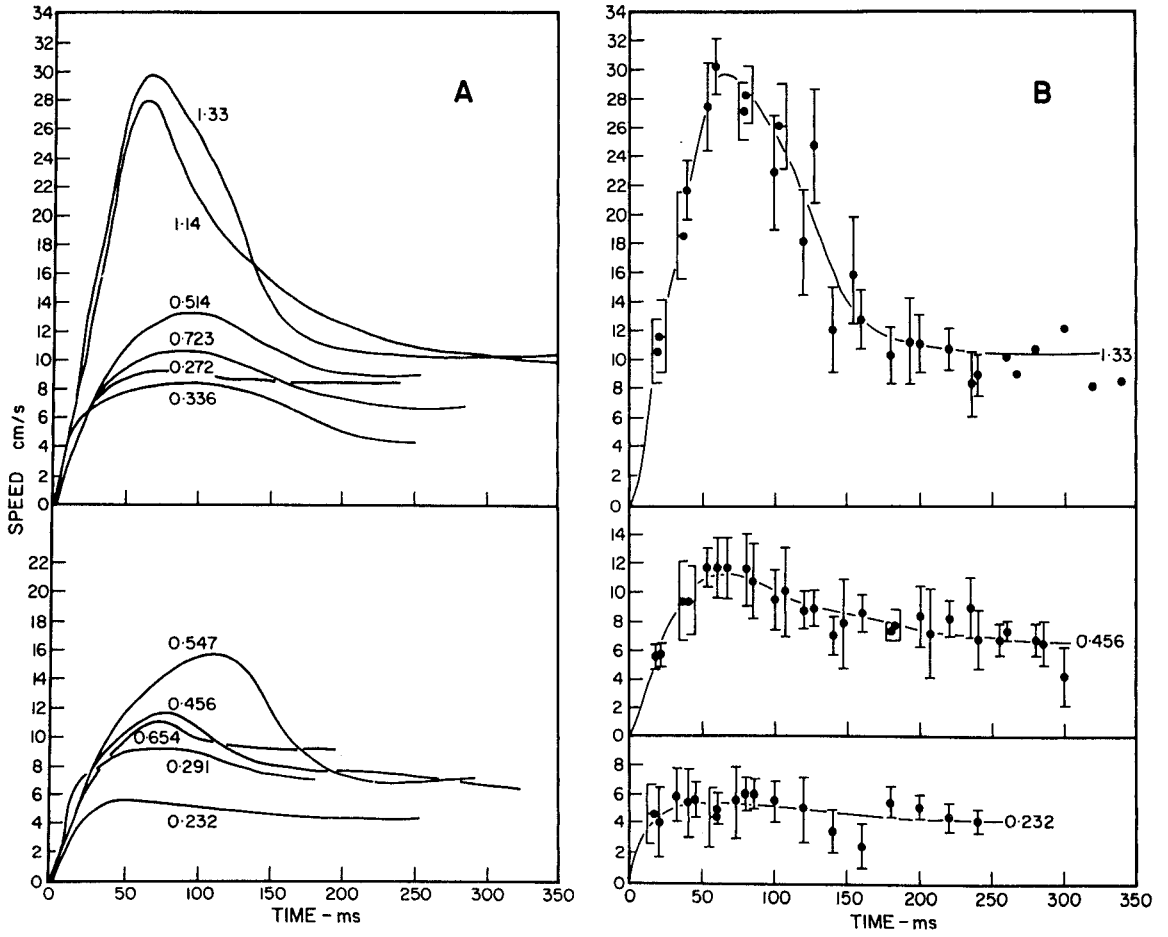

FIGURE 3.—Relationships between swimming speed and time during a burst for 11 groups of northern anchovy larvae ranging in mean total length from 0.23 to 1.33 cm. Panel A shows mean curves, separated into two groups for clarity. Panel B indicates the nature of the data from which the curves were constructed. Curves were fitted by eye. Vertical bars show ± 2 SE.

DISCUSSION

Northern anchovy larvae are important planktonic predators as well as being prey items for other organisms. Burst swimming speeds and burst swimming response ability will be important in this predator-prey role because the ability to rapidly strike prey and to escape strikes by predators will make major contributions to survival.

Response ability was assayed following an electric shock stimulus. While this is not a normal stimulus, observations on adult fish suggest responses to electric shock and more typical stimuli are comparable (Eaton et al. 1977; Webb 1978, 1979). For the larval northern anchovy, response patterns to electric shock correlated with expectations based on the onset of intermittent swimming and feeding (Figure 1). Similar patterns of maturation of the nervous system, especially the eyes (O'Connell in press), and reduced vulnerability to predators (Lillelund and Lasker 1971) suggest the stimulus is a suitable assay for maturation of locomotor coordination systems.

Following maturation of response capabilities, the effectiveness of a larva as a predator and in avoiding predation will depend to a large extent on locomotor performance (Lillelund and Lasker 1971). A model by Howland (1974) showed speed and maneuver were major factors in catch and avoidance behavior that contribute to success in predator-prey encounters. Larvae may be pursued

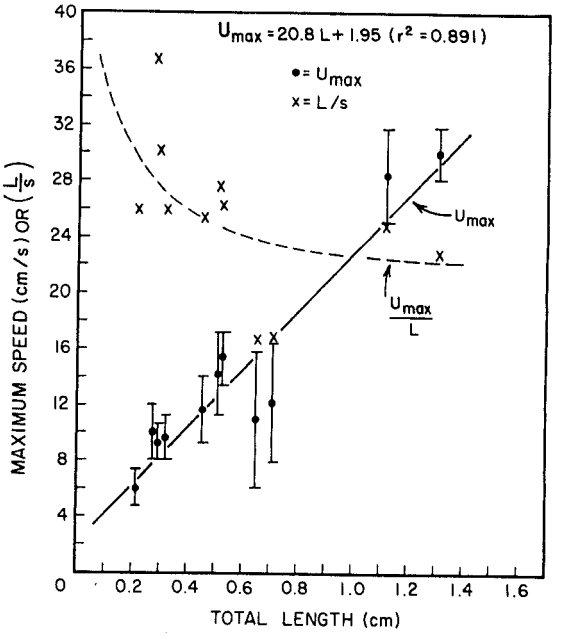

FIGURE 4.—Maximum burst speeds (U_{max}) as a function of total length (L) for northern anchovy larvae. Solid circles are absolute speeds (cm/s). Crosses show specific speeds in body lengths (L/s) calculated as U_{max}/L. Vertical bars show ± 2 SE.

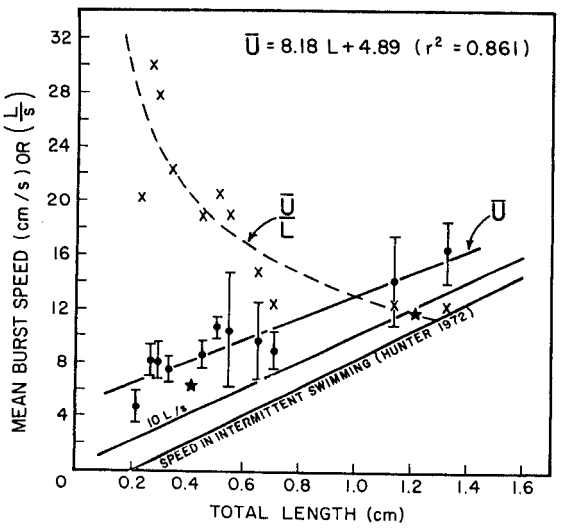

FIGURE 5.—Mean burst speeds ($\bar{U}$) as a function of total length (L) for northern anchovy larvae. Solid circles are absolute speeds (cm/s) and crosses show specific speeds ($\bar{U}/L$). Vertical bars show ± 2 SE. The 10 body length/s relationship is based on Blaxter (1969). The intermittent swimming speed relationship is taken from Hunter (1972). Stars show mean voluntary burst speeds, from Hunter (1972).

by predators so that endurance must be added to these components of predator-prey behavior. Of these three factors the physical ability to turn seems least important. Fish can turn in extremely small radius circles (Webb 1976; Eaton et al. 1977; Kimmel et al. in press) so that the optimal escape strategy of turning inside a predator's turning radius, forcing the predator to stop and reorient (Howland 1974), is probably impractical. For artificial predators, nets, the scale of the net makes turning ability unimportant. Therefore, speed is expected to be the major performance component of larval behavior contributing to the outcome of encounters with their prey, while both speed and endurance will affect interactions with predators and nets.

Hunter (1972) found that northern anchovy larvae accelerated over 8-16 ms to reach their prey. He found that a 0.8 cm larva would travel about 0.04 cm in that time, and a 1.3 cm larva about 0.09 cm. In the present experiments, the distance traveled was 0.03 and 0.09 cm in 12 ms for larvae of 0.8 and 1.3 cm TL, respectively. This shows that northern anchovy larvae use their maximum burst performance in attacking their prey.

Northern anchovy larvae are also prey items for a variety of fish and invertebrates (Hunter 1977, in press) so that the larvae would require a variety of response patterns to attempt to escape from predation. For example, lunging predators typically overshoot the prey location (Hoogland et al. 1956; Hunter 1972) when the rapid acceleration in a fast start would facilitate escape by quickly removing the potential prey from the predator's strike path. The rapid improvement in maximum burst speed with size (Figure 4) should reduce the vulnerability of larger northern anchovy to such predators. Chasing predators, for example, juvenile fish and larvae of more active species such as scombrids, are at the opposite extreme to lunging predators. Northern anchovy larvae should have reduced vulnerability to such predators as they grow because of improved mean swimming speed during a burst (Figure 5). In addition, the distance traveled per burst increases with size, implying improved stamina with increasing total length which should further facilitate escape of larger larvae from chasing predators.

The effect of size on the ability of northern anchovy larvae to escape natural predators and the mechanisms involved in escape behavior have received little attention. Decreased vulnerability of larger larvae to predation by copepods and

euphausids has been documented (Lillelund and Lasker 1971; Theilacker and Lasker 1974), but since experiments were performed in the dark, the factors leading to reduced vulnerability are not known. An alternative approach to assessing the importance of changing swimming performance with larval size is to consider an artificial "predator," a net, which simulates some actions of certain natural predators, such as filter feeders. The problem of sampling bias by nets has provided a variety of observations and models suitable to evaluate size-performance effects on vulnerability.

Most studies of net avoidance start with, or parallel, Barkley's (1964) model on selectivity of towed nets. This model identified three factors determining escape (and catch) probabilities: reaction distance, speed, and orientation of the escape path. Endurance must be added. In the absence of adequate data on the relevant parameters for fish larvae, results of sensitivity analyses have been fitted to catch data (Barkley 1964, 1972). The present data can be used to compare scaling relationships between escape probability and burst swimming performance to evaluate the importance of the latter in determining vulnerability of northern anchovy larvae to net "predators." Such a scaling approach allows some simplification because it is reasonable to assume that probability distributions for orientation of escape paths do not scale with size.

Escape probabilities, as a function of length, can be estimated from a comparison between day and night catches using towed nets. The ratio of night/day catches as a function of larval northern anchovy length is well known to be linear (Ahlstrom 1954; Zweifel and Smith in press) which means that the relationship between escape probability and size is curved, rapidly approaching an asymptote (Figure 6). The data shown in Figure 6 were obtained with a 1 m diameter ring net towed obliquely at about 125 cm/s (Zweifel and Smith in press). Ninety percent avoidance is reached by 1.0 cm larvae, with rather small improvements in escape probability at greater lengths. The decline in escape probability cannot be attributed to the capture of starving or sick larvae (Isaacs 1965) because O'Connell (1980) found no emaciated larvae >1 cm TL in net-caught samples.

In order to compare performance data with the catch probabilities, mean speeds and distances traveled in a burst were normalized about the performance measured for 1 cm larvae (Figure 6). The

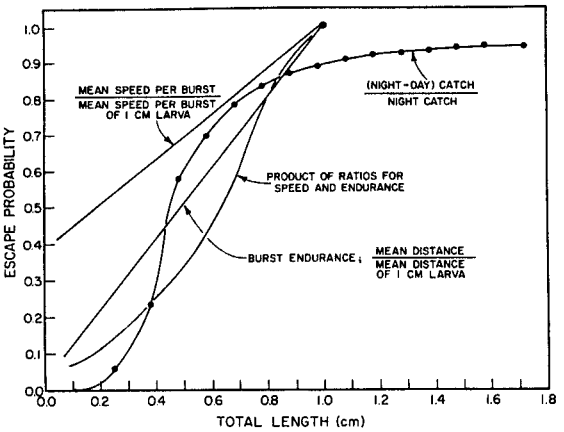

FIGURE 6.—Escape probabilities, estimated from day-night plankton net hauls, and those possible on the basis of burst swimming speed, burst endurance, and their product as a function of total length of northern anchovy larvae. Performance data are normalized with respect to a larval length of 1 cm, where the escape probability reaches 90%. Data for day-night catches were taken from Zweifel and Smith (in press).

scaling relationship for mean speeds in a burst, assuming bursts are repeated until a larva escapes, obviously do not parallel escape probabilities (Figure 6). Endurance in a burst shows a greater length effect, which is further accentuated by the interaction (product) of speed and endurance. This latter curve has the steepest slope, most closely paralleling escape probability, such that it is apparent that speed and endurance are major determinants of avoidance ability.

However, the shape of the curves suggests avoidance is underestimated for larger larvae between about 0.4-1.0 cm long. Length dependent maturation of sensory systems and motor control (O'Connell 1980) may contribute to increased escape probability of larger larvae. A behavioral factor may also contribute. Dill (1974) has shown that experienced juvenile zebra danio respond earlier to a predator than do inexperienced fish. Since the predation rate is high for northern anchovy larvae, then larger larvae are likely to be much more experienced with diverse attacks than are smaller larvae. Response thresholds decreased linearly with contacts up to 10 encounters in Dill's experiments, but this effect would undoubtedly decline with larger numbers of encounters, when a minimum threshold would presumably be obtained. Therefore, an age (experience) dependent decrease in reaction distance may contribute to net avoidance and the declining rate of catch probability at larger sizes.

Finally, it should be noted that improvements in plankton nets and catch techniques would shift the position of the curves in Figure 6. This would require different normalization points in evaluating effects of performance on escape probability, taking into account the new point at which larvae out-swim the net. However, such changes would not alter the nature of the arguments nor the conclusions concerning the importance of swimming performance in determining escape probability.

ACKNOWLEDGMENTS

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AGE AND GROWTH OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, AS INDICATED BY DAILY GROWTH INCREMENTS OF SAGITTAE

JAMES H. UCHIYAMA[1] AND PAUL STRUHSAKER[2]

ABSTRACT

Counts of the daily growth increments on otoliths provided the means for establishing growth curves for central Pacific skipjack tuna, *Katsuwonus pelamis*, up to 3 years old and for central Pacific yellowfin tuna, *Thunnus albacares*, up to 2 years old. The data indicated three stanzas of linear growth for 51 skipjack tuna ranging in size from 3 to 80 cm fork length. Estimated daily growth rates were 1.6 mm/day for fish up to a length of about 27.0 cm; 0.8 mm/day for fish between 27.0 and 71.4 cm; and 0.3 mm/day for fish between 71.4 and 80.3 cm. Growth data for 20 eastern Pacific skipjack tuna ranging in size from 38 to 65 cm fork length suggested that skipjack tuna in the eastern Pacific grew at a slower rate than those from the central Pacific.

Age determinations of 14 central Pacific yellowfin tuna suggested possibly two stanzas of linear growth. Estimated growth rates are 1.4 mm/day for fish up to a length of 64.2 cm and 0.9 mm/day for fish between 64.2 and 93.0 cm. Growth curves from this study were compared with published growth curves based on other methods.

The validity of daily growth increments was tentatively determined by observations on skipjack and yellowfin tunas held in captivity. Agreement of our growth curves with those of previous studies on the same stock of tunas using other growth estimating techniques also suggests that our aging technique is acceptable. However, the day-to-growth increment relation and the effect of various variables on the formation of growth increments of tunas need to be investigated further.

The many studies on age and growth of skipjack tuna, *Katsuwonus pelamis*, have primarily utilized three basic methods. Brock (1954), Schaefer (1961), Kawasaki (1965), Joseph and Calkins (1969), Yoshida (1971), Marcille and Stequert (1976a), and Diaz[3] determined growth rate and estimated the age of skipjack tuna by examining modal progression in length-frequency distributions. Yamashita and Waldron (1959), Shaefer et al. (1961), Clemens and Roedel (1964), Rothschild (1967), and Joseph and Calkins (1969) used data from tagged skipjack tuna to determine growth rates. Wild and Foreman (1980) estimated the growth rate of eastern Pacific skipjack tuna from the recapture fork length, the known period of growth, and the linear change in an otolith dimension following a tetracycline injection which was used to estimate length at marking. Marks on hard parts such as vertebrae and dorsal spines were interpreted to determine age and growth of skipjack tuna by Aikawa and Kato (1938), Yokota et al. (1961), Shabotiniets (1968), Batts (1972), and Chi and Yang (1973). Numerous reviews have been written on the subject and the lack of agreement on the aging and growth rate of skipjack tuna has frequently been noted.

Likewise, many studies have been conducted on age and growth of yellowfin tuna, *Thunnus albacares*. Moore (1951), Yabuta and Yukinawa (1957), Hennemuth (1961), Davidoff (1963), Diaz (1963), Le Guen et al. (1969), Yang et al. (1969), Le Guen and Sakagawa (1973), and Marcille and Stequert (1976b) have estimated age and growth rate by the analysis of modal progression in either length or weight frequencies. Blunt and Messersmith (1960), Schafer et al. (1961), and Bayliff[4] used results of their tagging experiments to determine the growth rate of yellowfin tuna in the eastern Pacific. Wild and Foreman (1980) estimated the growth rate of eastern Pacific yellowfin tuna by

[1]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii; present address: Easy Rider Corporation, 1050 Koloa Street, Honolulu, HI 96816.

[3]Diaz, E. L. 1966. Growth of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean. Unpubl. rep., 18 p. Inter-Am. Trop. Tuna Comm., La Jolla, Calif.

[4] Bayliff, W. H. 1973. Observations on the growth of yellowfin tuna in the eastern Pacific Ocean derived from tagging experiments. Unpubl. rep., 26 p. Inter-Am. Trop. Tuna Comm., La Jolla, Calif.

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their tetracycline-otolith method. Aikawa and Kato (1938), Nose et al. (1957), Yabuta et al. (1960), Tan et al. (1965), and Shabotiniets (1968) interpreted marks on scales, dorsal spines, and the centrum of vertebrae to estimate age and growth. These studies were performed on commercial-sized fish (>2 kg); growth during early life (<2 kg) has yet to be examined.

Pannella's reports (1971, 1974) provided circumstantial evidence that the smallest discernible growth increments in the sagittae (otoliths) of fish are deposited daily. More recent studies provide direct evidence that these growth increments are diel phenomena in sagittae of temperate (Brothers et al. 1976; Taubert and Coble 1977; Barkman 1978) and tropical (Struhsaker and Uchiyama 1976; Wild and Foreman 1980) species of teleosts. In the study of the short-lived engraulid *Stolephorus purpureus*, the information gained from the reading of sagittae was utilized in the construction of a growth curve for the first 190 d after yolk-sac absorption (full life cycle) (Struhsaker and Uchiyama 1976). In the present paper, growth curves are presented for central Pacific skipjack tuna to an age of about 3 yr, based on a sample of 51 fish, and for yellowfin tuna to about 2 yr, based on 14 fish. Counts on sagittae from 20 skipjack tuna from the eastern Pacific and 5 skipjack tuna from Papua New Guinea are also given. The results are discussed in relation to earlier age and growth studies of these species.

METHODS

Otolith Preparation and Counting

The central Pacific skipjack and yellowfin tunas were caught in the vicinity of the Line Islands and Hawaii. All specimens >20 cm FL (fork length) are samples taken from commercial fisheries or caught by trolling. Specimens <20 cm FL are from stomach contents of troll-caught skipjack tuna and regurgitations of a seabird, *Sula* sp., after it landed on the deck of a research vessel.

Juvenile skipjack tuna from stomach contents were identified by vertebral counts and skeletal characters given by Godsil and Byers (1944) and Gibbs and Collette (1967). In one case, only the anterior portion of a juvenile skipjack tuna was collected; standard length (SL) was estimated from the length of the precaudal vertebrae using the equation given by Yoshida (1971). A small (7.0 cm FL) yellowfin tuna specimen was tentatively identified on the basis of skeletal characters given by Matsumoto et al. (1972) and descriptions of *Thunnus* livers by Godsil and Byers (1944) and Gibbs and Collette (1967).

The caudal rays were missing from most tuna specimens collected from stomachs. Fork lengths were estimated by increasing standard lengths by 3.3%(Matsumoto[5]).

Heads from which the sagittae were not immediately removed after collection were frozen or preserved in 75% isopropanol.

In tunas <100 cm FL, we obtained the sagittae by splitting or cutting the skull along the sagittal plane and teasing them from the semicircular canals. With experience, the cut could be made without damaging either of the sagittae. We cleaned the sagittae by teasing or brushing off the sacculus and nerve endings. Sagittae that were not mounted immediately were stored in distilled water or 40% isopropanol, but were then mounted within a year.

After removal and cleaning, sagittae from tunas >45 cm FL were etched in a 1% solution of HCl for 3-5 min. The otoliths were then rinsed with several changes of water, mounted in Euparal,[6] and, in most cases, permitted to clear for 4 wk or more. Short lengths of monofilament line prevented contact of the otolith with the glass cover slip.

Increment counts were made from the core,[7] the center of the nucleus, to the tips of the rostrum, antirostrum, and postrostrum (terminology of Messieh 1972) for most sagittae. On sagittae from fish >60 cm FL, counts were made only to the rostrum and postrostrum. When the edge of the rostrum and postrostrum was fringed with irregular projections, counts were made on the projections leading to the point. Specimens were examined at magnifications of 200-800×. A microscope with a zoom feature was found to be useful, as the width of daily increments varied.

Counting increments in whole mounted otoliths becomes progressively more difficult with increasing specimen size. Experience is best obtained by beginning with otoliths from young fish and progressing through older fish. The initial counts en-

[5]W. M. Matsumoto, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. October 1974.

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

[7]Terminology agreed upon at the Otolith Workshop, Scripps Institution of Oceanography and Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif., 12-16 July 1976.

able the investigator to determine the best path to follow from the core to the edge of the otolith. Eventually, the counts either converge on a value or repeated identical counts are obtained. The number of counts required to determine age is dependent on the readability of the otolith. An average of about 20 counts was made for fish >1 yr old. We found that yellowfin tuna sagittae were easier to read than those of skipjack tuna. In yellowfin tuna, the increments are wider and can be examined at a lower magnification (200×), which provides a broader view and greater depth of field. The increment counts on 15 skipjack tuna and 3 yellowfin tuna sagittae were verified by a second reader whose counts were within 9% (5.4% average deviation) of the original counts except for one which was 17% off the original count.

Statistical Analysis

The parameters of linear growth stanzas were determined by the use of LINFIT, a computer program (Kamer[8]) which used the ordinary least squares procedure to fit two or three straight lines to bivariate data. Join points, also known as break points, are the places where one regime ends and another begins; these are assumed to exist. The range of the explanatory variable in which the join points are expected to occur must be designated. Given the range for these join points, the program performs the ordinary least squares procedure on each possible combination of regimes. The resulting output indicates the partitioning scheme, the intercept and slope of each fitted line representing a regime, the residual sum of squares for each regime, the combined residual sum of squares for the model, and the values of the dependent and explanatory variables at the join points. The linear growth stanzas used in this paper were selected under the following conditions: 1) minimized combined residual sum of squares for the model and 2) each join point associated with a partitioning scheme has a value for the explanatory variable which lies between the last data value in the regime to the left and the first data value in the regime to its right.

On the assumption that the maximum number of increments approximates the age of the fish in days, we calculated a growth curve for central Pacific skipjack tuna, eastern Pacific skipjack tuna, and central Pacific yellowfin tuna for comparison with other studies. The von Bertalanffy growth parameters were estimated on an annual basis using the computer program BGC3 (Abramson 1971).

ESTABLISHING THE GROWTH INCREMENT-DAY RELATION

The only direct evidence we have that a number of growth increments equal the same number of days came from the serendipitous opportunity to examine skipjack and yellowfin tunas under known captive conditions. These fishes were not held under strict experimental conditions and their primary use was not for aging studies; however, a detailed record on the amount of food consumed by each fish during the experiment was maintained. The experiment was similar to that used for nehu, *S. purpureus* (Struhsaker and Uchiyama 1976), and was carried out at the Kewalo Research Facility of the Honolulu Laboratory.

The stress of being hooked, transported, and confined in the community tanks at the Kewalo Research Facility, as well as the taking of little or no food during the first week of captivity, probably all contributed to the formation of a check mark on the otolith (Figure 1a, b). When the tuna were sufficiently recovered to feed normally, they received a daily ration which apparently was adequate to maintain life but inadequate for normal increment formation. Perhaps very thin increments were formed during this period, which might have added prominence to the check mark. When these tunas were fed to satiation throughout the day, the widths of the increments increased and became countable.

Under low magnification (200×), growth increments formed on the edge of a sagitta during the experiment were not as well defined as those of a tuna captured in the wild. The increments appeared thinner than normal when examined under high magnification (400×). For this reason, a sagitta was first examined under low power (200×) to locate the check mark and then examined under high power (400×) to enumerate the growth increments formed during the experimental feeding period. Although growth increments occurred all along the periphery of the sagitta, the full array of increments corresponding

[8]Kamer, G. A computer program for fitting straight lines to regimented data. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii.

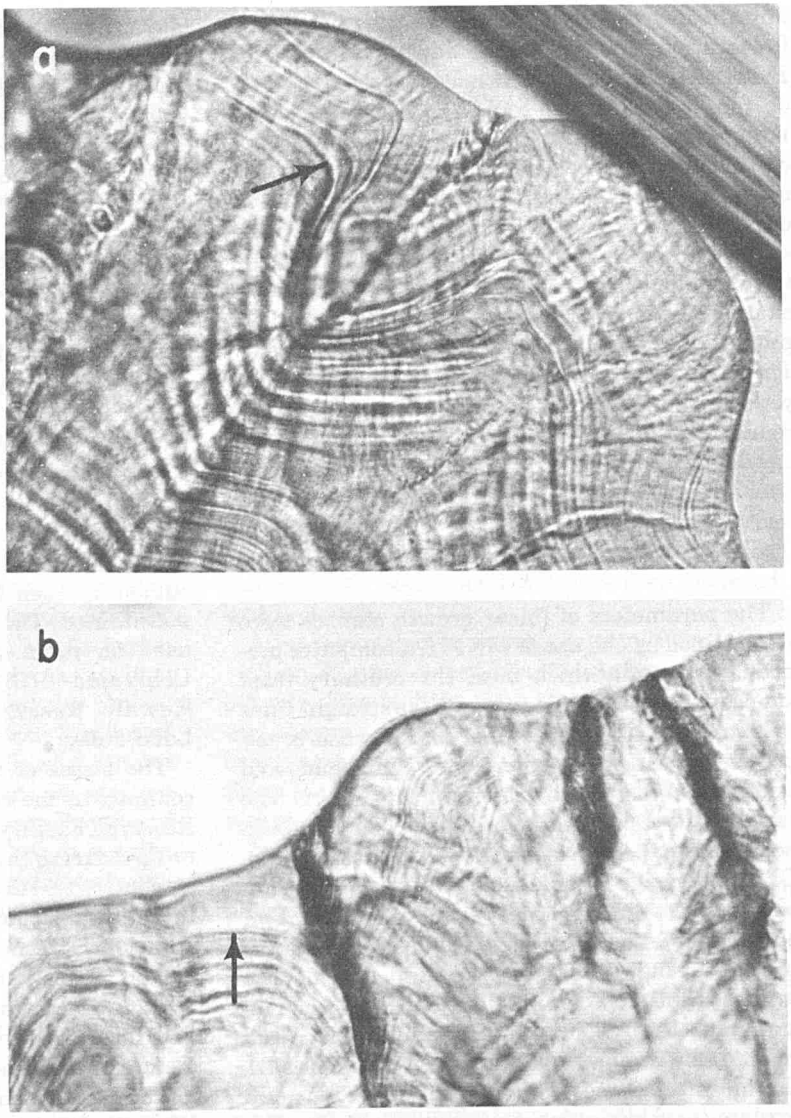

FIGURE 1.—Check mark, indicated by arrow, separates the environmentally marked increments from previous growth increments at a) tip of skipjack tuna sagitta rostrum; b) postrostrum of same skipjack tuna sagitta.

to the feeding period formed primarily on the tips of the rostrum and postrostrum (Figure 1a, b).

The highest count attainable corresponded with the number of days the tuna were fed to satiation, thus confirming the growth increment-day relation (Table 1). The number of increments formed after the check mark usually exceeded the number of feeding days because the tunas continued to live beyond the feeding period. During this latter period, the tunas either received a daily ration or starved. Great care was taken to avoid double counting of an increment where the sagitta was thin. The observations on these specimens were not long term and conditions were not fully controlled. Therefore, these data are considered tentative and in need of replication by rigorous experimental methods.

Wild and Foreman (1980) were able to show a 1:1 (day-to-growth increment) relationship for yellowfin tuna, 40-110 cm FL. However, their day-to-growth increment relation for skipjack tuna was significantly <1:1. Although an experiment where the fish lived in its natural environment was highly desirable, there was no control over variables and a record of variables which the fish might have encountered was unavailable.

Variables such as the amount of food a fish consumes (Struhsaker and Uchiyama 1976; Methot

TABLE 1.—Experimental data on marked daily growth increments in skipjack and yellowfin tunas.

Experimental animals	Fork length (cm)	Feeding period	Date of death per sampling	Length of feeding period (d)	No. of marked increments
Skipjack tuna 3	48.3	23 Aug.-22 Sept.	6 Oct.	30	33
Skipjack tuna 4	45.3	9-14 Oct.	27 Oct.	5	7
Skipjack tuna 5	49.3	15-22 Oct.	27 Oct.	7	8
Skipjack tuna 6	45.0	19-30 Oct.	4 Nov.	11	14
Yellowfin tuna 1	52.2	2-26 Aug.	4 Sept.	24	24
Yellowfin tuna 2	52.0	20 Aug.-19 Sept.	29 Sept.	30	31

and Kramer 1979), temperature (Taubert and Coble 1977; Methot and Kramer 1979), and age of fish (Pannella 1971; Brothers et al. 1976) have been demonstrated to affect the formation of daily growth rings on the sagitta. In our experiments with nehu, skipjack tuna, and yellowfin tuna, the amount of daily ration appeared to have an influence on otolith growth increments. Fishes fed once daily did not have clear otoliths with countable growth increments. Only when the fishes were fed to satiation throughout the day were countable growth increments formed. In the experiment on the effect of winter conditions on the formation of growth increments by Taubert and Coble (1977), the green sunfish, *Lepomis cyanellus*, lowered their activity level and fed less when the temperature fell below 10° C. Wild and Foreman (1980) also suggested that the difference in their results between yellowfin and skipjack tunas may have been due to feeding, citing the differences in the occurrence of full stomachs in the yellowfin and skipjack tunas from the Revillagigedo Islands area examined by Alverson (1963). Thus, it is evident that there is need for further research on the variables affecting day-to-growth increment relation of tuna otoliths.

RESULTS AND DISCUSSION

Skipjack Tuna

A plot of fork length versus age for 51 central Pacific tuna indicated three linear stanzas of growth (Figure 2). A least squares procedure was used to compute the lines of best fit for each stanza (Figure 2, Table 2). Von Bertalanffy growth parameters were also calculated (Figure 2). As there are no means available to statistically compare the von Bertalanffy growth curve, which has three parameters, with the three linear growth stanzas, which have a total of six parameters, the comparison was performed by examining the distribution of residuals (Figure 3). The residuals for the linear growth stanzas were distributed randomly about the x-axis, signifying a good fit (run's test: $Z = 0.39678$, $P \approx 0.6892$). On the other hand, the residuals for the von Bertalanffy curve oscillated about zero and were largest at breakpoints between linear stanzas and at the midpoint of the stanzas, thus suggesting a deviation from randomness (run's test: $Z = -3.32287$, $P<0.001$). Therefore, the linear stanzas appeared to be the preferable growth curve.

TABLE 2.—Length-age regression parameters for the three linear growth stanzas of skipjack tuna: N = number of data and RSS = residual sum of squares.

Stanzas	N	Intercept	Slope	RSS	Intersections: Years	Intersections: Fork length (cm)
1	11	0.0552	58.4167	3.0910		
					0.4616	27.0192
2	35	13.6402	28.9853	17.6038		
					1.9921	71.3812
3	5	51.6918	9.8838	0.2761		
Total RSS				20.9709		

It was noted earlier that the series of three linear growth lines appeared to provide a better fit to our data than the von Bertalanffy growth curve. However, since many of the earlier growth studies use the von Bertalanffy growth curve, it is of interest to compare the von Bertalanffy growth curve of this study with those of other growth studies on the central Pacific skipjack tuna stock (Figure 4). Growth rate estimates by Rothschild (1967) using corrected data of 35 long-term tag returns, by Joseph and Calkins (1969) using Rothschild's uncorrected data, and by Skillman[9] using 356 tag returns obtained during a 2-yr period, were all less than the rate obtained in this study. Brock (1954) analyzed the modal progression in length-frequency distributions obtained over a 5-yr period, and derived a growth curve similar to ours. Both curves show similar growth

[9]Skillman, R.A. Estimates of von Bertalanffy growth parameters for skipjack tuna, *Katsuwonus pelamis*, from capture-recapture experiments in the Hawaiian Islands. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii.

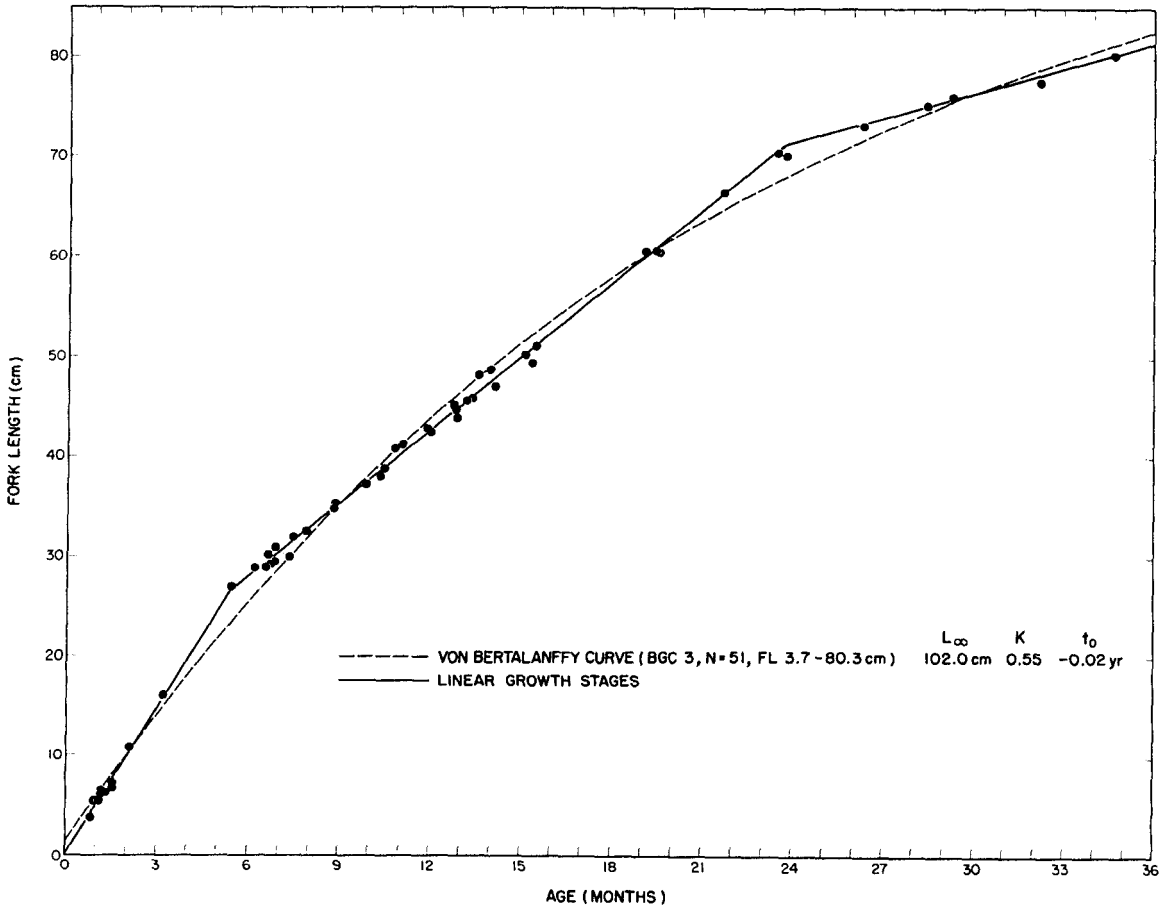

FIGURE 2.—Growth curve of skipjack tuna in the central Pacific as determined by otolith examination. Linear growth stanzas determined by LINFIT (see text). For parameters of growth stanzas, see Table 2.

rates up to 65 cm FL; beyond 65 cm FL, Brock's curve departs from ours and approaches an asymptote more rapidly. The difference in the growth rates above 65 cm may be due to two factors which would affect the modes of large (>6.8 kg) skipjack tuna: differential fishing or total mortality and temperature requirements of skipjack tuna. Barkley et al. (1978) hypothesized that large (>6.8 kg) skipjack tuna required cooler water than small skipjack tuna and therefore could tolerate the warmer surface water for relatively short periods. If so, the catchability of large skipjack tuna would be altered in the surface fishery and length-frequency modes of large skipjack tuna would be underestimated. Our otolith age determinations are not affected by these factors.

Otolith readings were also used to examine the age-length relationship of eastern Pacific skipjack tuna (Figure 5). Of the 20 specimens examined, 11 were caught off Baja California, Mexico. The other nine were caught in the eastern Pacific west of the Inter-American Tropical Tuna Commission's Yellowfin Regulatory Area. Most of these nine specimens had age-length relationships similar to those of fish caught off Baja California, but several had relationships similar to specimens taken in the central Pacific. Indications are that skipjack tuna in the eastern Pacific Ocean off Baja California grew at a slower rate than those in the central Pacific.

Our eastern Pacific skipjack tuna growth curve was compared with those of earlier studies from the eastern Pacific (Figure 5). A growth curve based on the progression of modes in length frequencies (Joseph and Calkins 1969) is similar to our curve; both show good agreement between 40

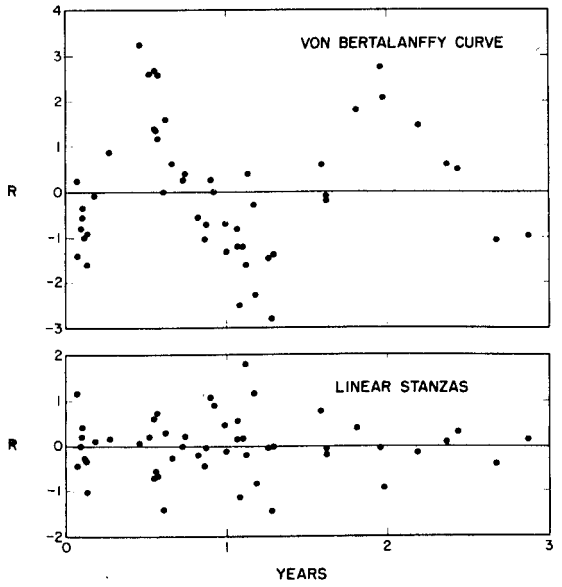

FIGURE 3.—Plot of residuals from von Bertalanffy growth curve and linear growth stanzas of central Pacific skipjack tuna shown in Figure 2.

and 65 cm FL. Growth curves determined from tagging data (Schaefer 1961; Joseph and Calkins 1969) showed slower growth.

The sagittae of five skipjack tuna from Papua New Guinea waters were examined (Figure 6). These fish grew more slowly than those from the central Pacific area.

Central Pacific Yellowfin Tuna

Two distinct stanzas of growth are evident for the sample of 14 central Pacific yellowfin tuna (Figure 7). Linear growth is apparent for about the first 14 mo of life, after which time the data suggest either the beginning of another linear growth phase or an asymptotic growth process. A segmented model with two linear phases was fitted to the data (Table 3). A von Bertalanffy growth equation was also fitted to the data and the following growth parameters were obtained: $L_\infty = 170.3$ cm; $K = 0.3864$, and $t_0 = 0.0366$ yr. Plots of residuals on age for both the segmental model and the von Bertalanffy growth curve were

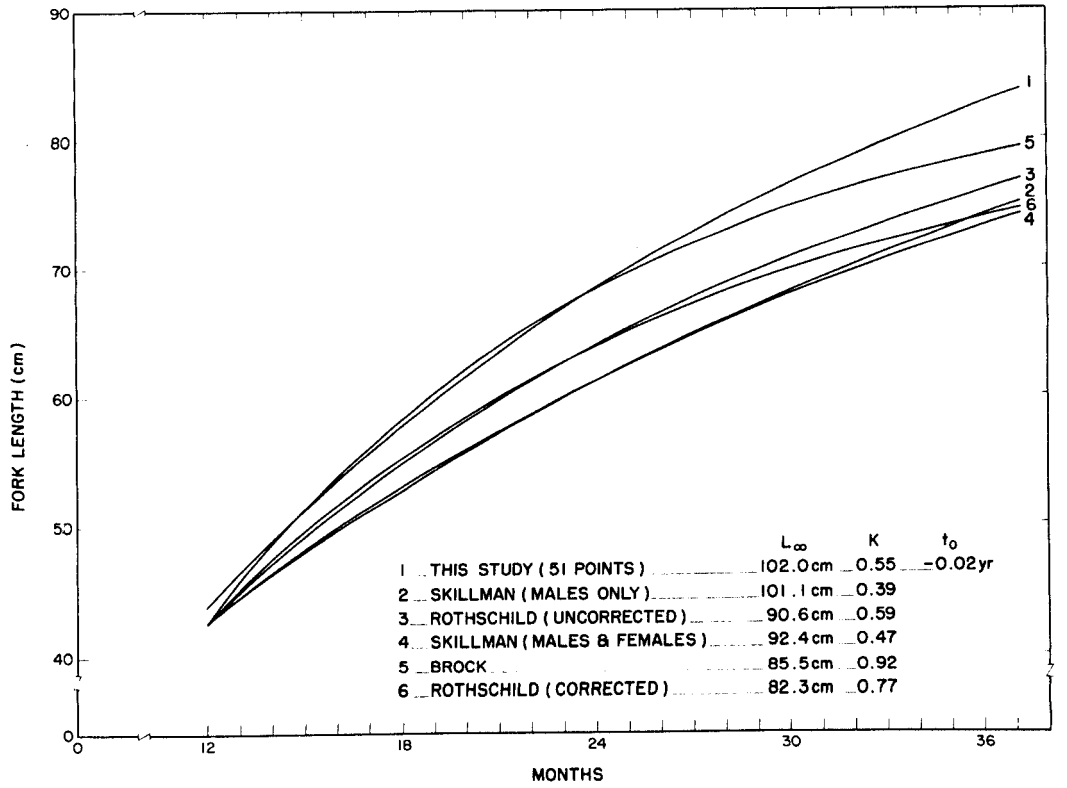

FIGURE 4.—A comparison of von Bertalanffy growth curves determined for central Pacific skipjack tuna (for full references, see text).

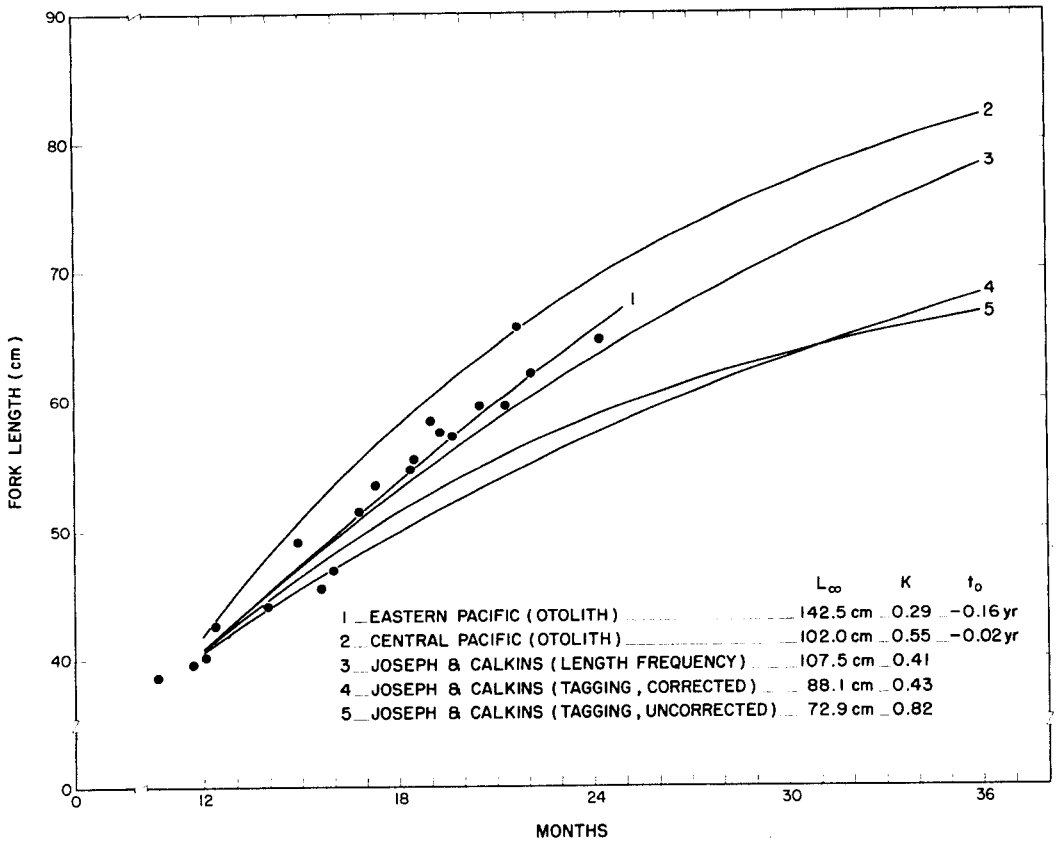

FIGURE 5.—The von Bertalanffy growth curve of skipjack tuna in the eastern Pacific as determined by otolith examination and its comparison with von Bertalanffy growth curves of previous studies from that area and the central Pacific (for full reference, see text).

TABLE 3.—Length-age regression parameters for the two linear growth stanzas of central Pacific yellowfin tuna: N = number of data and RSS = residual sum of squares.

					Intersections	
Stanzas	N	Intercept	Slope	RSS	Years	Fork length (cm)
1	10	0.8831	52.5837	5.7430	1.2047	64.2304
2	4	25.5653	32.0954	0.4620		
Total RSS				6.2050		

compared (Figure 8). As with skipjack tuna, the von Bertalanffy model gives a poorer fit than the linear segmental model. Although the probability for the distribution of residuals to be randomly distributed along the von Bertalanffy curve was significant at $P = 0.05$ (run's test, table of critical values: $r = 7$, $n_1 = 7$, $n_2 = 7$), clustering of pluses and minuses occurred. The run's test for the linear segmental model also showed randomness ($r = 9$, $n_1 = 6, n_2 = 8$; table of critical values, $P < 0.05$), and was an improvement over the von Bertalanffy curve with the increase in the number of runs from 7 to 9.

The results of our study on yellowfin tuna within the size range examined agree with most earlier studies for this species from the eastern and central Pacific Ocean. The results of aging by scales (Yabuta et al. 1960) and modal progression in length-frequency distributions (Hennemuth 1961) are given for comparison (Figure 6). It has been suggested that growth of yellowfin tuna in the eastern Pacific between the lengths of 50 and 100 cm is linear and that growth rates are 0.6-1.0 mm/d (Inter-American Tropical Tuna Commission 1972, 1974).

CONCLUSIONS

Daily growth information provides much greater insight into the growth patterns of teleost

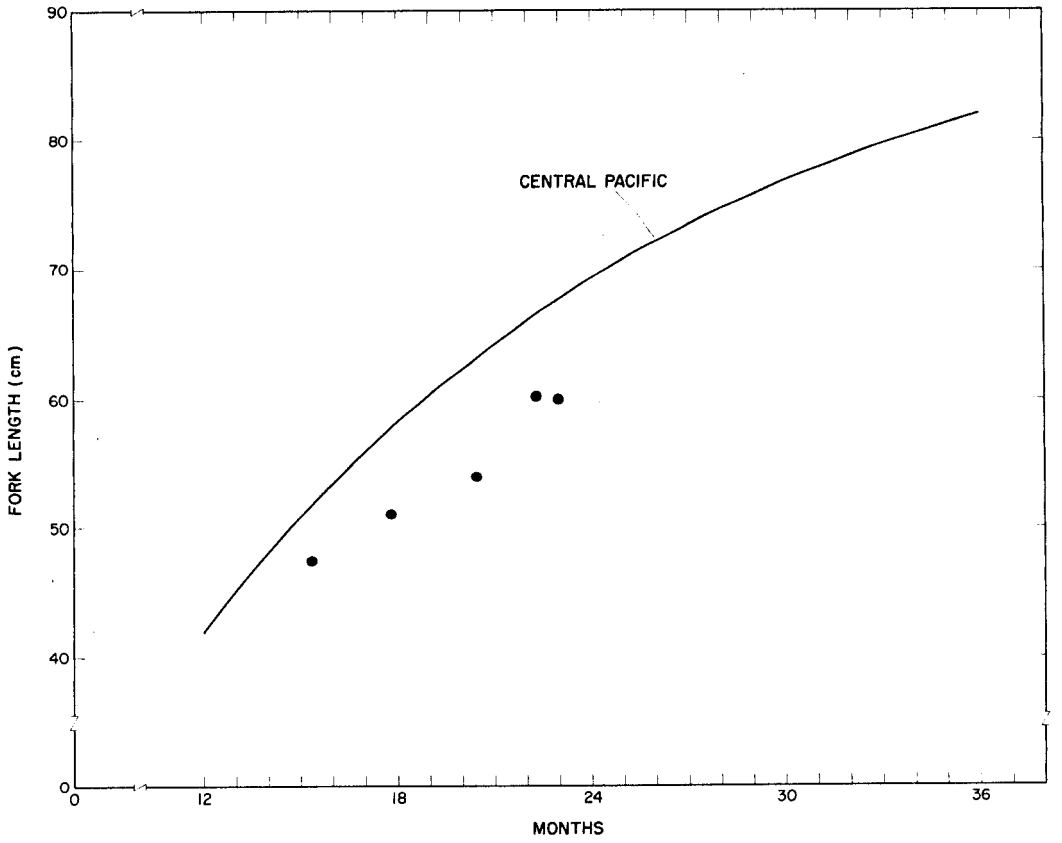

FIGURE 6.—Age determinations (points) of skipjack tuna from Papua New Guinea and comparison with the von Bertalanffy growth curve of central Pacific skipjack tuna derived in this paper.

fishes than can be gleaned using traditional annual techniques. Data presented here suggest three stanzas of linear growth for central Pacific skipjack tuna ranging in size from 3 to 80 cm FL, and that central Pacific yellowfin tuna from 7 to 93 cm FL have at least one stanza of linear growth.

Our assumption that the growth increments on the sagittae of skipjack and yellowfin tunas are deposited daily was supported by the deposition of experimentally induced increments on the sagittae of captive fishes and the relatively good agreement of our skipjack tuna and yellowfin tuna growth curves with those of previous studies utilizing other growth estimating techniques such as progression of modes in length-frequency distributions and interpretation of other hard parts. Growth studies on tunas based on tagging experiments have usually slower growth rates.

Otolith readings on specimens from three different areas suggest that there are geographical variations.

Estimation of growth rates from daily growth increments on sagittae is subject to at least two possible sources of error. One is that increments may not be deposited due to variables such as an inadequate ration, diet, temperature, age of fish, or during some physiologically stressful activity, such as reproduction. This is apparently the case for three species of boreal gadoids investigated by Pannella (1971). Another source is differential error during increment counting. If fewer rings are counted than actually exist, this, in addition to nondeposition of daily increments, would result in overestimation of growth rate.

ACKNOWLEDGMENTS

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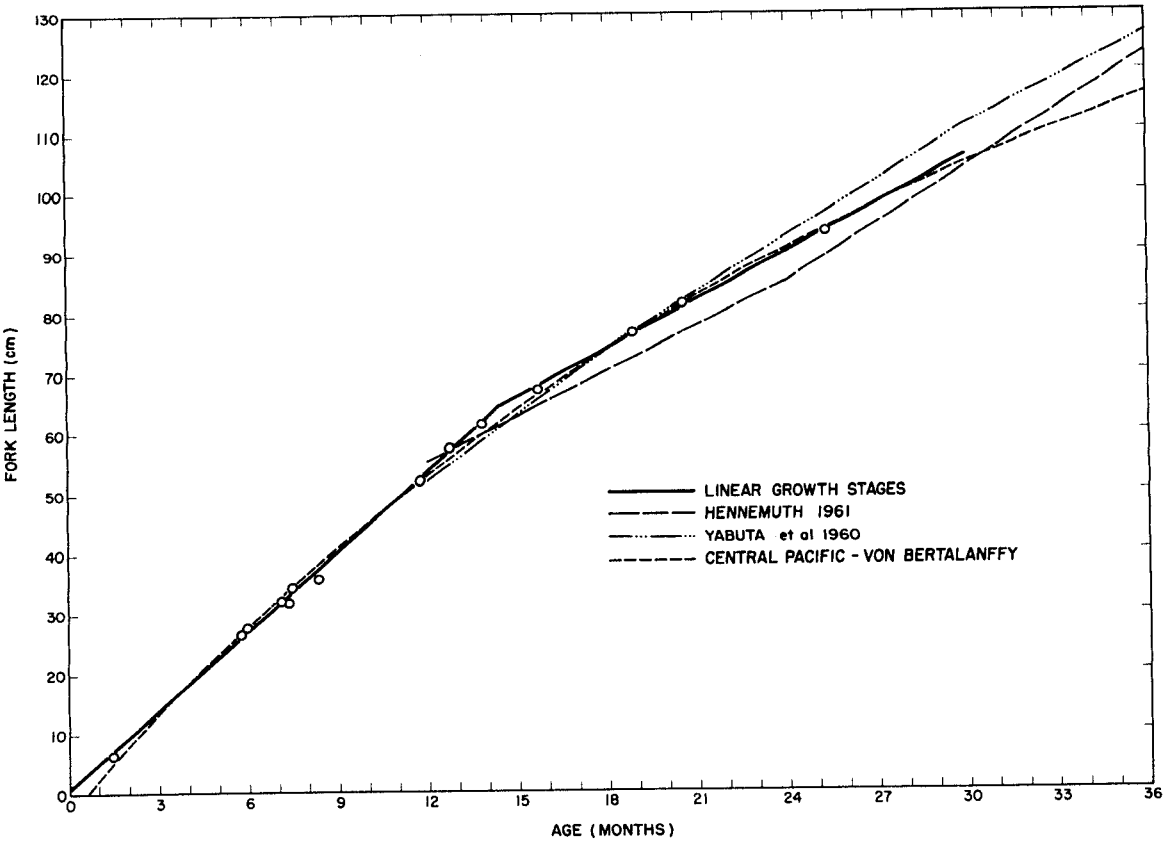

FIGURE 7.—Growth curve of yellowfin tuna in the central Pacific as determined by otolith examination and compared with growth curves of previous studies from that area and the eastern Pacific. Linear growth stanzas determined by LINFIT (see text). For parameters of growth stanzas, see Table 3.

pen and Howard O. Yoshida for their editorial help. We are especially indebted to Gary L. Kamer and Jeffrey J. Polovina for assisting with the statistical problems encountered. Marian Y. Y. Yong assisted with the data processing and Glen H. Sugiyama verified some of the age determinations. We are grateful to Sherry Steffel for sharing her data on feeding records and otoliths of skipjack and yellowfin tunas from her experiment.

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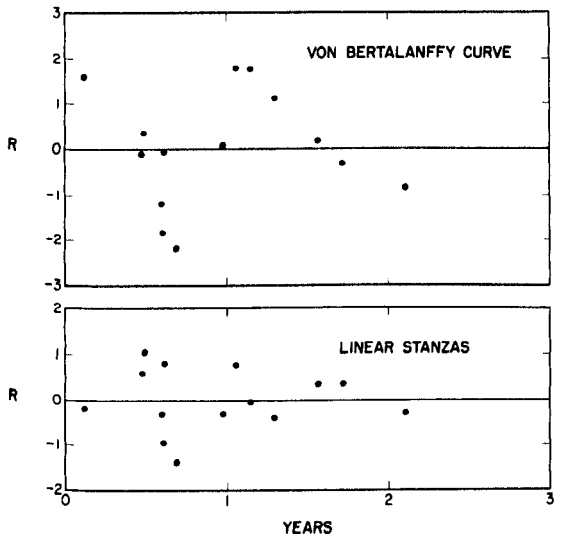

FIGURE 8.—Plots of residuals from von Bertalanffy growth curve and linear stanzas of central Pacific yellowfin tuna shown in Figure 7.

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PELAGIC EGGS AND LARVAE OF THE DEEPSEA SOLE, *EMBASSICHTHYS BATHYBIUS* (PISCES: PLEURONECTIDAE), WITH COMMENTS ON GENERIC AFFINITIES

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ABSTRACT

Two eggs of *Embassichthys bathybius* are 3.0 mm in diameter, pelagic, spherical, transparent, with a homogeneous yolk, narrow perivitelline space, and no oil globule. Embryos in late stage eggs have pigmentation characteristic of larvae, including pigment over the hindgut and three prominent postanal pigment bands. This pigment pattern and the high number of myomeres (>60) serve as distinguishing characters for larvae in the size series described from recently hatched specimens 9.8 mm standard length to a specimen beginning eye migration at 16.2 mm standard length.

Eggs and larvae of *E. bathybius* are extremely rare in extensive plankton and midwater trawl collections from the northeast Pacific with only eight specimens recorded to date. Occurrences were between March and June in the upper 185 m or less of the water column over bottom depths of 59-2,850 m.

Within the tribe Pleuronectini of the subfamily Pleuronectinae, larvae of *Glyptocephalus*, *Tanakius*, *Embassichthys*, and *Microstomus* form a distinct and logical group sharing similarities of a banded pigment pattern; angular, oblique jaw; elongate, slender form; and tendency toward a leptocephalus-like shape. If intense pigment banding and pronounced leptocephaluslike shape are derived characters, then the group is probably a naturally related one, with *Microstomus* the least and *Glyptocephalus* the most specialized.

The deepsea sole, *Embassichthys bathybius* (Gilbert), occurs in the northeast Pacific Ocean from Santa Catalina Island, southern California, to Pratt Seamount, Gulf of Alaska, in depths from 320 to 1,432 m but mostly >730 m (Miller and Lea 1972; Hart 1973). It grows to 47 cm and is reportedly uncommon (Miller and Lea 1972; Hart 1973). Life history data are minimal and nothing is known about its reproduction or early life.

Pelagic eggs and larvae of this species are described here for the first time based on collections taken off the Oregon coast. Knowledge of these early stages provides some insight into reproductive strategy as well as information on larval morphology which may be useful for examining systematic relationships.

METHODS

The pelagic specimens were collected (Table 1) with 70 cm bongos having 0.571 mm mesh nets and a 3.1 m Isaacs-Kidd midwater trawl with a 5 mm mesh liner and a 0.5 m diameter cod end of 0.571 mm mesh. The bongos were towed obliquely through the water column. The midwater trawl was towed near the surface in the upper 10 m.

All material was preserved in 10% Formalin[2] and stored in 5% Formalin except the 16.2 mm larva which was transferred to 36% isopropyl alcohol.

Measurements made on larvae included:

Standard length (SL) = snout tip to notochord tip until notochord is fully flexed and the posterior margin of the forming hypural elements is vertical, then to posterior margin of hypurals.

Head length = snout tip to cleithrum.

Snout to anus length = distance along body midline from snout tip to vertical through posterior margin of anus.

Eye diameter = horizontal diameter of pigmented portion of left eyeball.

Depth at cleithrum = vertical distance from dorsal body margin, excluding finfold or fin, to ventral tip of cleithrum.

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

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TABLE 1.—Collection data for eggs and larvae of *Embassichthys bathybius*.

Item	SL (mm)	Date	Gear	Lat. N.	Long. W	Distance from coast (km)	Bottom depth (m)	Depth of tow (m)
Eggs	—	22 May 1972	70 cm bongo	44°39.1′	124°45.7′	56	220	185-0
	—	20 March 1974	70 cm bongo	43°40.0′	124°33.0′	28	190	180-0
Larvae	9.8	27 March 1973	70 cm bongo	43°00.0′	125°01.7′	46	>1,000	102-0
	9.8	13 June 1972	70 cm bongo	44°39.1′	125°27.7′	111	2,850	120-0
	10.2	23 May 1972	70 cm bongo	44°39.1′	125°13.7′	93	1,300	165-0
	10.4	11 April 1972	70 cm bongo	44°39.1′	124°10.7′	9	59	48-0
	15.4	12 June 1972	70 cm bongo	44°39.1′	124°38.7′	46	330	115-0
	16.2	26 April 1965	3 m IKMT	44°39.1′	125°27.7′	93	1,300	≈10

Depth at anus = vertical distance from dorsal body margin, excluding finfold or fin, to anus.

Depth behind anus = vertical distance from dorsal body margin to ventral body margin, excluding finfold or fin, at point immediately behind anus where body depth decreases greatly compared with depth at anus.

Body lengths refer to standard length. Illustrations were made with the aid of a camera lucida.

IDENTIFICATION

The largest larva in the series, obviously a pleuronectid based on general body form and asymmetrical position of the left eye, had 60 myomeres (equivalent to vertebrae), 112 dorsal fin rays, and 97 anal fin rays. *Embassichthys bathybius* is the only pleuronectid occurring in the northeast Pacific which has these counts (Norman 1934; Miller and Lea 1972; Hart 1973). The larval series was linked together by the high number of myomeres and by pigment pattern, most notably three postanal pigment bands. Advanced embryos in the eggs had the same pigment pattern as the smallest larvae and the same high number of myomeres, providing positive identification.

DESCRIPTION

Eggs (Figure 1)

Two eggs identified as *E. bathybius* are spherical and transparent, 3.0 mm in diameter, with a homogeneous yolk, a relatively narrow perivitelline space, and no oil globule. The egg membrane is smooth and has a slight pinkish tinge in preserved material. Both eggs have well-developed embryos with three distinctive postanal pigment bands, including one at the tail tip. In the more advanced embryo (illustrated), the eyes are pigmented and the postanal bands are more intense. Pigment also occurs near the hindgut and extends out onto the yolk.

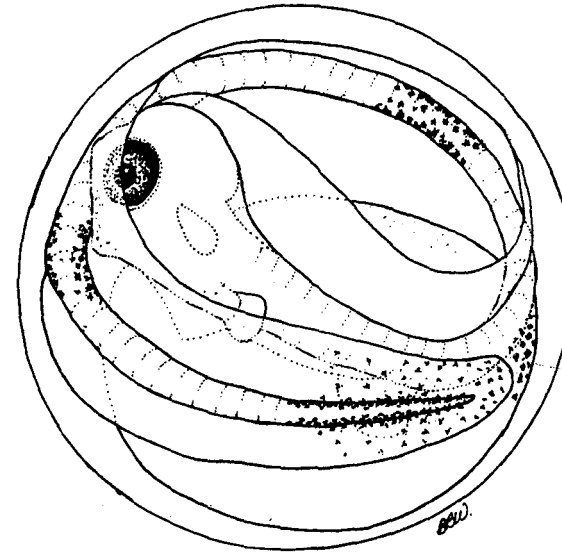

FIGURE 1.—Egg of *Embassichthys bathybius*, 3.0 mm in diameter.

Larvae (Figure 2; Table 2)

Six larvae identified as *E. bathybius* range from 9.8 to 16.2 mm SL. The two smallest specimens appear to be recently hatched, based on state of development compared with the most advanced embryo. A hatching size of about 9 mm (excluding shrinkage due to Formalin preservation) may be reasonable, based on the diameter-circumference relationship for a 3.0 mm diameter egg and the extent to which the advanced embryo encircles the yolk mass (Figure 1). The largest specimen, 16.2 mm, is beginning to undergo transformation as evidenced by the slight asymmetrical position of the left eye. The size at which the transformation process is complete is unknown.

Pigmentation on the smallest larvae is similar to that on the embryos, with melanophores present over the hindgut and in three bands postanally. Pigment in the anterior two of these three bands is generally more concentrated along the dorsal and

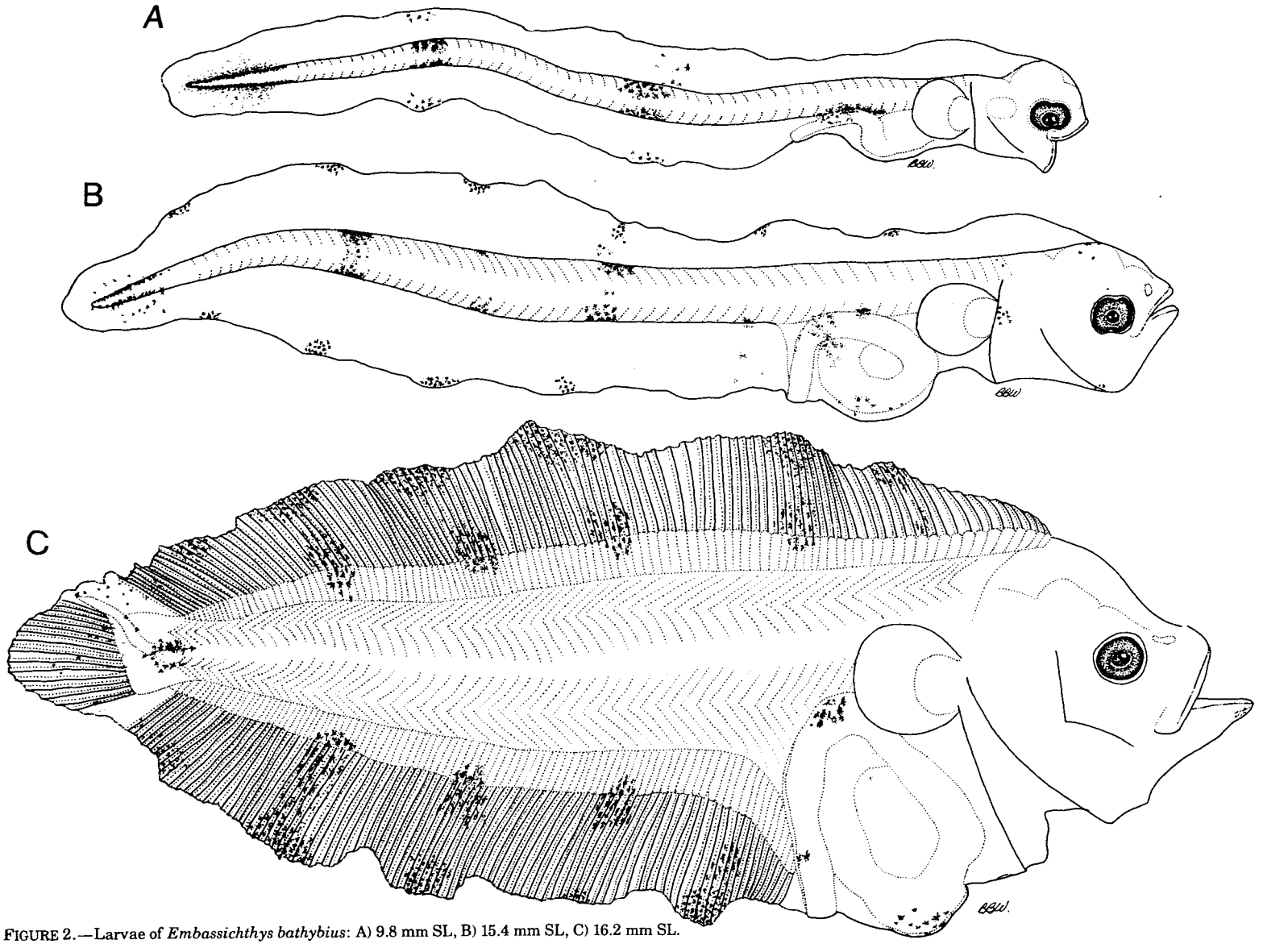

FIGURE 2.—Larvae of *Embassichthys bathybius*: A) 9.8 mm SL, B) 15.4 mm SL, C) 16.2 mm SL.

TABLE 2.—Measurements (millimeters) of selected body parts of larvae of *Embassichthys bathybius*.

SL	Head length	Snout to anus length	Eye diameter	Depth at cleithrum	Depth at anus	Depth behind anus
9.8	1.2	3.2	0.4	0.8	0.7	0.3
9.8	1.9	—	.5	1.3	—	.7
10.2	1.8	—	.5	1.2	—	.5
10.4	1.2	3.2	.4	.8	1.0	.5
15.4	2.0	5.3	.5	1.7	2.0	.8
16.2	3.7	6.4	.7	5.1	5.7	4.3

ventral body margins than laterally. Pigment also occurs on the finfold in the region of the bands, particularly at the finfold margins near the anterior two bands. During development, the most distinctive pigment additions occur along the fin fold (fin) margins, with seven patches forming along the dorsal fin and five along the ventral fin of the largest specimen. Pigment patches are also added to the dorsal and ventral body margins, generally in the vicinity of the fin fold (fin) patches, initially between the anterior two tail bands. With growth the original pigment bands become discontinuous laterally except for the one at the tail tip which eventually appears as a patch on the caudal peduncle. Some pigment is also added ventrally in the abdominal region.

Initially the larvae are relatively long and slender with body depth at the anus 7% SL in the smallest larvae and 13% SL by 15.4 mm. Body depth increases considerably by 16.2 mm when it is 35% SL at the anus. Snout to anus distance is 31-34% SL until 16.2 mm when it increases to 40% SL. Between 15.4 and 16.2 mm a number of events occur including notochord flexion; dorsal, anal, and caudal fin development; and formation of pelvic fin buds. By 16.2 mm, the adult complement of dorsal (109-117) and anal (94-98) fin rays (Miller and Lea 1972) is attained but the caudal fin rays are not fully developed, based on the incomplete count of 8 + 8, and pectoral fin rays are not yet formed. No head or body spines are apparent on any of the larvae.

COMPARISON

The only other pleuronectids occurring in the northeast Pacific with >60 vertebrae are *Reinhardtius hippoglossoides* and *Glyptocephalus zachirus* (Norman 1934; Miller and Lea 1972; Hart 1973). Eggs of *R. hippoglossoides* are 4.0-4.5 mm in diameter (Pertseva-Ostroumova 1961) and those of *G. zachirus* are 1.98-2.34 mm (Pearcy et al. 1977) compared with about 3.0 mm for *E. bathybius*. Larvae of *R. hippoglossoides* are lightly pigmented with melanophores lining the myosepta but never appearing as pronounced pigment bands on the body (Pertseva-Ostroumova 1961; Nichols 1971) as in *E. bathybius*. Small (< 11 mm) larvae of *G. zachirus* have four postanal pigment bands (Ahlstrom and Moser 1975) compared with three in *E. bathybius*. The bands in *G. zachirus* extend with uniform intensity from dorsal to ventral body margins whereas those in *E. bathybius* are concentrated along the dorsal and ventral margins and are less intense laterally. With development these bands persist laterally in *G. zachirus* while the anterior two bands persist only near the body margins in *E. bathybius*. Small (<11 mm) larvae of *G. zachirus* also have a relatively shorter snout to anus distance (range = 25.3-27.2% SL; mean = 26.2% SL based on four specimens) than *E. bathybius* (range = 30.8-32.7% SL; mean = 31.8% SL based on two specimens). Freshly preserved larvae of *E. bathybius* possess scattered orange chromatophores on the body whereas larvae of *G. zachirus* have none. Eye migration begins at a smaller size in *E. bathybius* (at least by 16.2 mm) than in *G. zachirus* [34-35 mm (Pearcy et al. 1977)] indicating that final transformation to juvenile may take place at a smaller size in *E. bathybius* compared with 45 mm or larger (Pearcy et al. 1977) for *G. zachirus*.

OCCURRENCE

Because of the paucity of specimens of *E. bathybius* little can be said about temporal and spatial distribution. All were collected between March and June (Table 1) which may indicate a winter-spring spawning period similar to that of many species off Oregon (Pearcy et al. 1977; Richardson and Pearcy 1977). Additional documentation is needed to determine whether such spawning periodicity actually exists in the deep habitat (generally >730 m) of the adults.

Specimens were collected in the upper 185 m or less of the water column over bottom depths of 59 to 2,850 m, with the largest larva taken in a surface (upper 10 m) tow (Table 1). The wide ranging occurrences of the pelagic eggs and larvae between 9 and 111 km from the coast probably reflects drift and dispersal by currents.

The larvae appear to be rare, at least off Oregon, based on over 3,000 midwater trawl and plankton collections that have been taken in that region

(table 1 in Pearcy et al. 1977). Such rarity could reflect the reported rarity of adults, or may indicate that the principal spawning occurs outside our sampling area, or that the primary occurrence of eggs and larvae may be at depths (>200 m) below those commonly sampled.

The reproductive strategy of *E. bathybius* involves production of a large egg, probably with an associated reduced fecundity compared with an equivalent sized pleuronectid producing smaller eggs. The egg likely has a moderate pelagic life span lasting at least a few weeks, based on time to hatching for eggs of the related northeast Pacific species *Microstomus pacificus* [38 d at 7.5° C; 27 d at 10° C; 18 d at 12.5° C (Williams[3])] which has eggs of 2.04-2.57 mm diameter (Pearcy et al. 1977). The larva of *E. bathybius* is well developed by the time it hatches and probably has an extended pelagic life lasting at least a few months, although size at which transformation is completed and growth rates are unknown. Pearcy et al. (1977) estimated that the related species *M. pacificus* and *G. zachirus* may have a pelagic phase lasting about 1 yr.

DISCUSSION

The most recent, broad based review of the family Pleuronectidae that implied relationships was by Norman (1934) who recognized five subfamilies. Within the subfamily Pleuronectinae the genera fall into two main groups: one in which the mouth is moderate to large and the jaws and dentition are well developed on both sides [tribe Hippoglossini of Nelson (1976), with ca. 10 genera, 18 species]; the other in which the mouth is small and asymmetrical, with the jaws and dentition more developed on the blind side [tribe Pleuronectini of Nelson (1976) with ca. 16 genera, 42 species]. Norman (1934) stated "The group of Pleuronectine genera including *Microstomus*, *Embassichthys*, *Tanakius* and *Glyptocephalus* have generally been marked off from the remainder of the small-mouthed members [tribe Pleuronectini] of the subfamily as a primary division [within the tribe], distinguished by a generally more elongate body and by an increased number of vertebrae, fin-rays and of scales in a longitudinal series. Such an arrangement is clearly an artificial one, and it is doubtful whether these [four] genera really form a natural group." He further said that *Embassichthys* is apparently closely related to *Microstomus* and *Glyptocephalus* is close to *Tanakius* whereas *Microstomus* is related to *Pseudopleuronectes* and *Tanakius* is apparently related to *Dexistes*.

Norman's (1934) discussion of intergeneric relationships was based mainly on external morphological features and therefore the phylogeny of the group was not really well defined. Additional evidence is needed to elucidate relationships. One source of additional information is the larval form of fishes which has been used to demonstrate or clarify systematic relationships in other groups of fishes, e.g., scoplarchids (Johnson 1974), gonostomatids (Ahlstrom 1974), myctophids (Moser and Ahlstrom 1974), myctophiforms (Okiyama 1974) marine teleosts in general (Ahlstrom and Moser 1976), bothids (Futch 1977), scombroids (Okiyama and Ueyanagi 1978), and serranids (Kendall 1979). Although larval characters that have been used are usually external morphological features such as body shape and form, spination, and melanistic pigmentation, character similarities have been consistently in agreement with intergeneric relationships.

With this paper, larvae of all species in the four pleuronectine genera mentioned by Norman (1934) are known (Table 3). Larvae are also known for 53 of the 60 pleuronectine species that occur in the North Pacific and North Atlantic (Ahlstrom and Moser 1979). With this knowledge it is possible to point out the similarity and distinctiveness of the larvae in the four-genus complex of *Microstomus*, *Embassichthys*, *Tanakius*, and *Glyptocephalus* which appear to form a logical group within the tribe Pleuronectini. Determination of whether this phenetically derived group is a

TABLE 3.—Selected references containing illustrations of larvae of species in the pleuronectid genera *Embassichthys*, *Glyptocephalus*, *Microstomus*, and *Tanakius*.

Species	References
Embassichthys bathybius	This paper
Glyptocephalus cynoglossus	Petersen 1904; Ehrenbaum 1905-09; Nichols 1971; Evseenko and Nevinsky 1975; Russell 1976.
G. stelleri	Dekhnik 1959; Pertseva-Ostroumova 1961; Okiyama 1963; Okiyama and Takahashi 1976.
G. zachirus	Ahlstrom and Moser 1975
Microstomus achne	Okiyama and Takahashi 1976
M. kitt	Nichols 1971; Russell 1976
M. pacificus	Hagerman 1952; Ahlstrom and Moser 1975
Tanakius kitaharae	Fujita 1965; Okiyama and Takahashi 1976

[3] S. Williams, Graduate student, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, unpubl. data, June 1976.

natural group comprised of related genera, in contrast with Norman's (1934) speculation, will depend on a detailed analysis of derived character states which is beyond the scope of this paper. However, based on other larval studies mentioned above, it seems probable that the larval similarities within the group may provide evidence to support the idea of intergeneric relationship. In an earlier study of larvae of *M. kitt*, *G. stelleri*, and *G. cynoglossus*, Pertseva-Ostroumova (1961) preliminarily concluded that larval evidence indicated a close relationship between *Microstomus* and *Glyptocephalus*.

Characters shared by larvae of members of this four-genus complex and not found in other members of the Pleuronectini include pigment pattern (preflexion larvae) consisting of three or four postanal pigment bands which may be continuous (from dorsal to ventral body margin) or discontinuous (concentrated only near the dorsal and ventral body margins); elongate, slender form of preflexion larvae; angular jaw with strongly oblique appearance; and tendency toward a leptocephaluslike shape with development. Among genera, similarities are greatest between *Glyptocephalus* and *Tanakius* which share the characters of continuous postanal pigment bands that, later in development, become concentrated mediolaterally; pigment addition as ventral patches between bands; preopercular spines; and pronounced leptocephaluslike shape. *Embassichthys* most closely resembles *Glyptocephalus* and *Tanakius*, having continuous postanal pigment bands initially which later become discontinuous, persisting only at the body margins; pigment addition as dorsal and ventral patches between bands; no head spination; a moderate leptocephaluslike shape. *Microstomus* is most distinct with postanal pigment bands discontinuous and not prominent; occipital spines in two of three species; much less tendency toward long leptocephaluslike shape with dorsoventral deepening of body instead. If strong pigment banding and pronounced leptocephaluslike shape can be shown to be derived character states, which they appear to be considering the rest of the Pleuronectini, this group of genera may indeed be related, with *Microstomus* being least specialized and *Glyptocephalus* most specialized.

Additional observations on head spine patterns, extremes in larval form, and eye position in relation to caudal fin development may prove to be useful in future studies assessing relationships within this group of genera. Evseenko (1979) theorized that the presence of head spines in flatfish larvae was indicative of their percoid ancestors and that a reduction in head spines within a genus was a derived character state. Both *M. achne* and *M. pacificus* of the North Pacific have prominent occipital spines (Hagerman 1952; Okiyama and Takahashi 1976) while *M. kitt* of the northeast Atlantic reportedly has none (Russell 1976; Evseenko 1979). This tends to offer support for the concept of a North Pacific origin of the genus *Microstomus* with *M. kitt* being a more specialized, derived form. All three species of *Glyptocephalus* reportedly have preopercular spines (Ahlstrom and Moser 1975; Russell 1976; Okiyama[4]) although total number and relative size have not been well documented for each species. It would be interesting to see if a reduction in preopercular spination occurs in *G. cynoglossus* of the North Atlantic, following a pattern similar to *M. kitt*.

Both egg size and size at transformation reach maxima in species of this generic complex in the northeast Pacific. Eggs of *E. bathybius* are about 3.0 mm in diameter and those of *M. pacificus* and *G. zachirus* are ≥2.0 mm (Pearcy et al. 1977). Larval lengths of up to 89 mm in *G. zachirus* and 65 mm in *M. pacificus* prior to transformation have been reported (Pearcy et al. 1977). The latter species develops an extremely deep bodied, highly compressed specialized larval form. The large egg size and size at transformation may possibly reflect an environmentally induced, specialized adaptation to the upwelling system (or deep habitat in the case of *E. bathybius*) and associated circulation patterns of the region.

Patterns of eye migration in relation to caudal fin development vary among genera. In *G. zachirus* the caudal fin forms entirely before the left eye begins to migrate whereas in *M. pacificus*, the eye begins to migrate as notochord flexion begins (Pearcy et al. 1977). Relatively few specimens of *G. zachirus* have been collected with the left eye on the middorsal ridge suggesting that once eye movement is initiated it proceeds rapidly, with transformation completed shortly thereafter. This is in contrast to *M. pacificus* where a large number of specimens in a wide size range (10-63 mm SL) have been collected with the eye on the middorsal

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ridge (Pearcy et al. 1977). These patterns have not been investigated fully in the other species and genera in the group although our limited *E. bathybius* series indicates eye migration may begin with notochord flexion. Larvae of *G. zachirus* appear to maintain symmetry until they are ready to settle and then transform rapidly, while asymmetry begins earlier and persists longer in the pelagic phase in *M. pacificus* and possibly the other genera. Perhaps the delay in eye migration in *Glyptocephalus* is a specialization associated with the prolonged pelagic period of all species in this genus.

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NOTES

EFFECTS OF SWIMMING PATH CURVATURE ON THE ENERGETICS OF FISH MOTION

Many respiration and other behavioral and physiological studies of larger pelagic fish species are carried out in round tanks (Fry 1957; Bainbridge 1958; Magnuson 1970; Neill et al. 1976). These tanks have structural and space advantages, since round tanks have the largest volume to surface area of any flat-sided enclosure.

However, circular tanks introduce an additional stress factor not usually encountered by wild fish. This is the centripetal force required for continued motion in a curved path. This force is proportional to the fish mass, and inversely proportional to the path radius. The tank radii are limited by the fact that respiration and heat transfer data are obtained from the medium, resulting in a requirement of relatively small volumes so that changes in the measured parameters (oxygen concentration, temperature, etc.) are enhanced.

As will be shown here, this constraint on tank size causes the centripetal contribution to the force balance to become dominant in certain experimental situations. I therefore developed a correction factor to be applied to data collected in round or annular tanks so as to make the data representative of fish swimming freely in a straight line, in open waters.

Analysis

For a neutrally buoyant fish swimming horizontally in a straight line at a constant speed the force balance in that plane (excluding forces due to buoyancy and its compensation) is, in absolute values,

$$T = D \qquad (1)$$

where T is the thrust and D is the total hydrodynamic drag. Equation (1) also describes the force balance in the tangential direction for curvilinear motion. However, an additional balance must be made between the natural centrifugal force F_c driving the fish to stay in a straight line and the countering centripetal force F causing it to remain on a curved path (see Figure 1A). This force

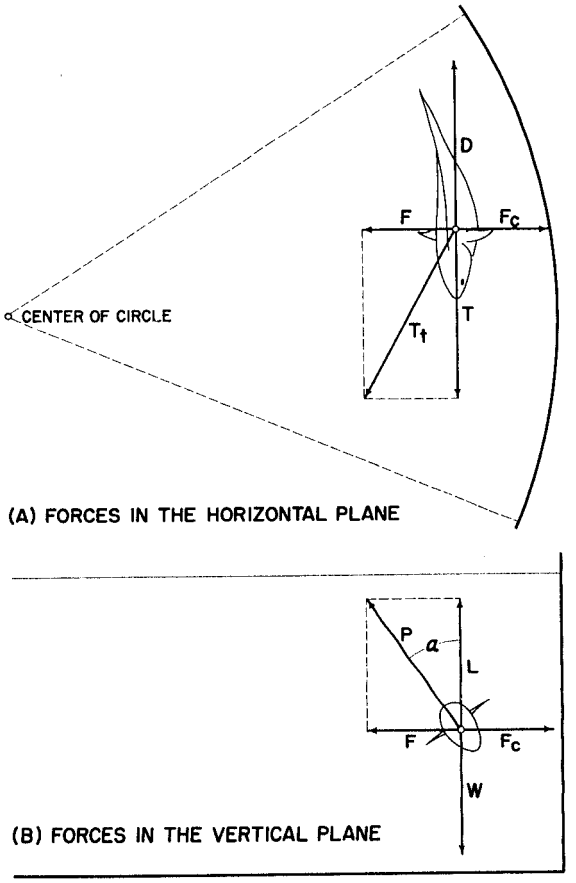

FIGURE 1.—Schematic description of forces acting on a fish when swimming in a curved path. A. Forces in the horizontal plane. B. Forces in the vertical plane.

F, which is equal in magnitude and opposite in sign to F_c, is of magnitude

$$F = \frac{m^1 U^2}{R} = \frac{VU^2}{R}(\rho_f + \rho_w \lambda) \qquad (2)$$

where m^1 is the virtual mass of the fish, ρ_f is the density (averaged) of the fish, V is its volume, U is the forward speed of the fish, λ is the longitudinal added mass coefficient, and R is the instantaneous radius of the curved path. The added mass coefficient λ is multiplied by the density of water ρ_w as the added mass is the volume of water dragged

along with the fish. The hydrodynamic drag can be written as (Hoerner 1965)

$$D = \frac{1}{2}\rho_w V^{2/3} U^2 C_{Dt} \tag{3}$$

where C_{Dt} is the total drag coefficient based on the two-thirds power of the volume, as reference area. Here drag includes gill drag, induced drag due to pectoral fin extension and lift, etc. (see Magnuson 1978 for an excellent description of the various components of drag).

To find the relative importance of the centripetal force, we divide Equation (2) by Equation (3), obtaining

$$\frac{F}{D} = 2\frac{V^{1/3}}{RC_{Dt}}\left(\frac{\rho_f}{\rho_w} + \lambda\right) \tag{4}$$

showing that the fish's velocity does not influence the ratio of centrifugal to drag forces in this case. Equation (4) can now be used to obtain the correction to the force produced by the fish, since the total force T_t that the fish requires for swimming in a circular path in the horizontal plane is, by vectorial addition,

$$T_t = \sqrt{D^2 + F^2}\,. \tag{5}$$

Dividing by D^2 and applying Equation (1), we obtain the required thrust increase for neutrally buoyant fish, as a function of what will now be called the correction factor F/D,

$$\frac{T_t}{T} = \sqrt{1 + \left(\frac{F}{D}\right)^2}\,. \tag{6}$$

Most studies of respiration and energetics in fish measure the aerobic oxygen consumption of the test animals as an indication of energy consumption. To obtain the correction required when the test data are obtained in a round tank, we recall that, for constant speed swimming

$$\dot{E} = TU \tag{7}$$

where $\dot{E}$ is the rate of working. Thus the ratio of work (per unit time) for a continually turning fish, compared with that of fish swimming in a straight line at the same speed, is

$$\frac{\dot{E}_t}{\dot{E}} = \frac{T_t U}{TU} = \frac{T_t}{T}\,. \tag{8}$$

The basic assumption of such respiration studies is that the oxygen uptake rate $\dot{V}_{O_2}$ is directly proportional to $\dot{E}$, so that

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = \frac{T_t}{T} \tag{9}$$

and with Equation (4) we can write this ratio in terms of experimentally measurable quantities:

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = \sqrt{1 + 2\frac{V^{1/3}}{RC_{Dt}}\left(\frac{\rho_f}{\rho_w} + \lambda\right)^2} \tag{10}$$

i.e., the equivalent oxygen uptake for a free-swimming fish moving in a straight line is always lower than that measured in a round tank. Also, for a given turning radius, the larger the fish, the greater the increase in oxygen uptake, or conversely, for a given fish, the oxygen uptake increases with decreasing turning radius. The increase is almost independent of swimming speed except for a possible weak Reynolds number dependence of C_{Dt}, neglected here.

The method shown above for obtaining the centripetal force by increasing the thrust is one possibility. A different way of getting the required forces is by means of hydrodynamic lift.

Negatively buoyant fish, such as most of the scombrids, produce lift by swimming continuously in order to maintain a horizontal course. This defines a hydrodynamical minimum swimming speed for horizontal motion (Magnuson 1970) and causes an additional effect due to swimming in a curved path.

The lift required is usually produced by the pectoral fins being placed at a small angle of incidence to the direction of motion. This force is at right angles to the longitudinal axis of the fish. It can therefore be applied to the production of the centrifugal force, by banking towards the center of curvature (see Figure 1B). Such behavior is an alternative to the added asymmetric thrust calculated above [Equations (4)-(6)], as no direct extra thrust is needed. However, the total lift force on the fins is now larger (Figure 1B), resulting in higher induced drag (Webb 1975; Magnuson 1978), which increases the thrust required.

For motion at a given speed we assume that the only component of drag that varies between straight-line and circular swimming is the induced drag. This is probably an underestimate, because the friction and form may also increase slightly, as mentioned in the previous section. Neglecting these, however, we find that the drag when turning D_t (the drag D, appearing in Equations (1)-(9), is D_t) is greater than the straight-line drag at the same speed D_s by

$$D_t - D_s = D_{it} - D_{is} \tag{11}$$

where D_{it} and D_{is} are the induced drag in turning and in straight-line swimming, respectively. The drag is usually (Hoerner 1965) written as a function of the fin lift force G

$$D_i = \frac{2G^2}{\epsilon\pi\rho b^2 U^2} \tag{12}$$

where b is the fin span and ϵ a fin shape factor. For our purposes, D_i can be written as

$$D_i = K\frac{G^2}{b^2U^2} \tag{13}$$

as the quantities collected in K are invariant for a given fish.

The fin span is variable, as many species of interest can adjust the sweepback angle, changing the span.

Substituting Equation (13) in Equation (11) and applying the geometrical relations of Figure 1B

$$D_t - D_s = \frac{K_1}{U^2}\left(\frac{P^2}{b_t^2} - \frac{L^2}{b_s^2}\right), \tag{14}$$

where b_t and b_s are the pectoral fin span in turning and in straight-line swimming, respectively. Dividing by D_s,

$$\frac{D_t}{D_s} = 1 + \frac{K_1}{U^2 D_s}\left[\frac{P^2}{b_s^2}\left(\frac{b_s}{b_t}\right)^2 - \frac{L^2}{b_s^2}\right]. \tag{15}$$

However, $D_{is} = K_1L^2/U^2b_s$, so that

$$\frac{D_t}{D_s} = 1 + \frac{D_{is}}{D_s}\left[\left(\frac{P}{L}\right)^2\left(\frac{b_s}{b_t}\right)^2 - 1\right]$$

$$= 1 + \frac{D_{is}}{D_s}\left[\left(\left(\frac{F}{L}\right)^2 + 1\right)\left(\frac{b_s}{b_t}\right)^2 - 1\right]. \tag{16}$$

In horizontal swimming $L = W$, so that

$$\frac{D_t}{D_s} = \frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}}$$

$$= 1 + \frac{D_{is}}{D_s}\left[\left(\left(\frac{F}{W}\right)^2 + 1\right)\left(\frac{b_s}{b_t}\right)^2 - 1\right], \tag{17}$$

and as $W = (\rho_f - \rho_w)gV$, by substituting Equation (2)

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = 1$$

$$+\frac{D_{is}}{D_s}\left[\left(\left(\frac{\rho_f + \lambda\rho_w}{\rho_f - \rho_w}\frac{U^2}{gR}\right)^2 + 1\right)\left(\frac{b_s}{b_t}\right)^2 - 1\right], \tag{18}$$

and again, as in Equation (10), the oxygen consumption is higher when the fish is swimming in a circular path. The two techniques, analyzed above are available to negatively buoyant fish, which can choose between producing the centripetal force by asymmetric thrust or by banking. Neutrally buoyant fish would have a more difficult time using the banking method [Equation (18)], as the vertical component L would cause upward motion, or complicated and strenuous compensatory motions.

Returning to the negatively buoyant species, such as skipjack tuna, *Katsuwonus pelamis*, it is reasonable to assume that they will choose the less costly method, or a combination of the two techniques. This will be studied quantitatively in the next section, but one can see immediately that the banking method is highly dependent on swimming speed. This indicates that there may be a threshold speed for each species above which the banking method is more costly.

Next, we estimate the influence of swimming in a curved path on the hydrodynamic minimum swimming speed (Magnuson 1970). At the minimum swimming speed, the pectorals are already producing the highest possible lift coefficient C_L (which will be designated as $C_{L\max}$). Banking the fins reduces the vertical component of the force (Figure 1B), since part of the hydrodynamic force is used to turn the fish. But the vertical force is prescribed by the weight, so that the swimming speed must be increased to obtain the required

forces. Thus, the minimum swimming speed for moving in a curved path is always higher than that for swimming along a straight line. This further increases the effort required to swim in circular tanks above and beyond the thrust corrections found before, when the fish wants or has to move at minimum speed.

At the minimum speed U_m

$$W = \tfrac{1}{2}\rho_w A_f C_{L\,max} U_m^{\,2} \tag{19}$$

where W is the submerged weight of the fish and A_f is the fin lifting area. If the fish turns (when it is confined to a round tank) and still remains at minimum speed, the pectoral fins are banked. The force produced on the fins is then (see Figure 1B)

$$P = \sqrt{W^2 + F^2} \tag{20}$$

or

$$\frac{P}{W} = \sqrt{1 + \left(\frac{F}{W}\right)^2}. \tag{21}$$

P is produced while the fins are at $C_{L\max}$ so that

$$P = \tfrac{1}{2}\rho_w A_f C_{L\max} U_t^{\,2} \tag{22}$$

where U_t is the minimum speed for a horizontal turn. This is a function of the turning radius, through F [see Equation (2)].

Substituting Equations (22), (19), and (2) in Equation (21) we have

$$\left(\frac{U_t}{U_m}\right)^2 = \sqrt{1 + \frac{m^1 U_t^{\,2}}{RW}} \tag{23}$$

$$\left(\frac{U_t}{U_m}\right)^4 = 1 + \frac{2m(1 + \lambda\rho_w/\rho_f)}{\rho_w R A_f C_{L\max}} \left(\frac{U_t}{U_m}\right)^2 \tag{24}$$

$$\text{from which } \frac{U_t}{U_m} = \left[B\left(1 + \sqrt{1 + \frac{1}{B^2}}\right)\right]^{1/2} \tag{25}$$

$$\text{where } B = \frac{m\left(1 + \lambda\rho_w/\rho_f\right)}{\rho_w C_{L\max} A_f} \frac{1}{R}.$$

From Equation (25) we see that $U_t > U_m$ for all finite values of R and that the minimum swimming speed grows as the radius decreases. The increase in minimum speed also is reflected in the total effort required for swimming in the round tank, as the rate of working goes up as the cube of the velocity. The induced drag changes [Equation (11)] are included since the fins are producing maximum lift coefficients both in straight-line swimming and in turning

$$\left(\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}}\right)_{\text{minimum speed}} = \left(\frac{U_t}{U_m}\right)^3. \tag{26}$$

Results and Discussion

To estimate the actual significance of the various corrections developed in the previous section, numerical values of the parameters are now substituted for a negatively buoyant species, the skipjack tuna.

Most of the quantities appearing in the oxygen consumption ratios [Equations (10), (18), and (26)] are easily measurable. The added mass and drag coefficients (λ and C_{Dt}) are more difficult to obtain, as both may also be dependent on the turning radius (due to higher drag when turning and additional added mass effects due to the fish body curvature). However, no such information is presently available, so both these quantities have to be estimated from data on rigid engineering structures.

The most complete set of data for estimation of D appears in Magnuson (1978, table 6) for skipjack tuna. These data will now be used to obtain a typical value of the correction factor Equation (4). The total drag for a 44 cm skipjack tuna swimming at 66 cm/s was estimated to be 19,780 dyn. The mass of the fish is approximately 1.67 kg (Nakamura and Uchiyama 1966), and with an average density of 1.09 (Magnuson 1978, table 3) the volume of the fish is 1,530 cm^3. The drag coefficient C_{Dt} (which is different from Magnuson's drag coefficient because of the different reference area) is found, from Equation (3), to be

$$C_{Dt} = \frac{2 \cdot 19{,}780}{1.025 \cdot (1{,}530)^{2/3} \cdot 66^2} = 0.067. \tag{27}$$

Magnuson's (1978) data are partially based on the study of ram ventilation by Brown and Muir (1970) which was carried out in the holding tanks of the National Marine Fisheries Service Kewalo Research Facility in Honolulu, which are of 7.3 m in

diameter. These allow a maximum path radius of about 300 cm. Recalling that the longitudinal added mass for a streamlined fish shape is $\lambda \approx 0.2$ (Webb 1975) and substituting the above values first into Equation (4), we obtain

$$\frac{F}{D} = 2\,\frac{(1{,}530)^{1/3}\ (1.06 + 0.2)}{300 \cdot 0.067} = 1.44. \quad (28)$$

This means that the centripetal force is actually larger than the total drag force under these circumstances. The total force exerted by the fish swimming in a circular path of 300 cm radius is thus, from Equation (6), $T_t/T = 1.76$, i.e., 76% greater than that required for straight swimming at the same speed. This is also, from Equation (9), the ratio of oxygen consumption. The ratio F/D grows essentially proportionally to fish length, so that larger fish expend an even greater proportion of energy in swimming in a curvilinear path.

We now look at the ratio of oxygen consumption obtained for fish swimming under the same circumstances while banking their fins. This is calculated from Equation (18), assuming that at this low (close to minimum) speed the pectoral fins are fully stretched so that $b_s/b_t = 1$. The ratio D_{is}/D_s is found from Magnuson's (1978) table 6, to be approximately 0.3;

$$\frac{D_t}{D_s} = \frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = 1 + 0.3\left[\left(\left(\frac{1.09 + 0.2 \cdot 1.025}{1.09 - 1.025}\,\frac{66^2}{981 \cdot 300}\right)^2 + 1\right) \cdot (1) - 1\right] = 1.026, \quad (29)$$

i.e., the increase in energy requirements is only 2.6%, much less than for the asymmetric thrust, nonbanked type of swimming. We can conclude therefore that skipjack tuna moving at low speeds in circular paths will use the banked swimming technique once they are adjusted. The banking angle can be obtained by banking the body and keeping symmetrical fin angles (as in Figure 1B), or by asymmetric deployment of the pectorals. An experimental program to study these angles by photography is underway at present, as this is the most obvious and easily measured prediction of the present theory. The predicted value of the banking angle (from the vertical) is obtained from Equation (20) as

$$\tan\alpha = \frac{F}{W} \qquad \alpha = \tan^{-1}\frac{m\left(1 + \frac{\lambda\rho_w}{\rho_f}\right)U^2}{RW}, \quad (30)$$

which for the skipjack tuna example above is 12.0°.

We see above that the banking technique is much more efficient at a relatively low swimming speed. However, the ratio of energy consumption [Equation (18)] is proportional to the speed to the fourth power, so it is important to check on its values at higher swimming speeds. There is no complete set of data available for such speeds, so we have to make some assumptions about the behavior of the various parameters. The ratio D_{is}/D_s is most probably not speed-dependent, as the total and induced drag are both proportional to the speed squared. Thus, we can use the value 0.3 found above. Next, we assume that fin extension is the same (at each speed) for straight-line swimming and turning (the extension can change as a function of speed, but the ratio remains constant). This assumption will also be checked in the experimental program mentioned before, as it is easily corrected in Equation (18).

Skipjack tuna can move at up to 10 body lengths/s, i.e., over 400 cm/s in the present case. Applying Equation (18) at different speeds (still for a turning radius of 300 cm), we obtain

U cm/s	66	100	120	150	175	200	300	400
$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}}$	1.026	1.137	1.285	1.696	2.289	3.199	12.13	36.18

i.e., at speeds of about 160 cm/s ($\approx$ 4 body lengths/s) the asymmetric thrust method, which is independent of speed, becomes the better way of compensating for circular swimming. One can therefore establish a general upper limit for the centrifugal increase in oxygen consumption from Equation (10), with the proviso that at lower speeds the banking method is more efficient.

Next, we calculate the increase in the minimum swimming speed of the tuna mentioned above, for which m = 1,670 g, $C_{L\max} = 1.0$, $A_f = 36$ cm^2 (Magnuson 1973), $\rho_w = 1.025$, $\lambda = 0.2$, and $R = 300$ cm. From Equation (25) we obtain $U_t/U_m = 1.093$. The measured minimum speed in the round tank is thus 10% higher than for the same fish moving in a straight line.

Using the allometric data of Magnuson (1973), we can obtain U_t/U_m as a function of fish size for various species. This appears in Figure 2 for the

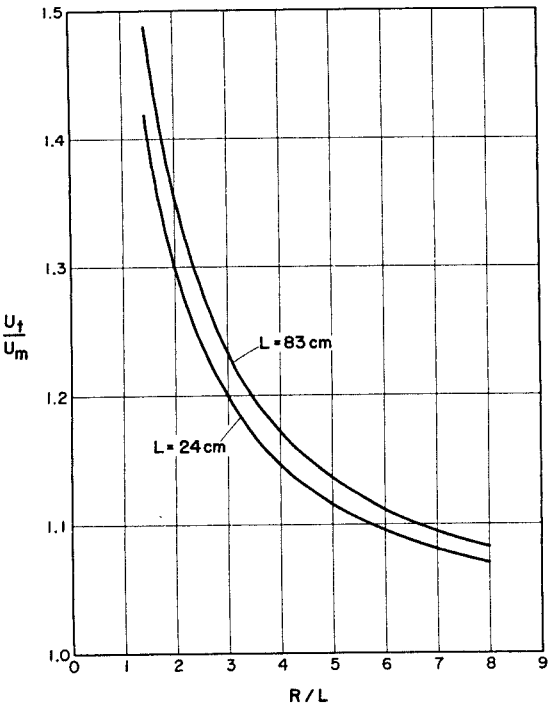

FIGURE 2.—Ratio of minimum speed when moving in a circular path, to the minimum speed in straight-line swimming versus the ratio of turning radius to fish length, for skipjack tuna, *Katsuwonus pelamis*.

skipjack tuna, for which $m = 0.00490L^{3.36}$ and $A_f = 0.00749L^{2.24}$, so that a slight dependence on fish length is retained, even after normalizing by the length. These curves can now be used to establish the increase in minimum energy consumption, with the aid of Equation (26).

In conclusion, it is seen that running fish in circular tanks can cause very significant additional stresses. These have to be taken into account when applying data collected under such circumstances to naturally occurring situations.

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DESCRIPTION OF STAGE II ZOEAE OF SNOW CRAB, *CHIONOECETES BAIRDI*, (OXYRHYNCHA, MAJIDAE) FROM PLANKTON OF LOWER COOK INLET, ALASKA

Chionoecetes bairdi Rathbun 1924 (subfamily Oregoniinae) is the only species of snow crab (genus *Chionoecetes*) that occurs in Cook Inlet, Alaska, and contributes about 20% of the total value of the commercial fisheries harvest of the area (Trasky et al. 1977). The larval stages of *C. bairdi* consist of one prezoeal, two zoeal, and one megalopal stage. The zoeae are readily distinguished from known zoeae of other genera of the subfamily Oregoniinae (*Hyas* and *Oregonia*) by size (the zoeae of *C. bairdi* are nearly twice as large as zoeae of *Hyas* and *Oregonia*) and by slight differences in morphology, especially setation of the antennule and length of the posterior lateral spines (Haynes 1973). The prezoeae, Stage I zoeae, and megalopa of *C. bairdi* have been described from known parentage (Haynes 1973; Jewett and Haight 1977). In this report, I describe the Stage II zoeae from plankton and compare them with other known Oregoniinae zoeae from the North Pacific Ocean.

Methods

Stage II zoeae of *C. bairdi* were collected in lower Cook Inlet in 1976 during a joint survey by the National Marine Fisheries Service and the Alaska Department of Fish and Game. The *C. bairdi* zoeae were collected near the southwestern tip of the Kenai Peninsula (Figure 1) in water 37-141 m deep. Collections were made with two 61 cm bongo nets fished side by side from near bottom to surface. The nets had 0.333 mm mesh, and cod end jars 0.571 mm mesh. The zoeae were captured by lowering the nets to about 1 m from the bottom and then retrieving them vertically at a velocity of slightly <1 m/s. After retrieval, zoeae were washed from the nets and preserved in a 5% solution of formaldehyde and seawater.

Drawings of the Stage II zoeae (Figure 2) were made from preserved specimens. The terminology, methods of measurement, techniques of illustration, and nomenclature of appendages are Haynes' (1973). Total body length includes telsonic furcations. Setation formulae refer to setae numbered from the distal to the proximal portion of the appendage. Comparison of morphological features was aided by first clearing the zoeae in 10% KOH. For clarity, setules on setae are usually omitted but spinulose setae are shown. Any variation in setal counts is noted in text.

Description of Stage II Zoeae

General shape characteristic of Stage II zoeae of *Chionoecetes* is shown in Figure 2A, B. Dorsal and rostral spines long, tapering, essentially

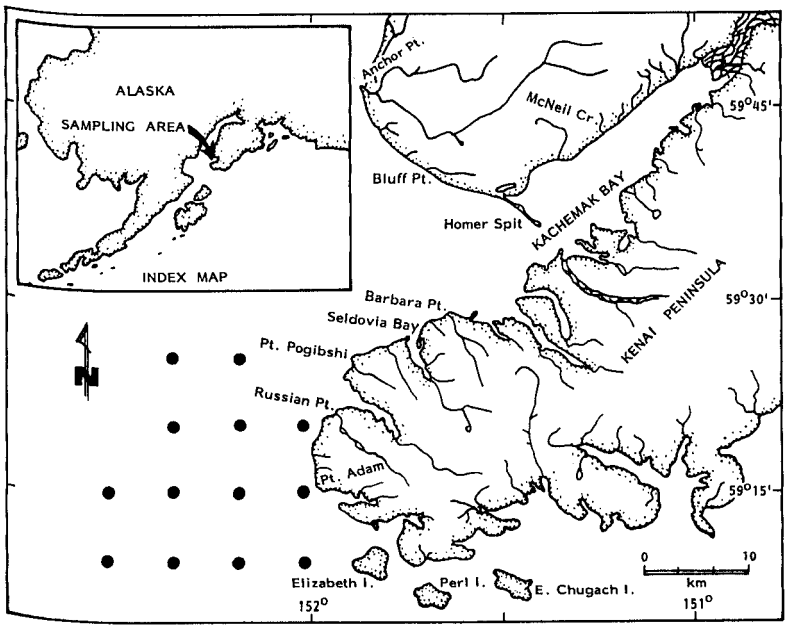
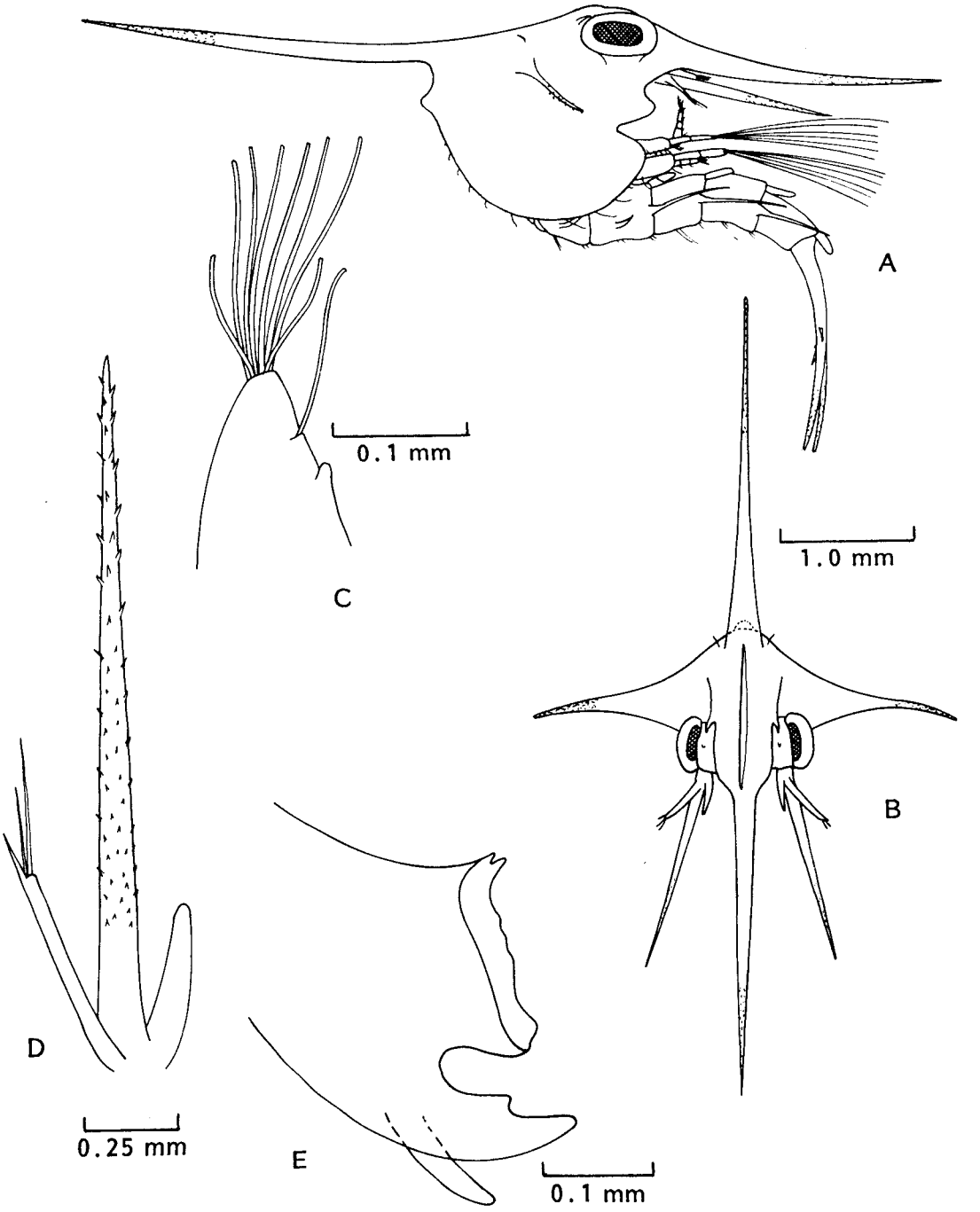


FIGURE 1.—Sampling locations in Cook Inlet, Alaska, where Stage II zoeae of *Chionoecetes bairdi* were captured in 1976.

straight; dorsal spine slightly longer than rostral; lateral spines long, at right angles to carapace, curving downward slightly. Distinct protuberance on carapace posterior to dorsal spine; minute hair on each side of carapace between lateral spine and base of dorsal spine; supraorbital spines present, 11 or 12 setae along posterior edge; lateral margin of carapace strongly indented just posterior to eye. Eyestalks short, articulated, each bears minute protuberance about midway between eye and carapace.

Average measurements: carapace length 1.04



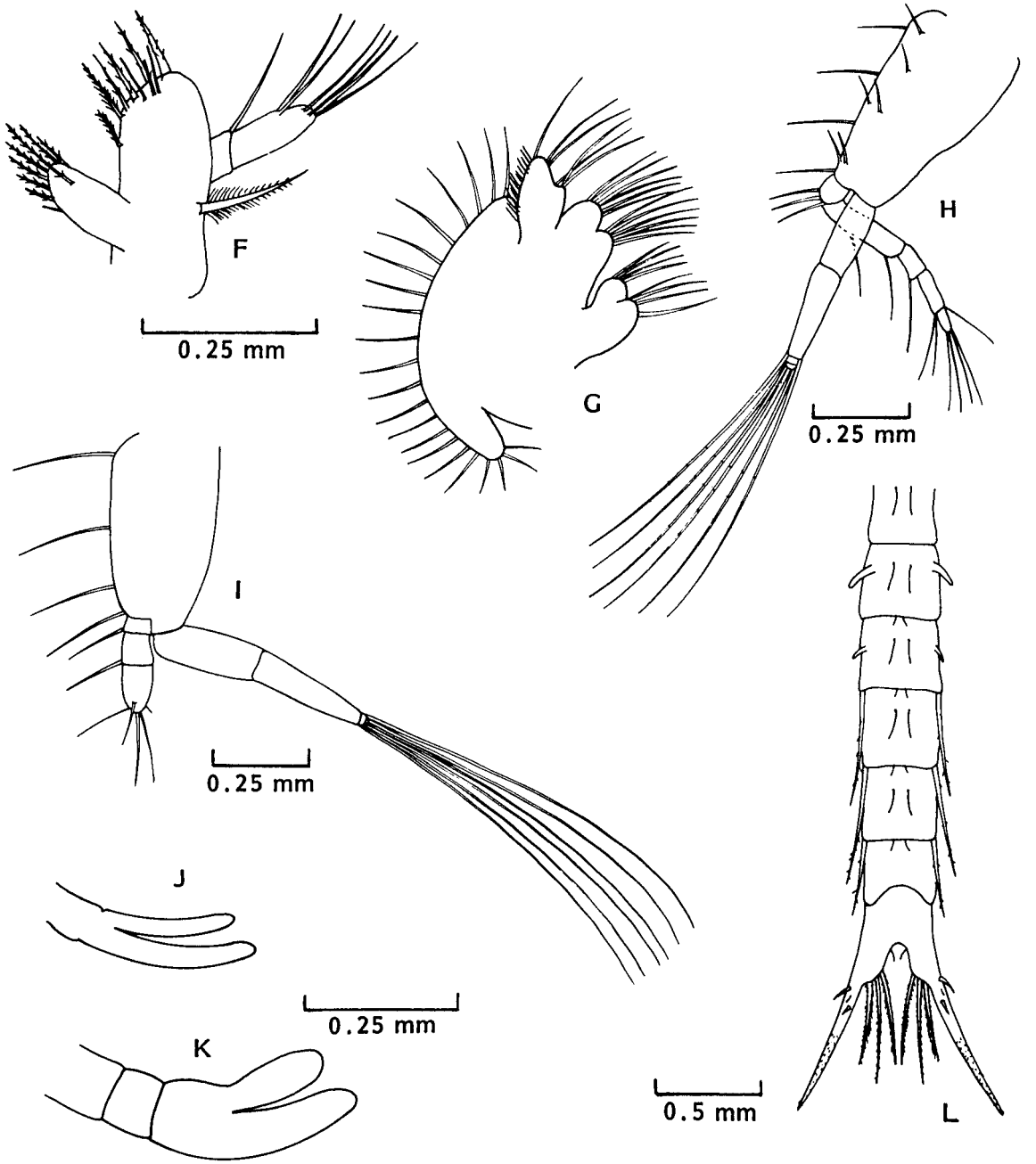


FIGURE 2. — Stage II zoea of *Chionoecetes bairdi*: (A) whole animal, right side; (B) whole animal, frontal; (C) antennule, dorsal; (D) antenna, dorsal; (E) left mandible, posterior; (F) maxillule, ventral; (G) maxilla, dorsal; (H) first maxilliped, lateral; (I) second maxilliped, lateral; (J) third maxilliped, lateral; (K) first pereopod, lateral; (L) abdomen, dorsal.

mm (range 0.98-1.12 mm, 10 specimens); dorsal-rostral length 6.15 mm (range 5.95-6.37 mm, 5 specimens); width between tips of lateral spines of carapace 2.89 mm (range 2.66-3.22 mm, 3 specimens); total body length 5.20 mm (range 4.55-5.95 mm, 9 specimens); rostral spine length 2.24 mm (all 4 specimens); dorsal spine length 2.45 mm (all 4 specimens).

ANTENNULE (Figure 2C). — First antenna, or antennule, conical and uniramous; bears eight terminal aesthetascs (six long and two of intermediate length); small budlike projection and single aesthetasc subterminally.

ANTENNA (Figure 2D). — Protopodite (spinous process) of antenna elongate, about two-thirds length of rostral spine, armed with numerous sharp spinules that increase in size distally; exopodite slender, less than one-half length of protopodite, two setae near sharp tip, each seta with two rows of many fine setules; endopodite naked, about two-thirds length of exopodite.

MANDIBLES (Figure 2E). — Right and left mandibles nearly identical; palps unjointed and naked; incisor composed of two large, rounded processes.

MAXILLULE (Figure 2F). — First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) bears nine spinulose spines, eight terminally and one subterminally. Median lobe (basipodite) bears nine spines distally: two setose spines, three simple spines, four spinous spines (especially stout) plus a large setose seta proximally. Endopodite two-segmented, originates from lateral margin of basipodite, bears seven setae (six on distal segment, one on distal margin of proximal segment).

MAXILLA (Figure 2G). — Bears platelike exopodite (scaphognathite) with 21-23 plumose setae along outer margin; no long, thick seta at proximal end. Endopodite unsegmented, bears six setae distally and fine hairs along outer margin. Basipodite bilobed; each lobe bears six setae. Bilobed coxopodite bears eight setae, four on each lobe.

FIRST MAXILLIPED (Figure 2H). — Exopodite completely segmented; bears six heavily plumose (natatory) setae on distal end. Endopodite five-segmented; setation formula 4, 3, 1, 2, 3. Basipodite bears 10 setae along posterior edge, all setae except natatory setae sparsely plumose.

SECOND MAXILLIPED (Figure 2I). — Exopodite completely segmented, bears six long, heavily plumose (natatory) setae terminally. Endopodite three-segmented, setation formula 5, 1, 1. Basipodite bears four setae along posterior margin, all except natatory setae, sparsely plumose.

THIRD MAXILLIPED (Figure 2J). — Not fully developed, unsegmented, bilobed.

FIRST PEREOPOD (Figure 2K). — Chela segmented from carpopodite, bilobed but not functional.

SECOND TO FIFTH PEREOPODS. — Small, uniramous, not segmented or bilobed.

ABDOMEN AND TELSON (Figure 2A, L). — Abdomen consists of six somites and telson. Somites 1-5 bear pair of simple setae middorsally; somites 2-5 also bear pair of simple setae near dorsal posterior margin. Second and third somites both bear pair of curved lateral processes; length of pair on second somite about half the height (Figure 2A) of second somite; pair on third somite about half the length of pair on second somite. Pair of long well-developed spines on posterior lateral margins of third, fourth, and fifth somites; those on third and fourth somites extend beyond posterior margin of adjacent somites to about midpoint of fifth and sixth somites, respectively. Spines on fifth somite extend to level of anus; lateral spines usually bear a few minute spinules. Undeveloped pleopods (Figure 2A) present on abdominal somites 2-5; length of pleopods about three-fourths height of abdominal somites. Telson bifurcate; furcations long, slender, finely spinulate, tips upcurved. Each furcation bears three articulated telsonic setae and one simple seta on mesial margin, a prominent spine laterally on outer margin, a smaller dorsal spine posterior to telsonic setae, and minute spinule about midway between the lateral and dorsal spines; lateral and dorsal spines on furcations minutely spinulate. Each telsonic seta, except pair of simple setae, bears two rows of spinules. Uropods (Figure 2A) on somite 6 undeveloped, length about four-tenths height of sixth somite.

Comparison of North Pacific Zoeae of the Subfamily Oregoniinae

The subfamily Oregoniinae comprises three genera, *Chionoecetes, Hyas,* and *Oregonia* (Garth 1958). Zoeae of the subfamily have been described, at least in part, for *C. opilio, C. japonicus, H. coarctatus alutaceus, H. lyratus,* and *Oregonia gracilis* (Hart 1960; Kurata 1963; Yamauro 1968; Haynes 1973; Motoh 1973). Based on these descriptions, Stage I and II zoeae of the Oregoniinae are readily separable from each other (Table 1). Stage I zoeae are characterized by sessile eyes, four natatory setae on the first and second maxillipeds, absence of pleopods, and three pair of setae on the inner margin of the telsonic furcations. Stage II zoeae bear stalked eyes, six natatory setae on the first and second maxillipeds, pleopods, and four pair of setae on the inner mar-

TABLE 1.--Morphological characteristics for distinguishing between Stage I and II zoeae of the subfamily Oregoniinae.

Characteristic	Stage I	Stage II
Supraorbital spines	absent	present
Eyes	sessile	stalked
Natatory setae:		
First maxilliped	4	6
Second maxilliped	4	6
Pleopods	absent	present
Pairs of setae on inner margin of telsonic furcations	3	4

gin of the telsonic furcations. In addition, the Stage II zoeae bear supraorbital spines which are lacking in the Stage I zoeae.

Hart (1960) reared and described the larvae of *H. lyratus* and *O. gracilis* from ovigerous females collected in British Columbia waters. Based on Hart's brief description, Stage II zoeae *H. lyratus* and *O. gracilis* are similar morphologically to Stage II zoeae of *C. bairdi,* but markedly smaller. Dorsal-rostral length of Stage II *H. lyratus* and *O. gracilis* averages 4.0 mm and 4.5 mm, respectively, compared with 6.5 mm for Stage II zoeae of *C. bairdi.*

Kurata (1963) described larvae collected off Hokkaido that he provisionally identified as *H. coarctatus alutaceus*. They can be distinguished from Stage II zoeae of *C. bairdi* by their smaller size (dorsal-rostral length averages 4.4 mm) and the lack of a distinct protuberance posterior to the dorsal spine.

Stephensen (1935) described zoeae from the collection of the Zoological Museum of Copenhagen previously identified by C.N. Rudolph and subsequently believed by Stephensen to be zoeae of *C. opilio*. Because of the numerous (14) natatory setae on the exopodites of the maxillipeds, Stephensen's zoeae are obviously not zoeae of the genus *Chionoecetes* nor even of the Oxyrhyncha. Stephensen's zoeae undoubtably belong to the Brachyrhyncha and likely the families Atelecyclidae or Cancridae.

Kurata (1963) described Stage I zoeae of *C. opilio elongatus* (=*C. opilio*[1]) reared in the laboratory from known parentage and the remaining larval stages from plankton of the Hokkaido area. Motoh (1973) described the zoeal and megalopal stages of *C. opilio* reared in the laboratory from an ovigerous female caught in the Sea of Japan. I confirmed Kurata's and Motoh's brief descriptions of Stage I and II zoeae by comparing their descriptions with specimens from the Sea of Japan sent to me by Tohshi Kon (see footnote 1). For both stages, zoeae of *C. bairdi* are morphologically identical with zoeae of *C. opilio* from Hokkaido and the Sea of Japan, except for length of the curved lateral processes on the third abdominal somite. In Stage I and II zoeae of *C. opilio* from Hokkaido and the Sea of Japan, the curved lateral processes reach the posterior margin of the third abdominal somite, but, in Stage I and II zoeae of *C. bairdi,* they are markedly shorter (Figure 2A, L).

Apparently larvae of *C. japonicus* are known; but, except for a brief comparison of their morphology with larvae of *C. opilio* by Yamauro (1968), I am unaware of their description in the literature. Based on Yamauro's comparison, Stage I and II zoeae of *C. japonicus* are distinguished from Stage I and II zoeae of *C. bairdi* by length of the posterior lateral spines on the third, fourth, and fifth abdominal somites. In *C. japonicus* zoeae the posterior lateral spines barely reach the posterior margin of the somite, but in *C. bairdi* zoeae they extend beyond the margin.

The following key is provided for distinguishing Stage II zoeae of *C. bairdi* from Stage II zoeae of *C. opilio, C. japonicus,* and the genera *Hyas* and *Oregonia.* In the key, length of the lateral processes on the third abdominal somite of *C. opilio* zoeae is based on specimens from the western Pacific Ocean. Stage II zoeae of *C. opilio* from the eastern Pacific Ocean have not been identified, and it is not known whether they can be distinguished from Stage II zoeae of *C. bairdi* by length of their lateral processes.

Key for Distinguishing Stage II Zoeae *C. bairdi*

1a. Dorsal-rostral length 4.0-4.6 mm .... *Hyas, Oregonia*
1b. Dorsal-rostral length 6.0-6.9 mm 2
2a. Lateral processes on third abdominal somite reach posterior margin of somite ..... *C. opilio*
2b. Lateral processes on third abdominal somite do not reach posterior margin of somite 3
3a. Posterior lateral spines on abdominal

[1]Rathbun (1924) designated *C. opilio* in the Sea of Japan as *C. opilio elongatus* based on the length/width relation of the second merus. According to Tohshi Kon, Fukui Prefecture Fishery Experimental Station, Tsuroga-shi, Fukui-Prefecture, Japan (pers. commun. November 1978), Kamita's (1941) findings invalidate Rathbun's subspecific designation.

somites 3, 4, and 5 barely reach margin of somite ..... *C. japonicus*

3b. Posterior lateral spines on abdominal somites 3, 4, and 5 extend beyond margin of somite ..... *C. bairdi*

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FEEDING RATE OF CAPTIVE ADULT FEMALE NORTHERN FUR SEALS, *CALLORHINUS URSINUS*[1]

Overexploitation of fishery stocks in the North Pacific and Bering Sea is thought by some to be contributing to a small but perceptible decline in the northern fur seal population (Gentry et al.[2]). To manage both fishery and fur seal resources intelligently it is necessary to know how much a northern fur seal eats and to identify the factors that affect its food intake. Our data show that feeding rate of captive adult females is variable and influenced by season of the year and body mass of the individual.

Methods

Ten adult northern fur seals (two males and eight females) were captured on St. Paul Island, Pribilof Islands, Alaska, in mid-October 1977.[3] The ages of the females were estimated at 5+ yr, based on the color of the vibrissae, which were completely white (Scheffer 1962). After a short observation period all seals were shipped by air freight to Mystic Marinelife Aquarium in Mystic, Conn. On arrival, the females were tagged with monel metal cattle ear tags[4] identical to those used in the National Marine Fisheries Service's Pribilof Fur Seal Program. One tag was placed on each seal's left foreflipper above the fur line. Numbers assigned were XCu01 through XCu08. Once acclimated, all seals were kept together in a large outdoor exhibit. Husbandry requirements, including feeding rate, were studied for the next 2 yr. This report deals only with the females.

Feeding rate was recorded daily for 356 days of 1978 (5 January through 27 December). Data are summarized in Table 1. The year was divided arbitrarily into three periods, each starting the day after the animals were weighed. Weights were taken 4 January (Period 1 = 5 January through 7 March), 7 March (Period 2 = 8 March through 25 September), and 25 September (Period 3 =

[1]Contribution No. 16, Sea Research Foundation, Inc.

[2]Gentry, R. L., J. H. Johnson, and J. Holt. 1977. Behavior and biology, Pribilof Islands. *In* Marine Mammals Division, Fur seal investigations, 1976, p. 26-39. Northwest Fish. Cent. Processed Rep.

[3]Permit No. 178, applied for under the Fur Seal Act of 1966 and issued 2 May 1977 by the National Marine Fisheries Service.

[4]NASCO, 901 Janesville Avenue, Fort Atkinson, WI 53538. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Feeding rate and body mass data for eight adult female northern fur seals from the Pribilof Islands, Alaska, 1977-78.

Tag no.	Acclimation (9 Oct.-4 Jan.) Mass[1] (kg)	Feeding rate (% body mass/d)	Mass change (%/d)	Period 1 (5 Jan.-7 Mar.) Mass (kg)	Feeding rate (% body mass/d)	Mass change (%/d)	Period 2 (8 Mar.-25 Sept.) Mass (kg)	Feeding rate (% body mass/d)	Mass change (%/d)	Period 3 (26 Sept.-27 Dec.) Mass (kg)	Feeding rate (% body mass/d)	Mass change (%/d)	Final mass 28 Dec.
XCu01	38.8	7.3	+0.17	44.6	9.4	−0.062	43.8	5.1	[2]	[2]	[2]	[2]	42.8
XCu02	30.4	8.4	+.57	45.5	12.2	+.31	50.0	4.5	−0.07	42.9	5.6	+0.07	45.5
XCu03	36.6	5.8	+.08	39.3	11.6	+.25	42.4	5.5	−.026	40.2	6.1	+.037	41.5
XCu04	39.7	6.6	+.23	47.8	10.4	+.15	50.0	4.3	−.13	37.5	7.4	+.36	49.6
XCu05	31.3	7.1	+.18	36.2	12.5	0	36.2	6.3	+.031	38.4	5.4	+.01	38.8
XCu06	34.8	9.2	+.059	36.6	13.1	+.19	38.8	7.1	−.092	37.1	7.0	−.01	36.6
XCu07	36.2	7.1	+.53	52.7	6.7	−.18	49.6	4.1	−.56	35.7	7.2	+.52	52.2
XCu08	44.2	5.3	+.15	50.0	7.9	−.28	45.5	4.9	+.31	52.7	4.7	+.057	55.4

[1]Initial mass recorded within 3 h of capture.
[2]Nursing a pup—no data collected.

26 September through 27 December). A final weight was recorded on 28 December, making a total of four weighing sessions in 1978. Air and water temperatures for the three periods are summarized in Table 2. Data collected during acclimation (9 October 1977 through 3 January 1978) were omitted from the calculations because the seals either were not feeding consistently, or were consuming abnormally large quantities of food. According to our experience, such behavior is not unusual.

Seals were fed individually. The food for each seal was weighed and the amount left over after a feeding was subtracted. All animals were fed to satiation and none ate to obesity. Feedings were at 0900, 1330, and 1530 h daily. Food fishes used primarily were Atlantic herring, *Clupea h. harengus*, and Atlantic mackerel, *Scomber scombrus*, purchased frozen and thawed shortly before feeding.

The animals were not fed on the morning they were weighed. Weighing sessions started at about 1000 h, after the pool was drained, and were finished shortly before noon. Seals were herded into individual cages and weighed on a hanging scale (±0.4 kg). Little food was present in the intestines at that point. Miller[5] showed that digestion in northern fur seals takes about 8 h.

Results

Multiple linear regression was performed using water temperature and animal mass as independent variables, and feeding rate as the dependent variable (Tables 1, 2), for all three periods combined. The equation obtained was

TABLE 2.—Mean monthly values for air and water temperatures during the feeding observations on captive northern fur seals.

Period	Month	Temperature (° C) Air	Water	Period	Month	Temperature (° C) Air	Water
1	Jan.	−1.9	9.6	2	Aug.	22.7	19.4
	Feb.	−2.4	8.3		Sept.	17.6	18.1
	Mar.	2.7	9.8		Mean	17.0	15.8
	Mean	−1.9	8.8	3	Oct.	12.3	15.8
2	Apr.	9.4	11.5		Nov.	7.7	13.1
	May	15.7	14.5		Dec.	3.2	11.1
	June	20.7	16.8		Mean	8.3	13.8
	July	22.5	19.1				

$$F = -0.782\,T_w - 0.096\,M + 25.77$$

where F is feeding rate (as percentage of body mass per day), T_w is water temperature (degrees Celsius), and M is body mass (kilograms). The coefficient of multiple correlation (r) was 0.927 and the standard error of estimate 1.05. An attempt to relate the same data with air temperature resulted in poorer correlation ($r = 0.879$, $s_{y.x} = 1.34$).

Feeding rate and initial body mass are strongly related, as is the feeding rate for all seals combined when considered seasonally. This is evident from data in Table 1 and the linear regressions of Figure 1. Large seals required a smaller percentage of body mass per day in all three periods. The steepest slope is in Period 1, in which differences between body and ambient temperature were greatest. Analysis of covariance demonstrated that Periods 1, 2, and 3 cannot be pooled for purposes of regression. Taken separately, regression produced correlation coefficients indicating high significance ($P \leq 0.01$ for Periods 1 and 2, and $P \leq 0.05$ for Period 3).

Discussion

Bigg et al. (1978) and Bigg[6] showed that the fluctuation in body mass of adult females in

[5]Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Rep. MMC-75/08, U.S. Mar. Mam. Comm., Wash., D.C., 27 p. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB-275 296.

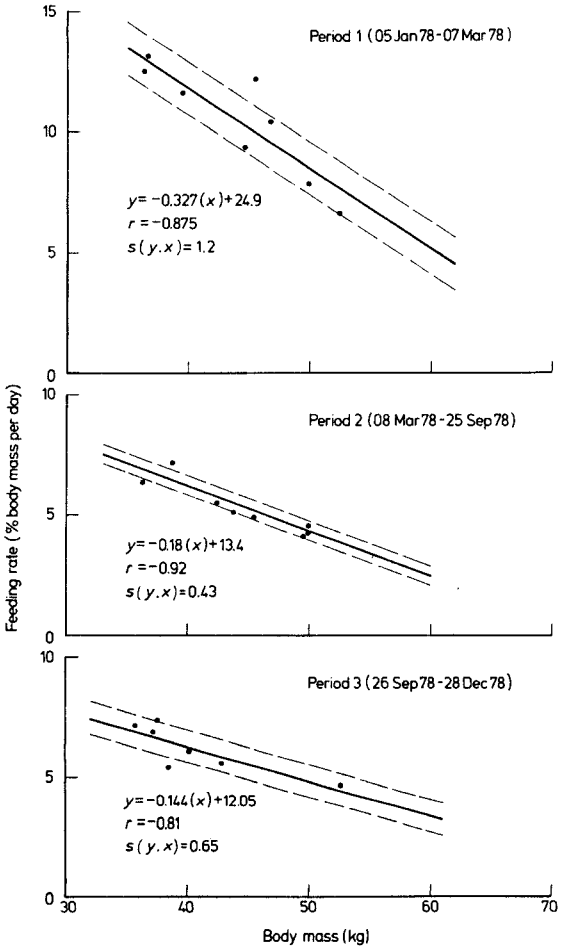

FIGURE 1.—Feeding rate versus individual body mass for eight adult female northern fur seals for Periods 1-3. Standard error of estimate ($s_{y.x}$) is indicated by the broken lines.

captivity follows a predictable pattern, implying a precise mechanism for weight control that is seasonally synchronized. Our findings are further confirmation of this. Food intake (and therefore body mass) was greatest from late autumn to late spring. Changes in mass reflected variations in blubber thickness, because all animals were fully mature.

Changes in water temperature probably account for the seasonal variation in food consumption shown by our seals, although individual differences in metabolism probably were important. In Period 1, when water temperature averaged 8.8° C, the smaller seals required a greater percentage ration than the larger animals, as shown by the slope of the line in Figure 1 (−0.327). In Periods 2 and 3, when water temperatures were similar, the variation in feeding rate versus body mass was less, and the slopes of the lines also were similar, as shown in Figure 1 (−0.18 and −0.144, respectively).

The above equation allows the feeding rate of captive adult females to be predicted with reasonable accuracy, given water temperature and body mass. The artifact introduced by captivity was to allow the seals to enter and leave the water at will. Future studies should be made using adult females that are confined to the water and not allowed to haul out for a length of time (and at a water temperature) that simulates the pelagic phase of the life cycle.

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INDUCED SPAWNING OF A TUNA, *EUTHYNNUS AFFINIS*

Investigations into the biology of young tuna have been hampered by the difficulty of capturing and maintaining live larvae or early juveniles from the wild. The production of young in captivity would provide an obvious solution; however, the inherent difficulties of maintaining and working with such powerful, fast-swimming, pelagic fishes under conditions of close confinement have discouraged attempts to artificially stimulate their spawning. The following describes what we believe to be the first induced spawning of any tuna, accomplished with specimens of *Euthynnus affinis*, one of the smaller sized of the true tunas (taxonomic relations of tunas were recently reviewed by Collette (1978)). These were held captive in tanks at the Kewalo Research Facility of the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA.

The specimens used in these spawning trials were three females in captivity for 2-4 wk and three males in captivity for about 4 mo. All were captured by hook and line and transported to the laboratory in the baitwells of either a commercial fishing vessel or the NOAA Ship *Townsend Cromwell*. They were maintained outdoors in circular, 7.3 m in diameter by 1.1 m deep tanks with water flow of about 3.0-3.5 l/s and temperatures ranging from 23.3° to 26.2° C. They were fed thawed surf smelt, *Hypomesus pretiosus*, and squid *Loligo opalescens* at a rate of about 15-20% of their body weight per day.

Sex and gonadal maturation of each specimen were determined by biopsy, with samples obtained by catheterization through the urogenital aperture (Shehadeh et al. 1973). While the fish were physically restrained for the biopsies, each was marked with an identifying numeral or letter with silver nitrate (Thomas 1975). Males in advanced stages of maturation could be recognized by the presence of milt in the catheter, while females in any stage of maturation could be identified from the biopsied ovarian tissue. The diameters of 25 ova of the largest size class present in the catheterized sample were measured with an ocular micrometer and the average diameter calculated as an index of ovarian maturation.

Gonadal maturation of captive specimens was monitored by monthly biopsies, starting in March 1979 with 37 specimens maintained since the preceding January and February. After March, newly captured specimens were also biopsied on the day of delivery to the laboratory. The most advanced ovaries in our captive fish between March and August 1979 were in three females delivered to the laboratory on 6 June. Their largest ova averaged 0.54, 0.48, and 0.44 mm on arrival and 0.55, 0.53, and 0.50 mm, respectively, when biopsied again 2 wk later on 19 June. The first two (females A and B, Table 1) were used in the first spawning trial, which started that same day, on 19 June. The third female (female C, Table 1) was biopsied again after an additional 2 wk, and its largest ova had increased to an average diameter of 0.56 mm. It was used in the second spawning trial, which started that same day, on 2 July. Males from groups captured earlier in January and February were also biopsied on the starting dates of the spawning

TABLE 1.—Spawning responses of *Euthynnus affinis* to treatment with salmon pituitaries (SP), human chorionic gonadotropin (HCG), and pregnant mare serum (PMS). Ova sizes represent mean diameters of 25 spawned ova after preservation in 3-5% Formalin,[1] or the largest size class in fresh biopsied samples.

	Day 1			Day 2			Day 3		
	Ova (mm)			Ova (mm)			Ova (mm)		
Specimen	Mean	SD	Treatment	Mean	SD	Treatment	Mean	SD	Response
Trial 1:									
Female A	0.53	0.03	SP 5 mg HCG 100 IU	0.54	0.04	SP 5 mg HCG 100 IU PMS 1,000 IU	0.55	0.04	Did not spawn.
Female B	0.55	0.05	SP 10 mg HCG 500 IU	0.57	0.04	SP 10 mg HCG 500 IU PMS 2,000 IU	0.77 0.98	0.02 0.02	Spawned (>35,000 released spontaneously; <10,000 stripped and fertilized).
Male A			HCG 100 IU			HCG 100 IU			No hydration of milt.
Male B			HCG 500 IU			HCG 500 IU			Hydration of milt.
Trial 2:									
Female C	0.56	0.03	SP 10 mg HCG 500 IU	0.70	0.04	SP 10 mg HCG 1,000 IU PMS 2,000 IU	0.78 1.02	0.03 0.03	Spawned (>185,000 released spontaneously; >40,000 stripped and fertilized).
Male C			HCG 1,000 IU			HCG 1,000 IU PMS 1,000 IU			Hydration of milt.

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

trials, and specimens yielding milt in the catheter were selected. The selected males and females were transferred to a spawning tank identical in dimensions to the holding tanks but with water depth reduced to 0.61 m. Two females and two males were used in the first trial, and one female and one male in the second. Their sizes ranged from 47.0 to 52.9 cm fork length and 2.25 to 3.04 kg.

Hormone treatments administered were modified after those used by Leong (1977) to spawn Pacific mackerel, *Scomber japonicus*. Combinations of triturated, acetone-dried salmon pituitary glands (SP), human chorionic gonadotropin (HCG), and pregnant mare serum gonadotropin (PMS) were injected into the dorsal musculature with tuberculin syringes and 24-gage needles. The hormone preparations were suspended or dissolved in physiological saline and administered in injection volumes of 0.10-0.50 ml (Table 1). Each treatment consisted of two series of injections 24 h apart, starting at 2 p.m. in the first trial and 6 p.m. in the second. Responses of females were monitored by ovarian biopsies taken immediately preceding each series of injections, and spawning was detected by the appearance of the buoyant, pelagic ova in plankton nets (egg strainers) placed in the outflow from the treatment tank. Responses of males were based on subjective evaluation of hydration of milt, on the basis of whether milt could be expressed by moderate stripping pressure, and the fluid consistency of the milt obtained.

In the first trial, neither female showed any significant increases in sizes of largest ova within 24 h after the first injections (Table 1). However, ova were found in the strainers the next morning at about 8:15, about 19 h after the second injections. Biopsy of both females indicated that ovulation had been induced only in the one treated with higher dosages; similarly, examination of both males indicated that milt could be expressed only from the individual treated with the higher dosages. Eggs and milt were stripped from the responsive pair to effect fertilization. Most of the ova from this spawning were not viable and sank when placed in seawater, and of those that remained buoyant none progressed beyond early cleavage stages. This poor viability was probably caused by our failure to detect or respond to this induced ovulation early enough, with a consequent deterioration of the ovulated eggs within the ovarian lumen (Stevens 1966).

In the second trial, biopsy of the female indicated that its largest ova had increased in mean diameter from the original 0.56 to 0.70 mm within 24 h after the first injections. Ova were found in the strainer at 5:30 the next morning, 12.5 h following the second injections. Milt could be easily expressed from the male at this time, and the pair were stripped to effect fertilization. At incubation temperatures which ranged between 21° and 26° C, the first cleavage divisions were observed about 1 h after fertilization and the first hatching at about 31 h. With limited facilities for maintaining the developing embryos, we were able to sustain only a small fraction of the fertilized eggs obtained. About 300 larvae were hatched and they developed and absorbed their yolk sacs over 2 d. It was not our intent or purpose at this stage of these investigations to attempt to feed or rear these larvae, and they all died by the end of the third day.

Previous attempts to produce young tuna in captivity have been concentrated in Japan, and along two lines of effort. One is the fertilization at sea of ova obtained by stripping freshly captured, running-ripe fish (Yasutake et al. 1973; Harada 1978; Ueyanagi 1978). Since running-ripe females are only infrequently taken in current commercial fishing operations, these efforts have produced only occasional successes. The other approach is to maintain adult-sized specimens in large, netted enclosures in coastal waters with the hope that they will eventually start spawning naturally. (By coincidence, the first known spawning of a species of tuna in such a situation was reported to have occurred with bluefin tuna, *Thunnus thynnus*, on 20 June 1979 (Sōgō 1979) at the same time that our first induced spawning of *E. affinis* was taking place.) Whether either of these two approaches can be developed into reliable spawning operations for tunas remains to be determined. The two consecutive hormone-induced spawnings that we achieved with *E. affinis* suggest that this technique can be developed into a routine procedure, at least for this species. Work is expected to continue at the Honolulu Laboratory on refinement of effective treatments and to be initiated on rearing of the resultant larvae.

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TROPHIC IMPORTANCE OF SOME MARINE GADIDS IN NORTHERN ALASKA AND THEIR BODY-OTOLITH SIZE RELATIONSHIPS

Natural marine ecosystems are being subjected to ever increasing human-induced stresses, including expanding commercial fisheries and activities associated with the exploration and development of offshore petroleum resources. Numerous studies of the food habits and trophic interactions of marine vertebrate consumers have been undertaken in Alaska during the last 5 yr in response to increased demand for multispecies approaches in fishery management plans and the legal requirement for environmental assessments prior to petroleum development. Through these and other studies the importance of three species—walleye pollock, *Theragra chalcogramma*, saffron cod, *Eleginus gracilis*, and Arctic cod, *Boreogadus saida*—in Arctic and subarctic ecosystems has become increasingly apparent (Klumov 1937; Andriyashev 1954; Lowry and Frost in press; Pereyra et al.[1]). These species are widespread and locally abundant, are major secondary consumers, and are important prey of other species (Table 1).

Walleye pollock are found throughout the North Pacific and in greatest abundance along the continental shelf break of the Bering Sea. Abundance decreases rapidly north of St. Matthew Island, and they are caught only rarely north of Bering Strait (Pereyra et al. footnote 1). The species supports a commercial fishery of almost 1 million t annually, one of the largest in the world. Walleye pollock form a major portion of the diet of all pinnipeds in the southern Bering Sea, except bearded seals and walruses, and are eaten by at least 4 species of cetaceans, 13 species of seabirds, and 10 species of fishes in that area.

Saffron cod occur in the eastern Bering and Chukchi Seas and throughout the western Arctic Ocean (Andriyashev 1954). They are also present, but less abundant, in the Beaufort Sea. Saffron cod are utilized for food by coastal Eskimos. They make up a major portion of the diet of ringed and spotted seals and white whales in the northern Bering and southern Chukchi Seas. They are also

[1]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Processed rep., 619 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

TABLE 1.—Marine mammals, birds, and fishes reported to eat walleye pollock, saffron cod, and Arctic cod.

Species	Walleye pollock	Saffron cod	Arctic cod
Marine mammals:			
Northern fur seal, *Callorhinus ursinus*	9		
Steller sea lion, *Eumetopias jubatus*	3, 10, 31		
Pacific harbor seal, *Phoca vitulina richardsi*	23, 24, 31		
Spotted seal, *P. largha*	22, 23, 31	32	22, 23
Ribbon seal, *P. fasciata*	14, 23, 31	14, 23	22, 23
Ringed seal, *P. hispida*	32	11, 23	2, 6, 11, 23
Bearded seal, *Erignathus barbatus*	31, 32	8, 23	2, 11, 32
Fin whale, *Balaenoptera physalus*	5, 13	5	1, 5
Minke whale, *B. acutorostrata*	5, 25	5	1, 5
Sei whale, *B. borealis*	5		5
Humpback whale, *Megaptera novaengliae*	5	5	1, 5
White whale, *Delphinapterus leucas*		5, 25	1, 2, 25
Harp seal, *Phoca groenlandica*			1
Narwhal, *Monodon monocerus*			1, 2, 18
Harbor porpoise, *Phocoena phocoena*		25	
Polar bear, *Ursus maritimus*			1
Birds:			
Glaucous gull, *Larus hyperboreus*	20		12
Herring gull, *L. argentatus*			12
Sabine's gull, *Xema sabini*			15
Ross's gull, *Rhodostethia rosea*			17
Ivory gull, *Pagophila eburnea*	20		17
Black-legged kittiwake, *Rissa tridactyla*	20, 21	30	1, 12, 30
Red-legged kittiwake, *R. brevirostris*	20, 21		
Common murre, *Uria aalge*	16, 21	30	7, 21, 30
Thick-billed murre, *U. lomvia*	16, 21	30	7, 28, 30
Black guillemot, *Cepphus grylle*	20		1, 12, 28
Pigeon guillemot, *C. columba*			12
Tufted puffin, *Lunda cirrhata*	21		12
Horned puffin, *Fratercula corniculata*	21		12
Kittlitz's murrelet, *Brachyramphus brevirostre*			15
Parakeet auklet, *Cyclorrhynchus psittaculus*	21		15
Least auklet, *Aethia pusilla*	21		
Arctic tern, *Sterna paradisea*			4
Fulmar, *Fulmarus glacialis*	21		28
Shearwaters, *Puffinus* spp.			15
Pelagic cormorant, *Phalacrocorax pelagicus*			12, 15
Red-faced cormorant, *P. urile*	21		
Red-throated loon, *Gavia stellata*			15, 19
Jaegers, *Stercorarius* spp.			1
Fishes:			
Atlantic cod, *Gadus morhua*			1
Pacific cod, *G. macrocephalus*	4, 26, 32		
Walleye pollock, *Theragra chalcogramma*	26, 32		
Saffron cod, *Eleginus gracilis*		4	4
Pacific halibut, *Hippoglossus stenolepis*	29		
Greenland halibut, *Reinhardtius hippoglossoides*	26, 32		
Sablefish, *Anoploploma fimbria*	26		
Flathead sole, *Hippoglossoides elassodon*	29, 32		
American plaice, *H. platessoides*			1
Arrowtooth flounder, *Atheresthes stomias*	26, 29		
Snailfish, *Liparis* sp.	32		
Eelpout, *Lycodes* spp.	32		
Sculpins, *Icelus spiniger*, *Myoxocephalus* spp.	32	32	
Sheefish, *Stenodus leucichthys*		32	
Arctic char, *Salvelinus alpinus*		32	27, 28
Atlantic salmon, *Salmo salar*			1

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prey of other cetaceans and numerous birds and fishes.

Arctic cod are circumpolar in Arctic waters extending south to at least lat. 60° N on the Alaska coast, typically in association with sea ice (Andriyashev 1954). They are a species of key trophic importance upon which many other far northern marine consumers depend entirely for a major portion of their yearly nutritional requirements. They are eaten by at least 12 species of marine mammals, 20 species of birds, and 5 species of fishes. Arctic cod are especially important because in the areas and at the times when they are abundant they are the only forage fishes present.

Investigations of food habits of marine animals almost invariably involve analysis of stomach contents. Morrow (1979) published preliminary keys to otoliths of 16 families of fishes found in Alaskan waters including the Gadidae, whereby fishes eaten by predators can be identified from otoliths even after soft parts and bones have been digested. In most instances the size of the fish or meal can also be determined from otoliths through back calculation of fish length and/or weight from various measurements of otolith size (Morrow 1951; Templeman and Squires 1956; Southward 1962; Gjosaeter 1973).

In this paper we present relationships of otolith length to fish length and weight for pollock, saffron cod, and Arctic cod of the Bering, Chukchi, and Beaufort Seas.

Methods

Samples of fishes were obtained by otter trawling in the Bering, Chukchi, and Beaufort Seas (Table 2). Soon after capture all fishes were identified, weighed to the nearest 0.1 g, and fork length measured to the nearest millimeter. The sagittal otoliths were removed and length and width measured to the nearest 0.1 mm with vernier calipers.

When otolith lengths and widths were plotted against fish lengths as scatter diagrams, the relationship between otolith length and fish length was found to be less variable than that of otolith width and fish length. For this reason otolith length was taken as the criterion for otolith size and used in subsequent calculations. Casteel (1976) discussed in detail the reasons for using length as the best measure of otolith size.

We chose a double regression method for relating otolith size to fish size (Fitch and Brownell 1968; Casteel 1976). For each species the relationships of otolith length to fish length and fish length to fish weight were calculated. In cases where two equations were required to fit a single relationship, the inflection point was determined by iteration. The specified inflection point was varied by increments of 0.1 and the pair of equations which minimized the combined deviation was selected.

Results and Discussion

Regressions of fish fork length on otolith length differed markedly among the three species. Those of walleye pollock and saffron cod formed two distinct straight-line sections each, with inflection points at otolith lengths of 10 mm in walleye pollock (fish length 22 cm) and 8.5 mm in saffron cod (fish length 15 cm) (Figures 1, 2). The regression for Arctic cod was rectilinear over the range of samples (Figure 3).

Several sources of error are possible when estimating the size of a fish from its otoliths, among which are normal variability in the ratio of fish length to otolith length and differences in lengths of left and right otoliths of the same fish. The calculated regression coefficients show that such variability is quite small. Deviation between actual measured and calculated fish lengths was usually <5%. Since food habits studies deal with

TABLE 2.—Sources of Alaskan marine gadids measured to determine otolith length-fish size relationships. T = *Theragra chalcogramma*; E = *Eleginus gracilis*; B = *Boreogadus saida*.

Vessel and cruise no.	Date	Area	Depth range (m)	Trawls (no.)	Species
NOAA[1] Ship *Surveyor* (RP-4-SU-76AI&II)	Mar.-Apr. 1976	Bering	79-173	39	T
NOAA Ship *Discoverer* (RP-4-DI-76BIII)	Aug. 1976	Bering/Chukchi	18-55	18	B, E
USCGC[2] *Glacier* (AWS76)	Aug. 1976	Beaufort	40-123	2	B
NOAA Ship *Miller Freeman* (RD-4-MF-76BII)	Oct. 1976	Bering	15-55	75	B, E
NOAA Ship *Surveyor* (RD-4-SU-77AII, III)	Mar.-Apr. 1977	Bering	28-150	45	T, E
NOAA Ship *Discoverer* (RD-4-DI-77AVI)	May-June 1977	Bering	30-150	36	B, T
NOAA Ship *Surveyor* (RD-4-SU-77BII)	June-July 1977	Bering/Chukchi	13-57	17	B, E
USCGC *Glacier* (AWS77III)	Aug.-Sept. 1977	Chukchi/Beaufort	31-400	33	B
ADF&G[3] skiff (Shishmaref 78)	Mar. 1978	Chukchi	5-10	5	E
NOAA Ship *Surveyor* (RP-4-SU-78AV, VI)	May-June 1978	Bering	17-210	78	T, E

[1]National Oceanic and Atmospheric Administration.
[2]United States Coast Guard Cutter.
[3]Alaska Department of Fish and Game.

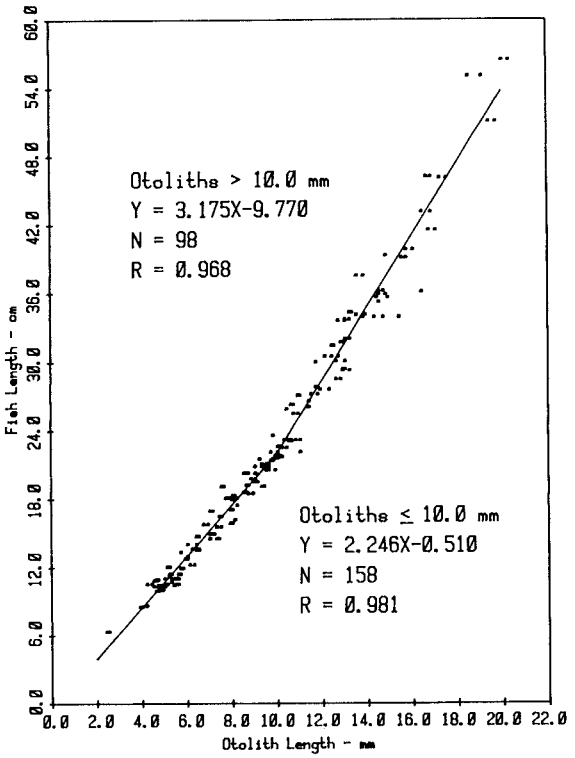

FIGURE 1.—Scatter diagram and regression lines and equations of otolith length against fish fork length for *Theragra chalcogramma*.

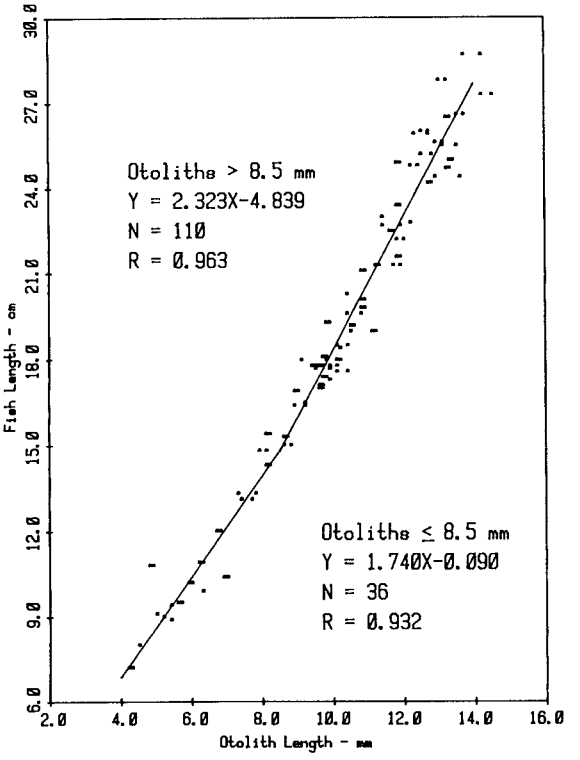

FIGURE 2.—Scatter diagram and regression lines and equations of otolith length against fish fork length for *Eleginus gracilis*.

mixed collections of otoliths, the cumulative importance of these differences should be minimal.

The relationships between fish lengths and weights of the three species were best fit by exponential equations of the form: weight = a (length)^b (Table 3). These relationships may vary somewhat with time of year, geographic location, sex, reproductive status, or fullness of stomach. Variation is probably most pronounced in sexually mature individuals with mature reproductive products, a condition which persists for only a few months of the year. Since small (juvenile) fishes are eaten by most marine mammals (Frost and Lowry 1980), birds (Hunt et al. in press), and other fishes (Frost and Lowry unpubl. data), this is probably a small source of error. Significant differences in weight-at-length by sex and geographic area were found for Arctic and saffron cods by Wolotira et al.[2] but they justified use of a single regression equation since the differences were small (3-7%). Similar differences have been noted for walleye pollock (Bakkala and Smith[3]).

Otoliths are valuable indicators of the diet of piscivorous marine consumers. Published keys such as Morrow (1979) allow determination of the species and numbers of fishes represented by otoliths in stomachs, intestines, or scats. By using the relationships between otolith size and body

TABLE 3.—Length-weight relationships observed for walleye pollock, saffron cod, and Arctic cod in the Bering, Chukchi, and Beaufort Seas (weight = a(length)^b).

Species	Number sampled	Range in fork length (cm)	a	b	Regression coefficient (r)
Walleye pollock	109	6-57	0.0077	2.906	0.998
Saffron cod	104	6-29	.0050	3.095	.991
Arctic cod	118	7-21	.0018	3.500	.987

[2]Wolotira, R. J., Jr. 1977. Demersal fish and shellfish resources of Norton Sound, the southeastern Chukchi Sea and adjacent waters in the baseline year 1976. Processed rep., 292 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

[3]Bakkala, R. G., and G. B. Smith. 1978. Demersal fish resources of the eastern Bering Sea: Spring 1976. Processed rep., 233 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

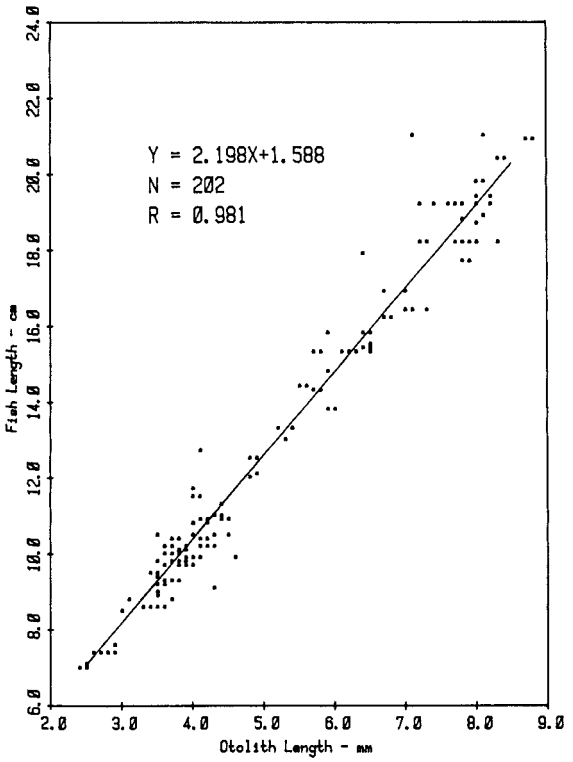

FIGURE 3.—Scatter diagram and regression lines and equations of otolith length against fish fork length for *Boreogadus saida*.

size it is possible to obtain additional information such as sizes and quantities of fishes eaten by consumers (Frost and Lowry 1980).

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CAROLINIAN RECORDS FOR AMERICAN LOBSTER, *HOMARUS AMERICANUS*, AND TROPICAL SWIMMING CRAB, *CALLINECTES BOCOURTI*. POSTULATED MEANS OF DISPERSAL

Recent reports of distributional extension for decapod crustaceans occurring along the east coast of the United States include two poorly substantiated records of American lobster, *Homarus americanus* H. Milne Edwards, and none of the tropical swimming crab, *Callinectes bocourti* A. Milne Edwards, from the Carolinas south of Cape Hatteras, N.C. (Williams 1965, 1974 [Carolinas]; Cerame-Vivas and Gray 1966 [Cape Hatteras]; Williams et al. 1968 [North Carolina]; Musick and McEachren 1972 [North Carolina-Virginia]; Milstein et al. 1977 [New Jersey]; Bowen et al. 1979 [Middle Atlantic area]; Herbst, Weston, and Lorman 1979 [Cape Hatteras]; Herbst, Williams, and Boothe 1979 [Capes Hatteras and Lookout]; Wenner and Boesch 1979 [Norfolk Canyon area]; Perschbacher and Schwartz 1979 [North Carolina]). Occurrences of both species in the Carolinas south of Cape Hatteras are documented here along with discussion of their postulated means of dispersal.

Specimens are deposited in the U.S. National Museum of Natural History (USNM), or are living in aquaria at the North Carolina Marine Resources Center, Bogue Banks (NCMRC), and the Hampton Mariners Museum, Beaufort (HMM).

Occurrence of Species

Homarus americanus.—Distribution of the American lobster has been given as, "East coast of America from the Strait of Belle Isle, Newfoundland (Canada) to Cape Hatteras, North Carolina (U.S.A.)," at depths of 0-480 m, usually 4-50 m (Holthuis 1974). Reported occurrences of this species south of Cape Hatteras are: one caught in a

crab pot near Cedar Island, Carteret County, N.C., in December 1958 (Williams 1965), and one doubtful occurrence near Beaufort, N.C. (Hay and Shore 1918). New substantiated records are given in Table 1.

Callinectes bocourti.—The distribution of *C. bocourti* has been given as, "Jamaica and British Honduras to Estado de Santa Catarina, Brazil," with "extraterritorial occurrences in southern Florida and Mississippi..." (Williams 1974). Gore and Grizzle (1974) confirmed Florida occurrences with a note on a mature male from the Indian River, Vero Beach, Fla., slightly larger than our specimens (Table 1). At the time our female was caught, it had a dorsal coloration much as that pictured for the female in color photo 5 by Taissoun (1972), i.e., carapace very dark olive green, but chelipeds moderate "brick" red, much as the male described by Gore and Grizzle (1974), and underparts white. By December, the dorsal greenish coloration of the carapace had faded somewhat, yielding an underlying reddish tone somewhat resembling the color of the male in color photo 5 by Taissoun (1972).

Discussion

What are the explanations for these marginal occurrences? Available evidence comes from known life histories (rates of development and growth, and movements deduced from seasonal and areal sampling), current regimes of waters in which the animals may have lived, and indication of migrations from tagged individuals that have been recaptured.

Lobsters.—There are no known breeding populations of American lobsters south of Cape Hatteras which is generally regarded as the southernmost extent of the cool temperate Virginian Province (Wells 1961; Cerame-Vivas and Gray 1966). Scott (1973), in a general review of lobster life history, pointed out that: 2 yr elapse between mating and hatching of eggs; hatched larvae drift from 2 wk to 2 mo before becoming permanent bottom dwellers; lobsters can be reared experimentally in waters of 22.2° C (72° F) to 0.37 kg (1 lb) weight in 2 yr, but require 5½ yr to reach this size in waters around Martha's Vineyard, Mass., and 8 yr to reach it in Canada.

Movements of tagged lobsters in the region of southern New England analyzed by Uzmann et al. (1977) showed that although courses from point of release to point of recapture cannot be interpreted as straight lines, "...maximum movement of any recapture was 186 nautical miles (345 km) in 71 days (2.6 miles/day)," and other tracks in excess of 100 mi (185 km) in from 29 to 86 days were recorded. Shorter "...apparently directed tracks of 50-87 miles (93-161 km)..." were traversed "...within 22-41 days," the calculated ground speeds of all these ranging from 1 to 5.5 mi (1.8-10.2 km)/day, indicating "...that directional movements in excess of 1 mile (1.8 km) per day are not uncommon...." Moreover, these authors showed that offshore lobsters tend to aggregate along the outer edge and slope of the continental shelf during January-April, but become widely dispersed by migration or random movement in the shoaler, warmer water off southern New England during May through December.

The approximate distance by water from Cape

TABLE 1.—Records of *Homarus americanus* and *Callinectes bocourti* from the Carolinas south of Cape Hatteras. Measurements (millimeters): CL = carapace length in midline, including rostrum of *Homarus*; TL = total length in midline; CW = carapace width including lateral spines, *Callinectes*.

Species	Sex	Measurements		Collection Data	Depository
				North Carolina	
H. americanus	♂	120 CL	257 TL	Jarratt Bay, Core Sound, 25 Oct. 1978, crab pot, R. R. Seely	
	♂	100 CL	230 TL	Bogue Sound off Salterpath, 12 Nov. 1978, crab pot, R. O'Neal	NCMRC living
	♀[1]	95 CL		Nelson Bay, Core Sound, 21 Nov. 1978, crab pot, R. R. Seely	USNM 172262
	♀[2]	95 CL		Near Davis, Core Sound, 29 Mar. 1979, crab pot, P. Apperson	USNM 173231
	♀[3]	110 CL	247 TL	Off Atlantic, Core Sound, 13 Nov. 1979, crab pot, L. Hill, Jr.	NCMRC living
	♀[4]	98 CL	222 TL	Drum Inlet, Core Banks, 28 Nov. 1979, D. Cavett	HMM living
	♂[5]		254 TL	0.8 mi off Rich Inlet, 15 May 1978, trawl, L. Holden on MV *Capt. Jason*	USNM photos
C. bocourti	♀	63 CL	130 CW	Sound behind Carolina Beach, mid-Oct. 1977, crab pot, by fisherman	USNM 170863
				South Carolina	
	♂	67 CL	128 CW	Wando R., Charleston, 4 Oct. 1977, crab pot, G. Steele, P. Eldridge, V. A. Burrell, Jr.	USNM

[1]Rostrum tip broken, length approximate; abdomen damaged.
[2]Maintained in aquarium in NCMRC until 4-5 October 1979 when killed at night by tank mate; abdomen damaged.
[3]Carapace encrusted with two species of barnacles, singly and in patches. Largest of these removed and measured at greatest diameter 24 December 1979: *Chelonibia patula* (Ranzani), 7.6 × 9.0; *Balanus venustus* Darwin, 6.4 × 6.8.
[4]Few small *B. venustus* on carapace.
[5]Measurement given to us.

Hatteras to Rich Inlet, around Cape Lookout, is 130 nmi (240 km). A narrow, southerly longshore current of Virginian water continues past Cape Hatteras (Bumpus 1973), reaching well beyond Cape Lookout in some winters (Wells 1961), which conceivably could aid southward movement of lobsters. The current contributes to what Watling (1979) and others have considered as part of a shallow nearshore and estuarine "transhatteran" zone. While the lobster larval phase might be dispersed southward from breeding populations living in cooler water by this means, survivors of such movement must be rare and would have to exist for at least two seasons in warm temperate Carolinian waters that are heavily trawled for penaeid shrimps in order to attain the sizes recorded in Table 1 (from growth rates calculated by Hughes and Mathiessen 1962, and accelerated growth rates indicated by Scott 1973). The dispersed phase of older lobsters (Uzmann et al. 1977), however, might utilize this nearshore southerly drift, and migrate southward in one season when they had reached essentially the size at which they were caught.

Crabs.—The northernmost occurrences of tropical crabs such as *C. bocourti*, *C. danae* Smith, and *C. marginatus* A. Milne Edwards in the western Atlantic have been attributed to drift of larvae entrained in currents associated with the Gulf Stream, or to drift of postlarval crabs (juveniles or subadults) with debris, or transport on boats (Williams 1974). Zoeae spawned in southern Florida, or perhaps Cuban waters, conceivably could be swept northward in favorable warm seasons to be introduced to shores of the Carolinian Province (Williams 1965). Later growth stages of crabs might be transported with the aid of swimming or in association with flotsam. Evidence of drift from the tropics deposited along the Carolina shores is provided by strandings of 22 species of sea-beans (*Mucuna* spp.), red mangrove (*Rhizophora mangle* Linnaeus) seedlings, and mango fruits (*Mangifera indica* Linnaeus) (Gunn and Dennis 1976), palm trunks and coconuts, bamboo, Portuguese man-of-war (*Physalia*), gulfweed (*Sargassum*), etc. observed along Bogue Banks, Core Banks, and Cape Lookout, especially following southerly storms.

Perschbacher and Schwartz (1979) reported *C. danae*, *C. marginatus*, and *C. ornatus* in the Intracoastal Waterway south of Carolina Beach Inlet, New Hanover County, in mid-September 1977, and in the nearby Cape Fear River in mid-October 1977; *C. ornatus* was already known from the Carolinas and *C. marginatus* recorded once near Beaufort (Williams 1974). Milstein et al. (1977) reported another tropical species, *Cronius ruber* Lamarck, collected off Little Egg Inlet, N.J., on 27 September 1974 (size unrecorded), from an engine block.

Callinectes specimens of the sizes reported here and by Perschbacher and Schwartz (1979) are mature (Williams 1974). The growth rates of *C. bocourti*, *C. marginatus*, *C. danae*, and *C. ornatus* are unknown, but if they are similar to that of *C. sapidus* these crabs were at the end of their second summer of life when caught. Their presence in the Carolinas at this size in late summer-early fall would have to result from: 1) transport of zoeae or megalopae into Carolinian waters during the previous summer or fall, and overwintering as juveniles to mature during the second summer of residence; 2) transport to Carolinian waters as juveniles in spring to mature during their second summer; or 3) transport to the Carolinas as subadults or adults sometime during the summer preceding capture. Presence of four tropical species together, two in considerable numbers, far beyond their normal range (Perschbacher and Schwartz 1979), suggests something other than casual transport, perhaps an unusually mild winter preceding the season of capture, a major eddy(ies) in the Gulf Stream, or major southern storm(s).

Callinectes sapidus requires temperatures >20° C for hatching, development, and survival of larvae (Costlow and Bookhout 1959; Costlow 1965, 1967). During larval development, the zoeal stages of *C. sapidus* are found at sea seasonally (see Williams 1974 for review), but megalopae return to estuaries for development into adults. Estuarine water temperatures in the Beaufort area commonly fall below 10° C in winter (Williams et al. 1967); in South Carolina such temperatures are normally higher, 9.4° C and above in 1973-74 (Mathews and Shealy 1978), for example. The winter of 1976-77 was abnormally cold in the eastern United States, the subnormal trend continuing into summer at sea (Ingham 1979). January water temperatures as low as 2° C were recorded in the bight of Cape Lookout (R. S. Fox[1]).

[1]R. S. Fox, Department of Biology, Lander College, Greenwood, SC 29646, pers. commun. May 1979.

Presumably the above tropical species have development similar to that of *C. sapidus*. If they could survive winter temperatures such as those given above, their normal ranges would extend to Cape Hatteras; therefore, overwintering as juveniles in Carolinian waters during 1967-77 seems unlikely.

Spin-off eddies along the western boundary of the Gulf Stream are regular features (Lee 1975). These cyclonic current reversals are not wind or

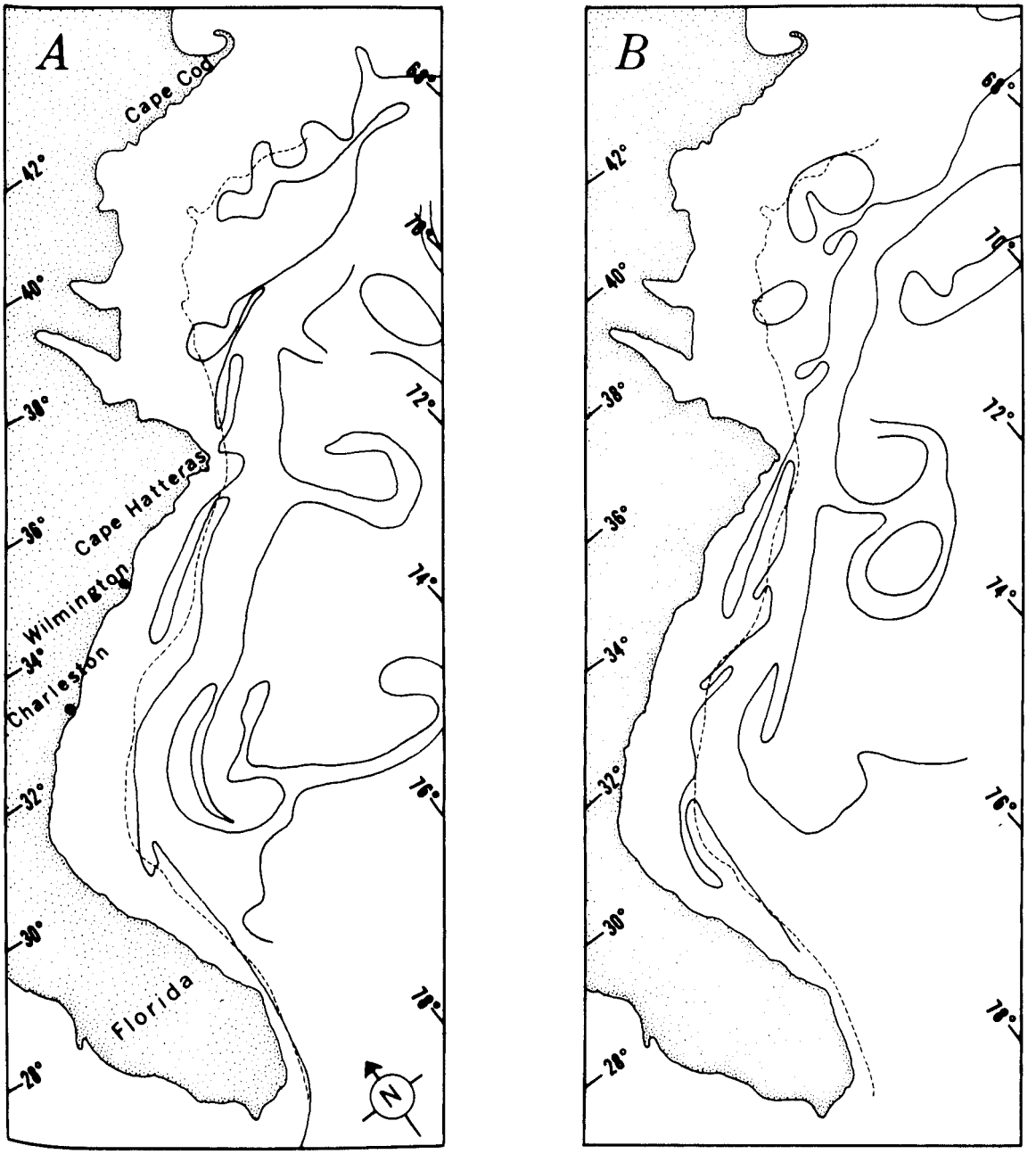

FIGURE 1.—Gulf Stream off eastern United States between Florida and Cape Cod; isopleths represent maximum thermal gradients at edges of spin-off eddies near shore and Gulf Stream meanders seaward as viewed by National Environmental Service Satellite and analyzed by Miami Satellite Field Services Station for weekly loop periods. Example plots: *A*, 26 April-2 May 1977; *B*, 10-16 May 1977.

tide induced. Figure 1 shows reproductions of Gulf Stream surface features taken from National Environmental Satellite Service charts analyzed by the Miami Satellite Services Station for two weekly periods in April and May 1977. The warm season is judged to be roughly the time during which surviving juvenile or adult crabs might be carried into the Carolinian Province by such eddies, hence accounting for the tropical *Callinectes* spp. collected in 1977. During late April to mid-June of this period, prominent spin-off eddies were developed along the coast (least evident at the surface when summer gradients are minimal). There is nothing to suggest that spin-offs during summer 1977 were unusual, but they appear to have been more prominent than such features indicated by surface isotherms in 1976 (Deaver 1979). These currents augment inshore and southerly drift indicated by drift-bottle returns in shelf waters along the Carolinas in May-June (indeterminate in July), August and September (Bumpus 1973; Barans and Roumillat 1978), and seabed drifter returns during the same period (Bumpus 1973). A mechanism to aid shoreward movement of tropical crabs seems to be present.

There is no record of unusual southerly storms during spring-summer of 1977 (Anonymous 1977a, b).

Are juvenile or adult *Callinectes* spp. ever found at sea? Admittedly, there is little evidence at hand. Most records of distribution for members of the genus are nearshore or estuarine, but Franks et al. (1972) recorded both *C. sapidus* and *C. similis* in trawl samples taken at depths of 9-90 m off Mississippi and on 29 May 1968 observed hundreds of nocturnally swimming small *C. similis* (40 mm carapace width) at the surface in 9 m water in an apparent inshore migration. *Callinectes sapidus* has been observed to move 90 mi (144.8 km) in 10 d in Chesapeake Bay (R. E. Miller[2]). Gunter (1950) reported mature female *C. danae* (= *similis*) at the surface several miles from the Texas shore in the Gulf of Mexico. All species of *Callinectes* have broad salinity tolerances. Although Norse (1978) regarded *C. bocourti* as occurring mainly in low salinities, he ordered *C. danae*, *C. marginatus*, and *C. ornatus* at the high end of the salinity tolerance scale for the genus, indicating ability to exist in full seawater.

Data on geographic ranges of species result from the amount of field work expended in finding them, coupled with study and identification. The marine species list for the Carolinas has expanded greatly in this century with the growth of laboratories in the area. So-called rare occurrences may result from simple lack of collecting, but in this case we feel that rarity is genuine because of the intense sampling effort expended in the area during the time considered. The South Carolina Marine Resources Center maintained an intensive estuarine benthic survey along the state's coast for 2 yr, 1973-74 (Bishop and Shealy 1977; Mathews and Shealy 1978); F. J. Schwartz[3] maintained an intensive gill net and trawl survey of the lower Cape Fear River, N.C., and adjacent waters in all seasons of the year from 1973 to 1978, consisting of 10,646 units of effort (6,828 20-min river trawls, 3,818 24-h river gill net sets, 1,531 30-min ocean trawls). The above crab records, with one exception, come from the latter effort or from personnel associated with the former, and are the only such occurrences recorded during this period.

Acknowledgments

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[2]R. E. Miller, Horn Point Environmental Laboratories, University of Maryland, Cambridge, MD 21613, pers. commun. October 1979.

[3]F. J. Schwartz, University of North Carolina Institute of Marine Sciences, Morehead City, NC 28557, pers. commun. August 1979.

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MORTALITIES OF ATLANTIC HERRING, *CLUPEA H. HARENGUS*, SMOOTH FLOUNDER, *LIOPSETTA PUTNAMI*, AND RAINBOW SMELT, *OSMERUS MORDAX*, LARVAE EXPOSED TO ACUTE THERMAL SHOCK

Entrainment of larval fishes through condenser cooling systems of electric generating stations often results in acute physical, chemical, and thermal stresses. These stresses are often lethal and the resulting mortalities could have adverse effects on populations proximal to the cooling water intake site. This is particularly true for fishes which have planktonic larvae (Schubel et al. 1978).

The rapid increase in temperature associated with passage through condenser cooling systems is seldom if ever experienced by organisms in the natural environment. Little is known of the ability of the larvae of most species of fish to withstand this kind of thermal stress. In assessing thermal stresses it is important not only to investigate the effect of different increases in temperature from some base temperature (ΔT), but also to investigate the effect of the duration of the exposure. The simplest simulation experiment, then, is one in which larvae are exposed to a rapid increase in temperature, are held at the elevated temperature for a period of time, and are then returned rapidly to the original base temperature.

Our experiments were designed to evaluate the thermal tolerances of three species of larval fish occurring in the Gulf of Maine and its estuaries: Atlantic herring, *Clupea h. harengus*, smooth flounder, *Liopsetta putnami*, and rainbow smelt, *Osmerus mordax*. These fish, although differing somewhat in their life histories, are all common in inshore areas during some part of their larval life, and are therefore subject to power plant entrainment. This paper presents the results of thermal tolerance experiments which encompassed the range of temperatures planktonic organisms encounter in condenser cooling systems.

Methods

All larvae used in the experiments were reared in the laboratory. Atlantic herring eggs and milt were stripped from ripe adults captured off Gloucester, Mass. The eggs were fertilized and held in 2 l shallow glass bowls of filtered seawater (31.8‰) at approximately the ambient temperature where the adults were collected (8°±1° C). Most of the larvae hatched after 13 d. Ripe adult smooth flounder were collected from Montsweag Bay, part of the Sheepscot River estuary, Maine. Eggs and milt were stripped from the adults, the eggs fertilized, and also kept in 2 l shallow glass bowls of filtered seawater (25.5‰) at the ambient temperature (4°±1° C). The larvae began to hatch after 21 d but the majority hatched after 27 and 28 d. Fertilized rainbow smelt eggs were collected directly from a spawning site in Wiley Brook, a tributary of the Damariscotta River estuary, Maine. The eggs were kept in 40 l aquaria with filtered brook water at the ambient temperature (13°±1° C). The brook water was treated with streptomycin and penicillin according to methods described in Shelbourne (1964) and malachite green hydrochloride was added to control fungal growth. Some of the rainbow smelt larvae began to

hatch immediately upon collection but most hatched 2 and 3 d later.

Thermal tolerance experiments were performed using a thermal gradient apparatus. Details of the design and the operating characteristics are given in Barker and Stewart (1978). In each experiment groups of 10-15 larvae were transferred from the ambient temperature water to test tubes containing 25 ml of water at the test temperatures in the thermal gradient apparatus and were exposed for 5-60 min. After exposure the larvae were returned to the ambient water. The addition of the larvae to the apparatus also involved the addition of about 5 ml of ambient temperature water which resulted in a slight lowering of the test temperatures. About 10-15 min were needed for the test temperatures to be reached again, so the temperatures given in the results section for the 5 min exposures were those reached after 5 min.

A control was maintained outside of the thermal gradient apparatus for all experiments. These larvae were held at ambient temperatures and were subjected to the same handling procedures as those larvae which received the exposures to elevated temperatures.

All larvae were observed for mortality 2 h after testing, at which time any dead larvae were removed. The remaining larvae were observed again after 24 h. Dead larvae could usually be recognized by their opaque appearance and any larvae that showed no movement when prodded were also considered dead.

Each experiment was replicated once for the smooth flounder larvae and the Atlantic herring larvae. The replicate experiments were performed for the rainbow smelt larvae in brook water and also in seawater (28.8‰, after acclimation for 1 d at 13°±1° C). All larvae tested were <5 d old and had yolk sacs.

Results

The results of all experiments are presented in Table 1. The Atlantic herring larvae were exposed to ΔT's ranging from 16° to 25° C for exposures of 5, 15, 30, and 60 min. It appears that the larvae acclimated to 8° C survived ΔT's up to 17° C for up to 60 min. The larvae survived higher temperatures at shorter exposure times. In all cases, except the 5 min exposures, the mortalities increased from approximately 0 to 100% over a range of 2° C.

The smooth flounder larvae were exposed to

TABLE 1.—Percentage mortalities of larvae of Atlantic herring, *Clupea h. harengus*, smooth flounder, *Liopsetta putnami*, and rainbow smelt, *Osmerus mordax*, in fresh and saltwater, under different time-temperature combinations. Values for each of the replicate experiments are listed. The temperature values in parentheses indicate the adjusted temperatures for the 5 min exposures as explained in the text.

Species	Time (min)	Temperature (° C)					
		[1]8.0	25.0 (24.0)	27.0 (26.0)	29.1 (27.9)	31.0 (29.8)	33.0 (32.7)
Clupea h. harengus	5	0	0	0	0	76.5	100
		0	0	0	6.7	18.8	100
N = 704	15	—	0	0	6.7	100	100
		0	0	0	12.5	100	100
	30	6.7	0	0	100	100	100
		0	0	0	100	100	100
	60	7.1	6.7	81.2	100	100	100
		0	0	100	100	100	100
		[1]4.0	25.4 (24.0)	27.6 (25.2)	29.8 (28.4)	32.0 (30.5)	34.2 (33.9)
Liopsetta putnami	5	0	0	6.7	26.7	46.7	100
		0	0	6.7	20.0	100	100
N = 525	30	6.7	20.0	0	90.9	100	100
		6.7	6.7	18.8	68.8	100	100
	60	0	0	80.0	100	100	100
		6.2	7.7	26.7	100	100	100
		[1]13.2	24.9 (24.5)	26.8 (26.6)	28.8 (28.6)	30.8 (30.6)	32.6 (32.4)
Osmerus mordax (freshwater)	5	6.7	0	0	7.1	0	100
		0	6.7	0	7.1	7.1	100
	30	0	0	0	0	100	100
		0	0	0	40.0	100	100
N = 525	60	6.7	0	0	57.1	100	100
		0	0	0	62.5	100	100
		[1]13.0	24.9 (24.5)	26.9 (26.7)	28.8 (28.6)	30.8 (30.6)	32.6 (32.4)
Osmerus mordax (saltwater)	5	0	14.3	0	11.1	11.1	100
		20.0	0	22.2	27.3	40.0	100
	30	10.0	60.0	50.0	100	100	100
		10.0	40.0	50.0	100	100	100
N = 346	60	20.0	50.0	90.9	100	100	100
		50.0	40.0	88.9	100	100	100

[1]Control (ambient temperatures).

ΔT's ranging from 20.0° C to 30.2° C for exposures of 5, 30, and 60 min. The larvae acclimated to 4° C survived ΔT's up to 21.4° C for 60 min with negligible mortality. The mortalities increased from approximately 0 to 100% over a range of about 5° C in the 30-60 min exposures. At the 5 min exposure mortality increased from 6.7% (considered background mortality) to 100% over a 8.7° C range (25.2°-33.9° C).

The rainbow smelt larvae held in freshwater were exposed to ΔT's ranging from 11.3° to 19.4° C for exposure times of 5, 30, and 60 min. The larvae survived a ΔT of 13.6° C for up to 60 min, and at exposures of shorter duration the larvae survived higher exposure temperatures. For exposures of 30-60 min the mortalities increased from 0 to 100% over a range of 4.0° C (26.8°-30.8° C). This range was 1.8° C for the 5 min duration exposure.

The rainbow smelt larvae which had been acclimated in seawater at 13°±1° C, after hatching in freshwater, were exposed to ΔT's ranging from

11.9° to 20.9° C for exposure times of 5, 30, and 60 min. The lowest ΔT at which 100% mortality was observed was 15.8° C. This occurred in larvae exposed 30 and 60 min. In the case of the 5 min exposure, some larvae survived up to a 19.4° C ΔT before experiencing 100% mortality. There was a high background mortality in these experiments which was probably due to stress resulting from the immediate transfer of larvae to seawater 1 d prior to treatment. This was not an unnatural stress, however, since in nature the larvae are immediately washed from the brook into the estuary, <50 m away, once they hatch from the adhesive eggs.

Discussion

The larvae of all three species appear to be able to survive ΔT's of short duration which are near the upper limits of cooling systems in most normally operating nuclear power plants (18.6° C, Schubel et al. 1978). Our results show that the Atlantic herring larvae are much more tolerant to brief (<60 min) increased temperature exposures than to the longer term exposure (24 h) reported by Blaxter (1960). It should be noted that Atlantic herring larvae are usually older and developed beyond the yolk-sac stage when they arrive at the inshore nursery areas from the spawning grounds and the results of these experiments should be considered in light of that fact. Smooth flounders, on the other hand, spawn in the estuaries and inshore areas of the Gulf of Maine and the larvae are susceptible to entrainment by power plants at an early age.[1] These larvae have a greater thermal tolerance than Atlantic herring and appear to be able to survive ΔT's in excess of those normally encountered during entrainment. Rainbow smelt larvae differ from both the Atlantic herring and smooth flounder. Rainbow smelt normally spawn in freshwater brooks during April and May in coastal Maine and almost immediately upon hatching the larvae are swept downstream into saltwater where they experience a sudden increase in salinity. The rainbow smelt larvae which we tested in brook water showed thermal tolerances very similar to smooth flounder larvae but those tested in seawater showed the lowest temperature tolerance of all the experiments. It appears, then, that if rainbow smelt larvae are entrained at this time the effects of increased salinity might act synergistically with the temperature increase to produce a lethal stress.

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FOOD OF 10 SPECIES OF NORTHWEST ATLANTIC JUVENILE GROUNDFISH

The food of fishes in the northwest Atlantic has been studied over many years. Verrill (1871) was one of the first investigators to document the food of marine fish. Recent investigations have identified the food of commercially important fish or fish currently composing a large portion of the fish biomass in the northwest Atlantic (Edwards and Bowman 1979; Langton and Bowman 1980), but still little is known about the diet of juvenile groundfish.

Most groundfish larvae are wholly planktonic until they either become demersal or grow large

enough and active enough to live independently of the currents (Graham 1956). This change in life style usually occurs during their first year of life and is reflected in their diet because they change from feeding mainly on plankton to benthic organisms (Nikolsky 1963). This paper identifies the types of food eaten by several species of juvenile groundfish, and further examines their change in diet with fish length.

Methods

Stomachs were collected from juvenile fish caught during annual spring and fall groundfish surveys conducted by the National Marine Fisheries Service (NMFS). A scheme of stratified random sampling was conducted within the five geographic areas of the northwest Atlantic (Figure 1). All bottom trawl tows were 30 min in duration and fishing continued over 24 h/d. (Further details of the bottom trawl survey techniques may be obtained from the Resource Surveys Investigation, Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA, Woods Hole, MA 02543.) The feeding data for all species except haddock are based on collections made from 1969 through 1972; juvenile haddock were collected from 1953 to 1976, inclusive. The species collected were: Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; silver hake, *Merluccius bilinearis*; pollock, *Pollachius virens*; red hake, *Urophycis chuss*; white hake, *U. tenuis*; spotted hake, *U. regius*; fourbeard rockling, *Enchelyopus cimbrius*; American plaice, *Hippoglossoides platessoides*; and yellowtail flounder, *Limanda ferruginea*. All of these species reach maturity when 2 or 3 yr old. This paper deals only with fish approximately 1 yr old or younger. The length, fork length (FL) when applicable, otherwise total length (TL), attained by each species when approximately 1 yr old is given at the bottom of Table 1 as the maximum length in each length range. Fish were either saved whole or their stomachs were excised aboard ship, labeled, and individually wrapped in gauze. All samples were preserved in 3.7% formaldehyde. The stomach contents of 3,065 fish, from 10 species, were analyzed. In the laboratory the individual stomachs were opened and their contents emptied onto a screen sieve with mesh openings of 0.18 mm. The contents were washed and then transferred into a dish from which the various prey items were manually sorted and counted. Prey were identified to the lowest taxonomic grouping possible, damp dried on absorbent paper, and immediately weighed to the nearest 0.001 g. Well-digested prey which were only identified within major prey categories (i.e., Crustacea and Pisces) or species within a major prey category which amounted to <0.1% of the diet of all predators are listed as "Other" in Table 1. Organisms of little apparent dietary significance and not belonging to any of the major prey categories listed make up the values calculated for the "Miscellaneous" category.

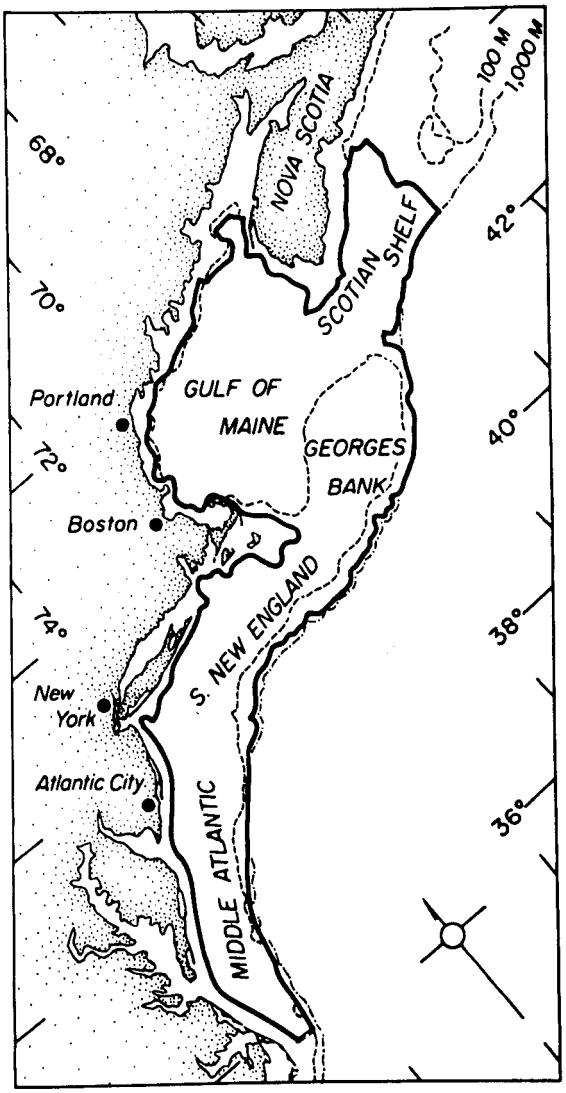

FIGURE 1.—Geographic areas of the northwest Atlantic, where the feeding habits of juvenile fish were studied. Fish were caught during bottom trawl surveys conducted from 1953 through 1976.

TABLE 1.—Summary of the stomach contents of juvenile groundfish from the northwestern Atlantic, expressed as a percentage of total food weight, for fish collected between the years of 1953 through 1976. Subtotals are italicized and a "+" indicates present in the diet but <0.1%. Dietary differences related to predator length are given in the text

Stomach contents	Atlantic cod	Haddock	Silver hake	Pollock	Red hake	White hake	Spotted hake	Fourbeard rockling	American plaice	Yellowtail flounder
Polychaeta	*0.4*	*13.6*	*0.3*	*0.7*	*2.4*	*2.9*	—	—	*72.1*	*3.0*
Crustacea	*81.6*	*62.3*	*89.0*	*68.2*	*90.1*	*94.9*	*85.9*	*33.3*	*21.1*	*94.4*
Amphipoda	22.5	27.6	6.6	1.5	19.4	15.4	77.1	33.3	17.3	38.8
Decapoda	11.2	11.5	30.4	0.3	41.6	58.2	+	—	+	3.7
Isopoda	—	0.7	+	1.2	0.1	—	—	—	—	1.0
Cumacea	0.2	0.7	0.1	—	0.5	—	—	—	+	10.2
Euphausiacea	18.0	13.0	44.4	55.8	6.4	—	—	—	—	—
Mysidacea	12.9	1.5	2.6	—	3.6	—	—	—	3.8	33.4
Copepoda	4.8	0.6	0.1	0.2	1.3	—	7.0	—	+	+
Other Crustacea	12.0	6.7	4.8	9.2	17.2	21.3	1.8	+	+	7.3
Mollusca	*0.1*	*0.1*	+	—	*0.2*	—	—	—	+	—
Chaetognatha	+	*0.2*	*0.8*	—	*0.3*	—	+	—	—	—
Echinodermata	—	*1.2*	—	—	+	—	—	—	—	—
Echinoidea	—	0.1	—	—	—	—	—	—	—	—
Ophiuroidea	—	1.1	—	—	+	—	—	—	—	—
Pisces	*16.0*	*5.0*	*8.5*	+	*1.9*	—	—	—	—	—
Ammodytes americanus	—	—	3.0	—	—	—	—	—	—	—
Merluccius bilinearis	—	2.2	—	—	—	—	—	—	—	—
Gadidae	—	—	2.1	—	—	—	—	—	—	—
Cottidae	—	—	2.3	—	—	—	—	—	—	—
Other Pisces	16.0	2.8	1.1	+	1.9	—	—	—	—	—
Miscellaneous	*0.1*	*0.6*	*0.7*	*5.8*	*0.2*	*0.1*	+	—	+	*0.2*
Unidentified	*1.6*	*15.5*	*0.7*	*24.9*	*4.9*	*1.3*	*14.1*	*66.7*	*3.9*	*2.0*
Sand	*0.2*	*1.5*	+	*0.4*	+	*0.8*	—	—	*2.9*	*0.4*
Number examined	107	2,159	440	22	229	23	16	3	10	56
Number empty	21	144	74	1	6	1	6	2	5	3
Mean weight per stomach (g)	0.064	0.107	0.086	0.271	0.061	0.085	0.038	0.020	0.010	0.043
Mean fish length (cm)	7 FL	13 FL	9 FL	17 FL	7 TL	9 TL	6 TL	8 TL	5 TL	7 TL
Length range (cm)	3-19 FL	2-20 FL	3-20 FL	4-20 FL	2-20 TL	5-20 TL	4-10 TL	6-9 TL	4-7 TL	4-9 TL

The stomach content data are summarized on a weight basis as the percentage weight each prey category made up of the total stomach contents weight for each of the 10 predators. Empty stomachs were included in the calculation of the mean weight per stomach for each species. In the text, the percentage weight is included in parentheses after the first mention of a particular prey to quantify the importance of that prey in the diet. Also included in the text, for each species of fish, is a two-part evaluation of the food based on fish length (given only for predators for which sufficient food data were available). This evaluation was made to determine the smallest fish collected of each species, which exhibited signs of feeding on the bottom, and also to discern, based on the available data, at what fish length the food was made up predominantly of prey usually associated with the bottom.

The nomenclatural distinctions categorizing prey species as either planktonic or benthic were taken from Gosner (1971). Planktonic organisms include the euphausiids and calanoid copepods. Benthic forms are typically noted as including most of the polychaetes, amphipods, and decapods. The distinction of these two generalized prey groupings, and what percentage they make up of the diet with fish length, indicates the fish's degree of association with the bottom when feeding. For the purpose of this paper it is assumed that when a fish's diet changes from primarily planktonic organisms to 50% or more benthic organisms (occurring when the fish has grown to within some specified length range), the fish can appropriately be referred to as "demersal." Before this change in diet occurs the fish are only loosely associated with the bottom and are therefore more likely to move off bottom in search of food.

Results

Table 1 summarizes the stomach contents of 10 species of juvenile groundfish collected during the years from 1953 through 1976. Only small numbers of such species as fourbeard rockling and spotted hake were available for stomach content analyses. Since little is known about their diets the data were included.

Atlantic Cod

Crustacea represented the largest portion of the diet of juvenile Atlantic cod (81.6%). Amphipods were the largest contributor to the crustacean prey (22.5%) and those identified were Gammaridae (6.5%) and Caprellidae (12.9%). Euphau-

siacea (mostly *Meganyctiphanes norvegica*) made up 18.0% of the stomach contents. The Mysidacea (12.9%) were primarily *Neomysis americana* (3.7%), and the Decapoda (11.2%) consisted mainly of *Crangon septemspinosa* (2.8%). Copepoda (4.8%) and Cumacea (0.2%) made up the rest of the crustacean portion of the Atlantic cod diet. None of the species of fish were identified (16.0%). The remaining prey were the Polychaeta (0.4%), Mollusca (0.1%), and Chaetognatha (+).

The predominant food of Atlantic cod 9 cm FL and longer was benthic organisms such as Gammaridae, Caprellidae, and Cumacea, which made up more than 50% of the diet. Plankton (i.e., copepods and euphausiids), the main food found in the stomachs of cod <9 cm FL, made up a progressively smaller percentage of the diet as the size of the fish increased. Small quantities of sand and gammarid amphipods were found in the stomachs of the smallest fish collected (3 cm FL).

Haddock

Small crustaceans accounted for 62.3% of the haddock diet. Amphipod crustaceans were the single most important food (27.6%). Corophiidae (primarily *Unciola* sp.) were by far the most common amphipod identified in the stomach contents (5.0%). Other amphipod groups frequently found as prey were, in order of dietary importance, Caprellidae (mainly *Aeginina longicornis*), Ampeliscidae, Aoridae, Hyperiidae, Gammaridae, and Pontogeneiidae. The Euphausiacea (chiefly *Meganyctiphanes norvegica*) accounted for 13.0% of the juvenile haddock diet. *Crangon septemspinosa* (2.6%) made up the largest part of the decapod prey. Crustaceans of lesser dietary importance to haddock were the Mysidacea (1.5%), Isopoda (0.7%), Cumacea (0.7%), and Copepoda (0.6%).

The largest contributor to the identified polychaete prey (13.6%) was nereidiform worms (almost 5%), with *Eunice* sp. being the most common nereidiform found in the stomach contents (1.0%). Other polychaete groups identified in the stomach contents included the suborders Spioniformia, Scoleciformia, Capitelliformia, Terebelliformia, and Sabelliformia.

Fish made up 5.0% of the diet, with silver hake composing almost half (2.2%) of this prey group. Small quantities (+) of Atlantic herring, *Clupea h. harengus*, and Bothidae were the only other fish identified. Echinodermata (1.2%), Chaetognatha (0.2%), and Mollusca (0.1%) were of little importance in the diet of juvenile haddock.

Haddock approximately 8 cm FL and longer fed heavily on the benthos (i.e., amphipods, decapods, and polychaetes). Pelagic organisms such as copepods and euphausiids were the predominant food of fish <8 cm FL. Benthic amphipods and cumaceans were found in the diet of haddock 2 cm FL.

Silver Hake

Silver hake preyed heavily on Crustacea (89.0%). Euphausiids were the single most important food (44.4%). *Meganyctiphanes norvegica* (22.8%) and *Thysanoessa* sp. (2.0%) were the common euphausiids identified in the stomach contents. Decapods (30.4%) included *Crangon septemspinosa* (21.5%) and pandalid shrimp (7.9%). Most of the pandalid shrimp were identified as *Dichelopandalus leptocerus* (3.8%). Amphipod prey (6.6%) came mostly from the families Ampeliscidae (1.9%) such as *Ampelisca* sp. (0.4%), or Tironidae (0.6%) which were identified as *Syrrhoe crenulata* (0.6%). Mysids (2.6%) taken by silver hake were all identified as *Neomysis americana* (2.0%). Cumaceans (0.1%), copepods (0.1%), and isopods (+) contributed little to the silver hake diet.

Small fish and fish larvae composed 8.5% of the silver hake food. The American sand lance, *Ammodytes americanus* (3.0%); sculpins (2.3%); and hakes (2.1%) were the only fish identified in the diet. Chaetognatha (0.8%), Polychaeta (0.3%), and Mollusca (+) were not important contributors to the food of juvenile silver hake.

Crangon septemspinosa and bottom living amphipods were found in the stomachs of the smallest (3 cm FL) silver hake collected. However, the benthos did not increase in importance in the diet of the larger silver hake. The primary prey of all silver hake collected (3-20 cm FL) was the euphausiid, *Meganyctiphanes norvegica*.

Pollock

Crustaceans (68.2%) were the most important food of pollock. Euphausiacea, primarily *Meganyctiphanes norvegica* (40.9%) and small quantities of *Thysanoessa inermis* (2.3%), made up 55.8% of the crustaceans found in the stomachs. *Byblis serrata* (1.3%), along with small amounts of Caprellidae and Haustoriidae, accounted for the majority of the amphipod prey (1.5%). Decapod

larvae (0.3%), isopods (1.2%), and calanoid copepods (0.2%) made up the remainder of the crustacean prey. Items of little dietary importance to pollock were polychaetes (0.7%) and fish (+).

Only one small pollock (4 cm FL) was collected for stomach content analysis. The remainder of the fish ranged from 15 to 20 cm FL. Since only unidentified crustaceans were found in the stomach of the 4 cm fish, no data are available to discern at what length they first feed on the benthos.

Red Hake

Crustaceans (90.1%) accounted for most of the diet of red hake. The single most important crustacean prey was the decapod shrimp *Crangon septemspinosa* (40.6%). *Pagurus* sp. (0.4%) and *Hyas* sp. (0.1%) were the only other decapods identified in the stomach contents. Amphipod prey (19.4%) included Oedicerotidae (5.9%), Corophiidae (2.3%) [mainly *Unciola* sp. (1.9%)], and a large percentage of unidentified Gammaridea (7.1%). Euphausiids (6.4%), primarily *Meganyctiphanes norvegica* (1.6%), and mysids (3.6%) were the only other crustacean prey of importance to red hake. Only small quantities of copepods (1.3%), cumaceans (0.5%), and isopods (0.1%) were found in the stomach contents. Polychaeta (2.4%), Pisces (1.9%), Chaetognatha (0.3%), Mollusca (0.2%), and Echinodermata (+) contributed little to the food of red hake.

Red hake 6 cm TL fed predominantly on benthic foods such as Gammaridae, *C. septemspinosa*, and Cumacea. The food of fish <6 cm TL was mostly copepods and chaetognaths. *Crangon septemspinosa*, amphipods, and sand were found in the stomachs of red hake 3 cm TL.

White Hake

White hake preyed almost exclusively on crustaceans (94.9%). *Crangon septemspinosa* (57.9%) was of major dietary importance. Hermit crabs (0.3%) were the only other decapod eaten. Amphipods (15.4%) included Corphiidae (*Leptocheirus pinguis*) (4.6%), Aoridae (2.0%), Hyperiidae (0.5%), Pontogeneiidae (0.4%), Ampeliscidae (0.3%), and Caprellidae (0.2%). Polychaete worms made up 2.9% of the diet.

The stomachs of the smallest white hake collected (5 cm TL) contained sand and bottom living animals such as gammarid amphipods. Planktonic organisms were not found in any of the stomachs.

Spotted Hake

The most important prey of spotted hake were Crustacea (85.9%). Amphipods (all identified as Gammaridea) composed 77.1% of this juvenile fish's diet. Other crustacean groups were calanoid copepods (7.0%), small amounts of *Crangon septemspinosa* (+), and hermit crabs (+). The only other prey identified as part of the spotted hake diet was the Chaetognatha (+).

Although only 16 spotted hake were collected, the stomach content data showed that small quantities of hermit crabs (+) were eaten by a fish of only 4 cm TL (1 of 3 fish). Calanoid copepods made up the rest of the stomach contents of the 4 cm fish and were found in all three stomachs. At 5 cm TL (seven fish) spotted hake were eating bottom living organisms such as gammarid amphipods and *Crangon septemspinosa* (approximately 50% of their diet).

Fourbeard Rockling

Only one fourbeard rockling stomach contained food (two of the three stomachs collected were empty). Gammarid amphipods (33.3%) and small quantities of hermit crabs (+) were the only dietary items identified. The fish whose stomach contained food was 9 cm TL.

American Plaice

Polychaeta (72.1%) was the primary prey of the five specimens of American plaice which contained food (10 fish were collected in total). Only two families of polychaetes were identified, Capitellidae (10.6%) and Sabellidae (2.9%).

Crustacea (21.1%) and Mollusca (+) made up the remainder of the prey identified in American plaice stomachs. The crustacean dietary components were gammarid amphipods (17.3%), mysids (3.8%), small amounts of copepods [identified as *Centropages* sp. (+)], cumaceans (+), and hermit crabs (+). The molluscan (+) portion of the diet was identified as Dentalidae.

Worms (Sabellidae) and other benthic organisms, such as cumaceans and dentalids, made up most of the diet of the smallest American plaice collected (4 cm TL).

Yellowtail Flounder

Crustacea was the predominant prey of juvenile yellowtail flounder (94.4%). Amphipods (38.8%) were represented by the families Gammaridae (5.2%), Caprellidae (0.5%), Aoridae (+), Ampeliscidae (+), and Oedicerotidae (+). The Mysidacea (33.4%) were mostly *Erythrops* sp. (9.9%). Cumaceans (10.2%), decapods (composed of *Crangon septemspinosa*, 3.4%, and hermit crabs, 0.3%), isopods (1.0%), and copepods (+) made up the rest of the crustacean prey. Polychaeta (3.0%) was the only other dietary item noted in yellowtail flounder stomachs. They consisted mainly of Nerediformia (2.1%); most of which were identified as *Phyllodoce* sp. (0.9%).

The smallest yellowtail flounder collected (3 cm TL) ate organisms such as gammarid amphipods, cumaceans, and hermit crabs.

Discussion

A number of investigators have described the foods of juvenile groundfish. Although many of their studies were not conducted on the same species of fish or in the same geographic area as the present research, they provide evidence that the food of many juvenile fish species is similar. Arntz (1974), for example, studied the feeding of juvenile cod >11 cm FL in the western Baltic. His work showed that juvenile cod feed mostly on small bottom living crustaceans. Daan's (1973) results from studies on cod >8 cm FL in the North Sea also indicate that juvenile cod feed predominantly on small benthic organisms. Homans and Needler (1944) and Wigley (1956) included data on the food of juvenile haddock in their investigations. They found that small haddock generally eat crustaceans associated with the bottom, and polychaete worms. The diet of several juvenile flatfish species found in the North Sea consists mainly of small benthic crustaceans and polychaete worms (Braber and DeGroot 1973). The food of 33 juvenile demersal fish species collected in Long Island Sound, N.Y., was identified by Richards (1963); her data showed that when most inshore fishes are 1 yr old, they feed predominantly on the benthos.

Studies conducted on larval fish indicate that most groundfish species undergo several pelagic stages, and during these stages they feed predominantly on planktonic organisms (Rae 1953; Marak 1960, 1974; Laurence 1974, 1977; Last 1978). During their first year of life the majority of groundfish take up a bottom living habit and feed primarily on the benthos (Graham 1956). Assuming that the type of food found in a fish's stomach is indicative of its life stage, then the diet can give some approximation of a fish's age (length) when it makes the transition from pelagic to demersal living. Fish such as cod, for example, have been described as "seeking the bottom" when just over 2 cm FL (Hardy 1959) and stomachs from Atlantic cod 3 cm FL examined during this study contained small amounts of sand and benthic gammarid amphipods. Most of their food, however, was identified as copepods and euphausiids, indicating that the transition from feeding on principally plankton to other foods is a gradual change rather than an abrupt one.

The transition from pelagic to demersal habits of other gadoid fishes is apparently similar to that of cod. Haddock >8 cm FL tend to eat fewer pelagic organisms and prey more heavily on the benthos, but the stomachs of the smallest haddock collected (2 cm FL) contained some benthic animals, suggesting a slow change from a pelagic to demersal life. The same trend was noted for red hake, white hake, and spotted hake. The smallest fish collected had eaten small quantities of benthic organisms, but their primary food was copepods, euphausiids, and chaetognaths. The larger fish (>5 cm TL) fed mostly on bottom living organisms. Silver hake and pollock were rather unusual in that all the fish collected had consumed large quantities of euphausiids. They are less dependent on the benthos as a food even as adults than most other gadoids (Langton and Bowman 1980). Because of this it is difficult to distinguish, based on their diet, when they become demersal.

Only the two flatfish, American plaice and yellowtail flounder, where dependent on the benthos as a food source at the smallest fish lengths collected (3-4 cm TL). Since plaice and other flatfish metamorphose early in life (most have completed metamorphosis by 11 wk of age when they are between 1 and 2 cm TL) they take up life on the bottom at very small sizes (Hardy 1959). Winter flounder, *Pseudopleuronectes americanus*, was studied by Pearcy (1962), and it serves as a typical example of how the feeding habits of the flatfish change with age. He noted that the predominant food of metamorphosing larvae and juvenile winter flounder up to 1 cm TL is copepods; when the juveniles range in length from 1 to 2.5 cm TL, amphipods and polychaetes are their most

important food. Polychaetes become increasingly important in the diet of older winter flounder, thus indicating a strong association with the bottom.

Overall, the analysis of the stomach contents reported on here indicates that relatively few prey species make up a large portion of the food of juvenile fish. Before groundfish begin to depend on the benthos as a food source, calanoid copepods and euphausiids (mostly *Meganyctiphanes norvegica*) are extremely important foods. The diet of most species of larger juvenile fish, which depend primarily on benthic animals as food, includes gammarid amphipods such as *Unciola* sp. and *Byblis serrata*, along with the caprellid amphipod *Aeginina longicornis*. Decapods found in the diet were represented by *Crangon septemspinosa* more than any other species. The only other prey which stands out as important in the diet of the juvenile fish reported on here was the mysid *Neomysis americana*.

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DIFFERENCE IN SEX RATIOS OF THE ANADROMOUS ALEWIFE, *ALOSA PSEUDOHARENGUS*, BETWEEN THE TOP AND BOTTOM OF A FISHWAY AT DAMARISCOTTA LAKE, MAINE[1]

The Damariscotta River alewife, *Alosa pseudoharengus*, fishery has been monitored by the Maine Department of Marine Resources every year since 1971 for abundance of fish, length and weight frequencies, age distribution, and sex ratios. From 1977 through 1979, sampling plans were also devised to estimate numbers, size, and sex composition of ripe alewives escaping the fishery and entering the lake to spawn. (Throughout this paper they will be collectively referred to as escapements.)

While sampling the 1977 escapement run it became evident that a greater number of males than females were entering the lake to spawn. This male dominance was not unusual as it was reported in other alewife runs, as well. Bigelow and Schroeder (1953) stated that as a rule males greatly outnumber females on the spawning grounds. What prompted this investigation was the fact that while the escapement runs had significantly more males than females, the samples from the commercial catch revealed a consistent sex ratio of 1:1. Similar disproportionate ratios were observed in the 1978 and 1979 escapement runs, while the commercial catch ratios were 1:1 each year. In this paper I will examine these varying sex ratios and offer considerations for further investigation.

Study Area

The Damariscotta River fishery is located in the adjoining towns of Nobleboro and Newcastle and is one of the largest alewife fisheries in the state, composing about 30% of the annual total landings (Cating 1958). This area was selected for study because of the easy access to sampling both the commercial catch and the escapement run. The objectives of the study were: 1) to estimate the abundance of spawning adults, 2) to determine the escapement level which will maximize subsequent recruitment, and 3) to determine population characteristics of the Damariscotta River alewife stock such as stock size, age, distribution, and growth rates.

Damariscotta Lake, in Lincoln County, Maine, is a narrow, north-south oriented body of water 17 km long and 1,806 ha in area. There are three major outlets in a dam at the southeastern end of the lake: the first supplies water to a hydroelectric power station, the second is the main outflow controlled by two spillways, and the third is a man-made fishway. In 1803, the start of a commercial run was created (Atkins 1887), and a fishway made of stones set to form a series of irregular pools and raceways was constructed beside the main outflow. The fishway is about 150 m long with a 16 m vertical rise.

The spawning migration of this fishery's alewives consists of a 29 km swim up the Damariscotta River to head of tide at Great Salt Bay. The fish then enter the outflow of Damariscotta Lake via a tidal stream about 50 m long. The stream divides in two and the right branch becomes the entrance to the fishway. The left branch leads past two dipping bins used by the commercial fishery and then to the spillways. The spillways are opened to allow a sufficient amount of water into the stream to attract alewives into the bins. The alewives in this stream have a choice of swimming either into the left branch and the dipping bins or into the right branch and into Damariscotta Lake via the fishway.

Due to the type of construction and the lay of the embankment, the fishway is not consistent in its rise from pool to pool. The bottom and top sections are steepest, while the middle levels out, moderating the waterflow. The resting pools are of varying sizes and some of them appear to be too small, causing overcrowding of the alewives. Some of the connecting raceways are long and narrow, allowing for a faster current than is present in other raceways. The combination of a small pool and a difficult raceway lowers the efficiency of this fishway. From the appearance of alewives passing through the fishway, it is a difficult and exhausting run.

Methods

From 1977 to 1979, when escapement counts were made, a wood and wire mesh trap, 3 m long by 1.2 m wide by 0.8 m deep, was placed in the lake side of the dam at the top of the fishway. The trap's entrance covered the dam opening, where the es-

[1]This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 89-304, as amended, Commercial Fisheries Research and Development Act, Projects AFC-18-(2,3) and AFC-21-1.

capement fish passed from the fishway into the lake. During 1977 and 1978, a stratified random sampling plan was used to estimate total numbers entering the lake. The total duration of the run was divided into successive 5-d strata with 2 d randomly selected out of each stratum. All fish entering the trap during a 24-h period were visually counted and released. During each day sampled, approximately 25 alewives were measured for total length and sex was determined by stripping.

In 1979 a Smith-Root[2] 602A electronic fish counter was installed in the trap. Saila et al. (1972) used the system 602 counter with two separate tunnels for counting direction movement, whereas the 602A has one tunnel for counting upstream and downstream passage. The tunnel was 20 cm in diameter and 35 cm long. During most of the run, alewives that passed through the tunnel were held in the trap and later counted to discover any errors and to make necessary adjustments to the instrument.

A separate sampling plan was used at the bottom of the fishway for the commercial catch. On randomly selected days during the run, 9 d in 1977 and 15 d in 1978, 50-100 fish were taken from the catch. In 1979 the number of days sampled was 31, with 50 fish taken each day. Total length, weight, sex, and scales were taken from these alewives. In 1979, otoliths were also removed for aging.

Mean lengths and weights were computed for each day sampled and for each sex. Length measurements were taken from the total length of the fish. Each mean length and weight was weighted by the number of fish caught or counted on that day for total mean length and weight results. The number of fish harvested each year was estimated by dividing total weight by the mean weight per fish.

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

Results

Each year the alewife run began in early May and ended in early June. The commercial harvest contained 1,277,642 fish in 1977, 999,484 in 1978, and 777,941 in 1979. The respective escapements into Damariscotta Lake (±SE) were 26,813±2,624, 53,180±9,147, and 20,313±4,145 ripe alewives. The resulting escapement was 2.0%, 5.0%, and 2.6% of the commercial catches for 1977, 1978,and 1979, respectively.

Sex ratios in the commercial catch samples showed no significant differences from the beginning of the run to the end in all but a few samples each season. The overall combined samples for each year showed no significant difference on χ^2 tests ($P \geq 0.05$) between numbers of males to females (Table 1).

Early immigrants into Damariscotta Lake had significantly different sex ratios in which males always outnumbered females and as the run progressed these ratios had a tendency toward a nonsignificant ratio of 1:1 (Figure 1). This persistency in male dominance was evidenced by significant (χ^2 $P < 0.05$) totals in the ratios of 2.1:1 for 1977, 1.9:1 for 1978, and 2.6:1 for 1979 (Table 1).

Age distribution of commercial and escapement runs ranged from 3 to 9 yr old. The age distribution for each sex in the commercial catch displayed greater percentages of younger males than younger females; conversely, there were greater percentages of females at older ages than males in

TABLE 1.—Sex ratios (M:F) and number of alewives sampled in 5-d consecutive periods for the commercial and escapement runs at the Damariscotta Lake fishway, Maine, 1977-79. The samples columns refer to the number of combined samples in the 5-d consecutive periods.

	1977						1978						1979					
	Commercial			Escapement			Commercial			Escapement			Commercial			Escapement		
	Samples	Ratio	*n*	Samples	Ratio	*n*	Samples	Ratio	*n*	Samples	Ratio	*n*	Samples	Ratio	*n*	Samples	Ratio	*n*
	1	2.7:1*	37	2	3.1:1*	111	3	1.1:1	300	2	3.4:1*	131	5	1.3:1*	247	3	3.0:1*	92
	1	1.1:1	19	2	3.3:1*	525	3	0.8:1*	300	2	2.1:1*	203	5	1.1:1	228	2	3.3:1*	113
	1	0.5:1	19	2	2.8:1*	569	3	0.7:1*	300	2	1.9:1*	280	5	1.0:1	252	1	4.1:1*	56
	3	1.2:1	128	3	1.2:1*	380	2	1.1:1	179	2	1.6:1*	118	5	0.9:1	251	1	3.2:1*	54
	1	0.8:1	54		—		2	1.2:1	223	2	1.3:1	155	5	1.1:1	243	1	1.7:1	30
	2	1.1:1	33	2	1.0:1	115	2	1.0:1	175	1	1.2:1	20	4	0.9:1	195	3	1.6:1	72
				1	1.1:1	66							2	1.1:1	100	2	1.1:1	44
				2	1.3:1	101												
				1	1.4:1	40												
Pooled samples		1.1:1			2.1:1*			1.1:1			1.9:1*			1.0:1			2.6:1*	

*χ^2 significance at $P \leq 0.05$.

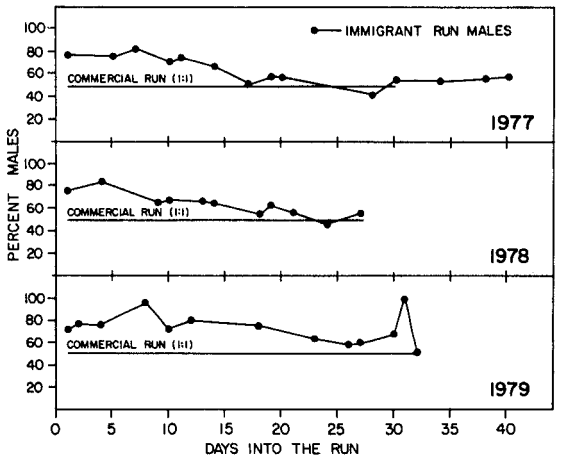

FIGURE 1.—Percentage of males from samples taken during the escapement run at Damariscotta Lake fishway, Maine, compared with the consistent (1:1) sex ratio of the commercial run, 1977-79.

each year. The greater proportion of ages III and IV were males, while ages V and VI were dominated by females in 1977 and 1979. In 1978 males dominated ages III through V. There is no evident trend in ages VII and older for either sex, probably due to the small sample sizes at these ages. The percentage at age of sexes in the escapement runs showed about the same distribution as was found in the commercial runs (Table 2). The trend in size and age at the Damariscotta Lake alewife run was larger and older fish arriving early and regressing to smaller and younger fish through time (Table 3).

Discussion

There have been other observations of early male alewife predominance in fishways and on spawning grounds. Dominy[3] showed a male predominance ratio of 2.4:1 at the start and a 0.7:1 ratio by the end of the run in the Gaspereau River, White Rock, Nova Scotia. Kissil (1974) at Bride Lake, Conn., observed more males during the early part of the run declining to an equal number with females for the remainder. Cooper (1961) reported that males gradually declined from 65% at the beginning to 35% at the end of the run at Pausacaco Pond, R. I. Rideout (1974) found a high percentage of males in most samples from the Parker River, Mass. Havey (1961) observed a 1.28:1

[3]Dominy, C. L. 1971. Evaluation of a pool and weir fishway for passage of alewives (*Alosa pseudoharengus*) at White Rock, Gaspereau River, Nova Scotia. Dep. Fish. For. Can. Resour. Dev. Branch, Halifax, Progr. Rep. 3:22.

TABLE 2.—Percentage of male and female alewives at age from the commercial and escapement runs at the Damariscotta Lake fishway, Maine, 1977-79.

		Commercial fishery								Escapement runs							
Year	Sex	III	IV	V	VI	VII	VIII	IX	Total	III	IV	V	VI	VII	VIII	IX	Total
1977	Males	0.3	34.6	13.8	1.6	0.7	0	—	51.1	0.5	37.4	26.0	1.8	0.9	0.1	—	66.6
	Females	.1	20.2	24.8	2.7	.7	.2	0.2	48.9	.2	14.4	15.5	2.9	0.3	.1	0	33.4
1978	Males	.1	14.1	28.1	6.6	2.0	.4	—	51.2	0	10.6	33.8	12.8	3.8	.8	—	61.9
	Females	.1	10.3	26.9	9.2	2.1	.2	—	48.8	.3	8.1	19.5	8.1	1.7	.4	0	38.1
1979	Males	.3	22.5	22.5	3.3	1.7	.2	—	50.4	.3	31.0	32.1	5.6	3.6	.1	—	72.7
	Females	.1	15.7	28.0	4.6	1.0	—	0.2	49.6	—	8.1	16.5	2.1	0.3	—	—	27.3

TABLE 3.—Age distribution (percent) and mean total length (millimeters) of alewives for three equal periods during the Damariscotta Lake, Maine, commercial run, 1977-79.

Date	Sex	III	IV	V	VI	VII	VIII	IX	Total	Mean length
4-13 May 1977	Males	—	22.0	28.1	5.4	3.1	0.9	—	59.6	304.0±2.0
	Females	—	10.3	25.3	4.9	—	—	—	40.4	309.4±2.0
14-23 May	Males	0.4	37.0	13.1	1.7	.9	—	—	53.1	292.6±1.4
	Females	.1	19.3	24.0	2.1	.9	.2	0.2	46.9	304.9±1.5
24 May-3 June	Males	.2	28.2	15.4	1.1	—	—	—	45.0	295.6±1.7
	Females	—	23.2	27.2	4.5	—	—	—	55.0	300.7±1.2
6-15 May 1978	Males	—	1.7	24.6	14.4	4.5	1.5	—	46.7	310.0±0.7
	Females	—	3.4	29.0	15.8	4.5	.6	—	53.3	317.5±0.7
16-25 May	Males	.1	11.2	29.3	6.9	2.5	.1	—	50.2	302.3±0.8
	Females	—	7.7	28.8	10.8	2.3	.3	—	49.8	313.7±0.8
26 May-3 June	Males	.3	22.5	27.3	3.7	.2	.4	—	54.4	295.7±0.8
	Females	.3	16.7	23.0	4.5	1.2	—	—	45.6	306.7±1.0
7-17 May 1979	Males	—	15.8	27.1	5.5	4.0	.5	—	52.9	299.6±1.0
	Females	—	9.3	29.4	6.6	1.3	—	.5	47.1	309.6±1.3
18-28 May	Males	.2	22.7	22.1	2.8	1.4	.1	—	49.2	292.1±0.8
	Females	—	16.4	28.9	4.0	1.2	—	.1	50.2	302.9±1.0
29 May-8 June	Males	.7	28.6	19.4	2.3	.4	—	—	51.3	288.3±1.0
	Females	.3	20.0	24.5	3.5	.4	—	—	48.7	299.5±1.2

(M:F) ratio at Long Pond, Maine, although this was not statistically significant.

Sex dominance in a species of fish that is assumed to have an equal sex ratio may be attributed to sampling and catch methods. For example, Casselman (1975) noted that the sex ratio of northern pike, *Esox lucius*, caught by anglers favored females because of their greater activity in foraging for food at the time of fishing. Early male alewife predominance is attributed to males maturing a year earlier than females (Havey 1961; Kissil 1974) and males ripening earlier in the season, thus beginning the spawning run sooner (Cooper 1961). Marcy (1969) at Bride Lake found that 68% of males were age IV and 68% of females were age V. The alewives in Damariscotta Lake have shown this same attribute of male dominance as in these other investigations. As fish begin entering the lake there were many more males present than females. The presence of significant heterogeneity revealed that this male dominance of early escapements into the lake is not consistent throughout the run. A comparison of percentage of males per sample in the fishway run to the hypothetical 1:1 ratio in the commercial catch showed a trend of diminishing male dominance.

The reasons cited earlier for male dominance in alewife runs do not explain the disproportionate ratio in these other runs or at Damariscotta Lake. The theory that earlier maturing or earlier ripening males in an alewife stock contribute to the greater male to female ratio does not correspond to the size and age trend of the Damariscotta spawning runs. As was shown, these runs had the largest fish arriving first. Other investigators have shown this to be the case in other alewife spawning migrations: Havey (1961) reported older fish running early; a decreasing trend in mean fork length for each sex during the spawning run was shown by Cooper (1961), Kissil (1974), and Rideout (1974). If larger alewives are the earliest to arrive, the greater proportion of males to females would not occur at the first of the run. The larger proportion of males would occur later or at the end of the run when the younger fish begin arriving. The main reason in searching for other explanations is the fact that the sex ratios in the commercial catch (located near the bottom of the fishway) had generally nonsignificant ratios throughout the run in each of the 3 yr. Age distribution of the commercial catches does show more younger males (III-IV), but the older ages contain more females (V-VII). The greatest proportion of the commercial catch (85-90%) is made up of 4- and 5-yr-old fish and they are always present throughout the run. This mixing of 4-yr-old males and 5-yr-old females caused the 1:1 sex ratio in the commercial catch.

The explanation for this abrupt change in the sex ratio from the tidal area to the lake appears to be an effect of the fishway. The greatest disproportionate ratio of male to female alewives occurred at the first part of the escapement run when the largest fish were in the fishway. It seemed that the construction of the fishway was selective against the largest or heaviest fish which were the females at that time. As the size of females tended to decrease, the male to female ratio became more equal.

Future investigations that deal with the sex ratio of alewives on the spawning grounds would do well to examine the alewife stock before it made any arduous runs through a difficult section of water or fishway. The reasons for a significantly different sex ratio on the spawning grounds could be from the physical aspects of the migration route rather than any biological factors of the alewife.

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PROXIMATE COMPOSITION AND NUTRITIVE VALUE OF SOME IMPORTANT FOOD FISHES FROM THE ARABIAN GULF

The unique value of fish for supplementing the nutritional qualities of man's diet, as also for animal feeding, is well recognized. Literature on the composition and calorie value of fish reported from various parts of the world is exhaustive. Love (1970), Sidwell et al. (1973, 1974), Bonnet et al. (1974), Stansby (1976), Sidwell, Loomis, Loomis, Foncannon, and Buzzell (1978), and Sidwell, Loomis, Foncannon, and Buzzell (1978) have provided good reviews on the subject.

The Arabian Gulf countries, including Kuwait, have rich fish faunas and Kuwait with a coastline of about 140 km, has at least 131 fish species in 64 families which are taken in commercial trawls (Kuronuma and Abe 1972). The total quantity of fish sold in Kuwait market in 1976 was 4,452 t as estimated by the Kuwait Ministry of Planning (Anonymous 1977). In a recent survey of the fish consumption of local populations in Kuwait, Afzal and Hayat (1977) reported that the consumption of fish in Kuwait is fairly high and that a majority of respondents had no clear idea about the nutritive value of fish. It was emphasized that a program was necessary to disseminate such information.

With the exception of the work of Das et al. (1976) on a few fishes from Shatt Al-Arab and the Arabian Gulf, nothing seems to have appeared on nutritional values of Arabian Gulf fishes. Here we report on the proximate composition and nutritive value of some of the important food fishes from Kuwait for use of consumers, dieticians, and the fishing industry.

Methods

The study was based on fish samples obtained from the local fish market. These are caught by shrimp trawlers and dhow boats operating in the Arabian Gulf. For each species, fresh specimens representing the common marketable size were selected (Table 1). Analysis used minced muscle from the trunk portion of each individual from which skin and all bony elements had been removed. Standard methods of chemical analysis were used (Horwitz 1975). Gross energy content was calculated from the mean values of fat, protein, and carbohydrate following equivalents as used by Jafri et al. (1964). All samples were taken during November and December 1978.

Results

Most of the fishes were found to be fairly high in protein content. The maximum value (22.6%) was observed in the barred Spanish mackerel whereas

TABLE 1.—Average proximate composition (± standard error of the mean) and energy content of some important food fishes sampled in November and December 1978 from the Arabian Gulf.

Species	No.	Total length (cm)	Protein (%)	Fat (%)	Moisture (%)	Ash (%)	Energy (cal/100 g)
Spotted Spanish mackerel, *Scomberomorus guttatus*	7	47.1±0.6	20.5±0.0	3.4±0.4	73.9±0.3	1.4±0.0	119.0
Barred Spanish mackerel, *S. commersoni*	5	103.5±7.2	22.6±0.6	1.8±0.2	73.5±0.1	1.5±0.0	111.7
Silvery croaker, *Otolithus argenteus*	5	33.4±1.1	21.8±0.3	1.1±0.3	74.5±0.4	1.3±0.0	104.8
Four-thread threadfin, *Eleutheronema tetradactylum*	5	53.0±0.6	20.7±0.2	5.3±1.1	72.1±0.7	1.3±0.0	136.6
Silvery grunt, *Pomadasys argenteus*	7	55.4±2.0	20.5±0.2	.5±0.1	77.6±0.3	1.2±0.0	89.4
Silvery pomfret, *Pampus argenteus*	5	30.4±6.4	18.5±0.3	1.4±0.3	78.3±0.3	1.3±0.0	91.0
Mullet, *Liza macrolepis*	12	17.5±0.2	17.2±0.2	1.1±0.0	79.6±0.2	1.3±0.0	83.9
Yellow finned black porgy, *Acanthopagrus latus*	5	31.2±0.8	19.7±0.3	.3±0.1	77.9±0.5	1.2±0.1	87.6
Crimson snapper, *Lutjanus coccineus*	5	64.0±1.4	19.1±0.3	.2±0.1	77.6±0.2	1.2±0.0	87.7
Brown-spotted grouper, *Epinephelus tauvina*	5	84.3±1.5	19.5±0.3	.5±0.0	74.1±0.1	1.2±0.0	104.1

the minimum value (17.2%) was noted in the mullet. Other fishes with high protein content were silvery croaker, four-thread threadfin, silvery grunt, and spotted Spanish mackerel. The value of protein observed for the silvery pomfret was found to be higher than the value reported by Das et al. (1976) for this species from Shatt Al-Arab.

The fat content ranged from 0.2% in crimson snapper to 5.3% in four-thread threadfin. Except for the four-thread threadfin and mackerels, fishes were generally low in fat content. The magnitude of variation in fat values for individual species was higher in comparison to that observed for protein. Of the various constituents of the fish body, fat is perhaps the most variable component varying with factors like age, sex spawning cycle, feeding, season, etc. Generally low fat values observed during the present investigation could possibly be the result of relatively poor winter condition of these fishes.

Moisture content varied from 72.1% in four-thread threadfin to 79.6% in mullet.

Ash content varied little. Except for the mackerels which showed slightly higher values, ash content varied between 1.2 and 1.3%.

Gross energy content was highest (136.6 cal/100 g) in the muscle of the four-thread threadfin, followed by mackerels and silvery croaker. Lowest value (83.9 cal/100 g) was noted for the mullet. The energy content for the silvery pomfret and silvery grunt resemble closely the values reported by Sidwell et al. (1974). The energy content for the various species of mullet quoted by Sidwell et al. (1974) was, however, higher than that obtained for *Liza macrolepis*.

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Seattle, Washington

1981

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THE SPAWNING ENERGETICS OF FEMALE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

J. ROE HUNTER AND RODERICK LEONG[1]

ABSTRACT

The seasonal pattern in incidence of postovulatory follicles in northern anchovy females indicated that they spawn about 20 times per year. The maturation rates of females in the laboratory indicated that they were capable of maturing a spawning batch of eggs at weekly intervals. Examination of the egg size frequency distributions in sea-caught specimens indicated that vitellogenesis and egg maturation continued until the last spawning. We evaluated for northern anchovy the fat-water balance, caloric values of tissues, annual fat cycle, seasonal changes in egg weight, total calories present in a mature ovary, batch fecundity; and determined in the laboratory the gross caloric conversion efficiency (12.8%). These measurements indicated that the caloric equivalent of only two spawning batches are present in a mature ovary at any time and that two-thirds of the annual cost of 20 spawnings could be supplied by fat stores. Estimates of annual reproductive effort (egg calories/ration calories × 100) ranged from 8% for 1 year to 11% for 3-year-old females. A daily ration of copepods equivalent to 4-5% of female wet weight per day is required to support the annual cost of growth and reproduction.

Histological evidence indicated that female northern anchovy, *Engraulis mordax*, spawned about once a week in February 1978 (Hunter and Goldberg 1980) and at 7-10 d intervals from late January through the middle of April 1979 (Hunter and Macewicz 1980). Egg and larva survey data indicate that some spawning occurs throughout the year, although about 50% of the annual production of northern anchovy larvae occurs during the peak months of spawning (February to April) (Lasker and Smith 1977). These findings indicate that northern anchovy females spawn many times per year. Thus, the annual fecundity of northern anchovy is higher than originally suspected by MacGregor (1968) and may be regulated by availability of food. Energy regulation of fecundity has been suggested for other marine fish stocks and could be important as a density-dependent population regulation mechanism (Bagenal 1973).

The objectives of this study were: to validate recent work on northern anchovy spawning by determining if such a high frequency of spawning is developmentally and energetically possible; to estimate the annual energy cost of reproduction; and to discuss the sources of variation. We estimated the average number of spawnings by northern anchovy females in a year and tested the hypothesis that they are capable of maturing eggs at the required rate. We considered the energy cost of reproduction, factors that affected variation in costs, and related reproductive costs to fat stores. Finally we estimated the annual reproductive effort (egg cal/ration cal). In addition to data collected specifically for this study, we used data available at the Southwest Fisheries Center (SWFC), La Jolla, Calif., including many unpublished sources.

METHODS

Field Data

To estimate the annual number of spawnings by northern anchovy, we used the data of Hunter and Goldberg (1980) and Hunter and Macewicz (1980) on the incidence of 24-h-old postovulatory follicles. The proportion of mature females with 24-h-old postovulatory follicles was considered equivalent to the fraction of females spawning per day during a cruise (Hunter and Goldberg 1980). All samples were taken in the Southern California Bight in 1977-79; the number of females analyzed per cruise was 148 from March 1977; 14 from September 1977; 295 from February 1978; 395 from January-February 1979; 557 from March-April 1979; and 33 from June 1979. Data were plotted at the mid-date for the cruises which were 10-22 d long.

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

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To estimate the rate of egg maturation required for weekly spawning, we used the frequency distributions of egg size in mature northern anchovy ovaries of females taken at sea. We measured distributions in 10 females taken in the Southern California Bight in February 1979, and in 6 taken in Monterey Bay in March 1979 by Hunter and Macewicz (1980). Five of the females from the Southern California Bight had 24-h-old postovulatory follicles indicating spawning had occurred on the day before they were captured, and the other five were mature without evidence of recent spawning. The ovaries of the six females from Monterey were highly atretic and in post-spawning condition, but had yolked eggs (Hunter and Macewicz 1980). This latter group was used to illustrate the condition of ovaries at the cessation of spawning. Our method of measuring the egg size-frequency distributions was similar to that of MacGregor (1968). We counted and measured to the nearest 0.05 mm all eggs >0.05 mm (major axis) in a weighed sample of the ovary.

Seasonal changes in fat content of female northern anchovy were calculated using the original data summarized by Lasker and Smith (1977). Their samples were taken at roughly monthly intervals from February 1965 to June 1967 (n = 593). Their data, supplemented by additional data (n = 338) taken in the summer and fall of 1979, were used to estimate the relation between wet weight without gonad (W) and fat content (F) and dry weight (without fat) (D). The multiple regression equation for this relation was

$$W = -0.018 + 0.320\,F + 5.469\,D \qquad (1)$$

where all variables are in grams, r^2 = 0.969, and n = 981. This equation permitted calculation of wet weight of northern anchovy females after fat gain or loss. Wet weight changes only slightly with fat loss because water content increases as fat decreases (Iles and Wood 1965) (Table 1). The same data were used to establish the relation between dry weight (without fat) (D) and standard length (L) where

$$\log_{10} L = 0.313 \log_{10} D + 1.930, \qquad (2)$$

r^2 = 0.974. Thus, wet weight can be estimated for northern anchovy of any standard length given the fat content.

Ahlstrom[2] measured the major and minor axes of 50-150 northern anchovy eggs taken in each of 58 standard ichthyoplankton tows (Smith and Richardson 1977) along the coast of California and Baja California in 1955, 1956, 1957, and 1965. These data, combined with an additional 30 tows (100 eggs measured/tow) taken in the same region in 1969, were used to estimate seasonal changes in the size of northern anchovy eggs. We calculated monthly mean egg dimensions for the combined data; number of tows per month varied from 9 to 16 (February-July) and from 1 to 4 in the period of low egg abundance (August-December). We calculated the mean volume of the eggs per month from average egg dimensions using the equation for a prolate spheroid. The volume (V) in cubic millimeters was converted to dry weight (E) in milligrams with the relation established in the laboratory using freshly spawned eggs

$$E = 0.0012 + 0.0930\,V \qquad (3)$$

where r^2 = 0.646 and n = 32.

Laboratory Data

Three groups of northern anchovy of 1,200-1,300 fish each were matured in the laboratory to measure the rate of ovarian maturation and to estimate gross growth efficiency. The fish were

[2]E. H. Ahlstrom, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, unpubl. data, 1979.

TABLE 1.—Relationship between fat-free dry weight or length and wet weight for northern anchovy at the average seasonal minimum and maximum fat content. Relationships calculated from regressions; all body weights are without gonads.

Standard length[1] (mm)	Fat-free dry weight (g)	Wet weight and water content at minimum (15%)[2] fat content			Wet weight and water content at maximum (41%)[2] fat content		
		Fat (g)	Wet weight[3] ± 95% C.I.	Water[4] (%)	Fat (g)	Wet weight[3] ± 95% C.I.	Water[4] (%)
106	2.000	0.353	11.03 ± 0.19	79	1.390	11.36 ± 0.11	70
118	2.891	0.510	15.96 ± 0.13	79	2.009	16.44 ± 0.18	70
131	4.000	0.706	22.08 ± 0.12	79	2.780	22.75 ± 0.35	70

[1]From Equation (2) in text.
[2]Percentage of the dry weight including fat.
[3]From Equation (1) in text; 95% confidence intervals calculated using Gauss multipliers (Snedecor and Cochran 1967).
[4]$[W - (D + F)/W] \times 100$, where W = wet weight without ovary, D = fat-free dry weight, and F = weight of fat.

purchased from bait dealers from September to October in 1977 and 1978 and held in circular tanks 4.6 m in diameter × 1 m deep (volume 16.6 m^3) with a fresh seawater inflow of 20 l/min. The fish were exposed to the natural photoperiod but were shielded from direct sunlight. They were fed a ration of Oregon Moist Trout Pellets[3] 6 d/wk. The pellets were dispensed with an automatic feeder over a 4-5 h feeding period beginning at 0800 h (Leong 1971).

To estimate the rate of egg maturation (group 1), 8-12 females were sampled twice weekly for 6 wk. The ovaries of nearly all females were immature (no yolked oocytes) when sampling began; the mean standard length (SL) of females was 112.4 mm increasing to 116.4 mm in 6 wk. The fish were held at ambient temperatures which ranged from 17.9° to 22.0° C and averaged 19.7° C; daily temperatures closely followed those taken at the Scripps Institution of Oceanography pier. We measured standard length, wet weight, and determined the frequency distribution of egg sizes within the ovary for each female sampled. We used as a measure of the state of sexual maturity, the mean size of eggs (major axis) within the most advanced spawning batch. The number of eggs within a batch was calculated from the wet weight of the female using the batch fecundity equation of Hunter and Macewicz (1980)

$$\log_e T = 4.248 + 1.620 \log_e W. \qquad (4)$$

(Equation corrected for bias in taking the antilog; Beauchamp and Olson 1973), where T = total number of eggs in a spawning batch and W = female wet weight (without ovary) in grams.

To measure growth efficiency, two groups (groups 2 and 3) were held under similar tank conditions, but were sampled at 2-wk intervals beginning at the end of November and ending in mid-February. Group 2 was in captivity for about 1 mo and group 3 for 2 wk prior to sampling. Group 2 was held at 15.6° C while group 3 was held at ambient temperatures which ranged from 15.2° to 17.0° C and averaged 16.0° C. Mean standard length of fish in groups 2 and 3 was 107.2 mm at the beginning and 121.4 mm at the end of the experiment.

The stomach contents of each fish sampled from groups 2 and 3 were weighed and used to determine the mean ration for the experiment. The ration was calculated from the equation

$$R = r \cdot s \cdot t + S_e \qquad (5)$$

where R = ration, expressed as wet weight food consumed/wet weight fish (in grams); r = rate of gastric evacuation (dashed line, Figure 1); s = average weight of food in stomach/fish weight during the period of gut filling (solid line, Figure 1); t = duration of feeding (4 h, group 2; 5 h, group 3); and S_e = weight of food in stomach/fish weight

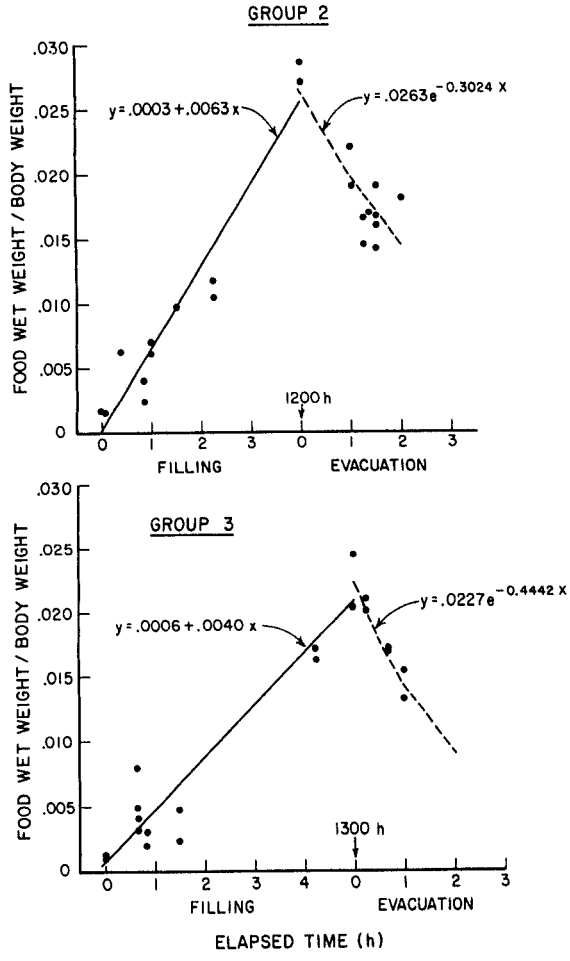

FIGURE 1.—Rate of stomach filling and gastric evacuation in two groups of northern anchovy fed Oregon Moist Trout Pellets. Weight of stomach contents expressed as a proportion of fish weight; each point is mean for 8-12 fish; feeding began at 0 h (filling) and ended at 0 h (evacuation) (arrow); time of day when feeding ended is above arrow. Daily ration calculated from these data was 4.4% body weight/d, group 2; and 4.6% body weight/d, group 3.

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

at end of feeding period. Similar functions have been used by Tyler (1970), discussed and used by Eggers (1977), and discussed by Elliot and Persson (1978). The daily pattern of feeding and evacuation and the data used to calculate the parameters for the ration equation are given in Figure 1. We use an exponential equation to estimate rate of gastric evacuation (r) because it is required by theory and the above model and use a linear regression equation for gut filling because the equation is used only to provide an empirical estimate of the mean stomach contents (s) during feeding.

The mean ration for a feeding day was 0.0437 g/g body wet weight (group 2) and 0.0462 g/g body wet weight (group 3); these values were multiplied by the mean wet weight of fish sampled (18.6 g, group 2; 17.6 g, group 3) to express the ration in terms of the average fish weight in each experiment. This value was adjusted by the ratio, total number of feeding periods/duration of the experiment (days) (ratio = 59/69, group 2; 67/78, group 3), to adjust the ration for days when no feeding occurred. This daily ration for the experiment was converted to calories by multiplying by 0.656 (average ratio of dry to wet weight for stomach contents of northern anchovy fed Oregon Moist Trout Pellets) and by 4,912, the caloric value per gram for this food (Table 2). The daily ration for fish in group 2 was 2,238 cal/d and was 2,245 cal/d for fish in group 3.

TABLE 2.—Mean calories per gram dry weight of various northern anchovy tissues and food.

Tissues or food	n	Mean calories	SD
Anchovy fat	4	9,227	40
Anchovy eggs (including fat)	4	5,450	90
Whole female anchovy, less ovary (fat free)	11	4,129	176
Anchovy ovary (fat free)	29	4,960	79
Anchovy ovary with 18%[1] fat	—	5,710	—
Oregon Moist Trout Pellets	4	4,912	214

[1] 18% is the mean fat content of northern anchovy ovaries; caloric value was calculated from the values for fat and fat-free ovary.

Dry weight and fat content of northern anchovy were determined for the first and last samples of groups 2 and 3. Fish were dried in an oven at 60° C until constant weight and fat extracted using Soxhlet extraction with chloroform-methanol (Krvarić and Mužinić 1950).

Caloric values of northern anchovy oil, newly spawned eggs, ovaries and whole females (without ovaries), and Oregon Moist Trout Pellets were estimated using a Parr bomb calorimeter and standard techniques (Table 2). Laboratory fish were used for all measurements except for the caloric value of northern anchovy oil where sea-caught specimens were used.

SPAWNING FREQUENCY AND RATE OF EGG MATURATION

Number of Spawnings per Year

We plotted the fraction of females spawning per day (females with 24-h-old postovulatory follicles) as a function of sampling date to estimate the number of spawnings produced by female northern anchovy in 1 yr. The seasonal change in the fraction of females spawning followed the seasonal change in the average relative larval abundance for 1953-60 (Lasker and Smith 1977) (Figure 2). The fraction of females spawning was the highest during peak spawning months and declined to zero by September. In peak spawning months the percentage of mature females spawning per day was 16-14%, indicating that individual females spawned every 6-7 d. The seasonal decline in the fraction of females spawning per day could be caused by an increase in the interval between spawnings in individual females, or by a complete cessation of spawning by an increasingly larger proportion of the population, or by a combination of these events.

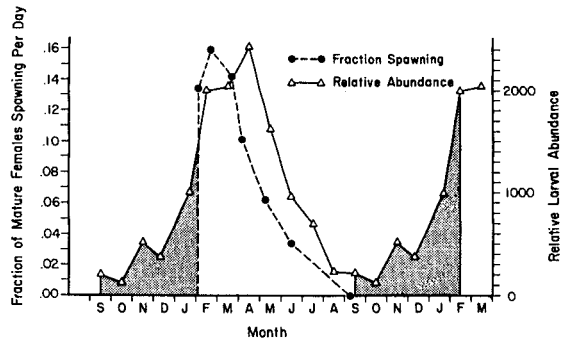

FIGURE 2.—Fraction of mature northern anchovy females from the Southern California Bight spawning per day during various months (dots). Fraction calculated from incidence of females with 24-h-old postovulatory follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980). Triangles indicate relative larval abundance per month from 1953 to 1960 (Lasker and Smith 1977). Shaded areas indicate months where spawning fraction was not estimated; total spawnings per year by northern anchovy females was estimated from areas under the two curves (see text).

The area under the curve for fraction of females spawning per day is an estimate of the number of spawnings produced per female from February to September. This calculation indicated that each mature female northern anchovy spawned on the average 15 times between February and September. The number of spawnings that occurred in October-January (shaded area, Figure 2) had to be estimated indirectly because no ovary samples existed. We assumed that the number of spawnings was proportional to the relative larval abundance in October-January, adjusted by the ratio of the areas under the spawning fraction and larval abundance curves for Feburary to September. This calculation indicated that about five spawnings would have had to occur in October-January to account for the abundance of larvae in that period; this brings the total number of spawnings for female to 20 for the year.

Form of Frequency Distribution of Egg Size

The form of the egg size distribution in mature northern anchovy ovaries is illustrated for a female taken 24 h after spawning and a mature female without evidence of recent spawning (nonspawning) (Figure 3). Ovarian egg size distributions typically resemble these except for females with hydrated eggs, where the hydrated eggs stand out as a discontinuous group of large eggs. In mature females (without hydrated eggs) the egg size distributions are continuous and typically have one or two modes as illustrated. In the nonspawning female a major mode of large yolked eggs existed between 0.6 and 0.8 mm (major egg axis) and in the spawned female the first modal group occurred at about 0.5 mm. Eggs <0.2 mm are the most abundant size class in both ovaries. These small eggs, also abundant in immature ovaries, form part of the reservoir of immature unyolked eggs which are matured during each spawning season.

Yolk appears in the egg when the major axis of the egg reaches about 0.4 mm. The ovary of the spawned female (20.2 g) in Figure 3 contained 9,384 yolked eggs, whereas that of the nonspawning female (25.3 g) contained 26,761 yolked eggs. The batch fecundity equation (Equation (4)) predicts a batch size of 9,110 eggs for the spawned female and 13,120 eggs for the nonspawning female. Hence, about one spawning batch of yolked eggs existed in the spawned female and about two

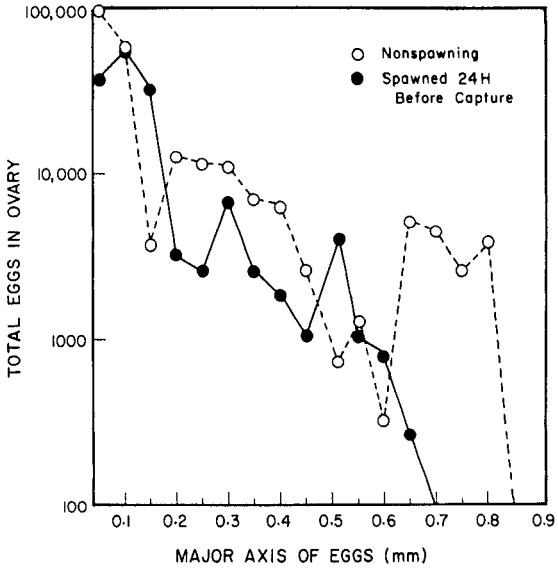

FIGURE 3.—Total eggs in ovary ($\log_{10}$ scale) as a function of the major egg axis for a 20.2 g female northern anchovy (ovary-free weight) captured 24 h after spawning and for a 25.3 g female, showing no evidence of recent spawning (nonspawning). Smallest eggs measured were 0.05 mm; measurements were made in increments of 0.05 mm. Females were captured in January to February 1979 in the Southern California Bight.

in the nonspawning female. If a female were to spawn more than a few times in one season, it would have to mature and yolk many of the small unyolked eggs in the ovary. If spawning were to occur at weekly intervals for months, this would be a continuous process.

Rate of Egg Maturation Required for Continuous Production of Eggs Compared With Laboratory Maturation Rate

For northern anchovy to continually mature and add yolk to a series of egg batches, the abundance of egg sizes in the ovary must vary inversely with the rate of egg maturation. Thus, a hypothetical curve for the rate of maturation of anchovy eggs can be constructed from the average size of eggs in each potential spawning batch within an ovary, if the time between batches or spawning frequency is known. This hypothetical rate can then be compared with the rate of egg maturation in the laboratory to determine if the predicted rate is possible.

To conduct this test for northern anchovy, we partitioned the total number of eggs in the ovary of 10 sea-caught fish into successive spawning

batches (starting with the largest eggs) and calculated the mean major axis of eggs in each successive batch. The number of eggs per batch was estimated from the wet weight of the females using the batch fecundity Equation (4).

As might be expected, the mean major axis of eggs in each of the potential spawning batches for the five females taken 24 h after spawning was about one spawning batch out of phase from the five nonspawning fish (Figure 4, upper). When the most advanced spawning batch of the recently spawned group was lagged by one spawning interval, the function was the same for both groups (Figure 4, lower) and similar to data on "nonspawning females" in Hunter and Goldberg (1980). The lower curves indicate that about four spawning batches of eggs >0.15 mm exist in the ovary of females near spawning condition. Hunter and Goldberg (1980) determined for 38 mature nonspawning females that the mean size of eggs in the most mature batch was 0.59 mm; and in the 5 females in the present analysis, the mean size was 0.71 mm. Thus a batch of eggs of 0.15 mm mean size major axis would have to reach about 0.6-0.7 mm in about 4 wk (28 d) if females were to spawn five or more times at weekly intervals.

The ovaries of all laboratory females were immature when the maturation experiment began (elapsed time = 0, Figure 5) although the mean size of eggs in the most advanced spawning batch was quite variable among females (mean egg size ranged from 0.13 to 0.48 mm). To illustrate the rate of ovarian maturation we used the average of the mean egg size in the spawning batch of individual females (Figure 5). The rate of maturation of ovaries in the laboratory group was similar to that predicted from egg size frequency distributions of wild fish, if one assumes spawning in the sea occurs weekly (line, Figure 5). The average of the mean size of eggs in the most advanced spawning batch was 0.15 mm after the first week of the experiment and was 0.62 mm 4 wk later. Thus maturation of eggs from 0.15 to 0.62 mm occurred in four wk and is about the same as the theoretical estimate based on egg size distributions in sea-caught specimens. This demonstrates that the rate of egg maturation required for continuous production of egg batches

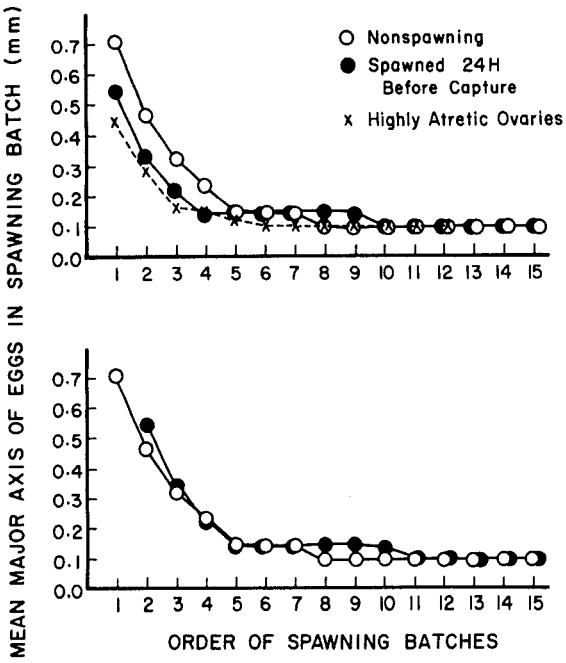

FIGURE 4.—Mean major axis of eggs in successive spawning batches within the ovary of northern anchovy. Number of eggs per batch estimated for each female from Equation (4). Numbers on abscissa indicate order of spawning batch with 1 = the most advanced batch. Circles are means of five nonspawning females (no evidence of recent spawning), and dots are means for five females having spawned within 24 h (females taken in the Southern California Bight); the X's are means for six females with highly atretic ovaries taken in Monterey Bay in 1979. The lower panel illustrates the correspondence between average egg size in successive batches in nonatretic ovaries when recently spawned females are lagged by one spawning batch interval. Only the 15 batches containing the largest eggs are shown.

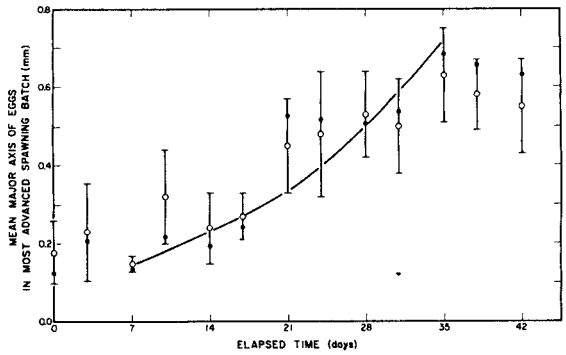

FIGURE 5.—Maturation of eggs in the most advanced spawning batch of laboratory-held northern anchovy as a function of elapsed time. Maturity is achieved when average egg size in batch attains 0.6-0.7 mm. Circles are averages of the mean size of eggs in the most advanced spawning batch of females sampled on a particular day, dots the median, and bars are ±2 SE. Number of eggs used to calculate the mean for each female was determined using Equation (4). The solid line is hypothetical maturation rate of egg batches from 0.15 mm (major egg axis), assuming females spawn at weekly intervals; the line is derived from data in Figure 4.

at 7-10 d intervals occurs in the laboratory and could occur in the sea. In addition, the forms of the theoretical and the laboratory maturation curves were similar, with maturation of small unyolked eggs being much slower than that of larger yolked eggs.

Cessation of Spawning

An assumption of some fecundity studies of multiple spawning fishes is that all eggs to be spawned in a season are yolked at the beginning of the season and spawning ends when these yolked eggs are depleted. The preceding analysis indicated that yolking of eggs from the reservoir of small unyolked eggs is a continuous process in northern anchovy. In this section we determined whether spawning ceases because of a lack of eggs of an appropriate size for maturation. We compared egg size-frequency distributions from six females with highly atretic ovaries with those of reproductively active females. Although the ovaries of the six females contained yolked eggs, they were highly atretic and judged to be in post-spawning condition, using histological criteria presented by Hunter and Macewicz (1980).

The form of the line relating the mean major axis of eggs to successive spawning batches (dashed line, Figure 4, upper) was similar in form to those of the other groups. The eggs in the most advanced spawning batch were smaller (0.45 mm) in atretic ovaries than in those of females that had spawned 24 h before capture (0.55 mm). Hunter and Goldberg (1980) showed that the mean major axis of the most advanced eggs (excluding hydrated eggs) was 0.46 mm in females captured on the night of spawning. This value is very close to the mean for highly atretic ovaries. Thus, oocyte maturation, at least in these six females, probably continued up to the time of the last spawning, whereupon maturation ceased and the remaining oocytes became atretic. Spawning did not cease because of lack of yolked eggs; the atretic ovaries of these six females had the same distribution of egg sizes as any female ovary immediately after spawning.

ENERGY COST OF SPAWNING

We consider here three variables affecting the cost of reproduction: Number of eggs in a spawning batch, size of eggs, and the energy existing in a mature ovary. Factors not considered include the metabolic costs of egg maturation and reproductive behavior and variation in the caloric content of eggs.

Number of Eggs

The spawning batch fecundity (number of hydrated eggs) of northern anchovy varies exponentially with female weight (Equation (4)). Similar to many other fishes (Bagenal 1973), fecundity among females of the same size or weight is highly variable. Variability may be caused by variations in egg size, food availability, and number of previous spawnings within the season.

Feeding conditions may not greatly affect batch fecundity in northern anchovy. Females matured in the laboratory (groups 2 and 3) were fed a high ration and grew about four times faster than those in the sea, yet the batch fecundity was about the same as field-caught specimens, which consume a lower ration (Table 3). Although the laboratory females had not begun spawning, their batch fecundity was similar to that of fish taken in the sea between January and April. This indicates that the average batch fecundity may not change over the first months of spawning. The fact that fecundity of females captured in March-April 1979 was about the same as that for January-February 1979 (Hunter and Macewicz 1980) also supports

TABLE 3.—Comparison of the batch fecundity of northern anchovy females matured in laboratory and in the sea within two weight classes.

Weight class (g)	Locality	n	Mean weight (without ovary) (g)	Batch fecundity (total eggs)	
				Mean ± 2 SE	Estimated for mean weight from fecundity equation for sea-caught female[1]
15-19.9	Laboratory[2]	38	17.9	8,910 ± 1,210	7,420
	Sea[3]	17	16.7	6,800 ± 1,150	6,690
20-24.9	Laboratory[2]	12	22.8	11,900 ± 950	11,100
	Sea[3]	21	22.6	10,400 ± 1,540	10,900

[1]From Equation (4) (Hunter and Macewicz 1980); intercept increased by 0.0647 ($\frac{1}{2}s^2$) to adjust for bias in taking antilog (Beauchamp and Olson 1973).
[2]Batch fecundity = number eggs in most advanced mode in ovary where mean egg size ≥0.65 mm (major axis; eggs not hydrated).
[3]Batch fecundity = number of hydrated eggs in females without new postovulatory follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980).

this view. We conclude that, at least over the first few months of spawning, the mean number of eggs per spawning batch may be independent of past spawning history.

Size of Eggs

The size of spawned northern anchovy eggs varies seasonally as do those of other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Smith and Richardson (1977) demonstrated that the major axes of northern anchovy eggs spawned in February 1972 were larger than those of eggs spawned in August 1972 ($P = 0.05$). The seasonal trend in dimensions of northern anchovy eggs is illustrated in Figure 6 (upper). The dry weight of eggs (calculated from their volume (Equation (3)) varies by about 20% over the spawning season; thus, females could produce about five more spawnings/yr at the minimum egg size than at the maximum with no increase in energy demand. The seasonal trend in egg dry weight is similar to the relative larval abundance (shaded area of Figure 6), with the largest eggs produced in February to April when most of the spawning occurs and the smallest eggs late in the summer when the least spawning occurs. Several possible explanations exist for the seasonal trend in egg size. Females may produce smaller eggs as the spawning season progresses or, alternatively, large females which begin spawning earlier may produce larger eggs than small females. Regardless of the mechanism, it probably is adaptive to produce larger eggs early in the spawning season when water temperatures are cooler since the advantage falls to larger eggs as water temperature declines, because incubation periods are longer (Ware 1975).

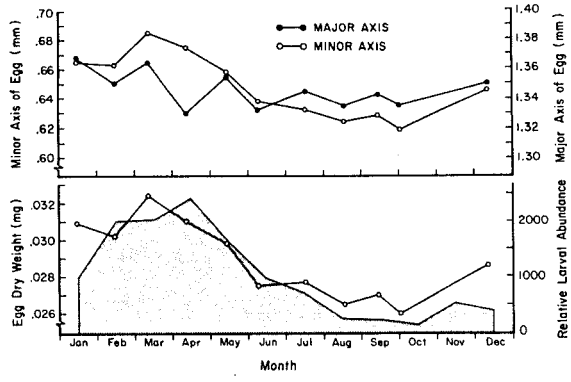

FIGURE 6.—Mean size of northern anchovy eggs taken in routine plankton tows by month. Upper, mean major and minor axes of eggs; lower, mean weight of eggs calculated from average dimensions of eggs given in upper figure using Equation (3); shaded area is the relative larval abundance for years 1953-60, from Lasker and Smith (1977).

Maturation of Eggs

Northern anchovy eggs < 0.1 mm are spherical; they become oblate spheroids between 0.1 and 0.25 mm (major axis) and thereafter retain the same proportionality between axes through hydration and spawning (Figure 7, upper). Hydration of the spawning batch of eggs (rapid uptake of fluid) begins about 12 h before spawning (Hunter and

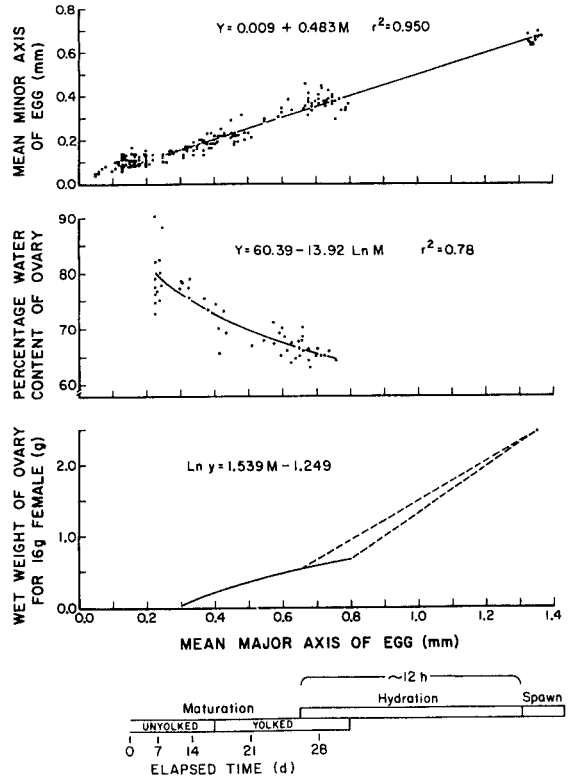

FIGURE 7.—The mean length of the minor egg axis (upper), water content of the ovary (middle), and ovary wet weight of a 16 g northern anchovy female calculated from Equation (6) (bottom), as functions of the mean major egg axis of eggs in the most advanced spawning batch (natural logarithms were used). Original data for Equation (6) (solid line, bottom) given in Hunter and Goldberg (1980); dashed lines indicate the range of egg sizes that may hydrate; and they converge at the average weight of a hydrated ovary in a 16 g female. Time scale on abscissa is based on hypothetical rate of egg maturation required for weekly spawning (see Figure 4).

Macewicz 1980), resulting in a rapid increase in ovary wet weight (Figure 7, lower) but no change in dry weight (Le Clus 1979). The mean size of eggs in a spawning batch, just before hydration, ranges from 0.6 to 0.8 mm; eggs >0.8 mm nearly always show histological signs of hydration. The average size of eggs that are hydrated would be expected to vary since the size of spawned eggs is variable.

The wet weight of the ovary (G) increases during maturation and is a function of the mean major axis of the eggs in the most mature spawning batch (M) and female wet weight without ovary (W); in northern anchovy this function is expressed as

$$\log_e G = -4.213 + 1.069 \log_e W + 0.555\, M \log_e W \quad (6)$$

(Hunter and Goldberg 1980) (Figure 7, lower). The water content of the ovary of laboratory females (group 1) declined during maturation from 80 to 65% just before hydration (Figure 7, center). The fat content did not change significantly over the maturation period; mean ovarian fat content of laboratory-matured northern anchovy was 18.6±1.2% (±2 SE of mean, n = 41) of ovary dry weight. As the fat content did not change, the caloric value of ovarian tissue can be considered to be constant at 5,710 cal/g dry weight (Table 2).

Using Equation (6), caloric values (Table 2), and water content of ovary (Figure 7), we estimate the ovary of a 16.4 g female contains 933 cal just after spawning when the mean major axis of most advanced eggs = 0.46 mm (Hunter and Goldberg 1980). The spawning batch of a 16.4 g female contains 6,500 eggs or 1,066 cal (from Equation (4)). Thus, just before spawning the ovary contains about 2,059 cal and the most advanced spawning batch constitutes about 52% of the calories in the ovary (documentation given in Table 4). Similar calculations can be made using the volume of eggs in the ovary and egg dimensions given in Figure 7 (upper) or by calculating the wet weight of the ovary at 0.46 mm egg major axis (after spawning) and at 0.81 mm egg major axis (at onset of hydration) using Equation (6). All calculations yield similar results when converted to dry weight or calories, i.e., about one-half of the calories in the ovary are lost in one spawning. We conclude that the calories invested in a mature ovary are small relative to the total reproductive cost of 20 spawnings.

ANNUAL FAT CYCLE AND SPAWNING

As the caloric equivalent of only two spawnings exists in the ovary at one time, northern anchovy must use energy stored in other tissues and food income to support reproduction. Lasker and Smith (1977) showed that the fat content of northern anchovy, like many other clupeoids (Blaxter and Holliday 1963; Shul'man 1974) varies seasonally. The fat accumulates in the body rapidly between April and July, matching the annual spring bloom of zooplankton (Lasker and Smith 1977). It usually remains high through December and then declines to a minimum between February and May (Figure 8). The decline in fat occurs during the months of maximum spawning. Thus, fat stored

TABLE 4.—Reproductive characteristics for the average female northern anchovy.

Item	Value	Explanation and data source
Weight and fecundity:		
Mean female wet weight, less ovary	16.4 g	For 1978 and 1979 (Hunter and Macewicz 1980)
Ovary wet weight after spawning[1]	.601 g	Equation (6) where M = 0.46 mm
Ovary dry weight after spawning[1]	.174 g	Percentage water in ovary from Figure 7 (center)
Number of eggs in one spawning batch	6,500 eggs	Equation (4)
Number of eggs spawned/yr	130,000 eggs	Assume 20 spawnings (Figure 2)
Dry weight one spawned egg	.0301 mg	Mean of monthly dry weight: (Figure 6) weighted by relative monthly larval abundance (Lasker and Smith 1977)
Caloric content of ovaries and spawn:		
Calories in one spawning batch	1,066 cal	Caloric value of eggs = 5,450 cal/g (Table 2)
Calories in ovary after spawning	993 cal	Caloric value of ovary = 5,710 cal/g (Table 2)
Calories in ovary just before spawning	2,059 cal	
Percentage of calories in ovary lost in one spawning batch	52%	
Daily spawning cost during peak spawning months	152 cal/d	Assume spawning interval = 7 d
Spawning related to fat stores:		
Maximum fat in body	2.009 g	Equation (1) where 41% of dry weight = fat
Minimum fat in body	.510 g	Equation (1) where 15% of dry weight = fat
Total fat stores	13,831 cal	Caloric value of fat = 9,227 cal/g (Table 2)
Fat stores in spawning batch equivalents	13 batches	

[1]Females with postovulatory follicles < 24 h old.

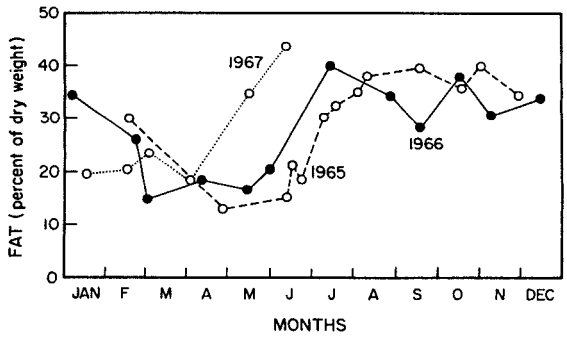

FIGURE 8.—Annual fat cycle of northern anchovy. Fat content expressed as a percentage of dry weight for various months in 1965, 1966, and 1967. Data from Lasker and Smith (1977).

from the previous spring and summer may be used the following year to support reproduction. Fat stores may not be used directly to promote egg production, which are largely protein, but rather to provide energy needed for metabolism, permitting energy from food to be used for egg maturation.

We calculated the number of spawnings that could be financed by the annual decline in fat stores, assuming that this energy or its equivalent is used for reproduction. We used the average minimum and maximum fat level for the 3 yr (Table 5) to estimate the grams of fat annually available for reproduction. Using the dry weight, fat, and wet weight relation (Equation (1)), we calculate that a 16.4 g female would store annually 13,831 cal of fat (Table 4) which is equivalent to 13 spawning batches. Thus, about two-thirds of the annual cost of egg production can be accounted for by the annual decline in fat stores.

The rate of increase in fat in the spring was similar in the 3 yr (1965-67) although the timing of the onset varied by 2-3 mo. The maximum rate occurred in the late spring or summer over a period of about 63 d (Table 5). Nearly all fat stores were accumulated over this period; on the average fat increased from 16.5 to 40.5% of the dry weight

TABLE 5.—Maximum and minimum fat content of female northern anchovy from Southern California Bight in 1965-67.[1]

	Fat content (% dry weight)				Period of maximum rate of increase in fat stores	
	Minimum		Maximum			
Year	Mo.	%	Mo.	%	Mo.	Total days
1965	Apr.	13.0	Nov.	39.8	June-Aug.	59
1966	Mar.	15.0	July	40.0	May-June	60
1967	Apr.	18.2	June	43.5	Mar.-May	69
Mean		15.4		41.1		63

[1]Data illustrated in Figure 8; from Lasker and Smith (1977).

over the 63 d. Thus, calories would accumulate in a 16.4 g fish at a rate of about 200 cal/d or the caloric equivalent of one spawning batch would be stored about every 5 d.

This analysis indicates that the annual spring bloom might regulate the reproductive potential of the northern anchovy population. This effect may have a 1-yr lag because fat accumulated in the late spring and summer would presumably be used to support reproduction the following year because most spawning occurs in February through April. On the other hand, if 20 spawnings occur, about one-third of them would have to be supported from energy gained during the current year. Thus, production of plankton might have an effect on egg production late in the spawning season, but the major effect of the spring bloom on reproduction may occur the following year.

ENERGY BUDGET FOR FEMALE GROWTH AND REPRODUCTION

In this section we calculate an annual energy budget for reproduction and growth in female northern anchovy based on relationships established in past sections and in the laboratory ration study outlined below. Food ration (R) may be partitioned into energy losses of metabolism (Q), excretion (X), digestive losses (I), reproductive costs (S), gains in growth (N) and fat stores (F) where

$$R = Q + X + I + S + N + F. \quad (7)$$

We do not estimate Q, X, or I, but rather calculate for laboratory females the gross conversion efficiency (C) where

$$C = \frac{S + N + F}{R}. \quad (8)$$

Variables N and F were calculated by subtracting weight and fat content of females determined at the beginning of the experiment from that determined at the end (Table 6); reproductive cost S was simply the increase in weight of the ovary since the fish did not spawn during the experiment; and R was calculated using Equation (5).

The coefficient C was used to estimate ration for natural populations using

$$R = \frac{S + N}{C}. \quad (9)$$

TABLE 6.—Calories gained per day and daily ration of two groups of northern anchovy fed Oregon Moist Trout Pellets.

Item	Standard length (mm)		Fat-free dry weight (without ovary) (g)		Fat in body (without ovary) (g)		Ovary dry weight (including fat) (g)	
	Beginning	End	Beginning	End	Beginning	End	Beginning	End
			Group 2					
Mean	108	120	2.38	3.27	1.17	2.66	0.14	0.38
SE of mean	.86	1.04	.09	.12	.30	.18	.02	.02
Number of fish	21	19	21	19	21	19	21	21
			Group 3					
Mean	106	122	2.16	3.30	.70	2.54	.04	.38
SE of mean	1.51	1.31	.10	.08	.03	.11	.02	.03
Number of fish	24	18	24	18	24	18	24	18

Group	Duration of experiment (d)	Daily ration[2] (cal)	Calories gained per day[1] Body (less ovary) (fat free)	Fat	Ovary (including fat)	Total
2	69	2,238	53	199	19.8	271
3	78	2,245	60	218	24.9	303
Mean	73.5	2,241	56	208	22.4	287
Percentage of ration			2.5	9.2	1.0	12.8

[1]Caloric values in Table 2.
[2]Method of calculation of ration outlined in methods.

Fat stores (F) are included in calculation of C in the laboratory work (Equation (8)) but not in the ration for natural populations (Equation (9)) because on an annual basis it is assumed to be subsumed in the annual cost of reproduction. The caloric value used for growth was set at the minimum fat content of the year (15.4% of the dry weight) using values in Table 2 and Equation (1).

Laboratory Growth Efficiency

Northern anchovy (groups 2 and 3) maintained in the laboratory grew much faster than those in the sea. The growth in length was about four times that estimated for wild northern anchovy by Spratt (1975) but was seven times faster when Spratt's data were converted to wet weight using the length-weight conversion for females of Collins (1969) (solid line, Figure 9). Thus, the average ration consumed by northern anchovy in the laboratory, 2,241 cal/d (about 124 cal/g fish wet weight per d) is probably much larger than the one consumed in the sea. On a wet weight basis, the laboratory ration (4.5% of fish wet weight/d) is deceptively low because the pelleted food had a much lower water content (35%) than natural foods (85%). A caloric equivalent ration of natural foods (copepods) would be about 16% of the wet weight/d.

Spawning did not begin during the experiment, hence the proportion of the daily ration incorporated into the ovaries (0.8%) was a function of only maturation of the ovary (Table 6). The median of the mean major axis of the eggs in the most advanced batch in the ovary increased from 0.55 to 0.63 mm in group 2 and from <0.25 to 0.63 mm for group 3. Most of the caloric gain was in fat; the percentage of the dry weight that contained fat increased from 32.6 to 44.2% in group 2 and from 24.5 to 43.2% in group 3 and accounted for about 9.2% of the daily ration. The caloric conversion efficiency for the total gain of calories in the body (including ovary and fat) was 12.8%. We calculated from data of Takahashi and Hatanaka (1960)

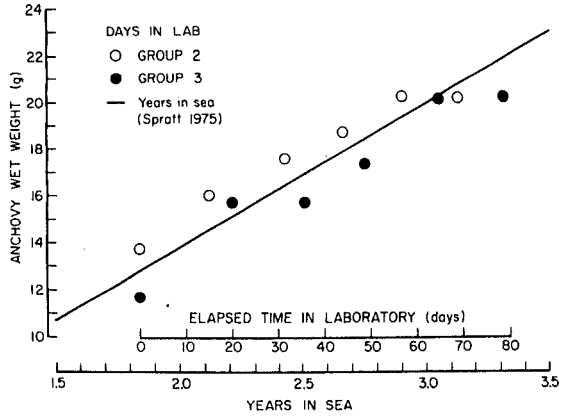

FIGURE 9.—Growth in days of two groups of northern anchovy in the laboratory (dots and circles) compared with the growth over years of northern anchovy in the sea (solid line). Growth in the laboratory is plotted using upper scale (elapsed time days), and growth in sea (solid line, from Spratt 1975; Collins 1969) is plotted on lower scale (years); and ratio between scales is about 1:7. Each point is mean weight for 8-12 fish. Laboratory fish were fed a pelleted trout ration which was the caloric equivalent in natural foods of about 16% of the fish wet weight per day.

that the Japanese anchovy, *Engraulis japonicus*, fed *Euphausia pacifica* in the laboratory, had a gross growth efficiency (in calories) of 11.9%, which is similar to our estimate of 12.8% for *E. mordax*.

Energy Budget

Growth of northern anchovy in the sea from age 1 to 2 yr is equivalent to a gain of 6.2×10^3 cal, and the energy cost of 20 spawnings for a 1-yr-old female is about 10×10^3 cal (documentation given in Table 7). Assuming that the caloric conversion efficiency for northern anchovy in the sea is the same as in the laboratory (12.8%), 1-yr-old females (mean weight 10.3 g) consume annually about 127×10^3 cal of which 8% would be used for reproduction and 5% for growth. This implies a daily rate of consumption in the sea of 348 cal/d, or, on a wet weight basis, about 4% body wet weight/d in copepods (copepods = 5,252 cal/g dry weight, Laurence (1976); water content of *Calanus* = 84.7%, Lovegrove (1966)). Sirotenko and Danilevskiy (1977) estimated from stomach content analysis that the Black Sea anchovy, *E. encrasicholus*, consumed 1.5-3.7% of their body weight/d; Mikhman and Tomanovich (1977) estimated from field captured specimens that *E. encrasicholus* consumed 1.4-3.0% of their body weight/d when they fed upon phytoplankton, 3.4% when they ate zooplankton, and 9.3% when they ate benthic animals. Our estimate of 4-5% body weight/d for females 1-3 yr old is within the range of these values.

DISCUSSION

Spawning Frequency

Northern anchovy females matured eggs in the laboratory at the rate required for weekly spawning, thus supporting the conclusions of Hunter and Goldberg (1980) and Hunter and Macewicz (1980). Our estimates of reproductive effort (egg calories/ration calories) of 8-11% (Table 7) seem reasonable, thereby supporting our estimate of 20 spawnings/female per year. Our calculations indicate that this effort could be sustained by a daily ration of natural foods of 4-5% of the fish wet weight/d which is similar to the natural ration of *E. encrasicholus* (Sirotenko and Danilevskiy 1977; Mikhman and Tomanovich 1977). Few estimates of reproductive effort exist for fishes. Lasker (1970) estimated that the cost of reproduction in Pacific sardine, *Sardinops sagax*, was about 1% of the total annual caloric requirement. He assumed the caloric equivalent of the ovary is spawned per year, which now seems an underestimate. Constantz (1976) estimated that reproductive effort ranged from 4 to 15% in two populations of *Poeciliopsis occidentalis*. Hirshfield (1977) found in laboratory studies that reproductive effort was related in a complex fashion to temperature and ration in medaka, *Oryzias latipes*; he estimated reproductive effort ranged from 10 to 18% in two natural Japanese populations. We conclude that 20 spawnings/yr is a reasonable estimate of the number of spawnings produced by females in the northern anchovy central subpopulation. The fact that two-thirds of the cost could be supported by the average annual decline in fat stores supports this conclusion.

An implication of this study is that egg maturation and vitellogenesis are continuous during peak spawning months. Evidence for this includes: the large fraction of the females in the population spawning per day during peak spawning months (10-16%); the presence of the caloric equivalent of only one or two spawning batches in the ovary at any time; the inverse relation between the abundance of egg sizes in the ovary and oocyte maturation rate; and the continuation of egg maturation until the last batch of eggs is spawned. Although maturation and vitellogenesis probably continue for extended periods, the rates probably vary. The seasonal decline in the fraction of females in the

TABLE 7.—Annual energy budget for female northern anchovy.

Age (yr) Beginning-end	SL[1] (mm) Beginning-end	Wet weight[2] (g) Beginning-end	Annual energy budget (thousands of calories)			Percentage of ration	
			Growth[3]	Reproduction[4]	Ration[5]	Growth	Reproduction
1-2	93-112	7.33-13.25	6.24	10.00	127	5	8
2-3	112-126	13.25-19.33	6.38	21.0	214	3	10
3-4	126-136	19.33-24.69	5.60	34.3	312	2	11

[1]From Spratt (1975).
[2]From Equations (1) and (2) where 15.4% of dry weight = fat.
[3]Gain in calories assuming 15.4% of dry weight = fat; caloric values in Table 2.
[4]Caloric content of 20 spawning batches; batch size calculated for mean female wet weight over the year (method illustrated in Table 4).
[5]Reproduction calories + growth calories/0.128, where 0.128 is growth conversion efficiency determined in laboratory (Table 6).

population spawning per day indicates that either the interval between spawnings in individual females increases in the latter part of the spawning season, or that an increasing number of females cease spawning as the season progresses, or a combination of both events. Rates of egg maturation and vitellogenesis probably also vary within a single maturation-spawning cycle. The caloric content of a northern anchovy ovary about doubles over the interval between spawnings (7-10 d in peak spawning months), indicating a rapid rate of vitellogenesis after spawning. In *Brachydanio rerio*, which spawns at 5-d intervals, a marked increase in gonadotropic activity occurs in the pituitary immediately after spawning (Lambert and van Oordt 1974), followed 1-2 d later by histological signs of an increase in lipoprotein production in the liver correlated with an increase in vitellogenesis (Peute et al. 1978). Similar processes may occur in northern anchovy, causing cyclic changes in the rates of vitellogenesis and egg maturation within the interval between spawnings.

Our estimate of 20 spawnings/yr is much higher than the number of spawnings estimated for many other pelagic spawning clupeoid fishes or for pelagic spawners in general. Multiple spawning fishes such as pilchards, sardines, anchovies, jack mackerels, and mackerels are often believed to produce one to three and possibly more spawning batches per year. These conclusions are based on the fact that frequently two modes of yolked eggs and sometimes three (in females with hydrated eggs) are observed in frequency distributions of ovarian egg sizes. Eggs are distributed in the same way in the northern anchovy (MacGregor 1968; Hunter and Goldberg 1980), but as present studies indicate, estimates of one to three spawnings would be in error by a factor of about 10. Thus, comparisons of annual fecundity among pelagic spawning clupeoids are meaningless at present, and spawning biomass estimated from egg and larval surveys may be in error because the total fecundity is inaccurate. Because of this it is essential that spawning frequency be estimated for additional species.

The best approach, at present, is the histological technique of Hunter and Goldberg (1980), but counts of the number of females with hydrated eggs could be used if histological techniques are impractical. Females with hydrated eggs are often rare in collections of clupeoid females taken during the spawning season (Higham and Nicholson 1964; Leary et al. 1975). Females with hydrated eggs may be available for sampling for only a short period of each day because hydration is rapid and spawning soon follows hydration. In northern anchovy, hydration is completed in about 12 h, but the earliest stage may not be evident without histological examination. In tropical species the time available for sampling females with hydrated eggs may be even less because of elevated temperature. The daily pattern of hydration and spawning must be known to use hydrated eggs as a measure of spawning frequency. It may also require sampling of fish in the day, because many pelagic spawners such as the northern anchovy begin spawning at sunset (Blaxter and Holliday 1963; Leary et al. 1975; Hunter and Macewicz 1980).

Variation in Egg Production and Reproductive Effort

Annual egg production and/or reproductive effort in northern anchovy populations can be modulated by changes in batch fecundity, annual number of spawnings, female size at first maturity, egg size, and egg cannibalism. Some evidence exists for each of these mechanisms in northern anchovy populations; we consider the evidence below.

Batch fecundity was relatively constant over 1978-79 (Hunter and Macewicz 1980) and was similar to that of laboratory specimens fed a large food ration. On the other hand, MacGregor (1968) estimated a somewhat higher fecundity for the central stock in the 1950's than Hunter and Macewicz (1980) did for the 1970's, and Laroche and Richardson (1981) found that batch fecundity of the northern subpopulation (Oregon coast) was much higher than all estimates for the central stock. Batch fecundity certainly differs between central and northern subpopulations, and it seems possible that it may have varied within the central stock over the last decades. Nevertheless, batch fecundity within a subpopulation may be a relatively more stable reproductive characteristic than other reproductive traits.

Weight at first maturity and age structure of the spawning population have a major effect on egg production, since batch size in northern anchovy increases exponentially with weight. Clark and Phillips (1952) concluded for females taken in 1946-52 from the central subpopulation that 50% of northern anchovy reach maturity at 130 mm SL

whereas Hunter and Macewicz (1980) estimated for 1979 that 50% of females of 96 mm SL were mature. Laroche and Richardson (1981) reported that only 31% of females 85-100 mm SL from the northern stock were mature. Thus, size at sexual maturity varies between subpopulations and may have varied within the central subpopulation over the last decade.

The relatively short 2-mo spawning season of the northern subpopulation of northern anchovy (perhaps 4 to 8 spawnings, Hunter and Macewicz 1980) compared with the central subpopulation (20 spawnings) is evidence of the great plasticity in the annual number of spawnings. Plasticity in the number of spawnings of the central stock is also indicated by the dynamics of the central population over the last decades. Smith (1972) pointed out that the decline of the Pacific sardine population was accompanied by an increase in the duration of the northern anchovy spawning period. Before the Pacific sardine decline, most northern anchovy spawning occurred in the winter quarter, whereas now larval production in both quarters is about equal. This increase in the duration of the peak period of spawning indicates that the annual number of spawning batches produced by northern anchovy has changed significantly since the demise of the Pacific sardine population. Food made available by the collapse of the Pacific sardine population may have been used by the northern anchovy population to increase the number of spawning batches produced annually. The fact that these additional spawnings occurred during the period Pacific sardine normally spawned may have had an important effect on the Pacific sardine population.

The annual seasonal decline in egg size in northern anchovy population (central stock) resembles that reported for other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Production of smaller eggs late in the season may be an energy-sparing mechanism whereby fecundity is maintained constant but at a lower reproductive effort. This could represent a 20% savings in reproductive costs in northern anchovy. Bagenal (1973) concluded in his review of the literature that it seems likely a negative correlation exists between fecundity and egg size. Several other mechanisms are possible; egg size may increase with female age (Hirshfield 1977), and the seasonal change could be caused by seasonal changes in the age structure of the spawners. In this case smaller eggs may compensate for the energy cost of faster growth in young fish. Alternatively, egg size may decline in females as ration increases during the spring and summer. Bagenal (1969) found that higher ration in brown trout resulted in more and smaller eggs. On the other hand, Hislop et al. (1978) found that the dry weight of eggs produced by haddock in the laboratory declined with successive spawnings and that the dry weight of eggs tended to be lower in females fed a lower ration. In northern anchovy, there may be a change in the partitioning of energy between growth and reproduction during late spring and summer when the potential for growth is higher, and this could result in the production of smaller eggs. As egg size alters the survival potential of the larva (Blaxter and Hempel 1963), any of these mechanisms could have important consequences because it could alter the relative contribution to recruitment of spawn produced in the latter part of the spawning season.

Egg cannibalism may also be an important factor regulating the effective egg production, as intensity of cannibalism could change with population size. Hunter and Kimbrell (1981) concluded that ingestion of eggs by northern anchovy could account for 17% of the daily egg production during peak spawning months.

This discussion indicates that egg production and reproductive effort of northern anchovy populations probably changes in a complex manner in relation to food, growth, temperature, population size, and age structure. All the reproductive parameters we have discussed may vary to some degree over years, between subpopulations, or within a season.

Studies of the reproductive energetics of northern anchovy populations will eventually require consideration of males as well as females. We know little about males at present. Our laboratory data indicated that males consume slightly less food than females, but no difference existed when consumption was expressed on a unit weight basis. Growth curves for male and female northern anchovy (Collins 1969) indicate that females are slightly longer than males of the same age, but the difference is small (about a 2% difference in length) and probably not statistically significant. Other than this small difference in size, no obvious sexual dimorphic characters exist. Schools have highly biased sex ratios (Klingbeil 1978), and males predominate in actively spawning schools (Hunter and Goldberg 1980). This suggests that

males may remain reproductively active for longer periods within the spawning season and may not have as well defined spawning cycles as do females. These differences are small relative to the overall great similarity between the sexes.

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DEVELOPMENT OF LARVAE AND JUVENILES OF THE ROCKFISHES *SEBASTES ENTOMELAS* AND *S. ZACENTRUS* (FAMILY SCORPAENIDAE) AND OCCURRENCE OFF OREGON, WITH NOTES ON HEAD SPINES OF *S. MYSTINUS*, *S. FLAVIDUS*, AND *S. MELANOPS*[1]

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ABSTRACT

Developmental series of larvae and juveniles of two species of northeast Pacific rockfishes (Scorpaenidae: *Sebastes*) are described and illustrated: *S. entomelas* (9.9-74.5 mm standard length) and *S. zacentrus* (7.4-74.8 mm standard length). Descriptions include literature review, identification criteria, distinguishing features, general development, morphology, fin development, spination, scale formation, and pigmentation.

Ontogeny of *S. entomelas* is very similar to that of *S. flavidus* and *S. melanops* among species for which development is known. All have moderately slender bodies and moderately developed head spines. Pigment patterns develop similarly but pigmentation is less intense in *S. entomelas*. Larval and juvenile *S. entomelas* within the size range described are distinguished by presence of preocular and supraocular spines, pectoral fin rays usually 18, dorsal fin rays usually ≤8, lateral line pores 52-56, and lack of melanophores at the articulation of dorsal and anal fin rays. Ontogeny of *S. zacentrus* is rather distinctive among species for which development is known. Larvae and juveniles are relatively deep bodied with large head spines. They are distinguished by presence of preocular and absence of supraocular spines, pectoral fin rays usually 17, dorsal fin rays usually 14, anal fin rays usually 7, lateral line pores 38-48, gill rakers 32-37, and relative lack of pigment.

Young of *S. entomelas* were taken March-July and *S. zacentrus* August-December off Oregon. Larvae of *S. zacentrus* seemed to have a more restricted offshore distribution than reported for most other species, possibly a function of seasonal wind and current regimes.

Additional new information concerning variation in supraocular spine patterns is presented as supplemental data to aid in identification and separation of four similar species, *S. entomelas*, *S. flavidus*, *S. melanops*, and *S. mystinus*.

The rockfish, *Sebastes* spp., resources of the northeast Pacific Ocean are being subjected to increasing fishing pressure. In 1978, trawl landings of rockfishes (all species) by the United States and Canada were 26,000 metric tons (t) or 38% of total Pacific landings (Pacific Marine Fisheries Commission 1964-78). This represents a sizable increase in the catch of "other rockfish" from previous years, e.g., 20,100 t in 1978 compared with 15,700 t in 1977 and 9,900 t in 1976 (Pacific Marine Fisheries Commission 1964-78). Since many rockfish species are long lived, living over 20 yr (Phillips 1964; Westrheim and Harling 1975), overfishing could have serious consequences. Rational utilization of these important resources requires an understanding of the life history and biology of each species involved. Yet, such information is still lacking for most of the rockfishes.

This paper provides some of the first information on the early life history of *S. entomelas*, widow rockfish, and *S. zacentrus*, sharpchin rockfish. *Sebastes entomelas* was one of five principal species in Oregon bottom trawl landings of "other rockfish," composing 13% of the catch during the years 1963-71, although annual catches fluctuated from 168 to 1,074 t (Niska 1976). Introduction of midwater trawl fishing for rockfish has recently focused attention on *S. entomelas* since large catches have been landed, e.g., during a 4-mo period in 1979 >90% of the 909 t of rockfish landed in Oregon were *S. entomelas* (Barss[3]). *Sebastes*

[1]From a final report for NOAA-NMFS Contract No. 79-ABC-00087 submitted to Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, on 31 July 1979.

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[3]William Barss, Fishery Biologist, Oregon Department of Fish and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. July 1979.

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zacentrus was landed in Oregon from 1963 to 1971 but never in large quantities (Niska 1976), possibly due to its reported preference for a rough bottom (Gunderson[4]).

Development of larvae and juveniles of *S. entomelas* and *S. zacentrus* is described and compared with other species of *Sebastes* for which young stages are known. Occurrence of young off Oregon is discussed. Additional new information is presented on head spine patterns and variability among the group of four similar species, *S. entomelas*, *S. flavidus*, *S. melanops*, and *S. mystinus*, which cooccur off Oregon. This information will aid in identification and separation of these species, particularly of specimens with variant head spine patterns.

METHODS

Specimens described in this paper came from collections in the School of Oceanography, Oregon State University. Most collections were obtained with 70 cm bongo nets, neuston nets, meter nets, purse seines, Isaacs-Kidd midwater trawls, beam trawls, otter trawls, and commercial midwater trawls off the Oregon coast since 1961. Samples were taken during all months of the year and along the entire Oregon coast but were concentrated along an east-west transect off Newport, Oreg. (lat. 44°39.1′ N). Benthic juveniles of *S. entomelas* were taken from adjacent California waters (lat. 40°12.2′ N, long. 124°23.4′ W). All specimens were preserved in 5 or 10% Formalin[5] and transferred to 40% isopropyl alcohol.

Our approach to identification, methods of making counts and measurements, and terminology for development and spination follow Richardson and Laroche (1979) and Laroche and Richardson (1980). Body parts measured include:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Snout to anus length = distance along body midline from snout tip to vertical through posterior margin of hindgut at anus.

Head length (HL) = snout tip to cleithrum until no longer visible, then to posteriormost margin of opercle.

Snout length = snout tip to anterior margin of orbit of left eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest diameter of left orbit.

Interorbital distance = distance between dorsal margins of orbits.

Body depth at pectoral fin base = vertical distance from dorsal to ventral body margin at base of pectoral fin.

Body depth at anus = vertical distance from dorsal to ventral body margin immediately posterior to anus.

Caudal peduncle depth = shortest vertical distance between dorsal and ventral margins of caudal peduncle.

Caudal peduncle length = horizontal distance from base of posteriormost dorsal ray to posterior margin of hypural elements.

Pectoral fin length = distance from base to tip of longest ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic spine length = distance from base to tip of pelvic spine.

Pelvic fin length = distance from base to tip of longest ray.

Snout to origin of pelvic fin = distance along body midline to vertical through insertion of pelvic fin.

Parietal spine length = distance along posterior margin of parietal spine from insertion to tip.

Nuchal spine length = distance along posterior margin of nuchal spine from insertion to tip.

Preopercular spine length (third spine; posterior series) = distance from tip to basal insertion if visible, or to a line connecting the points of deepest indentation between preopercular spines 2 and 3 and spines 3 and 4 (posterior series).

Longest dorsal fin spine = distance from base to tip.

Longest dorsal fin ray = distance from base to tip.

Longest anal fin spine = distance from base to tip.

All body lengths given refer to standard length unless noted otherwise. When the two posteriormost dorsal and anal fin rays arise from the same pterygiophore, they are counted as one.

[4]Gunderson, D. 1976. Proceedings of the 1st rockfish survey workshop. Processed rep., 14 p. Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

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

SEBASTES ENTOMELAS (JORDAN AND GILBERT)

Literature (Figures 1-3).—The pigment pattern of preextrusion *S. entomelas* larvae was described by Harling et al.,[6] including a figure, and Westrheim (1975). Preextrusion larvae, mean 4.8, 5.0 mm TL, have a row of usually <16 melanophores along the ventral body midline which stops short of the anus by at least four myomeres. The gut is pigmented in the vicinity of the anus. Pigment is absent from the dorsum, head, and hypural region. In reared larvae, the number of ventral midline melanophores increases to >16 (Westrheim 1975).

Identification (Tables 1-3; Appendix Table 1).—Fifty-three specimens of *S. entomelas* (9.9-74.5 mm) were selected for the development series from 444 larval and juvenile specimens identified. Juveniles were identified using the following combination of characters observed in juvenile and adult specimens examined:

Gill rakers = 34-39
Lateral line pores = 52-56

[6]Harling, W. R., M. S. Smith, and N. A. Webb. 1971. Preliminary report on maturity, spawning season, and larval identification of rockfishes (*Sebastodes*) collected during 1970. Fish. Res. Board Can., Manuscr. Rep. Ser. 1137, 26 p.

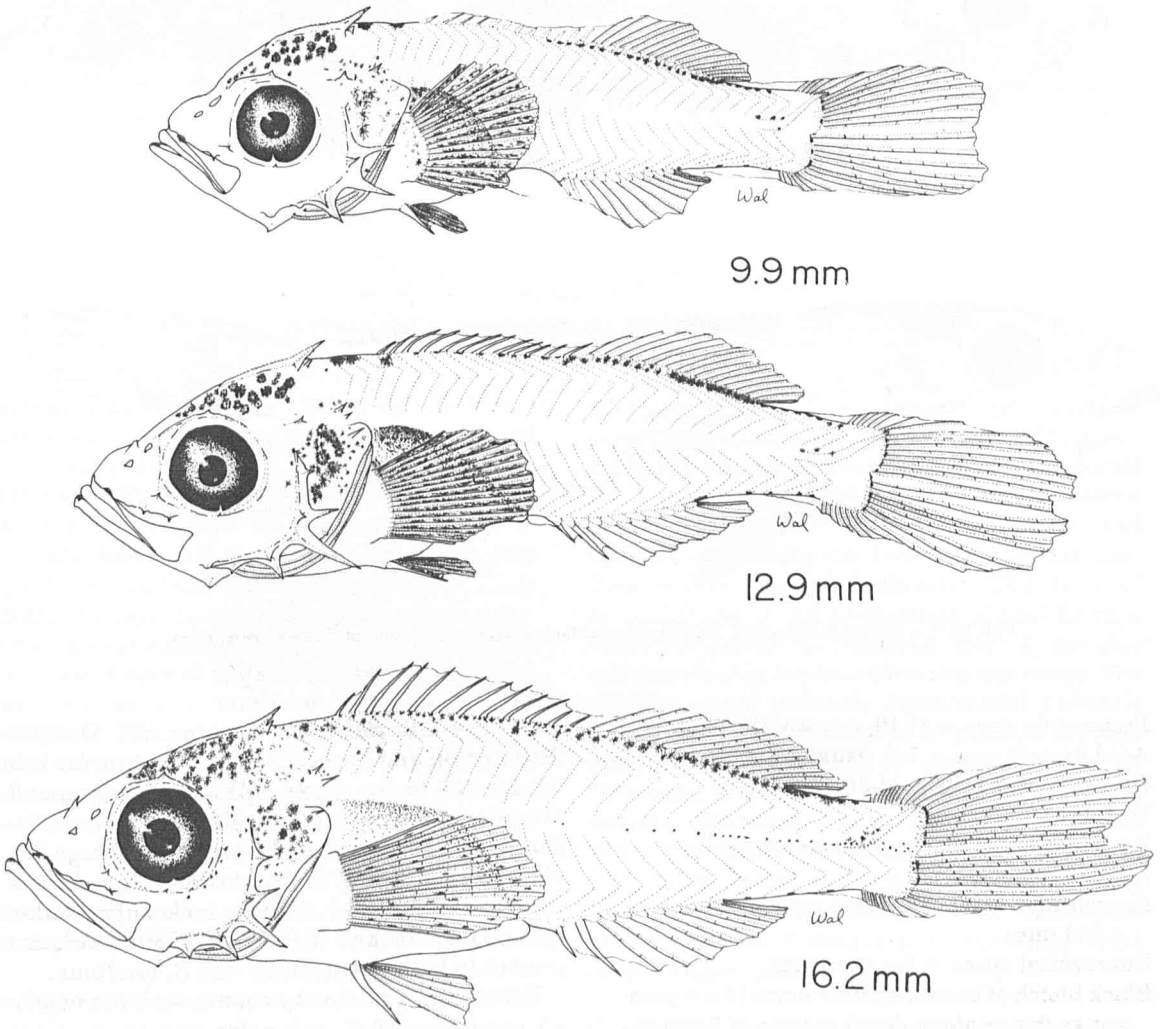

FIGURE 1.—Pelagic larvae of *Sebastes entomelas*.

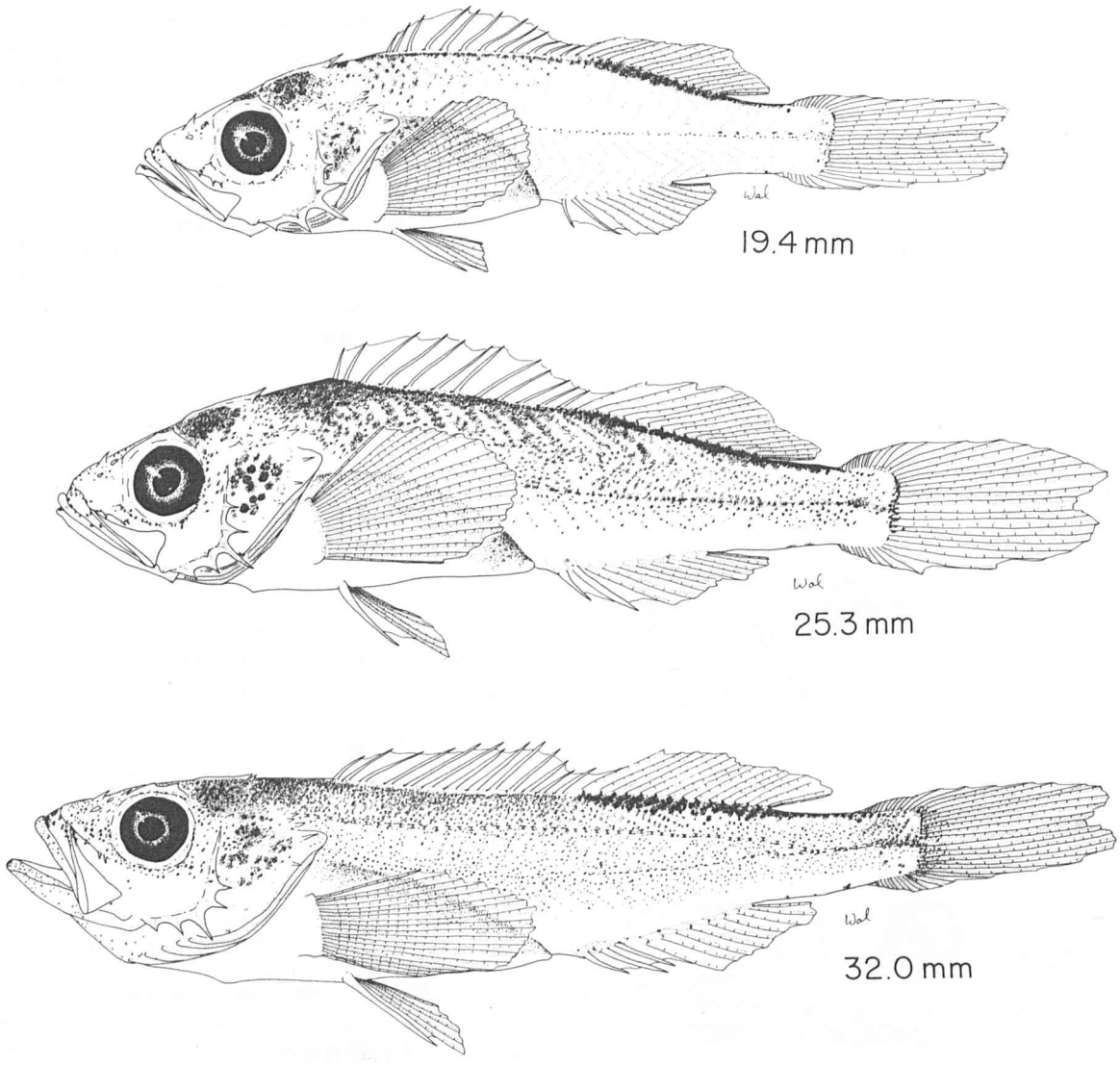

FIGURE 2.—Pelagic larvae (19.4, 25.3 mm) and pelagic juvenile (32.0 mm) of *Sebastes entomelas*.

Pectoral fin rays = 17-19, usually 18
Anal fin soft rays = 7-9, usually 8
Dorsal fin soft rays = 14-16, usually 15
Vertebrae = 26
Preocular spine = present (specimens <343 mm)
Supraocular spine = present (specimens <343 mm)
Interorbital space = flat to convex
Black blotch at base of spinous dorsal fin = present as fringe along distal margin of fin membrane.

Of the 36 *Sebastes* species off Oregon (Richardson and Laroche 1979), *S. entomelas* has the best fit to the above characters. Larvae and juveniles of *S. entomelas* are similar to those of *S. flavidus*, *S. melanops*, and *S. mystinus*. Large larvae and juveniles of *S. flavidus* and *S. melanops* lack preocular and usually lack supraocular spines (Laroche and Richardson 1980) which are present in both *S. entomelas* and *S. mystinus*.

Dorsal and anal fin ray counts separate nearly all specimens of *S. entomelas* and *S. mystinus* based on count frequency statistics given by

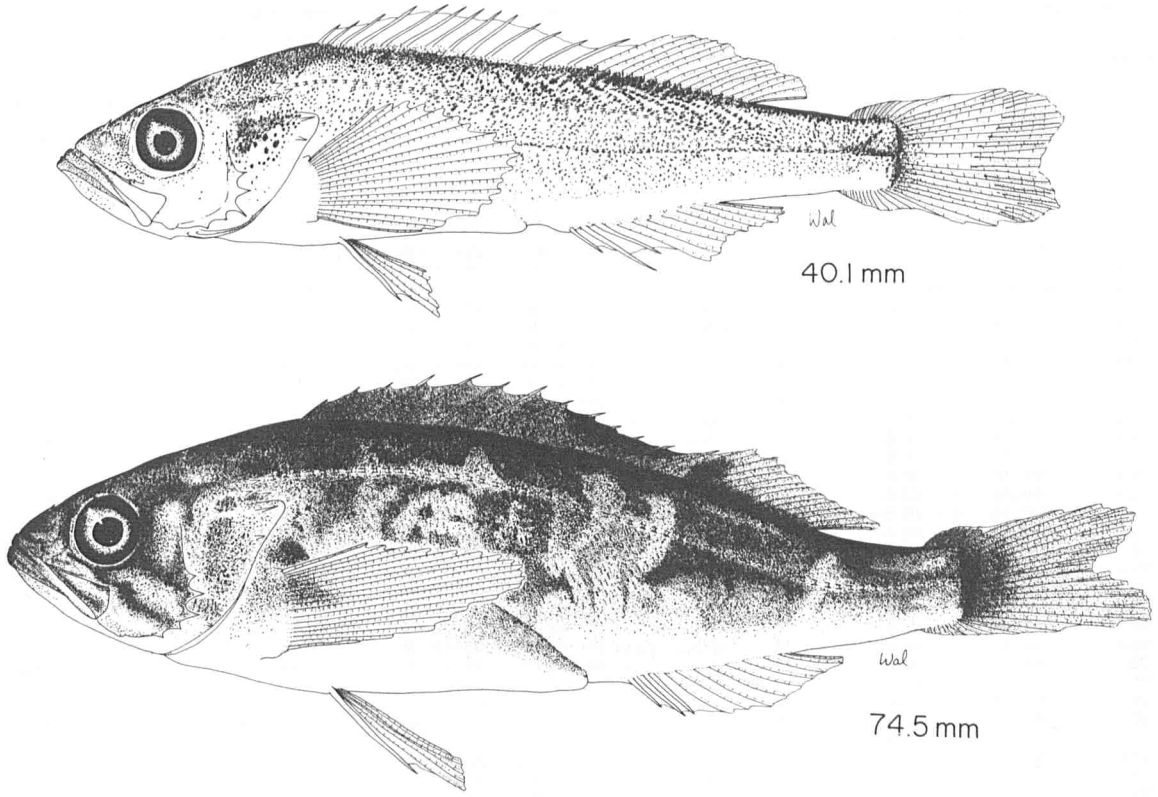

FIGURE 3.—Pelagic juvenile (40.1 mm) and benthic juvenile (74.5 mm) of *Sebastes entomelas*.

Laroche and Richardson (1980). Of 79 *S. entomelas* examined 94% had dorsal fin rays ≤15 and 96% had anal rays ≤8. Of 62 *S. mystinus* examined 92% had dorsal fin rays ≥16 and 90% had ≥ 9 anal fin rays. Only one specimen of *S. entomelas* had >15 dorsal fin rays and >8 anal fin rays. No *S. mystinus* had <16 dorsal fin rays and <9 anal fin rays. In specimens with outlyer dorsal or anal fin ray counts, the numbers of lateral line pores and diagonal scale rows below the lateral line resolved any questions in all cases (see Laroche and Richardson 1980, appendix table 1). To insure that no *S. mystinus* were accidentally included in the developmental series of *S. entomelas*, specimens with either >15 dorsal fin rays or >8 anal fin rays were intentionally excluded.

Pigment pattern and body morphology were also useful in linking smaller specimens to the developmental series.

Distinguishing Features.—Characters useful to distinguish *S. entomelas* larvae (9.9-18 mm) from those of other *Sebastes* species are fin element counts, gill raker counts, moderate pigmentation on pectoral and pelvic fins, presence of pigment along the dorsal body surface beneath the dorsal fin, internal and/or external melanophores above the notochord near the point of flexion, and melanophores along the dorsal and ventral margins of the caudal peduncle. The lack of melanophores at the articulation of anal fin rays helps distinguish *S. entomelas* from *S. flavidus* and *S. melanops* larvae within this size range. The smaller caudal peduncle depth/caudal peduncle length ratio and presence of 18 pectoral fin rays also help to distinguish *S. entomelas* from *S. melanops*. For larvae and juveniles >18 mm, meristic characters, presence of preocular (specimens >22 mm) and supraocular (specimens >18 mm) spines, flat to convex interorbital space, body and fin pigmentation, and body morphometry together serve to distinguish *S. entomelas* from other Oregon species.

General Development.—Notochord flexion is completed by ≈14 mm in *S. entomelas*. Transformation

TABLE 1.—Meristics from larvae and juveniles of *Sebastes entomelas* based on unstained specimens. Counts of left and right pelvic fin rays (I,5; I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7,7) were constant throughout the series. Specimens above dashed line are undergoing notochord flexion.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
9.9	IV+I[1],15	II[1],8	18	18	21+ 8=29	—	—	—	—	—
10.0	[2]	[2]	18	18	20+ 7=27	20+ 6=26	—	—	—	—
10.9	XIII[1],14	III[1],7	18	18	22+ 9=31	22+ 8=30	—	—	—	—
11.0	XIII[1],15	III[1],8	18	18	22+ 8=30	21+ 8=29	—	—	—	—
11.9	XIII[1],15	III[1],8	18	18	22+ 8=30	23+ 8=31	—	—	—	—
12.0	XIII[1],14	III[1],8	18	18	22+ 7=29	22+ 8=30	—	—	—	—
12.9	XIII[1],15	III[1],8	18	18	23+ 8=31	22+ 8=30	—	—	—	—
13.7	XIII[1],15	III[1],8	18	18	24+ 8=32	24+ 8=32	—	—	—	—
14.0	XIII[1],15	III[1],8	18	18	23+ 8=31	23+ 8=31	—	—	—	—
14.9	XIII[1],15	III[1],8	18	18	25+ 9=34	24+ 9=33	—	—	—	—
15.2	XIII[1],15	III[1],8	18	18	24+ 9=33	23+ 9=32	—	—	—	—
16.2	XIII[1],15	III[1],8	18	18	24+10=34	23+ 9=32	—	—	—	—
16.8	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
17.2	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
18.4	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
18.5	XIII[1],15	III[1],8	18	18	24+ 9=33	25+ 9=34	—	—	—	—
19.4	XIII[1],15	III[1],8	18	18	24+10=34	24+10=34	—	—	—	—
20.4	XIII[1],15	III[1],8	18	18	26+10=36	25+10=35	—	—	—	—
20.8	XIII[1],14	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
21.0	XIII[1],15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]21.7	XIII[1],15	III[1],8	18	18	25+ 9=34	24+ 9=33	—	—	—	—
[3]22.3	XIII[1],15	III[1],8	18	18	26+ 9=35	25+ 9=34	—	—	—	—
[3]22.9	XIII[1],15	III[1],8	18	18	25+10=35	26+10=36	—	—	—	—
[3]23.9	XIII[1],15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]24.5	XIII[1],15	III[1],8	18	18	26+10=36	26+ 9=35	—	—	—	—
[3]24.5	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
[3]25.3	XIII[1],15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]25.9	XIII[1],15	III[1],8	18	18	24+ 9=33	25+ 9=34	—	—	—	—
[3]26.5	XIII[1],15	III[1],8	18	18	27+10=37	26+ 9=35	—	—	—	—
[3]26.7	XIII[1],15	III[1],8	18	18	25+10=35	25+ 9=34	—	—	—	—
[3]27.2	XIII,15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]27.9	XIII,15	III[1],8	18	18	26+10=36	25+10=35	—	—	—	—
[3]28.5	XIII,15	III[1],8	18	18	26+10=36	25+10=35	—	—	—	—
[3]29.1	XIII,15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]29.7	XIII,15	III[1],8	18	18	25+10=35	26+10=36	—	—	—	—
[3]30.6	XIII,15	III[1],8	18	18	26+ 9=35	25+10=35	—	—	—	—
[4]30.8	XIII,15	III,8	18	18	26+11=37	26+11=37	—	54	—	—
[4]31.6	XIII,15	III,8	18	18	27+10=37	26+10=36	—	53	—	—
[4]32.0	XIII,15	III,8	18	18	26+10=36	26+10=36	—	52	—	—
[4]33.4	XIII,14	III,8	18	18	25+10=35	25+10=35	—	51	—	—
[4]35.7	XIII,15	III,8	18	18	26+10=36	26+10=36	—	53	—	—
[4]36.8	XIII,15	III,8	18	17	24+10=34	26+10=36	—	—	—	—
[4]40.1	XIII,15	III,8	18	18	26+10=36	26+11=37	—	52	—	—
[5]45.0	XIII,14	III,8	18	18	24+11=35	24+11=35	56	54	—	—
[5]47.7	XIII,14	III,7	18	18	27+11=38	28+11=39	52	54	—	—
[5]55.5	XIII,14	III,8	18	18	26+11=37	27+11=38	55	54	—	—
[5]55.7	XIII,15	III,8	18	18	26+11=37	26+10=36	56	55	—	—
[5]64.4	XIII,15	III,8	18	18	26+10=36	26+10=36	53	52	—	—
[5]65.0	XIII,15	III,8	18	18	27+11=38	27+11=38	53	53	64	63
[5]66.1	XIII,15	III,8	18	18	26+11=37	27+10=37	54	56	61	65
[5]71.2	XIII,15	III,8	18	18	26+11=37	26+11=37	54	54	62	66
[5]74.1	XIII,15	III,8	18	18	26+10=36	26+11=37	54	52	66	62
[5]74.5	XIII,15	III,8	19	19	27+11=38	27+10=37	53	56	64	68

[1]Posteriormost dorsal or anal spine appears as a soft ray.
[2]Forming.
[3]Transforming.
[4]Pelagic juvenile.
[5]Benthic juvenile.

from postflexion larvae to pelagic juveniles occurs between ≈22 and 31 mm as indicated by structural change of the dorsal and anal fin "prespines" to sharp, hard spines. Melanistic pigmentation gradually increases over the body through the larval and transformation periods and does not change markedly during transformation. Transition from pelagic to benthic habitat, based on all specimens examined, probably occurs chiefly between 55 and 75 mm. The largest pelagic juvenile was 40.1 mm, and the smallest juvenile taken in a beam trawl was 42 mm long.

Morphology (Tables 2, 3).—Various body parts were measured on 53 selected specimens of *S. entomelas* (9.9-74.5 mm). Relative growth trends are summarized in Table 2.

Perhaps the most distinctive morphometric aspect of larval and small juvenile *S. entomelas* is the relatively slender body. Body depth decreases

TABLE 2.—Body proportions of larvae and juveniles of *Sebastes entomelas* and *S. zacentrus*. Values given are percent of standard length (SL) and head length (HL) including mean, standard deviation, and range in parentheses. Number of specimens measured may be derived from number of measurements listed by stage, indicated in footnotes, in Tables 3 and 6.

Item	*Sebastes entomelas*	*Sebastes zacentrus*
Body depth at pectoral fin base/SL:		
Flexion	29.0±0.87(27.9-30.0)	35.2±1.36(33.8-36.5)
Postflexion	27.5±1.56(24.5-29.9)	34.4±1.07(33.1-35.9)
Transforming	25.2±0.80(23.9-26.3)	32.5±1.49(30.4-35.0)
Pelagic juvenile	23.9±0.48(23.1-24.4)	30.0±1.02(27.7-32.0)
Benthic juvenile	27.8±2.44(24.1-31.3)	32.0±1.08(31.1-33.8)
Body depth at anus/SL:		
Flexion	22.3±1.01(20.9-23.9)	24.7±1.53(23.0-25.9)
Postflexion	22.4±1.48(20.2-24.8)	25.8±1.33(23.3-27.4)
Transforming	20.6±0.56(19.3-21.8)	26.1±1.07(25.0-28.4)
Pelagic juvenile	19.7±0.55(18.6-20.2)	24.3±0.82(22.8-25.8)
Benthic juvenile	23.1±1.31(21.1-24.6)	25.8±1.04(24.3-26.7)
Snout to anus length/SL:		
Flexion	56.5±2.09(53.0-58.8)	52.5±1.78(50.6-54.1)
Postflexion	58.5±2.10(54.8-61.2)	57.0±2.34(53.8-62.4)
Transforming	59.4±1.72(55.3-62.3)	60.4±1.84(57.0-62.4)
Pelagic juvenile	61.0±1.24(59.8-62.7)	60.9±1.76(57.4-64.1)
Benthic juvenile	61.5±2.18(59.4-65.1)	58.7±1.62(56.9-61.3)
Snout to pelvic fin origin/SL:		
Flexion	39.4±1.55(37.0-41.2)	38.7±0.61(38.0-39.2)
Postflexion	37.7±2.12(35.1-40.9)	40.6±1.48(37.8-42.4)
Transforming	36.8±1.49(33.3-39.5)	40.8±1.85(38.1-44.8)
Pelagic juvenile	36.3±3.19(33.2-41.9)	39.4±1.43(36.2-42.3)
Benthic juvenile	37.0±1.83(34.8-40.3)	40.9±1.01(40.2-42.5)
Head length/SL:		
Flexion	39.7±2.09(37.2-43.1)	41.9±2.75(39.2-44.7)
Postflexion	36.3±1.82(34.1-39.4)	42.6±2.08(40.2-45.6)
Transforming	35.0±1.75(32.4-38.4)	40.4±1.53(37.6-43.1)
Pelagic juvenile	32.5±1.40(31.2-35.0)	37.5±1.70(34.4-40.4)
Benthic juvenile	32.2±1.90(29.5-35.6)	36.9±0.98(35.8-37.7)
Eye diameter/HL:		
Flexion	31.2±1.90(28.0-33.3)	33.1±2.08(31.6-35.5)
Postflexion	30.1±1.38(28.4-32.7)	32.0±2.13(28.3-34.8)
Transforming	26.8±1.28(25.0-29.1)	29.4±1.74(26.2-32.4)
Pelagic juvenile	26.7±0.92(25.2-28.2)	29.1±1.40(26.7-32.6)
Benthic juvenile	25.8±0.92(24.3-27.3)	31.1±1.96(29.1-33.2)
Upper jaw length/HL:		
Flexion	35.3±4.30(31.2-41.0)	45.9±1.27(45.2-47.4)
Postflexion	41.5±2.61(38.4-45.9)	43.7±2.31(38.6-45.7)
Transforming	39.5±1.90(36.5-43.1)	41.3±2.68(36.4-46.3)
Pelagic juvenile	42.1±1.59(40.2-43.8)	41.0±2.54(35.6-45.3)
Benthic juvenile	39.2±2.57(35.7-43.2)	42.2±2.48(39.7-46.1)
Snout length/HL:		
Flexion	28.3±3.27(22.6-32.0)	26.2±3.27(23.2-29.7)
Postflexion	27.4±1.79(23.9-29.6)	27.9±1.23(26.2-29.6)
Transforming	27.7±1.77(24.4-31.7)	26.4±1.72(24.2-28.8)
Pelagic juvenile	27.2±1.53(26.1-29.8)	26.2±2.12(22.0-31.4)
Benthic juvenile	25.4±2.68(21.1-28.2)	21.8±3.13(18.4-25.2)
Interorbital distance/HL:		
Flexion	30.9±2.04(28.0-33.3)	29.4±2.00(27.7-31.6)
Postflexion	28.8±1.18(25.7-30.1)	28.0±1.76(24.5-31.0)
Transforming	25.1±1.30(23.0-26.7)	25.5±1.85(23.0-29.6)
Pelagic juvenile	23.4±0.79(22.7-24.7)	21.5±1.48(19.1-23.8)
Benthic juvenile	22.6±1.22(20.6-25.0)	16.6±0.81(16.2-17.7)
Angle gill raker length/HL:		
Flexion	10.5±1.52(9.0-12.8)	9.4±1.48(8.4-10.5)
Postflexion	13.4±0.92(11.9-15.1)	13.3±1.16(10.9-14.8)
Transforming	13.2±0.94(11.7-14.7)	15.1±0.95(13.5-16.9)
Pelagic juvenile	14.4±0.75(13.1-15.5)	15.6±1.07(13.3-17.5)
Benthic juvenile	15.9±1.53(13.5-18.0)	16.0±0.32(15.6-16.4)
Longest dorsal spine length/HL:		
Flexion	12.2±3.00(7.7-15.8)	12.4±5.58(6.1-16.8)
Postflexion	24.8±5.64(17.4-32.4)	25.6±3.83(20.9-31.5)
Transforming	28.5±2.64(25.0-31.0)	36.6±3.21(28.8-39.4)
Pelagic juvenile	34.8±2.09(32.8-36.8)	38.0±2.57(33.9-42.9)
Benthic juvenile	32.9±2.20(30.0-36.5)	37.7±2.54(34.2-40.2)
Longest dorsal ray length/HL:		
Flexion	25.5±7.58(10.8-35.7)	24.9±6.54(20.0-32.3)
Postflexion	33.6±4.45(25.5-42.5)	31.1±3.40(27.3-37.0)
Transforming	35.8±2.93(29.8-39.6)	38.4±3.22(33.9-42.9)
Pelagic juvenile	39.8±2.26(36.4-43.3)	40.8±2.56(37.0-45.2)
Benthic juvenile	39.2±2.46(35.7-42.8)	44.6±2.38(40.9-47.0)
Longest anal spine length/HL:		
Flexion	10.2±2.25(7.4-12.9)	13.6±0.92(12.9-14.2)
Postflexion	21.4±4.76(13.8-26.8)	22.4±4.79(16.7-31.5)
Transforming	25.5±3.52(18.8-31.4)	35.3±3.44(30.5-41.6)
Pelagic juvenile	31.9±1.25(30.8-34.2)	41.1±1.96(37.9-44.8)
Benthic juvenile	35.1±3.73(28.2-39.7)	50.7±4.29(46.1-54.9)
Pectoral fin length/SL:		
Flexion	17.1±1.34(15.0-18.6)	15.3±2.30(13.0-17.6)
Postflexion	21.9±1.45(19.3-24.0)	21.5±1.18(20.2-23.6)
Transforming	23.1±1.11(21.5-25.3)	25.2±1.88(21.4-28.1)
Pelagic juvenile	24.2±0.33(23.7-24.6)	26.7±1.27(24.9-29.0)
Benthic juvenile	25.6±1.23(23.4-26.8)	26.4±0.68(25.4-26.9)
Pectoral fin base depth/SL:		
Flexion	10.0±0.77(9.2-11.0)	13.0±1.07(11.8-13.9)
Postflexion	8.8±0.58(8.2-10.2)	10.6±0.69(9.8-12.0)
Transforming	8.0±0.22(7.6-8.4)	9.3±0.39(8.7-10.0)
Pelagic juvenile	7.6±0.16(7.3-7.8)	8.8±0.44(7.9-9.8)
Benthic juvenile	8.4±0.63(7.3-9.1)	9.8±0.25(9.6-10.2)
Pelvic fin length/SL:		
Flexion	10.3±1.34(8.6-11.8)	13.7±1.68(11.9-15.2)
Postflexion	13.8±1.19(11.4-15.7)	17.5±1.75(15.2-21.0)
Transforming	14.5±0.89(12.7-16.0)	20.1±1.27(17.9-21.7)
Pelagic juvenile	16.1±0.34(15.7-16.6)	19.5±0.93(17.3-21.0)
Benthic juvenile	17.5±1.03(16.4-20.0)	21.3±1.04(20.3-22.6)
Pelvic spine length/SL:		
Flexion	6.0±1.82(3.7-8.4)	9.0±3.46(6.5-11.4)
Postflexion	12.0±1.30(10.0-13.6)	15.9±1.80(13.9-19.4)
Transforming	12.2±1.60(9.9-14.4)	19.7±0.80(18.4-20.7)
Pelagic juvenile	13.7±0.51(13.0-14.6)	17.7±1.52(15.3-20.0)
Benthic juvenile	12.7±0.56(11.7-13.4)	15.5±0.92(14.7-16.9)
Parietal spine length/HL:		
Flexion	10.2±1.80(8.4-13.3)	22.6±5.12(16.8-26.5)
Postflexion	8.7±2.56(6.4-11.6)	14.3±2.24(11.9-17.3)
Transforming	3.8±1.30(2.8-5.6)	10.4±1.83(7.7-14.1)
Pelagic juvenile	—	6.9±2.42(3.8-10.7)
Benthic juvenile	0.9±0.47(0.35-1.9)	2.6±0.98(1.6-4.0)
Nuchal spine length/HL:		
Flexion	1.4±1.70(0.0-4.4)	1.5±1.61(0.0-3.2)
Postflexion	3.4±0.65(2.2-4.1)	5.1±1.36(2.3-7.4)
Transforming	2.0±0.47(1.4-3.0)	4.6±1.74(0.0-6.2)
Pelagic juvenile	1.7±0.33(1.5-2.1)	3.3±1.30(1.2-5.6)
Benthic juvenile	0.0±0.00(0.0-0.0)	0.0±0.00(0.0-0.0)
Preopercular spine length/HL:		
Flexion	20.3±0.69(19.6-21.3)	32.9±8.20(27.1-38.7)
Postflexion	20.1±2.79(15.5-24.1)	25.3±2.35(22.2-29.5)
Transforming	10.8±1.31(8.8-12.3)	22.3±2.96(16.0-25.9)
Pelagic juvenile	5.3±1.60(3.8-7.0)	12.7±4.37(6.7-19.5)
Benthic juvenile	4.2±0.95(3.4-6.5)	4.0±0.87(3.1-5.1)
Caudal peduncle depth/SL:		
Flexion	12.4±0.83(10.9-13.6)	11.8±1.06(10.8-12.9)
Postflexion	11.1±0.71(10.1-12.4)	11.0±0.50(9.9-11.6)
Transforming	9.6±0.37(8.9-10.1)	10.6±0.49(9.8-11.5)
Pelagic juvenile	8.7±0.53(7.8-9.2)	9.6±0.41(8.6-10.3)
Benthic juvenile	9.1±0.34(8.8-9.9)	9.3±0.24(9.0-9.6)
Caudal peduncle length/SL:		
Flexion	15.6±0.78(14.5-16.7)	16.0±0.62(15.3-16.5)
Postflexion	15.3±0.58(14.3-16.2)	14.5±0.86(12.9-15.2)
Transforming	15.4±0.70(14.1-16.7)	14.7±0.68(14.0-15.7)
Pelagic juvenile	15.5±0.98(14.2-16.6)	14.0±0.99(12.4-16.5)
Benthic juvenile	14.6±0.68(13.7-15.7)	13.9±0.33(13.5-14.4)
Caudal peduncle depth/caudal peduncle length:		
Flexion	0.80±0.085(0.70-0.94)	0.74±0.095(0.67-0.85)
Postflexion	0.73±0.051(0.67-0.81)	0.76±0.061(0.67-0.88)
Transforming	0.63±0.030(0.58-0.67)	0.72±0.040(0.68-0.83)
Pelagic juvenile	0.57±0.055(0.47-0.63)	0.69±0.048(0.59-0.79)
Benthic juvenile	0.63±0.028(0.58-0.66)	0.67±0.022(0.65-0.70)

TABLE 3.—Measurements (millimeters) of larvae and juveniles of *Sebastes entomelas*. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal-hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
9.9	12.5	5.4	3.9	1.0	—	1.2	1.2	2.8	2.1	1.2	1.6	1.8	1.0	0.50	0.90	3.8	0.52	0.04	—	0.36	0.30	0.92	0.24
10.0	12.5	5.3	3.9	0.88	1.6	1.3	1.3	3.0	2.2	1.2	—	1.5	1.1	0.39	0.86	3.7	0.36	(4)	0.80	0.36	—	0.42	—
10.9	13.7	6.3	4.7	1.3	1.9	1.5	1.4	3.2	2.6	1.4	1.7	1.8	1.0	0.98	1.2	4.4	0.45	0.04	1.0	0.47	0.58	1.4	0.50
11.0	14.0	6.4	4.2	1.3	1.4	1.4	1.4	3.3	2.5	1.5	1.6	1.8	1.2	0.72	1.0	4.2	0.48	0.10	0.84	0.38	0.50	1.5	0.32
11.9	15.2	7.0	5.0	1.6	1.7	1.4	1.4	3.5	2.7	1.5	1.8	2.2	1.2	1.0	1.4	4.9	0.42	0.22	0.98	0.60	0.76	1.3	0.54
12.0	15.3	6.8	4.7	1.4	1.5	1.4	1.5	3.4	2.7	1.5	2.0	2.0	1.1	0.76	1.4	4.9	0.44	(4)	0.92	0.60	0.50	1.2	0.56
12.9	16.2	7.3	4.8	1.4	1.5	1.5	1.4	3.6	2.7	1.4	2.0	2.4	1.2	1.0	1.4	5.1	—	—	1.0	0.54	0.76	1.3	0.62
13.7	17.5	8.1	5.4	1.4	2.1	1.6	1.6	4.1	3.4	1.7	2.1	2.9	1.4	1.4	1.8	5.6	0.66	0.22	1.3	0.64	0.94	1.5	0.81
14.0	17.3	8.5	5.5	1.6	2.2	1.7	1.5	3.9	2.9	1.6	2.0	2.7	1.2	1.4	1.6	5.7	0.62	0.22	1.2	0.75	—	1.4	0.76
14.9	19.2	9.1	5.4	1.6	2.3	1.7	1.6	4.2	3.6	1.8	2.3	3.1	1.3	1.7	1.8	5.7	0.36	0.22	1.1	0.76	1.3	1.8	1.2
15.2	19.0	9.3	5.5	1.6	2.3	1.8	1.6	4.5	3.7	1.8	2.4	3.0	1.4	—	2.0	6.1	0.64	0.12	1.2	0.72	0.96	1.7	0.82
16.2	20.7	9.4	6.1	1.8	2.7	1.9	1.8	4.7	3.8	1.8	2.5	3.4	1.5	—	2.2	6.3	—	0.22	—	0.74	—	1.9	—
16.8	21.0	9.9	6.2	1.7	2.8	1.8	1.8	4.6	3.7	1.9	2.6	3.6	1.5	—	2.3	6.6	—	—	—	0.88	—	—	—
17.2	22.1	10.3	6.1	1.7	2.8	1.9	1.8	4.7	3.9	1.9	2.5	4.0	1.6	2.2	2.6	6.3	0.50	0.22	1.3	0.86	1.7	2.3	1.5
18.4	23.4	10.6	7.0	1.8	2.8	2.0	1.8	5.2	4.2	2.0	2.9	4.2	1.5	2.5	2.7	6.8	0.45	0.18	1.2	0.92	1.8	2.4	1.4
18.5	23.6	10.2	6.3	1.8	2.5	1.8	1.8	4.7	3.9	2.0	3.0	4.2	1.6	2.3	2.5	6.5	0.42	0.24	1.2	0.84	1.8	2.2	1.5
19.4	24.7	10.9	6.7	1.8	2.6	1.9	1.9	5.2	4.2	2.0	3.0	4.4	1.6	2.5	2.7	6.8	—	0.26	—	0.84	—	2.3	1.6
20.4	25.6	12.0	7.3	1.9	2.9	2.2	2.1	5.4	4.3	2.1	3.1	4.9	1.7	—	3.0	7.6	—	0.20	—	0.94	—	2.6	1.8
20.3	26.5	11.4	7.1	1.7	3.1	2.2	2.1	5.1	4.2	2.1	3.0	4.8	1.7	—	3.0	7.3	0.46	0.22	1.1	1.0	2.3	2.5	1.9
21.0	26.4	12.3	7.3	1.9	2.8	2.1	2.2	5.6	4.6	2.2	3.3	4.8	1.8	2.6	3.3	7.6	—	0.22	—	1.1	—	3.1	1.9
[5]21.7	27.0	13.1	8.0	2.2	3.1	2.1	2.1	5.6	4.5	2.2	3.5	4.9	1.8	2.5	3.2	8.4	0.45	0.24	—	1.0	—	2.7	1.5
[5]22.3	—	13.9	8.4	2.2	3.2	2.4	2.1	5.7	4.7	2.2	3.4	4.8	1.8	—	3.3	8.8	0.24	0.16	1.0	1.1	2.1	2.5	1.9
[5]22.9	29.1	13.6	8.1	2.1	3.1	2.2	2.1	6.0	4.8	2.3	3.5	5.2	1.8	2.5	3.1	8.5	0.32	0.22	1.0	0.96	—	2.7	1.9
[5]23.9	30.0	14.3	8.3	2.2	3.5	2.4	2.0	6.0	4.8	2.4	3.7	5.8	1.9	3.2	3.6	8.6	—	0.16	0.90	1.2	2.5	2.9	—
[5]24.5	30.8	14.5	8.7	2.5	3.5	2.2	2.3	6.3	5.1	2.4	4.1	5.7	2.0	2.5	3.5	9.2	—	—	—	1.2	—	3.0	2.0
[5]24.5	30.8	14.5	9.4	2.6	3.7	2.4	2.2	6.4	5.1	2.4	3.7	5.6	1.9	3.0	3.4	9.2	—	0.16	—	1.2	2.7	—	2.6
[5]25.3	32.0	14.9	8.6	2.1	3.2	2.3	2.3	6.4	5.1	2.5	4.1	5.9	2.0	2.5	3.7	9.3	—	—	—	1.2	—	3.4	2.5
[5]25.9	33.9	15.1	9.3	2.8	—	2.4	2.4	6.4	5.3	2.3	4.0	5.9	2.1	—	3.8	9.6	—	—	—	1.3	—	3.1	2.1
[5]26.5	33.2	16.2	8.6	2.4	—	2.5	2.3	6.5	5.4	2.5	4.2	—	2.1	3.2	3.6	10.1	—	—	—	1.2	—	—	—
[5]26.7	33.0	15.1	9.4	2.6	3.8	2.5	2.4	6.5	5.5	2.5	4.1	5.8	2.2	—	3.4	9.8	0.26	0.18	1.1	1.1	2.4	3.2	2.4
[5]27.2	—	16.6	8.8	2.3	3.6	2.4	2.3	6.5	5.4	2.6	4.0	—	2.2	—	3.8	9.6	—	0.20	—	1.1	2.7	3.4	2.4
[5]27.9	33.4	16.7	10.0	2.9	—	2.5	2.3	7.2	5.8	2.8	4.2	6.6	2.2	4.0	4.3	10.4	—	0.14	0.94	1.2	3.1	3.6	2.8
[5]28.5	35.8	16.9	9.6	2.8	3.5	2.5	2.4	7.5	6.2	2.8	4.5	7.2	2.4	—	4.5	10.2	—	—	—	1.3	—	3.8	—
[5]29.1	35.8	16.1	9.7	2.7	3.9	2.7	2.4	7.2	5.9	2.6	4.1	6.5	2.2	3.8	4.1	9.7	—	0.18	—	1.3	—	3.7	—
[5]29.7	—	17.5	10.4	3.3	4.0	2.7	2.5	7.3	6.1	2.8	4.2	6.6	2.3	—	—	10.5	—	0.22	1.1	1.3	—	3.8	2.8
[5]30.6	36.9	18.7	10.2	2.8	4.4	2.8	2.4	7.3	5.9	2.9	4.8	7.6	2.5	4.4	4.9	11.0	—	0.16	0.90	1.5	—	4.0	3.2
[6]30.8	38.5	18.5	9.7	—	—	2.6	2.4	7.4	6.1	2.8	5.1	7.3	2.3	4.2	5.1	11.3	—	0.18	—	1.4	—	4.2	3.0
[6]31.6	39.1	19.8	10.7	2.8	4.3	2.7	2.5	7.3	6.1	2.7	4.5	7.6	2.4	4.6	5.0	11.4	—	0.19	—	1.4	—	3.9	3.3
[6]32.0	39.7	19.4	10.3	2.8	4.2	2.7	2.4	7.6	6.3	2.7	5.1	7.7	2.4	4.4	5.2	10.9	—	0.22	—	1.6	—	4.2	3.2
[6]33.4	41.9	20.9	11.7	—	—	3.3	2.6	8.1	6.2	2.6	5.5	8.2	2.6	4.4	5.5	14.0	—	0.18	—	1.7	3.9	4.6	3.7
[6]35.7	44.0	21.9	11.4	3.4	4.8	3.1	2.7	8.7	7.1	3.3	5.2	—	2.6	4.9	5.6	13.9	—	0.18	0.80	1.6	4.2	—	3.9
[6]36.8	45.7	22.0	11.5	3.0	5.0	3.1	2.7	8.7	7.4	3.3	5.4	9.0	2.8	4.8	5.9	12.2	—	0.24	0.60	1.7	4.2	4.6	3.8
[6]40.1	—	24.0	12.8	3.4	5.6	3.4	2.9	9.8	8.1	3.7	6.4	9.8	3.1	5.5	6.4	13.4	—	0.16	0.48	1.9	4.2	5.0	4.1
[7]45.0	54.2	28.2	15.0	4.2	5.8	4.1	3.3	11.0	9.5	4.2	6.7	11.0	3.3	—	7.6	16.3	0.06	—	0.98	2.2	5.3	5.4	4.6
[7]47.7	58.2	30.9	17.0	4.7	6.5	4.3	3.5	12.4	10.9	4.7	7.1	11.7	3.8	6.1	8.0	18.9	0.06	—	0.84	2.3	5.3	6.5	4.8
[7]55.5	66.7	33.2	17.0	4.8	6.5	4.3	3.8	13.4	12.0	4.9	8.5	13.0	4.3	6.5	9.1	20.2	0.16	—	0.80	2.8	5.5	7.0	5.5
[7]55.7	67.2	34.9	18.5	5.0	6.6	4.6	4.1	14.0	12.0	5.0	8.4	13.7	4.5	6.8	9.3	21.4	0.18	—	0.78	2.5	5.7	6.6	6.8*
[7]64.4	78.9	38.5	19.4	4.1	8.3	5.1	4.6	17.3	15.0	5.7	8.8	16.9	5.7	8.0	11.0	23.6	0.24	—	0.66	3.5	6.4	8.3	7.7*
[7]65.0	79.2	42.3	22.0	5.4	8.3	5.6	5.0	19.7	16.0	6.1	9.6	17.2	5.9	8.5	13.0	26.2	0.16	—	0.80	3.7	6.6	8.1	7.5*
[7]66.1	81.1	39.4	21.7	5.0	8.7	5.8	5.0	19.3	16.2	6.1	10.4	17.7	5.8	8.6	11.9	23.0	0.20	—	0.88	3.4	7.1	8.9	7.7
[7]71.2	86.1	42.3	22.0	5.6	9.5	5.8	5.0	20.5	16.7	6.3	9.9	18.9	6.1	9.6	12.7	25.4	0.24	—	0.80	3.8	7.8	9.1	8.4
[7]74.1	89.1	45.6	23.9	6.6	8.6	5.8	5.1	20.4	17.6	6.6	10.4	19.4	6.6	9.1	12.9	26.2	0.10	—	0.92	3.9	7.5	9.5	8.8
[7]74.5	90.5	44.7	22.0	4.8	9.0	5.8	5.5	21.9	18.2	6.8	10.4	20.0	6.8	9.8	13.1	27.2	0.24	—	0.78	3.8	8.4	9.1	8.9*

[1]Usually fourth or fifth spine.
[2]Usually in anterior one-fourth of fin.
[3]Where indicated by (*) second and third spines equal or the third, otherwise the second measured.
[4]Bump.
[5]Transforming.
[6]Pelagic juvenile.
[7]Benthic juvenile.

from 29 to 24% through the pelagic juvenile period after which it deepens to 28% SL.

Fin Development (Tables 1-3).—The adult complement of 17-19 (usually 18) pectoral fin rays is present in the smallest larva (9.9 mm). Pectoral fin length increases from 17 to 26% SL between flexion and benthic juvenile stages. The smallest larvae (≈10 mm) have the adult pelvic fin complement (I,5). Pelvic fin length is moderate, increasing from 10 to 18% SL between flexion and benthic juvenile stages. Pelvic spine length increases from 6 to 12-14% SL.

The adult complement of 8 + 7 principal caudal fin rays can be counted on the smallest (9.9 mm) flexion larva. Seven benthic juvenile *S. entomelas*,

59-73 mm, had superior and inferior secondary rays: 12/13 (two specimens), 13/13 (three specimens), and 13/14 (two specimens), as determined from radiographs.

Adults' complements of dorsal and anal fin spines and rays can be counted by ≈11 mm, although ray bases can be counted in the smallest specimen. The dorsal and anal fin prespines become spines by ≈27 and 31 mm, respectively.

Spination (Tables 2, 4).—Spines on the left side of the head of the smallest *S. entomelas* include the parietal; nuchal; first and third anterior preopercular spines; first (as a bump), second, third, and fourth posterior preopercular spines; superior opercular spine (as a bump); postocular; first inferior infraorbital spine; first and fourth superior infraorbital spines; pterotic; and the inferior posttemporal spine.

The parietal spine and ridge are finely serrated on all specimens <33 mm long. Parietal spine length decreases with development becoming overgrown in large juveniles and adults. The nuchal spine, always shorter than the parietal, is usually present in larvae and pelagic juveniles. It begins to fuse with the parietal spine at ≈26 mm and is fused and not recognizable in benthic juveniles (≥45.0 mm).

All five spines of the posterior preopercular series are present on larvae by ≈11 mm and persist through adults. The third spine is always longest but decreases from 20% HL in flexion larvae to 4% HL in benthic juveniles. The second, third, and fourth posterior preopercular spines and the anterior edge of the first spine of the anterior preopercular series are weakly serrated in specimens <30 mm long. Serrations persist on the third posterior preopercular spine to ≈33 mm. The second anterior preopercular spine was present on the left side only in one flexion larva (12.0 mm). The first and third anterior preopercular spines are present on all flexion and postflexion larvae, are reduced to blunt bumps in ≈25 mm transforming larvae, and are no longer recognizable by ≈30 mm.

The superior opercular spine appears well developed and sharp tipped between 10 and 14 mm. The inferior opercular spine appears as a blunt bump at 15 mm, and as a sharp spine in specimens >21 mm. The interopercular spine appears as a blunt bump at ≈11 mm, as a small sharp spine by 22 mm, and is usually reduced to a blunt bump in benthic juveniles >44 mm.

The ridge anterior to the postocular spine is finely serrated on specimens <28 mm. The supraocular spine appears as a bump at ≈18 mm and as a sharp spine by ≈19 mm. The preocular spine appears as a blunt bump at ≈22 mm and as a sharp spine in all specimens >31.6 mm. The first inferior infraorbital spine is present in all specimens <55 mm, and is absent in specimens >56 mm. The second inferior infraorbital spine appears between 10 and 12 mm, is present in all specimens to ≈35 mm, appears only as a blunt bump between ≈33 and 55 mm, and is no longer visible in specimens >55 mm. The third inferior infraorbital spine appears at ≈15 mm, is present between 35 and ≈55 mm, and is usually absent in specimens >55 mm. The first superior infraorbital spine is present in all specimens <26 mm, is present as a blunt bump between 25 and 32 mm, and is absent in specimens >32 mm long. The second superior infraorbital spine is occasionally present between 16 and ≈30 mm and is absent in larger and smaller specimens. The third superior infraorbital spine is usually present in specimens ≈13-31 mm and usually absent in other sized specimens. The fourth superior infraorbital spine is usually present as a sharp spine in specimens <32 mm, as a sharp spine or blunt bump between 32 and 41 mm, and is usually absent in specimens >41 mm. The nasal spine appears as a bump between 11 and 12 mm and as a sharp spine in all specimens >12 mm.

The tympanic spine appears as a blunt bump between ≈28 and 35 mm and usually as a small sharp spine in specimens >35 mm. The pterotic spine is present as a sharp spine in all specimens <25 mm, as a blunt bump in specimens 25-37 mm, and is absent in specimens >37 mm. The inferior posttemporal spine is present in all specimens of the series. The supracleithral spine appears at ≈12 mm and is present in all larger specimens. The superior posttemporal spine appears as a blunt bump at ≈16 mm and as a sharp spine in all specimens >17 mm. The cleithral spine is present in most specimens >40 mm as a weak, flexible spine.

Scale formation.—Lateral line organs, indicated by a row of light colored spots on the flesh, are visible on the smallest larva and on most larger larvae which lack scales. Developing scales are first visible on unstained specimens at ≈22 mm in the region above the pectoral fin, near the posttemporal and supracleithral spines. The body is scale covered by ≈26 mm.

TABLE 4.—Development of spines in the head region of *Sebastes entomelas* larvae and juveniles. Specimens

Standard length (mm)	Parietal	Nuchal	Preopercular							Opercular		Inter-opercular	Sub-opercular	Pre-ocular	Supra-ocular	Post-ocular
			Anterior			Posterior										
			1st	2d	3d	1st	2d	3d	4th	5th	Superior	Inferior					
9.9	+	+	+	–	+	(1)	+	+	+	–	(1)	–	–	–	–	–	+
10.0	+	(1)	+	–	+	(1)	+	+	+	–	(1)	–	–	–	–	–	+
10.9	+	+	+	–	+	+	+	+	+	–	+	–	(1)	–	–	–	+
11.0	+	+	+	–	+	+	+	+	+	(1)	+	–	(1)	–	–	–	+
11.9	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
12.0	+	(1)	+	+[2]	+	(1)	+	+	+	(1)	(1)	–	(1)	–	–	–	+
12.9	+	+	+	–	+	+	+	+	+	+	(1)	–	(1)	–	–	–	+
13.7	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
14.0	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
14.9	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
15.2	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
16.2	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
16.8	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
17.7	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
18.4	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	(1)	+
18.5	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
19.4	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	(1)	+
20.4	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
20.8	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
21.0	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	(1)	+
[3]21.7	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
[3]22.3	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]22.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]23.9	+	+	+	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]24.5	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]24.5	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]25.3	+	–	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]25.9	+	+	+	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]26.5	+	+	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]26.7	+	+	(1)	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]27.2	+	+	+	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]27.9	+	+	(1)	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]28.5	+	+	–	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]29.1	+	+	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]29.7	+	+	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]30.6	+	+	–	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[5]30.8	+	+	–	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[5]31.6	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]32.0	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]33.4	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]35.7	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]36.8	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]40.1	+	+	–	–	–	+[6]	+	+	+	+	+	+	+	–	+	+	+
[7]45.0	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]47.7	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	–[9]	+
[7]55.5	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]55.7	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]64.4	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]65.0	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	+	(1)	+	+	+
[7]66.1	+[8]	+[8]	–	–	–	(1)	+	+	+	+	+	+	+	+	+	+	+
[7]71.2	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	+	(1)	+	+	+
[7]74.1	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	+	+	+	+	+
[7]74.5	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	(1)	+	+	+

[1]Bump, indicating beginning of spine formation or last stage before spine is overgrown.
[2]– on the right side.
[3]Transforming.
[4]Spine is bifid.
[5]Pelagic juvenile.
[6]Spine tip directed posteriorly.
[7]Benthic juvenile.
[8]Parietal and nuchal spines fused, only one tip visible.
[9]+ on the right side.

Pigmentation.—The smallest larval *S. entomelas* has melanistic pigment on the head over the brain. Melanophores are present on the inside tip of the lower jaw, along the anterior margin of the maxillary, around the pterotic and posttemporal spines, and on the operculum. An internal melanistic shield covers the gut appearing darkest on the dorsal surface. Melanophores are present dorsally on the nape, beneath the posterior one-third of the spinous dorsal fin, beneath the soft dorsal fin, and along the dorsal surface of the caudal peduncle. Internal and external melanophores are present on the lateral midline of the caudal peduncle in the vicinity of notochord flexure, above the posterior portion of the anal fin, and along the ventral margin of the caudal peduncle. Melanophores line the margin of the hypural elements. The pectoral and pelvic fin blades are moderately pigmented with expanded, somewhat elongated melanophores. External and a few internal melanophores are

above dashed line are undergoing notochord flexion. + denotes spine present and – denotes spine absent.

Standard length (mm)	Infraorbital							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supra-cleithral	Cleithral
	Inferior			Superior								Superior	Inferior		
	1st	2d	3d	1st	2d	3d	4th								
9.9	+	–	–	+	–	–	+	–	–	–	+	–	+	–	–
10.0	(1)	–	–	+	–	–	(1)	–	–	–	+	–	+	–	–
10.9	+	+	–	+	–	–	(1)	–	–	–	+	–	+	–	–
11.0	+	–	–	+	–	–	–	(1)	–	–	+	–	+	–	–
11.9	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
12.0	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
12.9	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.7	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
14.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
14.9	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
15.2	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
16.2	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	–
16.8	+	+	+	+	+	+	+	+	–	–	+	(1)	+	+	–
17.7	+	+	+	+	+	+	+	+	–	–	+	+	+	+	–
18.4	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
18.5	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
19.4	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
20.4	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
20.8	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
21.0	+	+	+	+	+	+	+	+	–	–	+	+	+	+	–
[3]21.7	+	+	+	+	+	+	+	+	–	–	+	+	+	+	–
[3]22.3	+	+	+	+	+	+	+	+	–	–	+	+	+	+	–
[3]22.9	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
[3]23.9	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
[3]24.5	+	+	+[4]	+	+	+	+	+	–	–	(1)	+	+	+	–
[3]24.5	+	+	+	+	+	+	+	+	–	–	+	+	+	+	–
[3]25.3	+	+	+	+	–	(1)	+	+	–	–	+	+	+	+	–
[3]25.9	+	+	+	(1)	–	(1)	+	+	–	–	+	+	+	+	–
[3]26.5	+	+	+	(1)	+	+	+	+	–	–	(1)	+	+	+	–
[3]26.7	+	+	+	(1)	+	+	+	+	–	–	(1)	+	+	+	–
[3]27.2	+	+	+	(1)	+	+	+	+	–	–	+	+	+	+	–
[3]27.9	+	+	+	(1)	+	+	+	+	–	(1)	+	+	+	+	–
[3]28.5	+	+	+	(1)	+	+	+	+	–	(1)	(1)	+	+	+	–
[3]29.1	+	+	+[4]	(1)	–	+	+	+	–	(1)	(1)	+	+	+	–
[3]29.7	+	+	+	(1)	+	+	+	+	–	(1)	(1)	+	+	+	–
[3]30.6	+	+	+	(1)	–	–	(1)	+	–	(1)	(1)	+	+	+	–
[5]30.8	+	+	+[4]	(1)	–	+	+	+	–	(1)	(1)	+	+	+	–
[5]31.6	+	+	+	(1)	–	–	+	+	–	(1)	(1)	+	+	+	–
[5]32.0	+	+	+	(1)	–	–	(1)	+	–	(1)	(1)	+	+	+	–
[5]33.4	+	+	+	–	–	–	(1)	+	–	(1)	(1)	+	+	+	–
[5]35.7	+	(1)	(1)	–	–	–	+	+	–	(1)	–	+	+	+	–
[5]36.8	+	+	+	–	–	(1)	+	+	–	+	(1)	+	+	+	–
[5]40.1	+	+	+	–	–	–	+	+	–	+	–	+	+	+	(1)
[7]45.0	+	–	(1)	–	–	–	–	+	–	+	–	+	+	+	+
[7]47.7	+	(1)	(1)	–	–	–	–	+	–	(1)	–	+	+	+	+
[7]55.5	(1)	(1)	(1)	–	–	–	(1)	+	–	+	–	+	+	+	+
[7]55.7	(1)	(1)	–	–	–	–	–	+	–	+	–	+	+	+	+
[7]64.4	–	–	–	–	–	–	–	+	–	+	–	+	+	+	+
[7]65.0	–	–	(1)	–	–	–	–	+	–	+	–	+	+	+	+
[7]66.1	–	–	–	–	–	–	–	+	–	+	–	+	+	+	+
[7]71.1	–	–	–	–	–	–	–	+	–	+	–	+	+	+	+
[7]74.1	–	–	–	–	–	–	–	+	–	+	–	+	+	+	–
[7]74.5	–	–	–	–	–	–	–	+	–	+	–	+	+	+	–

present on the underside of the pectoral fin base. A discrete melanophore is present at the articulation of each of several dorsal fin rays near the center of the soft dorsal fin.

As larvae develop, pigment increases over the brain. Melanophores are added on the snout, interorbital region, tips of the upper and lower lips, along the maxillary, and on the cheek and operculum. Pigment increases around the orbit and around the posttemporal spine, extending anteriorly over the head. Melanophores line the anterior margin of the cleithrum beneath the operculum. Pigment on the gut becomes less obvious as body musculature increases. The dorsal body surface is pigmented from nape to caudal peduncle by ≈11 mm. Large stellate melanophores beneath the soft dorsal fin increase in number and are aligned along the muscles surrounding the dorsal pterygiophores. This is the densest pigmentation on larvae. Internal and external melanophores are added along the body midline anteriorly from the caudal peduncle forming a line along the notochord which extends to the head by ≈16.5 mm. Melanophores extend ventrolaterally from the

nape to the lateral midline by ≈16.5 mm and are added posteriorly along the dorsolateral body surface with development. The melanophores located above the posterior portion of the anal fin disappear by ≈18 mm. Discrete melanophores are added at the articulation of dorsal fin rays and spines until most soft rays have an associated melanophore by ≈14 mm and most spines have one by ≈19 mm. Melanophores are added along the caudal fin base, sometimes appearing as a line of pigment, and onto the fin membrane. Pigment decreases and then disappears on the pelvic fin and underside of the pectoral fin base by ≈18 mm and on the pectoral fin by ≈20 mm.

During transformation, ≈22-31 mm, pigment gradually continues to increase over the head and body. External melanophores are added on the lips, lower jaw, snout, and dorsolateral areas of the head. Pigment becomes continuous around the orbit by ≈30 mm. Melanophores over the dorsolateral surfaces of the body often appear aligned along the myosepta, but this pattern becomes obscured as melanophores are added between the myosepta, particularly along the dorsal one-third of the body.

Pelagic juveniles, 31-40 mm, undergo a general increase in pigment with development. The upper head, snout, lips, lower jaw, maxillary, cheek, and gular region become increasingly pigmented with small melanophores. Melanophores are added ventrolaterally on the body until all but the ventral one-eighth is pigmented. Pigment distinctly lines the caudal fin base.

Benthic juveniles, >44 mm, become increasingly pigmented as small melanophores are added on the head and appear on the scales and fins. Pigmentation at the anterior tips of the lips and along the maxillary intensifies. By ≈55.5 mm a dark bar of pigment extends the length of the maxillary, and two other bars extend from the posteroventral margin of the eye across the cheek. The most dorsal cheek bar extends completely across the opercle. Dark blotches appear on the dorsal surfaces of the body as scale-borne melanophores overlie the body pigment which developed during the transformation and pelagic juvenile stages. In small benthic juveniles these blotches appear as indistinct bands as melanophores are added ventrolaterally to them. However, a mottled pattern appears over the dorsal half of the body by ≈66 mm. Melanophores are added anteriorly and proximally on the first dorsal fin and are eventually scattered over the entire fin. A dark blotch develops in the posterior portion of the spinous dorsal fin by ≈45 mm and persists in the largest juveniles observed; however, as development proceeds the blotch becomes less intensely pigmented and more of a pigment fringe, rather than a blotch. The membranes of the spinous and soft dorsal fins and caudal fin become lightly covered with small melanophores by ≈56 mm. Also by ≈56 mm, a small patch of melanophores appears on the dorsal half of the pectoral fin ray bases and adjacent fin base.

Occurrence (Figures 4, 5).—Adult *S. entomelas* occur from Todos Santos Bay, Baja California, to Kodiak Island, Alaska (Miller and Lea 1972). Off Oregon they are reported to be most common on the continental shelf between 100 and 200 m depth

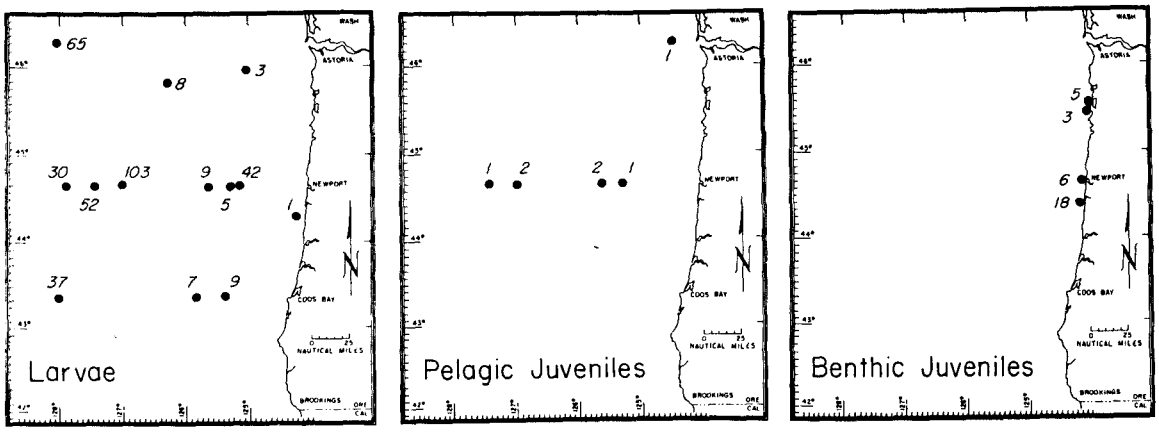

FIGURE 4.—Number of specimens and location of capture of larvae and juveniles of *Sebastes entomelas* off Oregon (1961-78) described in this paper.

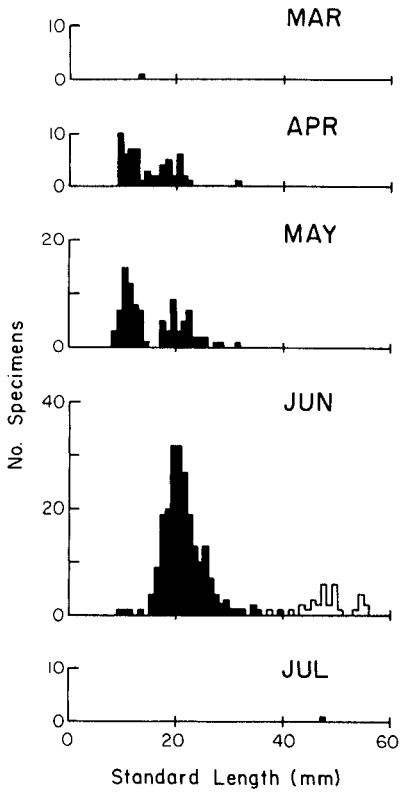

FIGURE 5.—Seasonal occurrence of larvae and juveniles of *Sebastes entomelas* off Oregon. Data from 1961 through 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

(Snytko and Fadeev[7]). Data from Niska (1976) show that ≈91% of the total Oregon trawl catch of *S. entomelas* landed from 1963 through 1971 was taken from depths of 110-218 m. Highest concentrations of *S. entomelas* found during the 1977 rockfish survey between Pt. Hueneme, Calif., lat. 34°00′ N, and Cape Flattery, Wash., lat. 48°29′ N, were at depths of 91-181 m between Cape Blanco, Oreg., lat. 43°00′ N, and Cape Flattery (Gunderson and Sample[8]). Larval and transforming *S. entomelas*, in our collections were captured at stations ≈9-306 km offshore. Pelagic juveniles appeared to range as extensively as larvae. Benthic juveniles were taken close to the coast at depths of 9-37 m.

Reported parturition times for *S. entomelas* are January through March off central California (Phillips 1958). Larvae <15 mm long were taken March through June, although most were taken in April and May. Larvae and pelagic juveniles >15 mm were taken April through June. Benthic juveniles were taken only in June. Lack of benthic juveniles in our collections from other months is probably due to inadequate sampling.

SEBASTES ZACENTRUS (GILBERT)

Literature (Figures 6-8).—The pigment pattern of *S. zacentrus* preextrusion larvae was described by Efremenko and Lisovenko (1970), including a figure; Westrheim (1975); Westrheim et al.[9]; and Harling et al. (footnote 6), including figures. Descriptions by Efremenko and Lisovenko (1970), Westrheim (1975), and Westrheim et al. (footnote 9) agree that preextrusion larvae (mean 4.2, 4.3, and 4.5 mm TL, respectively) have a postanal ventral row of melanophores (15-21, usually >16, and 15-20, respectively) which usually stops short of the anus by at least four myomeres with usually at least one melanophore in the hypural region. Melanophores also appear over the gut. No dorsal row of pigment is present. Harling et al. (footnote 6) described and illustrated two forms of *S. zacentrus* preextrusion larvae, both with mean 5.0 mm TL. One form had 15-18 ventral midline melanophores which stopped short of the anus by four myomeres, a hypural spot, and gut pigment. The second form had 18-21 ventral midline melanophores which did not stop short of the anus by four myomeres, 9-12 dorsal midline melanophores, considerable pigment encircling the yolk, a large lateral melanophore midway between the anus and tail tip, and several melanophores in the hypural region. It seems quite unlikely that the latter form is the same as the former and merely a result of within species variation as suggested by Harling et al. (footnote 6). Possibly it may reflect misidentification of the adult from which the larvae were taken. Since the two forms described by Harling et al. were consid-

[7]Snytko, V. A., and N. S. Fadeev. 1974. Data on distribution of some species of sea perches along the Pacific coast of North America during the summer-autumn seasons. Document submitted at the Canada-USSR meeting on fisheries in Moscow-Batumi, USSR-November 1974, 14 p. (Transl. 3436, Can. Transl. Ser.).

[8]Gunderson, D. R., and T. M. Sample. 1978. Distribution and abundance of rockfish off Washington, Oregon and California during 1977. Unpubl. rep., 45 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[9]Westrheim, S. J., W. R. Harling, D. Davenport, and M. S. Smith. 1968. Preliminary report on maturity, spawning season and larval identification of rockfishes (*Sebastodes*) collected off British Columbia in 1968. Fish. Res. Board Can., Manuscr. Rep. Ser. 1005, 28 p.

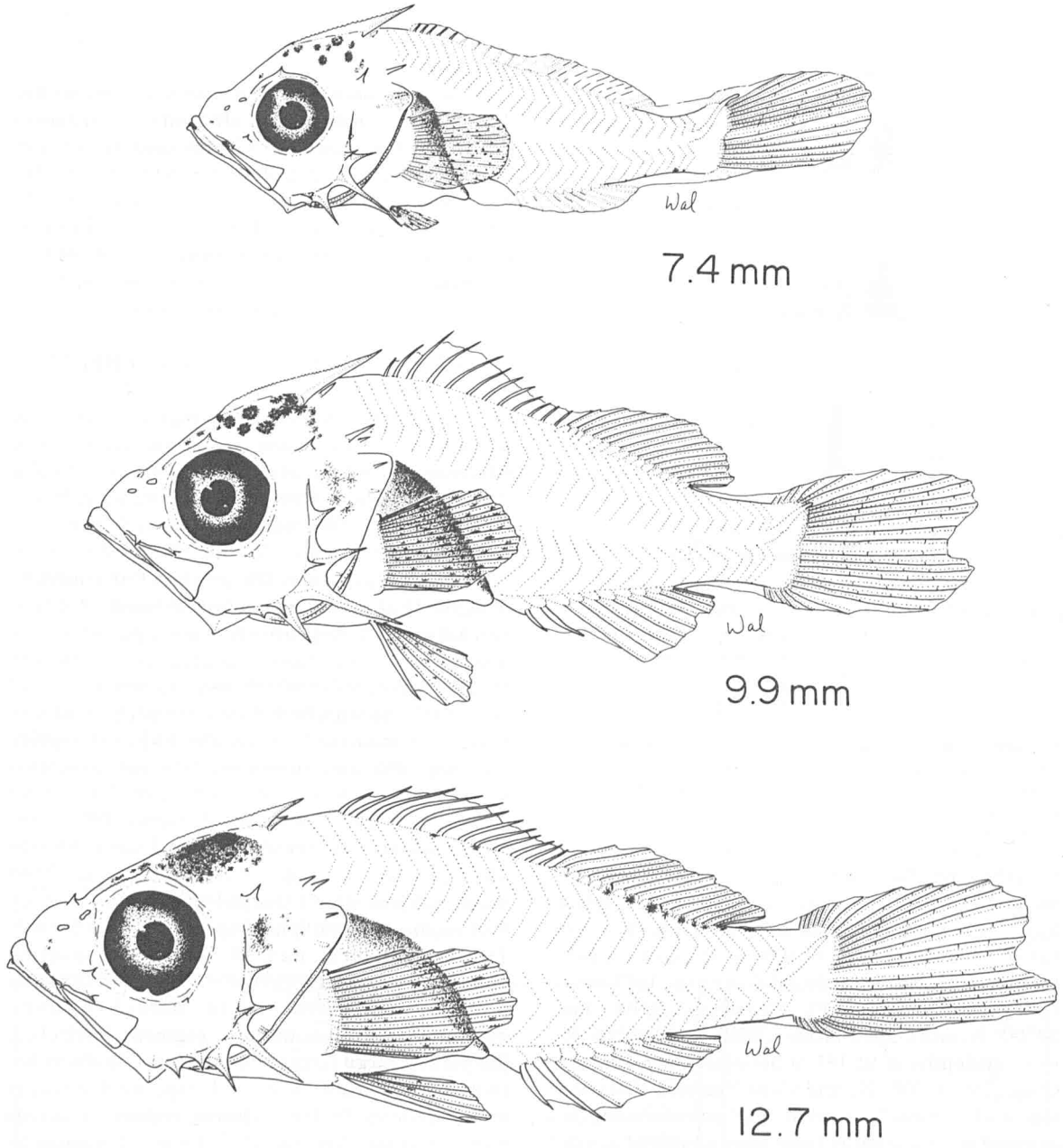

FIGURE 6.—Pelagic larvae of *Sebastes zacentrus*.

erably larger than those described by other workers (see above), there is some question about the identification of both.

Identification (Tables 5-7; Appendix Table 1).—Fifty-one specimens of *S. zacentrus* (7.4-74.8 mm) were selected for the developmental series from 181 larval and juvenile specimens identified. Juveniles were identified using the following combination of characters observed in juvenile and adult specimens examined:

Gill rakers = 32-37, usually 34-37
Lateral line pores = 38-48, usually 38-44

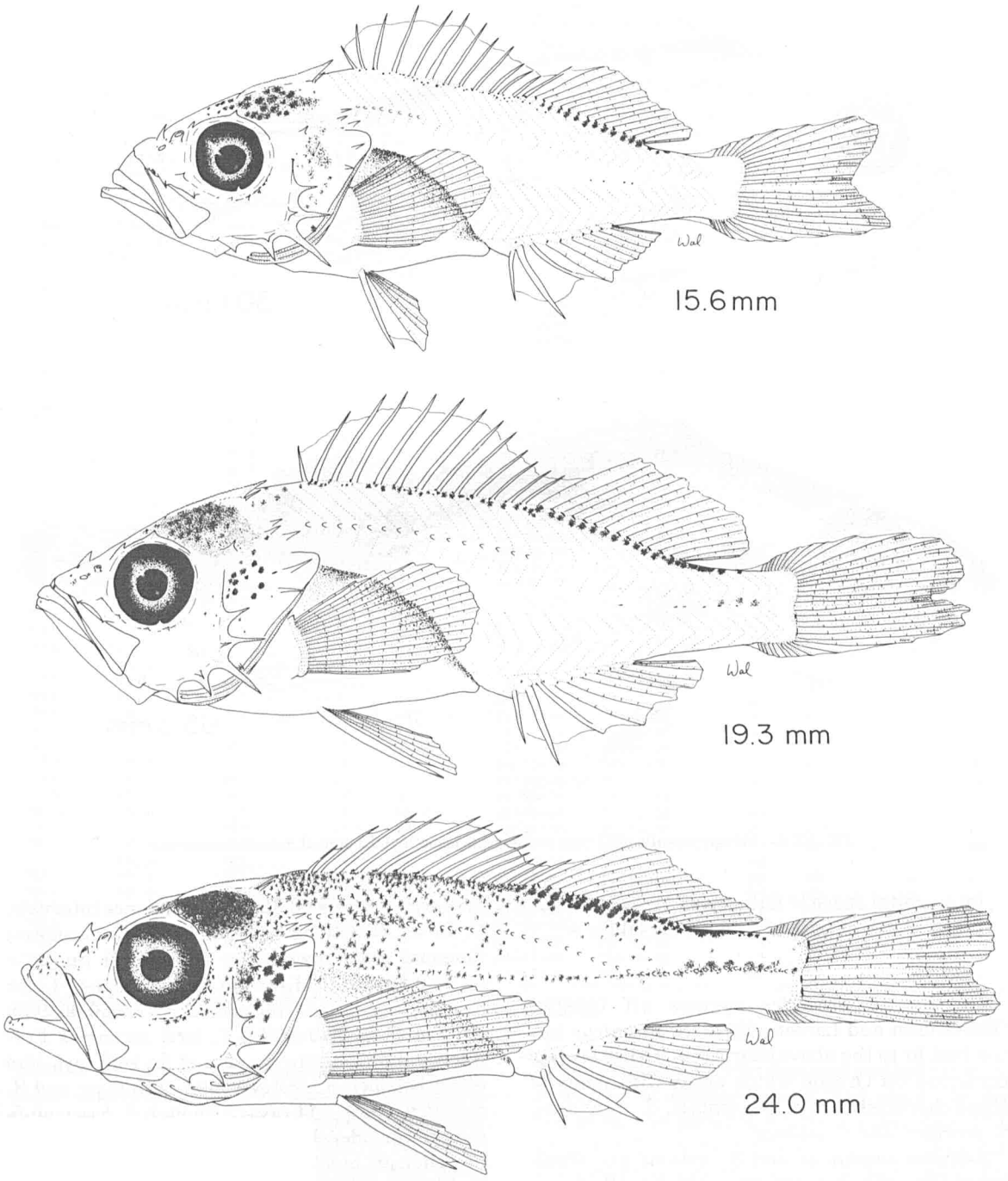

FIGURE 7.—Transforming larvae (15.6, 19.3 mm) and pelagic juvenile (24.0 mm) of *Sebastes zacentrus*.

Pectoral fin rays = 16-18, usually 17
Anal fin soft rays = 6 or 7, usually 7
Dorsal fin soft rays = 13-16, usually 14

Vertebrae = 27
Preocular spine = present (strong)
Supraocular spine = usually absent

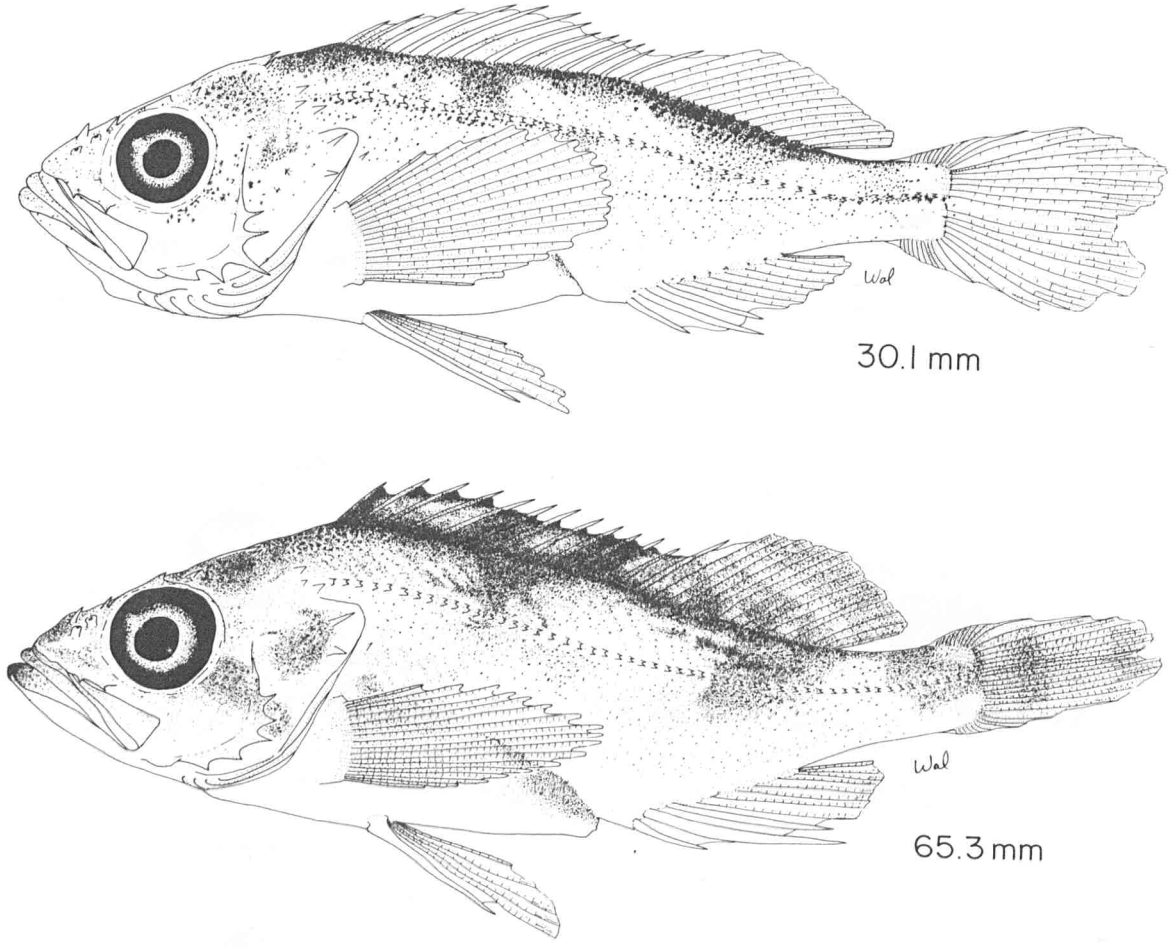

FIGURE 8.—Pelagic juvenile (30.1 mm) and benthic juvenile (65.3 mm) of *Sebastes zacentrus*.

Interorbital space = flat-convex
Black blotch at base of spinous dorsal fin = absent.

Of the 36 *Sebastes* species off Oregon (Richardson and Laroche 1979), *S. zacentrus* has the best fit to the above characters. Other species occurring off Oregon which agree with many of these characters are *S. brevispinis*, *S. emphaeus*, *S. proriger*, and *S. wilsoni*.

Sebastes emphaeus and *S. wilsoni* are eliminated since they have 39-43 and 38-42 gill rakers, respectively (see Appendix Table 1). *Sebastes wilsoni* also differs from *S. zacentrus* in soft anal fin ray count, usually 6 vs. usually 7, respectively (see Appendix Table 1). *Sebastes proriger* can be eliminated based on count frequency distributions (see Appendix Table 1): number of gill rakers on the first arch $\bar{x} = 38.3 \pm 0.35$ (95% confidence intervals, C. I.) vs. 35.3 ± 0.32 (95% C. I.) for *S. zacentrus*; diagonal scale rows below the lateral line $\bar{x} = 56.0 \pm 0.82$ (95% C. I.) vs. 50.2 ± 0.56 (95% C. I.) for *S. zacentrus*; lateral line pores $\bar{x} = 47.9 \pm 0.93$ (95% C. I.) vs. 41.8 ± 0.70 (95% C. I.) for *S. zacentrus*. Frequency distributions for dorsal fin soft rays also differ between *S. proriger*, 50% $\geq$15 rays, and *S. zacentrus*, 88% <14 rays. Although *S. brevispinis* differs considerably from *S. zacentrus* in body morphology, pigmentation, and relative strength and length of head and fin spines, the fin, scale, and lateral line pore count ranges are reported to overlap (Phillips 1957; Miller and Lea 1972; Hart 1973). Since count-frequency data have not been published for *S. brevispinis* and since we had only four large juvenile and adult specimens available for examination, it was necessary to rely on a

TABLE 5.—Meristics from larvae and juveniles of *Sebastes zacentrus* based on unstained specimens. Counts of left and right pelvic fin rays (I,5; I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7,7) were constant throughout the series. Specimens above dashed line are undergoing notochord flexion.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
7.4	V+I[1],14	III[1],7	17	17	—	—	—	—	—	—
7.9	XIII[1],13	III[1],7	17	17	18+ 7=25	17+ 7=24	—	—	—	—
8.5	XIII[1],14	III[1],7	17	17	18+ 8=26	19+ 8=27	—	—	—	—
9.2	XIII[1],14	III[1],7	17	17	20+ 8=28	19+ 8=28	—	—	—	—
9.9	XIII[1],14	III[1],7	17	17	20+ 9=29	21+ 9=30	—	—	—	—
10.1	XIII[1],14	III[1],7	16	17	21+ 9=30	21+ 8=29	—	—	—	—
10.6	XIII[1],14	III[1],7	17	17	22+ 8=30	21+ 9=30	—	—	—	—
11.2	XIII[1],14	III[1],7	17	17	21+ 9=30	21+ 9=30	—	—	—	—
11.7	XIII[1],14	III[1],7	18	17	21+ 9=30	23+ 9=32	—	—	—	—
12.4	XIII[1],13	III[1],7	17	17	22+ 9=31	22+10=32	—	—	—	—
12.7	XIII[1],14	III[1],7	17	17	24+ 9=33	23+ 9=32	—	—	—	—
13.3	XIII[1],14	III[1],7	17	17	23+ 9=32	22+ 9=31	—	—	—	—
[2]13.7	XIII,15	III[1],7	17	17	23+ 9=32	24+ 9=33	—	—	—	—
[2]14.0	XIII[1],14	III[1],6	18	17	24+ 9=33	24+ 9=33	—	—	—	—
[2]14.8	XIII[1],14	III[1],7	17	17	23+ 9=32	23+10=33	—	—	—	—
[2]15.0	XIII[1],14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]15.6	XIII,13	III[1],7	17	17	23+ 9=32	23+ 9=32	—	—	—	—
[2]16.3	XIII,14	III[1],7	17	17	24+10=34	23+10=33	—	—	—	—
[2]16.8	XIII,14	III[1],7	17	17	23+10=33	23+10=33	—	—	—	—
[2]17.3	XIII,14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]17.9	XIII,14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]18.0	XIII,14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]18.9	XIII,14	III[1],7	17	17	25+10=35	24+10=34	—	—	—	—
[2]19.3	XIII,14	III[1],7	17	17	25+10=35	24+10=34	—	—	—	—
[2]19.6	XIII,14	III[1],7	17	17	26+10=36	25+10=35	—	—	—	—
[3]20.3	XIII,14	III,7	17	17	26+10=36	25+10=35	—	—	—	—
[3]20.6	XIII,14	III,7	17	17	24+10=34	25+10=35	—	—	—	—
[3]21.0	XIII,14	III,7	17	17	25+10=35	25+10=35	—	—	—	—
[3]21.5	XIII,14	III,7	18	17	24+10=34	24+10=34	—	—	—	—
[3]22.0	XIII,14	III,7	17	17	25+10=35	24+11=35	—	—	—	—
[3]22.6	XIII,14	III,7	17	17	25+10=35	25+10=35	—	—	—	—
[3]23.3	XIII,13	III,7	17	17	25+10=35	25+10=35	—	41	—	—
[3]23.5	XIII,14	III,7	17	17	25+10=35	25+11=36	—	43	—	—
[3]24.0	XIII,14	III,7	17	17	26+10=36	25+10=35	—	43	—	—
[3]24.4	XIII,14	III,7	17	18	25+11=36	25+10=35	—	42	—	—
[3]25.6	XIII,14	III,7	17	18	24+10=34	25+10=35	42	—	52	—
[3]25.9	XIII,14	III,7	17	17	25+10=35	26+10=36	—	—	—	—
[3]26.3	XIII,14	III,7	17	17	24+10=34	25+10=35	43	41	48	50
[3]26.6	XIII,14	III,7	17	17	24+10=34	25+10=35	40	—	—	—
[3]27.6	XIII,14	III,7	17	17	25+10=35	24+10=34	—	—	—	—
[3]28.3	XIII,14	III,7	17	17	26+10=36	26+10=36	40	40	—	—
[3]30.1	XIII,14	III,7	17	17	25+10=35	25+10=35	42	41	—	—
[3]30.7	XIII,14	III,7	17	17	25+10=35	25+10=35	—	41	—	52
[3]31.2	XIII,14	III,7	17	17	25+10=35	24+10=34	40	—	—	—
[3]33.7	XIII,14	III,7	17	17	24+10=34	25+10=35	40	40	—	—
[3]35.3	XIII,14	III,7	17	17	25+10=35	25+10=35	44	43	—	—
[4]65.0	XIII,14	III,7	17	17	25+10=35	26+10=36	44	45	—	—
[4]65.3	XIII,13	III,7	17	16	25+10=35	26+10=36	41	43	—	—
[4]70.8	XII,14	III,7	17	17	24+10=34	26+10=36	44	43	—	—
[4]73.7	XIII,13	III,7	17	17	26+11=37	25+11=36	43	47	—	—
[4]74.8	XIII,14	III,7	17	17	24+10=34	24+10=34	43	42	—	—

[1]Posteriormost dorsal or anal spine appears as a soft ray.
[2]Transforming.
[3]Pelagic juvenile.
[4]Benthic juvenile.

number of characters for elimination of *S. brevispinis*. Characters useful for separating *S. brevispinis* from *S. zacentrus* are: weak or absent vs. strong supraorbital spines; 58-70 vs. 43-54 diagonal scale rows below the lateral line; 44-53 vs. 38-48, usually 38-44, lateral line pores; 26 vs. 27 vertebrae and myomeres; second anal spine about equal in strength and length to the third anal spine vs. second anal spine stouter and longer than the third anal spine. Larvae and small juveniles of 16 specimens, 14.9-28.1 mm, identified as *S. brevispinis* were found to have denser melanistic pigment over the head and body than *S. zacentrus* of similar length and more slender bodies at the pectoral fin base, averaging 26.1, 24.6, and 26.8% SL for larvae, transforming larvae, and pelagic juveniles vs. 35.2, 34.4, and 32.5% SL for comparable stages of *S. zacentrus*.

Distinguishing Features.—Characters useful to distinguish the smallest identified *S. zacentrus* larva, 7.4 mm, are fin counts; the moderately pigmented pectoral and pelvic fins; the general lack of body pigment; melanophores inside the tip of the

TABLE 6.—Measurements (millimeters) of larvae and juveniles of *Sebastes zacentrus*. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal-hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
7.4	9.1	4.0	3.1	0.92	1.4	1.0	0.86	2.5	1.7	0.80	1.2	0.96	0.98	0.48	0.88	2.9	0.82	0.04	0.84	—	0.19	0.69	([4])
7.9	10.0	4.0	3.1	0.72	1.4	1.1	0.98	2.8	2.0	0.92	1.3	1.2	1.1	0.90	1.2	3.0	0.76	([5])	1.2	0.26	0.52	1.0	0.40
8.5	10.9	4.5	3.8	0.98	1.8	1.2	1.1	3.1	2.2	1.1	1.3	1.5	1.0	—	1.2	3.3	0.64	0.12	—	0.40	0.54	0.76	0.54
9.2	11.8	5.2	4.2	1.1	1.8	1.3	1.2	3.3	2.5	1.0	1.4	1.9	1.1	1.3	1.5	3.8	—	0.22	—	0.55	0.90	1.2	0.70
9.9	12.8	5.6	4.4	1.2	1.7	1.4	1.2	3.5	2.6	1.1	1.5	2.0	1.1	1.4	1.5	4.2	0.76	0.20	0.98	0.58	0.92	1.2	0.78
10.1	13.0	5.6	4.2	1.1	1.8	1.4	1.3	3.4	2.6	1.0	1.5	2.1	1.1	1.4	1.6	4.1	0.68	0.24	1.1	0.52	1.0	1.4	0.88
10.6	13.3	5.7	4.4	1.3	2.0	1.5	1.2	3.6	2.7	1.2	1.6	2.2	1.1	1.6	1.9	4.2	0.75	0.10	1.3	0.48	1.1	1.2	0.92
11.2	14.4	6.4	4.6	1.3	2.1	1.6	1.3	4.0	3.0	1.3	1.7	2.4	1.1	1.8	1.9	4.7	0.66	0.21	1.2	0.68	1.3	1.7	1.2
11.7	14.9	6.8	5.3	1.5	—	1.5	1.3	4.0	3.0	1.3	1.6	2.4	1.2	1.9	2.0	4.9	0.66	0.30	1.3	0.72	1.3	1.5	1.1
12.4	15.9	7.0	5.4	1.5	2.4	1.7	1.5	4.3	3.4	1.4	1.6	2.8	1.3	2.4	2.6	4.9	0.64	0.28	1.2	0.73	1.7	1.8	1.7
12.7	16.2	7.2	5.1	1.4	2.3	1.7	1.5	4.2	3.1	1.4	1.8	3.0	1.3	2.2	2.4	4.8	0.64	0.29	1.3	0.72	—	1.6	—
13.3	16.9	8.3	5.4	1.6	2.4	1.6	1.5	4.4	3.1	1.4	1.9	3.0	1.3	2.2	2.4	5.4	0.68	0.40	1.4	0.78	1.6	1.8	1.3
[6]13.7	17.0	8.5	5.9	1.7	2.3	1.7	1.5	4.6	3.5	1.5	1.8	3.2	1.3	2.6	2.6	5.5	0.62	0.30	—	0.90	1.7	2.0	1.8
[6]14.0	17.9	8.0	5.4	1.5	2.5	1.6	1.6	4.9	3.9	1.5	2.2	3.4	1.4	2.9	3.0	5.7	0.76	0.32	1.4	0.87	1.9	—	1.8
[6]14.8	18.9	8.9	6.1	1.6	2.6	1.6	1.7	5.1	4.2	1.7	2.3	3.6	1.4	2.9	3.0	5.7	0.70	0.38	1.4	0.91	—	—	2.0
[6]15.0	18.0	8.8	6.1	1.5	2.6	1.7	1.6	5.1	4.0	1.6	2.2	3.7	1.4	3.0	3.1	5.9	0.70	0.37	1.5	0.88	—	—	2.1
[6]15.6	19.7	9.3	6.6	1.9	2.4	1.8	1.7	5.2	4.1	1.7	2.4	3.7	1.5	—	—	6.7	—	0.30	—	0.89	—	2.3	—
[6]16.3	20.8	10.0	6.6	1.6	2.8	2.1	1.7	5.1	4.3	1.7	2.4	4.1	1.6	3.0	3.0	7.3	0.62	—	1.5	0.96	2.4	2.6	2.3
[6]16.8	21.0	10.2	6.6	1.9	—	1.9	1.7	5.1	4.2	1.7	2.5	3.6	1.5	—	3.0	6.8	0.78	—	—	0.94	2.4	2.6	2.3
[6]17.3	—	10.8	6.9	1.7	2.7	2.0	1.7	5.4	4.4	1.9	2.5	4.4	1.5	—	—	7.4	0.64	0.22	1.6	1.1	—	2.5	2.3
[6]17.9	22.7	11.0	7.4	1.9	3.1	2.2	1.7	5.8	4.7	1.9	2.6	4.9	1.7	3.6	3.7	7.4	0.70	0.34	1.6	1.2	2.8	3.1	2.8
[6]18.0	22.8	11.1	7.5	1.9	3.2	2.3	1.8	5.7	4.5	2.0	2.7	4.9	1.7	3.7	3.9	7.4	—	—	1.2	1.1	2.9	2.9	3.0
[6]18.9	—	11.8	7.1	1.8	3.1	2.3	1.7	6.1	4.8	1.9	2.8	5.0	1.7	3.7	3.8	7.2	—	0.36	1.5	1.1	2.8	—	—
[6]19.3	24.4	11.0	7.5	1.9	3.0	2.3	2.0	6.0	4.9	1.9	2.7	5.1	1.7	3.6	—	7.7	0.58	0.32	—	1.1	2.9	—	—
[6]19.6	25.2	11.9	7.7	2.1	3.0	2.3	1.8	6.1	5.0	2.0	2.8	5.5	1.8	4.0	4.1	7.9	0.70	0.39	—	1.3	2.9	3.3	3.2
[7]20.3	25.6	12.0	8.1	2.1	3.4	2.3	1.9	6.3	5.1	2.1	3.0	5.4	1.8	—	4.2	8.1	0.66	0.37	1.4	1.3	3.1	3.0	—
[7]20.6	25.6	12.1	7.7	1.9	3.4	2.4	1.8	6.3	5.2	2.0	3.4	5.2	1.9	4.1	4.1	8.1	0.70	0.42	1.5	1.2	3.2	—	3.2
[7]21.0	25.7	13.2	8.4	2.1	3.6	2.4	2.0	6.3	5.0	2.0	2.8	6.1	1.9	—	—	8.4	0.62	0.34	1.2	1.4	3.6	—	3.3
[7]21.5	26.9	12.6	8.6	2.7	—	2.3	2.0	6.5	5.2	2.1	2.8	5.4	2.0	4.2	4.2	8.7	0.92	0.48	—	1.3	—	—	3.4
[7]22.0	—	13.5	8.5	2.5	3.2	2.5	1.8	6.8	5.3	2.1	2.9	—	1.9	—	—	9.3	0.57	0.30	—	1.2	3.2	—	3.3
[7]22.6	28.4	13.6	8.6	2.1	3.9	2.6	2.0	6.9	5.7	2.3	3.4	—	2.1	4.2	4.1	8.6	—	—	1.4	1.4	3.6	—	3.7
[7]23.3	29.6	13.9	9.0	2.4	3.6	2.6	1.9	6.7	5.5	2.2	3.2	6.3	2.1	4.2	4.7	9.2	—	—	1.5	1.2	3.6	3.6	3.7
[7]23.5	—	14.3	8.7	2.1	3.5	2.5	2.0	7.1	6.0	2.4	3.3	6.3	2.1	4.7	4.7	9.2	—	0.44	1.5	1.4	—	—	3.6
[7]24.0	30.5	14.8	9.7	2.7	4.0	2.9	2.0	7.2	5.9	2.4	3.6	6.6	2.2	4.2	4.7	9.7	—	0.32	—	1.4	3.5	3.6	—
[7]24.4	—	14.0	9.5	2.5	4.0	2.8	2.1	7.8	6.3	2.1	3.5	6.1	2.4	—	—	9.4	0.52	0.30	—	1.4	—	3.6	3.6
[7]25.6	32.0	16.4	9.4	2.5	4.0	2.8	2.1	7.7	6.0	2.4	3.9	6.8	2.2	4.3	4.9	10.4	0.36	0.24	1.0	1.6	3.6	4.0	3.9
[7]25.9	32.1	15.7	10.1	2.7	3.6	2.8	2.1	7.7	6.1	2.5	3.5	6.7	2.3	4.6	4.9	10.3	—	0.42	1.1	1.5	3.6	4.2	3.8
[7]26.3	32.7	15.6	9.6	2.7	4.0	2.8	2.1	8.3	6.6	2.5	3.6	—	2.3	4.6	5.1	10.4	0.38	0.24	—	1.6	3.6	4.0	4.3
[7]26.6	—	16.3	9.5	2.7	3.6	2.8	2.1	8.1	6.5	2.6	3.3	7.2	2.3	4.3	—	10.4	—	0.15	—	1.4	3.4	—	4.0
[7]27.6	34.7	16.3	10.0	2.2	4.2	3.1	2.1	7.8	6.6	2.7	3.9	7.5	2.4	—	5.8	10.0	—	0.16	—	1.5	3.8	—	4.3
[7]28.3	34.9	17.5	10.4	2.8	—	2.8	2.1	8.5	7.0	2.6	3.6	—	2.4	4.9	5.4	11.3	—	0.32	1.1	1.6	3.8	—	4.4
[7]30.1	37.4	18.6	10.9	2.7	4.6	3.1	2.2	9.2	7.1	3.0	4.4	8.6	2.7	4.6	6.1	11.9	—	0.36	—	1.7	4.2	4.5	4.7
[7]30.7	37.7	19.4	11.4	3.1	4.7	3.4	2.2	8.5	7.0	2.8	4.0	8.2	2.7	4.8	5.9	12.0	—	0.32	1.2	2.0	4.0	4.8	4.5
[7]31.2	39.1	19.2	11.5	2.7	5.0	3.5	2.2	9.4	7.3	2.9	4.6	8.8	2.6	—	6.2	12.0	—	0.30	0.82	1.9	3.9	5.2	4.8
[7]33.7	41.3	20.8	11.6	3.0	4.5	3.3	2.4	9.8	7.9	3.1	4.7	8.7	2.7	—	—	12.2	—	0.14	0.88	1.9	—	—	4.9
[7]35.3	42.6	22.3	12.3	3.1	4.6	3.4	2.4	10.3	8.5	3.4	4.8	8.8	2.8	—	6.1	14.6	—	0.24	0.82	1.8	—	5.2	—
[8]65.0	80.5	37.0	23.2	4.5	10.7	7.7	4.1	22.0	17.0	6.1	8.8	17.5	6.3	11.0	14.7	26.1	0.92	([9])	1.1	3.8	—	10.9	12.7
[8]65.3	79.7	40.0	23.4	4.3	10.0	7.5	4.0	20.7	16.4	6.3	9.0	17.2	6.3	10.4	14.5	27.0	0.60	([9])	1.2	3.8	9.4	10.8	12.0
[8]70.8	86.3	41.1	26.9	6.7	10.9	8.3	4.2	22.0	17.2	6.4	9.8	19.2	6.8	10.4	15.0	30.1	0.44	([9])	0.92	4.2	9.2	11.0	12.4
[8]73.7	89.7	43.5	27.8	7.0	11.7	8.1	4.6	23.5	19.6	7.0	10.6	18.7	7.5	11.4	15.0	29.7	0.46	([9])	1.0	4.4	10.5	12.2	12.9
[8]74.8	91.3	43.7	27.7	5.8	11.0	8.1	4.5	23.4	20.0	6.9	10.4	19.5	7.4	11.0	15.2	30.1	0.80	([9])	0.86	4.4	10.7	12.5	15.2

[1]Usually fourth or fifth.
[2]Usually midfin.
[3]The second spine.
[4]Forming.
[5]Bump.
[6]Transforming.
[7]Pelagic juvenile.
[8]Benthic juvenile.
[9]Nuchal spine overgrown.

lower jaw; narrow interorbital distance (27.7% HL); and long, deeply serrated, parietal spine (26.5% HL). Later stage larvae change little in overall appearance from the smallest larva, except for addition of melanophores along the dorsal body surface beneath the spinous and soft dorsal fins, along the dorsal surface of the caudal peduncle, and at the articulation of some dorsal soft fin rays of specimens >12.5 mm. A row of melanophores along the lateral midline and a strong, sharp preocular spine develop during the transformation period. Meristic characters, presence of a preocular and lack of a supraocular spine, the flat-convex shape and narrow width of the interorbital space, and stout, relatively long, second anal spine serve to distinguish pelagic and benthic juveniles.

General Development.—The smallest specimens (7.4-8.5 mm) of *S. zacentrus* are undergoing the

final stage of notochord flexion, which is completed by ≈9 mm. Transformation from postflexion larva to pelagic juvenile occurs between ≈13.5 and 20 mm as indicated by structural change of the dorsal and anal fin prespines to sharp, hard spines. Melanistic pigmentation gradually increases along the dorsal body surface under the dorsal fins and along the lateral midline of the caudal peduncle through the larval and transformation periods. A more rapid increase in pigment over the body, progressing anterior to posterior, is initiated at the beginning of the pelagic juvenile stage (≈20 mm). Transition from pelagic to benthic habitat takes place at lengths somewhere between 35 and 65 mm. The largest pelagic juvenile was 65.0 mm. Because of the long-term pelagic sampling effort off Oregon and the lack of specimens in the 35-65 mm length range, it seems likely that this species transforms at a relatively small size (≈35-40 mm). Small benthic juveniles would not be retained in the large mesh bottom trawls. The smallest benthic juvenile observed was 65.0 mm long.

Morphology (Tables 2, 6).—Various body parts were measured on 51 selected specimens of *S. zacentrus* (7.4-74.8 mm). Relative growth trends are summarized in Table 2.

This is a relatively deep-bodied form with body depth 35% SL in flexion larvae, decreasing to 30% in pelagic juveniles. It also has a rather large head, averaging 40-43% SL during the larval and transforming periods.

Fin Development (Tables 2, 5, 6).—The adult complement of 16-18, usually 17, pectoral fin rays is present in the smallest larva (7.4 mm). The pectoral fin is of moderate length, increasing from 15.3% SL in flexion larvae to 26.7 and 26.4% SL in pelagic and benthic juveniles, respectively.

The adult complement of pelvic fin spine and rays (I,5) is present on the smallest larva. The pelvic fin is moderately long increasing from 13.7 to 21.3% SL between flexion and benthic juvenile stages. The pelvic spine is also of moderate length, reaching 20% SL in transforming larvae.

The adult complement of 8+7 principal caudal fin rays can be counted on the smallest larva. Five benthic juveniles, ≈65-75 mm, had superior and inferior secondary caudal fin rays, respectively: 10/11 (three specimens) and 11/10 (two specimens), as determined from radiographs.

Dorsal fin spines and rays, including prespines, are completely formed by ≈8 mm but developing elements are countable in the smallest larva (7.4 mm). The dorsal and anal fin prespines become spines by ≈15.5 and 20 mm, respectively, marking the beginning of the pelagic juvenile stage.

Spination (Tables 2, 7).—Spines on the left side of the head of the smallest *S. zacentrus* include the parietal; nuchal; first and third anterior preopercular spines; first, second, third, fourth, and fifth (as a bump) posterior preopercular spines; superior opercular spine (as a bump); postocular; first inferior infraorbital; first superior infraorbital; pterotic; and the inferior posttemporal spine.

The parietal spine and ridge are serrated on all specimens <36 mm long. The relatively long (23% HL) parietal spine decreases in prominence to ≈3% HL by the benthic juvenile stage. The nuchal spine is always smaller than the parietal and is completely fused to it in benthic juveniles.

All five posterior preopercular spines are present as sharp spines by 8.5 mm and persist in adults. The third spine is relatively long (33% HL in flexion larvae) and decreases in length with development to 4% HL in benthic juveniles. Serrations are present on the first anterior preopercular spine of specimens <22 mm long, on the first and second posterior preopercular spines on specimens <26.5 mm, and on the third posterior preopercular spine to ≈34 mm. The first and third anterior preopercular spines are reduced to blunt bumps by ≈25 mm and are absent on all specimens >26.3 mm.

The superior opercular spine is sharp tipped by ≈8 mm. The inferior opercular spine appears as a blunt bump at ≈8 mm and becomes a sharp tipped spine by ≈13 mm. The interopercular spine appears as a blunt bump by ≈8 mm and as a small, sharp spine in all specimens >12 mm. The subopercular spine appears as a blunt bump by ≈13 mm, is usually present as a short, sharp spine between 13 and 23 mm, is reduced to a blunt bump on specimens 23-26 mm, and is usually absent on specimens >26 mm.

The ridge anterior to the postocular spine is serrated on specimens <27 mm. The preocular spine appears as a blunt bump at 14 mm and usually as a moderately strong, sharp spine on most specimens >15 mm. The first inferior infraorbital spine is present as a sharp spine on all specimens to 35 mm and as a blunt bump in the benthic juveniles examined (65.0-74.8 mm). The second

TABLE 7.—Development of spines in the head region of *Sebastes zacentrus* larvae and juveniles. Specimens

Standard length (mm)	Parietal	Nuchal	Preopercular								Opercular		Inter-opercular	Sub-opercular	Pre-ocular	Supra-ocular	Post-ocular
			Anterior			Posterior											
			1st	2d	3d	1st	2d	3d	4th	5th	Superior	Inferior					
7.4	+	+	+	–	+	+	+	+	+	(1)	(1)	–	–	–	–	–	+
7.9	+	(1)	+	–	+	+	+	+	+	(1)	+	–	(1)	–	–	–	+
8.5	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
9.2	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
9.9	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
10.1	+	+	+	–	(1)	+	+	+	+	+	+	(1)	(1)	–	–	–	+
10.6	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
11.2	+	+	+	–	+	+	+	+	+	+	+	(1)	–	–	–	–	+
11.7	+	+	+	–	+	+	+	+	+	+	+	(1)	+	–	–	–	+
12.4	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
12.7	+	+	+	–	+	+	+	+	+	+	+	+	(1)	(1)	–	–	+
13.3	+	+	+	–	+	+	+	+	+	+	+	+	+	+	–	–	+
[2]13.7	+	+	+	–	+	+	+	+	+	+	+	+	+	+	–	–	+
[2]14.0	+	+	+	–	+	+	+	+	+	+	+	+	+	+	–	–	+
[2]14.8	+	+	+	–	+	+	+	+	+	+	+	+	+	+	(1)	–	+
[2]15.0	+	+	+	–	+	+	+	+	+	+	+	+	+	+	(1)	–	+
[2]15.6	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[2]16.3	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[2]16.8	+	(1)	+	–	+	+	+	+	+	+	+	+	+	+	(1)	–	+
[2]17.3	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[2]17.9	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[2]18.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	–	+
[2]18.9	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[2]19.3	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[2]19.6	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]20.3	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]20.6	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]21.0	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]21.5	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]22.0	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]22.6	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]23.3	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	+
[3]23.5	+	+	+	–	+	+	+	+	+	+	+	+	+	(1)	+	–	+
[3]24.0	+	+	+	–	+	+	+	+	+	+	+	+	(1)	(1)	+	–	+
[3]24.4	+	+	+	–	(1)	+	+	+	+	+	+	+	+	(1)	+	–	+
[3]25.6	+	+	(1)	–	(1)	+	+	+	+	+	+	+	+	(1)	+	–	+
[3]25.9	+	+	(1)	–	+	+	+	+	+	+	+	+	+	(1)	+	–	+
[3]26.3	+	+	(1)	–	(1)	+	+	+	+	+	+	+	(1)	(1)	+	–	+
[3]26.6	+	+	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[3]27.6	+	+	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[3]28.3	+	+	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[3]30.1	+	+	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[3]30.7	+	+	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[3]31.2	+	+	–	–	–	+	+	+	+	+	+	+	(1)	(1)	+	–	+
[3]33.7	+	+	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[3]35.3	+	+	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[4]65.0	+[5]	+[5]	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[4]65.3	+[5]	+[5]	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[4]70.8	+[5]	+[5]	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[4]73.7	+[5]	+[5]	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	+
[4]74.8	+[5]	+[5]	–	–	–	+	+	+	+	+	+	+	(1)	–	+	–	(1)

[1]Bump, indicating beginning of spine formation or last stage before spine is overgrown.
[2]Transforming.
[3]Pelagic juvenile.
[4]Benthic juvenile.
[5]Parietal and nuchal spines fused, only one tip visible.

inferior infraorbital spine appears as a blunt bump at ≈8 mm and as a sharp spine in larger specimens. The first superior infraorbital spine is present as a sharp spine on all specimens <23 mm, as either a sharp spine or a blunt bump between 23 and 35 mm, and was absent in the benthic juveniles examined (65.0-74.8 mm). The second superior infraorbital spine is occasionally present between 15 and 30 mm. The third superior infraorbital spine is usually present as a sharp spine in larvae and pelagic juveniles 14 to 35 mm. Smaller larvae and benthic juveniles examined lacked this spine. The fourth superior infraorbital spine usually appears as a blunt bump in larvae 8-10 mm long and as a sharp spine in all larvae and pelagic juveniles >10 mm. This spine was absent in benthic juveniles. The nasal spine appears as a blunt bump in larvae ≈10-11 mm long and as a sharp spine in all larger specimens.

The tympanic spine appears as a blunt bump between 17 and 18 mm and as a sharp spine in all larger specimens. The pterotic spine is reduced to a blunt bump by 30 mm and is absent on benthic juveniles. The inferior posttemporal spine is pres-

above dashed lines are undergoing notochord flexion. + denotes spine present and – denotes spine absent.

Standard length (mm)	Infraorbital							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supracleithral	Cleithral
	Inferior			Superior											
	1st	2d	3d	1st	2d	3d	4th					Superior	Inferior		
7.4	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
7.9	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.5	+	(1)	–	+	–	–	(1)	–	–	–	+	–	+	+	–
9.2	+	+	–	+	–	–	+	–	–	–	+	–	+	+	–
9.9	+	+	–	+	–	–	(1)	(1)	–	–	+	–	+	+	–
10.1	+	+	–	+	–	–	(1)	(1)	–	–	+	–	+	+	–
10.6	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
11.2	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
11.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.3	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]13.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]14.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
[2]14.8	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
[2]15.0	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
[2]15.6	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
[2]16.3	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
[2]16.8	+	+	–	+	+	+	+	+	–	(1)	+	–	+	+	–
[2]17.3	+	+	–	+	+	+	+	+	–	(1)	+	(1)	+	+	–
[2]17.9	+	+	–	+	+	+	+	+	–	(1)	+	–	+	+	–
[2]18.0	+	+	–	+	(1)	+	+	+	–	(1)	+	+	+	+	–
[2]18.9	+	+	–	+	(1)	+	+	+	–	+	+	(1)	+	+	–
[2]19.3	+	+	–	+	+	+	+	+	–	+	+	+	+	+	–
[2]19.6	+	+	–	+	(1)	+	+	+	–	+	+	+	+	+	(1)
[3]20.3	+	+	–	+	(1)	+	+	+	–	+	+	+	+	+	(1)
[3]20.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
[3]21.0	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
[3]21.5	+	+	–	+	–	+	+	+	–	+	+	+	+	+	(1)
[3]22.0	+	+	–	+	–	+	+	+	–	+	+	+	+	+	–
[3]22.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	–
[3]23.3	+	+	–	(1)	+	+	+	+	–	+	+	+	+	+	+
[3]23.5	+	+	–	(1)	–	+	+	+	–	+	+	+	+	+	+
[3]24.0	+	+	–	(1)	–	+	+	+	–	+	+	+	+	+	(1)
[3]24.4	+	+	–	+	+	+	+	+	–	+	+	+	+	+	+
[3]25.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
[3]25.9	+	+	–	+	+	+	+	+	–	+	+	+	+	+	+
[3]26.3	+	+	–	+	+	+	+	+	–	+	+	+	+	+	+
[3]26.6	+	+	–	+	+	+	+	+	–	+	+	+	+	+	(1)
[3]27.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
[3]28.3	+	+	–	(1)	–	+	+	+	–	+	+	+	+	+	+
[3]30.1	+	+	–	+	(1)	+	+	+	–	+	(1)	+	+	+	+
[3]30.7	+	+	–	(1)	–	+	+	+	–	+	(1)	+	+	+	+
[3]31.2	+	+	–	(1)	–	–	+	+	–	+	(1)	+	+	+	+
[3]33.7	+	+	–	(1)	–	(1)	+	+	–	+	(1)	+	+	+	+
[3]35.3	+	+	–	(1)	–	+	+	+	–	+	(1)	+	+	+	+
[4]65.0	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
[4]65.3	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
[4]70.8	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
[4]73.7	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
[4]74.8	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+

ent in all specimens examined. The supracleithral spine appears by ≈8 mm and is present as a sharp spine on all larger specimens. The superior posttemporal spine appears as a blunt bump at ≈17 mm and is present as a sharp spine on all specimens >19 mm long. The cleithral spine appears as a blunt bump at ≈20 mm and is usually present as a sharp spine in specimens >23 mm.

Scale Formation.—Lateral line organs, indicated by a row of light colored spots on the flesh, are visible on the smallest larva and most larger larvae before scales form. Developing scales are visible on unstained specimens at 19.6 mm in the region above the pectoral fin, near the posttemporal and supracleithral spines. The body is scale covered by ≈30 mm.

Pigmentation.—The smallest *S. zacentrus* larva has melanistic pigmentation on the head over the brain, inside the tip of the lower jaw, and along the anteroventral margin of the maxillary. Melanophores are densely concentrated on the dorsal surfaces of the gut and are present in lesser concentrations on the body wall over the gut cavity. Four small melanophores are present along the ventral midline of the caudal peduncle. The pectoral and pelvic fin membranes are covered with

moderately large and elongate melanophores. Melanophores are also present along the ventral margin and underside of the pectoral fin base.

As larvae develop, pigment increases on the head over the brain, and a few small melanophores may appear on the snout in larvae >12 mm. Melanophores appear on the opercle by ≈8 mm and increase in number with development. By ≈12 mm, melanophores appear just above the opercle near the pterotic and inferior posttemporal spines. About one-half of larvae observed have at least one melanophore along the anterior margin of the cleithrum beneath the opercle. Gut pigmentation remains intense through the larval period. Melanophores begin to appear on the nape and along the dorsal surface of the body beneath the spinous and soft dorsal fins by ≈12 mm. This pigmentation beneath the soft dorsal fin is composed of large, expanded melanophores and always appears as the most densely pigmented area on larvae. The small melanophores along the ventral midline of the caudal peduncle usually disappear by ≈10 mm; two specimens, 12.4 and 13.3 mm, had one and two melanophores in this region, respectively. A single larva (11.7 mm) had one melanophore on the margin of the hypural plate. The pectoral and pelvic fin membranes are usually pigmented in larvae although the intensity and number of melanophores decreases with development. By 12 mm, melanophores entirely disappear from the pectoral fin base.

Early in the transformation period (≈14-20 mm), melanistic pigmentation rapidly appears over the dorsal surfaces of the snout, head, nape, body, and caudal peduncle and then continues to increase gradually ventrolaterally with development. Melanophores appear on the cheek, posteroventral to the eye by 14 mm, and begin to extend around the posteroventral portion of the orbit by ≈16 mm. Melanophores extend from the nape anteriorly joining the head pigment and laterally toward the body midline at the same time that pigment extends ventrolaterally from beneath the spinous dorsal fin. By ≈16 mm, some melanophores appear aligned along the myosepta over the anterior one-fourth of the body but never appear very distinct. By ≈15.5 mm, internal and external melanophores appear along the lateral midline anterior to the point of notochord flexion and just posterior to the head on specimens greater than ≈16 mm. Melanophores appear along the margin of the hypural elements in most specimens >16 mm. A melanophore appears at the point of articulation of most dorsal fin rays on specimens >15 mm, occasionally of some anal rays on specimens 13.5-19 mm, and of most anal fin rays on all specimens >19 mm. Melanophores are usually absent on the pelvic fin membrane on transforming larvae. Specimens >14 mm usually lack melanophores on the pectoral fin membrane. A single larva (19.3 mm) had a few small melanophores near the anterior base of the spinous dorsal fin membrane.

Melanistic pigmentation continues to intensify and increase gradually on pelagic juveniles, 20-35 mm. Melanophores cover the dorsal surface of the head and appear at the tips of the upper and lower lips by ≈24 mm. By ≈28 mm, melanophores extend over the cheek and around the posterior half of the orbit which becomes completely encircled by pigment at ≈30 mm. Melanophores appear on the gular region by ≈30 mm. Internal and external melanophores form a continuous irregular row along the lateral body midline by ≈20 mm. Melanophores also cover the ventrolateral area anterior to the soft dorsal fin between the dorsal margin and the lateral midline. At ≈21 mm, the large, expanded melanophores under the soft dorsal become concentrated along muscles surrounding the dorsal pterygiophores giving the appearance of vertical lines of pigment. Pigmentation on the body and caudal peduncle extends nearly to the ventral surface on specimens >28 mm. Areas of somewhat intensified pigmentation extend posteroventrally from the nape and spinous and soft dorsal fin bases appearing as faint saddles. A few small melanophores are occasionally present along the anterior portion of the spinous dorsal fin membrane near its base on pelagic juveniles <35 mm. The largest pelagic juvenile (35.3 mm) has melanophores scattered over the proximal two-thirds of the spinous dorsal membrane. Small melanophores appear on the caudal fin near its base by ≈25 mm.

Benthic juveniles, 65.0-74.8 mm, have about the same pigment pattern as that of the largest pelagic juvenile. However, they are more darkly pigmented due to the addition of numerous small melanophores over most surfaces of the head, body, and fins. The added pigmentation over the upper areas of the head and opercle, and on the body results from development of melanophores borne on the scales and skin tissue surrounding the scale pockets. This pigmentation overlies the larval and pelagic juvenile pigment which persists on benthic juveniles most obviously beneath the soft

dorsal fin where large melanophores remain. Melanophores on the dorsal portion of the opercle increase in number and intensify appearing as a patch of darker pigment. A single bar of pigment extends from the posteroventral margin of the eye across the cheek and opercle. Five faint saddles extend, one from the nape, two under the spinous dorsal fin, one under the soft dorsal fin, and one across the caudal peduncle, ventrolaterally from the dorsal surface of the body to just beneath the lateral midline. Spinous and soft dorsal fin membranes are covered by small melanophores with bands of more intense pigmentation extending across the fins as extensions of the body saddles. The largest benthic juvenile (74.8 mm) also has moderately intense pigmentation along the distal edge of the spinous dorsal fin membrane, concentrated immediately posterior to each dorsal spine. The caudal fin of benthic juveniles is lightly covered by small melanophores with sometimes a slightly darker bar of pigment apparent in the proximal third of the fin. A few small melanophores are present on the proximal half of the anal fin membrane, and small melanophores lightly cover the proximal half of the dorsalmost pectoral fin rays and the adjacent pectoral fin base.

Occurrence (Figures 9, 10).—Adult *S. zacentrus* occur from San Diego, Calif., to the Sanak Islands, Alaska, lat. 54.13° N, long. 161.37° W (Miller and Lea 1972; Hart 1973). Data from Niska (1976) show that 95% of the total Oregon trawl catch of *S. zacentrus* landed from 1963 through 1971 was taken from depths of 181-416 m. Highest concentrations of *S. zacentrus* found during a rockfish survey in 1977 between Pt. Hueneme and Cape Flattery were at depths of 183-272 m between Cape Blanco and the Columbia River, lat. 43°00′-47°30′ N (Harling et al. footnote 7). Larval *S. zacentrus*, including transforming specimens, in our collections were captured at stations ranging from 46 to 148 km offshore, ≈270-2,800 m depth. The data seem to indicate a more restricted offshore distribution for *S. zacentrus* larvae than for some other rockfish species: i.e., *S. entomelas*, 9-306 km; *S. pinniger*, 13-306 km; *S. flavidus*, 24-266 km; and *S. melanops*, 5-266 km (Richardson and Laroche 1979; Laroche and Richardson 1980). This is of interest as presumably the morphology of *S. zacentrus*, i.e., large head spines, stubby and deep body, would tend to enhance larval transport as suggested for *S. pinniger* (Richardson and Laroche 1979). The more restricted offshore occurrence of larvae may reflect the season of occurrence and associated wind regimes which are from the south and towards the coast in fall and winter. This would tend to minimize offshore dispersal. Pelagic juveniles occurred in about the same offshore area, 9-148 km offshore, as larvae. All demersal juveniles were taken from a single otter trawl haul made ≈40 km offshore, 91 m depth.

Reported parturition time for *S. zacentrus* is July off Oregon (Westrheim 1975). Larvae <10 mm were taken in August only, and larger pelagic specimens were taken August through December. Demersal juveniles were taken from a single October collection.

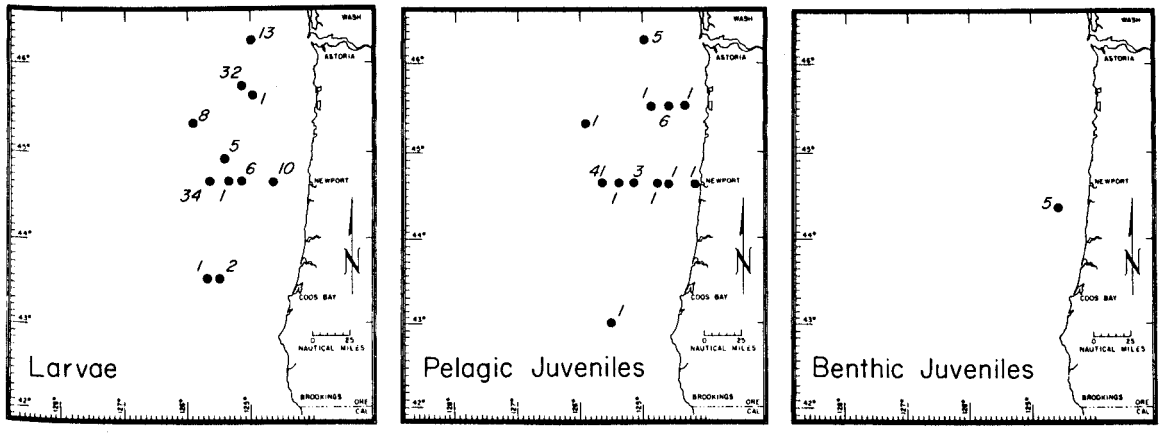

FIGURE 9.—Number of specimens and location of capture of larvae and juveniles of *Sebastes zacentrus* off Oregon (1961-78) described in this paper.

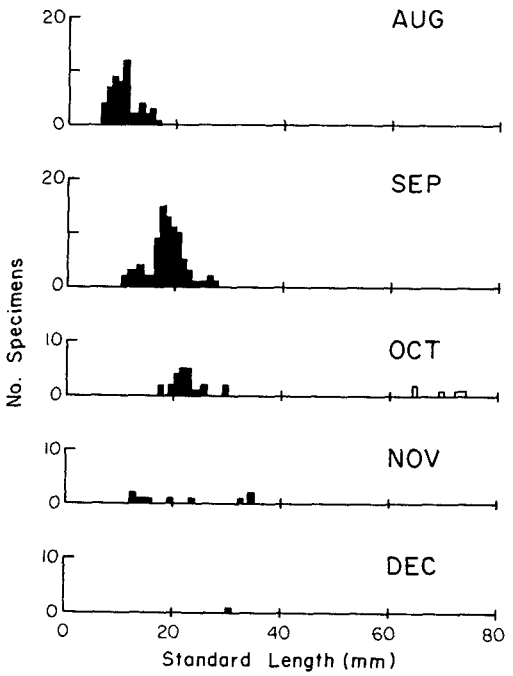

FIGURE 10.—Seasonal occurrence of larvae and juveniles of *Sebastes zacentrus* off Oregon. Data from 1961 through 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

COMPARISONS

Prior to this paper, developmental series of 12 of the 69 northeast Pacific (including Gulf of California) species of *Sebastes* had been described: *S. cortezi*, *S. crameri*, *S.* Gulf Type A, *S. flavidus*, *S. helvomaculatus*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanops*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger* (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980). Comparisons among a number of these species were discussed by Richardson and Laroche (1979) and Laroche and Richardson (1980).

Young stages of *S. entomelas* are relatively slender, with relatively light pigmentation, only moderate head spines, and pectoral and pelvic fins of moderate length. The ontogeny of *S. entomelas* is very similar to that of *S. flavidus* and *S. melanops* which also are moderately slender with only moderate head spines. Pigmentation develops in similar fashion in all three species, i.e., along the dorsal and lateral midlines, although it is less intense in *S. entomelas*. None of the three species develop pigment saddles. Larvae and juveniles of the three are separable by meristic characters.

Young *S. zacentrus* are comparatively deep bodied, with relatively large head and head spines, rather light pigmentation, moderately long pectoral fins, and relatively long pelvic fins especially in the early stages. Other deep-bodied (>30% SL) forms include *S. crameri*, *S. melanostomus*, and *S. pinniger*. Among these species, head spines are pronounced in all but *S. crameri*. The early lack of pigmentation and later development of five pigment saddles in *S. zacentrus* is shared with *S. crameri*, *S. helvomaculatus*, *S. levis*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger*, although the saddles of *S. zacentrus* are less distinct than in the other species. The presence of pigment along the dorsal body surface beneath the dorsal fins of postflexion larvae and pelagic juveniles of *S. zacentrus* is also seen in *S. flavidus*, *S. jordani*, and *S. melanops*. These three species develop a dense dorsolateral covering of melanophores that is not restricted to saddles. Larvae and juveniles of *S. zacentrus* are distinguishable from all of these species on the basis of meristic characters.

HEAD SPINE NOTES

A group of four similar species, *S. entomelas*, *S. flavidus*, *S. melanops*, and *S. mystinus* occur off Oregon and are difficult to identify and separate as larvae and juveniles. We have discovered that literature describing head spine patterns among this group of species is inaccurate and contradictory. After completion of our work on *S. flavidus* and *S. melanops* (Laroche and Richardson 1980) and during the course of our present work on *S. entomelas*, we found undescribed variation in head spine patterns among the species of this group. To insure accurate identification of variant specimens, we quantified and compiled data on spine pattern variation among this group of species. This new information is summarized here. It will aid in identification and separation of the species within the group, particularly of variant specimens.

The original description of *Sebastes entomelas* (Jordan and Gilbert 1880) described the preocular, supraocular, and postocular spines as minute, sharp, and concealed by scales. Phillips (1957) reported the above spines plus the tympanic spine were present on specimens "under about eight inches ..." (203 mm) long and become "nearly all obsolete" in large specimens with occasionally the

tips of the preocular spine weakly present. Hitz (1965) indicated that only the preocular spine is present. Hart (1973) stated that head spines are absent or weakly present, represented by the tip of the preocular spine. The original description of *S. mystinus* (Jordan and Gilbert 1881) stated that the "top of head" is without spines, with the exception of a very small nasal spine and sometimes a preocular spine present. Phillips (1957) and Hitz (1965) also reported this spine pattern. Miller and Lea's (1972) key to the rockfishes of California placed *S. mystinus* in the category of having head spines "weak or obsolete." Hart (1973) reported nasal and "... occasionally minute preopercular [sic = preocular] spines present" with other spines usually obsolete.

Supraorbital spines are small even in juveniles and have often been overlooked on *S. entomelas* and *S. mystinus*. We found that preocular, supraocular, postocular, and tympanic spines are usually present in both *S. entomelas* and *S. mystinus*, although the first two spines may be absent on one side of the head. The only exception observed was one juvenile *S. mystinus* which lacked both preocular spines. These spines eventually become overgrown by scales, tissue, and bone but using a dissecting microscope they are visible on all specimens examined including adults to 342 mm. However, scales and tissue must first be probed away before observation in *S. mystinus* >150 mm. In *S. entomelas* (115 pelagic juveniles, 49-78 mm) from Oregon, 4% lacked one preocular spine and 4% lacked one supraocular spine. In *S. mystinus* (135 pelagic juveniles, 51-71 mm) from Oregon, 6% lacked one preocular spine, and no specimen lacked a supraocular spine.

During our previous study of *S. flavidus* and *S. melanops* (Laroche and Richardson 1980) some variation in supraorbital head spine patterns (i.e., occasional presence of preocular and supraocular spines) was observed which could potentially cause confusion with *S. entomelas*. Although similar, *S. mystinus* has distinctive fin and scale counts (Laroche and Richardson 1980). Because we lacked material to quantify the spine variations, we excluded any variants (i.e., any specimens having preocular or supraocular spines) from the *S. flavidus* and *S. melanops* selected for the developmental series to insure positive identification. New data quantifying spine pattern variation in juveniles of these two species are presented here (Table 8). Presence of a preocular spine is quite rare but occurrence of a supraocular spine is more variable particularly in specimens from Oregon. Separation of *S. entomelas* from these two species is still possible for most specimens based on presence or absence of the preocular spine since >96% of *S. entomelas* and <2% of *S. flavidus* and *S. melanops* have one. Scale and fin ray counts further distinguish these species as described by Laroche and Richardson (1980).

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TABLE 8.—Percentage occurrence of preocular and supraocular spines in juvenile *Sebastes flavidus* and *S. melanops*.

Species	Preocular spines			Supraocular spines		
	Absent both sides	Absent one side	Present both sides	Absent both sides	Absent one side	Present both sides
S. flavidus:						
[1]British Columbia (*N* = 37;42-56 mm)	100	0	0	95	5	0
[2]Oregon (offshore) (*N* = 72;47-59 mm)	98	2	0	64	28	8
S. melanops:						
[1]British Columbia (*N* = 98;45-66 mm)	100	0	0	96	4	0
[2]Oregon (offshore) (*N* = 105;43-60 mm)	98	1	1	51	30	18
[1]Oregon (tidepools) (*N* = 101;43-60 mm)	100	0	0	69	23	8
[1]California (tidepools) (*N* = 80;41-53 mm)	80	0	0	70	9	1

[1]Benthic juveniles.
[2]Pelagic juveniles.

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APPENDIX TABLE 1.—Frequency distributions of soft fin rays, lateral line pores, diagonal scale rows below the lateral line, and gill rakers for juvenile and adult *Sebastes emphaeus*, *S. proriger*, *S. wilsoni*, and *S. zacentrus*.

		Pectoral fin rays			Dorsal fin soft rays				Anal fin soft rays			Lateral line pores																			
Species	Side	16	17	18	13	14	15	16	6	7	8	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	*N*	$\bar{x}$	SD
S. emphaeus[1]	Left	—	35	2	2	33	2	—	—	35	2	—	—	1	7	5	10	5	3	4	1	1	—	—	—	—	—	—	37	42.3	1.9
	Right	—	35	2								—	—	1	5	7	7	8	4	3	2	—	—	—	—	—	—	—	37	42.4	1.8
S. proriger[2]	Left	3	44	—	1	22	22	1	2	44	—	—	—	—	—	—	—	—	1	—	—	—	9	8	6	10	8	5	47	50.2	1.9
	Right	—	46	1								—	—	—	—	—	—	—	—	—	1	6	5	9	10	8	2	6	47	49.8	1.9
S. wilsoni[3]	Left	1	18	—	2	15	2	—	17	2	—	1	—	—	3	4	5	3	3	—	—	1	—	—	—	—	—	—	20	42.0	2.1
	Right	1	18	—								1	—	—	7	1	3	3	3	1	—	—	—	—	—	—	—	—	19	41.6	2.0
S. zacentrus[4]	Left	2	36	2	5	30	4	1	3	37	—	—	3	2	8	8	3	6	7	1	1	1	—	—	—	—	—	—	40	41.8	2.2
	Right	2	35	3								—	1	1	8	8	7	6	4	2	—	1	1	—	1	—	—	—	40	42.2	2.4

		Diagonal scale rows below lateral line																							
Species	Side	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	*N*	$\bar{x}$	SD
S. emphaeus	Left	1	2	2	9	8	8	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	37	45.0	1.6
	Right	—	—	2	4	6	13	4	3	1	1	—	—	—	—	—	—	—	—	—	—	—	34	45.9	1.6
S. proriger	Left	—	—	—	—	—	—	—	—	—	—	—	—	1	4	5	5	4	2	1	—	1	23	56.0	1.9
	Right	—	—	—	—	—	—	—	—	—	1	—	—	1	3	2	4	2	3	3	1	1	21	56.4	2.6
S. wilsoni	Left	—	—	1	1	1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	7	46.0	2.2
	Right	—	—	—	2	1	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	6	46.0	2.3
S. zacentrus	Left	—	—	—	—	4	4	2	4	5	3	1	—	—	1	—	—	—	—	—	—	—	24	47.9	2.2
	Right	—	—	1	1	4	4	3	2	5	3	—	—	1	1	—	—	—	—	—	—	—	25	47.6	2.7

		Gill rakers on lower bar of 1st gill arch									Gill rakers on upper bar of 1st gill arch					Total gill rakers on 1st gill arch														
Species	Side	23	24	25	26	27	28	29	30	31	9	10	11	12	13	32	33	34	35	36	37	38	39	40	41	42	43	*N*	$\bar{x}$	SD
S. emphaeus	Left	—	—	—	—	—	5	13	15	4	—	—	17	17	2	—	—	—	—	—	—	—	4	6	12	11	3	36	41.1	1.1
	Right	—	—	—	—	—	5	7	22	3	—	—	18	16	3	—	—	—	—	—	—	—	4	3	14	13	3	37	41.2	1.1
S. proriger	Left	—	—	—	11	17	18	1	—	—	—	7	32	8	—	—	—	—	—	1	11	18	12	4	1	1	—	48	38.3	1.2
	Right	—	—	—	8	23	12	2	1	—	—	9	35	2	—	—	—	—	—	2	11	18	13	1	—	—	—	45	38.0	0.9
S. wilsoni	Left	—	—	—	—	2	9	8	1	—	—	18	2	—	—	—	—	—	—	—	—	2	8	8	2	—	—	20	39.5	0.8
	Right	—	—	—	—	1	10	7	2	—	—	16	4	—	—	—	—	—	—	—	—	1	10	4	4	1	—	20	39.7	1.0
S. zacentrus	Left	1	7	17	14	1	—	—	—	—	1	34	5	—	—	1	—	6	18	10	5	—	—	—	—	—	—	40	35.3	1.0
	Right	1	3	17	18	1	—	—	—	—	3	34	3	—	—	1	—	4	16	16	3	—	—	—	—	—	—	40	35.4	1.0

[1]Thirty-five *S. emphaeus* collected at lat. 40°12.9′ N, long. 124°23.7′ W off northern California, and two specimens were collected from Hein Bank (lat. 48°21.5′ N, long. 123°02.5′ W).
[2]All *S. proriger* were collected off Oregon between lat. 43°59′ and 45°09′ N.
[3]*Sebastes wilsoni* were collected off Oregon and California between lat. 36°52′ and 45°56′ N.
[4]All *S. zacentrus* were collected off Oregon between lat. 43°23.7′ and 45°09′ N.

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CONTRIBUTION TO THE LIFE HISTORY OF THE DEEP-SEA KING CRAB, *LITHODES COUESI*, IN THE GULF OF ALASKA[1]

DAVID A. SOMERTON[2]

ABSTRACT

Lithodes couesi is a deepwater relative of the commercially important Alaskan king crabs, *Paralithodes camtschatica*, *P. platypus*, and *L. aequispina*. Compared with the *Paralithodes* species, which are primarily restricted to the continental shelf, *L. couesi* displays a variety of features which appear to be adaptations for life in deeper water on the continental slope, including elongated legs, red coloration, inflated branchial chambers, asynchronous spawning, and large eggs. Fecundity of *L. couesi* increases asymptotically with carapace length according to the relationship $E = 4{,}329 - 3.19 \times 10^9 e^{-0.172L}$. The size of 50% maturity is reached at 91.4 mm for males and at 80.2 mm for females.

The deep-sea king crab, *Lithodes couesi*, is a little known relative of the three species of king crab, *Paralithodes camtschatica*, *P. platypus*, and *L. aequispina*, commercially harvested in Alaska. Since its original description (Benedict 1895), *L. couesi* has been discussed only in taxonomic works (Rathbun 1904; Schmitt 1921; Makarov 1938; Sakai 1971); other than its geographical distribution (San Diego, Calif., to Onohama, Japan) and depths of occurrence (542-1,125 m), nothing has been reported concerning the life history of this species.

Considering its rather large size and conspicuous bright red color, it is surprising that *L. couesi* has not received more attention. One reason for this is that benthic sampling surveys infrequently reach the depths inhabited by *L. couesi*, and those that do typically are not designed to catch a large number of specimens. However, in 1979 a National Marine Fisheries Service (NMFS) cruise surveying the commercial fishing potential of seamounts in the Gulf of Alaska caught nearly 1,500 *L. couesi* in large baited traps. The present study is based on these specimens.

Although *L. couesi* is unlikely soon to become the target of a commercial fishery due to the great depths it inhabits, the high value of crab and the fluctuating supply of other Alaskan crab species may stimulate technological developments making deepwater crab fishing more economical. Such developments have already occurred in the fishery for another deepwater crab, *Geryon quinquedens*, along the east coast of North America (Wigley et al. 1975). This paper is intended to provide a comparison of life history characteristics between *L. couesi* and shallow-water king crabs, as well as to provide some information needed by fisheries managers in the event *L. couesi* were to become commercially important.

METHODS

Samples of *L. couesi* were collected between 31 May and 5 July 1979 on an NMFS stock assessment cruise to eight seamounts located in the central Gulf of Alaska (Figure 1). All specimens except three were captured in baited traps. Three types of trap were used: rectangular sablefish, *Anoplopoma fimbria*, traps measuring 0.8 m × 0.8 m × 2.5 m and covered with 8.9 cm (bar measure) webbing; conical sablefish traps measuring 0.7 m high × 1.2 m base diameter × 0.9 m top diameter and covered with 7.5 cm webbing; and rectangular king crab traps measuring 1.8 m × 1.8 m × 0.6 m and covered with 11.4 cm webbing. Traps were arranged at 91.5 m intervals along a 1,006.5 m groundline having surface floats connected to both ends. A typical set of gear included four or five of each type of sablefish traps, plus two king crab traps in 8 of the 25 sets. A total of 232 traps (102 conical, 114 rectangular, 16 king crab) were set. Three small specimens of *L. couesi* were obtained in one haul of a bottom trawl.

All seamounts were extremely steep sided, rising approximately 3,000 m from the seafloor to relatively flat summits composed of rock outcrops

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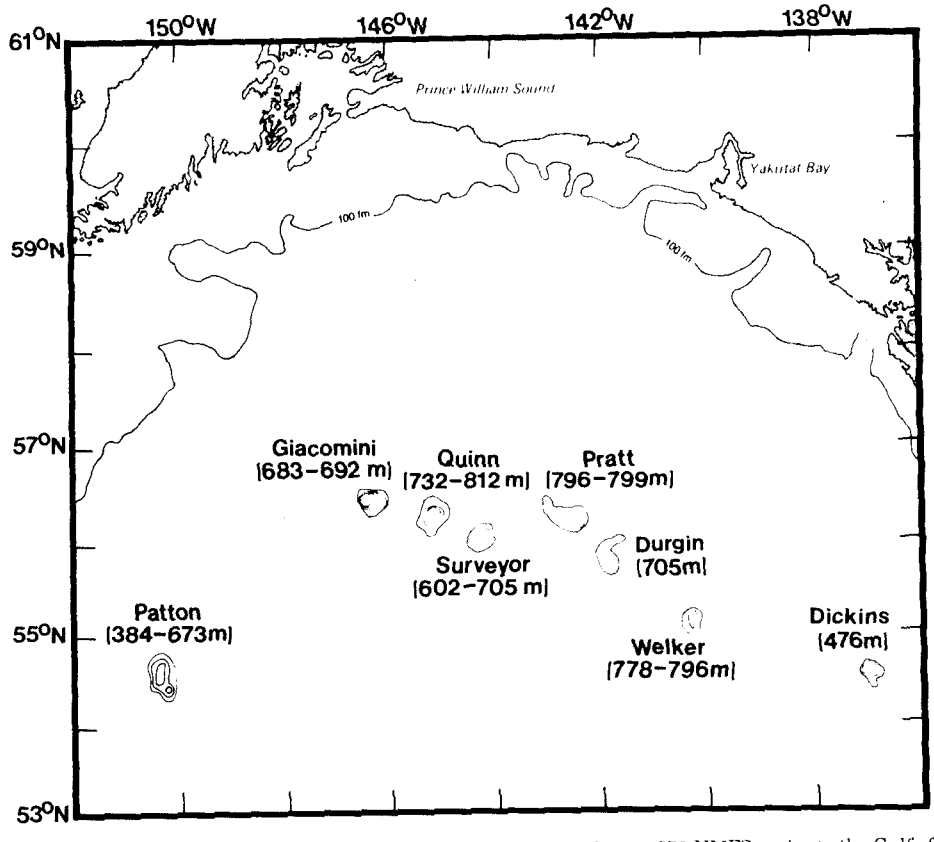

FIGURE 1.—Location of the eight seamounts which were surveyed on a 1979 NMFS cruise to the Gulf of Alaska. The range of sampling depths on each seamount is indicated.

with intervening sediments. This physiography limited sampling to the seamount tops. Sampling depths ranged from 384 m on the Patton Seamount to 850 m on the Quinn Seamount.

The carapace lengths of all crabs and the right chela heights of males were measured to the nearest 0.1 mm using vernier calipers (see Wallace et al. (1949) for a description of these two measurements). The reproductive condition of females was scored according to the following six-point scale:

1) Immature—white undeveloped ovaries and no egg remnants on the pleopod bristles.
2) Virgin—orange developed ovaries and no egg remnants on the pleopod bristles.
3) New eggs—orange external eggs with no evidence of embryonic eyes.
4) Developing eggs—tan external eggs with obvious dark embryonic eyes.
5) Hatching eggs—partial clutch of well-developed eggs, with remnants of hatched eggs attached to pleopod bristles and occasionally with prezoea on the egg mass.
6) Completely hatched—no external eggs, but remnants of eggs, especially the egg funiculi, attached to the pleopod bristles.

Abdomens, complete with attached eggs, were removed from a selected number of females and preserved in buffered 10% Formalin.[3] In the laboratory, the pleopods from females with new and developing eggs were removed and dried. After freeing the eggs from the pleopods, the total clutch was weighed and a subsample was weighed and counted. Total egg number was calculated by dividing total clutch weight by the average egg weight of the subsample. Maximum egg length was measured to 0.1 mm using an ocular micrometer. Measured eggs were well developed and

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

apparently close to hatching, and had been stored in 33% isopropyl alcohol after being fixed in Formalin.

RESULTS AND DISCUSSION

Depth Distribution

Specimens of *L. couesi* were collected in every trap set from the shallowest in 384 m to the deepest in 850 m. Four sets on two seamounts were at depths less than the depth range (542-1,125 m) previously recorded for this species (Sakai 1971).

Lithodes couesi occurs shallower on seamounts than on the continental slope. This hypothesis is supported by the results of a concurrent NMFS survey of the southeast Alaska continental slope that sampled roughly the same latitudes (54°-58° N) and depths (237-711 m) and used the same types of traps as the seamount study. Although depths <550 m were thoroughly sampled, specimens of *L. couesi* were not taken in <592 m (H. Zenger[4]).

The shallow distribution of *L. couesi* on seamounts may be due to the absence of a predator or competitor which is able to exclude it from similar depths along the continental slope. Because seamounts are isolated from the ocean surface and from coastal areas, they are essentially submarine islands inhabited only by species that are able to tolerate the available depth range and that possess sufficient dispersal capabilities to reach seamounts from the continental slope. If a predator or competitor were unable to colonize the seamounts, *L. couesi* may respond by expanding its range into shallower water. A similar pattern of competitive release and altitudinal expansion has been reported for birds on South Pacific islands (Diamond 1975).

Size Distribution

The size distribution of each sex was nearly unimodal with a mode at about 108 mm for males and 92 mm for females (Figure 2). The lack of an appreciable number of crabs <70 mm is probably due to size selectivity of the sampling gear, rather than a lack of small crabs on the seamount tops, because three of the four smallest specimens were caught with a bottom trawl in an area of the Patton Seamount where only larger crabs were obtained with traps.

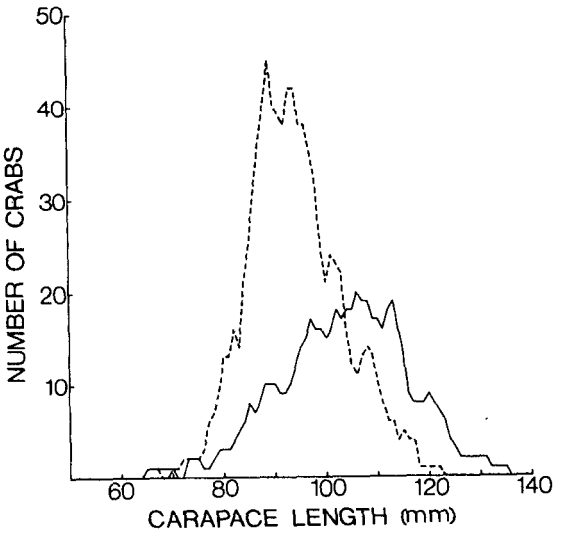

FIGURE 2.—Size distribution of male (solid line) and female (dotted line) *Lithodes couesi* by 2 mm size intervals from trap samples from Gulf of Alaska seamounts.

Other species of king crabs, especially *P. camtschatica* and *P. platypus*, display size stratification with depth; adults generally occur deeper than juveniles (pers. obs.). To determine if *L. couesi* also stratify, crab size was regressed against depth. Only the sizes of crabs from sablefish traps were used in the regression because king crab traps caught significantly larger crabs than sablefish traps when both types were fished together (t-test, $P<0.001$) and because king crab traps were not used on every seamount. For males, the slope of the regression line was not significant ($P = 0.289$). For females, the slope was significant ($P = 0.030$) and negative, indicating that larger females occur in shallow water. However, there was little variation in sampling depth on each seamount; thus, size variation with depth cannot be separated from size variation between seamounts.

Sex Ratio

In total, 880 females and 577 males were captured in 24 trap sets. The large preponderance of females suggested that the sex ratio may not be 1:1. If the sex of each specimen were independent of the sex of other specimens in the same set, then the observed proportion male, 0.40, is signifi-

[4]H. Zenger, Fishery Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. commun. June 1980.

cantly different than 0.50 ($Z = 7.8$, $P \leq 0.001$). Sex ratio, however, was not homogenous between trap sets ($\chi^2 = 137.5$, $P \leq 0.0001$), indicating that the sex of each specimen was not independent of other specimens but highly correlated. Thus, females tended to be caught with other females and males tended to be caught with other males. Segregation by sex is also commonly observed for *P. camtschatica* (pers. obs.).

Although the sexes of crabs within each set are correlated, the hypothesis of a 0.50 proportion male in the population can still be tested if each set is assumed to be an independent random sample. The test is made by calculating a *t*-statistic from the mean and variance of the proportion male within individual trap sets. Because the number of crabs within each set varied considerably, the mean proportion was calculated as a weighted average, with the weighting factors equal to the number of crabs in each set (Cochran 1943). The *t*-test was not significant ($t = 0.396$, $P = 0.86$); thus, a 1:1 sex ratio is not rejected.

Female Reproductive Condition

The number of female *L. couesi* in each of the six categories of reproductive condition is shown as a function of size in Figure 3. Eighty-six percent of the females examined were mature (categories 3-6). Virgin females had partially developed ovaries and appeared to have never spawned previously. Assuming virgin female *L. couesi* require the same length of time to complete maturity as "pubescent" female *P. camtschatica* (Powell et al. 1973), their first spawning will occur soon after their next molt in the following spring.

Mature female *L. couesi* display more heterogeneity in their reproductive condition than female *P. camtschatica*. This is exemplified in the following table, where the percentage of mature female *L. couesi* in each of the four mature reproductive categories is compared with the equivalent reproductive categories of female *P. camtschatica* collected in the eastern Bering Sea at the same time as the seamount survey.

Species	*New eggs*	*Developing eggs*	*Hatching eggs*	*Completely hatched eggs*
L. couesi	50	35	6	9
P. camtschatica	97	..... 2		1

Although no distinction was made between developing and hatching eggs for *P. camtschatica*, it is evident that *P. camtschatica* had nearly completed spawning and were carrying new eggs, whereas *L. couesi* had not completed spawning and were carrying eggs in a variety of developmental stages.

If *L. couesi* are similar to *P. camtschatica* in spawning soon after hatching the previous clutch, then the heterogeneity in their reproductive condition can be interpreted in either of two ways. First, *L. couesi* were sampled midway in their spawning season; therefore, the maturing eggs hatch later in the season. Second, *L. couesi* were sampled at the end of the spawning season; therefore, the maturing eggs are from spawning in the current season and hatch in the succeeding year. The difference in these interpretations

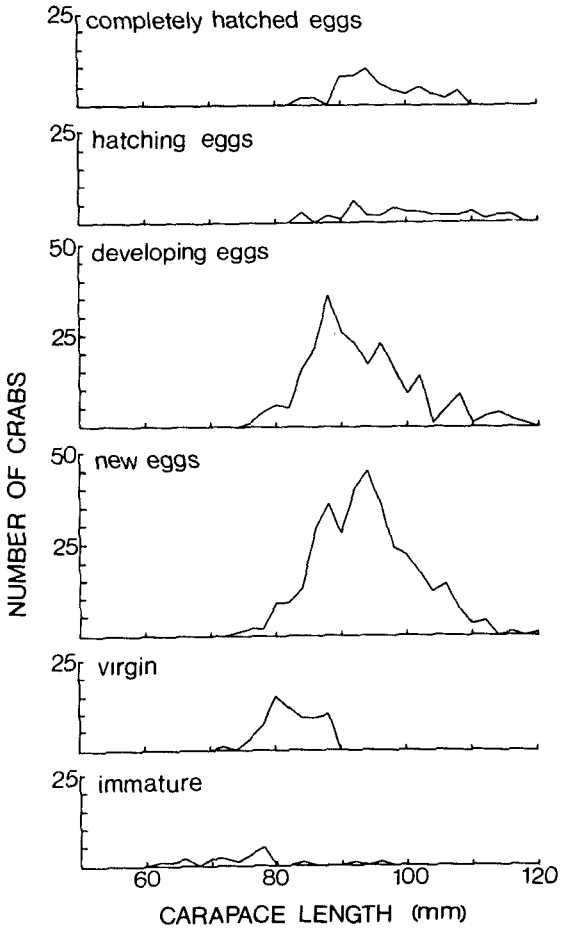

FIGURE 3.—Number of female *Lithodes couesi* by 2 mm size intervals in each of the six categories of reproductive condition described in the text.

reflects the degree of reproductive synchrony in the population. If the first interpretation were correct, *L. couesi* could be as synchronized as *P. camtschatica* and the heterogeneity in reproductive condition could merely be due to fortuitous timing of the survey. But if the second interpretation were correct, *L. couesi* would be quite asynchronous compared with *P. camtschatica* because, at least in *P. camtschatica*, the eyed (developing) eyes would have been spawned at least 4 mo previous to sampling (G. C. Powell[5]). Although the embryological development of *L. couesi* eggs was not studied—this would be necessary to completely resolve the question—I believe that the second interpretation, that *L. couesi* has an asynchronous spawning, is correct because the eggs classified as developing were clearly in a much earlier stage of development than were the hatching eggs.

The asynchronous spawning of *L. couesi* is probably related to the great depths which it inhabits. Temperate species having planktotrophic larvae typically have synchronous breeding cycles because of the rather brief periods which are optimum for larval survival. Since seasonal fluctuations are damped with depth, *L. couesi* may be unable to detect seasonal cues with precision, or more likely, may have larvae which do not rise to the euphotic zone and do not need to be synchronized with the surface production cycle. Asynchronous spawning was also observed for another deepwater crab, *Geryon quinquedens* (Haefner 1978). Crustaceans living at depths greater than *L. couesi* have such asynchrony in spawning that seasonal peaks in spawning activity are absent (Rokop 1977).

Size of Maturity

Maturity of females was determined by the presence of eggs or egg remnants on the pleopods. Thus, reproductive categories 1 and 2 were considered immature and categories 3 to 6 were considered mature. Maturity of males was determined from the size of the chela relative to the size of the carapace using a method discussed in Somerton (1980). This method assumes that when chela and carapace measurements are plotted against each other on a double logarithmic scale, the points lie along two straight lines, one describing the relative growth for juveniles, the other describing the relative growth for adults. A computer technique was used to iteratively fit two lines to the data until the best fit (minimal residual sum of squares) was achieved (Figure 4). Maturity was then based on the final assignment to one of the two categories.

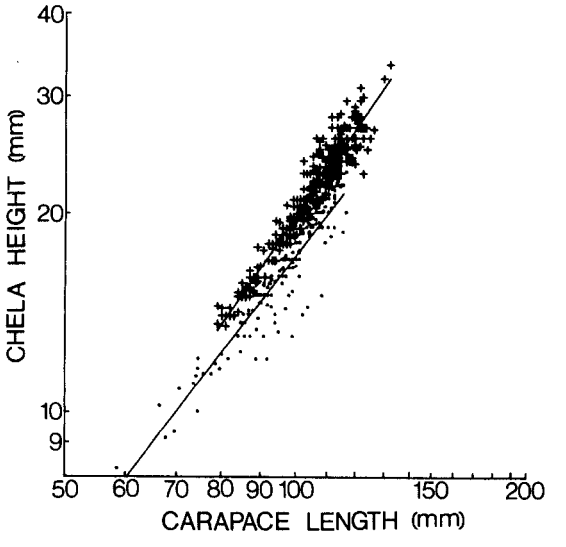

FIGURE 4.—Classification of male *Lithodes couesi* chela height and carapace length measurements into juvenile (dots) and adult (pluses) categories. The relative growth of the chela is described for juveniles by the lower line (CH = 1.52 CL − 4.17; SD for intercept and slope are 0.19 and 0.04) and for adults by the upper line (CH = 1.70 CL − 4.83; SD for intercept and slope are 0.13 and 0.03). Regression methods of Somerton (1980), see text.

The size of 50% maturity was estimated by fitting a logistic equation to the percentage mature by size using the methods discussed in Somerton (1980), then evaluating the fitted equation to determine the size corresponding to 50% mature. Percentage mature and the fitted logistic equation are shown for both sexes in Figure 5. Estimated sizes of 50% maturity were 91.4 mm for males and 80.2 mm for females.

Fecundity

Fecundity of *L. couesi* increases up to a size of 95 mm and remains fairly constant thereafter (Figure 6). The apparent curvilinear relationship between fecundity and size is similar to that reported for *P. platypus* (Sasakawa 1975) but unlike the strict linear relationships reported for

[5]G. C. Powell, Fishery Biologist, Alaska Department of Fish and Game, Division of Commercial Fisheries, P.O. Box 686, Kodiak, AK 99615, pers. commun. June 1980.

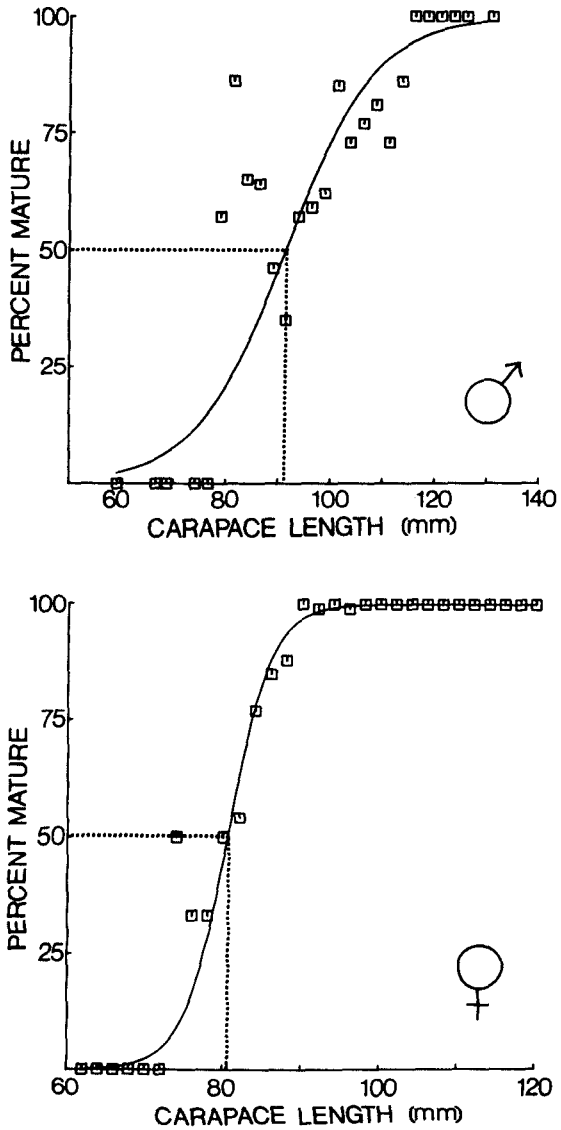

FIGURE 5.—Percentage of male (upper) and female (lower) *Lithodes couesi* classified adult as a function of size. The size of 50% maturity was estimated by first fitting a logistic equation to the data, then determining the size (shown by dotted lines) corresponding to 50% mature.

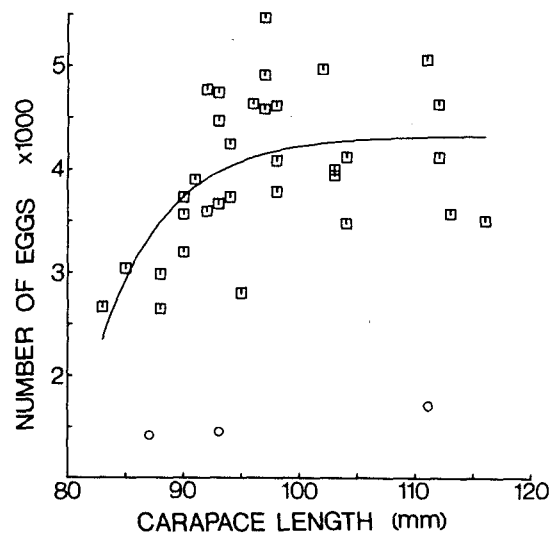

FIGURE 6.—Fecundity of *Lithodes couesi* as a function of size. An asymptotic curve was fit to the data using methods described in the text. Three specimens (shown by circles) had conspicuously fewer eggs. Although these females did not appear to be damaged, their fecundities were excluded from the analysis.

P. camtschatica (Haynes 1968), *L. aequispina* (Hiramoto and Sato 1970), and *L. antarctica* (Guzman and Campodonico 1972).

An attempt was made to develop an appropriate functional relationship to describe the fecundity and size of *L. couesi*. To determine whether or not this relationship should be curvilinear, the fit of a second degree polynomial was statistically compared with that of a straight line. The coefficient of the squared term of the polynomial was highly significant ($F = 12.23$, $P < 0.001$), indicating that the polynomial fit the data better than a straight line; however, a second degree polynomial was not a good relationship because the predicted fecundity did not increase monotonically with size. Since it is unlikely that fecundity reaches some maximum and then diminishes with size, an asymptotic curvilinear relationship was considered. The chosen equation is $E = E_\infty - Ae^{-BL}$, where E is egg number, L is carapace length, E_∞ is a parameter representing the theoretical maximum number of eggs that can be carried, and A and B are parameters controlling the rate at which the maximum egg number is achieved. Using nonlinear regression, the best fit was obtained when $E = 4{,}329 - 3.19 \times 10^9\ e^{-0.172L}$ (Figure 6).

If the number of eggs a female could carry were limited either by the length of the pleopods or by the volume of the brood chamber enclosed between the abdomen and the sternum, then fecundity should increase in proportion to the carapace length raised to a power of one or greater, that is, fecundity should be an upwards concave function of size. The best fitting equation is concave downwards, which indicates that some other mechanism limits fecundity in *L. couesi*. One possible explanation is that the low oxygen con-

centrations at the depth inhabited by *L. couesi* reduce the ability of females to aerate clutches larger than some fixed size.

One consequence of an asymptotic form to the fecundity and size relationship is that the reproductive effort, or the proportion of the total energy intake devoted to reproduction, must decrease over some part of the reproductive lifespan of *L. couesi*. Theory predicts and many animals display an increase in reproductive effort with age (Pianka and Parker 1975). Since fecundity appears to be fairly constant over approximately one-half of the mature size range of *L. couesi*, reproductive effort could increase only if either egg size increased with age or growth ceased. Individual dried egg weight, however, does not increase with crab size ($P = 0.15$), and the lack of wear and accumulation of epifauna on the exoskeleton suggests that molting, and presumably growth, continues throughout the life of females.

Egg Size

Lithodes couesi eggs in a late stage of development have a mean length of 2.3 mm (SD = 0.076, $N = 33$). This size is quite similar to previous estimates of mean or median egg size reported for other species in the genus *Lithodes*—*L. antarctica*, 2.2 mm (Guzman and Campodonico 1972); *L. aequispina*, 2.1 mm (Hiramoto and Sato 1970)—but roughly twice the egg size reported for species in the genus *Paralithodes*—*P. camtschatica*, 1.0 mm (Haynes 1968); *P. platypus*, 1.2 mm (Sasakawa 1975).

The larger size of *Lithodes* spp. eggs compared with *Paralithodes* spp. eggs conforms to a theory of egg size and pattern of larvae development first discussed by Thorson (1950), which proposes that benthic invertebrates generally have large eggs and lecithotrophic larvae in high latitudes or in deep water, but have small eggs and planktotrophic larvae in other areas. At great depths or at high latitudes water temperatures are low and larval development is protracted. Species may compensate for slow larval development by producing larger and more yolky eggs, which in turn result in larger larvae with greater energy reserves. These larval features may be necessary to allow the larvae either to migrate to the surface, to capture a broader array of food items, or to forgo feeding entirely. Stage 1 zoeae of *L. couesi* have conspicuously more yolk than *P. camtschatica* larvae in the same stage of development (J. Bowerman[6]), but it is unclear whether or not these larvae migrate to the surface. Unusually large eggs have been previously reported for abyssal shrimp (Zarenkov 1965) and abyssal crabs (Garth and Haig 1971).

Parasites

Of the 674 female *L. couesi* examined, 5 were parasitized by the rhizocephalan, *Briarosaccus callosus*. All five females were >90 mm and, on the basis of size alone, should have been mature, but none were carrying eggs and all had unusually small pleopods compared with uninfected crabs of similar size. Thus, similar to other species of crabs (Barnes 1974), *L. couesi* females are apparently castrated by *B. callosus*. One male *L. couesi* was also observed with the parasite; however, the abdomens of males were not routinely examined and other parasitized males could have been missed. *Briarosaccus callosus* has been previously reported as a parasite of *L. couesi* (Boschma 1970).

Adaptations for Life on the Upper Slope

Lithodes couesi is conspicuously different in appearance (Figure 7) from the shallow-water king crabs, *P. camtschatica* and *P. platypus*, because of three features: 1) bright red, 2) inflated branchial chambers, 3) elongated legs. All of these features are apparently adaptations for living in deeper water.

The red coloration of deepwater crustaceans has long been a subject for speculation, but the general consensus is that within some range of depth, red is cryptic due to the rapid attenuation of red light originating from the surface and the low in situ production of red light from bioluminescence (Marshall 1954). At depths greater than this range, the ambient light is too weak for visual predators and crustaceans are often white or transparent (Zenkevich and Birstein 1956); at depths shallower than this range, red may be too conspicuous to visual predators and the red cartenoid pigments are often complexed with proteins to produce blue, green, and brown pigments (Goodwin 1960).

Crabs living on the continental slope have branchial chambers which are more inflated than

[6]J. Bowerman, Fishery Biologist, Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615, pers. commun. June 1980.

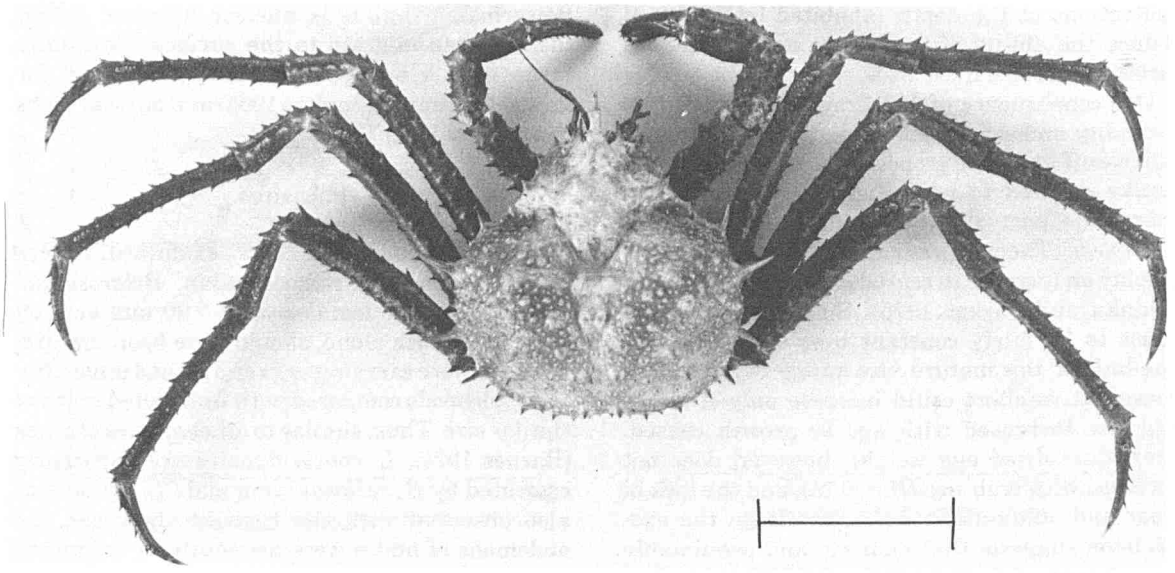

FIGURE 7.—A male specimen of *Lithodes couesi* (a 100 mm bar is included for scale). Generally, *L. couesi* are bright red with the carapace being somewhat lighter than the legs; however, occasional specimens will be light pink. Great variability was found in the length of the spines along the lateral margins of the carapace. The above specimen has especially long spines.

those of crabs living on the shelf. The degree of branchial inflation was quantified by Takeshita et al. (1978) for three anomuran crabs in the family Lithodidae—*P. camtschatica*, *L. aequispina*, *Paralomis verrilli*—and four brachyuran crabs in the genus *Chionoecetes*—*C. bairdi*, *C. opilio*, *C. japonicus*, *C. tanneri*—using moire photography. For both the anomuran and brachyuran crabs, the branchial chambers were more inflated in the species living at greater depths. In the present study, a similar type of assessment was not made for *L. couesi* due to a lack of suitable photographic equipment; however, the inflation of the branchial chambers appears to be greater than *L. aequispina* (a shallower species) and less than *P. verrilli* (a deeper species). Although I lack data to demonstrate that enlarged gills are associated with inflated branchial chambers, Rathbun (1893), in the original description of *C. tanneri* (a deep species), remarked that "The carapace is much swollen at the branchial regions" compared with *C. opilio* (a shallower species) and that the gills of *C. tanneri* are about two-fifths longer than the gills of an equal-sized specimen of *C. opilio*.

The inflation of crab branchial chambers with increasing depth is related to the distribution of oxygen in the sea. Typically, the concentration of dissolved oxygen decreases with depth until an oxygen minimum zone is reached, then increases thereafter. In the region of the Gulf of Alaska near the major seamounts, a minimum oxygen concentration of 0.5 ml/l, roughly 7% of the surface concentration, occurs at 1,000 m (Favorite et al. 1976). Since the combined depth ranges of the species considered by Takeshita et al. (1978) extend from 1,400 m to the intertidal, the deeper these species occur, the lower the oxygen concentrations they must deal with. Inflated branchial chambers or unusually large gills have been reported for a brachyuran crab, *Lophorochinia parabranchia* (Garth and Haig 1971), and a mysid, *Gnathophausia ingens* (Childress 1971a), both of which are primarily restricted to oxygen minimum zones.

Lithodes couesi has two additional morphological features allowing respiration in low oxygen concentrations: large exhalent openings and large scaphognathites (appendages located in the exhalent openings and used for pumping water over the gills). Enlargement of these features, compared with related shallow-water lithodid crabs, implies that a relatively greater volume of water is pumped over the gills. *Gnathophausia ingens* was also found to have a large ventilation volume compared with related shallow-water species (Childress 1971a).

To demonstrate that walking legs are more elongated for crab species inhabiting greater depths, two leg dimensions, merus length and propodus length, were compared between deep and shallow species (Table 1). Two trends in relative leg dimensions are evident. First, the legs become thinner with depth; that is, merus height to merus length decreases. Second, the distal portion of the legs becomes relatively longer with depth; that is, propodus length to merus length increases.

TABLE 1.—Merus height (MH) and propodus length (PL) of the right first walking leg, expressed as a fraction of merus length (ML), are shown for one adult male specimen of three species in the family Lithodidae and three species in the genus *Chionoecetes*. Under each taxonomic section, species are arranged according to depth, with the shallowest species at the top, except for *C. bairdi* and *C. opilio*, which occur at similar depths.

Species	MH/ML	PL/ML
Anomura:		
Paralithodes platypus	0.286	0.715
Lithodes aequispina	.255	.823
L. couesi	.189	.882
Brachyura:		
Chionoecetes opilio	.222	.578
C. bairdi	.209	.487
C. tanneri	.158	.655

The selective advantage of long slender legs for deepwater crabs is not obvious. Barnes (1974) suggested that: "Many abyssal crabs have long slender legs for crawling about over soft bottoms." Presumably, this means that the propodi and the dactyli are placed flat on the substrate and used, like snowshoes, to spread the body weight more evenly. However, underwater photographs of both *L. couesi* (Figure 8) and *Geryon quinquedens* (see Wigley et al. 1975, fig. 4) show individuals walking over apparently soft bottoms on the tips of the dactyli. An alternative explanation, suggested by Childress (1971b), is that reduced musculature in

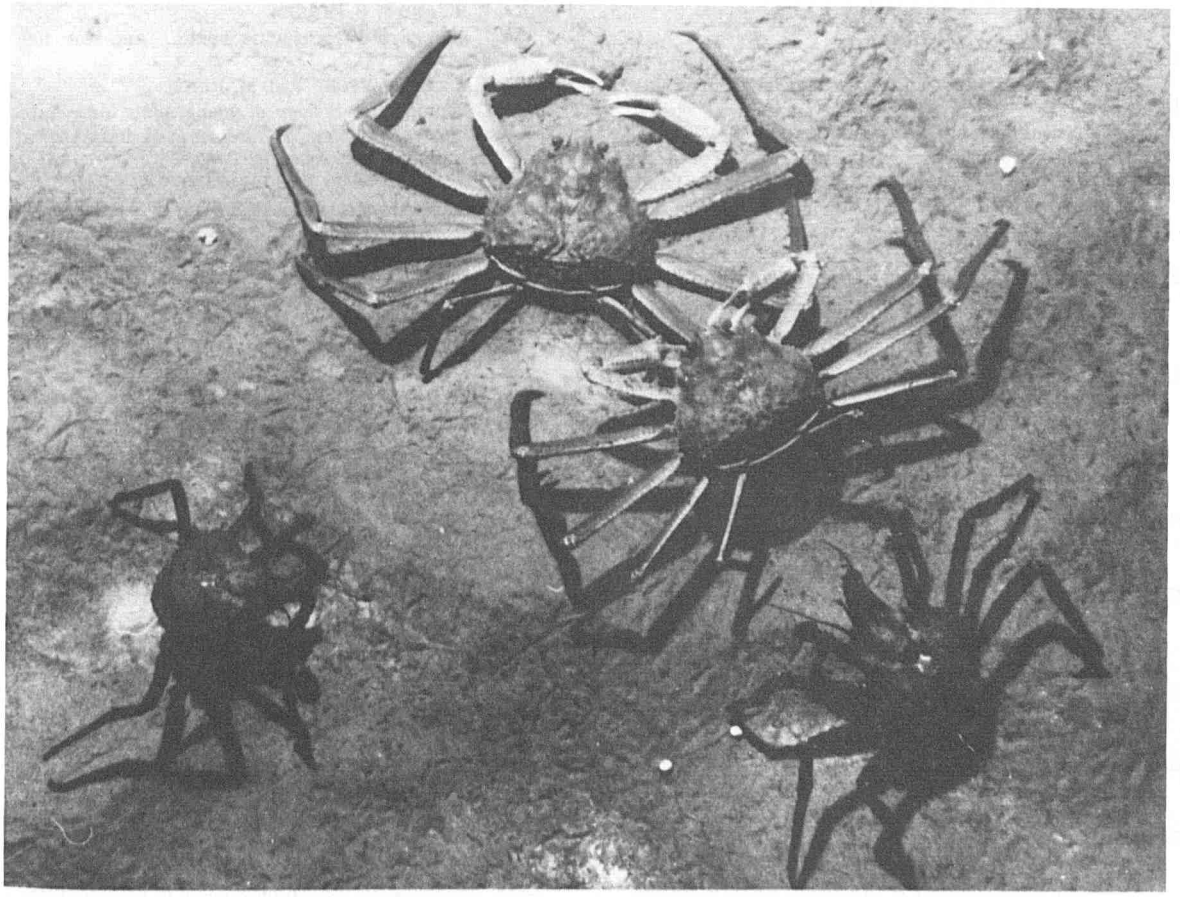

FIGURE 8.—Photograph on the Patton Seamount (500 m) of *Lithodes couesi* (lower) and *Chionoecetes tanneri* (upper) walking across a soft bottom on the tips of their dactyli (photograph taken by P. Raymore).

deepwater crustaceans requires less energy to maintain and thus represents an adaptation for energetic efficiency in a habitat where food is scarce. In addition, long legs may allow a crab to move more rapidly or more economically by taking fewer, larger steps to travel a given distance.

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THE EFFECT OF THE BOTTOM ON THE FAST START OF FLATFISH *CITHARICHTHYS STIGMAEUS*

P. W. WEBB[1]

ABSTRACT

Fast starts of the speckled sanddab, *Citharichthys stigmaeus*, were initiated by a 1 volt per centimeter direct current electric shock and recorded on movie film at 250 frames per second. Observations on kinematics and performance were made for fast starts of fish accelerating in the water column and from a grid located at a distance of 0, 1, 3, or 6 cm above the true bottom. During acceleration the body was bent into a U-shape relative to the bottom. The body sustained a direct push against the grid when accelerating from that grid. The amplitude of propulsive movements of fish accelerating from the grid was larger than acceleration movements of fish in the water column away from the bottom, because the potential for energy wastage due to recoil of the body was prevented by the grid. The distance between the grid and the bottom had no effect on fast starts, ruling out any hydrodynamic ground effect. Motion of fish accelerating in the water column was continuous and predominantly in the horizontal plane. There was little motion of fish accelerating from the grid until they started pushing against that grid. Motion was predominantly in the vertical plane. The resultant distance traveled by fish accelerating from the grid, measured at the end of the principal acceleration period exceeded that of fish accelerating in the water column. Velocities and acceleration rates were highest for fish accelerating from the grid. It was concluded that contact with the sea bottom would enhance fast-start performance of flatfish.

Fish of the order Pleuronectiformes are unique because the adults lie on one side. The habit of inclining to one side is common among other benthic fish that are normally vertically oriented, but no other group shows the specialized morphological adaptations of flatfish. Various observations on benthic fish suggest that inclining the body or lying on one side is advantageous for camouflage and crypsis (Norman 1966). Large locomotor advantages could also accrue, especially to flatfish orienting their body axis parallel to the ground.

Improvements in locomotor performance of flatfish could occur through two mechanisms: hydrodynamic ground effect and pushing against a rigid substrate. The hydrodynamic ground effect occurs through interaction of the downwash from propulsive surfaces with the ground (i.e., the sea bottom) and increases effective thrust and decreases effective drag (Bramwell 1976; Lighthill 1979). It has been described for birds (Withers and Timko 1977) and for pectoral fin propulsion of the mandarin fish, *Synchropus picturatus* (Blake 1979). Pushing against the substrate is obviously more energy efficient than pushing against water because more muscle power is converted into body motion rather than wasted in accelerating fluid. It is utilized by macrurous decapods (Webb 1979). The relative importance and effectiveness of these mechanisms will depend on how flatfish move their bodies near the ground.

The following experiments were performed to determine if the sea bottom could influence fast-start (acceleration) movements and performance of a typical flatfish. Emphasis was placed on fast starts because of their importance in evasion of predators and in catching elusive prey (Eaton and Bombardieri 1978; Webb and Skadsen 1980).

METHODS

Fish

Speckled sanddab, *Citharichthys stigmaeus* Jordan and Gilbert (family Bothidae) were used. Fish were caught in dip nets by divers along the southern California coast, hence avoiding the damage typical of trawl-caught specimens. Fish were held in a 60,000 l tank at 14° C. They were fed twice a week on frozen brine shrimp.

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Procedures

Individual speckled sanddabs were starved for 24 h. Each fish was lightly anesthetized (MS-222)[2] and a white thread was sewn above the center of mass of the stretched-straight body calculated from previous measurements on a subsample of fish. This reference facilitated later film analysis. Each fish was then placed in an observation arena and allowed to recover for 24 h overnight.

The observation arena consisted of a chamber 45 cm long, 30 cm wide, and 40 cm deep. A fast start is a short duration stereotyped activity during which fish travel short distances but accelerate at high rates to reach large speeds (Eaton et al. 1977; Webb 1978). The size of the arena would not interfere with fast-start activity but would prevent sustained high-speed swimming. This study is concerned only with the former activity.

The observation chamber had a false bottom made from a wire grid (2.5 cm squares made from 0.08 cm diameter wire). A solid bottom was located beneath the grid and could be set 0, 1, 3, or 6 cm beneath. Comparison of performance during fast starts with the grid set at various distances above the solid bottom was expected to show the importance of the hydrodynamic ground effect as differences in performances once physical contact with the grid had ended. Vertical reinforcers prevented the grid from acting as a spring when a force was applied by an accelerating fish. The observation chamber also allowed room for fish to swim in the water column for short distances permitting observation of fast starts in the water column remote from all possible ground interaction.

The bottom was located in one of the four positions beneath the grid while the sanddab became accustomed to the chamber overnight. Next morning a 1.0 V/cm d.c. electric shock was used to initiate a fast start either from the grid or when the sanddab was temporarily stationary in the water column clear of the grid and bottom. All experiments were performed at 14° C.

Fast starts were recorded on movie film at 250 frames/s. A 45° mirror above the observation chamber allowed simultaneous observation of top and bottom views. A floating lid prevented surface ripples distorting the top-view image.

Each fish was killed after an experiment. The body outline was traced on paper. Mass, total length, wetted surface area, location of the center of mass, and muscle mass were measured as described by Webb (1977).

There were no differences in these morphometric characteristics among various groups of speckled sanddabs. Combined values were (mean ±2 SE); mass, 28.96±3.78 g; length, 13.7±0.6 cm; the center of mass, located 5.2±0.2 cm from the nose; wetted surface area, 120±10 cm^2; muscle mass, free of skin and scales, 11.78±2.28 g.

Movie film was analyzed frame by frame to observe kinematics and to measure performance. Details are given by Webb (1978). Briefly, performance was measured for the motion of the center of mass of the stretched-straight body. This point approximates the instantaneous center of mass of the flexing body which is the point about which propulsive forces act. Coordinates for motion of the center of mass were measured in the horizontal and vertical planes. The resultant motion of the center of mass was calculated. Velocities and acceleration rates for these three motions (horizontal, vertical, and resultant) were calculated using moving point linear regression methods. Performance parameters were compared using the *t*-test, and significant differences between means are declared at the 5% level.

RESULTS

Kinematics

There were no differences in kinematics of fish accelerating from the grid set at various distances above the solid bottom. Fast-start kinematics for acceleration from the grids (Figure 1) showed the normal three stages originally described by Weihs (1973). During stage 1, the body was bent into a U-posture (0-80 ms in Figure 1A) comparable to the C-posture of other teleosts when viewed from above (Eaton et al. 1977; Webb 1978). The center of mass showed some recoil (i.e., lateral movement in the opposite direction to the tail, and normal to the fish axis) towards the grid because the fish adopted a posture with the body raised by the median fins before a fast start (Stickney et al. 1973). The body was always bent away from the bottom.

During stage 2 (80-120 ms in Figure 1A), the body was bent in the direction opposite to that of stage 1 as the body curvature traveled caudally along the body. Some point of the body remained in contact with the grid almost to the end of stage 2.

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

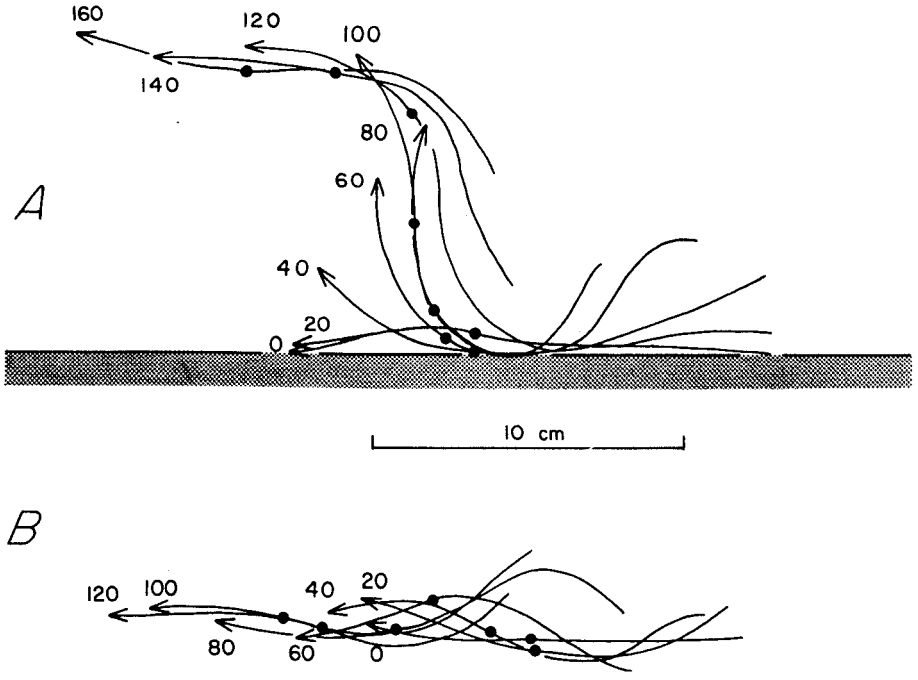

FIGURE 1.—Tracings of the body center-line (seen from the side) at 20 ms intervals to show the acceleration movements during fast starts of *Citharichthys stigmaeus*: A) Acceleration from contact with the grid. B) Acceleration in the water column. Dots show the location of the center of mass of the stretched-straight body. The extended and variable stage 3 following the major acceleration strokes has been omitted for clarity.

The center of mass was propelled vertically away from the ground.

Fast start stage 3, occurring after the major acceleration period, was variable, ranging from an unpowered glide to continued swimming with caudal propagation of propulsive waves sustained from the starting curvature in stage 2.

A typical fast start of a sanddab in the water column away from the bottom is illustrated in Figure 1B. Fast starts in the water column showed the same stages as fast starts from the grid. The amplitude of body movements was usually smaller than those of fish accelerating from the grid. Center of mass recoil, reduced during acceleration from the grid, was observed for fish accelerating in the water column, as seen in other teleosts.

The timing of various fast-start events was similar among groups of fish (Table 1). The duration of stage 1 showed a slight but nonsignificant tendency to decrease as the distance between the grid and the solid bottom increased. The fish accelerating from the grid lost contact after 112 ms, before the completion of stage 2 in 124 ms (Table 1).

Fast-Start Performance

The distance between the solid bottom and the grid had no significant effect on vertical and horizontal distances traveled by the center of mass of speckled sanddabs during fast starts (Figure 2) including distances traveled after losing contact with the grid. This showed that no measurable

TABLE 1.—Results for the duration of fast-start events for *Citharichthys stigmaeus* accelerating from a grid at various distances above a solid bottom and accelerating in the water column. Mean ±2 SE are shown, $n = 10$.

Timing	Acceleration in the water column	Distance between the grid and the solid bottom (cm)				Combined data for acceleration from the grid
		0	1	3	6	
Duration of stage 1, ms	58±8	65±6	65±14	62±8	60±8	63±5
Duration of stages 1 plus 2, ms	105±12	136±18	118±13	149±40	113±9	124±7
Time to end of ground contact, ms	—	116±19	108±9	116±15	113±9	112±6

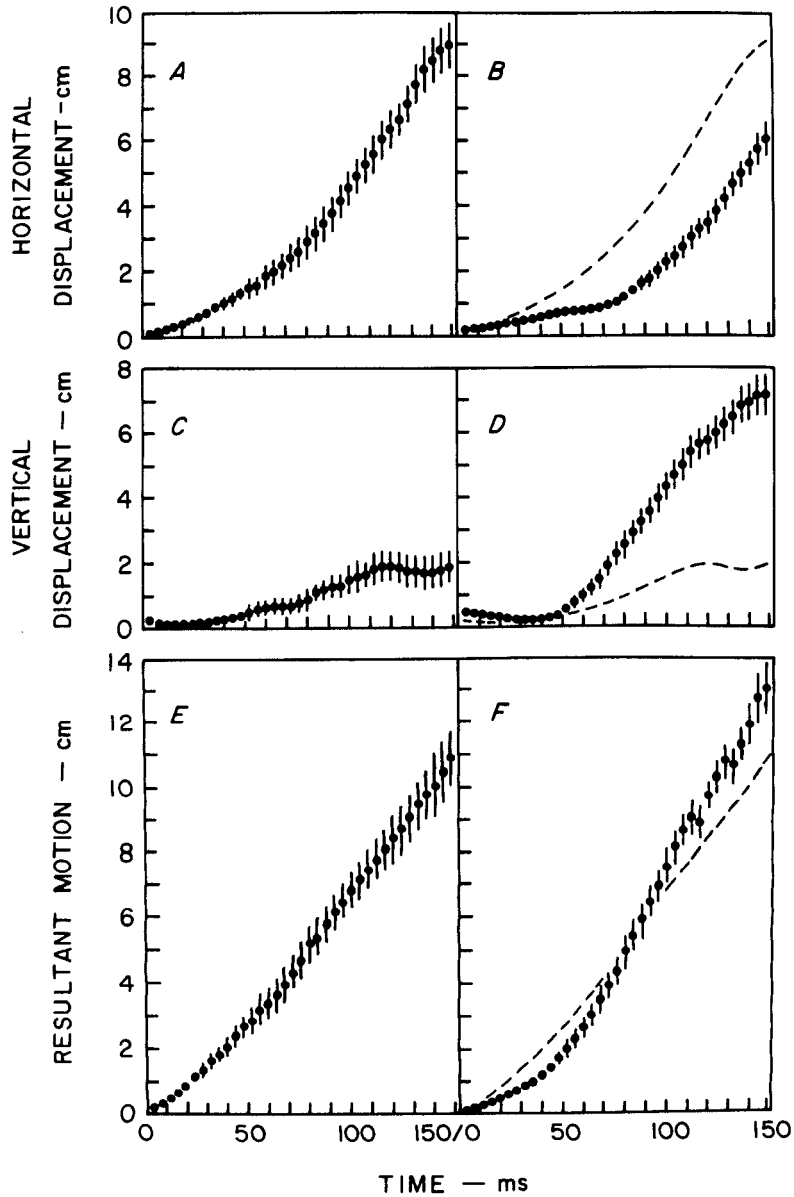

FIGURE 2.—Relationships between the distance traveled by the center of mass (the point about which propulsive forces act) and elapsed time during fast starts of *Citharichthys stigmaeus*. The motion of the center of mass was resolved into the distance traveled in the horizontal (A, B) and vertical (C, D) planes. These data were used to calculate the resultant distance traveled (E, F). Fast-start performance is shown for fish accelerating in the water column (A, C, E) and from the grid (B, D, F). The dotted lines in B, D, and F show the motions of the center of mass of fish accelerating in the water column from A, C, and E to facilitate comparison with fast starts from the grid. Vertical bars shown ±2 SE.

hydrodynamic ground effect influenced speckled sanddab fast starts. All data for fish accelerating from the grid were therefore combined for subsequent analysis and for comparison with fish accelerating in the water column.

The performance of fish accelerating from the grid differed from that of fish accelerating in the water column. The differences were seen in horizontal and vertical motions and in the net (resultant) motion. In the horizontal plane, fish accelerating from the grid traveled 0.8±0.2 cm in 63 ms at the end of stage 1, compared with 1.9±0.4 cm in the same time for fish accelerating in the water column. By the end of stage 2 fish starting from the grid had moved forward 3.9±0.9 cm in 124 ms. This was an improvement over stage 1, but still less than that of fish in the water column which moved forward 6.8±0.9 cm in the same time. The small initial displacement of fish in contact with the grid was probably due to frictional interactions between the fish and the grid (Arnold and Weihs 1978). The normal force at the point of con-

tact would also have been augmented by recoil forces generated by the tail and head tending to displace the fish downwards.

The motion of the center of mass in the vertical plane also differed between speckled sanddabs accelerating from the grid and in the water column (Figure 2C, D). For fish accelerating from the grid there was little vertical movement during fast-start stage 1 because of the presence of that grid. During stage 2, however, the center of mass was accelerated vertically upwards moving 6.0±2.4 cm in 124 ms. Fish accelerating in the water column showed little vertical motion, except that due to recoil (Figure 2C).

The resultant motion of the center of mass of the fish showed differences between acceleration in the water column and from the grid, but these differences were less marked than motions in the horizontal and vertical planes (Figure 2E, F). The increase in distance covered with time was initially greater for fish accelerating in the water column. They traveled a total of 3.7±0.6 cm in 63 ms compared with 2.9±0.4 cm for fish accelerating from the grid. However, once fish pushed against the grid in stage 2, performance improved. By the end of stage 2, they had traveled a cumulative distance of 10.2±1.2 cm in 124 ms, greater than that of 8.7±1.3 cm achieved by fish accelerating in the water column.

Velocities calculated for the center of mass reached maximum values close to the end of stage 2. Maximum values were significantly greater for fish accelerating from the grid compared with fish accelerating in the water column (Table 2). Mean acceleration rates would, of course, follow similar trends to velocities. Maximum acceleration rates only showed significantly improved performance for resultant motion of fish accelerating from the grid (Table 2).

TABLE 2.—Results of maximum acceleration rates and maximum velocities for *Citharichthys stigmaeus* accelerating from the grid and in the water column. Data (mean ±2 SE; $n = 10$) are shown for motion of the center of mass.

Item	Fast starts from the grid	Fast starts in the water column
Maximum acceleration rates, m/s^2:		
Horizontal	37±7	48±10
Vertical	54±10	44±9
Resultant	66±12	46±12
Maximum velocities, m/s:		
Horizontal	66±11	92±10
Vertical	92±12	17±4
Resultant	104±17	76±14

DISCUSSION

These experiments show that the bottom (grid) does influence fast starts in speckled sanddabs. Fast starts from the bottom were associated with large amplitude motions that would normally cause substantial recoil of the center of mass because the bottom prevents that recoil. Motions of fish accelerating from bottom contact were predominantly vertical compared with horizontal motions of fish accelerating in the water column. The relative magnitude of vertical and horizontal displacements of sanddab accelerating from the grid are comparable with those observed in crayfish under similar circumstances (Webb 1979). For both speckled sanddab and crayfish the marked vertical motion is caused by prolonged contact between the body and the ground. Unfortunately, these large vertical displacements in speckled sanddabs preclude any significant hydrodynamic interaction with the ground after contact is lost.

Withers and Timko (1977) give a succinct explanation of this hydrodynamic ground effect, where the ground influences the flow, increasing lift (thrust) and decreasing drag. Hydrodynamic ground effect rapidly declines as the ratio, y/s, increases, where y is the gap between the surface generating thrust and the ground, and s is the span (width) of that surface. Blake (1979) found that 80-90% of the ground effect vanished by the time y/s reached unity in hovering mandarin fish. The mean maximum span of speckled sanddab, located at the center of mass, was 6.7±0.2 cm. For this span, $y/s = 1$ after about 130 ms, 18 ms after the end of physical contact with the bottom (Figure 2D). The caudal fin had a maximum span of 2.4±0.3 cm, and a value of $y/s = 1$ is reached within about 16 ms after the tail loses contact with the bottom (Figure 1A). Thus, the vertical acceleration rapidly lifts the speckled sanddab out of the hydrodynamic influence of the ground so that there is insufficient time for any interaction to affect performance. However, the absence of this effect during a fast start does not preclude hydrodynamic ground interactions from improving steady swimming close to the sea floor.

Thus, the observations on fast starts of speckled sanddab from the bottom show that a single kinematic pattern is used, which sustains bottom contact for most of a fast start, but which prevents development of any significant hydrodynamic ground effect. However, a direct push against a

solid substrate will always convert more muscle energy into body motion than working against a fluid. It therefore appears that speckled sanddab utilizes fast-start behavior that makes the greatest use of the available ground interaction options.

However, the interaction with the ground cannot be assumed to be adaptive before considering the question of advantages and disadvantages. For example, the small initial displacement of the center of mass of fish accelerating from the ground might be disadvantageous in some circumstances, such as escaping from predators. However, significant protection is achieved by camouflage and cryptic behavior in pleuronectiform fishes, rendering this contingency unlikely.

The influence of the bottom is clearly advantageous in the capture of elusive prey, a second behavior in which fast starts play a key role (Eaton and Bombardieri 1978; Webb and Skadsen 1980). Elusive prey, e.g., fish and crustacea, are common dietary items for pleuronectiform fishes in the families Psettodidae, Bothidae, and Pleuronectidae (Liem and Scott 1966; Norman 1966). The bottom eliminates recoil so that the fish can rapidly accelerate the head vertically (Figure 1). Continued rapid vertical acceleration is facilitated by prolonged bottom contact through the major acceleration period of a fast start. Bottom contact also results in the acquisition of a superior final speed that would be advantageous in a continued attack. The time taken to accelerate from the bottom and reach maximum speed could also be reduced by resting in sand in a curved U-shaped posture. This may occur since flatfish often dig into sand with the eyes and tail at the surface, but the body buried, implying a curved posture (Hobson 1979). Thus, the morphology and behavior of the benthic sanddab appear to be adaptive in improving fast-start performance, as well as for camouflage. Such advantages undoubtedly apply equally to other members of the pleuronectiformes and therefore provide an additional functional explanation of the unique flatfish body form and habits.

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DAILY PATTERNS IN THE ACTIVITIES OF SWORDFISH, *XIPHIAS GLADIUS*, OBSERVED BY ACOUSTIC TELEMETRY

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ABSTRACT

Horizontal and vertical movements of swordfish were studied using acoustic telemetry. Five swordfish in the Pacific and one in the Atlantic were tagged with transmitters which provided information on location, depth, and surrounding water temperature. Two of the Pacific fish showed a clear daily cycle of movement between an inshore bank during the day and deep water offshore at night. All of the swordfish responded to light, swimming deep during the day and coming near the surface at night. In the Pacific depth during daylight appeared to be limited to about 100 m by the oxygen-minimum layer, but in well-oxygenated waters of the Atlantic, a midday depth of greater than 600 m was recorded and the fish appeared to follow an isolume. Depth of the Atlantic fish in daylight was related to changes in light caused by variation in water transparency. The vertical movements were associated with temperature changes of as much as 19° C within 2 hours. The implications of rapid vertical movements on buoyancy and swim bladder volume are discussed.

Despite their high commercial value and their significance as one of the large predators of the open ocean, relatively little is known about the habits and behavior of the swordfish, *Xiphias gladius*. The information which is available comes chiefly from observations made at the sea surface by commercial fishermen and from a few scientific studies based on commercial captures. Swordfish are large, fast-swimming fish that offer little opportunity for direct observation; however, some aspects of their behavior can be readily examined by telemetry from attached sensors.

Xiphias gladius is found throughout tropical and temperate waters. Its appearance in higher latitudes usually occurs in warm-season aggregations along the edge of the continental shelf and on offshore banks (Rich 1947; Wise and Davis 1973). The seasonal appearance of swordfish in both the western North Atlantic and Hawaiian fisheries (Uchiyama and Shomura 1974; Caddy[3]) coupled with the known distribution of their larvae and of adults with ripe gonads indicate a spawning migration to waters warmer than 23°-24° C (Arata 1954; Taning 1955; Gorbunova 1969; Markle 1974; Nishikawa and Ueyanagi 1974), while nonspawning fish appear to move between coastal and oceanic waters. Tagging studies show that some swordfish undertake long-distance movements. For example, a 12 kg swordfish tagged near the Mississippi Delta in March 1974 was recovered from Georges Bank at a weight of 86 kg in August 1977 (Casey[4]). The recovery of tagged swordfish near the point of release, even after several years at large (Beckett 1974), implies homing behavior if we assume that these fishes are regular migrators.

Longline fishery captures of swordfish occur primarily at night on hooks set at depths of 5-50 m. Deeper vertical excursions have been documented by DSV *Alvin* when the submersible was attacked by a swordfish at 610 m (Zarudski and Haedrich 1974) and by observation from *Deepstar* at 654 m (Church 1968). The harpoon fishery relies on the occurrence of swordfish near the surface during the day where they are commonly found resting in the warmer surface waters, often with their dorsal and upper caudal fins exposed. In this situation they can be approached and harpooned. This "basking" behavior may warm the fish and aid in the digestion of prey caught while foraging at greater depths. Spotter pilots for the harpoon fishery report that basking swordfish often defecate before sounding or breaching.

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[3]Caddy, J. F. 1976. A review of some factors relevant to management of swordfish fisheries in the northwest Atlantic. Environ. Can., Fish. Mar. Serv., Tech. Rep. 633, 42 p.

[4]John G. Casey, Apex Predator Program, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, Narragansett, RI 02882, pers. commun. 1978.

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Examination of swordfish stomach contents (Scott and Tibbo 1968; Ovchinnikov 1970) showed that they feed on cephalopods and a wide variety of nektonic fishes (e.g., anchovies, hake, mackerel) and micronektonic fishes (e.g., myctophids, paralepidids) and that a significant portion of their diet consisted of vertically migratory mesopelagic species. We have also found unusual items in their stomachs including birds and shrimp. Swordfish have been observed swimming through schools of fish, stunning them with their swords before eating them (Goode 1883). Fish removed from swordfish stomachs often show damage to the muscle and vertebral column from having been hit by the sword (Scott and Tibbo 1968). Swordfish have large eyes and are efficient visual predators even in dim light. Small phosphorescent lights are occasionally used to attract them to longline hooks, which indicates that they may also respond to bioluminescence.

Swordfish are aggressive and there are many accounts of their attacking and ramming their bills into ships, whales, and other objects (Goode 1883; Gudger 1938; Smith 1956; Jonsgard 1962). We have seen penetrating wounds in swordfish and Edlin[5] found a 15 cm fragment of a swordfish bill that entered near the heart of a 70 kg swordfish and was driven back into the body cavity, which may indicate that they strike each other. While they are generally solitary, longline fishermen say that in the Straits of Florida, a spawning area, swordfish may be encountered in twos with some regularity.

In the present study we investigate the horizontal and vertical movements of swordfish during their daily activities and attempt to determine the range of temperatures they encounter. We used acoustic telemetry to monitor data from depth and temperature sensors attached to the fish for periods of up to 5 d. The results presented here provide the first description of their activities based on continuous direct observations of individuals.

METHODS

We attempted to attach transmitters to seven swordfish and were successful with five in the Pacific, near Cabo San Lucas at the tip of Baja California, and one in the Atlantic, east of Cape Hatteras, N.C.

For the experiments off Baja California, the swordfish were located on the surface by aircraft and the transmitters harpooned into the free-swimming fish from the tracking vessel *Sea World*. In the Atlantic, the swordfish were taken on commercial longline fishing gear set by the tracking vessel FV *Diane Marie*. Weights of the fish were estimated by the fishermen.

Transmitters

Two types of sensors were used in the transmitters. Depth transmitters had a 500 or 1,000 lb/in^2g Biotek[6] strain gage pressure transducer. Temperature transmitters had a 300 kΩ Fenwall GA53M2 thermistor linearized with a series resistor. An up-down integrating circuit converted resistance changes in the sensor to a varying pulse rate. The pulses keyed an oscillator and output stage which drove a 1.27 cm long, 2.79 cm (outer diameter) cylindrical ceramic transducer (Marine Research TCD 5) with 30 ms pulses of ultrasound at an electrical power level of one to several watts. The transducers, which were mechanically resonant at 33 kHz, were operated at 32 kHz for temperature and 34 kHz for depth so that signals could be separated in experiments where both were used simultaneously.

Power was supplied by a battery of five 1.2-Ah lithium cells (Mallory L0325) which give a useful life of about 1 wk. Range was as great as 3-5 km at times, but much shorter when propagation conditions were poor.

The transmitters were 14 cm long, 4.5 cm wide by 3 cm thick and weighed 250 g in air and 90 g in water. They were cast in a strong epoxy plastic (Hysol 2039 resin, 3561 hardener) and tested to withstand hydrostatic pressures equivalent to a depth of 1,000 m. A miniature (6.5 cm long) swordfish dart was tied to the end of the transmitter with a 13 cm loop of twisted 200-lb (91 kg) test monofilament nylon (Figure 1). An adapter which fitted on a standard swordfish harpoon had a crosspiece which limited penetration of the dart to about 10 cm. In some experiments depth and temperature transmitters were tied in tandem and attached to the fish with a single dart. The swordfish showed no obvious reaction to the tags once they were attached.

The instruments were stable and accurate.

[5]Robert Edlin, P.O. Box 341303, Coral Gables, FL 33134, pers. commun. 1980.

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

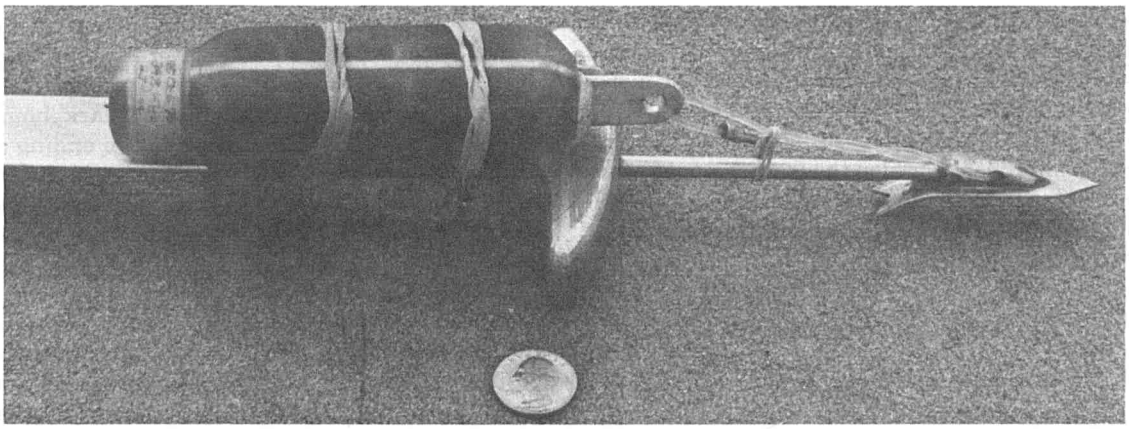

FIGURE 1.—Depth transmitter for swordfish. Rubber bands hold the transmitter to an adapter which fits on a standard swordfish harpoon. The crossbar on the adapter serves to limit penetration of the harpoon dart. A conductive path between two elements of a seawater switch turns the transmitter on when it enters the water. The coin is 24 mm in diameter.

Changing battery voltage did not affect the pulse rate of either type of transmitter, and the pulse rate of depth transmitters was not affected by temperature changes in the range 5°-30° C. In use we found that several days into an experiment the depth transmitters would still indicate <1 m when the fish was seen on the surface. A temperature transmitter recovered after 13 d on a fish was recalibrated and found to be within 0.1° C of the original calibration.

Receiving

We listened to the transmitters with a directional hydrophone constructed of seven ceramic transducer rings wired in parallel in a cylindrical array 10.5 cm long. The rings were backed with a layer of closed-cell polyethylene foam and cast in epoxy. A preamplifier in the hydrophone amplified the signal 100× and reduced problems from electrical noise picked up on the cables. The upper and rear surfaces of the horizontally mounted hydrophone cylinder were acoustically shielded with four alternating layers of 3 mm thick foam rubber and steel, leaving an approximately 140° sector uncovered and facing forward and down. The hydrophone was mounted at the bow of the vessel on a streamlined fin arranged so that it could pivot and follow the flow of water as the boat yawed. A shaft through the fin allowed the hydrophone to be rotated by a rope and pulley system from the bridge of the vessel.

The receivers (Lawson Instrument Company and CAI CR-40) were mounted on the bridge so that one person could follow the fish by rotating the hydrophone to find the strongest signal, then steering the boat in that direction. Data were recorded by timing a fixed number of pulses to the nearest 0.1 s with a stopwatch and converting the pulse rate to temperature or depth using a linear regression for the calibration curve. A 0.1 s counting error in a 30 s count produced a depth error of approximately 2 m. Data were taken routinely every 5 or 10 min and more frequently when the fish was changing depth. An automatic data recording system, based on a phase lock receiver, was used on 11 November 1977 and gave a continuous, detailed record of a swordfish rising to the surface in a series of steps.

Navigation

In the Baja California area we used radar to determine range and bearing to various peaks and headlands. The relative accuracy of this technique was good as checked by comparison of echo sounder depth with depth given on the chart at the plotted position. In the experiment near Cape Hatteras we used loran C with an accuracy better than 1 km. The position of the vessel was recorded when it was brought close to the fish and the plot of these positions used to approximate the fish's course.

Temperature

Temperature of the water was measured with expendable bathythermograph probes (XBT) (Sip-

pican T-6 and T-10) which were dropped routinely every several hours and more frequently when passing through boundaries between water masses. The XBT records were used to construct plots of isotherm depth. By superimposing the plot of swordfish depth on the isotherms, we could tell water temperature at the location of the fish in those experiments where a temperature transmitter was not used.

RESULTS

Swordfish No. 2, 19-24 April 1977, Baja California, Mexico

This 70 kg swordfish sounded when struck with the transmitter, but quickly came up and spent 20 min on the surface. It appeared to be in good condition and unaffected by the depth transmitter. During a 5-d period it showed a clear cyclical pattern of movement between an inshore bank during the day and offshore waters at night (Figure 2). Each day it occupied the same area along the 50-fathom (91 m) depth contour on the bank. Several hours before sunset it would move offshore, going out as far as 26 km from land, and remain in deep water all night. At first light of dawn, 1.0-1.5 h before sunrise, it would swim inshore again and return to the 50-fathom contour on the bank.

The fish remained close to the bottom while on the bank, coming to the surface during daylight only three times in 5 d. On 20 April it was usually 5-10 m up from the bottom and on the following days, usually 5-20 m above it. Each evening, an hour after sunset, swordfish no. 2 rose to the surface and spent the night in the upper 10 m. At first light, an hour before dawn, it descended and moved toward shore at depth with frequent vertical excursions.

Swordfish No. 3, 26-27 April 1977, Baja California, Mexico

This 70 kg fish was found close to where no. 2 had been tagged and was harpooned with both depth and temperature transmitters. It followed a similar pattern to no. 2, moving offshore before sunset and turning inshore at first light (Figure 3). Several hours before sunset both of these fish would leave their position on the 50-fathom contour of the bank and swim offshore into deeper water. They swam twice as fast, perhaps 3 km/h, when moving offshore as they had while on the bank. When on the surface several hours after dark, swimming speed usually slowed to 1 or 2 km/h. The movements during the dark hours showed a distinct offshore progression ending at an average distance of about 19 km offshore where the fish moved about slowly until first light. The journey back to the bank was again at a higher speed, about 3 km/h.

From 1100 to 1800 h on the second day, no. 3 remained in one spot and appeared to be resting on the bottom during part of this time (determined by positioning the boat over the fish and noting that the echo sounder depth was the same as that telemetered from the fish). At sunset it rose from the bottom and headed offshore. We lost it soon afterward when our equipment was damaged in rough water.

Swordfish No. 4, 30 April 1977, Baja California, Mexico

This 80 kg fish was harpooned in midmorning in 500 m of water some 24 km off the coast. It moved slowly in a westerly direction (Figure 4) staying uncharacteristically near the surface, frequently with its fins showing, and did not descend below 10 m. It was followed for only 2 h, then abandoned because of technical problems.

Swordfish No. 5, 30 April 1977, Baja California, Mexico

This fish weighed about 100 kg and was harpooned close to where we left no. 4. It also moved slowly westward, covering <3 km in the first 5 h (Figure 4). An hour before sunset it turned south and swam offshore over San Jose Canyon at a speed of 3.5 km/h. During the day it surfaced five times, spending alternate periods on the surface and at 100 m. Sunset marked a period of vertical activity and a gradual ascent to the upper 25-50 m. We lost the fish in rough weather that night as it was swimming offshore on a southerly course.

Swordfish No. 6, 3-6 May 1977, Baja California, Mexico

Swordfish no. 6 weighed about 140 kg and was harpooned with depth and temperature transmitters in an area about 24 km offshore, near where no. 4 and 5 had been tagged (Figure 4). It swam slowly westward as those fish had done,

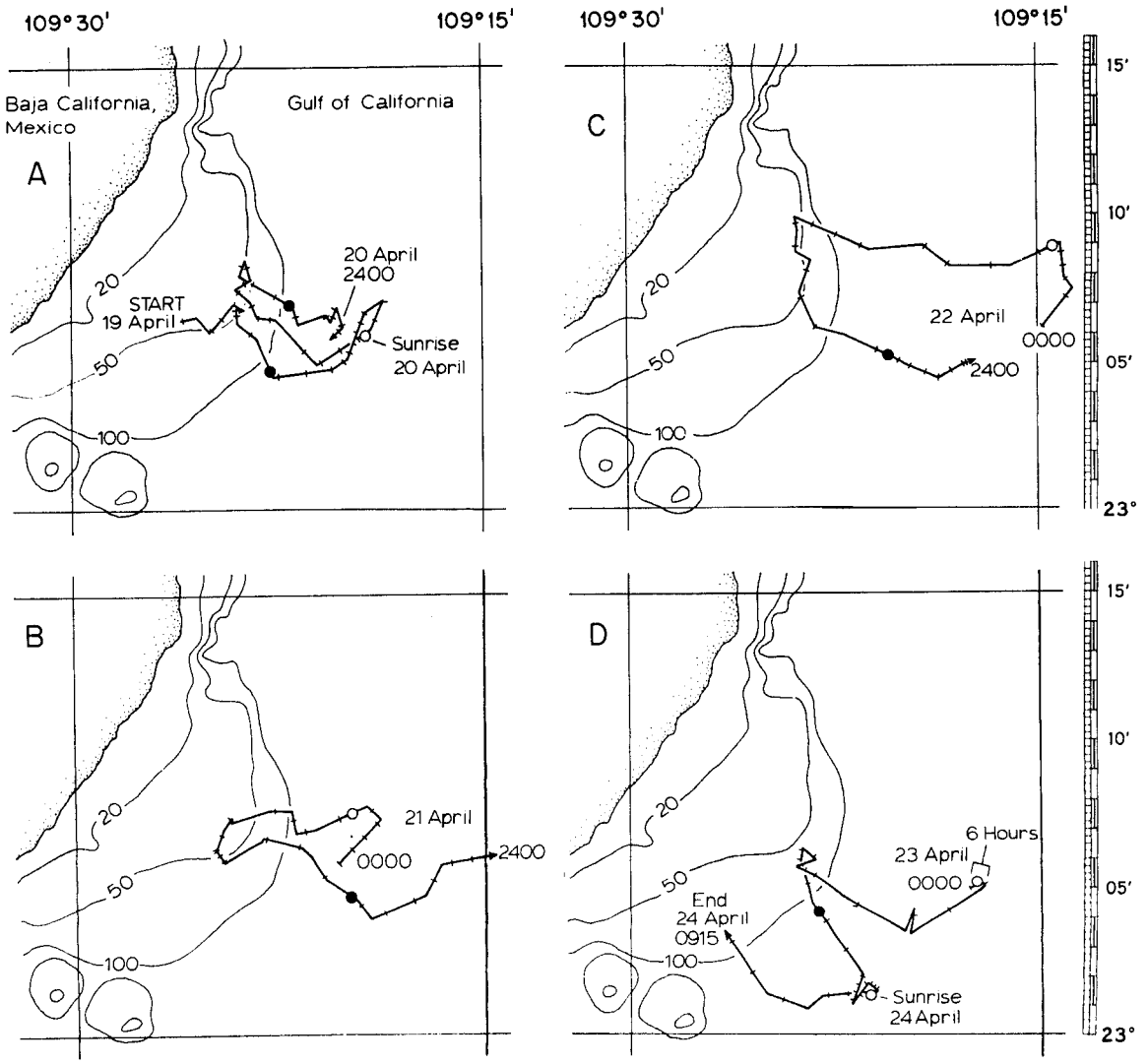

FIGURE 2.—Track of swordfish no. 2, Baja California, separated into four panels for clarity. Each day this fish moved inshore to the 50-fathom (91 m) curve on a bank then moved out over deep water at night. The turn inshore began about 1 h before dawn; the offshore movement began several hours before sunset. Compare with the depth record in Figure 9. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in fathoms.

moving 9 km in 5 h, then turned to the south at sunset and moved down the axis of San Jose Canyon. It continued in a southwest direction when it reached deep (2,000 m) water, and by dawn on 6 May when we abandoned it, it had gone 88 km in 44 h.

No. 6 showed the now-familiar pattern of vertical movements, staying near the surface at night and going deep during the day (Figure 5). Like no. 5 it made excursions to the surface during daylight hours, coming up five times to spend periods of 0.5-1.5 h on the surface, then returning to depths which averaged 75-100 m, but included much deeper excursions.

While on the surface during the day, no. 5 and 6 swam about actively. No. 6 moved at an estimated 1.6-3.2 km/h (1-2 kn) in a haphazard pattern with much turning, so that progression along its course was considerably slower than its swimming speed. It appeared to be responsive and moved after a live Pacific mackerel, *Scomber japonicus*, which was thrown to it. On one occasion we attempted to

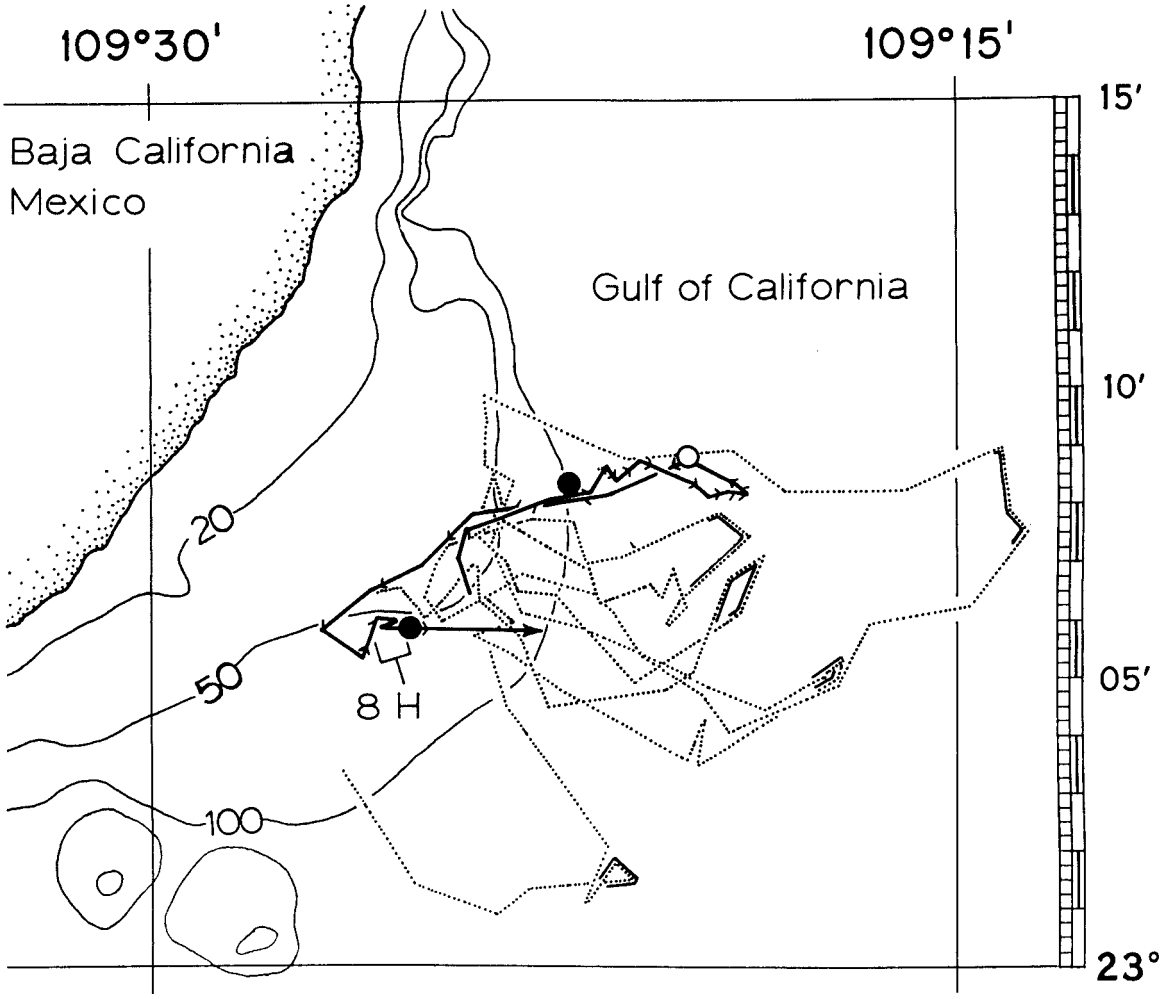

FIGURE 3.—Track of swordfish no. 3 (solid line) superimposed on track of swordfish no. 2 (dotted line), Baja California. No. 3 was on the bottom during much of the indicated 8-h period. The narrow solid lines near the track (dotted line) of no. 2 indicate positions where it was moving slowly on the surface at night. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in fathoms.

drive it down with the boat, but it sank just a few meters and avoided us. When hard pressed, it easily escaped in a series of long horizontal leaps, but did not go below a few meters depth until it had been on the surface for about 1 h.

Swordfish No. 7, 9-11 November 1977, Atlantic Ocean

This 70 kg swordfish was taken by longline about 100 km northeast of Cape Hatteras (lat. 36°00′ N, long. 74°40′ W) in a depth of 1,000 m (Figure 6). The fishing gear was left in the water for only 1 h to reduce the time that the fish would be struggling on the line. The fish was hooked in the tip of the lower jaw, a place where little damage would be expected; its bluish color and active movement gave the impression that it was in good condition. It was tagged with a depth transmitter and cut free within about 15 s after it had been brought alongside the boat.

The longline had been set in a patch of warm blue water (Figures 6, 7). When released the fish swam in a general southeast direction, a course which took it under a tongue of cold, grey-green shelf water. After several course changes, it came out from under this cold water on the second day and entered the Gulf Stream which swept it to

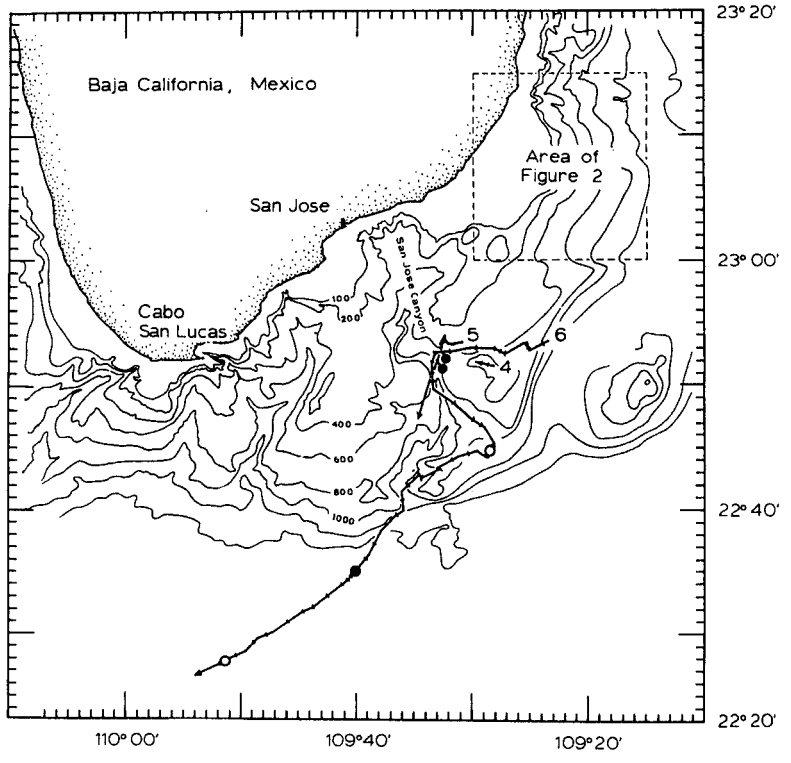

FIGURE 4.—Track of swordfish no. 4, 5, and 6, Baja California. These fish all moved west during the first afternoon; no. 5 and 6 then moved down the axis of San Jose Canyon after sunset. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in meters.

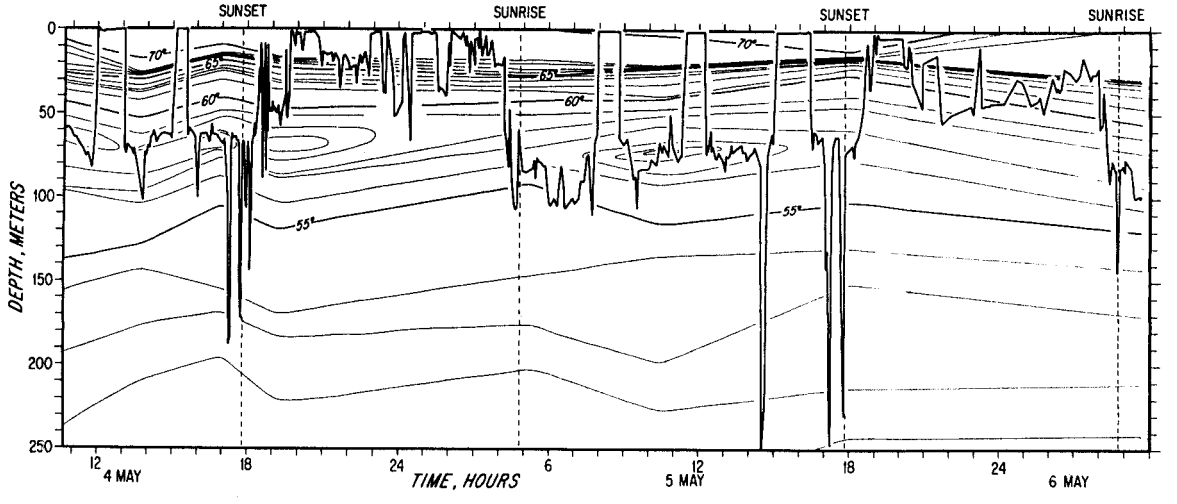

FIGURE 5.—Depth record for swordfish no. 6 off the tip of Baja California superimposed on an isotherm pattern drawn from bathythermograph lowerings. There was a full moon during this experiment and the usual nighttime depths were deeper than those on the moonless nights during experiments with swordfish no. 2 and 3. The fish generally swam below the thermocline during the day and was well into the oxygen-minimum layer, where oxygen concentration was estimated to be about 10% that on the surface. Isotherm interval 1° F.

the northeast. At the end of the third day the flattening of the deep isotherms (Figure 8) indicated that it had crossed the center of the Gulf Stream and entered the Sargasso Sea. When we abandoned the fish it had gone a distance of 240 km in 67 h.

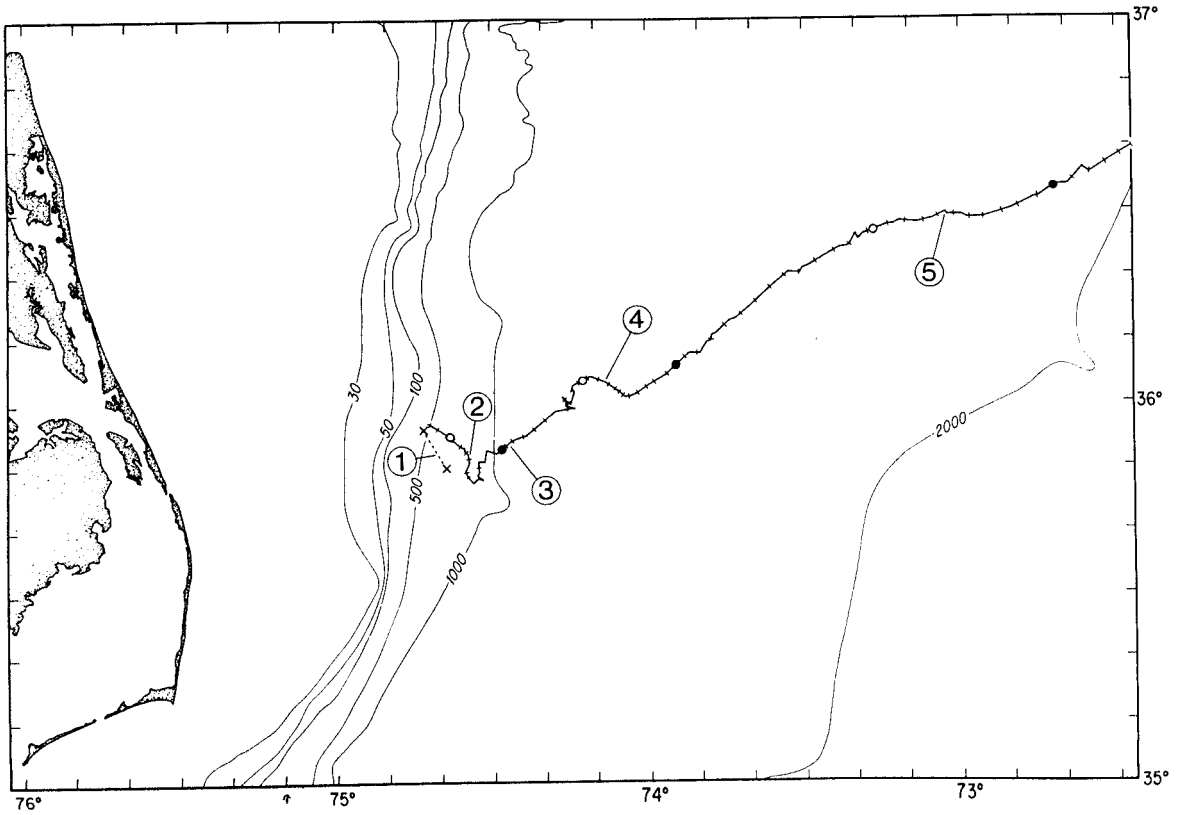

FIGURE 6.—Track of swordfish no. 7 in the Atlantic near Cape Hatteras, N.C. 1) Dotted line indicates position of longline gear where this fish was caught. 2) The swordfish moved beneath a layer of cold surface water at 1000 h on 9 November. 3) It emerged from beneath the cold surface layer at 2000 h on 9 November. 4) By 0500 h 10 November, it was in the Gulf Stream. 5) At 1500 h 11 November, it had crossed the Gulf Stream and entered the Sargasso Sea. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contour lines in fathoms.

During the first day, the vertical movements of no. 7 were complex. On the second and third day however, it followed a clear pattern of moving near the surface at night and going deep during the day. An hour before dawn on 10 November it was in 27° C water at a depth of 20 m (Figure 8). It began to descend and was in 8° C water at 400 m 2 h after sunrise. An hour before sunset it started back toward the surface and was at 20 m at twilight. No. 7 spent the night at about 20 m with four brief excursions to 100 m. Some of these were caused by our tracking vessel, for swordfish would often dive when we drove the boat over them and would do this even at night when the ship was darkened. The depth pattern on 11 November was similar to the previous day. Leaving the surface 1 h before dawn, it descended rapidly and was at 450 m shortly after sunrise. It continued to descend, reaching 617 m at noon, then starting back up, slowly at first, then more rapidly around sunset.

A continuous recording of the final ascent, made with the phase lock receiver, shows that it was done in steps with a rapid rise of 20-80 m, a pause for several minutes, then another rapid rise (Figure 8).

DISCUSSION

Horizontal Movements

Swordfish no. 2 and 3 showed clear cycles of movement between deep water and an inshore bank. During the day they occupied a rather narrow region, perhaps 8 by 1.5 km, along the 50-fathom (91 m) contour on the bank where the bottom fell off to the south and east (Figure 3). They stayed close to the bottom, moving slowly,

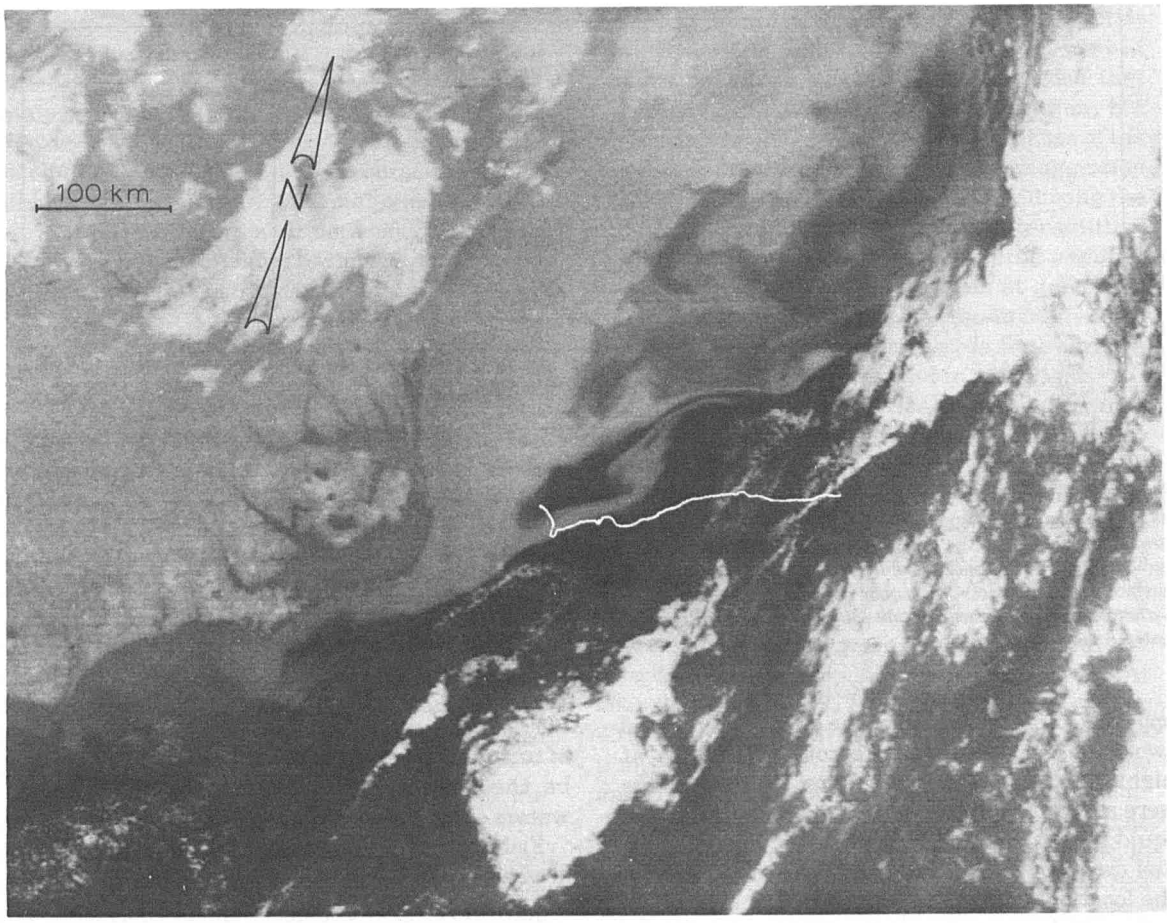

FIGURE 7.—Satellite infrared image of the Atlantic east of Cape Hatteras, N.C. (left center), with track of swordfish no. 7 superimposed. Light areas indicate cold water and dark areas warm water. The Gulf Stream moving past Cape Hatteras pulls off a streamer of cold shelf water. Swordfish no. 7 was tagged on the north side of this streamer, swam under it (see Figure 8), and crossed the Gulf Stream into the Sargasso Sea.

and may at times have been resting on it. Swordfish commonly feed on bottomfish (Scott and Tibbo 1968), and this location may have allowed them to prey on demersal fish moving on and off the bank.

In the evening no. 2 and 3 swam rapidly offshore and spent the night moving slowly in positions about 20 km from the coast (Figures 2, 3). A different area was visited each night, but they returned to the same spot on the bank every day. Squid, which were abundant on the surface at night, came to our lights in large numbers when we stopped. It is likely that the swordfish moved offshore to feed on the squid and other vertically migrating fauna which concentrate near the surface at night. The onshore-offshore movements which we observed may have been a feeding routine which allowed the swordfish to prey on demersal fish available in a prescribed spot on the bank during the day and to feed on squid and other prey wherever they were found over deep water at night.

In an area near Hawaii, Yuen (1970) used an acoustic transmitter to follow a skipjack tuna, *Katsuwonus pelamis*, for an 8-d period. He found that the fish remained with its school which spent the day on a bank and moved out over deep water at night. The nighttime positions were 20-100 km away from the bank, and like swordfish no. 2 and 3, a different area was visited each night. The behavior of the school during the day suggested to Yuen that the fish were foraging. A diel inshore-offshore movement cycle in the blue shark, *Prionace glauca*, near Catalina Island was reported by Sciarrotta and Nelson (1977). This cycle was

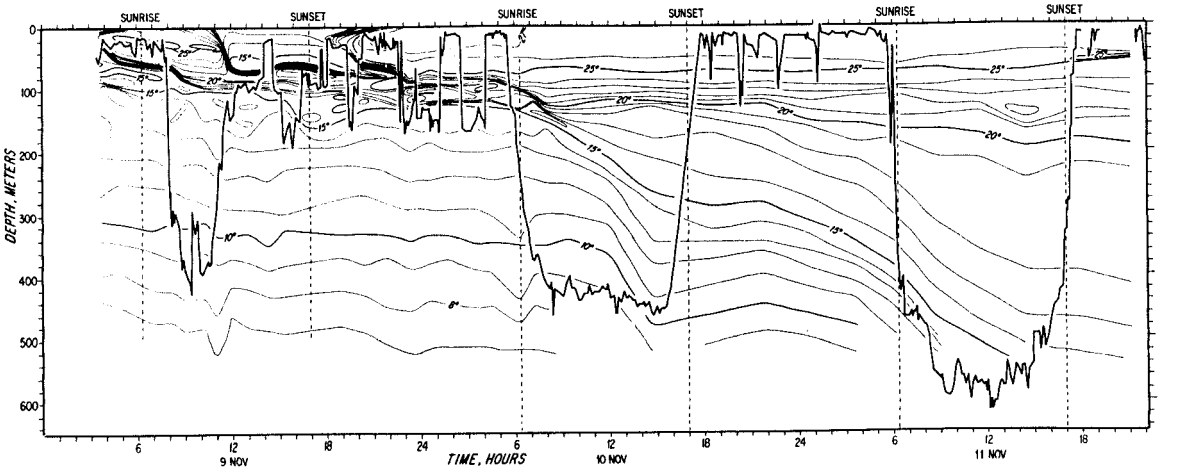

FIGURE 8.—Depth record for swordfish no. 7 off Cape Hatteras in the Atlantic superimposed on a 1° C isotherm plot drawn from expendable bathythermograph casts. On 9 November the fish passed under a cold streamer of shelf water (see Figure 7) and rose toward the surface in the middle of the day, probably in response to the decreased light. On 10 November the deepening isotherms indicate that the fish was following an isolume, descending 1 h before dawn, reaching its greatest depth at midday and coming to the surface 1 h after sunset. Continuous recording of depth on 11 November shows that the rise toward the surface at sunset was made as a series of steps with several minute pauses at each level. The flattening isotherms toward the end of the record indicate that the fish had entered the Sargasso Sea.

opposite in phase to that of the skipjack tuna and swordfish, with the sharks coming inshore at night. The authors suggested that the movements were associated with the nighttime availability of squid near the beach. It is likely that all of these diel cycles of movement are linked to changes in the location and availability of food.

Swordfish no. 4, 5, and 6, which were offshore in water 400-800 m deep, moved slowly west after they had been harpooned (Figure 4). We abandoned no. 4, but no. 5 and 6 continued until they were over San Jose Canyon, the most prominent submarine canyon in the area. Near nightfall, both of these swordfish changed course and moved south along the length of the canyon. The correspondence with the axis of the canyon is not exact, but the course change and the movement of both fish along the canyon suggests they were responding to the bottom topography. Commercial longline fishermen feel that the submarine canyons and hummocky areas along the edge of the continental shelf are good places to find swordfish.

Currents flowing over rough bottom produce eddies and flow separation features which may extend to the surface. The patterns of such turbulent flow affect the distribution of biological sound scattering particles and produce concentrations of organisms which can be seen in 200 kHz echograms made over Hudson Canyon in the Atlantic (Orr[7]). The concentration of organisms as a result of turbulence generated by the rough bottom may be the feature that attracts swordfish to the waters over submarine canyons.

Fishermen had suggested that swordfish in the area where no. 2 and 3 were followed were part of a resident population, while those in the area of no. 4, 5, and 6 were transient. Our results are consistent with this notion.

In the Atlantic, swordfish no. 7 swam in a southeasterly direction at a speed of 1.5-2.0 km/h during the first day. On the second day it entered the Gulf Stream as indicated by the deepening of the isotherms in Figure 8. While in the Gulf Stream it moved on a course a little north of east at a speed of 5.5 km/h, with most of this velocity contributed by the current which was flowing northeast. The course of the fish was to the south of the direction of the current, indicating that there was a southerly component to its swimming. It probably continued to swim on its original course and speed after entering the Gulf Stream. By the time we abandoned it on the third day, it had crossed the Gulf Stream, which is about 75 km wide at this point, and entered the Sargasso Sea. This can be seen from the flattening of the deep

[7]Marshall Orr, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1980, manuscr. in prep.

isotherms at the end of the track in Figure 8 and from the position of the Gulf Stream indicated on the 9 November 1977 Experimental Ocean Frontal Analysis Chart.[8] Swordfish concentrate along the edge of the continental shelf, but are widely distributed over the ocean. The course that no. 7 followed may have been a normal one for swordfish in the Hatteras area, or no. 7 may have been influenced to swim offshore by the trauma of being caught on longline fishing gear.

Vertical Movements and Light

The tagged swordfish showed a clear diel pattern of vertical movements, going deep during the daylight hours and coming to the surface at night (Figures 5, 8, 9). This is best illustrated by swordfish no. 7 on 11 November (Figure 8). The fish spent the night at about 20 m. About 1 h before dawn, when light was just noticeable in the east, it swam down rapidly, reaching a depth of 400 m by sunrise, and worked gradually deeper until it reached 617 m at midday. After noon the swordfish gradually rose again, increasing its rate of ascent sharply around sunset and reaching the surface about 1 h later.

There is an obvious relationship between the vertical movements of swordfish and light. The most rapid changes in depth were during a 2-h period at dawn and dusk when surface illumination changes by six or seven orders of magnitude (Brown 1952), and the greatest depth was reached at noon when light at the surface was at a maximum. The U-shaped pattern of the depth curve would be expected for an animal following an isolume (Blaxter and Parrish 1965; Boden and Kampa 1967).

The swordfish also appeared to respond to moonlight. There was no moon during experiment 2 (new moon, 21 April) and only a thin crescent for swordfish no. 3. On these nights, which were starlit and calm, the swordfish were usually at depths <10 m and often right on the surface (Figure 9). In the other experiments there was a full moon shining through clouds and it was windier. Nighttime depths for no. 5 and 6 were 10-50 m (Figure 5) and for no. 7 about 25 m (Figure 8). The fish were probably swimming at a greater depth in response to moonlight, although the wind might also have had an influence.

Guitart Manday (1964) analyzed the depth at which swordfish were taken in a Cuban fishery at various phases of the moon. He concluded that moonlight did not affect vertical migration, but noted that the fishermen felt that the phase of the moon was important and there is some suggestion in his data that fish were taken deeper during the full moon. Tesch (1978) used acoustic transmitters to follow the silver eel stage of *Anguilla anguilla* and reported that one which swam at a depth of 100 m while the moon was up rose to 50 m when the moon set. Our similar records for swordfish suggest that they also respond to moonlight.

If swordfish move vertically to maintain a constant level of illumination, the light level they follow should be somewhat greater than that on the clear, starry nights when they came to the surface and somewhat less than in moonlight when they swam at 10-50 m depth. We may use the values for irradiance of 3×10^{-1} μW/cm^2 under a clear night sky with full moon, 3×10^{-3} μW/cm^2 for a clear sky with no moon, and 3×10^{-4} μW/cm^2 for a dark night from Clarke and Kelly (1964). At noon, 11 November 1977, swordfish no. 7 was at lat. 35° N and at a depth of 600 m. Surface illumination, I_0, for this time, recorded in Woods Hole and corrected for latitude, was 5×10^4 μW/cm^2 (Payne[9]). Light, I, at depth, L, of the fish can be calculated assuming an attenuation coefficient, k, of 0.028 for the clear Gulf Stream-Sargasso Sea water in this area, (Clarke and Backus 1964). The relationship

$$I = I_0 e^{-kL}$$

gives 2.5×10^{-3} μW/cm^2, a value similar to that on a clear, moonless night when the fish might be expected to come to the surface. The fact that swordfish may also come to the surface during the day indicates that they are not locked to an isolume, but under some conditions they do appear to adjust their vertical position in a manner which would maintain a constant, dim illumination throughout the day.

Vision is obviously important to swordfish. The eyes of a 150 kg fish are as large as an orange and almost touch in the midplane of the skull. The amount of light we calculate for the isolume followed by swordfish is many orders of magnitude greater than the 3×10^{-10} μW/cm^2 suggested as a

[8]U.S. Navy Oceanographic Office NSTL Station, Bay St. Louis, MS 39522.

[9]R. E. Payne, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1977.

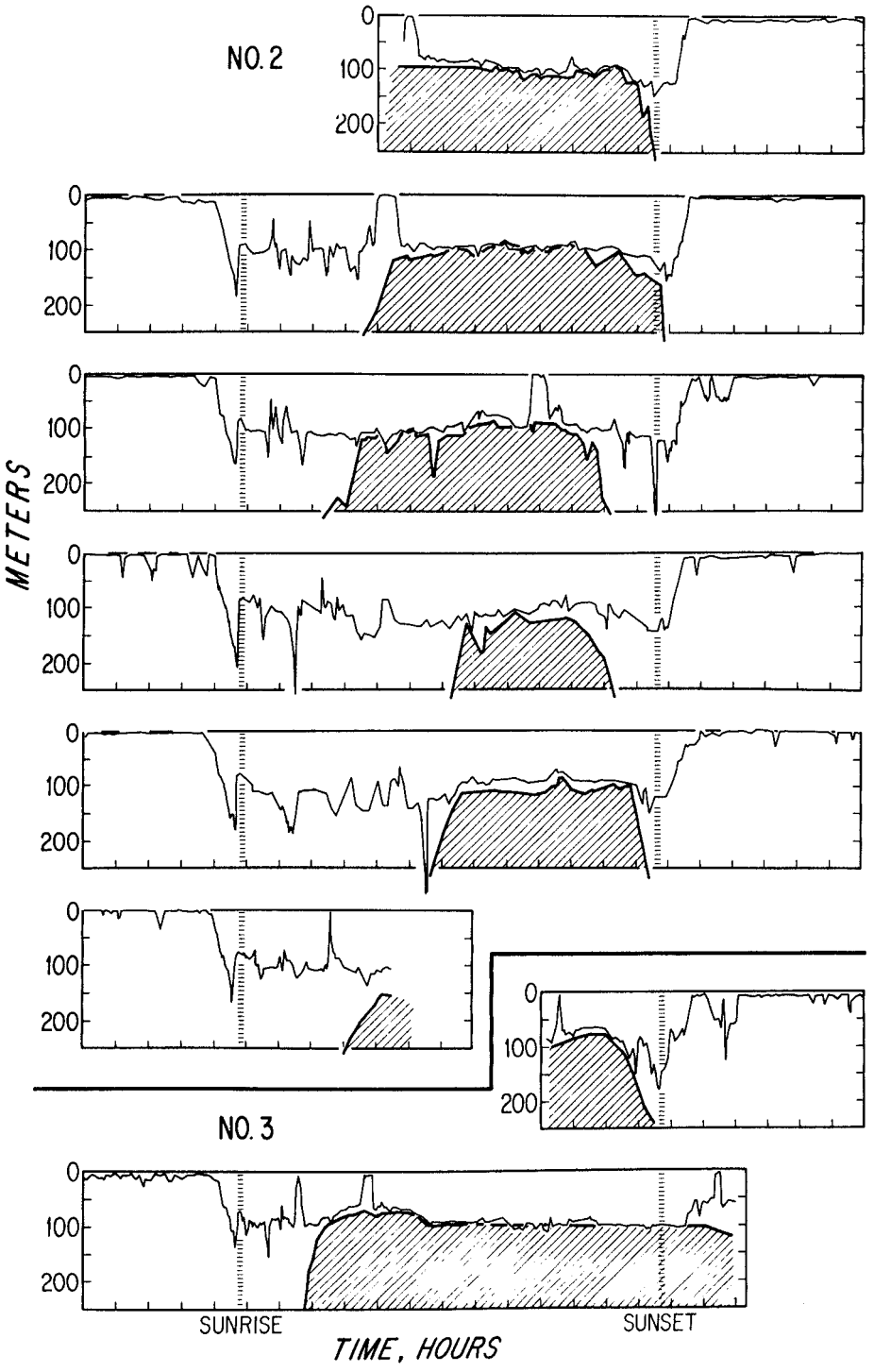

FIGURE 9.—Depth records for swordfish no. 2 and 3, Baja California, plotted from midnight to midnight. The crosshatched area indicates a bank. The fish swam near the surface at night and at a depth of about 100 m during the day. The morning dive about 1 h before sunrise carried the fish below its usual daytime depth.

threshold for vision in deep-sea fish (Denton and Warren 1957; Clarke and Denton 1962). The swordfish should be able to locate its prey visually in its dimly lit environment both day and night.

Our depth records for swordfish show many variations from the U-shaped pattern expected if they are following isolumes. Much of this variation can be explained as modification of a response to light by other environmental factors. On 10 November the depth record for no. 7 was skewed, with the greatest depth reached late in the afternoon (Figure 8). The deepening isotherms during this day indicate that the fish was moving from shelf and slope water into the warm, clear water of the Gulf Stream. Light attenuation is much greater inshore than in the Gulf Stream (Jerlov 1968) where the same level of illumination occurs at greater depths. The gradual increase in depth during the fading daylight on this afternoon coincided with the movement from slope to Gulf Stream water and can be interpreted as the fish maneuvering deeper to maintain a constant light intensity in the clearer water.

On 9 November, no. 7, which had reached 400 m by midmorning, returned to 100 m at noon. This unexpected midday rise from depth occurred when the fish left a region of clear blue slope water and passed under a streamer of dark grey-green shelf water (indicated as a marked thermal inversion in Figure 8 and as a light-colored region in the satellite infrared image, Figure 7). Swimming under this dark shelf water, the swordfish entered a shadowed area. By rising toward the surface it would have returned to a light level which prevailed at greater depth in the blue water. A change of attenuation coefficient from 0.035 in blue water to 0.140 in shelf water would result in the same light intensity at 400 m as at 100 m depths, respectively. These are reasonable attenuation values and it is possible that the swordfish was maintaining a constant light level during this vertical movement.

Oxygen

A vertical movement in response to sunrise and sunset occurred in all of the Baja California experiments. An interesting feature is apparent when these depth records are aligned vertically (Figure 9). The rapid descent which began about an hour before dawn each morning reversed at sunrise when the fish came back up to about 100 m. A well-developed oxygen-minimum layer exists in this area of the eastern tropical Pacific and the oxycline at the top of the low oxygen region is parallel to the thermocline, but at somewhat greater depth (Griffiths 1968, fig. 11 and 27). In its normal movement away from the surface with increasing light at dawn, the swordfish penetrated deeply into this low oxygen layer, then returned to spend most of the day at shallower depths with higher oxygen concentration. The presence of the oxygen-minimum layer caused the swordfish to spend the day at a shallower depth and higher light level than normal.

In Baja California swordfish frequently came up during the day to bask on the surface with the tips of their dorsal and caudal fins out of the water for periods of 15-80 min. This basking behavior, at a time of day when we would expect them to be at their greatest depth, may be related to the low oxygen concentration at depth. The depth record for no. 6 superimposed on an isotherm pattern in Figure 5 shows that the fish was well below the thermocline during much of the day. We did not measure oxygen, but using the data in Griffiths (1968) we can infer concentrations from water temperature and depth. When swordfish no. 5 and 6 were below the thermocline, they were in an environment with an oxygen concentration only 10 to 20% that of air-saturated water. This is a much lower concentration than the 60% saturation suggested as the lower limit for skipjack tuna in the vicinity of an oxygen-minimum layer (Ingham et al. 1977). The less active swordfish, with its large mass of white muscle, might be more resistant to anoxia and able to accumulate an oxygen debt. If so, the periodic excursions to well-aerated surface waters would allow it to recover from anoxia. There appears to be a rough correlation between time spent on the surface and the length of the preceding period below the thermocline, as would be expected if this were a recovery process: $T_s = 0.2\ T_L + 16$ ($r = 0.6$; $n = 10$) where T_s is time on surface in minutes and T_L is time at depth in minutes.

In the Baja California area, there was a marked difference between frequencies at which the inshore and offshore swordfish came to the surface during the day. The inshore fish surfaced six times in 7 d and spent 2.8% of the daylight hours on the surface. The offshore fish surfaced 10 times in 2.5 d, spending 25.7% of the daylight hours on the surface. This difference may be related to oxygen concentrations, for the inshore fish were near the mouth of the Gulf of California where the oxygen-

minimum layer is not well developed. They would probably encounter less anoxic conditions than the offshore fish which were well into the Pacific. Because of this, an attempt to compare abundance of swordfish in these two areas from the numbers seen on the surface could be grossly misleading.

On the continental shelf off the northeastern United States and Canada where swordfish can be seen "finning" on the surface during the warm months, the water is well oxygenated from surface to bottom. However, temperatures on the bottom can be quite cold, and the swordfish which are feeding deep may be coming to the surface to warm their muscles or as an aid in digestion. Basking behavior by swordfish may be part of a recovery from a variety of stresses experienced at depth.

Buoyancy

Swordfish swimming on the surface seem to have neutral or sufficient positive buoyancy to raise the dorsal and caudal fins out of the water. Swordfish taken on longline frequently float, swim bladders distended, when hauled to the surface, and would have been at neutral buoyancy at a pressure of a few atmospheres. The swordfish are clearly able to inflate their bladder to a volume which will give them neutral density at some near-surface depth. The capillary retia mirabilia of the gas gland are short, about 1 mm long, and similar to those of surface dwellers such as the flying fish (Marshall 1960, see footnote 10). Thus the structure of the gas gland does not seem suitable for rapid pumping of large volumes of oxygen under pressures up to 60 atm at 600 m. Our depth records (Figures 5, 8) show many examples of rapid vertical movements with the fish sometimes moving from 100 m to the surface in <5 min. Such changes in depth could cause a 10-fold expansion in the volume of a free bubble. It seems unlikely that the swordfish could pump gas into and out of its swim bladder rapidly enough to maintain constant volume during these excursions. The necessity for doing this could be avoided if the bladder were allowed to compress with hydrostatic pressure as the depth increased. This would increase the density of the fish, but even with the bladder partially collapsed at depth, the high lipid content and porous fatty bone of the swordfish would lower its density and the flattened bill and fixed pectoral fins would give it hydrodynamic lift while swimming.

When at rest at depth, excess density would prevent the swordfish from hovering easily and it might find resting on the bottom to be a convenient position. While on the bottom the fixed pectoral fins would form an effective tripod with the tail (R. H. Backus[11]). Frequent records of swordfish caught in bottom trawls indicate that resting on the bottom may be common in this species (Bigelow and Schroeder 1953; Eschmeyer 1963). Martin Bowen,[12] a National Marine Fisheries Service (NMFS) observer on foreign squid trawling vessels working between Cape Hatteras and Cape Cod, Mass., reported 28 swordfish taken in bottom trawls during 72 d at sea in 1977. Observers in research submarines have seen swordfish lying on the bottom (Zarudski and Haedrich 1974), and in our records it appears that swordfish no. 3 was on the bottom for several hours.

Temperature

Water temperatures encountered by swordfish in the Baja California area are illustrated in Figure 5. A 10° C (18° F) gradient was present between the surface and the depth of the deepest dive, 300 m. The gradient between surface and the usual daytime depth was 5°-7° C. The fish made frequent excursions through the thermocline, passing such gradients in a few minutes. While these are significant temperature changes, they did not seem to affect the activities of the fish, which in this area appear to be more influenced by the presence of anoxic water.

Our record for swordfish no. 7 in the North Atlantic shows the impressive ability of this species to penetrate marked thermal boundaries (Figure 8). The greatest temperature change occurred on the morning of 10 November when this fish moved from 27° C water on the surface to 8° C water at 420 m, a 19° C excursion in 2.5 h. This is a large change for any heterothermal organism to undergo and remain active. It was not just a brief excursion, for it remained in the cold water all day. The thermal history of the fish before this dive was complex, but the preceding

[10]N. B. Marshall, Park Lane, Saffron Walden, Essex, Engl., pers. commun. 1975.

[11]R. H. Backus, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1972.

[12]M. Bowen, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun. 1978.

4.5 h included 1.5 h at 27° C, 1.5 h at 14° C, and 1.5 h at 27° C for an average water temperature of 22°-23° C before the descent. The swordfish is clearly able to function over a wide range of ambient temperatures.

The coldest water which no. 7 entered was 8° C. This may represent a lower preferred limit for swordfish, as it agrees with the 8° C temperatures reported for deeper sightings from research submarines (Zarudski and Haedrich 1974). The 8° C temperature may only be coincident with a light or depth limit or the location of prey; we look forward to experiments with swordfish in areas where water <8° C is readily available.

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GROWTH RATES OF NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, BASED ON TAG RETURNS

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ABSTRACT

Estimates of growth parameters for North Pacific albacore, *Thunnus alalunga*, were based on tag-recapture statistics, using the standard von Bertalanffy model and an extended model. Sequential estimation of L_∞ and K allowed us to test hypotheses concerning variation in growth rate between tagged albacore recaptured in different ocean regions.

Significantly lower growth rates were found in albacore recaptured off Japan and the United States north of latitude 40° north compared with those recaptured off the United States south of latitude 40° north. The differences in estimated growth rate were generally consistent with differences in length-frequency distributions of albacore taken off the United States north and south of latitude 38° north during the period when most recaptures were made. The findings add to a growing body of evidence that the North Pacific albacore population is not homogeneous; rather, at least two different subpopulations may exist.

Growth rates of North Pacific albacore, *Thunnus alalunga* (Bonnaterre), have been estimated by counting vertebral rings (Uno 1936; Aikawa and Kato 1938; Partlo 1955), examining scale circuli (Nose et al. 1957; Bell 1962; Yabuta and Yukinawa 1963), tracing progressions of length modes (Brock 1943; Suda 1954), and by measuring tagged fish at release and recapture (Otsu 1960; Clemens 1961). Of these techniques, only tagging provides direct estimates of growth rate, and the tagging results of Otsu and Clemens are reasonably consistent with the conclusions of Yabuta and Yukinawa's scale analysis and Suda's modal progression work. However, as Shomura (1966) noted in a review of tuna growth studies, comparisons are complicated by the biases and uncertainties peculiar to each method. For example, in the case of tagging we assume that the growth rate is unaffected by stresses resulting from capture, handling and tagging, and from the burden of carrying the tag itself. Conclusive results will require that the basic assumptions of any particular method be tested and verified.

In this paper, we present new estimates of growth parameters based on recent tag-recapture experiments conducted jointly by the National Marine Fisheries Service (NMFS) and the American Fishermen's Research Foundation (AFRF).[3] We use the standard von Bertalanffy growth model, but also briefly explore an extension. Sequential estimation of the parameters L_∞ and K allows us to test hypotheses concerning variation in growth rate between tagged fish recaptured in different ocean regions.

Transpacific recaptures of albacore tagged in the eastern North Pacific off North America and in the western North Pacific off Japan have established the interdependence of the United States and Japanese North Pacific albacore fisheries, and have also fostered the hypothesis of a single, common stock (Ganssle and Clemens 1953; Clemens 1961; Otsu and Uchida 1963). However, our results add to growing evidence (Laurs and Lynn 1977) that the North Pacific albacore population is not homogeneous, as usually assumed, but is composed of at least two subgroups with different migration patterns and growth histories.

METHODS

Tagging Procedures

Albacore were caught in the eastern North Pacific and tagged aboard U.S. commercial jig and

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[3]AFRF administers revenues derived from a landing assessment paid by the U.S. albacore industry on U.S.-caught albacore.

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bait fishing vessels on charter to AFRF. Approximately 70% of the tagging was done by commercial fishermen trained in tagging procedures, the rest by NMFS technicians. Single Floy[4] spaghetti-dart tags were inserted on the left side below the second dorsal fin with the aid of a beveled stainless steel tube so that the tag barb was lodged in the pterygiophores of the fin. Only fish judged to be in very good condition were tagged; fish hooked in the roof of the mouth or showing signs of extreme exhaustion or severe bleeding were rejected. For each tagged fish a record was kept on 1) tag number, 2) date and time of release, 3) fork length at time of release, 4) condition at tagging, and 5) longitude and latitude of release. Additional tagging details are given in Laurs et al. (1976).

Recovery Procedures

Recoveries were made by sport and commercial fishermen, unloaders, and cannery workers. Information was obtained on 1) tag number, 2) date of recapture, 3) fork length at time of recovery, and 4) longitude and latitude of recapture. Most recapture locations were given as loran coordinates, which were converted to longitude and latitude, but the recapture locations for tags recovered by unloaders and cannery workers were often reported inexactly, e.g., as "off central California." Direct measurements of fork length were available for about one-half the fish recovered. For most of the remainder only the weight at recovery was given, and fork length was estimated using Clemens' (1961) weight-length relation. Observed fork lengths were measured to the nearest centimeter. Bias in estimating fork length from observed weight using the inverted weight-length relationship was judged to be <0.5 cm in absolute value over the length range represented in the recapture sample, so subsequent growth analyses were based on the combined sets of observed and estimated lengths.

[4]Mention of a commercial company or product does not constitute an endorsement by the National Marine Fisheries Service, NOAA.

Data Screening

The tag return data were screened to exclude cases where information was incomplete, unreliable, or clearly inaccurate. Out of 741 tag returns made from 1971 through 1978, 305 were rejected (Table 1). In 15 cases length at release was not measured, in 116 cases the recapture date was unknown, and in 68 cases neither length nor weight was measured at recovery. In 79 other rejected cases the length at recovery was not measured and the weight only guessed without the use of scales. Additionally, in 27 instances a gross error was apparent in the measurement of fork length either at release or recovery.

The final accepted data set of 436 cases includes observations on 28 albacore showing negative estimated growth. We assume these are a result solely of measurement error or error in estimation in cases where the recovery weight was converted to length, and we assume such error occurs throughout the data set independently of size or time between release and recapture (time out).

One of the common steps in screening tag recovery data for growth studies is to partition the data according to length at release, compute linear regressions of growth increment on time out within each subset, and then reject rare observations, usually those departing from expectations by more than two standard deviations (Schaefer et al. 1961; Joseph and Calkins 1969). We abandoned this step because the number of

TABLE 1.—Summary of number of tagged fish released, recovered, rejected, and accepted for analysis of albacore growth.

Year	No. tagged fish released	No. tagged fish recovered	Rejected tag recoveries (no.)						No. tag recoveries accepted for analysis
			Missing release length	Missing recapture date	Missing recovery size	Weight at recovery estimated	Measurement error	Total	
1971	887	34	2	6	5	1	0	14	20
1972	1,557	132	1	23	13	16	10	63	69
1973	1,805	111	0	23	10	12	2	47	64
1974	2,486	175	4	22	16	22	8	72	103
1975	1,349	115	1	17	13	15	2	48	67
1976	1,581	85	0	15	8	10	3	36	49
1977	1,221	25	0	4	0	3	0	7	18
1978	2,719	58	1	6	3	0	2	12	46
Unknown	—	6	6	—	—	—	—	6	0
Total	13,605	741	15	116	68	79	27	305	436

"outliers" it identified was consistent with the number expected due to chance alone, because the procedure has no sensible stopping rule, and because even with length at release fixed, the expected relationship between growth increment and time out is nonlinear.

Grouping of Data

The selected data were cross-classified by location of tagging and location of recapture (Table 2). Nearly 66% of the 436 tagged fish were released inshore,[5] and of these 74% were released south of lat. 40° N, the remainder north of this latitude. Eighty-four percent of recaptured fish released inshore south of lat. 40° N were recovered in the same area, 5% were recovered inshore north of lat. 40° N, 1.4% were taken in the offshore area east of long. 180°, and 8.4% were recovered in the western Pacific. Of the recovered fish tagged and released inshore north of lat. 40° N, only 8.2% were recaptured inshore south of lat. 40° N, 1.4% were taken east of long. 180° in the offshore area, 27.4% were recovered in the area of tagging and 63% were recovered in the western Pacific. Of the recovered fish tagged offshore, 70.5% were recaptured either inshore north of lat. 40° N or west of long. 180°, and only 27.5% were recovered in the southern inshore area.

For purposes of constructing and testing hypotheses about differences in growth rates, tag returns were grouped into three categories depending on recapture location: 1) Group A includes all fish recaptured inshore south of lat. 40° N, except those released inshore north of lat. 40° N (221 fish). 2) Group B consists of tag recoveries made inshore north of lat. 40° N, excluding those released inshore south of lat. 40° N (75 fish). 3) Group C consists of all tag recoveries made west of the 180° meridian (114 fish). The three groups together comprise 410 recaptures. Excluded are 6 fish tagged inshore north of lat. 40° N and recovered south of this line the following year or later; 11 fish released south of lat. 40° N and recaptured in the northern inshore area (1 the same season, 10 in following years); 6 fish recaptured offshore east of long 180°; and 3 fish whose recapture locations are unknown.

[5]Fish released (recaptured) east of long. 130° W in the area south of lat. 49° N, or east of long. 135° W between lat. 49° and 54° N were considered to be released (recaptured) inshore. Demarcation of the inshore area boundary is based on analysis of tag recoveries discussed in Laurs and Lynn (1977).

TABLE 2.—Classification of selected tag data by locations of release and recapture.

Recapture location	Release location: Inshore[1]—from lat. 40° N: South	North	Total	Offshore	Grand total
East of long. 180°	194	27	221	98	319
Inshore[1]	191	26	217	96	313
South of lat. 40° N	180	6	186	41	227
North of lat. 40° N	11	20	31	55	86
Offshore	3	1	4	2	6
West of long. 180°	18	46	64	50	114
Unknown	2	0	2	1	3
Grand total	214	73	287	149	436

[1]See text footnote 5.

Growth Models

We used observations of growth increment, length at tagging, and time at liberty to estimate the growth rate, K, and the asymptotic length, L_∞, of the standard deterministic von Bertalanffy model. In addition, we considered an extension of the von Bertalanffy model which allows the growth rate to vary with age in a simple manner. In general terms, we assumed that the expected growth increment for the jth fish in the ith group ($i = 1,\ldots, m$; $j = 1, 2,\ldots, n_i$), given the initial length and time out, could be stated as

$$E(\Delta L_{ij}) = \int_{t_{ij}}^{t_{ij}+\Delta_{ij}} G(u)\,(L_\infty - L(u))\,du,$$

where $E(\Delta L_{ij})$ = expected growth increment of jth tagged fish in ith group during $(t_{ij}, t_{ij} + \Delta_{ij})$
$= L(t_{ij} + \Delta_{ij}) - L(t_{ij})$
t_{ij} = age of jth fish in ith group at time of release
Δ_{ij} = time at liberty for jth fish in ith group
$L(u)$ = length at age u
L_∞ = asymptotic length
$G(u)$ = unspecified age-dependent growth rate.

If we set $G(u) = K$ = constant, we have the standard von Bertalanffy model, and

$$E(\Delta L_{ij}) = (L_\infty - L_{1_{ij}})\,[1 - \exp(-K\Delta_{ij})],$$

where $L_{1_{ij}} = L(t_{ij})$.

We call this Model 1. (We omit subscripts on

parameters, even though group-specific parameters are implied.)

In Model 1 we assume that the ratio of instantaneous growth rate, $dL(u)/du$, to potential growth, $L_\infty - L(u)$, is K, a constant. Instead, we may suppose generally that this ratio varies with age. We considered one such situation. In this model, Model 2, we assume that stresses due to capture, handling, and tagging will initially reduce the growth rate of a tagged fish below its usual level, but that as time passes the normal growth process will be restored. Specifically, in our analysis of Model 2 we assume the standard model holds for untagged fish but that when a fish is tagged its normal growth pattern is interrupted, such that

$$G(u) = K, \qquad 0 < u < t_{ij}$$
$$G(u) = K/\{1 + \alpha \exp[-\beta(u - t_{ij})]\} \qquad t_{ij} \leqslant u.$$

We assume $K \geqslant 0$, $\beta > 0$, and $\alpha \geqslant 0$. Model 2 says that following tagging the growth rate is immediately reduced to a fraction $(1 + \alpha)^{-1}$ of its normal value, K, and then returns to K asymptotically (Figure 1). L_∞ is assumed to be unaffected.

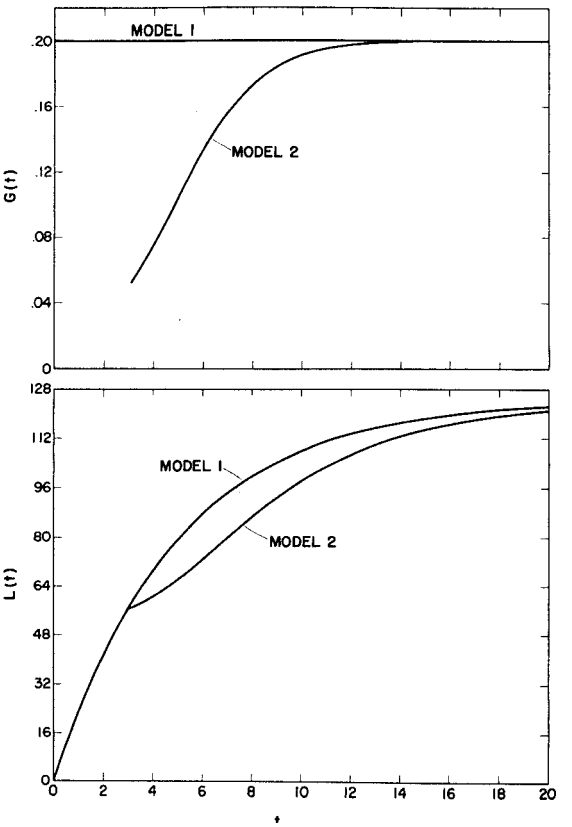

FIGURE 1.—Standard von Bertalanffy growth model (Model 1), and an extension (Model 2) incorporating a temporary reduction in growth rate, $G(t)$, following tagging. The resulting growth pattern, $L(t)$, is altered. Time units are arbitrary.

Parameter Estimation

In the standard von Bertalanffy model as applied to tag recapture data, there are two parameters to be estimated, K and L_∞. The usual approach is to estimate them simultaneously, and we did so using the FORTRAN program BGC 4 written by Tomlinson (1971). This routine finds $\hat{K}$ and $\hat{L}_\infty$ as those parameter values which minimize

$$S = \sum_{j=1}^{n_i} \left\{ L_{2_{ij}} - [L_\infty - (L_\infty - L_{1_{ij}}) \exp(-K\Delta_{ij})] \right\}^2,$$

where $L_{2_{ij}} = L(t_{ij} + \Delta_{ij})$. Since $E(L_{2_{ij}})$ is a nonlinear function of K, parameter estimates derived using this procedure are prone to serious bias unless observations on $L_{2_{ij}}$ are made over a wide range of $L_{1_{ij}}$ and Δ_{ij}. Presumably, it is also desirable that they be made uniformly in the plane of these two variables.

The parameters of Model 2 may also be estimated jointly using nonlinear least squares methods, but estimates of L_∞ and correlated parameters suffer the same drawbacks as estimates of the standard von Bertalanffy model parameters derived from BGC 4

An alternative approach in fitting both models is to estimate L_∞ and the other parameters sequentially. Where the oldest members of the population have been intensively sampled and an upper asymptote to length is clearly demonstrated in the data, a reasonable estimate of L_∞ is the length of the largest fish seen in the catches, or the average length of the largest specimens observed. Which estimator to use depends on one's conceptual model of the growth process—L_∞ can be regarded as the mean of a distribution of asymptotic lengths in the population, or strictly as an upper bound to the length any fish in the population can achieve. With the value of

L_∞ determined, the other parameters may be estimated by the least squares method using the general model:

$$Y_{ij} = -\ln\left(\frac{L_\infty - L_{2_{ij}}}{L_\infty - L_{1_{ij}}}\right) = \int_{t_{ij}}^{t_{ij}+\Delta_{ij}} G(u)\,du + \epsilon_{ij},$$

where we assume that ϵ_{ij} are independent errors with zero means and variances σ^2_{ij}.

This approach handily accommodates any well-behaved form of $G(u)$. In the case of Model 1, the problem of estimating K reduces to a simple linear regression:

$$Y_{ij} = K\Delta_{ij} + \epsilon_{ij}. \quad (1)$$

When a reasonably accurate estimate of L_∞ can be made by sampling the catches, this sequential estimation procedure for Model 1 has the advantage that the range of observations on $L_{1_{ij}}$ and Δ_{ij} is not so critical.

With Model 2, the sequential method may be applied to estimate K, α, and β using the equation:

$$Y_{ij} = K\Delta_{ij} - \left(\frac{K}{\beta}\right)\ln\left\{(1+\alpha)/[1+\alpha\exp(-\beta\Delta_{ij})]\right\} + \epsilon_{ij}. \quad (2)$$

The desirability of fitting this nonlinear model to any particular set of data may be judged by examining the residuals around the least squares fit of Model 1 (Equation (1)). As is evident from Figure 2, the detection of nonlinearity in this manner requires that observations be available uniformly over a broad range of Δ_{ij}.

Covariance Analysis

One of our chief objectives was to determine whether growth rates differed between groups of fish, based on estimates of parameters of the standard von Bertalanffy model. Since BGC 4 estimates of K and L_∞ are highly correlated, particularly when few large fish are in the sample, and since probability statements concerning intergroup comparisons of both K and L_∞ were not possible, we used the sequential estimation procedure. For the ith group of fish we assumed

$$E(Y_{ij}) = K_i\,\Delta_{ij}, \quad (3)$$

where $Y_{ij} = -\ln\left(\frac{L_\infty - L_{2_{ij}}}{L_\infty - L_{1_{ij}}}\right)$

and specified a fixed value for L_∞. Then we developed and applied a weighted zero-intercept covariance analysis to test hypotheses of the form:

$$H: K_1 = K_2 = \ldots = K$$

on the basis of F-statistics. Statistical weights were computed on the assumption that $\sigma^2_{ij} \sim \Delta_{ij}$, as suggested by Figure 2.

RESULTS

Standard Model

Joint estimates of K and L_∞ for Groups A, B, and C, based on the BGC 4 program, are shown in Table 3. We consider the estimates inaccurate, owing to sampling biases discussed earlier. In particular, we think the unexpectedly low L_∞ estimates (and correspondingly high K estimates) are due to the absence of very large albacore in the release and recovery samples. Of the 410 selected tag returns, 141 exceeded 80 cm fork length at recapture, but only 42 were >85 cm and just 11 were >90 cm. The average fork length of tagged albacore at time of release was 63.7 cm (range 45-89 cm), and at recovery, 75.7 cm (range 51-103 cm).

Because of the difficulties with BGC 4 estimates, we based intergroup comparisons on estimates of K from the sequential estimation procedure. A preliminary F-test showed no significant difference in $\hat{K}$ between fish whose lengths at recovery were measured and those whose lengths were estimated from the inverted weight-length relationship. Further sequential analyses (as well as the earlier BGC 4 estimates) were therefore based on all data, regardless of how recovery length was determined.

L_∞ was fixed at 125 cm, a reasonable choice well supported by available length-frequency data. Although Otsu and Sumida (1970) reported an albacore measuring 132.7 cm from the

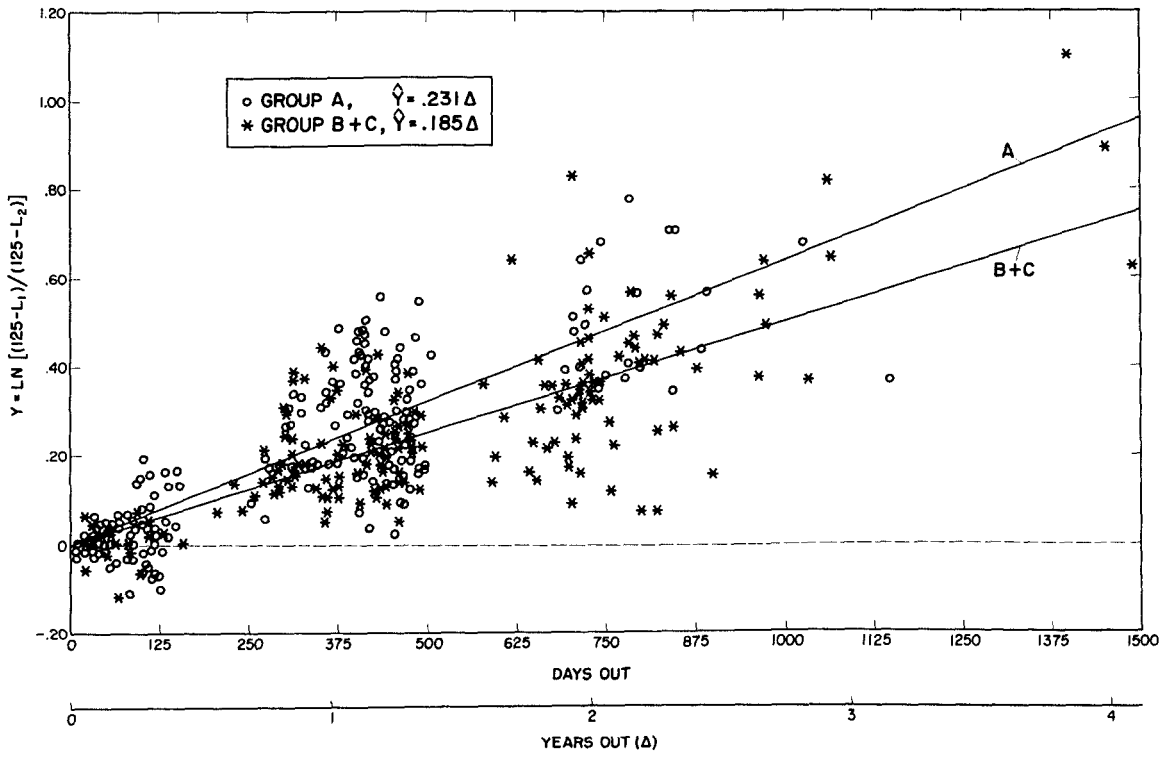

FIGURE 2.—Regression of growth variable, Y, on years between release and recapture for albacore of Groups A (221 fish) and B + C (189 fish). The slopes are estimates of the von Bertalanffy growth parameter, K, and they are significantly different.

TABLE 3.—Estimates of von Bertalanffy growth parameters for North Pacific albacore by recapture group and estimation method, assuming stock boundary at lat. 40° N.

Recapture group	Sample size	BGC4 estimates		Sequential estimates		Average time out Δ (d)
		$\hat{L}_\infty$ (cm)	$\hat{K}$ (yr^{-1})	Fixed L_∞ (cm)	$\hat{K}$ (yr^{-1})	
A	221	94.5	0.505	125.0	0.231	313
B	75	107.5	.272	125.0	.193	400
C	114	98.5	.345	125.0	.184	588
B + C	189	102.1	.310	125.0	.185	513
A + B + C	410	100.9	.342	125.0	.199	405

Hawaiian longline fishery, which harvests the largest North Pacific albacore known, specimens >125 cm are extremely rare. With L_∞ fixed at 125 cm, Group A had the highest growth rate estimate, $\hat{K}_A = 0.231$/yr (Table 3). Group B and $\hat{K}_B = 0.193$, and Group C had the lowest growth rate estimate, $\hat{K}_C = 0.184$. When Groups B and C were pooled into a "North" category, the resulting $\hat{K}_N$ was 0.185. The estimate of K for all three groups combined was 0.199.

Table 3 also shows the statistics on average time between release and recapture. Group A fish were at liberty an average of 313 d, while Group B fish were out 400 d, and Group C fish, 588 d. Tagged fish from Groups B and C combined were at large an average of 513 d.

The estimates suggest that the North fish, Groups B and C, had a lower growth rate than the South fish of Group A. Such a difference might arise if, as we suppose, the North fish budget more of their available energy for migration compared with the South fish, and relatively less energy for growth. Tag release and recovery results indicate that the North fish make longer migrations, traveling between coastal waters off the United States Pacific Northwest and coastal waters off Japan, while the South fish undertake shorter migrations between coastal waters south of Cape

Mendocino, Calif., and the central North Pacific east of 180° (Laurs[6]).

The hypothesis of equal growth rates was tested using the weighted zero-intercept analysis of covariance, and was rejected at the 0.5% significance level (Table 4, Figure 2). In pairwise comparisons between individual groups, the only nonsignificant difference in growth rate was between Groups B and C.

Are the observed differences in growth rates of tagged albacore consistent with other information? To check this, we examined the length composition of albacore catches along the U.S. west coast (Figure 3). The length-frequency plot for catches north of lat. 38° N during the period when most recaptures were made, 1972-78, showed modes at about 64 and 76 cm and a hint of one at 54 cm. Catches south of lat. 38° N showed the 54 cm mode, but had primary modes at about 66 and 79 cm. The discrepancy between modes of the older albacore is further evidence of a slower growth rate for North fish, assuming these modes represent fish of the same age. To see if length-frequency data and tag data agreed, we computed the expected fork lengths under each $\hat{K}$ at annual time steps and compared these with observed modes in the length-frequency distributions. Starting with some initial fork length, L_1, we used the equation $L_i = a + bL_{i-1}$, $i = 2, 3, \ldots$, where $a = L_\infty (1 - \exp(-K))$ and $b = \exp(-K)$. Setting $L_1 = 54$ and $L_\infty = 125$ cm, we found the sequence of lengths 54.0, 66.0, and 76.0 cm for the North group albacore; and 54.0, 68.6, and 80.3 cm for the South fish. These are reasonably consistent with the observed sequences of length modes.

Extended Model

Plots of residuals from the standard model against days out (Figure 4) showed a tendency toward negative deviations during the first several months after tagging, suggesting that some of the residual variation could be attributed to "lack of fit" (Draper and Smith 1966). For example, of the 221 recaptures analyzed in Group A, 90 were taken within 6 mo of tagging, and 70%of the Model 1 residuals corresponding to these early recaptures were negative. We therefore fit Model 2 to each set of data, using the sequential estimation procedure (Equation (2)) with $L_\infty = 125$ cm. Resulting estimates of K were 3-6%larger than the corresponding estimates from the standard linear model; thus, if Model 2 is correct, systematic bias in the latter estimates does not appear to be serious.

However, estimates of α and β were relatively large in all cases, suggesting that the growth rate may drop abruptly to near zero immediately after

TABLE 4.—Analysis of covariance comparing growth rate of Group A North Pacific albacore with growth rate of Group (B + C) albacore, assuming stock boundary at lat. 40° N. Probability of obtaining F statistic this large under null hypothesis is <0.005.

Source of variation	df	Residual SS	MS	F
Individual lines:				
A	220	1.1476		
B + C	188	1.7362		
Pooled	408	2.8837	0.0071	
Common line	409	3.1009		
Difference	1	.2172	.2172	30.72

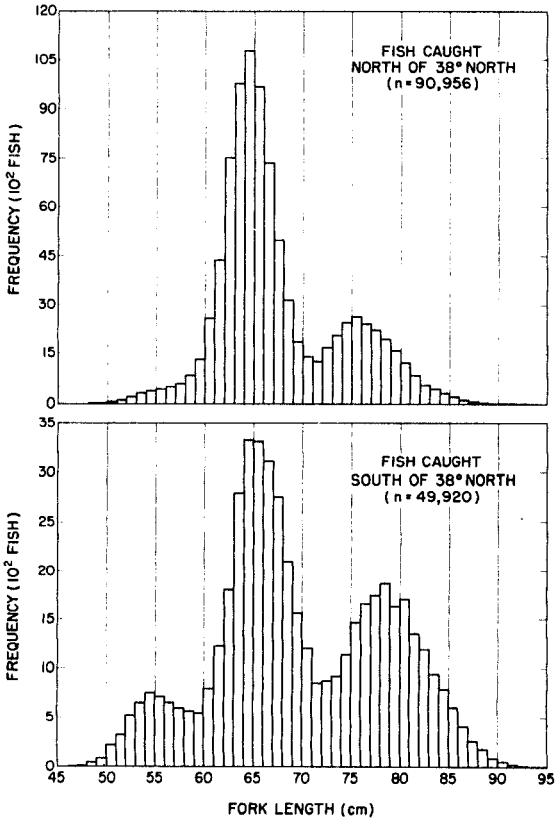

FIGURE 3.—Composite length-frequency distributions for North Pacific albacore caught north of lat. 38° N and south of lat. 38° N off the U.S. west coast during the 1972-78 fishing seasons.

[6]Laurs, R. M. 1979. Results from North Pacific albacore tagging studies. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-17, 10 p.

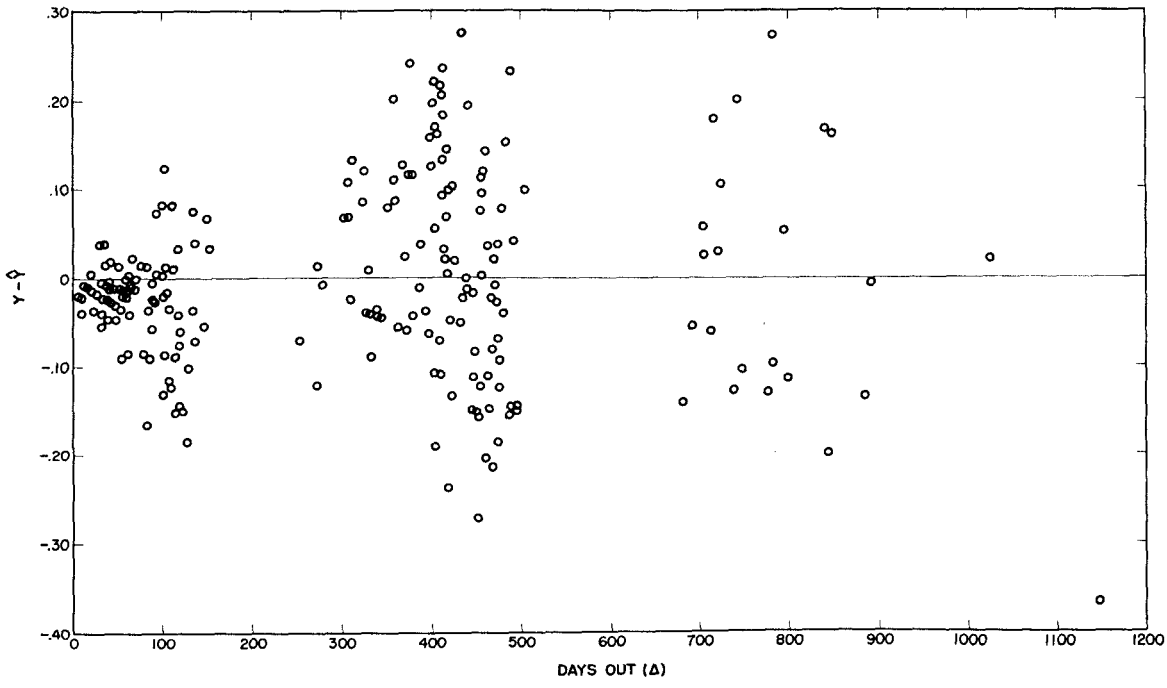

FIGURE 4.—Residuals from the fit of Model 1 to the Group A albacore data, as a function of days out.

tagging and then recover to normal within the first year of liberty. While this basic response to tagging stress appears to be a reasonable hypothesis, the estimates of α and β were very unstable and little confidence could be placed on projected growth rate recovery patterns. Further, although the extended model fits the data better than the ordinary von Bertalanffy in the sense of reducing residual variation, as expected, this improvement is only slight; considering the high variance displayed in the data we do not reject the simpler von Bertalanffy model.

DISCUSSION AND CONCLUSIONS

The results of our growth analysis are strengthened by their consistency with other findings, but the assumptions of our analysis need to be tested. In particular, we assumed that our estimate of L_∞, 125 cm, was the same for all groups of North Pacific albacore. If $L_\infty(B + C) > L_\infty(A)$, our conclusions concerning differences in growth rate are reinforced. But if the South fish, Group A, actually tend toward a larger asymptote in fork length than the North fish of Groups B and C (there is no evidence of this), then the differences between estimates of K might not be significant. For example, if we assume $L_\infty(A) = 130$ cm and $L_\infty(B + C) = 120$ cm, the differences vanish. More to the point, unless the L_∞'s are the same, the comparison of growth rates between groups is no longer conveniently reduced to a comparison of K estimates. When the assumption of equal L_∞ is valid, the actual value of L_∞ assumed is relatively unimportant as far as the covariance analysis is concerned; our conclusions were the same when L_∞ was fixed at 120, 130, and 135 cm.

In Model 1, the standard von Bertalanffy model, we also assumed that the growth rate was unaltered by the presence of the tag or by the stress imposed in its application. In our analysis of Model 2 we explored the question of whether tagging might have affected growth rate in a specified way, and Model 2 fits our data only slightly better than Model 1. However, effects of the sort we hypothesized might easily be masked by high variance in the data. Nevertheless, if the effect of tagging were simply to reduce the normal growth rate, K, suddenly and permanently to a lower level, K', it would go undetected by our analysis. To determine the validity of the tag-effect assumption, we need to compare the growth rates of tagged fish with those of untagged, "control" fish.

Such a comparison was recently made for bait-boat-caught southern bluefin tuna, *T. maccoyii*, by Hearn,[7] who found that fish caught 3 wk after being tagged weighed 14% less than untagged fish of the same length in the same schools. Assuming the tagged bluefin tuna also grew less in length than their untagged counterparts, this 14% weight loss would be an underestimate. At any rate, after 1 yr at liberty no difference in weight was discernible.

We found that the growth rate of North Pacific albacore recaptured either off the coast of North America north of lat. 40° N or in the western North Pacific off Japan was significantly lower than for tagged albacore recaptured off North America south of lat. 40° N during 1972-78. The differences in growth rate of tagged fish are remarkably consistent with differences in length-frequency distributions of albacore caught off North America north and south of lat. 38° N during the period when most recaptures were made. These findings add to a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs et al.[8]; Laurs and Lynn[9]) that North Pacific albacore are not as homogeneous as usually assumed, and that there may be at least two subgroups of albacore: one which supported the Japanese pole-and-line fishery and the United States and Canadian fisheries in waters north of about lat. 40° N from 1972 to 1978, and another which did not contribute significantly to the Japanese surface fishery, but supported the United States coastal fishery south of lat. 40° N during this period. If such a distinction is valid, the situation is surely more complex and dynamic than we have supposed, with each stock's contribution to each fishery varying from year to year. Presumably such variation would be tied directly to changes in oceanographic conditions. And undoubtedly the latitudinal boundary was not fixed exactly at lat. 40° N during 1972-78, as we assumed, but analyses based on assumed boundaries at lat. 38° and 42° N gave the same results. If an accurate assignment of tagged fish to stock were possible, a more powerful test of growth differences could be made.

A finding that more than one subpopulation or stock is involved in the North Pacific albacore fisheries would have important consequences, of course, both for stock assessment, fishery evaluation and management policy analysis, and for development of accurate catch forecasting systems. It is important that further work be done to identify stocks, and to elucidate their origins, migratory habits, and degree of interchange.

[7]Hearn, W. S. 1979. Growth of southern bluefin tuna (*Thunnus maccoyii*). Commonwealth Scientific and Industrial Research Organization, Division of Fisheries and Oceanography, Cronulla, New South Wales, Australia, Unpubl. manuscr.

[8]Laurs, R. M., R. J. Lynn, and R. N. Nishimoto. 1975. Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1975. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-75-84, 49 p.

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ECONOMIC FEASIBILITY OF DOMESTIC GROUNDFISH HARVEST FROM WESTERN ALASKA WATERS: A COMPARISON OF VESSEL TYPES, FISHING STRATEGIES, AND PROCESSOR LOCATIONS

C. M. LYNDE[1]

ABSTRACT

An economic model relating fishing costs to vessel characteristics and operating conditions was used to estimate the costs and benefits to U.S. fishermen of harvesting groundfish under a variety of conditions. Comparisons were made between 1) two vessel types, 2) two modes of operation: delivering to a floating processor and delivering to a shore-based processor, and 3) three fishing strategies in Alaskan waters.

Fishing costs were about 50% less and fuel efficiency was 28% higher for the smaller of the two vessels. Costs for either vessel decreased by 30% and fuel efficiencies increased by 35% when delivering the catch to a floating processor rather than delivering to port. Cost estimates for both sea delivery and port delivery were sensitive to changes in fuel price. A $0.026/l ($0.10/gallon) increase in fuel price increased the break-even ex-vessel prices by $6/t for sea delivery and $8/t for port delivery in one example.

Given the ex-vessel prices currently offered by two joint venture firms and a fuel price of $0.277/l ($1.05/gallon), break-even catch rates were calculated for each vessel type and targeting strategy, assuming sea delivery. All of the catch rates were considered highly feasible when compared with the average catch rates of foreign trawlers and experimental U.S. fisheries in the area. Assuming similar prices were offered by shore-based processors, the break-even catch rates, although higher than under the sea delivery mode, were still considered feasible. However, the margin for profit is narrower and could be negative with increases in fuel price.

Since the implementation of the U.S. 200 mi economic zone (public law 94-265, 13 April 1976), a great deal of interest has been generated by the large stocks of groundfish off the western Alaska coast. The combined annual optimum yield of walleye pollock, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*; sablefish, *Anoplopoma fimbria*; flatfish, and rockfish from the eastern Bering Sea, Aleutians, and western Gulf of Alaska (Kodiak Island westward; Figure 1) has been estimated to be over 1.6 million t (North Pacific Fisheries Management Council 1978a, b). In perspective, this potential is equivalent to 58% of the total 1978 U.S. commercial landings of all species from all areas (U.S. Department of Commerce 1979). Although the Fisheries Conservation and Management Act of 1976 grants preference to U.S. harvesters over foreign fishing fleets, a domestic trawl fishery for groundfish has been slow to develop, and the precise set of conditions necessary to stimulate growth has been a topic of considerable concern (Sullivan and Heggelund 1979; Gorham[2]; Little[3]; Alaska Fisheries Development Foundation[4]; Combs[5]).

In this paper I demonstrate the utility of an economic model which estimates fishing costs based on vessel characteristics and operating conditions. The model is used to predict the fishing costs and the catch rates required to cover costs under conditions that are likely to occur during future domestic groundfish harvests from western Alaska. These catch rates are then compared with actual catch rates observed in foreign and experimental domestic fisheries in the area. In this way I seek to contribute to the development of an appropriate methodology for evaluating the economic feasibility of domestic groundfishery expansion in Alaska.

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[4]Alaska Fisheries Development Foundation. 1978. Development proposal for bottomfish off Alaska, 37 p.

[5]Combs, E. R. 1979. Prospectus for development of the United States fisheries. Alaska groundfish, p. 25-112, 327-362. Prepared for Fisheries Development Task Force, NMFS, NOAA.

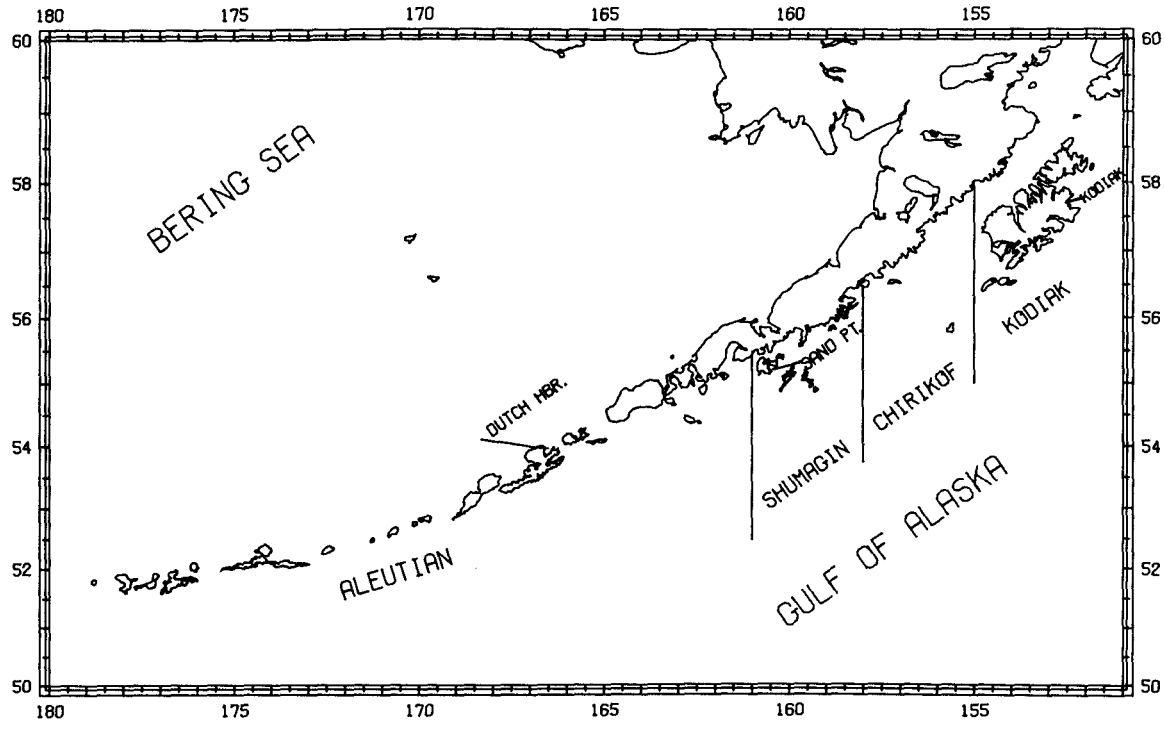

FIGURE 1.—Western Gulf of Alaska and eastern Bering Sea and selected International North Pacific Fisheries Commission areas.

In addition, an economic model such as the one described in this paper may be helpful to fishermen considering future diversification. The model could be easily adapted for use with a programmable calculator or onboard microcomputer. After tailoring the parameters to his vessel, the vessel owner need only key in a few pertinent variables such as expected ex-vessel price, distance to the fishing ground, and fuel price and receive an immediate estimate of the average catch rate required to cover his expenses.

One advantage of the modeling approach is that it allows one to examine the effects of individual factors of interest by allowing these factors to vary while holding all others constant. This paper examines the effects upon fishing costs and fuel efficiency (fish harvested per fuel consumed) of the following factors: vessel type, processor location, fishing strategy, and fuel price. Costs and benefits are estimated only within the harvesting sector. A consideration of economic feasibility within the processing and marketing sectors of the industry is beyond the scope of this paper.

THE ECONOMIC MODEL

Given a set of operating conditions, such as distance to the fishing grounds and number of crew required, a set of vessel characteristics, such as cruising speed and hold capacity, as well as a schedule of capital expenses, such as the vessel's initial value and finance rate, the model projects the costs of a single fishing trip and computes a set of catch rates and corresponding ex-vessel prices required to balance fishing costs with net revenue.

Assuming the crew (including skipper) receives shares of the revenue as remuneration, the benefit (B_{ij}) to the vessel owner of a single fishing trip is simply:

$$B_{ij} = (1 - S_{ij}) \cdot U \cdot P$$

where S_{ij} = total crew shares (expressed as decimal fraction) for the ith vessel type and jth mode of operation, U = total catch, and P = ex-vessel price.

Fishing costs are commonly categorized as fixed

or variable. Fixed annual costs are invariate with respect to the amount of vessel use per year. Using the subscripts i and j as before, the fixed annual costs can be prorated over the length of the fishing trip, allowing for yearly down time due to bad weather, maintenance, and vacations, according to the formula:

$$F_{ij} = [T_{ij}/(365 - D_i)]A_i$$

where F_{ij} = fixed costs per trip, T_{ij} = length of trip in days, D_i = total inoperative days per year, and A_i = annual fixed costs.

Assuming the crew pays a share of certain variable costs, the total fishing costs (C_{ij}) incurred by the vessel owner per trip can be expressed as:

$$C_{ij} = F_{ij} + V_{ij} + (1 - S_{ij})W_{ij}$$

where V_{ij} = variable costs incurred only by vessel owner and W_{ij} = variable costs incurred by owner and crew.

Setting benefits equal to costs and solving for ex-vessel price gives:

$$P = \left[\frac{F_{ij} + V_{ij}}{1 - S_{ij}} + W_{ij}\right] \frac{1}{U} . \qquad (1)$$

This equation defines the ex-vessel price, P, required to break even for a fishing trip with catch rate U. Conversely, Equation (1) can be used to compute the catch rate required to break even for a fishing trip when the ex-vessel price is P. A computer program (TRAWL)[6] was written to calculate solutions for P over a range of catch rates for a given vessel type and mode of operation.

A tacit assumption has been made that the criterion for economic feasibility of a fishery is met if a fisherman can receive enough revenue to balance the variable and fixed costs of fishing. In fact, if the vessel and gear already exist and no other more profitable fisheries are available, it will be economically advantageous for the fisherman to enter the fishery in question if it provides enough revenue to cover variable costs alone, since the fixed costs will be incurred whether fishing or not. However, the objective of this paper is to examine the conditions under which the fisherman can cover both fixed and variable costs.

The model relies on a number of assumptions which relate fishing costs to the vessel type and the mode of operation. Table 1 lists these assumptions according to a cost accounting format similar to that suggested by Smith (1975). A description of the cost derivations and the sources of their estimates can be found in Appendix I. Note that, unlike Smith's cost accounting procedures, the average annual cost of financing is included here as a fixed cost. Variable costs IIB-D (Table 1), represented in total by symbol W_{ij} in the above development, are commonly deducted from the gross revenue before the crew shares are taken. Fixed costs IA-F and variable costs IIA are in turn represented by symbols A_i and V_{ij} above. Crew

[6]Written in Fortran IV. A program listing and user's guide are available from the author on request.

TABLE 1.—Fixed and variable fishing costs as a function of vessel characteristics and operating conditions.

Cost category	Parameter values and variables
I. Fixed annual costs:	
A. Routine boat and engine maintenance	\$0.07 × vessel's initial value (VIV)
B. Insurance:	
1. Hull	0.021 × VIV
2. P & I	2,100.0 × no. in crew
C. Depreciation	0.0533 × VIV
D. Association dues	2,500.0
E. Contingencies/miscellaneous	0.05 × (above total)
F. Average annual finance cost n = no. of payment periods i = interest rate per period	$1.0 \times \text{VIV} \times \left[\frac{\%\text{ financed}}{\text{yr financed}}\right] \times \left[\frac{ni(1+i)^n}{(1+i)^n - 1} - 1\right]$
II. Variable costs:	
A. Fishing gear repair and replacement (see Append. I)	\$1.0 × gear costs/h × towing h
B. Fuel:	
1. Cruising	0.2105 × horsepower × travel h × fuel price/l
2. Towing	0.1579 × horsepower × towing h × fuel price/l
3. Stove and auxiliaries	30.283 × trip h × fuel price/l
4. Lube oil	0.235 × trip h × price/l
C. Food	13.50 × trip d × no. in crew
D. Ice	$25.00 \times \frac{\text{capacity for groundfish (wt)}}{1 + (\text{fish:ice wt ratio})}$

shares, composing S_{ij}, are assumed to be 12% for the skipper and 7% for each additional crew member.

FACTORS OF INTEREST

Vessel Types

Two representative vessel types were considered: a 33 m (108 ft) combination crabber/trawler and a 25-28 m (80-92 ft) bottom trawler or combination shrimp and groundfish trawler. These vessel types are thought to be representative of many of the U.S. vessels likely to participate in future western Alaska groundfish harvests.

The vessel characteristics and capital expenses for the two vessel types are listed in Table 2. The vessel characteristics are based on statistical analyses of vessels registered with the State of Alaska as performed by Katz et al.[7] The characteristics of vessel type 1 are average values for a group of combination crabber/trawler vessels fishing for king and tanner crab in Alaska (class 8.5 of Katz et al. (footnote 7)). Similarly, the characteristics of vessel type 2 are representative of a group of Alaska shrimp trawlers and smaller crabber/trawlers (class 8.3 of Katz et al.). Type 2 vessel characteristics are also believed to be representative of the larger groundfish trawlers of California, Oregon, and Washington. The capital expenses incurred by owners of these vessel types were estimated with the help of industry personnel (Pigott[8]; Jaeger[9]).

TABLE 2.—Vessel characteristics and capital expenses for two representative vessel types (see text).

Item	Vessel type 1	Vessel type 2
Vessel characteristics:		
Age, yr	1-2	5
Keel length, m (ft)	33 (108)	25-28 (80-92)
Engine type	Diesel	Diesel
Horsepower	1,000	650
Cruising speed, kn/h	11.5	10.0
Hold volume, m^3 (ft^3)	225 (8,000)	140 (5,000)
Capacity for groundfish, t	150	115
Capital expenses:		
Vessel's initial value, $	1,500,000	500,000
Amount financed, %	80	80
Annual finance rate, %	10	8.5
Amortization, yr	20	15
Payment period	Monthly	Monthly
Interest per period (i), %	0.7174	0.6821
No. of payment periods (n)	240	180

Processor Location and Mode of Operation

Two modes of operation were compared: delivering the catch at sea to a floating processor and delivering the catch to a land-based processor. The method of sea delivery is currently being employed by U.S. fishermen participating in two international joint fishing ventures for groundfish off the western Alaska coast. Under the arrangements of these joint ventures, the U.S. trawlers transfer their catch at sea via detachable cod ends to large floating processors provided by the foreign partner. The fish are then processed aboard the factoryships and the resulting product is taken to foreign ports and sold on the foreign market.

During the sea delivery mode of operation, it is assumed that: 1) the floating processor is on or near the fishing grounds, 2) fishing vessels have at least two cod ends so replacement after each haul is not delayed, 3) full cod ends are towed to the processor and empty cod ends are returned to the fishing vessel periodically by a motor launch, and 4) the processing rate of the factory vessel is not limiting.

Table 3 lists the estimated operating conditions for the sea delivery and land delivery modes of operation. Differences between the two modes are as follows:

TABLE 3.—Operating conditions for vessels harvesting groundfish from western Alaska. Delivering the catch at sea versus delivering to a land-based processor.

Item	Mode of operation: Sea delivery	Land delivery
No. of crew required (including captain)	4	5
Maximum trip length:		
Vessel type 1	28	7
Vessel type 2	26	7
Fish:ice weight ratio (if applicable)	N.A.	2:1
Search time per trip, h	6	6
Towing time per day on grounds, h	9	9
Time spent in port replenishing supplies, refueling, and unloading	24	24
Distance to fishing grounds:		
Gulf of Alaska	75	75
Bering Sea:		
Walleye pollock or Pacific cod	65	65
Sole species	220	220
Gear costs per hour of towing:		
Vessel type 1	20.57	20.57
Vessel type 2	16.90	16.90

[7]Katz, P. L., K. C. Lee, L. J. Bledsoe, and J. Buss. 1976. The classification, enumeration, characteristics and economic performance of Alaska shellfish vessels. Part 1-Classification, enumeration and vessel characteristics. Norfish Tech. Rep. 61, 59 p.

[8]George M. Pigott, University of Washington, Department of Food Science, Seattle, WA 98195, pers. commun. December 1979.

[9]Sig Jaeger, President, North Pacific Vessel Owners Association, Fishermen's Terminal, Seattle, WA 98119, pers. commun. January 1980.

1) The maximum trip length when delivering at sea is limited only by the storage capacities for fuel, water, and supplies, while the maximum trip length when delivering onshore is limited by the iced storage life of the catch. In the first case, the maximum trip length has been estimated as 28 d for vessel type 1 and 26 d for vessel type 2. In the latter case, a 5-d storage life for fresh walleye pollock (Sea Fisheries Institute and National Marine Fisheries Service[10]) limits the trip to a maximum of 7 d (including time traveling to the grounds and time in port). At higher catch rates the actual trip length may be further limited by the hold capacity for groundfish and ice.

2) No ice is required when delivering at sea.

3) Fewer crew members are needed when delivering the catch at sea since no sorting or stowage of the catch is required. Jaeger[11] predicted that two fewer crew members would be required if delivering at sea. This proved true for at least one vessel owner participating in the joint venture for Pacific whiting (formerly known as Pacific hake) off the coast of Oregon during 1978 and 1979 (Fisher[12]). However, in this analysis, a conservative estimate of one fewer crew member has been adopted.

The search time, towing time, and the time in port have all been assumed to be the same for both modes of operation. The search time, or time spent prospecting for fish, and the time spent in port replenishing supplies, refueling, and unloading (if applicable) have been estimated to be 6 and 24 h, respectively. The towing time per day on the grounds has been taken to be 9 h after Jaeger (footnote 11). Again, these assumptions are conservative. If vessels delivering their catch at sea are fishing for a joint venture operation, the information sharing that is likely to occur may reduce the search time per trip. It has also been argued that the cod end transfer system employed in the sea delivery mode requires less rerigging time and therefore allows more towing time per day on the grounds (Fisher footnote 12).

[10]Sea Fisheries Institute, Gdynia, Poland, and National Marine Fisheries Service, Seattle, Wash. 1977. Preliminary report Gulf of Alaska research cruise. First leg, July 1977, 21 p.

[11]Jaeger, S. 1977. Presentation to the North Pacific Fishery Management Council on the subject of foreign joint ventures. August 5, 1977. Seattle, Wash.

[12]Barry Fisher, Vessel Owner/Operator, Newport, OR 97065, pers. commun. with R. Major, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112, November 1979.

Fishing Strategy

Three different fishing strategies were examined based on the following stocks as targets: Pacific cod and walleye pollock in the western Gulf of Alaska, walleye pollock in the Aleutian area, and sole, especially yellowfin sole, *Limanda aspera*, in the eastern Bering Sea. The distances to the fishing grounds are based on the locations of the nearest of the most productive foreign fishing locations during 1977 and 1978 (Smith and Hadley[13]). Table 4 lists these locations and their approximate distances to the nearest port.

Fuel Price

For most of the following comparisons the fuel price was taken to be \$0.277/l, which was the current price for no. 2 diesel fuel at Dutch Harbor as of the time of this writing (1980). A subsequent section details the sensitivity of cost estimates to increases in fuel price.

RESULTS

Delivering at Sea Versus Delivering to Port

At any given catch rate for vessel type 1, the break-even ex-vessel price when delivering to a floating processor is at least 31% lower than when delivering to port. For example, at a catch rate of 10 t/d on the fishing grounds, vessel type 1 would require an ex-vessel price of \$421/t to cover costs if unloading in port while requiring only \$290/t if transferring the catch at sea. A plot of the relationship between break-even price and catch rate [described by Equation (1)] for vessel type 1 operating in the Gulf of Alaska delivering to a floating processor (solid) and delivering to a land-based processor (dashed) is shown in Figure 2.

Similar results were obtained from the analysis of vessel type 2 operating in the Gulf of Alaska (Figure 3). Under the sea delivery mode of operation break-even ex-vessel prices are at least 33% lower than under the port delivery mode. At a catch rate of 10 t/d the required break-even prices are \$146/t and \$217/t for sea delivery and port delivery, respectively. These results are in general agreement with Jaeger's (footnote 11) analysis in

[13]Smith, G. B., and R. S. Hadley. 1979. A summary of productive foreign fishing locations in the Alaska region during 1977-78: trawl fisheries. Alaska Sea Grant Rep. 79-7, 287 p.

TABLE 4.—Foreign catches from western Alaska waters during 1977 and 1978. Source: Smith and Hadley (text footnote 13).

Nation	Predominant species	Location		Nearest port	Distance (nmi)
		lat.	long.		
R.O.K.	Walleye pollock and Pacific cod	54°18′ N,	160°23′ W	Sand Point	75
U.S.S.R.	Walleye pollock and Pacific cod	56°30′ N,	152°30′ W	Kodiak City	75
Japan	Walleye pollock and Pacific cod	56°30′ N,	152°30′ W	Kodiak City	75
U.S.S.R.	Sole species	57°31′ N,	166°55′ W	Dutch Harbor	220
R.O.K.	Walleye pollock	53°25′ N,	166°15′ W	Dutch Harbor	65

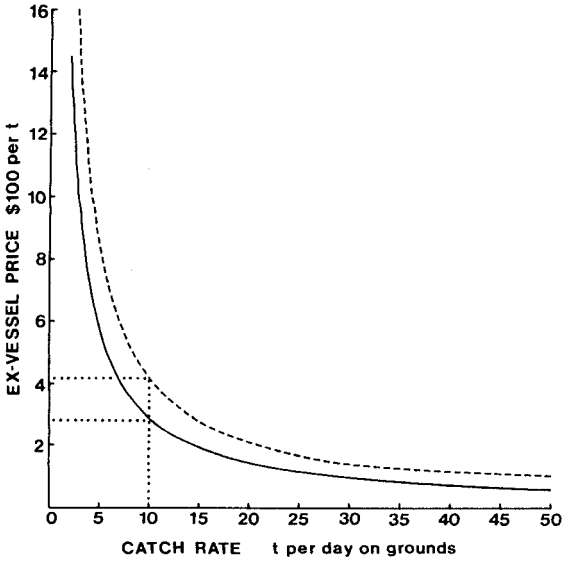

FIGURE 2.—Break-even price versus catch rate for vessel type 1, delivering to a floating processor (solid) and delivering to a shore-based processor 75 nmi from the fishing grounds (dashed). Dotted lines indicate required ex-vessel prices for a catch rate of 10 t/d.

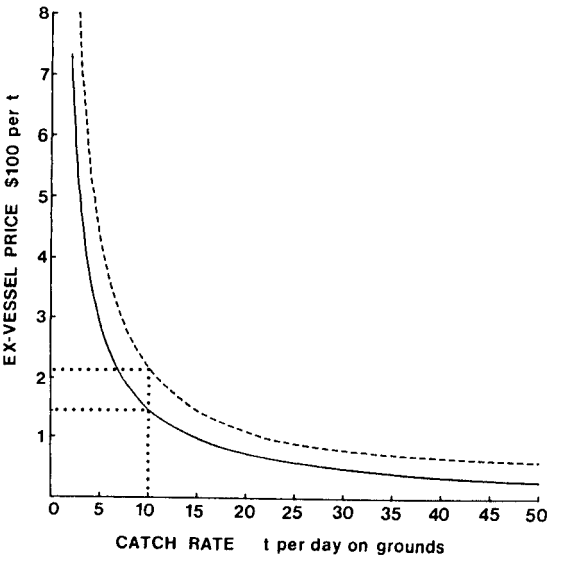

FIGURE 3.—Break-even price versus catch rate for vessel type 2, delivering to a floating processor (solid) and delivering to a shore-based processor 75 nmi from the fishing grounds (dashed). Dotted lines indicate required ex-vessel prices for a catch rate of 10 t/d.

which it was found that ex-vessel prices under the sea delivery mode could be 50% less than under the port delivery mode and still yield the same profit to the fisherman.

Another criterion for comparing harvest methods is the weight of whole fish harvested per volume of diesel fuel consumed, hereafter referred to as the fuel efficiency. At a catch rate of 10 t/d the fuel efficiency for vessel type 1 is 3.2 kg/l if delivering to port and 4.3 kg/l if delivering at sea. For vessel type 2 fuel efficiencies at 10 t/d are 4.0 kg/l and 5.5 kg/l for port and sea delivery modes, respectively. Thus, the fuel efficiencies increase by 34% (vessel 1) and 36% (vessel 2) under the sea delivery mode.

If the expected average catch rate is high (> 29 t/d for vessel 1 or >22 t/d for vessel 2), then the relative advantages of sea delivery increase since the hold capacity becomes limiting under the port delivery mode.

Comparison of Vessel Types

Based on the above results, it can be seen that the break-even price required by vessel type 2 is about 49% less than that required by vessel type 1, given the same catch rate. Alternatively, for any given ex-vessel price, the catch rate required by vessel type 1 to cover costs is about twice as high as that for vessel type 2. Furthermore, fuel efficiencies for the second vessel type are about 28% higher than those of vessel type 1.

Sensitivity to Changes in Fuel Price

The effect of changes in the price of fuel upon the relationship between the break-even price and catch rate will now be examined. For a given set of vessel characteristics and operating conditions, the fixed and variable costs are constant over a range of catch rates (assuming hold size is not limiting) and Equation (1) can be reduced to:

$$P = \frac{C_1}{U} + \frac{C_2 D}{U} \qquad (2)$$

where C_1 and C_2 are constants (C_2 = volume of fuel consumed), D = fuel price, P = break-even ex-vessel price, and U = total catch. Thus, the effect of the price of fuel upon the break-even ex-vessel price depends upon the catch rate and, of course, the vessel type and mode of operation. Once again using 10 t/d as a point of reference, Equation (2) predicts that for each \$0.026/l (\$0.10/gal) increase in the price of fuel, a \$6/t increase in the break-even ex-vessel price results (vessel type 1, delivering at sea, distance = 75 nmi). The same increase in fuel price for vessel type 1 unloading in port results in an \$8/t change in the break-even ex-vessel price. An equivalent increase in fuel price for vessel type 2 results in \$5/t and \$7/t increases in the break-even ex-vessel price for the sea delivery and land delivery modes, respectively. Thus, any estimates of economic feasibility will be moderately sensitive to changes in fuel price.

Comparison of Fishing Strategies

In the above comparisons, the distance from fishing grounds to the nearest port was fixed at 75 nmi, which is the expected distance if targeting on Pacific cod and walleye pollock in the western Gulf of Alaska. For the two alternative strategies, targeting on walleye pollock in the Aleutians area and targeting on yellowfin sole in the eastern Bering Sea, the expected distances are 65 and 220 nmi, respectively (Table 4). Accordingly, the model was run and Equation (1) was solved for a range of catch rates using these latter distances.

Figure 4 shows the ex-vessel prices required by vessel 1 under both modes of operation when the distance is 65 nmi and when the distance is 220

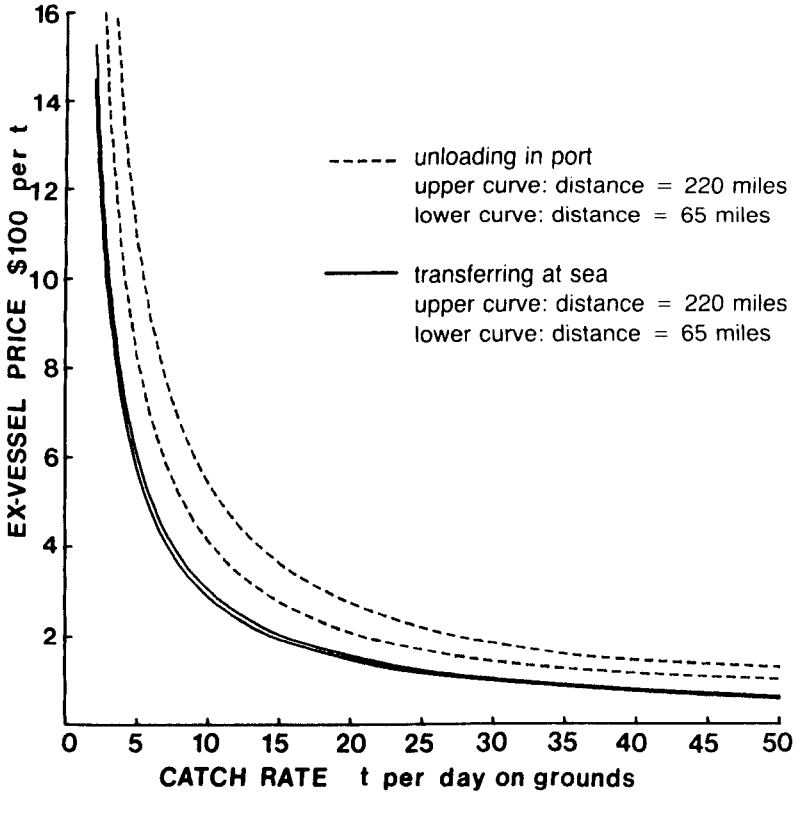

FIGURE 4.—Break-even price versus catch rate for vessel type 1, sea delivery and shore delivery, for distances of 65 and 220 nmi to the nearest port.

nmi. Similar curves result for vessel 2. It can be easily seen that under the port delivery mode a large increase in break-even price results from increasing the distance from 65 to 220 nmi (at 10 t/d these prices are \$414/t and \$545/t, a 32% increase). Under the sea delivery mode, however, the increased distance results in only a 6% increase in price (\$289/t to \$305/t at 10 t/d). Thus, any estimates of feasibility for the sea delivery mode are liable to be insensitive to changes in the distance to the fishing ground.

Feasibility of Groundfish Harvest

Table 5 lists the average species composition of the catches of three U.S. vessels fishing for two joint venture corporations in the Gulf of Alaska during 1979 and presumably targeting on Pacific cod and walleye pollock. In addition, the species composition obtained by Soviet factory trawlers targeting on sole in the Bering Sea and Korean factory trawlers targeting on walleye pollock in the Aleutians during 1978 is given (National Marine Fisheries Service[14]). Also listed in Table 5 are the ex-vessel prices offered by one of the joint venture firms as of the end of 1979. If U.S. trawlers catch the same species mix and receive the same prices, the expected average ex-vessel price per metric ton will be \$169 if targeting on Pacific cod and walleye pollock, \$217 if targeting on sole, and \$121 if targeting on walleye pollock. Table 6 presents the average catch rates, as predicted by the model, which would allow owners of vessel types 1 and 2 to break even, given the expected ex-vessel price and operating conditions for each of the three targeting strategies. I would now like to determine if these catch rates are feasible. Unfortunately, since the trawl fishery for groundfish in western Alaska is new to U.S. vessels, there is a paucity of U.S. commercial catch rate data.

Although the average catch rate for the three U.S. vessels fishing for joint ventures in 1979 was not available, a single U.S. vessel (25 m in length) fishing experimentally for one of the joint venture companies in the Shumagin area during 1978 averaged 11.8 t/d on the grounds. This vessel fished for only a short period, but the catch rate steadily increased from 4.8 to 22.3 t/d as the weather improved and experience was gained (Ely[15]). In light of these results, the catch rates of 17 and 9 t/d required by vessel types 1 and 2, if targeting on Pacific cod and walleye pollock and delivering to a floating processor, are considered feasible. Even the catch rates of 25 and 13 t/d required by the same vessels if landing their catch in port may be feasible; however, the vessel owner's margin for profit (if any) is substantially reduced. Again, these catch rates are fairly sensitive to the price of fuel (considered here to be \$0.277/l). An increase in the price of fuel to, say, \$0.528/l (\$2.00/gal) without a subsequent increase in groundfish prices, would lead to required catch rates of 21 and

[14]National Marine Fisheries Service, Foreign Observer Department. 1980. Unpubl. manuscr., n.p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

TABLE 5.—Recent ex-vessel prices offered by a joint venture corporation and average species composition and average catch rates of groundfish taken by: 1) U.S. vessels fishing for joint ventures in the Gulf of Alaska during 1979, 2) Soviet factory trawlers fishing in the eastern Bering Sea during 1978, and 3) Korean factory trawlers fishing in the Aleutians area during 1978. Source: National Marine Fisheries Service (text footnote 14).

Species	Ex-vessel price	Percentage composition		
		U.S.	U.S.S.R.	R.O.K.
Walleye pollock	\$132	38.5	4.1	84.2
Pacific cod	187	47.0	2.1	5.1
Sole[1]	242	5.0	85.9	0
Rockfish	308	6.0	0	.1
Others	—	3.5	7.9	10.6
Catch rate, t/d		11.8	43.2	61.0

[1]Yellowfin sole and Alaska plaice.

[15]R. C. Ely, American Fisheries Corporation, Anchorage, AK 99503. Report on progress of the KMIDC/Davenny pollock joint venture in the Gulf of Alaska. Report given to the North Pacific Fishery Management Council in public hearings. November 30, 1978.

TABLE 6.—Expected ex-vessel prices and required break-even catch rates by target strategy, vessel type, and mode of operation.

Target species	Area	Price/t	Vessel type	Required break-even catch rate (t/d on grounds)	
				Sea delivery	Land delivery
Pacific cod and walleye pollock	Gulf of Alaska	169	1	17	25
			2	9	13
Sole species	Bering Sea	217	1	14	25
			2	7	14
Walleye pollock	Aleutian Islands	121	1	24	37
			2	12	17

12 t/d for the two vessel types if delivering at sea and 30 and 17 t/d if delivering to port.

The catch rates that can be expected by U.S. groundfish trawlers operating in the Bering Sea and Aleutians are even more nebulous. The Soviet trawlers targeting on sole in the Bering Sea during 1978 were much larger (76-89 m, 2,000 hp) than the U.S. trawlers under consideration (Pruter[16]). However, much of the factory trawler's size is devoted to supporting crews of 87-96 for periods up to 90 d at sea. In addition, these vessels must have space for large processing and storage facilities. The U.S. vessels, on the other hand, with crews of four or five and no processing facilities, are more efficient for their size as catchers. Therefore, the break-even catch rates of 14 and 7 t/d for vessel types 1 and 2 targeting on sole and delivering to sea seem quite feasible when compared with the Soviet's average of over 43 t/d. Even though the catch rates required if delivering to port (25 t/d for vessel type 1, 14 t/d for vessel type 2) are nearly twice as high as required when delivering at sea, they still may be considered feasible when compared with the average Soviet catch rate.

If instead, U.S. trawlers similar to types 1 and 2 target primarily on walleye pollock in the Aleutians as did large Korean factory trawlers (89-111 m, 3,500-6,000 hp, Pruter footnote 16) the U.S. vessels would require catch rates of approximately 24 and 12 t/d if delivering at sea. The corresponding catch rates if delivering to port are 37 and 17 t/d. Although these catch rates are higher than under the previous strategies, they may be feasible considering the high availability of walleye pollock in the area. In fact, none of the above catch rates can be considered unfeasible since the average Korean catch rate in the Aleutian area exceeded 61 t/d.

DISCUSSION

Recently a number of events have occurred which have made fishing for groundfish in western Alaska relatively more attractive.

1) A market for potentially large quantities of groundfish has developed with the initiation of the two international joint ventures in western Alaska.

2) Groundfish markets in California, Oregon, and Washington have been erratic and prices have been generally low (Sorensen[17]).

3) Vessel profits from the western Alaska shellfisheries have decreased due to:

a) declining abundance of pandalid shrimp (Jackson et al.[18]) and snow crab stocks (Somerton[19]),

b) a drop in the ex-vessel price for king crab from $2,460/t ($1.23/lb) in 1978 to $1,720/t ($0.86/lb) in 1979 (Browning[20]), and

c) expansion of the king crab fleet (from 60 boats in 1977 to 226 in 1979) leading to shortened seasons and reduced average vessel shares of the relatively constant quota.

The results of this analysis indicate that given a market with ex-vessel prices similar to those being offered by the joint venture firms, U.S. fishermen may currently find it economically attractive to participate in a trawl fishery for groundfish in western Alaska. In fact, some 23 vessels are committed to fish for the joint venture operations in western Alaska during 1980 (Blackburn[21]). It would seem, from this analysis, that operators of vessels similar to vessel types 1 or 2 can currently cover both fixed and variable costs given the above ex-vessel prices whether delivering at sea or delivering to port. However, the profits if delivering to port would be less. To equal the vessel profits under the sea delivery mode, land-based processors would have to offer ex-vessl prices at least 45% higher than those offered at floating processors would have to offer ex-vessel prices at least delivering at sea should increase with increased fuel costs. As fuel prices increase, owners of larger vessels with high horsepower, such as vessel type 1, will have a harder time making a profit in a western Alaska groundfish trawl fishery than owners of smaller vessels such as type 2.

This paper has not examined the economic feasibility of domestic processors. However, since

[16]Pruter, A. T. 1980. Preliminary analysis of data obtained by foreign fishery observers in 1978. Processed Rep. 80-7, 58 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[17]Sorensen, S. 1979. Statement to the International Trade Commission. Reprinted in Alaska Fisherman's J. 2(12):20-21.

[18]Jackson, P. B., P. Holmes, A. Spalinger, and J. Nickels. 1979. Shrimp research. *In* Westward Region Shellfish Report to the Alaska Board of Fisheries, April, 1979, p. 216-242. Alaska Dep. Fish Game, Kodiak.

[19]Somerton, D. 1979. A reappraisal of the declining trend of recruitment to the Bering Sea stock of tanner crab (*Chionoecetes bairdi*). Norfish Tech. Rep. 92, 16 p.

[20]Browning, R. 1979. Crab season cut short as Bering boats fill quota. Natl. Fisherman 60(8):11.

[21]Blackburn, C. 1979. Plans progress for KMIDC fish purchases. Kodiak Daily Mirror 39(185):1-3.

U.S. fishermen are restricted by law to using only U.S. built vessels for fishing related activities, any domestic floating processors are likely to be either new vessels or extensive conversions, both of which may be cost prohibitive. On the other hand, distant water fishing nations, faced with increasing area and quota restrictions, may have factory vessels which are receiving less than optimal use (Kaczynski and LeVieil[22]). For this reason, international joint fishing ventures may be the only viable option for potential domestic groundfish trawlers in western Alaska in the near future. Although it has been argued that international joint fishing ventures may hinder the development of domestic land-based processors (Sullivan and Heggelund 1979), and the long-term net benefits to the domestic industry as a whole may be negative (Gorham footnote 2), the immediate benefits to the U.S. fishermen involved are positive.

CONCLUSIONS

On the basis of the economic model and assumptions applied in this study it was shown that:

1) Delivering the catch at sea via detachable cod ends is more economically efficient for U.S. fishermen than landing the catch in port. This is particularly true of fisheries for species with high spoilage rates, such as walleye pollock. The cost savings in this analysis amounted to over 30% and derive primarily from the following factors:

a) Fewer crew members are required when delivering the catch at sea.
b) A much higher percentage of the season can be devoted to trawling time when delivering to a sea-based processor.
c) Less fuel per season is spent running back to port, thus the fuel efficiency is greater when delivering the catch at sea.

These cost savings apply whether fishing for an international joint fishing venture or delivering the catch to a domestic floating processor.

2) Increasing the distance to the fishing grounds, while largely affecting the economic efficiency if delivering to port, had little effect if delivering at sea.

3) The relationship between catch rate and break-even ex-vessel price is sensitive to increases in fuel price for both the sea delivery and land delivery mode of operation. However, it is slightly less critical for the sea delivery mode. Each increase of $0.026/l ($0.10/gal) should lead to an increase of $6/t in the break-even ex-vessel price for a vessel similar to type 1 delivering at sea (distance to grounds = 75 nmi) and averaging 10 t/d. For the same vessel delivering to port, such an increase in fuel price should lead to an increase in $8/t in the required ex-vessel price.

4) Fuel efficiencies (weight of fish caught per volume of fuel consumed) were 28% higher for vessel type 2 (25-28 m) than for vessel type 1 (33 m), and were about 35% higher for both vessels for sea delivery than for port delivery.

5) U.S. fishermen operating vessel types similar to the 33 m crabber/trawler and the 25 m trawler considered in this analysis may find it economically attractive to participate in joint fishing ventures for groundfish in the western Gulf of Alaska and the eastern Bering Sea given the ex-vessel prices currently being offered by the joint venture companies and the large volumes of fish in which these companies are interested.

It was considered feasible for these U.S. vessels to attain average catch rates sufficiently high to cover the fixed and variable costs of fishing under each of three fishing targeting strategies in which the target stocks are: 1) Pacific cod and walleye pollock in the western Gulf of Alaska, 2) sole in the eastern Bering Sea, and 3) walleye pollock in the Aleutians area.

ACKNOWLEDGMENTS

I would like to thank S. Jaeger, V. Kaczynski, and G. M. Pigott for contributing helpful information and suggestions during the development of this paper. Thanks are also due to D. Somerton and L. J. Bledsoe for their helpful critiques.

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APPENDIX I.—COST DERIVATIONS AND SOURCES OF ESTIMATES

I. A. Boat and engine routine maintenance. 7% of the vessel's initial value (VIV) is based on Marine Economics Data Sheets[23-27] for bottom draggers which indicate boat and engine repairs ranging from 5.1 to 11.4% (average 7.0%) of the vessel's market value. Katz and Lee[28] used a "rough estimate" of 6% for crab vessels.

B. Insurance. 2.1% of VIV for hull is a midpoint estimate based on a range of 1.7 to 2.5% (Jaeger footnote 11; Katz and Lee footnote 28).

C. Depreciation. Based on the following assumptions for vessel type 1 (Jaeger footnote 9):

	Cost	*Useful life (yr)*
Electronics	$ 100,000	6
Engine	$ 250,000	10
Hull	$1,150,000	30

Over a 30-yr period, assuming constant replacement costs, costs due to depreciation will be 5 × $100,000 + 3 × $250,000 + $1,150,000 = $2,400,000. The yearly cost is then $80,000 which equals 0.0533 VIV. Assuming equal cost proportions for vessel type 2 (electricity 6.7%, engine 16.7%, and hull 76.6% of VIV) also yields 0.0533 VIV.

D. Association dues. From Katz and Lee (footnote 28) updated to current values based on insurance cost index (U.S. Bureau of the Census 1978).

E. Contingencies/Miscellaneous. From Smith.[29]

F. Average annual cost of financing. Assumes 80% VIV financed and amortization through equal monthly payments. Financing for vessel type 1 is for 20 yr at 10% annual interest. Financing for vessel type 2 is for 15 yr at 8.5% interest. Differences in interest rates are due to different times of purchase.

[23]Marine Economics Data Sheets. 1971a. Seattle drag fishing business. Oregon State University Extension Service SR500-9.
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II. A. Gear repair and replacement. It is generally agreed that fishing gear maintenance and repair is roughly proportional to the amount of fishing time, but very little data are available which describe this relationship. The estimate of $20.57/h for vessel type 1 is based on the following estimates of Jaeger (footnote 11):

Total gear maintenance costs per year	$20,000
Total towing hours per year	972

The hourly costs for vessel type 1 are taken to be the same ($20,000/972) as for the vessel described by Jaeger. Since the trawl used by vessel type 2 would be smaller and hence less expensive than that of vessel type 1, its hourly costs were reduced by a factor based on the values of one net (including roller gear and floats) as estimated by Hurd.[30]

	Value of net
Vessel type 1	$7,000
Vessel type 2	$5,500-$6,000

B. Fuel costs. Gal/h:hp ratios as estimated by Jaeger (footnote 9). Fuel price of $0.277/l ($1.05/gal) based on current price at Dutch Harbor, Alaska.

C. Food costs. Based on Katz and Lee (footnote 28) and Jaeger (footnote 11) and updated by cost index (U.S. Bureau of the Census 1978).

D. Ice. Based on Bledsoe and Mesmer[31] and updated by cost index (U.S. Bureau of the Census 1978).

E. Crew and captain's shares. Katz and Lee (footnote 28), Jaeger (footnote 11).

[30]Rod Hurd, Seattle Marine and Fishing Supply Co., Seattle, Wash., pers. commun. December 1979.

[31]Bledsoe, L. J., and K. Mesmer. 1978. Summary of regional fishery system simulator configuration for N.E. Pacific shellfishery studies (NEPAC model and simulator). Norfish Pap. NM46, 19 p.

A STOCHASTIC MODEL FOR THE SIZE OF FISH SCHOOLS[1]

JAMES JAY ANDERSON[2]

ABSTRACT

A model is presented that reproduces the frequency distribution of fish school diameters observed acoustically in waters off southern California. The rate of change of school diameter is described by an equation that includes an entrance rate of fish into a school, which is independent of the number of fish in the school, and an exit rate, which is proportional to the number. The number in a school is assumed to be proportional to the square of the school diameter implying the average shape is disklike. Fluctuations in school size from unknown factors are approximated by stochastic rate terms for the entrance and exit rates and the diameter-number relation. This gives a stochastic dynamic equation for the rate of change of diameter and the probability distribution of the diameter is analyzed with a Fokker-Planck probability equation. A sensitivity analysis indicates two basic distribution types occur. Large exit rates and small stochastic fluctuations produce a narrow range of small diameters, while large entrance rates and large fluctuations produce a wide range of large diameters. Qualitative inferences from the model indicate schools of large fish should have a wide range of large diameters while small fish should have a narrow range of small diameters. Also fishing activity could decrease entrance rates and increase exit rates, and the combination would shift the probability distribution to a narrow range of small diameters.

When fish are mutually attracted they form schools, either in random orientation or in highly organized structures (Shaw 1978). The shape of the schools are diverse and changeable, and typically range from ribbonlike to spherical with the latter being uncommon (Radakov 1973). The attraction is mostly keyed visually and in northern anchovy, *Engraulis mordax*, schools off southern California the shape is disklike during the day and generally more diffuse and elongated at night (Squire 1978). Often within a school fish arrange in a lattice structure with the density of fish per unit volume related to fish length (Breder 1976; Serebrov 1976).

Models for the interactions of fish in a school have been postulated by a number of authors (see Breder 1976 for review and Okubo et al. 1977), but the processes controlling the size of a school in terms of the number of fish in a school or its physical dimensions have not been considered in mathematical terms. Considering what factors may be important in controlling size it is apparent the problem is complex and could include species behavior, light, predator-prey interactions, turbulence, life cycle stages, the stock population, and the size of the schools themselves.

An interesting set of observations on the size-frequency distribution of unidentified schools off southern California, shows a well-defined peak frequency at a diameter of about 15 m (Smith 1970). Towards larger and smaller diameters the frequency distribution decreases in an exponentiallike manner (Figures 1, 2).

This simple, and relatively stable, distribution is particularly interesting considering the possible complexity of the schooling process. The observations might be produced in one of two funda-

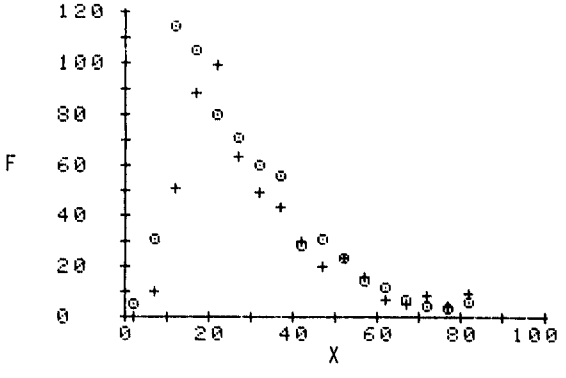

FIGURE 1.—Frequency distribution of fish schools (F) vs. school diameter (X) for unidentified schools observed with sonar by Smith (1970) from San Francisco, Calif., to Cabo San Lazaro, Baja California, in May 1969 (⊖) and June 1969 (+). F in numbers of schools and X in meters.

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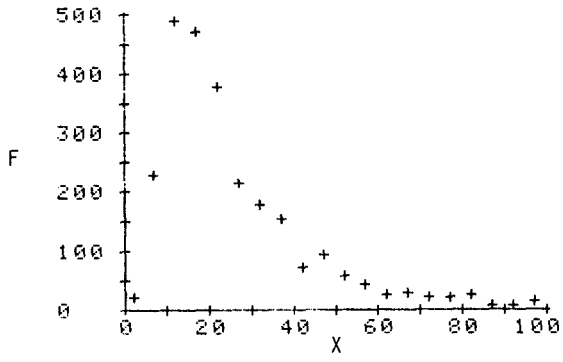

FIGURE 2.—Frequency distribution of fish schools (F) vs. school diameter (X) for composite of Smith's (1970) sonar surveys off California and Mexico in January, February, April, May, June, and July 1969.

mental ways. Either the frequency distribution is coupled to the school size or it is coupled to other factors such as the species composition of the observations. In the first case, the factors relating to environmental conditions, species, and stock numbers may also be acting on the school size but could be hidden in the averaging, inherent in the frequency mode of data display. In the second case, size may be insignificant and the distribution might reflect other factors. For example, if each species has a preferred school size, then a particular frequency distribution of species could produce an apparent frequency size correlation.

In this paper I explore the situation where the schooling dynamics are dependent on the school size and other factors, like species composition, have effects randomly distributed over the range of school sizes.

OBSERVATIONS

Smith (1970) observed fish schools over a 200,000 nmi^2 area between San Francisco, Calif., and Cabo San Lazaro, Baja California. The targets were recorded using sonar with a transducer fixed at a 90° relative bearing giving a beam perpendicular to the path of the ship. A 30 kHz frequency was used with a 10° conic beam (at −3 dB), at ranges from 200 to 450 m from the ship. Observations were made during daylight hours only and a complete survey of the area could be made in <2 mo. The dimensions of the schools were measured at right angles and parallel to the ship and the number of schools in 5 m intervals of diameter was estimated, correcting for bias from schools that only fell partially within the 200-450 m observation window of the sonar.

Frequency distributions for surveys in May and June 1969 were composed of 525 and 650 observations, respectively, in the diameter range 0-99 m (Figure 1). A composite frequency distribution of surveys in January, February, April, May, June, and July 1969 contained 2,549 observations of schools between 0 and 99 m diameter (Figure 2).

Smith (1970) estimated to a first order that about 30% of the observed schools were adult northern anchovy. Other common schooling fish in the area, the CalCOFI area, include northern anchovy juveniles; jack mackerel, *Trachurus symmetricus*, juveniles; Pacific bonito, *Sarda chiliensis*; Pacific mackerel, *Scomber japonicus*; and Pacific sardine, *Sardinops sagax*.

THE MODEL

To describe the frequency distribution of school diameters first consider an equation for the rate of change of the number of fish in a school. Define this rate in terms of a deterministic equation, which is related to school size, plus a stochastic equation which is taken to approximate the remaining unknown fluctuating behavior of the rate. The deterministic and stochastic equations are combined to give a stochastic dynamic equation for the rate of change of fish in a school as

$$\frac{dN}{dt} = \alpha + \delta(t) - \beta N + \gamma(t)N. \qquad (1)$$

The number of fish in a school is N and its change with time is determined as the difference between the rate fish enter the school, which is independent of N, and the rate fish exit from the school, which is proportional to N. The deterministic entrance and exit rates are α and βN where α and β are constant and represent averages over an ensemble of schools. The stochastic entrance and exit rates are $\delta(t)$ and $\gamma(t)N$ where $\delta(t)$ and $\gamma(t)$ represent white noise fluctuations which vary rapidly compared with variations in N, and are not affected by past conditions. The mean values of the stochastic terms are zero and so the stochastic parts represent fluctuations about the deterministic rate terms.

To express the frequency distribution in terms of school diameters we note Squire's (1978) observations in which the average shape of northern an-

chovy schools during the daylight hours is disklike. Including unknown factors that alter the three-dimensional shape through a stochastic term the relation between the school diameter and number is expressed as

$$N = X^2(\rho + \epsilon(t))\ \pi/4 \tag{2}$$

where X is the diameter of a school with a disklike shape, ρ is the average density of fish per unit horizontal area, and $\epsilon(t)$ is the stochastic variation on the density and has white noise character. Rewrite Equation (2) as

$$N = pX^2(1 + h(t)) \tag{3}$$

where p is a generalized density with $p = \rho\pi/4$ and $h(t)$ is the stochastic density normalized to p giving $h(t) = \epsilon(t)/p$.

Using Equation (3) in Equation (1) and differentiating yields

$$\frac{dX}{dt} = \frac{\alpha}{2pX(1+h(t))} - \frac{\beta X}{2} + \frac{\delta(t)}{2pX(1+h(t))} + \frac{\gamma(t)X}{2} + \frac{dh(t)/dt}{2(1+h(t))}. \tag{4}$$

To separate the deterministic and stochastic parts of Equation (4) assume $\rho > |\epsilon(t)|$ so $h(t)^2 < 1$ giving the convergent series

$$\frac{1}{1+h(t)} = 1 - h(t) + h(t)^2 - h(t)^3 + \ldots = 1 + \sum_{m=1}^{\infty} (-h(t))^m. \tag{5}$$

Using Equation (5) in Equation (4) and separating deterministic and stochastic parts in powers of X yields the stochastic dynamic equation for X as

$$\frac{dX}{dt} = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{i(t)}{2pX} + \frac{j(t)X}{2}. \tag{6}$$

The first term on the right side of Equation (6) is the deterministic expansion rate of a school and the second term is the deterministic contraction rate. The third term is the stochastic expansion rate and is principally related to the stochastic entrance rate. The stochastic component in expanded form is

$$i(t) = \delta(t) + (\alpha + \delta(t)) \sum_{m=1}^{\infty} (-h(t))^m.$$

The last term in Equation (6) is the stochastic contraction rate and is related to the stochastic exit rate according to the relation

$$j(t) = \gamma(t) + \frac{dh(t)}{dt} \sum_{m=0}^{\infty} (-h(t))^m.$$

We assume the components $i(t)$ and $j(t)$ are stationary random processes with zero mean values. Then their statistics can be characterized by the relations

$$\overline{i(t)i(t+t')} = \sigma_i^2\, q_i(t')$$

$$\overline{j(t)j(t+t')} = \sigma_j^2\, q_j(t') \tag{7}$$

where $\sigma^2{}_i$ and $\sigma^2{}_j$ are positive constants that quantify the level of the stochastic inputs and are referred to as "incremental variances." The $q(t')$ terms are autocorrelation functions that quantify the spectrum characteristics of the stochastic inputs as a function of separation time t'.

To investigate the probability characteristics of X in Equation (6) we must combine the stochastic terms into a single stochastic input, in a manner that retains the statistical characteristics of the terms. From Equation (7) we define the ratio

$$r(t')^2 = \frac{\overline{i(t)i(t+t')}}{\overline{j(t)j(t+t')}} = \frac{\sigma_i^2\, q_i(t')}{\sigma_j^2\, q_j(t')}.$$

We assume the correlation functions are similar enough to make the simplification $q_i(t')/q_j(t') \approx 1$. Then we relate the two stochastic terms in Equation (6) as

$$i(t) = rj(t) \tag{8}$$

where r is the ratio of the intensities of the inputs and is defined as

$$r = \sigma_i/\sigma_j. \tag{9}$$

In effect with Equations (8) and (9) we are taking the ratio of the two stochastic terms to be equal to

the ratio of their "incremental standard deviations." These are not the typical standard deviations, but if the correlation functions q_i and q_j are similar the ratio of the incremental standard deviations should approach the ratio of the typical standard deviations of the variables, i.e., $r \rightarrow \mathrm{SD}(i(t))/\mathrm{SD}(j(t))$ as $q_i(t')/q_j(t') \rightarrow 1$.

Now the stochastic dynamical equation for fish school diameter is written

$$\frac{dX}{dt} = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{j(t)}{2}\left[\frac{r}{pX} + X\right]. \quad (10)$$

The probability characteristics of X can be analyzed according to the Fokker-Planck equation (Goel and Richter-Dyn 1974). This is also known as the forward diffusion equation for probability in X and t. The probability density for the system having a diameter X at time t when it had diameter Y at time zero is denoted $P(X/Y,t)$ and for Equation (10) the Fokker-Planck equation is

$$\frac{\partial P(X,t)}{\partial t} = -\frac{1}{2}\left\{\frac{\partial}{\partial X}\left[\left[\frac{\alpha}{pX} - \beta X + \frac{\sigma^2}{8}\frac{\partial}{\partial X}\left(\frac{r}{pX} + X\right)^2\right]P(X,t)\right]\right\} + \frac{\sigma^2}{8}\frac{\partial^2}{\partial X^2}\left(P(X,t)\left(\frac{r}{pX} + X\right)^2\right). \quad (11)$$

The term σ^2 is the incremental variance of the diameter shrinkage rate and is in fact equivalent to σ^2_j in Equation (7). The term has a dimension of t^{-1} and is also the diffusion coefficient of probability $P(X,t)$ in X space. In this manner it quantifies the level of randomness in the schooling process.

For the Fokker-Planck equation the growth rate of the mean value of X is

$$M_1(X) = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{\sigma^2}{2}(r/pX + X)(1 - r/pX^2) \quad (12)$$

and the growth rate of the variance of X is

$$M_2(X) = \frac{\sigma^2}{4}(r/pX + X)^2. \quad (13)$$

From the similarity of frequency distributions for different months (Figures 1, 2) we assume a steady-state probability distribution and from Goel and Richter-Dyn (1974) this is expressed as

$$P(X) = \frac{C}{M_2(X)} \exp\left\{\int_0^X 2\frac{M_1(s)}{M_2(s)}\, ds\right\} \quad (14)$$

where C is a constant determined by the condition that the total probability equals one

$$1 = \int_0^\infty P(X)dX. \quad (15)$$

Using Equations (12) and (13) in Equation (14) the steady-state probability distribution, or probability density, for school diameter is

$$P(X) = \frac{kXe^{-2(a+bc)/(c+X^2)}}{(c+X^2)^{(1+2b)}} \quad (16)$$

where

$$a = \alpha/p\sigma^2,\ b = \beta/\sigma^2,\ c = r/p,$$
$$k = 4C/\sigma^2. \quad (17)$$

The dimensions of the above constants with l for length, t for time, and n for number of fish are as follows. The parameters a and c have dimensions of l^2, b is dimensionless, and k has dimensions of l^{1+4b}. The dimension of α is lt^{-1}, β and σ^2 have t^{-1}, p has nl^{-2}, r has n, and C has $t^{-2}l^{1+4b}$.

FITTING THE MODEL TO DATA

Equation (16) can be fit to Smith's (1970) data through a number of methods all of which adjust the free parameters a, b, and c to obtain a best fit according to visual or statistical criterion. To obtain a first order estimate of the free parameters we will use a simple algorithm in which the probability curve is made to go through the observed

probability distribution at the most common, or peak, diameter and one other diameter in the distribution. This fixes two of the free parameters and with trial values of the remaining free parameter the model is fit to observations.

We begin by converting the probability equation to the frequency equation

$$F(X) = \frac{k^*}{k} P(K) \tag{18}$$

where $F(X)$ is the number of fish observed at diameter X and k^* is a constant that is a function of the number of schools observed. At the most common diameter X_0, the frequency is maximum so $dF(X_0)/dX = 0$ and from Equations (16) and (18) we obtain

$$a = X_0^2 \left(b + \frac{1}{4}\right) - \frac{1}{4} c^2/X_0^2. \tag{19}$$

With Equation (19) in $F(X)$ the log of $F(X)$ yields equations for b and k^*. These can be solved explicitly with observations $F(X_0), F(X_1), X_0, X_1$, and the free parameter c where X_1 is a diameter greater than the peak diameter X_0. The equations are

$$b = \frac{A(X_1) - A(X_0) + C(X_1) - C(X_0)}{B(X_1) - B(X_0)} \tag{20}$$

$$k^* = \exp\left\{-A(X_0) + bB(X_0) - C(X_0)\right\} \tag{21}$$

where $A(X_i) = \frac{1}{2}(c^2/X_0^2 - X_0^2)/(c + X_i^2) + \ln(X_i/(c + X_i^2)$

$B(X_i) = 2(c + X_0^2)/(c + X_i^2) + 2\ln(c + X_i^2)$

$C(X_i) = -\ln(F(X_i))$

with $i = 0$ and 1.

For the composite of observations depicted in Figure 2 we take $X_0 = 14$ m, $X_1 = 40$ m, $F(X_0) = 491$, and $F(X_1) = 115$. A good fit (Figure 3) is obtained with $c = 60$ m^2 and the remaining constants from Equations (19), (20), and (21) are $a = 133$ m^2, $b = 0.452$, and $k^* = 4716244$.

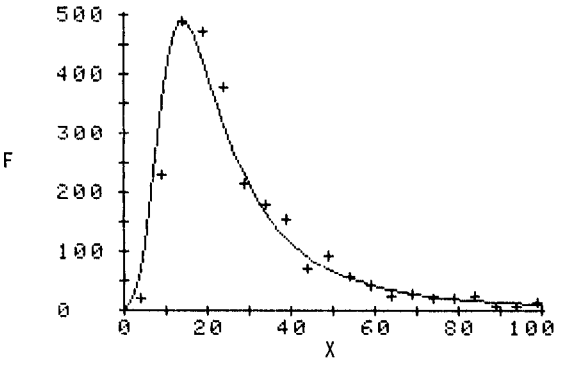

FIGURE 3.—Fit of probability equation of school diameter to frequency distribution of Figure 2. Probability Equation (16) is equated to frequency according to Equation (18).

SENSITIVITY ANALYSIS

The sensitivity of $P(X)$ to variations in the model parameters has been investigated for $P(X)$ in the configuration of the observed distribution (Figure 3).

We note that the curve $P(X)$ is defined by three free parameters a, b, and c which are in effect fitting parameters. These are ratios of the coefficients of the stochastic dynamic Equation (10). The coefficients are the dynamic parameters of the system and are α, β, σ, σ_i, and p. The relationship between the fitting parameters and the dynamic parameters is given by Equation (17) where σ_i is related to r by Equation (9). Because the dynamic parameters are only known in ratios in this model we can only investigate their effect on $P(X)$ in terms of relative changes. The relative value y', of a dynamic parameter y, can be defined

$$y' = y/y_o \tag{22}$$

where y_o is the value of the dynamic parameter corresponding to the fit to the observed frequency distribution.

To investigate the equation sensitivity, each dynamic parameter is varied while the others are held constant at their y_o values. For each set of

dynamic parameters generated in this manner $P(X)$ is calculated for X from 0 to 100 m. For each set of parameters the constant k in Equation (16) is determined according to the condition expressed by Equation (15) by numerically integrating the integral

$$1/k = \int_0^{X^*} \frac{Xe^{-2(a+bc)/(c+X^2)}}{(c+X^2)^{(1+2b)}}\, dX\,. \qquad (23)$$

Using Simpson's rule for integration $1/k$ is evaluated within a few percent accuracy with a 1 m integration step and $X^* = 300$ m.

The response of $P(X)$ to variations in the dynamic parameters is illustrated in Figures 4-8,

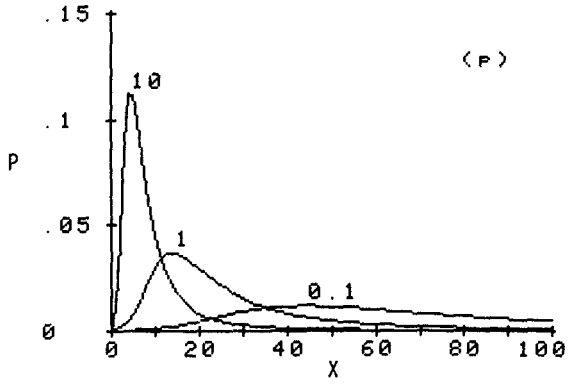

FIGURE 4.—Probability distribution (P) vs. school diameter (X), in meters, for relative schooling density parameter values p′ = 0.1, 1, and 10.

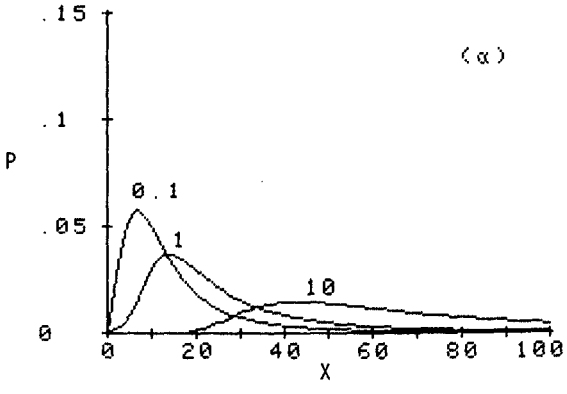

FIGURE 5.—Probability distribution (P) vs. school diameter (X) for relative entrance rate values $\alpha' = 0.1$, 1, and 10.

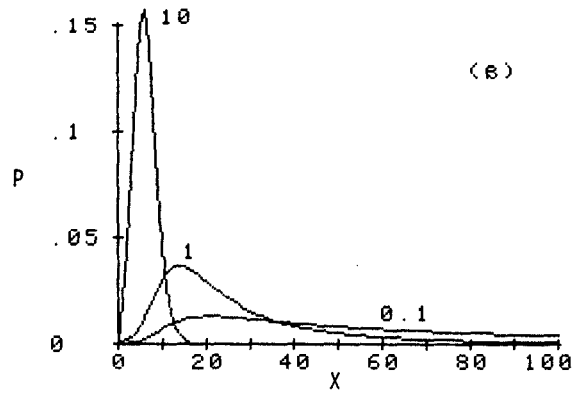

FIGURE 6.—Probability distribution (P) vs. school diameter (X) for relative exit rate parameter values $\beta' = 0.1$, 1, and 10.

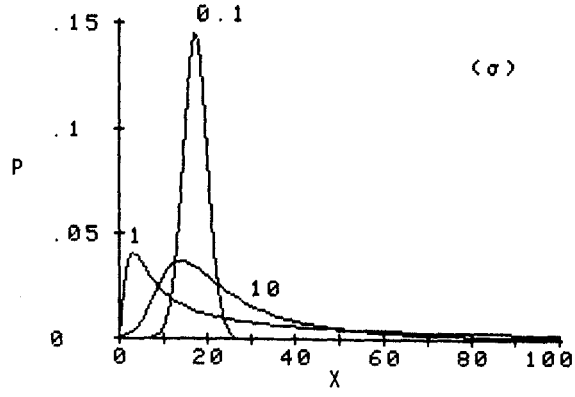

FIGURE 7.—Probability distribution (P) vs. school diameter (X) for relative shrinkage rate standard deviation values $\sigma' = 0.1$, 1, and 10.

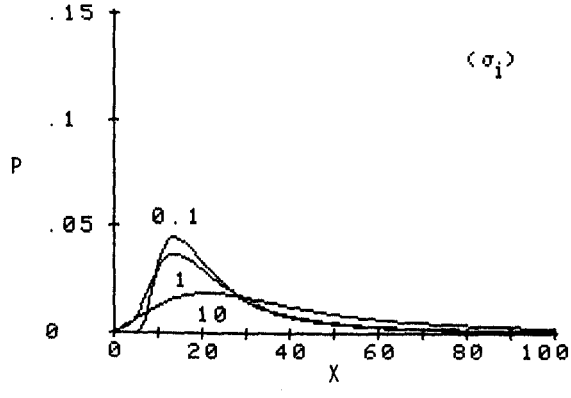

FIGURE 8.—Probability distribution (P) vs. school diameter (X) for relative expansion rate standard deviations values $\sigma'_i = 0.1$, 1, and 10.

which show $P(X)$ vs. X for each parameter varied with relative values $y' = 0.1, 1, 10$, where $y' = 1$ is the relative value corresponding with the fit to the observed distribution (Figure 3). In the figures the shape of $P(X)$ varies between a well-defined sharp peak, in which only a narrow range of diameters are probable, and a broad low peak, in which a larger range of somewhat larger diameters are probable. A brief discussion of the sensitivity and some possible biological implications follows.

p

The density, or number of fish per square meter of horizontal area of a school, has a strong effect on the probability distribution (Figure 4). A dense grouping of fish, corresponding with large values of p, favors a narrow range of small school diameters while a low density favors a wide range of larger diameters. Serebrov (1976) illustrated that the density of fish in a school is highly correlated to fish length according to the relation $\rho = 1/(LK)^3$ where ρ is the density in number of fish per cubic meter, L is fish length in centimeters, and K is a constant, with average value 2.44. If we assume the density per square meter is proportional to the density per cubic meter, then with Serebrov's relation, p responds to the one-third power of fish length averaged over the ensemble of schools making up the observations. Fish length becomes a sensitive parameter, e.g., the relative change in p from 1 to 10 in Figure 4 corresponds to a relative change in the average fish length from 1 to 0.46.

α

For small values of the entrance rate into schools, small diameters are favored, and as the entrance rate increases a wide range of large schools is favored (Figure 5).

The rate α has units of number of fish entering the school per unit time, and if we envision the entrance event as the chance encounter and joining of two schools, then α should be proportional to the average number of fish in the schools divided by the average time interval between encounters of schools. The time interval between encounters could decrease as the stock population increases if the number of schools per unit area increases. Thus, the entrance rate could increase with increases in the stock population of an area. This reasoning suggests that larger stocks would contain a wide range of school sizes and small stocks would contain a narrow range of small school sizes.

β

The parameter β is the coefficient for the average exit rate of fish from a school and has units of t^{-1}. If we envision the loss mechanism as a random dividing of the school into two fractions, with the time interval between the divisions being random, then the average time interval is proportional to β^{-1}. Thus, larger values of β correspond to short time intervals between divisions and small values correspond to large time intervals between school divisions. The interval as expressed by β has a significant effect on the probability distribution $P(X)$, with small values favoring a narrow range of small diameters and large values favoring a wide range of larger diameters (Figure 6).

σ

The randomness in the schooling process is quantified in the model by the incremental standard deviation σ, which has units of $t^{-1/2}$. For small levels of randomness, small σ, the probability distribution converges on the deterministic steady-state diameter which is defined

$$\bar{X}_0 = (\alpha/p\beta)^{1/2} = (a/b)^{1/2}.$$

For the model fit this gives $\bar{X}_0 = 17.3$ m. The convergence is evident in Figure 7 in which X_0 changes from 3 to 14 to 17 with σ changing from 10 to 1 to 0.1. At larger values of σ the system has more random character and the probability distribution spreads away from the deterministic value $\bar{X}_0$. Expressed as the incremental variance σ^2, with the dimension t^{-1}, the term is the diffusion coefficient of probability in X space, since the Fokker-Planck equation is in fact a diffusion equation of probability in X and t.

σ_i

The incremental standard deviation of the expansion rate, σ_i is defined by Equation (7) and is related to the probability equation through r according to Equation (9). It has a small effect on the probability distribution with larger values producing a broadening of the probability distribution and a shift towards larger diameters. Increasingly, smaller values asymptotically approach a stable

distribution as is evident by the similarity of the curves for relative values $\sigma_i = 0.1$ and 1 (Figure 8).

DISCUSSION

The frequency distribution of fish school diameters observed acoustically off the coast of southern California by Smith (1970) has a well defined most frequent, or peak, diameter. The distribution is also skewed towards small diameters and is relatively stable from one month's observations to the next. These data likely represent a range of fish sizes and species with northern anchovy probably being the dominant group.

The frequency distribution can be modeled by a probability equation that is based on a dynamic equation that contains deterministic and stochastic rates for the entrance and exit of fish from a school. The entrance rates are taken to be independent of the number of fish in a school while the exit rates are taken to be proportional to the number. The number of fish in a school is transformed to a diameter by assuming the average school shape is disklike so the number is proportional to the horizontal area, as expressed by the square of the diameter.

The effects of environmental conditions, fish sizes, species, predator-prey interactions, and stock size are assumed to be contained in the stochastic parameters of the dynamic equation. This assumption requires these basically unknown factors have white noise character.

In effect the deterministic behavior of the rate of change of diameter is represented by a dynamical equation, $dx/dt = f(x)$, where $f(x)$ is the deterministic rate and is a function of x. The remaining unknown fluctuating behavior, due to other factors, is approximated by $e(x)j(t)$ where $j(t)$ is white noise fluctuation and $e(x)$ gives the x dependence of the stochastic rate. Combining the rates we obtain a dynamical stochastic equation for x and the probability analysis of the process can be carried out using a Fokker-Planck equation, which is a diffusion equation for probability in x and t. The solution of the Fokker-Planck equation gives the probability curve $P(X)$.

Fitting the curve $P(X)$ to Smith's (1970) observations yields the equation constants or fitting parameters a, b, and c. These fitting parameters are ratios of the dynamic parameters of the dynamical stochastic equation for x.

The sensitivity analysis of $P(X)$ to relative changes in the dynamic parameters indicates two basic probability distributions can be produced: 1) a narrow probability distribution, favoring a narrow range of small diameters with the occurrence of large schools unlikely and 2) a wide distribution in which a wide range of larger diameters have low but essentially equal probabilities, and small diameters are unlikely. Wide distributions are favored by large entrance rates and a large amount of randomness to the schooling process. Narrow distributions are favored by large exit rates and low randomness in the schooling process. Additionally, wide distributions are favored for schools with a low fish density per cubic meter, and narrow distributions of diameters are favored with high density schools. The density of fish in schools is related to the fish length so the analysis infers that large fish should have a wide probability distribution of large diameters and small fish should develop a narrow probability distribution of small diameters.

From a commercial fishing viewpoint factors that affect school sizes are important and so, briefly, we consider a possible qualitative response of school diameter to fishing activity. If we envision the fishing process as an event that divides a school and removes one of the fractions, then we expect fishing should at least affect the deterministic parameters of the model. The dividing of the school, by fishing, decreases the mean time interval between school divisions and this, in turn, would increase the exit rate coefficient β. The fact that part of the stock is removed by fishing may increase the time interval between school encounters and thus decrease the entrance rate α. A con-

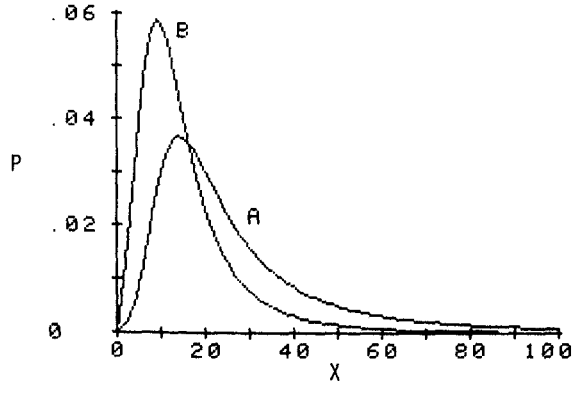

FIGURE 9.—Probability distribution (P) vs. school diameter (X) in meters. Curve A, distribution corresponding to Smith's (1970) observations. Curve B, distribution postulated for fishing activity that increases β and decreases α by 50%.

comitant increase in β and decrease in α would shift the probability distribution towards a narrow range of small diameters. For example, if we assume an increase in fishing activity off southern California decreases α and increases β by 50%, then there would be a noticable decrease in the occurrence of schools >20 m diameter (Figure 9).

ACKNOWLEDGMENT

I wish to thank Akira Okubo for his discussion on this problem.

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RECRUITMENT AND EXPLOITATION OF GULF MENHADEN, *BREVOORTIA PATRONUS*[1]

DEAN W. AHRENHOLZ[2]

ABSTRACT

Gulf menhaden, *Brevoortia patronus*, range along the Gulf of Mexico coast from Cape Sable, Florida, to Veracruz, Mexico, and are exploited by a purse seine fishery from Alabama to eastern Texas. Rates of exploitation, population movement, and recruitment into the fishery were estimated from returns of tagged juveniles and adults. The annual instantaneous rate of natural mortality (M = 1.0935) was estimated from recoveries of tagged adults. Recruitment patterns were determined and exploitation rates were estimated from returns of fish tagged as juveniles in specific geographic regions along the northern Gulf of Mexico. During 1971-73, fish tagged as juveniles from either the eastern or western extremes of the northern gulf coast were exploited as 1-year-olds at a mean rate of only 5%. The rate increased to a high of 51% for 1-year-olds tagged near the Mississippi Delta, the center of the fishery. During 1972-74, 2-year-old fish tagged as juveniles were exploited at rates ranging from 18 to 55%. Fish from the eastern and western ends of the range dispersed toward the center of the range as they grew older.

Gulf menhaden, *Brevoortia patronus*, range along the coastline of the Gulf of Mexico from Cape Sable, Fla., to Veracruz, Mex. (Reintjes 1969). They are exploited from April to October by a purse seine fishery that operates in nearshore waters from Alabama to Texas. Gulf menhaden move offshore in the fall before spawning in the winter. The larvae move into estuaries in late winter and spring, where they metamorphose into juveniles and remain there until the following autumn.

The fishery is dependent on age-1 and age-2 fish, with few fish being taken that exceed 3 yr of age. The catch, processed into meal and oil, increased from 8,900 t in 1946 to 728,500 t in 1971, and has fluctuated between 447,000 and 820,000 t since then. Yellowfin menhaden, *B. smithi*, and finescale menhaden, *B. gunteri*, occur in the area fished, but Gulf menhaden compose approximately 99% of the landings. At present, catches are processed at 11 reduction plants, located at six ports along coastal Louisiana and Mississippi (Figure 1). Large, refrigerated purse seine vessels, supported by spotter aircraft, range up to about 320 km from port. During recent years the number of operating plants has varied from 10 to 13, and the number of active ports has varied from 6 to 8 (Nicholson 1978).

To determine if fish reared outside the range of the fishery are exploited and to determine the rate of exploitation of individuals reared within the range, juvenile menhaden (young-of-the-year) have been tagged since 1970 in selected estuaries from Florida to the Mexican border. I analyzed returns from fish tagged as juveniles from 1970 to 1972 to determine if fish reared outside the range of the fishery contribute to landings and to estimate rates of exploitation by age and estuarine area of origin.

I also analyzed returns from a second (independent) adult tagging program to obtain an estimate of natural mortality and a preliminary estimate of rate of fishing on fully recruited fish to complement my analysis of the first (juvenile) tagging program. In the second study, reported by Pristas et al. (1976), Gulf menhaden were tagged as recruited fish (adults) on the fishing grounds from 1969 to 1971.

TAGGING METHODOLOGY

Since all tags that are recovered from both tagging programs are from "adult" fish caught by the fishery, a distinction in terminology is made in this paper for clarity in separating results: "tagged as adults" or "adult recoveries" refers to the study reported by Pristas et al. (1976) and "tagged as juveniles" or "juvenile recoveries" refers to the present study.

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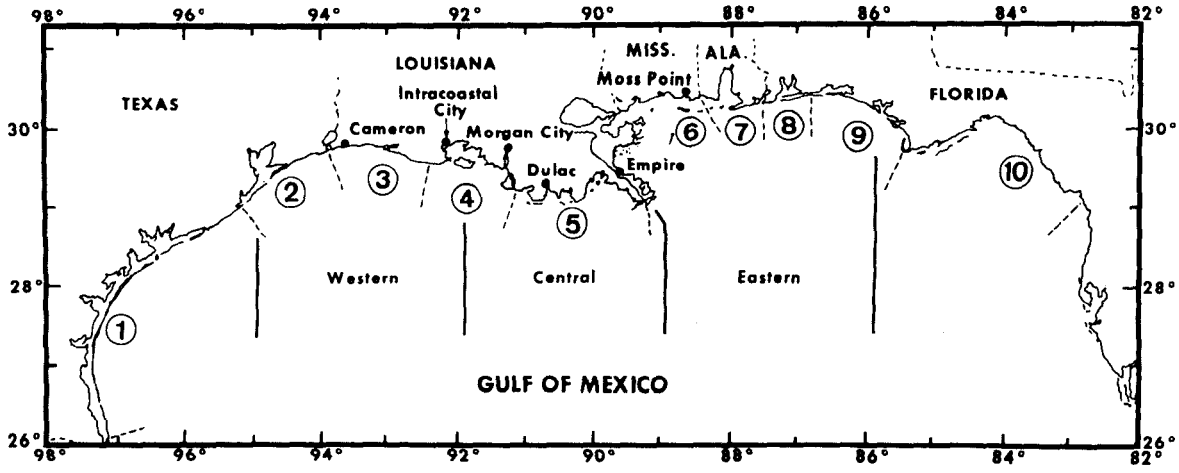

FIGURE 1.—Location of Gulf of Mexico ports where catches of Gulf menhaden are currently landed (dots), major fishing and tagged adult release areas (vertical lines), and division of the U.S. gulf coast into tagged juvenile Gulf menhaden release areas (numbered circles and dashes).

Methods of tagging and tag recovery are well documented (Pristas and Willis 1973; Parker 1973; Dryfoos et al. 1973). Numbered stainless steel ferromagnetic tags, 7.0 × 2.5 × 0.4 mm for juveniles, and 14.0 × 3.0 × 0.5 mm for adults, were injected into the body cavity. Juveniles were tagged in estuaries during late summer or early fall just before emigration. Adults obtained from fishing vessels on the fishing grounds were tagged during late spring.

Tags were recovered on magnets located in reduction plants; however, not all tags that entered a plant were recovered. To estimate the fraction of tags recovered at each plant, 100 tagged fish were put in the catch of a selected vessel each week. Field recoveries were adjusted for loss rates within a plant by multiplying the inverse of the test recovery fraction by the number of field tags actually recovered at each plant.

For analyzing juvenile tag recoveries, the northern Gulf of Mexico coast was divided into 10 release areas, numbered, and geographically named for reference (Figure 1, Table 1). In some areas, fish were tagged in only one estuary; in other areas, they were tagged in several estuaries. For analyzing adult tag recoveries, the coast was divided into three areas: western, central, and eastern (Pristas et al. 1976) (Figure 1).

TABLE 1.—Numbers of tagged juvenile Gulf menhaden released in estuarine waters by area and year, 1970-72. Areas are depicted in Figure 1.

Release area	1970	1971	1972
1. Southeast Texas	3,199	3,263	3,900
2. Galveston Bay	892	1,200	1,000
3. Western Louisiana	1,000	2,500	2,500
4. Central Louisiana	—	1,500	640
5. Western Delta	200	600	1,200
6. Eastern Delta-Mississippi	1,622	1,248	1,800
7. Mobile Bay	1,199	2,500	—
8. Pensacola Bay	600	1,000	1,700
9. Choctawhatchee Bay-St. Andrew Bay	—	200	2,482
10. Apalachee Bay	—	400	100
Total	8,712	14,411	15,322

MOVEMENT AND RECRUITMENT OF JUVENILE TAGGED FISH

The eventual distribution of fish tagged in specific estuaries would be an indication of the degree and direction of movement of fish from each estuary. Because there is no way of knowing exactly where a tagged fish was caught, and because levels of effort may vary between ports (and thus numbers of fish actually landed), the distributions must be inferred from estimates of the relative availability of tagged fish to each port rather than from just the distribution of recoveries of tagged fish to each port. Because vessels tend to fish more intensively in areas near their home ports, most tags recovered at a specific port were assumed to have been from fish caught in waters closest to that port. The measure of standardized effort (f') used in availability calculations is the vessel-ton-week (computed as net-registered-tonnage times number of weeks fished), the unit of fishing effort currently employed for this fishery (Chapoton 1972; Schaaf 1975), adjusted for differences in vessel catch efficiency in numbers of fish

between ports and between years. (Landing and effort data from a former plant at Sabine Pass, Tex., were combined with Cameron, La., data for 1971.) This adjustment, made by multiplying the actual effort by the ratio of actual catch per unit effort in numbers of individuals to the overall port's and year's mean catch per unit effort (in numbers), makes all measures of effort by port equivalent with respect to numbers of fish landed.

Relative availabilities were calculated for juveniles tagged in nine specific areas from 1970 to 1972. No tags were recovered from fish tagged in area 10, probably because so few were tagged. For each of six ports, the estimated number of tags recovered annually from fish tagged in specific areas was divided by the number of tags recovered at all ports over all years. The quotient was divided by the amount of standardized fishing effort for the port during the year considered, and a three-dimensional matrix of relative availabilities by age of capture, port, and year class was calculated for each release area. The equation used for these calculations is:

$$\overline{RAV}_{ijk} = (R_{ijk} / \sum_i \sum_j R_{\cdot\cdot k}) / f'_{jm} \qquad (1)$$

where f'_{jm} = standardized effort,
R_{ijk} = number of recoveries, and
$\overline{RAV}_{ijk}$ = relative availability to a unit of effort.

Here, i refers to age at capture, j refers to port, k refers to year class, and $m = k + i$ (year captured).

The relative availability estimates at the different ports for each release area were similar between year classes and so were averaged for all years (Figure 2). These results support the hypothesis advanced by Kroger and Pristas (1975) that there is little or no exchange of fish between areas east and west of the Mississippi Delta. Large numbers of fish tagged east and west of the delta were recovered at Empire, La., plants; since vessels from these plants fish both sides of the delta there is no way of knowing on which side fish bearing these tags were actually captured. The few tags recovered at plants east of the delta of fish tagged west of the delta may actually have been taken by vessels from plants east of the delta fishing west of the delta, and vice versa. It is noteworthy that of the few tags recovered at plants west of the delta of fish tagged east of the delta nearly all were recovered at Morgan City and Dulac, La. Vessels from these ports were more likely to have fished east of the delta than were vessels from the two most western ports, Intracoastal City and Cameron, La. Almost no fish tagged east of the delta were recovered at these ports.

As fish age, there appears to be a slow dispersal toward the delta of fish from eastern and western areas. Fish tagged in the two most western areas were captured in greater numbers their second year after release at the two more central ports, Morgan City and Dulac. Although the fish tagged in the other three western areas were captured in greatest numbers their first year after release, they became progressively more available as 2-yr-olds to the three central ports than they were to the most western port at Cameron. However, 1-yr-old fish from these three western areas (3, 4, and 5) were disproportionately more available to the western extreme of the fishery than to the more central area. Fish tagged in the three most eastern areas were captured in greater numbers the second year after release at the Moss Point, Miss., and Empire plants. Fish tagged in the eastern area adjacent to Moss Point, although captured in greater numbers the first year after release, appeared to be more available as 2-yr-olds to Empire vessels than to Moss Point vessels.

As a consequence of the fishery being concentrated in Mississippi and Louisiana waters, fish reared as juveniles in the extreme eastern (Alabama and Florida) and western portions (Texas to the Mexican border) of the range are recruited at a lesser rate than fish reared in the center of the range. Fish moving toward the center of the range probably are recruited progressively later in the season as age 1, and many may not be recruited until age 2, whereas nearly all fish reared in the center of the range probably are recruited early in the season at age 1.

The gradual shift toward the center of the fishing area as a year class ages, indicated by the pattern of juvenile tag recoveries, is also indicated by the age composition of the catches. Age-1 fish compose a higher percentage of catches at plants or longitudes at the eastern and western ends than at plants or longitudes in the center (Nicholson 1978). The observed age composition is not due to greater fishing pressure on fish at either end of the fishing grounds, since attrition rates of fish tagged in the more central areas, implied by catch curves of tag recoveries, are equal to or greater than rates observed for fish tagged in either extreme (Figure 3). This shifting is apparently superimposed over

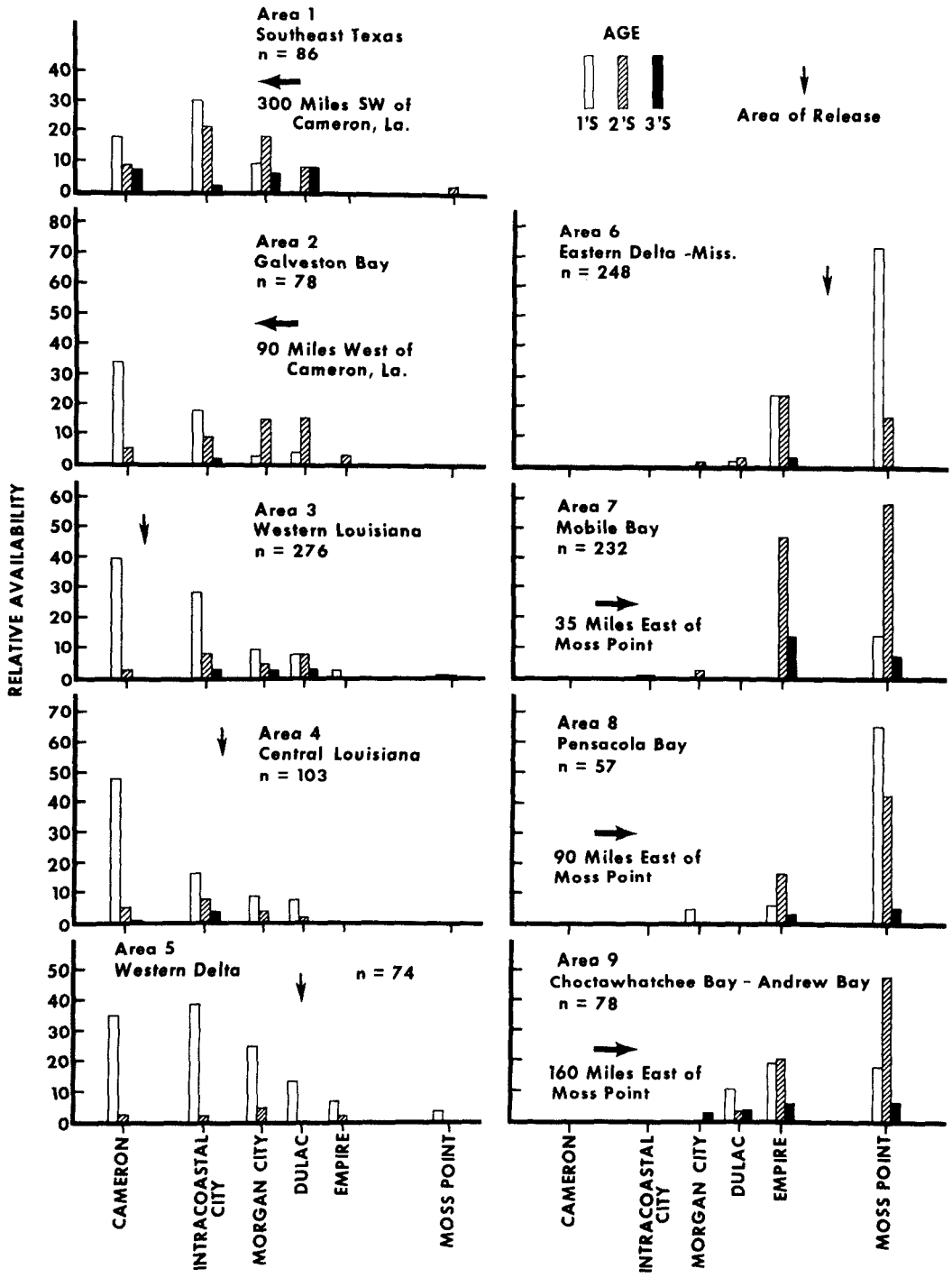

FIGURE 2.—The mean release area-specific availability by age of Gulf menhaden tagged as juveniles to individual ports in the Gulf of Mexico. Vertical arrows denote approximate release location with respect to the ports, horizontal arrows denote release locations beyond the range of the figure. The actual (unadjusted) number of tag returns is given for each release area.

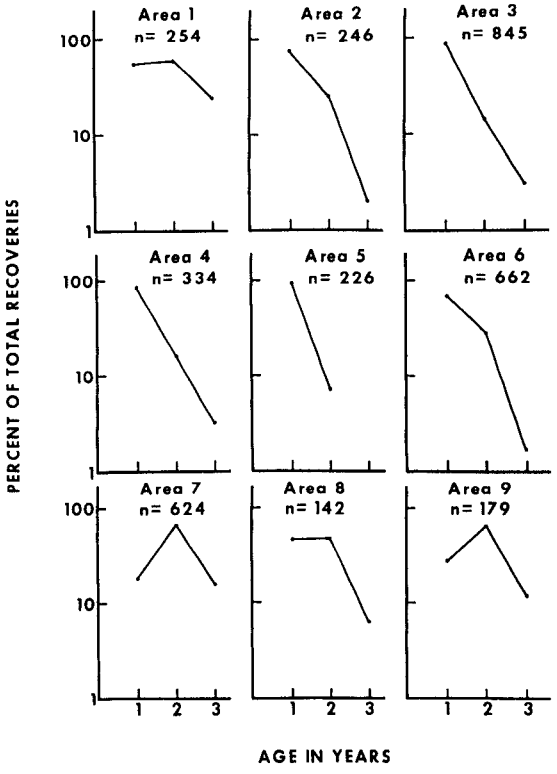

FIGURE 3.—The frequency of recoveries for a standard 100 tags for each juvenile Gulf menhaden release area (ordinate logarithmically scaled) and the adjusted number of recoveries from each release area, Gulf of Mexico.

an annual fall-spring, offshore-onshore migration (Roithmayr and Waller 1963).

The lack of precise recapture location information and the limited range of the fishery relative to the range of the species prevents the formulation of a more detailed and possibly more accurate description of dispersal patterns of Gulf menhaden. For instance, it is possible that fish from nursery areas outside the fishing grounds disperse at a more or less equal rate towards and away from the fishery. However, the relatively strong showing of tags from outside the fishery 2 and 3 yr after release and the relatively few schools of Gulf menhaden that are sighted at the extremes of the range indicate that dispersal is probably stronger towards the center of the range, where the fishery is heaviest, rather than away from it.

MORTALITY RATE ESTIMATION FROM ADULT TAG RECOVERIES

To estimate the age specific exploitation rate of Gulf menhaden from different geographic nursery areas, I needed an estimate of the instantaneous natural mortality rate (M) and an estimate of the exploitation rate (u) of fully recruited fish. I used the tag recovery data from the adult tagging study reported by Pristas et al. (1976) to estimate these parameters, because these fish (being obtained from commercial purse seine sets) were assumed to be fully recruited when tagged, and the adult tagging study is independent from the juvenile tagging study which will be used as the data base for the area and age specific exploitation estimation. Before mortality rates were estimated, however, adjustments were made to the adult tag-recovery data to remove the potential for systematic errors in the results.

A, B, and C errors (Ricker 1975) are commonly associated with tagging studies attempting to estimate rates of survival and fishing. Type A errors can occur when tagged fish die as a result of marking or shed their tag shortly after tagging and also during the recovery phase when reporting of recoveries is incomplete (in this case loss of tags within a reduction plant). Type A errors are characterized by affecting estimates of rate of fishing (hence rate of natural mortality) but not rates of total mortality when these parameters are estimated by rates of recovery over several time intervals.

Adjustments of numbers recovered for incomplete recovery of tags from harvested tagged fish is straightforward and is outlined in the Tagging Methodology section. Adjustments of numbers released entailed adjusting for any significant difference in recovery rates associated with different taggers and then determining a realistic estimate of rate of loss due to death and shedding shortly after tagging, which is applicable to all taggers. Since only three taggers were employed in this study, and one only tagged 200 fish in 1971, a recovery comparison was conducted between the two taggers who tagged the greatest number (99.7%) of the fish. Because the recovery rate for fish tagged by one individual (tagger B) was much lower than the rate for fish tagged at the same time by the other (tagger A) (Table 2), the number of tags applied during 1969 by this tagger was adjusted downward. The adjustment was made by multiplying tagger B's number released for each area by the ratio of the recovery rate of tagger B to tagger A for each area. All of the remaining releases (1970 and 1971, with the exception already noted above) were tagged by tagger A. Adjusted recov-

TABLE 2.—Comparison of differences in recovery rates between taggers for paired tagging of adult Gulf menhaden conducted in 1969 in the Gulf of Mexico. All chi-square values obtained from 2×2 contingency tables were highly significiant ($P < 0.001$).

Area	Tagger	No. tagged	Actual recoveries	Chi-square
Eastern	A	6,700	1,118	77.05
	B	6,300	713	
Central	A	1,900	402	36.54
	B	1,800	245	
Western[1]	A	4,100	456	120.04
	B	3,700	163	

[1]Release totals in Table 3 contain an additional 2,500 tags released by tagger A working alone.

eries and numbers released with adjustments for differential tagger induced mortality (1969 only) for the adult study are given in Table 3. (The number of adjusted recoveries differs from the number published by Pristas et al. (1976), probably because slightly different methods were used to adjust known recoveries and somewhat different criteria were used to judge the suitability of some returns.)

Adjustments of numbers released to account for tags lost from initial mortality and shedding had to be somewhat arbitrary. Kroger and Dryfoos (1972) reported on a series of short-term tagging mortality and shedding studies on Atlantic menhaden, *B. tyrannus*, which tested a variety of methods of insertion, fish size, chemical treatment of tags, and tag size. Of this series, two were with fish size and tagging methodology similar to the Gulf adult study. Losses due to mortality and initial shedding in these two experiments were 10 and 24%. Since these experiments were conducted under better conditions than field tagging, I selected a value nearer the higher of the two estimates, 20%, as a realistic mean rate of Type A tag loss, and 10-30% as a range for testing the sensitivity of this assumption.

Type B errors can occur when tags are shed throughout the recovery period, when tagged fish have a higher rate of mortality, or when tagged fish emigrate from the fishing grounds. Errors of this type will cause overestimation of total mortality and natural mortality but not necessarily rate of fishing. No corrections were made for Type B errors because no long-term studies of shedding or mortality under this category have been conducted with menhaden. Since tagging wounds heal within a few weeks after tagging (Kroger and Dryfoos 1972) and the internal tag is stainless steel with rounded, smooth edges, I would expect Type B losses to be minimal. Emigration from the fishing grounds is unlikely (see Recruitment section above).

Type C errors occur when the tagged individuals are either more or less susceptible to capture than untagged fish during the first year after release. Recovery rates for later years may be representative, however. Adjustment for Type C error is made in the estimating method, as will be shown later.

The Gulf menhaden tag-recovery data are subject to an additional type of error. Sometimes tags from recaptured fish lodged in plant machinery and were not recovered until 1 or more years after entering a reduction plant (Table 4). The retention of tags in plants for more than one season prior to their recovery will cause estimates of total mortality to be too low. Since trial calculations (of simulated data) showed that the rates of tag retention noted would cause underestimation by only about 5.4% for fish marked with large (adult) tags and 3.8% for fish marked with small (juvenile) tags, and attempts to adjust for this bias may introduce additional error, the effects were ignored. [Tag retention rates were not as large as reported by Nicholson and Schaaf (1978). The most serious discrepencies were for two plants during 1972, where retention rates were reported as 5 and 6%. It was discovered that 34 of the 59 tags reported as retained for 1 yr in one plant and 92 of the 93 tags reported as retained in the other plant were erroneously recorded. Corrected retention rates are 2 and <0.1% for the two plants.]

Plots of log frequencies of adult recoveries for each release year and area (Table 3) on years-at-

TABLE 3.—Number of adult Gulf menhaden tagged in late spring, by area, year, and adjusted number recovered, Gulf of Mexico.

			No. recovered in year			
Area	Year	No. tagged	1	2	3	4
Western Gulf	1969	[1]8,065	1,363	509	68	6
	1970	9,100	3,619	838	15	4
	1971	7,400	2,622	235	24	1
Central Gulf	1969	[1]3,056	1,311	215	21	—
	1970	5,100	2,168	408	22	—
	1971	5,200	1,617	94	11	6
Eastern Gulf	1969	[1]10,965	2,305	1,123	134	22
	1970	3,575	1,315	321	33	7
	1971	10,200	2,694	742	89	9

[1]Adjusted for tagger induced mortality.

TABLE 4.—Mean percentage of large (adult) and small (juvenile) test tags recovered in Gulf menhaden reduction plants, Gulf of Mexico.

Tag type	Release years	Percentage recovered in season of release	Percentage recovered in seasons after release		
			1st	2d	3d
Large	1969-71	51	0.56	0.05	0.02
Small	1970-72	34	.38	.02	.01

large indicate that mortality rates were generally similar for all areas and years (Figure 4). Since not all areas and years had 4 yr of recoveries, and two of the three areas did not have strongly linear plots (hence a constant annual Z) for 1970 releases, I selected the more linear 3 yr of recovery data from each area for 1969 and 1971 for further analysis (points joined by solid lines on Figure 4). Based on the plotted data of Figure 4, I assumed that Z (hence survival and rate of fishing) was constant for years 1-3 following release for the western area in 1971 and the central area in 1969 and 1971. I assumed a Type C error condition for the first year after release for the western area in 1969 and the eastern area in 1969 and 1971 and assumed Z to be constant for years 2-4 in these three data sets. I also assumed that all the fish tagged as adults, which were released in late spring just after fishing had begun, were subjected to a full season of natural mortality.

I used the slope of a weighted regression of the natural logarithms of recoveries on years-at-large where mortality was assumed constant as an estimate of Z. Each regression point was weighted by the number of unadjusted recoveries that provided the basis for that point.

For release groups with an estimate of constant Z for years 1-3, called here Z_1, the constant annual exploitation rate (u_1) was estimated directly by (Ricker 1975):

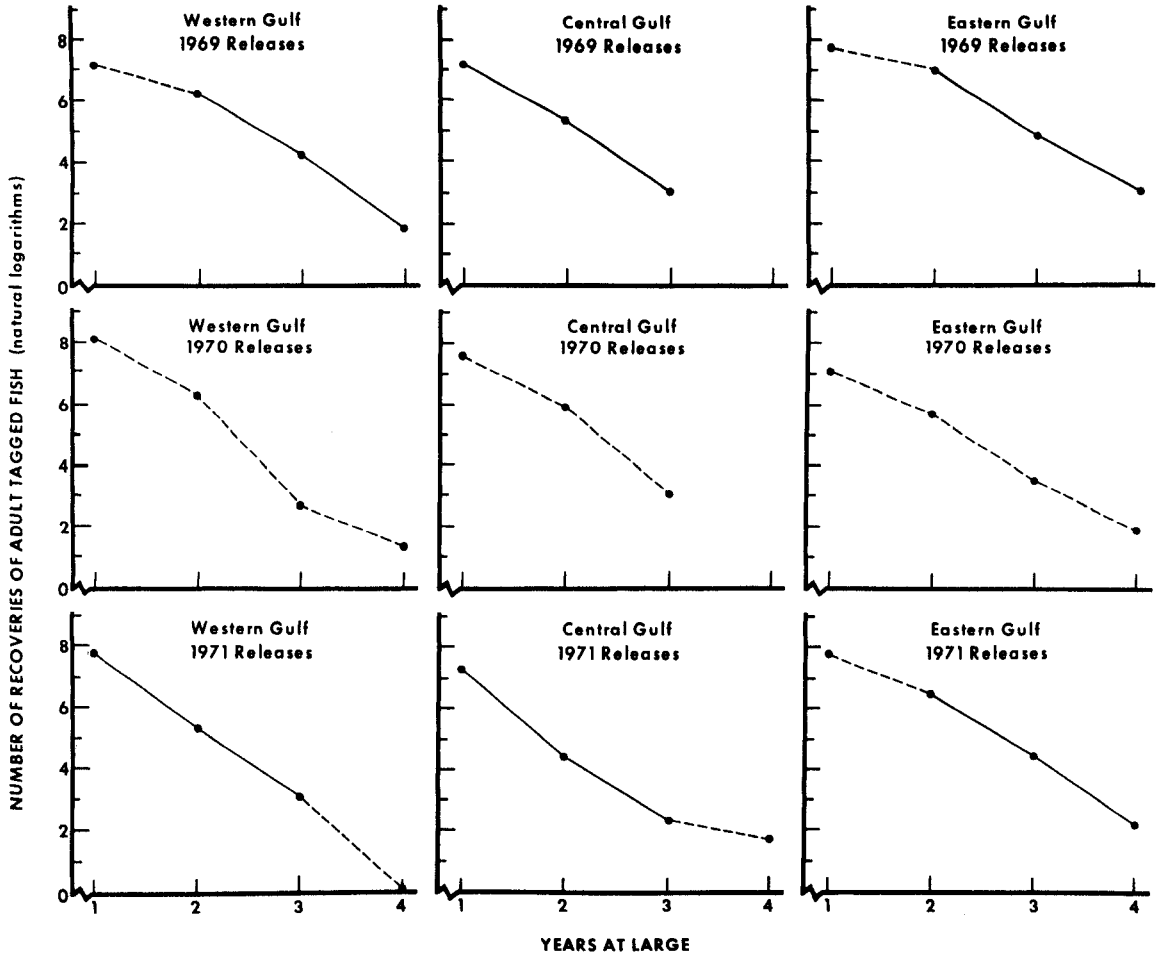

FIGURE 4.—Natural log frequency of recoveries by years at large for tagged adult Gulf menhaden by fishing area and release year, Gulf of Mexico. Lines connect points used to estimate instantaneous total mortality rate (Z) (assumed constant for 3 consecutive years), and dashes connect points not used in the estimation procedure for Z.

$$u_1 = \frac{R_1 + R_2 + R_3}{M'(1 + S_1 + S_1^2)} \quad (2)$$

where M' = the number tagged and released, adjusted for tagging loss,
$S_1 = e^{-z}$, the constant annual survival rate, and
R_n = number of adjusted recoveries for years-at-large n.

For release groups with an estimate of constant Z for years 2-4, called here Z_2, the constant exploitation rate (u_2) had to be estimated by trial, since the rate for the first season could not be assumed a constant for later years (Type C error condition). A trial value of Z_1 for the first year-at-large also provided first year trial values of S_1 and A_1 (total annual mortality rate); u_2 was estimated for the second and later years-at-large by (Ricker 1975):

$$u_2 = \frac{R_2 + R_3 + R_4}{S_1 M'(1 + S_2 + S_2^2)} \quad (3)$$

and also by:

$$u_2 = \frac{A_2}{Z_2}\left(Z_2 - Z_1 + \frac{R_1 Z_1}{M' A_1}\right). \quad (4)$$

The trial value of Z_1 was adjusted until Equations (3) and (4) converged on virtually equivalent estimates of u_2.

The annual instantaneous rate of fishing mortality (F) was estimated by:

$$F = \frac{uZ}{A} \quad (5)$$

where $A = 1 - e^{-z}$, the total annual mortality rate, and u, Z, F, and A are subscripted 1, where Z was constant through years 1-3, and 2 where Z was constant through years 2-4.

The annual instantaneous rate of natural mortality (M) was estimated by:

$$M = Z - F \quad (6)$$

where, as above, Z and F are subscripted 1 for constant mortality years 1-3 and 2 for constant mortality years 2-4.

The central area had the greatest variation in parameter estimates between years, while the western area had the least (Table 5). I averaged all estimates of M and u for each tagging loss rate examined to obtain unweighted means (Table 6). A change in the estimate of tagging loss resulted in a slightly greater than 1:1 fractional change in the estimates of M and u.

TABLE 5.—Estimated annual instantaneous natural (M) and fishing (F) mortality rates and exploitation rates (u) for tagged adult Gulf menhaden in the Gulf of Mexico, assuming a 20% initial tag loss to shedding and mortality.

Area	Year	M	F_1	F_2	u_1	u_2
Western Gulf	1969	1.1672	—	0.9300	—	0.3890
	1971	1.2287	1.1665	—	0.4426	—
Central Gulf	1969	.6927	1.2043	—	.5396	—
	1971	1.6083	1.1367	—	.3875	—
Eastern Gulf	1969	.8805	—	1.1673	—	.4965
	1971	.9835	—	1.1662	—	.4793

TABLE 6.—Estimates of mean annual rate of exploitation (u) and instantaneous natural mortality rate (M) for Gulf menhaden in the Gulf of Mexico, estimated from recoveries of tagged adults, with varied levels of tagging mortality.

	Tagging loss rate				
Parameter	10%	15%	20%	25%	30%
u	0.4122	0.4328	0.4558	0.4815	0.5106
M	1.2019	1.1506	1.0935	1.0293	0.9568

Since the earlier estimates of each Z were from weighted regressions with only three data points and hence only one degree of freedom for estimating confidence intervals (C.I.), I conducted a combined analysis of scaled data for the six sets of release-recovery data for 1969 and 1971 (which consist of 18 data points and, hence, 16 df) to determine the stability of the estimate of M relative to the variance about the estimate of Z. After scaling the data, each release-recovery set summing to 10,000, I estimated the unweighted predictive regression slope estimate of Z_2 and its 95% C.I. by standard methods (Draper and Smith 1966). Assumptions on which years represented periods of constant total mortality were the same as for the earlier analysis. Equations (3) and (4) were used to estimate u_2 from the scaled estimate of Z_2 and for the high and low extremes of the 95% C.I. F_2 and M were estimated by Equations (5) and (6) as before. The resulting estimate of M and its approximate 95% C.I., although slightly lower than the earlier estimate, represent very similar values, and relative to the variance about the estimate of Z_2, M is quite stable (Table 7).

To determine if the arbitrary selection of 3 yr of recovery data for analysis, adjustment for Type C error, and use of weighted regressions had a major altering effect on the resulting estimate of M, I estimated M using all recovery data points for the

TABLE 7.—Estimates from scaled data of total annual instantaneous mortality rate (Z_2), rate of exploitation (u_2), instantaneous fishing mortality (F_2), instantaneous natural mortality (M), and their approximate 95% confidence intervals (C.I.), for Gulf menhaden tagged as adults in the Gulf of Mexico.

Parameter	Estimate	High 95% C.I. limit	Low 95% C.I. limit
Z_2	2.2241	2.4356	2.0126
u_2	0.4692	0.5041	0.4307
F_2	1.1701	1.3456	1.0005
M	1.0540	1.0900	1.0121

1969 and 1971 releases, no Type C correction, and an unweighted predictive regression estimate for Z. The resulting mean estimate for M, 1.0852, is very similar to the estimate of M, 1.0935, obtained from the more refined analysis. Inclusion of the 1970 release-recovery data in this analysis resulted in a somewhat lower mean estimate of M, 1.0089. The lower M estimates for the 1970 releases probably resulted from a lower rate of tagger induced mortality than for the 1969 and 1971 release groups, as the 1970 tagged fish were larger than the fish tagged during the other 2 release years.

As evidenced by the similarity of results from the two modified analyses and the results depicted in Table 6, the estimate of M is apparently more sensitive to the correction factor for tagging mortality loss than the estimates of other parameters used in its estimation. Unfortunately, data on the nature of the statistical distribution on which to base variance estimates and hence approximate 95% C.I. are lacking. Based on the current knowledge of tagging mortality for menhaden, the estimates obtained for a 20% tagging loss and the weighted regression technique (M = 1.0935 and u = 0.456) are the best estimates currently available.

AREA-SPECIFIC AND AGE-SPECIFIC EXPLOITATION RATES

To estimate area-specific and age-specific exploitation rates from recoveries of tagged juveniles, it is necessary to estimate the number of tagged fish alive at the beginning of each fishing season. These numbers can be estimated from the number of recoveries by sequential analysis (Ricker 1975). The data and parameters needed are the number of recoveries (R_n) by age (n), an estimate of M, and an estimate of u for a given cohort during its last year in the fishery.

The numbers of tags recovered in all years for fish released in specific areas were pooled by age of capture and, with one exception, were unweighted (Table 8). For three estuaries, which constituted the southeast Texas area, the recoveries were weighted so that each estuary contributed equally to the totals.

TABLE 8.—Area-specific annual exploitation and fishing mortality rates estimated by sequential analysis of recoveries of tagged juvenile Gulf menhaden in the Gulf of Mexico. Numbers in parentheses are initial rates of exploitation obtained from the analysis of adult-tagged fish.

Area	Age	N_n	u	F	S	R_n
1. Southeast Texas[1]	1	2,557	0.050	0.086	0.3074	129
	2	786	.184	.348	.2366	145
	3	186	(.456)			85
2. Galveston Bay	1	656	.270	.549	.1935	177
	2	127	.505	1.351	.0868	65
	3	11	(.456)			[2]5
3. Western Louisiana	1	2,096	.338	.737	.1603	709
	2	336	.330	.715	.1639	111
	3	55	(.456)			25
4. Central Louisiana	1	763	.373	.843	.1442	284
	2	110	.390	.901	.1361	43
	3	15	(.456)			7
5. Western Delta	1	412	.509	1.373	.0849	210
	2	35	(.456)			16
6. Eastern Delta-Mississippi	1	1,748	.265	.538	.1956	464
	2	342	.547	1.563	.0702	187
	3	24	(.456)			11
7. Mobile Bay[3]	1	3,896	.027	.045	.3203	105
	2	1,248	.343	.753	.1578	429
	3	197	(.456)			90
8. Pensacola Bay	1	587	.112	.200	.2743	66
	2	161	.417	.992	.1242	67
	3	20	(.456)			9
9. Choctawhatchee Bay-St. Andrew Bay	1	977	.049	.084	.3080	48
	2	301	.368	.830	.1461	111
	3	44	(.456)			20

[1]Weighted recoveries for this subarea only.
[2]Pooled age-3 and age-4 recoveries.
[3]Estimates are unrealistic; see Table 9 and text.

The number of tagged fish alive (N_n) in their last representative year in the fishery at the beginning of a fishing season was estimated by:

$$N_n = \frac{R_n}{u} \tag{7}$$

where u = 0.456 from the adult tagging analysis.

An estimate of S_{n-1} was required to estimate the number of 2-yr-old tagged fish alive (N_{n-1}) at the beginning of a fishing season from the equation:

$$N_{n-1} = \frac{N_n}{S_{n-1}}. \tag{8}$$

S_{n-1} was estimated by substituting trial mortality estimates (assuming M = 1.0935) into the following equation until the right side equaled the number of recoveries at age n − 1 (Ricker 1975):

$$R_{n-1} = N_n \left[\frac{F_{n-1} A_{n-1}}{S_{n-1} Z_{n-1}} \right]. \quad (9)$$

By repeating this procedure, Equations (9) and (8), using N_{n-1} as an estimate of 2-yr-olds alive at the beginning of a fishing season, the number of tagged 1-yr-olds (N_{n-2}) alive at the beginning of a fishing season was estimated.

Age (n) specific exploitation rates were estimated for each release area by using the estimated age specific mortality rates in:

$$u_n = \frac{F_n A_n}{Z_n}. \quad (10)$$

Except for fish tagged in the Mobile Bay, Ala., area (Alabama coastal waters are closed to purse seining) the exploitation rates for both age-1 and age-2 fish declined progressively as the distance from the delta increased. The decline was much greater for age-1 than for age-2 fish (Figure 5). The low rates of entry of fish from the extremes of the range and the purse seine closure imposed for coastal Alabama waters may enable a small buffer stock to survive in the event of heavy exploitation.

For fish tagged in Mobile Bay, the number estimated to have been alive at the beginning of the first fishing season exceeded the number of fish tagged, an obvious impossibility (Table 8). In outside waters, Gulf menhaden are taken incidentally by the industrial bottom trawl fishery (Roithmayr and Waller 1963) and by the shrimp fishery in inside and outside waters. The overestimate of N_1 may have been the result of estimated M being too high for this group of fish. One possibility for M being too high is that the loss of tagged fish to other causes, which is included in the estimate of M, may be lower than for fish tagged in all other areas.

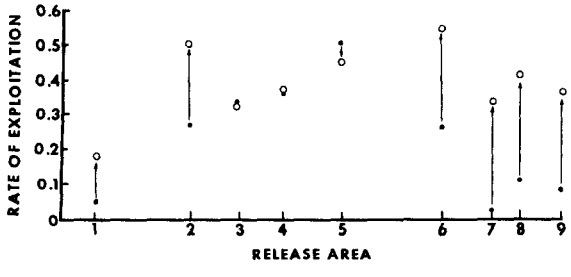

FIGURE 5.—The rate of exploitation by release area for age-1 (dots) and age-2 (circles) Gulf menhaden tagged as juveniles in estuaries on the Gulf of Mexico. Arrows indicate degree and direction of change between years.

Estimates of initial tag loss from shedding and death were made by comparing the number of fish estimated to have been alive at the beginning of the first season with the number that should have been alive if only natural mortality ($M = 1.0935$) had caused deaths during the approximately 8 mo (0.67 yr) following tagging. The apparent tagging loss estimates (L) were calculated by estimating the fraction by which M' would have to be reduced to equal N_1 prior to undergoing 8 mo of natural mortality, i.e.:

$$(M' - LM')e^{-0.67M} = N_1$$

by solving for L and simplifying,

$$L = 1 - \frac{N_1}{M'(e^{-0.67M})}. \quad (11)$$

The resulting estimates, expressed as a percentage of the number of fish tagged, ranged from 22.1 to 63.0% (Table 9). These estimates seemed realistic in view of the loss rates reported by Kroger and Dryfoos (1972) for Atlantic menhaden of similar size tagged with small (juvenile) tags. These estimates do not, however, have any bearing on the 20% tagging loss estimate used for the adult study, as this study used larger fish and larger tags.

TABLE 9.—Numbers of juvenile Gulf menhaden tagged in autumn, numbers estimated by sequential analysis to have been alive the following April, and effectual tagging loss rates, Gulf of Mexico.

Release area	Number tagged	Number estimated alive	Effectual tagging loss
1. Southeast Texas[1]	13,460	2,557	0.605
2. Galveston Bay	3,092	656	0.559
3. Western Louisiana	6,000	2,096	0.273
4. Central Louisiana	2,140	763	0.258
5. Western Delta	2,000	412	0.571
6. Eastern Delta-Mississippi	4,670	1,748	0.221
7. Mobile Bay[2]	3,699	3,896	—
8. Pensacola Bay	3,300	587	0.630
9. Choctawhatchee Bay-St. Andrew Bay	2,682	977	0.242

[1]Weighted data for this area only.
[2]Unrealistic results, see text.

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NATURAL STABLE CARBON ISOTOPE TAG TRACES TEXAS SHRIMP MIGRATIONS[1]

BRIAN FRY[2]

ABSTRACT

A 1978 spring and early summer survey of Texas brown shrimp, *Penaeus aztecus*, showed that stable carbon isotope ($^{13}C/^{12}C$ or $\delta^{13}C$) analysis is useful for tracing shrimp movements. At least four isotopically distinct shrimp feeding grounds (three estuarine and one offshore) exist along the Texas coast. Mean $\delta^{13}C$ values for brown shrimp in these feeding grounds during the spring and early summer were −12.8 to −15.4 (sea grass meadows), −16.2 to −16.8 (offshore), −17.9 to −19.6 (open bays, group 1), and −20.1 to −21.7 (open bays, group 2). Longer term seasonal studies offshore and at two sea grass stations showed that shrimp $\delta^{13}C$ values become less negative by 1.2 to 2.4‰ in the fall versus spring/early summer. Many small subadult brown shrimp collected offshore and during outgoing tides in a channel leading to the offshore Gulf of Mexico had $\delta^{13}C$ values typical of individuals in sea grass meadows. These and possibly other shallow-water habitats appear to supply more shrimp to south Texas offshore fisheries than do deeper estuarine bays.

Migratory movements of many commercial marine species are difficult to follow. Traditional methods include mark-recapture techniques to follow individual growth and movement while sequential trawling studies follow mass migrations. Newer techniques based on underwater acoustics or genetic differences among stocks have expanded our ability to follow marine migrations, but many movement patterns remain unresolved.

Recently, the study of stable carbon isotope ratios, $^{13}C/^{12}C$ or $\delta^{13}C$, has shown that animals acquire a natural isotopic label or tag from their diet. The carbon in animals is generally isotopically similar within a range of ±2‰ to the carbon in the diet (DeNiro and Epstein 1978; Fry et al. 1978; Teeri and Scholler 1979). Photosynthesis introduces $\delta^{13}C$ variations among different plant species (Park and Epstein 1960; Smith and Epstein 1971), and the $\delta^{13}C$ values of animals may be interpreted in terms of the relative carbon contributions from plants at the base of food chains. In the Gulf of Mexico, marine sea grass species have the least negative $\delta^{13}C$ values (−3 to −15‰) while phytoplankton and particulate organic carbon are usually more negative (−18 to −25) and other species of marine algae are intermediate (−12 to −20) (Craig 1953; Parker 1964; Smith and Epstein 1971; Eadie and Jeffrey 1973; Fry and Parker 1979). Animals in sea grass meadows are usually less negative than animals found offshore, reflecting the general $\delta^{13}C$ difference between sea grass plants and phytoplankton (Parker and Calder 1970; Thayer et al. 1978; Fry and Parker 1979; McConnaughey and McRoy 1979).

This study assesses the potential of using $\delta^{13}C$ variations to trace shrimp movements. Since food availability differs between habitats such as sea grass meadows and phytoplankton-dominated open bays, the $\delta^{13}C$ label acquired during feeding will differ between such habitats. Measuring the $\delta^{13}C$ values of migrating shrimp should provide an indication of which habitats they came from and a basis for evaluating which habitats are relatively important numerical contributors to commercial shrimp fisheries.

During 1978, I analyzed the $\delta^{13}C$ values of the migratory brown shrimp, *Penaeus aztecus*, and to a lesser extent, of the pink shrimp, *P. duorarum*. These shrimp share a similar life history pattern of offshore spawning, juvenile growth in estuaries, subsequent offshore migration of subadults, and final maturation to adults that spawn offshore (Cook and Lindner 1970). Several nonmigratory shrimp and one offshore stomatopod species were also collected to facilitate interpretation of $\delta^{13}C$ patterns as due to local conditions vs. migration. Seasonal studies assessed the rate at which local food variations cause a change in shrimp $\delta^{13}C$.

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METHODS

Shrimp samples were collected at 22 bay and 3 offshore stations along the Texas coast (Figure 1). Most bay sampling was done by the Texas Parks and Wildlife Department, Coastal Fisheries Division, as part of their 1978 spring shrimp survey. Depths at bay stations were 1-2 m; offshore trawling areas were located in 27-29 m depths. Open bay stations had unvegetated mud bottoms and were not within 0.25 km of a major swamp, sea grass meadow, or marsh. Sea grass stations were all in or on the edge of large sea grass meadows measuring at least 5 ha.

Four open bay stations deserve individual mention. Clear Lake (station 100) and the old Arroyo Colorado (station 13) receive substantial amounts of domestic sewage. Station 94, at the mouth of the Tres Palacios River, had the lowest salinities of any station. Station 92 in Turtle Bay was in the open bay, but well-developed *Spartina* sp. marshes were present on the shore.

Shrimp were collected either with bar seines or trawls and then frozen in seawater for later identification and $\delta^{13}C$ analysis. Surface temperature and salinity were measured at the time of collection. Spring samples were mostly collected during a 6-wk period from mid-April to 1 June 1978. Offshore samples were collected 26 July 1978.

White muscle tissue was dissected from shrimp abdomens for $\delta^{13}C$ analysis. Both composite and individual samples were prepared. Composite samples contained equal-weight tissues from individual shrimp. Preliminary analysis of the number of pooled brown shrimp required for an accurate estimate of mean shrimp $\delta^{13}C$ showed that combining five or six individuals is generally sufficient (Figure 2); accordingly, composite sample sizes were ≥10 for all shrimp, and averaged 34 individuals/sample. For individual shrimp, mus-

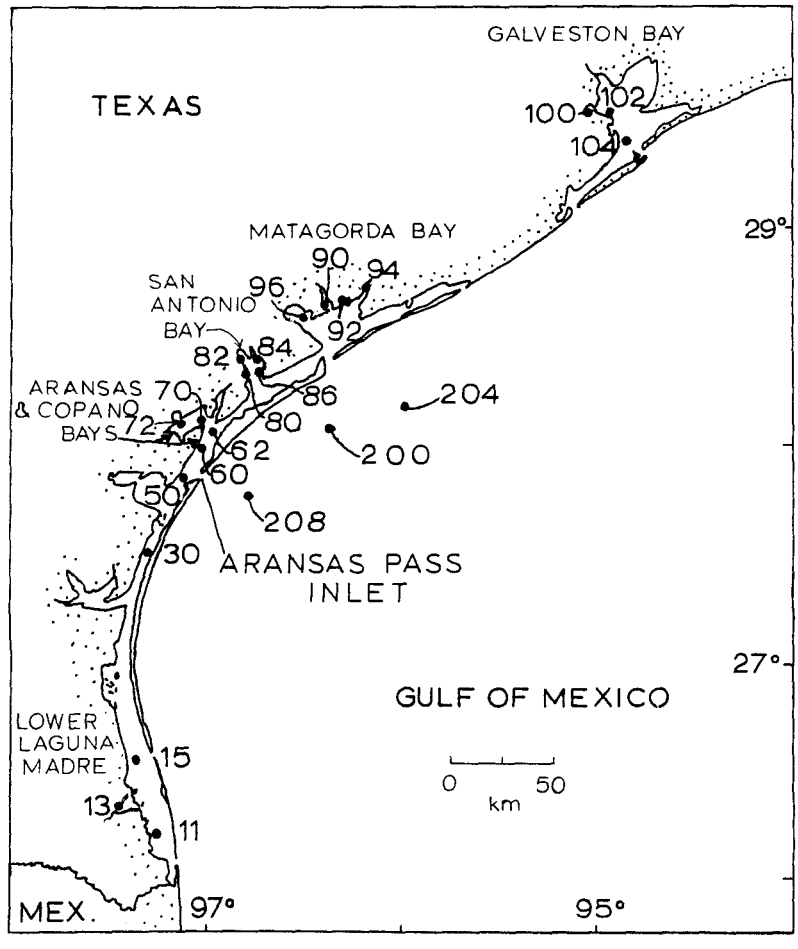

FIGURE 1.—Shrimp collection stations in the northwestern Gulf of Mexico.

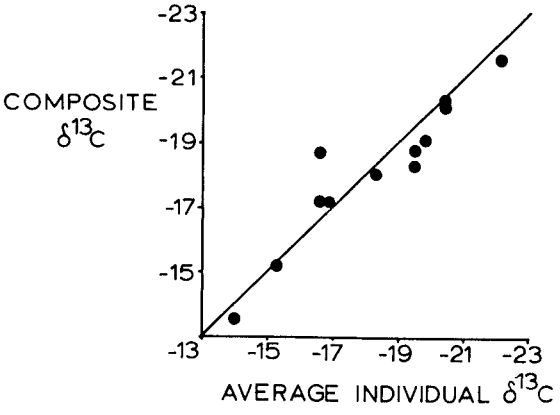

FIGURE 2.—Agreement between two methods of estimating mean shrimp $\delta^{13}C$ at 12 bay stations. The mean $\delta^{13}C$ value of five or six individuals is plotted as the x coordinate; the $\delta^{13}C$ value of the composite sample from which the individuals were subsampled is plotted as the y coordinate. The 45° reference line indicates complete agreement between the two methods.

cle tissue taken from the same shrimp showed a maximum $\delta^{13}C$ range of 0.3‰ (three shrimp, each sampled thrice), and subsampling one piece of tissue per shrimp was therefore considered adequate.

Shrimp were sorted by species by hand, and identification checked with a dissecting microscope on 5-10 specimens per composite sample using several keys (Zamora and Trent 1968; Pérez-Farfante 1970; Wood 1974).

Composite and individual samples were dried in an oven or freeze dryer, then shredded through a #40-mesh screen with a Thomas-Wiley Mill[3] or ground to a fine powder with mortar and pestle. Samples were combusted in a modified Leco radio frequency furnace (Parker et al. 1972) and analyzed for $\delta^{13}C$ values using a Nuclide 6-60 dual collector isotope ratio mass spectrometer. All results are expressed relative to the international PDB[4] standard where:

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{standard}} - 1 \right) \times 10^3.$$

Based on analysis of 53 paired replicate samples, the mean error ±95% confidence limits was 0.45±0.77‰.

RESULTS

Bay Shrimp

Figure 3 shows the $\delta^{13}C$ values of brown shrimp from all bay stations sampled during the spring and early summer. The sampling effort was unequal at these stations, primarily due to fluctuations in shrimp numbers from week to week. At most stations, three or more composite samples were collected at irregular intervals over the 2-mo period; individual subsamples of pooled composite samples were collected between 1 and 15 May.

Analysis of variance showed highly significant differences between station means computed from composite samples ($P<0.01$). The LSD multiple range test showed that bay stations formed at least three significantly different groups on the basis of their mean $\delta^{13}C$ values (Figure 3; vertical bars at right margin). Most stations were open bay stations and had mean $\delta^{13}C$ values between −17.9 and −19.6‰ (stations 60-84). Mean $\delta^{13}C$ values were higher in sea grass meadows, −12.8 to −15.4‰. Several open bay stations formed a third group, having more negative average values of −20.1 to −21.7‰ (stations 80-13).

Analysis of the open bay stations showed that the more negative shrimp $\delta^{13}C$ values tended to occur in lower salinity bays which have been historically well flushed by freshwater inflows (Table 1).

TABLE 1.—Brown shrimp $\delta^{13}C$ and salinity at open bay stations and freshwater flushing rates for five Texas bays and the Gulf of Mexico.

Bay	$\delta^{13}C$[1] mean±SD(*N*)	Salinity[2] mean±SD(*N*)	Mean bay turnover rates (times/yr)[3] Historical	1951-68
Galveston	−20.0±0.9(19)	20.2±2.5(24)	3.9	3.1
San Antonio/ Espiritu Santo	−19.2±1.1(17)	16.7±4.8(25)	2.6	2.2
Matagorda	−18.3±1.3(17)	20.9±5.0(25)	1.3	1.3
Copano/Aransas	−17.7±0.6(9)	22.5±2.2(30)	.2	.2
Laguna Madre[4]	−17.6±0.6(2)	32.0±4.4(3)	.02	.02
Offshore, July	−16.5±0.6(15)	≈36	≈0	≈0

[1]Based on composite samples only.
[2]Salinity taken at the time of shrimp collection (mid-April to mid-June 1978).
[3]Turnover rate is the ratio of annual freshwater inflow volume to the volume of a bay. Calculated from Table 8, Diener 1975.
[4]Station 13 in the Old Arroyo Colorado is not included in this average.

Size and Bay Brown Shrimp $\delta^{13}C$

Systematic $\delta^{13}C$ changes with size might be expected if shrimp foods available to different size classes possessed different $\delta^{13}C$ values. Shrimp sizes ranged from 20 to 110 mm total length (TL),

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
[4]Abbreviation in the isotopic literature for a fossil belemnite, *Belemnitella americana*, from the PeeDee formation in South Carolina.

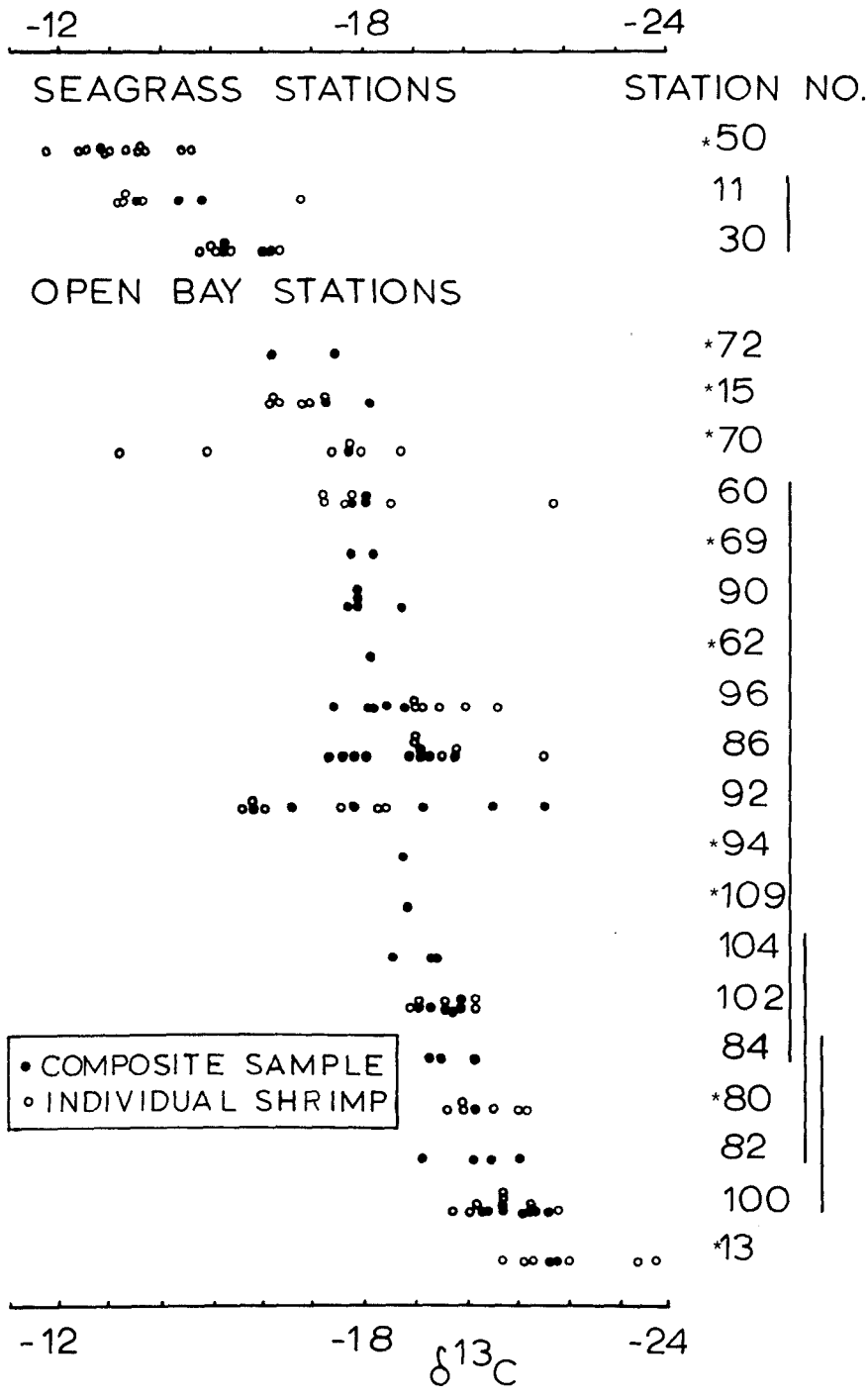

FIGURE 3.—Bay brown shrimp $\delta^{13}C$ by station, mid-April through mid-June 1978. Vertical lines (right margin) connect stations that, on the basis of their composite samples, were not significantly different ($P<0.01$, LSD multiple range test). Stations denoted by an asterisk had one or two composite samples and were not subjected to this analysis, although they are included for completeness. Stations 69 and 109 are composites of several stations in Aransas and Galveston Bay, respectively.

generally progressing throughout the spring sampling period. Both individual and composite bay brown shrimp samples were examined by station and station group (Figure 3) using graphic, linear, and multinomial regression analysis for correlations of shrimp length, weight, or date of collection with shrimp $\delta^{13}C$. These analyses were significant only rarely, <1 case in 10, so that no consistent $\delta^{13}C$ relationships with size or date were evident.

Offshore Samples

In addition to migratory brown shrimp, three other shrimp and stomatopod species were collected offshore at stations 200, 204, and 208. These species, *Trachypenaeus similis*, *Sicyonia dorsalis*, and *Squilla empusa*, are normally resident offshore and only occasionally enter estuaries (Hoese et al. 1968). Composite samples of these species fell within a narrow $\delta^{13}C$ range of -16.2 to -16.9‰ (Table 2). Forty-three individual rock shrimp, *Sicyonia dorsalis*, also collected at these stations showed a slightly larger $\delta^{13}C$ range of 1.9‰, -15.5 to -17.4 (Table 2). Mean $\delta^{13}C$ values of migratory brown shrimp were very similar to values of the resident species, although some $\delta^{13}C$ values of smaller brown shrimp differed significantly from mean values of the offshore species (Figure 4A, B). Several other samples of small brown shrimp collected offshore or during outgoing tides 24 May and 21 June 1978 at Aransas Pass Inlet also showed $\delta^{13}C$ values significantly different from the July offshore species (Figure 4A, B). These individual and composite analyses showed that small brown shrimp may enter the offshore regions with widely differing $\delta^{13}C$ values (-12.5 to -19.1‰, Figure 4). But as brown shrimp feed and grow offshore, their $\delta^{13}C$ values rapidly converge on the -16 to -17‰ $\delta^{13}C$ values characteristic of offshore, nonmigratory species.

TABLE 2.—$\delta^{13}C$ values of shrimp species caught at three offshore stations, July 1978. The standard deviation and the number of samples (N) are given after the means that contain more than one sample.

Item	Station 200	204	208
Composite samples:			
Offshore stomatopod			
Squilla empusa	−16.4	−16.2	−16.4
Offshore shrimp			
Trachypenaeus similis	−16.4	−16.6	−16.2
Sicyonia dorsalis	−16.4	−16.6	−16.9
Migratory brown shrimp	−16.6 ±.6(4)	−16.8 ±.2(4)	−16.2 ±.5(7)
Individual shrimp:			
Offshore *S. dorsalis*	−16.5 ±.4(12)	−16.2 ±.5(13)	−16.7 ±.4(16)
Migratory brown shrimp	−16.0 ±.7(12)	−16.2 ±1.0(12)	−15.9 ±1.2(16)

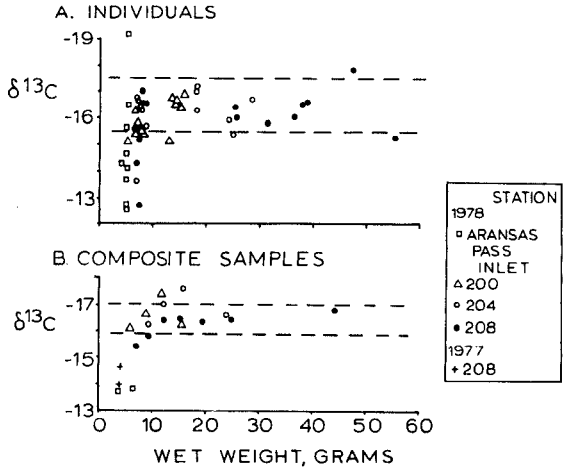

FIGURE 4.—Size dependence of brown shrimp $\delta^{13}C$ values at three offshore stations and from an outgoing tide at a major migratory pass opposite these stations. Dashed lines indicate 95% confidence limits beyond which single brown shrimp samples differ significantly from the -16.5‰ mean of resident offshore shrimp species listed in Table 2 (Sokal and Rohlf 1969).

Seasonality

To supplement the late spring bay collections, a longer term seasonal study was undertaken at sea grass station 30. In addition to the migratory pink and brown shrimp, three small, 20-50 mm TL, nonmigratory shrimp species were also collected: grass shrimp, *Palaeomontes* sp.; arrow shrimp, *Tozuema carolinense*; and snapping shrimp, *Alpheus heterochaelis*. Mean values of these two migratory and three nonmigratory species showed a sigmoidal variation from -15.6 in late April to -13.0 to -13.2 in late August through late October to -14.2 in early December (Figure 5). Regression analysis showed that mean $\delta^{13}C$ did not correlate significantly with either temperature or salinity. Collections offshore and at sea grass station 50 showed a similar pattern in shrimp $\delta^{13}C$ variation between early summer and late fall, although collections at these stations were not made regularly as at station 30. Late October offshore composite samples averaged 1.2‰ less negative than late July samples (N = 18 and 23, respectively); at sea grass station 50, late September composite samples averaged 2.2‰ less negative than late June samples (N = 4 and 2, respec-

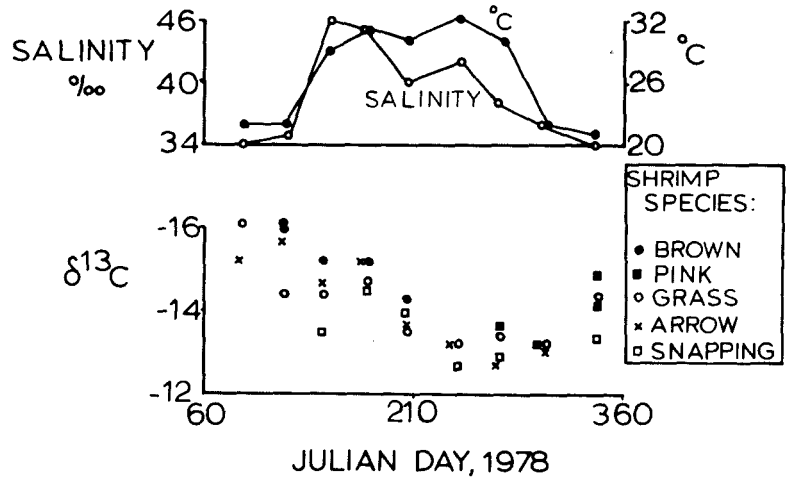

FIGURE 5.—Seasonal trends in shrimp $\delta^{13}C$ at bay sea grass station 30. All samples are composite samples; temperatures were taken between 0900 and 1200 h on each collection date.

tively). These seasonal differences between means were significant offshore ($P<0.01$, t-test) but not at sea grass station 50 ($P>0.05$, t-test).

DISCUSSION

To use $\delta^{13}C$ data to monitor shrimp migrations, isotopically distinct feeding grounds must be identified in which shrimp acquire significantly different, unique isotopic tags during feeding and growth. When the relationship between shrimp foods and shrimp tissue $\delta^{13}C$ is more precisely known, it should be possible to predict shrimp tissue $\delta^{13}C$ at any locality from the $\delta^{13}C$ value of locally available shrimp foods (Fry in prep.). This study relied on a more indirect method of identifying these isotopically distinct feeding grounds, i.e., monitoring the tissues of the mobile shrimp. In most cases, mean shrimp $\delta^{13}C$ values are probably a reliable index of local feeding conditions, as evidenced by the close $\delta^{13}C$ similarity of migratory brown shrimp and resident nonmigratory shrimp both offshore (Table 2) and in sea grass meadows (Figure 5).

Tests for significant differences among stations showed that sea grass stations were distinct from open bay stations which were in turn divided into two groups (Figure 3). The $\delta^{13}C$ distinction between sea grass and the more positive group of bay stations has been previously observed (Parker and Calder 1970; Fry et al. 1977; Fry and Parker 1979). These open bay stations occurred throughout the Texas bay system (Figure 3). The more negative open bay stations were found in areas which are more heavily influenced by terrestrial inputs such as sewage (stations 100 and 13) or river-borne debris (stations in Galveston and San Antonio Bays). Numerous sediment studies have documented that river-borne detritus derived from terrestrial sources averages −25 to −30‰ (e.g., Hunt 1970; Shultz and Calder 1976). Brown shrimp consumption of this detritus should result in the observed more negative shrimp $\delta^{13}C$ values.

Seasonality

The seasonal cycle observed in shrimp $\delta^{13}C$ is roughly correlated with the warmer growing season when the temperature increases and the species composition and abundance of food sources also change. These effects are difficult to separate with the present data. Marine plant species are sometimes enriched in ^{13}C when grown at higher temperatures (Sackett et al. 1965; Degens et al. 1968; Wong and Sackett 1978), although this effect does not appear to consistently apply to sea grasses (Thayer et al. 1978) nor to natural phytoplankton populations existing at temperatures typical of Texas bays (Sackett et al. 1974).

Seasonal changes in species composition and abundance occurring in sea grass meadows could also change the mean isotopic composition of shrimp foods; probably, the larger seasonal variations observed in sea grass meadows are due in part to the increasing dominance of sea grass carbon in food chains leading to shrimp. The lack of correlation between shrimp $\delta^{13}C$ values and temperature at a time when shrimp $\delta^{13}C$ values could change rapidly (mean weight increased 20-50 × over the spring sampling period) argues against a

direct temperature effect on the carbon metabolism of shrimp.

Offshore Migrations

As brown shrimp migrate offshore from the estuaries, they encounter a new feeding ground. During subsequent offshore growth, shrimp metabolize away the estuarine carbon present in their tissues, and dilute the remainder of this old carbon with new offshore carbon. Summer $\delta^{13}C$ values of nonmigratory offshore shrimp were quite constant around $-16.5‰$ and the offshore feeding grounds appeared to be isotopically uniform over the three stations sampled (Table 2). A model that incorporates these features and predicts the change of shrimp $\delta^{13}C$ during offshore growth is shown in Figure 6. This simple model is a first approximation in that only dilution of the old estuarine carbon during offshore growth is considered, while metabolic loss of this estuarine carbon is ignored. The $\delta^{13}C$ value of shrimp at any time after emigration can be calculated from the equation:

$$\delta^{13}C = \frac{\delta^{13}C_{old}(W_e) + (W_c - W_e)(\delta^{13}C_{new})}{W_c}$$

where W_e = initial weight at emigration,
W_c = weight at time of collection offshore,
$\delta^{13}C_{old}$ = $\delta^{13}C$ at emigration,
$\delta^{13}C_{new}$ = mean offshore shrimp $\delta^{13}C$.

The weights and $\delta^{13}C$ values at the time of offshore emigration shown in Figure 6 represent two individual brown shrimp collected in May at Aransas Pass Inlet (see Figure 4A). The 5 g wet weight is typical of most brown shrimp during the annual peak spring and early summer migrations (Copeland 1965; Trent 1966; Parker 1970; King 1971; pers. obs. 1978).

The model predicts that these migrating 5 g shrimp will rapidly become isotopically indistinguishable from resident shrimp during offshore growth (Figure 6). This prediction agrees well with the results shown in Figure 4 in which shrimp weighing >15 g are generally not significantly different than the –16.5 average of nonmigratory resident shrimp. Growth from 5 to 15 g should occur in about 1.1 and 2.9 mo for female and male brown shrimp, respectively (Parrack 1979), so that the effective offshore life of the estuarine tag is rather brief. Larger weights at emigration and increased differences between δ_{old} and δ_{new} result in a more gradual approach to the mean offshore value, while smaller weights, decreased $\delta_{old} - \delta_{new}$ differences, or metabolic loss of estuarine carbon during offshore growth would result in a shorter detectable life for this estuarine $\delta^{13}C$ tag.

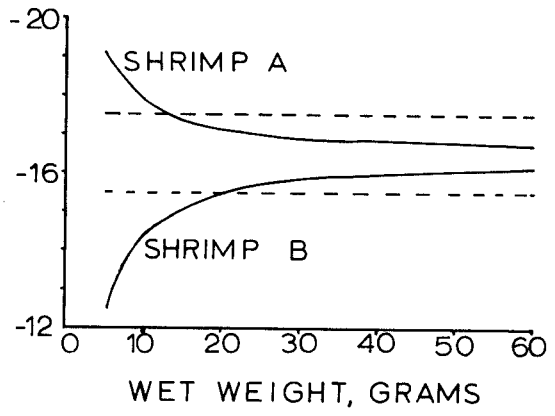

FIGURE 6.—Isotopic diet-change model for two shrimp migrating offshore from Texas estuaries. During offshore growth, these two shrimp gradually approach the characteristic $\delta^{13}C$ value of the offshore area, $-16.5‰$, according to the equation presented in the text. Dashed lines as in Figure 4 indicate $\delta^{13}C$ values at which the estuarine $\delta^{13}C$ tag is no longer distinguishable from normal offshore values.

The data presented in Figure 4 allow a preliminary assessment of the probable estuarine origins of most brown shrimp recruits to the offshore fishery. A trend among smaller shrimp towards $\delta^{13}C$ values more typical of sea grass meadows, rather than those typical of open bays, was evident at both Aransas Pass Inlet in May and June and offshore during late July (Figure 4). Shrimp from two other shallow-water habitats, salt marshes (Haines and Montague 1979), and blue-green algal mats (Fry, unpubl. data) also have isotopic compositions similar to shrimp from sea grass meadows. The $\delta^{13}C$ label thus distinguishes deeper water, open bays from shallow marsh, algal mat, or sea grass habitats. These initial results suggest that the shallow-water habitats are the more important feeding grounds for shrimp that enter the south Texas offshore commercial fishery. This conclusion is in good agreement with other studies that show that shrimp are exceptionally abundant in sea grass meadows (Loesch 1965; Young 1978) and that sea grass meadows are quite extensive in south Texas estuaries (Diener 1975).

Bay Migrations

The $\delta^{13}C$ data also trace migrations between different estuarine habitats. Brown shrimp are smaller and grow more rapidly in estuaries than offshore, further abbreviating the useful life of the initial $\delta^{13}C$ tag a shrimp possesses when entering a new feeding ground. Despite this, brown shrimp $\delta^{13}C$ values were highly variable at bay stations 60, 70, 86, and 92 (Figure 3). High variability may indicate that these stations lie on migration routes where shrimp converge from several isotopically distinct feeding grounds. In support of this idea, one may note that a high $\delta^{13}C$ range, 6.7‰, was observed among migrating individuals at Aransas Pass Inlet, and that offshore, small migrating brown shrimp caused a larger $\delta^{13}C$ range than that found in offshore resident species (Figure 4).

To identify which stations lie on migratory routes, one must distinguish the normal variability expected from local feeding conditions from a higher variability due to migration. Local variation is probably 2.2‰ or less and 3‰ or less for composite and individual samples, respectively. These estimates are based on the $\delta^{13}C$ ranges observed at frequently sampled bay stations, i.e., stations 90, 100, and 102 for composite samples and station 50 for individual samples (Figure 3). Further study will undoubtedly refine these estimates, or, alternatively, future studies may use large differences between shrimp tissue $\delta^{13}C$ and local food $\delta^{13}C$ as a criterion to identify locations where migratory activity occurs. These techniques should allow the delineation of underwater migratory routes whose existence has been suggested by Parker (1970).

CONCLUSION

This paper proposes to trace shrimp movements by matching the $\delta^{13}C$ values of migrating shrimp with the $\delta^{13}C$ values of shrimp living in habitats such as sea grass meadows and planktonic bays where available shrimp foods, and hence the shrimp themselves, differ substantially in their $\delta^{13}C$ values. There are several limitations to this method, as well as some advantages. The utility of the method is limited by the number of habitats that $\delta^{13}C$ analysis can differentiate. Future analyses of other stable isotopes such as hydrogen/deuterium may allow additional distinctions between habitats such as marshes and sea grass meadows. The rapid growth rate of shrimp imposes a second limitation. The maximum amount of information about migratory movement is gained by sampling slower growing animals soon after they begin their migrations. For shrimp, sampling males offshore or in migratory passes during the times of peak migrations will give clearest results. Seasonal changes in shrimp $\delta^{13}C$ occur, but are gradual and can be avoided by sampling during the 1-3 mo peak migration period.

This method should be equally applicable to other migratory animals, both terrestrial and aquatic. Fish movements may be easier to analyze than those of shrimp because of the age-specific $\delta^{13}C$ historical records that fish lay down in their scales. Such analyses could yield information not only about which areas an animal had fed in, but also at what stage in the life cycle and with what frequency these feeding episodes occurred. The initial data presented for the south Texas coast show that shallow water habitats such as sea grass meadows are important suppliers of shrimp to commercial fisheries. Direct extensions of these investigations should yield quantitative information on which estuarine habitats supply the bulk of shrimp and fish caught in commercial fisheries.

ACKNOWLEDGMENTS

Gill Gilmore and the staff of the Coastal Fisheries Division, Texas Parks and Wildlife Department, kindly made their spring shrimp collections available for analysis. P. L. Parker and R. S. Scalan provided support and technical assistance. Chris L. Kitting, Joan Holt, and two anonymous reviewers made useful criticisms of early drafts of this manuscript. This work was supported by NSF grant OCE 77-27009.

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NOTES

ANNUAL REPRODUCTION, DEPENDENCY PERIOD, AND APPARENT GESTATION PERIOD IN TWO CALIFORNIAN SEA OTTERS, *ENHYDRA LUTRIS*

There are various estimates of the frequency of pupping, dependency period and gestation period for the sea otter, *Enhydra lutris*. Based upon an evaluation of female urogenital tracts taken at various times of the year and comparing observed population growth rates with theoretical growth rates, Kenyon (1969) and Schneider[1] concluded that female sea otters probably reproduced every 2 yr. Sinha et al. (1966) demonstrated that delayed implantation of the blastocyst probably occurred in sea otters. Kenyon (1969) suggested 12-13 mo total gestation period (7-8 mo unimplanted and 4.5-5.5 mo implanted) and 11-12 mo for rearing the pup, and a few months rest between weaning and the next estrus. This cycle could be shortened if the female prematurely lost a pup (Schneider footnote 1). Schneider[2] assumed the reproductive cycle included a 7.5 mo gestation period; Barabash-Nikiforov (1935) estimated an 8-9 mo gestation period; he later stated that sea otters breed once a year (Barabash-Nikiforov 1969). Lensink (1962) believed that females bred every year, at least when food was not limiting, and recent evidence presented by Johnson and Jameson[3] indicates annual reproduction in at least some Prince William Sound sea otters. Vandevere (1972) suggested that pup dependency period was less than a year, based on an annual February peak in pupping in California.

This note describes observations of two tagged female sea otters in California, one seen with a different pup for 6 consecutive yr and the other seen with four different pups in about 5 yr. We also report estimates on the apparent gestation period and pup dependency period for these two sea otters.

The first sea otter was a female [No. 34; marked with aluminum tags (Loughlin 1977)] weighing 22 kg when captured on 7 March 1976 near Monterey, Calif. It was noted at the time that this female had protruding nipples, a distended abdomen, an enlarged pelvic area, indicating that she may have been pregnant. She was subsequently seen on 13 March 1976 with a newborn pup. The female-pup pair was last sighted on 2 April 1976, although the female was sighted often in May 1976 without a pup. The pup was apparently lost after only 2 mo and probably died. On 9 May 1977, female No. 34 was seen with a second pup estimated to be 1-3 mo old near San Simeon, Calif. (approximately 140 km south of Monterey). The last sighting of this pup was on 10 August 1977 at which time it was assumed to be 4-6 mo old. [The pups were not marked, except for No. 34's third pup, and since sea otters are not known to adopt strange pups, we assumed that the pups observed were the same during any 1 yr. Estimates of age for pups were based upon a subjective appraisal of physical appearance and behavior (Lensink 1962; Kenyon 1969; Sandegren et al. 1973). The reader is cautioned that our estimates of gestation period are based upon this subjective appraisal.] A third pup, a 3.6 kg female probably not over 1.5 mo old, was captured along with No. 34 on 2 March 1978 back near Monterey. This pup was marked with a small tag in one ear and was sighted only once about a week later. It is presumed to have died. Number 34 was observed on 9 January 1979 with a fourth pup. Both were resighted on many occasions through 13 September 1979 when this pup was assumed to be slightly over 8 mo of age. This same female was seen with a fifth newborn pup on 27 March 1980. This mother-pup pair was seen on at least two subsequent occasions, the last being 8 April 1980, but by 5 May 1980 she again was without a pup and it presumably died. Number 34 was seen with her sixth pup, judged to be 1 mo old, on 9 March 1981 and it was still with the female at the time of writing (Table 1). (Identification of No. 34 is now difficult since she lost her right flipper tag and the left is loose.)

The second female sea otter (No. 41) weighed 25 kg when captured and marked on 15 August 1976 near Monterey. She was observed on 8 January 1977 with a newborn pup and both were subsequently resighted on many occasions. Eight months later, on 8 September 1977, she had a red swollen nose which is indicative of recent copulatory behavior (Kenyon 1969) and was without her

[1]Schneider, K. B. 1972. Reproduction in the female sea otter. Alaska Department of Fish and Game, Sea Otter Rep. I, 36 p.

[2]Schneider, K. B. 1973. Reproduction in the female sea otter. Alaska Department of Fish and Game, Sea Otter Rep. II, 13 p.

[3]Johnson, A. M., and R. Jameson. 1979. Evidence of annual reproduction among sea otters. (Abstr.) Third Biennial Conference on the Biology of Marine Mammals, Oct. 7-11, Seattle, Wash., p. 31.

TABLE 1.—Observation data on sea otter No. 34 and her six pups.

Pup	Date pup first seen	Approximate age of pup when first seen	Date pup last seen	First date female seen without pup	Approximate dependency period	Apparent gestation period
First	13 Mar. 1976	Newborn	2 Apr. 1976	10 May 1976	Presumed dead	No estimate
Second	9 May 1977	1-3 mo	10 Aug. 1977	12 Aug. 1977	4-6 mo	About 5 mo
Third	2 Mar. 1978	About 1.5 mo	7 Mar. 1978	15 Mar. 1978	Presumed dead	No estimate
Fourth	9 Jan. 1979	Newborn	13 Sept. 1979	22 Sept. 1979	8.5 mo	6 mo
Fifth	27 Mar. 1980	Newborn	8 Apr. 1980	5 May 1980	Presumed dead	No estimate
Sixth	9 Mar. 1981	About 1 mo	Still with female at time of writing			

TABLE 2.—Observation data on sea otter No. 41 and her four pups.

Pup	Date pup first seen	Approximate age of pup when first seen	Date pup last seen	First date female seen without pup	Approximate dependency period	Apparent gestation period
First	8 Jan. 1977	Newborn	27 Aug. 1977	8 Sept. 1977	8 mo	4 mo
Second	28 Feb. 1978	About 1.5 mo	7 Sept. 1978	27 Sept. 1978	8 mo	4 mo
Third	13 Mar. 1979	About 1.5 mo	5 May 1979	10 July 1979	3.5-5.5 mo	No estimate
Fourth	31 Dec. 1980	About 1.5 mo	Still with female at time of writing			

pup (Table 2). She was seen with a second pup judged to be about 1.5 mo old on 28 February 1978. This mother-pup pair was seen on numerous occasions through 7 September 1978. Apparently the mother and pup separated after about 8 mo. Number 41 was observed with a third pup, also judged to be approximately 1.5 mo old, on 13 March 1979. This pair was observed often through 5 May 1979. Neither was seen again until 10 July 1979 when No. 41 was seen, red nosed, with a male but without her pup. The third pup, therefore, probably was 3.5-5.5 mo old when separated from its mother. Number 41 was seen with a fourth pup, judged to be 1.5 mo old, on 31 December 1980, and was still with the female at the time of writing.

Since it is not possible to determine with certainty when conception or blastocyst implantation occurred, we can only speculate on the gestation period for the pups of No. 34 and 41. On 10 August 1977, No. 34 was seen with a second pup and on 12 and 13 August 1977 she was seen without her second pup and with a male escort. Photographs of her head region taken on 13 August 1977 showed nose damage indicating recent copulation. She was subsequently recaptured on 2 March 1978 with a third pup that weighed 3.6 kg. Assuming the pup was 1.5 mo old at capture and that conception occurred in mid-August 1977, the gestation period was about 5 mo. Number 34 and a fourth pup were last seen together on 13 September 1979. She was seen without a pup and with a male companion on 22 September 1979 and by 24 September 1979 her nose again exhibited evidence of recent copulation. We monitored No. 34 closely for the next several months. She was last seen without a pup on 14 March 1980; then with a fifth pup on 27 March 1980. If conception took place on 22-24 September 1979, gestation was close to 6 mo.

Number 41 was separated from a pup in early September 1977, coincident with the appearance of a male companion. She had a swollen nose on 8 September 1977 and on 28 February 1978 was seen with an estimated 1.5-mo-old pup. Assuming conception occurred in early September, the gestation period was a little over 4 mo. Her second pup was "weaned" in early September 1978. A third pup, judged to be about 1.5 mo old when first observed on 13 March 1979, was also born just over 4 mo after separation of the second.

Our observations indicate that at the time of separation (weaning) three of the eight separated pups were large enough at 8-8.5 mo of age to have a good chance of survival. Two pups between about 3.5 and 6 mo, although rather small, may have survived. Some independent animals have been documented in the 9-12 kg range (Loughlin 1977; Wild and Ames[4]). The remaining three almost certainly died.

Estimates of the gestation period for captive sea otters, presumably based upon more definitive data, range from 5.5 to 8 mo (Brosseau et al. 1975; Antrim and Cornell 1980; Antrim[5]). Our esti-

[4]Wild, P. W., and J. A. Ames. 1974. A report on the sea otter, *Enhydra lutris* L., in California. Calif. Dep. Fish Game, Mar. Resour. Tech. Rep. 20, 93 p.

[5]J. Antrim, Curator of marine mammals, Sea World, Inc., 1720 South Shores Road, San Diego, CA 92109, pers. commun. June 1980.

mates of 4-6 mo gestation periods, which assume that copulation and conception do not occur until after weaning, seem reasonable if the blastocyst is implanted soon after conception, partially skipping or entirely skipping the delay period. Our field data and that from captive studies indicate that the gestation period in sea otters may be variable and depend on an external stimulus or the general well being of the female.

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MASS MORTALITY OF FEMALE DUNGENESS CRAB, *CANCER MAGISTER*, ON THE SOUTHERN WASHINGTON COAST

Studies of growth and age of Dungeness crab, *Cancer magister*, populations from California to British Columbia have amply elucidated developmental rates for this species (Cleaver 1949; Waldron 1958; Butler 1961; Poole 1967), but no information is contained in such reports on mortality and its causes, apart from reference to known predators and cannibalism. Natural mortality for highly mobile crustaceans is difficult to investigate because animals simply do not expire in easily observed locations or are quickly removed by scavengers once dead. Consequently, there has been no documentation of extensive crustacean mortality by causes such as disease or pollution on the Pacific coast of the United States, and therefore loss from a population throughout its life cycle due to a generalized predator category (including fishing and cannibalism for *C. magister*, Botsford and Wickham 1978) remains the traditional mortality component of the literature on many crustaceans including Dungeness crabs.

On 18 April 1979 large numbers of dead Dungeness crabs on the beach at Grayland, Wash. (Figure 1), were reported to the Westport Field Office of the Washington Department of Fisheries (WDF). Inspection of the beach between Westport and the northern end of Willapa Bay confirmed that many Dungeness crabs had been washed ashore and, contrary to our initial supposition, were not exuvia which are often mistaken for dead crabs by the public. Preceding this instance, we had reports of dead crabs in the pots of commercial fishermen in Willapa Bay in February 1979, and these findings were verified by WDF personnel.

In response to the report of 18 April, five locales on the beach from Grays Harbor to Willapa Bay (Figure 1, Table 1) were quantitatively examined for dead crabs and the shoreline between these points was inspected from a car. All crabs along the five transects were counted and sexed, if possible, and 42 Dungeness crabs at transect 3 were measured to the nearest millimeter across the carapace inside the tenth anterolateral spines.

Results

Dead crabs found on the beach between Grays Harbor and Willapa Bay were confined to the line of previous high tide in a swath about 8-10 m wide.

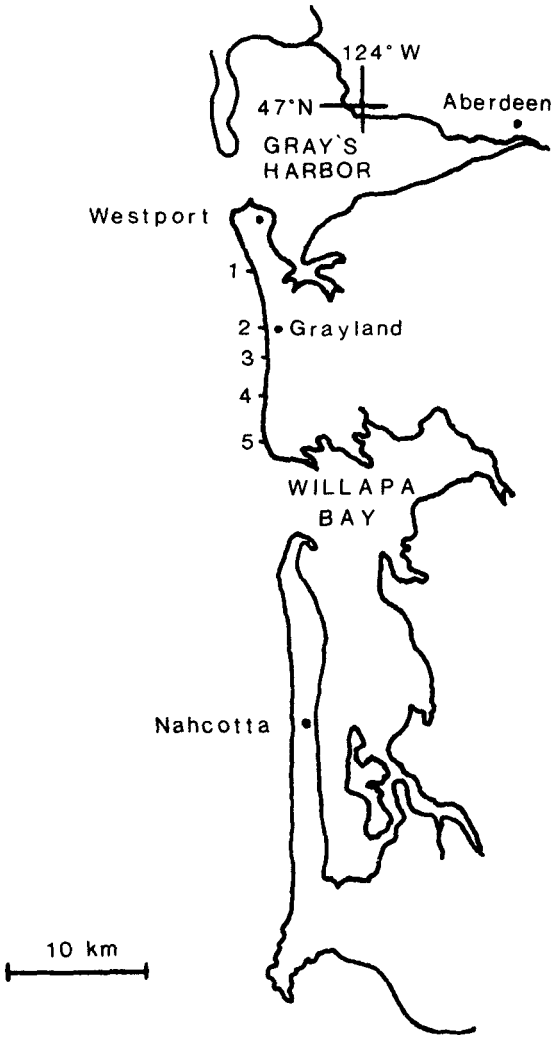

FIGURE 1.—Southern Washington coast and locations of numbered transects.

Nearly all animals examined contained musculature in the appendages and thoracic region and relatively few exuvia were found (Table 1). Because of decomposition and some bleaching of shells, animals were judged to have been on the beach 1-3 d and a relatively high percentage had been damaged by scavenging birds, thereby precluding identification of sex in those instances. Still, all Dungeness crabs sexed were females which, of the 42 measured, averaged 147 mm carapace width (range 110-162 mm).

TABLE 2.—Estimated number of dead Dungeness crabs, Grayland to North Cove, Wash., 18 April 1979.

Area	Crabs/m[1]	Distance between transects (m)	Estimated total no. dead crabs between transects
Grayland to county line (transects 2 to 3)	1.09	1,800	1,962
County line to Midway (transects 3 to 4)	1.15	2,700	3,105
Midway to North Cove (transects 4 to 5)	0.41	3,400	1,394
Total			6,461

[1]Average of two successive transects.

Substantial numbers of dead crabs were found with densities of up to 1.64 crabs/m of shoreline (in the 8-10 m band of upper high tide) computed at transect 3 (Table 1). Generally, the numbers of dead crabs observed between transects seemed consistent with the densities recorded along transects. Estimation of the total number of dead crabs on the beach between Grayland and North Cove (7.9 km) was 6,461 animals (Table 2).

Discussion

Mass mortality of *C. magister* has not, to our knowledge, been previously reported for any locale within this species range from central California to Alaska. At the time of the incidence we describe for southern Washington, there were no similar reports of mortality along Oregon beaches according to Dale Snow.[1] Furthermore, he had never verified an occurrence of extensive crab mortality in that state during 17 yr of fisheries research.

Does our report then, describe an isolated or rare phenomenon of this species or does an event such as mass mortality go undetected, observed but not interpreted for what it is? Along the Wash-

[1]Dale Snow, Oregon State Department of Fish and Wildlife, Newport, Oreg., pers. commun. April 1979.

TABLE 1.—Dead Dungeness crabs along measured beach transects in southern Washington (shown in Figure 1).

Area and transect no. on map	Dead crabs				Exuvia	Transect length (m)	Crabs/m	Cumulative distance (km)
	M	F	Unknown	Total				
Twin Harbors - 1	0	0	0	0	3	152	0.00	0.0
Grayland - 2	0	26	5	31	1	61	0.54	4.3
County Line - 3	0	81	21	101	2	61	1.64	6.1
Midway - 4	0	14	27	41	5	61	0.66	8.7
North Cove - 5	0	4	5	9	0	61	0.16	12.2

ington coast, *C. magister* females generally molt and breed in April through June (Cleaver 1949), and local residents are accustomed to the presence of numerous cast shells on the beach at that time. Since it occurred in the spring, the mortality, prior to our investigation, was probably mistaken for normal molting by many people including patrolmen of the local state parks. It is possible, therefore, that similar occurrences have gone unreported in the past due to such confusion; careful examination of the shells is required to detect tissues and distinguish dead animals from exuvia.

Since the original drafting of this report, two additional mortalities have come to our attention. On 29 November 1979, Walt Cooke[2] observed a large number of dead female Dungeness crabs on the beach from Ocean Park to Long Beach, Wash. (15.6 km). He estimated their number to be 955-1,910, of which only 2.5% were exuviae, and 93% of the remainder were females averaging 146 mm (n = 58) carapace width. On 30 January 1980, Darrell Demory[3] estimated a mortality of 68 crabs/km from the Umpqua River mouth north to Tahkenitch Creek, Oreg., (13.9 km) for an estimated total of 947, of which approximately 95% were females. Conditions of both these occurrences were similar to the April mortality; each consisted almost entirely of large female crabs confined to the high tide line, and occasionally in patches.

It is noteworthy that several instances of dead Dungeness crabs in commercial pots from Willapa Bay prompted investigations by one of the authors, David Armstrong, and personnel from WDF and the National Marine Fisheries Service in February and March 1979 (Tufts[4]). Moribund and dead crabs (male and female) were found in pots checked every 24 h, and some were recovered from shallow intertidal areas. This indicates that animals attracted to bait were healthy enough to enter pots, and then died within a short time thereafter. These observations were made following a severe cold spell during which the air temperature was below freezing for 2 wk, and parts of Willapa Bay had frozen over suggesting temperature stress associated with the mortalities.

Causes of the mortality of April 1979 are only speculative, since crabs could not be examined histologically. Immediately after verifying the report, we questioned WDF personnel to learn if nearshore groundfisheries might account for extensive crab mortality by trawling activity, and learned that no trawlers were known to be operating just prior to 18 April offshore from the transect locations. We surmise that death was due to disease, and the specificity shown for large, older females indicates a causative agent linked perhaps to a decline in vigor with old age. Female *C. magister* reach sexual maturity at about 100 mm carapace width in their second year and relatively few animals exceed 145-150 mm (Butler 1961; Poole 1967). The average carapace width of 147 mm for dead crabs at transect 3 shows a preponderance of older females were affected, perhaps because they were more susceptible to possible lethal stresses than younger animals.

Tissue samples dissected from moribund animals in Willapa Bay in March 1979 were studied for histopathological anomalies, and preliminary results indicate a systemic bacterial infection as a possible causative agent according to Sparks.[5] Lethal diseases among wild populations of *C. magister* are unknown but mortalities of laboratory-held animals have been attributed to such pathogens as fungus and ciliates (Armstrong et al. 1976; Armstrong and Sparks[6]). It seems likely that bacteria or various pathogenic protozoans may take a toll in wild populations, particularly in a segment of the population weakened or predisposed by contributing factors such as old age.

Demory (footnote 3) concluded that the mortality observed in January 1980 on the Oregon beaches may have been the result of stress on crabs trapped in pots that were "sanded in" during a period of adverse weather immediately preceding the observation, when fishermen could not pull these pots for several days. No diseases or parasites were found in specimens obtained from this mortality.

Although examples of mass mortality in crustacean populations are rare, the presence of numerous dead *C. magister* along a beach is reminiscent of the "Gray Crab Disease" affecting *Callinectes sapidus* on the east coast of the United States. Lethal infections attributed to the amoeba

[2]Walt Cook, Washington Department of Fisheries, P.O. Box 158, Ocean Park, WA 98640, pers. commun. 2 June 1980.

[3]Darrell Demory, Oregon State Department of Fish and Wildlife, Newport, Oreg., pers. commun. 5 February 1980.

[4]Dennis Tufts, Washington Department of Fisheries, P.O. Box 158, Ocean Park, WA 98640, pers. commun. 11 July 1980.

[5]Albert Sparks, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, Wash., pers. commun. March 1979.

[6]D. Armstrong and A. Sparks, College of Fisheries, University of Washington, Seattle, WA 98195, unpubl. data on blood ciliates.

Paramoeba perniciosa have been found from Maryland to Georgia (Sprague et al. 1969; Mahood et al. 1970), and strong correlations were established between mass mortalities of blue crabs, high incidences of infection, and declines in commercial fishery landings (Mahood et al. 1970). Percentages of blue crabs infected with the disease range from 20 to 35% of captive animals in holding boxes (Sprague and Beckett 1966; Sawyer 1969) and from 7 to 17% in wild populations during the summer (Sawyer 1969; Sawyer et al. 1970; Newman and Ward 1973). As noted by Newman and Ward, epizootics attributed to this disease can be of short duration, killing significant numbers of animals and leaving no indication of the severity even to investigators purposefully seeking clues on occurrence and extent of infection.

The importance of these observations is, in part, as a reminder that significant loss from a population can result from factors other than predation. The nature of other mortality factors (be they disease, physical-chemical, or pollution) and the magnitude of their effects are largely unknown, particularly for highly mobile crustaceans. Still, the presence of over 6,400 dead adult female crabs along a segment of coastline in conjunction with the other two reports of mass mortality noted, indicates *C. magister* is susceptible to conditions and events that may occur on a seasonal basis. It is reasonable to assume that the crabs observed dead at the high watermark were only a fraction of the numbers affected offshore and, if so, then the magnitude of the mortality in this instance was certainly greater than that observed.

Whatever the cause of the mortality to *C. magister* in this case, and whether such an event is a common seasonal occurrence or a rare catastrophe, a partial loss of this reproductively significant age-group could have important consequences for the commercial fisheries.

Acknowledgments

We express our appreciation to Walt Cooke and Dennis Tufts of the WDF, to Albert Sparks of the National Marine Fisheries Service, and to Darrell Demory of the Oregon Department of Fish and Wildlife for sharing their observations with us.

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FISHES NEW TO THE EASTERN BERING SEA

A joint Japan-United States groundfish survey was conducted during the summer of 1979 on the continental shelf and slope in the eastern Bering Sea. Of the more than 100 species of fishes taken during the survey, 1 has not been previously reported from the Bering Sea—*Kali indica* Lloyd 1909 (Chiasmodontidae)—and 3 others have been recorded, but no specific localities in the eastern portion have been attributed as capture sites: *Percis japonicus* (Pallas 1772) (Agonidae); *Laemonema longipes* Schmidt 1938 (Moridae); and *Macropinna microstoma* Chapman 1939 (Opisthoproctidae). In this paper we document the capture of the four species from the eastern Bering Sea.

Collection Information (Table 1)

Specimens of the four species were captured with a 53.4 m (headrope length) commercial bottom trawl fished by a 350-ton land-based trawler, the *Yakushi Maru No. 21*, chartered by the Fisheries Agency of Japan. As no closing devices were used, capture depths are unknown. Presumably, the specimens of *Kali*, *Laemonema*, and *Macropinna* species were captured in midwater as the trawl was lowered or raised, for the species have been collected previously almost exclusively by midwater trawls. Specimens are deposited in the Laboratory of Marine Zoology, Hokkaido University, Hakodate (HUMZ), and the U.S. National Museum of Natural History, Washington, D.C. (USNM). Other specimens of *Percis japonicus* and *Laemonema longipes* were examined from the collections of the Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, Kodiak, Alaska, and the College of Fisheries, University of Washington, Seattle, Wash. (UW), respectively.

TABLE 1.—Collection data for the eastern Bering Sea fish specimens (summer 1979).

Station no.	Date (GMT)	Position (middle of tow)	Bottom depth (m)	Water temp. (°C)	
				Surface	Bottom
22	27 June	59°47.9′ N 178°47.3′ W	930	7.5	3.0
28	27 June	59°53.0′ N 178°54.3′ W	580	7.2	3.7
43	27 June	59°28.6′ N 178°12.5′ W	280	6.5	—
124	23 June	58°22.1′ N 175°01.8′ W	740	6.3	—
225	7 July	57°00.6′ N 170°16.2′ W	510-440	8.1	3.2
251	18 June	56°00.9′ N 169°16.5′ W	610	6.8	—

Kali indica Lloyd 1909
Figure 1 (upper)

One specimen, HUMZ 81941, taken at station 124. This bathypelagic chiasmodontid is widely distributed in tropical seas and has been taken in the temperate South Atlantic and North Pacific as well (Johnson 1969; Johnson and Cohen 1974). Hubbs et al. (1979) have recently reported it from off California based on two specimens (lat. 32°37.7′ N, just north of the United States-Mexican border; and about lat. 33° N, long. 119°20′ W; locality information from L. J. Dempster[1]). The Bering Sea specimen is the most northern record of the species, the first from boreal waters, and an addition to the fish fauna of Alaska.

Counts: D. XIII+24; A. I,25; P. 11; V. I,5; branchiostegal rays 6. Teeth: in lower jaw 5 (outer row) and 3 (inner row); in upper jaw 6 (outer) and 3 (inner); on palatine 4. Measurements in millimeters: standard length 175.3; predorsal 48.5; preanal 95.8; greatest body depth 30.1; least depth caudal peduncle 7.6; length caudal peduncle 20.6; pectoral fin length 30.9; head length 41.6; snout 14.5; eye diameter 6.2; postorbital length of head 22.8; width bony interorbital 11.6; length upper jaw 34.2; length lower jaw 37.2; largest teeth on upper jaw 8.9.

Percis japonicus (Pallas 1772)
Figure 1 (lower)

One specimen, HUMZ 84945, taken at station 43; another deposited in the Northwest and Alaska Fisheries Center Kodiak Laboratory, NMFS, from lat. 57°16.3′ N, long. 172°56.5′ W (RV *Oregon* cruise 794, haul 90, 23 July 1979). Other specimens have been taken from the eastern Bering Sea northwest of Unalaska.[2] This agonid is common in Japanese waters and is also known from the Okhotsk Sea and the Asiatic coast of the

[1]Lillian J. Dempster, Associate Curator, Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, pers. commun. January 1980.

[2]Doyne Kessler, Fishery Biologist, Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615, in litt., 5 August 1980, and James Long, student, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, pers. commun. 9 September 1980.

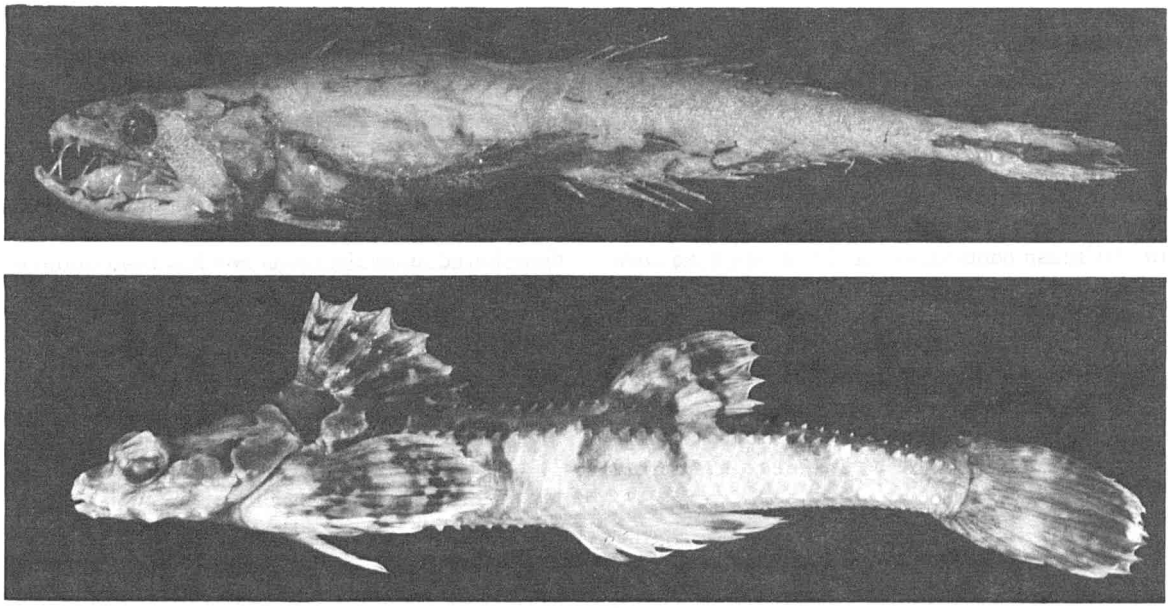

FIGURE 1.—Specimens of *Kali indica*, HUMZ 81941 (top) and *Percis japonicus*, HUMZ 84945 (bottom) taken in the eastern Bering Sea.

Bering Sea (Jordan and Gilbert 1899; Andriashev 1937; Schmidt 1950). Schultz (1967) quoted a letter from Teodor Nalbant which mentions a capture in the south-central Bering Sea, but without an exact locality. The present specimens are the first certain records of the species from the eastern Bering Sea and an addition to the fauna of North America.

Counts (HUMZ 84945 first): D. VI+7, VI+7; A. 8, 8; P. 12, 12; V. I,2, I,2; lateral line plates 30, 37; vertebrae (excluding ural centrum) 40, —. Measurements in millimeters (HUMZ 84945 first): standard length 241, 215; predorsal 66.0, 60.3; preanal 131.0, 122.6; preventral 61.2, 61.8; greatest body depth 40.5, 35.9; least depth caudal peduncle 16.8, 17.5; pectoral fin length 56.0, 50.2; ventral fin length 31.5, 29.2; first dorsal fin base 48.2, 39.8; second dorsal fin base 33.1, 32.2; anal fin base 69.1, 40.3; head length 60.8, 55.4; snout length 15.4, 15.7; eye diameter 12.2, 8.9; interorbital width 16.2, 16.1; upper jaw length 15.3, 13.0.

Laemonema longipes Schmidt 1938

Two specimens, HUMZ 82892 and USNM 220877, were collected at station 251; a third example, UW 20772, eastern Bering Sea, summer 1978, was also examined. This elongate morid is locally abundant in the western North Pacific, ranging from off Owase, Mie Prefecture (specimens in the collections of the University of Kyoto, Maizuru), to the Okhotsk and Bering Seas. Large trawl catches from Suruga Bay have been noted by Matsubara (1955), and >1,000 individuals were found in the stomach of a whale in the Kurile-Kamchatka Trench (Rass 1954). Although Fedorov (1973) listed the species from the Bering Sea, apparently no specimens or precise localities documenting the record have been published. These specimens are new additions to the fauna of North America.

Counts (HUMZ 82892 first, followed by USNM 220877 and UW 20772): D. 6+52, 6+52, 6+50; A. 49, 50, 50; P. 17, 17, 18; V. 2, 2, 2; caudal rays 23, 25, 22; gill rakers 7+18, 8+21, 8+22; branchiostegal rays 7, 7, —; vertebrae (not including ural centrum) 52, 53, 50. Measurements in millimeters: standard length 178, 219, 205; predorsal 46.9, 57.1, 54.7; preanal 68.7, 78.1, 77.1; preventral 34.8, 40.1, 38.1; greatest body depth 39.9, 34.0, —; pectoral fin length 39.8, 46.2, 43.9; ventral fin length 71.0, 78.4, 64.5; head length 42.9, 49.6, 46.3; snout 13.0, 15.8, 14.2; eye diameter 7.4, 9.3, 8.6; width interorbital 9.4, 15.2, 12.8; length upper jaw 20.0, 23.3, 22.1.

Macropinna microstoma Chapman 1939

Three specimens were taken: HUMZ 81966 (stn. 22), HUMZ 81975 (stn. 28), and USNM 220876

(stn. 225). This bizarre, tube-eyed opisthoproctid fish is a characteristic member of the mesopelagic fauna in the temperate eastern North Pacific, where it has been caught between the Gulf of Alaska and northern Baja California (Berry and Perkins 1966; Quast and Hall 1972). It also has been taken in the southeastern Pacific west of the Juan Fernández Islands (Craddock and Mead 1970). Although no localities have been presented, western Pacific captures are mentioned from the Kurile-Kamchatka Trench (as Macropinnidae; Rass 1955) and listed from the northwestern Pacific (Parin 1961). Fedorov (1973) listed the species from the Bering Sea without documentation. The three specimens reported upon here are the first verified records of the species from the Bering Sea.

Counts and measurements of HUMZ 81966 (eyes, distal portion of ventral fin, and skin lost), HUMZ 81975 (eyes, dorsal fin, and skin lost), USNM 220876 (eyes lost). Counts: D. 11, —, 12; A. 14, 14, 14; P. 17, 17, 17; V. 10, 10, 10; branchiostegals 3, 3, 3. Measurements in millimeters: standard length 96.4, 112.8, 56.7; predorsal 68.6, —, 42.7; preanal 76.7, 82.5, 41.9; preventral 53.3, 61.7, 33.1; vent to anal origin 22.1, 18.0, 6.1; greatest body depth 36.6, 36.8, 20.3; least depth caudal peduncle 13.2, 14.3, 7.3; pectoral fin length 21.6, 17.8, 16.5; ventral fin length —, 48.9, 28.0; dorsal fin base 15.8, —, 8.8; anal fin base 14.3, 18.4, 9.6; head length 38.0, 47.8, 26.6.

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SCHOOLING OF THE SCALLOPED HAMMERHEAD SHARK, *SPHYRNA LEWINI*, IN THE GULF OF CALIFORNIA

Groups of sharks have been witnessed occasionally by airborne or shipboard observers (Bass et al. 1975; Clark 1963; Springer 1967; Kenney 1968). Such remote observations, augmented with inferences from fishery records (Ford 1921; Olsen 1954; Jensen 1965), have provided fragmentary descriptions of these groups and speculations on their function. We have studied polarized schools of the scalloped hammerhead shark, *Sphyrna lewini*, by free diving among them at several offshore sites in the Gulf of California. Here we report preliminary observations on the sizes, depths, movements, and compositional dynamics of these schools, and the sizes, sexes, and behavior of the school members. Based upon these observations, we discuss the possible function of such schools.

Previous sightings by others indicated that schools of *S. lewini* might be encountered during the summer at three locations near La Paz, Baja California Sur, Mexico: Las Arenitas Rocks (Isla Cerralvo), El Bajo Espiritu Santo, and Isla Las Animas (Figure 1). These locations were visited between 26 July and 6 August 1979 aboard either our 7 m fiber glass skiff or the 23 m ferrocement research vessel, the *Juan de Dios Batiz*. At these locations and others, four search techniques were employed: 1) Free diving and surface swimming; 2) scuba; 3) baiting with ground Pacific mackerel, *Scomber japonicus*; and 4) playback of pulsed, low-frequency sounds (for description, see Myrberg 1978). Scalloped hammerheads were most easily discovered and approached by free diving, and data were recorded on small plastic slates. Relatively few scalloped hammerheads were observed by divers with scuba, even in areas where this species was abundant. This was probably due to their avoidance of the divers' sounds

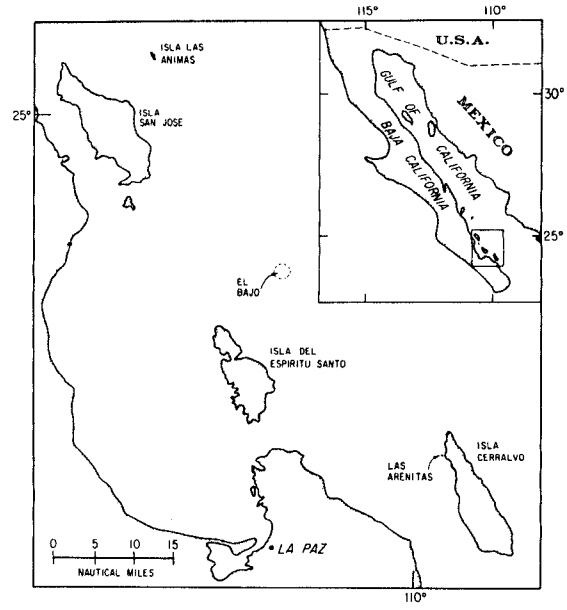

FIGURE 1.—The La Paz study area in the Gulf of California. Grouped scalloped hammerhead sharks were encountered at three sites: 1) Las Arenitas, a cluster of rocks 100 m from Isla Cerralvo; 2) El Bajo Espiritu Santo, a seamount rising to within 14 m of the sea surface; and 3) Isla Las Animas.

and visually conspicuous bubbles. Only three scalloped hammerheads were attracted in 11.5 h of baiting and none during 40 min of sound playback, indicating a lack of interest in these feeding stimuli.

Both individuals and schools of *Sphyrna lewini* were seen. Generally the sharks within schools swam in a polarized manner, remaining relatively equidistant from each other and swimming forward and changing direction together (Figure 2A, B). For the purposes of data sampling, sharks were counted during discrete "observation dives," which usually consisted of free dives, but included some observations from the surface. Scalloped hammerheads were encountered on 91% of the free dives at El Bajo, 58% at Isla Las Animas, and 34% at Las Arenitas Rocks. These percentages are a rough index of relative abundance because they are probably affected by differences in search success and water clarity. School sizes at El Bajo were larger than those at Las Arenitas Rocks and Isla Las Animas, but no large difference existed between group sizes at Las Arenitas Rocks and Isla Las Animas.

The number of scalloped hammerhead sharks in the vicinity of El Bajo was estimated by using the

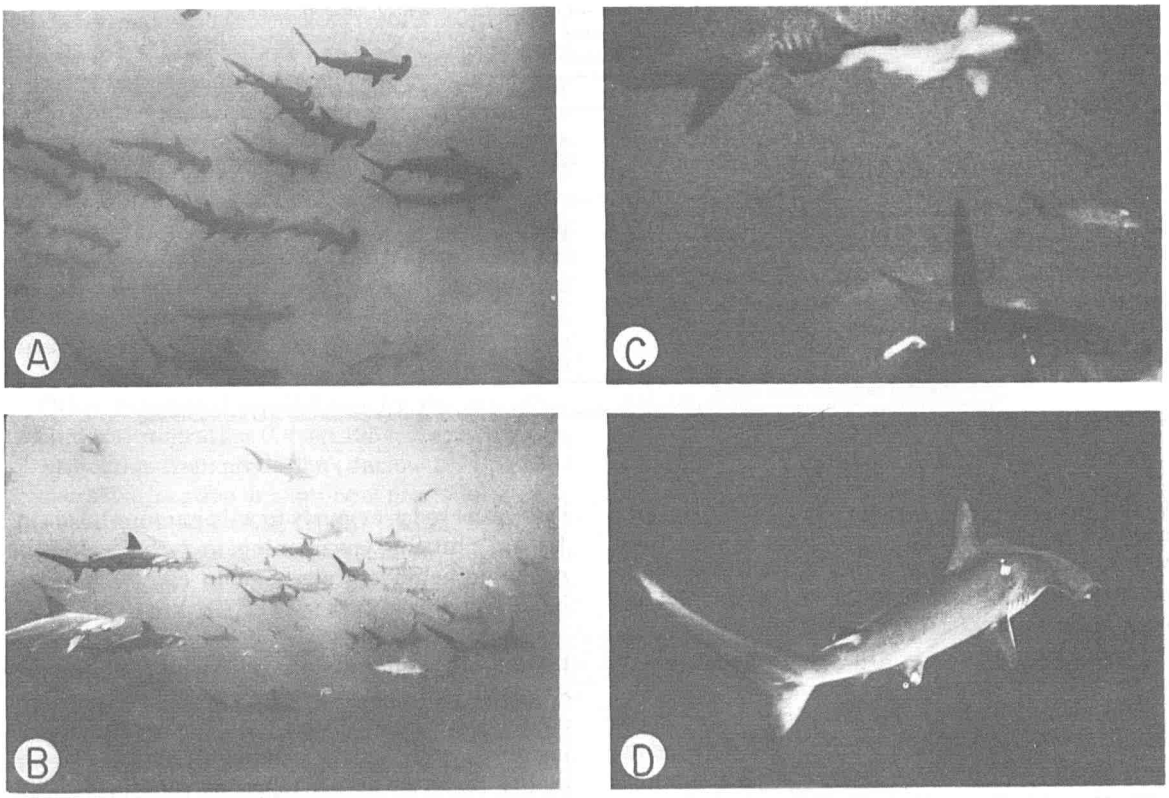

FIGURE 2.—Scalloped hammerhead sharks photographed in the Gulf of California: A. Hammerhead school as viewed obliquely from below. Note leading edge of school, orientation of sharks in same direction, and similar spacing between sharks. B. Side view of school. C. Shark in upper right-hand corner performing headshaking behavior. Note shark with color-coded streamer tag beneath headshaking shark. D. Female hammerhead possessing ellipsoid scar (above last gill slit), possibly inflicted during courtship.

Lincoln Index capture-recapture analysis, modified for observational data. On the morning of 3 August, 21 sharks were tagged with color-coded, plastic-streamer dart tags. Upon spear application of the tags, the sharks often accelerated momentarily, but usually remained within their groups. That afternoon, 9 tagged sharks were observed again within a group of 225, yielding an estimate of 525 sharks in the seamount vicinity (2-4 ha). We feel that this estimate was unbiased because all 21 of the tagged sharks dispersed among various groups after tagging.

We observed groups of 3 to 225 scalloped hammerhead sharks per dive with a mean of 19 (Table 1). Groups of sharks were encountered on 83% of the dives, two sharks on 7%, and single shark on 20% of the dives. Group size varied greatly; this in part reflected the dynamic composition of the groups as sharks left and returned. This was tested by noting the number of sharks associated with a tagged shark when it was reobserved. Tagged sharks (39 were tagged at El Bajo over the study period) were reobserved with varying numbers of accompanying sharks. For example, shark no. 19 was reobserved on four occasions during 135 min on the morning of 6 August with successive groups of 50, 15, 100, and 10 sharks. Such dynamics also were evident to an observer who remained for 120 min above one large group, which varied over that time from 50 to 225 sharks. Subgroups of up to 50 sharks departed and returned to this main group. Groups either appeared to remain at one certain spot (e.g., just upcurrent of the seamount at El Bajo) or repeatedly to follow a path within a relatively small area (ca. 2 ha). At Las Arenitas Rocks a group of ca. 50 scalloped hammerheads repeatedly traveled a particular oblong circuit once each 15 min.

There appeared to be some departures of sharks from El Bajo. Although 16 of the 21 sharks tagged the morning of 4 August were reobserved later

TABLE 1.—School size, depth, shark length, and sex composition of schools of scalloped hammerhead sharks at Las Arenitas Rocks, El Bajo Espiritu Santo, Isla Las Animas, and all locations in the Gulf of California. Numbers in parentheses refer to numbers of observations.

Descriptive categories	Las Arenitas Rocks	El Bajo	Isla Las Animas	All locations pooled
[1]School size, no.:				
Mean (*n*)	12(128)	44(54)	11(43)	19(225)
Maximum	100	225	50	225
[2]Individuals depth, m:				
Minimum	.6	.6	.6	.6
Mean (*n*)	10.1 (114)	10.7 (43)	11.7 (43)	10.4 (200)
Maximum	22.7	22.7	22.7	22.7
Variation around mean	4.3 (6)	8.5 (11)	3.1 (4)	6.7 (21)
Total length, m:				
Minimum	.9	.9	.9	.9
Mean (*n*)	1.6 (39)	1.8 (28)	1.7 (7)	1.7 (74)
Maximum	2.3	3.4	2.4	3.4
Sex ratios:				
Male:female (*n*)	1:1.6 (63)	1:3.8 (84)	1:3.1 (65)	1:2.7 (212)

[1]School defined as three or more sharks.
[2]Individuals' mean and maximum depths based only on observable sharks, since at times (particularly at El Bajo) schooling sharks extended to depths beyond our vision.

that day, only 5 were reobserved 2 d later, despite the fact that an equivalent amount of searching was conducted. The possibility of such migratory or dispersal movements was supported by the occasional observation of single scalloped hammerhead moving slowly at the surface over deep water between islands.

The mean depth of the schooling individuals was 10.4 m with sharks as shallow as 0.6 m and as deep as 22.7 m (Table 1). Depths were estimated with the aid of wrist-worn depth gages. Small groups of sharks were seen swimming close to the sandy or rocky substrate and at times appeared to explore rocky crevices.

The scalloped hammerhead schools were composed of sharks of variable size; both sexes were present in a school, but females were more common (Table 1). The largest individuals, which appeared to be females, often remained at the top of the schools. The sharks at El Bajo were larger than those at Las Arenitas Rocks, but no difference existed between those at El Bajo and Isla Las Animas and at Las Arenitas Rocks and Isla Las Animas. Females were more prevalent at all three sites with male:female ratios ranging from 1:3.8 at El Bajo to 1:1.6 at Las Arenitas Rocks (Table 1).

Within the groups, sharks performed a number of behavior patterns, including the following (in order of decreasing frequency): 1) tilting the body laterally; 2) accelerated swimming with headshaking (Figure 2C); 3) accelerated swimming, dorsal or ventral surface upward, while thrusting the midsection; 4) accelerated corkscrew swimming, rotating 360° around the longitudinal axis; 5) hitting of conspecific with the snout; 6) jaw opening; and 7) clasper flexion. Headshaking has been observed previously in wild hammerheads by Herald[1]; hitting, jaw opening, and clasper flexion resemble behaviors observed in captive bonnethead, *S. tiburo* (Myrberg and Gruber 1974).

Sharks of all sizes and both sexes performed tilting. This generally occurred when a diver was swimming above or behind the shark, perhaps enabling the shark to see the diver better. In one instance, while tilting, a shark flexed his clasper in the direction of an adjacent conspecific. Six males and three females varying from 1.5 to 1.8 m long were observed headshaking. Medium-sized sharks also performed corkscrewing; the sex of the single shark identified was male. Although jaw opening, apparently directed at divers, occurred in sharks outside of groups, headshaking, midsection thrusting, and corkscrewing usually occurred within the group, often at long distances from the diver. On two occasions sharks followed headshaking and corkscrewing by hitting their snouts against adjacent individuals, lateral or anterior to the first dorsal fin.

Many sharks bore abrasions (Figure 2D). These were small, recently inflicted, whitish patches (estimated diameter 4-8 cm), or partially healed black patches. In 21 out of 27 sharks, these were located lateral or anterior to the first dorsal fin, and if two patches were present, at times appeared bilaterally symmetrical. Possessors were predominately female (23 out of 27) and ranged from 1.2 to 2.1 m long ($\bar{x}$ = 1.7 m). These scars may be inflicted by males during mating. Captive, small

[1]Herald, E. The shimmy behavior of the hammerhead shark. Unpubl. manuscr., 4 p. Steinhart Aquarium, San Francisco, Calif., available from authors.

male bonnetheads accelerated from a position just above and behind a large female and scraped her dorsum between the first and second dorsal fins with their heads, often leaving similar scrapes (Myrberg and Gruber 1974). Bite scars, often consisting of a row of teeth marks, are inflicted during courtship in some sharks (Stevens 1974; Klimley 1980). The presence of these scarred females raises the possibility that the scalloped hammerhead schools may have a reproductive function. Grouping for reproduction has been speculated for *Galeorhinus australis* (Olsen 1954) and *Squalus acanthias* (Jensen 1965).

Other functional possibilities for the schooling include: 1) migration (Olsen 1954; Kenney 1968), 2) protection from predation (Barlow 1974), and 3) cooperative location or capture of prey (Coles 1915; Bigelow and Schroeder 1948). Other than the departure of tagged sharks from El Bajo, little evidence for or against the first hypothesis can be marshalled. The second hypothesis seems unlikely due to the absence of known predators. We do, however, have some evidence against the last hypothesis. Feeding was not observed, although scalloped hammerheads were often swimming through large schools of fishes. No feeding responses were directed at baits placed either among or above large numbers of scalloped hammerheads. Although fishing was carried out continuously, only a single male was captured. Feeding readiness was also tested by playing back sounds, attractive to many species of sharks including *Sphryna* sp. (Nelson and Johnson 1972), and baiting immediately after encountering grouped sharks. In 20 min of sound playback and 125 min of baiting, only a single shark was attracted. The phenomenon of grouped hammerhead sharks presents a unique opportunity for the further understanding of shark social behavior, since the sharks are found in sufficiently clear water for observation, shallow enough for free diving, remain in a sufficiently limited area for prolonged observations, and tolerate the approach of divers.

Acknowledgments

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CLEANING SYMBIOSIS BETWEEN TOPSMELT, *ATHERINOPS AFFINIS*, AND GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, IN LAGUNA SAN IGNACIO, BAJA CALIFORNIA SUR, MEXICO

Many species of marine fishes are known to engage in various forms of cleaning symbiosis (Limbaugh 1961; Hobson 1969, 1971). The cleaners, generally small or juvenile fish, remove ectoparasites and necrotic tissue from larger host fish. This promotes the well-being of the host and provides food for the cleaner. Cleaning symbiosis between topsmelt, *Atherinops affinis*, cleaners and gray whale, *Eschrichtius robustus*, hosts was observed during the author's study of breeding gray whales in Laguna San Ignacio, Baja California Sur, Mexico, supported by the United States Marine Mammal Commission, the National Geographic Society, and the World Wildlife Fund-U.S. (Swartz and Jones[1]). Topsmelt are perennial residents of the lagoon and gray whales occupy the lagoon for 3 to 4 mo each winter. As we photographed gray whales from our skiff, schools of topsmelt were seen accompanying the whales and picking at clusters of parasitic barnacles, *Cryptolepas rhachianecti*, and whale lice, *Cyamus* sp., which incrust these cetaceans (Rice and Wolman 1971).

Topsmelt in association with gray whales were collected during the 1978-79 winter with a "mackerel rig" consisting of 1 m of monofilament line with four No. 6 brass hooks spaced 10 cm apart. The standard length (SL) of each fish was measured and its gut contents examined. A second series of topsmelt were collected during the same winter in the absence of gray whales.

The topsmelt ranged from 17 to 29 cm SL. All 38 specimens collected in association with gray whales contained bits of sloughed gray whale epidermis and whale lice appendages. No barnacle appendages or other material was found in these fish. None of 25 topsmelt collected in the absence of whales contained any gray whale epidermis or whale lice; rather they contained bits of filamentous brown algae, *Ectocarpus* sp., and gammarid amphipods.

Topsmelt are described as opportunistic feeders on marine plants, small crustaceans, bryozoans, and hydroids (Frey 1971). During the breeding season of the gray whale, topsmelt in Laguna San Ignacio supplement their diets by cleaning sloughing epidermal tissue and external parasites from gray whale hosts.

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MORPHOLOGICAL FEATURES OF THE OTOLITHS OF THE SAILFISH, *ISTIOPHORUS PLATYPTERUS*, USEFUL IN AGE DETERMINATION[1]

Because of its spectacular runs and leaps, sailfish, *Istiophorus platypterus*, is highly valued by sport fishermen, and the fishery contributes substantially to the economics of coastal regions (de Sylva 1969). However, information on the biology of sail-

[1]Swartz, S. L., and M. L. Jones. 1978. Gray whales, *Eschrichtius robustus*, during the 1977-1978 and 1978-1979 winter seasons in Laguna San Ignacio, Baja California Sur, Mexico. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB-289 737, 35 p.

fish, even though critical to resource management, is limited.

Age estimates and growth rates are necessary to prepare accurate stock statistics. Age determinations in fish are generally indirect measures and are made from length-frequency analyses (Petersen's method) or annual events in hard tissue (Bagenal 1974). The length-frequency method has been applied to sailfish (de Sylva 1957; Koto and Kodama 1962), but the results are inconclusive at best. Annual events recorded in hard tissues are a more accurate method of age determination, and Jolley (1974, 1977) counted the rings in dorsal fin spines to estimate the age of sailfish. The length-frequency data (de Sylva 1957; Koto and Kodama 1962) and proposals of Maksimov (1971) from length-frequency data indicated a rapid growth rate and relatively short lifespan of 3-5 yr for a sailfish. Jolley's (1974) analysis also indicated a rapid growth rate but a possible lifespan of about 10 yr, so at present, age determination in sailfish is unresolved.

Otoliths have been shown to be accurate indicators of age (Bagenal 1974; Six and Horton 1977) and are particularly useful on species of fish which lack scales or have minute scales such as those species in the family Istiophoridae. Otoliths are composed of calcium carbonate in the form of aragonite (Irie 1955; Degens et al. 1969) and are formed in the labyrinth of teleost fish. There are three otoliths (sagitta, lapillus, and asteriscus) on each side of the brain cavity in the inner ear (Lowenstein 1971) and the morphology of these calcified structures is species specific (Hecht 1978; Morrow 1979). The sagitta is usually the largest otolith and the one most often used for age determinations, but the other two otoliths have not been adequately studied and might also be of use. The otoliths of sailfish and other billfishes (families Istiophoridae and Xiphiidae) have been thought to be so small that they would not be useful in age determinations (Jolley 1974; Beckett 1974). Consequently, age and growth data are lacking for these important recreational and commercial species. In this study we analyzed 65 sailfish and described the morphology of the otoliths. A mathematical relationship between the wet weight of the fish and morphological features of the sagitta, enabled us to estimate the age of all but one specimen. Ages of very large fishes, previously difficult to measure, were readily amenable to otolith age analysis.

Methods

Otoliths were collected from sailfish at taxidermy facilities in Florida in fall 1978. Total lengths (TL) and wet weights were recorded from the tags placed on the fish at the dock and otoliths were extracted from 65 fish. The otoliths of sailfish were extremely small and required careful dissection. A saggital cut was made on the midline of the head and the semicircular canals dissected from the brain area. All three otoliths were removed from the semicircular canals and cleaned. Dried otoliths were attached to aluminum stubs; gold-coated otoliths were viewed in a Cambridge Stereroscan Mark 2A[2] scanning electron microscope (SEM).

The internal structure of the sagitta was observed by attaching the sagitta to a SEM stub with 5 min epoxy and fracturing it through the core region. The fractured otoliths were etched for 5 min in 7% ethylenediaminetetraacetic acid (pH 7.4) and then coated with gold before viewing. The lapilli of sailfish were viewed with reflected light microscopy to determine if this would be a viable alternative to SEM preparations.

Results

The morphological nomenclature we use to describe sagitta is that of Hecht (1978) and Morrow (1979). The otoliths are extremely small, from 0.75 to 1.5 mm long. The medial or concave surface (Figure 1) has a deep and well-defined sulcus and the depth of the sulcus increased with fish weight. The sagitta has no collum and lacks anterior and posterior cristae. The excisural notches are distinct and V-shaped and have two lobes which fold onto each other. The antirostrum is one-third as long as the rostrum and well separated from the rostrum. Consequently sagitta had a different configuration from most sagitta, as the rostrum is exaggerated. The surface of the concave portion of the sagitta is granular with crystalline palisade configurations.

There are distinct ridges on the side of the rostral lobe (Figure 2) which we interpret as annual events, as there is an increase in ridge number with weight (Figure 3). The sagitta of a sailfish

[1]Contribution No. 397 of the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina.

[2]Reference to trade names doesnot imply endorsement by the National Marine Fisheries Service, NOAA.

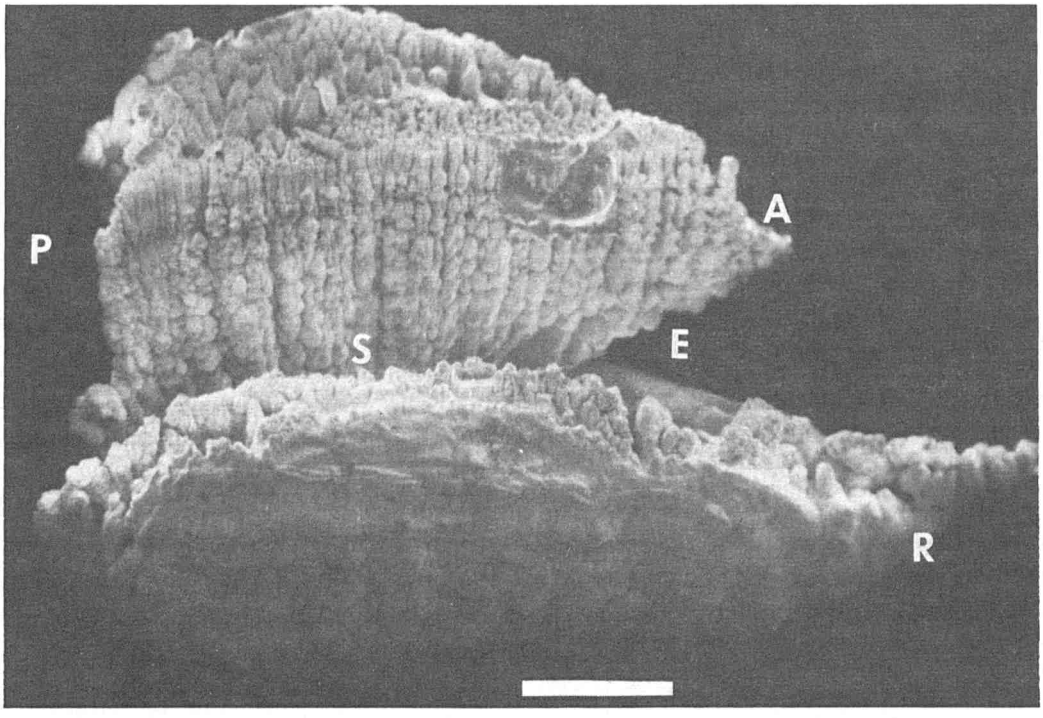

FIGURE 1.—The concave medial surface of the left sagitta from a sailfish that weighed 27.7 kg (18×): A, Antirostrum; E, Excisural notch; S, Sulcus; P, Posterior. Bar = 0.5 mm.

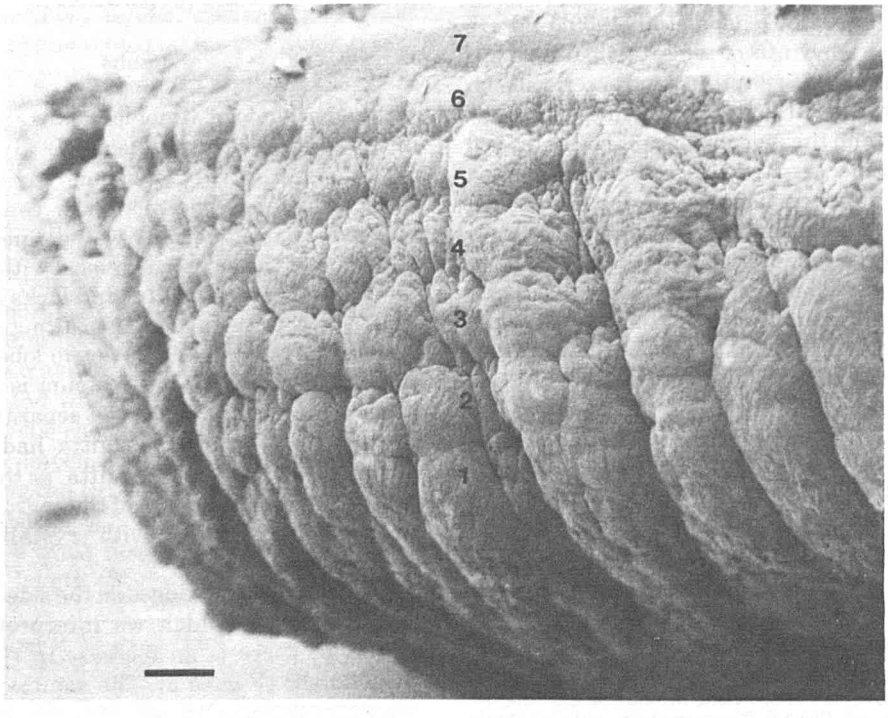

FIGURE 2.—Rostral lobe of the left sagitta of a 27.7 kg sailfish (60×). Numbers indicate ridges. Bar = 0.1 mm.

that weighed 27.7 kg and was 226 cm TL had 7 ridges (Figure 2), while the sagitta of a sailfish that weighed 12.7 kg and was 183 cm TL had 3 ridges (Figure 4). These ridges are distinctive and easily counted, and of a sample of 65 sailfish only 1 specimen had uncountable ridges on both sagittae.

The convex or lateral surface of the sagitta (Figure 5) was moderately smooth and the two lobes were joined in the core region. The convex surface did not have the distinctive configuration seen on the side of the rostral lobe. A medial section of the sagitta revealed internal structures which indicated incremental otolith growth and progressive deposition (Figure 6).

The asteriscus and lapillus (Figure 7) are much smaller than the sagitta and also show internal features that appear to have progressive deposition. The asteriscus is very fragile and was often broken during dissection, but its growth features support the sagittal ridge counts. The lapillus was much heavier in structure than the asteriscus and also showed internal growth features that appear to be age related (Figure 8). The lapillus showed layers that correspond to the number of ridges found on the sagitta when viewed under transmitted light (Figure 9). The lapilli age counts were identical to sagittal ridge counts 85% of the time and ±1 yr in the other counts. The possibility exists that age estimates could be obtained by light microscope techniques, although the sagittal

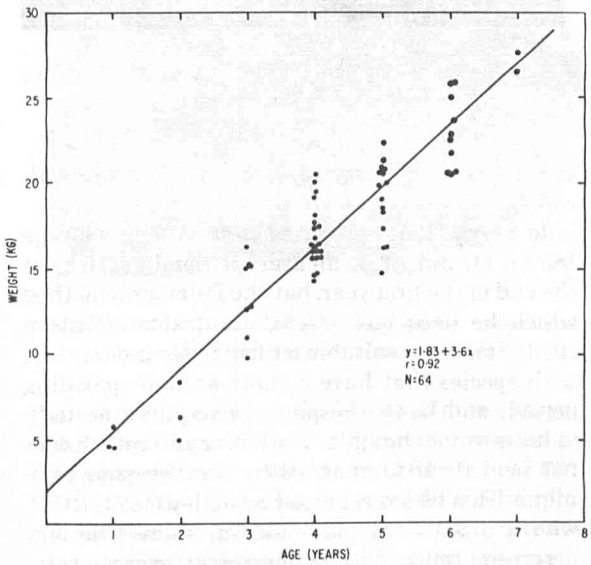

FIGURE 3.—Relationship between the weight of the sailfish and the number of ridges (years) on the sagitta.

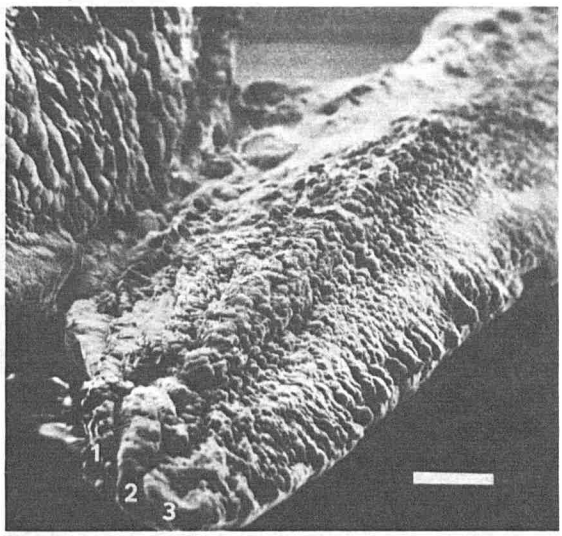

FIGURE 4.—The rostral lobe of the left sagitta from a 12.7 kg sailfish with three ridges (85×). Numbers indicate ridges. Bar = 0.1 mm.

ridges were very distinct in SEM preparations which we feel would be more accurate.

The ridges on the sagitta of 64 sailfish were counted and compared with body weight and a strong correlation was found (Figure 3). The ridges appear to be annual events and fish with four ridges were the most numerous in our sample. We did a log transformation of the allometric growth curve equation or power curve fit of the data (Table 1) so we could compare our data directly with that of Jolley (1977) for which summary statistics only are available. The data used for statistical analysis were selected from the Jolley (1977) regressions. An F-test for difference between the regression coefficients gave $P>0.05$, so there is no apparent difference between the slopes of Jolley's data and ours. The data indicate that the sailfish develop a large muscle mass in a short period of time (<4 yr), and our results are similar to Jolley's over the same time span.

TABLE 1.—Age-weight relationships ($Y = \alpha x^b$) for the Atlantic sailfish as expressed by predictive power equations, $\log_{10}$ transformed for purposes of testing difference in regression coefficients between the data presented in this paper and those of Jolley (1977).

Source	N	Regression coefficient	Y-intercept	r	P (F-test)
Present study	64	0.883	4.64	0.86	>0.05
Jolley (1977):					
Males	74	.888	1.48	.85	>0.05
Females	73	1.048	1.33	.88	>0.05

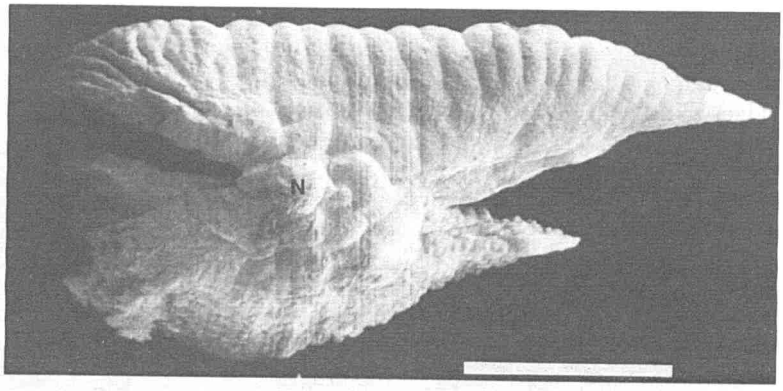

FIGURE 5.—The convex distal surface of the left sagitta of a 27.7 kg sailfish; N indicates nuclear (core) region (18×). Bar = 1 mm.

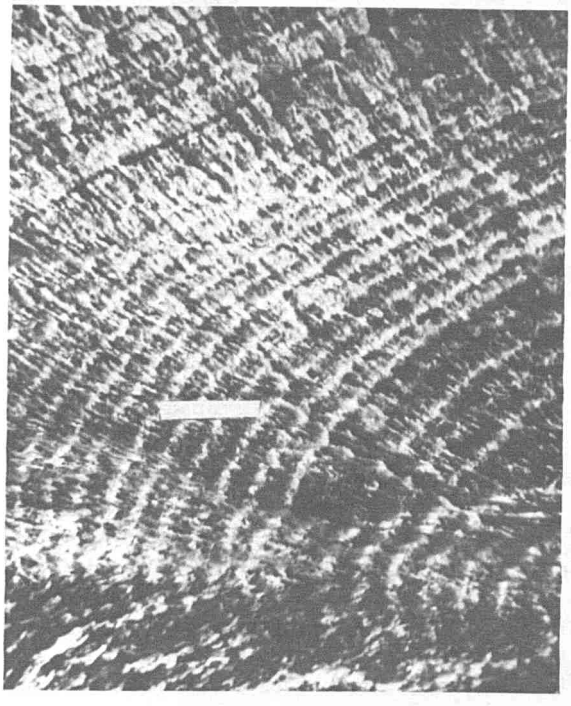

FIGURE 6.—Cross section of the rostral lobe of a sailfish sagitta that shows incremental growth in the internal structure (1,100×). Bar = 10 μm.

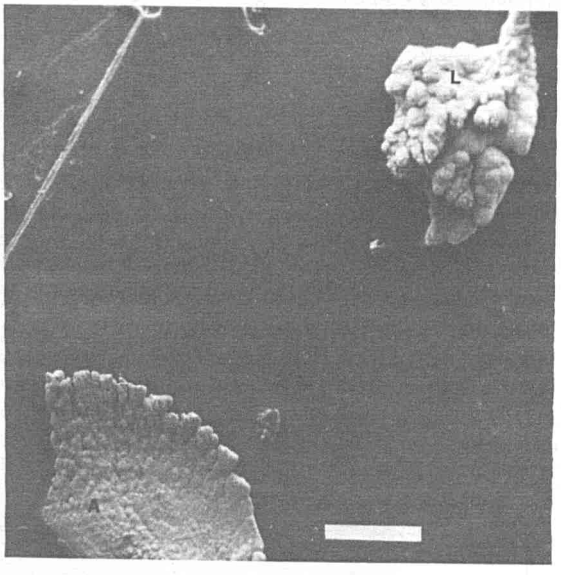

FIGURE 7.—The left lapillus (L) and asteriscus (A) of a 27.7 kg sailfish (18×). Bar = 0.5 mm.

Discussion

The otoliths from sailfish are very small in relation to the size of the fish and appear to be unique, as their prominent ridges on the rostral lobe are different from the morphology of other teleost otoliths. For comparison of morphological features, excellent surveys of otoliths from a broad range of families and geographic areas are found in Hecht (1978) and Morrow (1979). The external ridge feature makes it possible to use the sagitta of the sailfish for determination of age and growth rates.

de Sylva (1957) proposed that sailfish average 183 cm TL and attain an average weight of 10 kg at the end of the first year, but the Petersen's method which he used has several limitations (Watson 1964). It is most suitable for fish in their early life, with species that have a short annual spawning period, and large samples are required as individuals cannot be aged. The biology of sailfish does not lend itself to analysis by the Petersen technique. This was recognized by Jolley (1974, 1977), who utilized hard parts (dorsal spines) for age determinations. Our estimates of growth rates and age estimates are similar to his. However, Jolley (1977) found that only 24% of the samples

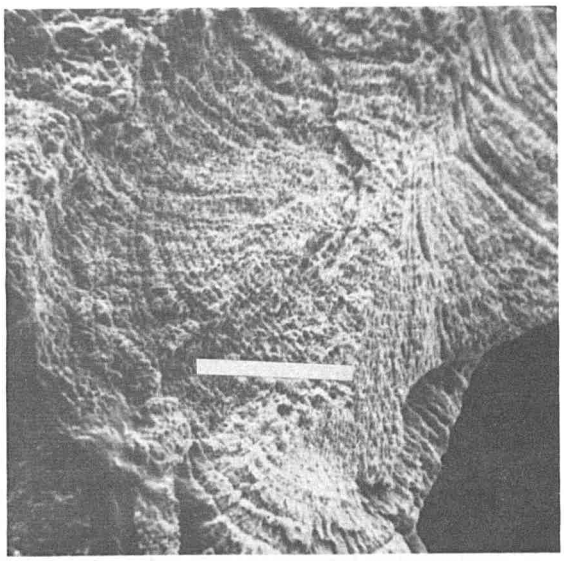

FIGURE 8.—The internal structure of the lapillus of a 20.5 kg sailfish (400×). Bar = 50 μm.

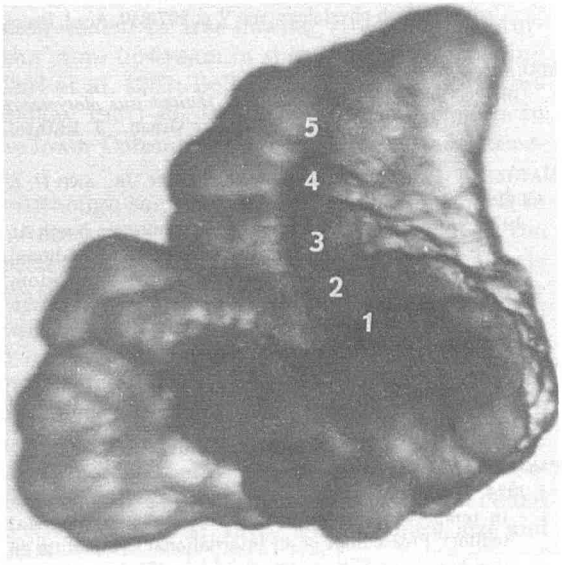

FIGURE 9.—The lapillus of a 20.5 kg sailfish viewed under transmitted light. Five layers are shown (40×).

he examined could be aged by the spine analysis, and it was particularly difficult for him to age larger specimens, while we read 64 of 65, or 98%, of the otoliths. Our percentage might be lower for a larger sample or older fish, but an age estimate was usually possible from one of the two sagitta present in the fish. We did not find it difficult to resolve the age of our largest specimens.

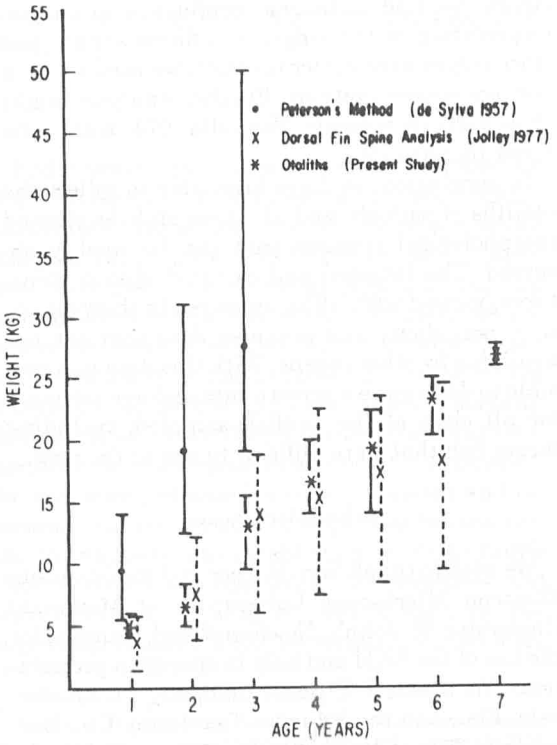

FIGURE 10.—Comparison of relationships between the mean weight of sailfish and estimated age. Bars represent ranges.

The age-weight relationship developed in our study from otoliths, and by Jolley (1977) from analysis of dorsal fin spines (Figure 10) indicates that weight attained at ages 1 through 3 are about 50% less than those estimated by de Sylva (1957) and Koto and Kodama (1962). Tag data (Mather et al. 1974) are inconclusive due to the small number of returns. Our two largest specimens (estimated age 7) weighed 26.4 and 27.7 kg and were 228.6 and 226.1 cm TL. This is similar to Jolley's largest fish of 26 kg at our equivalent age 6, but his larger fish could not be aged with the fin spine method.

Sailfish are multiple spawners (Jolley 1977), which could account for the range of weights in the different age-groups. A study of internal patterns in otoliths might make it possible to determine when an individual fish spawned. The internal microstructure could be a permanent calendar of the physiological history of the fish. Further study on the micromorphology and internal structure of the otolith should reveal valuable information. The internal increments occurred at a frequency of 13 or 14 increments in each major assemblage which could be evidence of a lunar periodicity.

Hence, we had additional confidence in our interpretation of the ridges as annual events and since ridges were easier to count, we used them in our age determinations. Further analysis might show daily increments (Pannella 1974) within the lunar increments.

In conclusion, we have been able to collect the otoliths of sailfish, and all three otoliths showed morphological features that can be readily observed. The internal and external otolith structures, viewed with SEM, appeared to show an annual periodicity and provided data that are not available by other means. With this data it is possible to determine a growth rate and age estimate for all sizes of the sailfish sampled, including larger fish that were difficult to age in the past.

Acknowledgments

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DIEL AND SEASONAL MOVEMENTS OF WHITE STURGEON, *ACIPENSER TRANSMONTANUS*, IN THE MID-COLUMBIA RIVER

The white sturgeon, *Acipenser transmontanus*, is a commercial and sport fish common to major river systems of the Pacific Coast from Monterey, Calif., to Alaska (Scott and Crossman 1973). However, there is considerable confusion concerning migration habits or seasonal movements of the species. Early workers (Jordan and Evermann 1908; Craig and Hacker 1940) considered white sturgeon anadromous. In free-flowing rivers, white sturgeon move upstream in spring prior to spawning (Carl et al. 1967; Bell 1973). Other investigators (Bajkov 1951) suggested seasonal movements in the lower Columbia River may be related to feeding.

Although some white sturgeon can be found in the ocean and may ascend rivers to spawn, the species is not truly anadromous. Many individuals remain in freshwater, and those found in the upper Columbia River and its tributaries are landlocked by a system of hydroelectric dams. However, permanent freshwater residents also show seasonal movements. Studies in 1975 and 1976, involving radio-tagged white sturgeon in the mid-Columbia River, indicated sturgeon movements >2 km occurred when river temperatures exceeded 13° C (Haynes et al. 1978). Furthermore, size and possibly sexual maturity influenced direction of movement in the river. Smaller white sturgeon moved downstream in summer, larger sturgeon moved upstream in summer and fall, and intermediate-sized sturgeon remained near release points. Although seasonal movements may be related to water temperature, no quantitative data exist on diel activity patterns of the species. To further evaluate seasonal movements in the free-flowing Hanford reach of the Columbia River, we fitted additional white sturgeon with radio transmitters in spring and early summer 1977 and continued monitoring fish which had been tagged in 1975 and 1976.

Methods

Radio-telemetry equipment was developed by the University of Minnesota, Bioelectronics Laboratory (Tester and Siniff[1]). Nineteen white sturgeon ranging from 98 to 236 cm total length were captured with trammel nets and angling gear at White Bluffs Pool (Figure 1), about 48 km upstream from Richland, Wash. Transmitters were selected so as not to exceed 2% of estimated sturgeon body weight and were attached dorsally (Haynes et al. 1978). Twelve transmitters had temperature sensors (precision ±0.2° C, Kuechle[2]). An automatic, channel-scanning receiver and recording station, capable of sequentially monitoring 16 channels, was established at White Bluffs Pool to record environmental temperatures and sturgeon movements in and out of the pool. Receivers operated on a carrier frequency of 53 MHz

[1]Tester, J. R., and D. B. Siniff. 1976. Vertebrate behavior and ecology progress report for period July 1, 1975-June 30, 1976. COO-1332-123. Prepared for U.S. Energy Research and Development Administration. Contract No. E(11-1)-1332 by Univ. Minn., Minneapolis, 63 p.

[2]V. B. Kuechle, Bioelectronics Laboratory at Cedar Creek, University of Minnesota, Minneapolis, pers. commun. 1977.

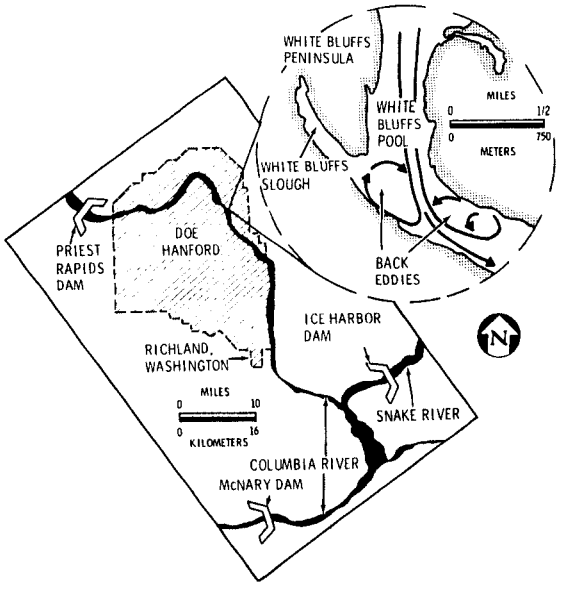

FIGURE 1.—White Bluffs monitoring area for white sturgeon movements in the Columbia River.

and were capable of distinguishing 100 discrete crystal-tuned transmitters. Sturgeon, including those radio-tagged in 1975 and 1976 (Haynes et al. 1978), were located once or twice per week with boat- and truck-mounted receiver gear. On several occasions, sturgeon locations were monitored manually over a 24-h period.

During the summer we measured Columbia River temperatures at numerous midchannel locations from Priest Rapids Dam to Richland, 95 km downstream (Figure 1). On these occasions river temperatures only varied about 1° C. Therefore, mean river temperatures (standard deviation = 0.5° C/d) during the study were calculated from 12 temperature readings taken daily at Priest Rapids Dam. Daily mean river temperatures were averaged weekly. Main current temperatures in White Bluffs Pool were monitored by a reference temperature transmitter in the pool and were also measured while tracking fish.

Analysis of variance was used to compare mean sturgeon environmental temperatures in six time periods (0200-0600, 0600-1000, 1000-1400, 1400-1800, 1800-2200, and 2200-0200 h) with the weekly mean river temperature from 19 June to 20 August 1977. Differences between sturgeon environmental temperatures and weekly average river temperatures were experimental units within each time period. Honest significant difference (HSD) tests (Snedecor and Cochran 1972) were used to establish which periods differed.

White Bluffs Pool is 1.5 km long and has three distinct habitats (Figure 1). Most of the pool is part of the deep, swiftly flowing main current of the Columbia River and has a rock bottom. A deep, slow-moving back eddy with a sandy bottom lies off the tip of White Bluffs Peninsula. White Bluffs Slough has a mud and rock bottom and extends 1 km upstream along the peninsula. The pool ranges in depth from 1 m in the slough to 20 m in midpool, and the main current is well mixed (Gray et al.[3]; Page et al.[4]). However, underground spring seepage areas, common in the region, are 1°-5° C lower, and slough areas are 2°-5° C higher, than mixed main currents in summer (Haynes 1978).

[3]Gray, R. H., T. L. Page, and E. G. Wolf. 1976. Report on aquatic ecological studies near WNP-1, 2, 4, Sept. 1974-Sept. 1975. WPPSS Columbia River ecology studies, Vol. 2, 115 p. Battelle, Pac. Northwest Lab., Richland, Wash.

[4]Page, T. L., R. H. Gray, E. G. Wolf, and M. J. Schneider. 1976. Final report on aquatic ecological studies conducted at the Hanford Generating Project 1973-74. WPPSS Columbia River ecology studies, Vol. 1, 206 p. Battelle, Pac. Northwest Lab., Richland, Wash.

Results and Discussion

Main current temperatures in White Bluffs Pool averaged within 0.5° C of Priest Rapids Dam temperatures and weekly standard deviations averaged 0.3° C throughout 1977. Therefore, deviations in daily and weekly midriver temperatures were small relative to temperature differences in spring seepage and slough areas in summer. Throughout the summer of 1977, individual sturgeon with temperature transmitters engaged in movements that often resulted in a 2°-4° C daily change in recorded temperature. The analysis of sturgeon environmental temperatures versus weekly average river temperatures during certain periods of the day (Table 1) indicated significant differences ($P<0.001$). Because deviations in main river temperatures were 8-25% less within and between days than changes in sturgeon environmental temperatures, recorded temperature changes indicated sturgeon moved into areas of differing environmental temperatures. Position determinations confirmed these movements and indicated sturgeon generally occupied midchannel areas from early morning until midafternoon. Movements into nearshore and slough areas were observed in late afternoon and evening.

During summer 1977 from 0200 to 1000 h, sturgeon environmental temperatures (Figure 2) were somewhat, but not significantly, lower (−0.35° C) than weekly average river temperatures, suggesting presence in deeper, and possibly spring-fed areas. During 1400-2200 h, sturgeon environmental temperatures were significantly ($P<0.05$ by HSD) higher (0.85° C) than the weekly average river temperature, indicating presence in warmer, shallow slough areas. During 1000-1400 h and 2200-0200 h, sturgeon environmental temperatures were somewhat higher (0.32° C) than the weekly average, suggesting transition periods when sturgeon moved between inshore and midchannel areas.

Although changes in sturgeon environmental temperatures documented movements among

TABLE 1.—Analysis of variance on differences in mean sturgeon environmental temperatures in six daily time periods (0200-0600, 0600-1000, 1000-1400, 1400-1800, 1800-2200, and 2200-0200 h).

Source	df	SS	MS	F
Among time periods (diel)	5	164.67	32.93	47.7**
Within time periods	701	485.28	0.69	
Total	706	649.95		

**$P<0.001$.

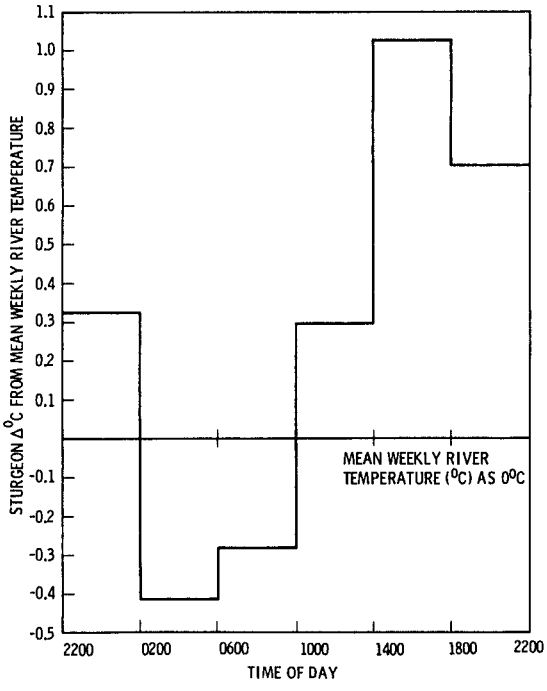

FIGURE 2.—Mean sturgeon environmental temperature deviation (Δ° C) from mean weekly Columbia River temperatures averaged over 4-h periods within the diel cycle, from 19 June through 20 August 1977.

habitats, we do not believe temperature differences in White Bluffs Pool caused diel sturgeon movements. Rather, diel movements are probably influenced by light. Movement to cool, deep areas occurred prior to sunrise and movement to warm, shallow areas peaked after sunset. Sturgeon were sensitive to light when captured for tagging and remained active until a towel was placed over their eyes. Bait angling for sturgeon was most successful during sunset and sunrise, and netting near shore was most productive at night. Evening movements to back eddy and slough areas of White Bluffs Pool, where benthic organisms and smaller fish are more abundant, may be related to feeding.

Sturgeon are bottom feeders and in freshwater reportedly eat crustaceans (*Daphnia* and copepods), molluscs (clams and snails), insect larvae (chironomids, stone flies, and ephemeropterans), and fish (Bajkov 1949; Semakula and Larkin 1968). Sturgeon in the mid-Columbia River at Hanford ingest crayfish, fish (including whitefish, suckers, and sculpins), midge and caddis fly larvae, snails, and periphyton (Gray et al. footenote 3; Page et al. footnote 4).

Daily environmental temperature records indicated sturgeon did not consistently engage in a diel movement pattern. Sturgeon sometimes spent one or more days in cooler, midchannel areas. Occasionally, sturgeon remained near inshore areas through midday, although variability within and among fish was common.

Haynes et al. (1978) suggested long-distance sturgeon movements in the mid-Columbia River were related to temperature. Data collected in 1977 confirm these observations. Sturgeon movements >2 km up- or downriver began in early summer when river temperature rose to 13° C and ended in fall when temperature dropped below 13° C (Figure 3).

The possibility that photoperiod plays a role in initiation of long-distance movement and termination of movement appears unlikely. Pacific Northwest drought conditions in 1977 resulted in extremely low Columbia River flows and higher-than-normal water temperatures. River temperatures in 1977 did not drop below 13° C until early November, and sturgeon movements continued throughout. In previous years, river temperatures

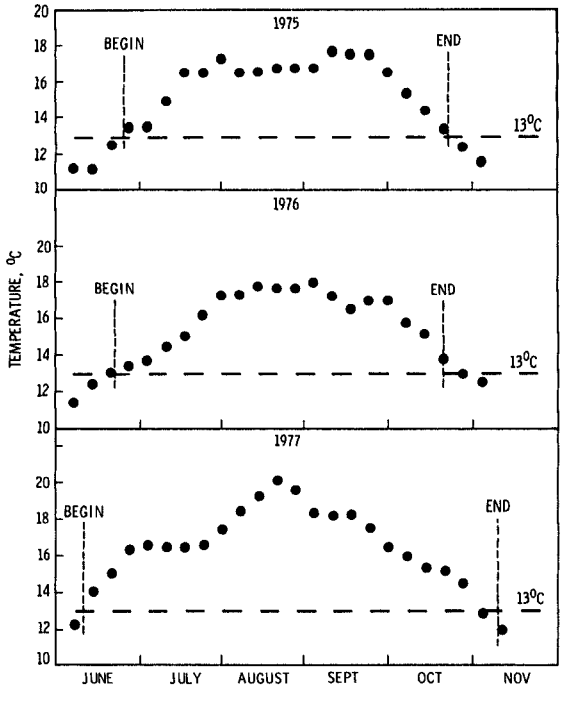

FIGURE 3.—Beginning and end of sturgeon movement (>2 km up- or downstream from release site) versus weekly average Columbia River temperatures in 1975 and 1976 (derived from Haynes et al. 1978) and 1977.

declined below 13° C and sturgeon movements ceased by mid-October. If photoperiod were involved, sturgeon movements in 1977 should have stopped at about the same time as they did in 1975 and 1976. Complete cessation of movement >0.5 km in autumn may be related to cold-induced inactivity.

Linear regression analyses comparing distances moved by sturgeon with river flows at Priest Rapids Dam produced scatter diagrams with regression coefficients approaching zero. In contrast to results of studies in the Snake River, Idaho (Coon et al.[5]), river flow apparently had no influence on long-distance sturgeon movements in the Columbia River at Hanford.

The complex interaction of water temperature, light cycle, feeding, urge to spawn, and other factors undoubtedly influence sturgeon movements in the mid-Columbia River. Although temperature is a major influence stimulating seasonal movements, light cycle and feeding probably influence diel movements.

Acknowledgments

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FEEDING PERIODICITY AND DIEL VARIATION IN DIET COMPOSITION OF SUBYEARLING COHO SALMON, *ONCORHYNCHUS KISUTCH*, AND STEELHEAD, *SALMO GAIRDNERI*, IN A SMALL STREAM DURING SUMMER

Throughout their native range in northwestern North America, juvenile coho salmon, *Oncorhynchus kisutch*, and steelhead, *Salmo gairdneri*, occur sympatrically in streams (Milne 1948). In these instances, social interaction between the two species leads to spatial segregation during the spring and summer, with coho salmon generally occupying pools and steelhead riffles (Hartman 1965; Allee 1974). A recent investigation of naturalized populations in the Great Lakes region has observed similar patterns of spatial segregation (Johnson and Ringler 1980).

It is generally accepted that social interaction among closely related fish species may lead to interactive segregation, with each species segre-

gating into a habitat which it is best suited to exploit (e.g., Nilsson 1967). In this respect, interactive segregation of juvenile coho salmon and steelhead enables the surface and drift forager, coho salmon, to inhabit pools and the more bottom-oriented steelhead to occupy riffles. Johnson and Ringler (1980) pointed out that in sympatry with coho salmon, steelhead are found in areas (riffles) where the standing crop of benthic invertebrates is the greatest, an obvious advantage in conjunction with their benthic habits. Conversely, coho salmon which feed predominantly from the drift presumably have a relatively long time interval in which to observe drifting prey because of decreased water velocities in pools.

Johnson and Ringler (1980) demonstrated that in sympatry the diet of subyearling coho salmon was closely associated with the composition of the drift, and the diet of subyearling steelhead was more closely associated with the bottom fauna. They found a low degree of overlap in the diurnal summer diet of coho salmon and steelhead due to the utilization of drifting terrestrial invertebrates by coho salmon and benthic invertebrates by steelhead. They speculated that since the composition of invertebrates on or within the substratum of a stream is much more stable over a 24-h period than the composition of the invertebrates drifting over it, that the diet of the drift feeder (coho salmon) would be more variable than the diet of the benthic forager (steelhead) over a 24-h period. The purpose of this study was to test this hypothesis while also gathering information sufficient to determine diel feeding periodicity, daily meal, and daily ration of juvenile coho salmon and steelhead.

Methods

Subyearling coho salmon and steelhead were collected from a 200 m section of Orwell Brook, Oswego County, N.Y. The stream discharges into the Salmon River which empties into Mexico Bay in the southeastern portion of Lake Ontario. Orwell Brook is a high quality spawning and nursery stream for salmonids migrating from Lake Ontario (Johnson 1980). The 200 m stream section generally consisted of a series of pools, runs, and riffles. The surface substrate consisted of gravel and pebbles. Maximum and minimum water temperatures recorded during the study period were 21° C at 1600 h (31° C air temperature) and 16° C at 0400 h (17° C air temperature).

The study was carried out in July 1979 since previous studies had shown that subyearling coho salmon and steelhead are most abundant in Orwell Brook at this time (Johnson 1980). Maximum numbers of coho salmon and steelhead in the stream were desired in order to facilitate collections and to prevent depletion of the populations of each species. Fish were collected at 4-h intervals commencing at 0800 h on 13 July and ending at 0400 h on 14 July 1979. During the study period sunrise occurred at 0436 h and sunset at 1943 h e.s.t. A minimum of 20 individuals of each species on 13 July 1979 was collected during each 4-h interval. Fish were collected with a 3 m seine, slit, and immediately placed in 10% Formalin[1] in order to halt digestive processes. Prior to the removal of their digestive tracts all fish were weighed (grams) and measured (millimeters total length, TL). Correction factors were used to account for weight gain and length shrinkage caused by preservation (Parker 1963; Stauffer[2]). Dietary items were identified to the family level for aquatic invertebrates and to the ordinal level for terrestrial invertebrates.

Dry weight estimates were obtained for individuals of each family of aquatic prey and each order of terrestrial prey (invertebrate taxa which had no life state occurring in the aquatic environment) to determine the relative contribution of food organisms in the fishes' diet. A representative number of individuals of each prey taxa (usually 10) were used to derive a dry weight estimate. Food items were placed in small preweighed pans and then dried at 105° C for 24 h. The pans were then placed in a desiccator for 6 h, and reweighed. The dry weight of the organisms in the pan was divided by the number of individuals in the pan giving an average dry weight estimate of an individual of that taxa. Dry weight determinations were used to estimate diet composition for both coho salmon and steelhead for each 4-h interval. In addition, dry weight estimates for each taxon were summed for the 24-h period to derive an estimate of diel diet composition.

To examine diel patterns of food consumption of both coho salmon and steelhead the total dry weight of the stomach contents per dry weight of

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

[2]Stauffer, T. M. 1971. Salmon eggs as food for stream salmonids and sculpins. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1776, 10 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

the fish was plotted for each 4-h interval. Dry weight estimates for each fish were based on the entire carcass. These estimates were derived experimentally using a dry weight to wet weight conversion (21.1%) based on the combined results of 15 individuals of each species.

Daily meal and daily ration of subyearling coho salmon and steelhead were determined by summing interval values for the 24-h period. The amount of food consumed at each 4-h interval, was estimated from the Elliott and Persson (1978) formula:

$$C_t = \frac{(S_t - S_0 e^{-R_t})R_t}{1 - e^{-R_t}}$$

where C_t = amount of food consumed in t hours
S_t = mean stomach contents at the end of the interval
S_0 = mean stomach contents at the beginning of the interval
R = exponential rate of gastric evacuation in t hours.

Estimates of R were derived using available information for subyearling rainbow trout (Windell et al. 1976).

Variability in the diet of coho salmon and steelhead over the 24-h period, and diet similarity between coho salmon and steelhead between sampling periods spaced 4 h apart were examined using the overlap formula of Morisita (1959) modified by Horn (1966):

$$C_\lambda = \frac{2 \sum_{i=1}^{s} X_i \cdot Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where C_λ = overlap coefficient
s = food categories
X_i = proportion of the total diet of fish species X contributed by food category i
Y_i = proportion of the total diet of fish species Y contributed by food category i.

C_λ can range from 0, when samples contain no food in common, to 1, when there is identical representation of food between samples.

Results

A total of 130 coho salmon and 142 steelhead were examined for diet composition and feeding periodicity (Table 1). Subyearling coho salmon which emerge approximately 6 wk earlier than subyearling steelhead were substantially larger at the time of collection. Terrestrial invertebrates were the major components (51.3-62.3%) in the diurnal diet of coho salmon fry, whereas aquatic invertebrates were the major prey utilized at night (89.5-96.9%) (Table 2). Predation on terrestrial invertebrates was greatest between 1600 and 2000 h and greatest on benthic invertebrates between 2000 and 2400 h. Of the aquatic taxa immature chironomids were the most important item (17.1%) during the 24-h period although some diel variation in importance is suggested. Other less important aquatic items include adult chironomids (7.7%), caenid (7.0%), and leptophlebiid (6.8%) mayfly nymphs along with hydropsychid caddisfly larvae (6.0%). Homopterans (6.5%), dipterans (5.4%), and coleopterans (4.8%) were the major terrestrial invertebrates consumed. Overall, aquatic invertebrates composed 74.7% and terrestrial invertebrates 25.3% of the diel diet of coho salmon (Table 2).

Aquatic invertebrates were the principal food of subyearling steelhead throughout the 24-h period (Table 2). Although steelhead did not utilize terrestrial invertebrates to the extent that coho salmon did during diurnal feeding, temporal patterns in the consumption of terrestrial prey were

TABLE 1.—Number examined, mean total length (millimeters ± 95% confidence limits), mean dry weight of fish (gram) and stomach contents (milligrams), and C_λ of subyearling coho salmon and steelhead. Data are from sampling intervals spaced 4 h apart, 13-14 July 1979, in Orwell Brook, N.Y.

	Coho salmon					Steelhead			
Time	Number	Length	Weight	Stomach contents	C_λ	Number	Length	Weight	Stomach contents
0800	20	70.9±4.1	0.63	1.83	0.70	24	49.7±2.7	0.23	1.40
1200	25	66.1±5.7	.53	2.01	.53	20	55.2±2.6	.32	1.66
1600	20	62.5±5.1	.45	.90	.42	28	53.7±1.6	.30	2.58
2000	21	71.0±3.5	.68	2.65	.64	24	55.1±2.5	.32	4.26
2400	22	68.4±3.9	.58	5.80	.82	24	51.1±2.4	.25	1.45
0400	22	64.4±4.6	.49	3.77	.91	22	49.0±2.8	.22	1.08

TABLE 2.—Percentage dry weight dietary composition of subyearling coho salmon and steelhead sampled at 4-h intervals over a 24-h period, 13-14 July 1979, in Orwell Brook, N.Y.

	Coho salmon							Steelhead						
Taxon	0400	0800	1200	1600	2000	2400	24-h total	0400	0800	1200	1600	2000	2400	24-h total
Oligochaeta	—	—	—	—	—	—	—	0.21	0.70	0.25	0.15	—	—	0.19
Ostracoda	—	—	—	—	—	—	—	—	.08	—	—	—	—	.01
Hydracarina	0.05	0.92	0.48	1.59	0.32	0.07	0.31	.27	.58	.16	.67	0.59	0.55	.52
Collembola	.06	—	.56	—	.09	—	.09	1.41	.14	.67	.10	.18	—	.29
Plecoptera:														
Chloroperlidae	.88	—	—	—	—	—	.20	1.53	—	—	—	—	—	.10
Leuctridae	4.64	6.28	—	—	—	2.46	2.62	4.12	—	—	1.24	—	1.13	.69
Perlidae	5.06	—	—	—	6.24	8.28	3.23	2.02	3.82	—	6.19	.36	.60	2.30
Unidentified	.05	—	1.96	1.25	—	.15	.33	—	1.01	1.08	—	.84	—	.54
Ephemeroptera:														
Baetidae	3.95	3.88	.81	—	.55	3.50	2.77	9.69	11.27	16.11	12.30	6.53	8.31	9.93
Caenidae	.25	1.74	.28	—	—	18.10	7.03	11.01	5.04	10.46	5.21	2.48	5.88	5.35
Ephemerellidae	2.27	3.13	—	—	—	4.38	2.47	1.19	1.39	—	1.60	.83	6.30	1.63
Ephemeridae	—	—	.98	—	—	3.88	1.55	—	—	—	—	—	—	—
Heptageniidae	.27	.29	—	2.24	—	2.71	1.21	2.94	—	—	—	—	2.99	.57
Leptophlebiidae	7.53	.47	1.15	—	—	13.33	6.83	4.00	1.31	1.89	2.00	1.18	1.94	1.75
Unidentified	1.65	.89	23.32	1.99	7.42	—	4.22	—	6.59	9.62	15.52	2.50	.77	6.30
Odonata:														
Aeshnidae	—	—	—	—	—	.54	.20	—	—	—	—	—	—	—
Trichoptera:														
Glossosmatidae	.16	.58	.14	—	—	.23	.19	—	—	—	1.76	.92	2.04	.95
Helicopsychidae	—	—	—	—	.26	—	.04	.59	—	—	—	.28	—	.14
Hydropsychidae	11.77	1.77	5.60	—	.72	6.55	5.98	4.12	5.37	2.60	.71	.66	15.91	3.51
Odontoceridae	—	—	—	—	—	—	—	2.10	—	—	1.53	—	1.06	.61
Philopotamidae	2.93	—	—	—	—	.27	.76	—	—	—	—	—	—	—
Polycentropodidae	.41	—	—	—	—	—	.09	—	—	—	.23	—	—	.05
Unidentified	4.76	8.35	2.52	—	2.81	2.64	3.66	2.24	.30	—	2.48	2.32	3.80	2.30
Hemiptera:														
Velliidae	.41	—	—	—	—	—	.10	—	—	—	—	—	—	—
Megaloptera:														
Sialidae	—	1.66	—	—	—	.12	.22	—	.20	—	—	—	—	.02
Coleoptera:														
Dytiscidae	.49	—	—	2.49	1.12	—	.41	—	—	—	—	—	—	—
Elmidae	.76	.80	—	2.12	—	1.36	.86	—	1.09	—	—	—	2.06	.37
Psephenidae	.37	4.39	—	—	—	.70	.81	—	1.22	.84	.63	.48	3.70	.99
Diptera:														
Ceratopogonidae	.10	.39	—	—	—	.17	.12	—	.11	—	—	.08	.50	.22
Chironomidae, immature	27.48	12.95	3.31	7.04	3.28	22.28	17.08	26.33	25.80	20.03	8.44	20.34	20.82	18.76
Chironomidae, adult	11.76	3.50	7.55	12.34	12.34	3.35	7.67	14.16	3.40	2.85	9.06	15.96	15.45	11.10
Dixidae	—	—	—	—	—	.19	.07	—	—	—	—	—	.88	.10
Simuliidae	.41	.75	—	—	—	.61	.40	—	—	1.41	—	.15	.35	.23
Tipulidae	1.02	11.75	.02	15.15	2.59	1.01	3.04	2.89	16.19	.25	.10	1.11	.56	2.64
Gastropoda:														
Physidae	—	—	—	—	—	—	—	1.88	—	—	—	—	—	.13
Fish larvae	.65	—	—	—	—	—	.14	—	5.92	—	1.15	—	—	.95
Aquatic food total	90.14	64.49	48.68	46.21	37.74	96.88	74.70	92.70	91.53	68.22	71.79	57.79	95.60	73.24
Annelida	—	—	—	19.29	—	—	.90	—	—	—	—	—	—	—
Arachnida	.91	1.27	1.93	—	—	.26	.63	—	.75	1.47	.98	.91	—	.80
Coleoptera	2.91	5.15	3.19	.47	19.16	.19	4.82	5.30	3.83	4.29	5.27	12.07	2.64	7.05
Dermaptera	—	—	1.04	—	.98	—	.27	—	.17	.23	.06	.87	—	.35
Diptera	1.18	5.94	9.21	18.37	13.48	1.16	5.39	.88	1.36	6.58	5.82	7.15	—	4.98
Hemiptera	.93	.88	11.64	2.33	2.35	.47	2.17	1.12	.44	6.63	6.44	3.21	1.76	3.67
Homoptera	3.77	13.93	10.33	10.96	14.59	.34	6.45	—	.95	1.46	2.00	14.01	—	5.49
Hymenoptera	.16	2.89	13.98	2.37	11.70	.70	4.09	—	.97	8.93	7.64	3.99	—	4.15
Lepidoptera	—	5.45	—	—	—	—	.58	—	—	2.19	—	—	—	.27
Terrestrial food total	9.86	35.51	51.32	53.79	62.26	3.12	25.30	7.30	8.47	31.78	28.21	42.21	4.40	26.76

identical for the two species. Terrestrial prey were most important in the diurnal diet of steelhead (28.2-42.4%) whereas nocturnal feeding was almost exclusively on autochthonous prey (92.7-95.6%). Like coho salmon, peak consumption of terrestrial invertebrates by steelhead occurred from 1600 to 2000 h while peak consumption of aquatic prey was from 2000 to 2400 h. Baetid, caenid, and leptophlebiid mayfly nymphs along with immature and adult chironomids were the only aquatic prey taxa which were well represented in the diet of steelhead during each 4-h interval (Table 2).

The two species exhibited diel differences in feeding intensity (Figure 1). Coho salmon fry fed heaviest from 2000 to 2400 h, while peak feeding of steelhead trout fry occurred from 1600 to 2000 h. (The feeding intensity of steelhead fry also increased substantially from 1200 to 1600 h.) In general, the greatest variation in the amount of

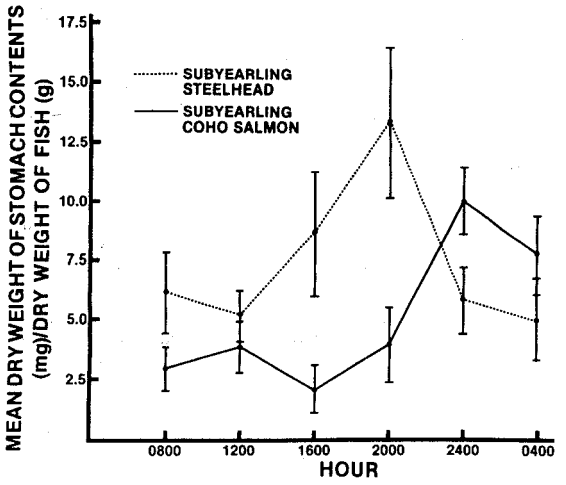

FIGURE 1.—Relative food contents (with 95% confidence limits) of subyearling coho salmon and steelhead at 4-h intervals, 13-14 July 1979, in Orwell Brook, NY.

food consumed among individual fish occurred during peak feeding periods in both species. Coho salmon appear to be primarily nocturnal feeders since their stomachs during periods of low light intensity (2000-0800 h) were much fuller ($\bar{x}$ = 6.87 mg stomach contents/g fish) than during daylight periods (0800-2000 h) ($\bar{x}$ = 3.23 mg stomach contents/g fish). Conversely, steelhead are predominately diurnal feeders. Their stomachs during the day ($\bar{x}$ = 9.03 mg stomach contents/g fish) were considerably fuller than at night ($\bar{x}$ = 5.60 mg stomach contents/g fish).

We estimated the daily meal (amount of food consumed per day) and the daily ration (amount of food consumed per day expressed as a percentage of the fish's body weight) for subyearling coho salmon and steelhead in Orwell Brook. The daily meal of coho salmon was estimated as 10.6 mg and the daily ration was 1.7% of their dry body weight. For steelhead the daily meal was estimated as 7.8 mg and the daily ration as 2.8%.

To investigate the hypothesis that the diet of coho salmon fry was more variable than that of steelhead fry over a 24-h period the overlap formula was used to compare diet similarity for each species between each 4-h sampling interval. When employing this formula, $C_\lambda \geq 0.60$ is assumed significant (Zaret and Rand 1971). Using this criterion, all possible combinations for steelhead are significant (Table 3). Only 4 of the 15 comparisons for coho salmon are significant while

TABLE 3.—Diet similarity values (C_λ) for subyearling coho salmon and steelhead between sampling periods spaced 4 h apart, 0800 h 13 July to 0400 h 14 July 1979.

		Steelhead					
		0800	1200	1600	2000	2400	0400
Coho salmon	0800		0.82	0.65	0.67	0.80	0.86
	1200	0.41		0.89	0.72	0.78	0.84
	1600	0.72	0.47		0.69	0.72	0.71
	2000	0.47	0.60	0.56		0.73	0.76
	2400	0.50	0.12	0.20	0.10		0.94
	0400	0.64	0.24	0.38	0.26	0.73	

their mean C_λ, 0.43, is much lower than that of steelhead, 0.77 (Table 4).

The diet of coho salmon and steelhead during similar 4-h intervals differed. The greatest overlap occurred between 2400 and 0400 h and the lowest from 1200 to 1600 h (Table 1). Overall, the mean diel overlap in diet between coho salmon and steelhead was significant (C_λ = 0.67).

Discussion

The results of this study support the hypothesis that the diet composition of subyearling coho salmon is more variable over a 24-h period than that of sympatric subyearling steelhead. The C_λ's for each species between different 4-h intervals (Table 4) indicate that the diet composition of coho salmon was variable, whereas that of steelhead was fairly uniform over the 24-h study period. In fact, the data show that at no time did the diet of steelhead fry (mainly aquatic invertebrates) differ substantially from diets at other 4-h intervals (e.g., all C_λ's were significant). The low similarity in the diel diet of coho salmon, as postulated, was due to the predominance of terrestrial prey in their daytime diet and predominance of aquatic prey in their nocturnal diet as C_λ's between daytime (0800-2000 h) and nocturnal (2000-0800 h) periods for coho salmon were generally the lowest ($\bar{x}$ = 0.32). Unfortunately, samples of the invertebrate drift were not taken at 4-h intervals concurrent with these fish collections. We suspect, however, that the variability in the diet of coho salmon was due to diel fluctuations in the composition of the drift, which are well documented in streams (Hynes 1970). In many streams during the summer, terrestrial invertebrates dominate the diurnal drift (Hinckley and Kennedy 1972; Johnson and Ringler 1980) while aquatic invertebrates dominate the nocturnal drift (Hynes 1970; Hinckley and Kennedy 1972). Since the diet of coho salmon fry in Orwell Brook has been shown to be significantly associated with the composition

of the drift, it is apparent why the diet composition, in synchrony with the drift, varies over a 24-h period.

Mason (1966) demonstrated nocturnal feeding activity of coho salmon fry. He attributed the night feeding habits of coho salmon to high retinal cone sensitivity, believing that it aided them in utilizing the increased drift of aquatic invertebrates during periods of low light intensity. Jenkins[3] observed that rainbow trout fed most actively at midday and that the diet at this time was composed mainly of terrestrial invertebrates which predominated in the drift. However, these fish were overyearlings, so a direct comparison with this study (fry) cannot be made since as salmonids grow older (and larger), not only do they occupy different habitats (Saunders and Smith 1962) but they also utilize different prey species (Kallenberg 1958), in addition to eating larger prey when available (Allen 1969). Tippets and Moyle (1978), however, did demonstrate that during the summer, rainbow trout fry fed predominantly on drifting invertebrates during the day in the McCloud River, Calif. In Orwell Brook in 1977, the diurnal diet of steelhead fry during the summer was found to be more closely associated with the composition of the bottom fauna rather than with the composition of the drift (Johnson and Ringler 1980). These differences in the feeding of steelhead may be due to social interaction between coho salmon and steelhead fry in Orwell Brook. In sympatry, during the summer, coho salmon occupy pools while steelhead utilize riffles (Hartman 1965; Allee 1974). In allopatry, although steelhead fry occupy both habitats, they prefer pools (Hartman 1965). If riffle versus pool occupancy influences the prey selection of coho salmon and steelhead as suggested by Johnson and Ringler (1980), the diets of steelhead fry in allopatric (predominately pools) and sympatric (predominantly riffles) situations with coho salmon may be expected to differ.

Although subyearling coho salmon actually consumed more food (10.6 mg daily meal) than subyearling steelhead (7.8 mg), because coho salmon were much heavier (Table 1), their daily ration was substantially less than steelhead (1.7 and 2.8% daily rations). Elliott and Persson (1978) suggested that, when using their formula to estimate daily food consumption, sampling intervals should be 3 h or less; larger intervals may result in inaccurate estimates. Since our sampling interval was 4 h and rates of gastric evacuation were determined from the literature (i.e., rainbow trout fry fed oligochaetes, Windell et al. 1976) using mean water temperatures (16°-21° C) for each 4-h interval, our results are, at best, rough estimates of the daily meal and daily ration of subyearling coho salmon and steelhead. However, our estimates are well within the range of juvenile sockeye salmon, *Oncorhynchus nerka*, in a lacustrine environment in Washington (Doble and Eggers 1978).

Johnson and Ringler (1980) found that the diurnal diet (0900-1500 h) of coho salmon and steelhead fry did not overlap substantially (i.e., $C_\lambda \geq 0.60$) from June through September in Orwell Brook during 1977. Interestingly, the only time that the diet of these two species did not overlap significantly in this study was during approximately the same period, 0800-1600 h (Table 1). The highest degree of overlap in the diets of coho salmon and steelhead occurred from 2000 to 0400 h when both species were feeding mainly on aquatic invertebrates. Inspection of diet overlap during twilight feeding periods (0400-0800 and 1600-2000 h) indicates significant overlap ($\bar{x} = 0.67$), which is distinctly intermediate between diurnal ($\bar{x} = 0.48$) and nocturnal ($\bar{x} = 0.87$) periods. The large diel fluctuations in diet similarity between these two species indicate that diel studies are necessary when examining aspects of their trophic ecology, at least when the species occur sympatrically. Daytime food studies could lead to the erroneous speculations that the diet of sympatric juvenile coho salmon and steelhead is not similar and that terrestrial invertebrates (at least during certain periods of the year) are the major component in the diet of coho salmon. Conversely, examination of the stomachs contents during nocturnal and crepuscular periods would indicate a great deal of similarity in diet and would not reflect the importance of allochthonous material in the daytime diet of coho salmon.

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THE OCCURRENCE OF *CIROLANA BOREALIS* (ISOPODA) IN THE HEARTS OF SHARKS FROM ATLANTIC COASTAL WATERS OF FLORIDA

Extensive depredation of catch triggered the closing of the only large commercial shark fishery on the Florida east coast (at Cape Canaveral) in October 1978. Shark catches had been affected throughout a 403 km stretch of nearshore waters from St. Augustine to Fort Pierce, Fla., from between 29 and 56 km offshore, at depths of 20-43 m. The organism responsible was a marine isopod, *Cirolana borealis* (Bowman[1]).

The presence of isopods (thought to be worms by the fishermen) in the heart of a shark was discovered in October 1977, when the pericardial

[1]Thomas E. Bowman, Curator, Crustacea, Department of Invertebrate Zoology, National Museum of Natural History, Washington, DC 20560, pers. commun. September 1978.

cavity of a freshly caught sandbar shark, *Carcharhinus milberti*, was accidentally opened. From January through May of 1978, increasing numbers of sandbar sharks with isopods in the gills and heart were taken. By spring, infestation was noted also in tiger sharks, *Galeocerdo cuvieri*, including one living animal in which isopods had entered the peritoneal cavity by chewing through the musculature from the right pectoral fin axil. Moderate isopod infestation of the gills was seen in one individual of a third shark species (*Sphyrna* sp.) in August 1978. Scavenging by isopods of dead sharks on setlines also increased dramatically during this period.

Shark catch declined sharply in June 1978, and up to 60% of the animals that were taken were affected by *C. borealis* (an average of 12 out of 20 sharks caught/400 hook set). The incidence rose to 100% of catch by August 1978 (an average of 22 sharks caught/400 hook set). Some of the sharks retrieved alive with isopods in their hearts showed no obvious external damage. A short pilot study in October 1978 identified the problem in the shark fishery (Bird[2]). Investigation was undertaken from June 1979 through April 1980 on the occurrence of *C. borealis*, the possible species of fishes affected, and the potential threat that the isopod posed to fisheries on the Florida Atlantic coast.

Cirolana borealis is normally a deepwater isopod. Its distribution on both sides of the Atlantic Ocean (usually at depths of 55-1,478 m) is temperature and Gulf Stream related (Richardson 1904; Schultz 1969). (One individual, a male, was noted by Menzies and Kruczynski (in press) in the Gulf of Mexico in 1967 at a depth of 55 m.) The occurrence in 1977 and 1978 off the Florida east coast in depths as shallow as 20 m appears to be a record for the species in that area. *Cirolana borealis* is eminently carnivorous, an active swimmer, and reputedly a voracious scavenger and has been noted as an occasional parasite by Sars (1899), Richardson (1905), and Halvorsen (1966). The species was recorded by Moreira and Sadowsky (1978) as an ectoparasite of *Squalus* spp. and *Raja* spp.; it was also recorded in the peritoneal cavity of *Raja* spp. *Cirolana borealis* is a morphologically capable predator. The incisors are heavily sclerotized for biting; the first three pairs of pereopods are prehensile, and the posterior pereopods are ambulatory (modified natatory).

The life cycles of most isopods are unknown (Overstreet 1978). There are few studies on the genus *Cirolana* other than those by Davis (1964), Nielsen and Stromberg (1965), Tjonneland et al. (1975), and Johnson (1976a, b). Cirolanids are not considered endoparasitic.

Methods

Fishes examined for isopods during the course of the investigation included commercially caught *Lutjanus campechanus*, *Epinephelus morio*, and *Mycteroperca microlepis* and numerous inshore and offshore species (*Dasyatis sabina*, *Raja eglanteria*, *Paralichthys lethostigma*, *Centropristis striata*, *Rhomboplites aurorubens*, *Sphyraena barracuda*, *Coryphaena hippurus*, *Haemulon plumieri*, *Euthynnus alletteratus*, *Echeneis naucrates*, *Balistes capriscus*, etc.) from fishing tournaments, shore fishermen, research vessels, and personal collection. Swordfish, *Xiphias gladius*, longline operations covering offshore areas from north of Cuba to Georgia were accompanied and their coincidental shark catches inspected for *Cirolana borealis*. Twenty-three species of sharks were examined altogether, including *Carcharhinus milberti*, *C. falciformis*, *C. limbatus*, *C. obscurus*, *Galeocerdo cuvieri*, *Sphyrna mokarran*, *Isurus oxyrinchus*, and *Ginglymostoma cirratum*.

As an adjunct to sampling, four seasonal field trails were undertaken at sites where infested sharks had been collected on setlines in 1978. Sites were "baited" for isopods with living and dead sharks placed on weighted lines and in wire cages on the bottom. Additionally, bottom samples from the area were obtained from shrimp and scallop trawlers. They were subsequently treated with rose bengal to stain organic material and screened for isopods. Faunal records and recent and historic benthic surveys were scrutinized for *Cirolana borealis* occurrence. Historic water parameters, currents, and eddies of the Florida Atlantic continental shelf were studied in regard to normal patterns and possible deviations.

Five shark samples with intact isopods were obtained. All samples were initially frozen and transferred into 10% buffered Formalin[3] on receipt. Samples 1 through 4 represented isolated

[2]Bird, P. M. 1978. Report on infestation by *Cirolana borealis* in sharks caught commercially on the Florida east coast. Fla. Sea Grant Rep. 04-8-M01-76, 14 p. Florida Sea Grant College, 2001 McCarty Hall, University of Florida, Gainesville, FL 32611.

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

sections from mature sandbar sharks collected by the fishery operator[4] from various sets in winter and spring 1978; he stated the animals were alive when retrieved from the lines. The samples consisted of: sample 1—ventricle complete with atrium, conus arteriosus, and short ventral aorta section; sample 2—ventricle as above and an epidermal section from the same animal; sample 3—ventricle as above within the pericardial chamber, intact with coracoid bar and transverse septum; sample 4—two branchial arches. Sample 5 was an entire male sandbar shark, 153 cm total length (TL), collected in July 1978; it was retrieved dead from the line.

Sample 1 was subsequently examined histopathologically; the entire specimen was serially sectioned and all sections studied microscopically. The material was paraffin embedded, cut to 6-7 μm thickness, and stained with hematoxylin and eosin.

Locations of isopods within the samples, sites of attachment, evidence of feeding, and morphological distinctions were noted on initial examination. Isopods removed during subsequent dissection were measured to the nearest 0.1 mm TL; length data were classed (2 mm classes) for frequency distributions. Species identification, sex, and stage of development were determined. Isopods were transferred into 70% isopropyl alcohol after detachment.

Results

Sampling

All teleost samples were negative for *C. borealis*. Those obtained during the pilot project in October 1978 were possibly within the chronological period of isopod occurrence in nearshore waters. Occurrences of other parasites and pathologies noted in the fishes (ectoparasitic crustaceans, cestodes, monogenetic and digenetic trematodes, nematodes, infections, etc.) were within normal levels. Reports from finfish processors and historic faunal records from the area are consistent with the finding that *C. borealis* are not a problem for teleostean fishes. Elasmobranchs collected in 1979 and 1980 were also negative for the isopods. No *C. borealis* were produced by the field trials.

Bottom samples were also negative. Historic faunal surveys revealed only one recent record of *C. borealis* (provisionally identified), taken in the South Atlantic Outer Continental Shelf Benchmark Study[5] that sampled continental shelf waters from Daytona Beach, Fla., through Georgia during 1977. The season and location in which the species was collected are unknown because Benchmark faunal lists are not yet keyed for retrieval of these data. The report would place *C. borealis* in Atlantic Shelf waters within the chronological period of shark infestation by the isopod.

Water Parameters

The currents and eddies off the Florida Atlantic coast are particularly dynamic. Recent data show that deep, cold, nutrient-rich Gulf Stream waters advect onto the continental shelf many times during the year (Atkinson et al. 1978). Spin-off eddies become larger north of Jupiter, and an established, persistent upwelling feature occurs to the north of Cape Canaveral. Lee et al. (in press) noted that eddy events appear in surface waters as warm, southward-oriented extrusions of the Gulf Stream, coupled to cold, upwelled cores. They documented an unusually strong eddy in April 1977; the eddy apparently coincided with the vertical stratification of the water, which strengthened the extrusion and brought it closer to shore. Water near the bottom (63 m depth) at the shelf break from St. Augustine south had the characteristics of water from depths of from 200 to 300 m. Its Gulf Stream origin was indicated by low temperature, salinity, oxygen content, and high nutrient concentration. The eddy, which was followed by a second strong eddy event, was 225 km long (parallel to the shelf) and approximately 35 km wide; upwelling of the cold core extended into the euphotic zone (45 m depth). Lee[6] stated that the coastal area from St. Augustine to Cape Canaveral in which *C. borealis* was found in sharks in 1977 and 1978 coincided with the area influenced by the especially strong eddies in spring of 1977.

[4]Joe D. Walker, P.O. Box 356, Cape Canaveral, FL 32920.

[5]South Atlantic OCS Benchmark Program, 1977 Report. 1979. Texas Instrument Contract AA550-CT7-2, Bureau of Land Management, Vol. 1-6. Bureau of Land Management, Department of the Interior, Federal Building, New Orleans, LA 70113.

[6]Thomas N. Lee, University of Miami, Department of Energy, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, pers. commun. March 1980.

Isopods in Shark Samples

Cirolana borealis (129 total individuals) were present only in shark samples 1-5 taken in 1978. One individual of a different isopod species and one copepod were also noted in the samples. Table 1 shows the *C. borealis* population composition for each sample. No manca larvae or true juveniles were found; all had completed the molt to seven peraeonal appendages, although the last pair of pereopods were small in some individuals in the 5 mm class. No ovigerous females or females with remnant marsupia were seen. A morphological distinction between isopods was noted in that the pleopods of individuals from the conus and ventricle were consistently swollen, while about half of those from the pericardial chamber, and only two of the isopods from the gills, showed this condition. The distinction was present prior to preservation of the samples, and was possibly an osmotic response to the body fluids of the host. The distribution of *C. borealis* in the same samples pooled by site of occurrence is shown in Table 2 (note relationships between the groups, particularly in the male to female ratios).

Shark Pathology

Intact isopods in the isolated shark samples were observed free within the pericardial chamber; others had their mouthparts attached to the tissues of the atrium and ventricle. In two instances (samples 1 and 3), a single, large female was attached in the conus arteriosus, caudad-directed, anterior to the proximal semilunar valves. There was no sign of external entry into the conus or aorta. Abrasions were evident on the exterior of the ventricles, and holes extended into the lumen; large isopods with guts distended and dark from feeding were present in pockets of tissue in the ventricular walls (Figure 1). Areas of possible necrosis were noted in these samples. Much of the gill tissue was destroyed on the branchial arches, exposing the cartilaginous gill rays. The epidermal section was abraded.

TABLE 2.—Distribution of *Cirolana borealis* by morphological site of occurrence in pooled *Carcharhinus milberti* samples (see text) collected off the Florida Atlantic coast in 1978.

Site of occurrence	Total number	Mean TL (mm)	% Male	% Female	% undifferentiated	M/F ratio
Epidermis	2	6.6	0	100.0	0	—
Gill	41	10.1	34.1	56.2	9.7	1:1.6
Pericardial cavity	56	10.0	28.6	71.4	0	1:2.5
Ventricle	28	12.1	14.3	85.7	0	1:6
Conus arteriosus	2	15.8	0	100.0	0	—

Two free isopods were in the pericardial chamber of the intact shark (sample 5). A small hole (chewed) through the coracobranchial musculature led into the chamber from the left posteriormost gill. No isopods were present in the interior of the ventricle, conus, or circulatory system. The tranverse septum was entire (as was that of sample 3). Two isopods were attached at the cloacal opening, and both claspers showed minor surface injury. The hide was deeply pitted at the axil of the pectoral fins and the soft areas at the median fin bases.

Histopathology of the Shark Heart

Histopathological examination of heart sample 1 showed several *C. borealis* in the atrium near the atrioventricular opening; the adjacent endocardium and myocardium surrounding one of the organisms had areas of necrosis, determined by observation of basophilic degeneration of myocardial fibers and loss of nuclei (Figure 2). No inflammation was evident. Isopods were present in the lumen of the ventricle. Isopod mouthparts

TABLE 1.—Population composition of *Cirolana borealis* present in five *Carcharhinus milberti* samples (see text) collected off the Florida Atlantic coast in 1978.

Item	1 Heart	2 Heart and epidermis	3 Heart	4 Gill	5 Intact shark	Pooled samples
Total number	7	30	47	38	7	129
Mean TL, mm	9.0	10.8	10.9	10.5	11.3	10.9
Male/female ratio	1:2.5	1:2.3	1:5.7	1:1.8	1:0.75	1:2.7
Number of males	2	9	7	12	4	34
TL range, mm	8.6-11.5	6.6-16.7	10.9-16.3	5.8-17.7	13.6-16.0	5.8-17.7
Mean TL, mm	10.1	11.3	13.6	11.5	14.7	11.6
Number of females	5	21	40	22	3	91
TL range, mm	5.4-15.9	5.5-18.8	5.4-19.4	5.3-18.3	6.5- 9.8	5.3-19.4
Mean TL, mm	9.0	10.8	10.2	11.3	7.7	10.5
Number undifferentiated	—	—	—	4	—	4
TL range, mm	—	—	—	4.8- 5.2	—	4.8- 5.2
Mean TL, mm	—	—	—	5.05	—	5.05

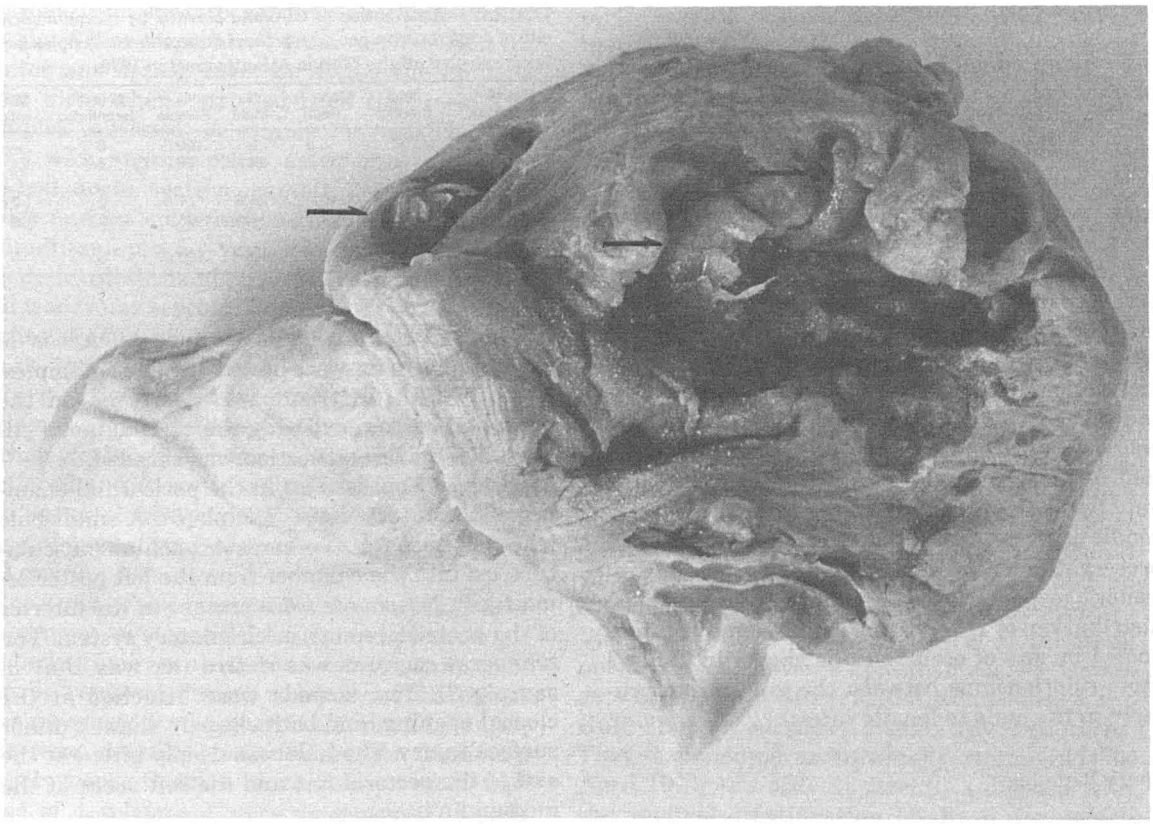

FIGURE 1.—Heart of a mature sandbar shark, *Carcharhinus milberti*, taken off the Florida Atlantic coast in 1978. Note *Cirolana borealis* enpocketed in the tissues of the ventricle.

were attached to the myocardium and on the endocardial surface of the ventricle; one area of the ventricle showed signs of endocardial and myocardial degeneration. The ventricular valves appeared morphologically normal (thus, the isopod in the conus in this sample had not entered from the ventricle). Isopod mouthparts were also attached on the pericardial surface, and there were foci of mononuclear cell infiltrate in the pericardium, indicating mild inflammation.

There was remarkedly little inflammation in the heart sample, but it is well documented that sharks demonstrate a surprising lack of inflammatory response to trauma (Sigel et al. 1968; Bird 1978). The pathologist[7] dated the time of necrosis development in the shark heart muscle as 18-24 h before death, because of the lack of inflammatory cells (as would be true in a human heart). He stated the lesion should be older, however, because of the loss of nuclei from the affected muscle cells.

Discussion

The occurrence of *C. borealis* in nearshore Atlantic waters and in the hearts of sharks appeared to be an unusual phenomenon. This is indicated by the absence of the species in historic records of faunal surveys and fishery operations in the area. The large shark fishery at Salerno, Fla., operated from 1935 to 1950 with no observed depredation of catch by *C. borealis* (Springer[8]). The occurrence in 1977 and 1978 might have passed unnoticed, however, had it not been for its effect on the Cape Canaveral fishery and the serendipitous opening of the heart cavity of a shark. It is probable that the isopods were

[7]William H. Luer, Department of Pathology, Tulane University, School of Medicine, 1430 Tulane Avenue, New Orleans, LA 70112, pers. commun. April 1980.

[8]Stewart Springer, Senior Research Associate, Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577, pers. commun. October 1978.

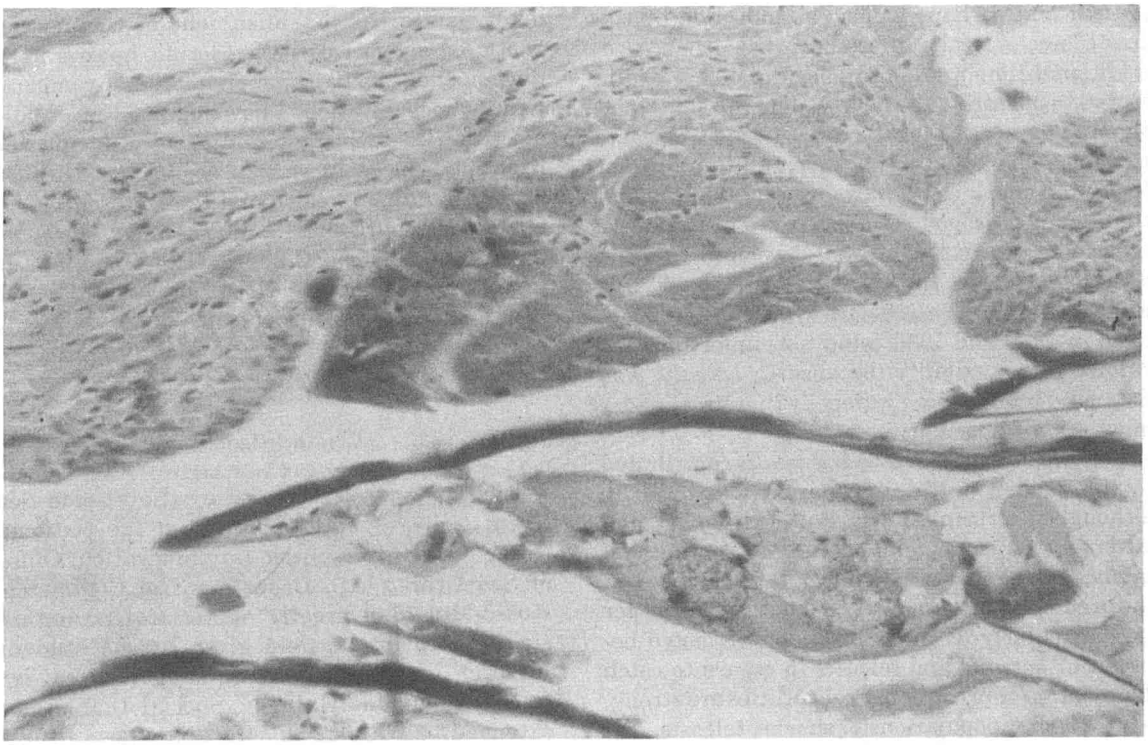

FIGURE 2.—Paraffin section of *Carcharhinus milberti* atrium; hematoxylin and eosin (100×); bright field illumination. Necrosis of heart tissue demonstrated by basophilic degeneration of muscle fibers and loss of nuclei. Note *Cirolana borealis* (delineated by darkly stained exoskeleton) directly below necrotic tissue.

carried near shore by an event (or repeated events) of particularly strong upwelling, possibly the eddy of April 1977. Gulf Stream intrusions are known to exert major influences on populations of shelf biota (Atkinson et al. 1978). The isopods were not observed in the area by 1979, however, and may not have been able to survive as a species in coastal waters subject to extremes of temperature, light, and salinity, parameters which remain uniform in the deepwater environment.

Factors indicate that the *C. borealis* population in nearshore waters was aberrant: the depths were shallower than previously recorded for the species in American waters; large-scale predation on living animals was heretofore unknown. Additionally, the shark samples containing isopods were collected during three seasons (winter, spring, and summer) in 1978; and while the life cycle of *C. borealis* is unknown, it was surprising to not find a few juveniles or females with remnant marsupia in any of the samples.

Opportunistic feeding by *C. borealis* occurred when isopods and sharks were concurrently inhabiting nearshore waters. Both groups of animals may have been drawn to common areas as a response to the olfactory stimuli of baited setlines. Dead sharks on the lines were extensively scavenged, but living animals on the lines were attacked as well. Predation by isopods on active sharks on the lines would have been facilitated by the restricted avoidance capabilities of the hooked fishes. A deliberate preference by the isopods for the heart of the shark is strongly indicated, both in its predatory and scavenging activities.

The pathologies observed in the shark hearts suggest that *C. borealis* might have attacked some free ranging sharks while in nearshore waters. Shark setlines were retrieved by the fishery within 10-12 h of set because prompt recovery of catch was essential in order to maintain the quality of shark meat marketed for human consumption (Walker[9]). Yet, necrosis in heart sample 1 developed at least 18-24 h prior to the death of the

[9]Joe D. Walker, P.O. Box 356, Cape Canaveral, FL 32920, pers. commun. October 1978.

animal and perhaps longer (as indicated by the loss of nuclei in the affected muscle cells). Also, additional time would have been required for the isopod to penetrate the body wall of the shark and into the heart, and for the heart tissue to become necrotic. The disparity between the number of hours the shark could have been on the line and the length of isopod residence time in the heart muscle as shown by the well-developed necrosis would, therefore, indicate that the shark was attacked by *C. borealis* before it was hooked. Field tests in 1979 and 1980 could not, unfortunately, resolve this possibility (because *C. borealis* was not found in nearshore waters by that time) and it must remain speculative.

There is no evidence that *C. borealis* contributed to the sudden decline in shark catch in 1978, although it certainly affected utilization of catch adversely. A coincident decline in commercial catches of snapper and grouper that occurred in the area also appears unrelated to the isopods per se, particularly as no association was noted between *C. borealis* and teleosts in regard to catch depredation or predation. Probabilities are strong, however, that populations of sharks, teleosts, and isopods were all influenced by common water parameters. Upwellings have historically been associated with declines in fish catch (Jones et al.[10]) and were shown by George and Staiger[11] to be dominant in inducing shifts in benthic invertebrate and demersal fish populations in the South Atlantic Bight.

The Cape Canaveral shark fishery might not have closed in 1978 had the nature of the isopod problem been known at that time. The operator thought the shark flesh was contaminated by the isopods and was afraid to sell it, thus needlessly lost his profitable market for the meat. This, combined with reduced profits from the pitted hides and the decline in shark catch, caused undue financial hardship. The encounter with a totally new problem, of an unknown future duration, doubtlessly contributed to the disillusionment of the operator. Occasional occurrences of *C. borealis* in shallow waters should not be considered a deterrent to the establishment of commercial shark fishing operations in Florida, however. The phenomenon, if it recurs, should be of comparatively short duration; knowledge of this should aid fisheries to budget realistically during the interim. Isopods in sharks do not constitute a hazard to human health and their presence does not render shark flesh unmarketable. More frequent collection of setlines and experimental sets to define areas of less isopod prevalence would help alleviate problems of shark fisheries during possible future occurrences of *C. borealis* in nearshore waters.

[10]Jones, R., R. Gilmore, Jr., G. Kulczycki, and W. Magley. 1975. Studies of the fishes of the Indian River region. *In* Indian River Study, Harbor Branch Consortium, Annual Rep., 1973-74, Vol. 1, p. 110-183. Harbor Branch Consortium, North Old Dixie Highway, RFD 1, Box 196, Fort Pierce, FL 33450.

[11]George, R., and J. Staiger. 1979. Epifauna: benthic invertebrate and demersal fish population of the South Atlantic/Georgia Bight. *In* South Atlantic OCS Benchmark Program, 1977 Report, Vol. 3, p. 237-279 (see footnote 5).

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A FLUSHING-CORING DEVICE FOR COLLECTING DEEP-BURROWING INFAUNAL BIVALVES IN INTERTIDAL SAND

In planning a study on the population dynamics and annual secondary production of deep-burrowing infaunal bivalves, a device was required which could take samples in shallow intertidal sand. Though many grabs or coring devices described in the literature (Brett 1964; Hopkins 1964; Maitland 1969; Kajak 1971) might have been suitable for taking short cores (20-30 cm deep) in intertidal or even subtidal areas, none were found suitable for taking large numbers of quantitative samples to a depth of 65-70 cm below the sediment surface. A device similar to one described by Van Arkel and Mulder (1975) was built to achieve this goal.

Materials

The device (Figure 1) was built according to the specifications outlined in Table 1. All materials are obtainable from either hardware or plumbing supply houses and are interconnected using polyvinyl chloride (PVC) cement, nuts, and bolts.

Operation

When intertidal samples are taken, the site is visited at high tide or when the water over the site

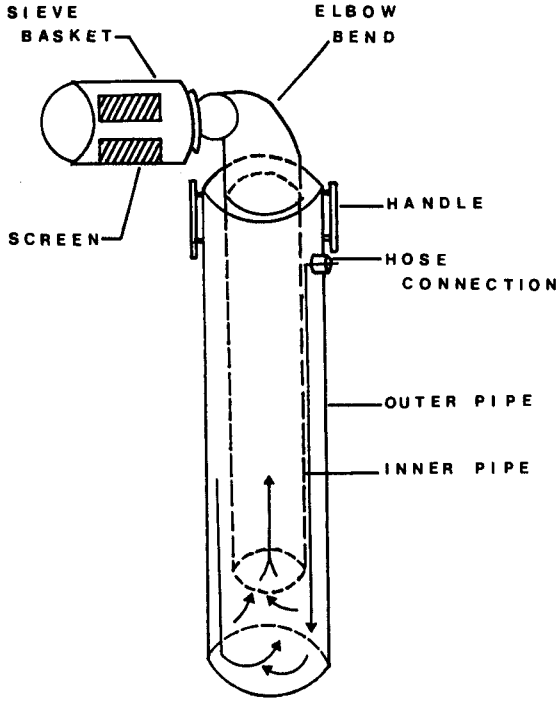

FIGURE 1.—Flushing-coring sampler. Arrows indicate direction of waterflow. Centrifugal water pump, gasoline engine, and water hoses are not shown.

TABLE 1.—Dimensions and materials used in the construction of the flushing-coring sampling system.

Item	Dimension (cm)		Material
	Diameter	Length	
Inner pipe	10.2	100.0	Polyvinyl chloride
Outer pipe	16.0	115.0	Polyvinyl chloride
Hose connection to sampler	5.1	5.1	Polyvinyl chloride
Elbow bend	10.2	—	Polyvinyl chloride
Sieve basket	16.0	30.0	Polyvinyl chloride
Side handles	2.54	20.3	Aluminum
Screen mesh (2 per sieve basket)	—	12.7	Aluminum
Hose (pump[1] to sampler)	5.1	1,000.0	Plastic
Hose (water supply to pump[1])	5.1	610.0	Heavy plastic

[1]High-pressure (22 m^3/h) water pump and 3-hp gasoline engine.

is at least deep enough to allow the pump intake hose to be submerged. The device may also be operated on exposed tidal flats if a water supply is within reach of the intake hose. The small screen over the end of the intake hose prevents debris from entering the water pumping system.

The boat is anchored and the sampling device lowered over the side and pushed several centimeters into the sediment prior to starting the pump. The operator may choose to stand in the water with waders in areas where currents and wind cause the boat to move a great deal resulting in an unstable work platform.

When the pump is activated, water is forced down the space between the inner and outer PVC pipes, forcing a suspension of sediment and all associated organisms up the smaller inner pipe and into the attached sieve basket. The operator forces the device down into the sediment to the desired depth, then the pump is shut off. At this point, the sieve basket contains all organisms and objects too large to pass through the screen. Most sediment washes easily through.

Discussion

After collecting more than 2,000 samples over a 1-yr period, no problems have been encountered with the system. A 2.5 mm mesh screen was used on the sieve basket. As the device was designed specifically to take quantitative samples of the deep-burrowing, stout razor clam, *Tagelus plebeius* Solander, for a secondary production study, the 2.5 mm mesh was adequate for sampling small bivalves and adults. Collections were made from small aluminum or fiber glass boats (3.8-4.9 m long). The system was also tested at a beach site where the water pump was placed on the shore while the operator carried the sampler into adjacent intertidal waters. Though possible, this method lacks the mobility of sampling from a boat.

Most bivalves were recovered in an undamaged condition (Table 2). In no case was a bivalve recovered with a shell broken such that shell length could not be measured, though in some specimens, small breaks in the shell allowed body fluids to escape resulting in a specimen unsuitable for an accurate biomass determination. The soft shell clam, *Mya arenaria*, and the stout razor clam have thin gaping shells that are much more susceptible to damage than the hard clam, *Mercenaria mercenaria*. Van Arkel and Mulder (1975) reported that damage to small polychaete worms was no more than if a hand corer and ordinary sieve had been used. Polychaetes were not specifically examined for damage in the present study. Many were collected in the sieve basket and though some were obviously broken, most were not.

TABLE 2.—Condition of bivalves recovered in 1,575 separate samples by the flushing-coring device.

Species	Collected (no.)	Broken[1] (no.)	Broken (%)
Tagelus plebeius	1,479	186	13
Mya arenaria	513	45	9
Mercenaria mercenaria	36	0	0
Ensis directus	3	0	0
Total bivalves	2,031	231	11

[1]Any break in the shell, no matter how small, that might allow loss of body fluids.

The maximum shell lengths (largest external dimension of the shell) of the collected specimens were 10.4, 9.15, 10.2, and 10.8 cm for *M. mercenaria*, *T. plebeius*, *Mya arenaria*, and *Ensis directus*, respectively. The heaviest bivalve, *Mercenaria mercenaria*, was estimated to weigh 200-300 g. Several of the large *M. mercenaria* were placed in the sediment and repeatedly "sampled" from the sand flat to the sieve basket to test the lifting capability of the system. The test specimens were always easily raised.

Direct visual observations in shallow water indicate that no water or sediment escapes under the outer pipe when in operation. The outer pipe has a large diameter (16 cm), thus the surface area of a single sample (0.02 m^2) is quite large.

The main advantages of this system are its mobility (as mobile as a small, shallow-draft boat) combined with the fact that deep cores can be taken and sieved in one fast process. Samples can routinely be taken to a depth of 65-70 cm below the sediment surface. Organisms can be immediately placed in storage containers, ready to be processed upon returning to the laboratory. The use of PVC parts and removable sieve basket screens allows the investigator to build and modify the device to one's own specifications depending on the particular goals of the study.

Acknowledgments

I wish to thank Czeslaw A. Bartusiak for providing assistance and a workshop in which to construct the device. This project was supported in part by an Old Dominion University, Institute of Oceanography (Norfolk, Va.), Graduate Fellowship.

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ERRATA

Fishery Bulletin, Vol. 79, No. 1

Gooding, Reginald M., William H. Neill, and Andrew E. Dizon, "Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*," p. 31-48.

1) Page 31, Abstract, first paragraph, line 9, correct to read:
independent of weight effects)—$\log_{10}\dot{V}_{O_2} = -1.20 + 0.19 \log_{10}W + 0.21\ S$. However, laboratory fish
2) Page 37, left column, first paragraph, lines 13 and 15, correct to read:
(grams) = $-2.657 + 3.532 \log L$ (centimeters);
$3.368 \log L$ (centimeters) (log = $\log_{10}$). This com-
3) Page 37, right column, the equation, correct to read:
$$S = 3.55 - 0.53 \log \overline{W} - 0.02t - 0.04 \cdot k$$
4) Page 37, right column, line above the heading Respiration Rate, correct to read:
$\log \overline{W}$ (Figure 2).
5) Page 38, right column, lines 1 and 6, correct to read:
body weight (Figure 2): $S = 3.14 - 0.53 \log \overline{W}$.
left with $\log \dot{V}_{O_2} = -0.54 + 0.08 \log \overline{W}$. Thus,
6) Page 43, left column, second paragraph, line 4, correct to read:
relation $S = 3.14 - 0.53 \log \overline{W}$. Magnuson
7) Page 44, left column, line 2, correct to read:
(Figure 9).

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Fishery Bulletin

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Seattle, Washington

1981

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THE OSTEOLOGY AND RELATIONSHIPS OF THE ANGLERFISH GENUS *TETRABRACHIUM* WITH COMMENTS ON LOPHIIFORM CLASSIFICATION[1]

THEODORE W. PIETSCH[2]

ABSTRACT

The shallow-water anglerfish, *Tetrabrachium ocellatum*, now represented by 36 specimens from Australian, New Guinean, and Indonesian waters, is redescribed and compared osteologically with its allies within the Antennarioidei. Phylogenetic analysis based on a search for shared, derived characters shows that *Tetrabrachium* is most closely related to *Antennarius*, and is classified on this basis as a sister-family of the Antennariidae. That the Tetrabrachiidae has entered a "new adaptive zone" relative to the Antennariidae is evidenced morphologically by a number of unique derived features. The most conspicuous of these include small, close-set eyes protruding from the dorsal surface of the head, and a peculiar webbing between the pectoral fin and the body, and between the pectoral and pelvic fins, characters that reflect a benthic existence in soft substrata (mud or fine sand).

It is further shown that a group including the Antennariidae and Tetrabrachiidae forms the primitive sister group of the Lophichthyidae and that these two groups together form the primitive sister group of the Brachionichthyidae. Although evidence is provided to establish a sister-group relationship between the Chaunacidae and Ogcocephalidae, no convincing synapomorphy is known at the present time that will establish monophyly for a group containing all six families. An analytical key to the major subgroups of the Antennarioidei is provided and a revised classification of the order Lophiiformes is proposed.

One of the more curious forms described by Günther (1880) in his report on the shore fishes procured by the *Challenger* Expedition of 1873-76, was a single specimen of an antennarioid anglerfish from off the southern coast of New Guinea. In reference to a peculiar, double pectoral fin and numerous ocellilike markings on the dorsal half of the body, the species was named *Tetrabrachium ocellatum*. Since the original description perhaps a dozen authors have cited Günther (1880), but none have been able to offer any new information on this species other than a report of the discovery of two additional specimens (Whitley 1935). For the purposes of this study, 36 specimens of *T. ocellatum* have been located, all collected from Australian, New Guinean, and Indonesian waters at depths of between approximately 5 and 55 m. Although a close phylogenetic relationship with the genus *Antennarius* has been implied (by recognition of a subfamily Tetrabrachiinae of the Antennariidae; Regan 1912, Berg 1940, Norman 1966), no evidence for this alignment has been provided.

The objectives of this paper are to describe the structure of *T. ocellatum*, to compare it morphologically with its nearest allies, and to speculate on the phylogenetic relationships of this and other members of the suborder Antennarioidei. Representatives of the six major antennarioid subgroups (here recognized as families) are considered in detail. In addition to *Tetrabrachium*, these are *Antennarius* Daudin, recognized here as the least derived genus (see Phylogenetic Relationships below) of some eight genera of the Antennariidae (a modification of Schultz 1957; Pietsch in prep.); *Lophichthys*, a monotypic genus recently described by Boeseman (1964) and heretofore not adequately placed within any higher taxonomic category (see Boeseman 1964 and Le Danois 1979); *Brachionichthys* Bleeker (= *Sympterichthys* Gill), containing approximately four southern Australian species, and recognized as constituting an antennarioid family by nearly all authors since Regan (1912); *Chaunax* Lowe, the only genus of the family Chaunacidae; and *Dibranchus* Peters, an underived genus of the Ogcocephalidae (see Bradbury 1967).

[1]Contribution No. 561, College of Fisheries, University of Washington, Seattle, Wash.

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FISHERY BULLETIN: VOL. 79, NO. 3, 1981.

METHODS AND MATERIALS

Standard lengths (SL) are used throughout. All measurements were taken on the left side and rounded to the nearest 0.5 mm. Head length is the distance from the anterior tip of the upper jaw to the posteriormost margin of the preopercle. The illicial bone is the first spinous dorsal ray (Bradbury 1967). Sockets indicating missing teeth in the jaws and on the vomer were included in total tooth counts. The analysis of relationships follows, in a general way, the phylogenetic approach suggested by Hennig (1966) with the exception that not all branching points in the cladogram are formally named. The loss of convenience in discussing individual sister groups by a single epithet is outweighed by the avoidance of adding a multiplicity of new taxonomic categories and names, as well as the necessity of altering names that are well established in the scientific literature. The relative primitiveness of character states is identified by the procedure of outgroup comparison as discussed by Eldredge and Cracraft (1980:63).

The osteology of *Tetrabrachium ocellatum* is based on two specimens (AMS IB.7177, 7178, 56 and 61 mm SL) cleared and stained with alizarin red S following the trypsin digestion technique of Taylor (1967). All additional material examined for comparative purposes is listed in the Appendix. Bone terminology follows Nybelin (1963), Bradbury (1967), and Pietsch (1972). In osteological drawings cartilage is stippled, and where necessary for clarity, open spaces are rendered in solid black.

Material is deposited in the following institutions:

AMS: Australian Museum, Sydney
BMNH: British Museum (Natural History), London
KFRS: Kanudi Fisheries Research Station, Konedobu, Papua, New Guinea
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge
NMV: National Museum of Victoria, Melbourne
RMNH: Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
USNM: National Museum of Natural History, Washington, D.C.
UW: College of Fisheries, University of Washington, Seattle
WAM: Western Australian Museum, Perth

SYSTEMATICS

Tetrabrachium ocellatum Günther
Figures 1, 2

Tetrabrachium ocellatum Günther 1880:44-45, 78, pl. 19, fig. C (original description, single specimen, 51 mm SL, holotype BMNH 1879.5.14.618, *Challenger* Station 188, south of New Guinea, 9°59′ S, 139°42′ E, 51 m). Gill 1883:551 (after Günther 1880; Pedicalidae of Günther 1880:78 a misprint for Pediculati). Regan 1912:283 (after Günther 1880; Tetrabrachiinae). Fowler 1928:476 (after Günther 1880; Pedicalidae after Günther 1880:78). Gregory 1933:394 (after Günther 1880). Whitley 1934:xxx (second known specimen). Whitley 1935:249 (second and third known specimens; Tetrabrachiidae). Berg 1940:499 (subfamily Tetrabrachiini of Antennariidae). Gregory 1951:224, fig. 9.154C (obliteration of postopercular cleft by branchiostegal membrane). Beaufort and Briggs 1962:222, fig. 50 (description, holotype reexamined). Le Danois 1964:141 (after Günther 1880, Whitley 1935). Norman 1966:590 (in key; Tetrabrachiinae of Antennariidae). Kailola and Wilson 1978:26, 58-59 (additional material, Papua New Guinea).

Material.—Thirty-six specimens, 17-67 mm SL.

Holotype of *T. ocellatum*: BMNH 1879.5.14.618, 51 mm SL, *Challenger* Station 188, south of New Guinea, 9°59′ S, 139°42′ E, 51 m.

Additional nontype material: AMS IB.5836, 64 mm SL, Townsville District, Queensland, 19°16′ S, 146°49′ E, trawled. AMS IA.6003, 17 mm SL, off Hayman Island, Queensland, 20°03′ S, 148°53′ E, 9 m. AMS IA.6136, 27 mm SL, Lindeman Island, Queensland, 1934. AMS IA.6759, 2(20 and 26.5 mm SL), Lindeman Island, Queensland, 20°27′ S, 149°02′ E, trawled. AMS IB.7173-7178, 6(42.5-61 mm SL), Gulf of Carpentaria, Queensland (56 and 61 mm SL specimens cleared and stained). AMS I.15557-281, 7(42-61.5 mm SL), Gulf of Carpentaria, Queensland, 17°29′ S, 140°24′ E, trawled, 5.5 m, 24 November 1963. AMS I.19289-003, 31.5 mm SL, *Alpha Helix*, Arafura Sea, 10°27.5′ S, 136°47.0′ E, trawled on bottom of mud, gravel, and shells, 55 m, 17 March 1975. AMS I.20907-041, 41.5 mm, south of Cooktown, Queensland, 16°01′ S, 145°29′ E, trawled on bottom of mud and shells, 20 m, 6 February 1979.

KFRS 871, 46 mm SL, northwest of Yule Island, Gulf of Papua, New Guinea, March 1963. KFRS 1483, 52 mm SL, Kerema Bay, Gulf of Papua, 5 May 1969. KFRS 2953, 62 mm SL, 6.5-8 km off Kerema Point, Gulf of Papua, prawn trawl, 14.6 m, 9 May 1973. KFRS 3017, 58 mm SL, Kerema Bay, Gulf of Papua, 9-13 m, September-October 1970. KFRS 3023, 61 mm SL, Kerema Bay, Gulf of Papua, 9-13 m, September-October 1970. KFRS 3082, 50 mm SL, FRV *Rossel*, Yule Island, Gulf of Papua, trawl, 18-24 m, January-February 1971.

USNM 177873, 52 mm SL, between Hayman and Magnetic Islands, Queensland, trawl, 18-46 m, May-June 1957.

WAM P.21473-001, 67 mm SL, Vansittart Bay, West Australia, 14°04′ S, 126°17′ E, 26 May 1968. WAM P.26130-001, 2(58 and 67 mm SL), Broome Bay, Napier, West Australia, 14°00′ S, 126°36′ E, 26 November 1968. WAM P.26832-001, 34 mm SL, Wokam and Uru Islands, Indonesia, 5°30′ S, 134°12′ E, 15 June 1970. WAM P.26833-001, 47 mm SL, Aru Island, Indonesia, 5°30′ S, 134°12′ E, 16 June 1971. WAM P.26540-001, 53 mm SL, Mermaid Passage, Dampier Arch, West Australia, 16°25′ S, 123°20′ E, prawn trawl, 8 September 1977. WAM P.26834-001, 35 mm SL, west of Dongara, West Australia, 29°15′ S, 114°01′ E, 20 March 1972.

Diagnosis.—Mouth small, opening dorsally, bones of jaws nearly vertical, nearly completely hidden by folds of skin; lower lip lined with small, cutaneous papillae; eyes small, close-set, protruding from dorsal surface of head; anterior half of frontals separate, posterior half meeting on midline; pterosphenoid present; parietals separated by supraoccipital; mesopterygoid absent; ectopterygoid triradiate, T-shaped; dorsal head of quadrate narrow, less than width of metapterygoid; interhyal with a medial, posterolaterally directed process; interopercle flat, broad; pharyngobranchial I present; epibranchial teeth absent; ceratobranchials toothless; toothed portion of ceratobranchial V expanded; hypohyals II and III bifurcated; ossified basibranchials absent; small basihyal present; neural spines of preural centra 14-22 short, spatulate, not interdigitating with proximal radials of soft dorsal fin; epurals absent; three dorsal fin spines without interconnecting membrane; illicial cavity absent (Bradbury 1967); illicium reduced, without esca, emerging anterior to eyes; second dorsal fin spine covered with cutaneous filaments, emerging from between eyes; third dorsal fin spine nearly completely covered with skin of head, distal tip emerging on posterior margin of cranium; illicial pterygiophore and pterygiophore of third dorsal fin spine with highly compressed, bladelike dorsal expansions, each expansion with a foramen within which lie medially directed prongs of proximal end of respective dorsal fin spine; soft dorsal fin rays 16-17; anal fin rays 11-12; pectoral fin rays 9, divided into dorsal portion of 4 rays interconnected by membrane, ventral portion of 5 interconnected rays, dorsalmost ray attached to lateral surface of body by membrane; pectoral lobe attached to posteriormost ray of pelvic fin by membrane; three pectoral radials; skin naked except for very few microscopic spinules associated with pores of acoustico-lateralis system.

Description (Figure 1).—Body strongly compressed, elongate (greatest depth <50% SL); head compressed, short (<32% SL); cranium strongly oblique in position, posterior end of cranium and anterior vertebrae raised forming a prominent convex hump; mouth small, width <16% SL;

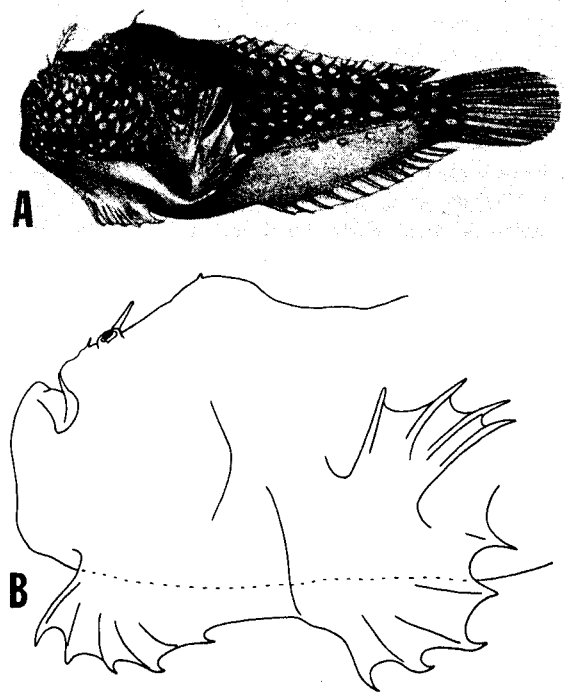

FIGURE 1.—*Tetrabrachium ocellatum*: A. Holotype, BMNH 1879.5.14.618, 51 mm SL, after Günther 1880; B. Diagram showing webbing between lower portion of pectoral fin and body, and between pectoral and pelvic fins.

anterior nostril opening on edge of upper lip, posterior nostril opening approximately half-way between edge of lip and eye; oral valve present lining both upper and lower jaw; gill opening small, situated just below and behind base of pectoral fin lobe; no opening behind fourth gill arch; holobranchs present on ventral half of ceratobranchial I, full length of ceratobranchials II and III, ventral half of epibranchial II, and ventral tip of epibranchial III; hemibranchs present on dorsal half of ceratobranchial IV and ventral tip of epibranchial IV; pseudobranch absent; swim bladder absent; ovaries paired.

Pterygiophore of illicium completely covered with skin of head; illicial bone short (<8% SL) and thin, tapering to a point; bases of soft dorsal and anal fins long (>48% and 42% SL, respectively), rays short; dorsal and anal fin rays enveloped in membrane; in some specimens (7 of 16 specimens examined) distal tips of first 9 rays of soft dorsal fin free, each terminating in a tight ball of tissue, remaining dorsal rays enveloped in membrane; caudal fin long (>30% SL), rounded.

Teeth small, slender, recurved, and depressible; each premaxilla with a single row of 22-25 teeth, each dentary with approximately 35 teeth arranged in two rows; vomerine teeth in two patches, about 25 teeth in each patch; palatine teeth absent; pharyngobranchials II and III and ceratobranchial V toothed.

Color in preservative white on lower half of body to brown on upper half of body, with numerous, small, white spots continuing onto soft dorsal fin, remaining fins white; oral cavity and viscera unpigmented.

Length to 67 mm SL.

Complete counts and measurements of representative material are given in Table 1.

Habitat.—Specific information on the habitat frequented by *T. ocellatum* is available for only two captures: a 31.5 mm SL specimen (AMS I.19289.003) and a 41.5 mm SL specimen (AMS I.20907-041) were trawled off a bottom of mud, gravel, and shell. A number of other specimens were collected in prawn trawls most likely fished over similar, soft-bottom substrates of mud or sand.

Distribution (Figure 2).—*Tetrabrachium ocellatum* is known from 36 specimens collected in shallow water (55 m or less) off the western (as far south as lat. 29° S) and northern coasts of Australia, the southern coast of Papua, New Guinea, and the south Molucca Islands, Indonesia.

Osteology of *Tetrabrachium ocellatum* Figures 3-13

The osteology of lophiiform fishes has been dealt with by numerous authors (Garman 1899; Regan

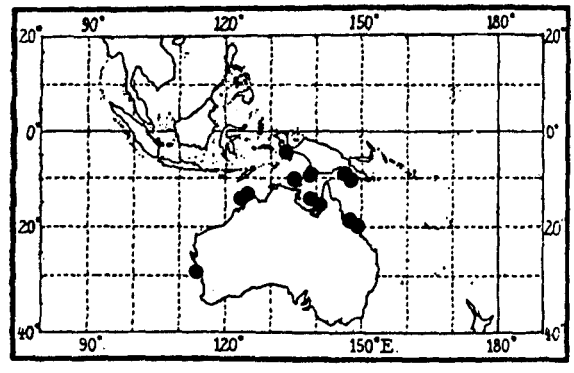

FIGURE 2.—Known distribution of *Tetrabrachium ocellatum*. One symbol may indicate more than one capture.

TABLE 1.—Counts and measurements (in percentage of standard length) of representative specimens of *Tetrabrachium ocellatum*.

	KFRS 3087	UW 20771	AMS IB.7173	KFRS 871	KFRS 3082	USNM 177873	AMS IB.7174	AMS IB.7175	KFRS 3023	KFRS 2953
Standard length, mm	39	39.5	42.5	46	50	50.5	54	56	61	62
Length:										
Head (snout to posteriormost margin of preopercle)	27.7	30.4	25.9	26.1	26.0	23.8	20.4	25.0	23.0	22.6
Snout to emergence of dorsal spine III	22.6	25.3	25.9	25.4	23.2	23.8	25.0	—	23.0	25.0
Illicial bone	7.2	4.6	2.6	4.1	4.0	4.0	3.3	—	—	4.8
Dorsal spine II	7.9	6.3	4.7	8.7	6.8	5.2	4.1	4.6	5.4	4.8
Base of soft dorsal fin	67.9	64.6	49.4	56.5	58.0	63.4	63.0	—	54.9	53.2
Base of anal fin	51.3	51.9	42.3	48.9	51.0	53.5	49.1	—	48.4	48.4
Caudal fin	43.1	36.2	39.3	34.8	32.0	35.6	36.1	36.7	37.7	33.9
Width:										
Between eyes (from center of lens)	11.0	12.4	10.6	11.1	10.4	9.9	9.1	—	10.8	10.3
Least between frontal bones	6.7	6.8	4.9	6.1	5.8	5.5	5.4	—	4.9	5.6
Greatest between sphenotic bones	20.2	19.7	19.8	20.6	19.4	19.2	17.2	17.9	20.5	20.2
Greatest body depth	38.5	43.0	35.3	46.7	46.0	45.5	42.6	37.5	42.6	41.9
Dorsal fin rays	16	17	16	16	16	17	16	16	17	16
Anal fin rays	11	11	11	11	11	12	12	11	12	12

1903, 1912; Gregory 1933; Eaton et al. 1954; Monod 1960; Le Danois 1964, 1974, 1979; Field 1966; Bradbury 1967; Rosen and Patterson 1969; and additional references cited by Pietsch 1972, 1974, 1978, 1979), yet no published osteological information on the genus *Tetrabrachium* is available. In the following account only those comparative aspects that differ from those previously described in other anglerfishes are discussed.

Cranium (Figures 3-6).—The ethmoid cartilage of *T. ocellatum* broadly covers the posterior half of the vomer meeting with the lateral ethmoids laterally and the supraethmoid medially. The supraethmoid forms a narrow, vertical interorbital septum lying between, but well separated from the orbital portions of the frontals. The laterally compressed, ventral end of the supraethmoid meets with the ethmoid cartilage anteriorly and lies within a groove on the dorsal surface of the parasphenoid posteriorly. The dorsal end of the supraethmoid is overlapped on each side by central extensions of the frontals. Each lateral ethmoid has a narrow, cylindrical posterior portion that lies ventral to an anterior extension of the respective frontal, and a larger, ventrally directed, anterior portion that meets with the ethmoid cartilage.

The head of the vomer lies ventral to the ethmoid cartilage. Its anterior margin is indented medially. The ventral surface of the vomer is strongly concave (as seen in anterior view, Figure 6). A laterally compressed, keellike posteromedial process emerges from the ventral surface of this bone and fits within a deep groove on the anteroventral surface of the parasphenoid; the ventral margins of the posteromedial process of the vomer and the anterior end of the parasphenoid are strongly convex (as seen in lateral view, Figure 4). Vomerine teeth are present in two lateral patches, each patch containing approximately 25 teeth arranged in perhaps three irregular rows.

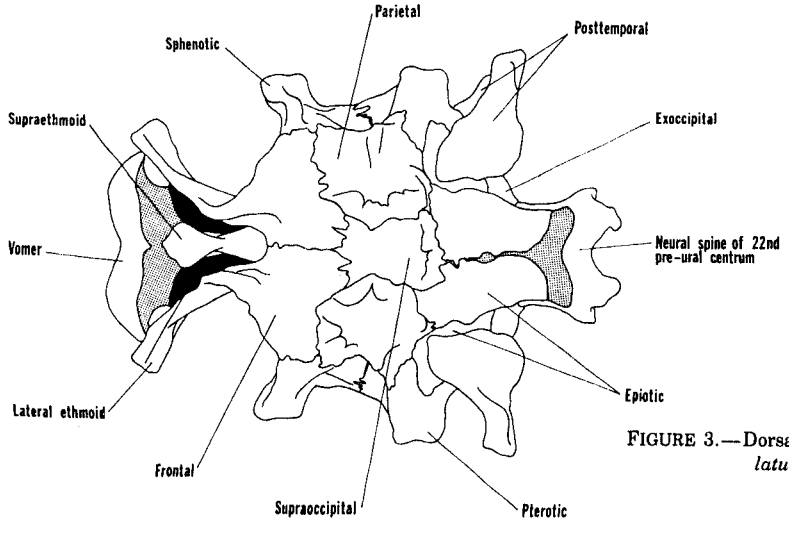

FIGURE 3.—Dorsal view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

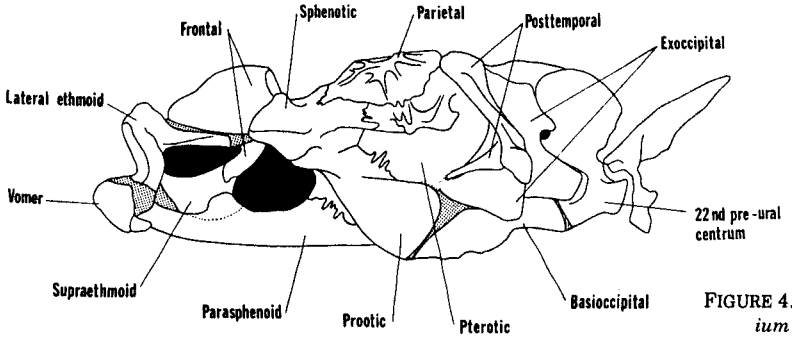

FIGURE 4.—Lateral view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

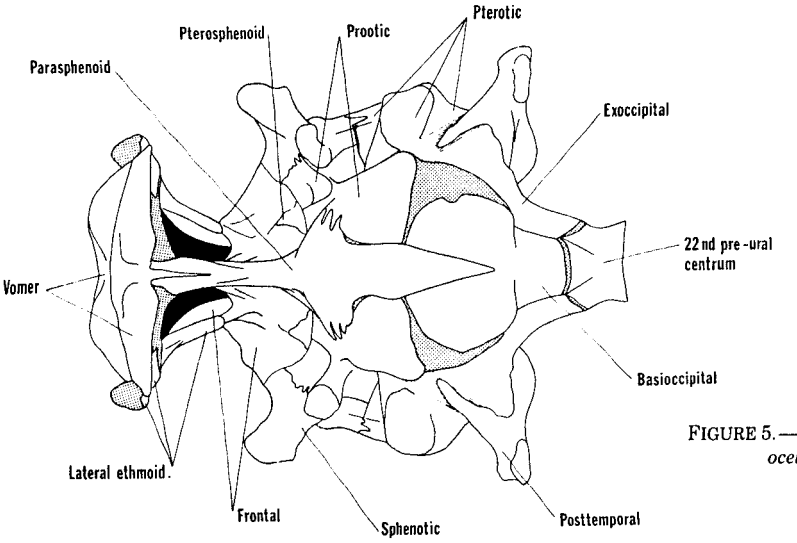

FIGURE 5.—Ventral view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

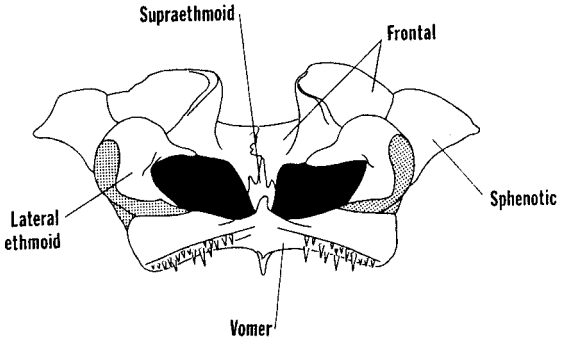

FIGURE 6.—Anterior view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

The frontals are relatively large and irregular in shape. Each has a laterally compressed, anterior half, well separated from its counterpart of the other side, and a dorsoventrally depressed posterior half that meets its counterpart on the midline. In dorsal view (Figure 3), the frontals form a relatively narrow orbital region to accommodate the closely set, dorsally directed eyes. In lateral view (Figure 4), the depressed posterior half of the frontals form a concavity between the elevated, laterally compressed anterior half of these bones and the posterior half of the cranium.

The parietals are irregularly shaped elements with deeply pitted and grooved external surfaces. They are well separated from each other by the supraoccipital. Each parietal overlaps the respective frontal anteriorly, the sphenotic and pterotic laterally, the supraoccipital medially, and the epiotic posteriorly.

A small pterosphenoid lies on the ventromedial surface of the frontal in contact with the prootic.

The orbitosphenoid and basisphenoid are absent in all lophiiforms.

The parasphenoid is a stout, well-ossified element with a convex ventral margin (Figure 4). Its anterior end is overlapped by the ethmoid cartilage dorsally and by the narrow shaft of the vomer ventrally. Medially, the dorsal surface of this bone forms a deep groove within which lies the laterally compressed, posteroventral part of the supraethmoid. Posteriorly, the parasphenoid is broadly connected with the prootics laterally and the basioccipital medially. At no point does the parasphenoid make contact with the frontals.

Each sphenotic forms a dorsoventrally depressed flange that extends outward in an anterolateral direction, considerably beyond the width of the ethmovomerine region of the cranium (Figure 3).

The remaining elements of the cranium (pterotics, epiotics, prootics, supraoccipital, and exoccipitals) do not differ substantially from those described for other lophiiforms (Regan 1912, fig. 5; Gregory 1933, fig. 265, 267-271; Pietsch 1972, 1974).

Otoliths (Figure 7).—The sagitta of *T. ocellatum* is roughly oval in shape with a length to height ratio of about 1.4:1. The sulcus is only slightly

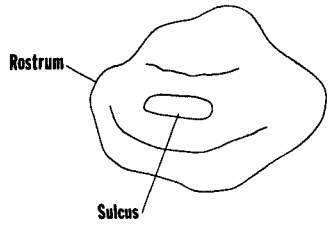

FIGURE 7.—Medial view of right sagitta of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

grooved. The rostrum is poorly developed, and an antirostrum is absent.

Mandibular arch (Figures 8, 9).—The premaxillae (Figure 8) are each characterized by having a narrow ascending process, nearly as long as the tapering toothed portion of the bone; a rounded articular process; and an elongate, spatulate postmaxillary process (pmpmx of Rosen and Patterson 1969, fig. 56A). The ascending and articular processes together form an oblique angle with the postmaxillary and toothed processes. The toothed portion of each premaxilla bears a single row of 22 to 25 depressible teeth, the largest at the symphysis, becoming progressively smaller posteriorly.

Each maxilla consists of a broad posterior portion (completely hidden from behind by a thick fold of skin when the mouth is closed), and an expanded anterior head that, in turn, consists of an anterior process that overlaps the respective premaxilla and a medially directed process that is attached by a short ligament to the articular process of the respective premaxilla. The dentaries, articulars, and angulars (Figure 9) are similar to those described for other lophiiforms (Gregory 1933, fig. 265, 266, 269-271; Pietsch 1972, 1974). Each dentary bears approximately 35 depressible teeth arranged in two rows.

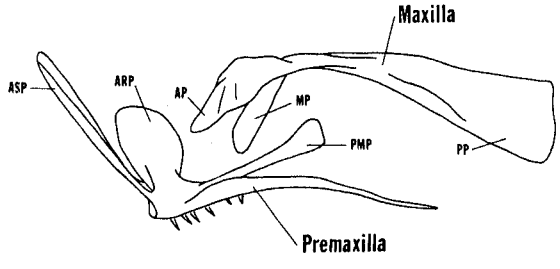

FIGURE 8.—Upper jaw bones of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. AP = anterior process of maxilla; ARP = articular process of premaxilla; ASP = ascending process of premaxilla; MP = medial process of maxilla; PMP = postmaxillary process of premaxilla; PP = posterior process of maxilla.

Palatine arch (Figure 9).—Each metapterygoid is in contact with four other bones: dorsally and posterodorsally with the hyomandibular, posteroventrally with the upper half of the symplectic, and ventrally with the quadrate and ectopterygoid. The ectopterygoid is large and T-shaped, overlapping the medial surface of the metapterygoid dorsally, the quadrate ventrally, and the palatine anteriorly. The mesopterygoid (cartilaginous or ossified) is absent. The palatine is unusually large, approximately twice the length of the ectopterygoid. Palatine teeth are absent.

Hyoid arch (Figures 9, 10).—Dorsally, each hyomandibular is forked forming two heads, both of which articulate with the cranium: an anterior head fits into a concavity formed by the sphenotic and prootic, and a posterior head articulates on the ventrolateral face of the pterotic (Figures 4, 5, 9). The symplectic is separated from the hyomandibular by cartilage dorsally, and lies within a shallow groove on the medial surface of the quadrate ventrally. The dorsal head of the quadrate is narrow, considerably less than the width of the metapterygoid. The interhyal bears a prominent medial, posterolaterally directed process that wraps around the posterior margin of the respective preopercle when the interhyal rotates upward (e.g., during a feeding event). This contact between the interhyal and the preopercle limits the dorsal rotation of the interhyal and, in turn, limits the extent of abduction of the lower jaw via ligamentous connections to the respective interopercle.

The epihyal and ceratohyal do not differ substantially from those described for other lophiiforms (Pietsch 1974, 1979). There are two hypohyals on each side (Figure 10), both of which are connected to the ceratohyal by a posteriorly directed strut. The dorsal hypohyal is further connected to an anterodorsal extension of the ceratohyal by a cylindrical piece of cartilage.

There are six branchiostegal rays all borne on the ceratohyal (Figure 10); the two anteriormost rays articulate on the medial surface, the four posterior rays on the lateral surface. Branchiostegal rays 3 and 4 are curved in an anteroventral direction, in contrast to the posterodorsal direc-

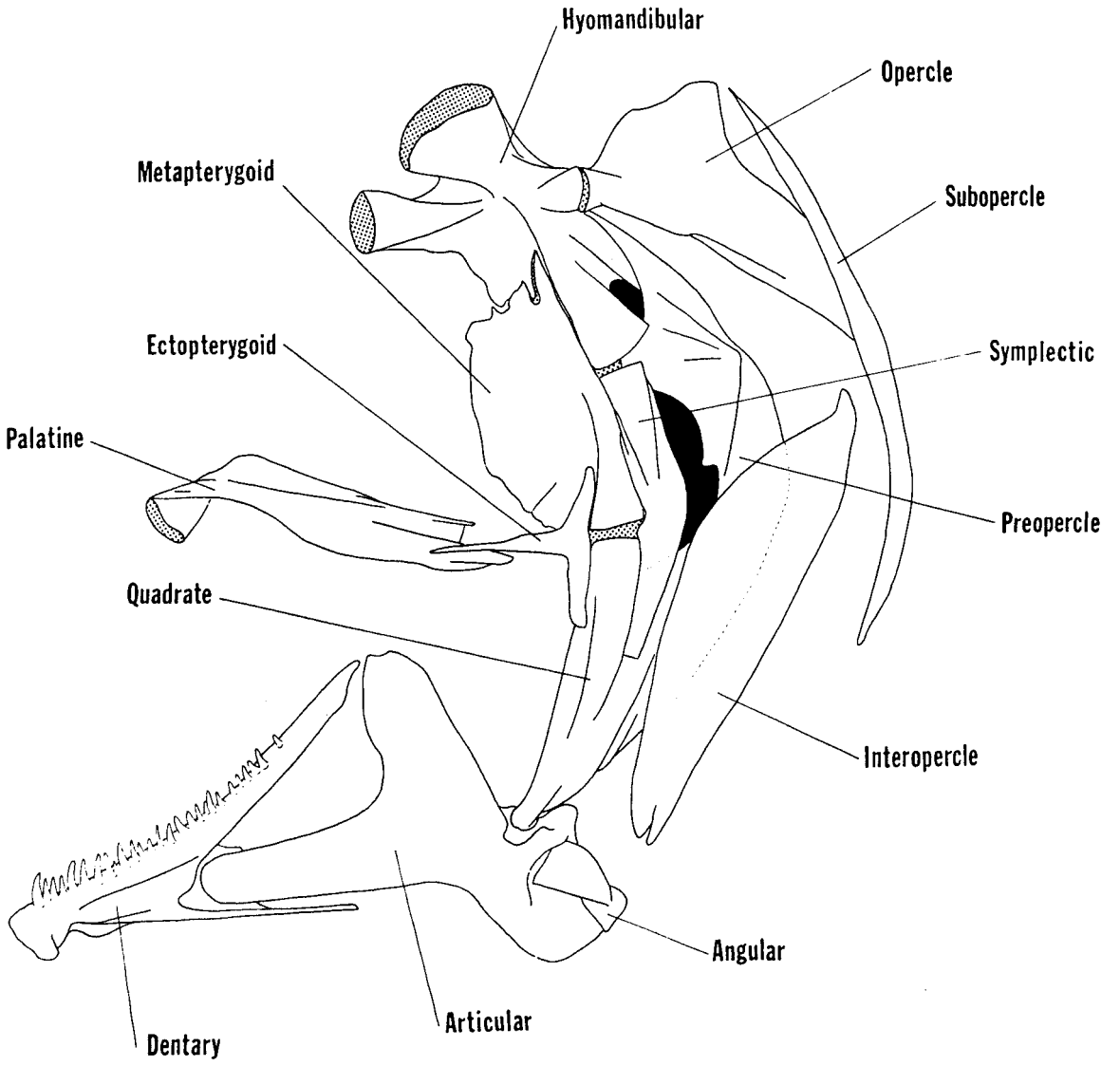

FIGURE 9.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL, right side.

tion of the remaining rays. On the left ceratohyal of the 61 mm cleared and stained specimen of *T. ocellatum* (Figure 10), the fifth branchiostegal ray is bifurcated at midlength, giving the impression of having seven total rays.

A small, triangular basihyal is present (Figure 10). The urohyal is absent in all lophiiforms.

Opercular apparatus (Figure 9).—The opercle is triangular in shape with a slightly concave posterior margin. An elongate, crescent-shaped subopercle lies medial to the ventral tip of the opercle. A subopercular spine is absent. The interopercle is large, flat, and broad. The crescent-shaped preopercle is also large, strengthening the entire length of the suspensorium.

Branchial arches (Figure 11).—There are three pharyngobranchials. That of the first arch is a small, toothless, suspensory pharyngobranchial; those of the second and third arches are considerably larger, tooth-bearing elements closely at-

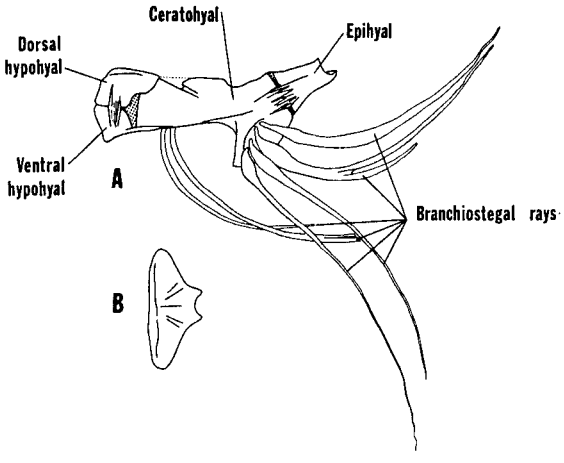

FIGURE 10.—Hyoid apparatus of *Tetrabrachium ocellatum*: A. AMS IB.7178, 61 mm SL, left lateral view; B. Basihyal, AMS IB.7177, 56 mm SL, ventral view, anterior to the left.

tached to each other and to the dorsal end of epibranchials II through IV. Epibranchial I is triradiate in shape, articulating with ceratobranchial I proximally, bearing pharyngobranchial I distally, and attached by a short ligament to the proximal end of epibranchial II medially. Ceratobranchials I through IV are toothless. The expanded, proximal end of each ceratobranchial V bears about 19 to 21 depressible teeth arranged in two rows. Hypobranchial I is a simple, rod-shaped

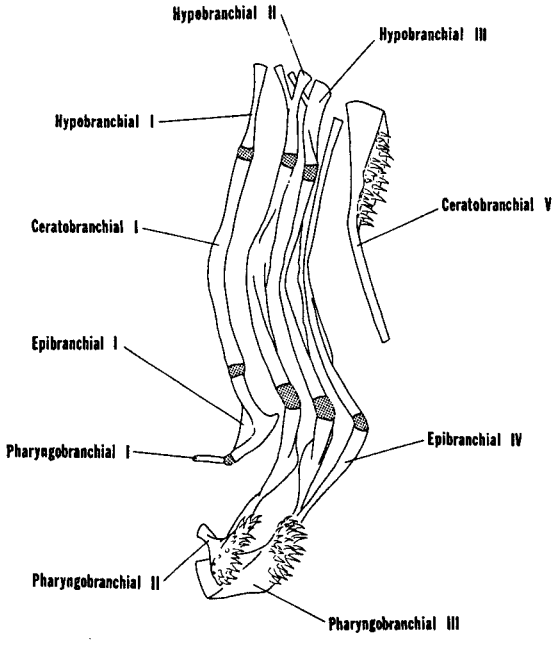

FIGURE 11.—Branchial arches of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

element. Hypobranchials II and III are bifurcated proximally. Ossified basibranchials are absent.

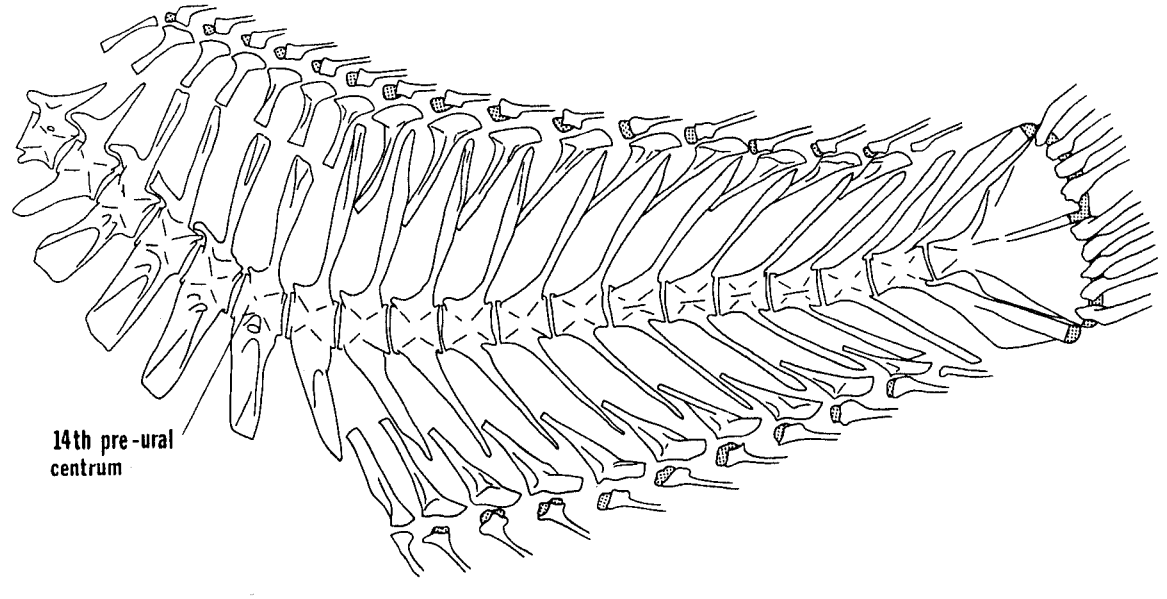

FIGURE 12.—Vertebrae, caudal skeleton, and median fins of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

Vertebrae and caudal skeleton (Figure 12).—In the two cleared and stained specimens of *T. ocellatum* examined, there are 22 vertebrae (including the last centrum to which is fused the hypural plate; Pietsch 1972:38). Preural centra 2 through 18 bear complete haemal arches and are considered caudal vertebrae. The neural spines of preural centra 14 through 22 are considerably shorter than those of the more posterior centra; correspondingly, the seven anteriormost proximal radials of the soft dorsal fin are also short so that they do not interdigitate with the respective neural spines. Further, there appears to be little if any connective tissue between the elements of the soft dorsal fin and the vertebral column in this region allowing for independent movement of the anterior portion of the fin relative to the axial skeleton. The haemal spines of preural centra 14 through 17 are unusually broad and laterally compressed.

The hypural plate, slightly notched posteriorly, bears the overlapping bases of nine principle caudal rays. The central seven caudal rays are bifurcated distally. There are no epurals.

Median fins and illicial apparatus (Figures 12, 13).—The spinous dorsal fin consists of three spines. The anteriormost two are supported by a single, elongate, horizontally situated pterygiophore (Figure 13) that is loosely attached to the dorsal surface of the cranium between the anterior halves of the frontal bones by three pairs of extrinsic illicial muscles (Bertelsen 1951:18, fig. 4; Bradbury 1967, fig. 2; Winterbottom 1974:284, fig. 44). The illicial bone (Bradbury 1967:401) is considerably reduced in size relative to other lophiiforms (Gregory 1933, fig. 265, 266, 267; Pietsch 1972, 1974, 1979). The second spine is considerably thicker and approximately three times longer than the first. The third spine, slightly longer and thicker than the second, is supported by a second, elongate, and horizontally placed, cephalic pterygiophore that is tightly connected to the posterior, dorsomedial surface of the supraoccipital and anterior, dorsomedial margins of the epiotics. The proximal end of each spine is bifurcated, each fork bearing a small, medially directed prong; the prongs of each spine fit within a large, rounded foramen located on a highly compressed, bladelike dorsal expansion of the respective pterygiophore.

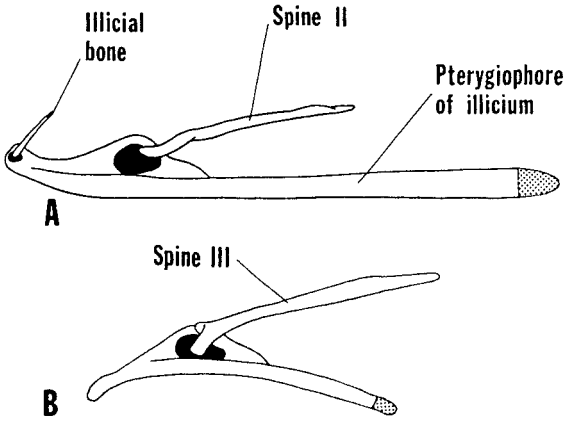

FIGURE 13.—Spinous dorsal fin of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL: A. Illicial apparatus, second dorsal spine, and common pterygiophore; B. Third dorsal spine and pterygiophore.

The soft dorsal fin consists of 16 biserial, segmented, and unbranched rays, each supported by a cartilaginous distal radial and an ossified proximal radial. The proximal end of the anteriormost proximal radial lies above the neural spine of the 19th preural centrum, while the proximal end of the last proximal radial lies between the neural spines of the fourth and fifth preural centra.

The anal fin consists of 11 biserial, segmented, and unbranched rays. The first two rays share a single supporting radial. The remaining rays are each supported by a small, cartilaginous distal radial and an elongate, ossified proximal radial. The proximal ends of the two anteriormost proximal radials lie between the haemal spines of the 12th and 13th preural centra. The proximal radials of the nine remaining anal fin rays have a one-to-one correspondence with the haemal spines, so that the radial of the last anal ray lies between the haemal spines of the fourth and fifth preural centra. The posteriormost rays of the dorsal and anal fins are broadly connected by a membrane to the dorsal and ventral margins of the caudal fin so that a caudal peduncle is absent.

Pectoral and pelvic girdles and fins (Figure 14).—The posttemporal is unusually large and connected to the posterolateral corner of the cranium in such a way as to allow for considerable movement (relative to the cranium) in an anterodorsal-posteroventral plane. The bone consists of a broad, dorsal flange that overlaps the dorsolateral surface of the epiotic, pterotic, and exoccipital. A large ligament originates on the posterodorsal margin of the prootic and inserts on the tip of

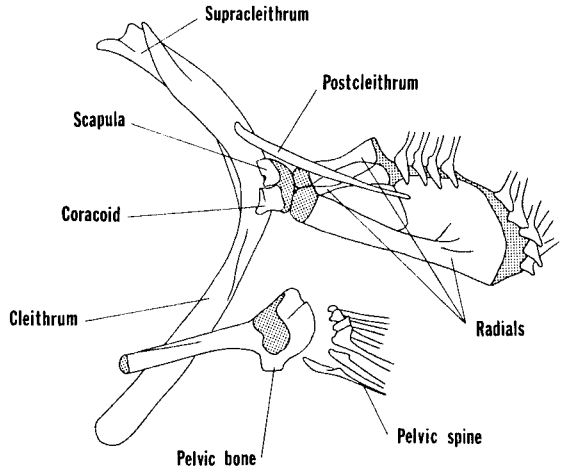

FIGURE 14.—Medial view of right pectoral girdle, and pectoral and pelvic fins of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. Cartilaginous radials supporting pelvic fin rays and cartilaginous distal radials supporting pectoral fin rays not shown; see text.

an elongate, ventromedially directed extension of the posttemporal.

The supracleithrum, cleithrum, coracoid, and scapula (Figure 14) are similar to those described for other lophiiforms (Gregory 1933, fig. 265; Pietsch 1972, 1974). A cleithral spine is absent. There is a single rodlike postcleithrum.

The pectoral fin is supported by three pectoral radials (Figure 14). The two dorsalmost radials are similar in size and shape. The third or ventralmost radial is considerably larger; its expanded distal portion bears the bases of nine unbranched, pectoral fin rays (each ray associated with a small, cartilaginous distal radial; not shown in Figure 14). The pectoral fin itself is divided into two portions: a dorsal portion consisting of four rays that are interconnected by a membrane, and a ventral portion consisting of five rays that are similarly connected to each other, but also to the lateral surface of the body. In a similar way, the pectoral fin lobe is connected by a membrane to the rays of the respective pelvic fin (Figure 1B). The pelvic bone, nearly as long as the ventralmost pectoral radial, bears on its expanded distal end a single spine and five unbranched pelvic fin rays (each ray associated with a small, cartilaginous radial; not shown in Figure 14).

Skin spines.—Dermal spines are absent except for the very rare occurrence of a tiny, crescent-shaped spinule associated with an individual pore of the acoustico-lateralis system of the head and trunk.

COMPARATIVE OSTEOLOGY OF ANTENNARIOID FAMILIES

The following discussion is based primarily on an osteological comparison of a representative of each of six major subgroups of the Antennarioidei (here recognized as families; see Phylogenetic Relationships and Appendix below): *Antennarius* Daudin, thought to be the least derived genus of the Antennariidae (see Phylogenetic Relationships below); *Tetrabrachium* Günther, the only genus of the Tetrabrachiidae; *Lophichthys* Boeseman, the only genus of the Lophichthyidae; *Brachionichthys* Bleeker, the only extant genus of the Brachionichthyidae (see p. 416); *Chaunax* Lowe, the only genus of the Chaunacidae; and *Dibranchus* Peters, an underived genus of the Ogcocephalidae (see Bradbury 1967). Only those comparative aspects that might have a bearing on the phylogenetic interrelationships of these taxa are discussed.

Cranium (Figures 3-6, 15-19).—In *Tetrabrachium* and *Antennarius* the ventral surface of the vomer is strongly concave (as seen in anterior view, Figure 6). A laterally compressed, keellike posteromedial process emerges from the ventral surface of this bone and fits within a deep groove on the anteroventral surface of the parasphenoid; the ventral margins of the posteromedial process of the vomer and the anterior end of the parasphenoid are strongly convex (as seen in lateral view, Figure 4). In all other antennarioids examined the posteromedial process of the vomer is flush with the more or less flat ventral surface of this bone; the ventral margins of the vomer and anterior end of the parasphenoid (as seen in lateral view) are straight to slightly concave.

Other osteological variation in the crania of antennarioids occurs primarily in the shape and relative position of the frontal bones. In *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Dibranchus* (Figures 15-17, 19) the frontals are broad and roughly triangular in shape, well separated from each other anteriorly, but meeting on the midline posteriorly. The narrow interorbital space formed by these elements in *Tetrabrachium* is absent (compare Figures 3 and 15). The anterior ends of the frontals of *Lophichthys* are exceptionally narrow, gradually tapering to a point (Figure

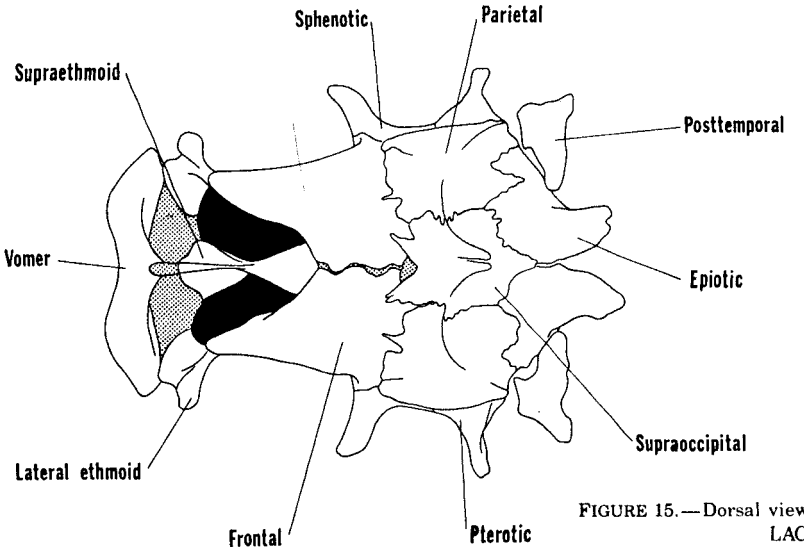

FIGURE 15.—Dorsal view of cranium of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

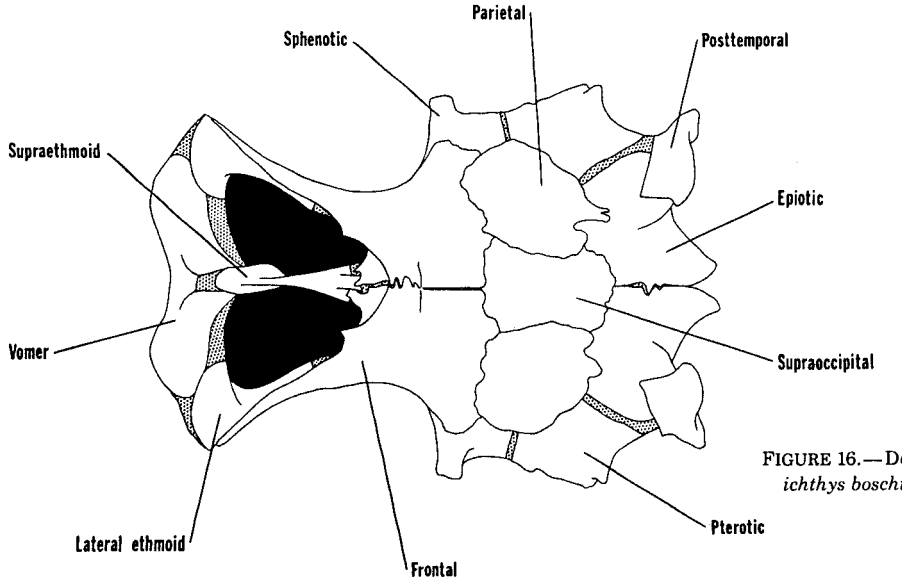

FIGURE 16.—Dorsal view of cranium of *Lophichthys boschimai*, UW 20773, 47 mm SL.

16); they diverge laterally to a much greater extent than in the other genera examined in response to a much wider vomer and laterally expanded lateral ethmoids.

In contrast to all other antennarioids examined, the frontals of *Chaunax* (Figure 18) are elongate and narrow, meeting on the midline for their entire length. The lateral ethmoids of this genus are also unusually long and narrow.

In *Antennarius*, *Lophichthys*, *Tetrabrachium*, *Chaunax*, and *Dibranchus* the parietals are well separated from each other by the supraoccipital. In *Brachionichthys*, however (Figure 17), these elements approach each other above the supraoccipital and meet on the midline, roofing over a small longitudinal passageway within which lies the posterior tip of the pterygiophore of the third dorsal fin spine.

Mandibular arch (Figures 8, 9, 20-25).—The premaxilla of *Antennarius* is very similar to that of *Tetrabrachium* (Figures 8, 20A); both genera

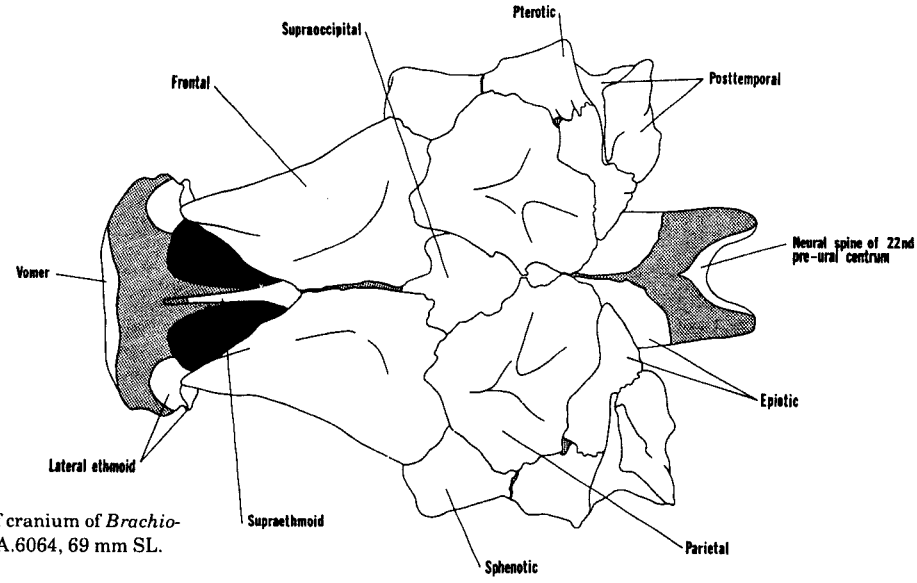

FIGURE 17.—Dorsal view of cranium of *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

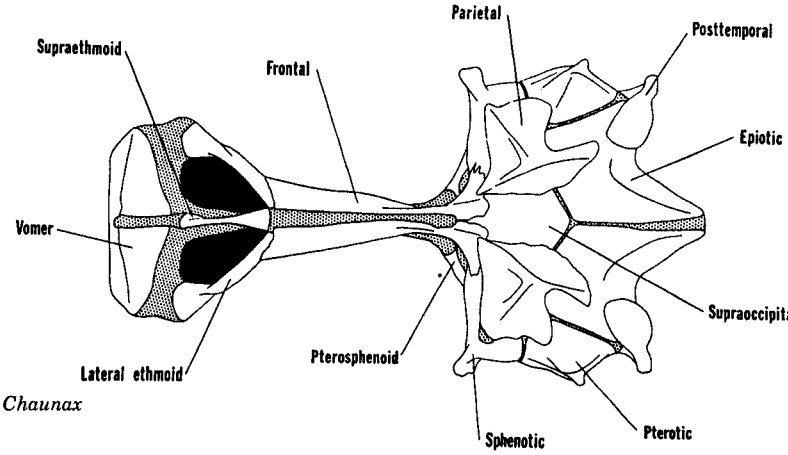

FIGURE 18.—Dorsal view of cranium of *Chaunax pictus*, UW 20770, 90 mm SL.

are characterized by having a spatulate postmaxillary process. The premaxilla of *Lophichthys* is also quite similar but bears a narrow, tapering postmaxillary process (Figure 20B). The premaxillae of the remaining antennarioid taxa examined are each somewhat different from these and from each other. In *Brachionichthys* (Figure 20C), the ascending and articular processes are at right angles to the toothed portion of the bone; the toothed portion is unusually short, about as long as the postmaxillary process and considerably shorter than the ascending process. In *Chaunax* (Figure 20D), the shape and relative proportions of the ascending, articular, and toothed processes of the premaxilla are similar to those of *Antennarius* and *Tetrabrachium*; the postmaxillary process, however, is represented by a large flange of bone, broadly connected to the toothed process. In *Dibranchus* (Figure 20E), the ascending and articular processes together form an acute angle with the postmaxillary and toothed processes; the articular process is nearly as long as the ascending process; and the postmaxillary process is connected by bone to the toothed process of the premaxilla for about half its length.

Palatine arch (Figures 9, 21-25).—A mesopterygoid is present in *Antennarius*, *Chaunax*, and

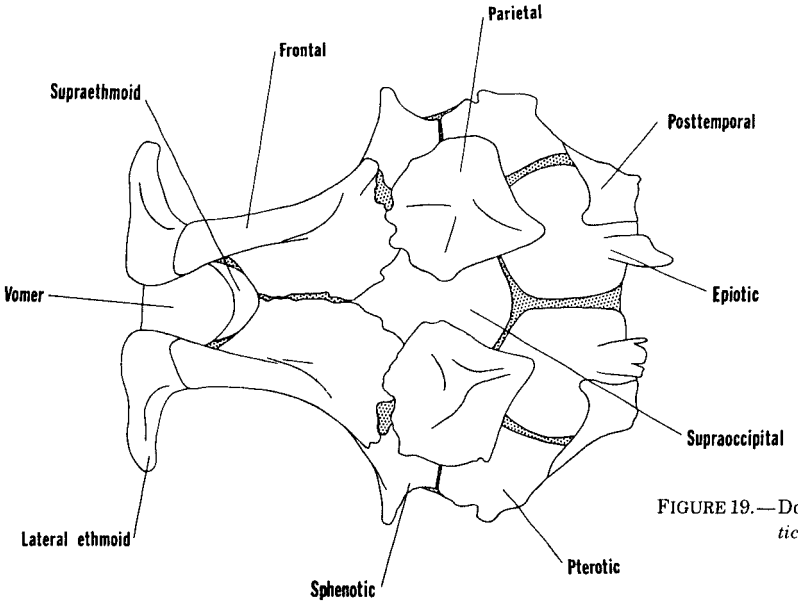

FIGURE 19.—Dorsal view of cranium of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Dibranchus (Figures 21, 24, 25), but absent in *Tetrabrachium*, *Lophichthys*, and *Brachionichthys* (Figures 9, 22, 23). The triradiate ectopterygoid of *Antennarius*, *Tetrabrachium*, and *Lophichthys* (T-shaped in *Tetrabrachium* and *Antennarius*, Figures 9, 21, but Y-shaped in *Lophichthys*, Figure 22) overlaps the medial surface of the metapterygoid dorsally; in *Chaunax* and *Dibranchus* the ectopterygoid is crescent-shaped and makes no contact with the metapterygoid. An ectopterygoid is absent in the larger (69 mm SL) specimen of *Brachionichthys* examined (Figure 23A) but represented by a small, weakly ossified remnant in the smaller specimen (42 mm SL) (Figure 23B).

The palatine is well toothed in *Antennarius*, *Lophichthys*, and *Chaunax*, but toothless in *Tetrabrachium* and in the single cleared and stained specimen of *Dibranchus* examined (palatine teeth are present in some ogcocephalid genera and sometimes in *Dibranchus*; Bradbury 1967: 409). In the absence of a mesopterygoid and reduced (or absent) ectopterygoid, the toothless palatine bone of *Brachionichthys* is widely separated from the suspensorium (Figure 23).

Hyoid arch (Figures 9, 10, 21-27).—In *Tetrabrachium* and *Antennarius* (Figures 9, 21) the dorsal head of the quadrate is relatively narrow, somewhat less than the width of the ventral head of the metapterygoid. In contrast, the quadrate of *Lophichthys*, *Brachionichthys*, *Chaunax*, and *Dibranchus* (Figures 22-25) is broad, making a much broader contact with an expanded metapterygoid. In *Dibranchus* the quadrate is exceptionally broad, the anterior half of the dorsal margin coming into contact with the mesopterygoid (Figure 25).

The interhyal of *Antennarius*, *Lophichthys*, and *Brachionichthys* is similar to that of *Tetrabrachium* (but in contrast to that of *Chaunax* and *Dibranchus*; Figures 24, 25) in having a prominent, medial, posterolaterally directed process that wraps around the posterior margin of the respective preopercle when the interhyal rotates upward (Figure 26). This contact between the interhyal and preopercle limits the dorsal rotation of the interhyal and, in turn, limits the extent of abduction of the lower jaw via ligamentous connections with the respective interopercle.

In shape and relative proportions, the branchiostegal rays of *Antennarius*, *Lophichthys*, and *Brachionichthys* are similar to those of *Tetrabrachium*; *Brachionichthys*, however, has lost the anteriormost element in this series (Table 2). In *Chaunax* and *Dibranchus* (Figure 27) the posteriormost branchiostegal ray is greatly enlarged, becoming ankylosed to the ventromedial margin of the subopercle in the later genus.

A small basihyal is present in *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Chaunax*, but absent in *Brachionichthys* and *Dibranchus*.

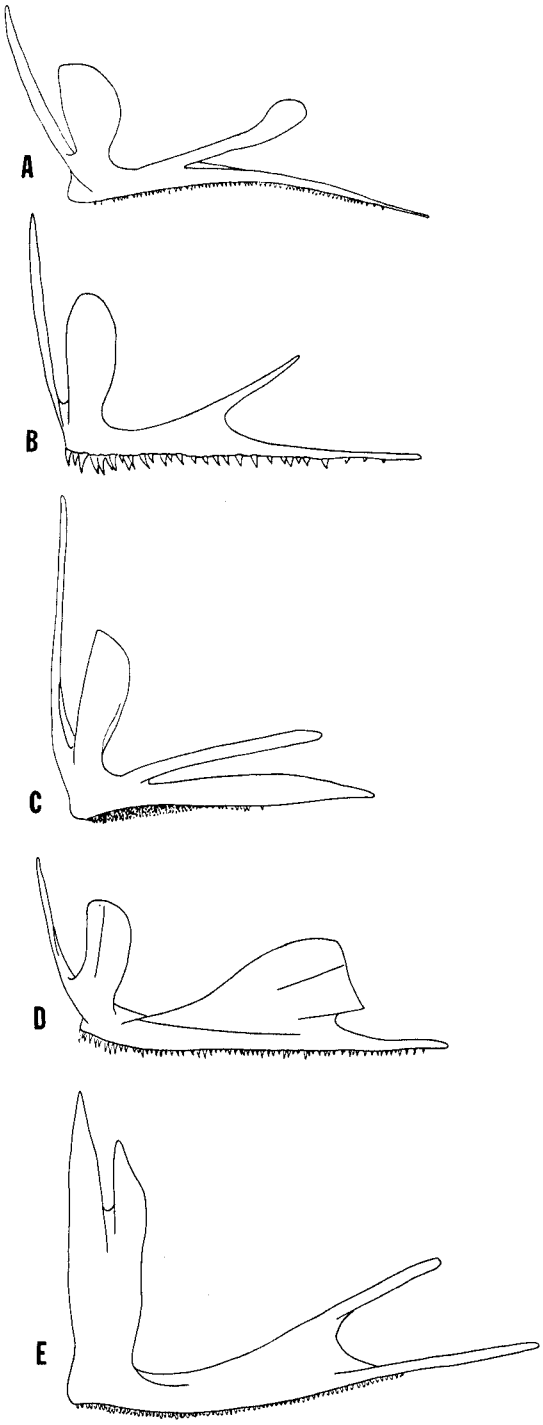

FIGURE 20.—Premaxillae, left lateral views: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Lophichthys boschmai*, UW 20773, 47 mm SL; C. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL; D. *Chaunax pictus*, UW 20770, 90 mm SL; E. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Opercular apparatus (Figures 9, 21-25).—The opercle and subopercle of *Antennarius*, *Tetrabrachium*, and *Brachionichthys* are similar except in the following details: both elements are considerably reduced in size in *Tetrabrachium* and *Antennarius* (Figures 9, 21); in contrast to the smooth, slightly concave (sometimes deeply incised), posterior margin of the opercle of *Antennarius*, *Tetrabrachium*, and *Lophichthys*, the posterior margin of this bone in *Brachionichthys* is broken into numerous, weakly ossified, bony filaments (Figure 23A); in contrast to the relatively broad, spined subopercle of *Antennarius* and *Lophichthys*, the subopercle of *Tetrabrachium* and *Brachionichthys* (Figures 9, 23A) is a narrow, crescent-shaped element lacking a subopercular spine.

In contrast to the small opercle and subopercle of *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Brachionichthys*, those of *Chaunax* and *Dibranchus* (Figures 24, 25) are greatly enlarged and expanded posteriorly. A well-developed subopercular spine is present in *Chaunax*, but absent in *Dibranchus*.

The interopercle of *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 21-23) is similar to that of *Tetrabrachium*; the interopercle of *Chaunax* and *Dibranchus* (Figures 24, 25) is much more slender and elongate.

Branchial arches (Figures 11, 28-32).—Pharyngobranchial I is represented by a simple, rod-shaped element in *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29). In the single specimen of *Chaunax* examined pharyngobranchial I is Y-shaped (Figure 31). This element is toothless in *Antennarius*, *Tetrabrachium*, and *Chaunax*, but bears a series of approximately eight small teeth in *Lophichthys* (Figure 29). Pharyngobranchial I is absent in *Brachionichthys* and *Dibranchus*. Pharyngobranchial IV is absent in all antennarioids.

In *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29), epibranchial I is triradiate in shape, toothless in *Antennarius* and *Tetrabrachium*, but bearing a single row of about 13 small teeth in *Lophichthys* (Figure 29). A similarly shaped epibranchial I, associated with three and two tooth plates is present in *Chaunax* and *Dibranchus*, respectively (Figures 31, 32). An L-shaped epibranchial I, associated with a single tooth plate, is present in *Brachionichthys* (Figure

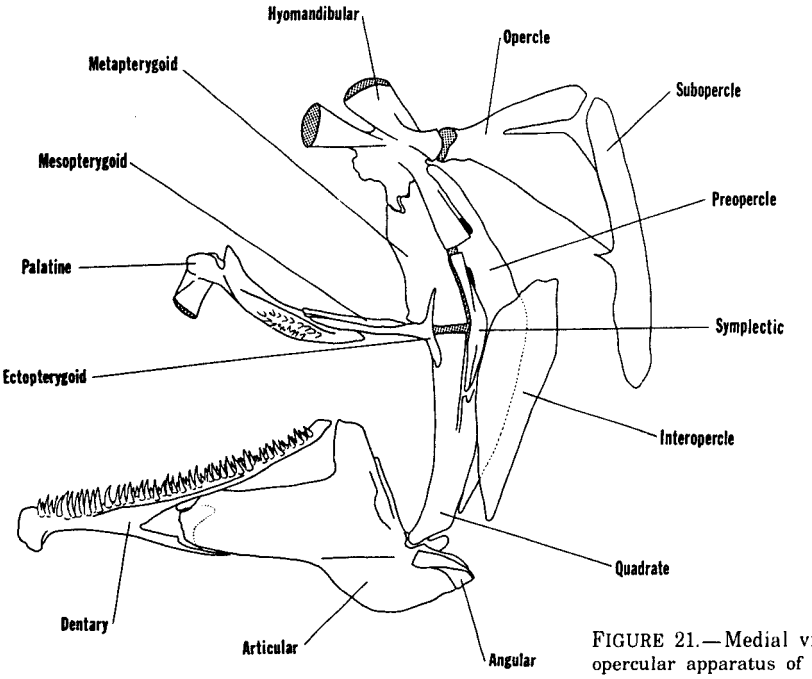

FIGURE 21.—Medial view of lower jaw, suspensorium, and opercular apparatus of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

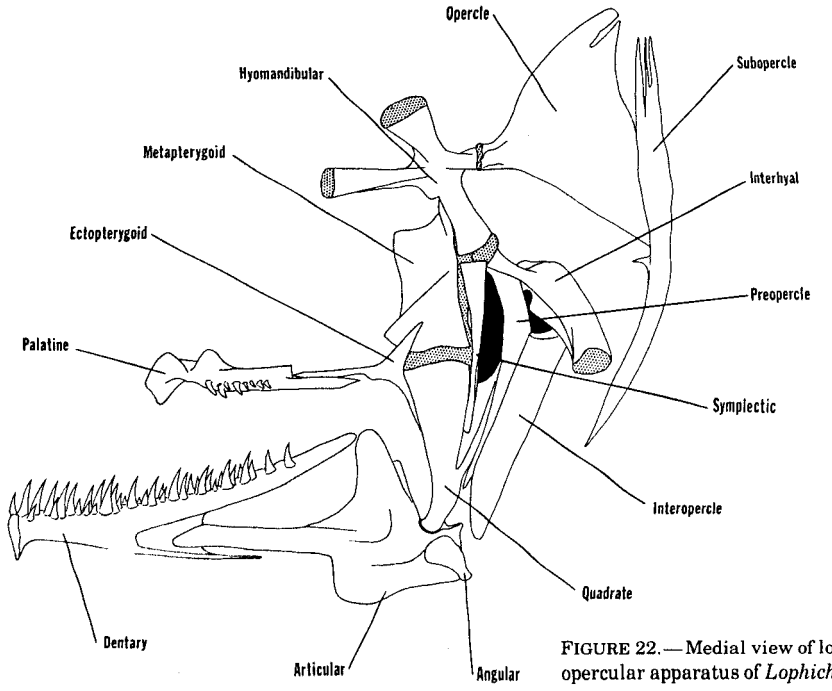

FIGURE 22.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Lophichthys boschmai*, UW 20773, 47 mm SL.

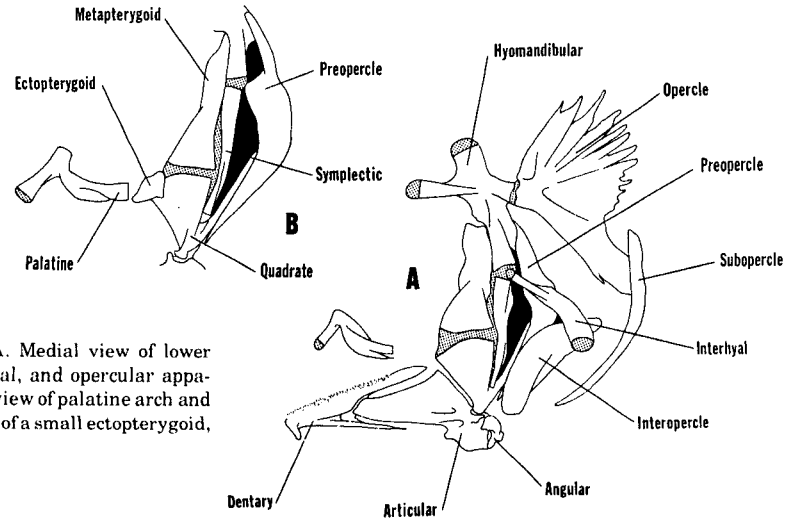

FIGURE 23.—*Brachionichthys hirsutus*: A. Medial view of lower jaw, palatine bone, suspensorium, interhyal, and opercular apparatus, AMS IA.6064, 69 mm SL; B. Medial view of palatine arch and suspensorium, right side, showing presence of a small ectopterygoid, UW 20769, 42 mm SL.

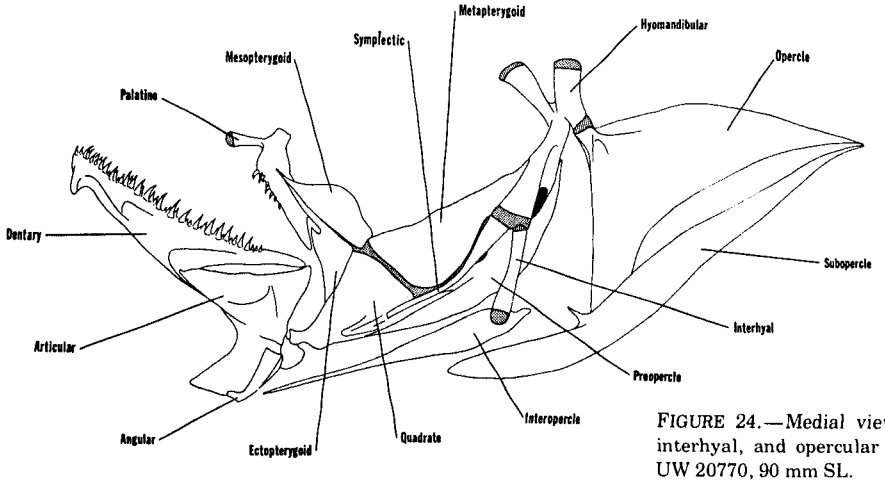

FIGURE 24.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Chaunax pictus*, UW 20770, 90 mm SL.

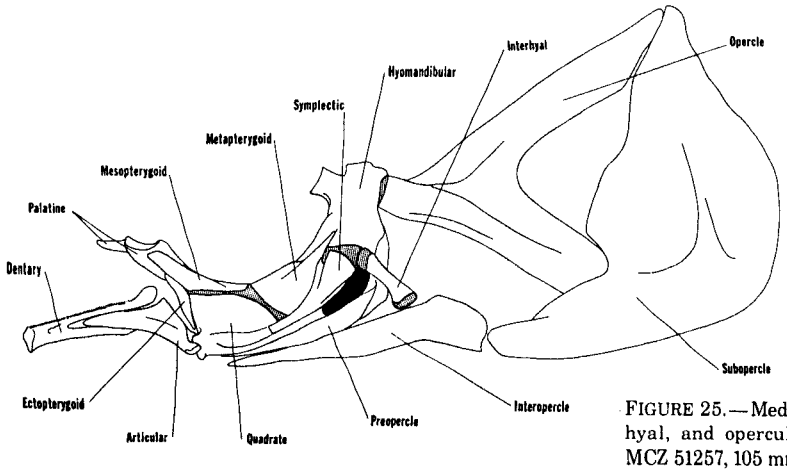

FIGURE 25.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

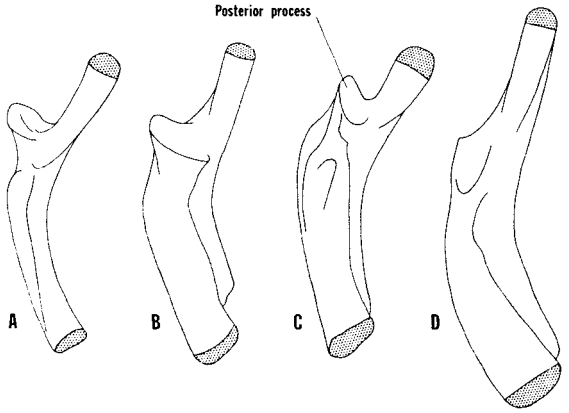

FIGURE 26.—Lateral view of interhyal, right side: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL; C. *Lophichthys boschmai*, UW 20773, 47 mm SL; D. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

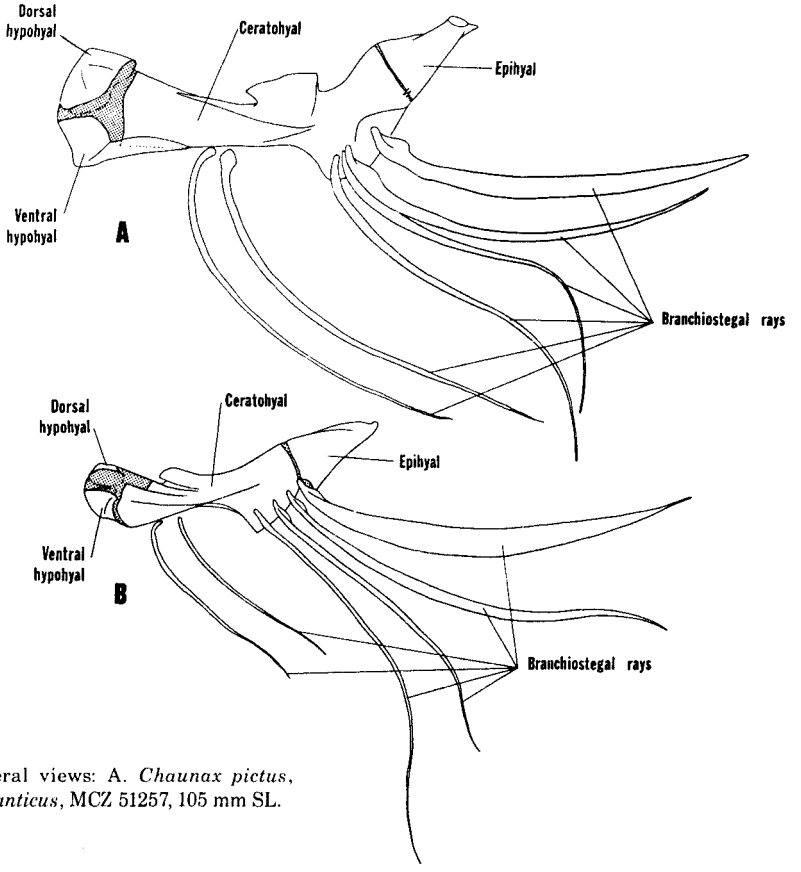

FIGURE 27.—Hyoid apparatus, left lateral views: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

TABLE 2.—Characters of representative genera of the major subgroups of the Antennarioidei.

Item	*Antennarius*	*Tetrabrachium*	*Lophichthys*	*Brachionichthys*	*Chaunax*	*Dibranchus*
Branchiostegal rays	2+4	2+4	2+4	1+4	2+4	2+4
Pharyngobranchial I	rod shaped (toothless)	rod shaped (toothless)	rod shaped (toothed)	absent	forked (toothless)	absent
Palatine teeth	present	absent	present	absent	present	absent
Epibranchial teeth						
Arch I	absent	absent	single row	1 plate	3 plates	2 plates
Arch III	absent	absent	absent	absent	absent	1 plate
Ceratobranchial teeth						
Arch I	absent	absent	absent	2 plates	present	present
Arch II	absent	absent	absent	1 plate	present	present
Arch III	absent	absent	absent	1 plate	present	present
Arch IV	absent	absent	absent	absent	present	present or absent
Hypobranchial II	bifurcated	bifurcated	bifurcated	simple	simple	absent
Hypobranchial III	bifurcated	bifurcated	bifurcated	simple	simple	absent
Pseudobranch	present	absent	absent	absent	absent	absent
Swim bladder	present	absent	absent	absent	absent	absent
Basihyal	present	present	present	absent	present	absent
Vertebrae (precaudal)	19(4)	22(4)	19(4)	22(4)	19(4)	19(6)
Epural	1	0	remnant present or absent	0	1	1
Dorsal fin rays	11-15	16-17	12-13	17	12	5
Anal fin rays	6-9	11-12	9	7	7	4
Pectoral fin radials	3	3	3	2	3	3
Pectoral fin rays	7-14	4+5	7	8	14	14
Pelvic fin rays	I+5	I+5	I+5	I+4	I+4	I+5

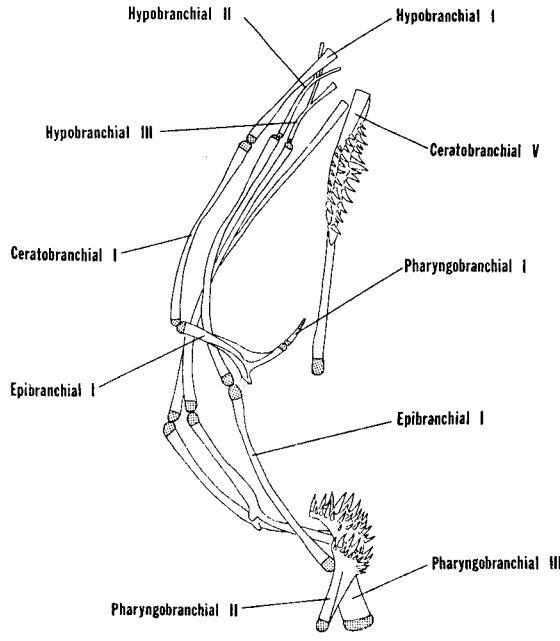

FIGURE 28.—Branchial arches of *Antennarius sanguineus*, LACM 8125, 76 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

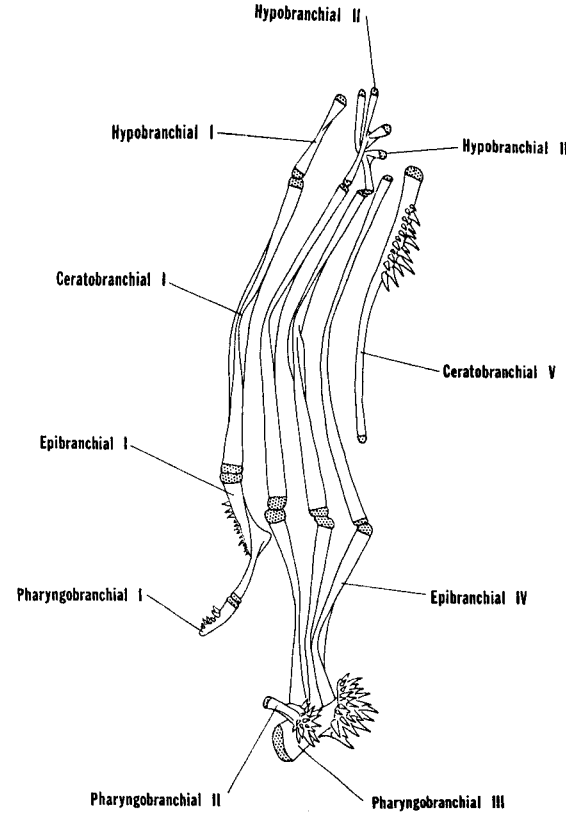

FIGURE 29.—Branchial arches of *Lophichthys boschmai*, UW 20773, 47 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

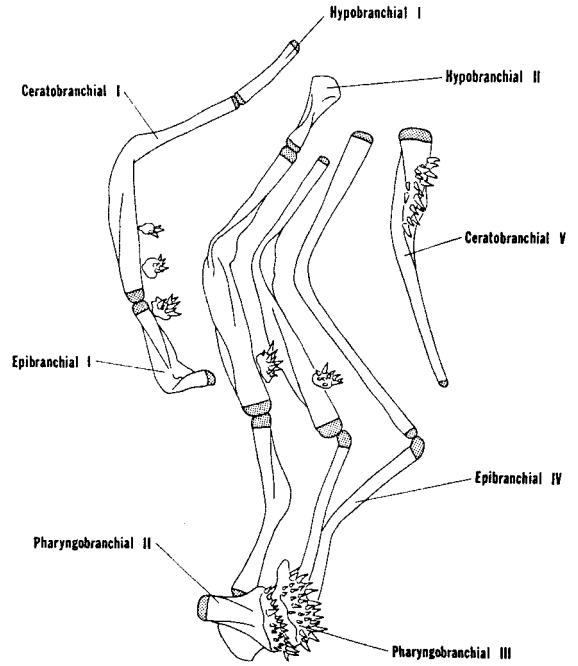

FIGURE 30.—Branchial arches of *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

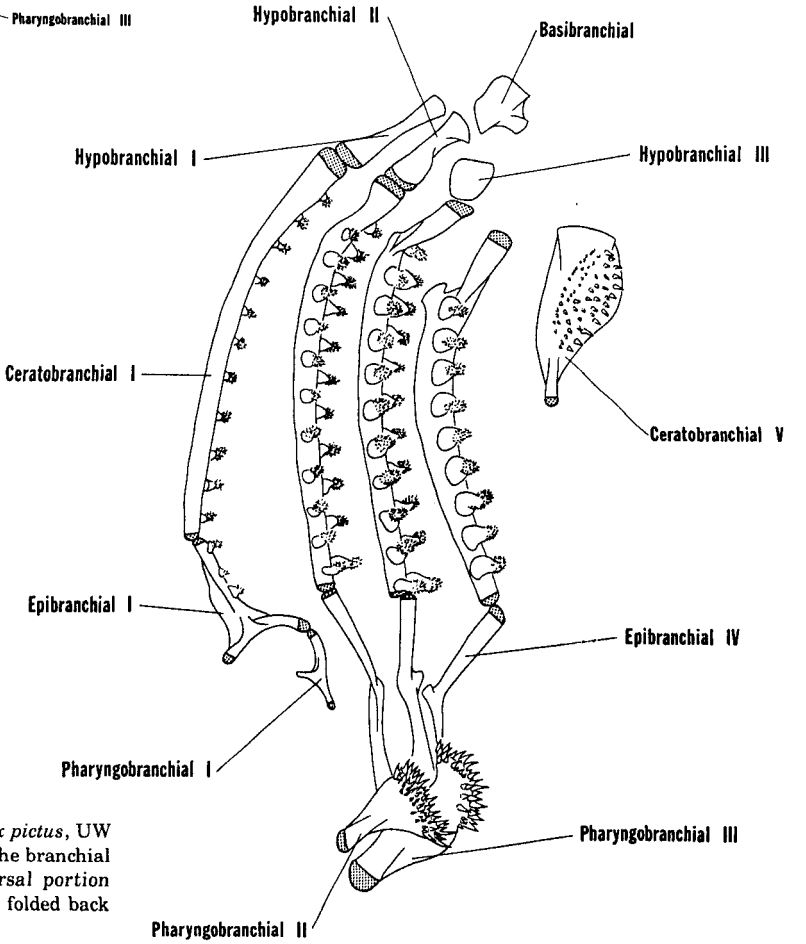

FIGURE 31.—Branchial arches of *Chaunax pictus*, UW 20770, 90 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

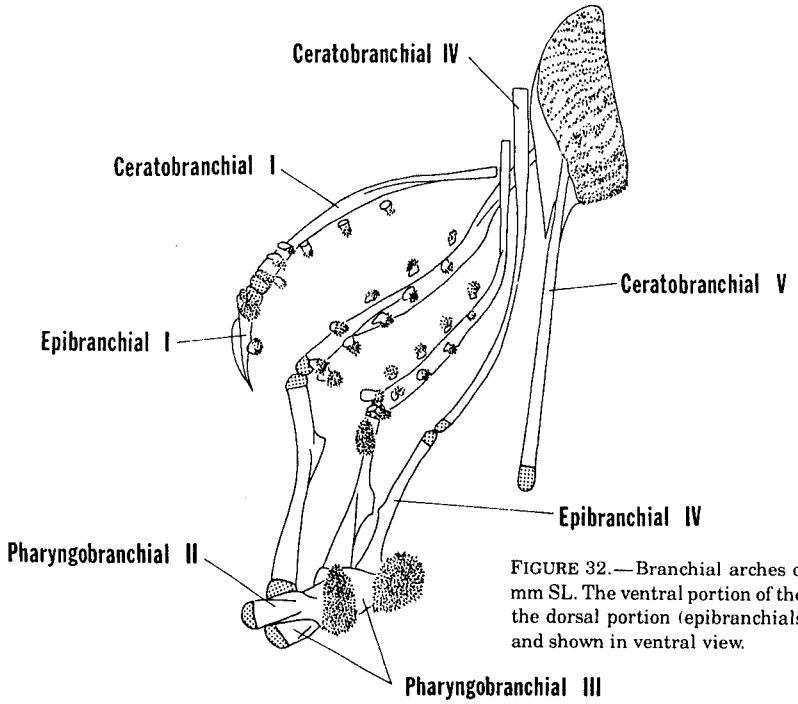

FIGURE 32.—Branchial arches of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL. The ventral portion of the branchial basket is shown in dorsal view. the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

30). Epibranchial III is toothless in all antennarioids examined except in *Dibranchus* (Figure 32) where this bone is associated with a single tooth plate.

Ceratobranchials I through IV are toothless in *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29). In *Brachionichthys* (Figure 30), one to three tooth plates are present on ceratobranchials I through III; in *Chaunax* (Figure 31), tooth plates are present on ceratobranchials I through IV; in *Dibranchus* (Figure 32), tooth plates are present on ceratobranchials I through III (but also sometimes present on ceratobranchial IV, see Bradbury 1967:408) (Table 2).

In contrast to the separate, individual teeth present on pharyngobranchial I and epibranchial I of *Lophichthys* (Figure 29), those present on epibranchial I and ceratobranchials I through IV of *Brachionichthys*, *Chaunax*, and *Dibranchus* (Figures 30-32) are born in clusters on individual tooth plates. The tooth plates of *Chaunax* and *Dibranchus* (Figures 31, 32) (and a number of other ogcocephalid taxa, see Bradbury 1967) differ from those of *Brachionichthys* (Figure 30) and from those of all other lophiiforms in being raised, pedicallike structures bearing a cluster of numerous, tiny teeth at the apex (but see Bradbury 1967, fig. 7, for other forms of gill teeth in ogcocephalids).

Ceratobranchial V is well toothed in all antennarioids examined. In *Tetrabrachium*, *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 11, 28-30), this bone consists of a narrow, toothed proximal portion and a tapering, cylindrical distal portion; in *Chaunax* (Figure 31) only a triangular, toothed portion is present. In *Dibranchus* (Figure 32), ceratobranchial V is greatly enlarged, consisting of a finely toothed, expanded proximal portion and a long, cylindrical distal shaft.

Hypobranchial I of *Tetrabrachium*, *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax* (Figures 11, 28-31) and hypobranchial II of *Brachionichthys* and *Chaunax* (Figures 30, 31) are simple, rod-shaped bones. Hypobranchials II and III of *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29) are bifurcated proximally (this feature is probably plesiomorphic for lophiiforms since a similar situation is present in all batrachoidids examined). Hypobranchial III is absent in *Brachionichthys* (Figure 30), but represented by a semicircular ossification in *Chaunax* (Figure 31). There are no ossified hypobranchials in the single specimen of *Dibranchus* examined (Figure 32, Table 2).

Basibranchials are represented by a single ossification in *Chaunax* (Figure 31), but are absent in *Antennarius*, *Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and *Dibranchus*.

Gill filaments are absent on arch I of *Chaunax* and *Dibranchus*. Filaments are present as holobranchs on arch I of *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Brachionichthys*, and on arches II and III of all antennarioids examined. Hemibranchs are present on arch IV of all antennarioids examined (filaments may sometimes be absent on arch IV of *Dibranchus*; Bradbury 1967:408).

A small pseudobranch is present in *Antennarius*, but absent in all other antennarioids examined.

Vertebrae and caudal skeleton (Figures 12, 33-35).—The vertebral column of *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 33, 34A) is similar to that of *Tetrabrachium* (Figure 12) in having the neural spines of three to four anterior vertebrae (preural centra 11-13 in *Antennarius*, Figure 33; 14-17 in *Tetrabrachium*, Figure 12; 12-14 in *Lophichthys*, Figure 34A; and 15-18 in *Brachionichthys*) short (spatulate in all antennarioids examined except for *Lophichthys*, *Chaunax*, *Dibranchus*, and a few specialized antennariid genera, i.e., *Echinophryne*, *Trichophryne*, and *Rhycherus*; see Appendix) and not interdigitating with the corresponding proximal radials of the overlying soft dorsal fin (this feature appears to be plesiomorphic for the Lophiiformes being more or less developed in nearly all taxa).

In *Chaunax* (Figure 35A), the neural spines are similar throughout the length of the axial skeleton. In *Dibranchus* (Figure 35B), the vertebral column and caudal skeleton are strongly modified for a benthic life-style. The neural and haemal spines of all centra are short and broad. Preural centra 14 through 18 are considerably more elongate than the remaining centra; the neural spines of these centra are expanded anteroposteriorly and compressed laterally to form a solid bony partition along the dorsal midline. Mobility in this region of the axial skeleton is severely reduced due to large, overlapping prezygapophyses (considerable movement is retained, however, between the two anteriormost centra, preural centra 18 and 19).

In both specimens of *Lophichthys* examined a peculiar bridging of bone is present between the distal tips of the haemal spines of the 14th through the 16th preural centra (Figure 34A). This kind of ossification has not been described for any other lophiiform.

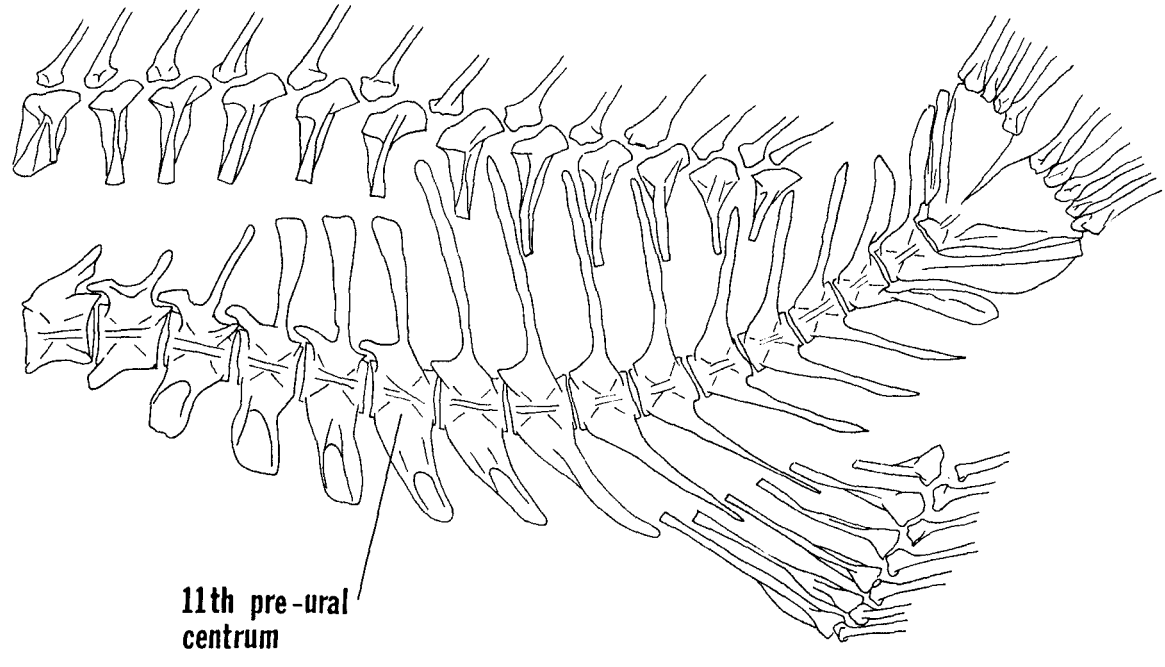

FIGURE 33.—Vertebrae, caudal skeleton, and median fins of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

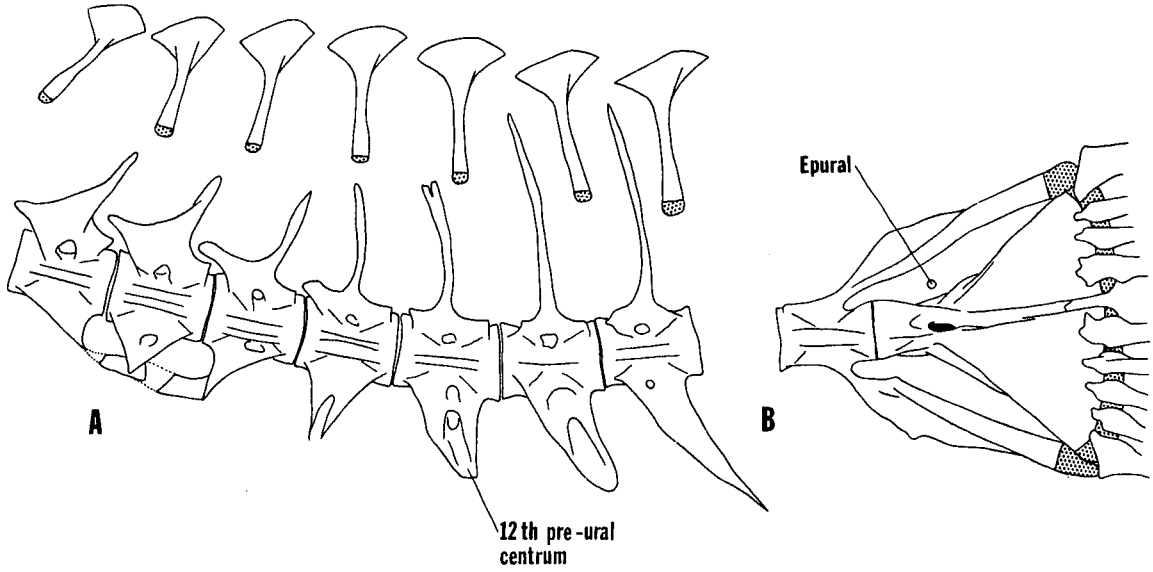

FIGURE 34.—*Lophichthys boschmai*, UW 20773, 47 mm SL: A. Preural centra 12 through 16, showing partially ossified connection between distal tips of haemal spines of preural centra 14 through 16; B. Caudal skeleton showing remnant of epural.

A single epural is present in *Antennarius*, *Chaunax*, and *Dibranchus* (Figures 33, 35) (oval and laterally compressed in the later genus). In the larger (47 mm) of the two specimens of *Lophichthys* (Figure 34B) examined, the epural is represented by a tiny circular ossification. No trace of this element is present in the smaller (44 mm) individual of *Lophichthys*, or in any other antennarioid examined.

Axial skeletal elements of the antennarioid taxa examined are compared in Table 2.

Medial fins and illicial apparatus (Figures 13, 36-39).—The spinous dorsal fin of *Tetrabrachium*,

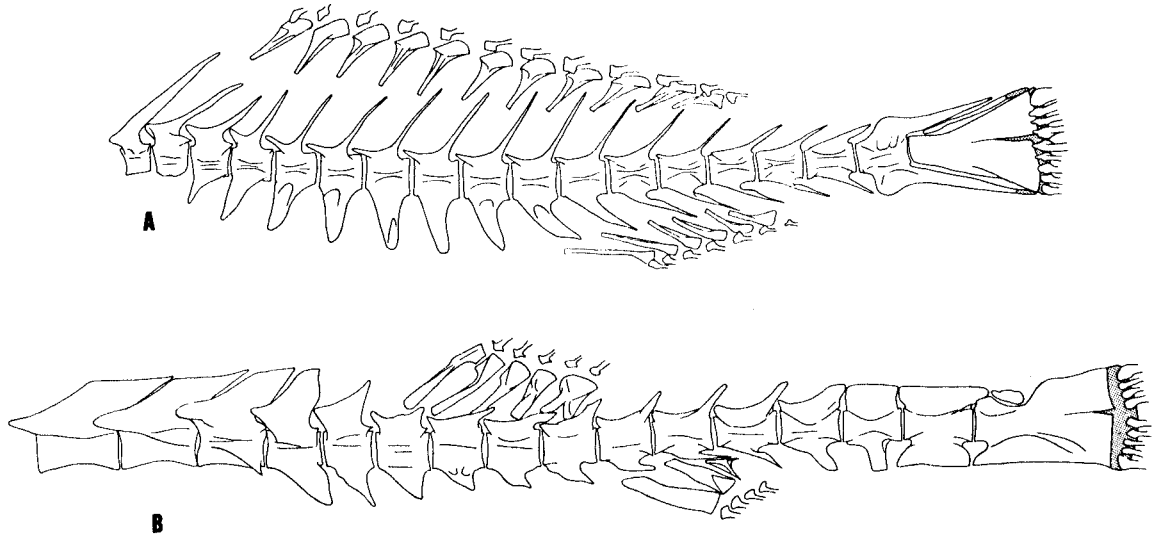

FIGURE 35.—Vertebrae, caudal skeleton, and median fins: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Antennarius, *Brachionichthys*, *Lophichthys*, and *Chaunax* consists of three spines. In *Antennarius*, *Brachionichthys*, and *Lophichthys* (Figures 36, 37) all three spines are well developed, extending above the skin of the head. In many species of *Antennarius* spines II and III are membranously attached posteriorly to the head; in *Brachionichthys*, and in some forms of *Antennarius* (e.g. *A. pauciradiatus* Schultz 1957:100, fig. 7; *A. randalli* Allen 1970:518, fig. 1, 2a), spine II is membranously attached to the full length of spine III, and spine III is, in turn, membranously attached posteriorly to the head.

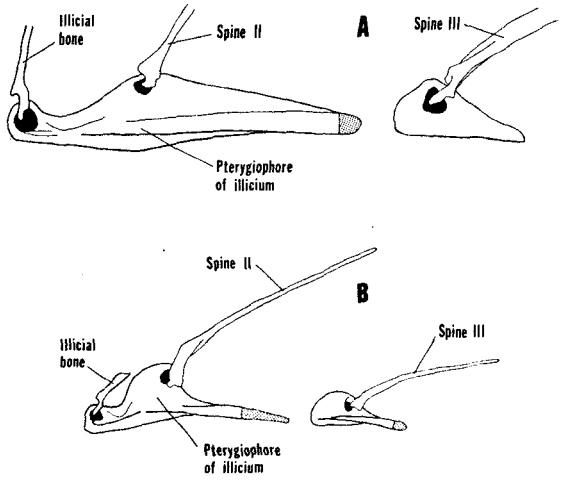

FIGURE 36.—Spinous dorsal fin, left lateral view: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

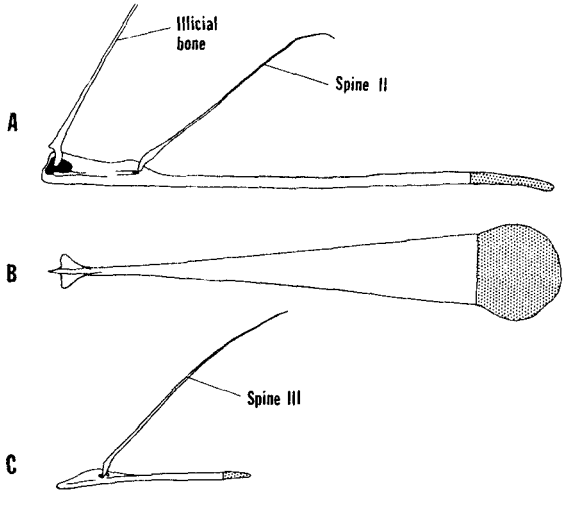

FIGURE 37.—Elements of spinous dorsal fin of *Lophichthys boschmai*, UW 20773, 47 mm SL: A. Anteriormost pterygiophore bearing illicial bone and dorsal spine II, left lateral view; B. Anteriormost pterygiophore, ventral view; C. Second pterygiophore bearing dorsal spine III, left lateral view.

In *Tetrabrachium* (Figure 13), all three dorsal fin spines are evident externally, but all are reduced in size; the greater part of spine III is covered by skin of the head, only the tip emerging. In *Chaunax* (Figure 38A), all three dorsal fin spines are relatively well developed, but spines II and III are laid back on the surface of the cranium completely covered by skin and apparently nonfunctional (a similar situation is found in *Histiophryne*, a highly specialized genus of the Antennariidae). The illicial bone (dorsal spine I), when retracted, comes to lie within an aperture on the face between the nostrils and eyes, called the illicial cavity (Figure 39A; Bradbury 1967).

In *Dibranchus* (Figure 38B), dorsal spine III and its pterygiophore are absent. Spine II is reduced to a small vestige of bone (the "H-shaped" bone of Bradbury 1967:402, fig. 1) lying on, or often fused to the anteriormost pterygiophore just behind the articulation of the pterygiophore and the illicial bone. As in *Chaunax*, the illicial bone, when retracted, comes to lie within an illicial cavity (Figure 39B, C).

In *Tetrabrachium*, *Antennarius*, *Lophichthys*, and *Brachionighthys* (Figures 13, 36-37), the anteriormost pterygiophore that supports the illicial bone and dorsal spine II, and the second pterygiophore that supports dorsal spine III have highly compressed, bladelike dorsal expansions. Each

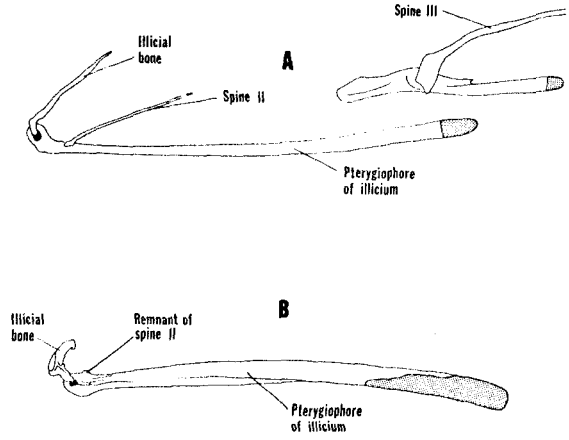

FIGURE 38.—Spinous dorsal fin, left lateral views: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

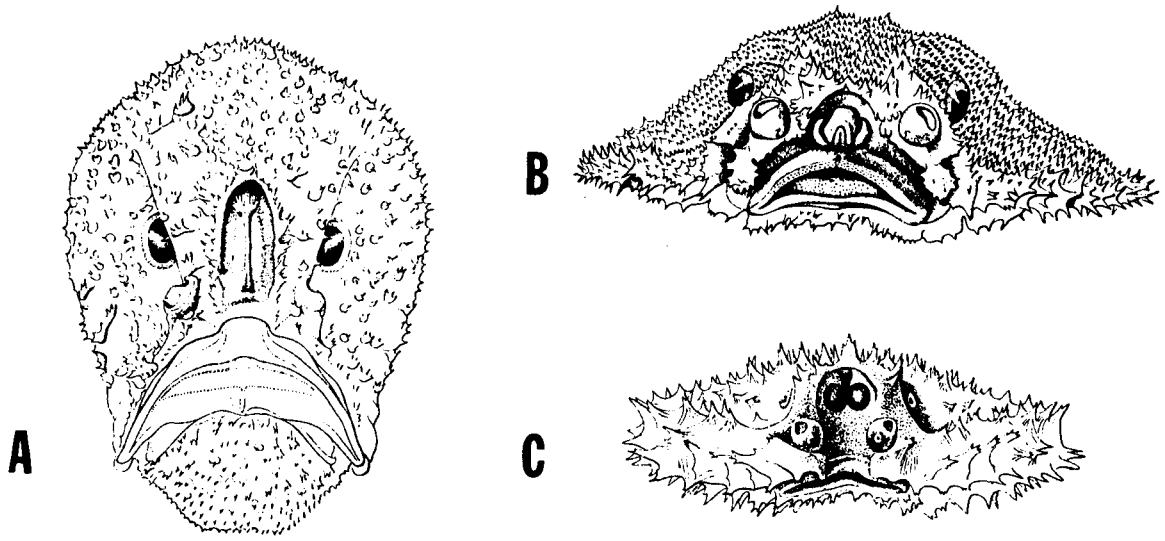

FIGURE 39.—Anterior views showing illicial cavity within which the illicial bone, when fully retracted, comes to lie: A. *Chaunax coloratus* Garman; B. *Dibranchus spinosa* (Garman); C. *Halieutopsis tumifrons* (Garman). After Garman (1899).

expansion is pierced by a large, circular foramen within which fits the bifurcated proximal end of the respective dorsal fin spine. The anteriormost pterygiophore of *Lophichthys* (Figure 37A, B) is unique among the antennarioids examined in being much more elongate, and in becoming greatly depressed and laterally expanded posteriorly. In *Chaunax* and *Dibranchus* (Figure 38), the pterygiophores of the dorsal fin spines are cylindrical in cross section along their entire length.

Dorsal and anal fin ray counts of the antennarioids examined are compared in Table 2.

Pectoral and pelvic girdles and fins (Figures 14, 40).—The posttemporal of *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax* is similar to that of *Tetrabrachium*, attached to the cranium in such a way that considerable movement in an anterodorsal-posteroventral plane is possible. In contrast, the posttemporal of *Dibranchus* is fused to the cranium.

The number and length of the pectoral fin radials varies somewhat among the antennarioids examined. There are three relatively short pectoral radials in *Tetrabrachium*, and *Antennarius* (Figures 14, 40A). The three radials of *Lophichthys* (Figure 40B) are exceptionally long and narrow; the second radial is reduced, tapering proximally to a slender filament. *Brachionichthys* (Figure 40C) has two, somewhat elongate pectoral

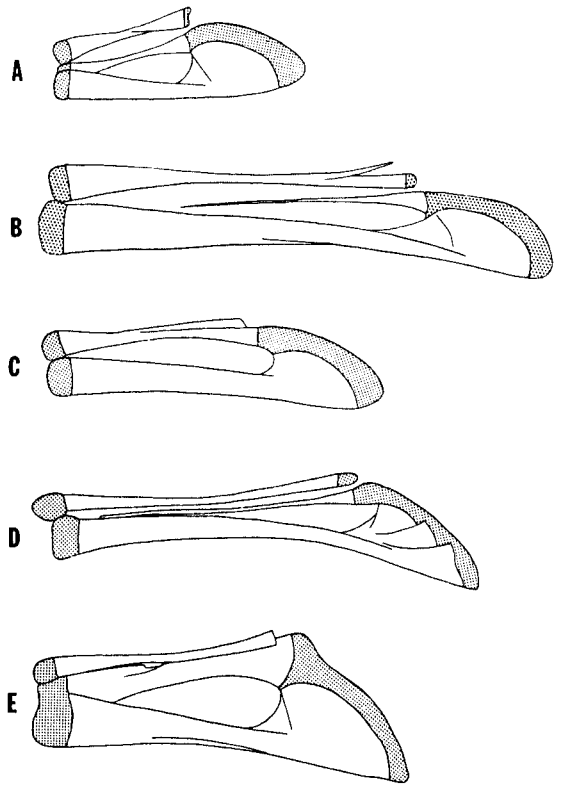

FIGURE 40.—Pectoral radials, lateral view, left side: A. *Antennarius striatus*, UW 20768, 67 mm SL; B. *Lophichthys boschmai*, UW 20773, 47 mm SL; C. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL; D. *Chaunax pictus*, UW 20770, 90 mm SL; E. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

radials. In the single osteological preparation of *Chaunax* examined (Figure 40D), there are three separate, relatively long radials, but the ventralmost element appears to be the result of fusion of three, perhaps indicating the presence of a total of five radials. In *Dibranchus* (Figure 40E) there are three, relatively short radials, the dorsalmost two lying side-by-side and fused to one another at their proximal and distal ends.

Skin spines.—Numerous, close-set dermal spines cover the head and body of *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax*; the spines are bifurcated in *Antennarius*, but simple in *Lophichthys*, *Brachionichthys*, and *Chaunax*. Dermal spines are absent in *Tetrabrachium*, except for the occasional presence of a spinule associated with an individual pore of the acoustico-lateralis system. The head and body of *Dibranchus* are nearly totally enclosed in a covering of thick, nonoverlapping tubercles (Bradbury 1967:404).

PHYLOGENETIC RELATIONSHIPS

The order Lophiiformes is an assemblage of 18 families, 59 genera, and approximately 255 living species of marine teleosts, the monophyletic origin of which seems certain based on the following list of synapomorphic features:

1) Spinous dorsal fin primitively of six spines, the anteriormost three of which are cephalic in position and modified to serve as a luring apparatus (involving numerous associated specializations, e.g., a medial depression of the anterior portion of the cranium, loss of the nasal bones [nasal of Rosen and Patterson 1969 = lateral ethmoid] and supraoccipital lateral-line commissure, and modifications of associated musculature and innervation);
2) Epiotics separated from parietals and meeting on the midline posterior to the supraoccipital;
3) Gill opening restricted to a small, elongate tubelike opening situated immediately dorsal to, posterior to, or ventral to (rarely partly anterior to) pectoral fin base;
4) Second ural centrum fused with the first ural and first preural centra to form a single hypural plate (sometimes deeply notched posteriorly) that emanates from a single, complex half-centrum (Rosen and Patterson 1969:441, text fig. 4E, 60);
5) Pectoral radials narrow and elongate, the ventralmost radial considerably expanded distally;
6) Eggs spawned in a double, scroll-shaped mucous sheath (Rasquin 1958).

Since Regan (1912), three major lophiiform taxa of equal rank have been recognized by nearly all authors. These taxa, together with their currently recognized families (the 11 families of the bathypelagic Ceratioidei excluded), are:

Suborder Lophioidei
  Family Lophiidae
Suborder Antennarioidei
  Family Antennariidae
  Family Brachionichthyidae
  Family Chaunacidae
  Family Ogcocephalidae
Suborder Ceratioidei

In attempting to place *Tetrabrachium* within the framework of this classification it became apparent that not all of the relationships expressed can be supported by an adherence to cladistic methodology. Although never questioned by any subsequent author, the monophyly of each of Regan's (1912) three major lophiiform taxa has not been established. Serious problems lie within the Antennarioidei: a number of synapomorphic features support a sister-group relationship between the Antennariidae and Brachionichthyidae (see below), and between the Chaunacidae and Ogcocephalidae, but no convincing synapomorphy is known at the present time that will link these two larger subgroups. Thus, the problems of interpreting the interrelationships of higher taxonomic categories within the Antennarioidei, and the relationships of this suborder to the Lophioidei and Ceratioidei are postponed. The following discussion is limited for the most part to *Tetrabrachium* and its relationship to the Antennariidae, to *Lophichthys* (here given familial rank as suggested by Boeseman 1964), and to the Brachionichthyidae. Synapomorphic features that establish monophyly for a group containing the Chaunacidae and Ogcocephalidae are also enumerated. The relative primitiveness of the character states utilized below was determined by examining their distribution among all available lophiiform material (47 of the 59 currently recognized genera;

material unavailable for comparison includes the lophioid genus *Sladenia* Regan, seven of the nine ogcocephalidid genera, and a number of rare and highly derived ceratioid genera), as well as representative taxa of the Batrachoidiformes (3 of the 12 nominal genera), the only group bearing evidence of sister-group relationship with the Lophiiformes (Regan 1912; Gregory 1933; Rosen and Patterson 1967) (see Appendix).

Antennarius, used here as the representative taxa of the Antennariidae, is recognized as the least derived genus of the family based on a comparative anatomical study of some eight nominal antennariid genera (Pietsch in prep., see Appendix). Except for synapomorphies that establish monophyly for *Antennarius*, all known characters of taxonomic importance found among the eight genera are present in *Antennarius* in the primitive state. For example, a mesopterygoid and an epural are present in *Antennarius* but absent in all other genera except *Histrio*; *Histrio* is clearly derived relative to *Antennarius* in having enlarged pelvic fins, a pectoral fin lobe that is detached from the body along most of its length, absence of skin spines, and a unique pelagic habitat in sargassum weed. Similarly, each of the remaining six antennariid genera possesses a number of autapomorphic features that indicate its derived nature relative to *Antennarius*. Although these and other data support the least derived position of *Antennarius*, this verification is not basic to the subsequent discussion of relationships since the synapomorphic features used to establish the sister groups proposed below are synapomorphic for all eight antennariid genera.

Tetrabrachium is most closely related cladistically to *Antennarius*, and is here classified on this basis as a sister-family, the Tetrabrachiidae (first proposed by Whitley 1935), of the Antennariidae (Figure 41). This hypothesis of relationship is supported by three synapomorphies:

1) Posteromedial process of vomer emerging from ventral surface as a laterally compressed, keellike structure, its ventral margin (as seen in lateral view) strongly convex (this character state is present in *Tetrabrachium* and in all antennariid taxa examined; in the batrachoidids and other lophiiforms examined the posteromedial process is flush with the ventral surface of the vomer, its ventral margin straight to slightly concave);
2) Postmaxillary process of premaxilla spatulate (this character state is present in *Tetrabrachium* and in all antennariid taxa examined; in the batrachoidids and other lophiiforms examined the postmaxillary process of the premaxilla is connected to the toothed portion of this element by bone, represented by a narrow, tapering structure, or absent);
3) Opercle similarly reduced in size (in *Tetrabrachium* and all antennariid taxa examined the width of the opercle is approximately $\leq 25\%$ the length of the suspensorium; in the batrachoidids and other lophiiforms examined this distance is $>40\%$).

Although the classification of taxa presented here is based on recency of common descent, the amount and nature of evolutionary change between the Antennariidae and the Tetrabrachiidae is an important part of their evolutionary histories. That the Tetrabrachiidae has entered a "new adaptive zone" relative to the Antennariidae is evidenced morphologically by a number of unique, derived features: eyes small, close set, protruding from the dorsal surface of the head; mouth small, superior, lower lip fringed with small cutaneous papillae; illicial apparatus reduced; pectoral fin double, the ventral portion membranously attached to the side of the body; and pectoral fin lobe membranously attached to the rays of the pelvic fin. The webbing between the pectoral fin and the body, and between the pectoral and pelvic fins is apparently used to remove soft-bottom substrate (fine sand or mud) from beneath by scooping material away in a lateral direction and simultaneously throwing material up and over to cover the animal; the fringed lip allows for intake of water while helping to prevent particles from entering the pharyngeal cavity. These and other characters listed above reflect a life style similar to that of a uranoscopid or synanceiid, lying for long periods of time buried up to the eyes in sand or mud, a mode of existence unlike that of any other antennarioid.

The results of this study further show that the Antennariidae and Tetrabrachiidae together form the primitive sister group of the Lophichthyidae and that these three taxa together form the primitive sister group of the Brachionichthyidae (Figure 41). The monophyly of a group including the Antennariidae, Tetrabrachiidae, and Lophichthyidae is supported by a single synapomorphy:

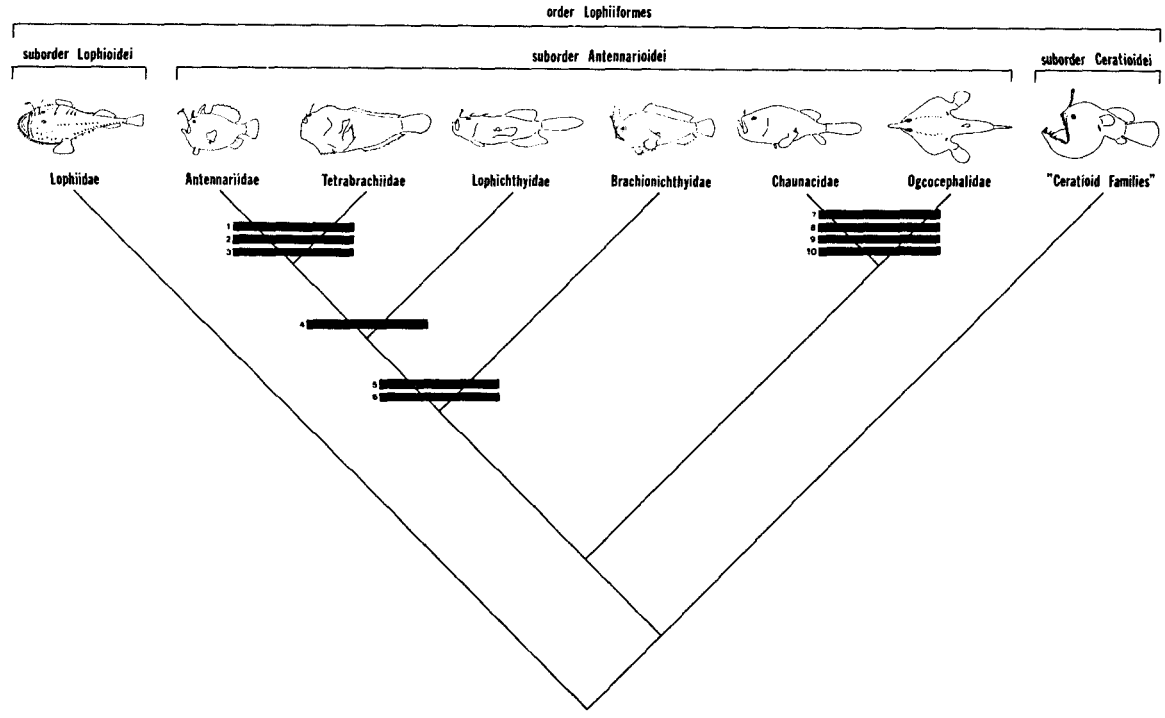

FIGURE 41.—Cladogram showing proposed phylogenetic relationships of major subgroups of the Lophiiformes. Note that not all sister-group relationships are supported by sufficient data. Black bars and numbers refer to synapomorphic features discussed in the text: 1) Posteromedial process of vomer emerging from ventral surface as a laterally compressed, keellike structure; 2) Postmaxillary process of premaxilla spatulate; 3) Opercle reduced; 4) Ectopterygoid triradiate; 5) Interhyal with a medial, posterolaterally directed process; 6) Illicial pterygiophore and pterygiophore of third dorsal fin spine with highly compressed, bladelike dorsal expansions; 7) Posterior-most branchiostegal ray exceptionally large; 8) Gill teeth tiny, arranged in a tight cluster at apex of pedicellike tooth plates; 9) Gill filaments of gill arch I absent; 10) Illicial bone, when retracted, lying within an illicial cavity. Drawings courtesy of The American Museum of Natural History.

4) Ectopterygoid triradiate, a dorsal process overlapping the medial surface of the metapterygoid (this character state is present in *Tetrabrachium*, *Lophichthys*, and all antennariids examined; in the batrachoidids and other lophiiforms examined this element is crescent shaped, making no contact with the metapterygoid).

That the Antennariidae, Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae constitute a monophyletic group is supported by two synapomorphies:

5) Interhyal with a medial, posterolaterally directed process that comes into contact with the respective preopercle (this character state *is present in Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and all antennariids examined; in the batrachoidids and all other lophiiforms examined this interhyal process is absent);
6) Illicial pterygiophore and pterygiophore of the third dorsal fin spine with highly compressed, bladelike dorsal expansions (this character state is present in *Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and all antennariids examined; in other lophiiforms examined these dorsal expansions are absent; this character does not extend to batrachoidids).

Gregory (1933:388, fig. 264) speculated that the membranous connection between the spines of the dorsal fin of *Brachionichthys* represents a primitive feature: "This is the most primitive condition among the typical pediculates" (= lophiiforms). On this assumption, in addition to a statement that the skeleton of *Brachionichthys* is relatively primitive in appearance, Gregory (1933:387) concluded that "...*Brachionichthys* is much less spe-

cialized [relative to antennariids and lophiids] and in fact seems to give several clues to the origin of the entire order." On the contrary, all evidence indicates that a membranous connection between the dorsal fin spines is apomorphic for anglerfishes; of the approximately 255 living species of the order this feature is present in the four nominal species of *Brachionichthys* and in two of the most derived species of the genus *Antennarius* (*A. pauciradiatus* and *A. randalli*; Pietsch in prep.). Besides this character, *Brachionichthys* possesses a set of autapomorphic features that clearly remove it from consideration as "the most primitive lophiiform." In addition to those autapomorphies listed in the analytical key below, Winterbottom (1974:284) has identified an apparently unique derived condition of the inclinator dorsales muscle of the second dorsal fin spine of *Brachionichthys*.

Although strikingly dissimilar at first glance, a number of synapomorphies support a hypothesis of sister-group relationship between the families Chaunacidae and Ogcocephalidae (Figure 41):

7) Posteriormost branchiostegal ray exceptionally large (in batrachoidids and all other lophiiforms examined the size of the posteriormost branchiostegal does not differ significantly from the adjacent branchiostegal);
8) Gill teeth tiny, arranged in a tight cluster at apex of pedicellike tooth plates (in batrachoidids and other lophiiforms examined the gill teeth are relatively large, and either single, or associated with a flat, rounded tooth plate);
9) Gill filaments of gill arch I absent (in batrachoidids and all other lophiiforms examined gill filaments are present on arch I);
10) Illicial bone, when retracted, lying within an illicial cavity (an illicial cavity is absent in all other lophiiforms examined; this character does not extend to batrachoidids).

Historically, chaunacids and ogcocephalids have been classified with antennariids and brachionichthyids by aspects of general similarity (i.e., they neither look like lophioids or ceratioids). Nearly all of these similarities are easily identified as character states that are plesiomorphic for antennarioids (or for lophiiforms as a whole); the synapomorphic nature of the few remaining similarities is unresolvable. Thus, despite a thorough osteological search, this study has failed to identify the sister group of a group including the Chaunacidae and Ogcocephalidae among the known members of the Lophiiformes. In the absence of any evidence for or against, these taxa are tentatively retained within the Antennarioidei (Figure 41).

Of the possible cladograms that could be constructed on the basis of the data provided in this study, the one shown in Figure 41 involves the least number of convergences. The preferred phylogeny requires four cases of convergence (Table 2), all of which, however, are loss characters that extend to other lophiiform taxa:

1) the independent loss of palatine teeth in the Tetrabrachiidae and Brachionichthyidae [also absent in some ogcocephalids (see Bradbury 1967:409) and in all ceratioids];
2) the independent loss of a pseudobranch in the Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae (also absent in chaunacids, ogcocephalids, and all ceratioids);
3) the independent loss of the swim bladder in the Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae (also absent in lophioids, chaunacids, ogcocephalids, and ceratioids);
4) the independent loss of the epural in the Tetrabrachiidae and Brachionichthyidae also absent in all antennariid genera examined except *Antennarius*, *Antennatus*, and *Histrio*; [although present in the Caulophrynidae (Pietsch 1979, fig. 11), the epural is absent in all other ceratioids].

Plesiomorphic and autapomorphic features of the major subgroups of the Antennarioidei are incorporated into the following analytical key:

1A. Spinous dorsal of three spines, emerging from dorsal surface of cranium, illicium not retractable within an illicial cavity; ectopterygoid present or absent, interopercle flat and broad 2
1B. Spinous dorsal of one spine (spines II and III reduced and embedded beneath skin of head or lost), illicium retractable within an illicial cavity; ectopterygoid present, crescent shaped; interopercle elongate and narrow 5
2A. Parietals well separated by supraoccipital; ectopterygoid triradiate; ceratobranchials I through IV toothless; hypobranchials II and III bifurcated prox-

imally; three pectoral radials; pelvic fin of one spine and five rays 3

2B. Parietals meeting on the midline dorsal to supraoccipital; ectopterygoid roughly oval in shape or absent; ceratobranchials I through III with one or more tooth plates; hypobranchial II simple, hypobranchial III absent; two pectoral radials; pelvic fin of one spine and four rays ..... Brachionichthyidae

3A. Vomer narrow, width between lateral ethmoids considerably less than between lateral margins of sphenotics; dorsal head of quadrate narrow, width less than that of metapterygoid; postmaxillary process of premaxilla spatulate; opercle reduced in size; pharyngobranchial and epibranchial of first arch toothless; bony connection between tips of haemal spines absent; pterygiophore of illicium short, posterior end cylindrical 4

3B. Vomer wide, width between lateral ethmoids nearly as great as between lateral margins of sphenotics; dorsal head of quadrate broad, width equal to or greater than that of metapterygoid; postmaxillary process of premaxilla tapering to a point; opercle expanded posteriorly; pharyngobranchial and epibranchial of arch I toothed; bony connection between tips of haemal spines of 14th through 16th preural centra; pterygiophore of illicium elongate, greatly depressed and laterally expanded posteriorly ..... Lophichthyidae

4A. Eyes lateral, dorsal fin spines well developed; mouth large; pectoral fin single, rays not membranously attached to side of body; pectoral fin lobe not membranously attached to rays of pelvic fin; soft dorsal fin rays 11 to 15, anal fin rays 6 to 9 ..... Antennariidae

4B. Eyes dorsal; dorsal fin spines reduced; mouth small; pectoral fin double, dorsalmost ray of ventral portion membranously attached to side of body; pectoral fin lobe membranously attached to rays of pelvic fin; soft dorsal fin rays 16 or 17, anal fin rays 11 or 12 ..... Tetrabrachiidae

5A. Body slightly compressed laterally; cleft of mouth nearly vertical; frontal bones narrow, meeting each other on the midline along their entire length; lateral ethmoids long and narrow; posteriormost branchiostegal ray free; dorsal fin spines II and III present, embedded beneath skin of head; pelvic fin of one spine and four rays; soft dorsal fin rays 11 to 13; anal fin rays 5 to 7 ..... Chaunacidae

5B. Body strongly depressed dorsoventrally; cleft of mouth horizontal; frontal bones triangular in shape, only their posterior halves meeting on the midline; lateral ethmoids short and stout; posteriormost branchiostegal ray ankylosed to ventromedial margin of subopercle; dorsal fin spine III absent, spine II reduced to a small remnant embedded beneath skin and lying on, or fused to, dorsal surface of pterygiophore just behind base of illicial bone; pelvic fin of one spine and five rays; soft dorsal fin rays 4 or 5; anal fin rays 4 ..... Ogcocephalidae

Although not all of the sister groups suggested are supported by sufficient data at this time, the following classification of the Lophiiformes is proposed. While the ranking of taxa is not dichotomous (see Methods), internested sets of vertical lines are used to indicate sister-group relationships:

Order Lophiiformes
- Suborder Lophioidei
- Suborder Antennarioidei
  - Family Antennariidae
  - Family Tetrabrachiidae
  - Family Lophichthyidae
  - Family Brachionichthyidae
  - Family Chaunacidae
  - Family Ogcocephalidae
- Suborder Ceratioidei

As a final note, the genus *Histionotophorus*, based on a single species, *H. bassani* (Zigno 1887) from the Eocene of Monte Bolca, Italy, should be mentioned. From the available fossil evidence, this genus does not appear to differ substantially from *Brachionichthys*, and probably should be synonymized with the latter (Rosen and Patterson 1969:442). Reconstructions and photographs of the few known specimens (Eastman 1904, text fig. C, pl. 1, fig. 1-3; Gill 1904; Le Danois 1964:141, fig. 75, 76) show the following brachionichthyid features: mouth horizontal; mesopterygoid greatly reduced or absent (?); ectopterygoid absent (?); 22 vertebral

centra; epural absent; dorsal of three well-developed cephalic spines; membrane between dorsal spines II and III (?); caudal fin rays elongate; two elongate pectoral radials.

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APPENDIX

The osteological evidence presented in this paper is based on the following list of specimens in addition to the lophiiform material listed in previous studies of the osteology and interrelationships of ceratioid anglerfishes (Pietsch 1972: 44, 1974:109, 1979).

Batrachoididae

Batrachoides pacifici (Günther): MCZ 41805, 153 mm.
Daector dowi (Jordan and Gilbert): LACM 31310-19, 1 (of 3), 97 mm.
Porichthys analis Hubbs and Schultz: LACM 22345, 1 (of 2), 125 mm.
Porichthys notatus Girard: LACM 22083, 1, 114.5 mm.
Porichthys porosissimus (Cuvier and Valenciennes): LACM 30727-11, 1 (of 4), 96 mm.

Lophiidae

Lophius americanus Valenciennes: MCZ 51259, 1, 121 mm.
Lophiodes caulinaris (Garman): MCZ 51260, 1, 33.5 mm.
Lophiodes monodi (Le Danois): MCZ 40928, 1, 92 mm.

Antennariidae

Antennarius avalonis Jordan and Starks: UW 20766, 1, 67 mm.
Antennarius maculatus (Desjardins): UW 20767, 1, 64 mm.
Antennarius sanguineus Gill: LACM 8125, 1 (of 2), 76 mm.
Antennarius striatus (Shaw and Nodder): UW 20768, 2, 65 and 67 mm.
Antennatus bigibbus (Latreille): LACM 32611-1, 1 (of 5), 63 mm.
Echinophryne crassispina McCulloch and Waite: NMV A537, 51 mm.
Histiophryne bougainvilli (Valenciennes): NMV A535, 64 mm.
Histrio histrio (Linnaeus): LACM 8975-1, 1 (of 6), 91 mm.
Histrio histrio (Linnaeus): MCZ 51261, 1, 68 mm.
Rhycherus filamentosus (Castelnau): NMV A536, 56 mm.
Tathicarpus butleri Ogilby: AMS IB.3043, 63 mm.
Trichophryne furcipilis (Cuvier): AMS IA.6631, 50 mm.

Tetrabrachiidae

Tetrabrachium ocellatum Günther: AMS IB.7177, 7188, 2, 56 and 61 mm.

Lophichthyidae

Lophichthys boschmai Boeseman: UW 20773, 2, 44 and 47 mm.

Brachionichthyidae

Brachionichthys hirsutus (Lacepede): AMS IA. 6064, 1, 69 mm.
Brachionichthys hirsutus (Lacepede): UW 20769, 1, 42 mm.
Histionotophorus bassani (Zigno): MCZ 5176A + 5176B, 35 mm; MCZ 5177A + 5177B, 37 mm; MCZ 5178, 33 mm.

Chaunacidae

Chaunax pictus Lowe: UW 20770, 1, 90 mm.

Ogcocephalidae

Dibranchus atlanticus Peters: MCZ 51257, 1, 105 mm.
Zalieutes elater (Jordan and Gilbert): LACM 8824-13, 1 (of 3), 98 mm.

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EARLY ZOEAL STAGES OF *LEBBEUS POLARIS*, *EUALUS SUCKLEYI*, *E. FABRICII*, *SPIRONTOCARIS ARCUATA*, *S. OCHOTENSIS*, AND *HEPTACARPUS CAMTSCHATICUS* (CRUSTACEA, DECAPODA, CARIDEA, HIPPOLYTIDAE) AND MORPHOLOGICAL CHARACTERIZATION OF ZOEAE OF *SPIRONTOCARIS* AND RELATED GENERA

EVAN HAYNES[1]

ABSTRACT

Stage I and II zoeae of *Lebbeus polaris*, *Eualus suckleyi*, and *E. fabricii* and Stage I zoeae of *Spirontocaris arcuata*, *S. ochotensis*, and *Heptacarpus camtschaticus* are described from individuals of known parentage. Larval development of *L. polaris* is more abbreviated than larval development of other hippolytid shrimp. Early stage zoeae of *L. polaris* can be distinguished from zoeae of *L. groenlandicus* by differences in morphology of antennal flagellum, maxillipeds, pereopods, and pleopods. Early stage zoeae of *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* can be distinguished from each other and other known hippolytid zoeae by slight differences in morphology, especially length of rostrum, armature of carapace and abdomen, setation of antennule and mouthparts, and development of pereopods. These new descriptions extend the range of morphological characters of zoeae for each genus and support the proposal that the *Spirontocaris* sensu lato unit be accorded suprageneric status rather than generic status.

Larvae of only a few of the 87 known species of hippolytid shrimp in the northern North Pacific Ocean have been described. Needler (1934) described Stage I zoeae of *Hippolyte clarki* Chace under the name *Hippolyte californiensis* Holmes, and Stage I zoeae of *Eualus herdmani* (Walker), *Heptacarpus brevirostris* (Dana), *H. paludicola* (Holmes), and *H. tridens* (Rathbun) under the generic name *Spirontocaris*. These zoeae were hatched in the laboratory from ovigerous females collected in British Columbia waters. Zoeae and megalopa of *Spirontocaris spinus* (Sowerby) and *S. lilljeborgii* (Danielssen) were described from known parentage and from plankton of eastern Atlantic waters (Pike and Williamson 1961). Pike and Williamson (1961) also described Stage II zoeae of *S. phippsii* (Krøyer) collected from plankton in the western Atlantic and all larval stages of *E. pusiolus* (Krøyer), a species found in the western Atlantic and northern North Pacific Ocean. In addition, Pike and Williamson (1961) described several stages of zoeae presumed to be zoeae of *Lebbeus polaris* (Sabine). Ivanov (1971) described Stage I zoeae of *Eualus macilentus* (Krøyer), *E. barbatus* (Rathbun), *Spirontocaris spinus* (= *S. spina intermedia* Kobjakova), and *Lebbeus groenlandicus* (Fabricius) hatched in the laboratory from ovigerous females collected in the Bering Sea and Gulf of Alaska. Haynes (1978) described the larval stages, including the megalopa, of *L. groenlandicus* from specimens hatched from ovigerous females collected in Kachemak Bay, Alaska.

In this paper, I describe and illustrate zoeal Stages I and II of *L. polaris*, *E. suckleyi* (Stimpson), and *E. fabricii* (Krøyer), and Stage I zoeae of *S. arcuata* (Rathbun), *S. ochotensis* (Brandt), and *H. camtschaticus* (Stimpson) hatched in the laboratory from ovigerous females collected in Kachemak Bay. I also compare the morphology of zoeae of *Spirontocaris* and related genera, and support Pike and Williamson's (1961) proposal to elevate *Spirontocaris* to suprageneric status.

METHODS

From late April to early May 1976, ovigerous *L. polaris*, *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* were caught in pots at depths of 20-30 m (11-16 fathoms) in Kachemak Bay. The females were transported

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to the laboratory and maintained as described by Haynes (1980) for ovigerous *Crangon franciscorum angustimana*. Most zoeae were released at night, about 1 wk after the females were captured. I do not know whether any of the larvae hatched as prezoeae.

For each species, 100 zoeae in groups of 10 zoeae each were placed by large-bore pipette into 500 ml beakers containing about 400 ml of filtered seawater. Seawater in the beakers was changed every other day. Newly hatched nauplii of brine shrimp, *Artemia salina*, from San Francisco Bay were offered, but none were eaten by the zoeae. The zoeae of each species were preserved in 5% Formalin[2] about 10 d after their release. Some of the zoeae of *L. polaris*, *E. suckleyi*, and *E. fabricii* had molted to Stage II.

To study segmentation and setation, I cleared some zoeae in 10% KOH and stained the exoskeleton with Turtox CMC-S (acid fuchsin stain mountant). Because the paired appendages of the zoeae are symmetrical, only the left members are figured. The mandibles, an exception, are drawn as pairs. For clarity in the illustrations, setules on setae are usually omitted, but spinulose setae are shown. Illustrations are partly schematic and represent typical setal counts. Any variation in setal counts is noted in the text.

DESCRIPTION OF ZOEAE

Terms used in the text, nomenclature of gills and appendages, and techniques of measurement and illustration are those given by Haynes (1976). Carapace length refers to the straight-line distance from posterior margin of the orbit to middorsal posterior margin of the carapace. Total body length refers to the distance from the tip of the rostrum to the posterior margin of the telson, not including telsonic spines. Stage I zoeae of *S. ochotensis* lack a rostrum; therefore, for this species only, total body length refers to the distance from anterior middorsal margin of the carapace to posterior margin of the telson. Telsonic setae or spines are numbered from an inner (medial) to outer (lateral) direction. The setation formulas proceed from the distal to the proximal ends of appendages. Principal morphological characteristics used to separate the species of zoeae described in this report are summarized in Table 1.

Lebbeus polaris—Stage I Zoeae

Mean total length of Stage I (Figure 1A), 5.4 mm (range 5.2-5.6 mm, 3 specimens). Rostrum slightly sinuate, without teeth, about one-half length of carapace. Carapace with a rounded prominence at base of rostrum and near posterior margin. Ventral margin of carapace smooth except for pterygostomian spine. No supraorbital spines.

Antennule (Figure 1B).—First antenna, or antennule, an unsegmented peduncle with conical projection and heavily plumose seta. Conical projection with four aesthetascs of various lengths.

Antenna (Figure 1C).—An inner flagellum (endopodite) and outer scale (exopodite). Flagellum two-segmented, slightly longer than scale; distal segment styliform, with terminal plumose seta and short spine. Proximal segment of flagellum has simple seta near joint. Scale distally divided into four joints, fringed with 11 heavily plumose setae. Protopodite with two simple spines: one at base of flagellum, other at base of scale.

Mandibles (Figure 1D).—Well developed, without palps. Four teeth on incisor process of left mandible in contrast to diserrate incisor process

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

TABLE 1.—Principal morphological characteristics of hippolytid zoeae described in this report.

Species	Rostrum	Supraorbital spine in Stage I	Abdominal somites bearing posterolateral spines in all stages	Pereopods bearing exopodites	Pereopods in Stage I
Lebbeus polaris	long	no	4, 5	[1]1, 2	5
Eualus suckleyi	long	no	5	[2]1-3	[3]5
E. fabricii	long	no	4, 5	[2]1-3	[3]5
Spirontocaris arcuata	short	no	4, 5	[4]1, 2	[3]5
S. ochotensis	absent	yes	4, 5	[4]1, 2	[3]5
Heptacarpus camtschaticus	minute	no	none	[4]1, 2	[3]5

[1]Small lobe in Stage I and II; absent in later stages.
[2]Poorly developed in Stage I and II; pereopods gradually develop in later stages.
[3]Undeveloped pereopods.
[4]Poorly developed in Stage I; pereopods gradually develop in later stages.

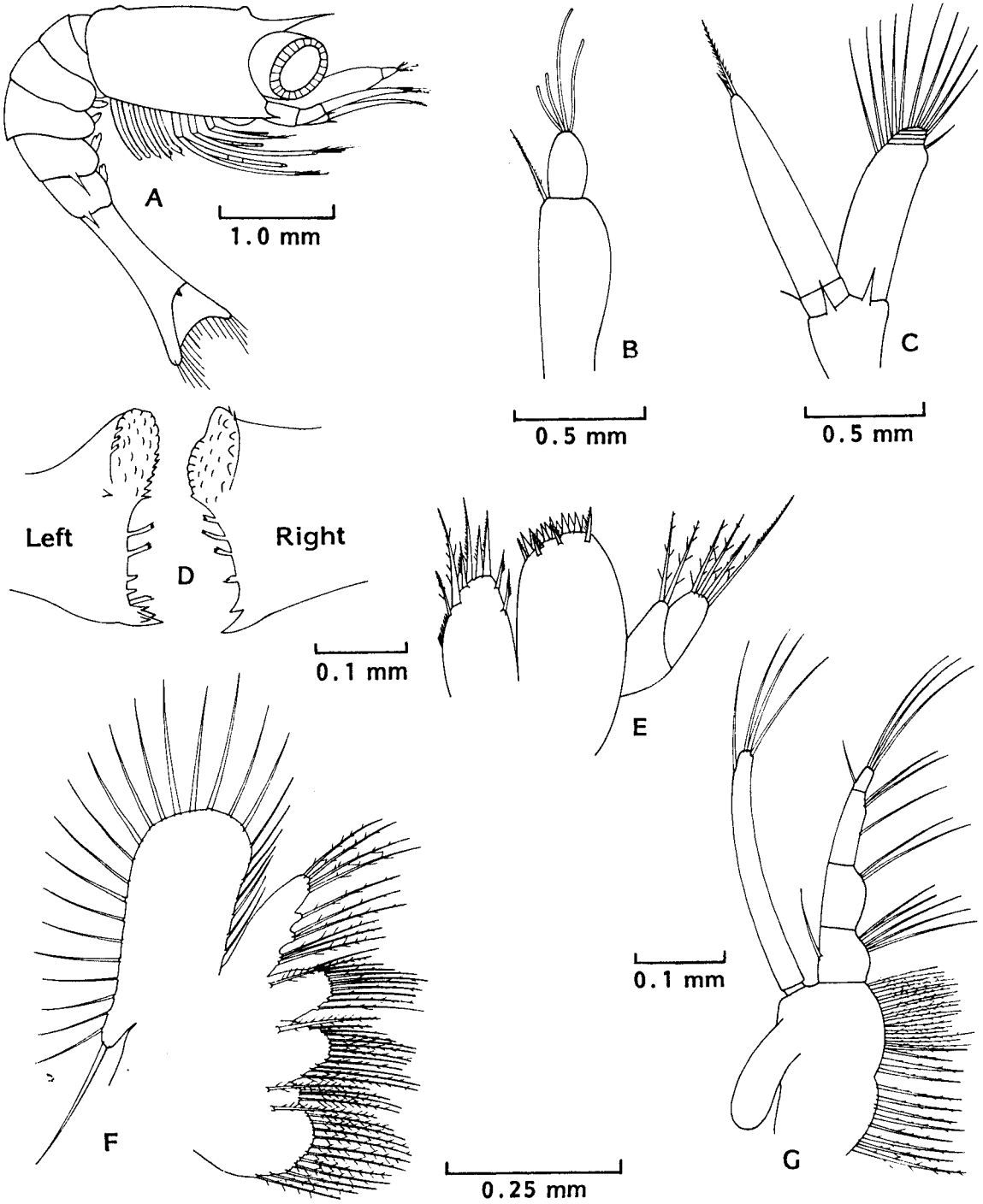

FIGURE 1.—Stage I zoea of *Lebbeus polaris*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, dorsal.

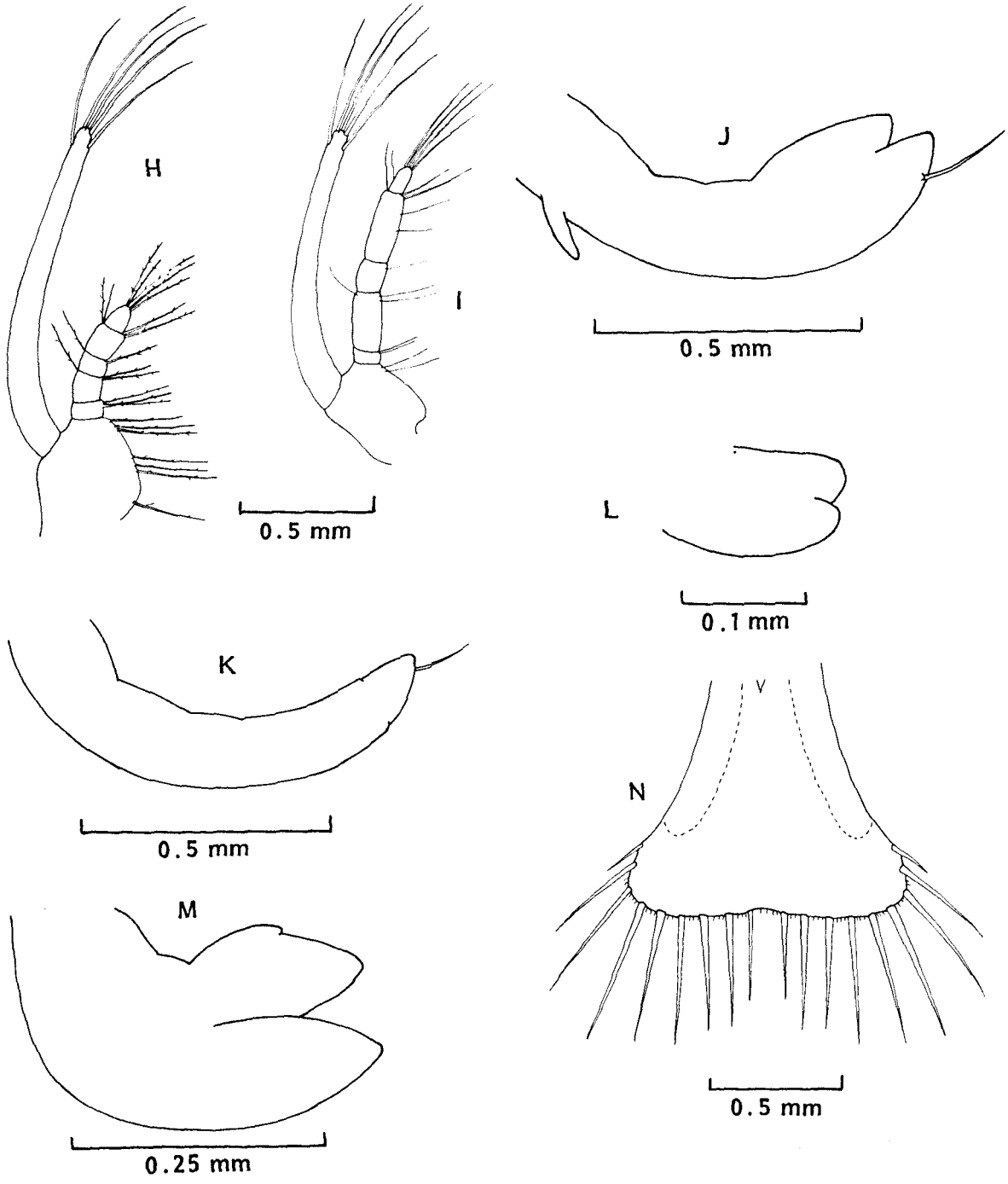

FIGURE 1.—Stage I zoea of *Lebbeus polaris*: H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, first pereopod, right side; K, third pereopod, right side; L, first pleopod, right side; M, second pleopod, right side; N, telson, ventral.

of right mandible. Lacinia mobilis adjacent to incisor process and subterminal tooth on left mandible; neither structure on right mandible.

Maxillule (Figure 1E).—With coxal and basial endites and endopodite on maxillule (first maxilla). Eight setae, all spinulose, on proximal lobe (coxopodite). Fifteen spines terminally (four spines spinulose) on median lobe (basipodite). Two-segmented endopodite on lateral margin of basipodite: distal segment with four, sometimes three, spinulose setae terminally (one seta especially long; remaining three, or two, about equal length); two spinulose setae terminally on proximal segment. No outer seta on maxillule.

Maxilla (Figure 1F).—Platelike exopodite (scaphognathite) with 25 long plumose setae and long thicker seta at proximal end. Both coxopodite and basipodite bilobed. Ten setae on unsegmented endopodite—all setae distinctly setulose. Basipodite with 23 setae: 11 on distal lobe, 12 on proximal lobe. Most, if not all, setae on basipodite and coxopodite setulose. Sixteen setae on coxopodite: 4 on distal lobe, 12 on proximal lobe.

First maxilliped (Figure 1G).—Unsegmented protopodite with 31 spinulose setae: 23 on basipodite, 8 on coxopodite. Endopodite four-segmented; setation formula 4, 3, 2, 6. Exopodite segmented at base, has four natatory setae. Epipodite a single lobe.

Second maxilliped (Figure 1H).—Seven sparsely spinulose setae on unsegmented protopodite. Endopodite five-segmented; fourth segment expanded somewhat laterally; setation formula 5, 4, 2, 3, 3. Exopodite about three times longer than endopodite, not segmented at base. Five natatory setae on exopodite. No epipodite.

Third maxilliped (Figure 1I).—Two simple setae on unsegmented protopodite. Endopodite five-segmented, nearly as long as exopodite; setation formula 5, 5, 1, 3, 2. Setae simple and, except for few terminal setae, minutely spinulose. Exopodite unsegmented at base, has five natatory setae. No epipodite.

First pereopod (Figure 1J).—Endopodite relatively short, wide, unsegmented; chela partially formed; dactylopodite with simple spine. Exopodite, a small lobe.

Second pereopod.—Similar to first pereopod except narrower, exopodite smaller, and chela more deeply cleft.

Third (Figure 1K), *fourth, and fifth pereopods.*—Nearly identical, except size decreases slightly from third to fifth pair. No exopodites.

Pleopods.—First pleopod (Figure 1L) blunt, slightly bilobed. Second pleopod (Figure 1M) bilobed; inner lamella with bud of appendix interna. Third, fourth, and fifth pleopods same as second pleopod. All pleopods without joints or setae.

Abdomen and telson (Figure 1A, N).—Five somites and telson (somite 6 fused with telson). Fourth and fifth abdominal somites with pair of posterolateral spines about half as long as the somites themselves—pair on fifth somite slightly shorter than pair on fourth somite. Telson slightly emarginated distally, has 9 + 9 densely plumose setae; small spinules between bases of all setae except last outer pair of setae. Enclosed uropods visible. Anal spine present but minute.

Lebbeus polaris—Stage II Zoeae

Mean total length of Stage II, 5.7 mm (range 5.6-5.8 mm, 4 specimens). Rostrum (Figure 2A) styliform, not sinuate, without teeth, about one-half length of carapace. Carapace with small supraorbital spine and pterygostomian spine; no spinules along posteroventral margin. Eyes stalked.

Antennule (Figure 2B).—Similar to Stage I antennule, except heavily plumose seta arises from small conical projection. Spine, or seta, and four aesthetascs on tip of large conical projection. Three plumose setae ventrally on distal portion of peduncle.

Antenna (Figure 2C).—Flagellum of antenna three-segmented: terminal segment spined at tip; proximal segment has simple seta. Scale and protopodite similar to scale and protopodite of Stage I.

Mandibles, maxillule, and maxilla.—Nearly identical to Stage I, except molar process of left mandible has several spines along outer margin. Eighteen setae on basipodite of maxillule; 12 setae on coxopodite of maxillule. About 30 setae on scaphognathite of maxilla.

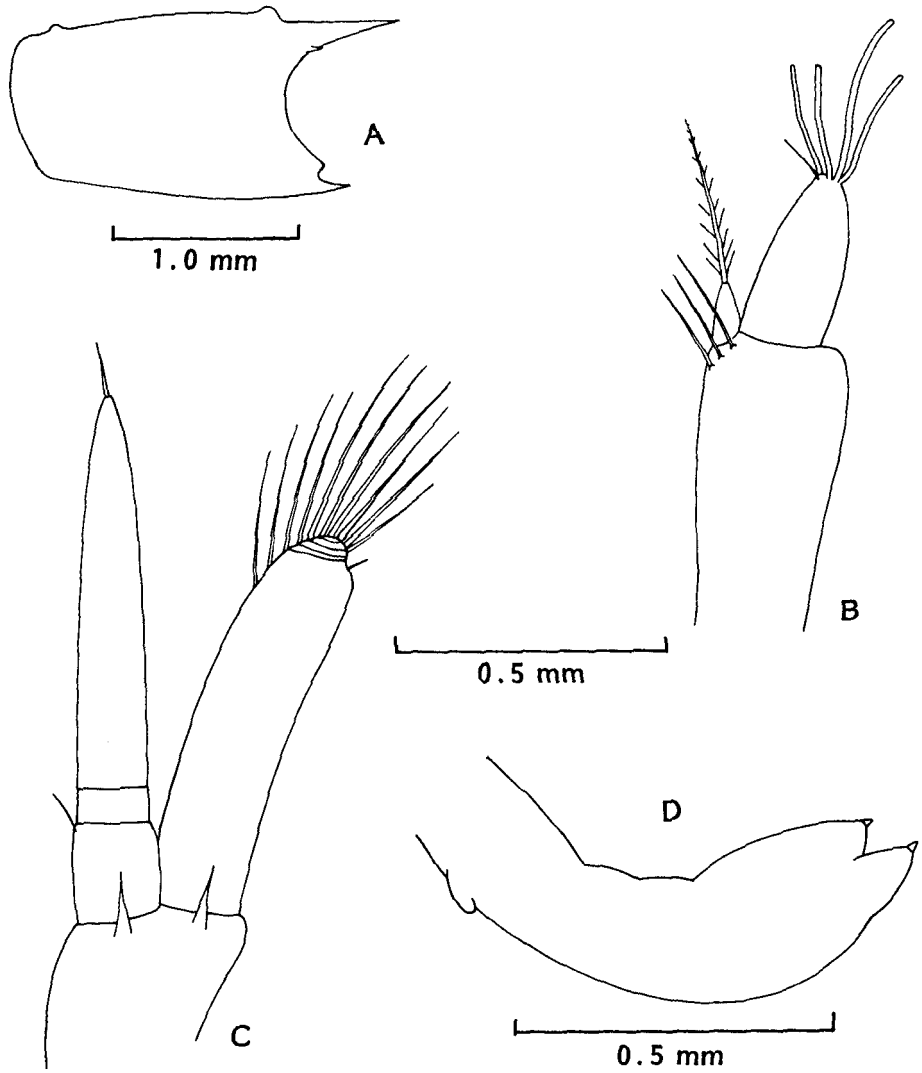

FIGURE 2.—Stage II zoea of *Lebbeus polaris*: A, carapace, right side; B, antennule, ventral; C, antenna, ventral; D, first pereopod, right side.

Maxillipeds.—Same as Stage I.

First pereopod (Figure 2D).—Unsegmented, slightly narrower than in Stage I. Propodite and dactylopodite tipped by small spine; dactylopodite without seta; exopodite remnant.

Second to fifth pereopods.—Similar to Stage I, except second pereopod slightly narrower, without exopodite. Third, fourth, and fifth pereopods with incipient segmentation.

Pleopods.—Similar to Stage I except more bilobed, appendices internae more distinct.

Abdomen and telson.—Nearly identical to Stage I, except sixth abdominal somite and telson jointed. Same number of telsonic setae as in Stage I. Uropods still enclosed.

Eualus suckleyi—Stage I Zoeae

Mean total length of Stage I (Figure 3A), 3.2

mm (range 3.0-3.5 mm, 10 specimens). Rostrum slender, spiniform, without teeth, slightly less than one-half length of carapace. Carapace with small, somewhat angular, dorsomedial prominences at base of rostrum and near posterior edge. Pterygostomian spines present, not hidden by sessile eyes. Several minute spines adjacent to pterygostomian spine: three or four spines on

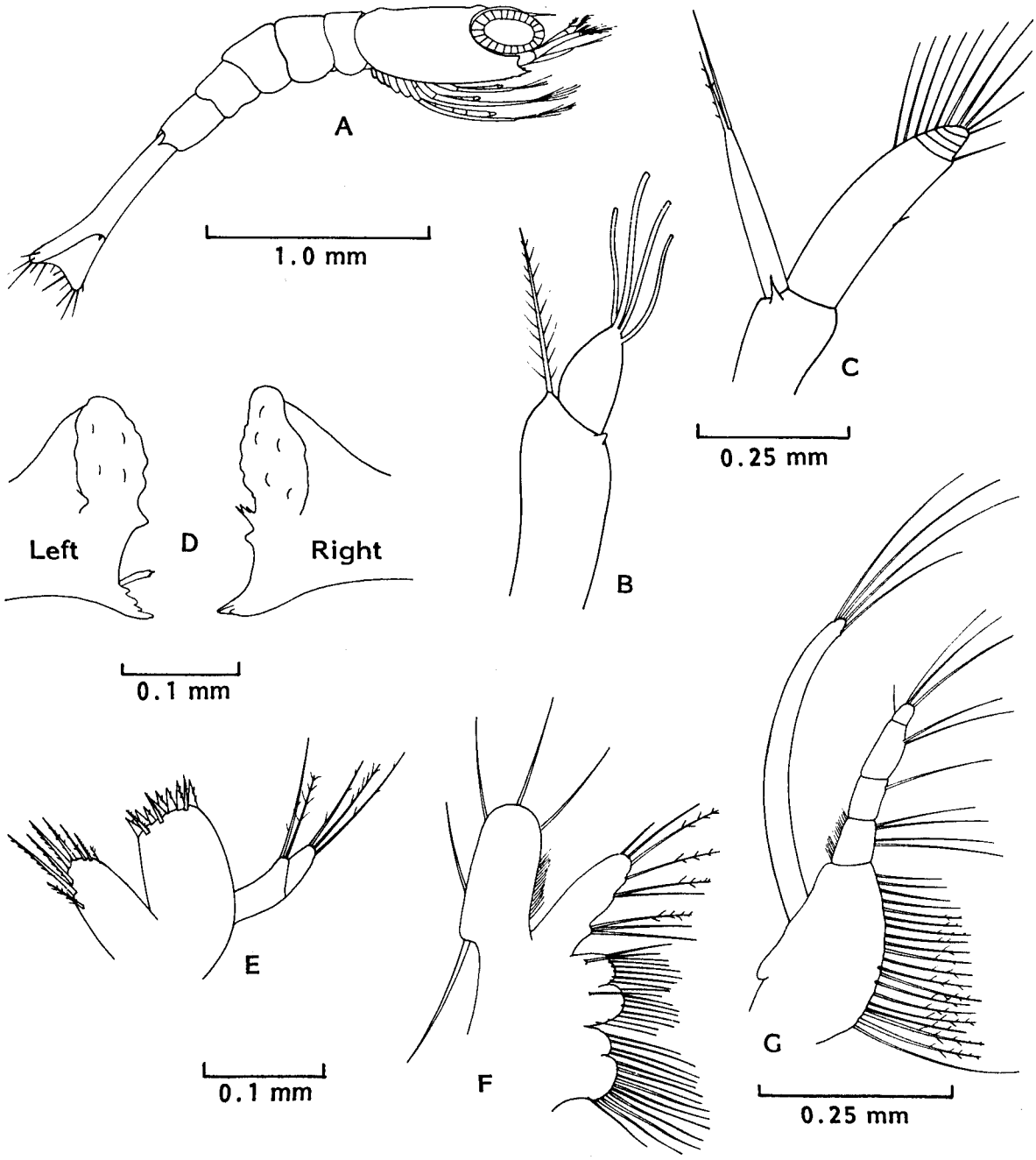

FIGURE 3.—Stage I zoea of *Eualus suckleyi*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, dorsal.

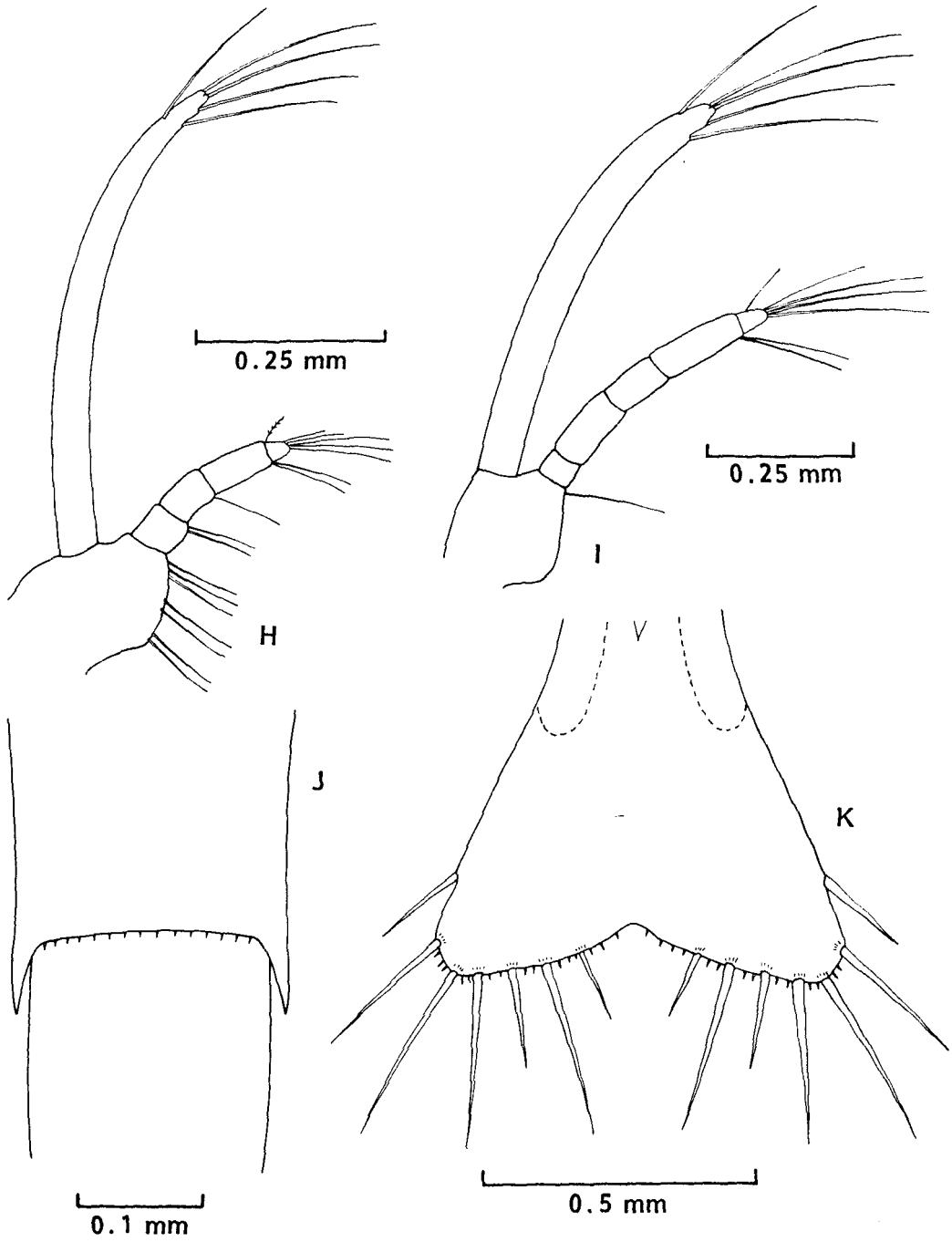

FIGURE 3.—Stage I zoea of *Eualus suckleyi*: H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, fifth abdominal somite, dorsal; K, telson, ventral.

ventral margin of carapace, one spine on anterolateral margin. No supraorbital spines.

Antennule (Figure 3B).—Unsegmented peduncle with conical projection and heavily plumose seta. Four aesthetascs of various lengths on conical projection. Small projection on peduncle near base of conical projection.

Antenna (Figure 3C).—Flagellum unsegmented, shorter and narrower than scale, terminally has plumose seta and shorter spinulose spine. Scale distally divided into four joints, fringed with 11 heavily plumose setae. Small plumose seta about midway on outer lateral margin. Protopodite with spine at base of flagellum but not at base of scale.

Mandibles (Figure 3D).—Well developed, without palps. Incisor process of left mandible with four teeth; incisor process of right mandible triserrate. Left mandible has lacinia mobilis adjacent to incisor process and subterminal tooth on truncated molar process.

Maxillule (Figure 3E).—Coxopodite with eight spinulose setae. Basipodite with 11 spinulose spines terminally. Two-segmented endopodite originating from lateral margin of basipodite has five spinulose setae: three on distal segment, two on proximal segment. Two setae especially spinulose, as shown. No outer seta on maxillule.

Maxilla (Figure 3F).—Scaphognathite with four long plumose setae, slightly longer thicker seta at proximal end, and series of fine hairs along inner margin of exopodite. Unsegmented endopodite with nine setae (four spinulose, as shown). Both basipodite and coxopodite bilobed. Basipodite with 17 setae: 8 on distal lobe, 9 on proximal lobe. Coxopodite with 14 setae: 4 on distal lobe, 10 on proximal lobe. Most, if not all, setae on basipodite and coxopodite setulose.

First maxilliped (Figure 3G).—Unsegmented protopodite with 20 setae; most setae heavily spinulose. Endopodite four-segmented; setation formula 4, 2, 1, 4; series of fine hairs on medial margin of proximal segment. Four natatory setae on exopodite. Epipodite, a small lobe.

Second maxilliped (Figure 3H).—Unsegmented protopodite with seven spinulose setae. Endopodite four-segmented; setation formula 6, 2, 1, 2. Exopodite about three times longer than endopodite, five natatory setae.

Third maxilliped (Figure 3I).—Usually one seta on unsegmented protopodite. Endopodite five-segmented, seven setae: five setae on distal, two on penultimate segment. Exopodite with five natatory setae.

Pereopods.—Poorly developed, unsegmented, and compacted tightly under cephalothorax. Pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 3A, J, K).—Five somites and telson (somite 6 fused with telson). Fifth somite with pair of spines on posterolateral margin that extend posteriorly about one-fifth length of fifth somite. Minute spinules along posterodorsal border of fifth somite (Figure 3J) (spinules most easily seen in cleared specimens at $\geq$100$\times$ magnification). Telson (Figure 3K) slightly emarginate distally, bears 7 + 7 densely plumose setae. Third setal pair shorter than second or fourth setal pair. Minute spinules along posterior margin and at base of all setal pairs except possibly outer (seventh) setal pair. Enclosed uropods visible. Anal spine present.

Eualus suckleyi—Stage II Zoeae

Mean total length of Stage II, 3.8 mm (range 3.5-4.2 mm, 8 specimens). Eyes stalked. Rostrum shaped as in Stage I. Carapace with small supraorbital spine, no spinules (Figure 4A).

Antennule.—Similar to Stage I, except peduncle two-segmented with two setae at joint.

Antenna.—Flagellum with terminal spine, no setae, almost same length as scale (Figure 4B). Tip of scale four-segmented, proximal segment incomplete. Scale with 13 plumose setae—no proximal seta near outer lateral margin.

Mandibles, maxillule, and maxilla.—Same as Stage I.

Maxillipeds.—Epipodite of first maxilliped distinctly lobed. Exopodites of maxillipeds 1, 2, and 3 have four, five, and five natatory setae, respectively.

Pereopods.—Poorly developed, tightly compacted under cephalothorax; pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson.—Somite 6 fused with telson. Abdomen retains spines on fifth somite.

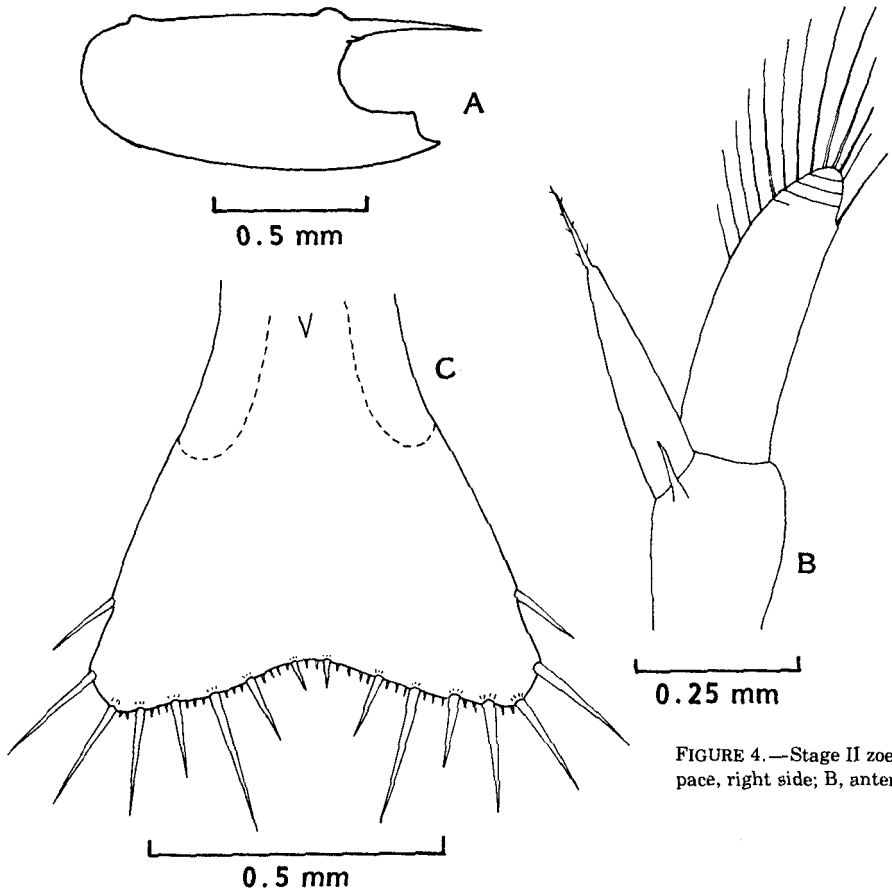

FIGURE 4.—Stage II zoea of *Eualus suckleyi*: A, carapace, right side; B, antenna, ventral; C, telson, ventral.

Telson with 8 + 8 plumose setae; setae noticeably shorter than in Stage I (Figure 4C). Uropods enclosed.

Eualus fabricii—Stage I and II Zoeae

Stage I and II *Eualus fabricii* are similar morphologically to Stage I and II *E. suckleyi*; however, they can be distinguished. Stage I and II of *E. fabricii* are slightly larger than Stage I and II *E. suckleyi*, and armature of the fourth and fifth abdominal somites and numbers of spines and setae differ between the two species.

Stage I Zoeae

Mean total length of Stage I, 3.7 mm (range 3.5-3.8 mm, 10 specimens). Carapace and rostrum similar to those of Stage I *E. suckleyi*, except no spines adjacent to pterygostomian spine on anterior margin of carapace.

Antennule.—Minute projection at base of conical projection of antennule (observable only under high [400×] magnification).

Antenna.—Same as antenna of Stage II *E. suckleyi* (Figure 4B), except flagellum about 1.5 times length of scale.

Mandibles.—Same as Stage I *E. suckleyi.*

Maxillule.—Seven spines on coxopodite; nine spines on basipodite.

Maxilla.—Three (sometimes 4) setae on distal lobe of coxopodite; 11 setae on proximal lobe. Six setae on each lobe of basipodite.

Maxillipeds.—Similar to Stage I *E. suckleyi* except no epipodite on first maxilliped.

Pereopods.—Same as Stage II *E. suckleyi.*

Pleopods.—Absent.

Abdomen and telson.—Pair of lateral spines on fourth and fifth somites. Lateral spines on fourth somite slightly smaller than lateral spines on fifth somite (Figure 5). Minute spinules on posterodorsal margin of fourth and fifth somites: usually one to three on fourth somite, about eight on fifth somite. Minute spinules somewhat variable in size and number, slightly larger than spinules of *E. suckleyi*. Telson same as Stage I telson of *E. suckleyi*.

Stage II Zoeae

Mean total length of Stage II, 4.1 mm (range 4.0-4.3 mm, 10 specimens). Carapace with two spinules immediately posterior to pterygostomian spine; small supraorbital spine present.

Antennule and antenna.—Similar to Stage II *E. suckleyi*, except antennules have only 1 small seta at joint of peduncle and scale with 16 or 17 plumose setae.

Mandibles, maxillule, and maxilla.—Same as Stage I *E. fabricii*.

Maxillipeds.—Exopodites of maxillipeds 1, 2, and 3 have 4, 9, and 10 natatory setae, respectively. Epipodite on first maxilliped undeveloped, not lobed.

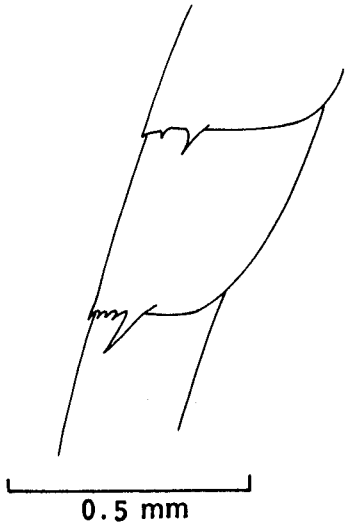

FIGURE 5.—Stage I zoea of *Eualus fabricii*: fourth and fifth abdominal somites, right side.

Pereopods.—Pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson.—Fourth and fifth somites with lateral spines, no spinules. Telson fused with sixth somite, has 8 + 8 densely plumose setae. Setae noticeably shorter than in Stage I *E. fabricii*. Uropods enclosed.

Spirontocaris arcuata—Stage I Zoeae

Mean total length of Stage I (Figure 6A), 4.2 mm (range 4.1-4.4 mm, 10 specimens). Rostrum (Figure 6B) spiniform, without teeth, about one-seventh length of carapace, projects downward paralleling contour of eyes. Carapace with small, somewhat angular, dorsal prominence at base of rostrum; another prominence near posterior edge. Pterygostomian spines present, not hidden by sessile eyes. Two or three minute spines along anteroventral margin of carapace. No supraorbital spines.

Antennule (Figure 6C).—Unsegmented peduncle with conical projection and several small simple setae (one seta especially longer than others). Four aesthetascs on small projection on peduncle near base of conical projection.

Antenna (Figure 6D).—Unsegmented flagellum shorter and narrower than scale. Flagellum with spinulose apical spine and several simple setae of various lengths. Scale distally divided into four segments, fringed with 11 heavily plumose setae, has small plumose seta proximally (near outer lateral margin). Protopodite with spine at base of flagellum but not at base of scale.

Mandibles (Figure 6E).—Well developed, without palps. Incisor process of left mandible has four teeth; incisor process of right mandible triserrate. Left mandible with relatively wide lacinia mobilis adjacent to incisor process, subterminal tooth on truncated molar process.

Maxillule.—Maxillule same shape as maxillule of Stage I *E. suckleyi* (Figure 3E). Coxopodite with seven spinulose setae. Basipodite with 10 (sometimes 11) spinulose spines terminally. Endopodite two-segmented, has five spinulose setae: three on

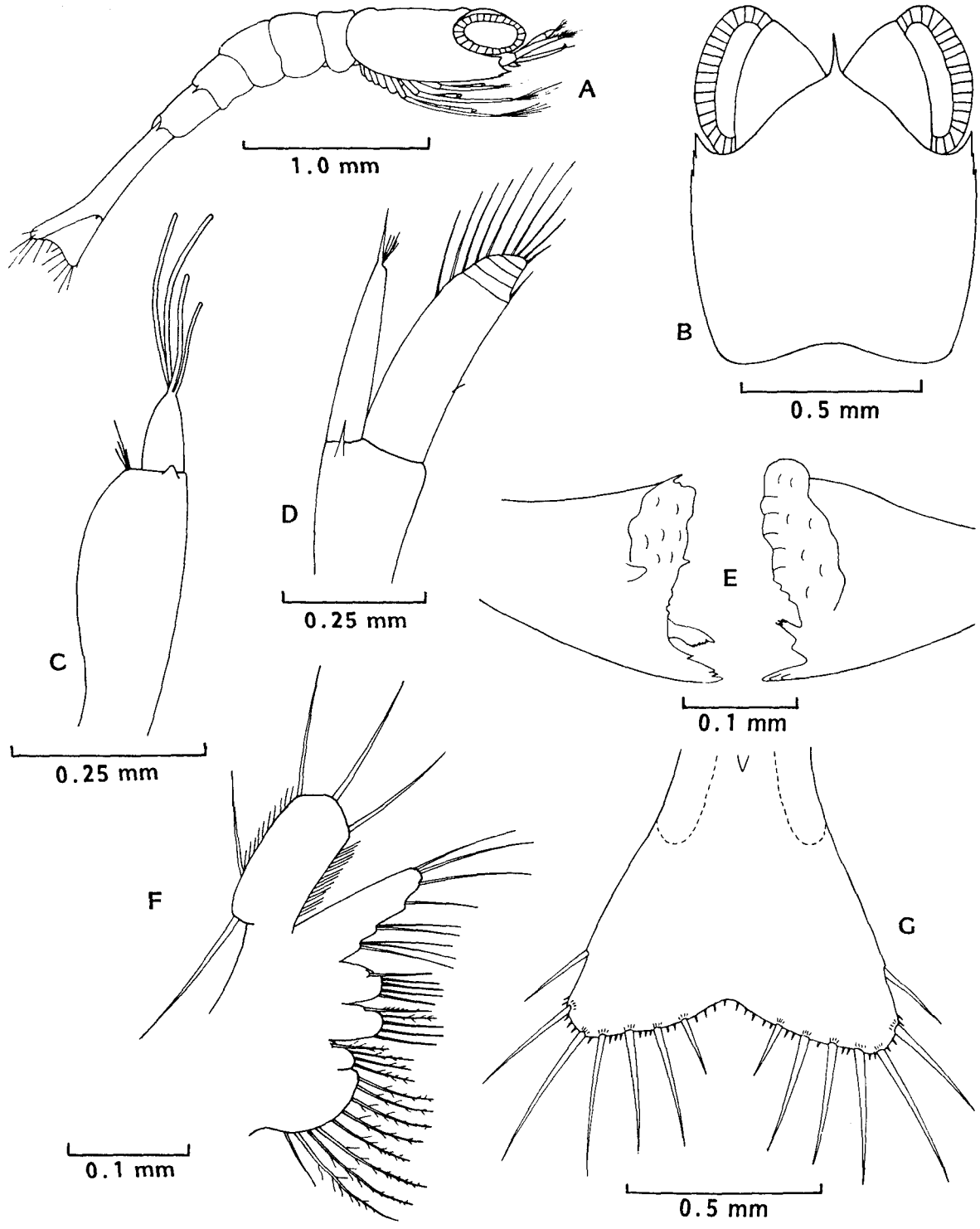

FIGURE 6.—Stage I zoea of *Spirontocaris arcuata*: A, whole animal, right side; B, carapace and eyes, dorsal; C, antennule, ventral; D, antenna, ventral; E, mandibles, left and right, posterior; F, maxilla, dorsal; G, telson, ventral.

distal segment, two on proximal segment. No outer seta on maxillule.

Maxilla (Figure 6F).—Four long plumose setae on scaphognathite; slightly longer, thicker seta at proximal end; series of fine hairs along inner margin; thinner series of hairs along outer margin. Nine setae on unsegmented endopodite. Basipodite and coxopodite bilobed. Basipodite with five setae on each lobe. Coxopodite with 13 setae: 4 on distal lobe, 9 on proximal lobe. Most setae on coxopodite setulose.

First, second, and third maxillipeds.—Maxillipeds similar to Stage I *E. suckleyi*; protopodite of first maxilliped has 25-27 setae; setation formula of endopodite of third maxilliped 5, 2, 1, 1, 4.

Pereopods (Figure 6A).—All five pairs present, poorly developed, unsegmented, and compacted under cephalothorax. Pairs 1 and 2 biramous, 3-5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 6A, G).—Five somites (somite six fused with telson). Fourth and fifth somites with spine but no spinules on posterolateral margins. Telson, shaped as in Stage I *E. suckleyi* (Figure 3K), has 7 + 7 densely plumose setae. Second and third pair of telsonic setae are same length. Minute spinules along terminal margin and at base of each seta except possibly last setal pair. Enclosed uropods visible. Anal spine present.

Spirontocaris ochotensis— Stage I Zoeae

Stage I *S. ochotensis* similar to Stage I *S. arcuata*. *Spirontocaris ochotensis* smaller than *S. arcuata* and lacks rostrum; morphology of carapace, antenna, mandibles, and maxilla slightly different. Characters not mentioned are identical to Stage I *S. arcuata*.

Mean total length of Stage I, 2.8 mm (range 2.7-2.9 mm, 10 specimens). Carapace of *S. ochotensis* without rostrum. Pterygostomian spine and usually a spine along anteroventral margin of carapace (Figure 7A). Minute supraorbital spines present.

Antenna.—Plumose seta three times length of terminal spine on tip of flagellum (Figure 7B).

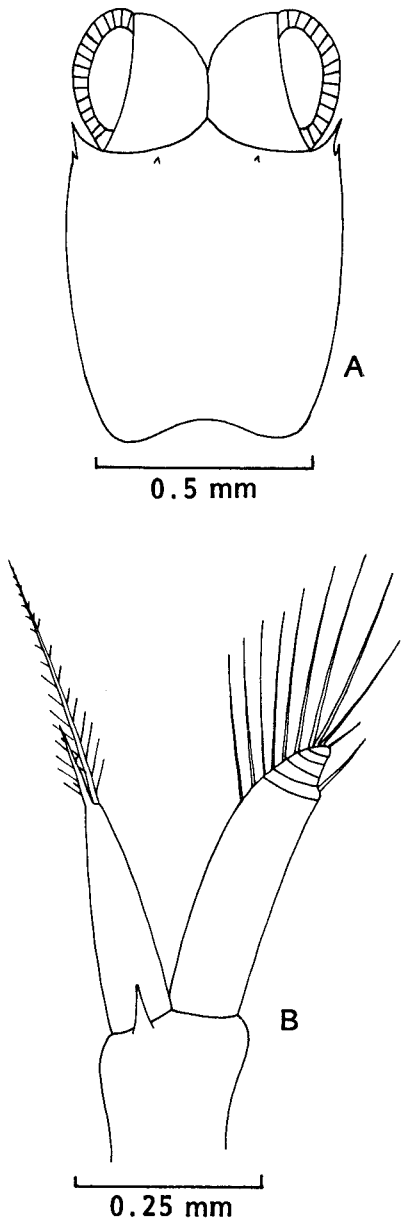

FIGURE 7.—Stage I zoea of *Spirontocaris ochotensis*: A, carapace and eyes, dorsal; B, antenna, ventral.

Mandible.—Narrow lacinia mobilis on left mandible (as in Stage I *E. suckleyi*, see Figure 3D).

Maxilla.—Seven (rarely eight) plumose setae on exopodite.

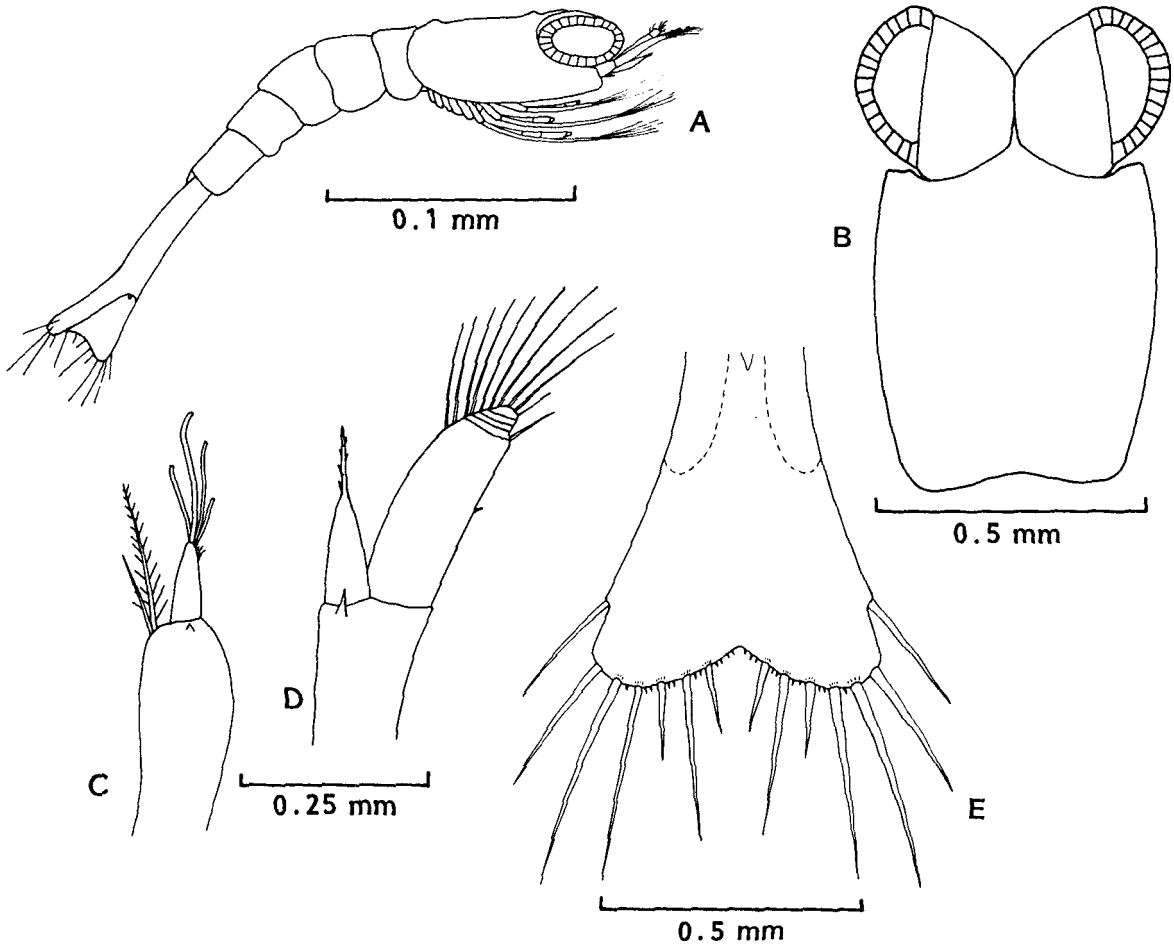

FIGURE 8.—Stage I zoea of *Heptacarpus camtschaticus*: A, whole animal, right side; B, carapace and eyes, dorsal; C, antennule, ventral; D, antenna, ventral; E, telson, ventral.

Heptacarpus camtschaticus— Stage I Zoeae

Mean total length of Stage I (Figure 8A), 2.9 mm (range 2.8-3.1 mm, 10 specimens). Carapace without spines; minute rostrum curves slightly downward following dorsal contour of sessile eyes (Figure 8B).

Antennule (Figure 8C).—Unsegmented peduncle with conical projection, plumose seta, simple spine, and small projection. Plumose seta about twice length of conical projection. Conical projection has four aesthetascs terminally, three small aesthetascs subterminally.

Antenna (Figure 8D).—Unsegmented flagellum about three-fourths length of scale, tipped by stout spinulose spine. Scale similar to scale of Stage I *E. suckleyi* (Figure 3C) except noticeably shorter and wider.

Mandibles, maxillule, maxilla, and maxillipeds.—Mouthparts similar to those of Stage I *E. suckleyi*, except coxopodite of maxillule has seven spinulose setae; basipodite of maxilla has six setae on each lobe; first maxilliped has no epipodite; setation formulas of the endopodites of the second and third maxillipeds are 5, 2, 1, 3 and 4, 2, 0, 0, 2, respectively.

Pereopods (Figure 8A).—All five pairs present: pairs 1 and 2 biramous; 3-5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 8A, E).—Abdomen similar in shape to abdomen of Stage I *E. suckleyi* except without spines or spinules. Telson emarginated, bears 7 + 7 relatively long densely plumose setae: longest (fifth) pair about three-fourths length of greatest telsonic width. Minute spinules along terminal margin of telson and at base of each seta to fifth setal pair. Anal spine present.

COMPARISON OF ZOEAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

In the literature, authors have identified or assigned names or stages to hippolytid larvae obtained from plankton. A comparison of their descriptions with my descriptions of zoeae of known parentage is useful in placing these earlier works in proper perspective (Table 2).

TABLE 2.—Presumed and corrected identities of hippolytid zoeae discussed in this report.

Author	Presumed identity	Conclusion from this study
Stephensen (1916)	*S. polaris* (= *L. polaris*) Stage I	Probably *L. polaris* Stage III or later
	Spirontocaris-larva Nr. 3	Not *E. fabricii*
	S. fabricii (= *E. fabricii*) "youngest" stage (Stage I)	Stage III
	"intermediate" stage (Stage II)	Stage IV
	"oldest" ("last") stage (Stage III)	Stage V or VI
Stephensen (1935)	*Spirontocaris*-larva No. 1	Unknown
	S. polaris (= *L. polaris*) Stages not specified	—
Frost (1936)	*E. fabricii* Late-stage larvae	Not *E. fabricii* Stage VI or VII
Makarov (1967)	*Lebbeus* sp. "C" Stage II	*Lebbeus* sp. Stage I
	Lebbeus sp. "D"	*Lebbeus* sp.; different species from *Lebbeus* sp. "C"
	Stage I	Stage I
	"*Eualus* sp. A" *E. fabricii*	Not *E. fabricii*
	Stage I	Stage I
	"*Spirontocaris* sp. A" *S. phippsii*	Not *S. arcuata*
	Stage I	Stage I
	"*Spirontocaris* sp. B" Stage I	Not *S. arcuata* Stage I

Lebbeus polaris

Krøyer (1842, in Pike and Williamson 1961) described an advanced embryo of *L. polaris* with all appendages, except uropods, present and segmented. The fourth and fifth abdominal somites each have a pair of small posterolateral spines. All three pairs of maxillipeds have natatory exopodites, but the pereopods have none. As far as can be compared, my Stage I zoeae of *L. polaris* are identical to Krøyer's embryo, except the pereopods and pleopods of my specimens are unsegmented.

Stephensen, in 1916, described a zoea from southern waters of Greenland that he assumed is a Stage I zoea of *S. polaris* (= *L. polaris*). As noted by Pike and Williamson (1961), Stephensen's zoea is similar to Krøyer's specimen. Stephensen's zoea has posterolateral spines on the fourth and fifth abdominal somites, lacks exopodites on the pereopods, and the appendages are larger and more developed than Krøyer's specimen. The carapace of Stephensen's zoea has supraorbital spines, and developing uropods are visible inside the telson. In addition, the chelae of the first and second pereopods of Stephensen's zoea are well developed; the carpopodite of the second pereopod had begun to develop joints; and the pleopods have well-developed appendices internae. The presence of appendices internae, well-developed chelae, and segmentation of carpopodite shows that Stephensen's zoea is in the last, or perhaps penultimate, zoeal stage and that the species passes through only three or, perhaps, four zoeal stages. Under the name "*Spirontocaris*-larva No. 1," Stephensen (1935) included several specimens collected from waters of western Greenland that he assumes are later stages of *S. polaris* (= *L. polaris*); one specimen bears exopodites on pereopods 1 and 2.

The characteristics of Stephensen's (1916) late-stage "*S. polaris*" zoea are typical of *Lebbeus* zoeae although his zoea differs somewhat from my *L. polaris* zoeae. Stephensen's zoea has an unsegmented antennal flagellum, and the telson is fused with the sixth somite; my zoeae of *L. polaris* have a two-segmented antennal flagellum in Stage I, and the sixth somite and telson are jointed in Stage II. If Stephensen was correct in assuming his specimen to be *L. polaris*, then *L. polaris* in Greenland waters has at least one more zoeal stage than *L. polaris* in Alaskan waters. Stephensen's (1935) descriptions of his "*Spirontocaris*-larva No. 1" zoeae are too brief to identify either the species or stage. At least one of Stephensen's specimens lacks the pair of spines on the antennal protopodite and must be a species other than *L. polaris*.

Makarov (1967) briefly described zoeae collected from plankton of the western Kamchatka Peninsula shelf. He thought these zoeae were probably

zoeal Stages I-IV of a species of *Lebbeus*. He also obtained one specimen each of "*Lebbeus* sp. D" and "*Lebbeus* sp. C"; these he thought were zoeal Stages I and II, respectively. My Stage I zoeae of *L. polaris* are similar to Makarov's Stage I zoea ("*Lebbeus* sp. D") except my zoeae are not as long (average length 5.4 mm compared with 6.4 mm). Makarov's Stage II zoea ("*Lebbeus* sp. C") is 7.6 mm long; the eyes are sessile; and the carapace lacks supraorbital spines. My Stage II zoeae of *L. polaris* are 5.7 mm (mean) long; the eyes are stalked; and the carapace has supraorbital spines. Development of Makarov's "*Lebbeus* sp. C" and "*Lebbeus* sp. D" zoeae shows that they are undoubtedly zoeae of the genus *Lebbeus*. Because his "*Lebbeus* sp. C" zoea has sessile eyes and does not have supraorbital spines, it must be a Stage I zoea rather than a Stage II zoea. "*Lebbeus* sp. C," therefore, is a species different from "*Lebbeus* sp. D."

Larvae of only one other species of *Lebbeus*, *L. groenlandicus*, have been completely described from known parentage (see Haynes 1978). At comparable zoeal stages, *L. groenlandicus* is more developed than *L. polaris*. The antennal flagellum of Stage I zoeae of *L. groenlandicus* is about twice as long as the scale and terminates in a narrow projection. In *L. polaris*, the antennal flagellum is only slightly longer than the scale and has a plumose seta and spine. Also, in Stage I zoeae of *L. groenlandicus*, the epipodite of the first maxilliped is bilobed; the second maxilliped has a single lobed epipodite; and pereopods and pleopods are either partially or fully segmented. In *L. polaris*, only the first maxilliped bears an epipodite (single lobed), and none of the pereopods or pleopods are either partially or fully segmented.

In Stage II zoeae of *L. groenlandicus*, the supraorbital spine is well developed; the antennule differs considerably from the antennule of Stage I; the antennal flagellum has setae; the antennal scale is fringed with plumose setae along nearly the entire inner margin; the pereopods are essentially adult in shape; and the pleopods are fully segmented. In Stage II *L. polaris*, the supraorbital spine is small; the antennule and antennae are similar to the antennule and antennae of Stage I; the pereopods are not adult in shape; and the pleopods are unsegmented.

Lebbeus groenlandicus has only three larval stages: two zoeal stages and one megalopal stage (Haynes 1978). Because larvae of *L. polaris* are somewhat less developed for a given stage than those of *L. groenlandicus*, *L. polaris* probably has three zoeal stages before molting to the megalopa.

Eualus suckleyi

Zoeal Stages I and II of *E. suckleyi* are similar to the same zoeal stages of *E. gaimardii* (H. Milne Edwards), *S. spinus*, and *S. lilljeborgii* (as Pike and Williamson [1961] described them from eastern Atlantic specimens); however, there are slight differences in setation, development of pereopods, and armature of carapace and abdomen. The antennal flagellum of Stage I zoeae of *E. suckleyi* has a spine and a seta; the antennal scale has a plumose seta at the base of each of the four segments; and pereopods 1-5 are present (pereopods 1-3 biramous, other pereopods uniramous). The antennal flagellum of Stage I zoeae of *E. gaimardii* has only a spine; the antennal scale has a small outer spine at the base of the four segments; and pereopods 1-4 are present and uniramous. Stage I zoeae of *S. spinus* and *S. lilljeborgii* lack minute spines on the anteroventral margin of the carapace, have a rudimentary supraorbital spine, and only pereopods 1 and 2 are biramous. Also, *S. spinus* has posterolateral spines on abdominal somites 4 and 5 rather than only on somite 5 as in *E. suckleyi*.

In Stage II zoeae of *E. suckleyi*, an outer plumose seta is at the base of the distal joints of the antennal scale; and exopodites on maxillipeds 1-3 have four, five, and five natatory setae, respectively. In Stage II zoeae of *E. gaimardii*, a somewhat stout spine is at the base of the distal joints of the antennal scale, and exopodites on maxillipeds 1-3 have five, seven, and seven natatory setae, respectively. Stage II zoeae of both *S. spinus* and *S. lilljeborgii* have a tuft of dorsal setae on abdominal somite 4; Stage II zoeae of *E. suckleyi* do not have this tuft.

Eualus fabricii

Stephensen's (1916) "*Spirontocaris*-larva Nr. 3" were the most abundant spirontocarid larvae in his plankton samples from Greenland waters. He thought the larvae were the same species as the most abundant adult and described and illustrated them as the "youngest" stage, "intermediate" stage, and "oldest" ("last") stage of *Spirontocaris fabricii* (= *Eualus fabricii*). Stephensen (1935) later described additional characteristics for the "first" and "last" stages. Frost

(1936) illustrated a whole zoea she believed was a zoeal stage of *E. fabricii* later than Stephensen's "last" stage. Pike and Williamson (1961), from development of zoeae of the genus *Eualus*, showed that Stephensen's "youngest" stage is Stage III; the "intermediate" stage is Stage IV; and the "oldest" stage is Stage V or VI. They believed that the zoea illustrated by Frost (1936) is probably Stage VI or VII.

Although Stephensen's and Frost's *E. fabricii* zoeae are later stages than my zoeae, they can be compared with my zoeae by the presence of posterolateral spines on abdominal somites, length of the antennal flagellum, and number of setae fringing the antennal scale. My *E. fabricii* zoeae have posterolateral spines on abdominal somites 4 and 5; Stephensen's and Frost's zoeae do not. The antennal flagellum in Stages I and II of my *E. fabricii* zoeae is about 1.5 times the length of the antennal scale, and the antennal scale has 13 setae in Stage I and 16 or 17 setae in Stage II. In the "youngest" stage (Stage III zoeae) described by Stephensen, the length of the antennal flagellum is still only about one-half the length of the antennal scale, and the number of setae on the antennal scale does not exceed 11. Stephensen's and Frost's zoeae apparently belong to a species other than *E. fabricii*.

Pike and Williamson (1961) noted that the zoeae described by Stephensen (1916, 1935) and Frost (1936) as *S. fabricii* (= *E. fabricii*) are similar to zoeae of *E. pusiolus*. The zoeae of both species lack abdominal spines and have exopodites on pereopods 1-4. However, *E. fabricii* zoeae are larger, have a longer rostrum, and have a well-developed antennal spine on the anterior margin of the carapace in late zoeal stages (compared with *E. pusiolus* zoeae). On the basis of Pike and Williamson's comparison of zoeae of *E. fabricii* and *E. pusiolus*, Makarov (1967) suggested that his "*Eualus* sp. A" series of zoeae from the west Kamchatka shelf is either *E. pusiolus* or *E. fabricii*. According to Makarov, "*Eualus* sp. A" zoeae are nearly identical to zoeae of *E. pusiolus* described by Pike and Williamson (1961), but because Makarov's zoeae are larger, especially in the later stages, he speculated that "*Eualus* sp. A" zoeae might be *E. fabricii* zoeae.

Stage I and II zoeae of Makarov's "*Eualus* sp. A" differ considerably from my Stage I and II zoeae of *E. fabricii*. The zoeae of "*Eualus* sp. A" are markedly smaller (Stages I and II of "*Eualus* sp. A" are 2.8 mm and 3.2 mm long, respectively; Stage I and II *E. fabricii* are 3.7 mm and 4.1 mm long, respectively). The rostrum of Makarov's zoeae is minute; the abdomen lacks spines; and the antennal flagellum is noticeably shorter than the antennal flagellum of my Stage I and II *E. fabricii*.

Spirontocaris arcuata

Pike and Williamson (1961) described a Stage I zoeae of *S. spinus* and *S. lilljeborgii* hatched from known parentage and a Stage II zoea of *S. phippsii* collected from plankton. My Stage I zoeae of *S. arcuata* are clearly different from these zoeae. Stage I zoeae of *S. arcuata* differ from those of *S. spinus* and *S. lilljeborgii* in shape of rostrum, armature of carapace and abdomen, and setation of antennule and antennae. Stage I *S. arcuata* zoeae have a short rostrum that does not project beyond the anterior margin of the eyes. In Stage I zoeae of *S. spinus* and *S. lilljeborgii* and Stage II zoeae of *S. phippsii*, a prominent rostrum projects anteriorly beyond the eyes to about three-fourths the length of the antennular peduncle. The carapace of my specimens of *S. arcuata* does not have supraorbital spines but has spines along the anteroventral margin. However, in Stage I *S. spinus* and *S. lilljeborgii* and Stage II *S. phippsii*, the carapace has a small supraorbital spine, and the anteroventral margin is smooth. Also, in Stage I zoeae of *S. arcuata*, the antennule and inner flagellum of the antenna have several setae terminally. Both the antennule and inner antennal flagellum of Stage I zoeae of *S. spinus* and *S. lilljeborgii* and Stage II zoeae of *S. phippsii* have a large seta terminally. Finally, Stage I zoeae of *S. lilljeborgii* have posterolateral spines only on the fourth abdominal somite; Stage I zoeae of *S. arcuata* have posterolateral spines on both fourth and fifth abdominal somites.

Makarov (1967) described Stage I zoeae of two unidentified species of *Spirontocaris* ("species A" and "species B") from plankton of the western Kamchatka Peninsula shelf. His zoeae can be separated from Stage I zoeae of *S. arcuata* by the relatively long rostrum in his species A and B. In addition, Makarov's Stage I zoeae of *Spirontocaris* sp. B are longer than those of *S. arcuata* (5.1 mm and 4.2 mm, respectively) and have pleopodal buds.

Ivanov (1971) briefly described four zoeae he assumed were *S. spina intermedia*. His zoeae are readily distinguishable from zoeae of *S. arcuata*

because *S. spina intermedia* has a tuft of setae on the dorsal surface of the fourth abdominal somite.

Spirontocaris ochotensis

When descriptions of hippolytid zoeae by other authors (Stephensen 1916, 1935; Webb 1921; Lebour 1931, 1932; Needler 1934; Frost 1936; Gurney 1942; Williamson 1957; Pike and Williamson 1961; Makarov 1967; Ivanov 1971; and Haynes 1978) are compared with my description of zoeae of *S. ochotensis*, my Stage I zoeae of *S. ochotensis* are the only described hippolytid zoeae of the northern North Pacific Ocean that have posterolateral spines on the fourth and fifth abdominal somites and lack a rostrum. Stage I zoeae of *S. arcuata* (described in this report) are similar to Stage I *S. ochotensis* zoeae but have a rostrum.

Heptacarpus camtschaticus

The only larvae of *Heptacarpus* identified are the first zoeal stages of three species that Needler (1934) described: *H. paludicola*, *H. tridens*, and *H. brevirostris*. These zoeae differ from *H. camtschaticus*: Needler's zoeae lack a rostrum, a spine adjacent to the plumose seta of the antennule, and a long proximal seta on the scaphognathite of the maxilla. Also, Needler's zoeae have pterygostomian spines, which are absent in Stage I zoeae of *H. camtschaticus*.

Stage I zoeae that resemble Stage I zoeae of *H. camtschaticus* include *E. pusiolus* and *E. occultus* found in European waters (Pike and Williamson 1961) and *E. macilentus* found in the Bering Sea (Ivanov 1971). All these Stage I zoeae lack posterolateral spines on the fourth and fifth abdominal somites and have a minute rostrum (although Stage I zoeae of *E. occultus* from British waters may lack a rostrum [Pike and Williamson 1961]). Stage I zoeae of *H. camtschaticus* differ from the other Stage I zoeae because *H. camtschaticus* zoeae have all pairs of pereopods, and the antennal flagellum projects only about three-fourths the length of the antennal scale. In Stage I, the other species lack pereopods, and the antennal flagellum projects to the tip of the antennal scale or just beyond. In addition, Stage I zoeae of *E. occultus* have a small dorsal tuft of setae on the fourth abdominal somite and a row of fine denticles on the posterior margin of the fifth abdominal somite; these structures are absent in Stage I zoeae of *H. camtschaticus*.

CHARACTERIZATION OF ZOEAE OF *SPIRONTOCARIS* S.S. AND RELATED GENERA

Holthuis (1947) redefined the genus *Spirontocaris* sensu lato (s.l.) and divided it into six genera: *Birulia*, *Eualus*, *Heptacarpus*, *Lebbeus*, *Spirontocaris* sensu stricto (s.s.), and *Thoralus*. Pike and Williamson (1961) categorized the zoeae of *Spirontocaris* s.l. by the number of zoeal stages, number of pereopods, morphology of the rostrum in Stage I, and number of pereopods with exopodites in the last zoeal stage. Because of the wide range in morphology of the zoeae, Pike and Williamson (1961) suggested that *Spirontocaris* s.l. be given suprageneric status. My descriptions of hippolytid zoeae partially invalidate Pike and Williamson's categorization, extend the range of larval characters of the genus *Spirontocaris* s.l., and confirm Pike and Williamson's suggestion that *Spirontocaris* s.l. be given suprageneric status.

In Pike and Williamson's (1961) categorization, the known larvae of *Lebbeus* and *Spirontocaris* s.s. form separate generic groups. They categorize identified larvae of *Eualus* spp. into two distinct groups. Group 1 includes *E. gaimardii*, which has five zoeal stages. In Stage I zoeae of Group 1, the rostrum is large, and four pairs of undeveloped pereopods are present; in later zoeal stages, exopodites are present on pereopods one through three. Group 2 includes *E. pusiolus*, *E. occultus*, *E. fabricii*, and *E. herdmani*, which probably have six to nine zoeal stages. In Stage I zoeae of Group 2, the rostrum is minute or absent, and there are no pereopods. In later zoeae, exopodites are present on pereopods one through four (evidence was incomplete for *E. fabricii* and *E. herdmani*). The lack of information on larvae of *Heptacarpus* spp. prevents any comparison of *Heptacarpus* spp. larvae to those of Group 2 *Eualus*.

My descriptions of zoeae of *L. polaris*, *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* increase the range of morphological variations of zoeal "generic" characters used by Pike and Williamson (1961) for these genera (Table 3). Pike and Williamson list the rostrum of *Lebbeus* spp. zoeae in Stage I as small, but the rostrum may also be large (about one-half the length of the carapace). They list the rostrum in Stage I zoeae of *Spirontocaris* s.s. as large, but the rostrum of Stage I zoeae of *S. arcuata* is small (about one-seventh the length of the carapace), and the rostrum of Stage I zoeae of *S.*

TABLE 3.—Range of morphological and developmental characters used to define zoeae of *Spirontocaris* s.s. and related genera. (? = unknown.)

Genus	Characters				
	Number of zoeal stages	Number of pereopods in Stage I	Rostrum in Stage I	Pereopods bearing exopodites in later zoeal stages	References[1]
Lebbeus sp.	2, 3	5	long	0	1, 2, 3
Eualus sp.	5-9	0, [2]4, [2]5	absent to long	3, 4	1, 3, 4, 5, 6, 7
Spirontocaris s.s.	5	[2]5	absent to long	2	1, 3, 4, 6, 8
Heptacarpus sp.	?	0, [2]5	absent, minute	?	1, 5
Thoralus sp.	9	0	absent, minute	3	4, 9, 10

[1]1) Haynes 1978, 2) this report, 3) Ivanov 1971, 4) Pike and Williamson 1961, 5) Needler 1934, 6) Williamson 1957, 7) Lebour 1940, 8) Lebour 1937, 9) Lebour 1932, 10) Lebour 1936.
[2]Undeveloped pereopods.

ochotensis is absent. Stage I zoeae of both *E. suckleyi* and *E. fabricii* have large rostrums (about one-half the length of the carapace) and, therefore, correspond to Pike and Williamson's *Eualus* Group 1 but also have some of the characters of Group 2. Additionally, zoeae of *E. suckleyi* and *E. fabricii* have five pairs of undeveloped pereopods rather than four pairs of undeveloped pereopods like Stage I zoeae of *E. gaimardii*. The genus *Heptacarpus* is characterized by Pike and Williamson (1961) by the absence of both rostrum and pereopods in Stage I, but Stage I zoeae of *H. camtschaticus* have both a minute rostrum and all five pairs of undeveloped pereopods.

Although my new descriptions of zoeae extend the range of morphological characters of the genus *Spirontocaris* s.l. and partially invalidate the generic groupings used by Pike and Williamson (1961), these new descriptions confirm their findings of great morphological variation of the zoeae of *Spirontocaris* s.l. The range of two to nine zoeal stages among the species is unequalled in any described genus. Usually Stage I zoeae of a caridean genus vary little in the degree of development at hatching, but *Spirontocaris* s.l. includes some species that have Stage I zoeae with all appendages, except uropods, present and segmented and other species of Stage I zoeae that have no trace of appendages posterior to the maxillipeds. The size of the zoeal rostrum is frequently of generic importance. Among species of the spirontocarid group, the rostrum varies from being absent to large. Also, the number of pereopods with exopodites in later zoeal stages is constant throughout known zoeae of nearly all caridean genera except *Spirontocaris* s.l., which may have 0, 2, 3, or 4 pereopods (Pike and Williamson 1961). The wide range in morphology of different species in the *Spirontocaris* s.l. supports Pike and Williamson's (1961) suggestion that it be accorded suprageneric, rather than generic, status.

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FEEDING BEHAVIOR AND BIOLOGY OF YOUNG SANDBAR SHARKS, *CARCHARHINUS PLUMBEUS* (PISCES, CARCHARHINIDAE), IN CHINCOTEAGUE BAY, VIRGINIA[1]

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ABSTRACT

During the summers of 1977, 1978, and 1979 the feeding behavior and biology of young sandbar sharks were investigated in Chincoteague Bay, Virginia, using catch data obtained from rod and reel fishing. Mean catch per unit effort for the study was 1.02 sharks per hour, but yearly differences in catch per unit effort were found. Sandbar sharks were not caught before the first week in June despite substantial fishing effort prior to this time, both in 1977 and 1978. Catch per unit effort was higher at night than during the day but was not related to tidal current stage or speed. Captures were made at surface, mid, and bottom fishing depths. During the day, catch per unit effort was highest at the bottom fishing depth but did not differ among the three depths during the night. The blue crab, *Callinectes sapidus*, was found in 41.3% of the stomachs examined; 20% of the stomachs were empty, and the remainder contained various crustaceans and fishes. The proportion of empty or nearly empty stomachs was greater for night captures than for day captures. Yearly differences in sex ratio existed and the total length distribution of sharks measured suggested the presence of relatively distinct size classes.

The natural history of the sandbar shark, *Carcharhinus plumbeus*, has received considerable attention and is relatively well known. Tag returns (Casey 1976) and analysis of commercial shark fishery records (Springer 1960) have provided valuable information on the distribution and long-term movements of this species. These studies show the sandbar shark to be an abundant, migratory shark distributed in the western North Atlantic from Cape Cod, Mass., to West Palm Beach, Fla., during the summer and from the Carolinas into the Gulf of Mexico in the winter. From spring until late fall, young sandbar sharks spend much of their time along the mid-Atlantic coast in nursery areas consisting of shallow bays and sounds. In late fall the young move farther offshore and south to wintering grounds between North Carolina and Florida. According to Casey (1976), the young may repeat this cycle for up to 5 yr and then begin to occupy areas farther offshore and undertake longer north-south migrations. Other studies have made contributions concerning growth (Wass 1973), reproduction (Taniuchi 1971), and general ecology (Bigelow and Schroeder 1948; Clark and von Schmidt 1965; Bass et al. 1973; Lawler 1977).

One area in which information is lacking, not only for this species but for sharks in general, concerns feeding behavior. Although work has been conducted on the prey items of sharks (Bigelow and Schroeder 1948) and the role of various sensory modalities in locating prey (Hobson 1963; Kleerekoper 1969; Myrberg et al. 1976; Hodgson and Mathewson 1978; Kalmijn 1978), these areas have received little attention and are little understood. Other areas of feeding behavior such as food requirements and feeding activity have received even less attention.

The specific objective of this study was to determine patterns of feeding activity of young sandbar sharks in relation to the time of day, tidal cycle, and vertical positions within the water column. Because information on sandbar sharks in nursery areas is scarce, data concerning the food items, abundance, sex ratio, and age-class composition of this species in Chincoteague Bay are also presented.

METHODS

This study was conducted from early May through late August during 1977 and 1978 and on

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12 July 1979 in the lower portion of Chincoteague Bay, Va. (Figure 1). Located within the summer distribution of this species, the bay supports a relatively large number of young sandbar sharks from early June through September (pers. obs.). Average water depth of the bay is 2 m, but many areas with strong current flow have depths as great as 12 m. A tidal inlet connects the bay with the Atlantic Ocean and tidal range varies from 0.75 to 2.00 m. Salt marshes with numerous tidal creeks, brackish to seawater salinities, and other conditions which seem typical of the nursery grounds of this shark along the middle Atlantic coast also characterize the area.

A 4.9 m outboard motorboat was used as a fishing platform and sharks were caught using sport fishing rods with 3/0 Penn[4] reels. Terminal tackle consisted of a 0.3 m wire leader with a straight-shank, ball-eye fishing hook. To increase fishing effort, two leaders were attached (0.5 m apart) on each fishing line. To facilitate captures over the entire size range of sharks in the area, each line was rigged with a 3/0 and a 8/0 hook. A lead sinker or cork float was attached to adjust the lines to the desired fishing depth. Cut pieces of freshly frozen Atlantic menhaden, *Brevoortia tyrannus*, were used as bait and each hook was rebaited hourly. Nothing was thrown into the water to attract sharks except the bait. Upon capture each shark was brought into the boat where it was identified, sexed, and measured. The shark was then either tagged and released or sacrificed for stomach content analysis.

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

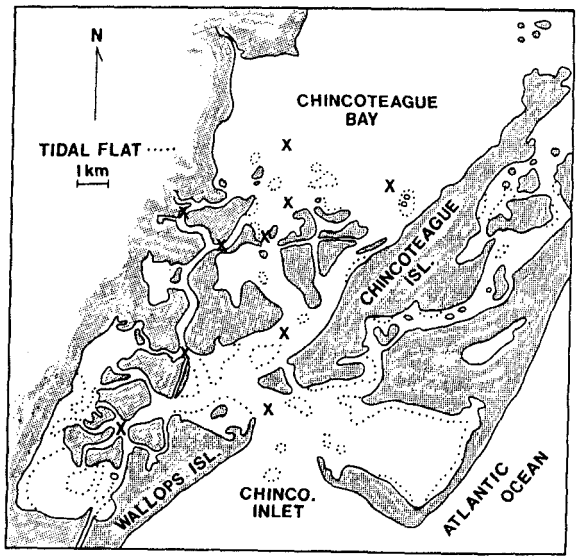

FIGURE 1.—Chart of the Chincoteague Bay study area (modified from National Ocean Survey Charts 12210 and 12211). ×'s give the locations of the 10 24-h fishing stations.

The type of fishing conducted fell into two categories. On 10 occasions, continuous fishing stations of approximately 24-h duration were completed (three in 1977, six in 1978, and one in 1979). These stations occurred at 10 different locations (Figure 1), each with a water depth >3 m. On all stations, the boat was anchored and three rods (rigged and baited as described above) were used with a rod fishing at the surface, middepth, and bottom. Fishing technique was standardized from station to station. After catching a shark, the rod was immediately replaced by another so that fishing effort was not interrupted. On 52 other occasions (20 in 1977 and 32 in 1978), shorter fishing periods were completed at randomly selected locations. The duration of these fishing periods and the time of day that they were conducted varied, but in a random fashion. The same fishing gear was employed at these times, but shallow as well as deep areas were fished. These shorter fishing periods are hereafter referred to as miscellaneous fishing stations. During both types of fishing, data concerning tidal current flow and water temperature were collected.

Strikes by fishes not captured were not included in the analysis of data. For each fishing station, catch per unit of effort (CPUE) was calculated by dividing the total number of sharks caught by the total number of hours spent fishing. CPUE is expressed as the number of sandbar sharks caught per hour of fishing using the three fishing rods previously described. CPUE was also calculated for various comparison categories within fishing stations such as day and night periods. For comparison categories involving fishing depth, CPUE at each depth was based on one fishing rod. Where mean CPUE is referred to in the results, the value is the arithmetic mean of CPUE values calculated for each fishing station. Because values of CPUE were not normally distributed, nonparametric methods of data analysis were employed. The tests used are described by Hollander and Wolfe (1973). Due to the large number of statistical comparisons made, many of the test names and probability values are given in tables rather than in the text of the results.

RESULTS

A total of 73 h from 17 fishing stations conducted in May 1977 and 1978 resulted in no catches. The first catch occurred on 6 June 1977 and on 1 June 1978 at water temperatures of 20.5° C and 21.0° C, respectively. After the initial catch, sandbar sharks were caught consistently and CPUE did not differ significantly among June, July, and August during either year (Table 1).

The number of catches and hours of fishing conducted after the arrival of sandbar sharks are summarized in Table 2. A total of 318 sharks were caught in 478 h of fishing. Mean CPUE for the 62 fishing stations was 1.02 sandbar sharks/h. CPUE varied among the 3 study yr (Table 3). CPUE in 1979 was 2.06 sandbar sharks/h, but was based on only one 24-h fishing station. In 1977 and 1978, CPUE was based on numerous fishing stations and was significantly higher in 1977.

Sandbar sharks were caught during all hours of the day and night. CPUE was calculated at 1-h intervals for each 24-h fishing station, but because of the relatively small sample size, numerous observations of zero CPUE, and great station-to-station variation in CPUE, these data were not sufficient for a statistical analysis of diel rhythmicity. Visual inspection did suggest a day-night difference in CPUE. On all but one 24-h station, CPUE was higher during the night than during the day. Grouping the data on this more general level and treating day and night observations (on CPUE) as samples paired on fishing station indicates CPUE was significantly higher during the night than during the day (Table 4).

CPUE did not differ significantly between flood and ebb tidal current periods (Table 4). During both current periods CPUE was higher during the night than during the day, but, because of multiple testing on the same data, the probability values given for the tests should be considered as only rough approximations (Table 4).

Catch data were grouped into four tidal current speed categories. Sandbar sharks were caught over the entire range of current speeds recorded during 24-h stations and CPUE was not significantly different among the four current speed categories (Table 5).

CPUE was calculated for the three fishing depths used during 24-h fishing stations. Although sandbar sharks were caught at all three depths, CPUE differed significantly among them (Friedman test, $P = 0.02$) and was higher at the bottom than at the surface or middepth. CPUE did not differ significantly between the surface and middepth (Table 6). The difference in CPUE among the depths was not the same for both day

TABLE 1.—Summary of fishing data for the 3 study mo of 1977 and 1978. The value given for "Mean rank" is the mean of the ranks assigned to the observations on CPUE in a Kruskal-Wallis test for differences in CPUE among months within the indicated year.

Year	Month	No. of fishing stations	Mean CPUE (sharks/h)	Mean rank	*P*-value
1977	June	13	1.46	16.1	
	July	5	1.63	13.4	0.46
	Aug.	5	.92	13.4	
1978	June	17	.63	17.3	
	July	12	.64	20.2	.47
	Aug.	9	1.21	22.8	

TABLE 2.—Summary of fishing data for 24-h stations, miscellaneous stations, and all stations combined.

Stations	Hours of fishing	No. of sharks caught	No. of stations	Mean CPUE (sharks/h)
24 h	232	160	10	0.67
Miscellaneous	246	158	52	1.07
Overall	478	318	62	1.02

TABLE 3.—Summary of fishing data for each study year. The value given for "Mean rank" is the mean of the ranks assigned to the observations on CPUE in a Mann-Whitney *U*-test.

Year	Hours of fishing	No. of sharks caught	No. of fishing stations	Mean CPUE (sharks/h)	Mean rank	*P*-value (2-tail test)
1977	128	119	23	1.39	39.2	0.005
1978	325	148	38	.76	26.0	
1979	25	51	1	2.06		

TABLE 4.—Summary of fishing data for various periods during 10 24-h fishing stations. The values given for "Rank sums" are the sums of the positive and negative differences of paired observations on CPUE in a Wilcoxon signed rank test. Differences for day-night and for day-night by current stage categories were for CPUE during the night minus CPUE during the day. Differences for the flood-ebb category were for CPUE during flood minus CPUE during ebb. Dusk and dawn periods were split equally between day and night categories.

Period	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sums (+)	Rank sums (−)	*P*-value (2-tail test)
Day	143	85	0.56	48	7	0.04
Night	89	75	.86			
Flood	115	90	.75	39	16	.28
Ebb	117	70	.55			
Flood-day	76	49	.62	45	10	[1].08
Flood-night	38	41	.78			
Ebb-day	67	36	.41	47	8	[1].04
Ebb-night	51	34	.65			

[1]Probabilities should be considered as rough approximations because of multiple testing on the same data.

TABLE 5.—Summary of fishing data for tidal current speed categories during the eight 24-h fishing stations in which current speed was recorded. The value given for "Rank sum" is the sum of the ranks assigned to the observations on CPUE for that current speed category in a Friedman test.

Current speed (m/min)	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sum	*P*-value
<10	36.5	25	0.65	24.0	
10-20	42.5	20	.51	16.5	$0.30<P<0.50$
20-30	52.0	35	.64	17.5	
>30	55.5	42	.63	22.0	

TABLE 6.—Summary of fishing data for the three fishing depths used during the 10 24-h fishing stations. The value for "Rank sum" is the sum of the ranks assigned to the observations on CPUE for that fishing depth in a Friedman test. Vertical lines are used to indicate significantly different CPUE ($\alpha = 0.05$, multiple comparisons based on Friedman rank sums).

Fishing depth	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sum
Surface	232	32	0.11	15.5
Middepth	232	42	.16	17.0
Bottom	232	85	.37	27.5

and night fishing periods. During the day, CPUE differed significantly among fishing depths and was highest at the bottom. In contrast, during the night no difference in CPUE was found among fishing depths (Table 7). At surface and middepth CPUE was substantially higher during the night than during the day on 9 out of 10 and 8 out of 10 fishing stations, respectively. In contrast, at the bottom CPUE differed little between day and night periods and was not consistently higher or lower during the night. These observations suggest that the above difference between day and night periods (i.e., depth differences in CPUE during the day but not during the night) was a result of increased CPUE at surface and middepth during the night rather than a decrease in CPUE at the bottom.

TABLE 7.—Summary of fishing data for time period-fishing depth categories during the 10 24-h fishing stations. The value given for "Rank sum" is the sum of the ranks assigned to the observations on CPUE for that category in a Friedman test. Vertical lines are used to indicate significantly different CPUE ($\alpha = 0.05$, multiple comparisons based on Friedman rank sums).

Time period-fishing depth	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sum
Day-surface	143	12	0.07	16.5
Day-middepth	143	21	.13	26.5
Day-bottom	143	52	.37	51.0
Night-surface	89	20	.22	32.5
Night-middepth	89	21	.23	38.5
Night-bottom	89	33	.36	48.5

The stomach contents of 80 sandbar sharks were examined to identify food items (Table 8). Items that could be identified included small crustaceans and fishes that are abundant in the study area (pers. obs.). The blue crab, *Callinectes sapidus*, of all sizes was found in 41% of the stomachs examined (and in over 52% of the stomachs not empty). Two or more different food items were found in 14 stomachs and several stomachs contained unidentifiable items but were very nearly empty. The proportion of empty or nearly empty stomachs (15 empty out of 27 examined) for sandbar sharks caught during the night was significantly greater than the proportion (16 empty out of 53 examined) for sharks caught during the day (2-tailed chi-square test for differences in probabilities, $P = 0.04$). Stomach contents were, in general, similar for the 3 study yr, both sexes, all sizes of sharks, and tidal current and capture depth categories.

The total number of male and female sharks caught (over all 3 yr) did not differ significantly, but yearly differences in sex ratio were found (Table 9). During 1978 and 1979 about equal numbers of male and female sandbar sharks were caught, but in 1977 significantly more females than males were caught. Sex ratios were consistent among the 3 study mo (June, July, and

TABLE 8.—Stomach contents of 80 young sandbar sharks.

Stomach contents	No. of stomachs found in	Percent of stomachs found in
Blue crab, *Callinectes sapidus*	33	41.3
Unidentified fish	9	11.3
Mantis shrimp, *Squilla* sp.	8	10.0
American eel, *Anguilla rostrata*	7	8.8
Calico crab, *Ovalipes ocellatus*	6	7.5
Puffer, *Tetraodon maculatus*	4	5.0
Atlantic menhaden, *Brevoortia tyrannus*	3	3.8
Rock crab, *Cancer irroratus*	3	3.8
Unidentifiable material	3	3.8
Unidentified crustacean	1	1.3
Unidentified crab	1	1.3
Unidentified shrimp	1	1.3
Bluefish, *Pomatomus saltatrix*	1	1.3
Spot, *Leiostomus xanthurus*	1	1.3
Mummichog, *Fundulus heteroclitus*	1	1.3
Empty stomachs	16	20.0

TABLE 9.—Number of male and female sandbar sharks caught and probabilities for chi-square goodness of fit test (2-tailed) for each year and the entire study.

Year	No. of males	No. of females	*P*-value
1977	24	48	<0.01
1978	60	58	$0.80<P<0.90$
1979	28	22	$.30<P<0.50$
Total	112	128	$.30<P<0.50$

August) both in 1977 and 1978, i.e., unbalanced in 1977 but balanced in 1978. For all study years taken together, the number of male sandbar sharks caught did not differ significantly from the number of females caught during day or night periods, during flood or ebb current periods, at any of the three fishing depths, or for any of the four current speed categories (2-tailed chi-square goodness of fit Test, $\alpha = 0.05$).

With the exception of one sandbar shark (137.0 cm TL), the catch ranged from 60.0 to 112.5 cm TL. The length distributions for 1977 and 1978 are presented in Figure 2. Both distributions were based on relatively small numbers of sandbar sharks and are no doubt rough approximations of the actual size distributions. The fact that the distributions were not continuous and were characterized by several well-defined peaks does, however, suggest that in both years, the population of sandbar sharks consisted of relatively distinct size classes. Based on only visual inspection of the distributions, it appears that at least 3 and possibly as many as 5 different size classes may have been present. In general, similar size distributions were found for sex, light, tidal current stage and speed, and fishing depth categories.

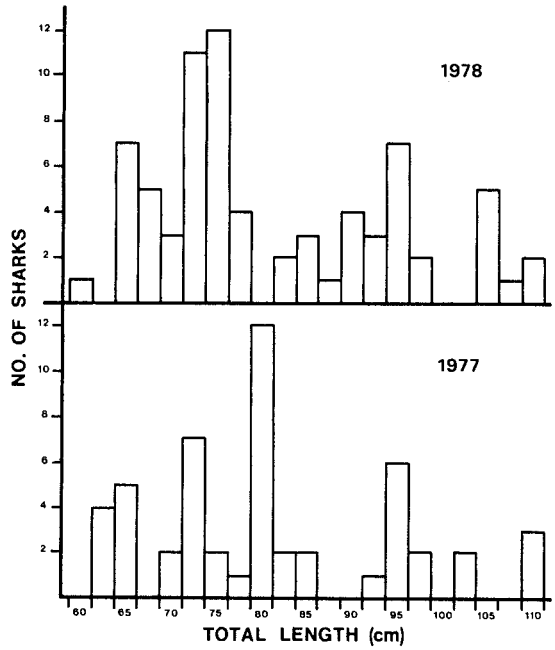

FIGURE 2.—Frequency distribution for total length of sandbar sharks caught and measured in 1977 and 1978. The total length given for each interval is the beginning length for that 2.5 cm wide interval.

DISCUSSION

Despite many hours of fishing, no sandbar sharks were caught before the first week of June either in 1977 or 1978, suggesting they were not present in the area during this time. Local fishermen who commonly catch numerous sharks in their gill nets also did not encounter sandbar sharks over this period; it appears that few, if any, sandbar sharks had migrated into the Chincoteague Bay area before the first week in June during these years. The consistency in CPUE among months within each year (Table 1) suggests that the abundance of sandbar sharks remained relatively constant in June, July, and August.

The mean CPUE of 1.02 sandbar sharks/h for the study indicates that the Chincoteague Bay area supports a large number of young sandbar sharks during the summer. The factors responsible for yearly differences in CPUE (Table 3) are unknown. Because fishing locations and times were selected in a random fashion and fishing technique was standardized over the entire study, it is unlikely that the differences were a result of the methods employed. Year-to-year changes in population numbers and/or shifts in distribution resulting in local differences in abundance may have been involved.

The significantly higher CPUE experienced during the night (Table 4) may relate to day-night differences in 1) the abundance of sandbar sharks in Chincoteague Bay, 2) the availability of prey, 3) the visual "attractiveness" of the bait, or 4) the feeding activity of young sandbar sharks.

Movements of sandbar sharks out of Chincoteague Bay to adjacent ocean waters during the day and back into the bay during the night could result in the observed differences. The movements of 23 sandbar sharks tracked in this area (Medved unpubl. data) were strongly oriented in the direction of tidal current flow and do not suggest a day-night pattern of movement into and out of the bay.

A decrease in the availability of various prey species could also account for increased CPUE during the night. Observations confirmed by local crab fishermen indicate that the blue crab (the most common food item found in the stomachs examined) is frequently found swimming near the water's surface during the night but rarely during

the day. This difference in behavior would seem to make the blue crab more accessible and would probably tend to decrease rather than increase CPUE during the night.

Differences in the visual attractiveness of the bait used to catch sharks may have existed, but the limited visibility (<1 m) in the turbid waters of the area suggests that vision was probably of little importance in feeding behavior. Experiments conducted on various species (Hobson 1963; Hodgson and Mathewson 1978; Kalmijn 1978) have shown the ability of sharks to locate food by means other than vision and that feeding behavior is directed towards almost any object present in a high concentration of olfactory material. These experiments indicate that the importance of vision may be only to direct the final act of feeding. It appears doubtful that day-night differences in the visual attractiveness of the bait were responsible for increased CPUE during the night.

Finally, the night hours may simply be a period of increased feeding activity for young sandbar sharks in this area. The existence of such a diel pattern would not be surprising in that similar rhythmicity for various activities (including feeding) has been reported for several sharks (Springer 1963, see footnote 5; Randall 1967; Hobson 1968; Nelson and Johnson 1970; Myrberg and Gruber 1974; Finstad and Nelson 1975; Sciarrotta and Nelson 1977).

Numerous catches at surface and middepth (Table 6) suggest that the young of this species occur throughout the vertical range of the water column. This would appear to be in conflict with Springer's (1960) statement that sandbar sharks are properly considered "ground sharks," rarely seen at or near the surface. However, most of Springer's observations were apparently made on adult sandbar sharks. The conflict may simply indicate differences between the young and adults of this species. The increase in CPUE at surface and middepth at night (Table 7) suggests that the tendency of sandbar sharks to move into these areas may have been greater at night and possibly related to the movements of blue crabs discussed earlier.

In general, food items taken by this shark (Table 8) agree with those reported by other authors (Bigelow and Schroeder 1948; Springer 1960; Clark and von Schmidt 1965; Bass et al. 1973; Lawler 1977). The fact that the blue crab was by far the major prey item may simply reflect its abundance in the area rather than a specific food preference. Wass (1973) indicated that food is retained within the stomachs of sandbar sharks for periods of 2-4 d or more, depending on the consistency of the item. The relatively large proportion of empty stomachs observed in this study would then indicate that the young of this species may frequently go at least several days without feeding. Whether this is by choice or imposed by difficulties in capturing food is uncertain. The higher proportion of empty stomachs observed for sandbar sharks caught during the night than for those caught during the day may relate to the possible day-night difference in feeding activity previously mentioned.

Selectivity in the fishing method employed may account for the observed yearly differences in sex ratio (Table 9). Assuming equal numbers of both sexes in the area, the method must have been selective for females in 1977 but not in 1978 and 1979. Considering that the same methods were employed in all years, it appears that the proportion of male and female sharks utilizing the area may have varied among years.

It seems that sandbar sharks >112.5 cm TL rarely occurred in the study area (Figure 2). The failure to capture larger sharks was not felt to be related to the fishing method because this method has yielded numerous large sandbar sharks in offshore areas (pers. obs.). A period of approximately 9 mo separates successive year classes of sandbar sharks (Springer 1960), and age determinations using vertebral annuli indicate relatively rapid rates of growth for the first several year classes (Lawler 1977). Lawler's growth rates suggest that the relatively distinct size classes apparent in this study were probably a reflection of the various year classes of sandbar sharks present in the area. The impression of the existence of 3 to 5 different age-classes given by the size distributions also agrees with Casey's (1976) contention that young sandbar sharks may occupy nursery ground areas for up to 5 yr before moving farther offshore.

ACKNOWLEDGMENTS

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[5]Springer, S. 1943. Sharks and their behavior. Special report to the Coordinator of Research and Development, U.S.N. Emergency Rescue Equipment Section.

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SEASONAL CHANGES IN SOFT-BODY COMPONENT INDICES AND ENERGY RESERVES IN THE ATLANTIC DEEP-SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*[1]

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ABSTRACT

The relationship between the energy storage cycle and gametogenesis was investigated over a 1-year period (March 1979-March 1980) in a population of the Atlantic deep-sea scallop, *Placopecten magellanicus*, from Boothbay, Maine. Soft body component indices, dry weights, lipid, and carbohydrate levels were measured in digestive gland, adductor muscle components, and gonadal tissue. In addition, mantle, mantle edge, foot, and kidney tissues were examined histochemically for glycogen and lipid content. Gametogenesis began in early winter (December-January) during a period when energy reserves and tissue indices were falling. Gonadal growth occurred concurrently with increases in body component indices, dry weights, and replenishment of lipid and carbohydrate levels in the digestive gland and adductor muscle (January-March). The accumulated springtime energy reserves in somatic tissues were lost in the late spring-summer, as maturation of gametes was completed. Following spawning in mid-September, a slight recovery of energy reserve levels and body component index values was evident for the digestive gland and quick component of the adductor muscle. Recovery did not occur in the gonad. Energy reserves, body component indices, and dry weights all declined throughout the late fall and early winter months. A buildup of energy reserves in the early spring appears essential for the later completion of gonadal maturation. Similarly, the autumn recovery of energy reserves within the somatic tissue may be important for the subsequent initiation of gametogenesis in early winter, as well as for meeting metabolic demands during the period of low food-availability.

The Atlantic deep-sea scallop, *Placopecten magellanicus* (Gmelin), supports an extensive commercial fishery throughout most of its western Atlantic range from the Strait of Belle Isle, Newfoundland, to Cape Hatteras, N.C. (Posgay 1957; Altobello et al. 1977; Serchuk et al. 1979). In spite of its economic importance, the underlying factors which affect reproductive success are poorly understood although the basic reproductive biology is well documented. The annual cycle of gametogenesis has been described both macroscopically (Coe 1945) and microscopically (Naidu 1970). Spawning seasons have been identified throughout most of the scallop's geographical range (Dickie 1955; Posgay and Norman 1958; Naidu 1970; Merrill and Edwards 1976). Larval development has been followed in the laboratory through settlement (Baird 1953; Culliney 1974; Drew 1906) and temperature and salinity effects on development have been investigated (Culliney 1974). The lack of consistent year-class recruitment, however, probably reflects the importance of environmental influences on reproductive success (Dickie 1955; Serchuk et al. 1979).

As an initial step toward a better understanding of reproductive success in any invertebrate species, the relationship between the buildup and utilization of energy reserves and the annual cycle of gametogenesis and spawning should be investigated (Giese and Pearse 1974). Thompson (1977) undertook such an approach using Atlantic deep-sea scallops collected from three populations in southeast Newfoundland. Although his main emphasis was on the seasonal changes in blood chemistry, biochemical analyses for glycogen, lipid, and protein levels were conducted on both gonadal and somatic tissues. Other contributions to an understanding of the energy reserve-reproductive cycle relationship have been made. Naidu (1970) presented gonad wet weight data, broken

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down by scallop age, over a 2-yr period, in addition to a histological description of the gametogenic cycle. Seasonal changes in total fat, sterol, and unsaponifiable fat within the adductor muscle have been described by Idler et al. (1964), and six major phospholipids identified from whole-body extracts by Shieh (1968).

The present study was undertaken to identify and localize the major energy reserves of *P. magellanicus*, to follow the levels of these reserves within each identified storage tissue over a 1-yr period, and to monitor the gametogenic cycle histologically.

MATERIALS AND METHODS

Deep-sea scallops were collected by divers at approximately 6-8 wk intervals from natural beds at the mouth of the Damariscotta River, off Farnham Pt., Linekin Neck, Boothbay, Maine, in 10-30 m of water. Deep-sea scallops ranged from 79.8 to 163.0 mm shell height ($\bar{X}$ = 119.0, SD = 17.5 mm, N = 165), although individual size varied considerably within each sample. Animals were transported to the laboratory in chilled seawater and maintained overnight in a running seawater system. Twenty deep-sea scallops (10 of each sex whenever possible) were chosen for subsequent analyses. Shell height was measured for each deep-sea scallop prior to dissection. Wet weights were recorded for total body (exclusive of mantle cavity water), shell, both catch and quick components of the adductor muscle, digestive gland, and "gonadal mass" (defined as all gonadal tissue, overlying epidermis, inclusive connective tissue, and intestinal loop). The contents of the intestinal loop were gently squeezed out prior to weighing. Similarly, the stomach and surrounding digestive gland were split open, and all food material flushed out with seawater. Gastric shield and crystalline style were excluded from digestive gland and gonadal mass wet weights. Tissues were individually frozen and stored at −20° C for subsequent biochemical analyses.

Body Component Indices

Individual soft-body component indices were calculated for catch adductor (CAI), quick adductor (QAI), digestive gland (DGI), and gonadal mass (GMI) according to Giese et al. (1967): body component index = wet weight of body component ÷ total wet body weight. Total wet body weight was determined by subtracting wet shell weight from total wet weight, and therefore includes the weight of extrapallial fluid which would have been lost if body weights were determined following separation of the animal from its valves. Linear regression analysis of body component index values (GMI, DGI, QAI, and CAI) on shell height revealed that all indices were independent of body size within the sampled range. The use of index values for comparisons between samples containing different size distributions of deep-sea scallops was therefore justified.

Histological and Histochemical Monitoring

Following wet weight determinations, a small piece of GMI tissue was fixed in Bouin's fluid for histological examination of gametogenesis. Tissues were later dehydrated, embedded in polyester wax (Steedman 1960), sectioned at 7 μm, and stained in 2% aqueous celestin blue. Gametogenic state was characterized as either early, mid, or late developing, ripe, partially spawned, or spent, based on a shortened version of the nine stages described by Naidu (1970). During early development, gonadal follicles are predominantly empty except for a few layers of spermatocytes or a single layer of oocytes closely oppressed to the follicular wall. In middeveloping follicles, the lumen is more restricted. Oocytes are enlarged in females, whereas in males, spermatids and spermatozoa become increasingly common although spermatocytes are still predominant. The follicular lumen is occluded by mature or maturing spermatozoa and oocytes in late-developing gonads, although immature stages are common toward the periphery of the follicles. In ripe gonads, follicles are tightly packed with mature gametes. Follicles show a progressive loss of ripe gametes as spawning proceeds, ultimately becoming empty when deep-sea scallops are completely spent.

Gametogenic values were assigned to each stage (early developing = 1, middeveloping = 2, late developing = 3, ripe = 4, partially spawned = 2, spent = 0). The mode, median, and range of gametogenic values were used for comparisons between sample dates.

To insure that tissues examined biochemically were sites of major energy reserves, a variety of tissues were fixed and histochemically examined from one or two animals of each sex during each sample period. In addition to the catch and quick

components of the adductor muscle, digestive gland, and gonadal mass, analyses were made on mantle, mantle edge, foot, and kidney tissue. For glycogen staining, tissues were fixed in Rossman's fluid (Humason 1972), embedded as before, and stained with Best carmine (Humason 1972). Control slides were incubated with 1% α-amylase in 0.2 *M* phosphate buffer (pH 7.0) at 40° C for 1 h. Lipid was localized in cryostat-sectioned material, postfixed in 10% calcium-Formalin[5] fixative (Humason 1972), and stained with supersaturated Oil red *O* (Lillie and Fullmer 1976). Control slides were immersed for 10 min in 95% ethanol to remove all lipid.

Biochemical Analysis of Tissues

As a result of the routine histochemical examinations, only adductor muscle, digestive gland, and gonadal mass were chosen for biochemical determinations of lipid and carbohydrate concentrations. No other tissues contained appreciable reserves of either lipid or carbohydrate at any time during the year. Tissues from the 20 deep-sea scallops chosen on each sampling date were pooled by sex into groups of 3-10 animals depending on the size of tissue sample and time of year. The pooled samples were freeze-dried to determine wet:dry weight ratios for each tissue. Subsamples of the dried tissue were used for biochemical analyses. Lipid concentrations were determined gravimetrically after extraction in acetone-isooctane (Peterson et al. 1976). Glycogen levels were determined on each of the four tissues using the glucose-oxidase method as described by Williams and Lutz (1975). All glycogen was first converted to glucose by a 2-h incubation at 55° C in 1% amyloglucosidase (Sigma A-7255). Glucose concentrations were then measured spectrophotometrically following a 30-min incubation at 37° C with a mixture of glucose-oxidase and peroxidase (Sigma Kit 510-A). The results give the combined concentrations of both glucose and glycogen for each tissue, and will hereafter be considered "carbohydrate." Since initial results indicated that wet:dry weight ratios, lipid, and carbohydrate concentrations were not significantly different in the catch and quick components of the adductor muscle (March-April samples), analyses of the smaller catch component was discontinued.

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

Standard Scallop

In order to account for the influences of animal size on seasonal body changes, body component dry weights, and biochemical constituents were calculated for a "standard scallop" of 120 mm shell height. This height was close to the mean (119.0 mm) and mode (115.2 mm) for the combined yearly samples. Predictive regressions of wet tissue weight (separately for gonadal mass, digestive gland, and quick adductor) on shell height were calculated for each sex within each sample. The resulting regression equations were solved for the standard deep-sea scallop (120 mm shell height). These wet weight values were converted to estimated dry weights of each tissue using the wet:dry weight ratios. By multiplying the estimated dry weights of each tissue by the corresponding concentrations of lipid and carbohydrate, total amount of each energy reserve per tissue was calculated. These energy reserve levels were then converted to caloric equivalents using the conversion factors from Crisp (1971) (carbohydrate = 4.1 kcal/g; lipid = 9.45 kcal/g). Since the calculations for dry weight, lipid, and carbohydrate were based on mean values of pooled tissue samples and regressions of wet tissue weight on shell height, confidence limits could not be estimated for the resulting values. All results have been presented as total amount of each energy reserve per standard animal.

RESULTS

Gametogenic Cycle

During most of the year, deep-sea scallops could easily be sexed by visual examination, due to the characteristic bright pink ovaries and opaque white testes. Histological sections, however, were necessary to determine the sex of spent individuals in the September-January samples. Spent gonads were shrunken, flaccid, and lacked characteristic coloration, instead possessing semitransparent epidermal and connective tissues.

Gametogenesis, as followed histologically, conformed to the description of Naidu (1970). The seasonal gametogenic cycle, based on modal gametogenic values for each sample, is presented in Figure 1. Modal values increased throughout the winter, spring, and into the summer as gametes differentiated and ripened. Spawning was evident in 67% of the males (N = 9) and 64%

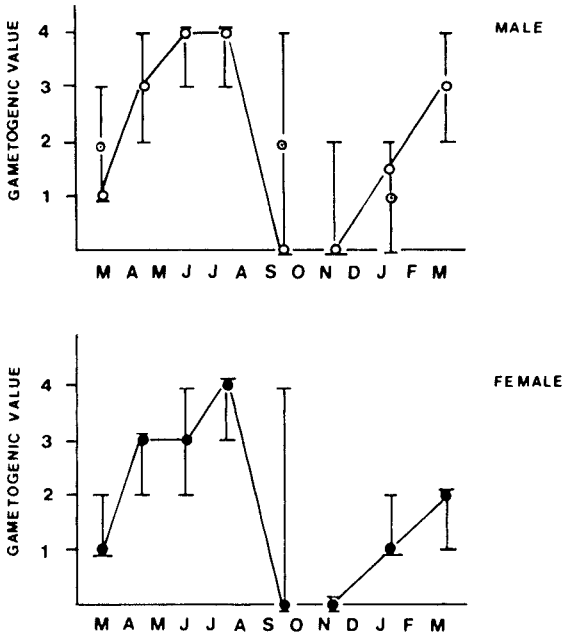

FIGURE 1.—Annual cycle of gametogenesis in *Placopecten magellanicus* based on assessment of histological sections for each sample date, March 1979-March 1980. Modal values of each sample indicated by • for females and ○ for males. Bars = ranges. Median values indicated by ⊙ in cases where median values differ from modal values.

of the females (N = 11) from the 14 September sample, resulting in a marked drop in modal rank. Variability within the population was greatest at this time since ripe, partially spawned, and spent individuals were all present in the population. By 5 November, virtually all deep-sea scallops sampled were spawned out. In January, modal values again rose. Gonial cells were distinguishable in the follicles and characteristic gonadal coloration became evident, although a few individuals showed signs of still being only partially spawned out.

Body Component Indices

Seasonal changes in mean body component indices are plotted in Figure 2. GMI, DGI, QAI, and CAI all varied significantly with time ($P<0.01$; analysis of covariance: body component index by sample date with scallop height as a cofactor). Similar analyses using raw tissue wet weights also point out significant changes between sampling dates ($P<0.01$). Since differences between the sexes were not significant for any of

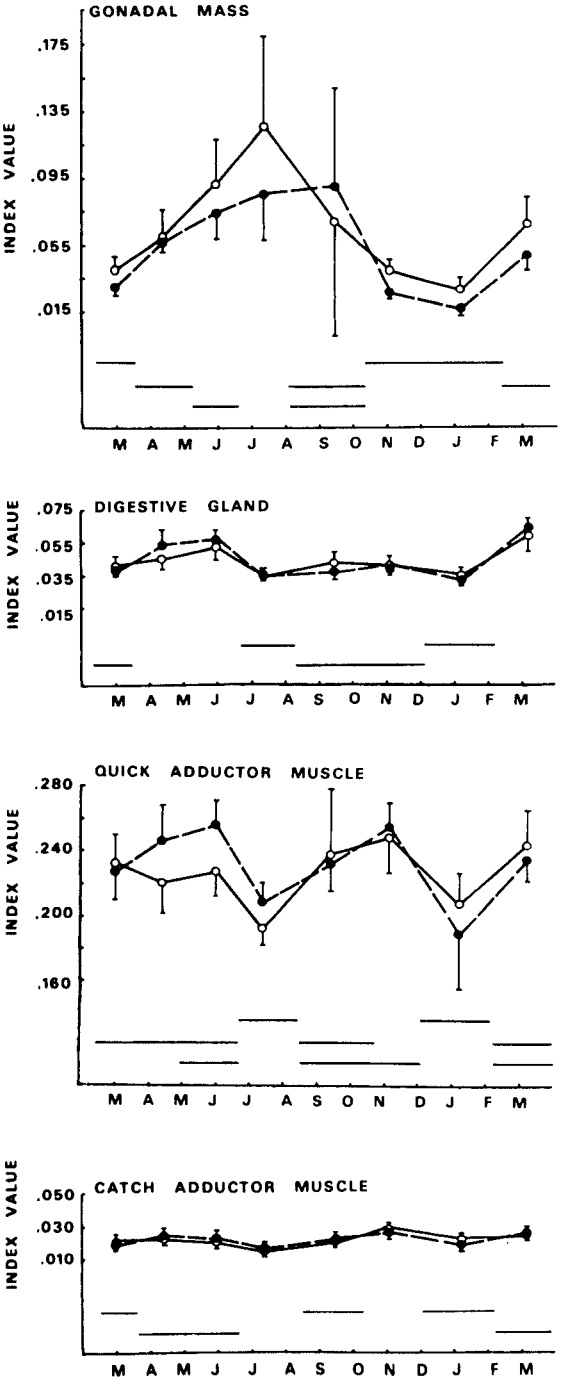

FIGURE 2.—Seasonal fluctuations in soft-body component indices for *Placopecten magellanicus*, March 1979-March 1980. Bars represent 95% confidence intervals; • = female; ○ = male; horizontal lines underscore samples which are not significantly different at the 95% confidence level (male and female data combined for each sample, least significant difference multiple range test).

the indices, data for each sex were combined. Multiple range tests (least significant difference) on the combined data indicated that GMI, DGI, and CAI values all rose in the spring. QAI, CAI, and DGI dropped in July, while GMI continued to rise until spawning in late summer. The September and November samples showed a recovery of QAI, CAI, and DGI, but a drop in GMI, representing a decline in the proportion of body mass attributable to the gonad following spawning. The late fall to early winter period showed a continued decline in all four indices except possibly GMI, with recovery evident by the subsequent March sample. Both GMI and modal gametogenic values (Figure 1) were much higher in the March 1980 sample than for the March sample of the previous year, probably reflecting the mild 1979-80 winter.

Differences in total wet animal weight and total wet body weight between samples were not significant (ANCOVA: $P > 0.05$). Variability of each of these components was too high to discern seasonal trends.

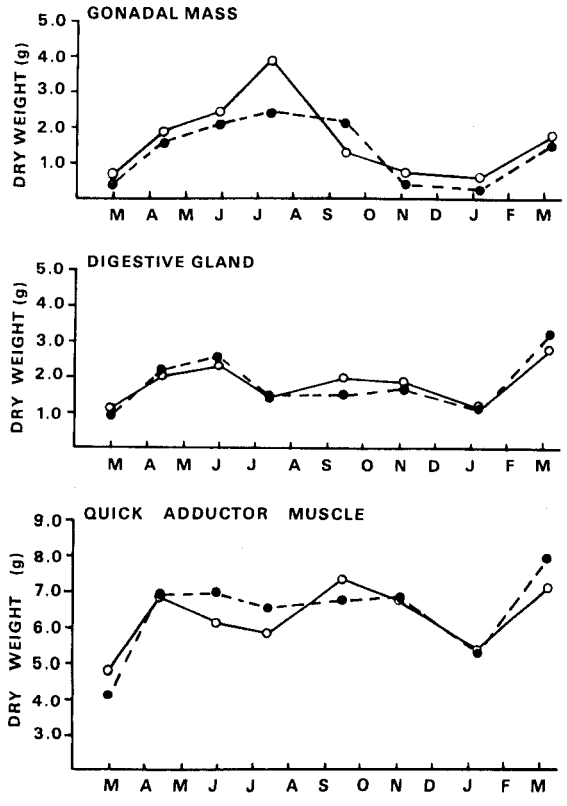

FIGURE 3.—Standard deep-sea scallop (120 mm shell height) annual tissue dry weight fluctuations. • = female; ○ = male.

Histochemical Localization of Energy Reserves

Appreciable concentrations of energy reserves were detected in only the adductor muscle, digestive gland, and gonadal mass. As indicated by routine histochemical examinations, a shift of energy reserves from these major areas to other tissues did not occur during the study period.

Glycogen was primarily concentrated in the adductor muscle, although significant levels were also seen in the digestive gland and the epithelium of both male and female reproductive ducts during most of the year. Concentrations were highest in the spring and early summer within the adductor muscle, ovary, and testes, but were only high in the spring within the digestive gland. Glycogen concentrations remained very low throughout the year in the mantle, mantle edge, foot, and kidney.

Lipid levels were highest throughout most of the year in the digestive gland, with peak levels in April-May 1979 and March 1980. High concentrations were also found in the ovary, increasing throughout the spring to a maximum in July, declining slightly in September, and dropping precipitously by November as a result of spawning. Significant lipid localization was not observed in any other tissue.

Dry Weight and Biochemical Analyses

Seasonal fluctuations in gonadal mass, digestive gland, and quick adductor muscle dry weights are presented in Figure 3 for standard deep-sea scallops of each sex. Following an initial increase in the weight of all tissues in the spring, gonadal dry weight continued to rise into July, whereas a concomitant decrease occurred in the weight of the adductor muscle and digestive gland. Gonadal dry weight fell throughout the autumn and early winter. The adductor and digestive gland on the other hand, recovered in the autumn to about their springtime levels, but then dropped during the early winter.

Calculated quantities of lipid and carbohydrate in tissues of standard scallops of each sex are shown in Figures 4 and 5. As with dry weights, both reserves showed an initial rise in the spring in all tissues although the rise in carbohydrate in the gonadal mass and digestive gland was slight. The amount of gonadal lipid and carbohydrate continued to increase into midsummer, whereas digestive gland lipid and adductor carbo-

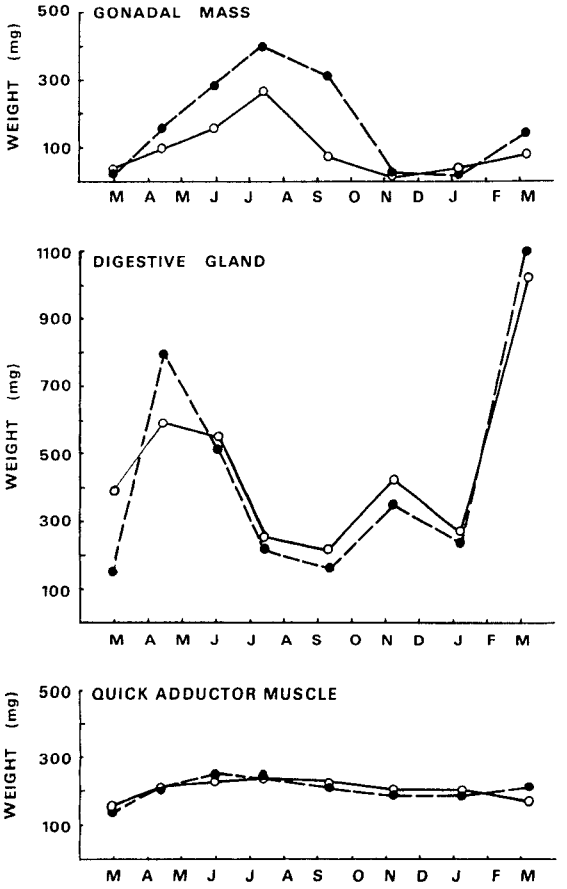

FIGURE 4.—Seasonal changes in tissue lipid content calculated for the standard deep-sea scallop (120 mm shell height). • = female; ○ = male.

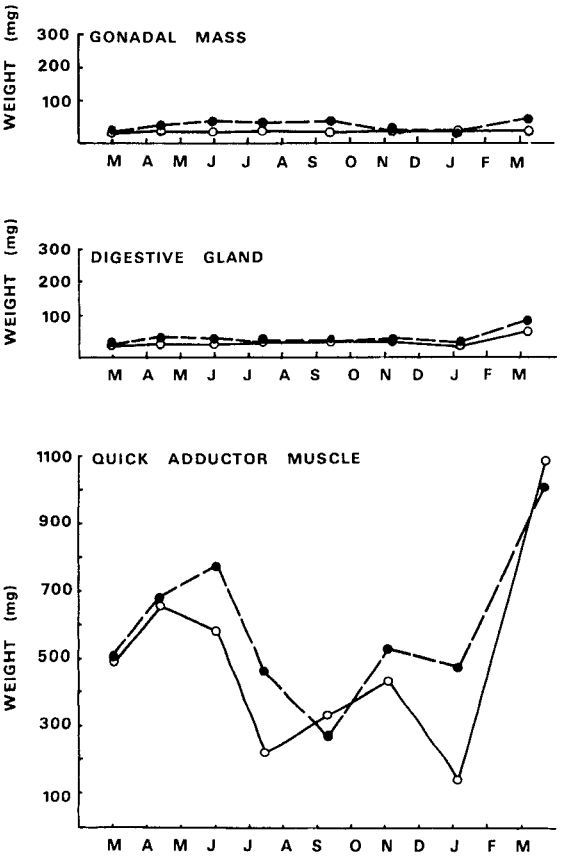

FIGURE 5.—Seasonal changes in tissue carbohydrate content calculated for the standard deep-sea scallop (120 mm shell height). • = female; ○ = male.

hydrate fell from late spring through September. Although present at lower amounts than in the gonadal mass and digestive gland, lipid in the quick component of the adductor muscle rose in the spring-summer and dropped in the autumn-winter.

Changes in caloric equivalents (kilocalories) of energy reserves from each tissue, presented in Figure 6, reflect the changes in lipid storage in both the gonadal mass and digestive gland, and fluctuations of carbohydrate in the quick component of the adductor muscle. Differences in energy reserves between the sexes are not significant, although females tend to show higher levels and greater fluctuations in energy content throughout the year. The drop in gonadal caloric equivalents in mid-September, in addition to the drop in GMI and gonadal dry weight, is indicative of spawning within the population and is corroborated by the histological appearance of the gonads.

DISCUSSION

Of the three tissues which contain appreciable reserves of either lipid or carbohydrate, only digestive gland and adductor muscle may properly be considered "storage organs" (i.e., temporary repositories of energy-rich substances which may later be utilized to meet either metabolic or reproductive demands). Energy-rich substances within the gonad, albeit temporary, are ultimately destined for gamete production and nourishment of the developing larvae. If these substances are completely lost at spawning, as is evident for *P. magellanicus*, they should not be considered as energy reserves for the adult scallop (Giese 1966), even though resorption of gametes by some

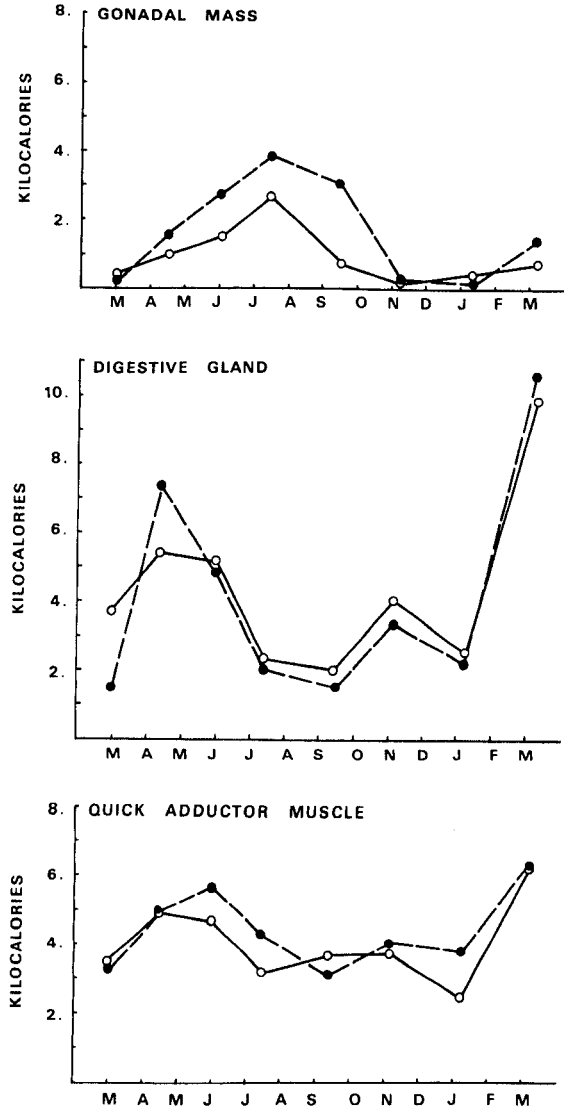

FIGURE 6.—Caloric equivalents (lipid + carbohydrate) for major energy storage tissues of the standard deep-sea scallop (120 mm shell height) over the 1-yr study period. • = female, ○ = male.

pectinids may occur at times of food shortage (Sastry 1966). Furthermore, neither lipid nor carbohydrate accumulates in the gonad immediately following spawning for use as an overwintering reserve (Thompson 1977; this study).

Histochemical tests do not reveal significant quantities of lipid in either the quick or catch components of the adductor muscle, whereas a substantial amount is detected biochemically. Quantities of sterols (e.g., 22-dehydrocholesterol, cholesterol, brassicasterol, and 24-methylenecholesterol) are present in adductor tissue (Idler et al. 1964) in addition to structural lipids. These high melting point lipids do not color with Oil red *O* and other Sudan dyes (Lillie and Fullmer 1976), and, therefore, cannot be localized histochemically. They are, however, readily extracted by the solvents used for gravimetric lipid analysis. When addressing the problem of distinguishing structural from reserve lipid, Giese (1966) has concluded that lipid levels >5.2% dry weight are reserve. Lipid levels in *P. magellanicus* adductor muscle are never high enough (2.3-4.1%) to meet this criterion.

Neither carbohydrate nor lipid concentrations in the quick component of the adductor muscle were significantly different from those in the catch component in the March and April 1979 samples. Analysis of the catch component was therefore discontinued. De Zwaan et al. (1980), however, found higher concentrations (2.5×) of glycogen in the phasic (= quick) than in the catch adductor of *P. magellanicus* sampled in July at a time when glycogen levels were at a peak. As with our samples, no difference in lipid concentrations was observed. Taken together, these results may indicate that both components of the adductor contain approximately the same carbohydrate levels during the winter and early spring, but that the quick component rapidly overbalances the catch adductor in importance as a site of carbohydrate reserves.

Gametogenesis is intimately related to energy-reserve fluctuations in *P. magellanicus*. In January, while gametogenesis has already reached the early-development stage (Figure 1), body component indices (Figure 2), dry weights (Figure 3), and energy reserves (Figures 4, 5) within the gonad, digestive gland and quick component of the adductor muscle have fallen to their lowest values. The initiation of gametogenesis, characterized by increased numbers of gonial cells and an apparent increase in mitotic activity, is first seen in early winter, at a time when energy reserves are declining. This initiation thus appears to be dependent on the energy reserves accumulated the previous season, although food availability data are not available to substantiate this hypothesis. Following the initiation of gametogenesis, storage products begin to accumulate in the digestive gland, adductor muscle, and gonad in the late winter to early spring (Figure 6). At the same time, gametogenesis proceeds into the middevel-

opment stage and gonad size increases. The accumulation of reserves is almost certainly due to spring phytoplankton blooms. Following this general buildup of energy reserves and continued maturation of gametes, a marked shift in the condition of the digestive gland and adductor muscle occurs. From June through July and probably into August, there is a sharp drop in DGI and QAI (Figure 2), lipid levels in the digestive gland (Figure 4), and carbohydrate in both the digestive gland and quick component of the adductor muscle (Figure 5). During this time, gametes are ripening, GMI values reach their peak and lipid generally reaches its highest level in the gonad. The completion of gametogenesis therefore seems largely dependent on energy reserves which were accumulated earlier in the spring.

Gonadal weight, glycogen, and lipid concentrations are inversely related to the weight and energy reserves of somatic tissues in a variety of other pectinids. In queen scallop, *Chlamys opercularis*, lipid content of body tissues declined as gonadal lipid increased (Taylor and Venn 1979). Similarly, inverse relationships have been shown for adductor and gonadal dry weights in *Pecten maximus* by Comely (1974) and digestive gland and gonadal indices in bay scallop, *Argopecten* (= *Aequipecten*) *irradians*, by Sastry (1966, 1970). Sastry (1966) has proposed however that the reciprocal relationship between index values may indicate that nutrients supplied by feeding might be rapidly utilized for growth and development without prior storage. Thus a decline in DGI would not represent a drop in actual digestive gland wet weight. However, direct evidence for the transfer of some quantity of materials from body tissues to the gonad has been demonstrated in *A. irradians* using ^{14}C-leucine (Sastry and Blake 1971), in *C. hericia* using lipid ^{14}C-labeled *Chlorella* extract (Vassallo 1973) and in other bivalves (vide Gabbott 1975; Sastry 1979).

During the spring and summer, the loss of energy stores from the digestive gland and adductor muscle could not have been due solely to the transfer of these substances to the gonad. From 13 April to 13 July, more calories were lost from the quick adductor and digestive gland (male, −4.75 kcal; female, −6.00 kcal) than were gained by the gonadal mass (male, +1.57 kcal; female, +2.27 kcal). The real energy loss was probably greater than indicated by these calculations, since contributions from the catch component of the adductor and other somatic tissues were not included in the calculations. Metabolic demands, due to warmer water temperatures and the completion of gonadal maturation probably accounted for the remainder of the lost energy reserves. The possibility that these reserves were used entirely for metabolic needs, while gonadal maturation depended solely on food intake, seems remote.

Following spawning, the condition of the digestive gland and adductor muscle improves, as evidenced by the increase in QAI, CAI, digestive gland lipid, and quick adductor carbohydrate. Reserves do not reach or exceed their springtime levels, such as occurs in *P. maximus*, (Comely 1974), *C. opercularis* (Taylor and Venn 1979), and *C. septemradiata* (Ansell 1974) populations from the Clyde Sea area. Postspawned *Placopecten magellanicus* from Georges Bank attain total fat levels as high as those reached during the springtime (Idler et al. 1964) whereas *P. magellanicus* from a southeast Newfoundland population (Thompson 1977) do not show postspawning, autumn increases in either carbohydrate, lipid or dry weight within the gonad, or somatic tissue. The autumn recovery pattern in Boothbay scallops appears to be intermediate between the Georges Bank and Newfoundland populations.

Reproduction is dependent to varying degrees on available food levels and energy reserves in different temperate marine bivalves. In *C. opercularis* (Taylor and Venn 1979) and *Pecten maximus* (Comely 1974) for example, energy reserves are utilized for both the initiation of gametogenesis and for subsequent gonadal growth. Reserves are apparently required for both these activities in the intertidal mussel, *Mytilus edulis*, as well (Gabbott 1975). In other bivalves, however, intake of food is necessary for vitellogenesis and gonadal growth and often for the initiation of gametogenesis. Gonadal growth in *A. irradians* cannot occur without feeding, since reserve material from the digestive gland and other body tissues are not adequate to sustain maturation (Sastry 1966, 1968, 1970). However, reserves within the digestive gland may supplement nutritional intake needed for gonadal proliferation (Sastry and Blake 1971). Similarly, in *Crassostrea gigas* and *C. virginica* (Gabbott 1975), gonadal growth is accompanied both by springtime feeding and decreased glycogen content of the tissues. Gonadal growth however is supported directly by springtime feeding in *Chlamys septemradiata* (Ansell 1974), although gametogenesis begins during the

winter months when food levels are low and energy reserves in the adductor are falling. In the southeast Newfoundland population of *Placopecten magellanicus*, the initial rise in gonadal DNA content preceeds the usual springtime phytoplankton bloom, occurring instead during the period when both gonadal and somatic dry tissue weights are at an ebb (Thompson 1977). The initiation of gonadal growth in this Newfoundland population, however, appears to be dependent on available food. From measurements of seasonal rates of respiration, excretion, consumption, and filtration in *P. magellanicus* from Narragansett Bay, Ehinger[6] has concluded that intake of food is necessary to meet the energy demands of reproduction. In the present study, the initiation of gametogenesis is shown to occur at a time when reserves, dry weights, and index values of the digestive gland, adductor, and gonad are all declining. Gonadal growth however occurs concurrently with an early spring replenishment of energy reserves. Final maturation of the gametes although dependent on the transfer of energy reserves per se, ultimately relies on the springtime availability of food for the buildup of these reserves.

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EFFECTS OF PHOTOPERIOD AND FEEDING ON DAILY GROWTH PATTERNS IN OTOLITHS OF JUVENILE *TILAPIA NILOTICA*

KUNIAKI TANAKA, YASUO MUGIYA, AND JURO YAMADA[1]

ABSTRACT

Effects of varying photoperiods and feeding times on the formation of daily rings in otoliths of juvenile *Tilapia nilotica* were studied with a scanning electron microscope. Two alternate concentric zones, each different in structure, were distinguished in the acid-etched ground plane: one thin and appearing as a groove (discontinuous zone) and the other thick and with well-developed, needlelike crystals (incremental zone). The number of incremental zones showed a good correlation with the chronological age in days after hatching for at least 28 days. The otolith showed a daily rhythm of growth under a photoperiod of 24 hours (12 light-12 dark). Growth of incremental zones started a few hours after lights-on and stopped or slowed down within a few hours of the following lights-on, during which time the discontinuous zone seemed to be formed. When the light and dark cycle was reversed, the cycle of otolith growth began to change on the second day and accommodated to the new photocondition 6 days after the reversal. A change in length of light and dark phases (18L-6D or 6L-18D) or a shift of feeding time did not affect the time of the discontinuous and incremental zone formation.

Otoliths have been widely used for aging fishes along with other hard tissues such as scales and vertebrae. Determinations of ages of larvae and juvenile fish will yield information on their early life history which is important for analyses of their population dynamics. However, accurate age determinations in terms of months or days have not been possible for young fish up to 1-yr-old until Pannella (1971, 1974) showed the presence of daily rings in otoliths (sagittae) of some temperate as well as tropical species. Brothers et al. (1976), Struhsaker and Uchiyama (1976), Taubert and Coble (1977), Timola (1977), Barkman (1978), and Radtke and Dean (in press) have studied the use of such rings, or daily increments, for determining the age in days of some larval and adult fish in temperate or tropical species. Their results showed good correlations between the number of rings and the ages in days after hatching in larval fish. However, the number of rings was often greater than the age in days in larval fish and less in adult fish, and the difference seemed to vary by species. This shows that otolith daily rings may be formed in the embryonic stage in some fish (Brothers et al. 1976; Radtke and Dean in press) and that the increments may not be formed in old fish by cessation of growth under some environmental conditions (Taubert and Coble 1977).

In order to accurately interpret otolith daily rings for age readings, it is necessary to understand the mechanisms which induce formation of individual rings. Taubert and Coble (1977) suggested that a 24-h light-dark cycle is essential for the formation of the ring pattern in the otolith of *Tilapia mossambica*. The morphological studies by Degens et al. (1969) and Pannella (1971, 1974) showed that the ring pattern of fish otoliths is composed of increments of two alternate light and dark bands: a thick band of well-developed aragonite crystals with their long axis roughly perpendicular to the outer margin of the otoliths and a relatively thin band intersecting the aragonite crystals.

Our study was undertaken to verify the presence of a daily growth rhythm in the otolith of *T. nilotica* and to determine the time of a day at which a new increment is formed. We investigated the effects of various photoperiods and the feeding time on the zone formation cycle of the otolith.

MATERIALS AND METHODS

Juveniles of *T. nilotica* (12-24 mm standard length) were used. They were obtained by natural fertilization and rearing by eight females in our laboratory. Eggs hatched about 4 d after fertilization and the larvae remained in their mothers' mouths for about 10 d. Immediately after leaving the mothers' mouths, the juveniles were trans-

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ferred to aquaria and used in the experiments. Water temperature was maintained at 27±0.5° C.

Experiments under 24-h Photoperiod

The juveniles were transferred to four 60 l aerated aquaria, each kept under a different photoregime: 12L-12D (light phase, 0800-2000 h), 12L-12D (light phase, 2000-0800 h), 18L-6D (light phase, 0800-0200 h), and 6L-18D (light phase, 0800-1400 h). For lighting, a daylight fluorescent lamp (20 W) was fixed 15 cm above the water surface. In all groups, fish were fed to satiation on fish food pellets supplied throughout the 24-h photoperiods. After acclimation to each condition for at least 12 d, 6-10 fish were killed every 3 h and their otoliths removed for measurement of completion of the newest increment. In addition, 10 fish in the first group (12L-12D, light phase, 0800-2000 h) were killed 19 and 28 d after hatching to compare the number of otolith rings with the fish's age in days.

Feeding Experiments

For experiments on effects of feeding we used two groups of juvenile fish of the same brood. Five days after leaving their mother's mouth, one group was fed for 3 h after each lights-on; and the other group was fed for 3 h before lights-off under 12L-12D cycle (light phase, 1200-2400 h). The experiment lasted 15 d. Five fish were killed from each group every 3 h during the last 2 d of the experiment and otoliths were examined for completeness of the newest increment.

Otolith Preparation for Scanning Electron Microscopy

Otoliths (sagittae) were removed from the fish under a dissecting microscope, washed in water, embedded in a few drops of epoxy resin (Bond E,[2] Konishi Co.), and placed on a glass microscope slide. After hardening, both otoliths from each fish were ground by hand with a whetstone to the mid-transverse plane, parallel to the long or short axis, and then polished with a compound whetting paste for sharpening microtome knives. The specimens were cleaned in xylene, etched with 0.5% HCl for about 20 s, and coated with gold in vacuum. The specimens were examined with a JSM-25 scanning electron microscope (SEM) at 15 kV for number of growth rings or for determination of completeness of the newest increment.

For the observation of the internal structure, otoliths were placed in a drop of water and broken into several pieces by a razor blade. The broken pieces were air-dried, coated with gold, and the nonetched fractured surface was observed with the SEM.

Measurement of Daily Growth Rhythm

In order to determine the exact hour when a new increment is formed in the otolith, we calculated the index of completion for current increment (C) by the following formula:

$$C = \frac{W_n}{W_{n-1}} \times 100$$

where W_n = width of current increment
W_{n-1} = width of previous complete increment.

Measurements were made on SEM photographs of specimens collected every 3 h. Following the change of C in time sequence, one can estimate the time of completion or start of zone formation when C suddenly drops from approximately 100% to a lower level. The area of the measurement of C was at the distal surface near the anterior or the posterior edge of the otolith, where increments are thick, discontinuous, and easily observed.

RESULTS

The sagitta of a juvenile *T. nilotica* takes the form of an oval disc. It lies vertically in the sacculus of the inner ear with its long axis parallel to the anteroposterior axis of the fish. The inner surface of the otolith facing the macula region of the sacculus is somewhat concave, whereas the other surface is slightly convex.

When the otolith is ground parallel to its long or short axis down to the core region, or the growth center, and then etched, it exhibits a concentric ring pattern (Figure 1A), with each ring composed of two alternate layers, each different in structure. One layer usually measures 2-8 μm wide and has needlelike crystals of the aragonite form $CaCO_3$

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

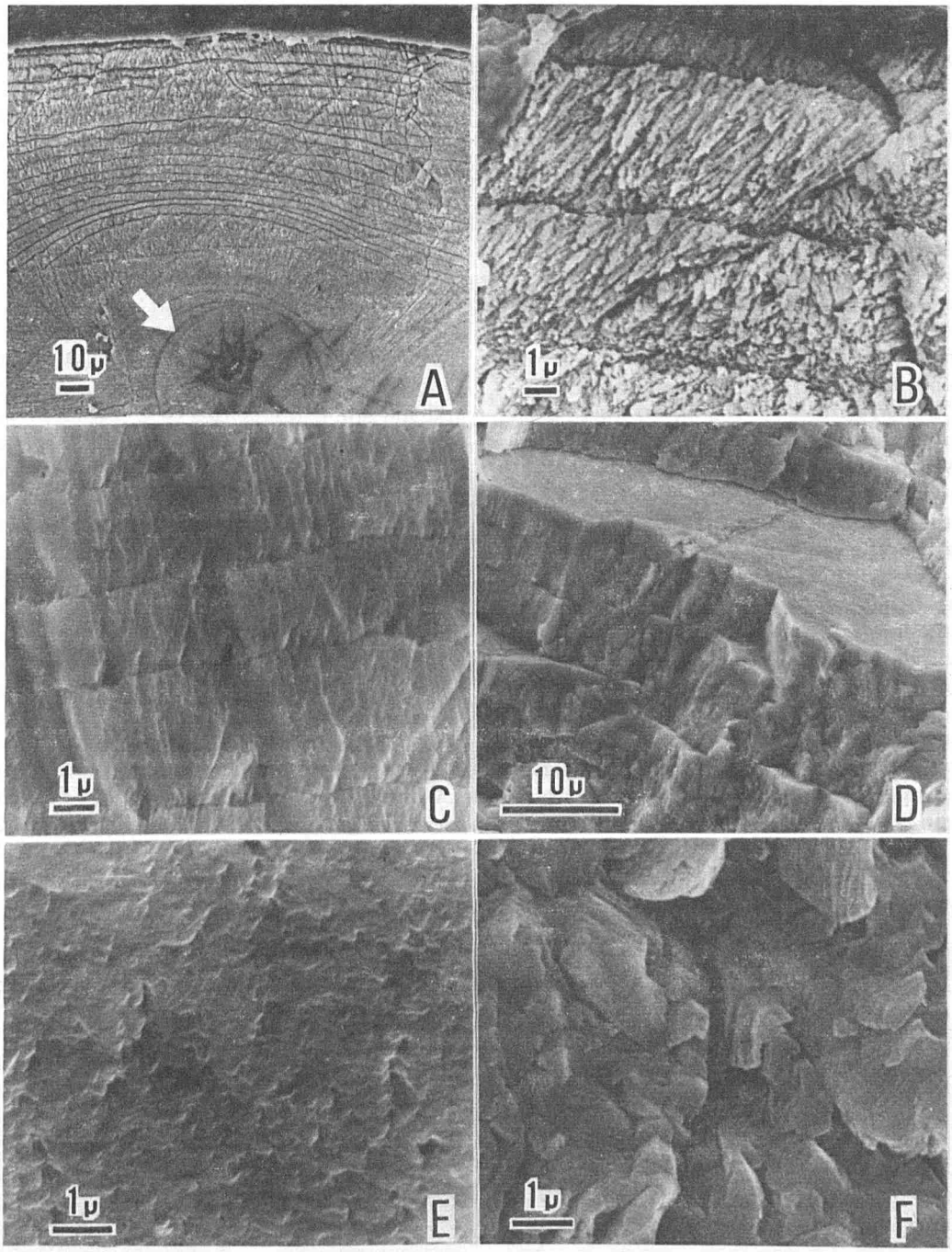

FIGURE 1.—Scanning electron microscope photographs of otoliths of juvenile *Tilapia nilotica*. A) Ground and etched otolith of a fish 28 d after hatching. The core region delimited by the innermost clear discontinuous zone (arrow) shows several vague, narrow bands. The center of the core region is deeply etched and has some spherules. B) Margin of a ground and etched otolith. The outermost incremental zone is not complete. C) Nonetched fracture plane of an otolith. The otolith is composed of a piling up of crystallized lamellae (incremental zone) with thin interstitial layers (discontinuous zone). D) Nonetched fracture plane of an otolith. The surface of a complete crystallized lamella at the boundary of the interstitial layer can be seen. E) Higher magnification of the surface of the crystallized lamella in D. F) Nonetched external surface of an intact otolith to show the growing surface of the outermost incremental zone.

with the long axis nearly perpendicular to the margin of the otolith, while the other is thin (about 0.2-0.5 μm wide) and appears as a concentric groove in slightly etched planes of the otolith (Figure 1B). Most of the grooves are not continuous around the whole area and fade out near the area along the long (anteroposterior) axis of the otolith. Usually, a few grooves in the area around the core region, which is delimited by the earliest clear circular groove, are weakly etched and set at wide intervals (Figure 1A).

On the other hand, examinations of nonetched fracture planes of the otolith revealed several thick crystallized lamellae piled up with narrow (<0.1 μm) interstitial layers between them (Figure 1C, D). The surface of a completed crystallized lamella that was fractured tangentially at the boundary to the interstice was observed to be flat and smooth (Figure 1D, E), while the growing surface of the otolith was rough with stacked crystals (Figure 1F). Therefore, we consider that the concentric grooves in acid-etched planes correspond to the interstitial layers where the growth of crystallized lamella was interrupted. The grooved zone is here defined as the discontinuous zone and the crystallized lamella as the incremental zone, both zones constituting a unit increment.

The core region, defined by the earliest clear discontinuous zone, was about 40 μm in diameter and had several, usually five or more, narrow unclear rings (Figures 1A, 2A). Ten or more spherules of crystals, about 1.5 μm in diameter, were aggregated at the center of the core region. Some of them had the relatively finely organized core surrounded by coarse granules along the margin (Figure 2B). The peripheral region of the aggregate of the spherules was often deeply etched and appeared as a hole.

Correlation between the Number of Otolith Rings and Age in Days after Hatching

The number of rings (incremental zones) was counted from preparations of otoliths from fish 19 and 28 d after hatching. In this case, unclear and narrow rings in the core region were not counted because they seemed to be formed during the embryonic stage. Sixteen otoliths from 8 fish 19 d after hatching and 14 otoliths from 7 fish 28 d after hatching showed 18.89 ± 0.23 and 27.12 ± 0.27 (mean $\pm$ SE) rings, respectively. The observed close correlations between the number of rings and the age in chronological days indicated that the ring formation proceeded on a daily basis until at least 28 d after hatching.

Formation of Otolith Rings Under a 12L-12D Photoperiod

When fish were acclimated to a 12L-12D photoperiod of lights-on at 0800 h and lights-off at 2000

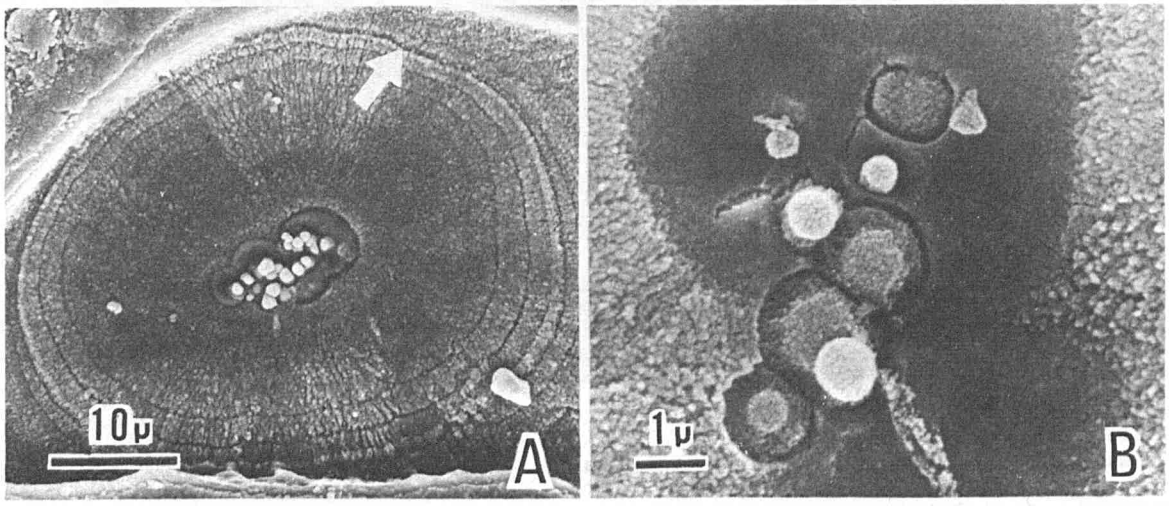

FIGURE 2.—Scanning electron microscope photographs of otoliths of *Tilapia nilotica* 1 d after hatching. A) Core region encircled by the first clear discontinuous zone (arrow). An aggregate of a number of small crystallized spherules is visible in the center. B) Crystallized spherules in the center area of the core region.

h, the otolith showed two phases, growth and rest, in a 24-h period (Figure 3A). The growth phase started between 0900 h and 1200 h and continued until 0500-0800 h next morning. The growth seemed to stop or slow down about the time of lights-on, resulting in the formation of a discontinuous zone. After several hours, the otolith started the next cycle of growth. This growth pattern occurred regularly for a consecutive 3-d period (Figure 3A). Accordingly, one incremental and one discontinuous zone were formed in the otolith in 24 h. When the photoperiod was reversed to lights-on at 2000 h and lights-off at 0800 h, the time of zone formation was also shifted about 12 h (Figure 3B), i.e., the growth phase started at sometime between 2100 h and 2400 h and lasted until about 2100 h. It should be noted that the formation of the incremental zone started a few hours after lights-on in both the experiments.

To see how the time of incremental zone formation shifts following a sudden reversal of light and dark phases (12-h shift), the index of completion for current increment at 2000 h was traced through the reversal (Figure 4). Under the ordinary photoperiod before the change, the index had been maintained at about 50% and persisted in the first day after the shift to the new photoperiod. However, the index at 2000 h became variable in the second day, and then gradually changed to a level of about 100% by the sixth day.

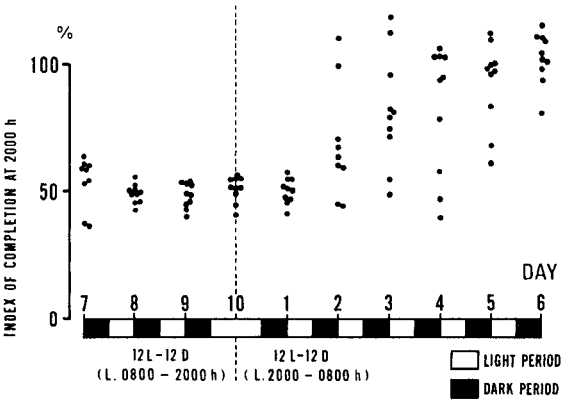

FIGURE 4.—Change in the index of completion for current increment at 2000 h in *Tilapia nilotica* otoliths when the fish were kept under a photoperiod of 12L-12D (light phase, 0800-2000 h) for 10 d and then transferred to the reversed light condition (light phase, 2000-0800 h). Each dot represents one otolith.

Formation of Otolith Rings Under 18L-6D and 6L-18D Photoperiods

The daily growth pattern was found to be the same in the group acclimated to photoperiods of lights-on at 0800 h and lights-off at 0200 h (18L-6D) and in the other with lights-off at 1400 h (6L-18D) despite the 12-h shift in the time of lights-off (Figure 5). The growth phase started about 3 h after lights-on and continued until about 0800 h the following morning. Thus, the discontinuous zones were formed sometime between 0800 h and 1100 h in both groups. It was also observed in both groups that the growth slowed down several hours before lights-on, as seen in 12L-12D experiments.

Feeding Time and the Formation of Otolith Rings

Two groups of fish were acclimated to different feeding schedules under the same photocondition (12L-12D, light phase, 1200-2400 h). One group

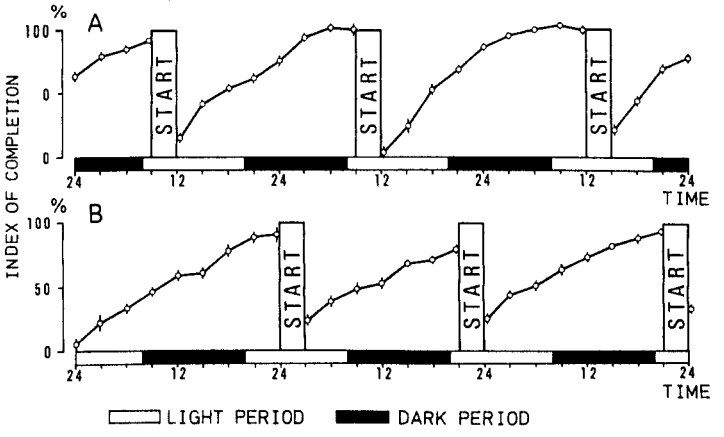

FIGURE 3.—Daily growth of *Tilapia nilotica* otoliths as represented by changes in the index of completion for current increment every 3 h for 72 h. The fish were maintained under two contrasting photoperiods: A) 12L-12D (light phase, 0800-2000 h); B) 12L-12D (light phase, 2000-0800 h). Each circle represents mean ± SE for six fish. START = start of new incremental zone.

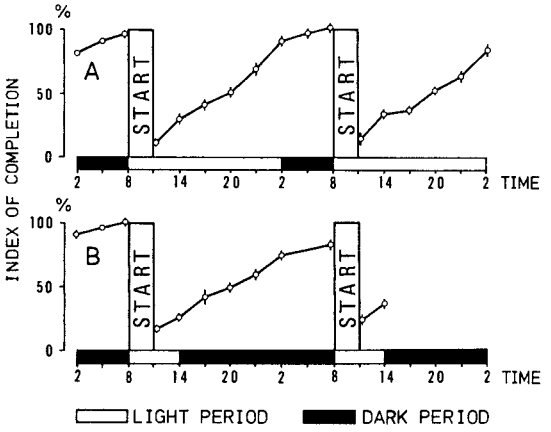

FIGURE 5.—Effects of long and short light periods on the daily growth of *Tilapia nilotica* otoliths. A) 18L-6D, light phase, 0800-0200 h; B) 6L-18D, light phase, 0800-1400 h. Each circle represents mean ± SE for five or six fish. START = start of new incremental zone.

was fed during the first 3 h of light phases while the other was fed during the last 3 h of light phases, giving a 9-h difference in the beginning feeding time. However, no significant difference was found in the time of discontinuous zone formation in both groups (Figure 6). The zone was completed 1 or 2 h after lights-on in both groups, showing that the feeding time had no apparent effect on the formation of otolith rings under the 12L-12D photoperiod.

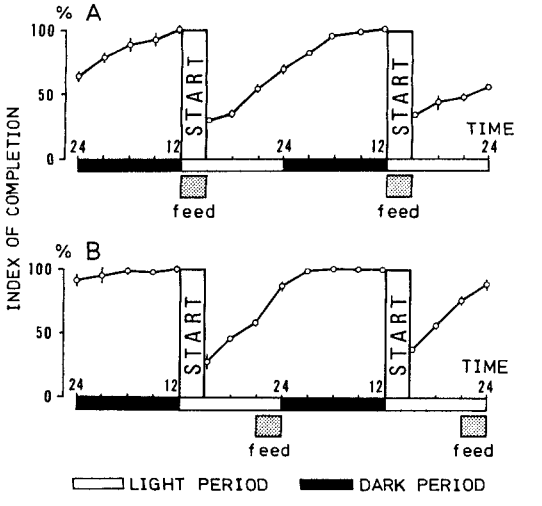

FIGURE 6.—Effects of feeding time on daily growth of *Tilapia nilotica* otoliths when the fish were reared under 12L-12D (light phase, 1200-2400 h). A) fed for 3 h after the onset of light phase; B) fed for 3 h before the end of light phase. Each circle represents mean ± SE for five fish. START = start of new incremental zone.

DISCUSSION

The ground and etched plane of otoliths of *T. nilotica* exhibited a concentric ring pattern of thick incremental and thin discontinuous zones. In other teleost otoliths, a unit increment has been described as composed of light and dark bands in light microscope observations of replicas of ground and etched planes (Pannella 1971, 1974) and light microscope (Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Barkman 1978) or SEM (Pannella 1974; Brothers et al. 1976; Timola 1977) observations of ground and etched specimens. The thickness of each band was variable but not as different as observed with the discontinuous and incremental zones in our results. This may be due to different ways of preparation and observation with different species of different ages. In particular, the thickness of discontinuous zones may vary depending on the concentration of acid and the etching time.

It has been considered that the band easily etched by acid contains more calcium and less organic materials (Brothers et al. 1976; Timola 1977). However, our observations of nonetched fracture planes in comparison with ground and etched planes indicated that acid effects thin interstitial layers between thick crystalline lamellae to form grooves, which are wider than the interstitial layers. This may be interpreted as caused by dissolution of calcium from the interstitial layers, and further, from the crystallized lamellae. The presence of organic materials intersecting growing crystals was reported in otoliths of various fishes (Degens et al. 1969; Pannella 1971). Dunkelberger et al. (1980) showed in a transmission electron microscope study of the *Fundulus* otolith that an interlamellar organic matrix interrupts each growth layer. Therefore, we consider that etching by acid discloses a layer containing more organic materials and less calcium and that acid infiltrated into the layer would affect crystalline layers at both sides. The discontinuous zones in the area along the anteroposterior axis of the otolith were not clear. Also, a few weakly etched discontinuous zones at wide intervals were found near the core region. This shows a possibility that clearness of a discontinuous zone reflects the growth rate of the otolith in relation to the ratio in amount of organic versus inorganic materials.

Results of our experiments in which the completeness of the outermost incremental zone was

measured every 3 h clearly showed that the ring is formed periodically every 24 h. This is supported with the observation that the number of rings (incremental zones), except those in the core region, is in good correlation with the chronological age in days after hatching of the fish. This also shows that the core region is formed during the embryonic stage. Several crystallized spherules found in the center of the core region indicate that the otolith rudiment is formed by fusion of many small primordia. Their presence is helpful to identify the plane that exactly passes through the center of the otolith.

The rate of otolith growth, judged from a change of the completeness of current increment, decreased or stopped for at least a few hours before and/or after the beginning of a light period in all the experiments. This may indicate that the growth of aragonite crystals at the margin of the otolith stopped or slowed down during this period of a day. On the other hand, growth of the otolith was apparent the rest of the time, showing that crystals deposited more rapidly. The structural difference observed between the surface of a complete crystalline layer and the outer surface of the growing otolith, flat and smooth in the former and rough with stacked crystals in the latter, also shows a difference in growth phases. These observations confirmed that in the fast growth phase an incremental zone is formed in the margin of the otolith and in the resting phase a discontinuous zone is formed. In relation to the structure of incremental and discontinuous zones discussed above, a cyclic deposition of organic materials or calcium or both seems to occur according to a daily photoperiod. Recently, Mugiya et al. (1981) reported that ^{45}Ca uptake by goldfish otoliths slowed down or stopped at sunrise and resumed in 3 h.

When a light and dark cycle was suddenly reversed, it took at least 6 d for the rhythm of the otolith growth to be adapted to the new photocondition. This indicates that otolith growth is primarily controlled by an endogenous rhythm synchronized with the environmental photoperiod. Taubert and Coble (1977) also presented a hypothesis that the formation of otolith rings is controlled by an internal, diurnal clock when fish are exposed to a 24-h photoperiod.

It was clearly shown that the otolith resumes its growth a few hours after lights-on, leaving a new discontinuous zone behind it. This pattern of growth was not affected by the change of the lengths of light and dark phases such as 18L-6D and 6L-18D. This shows that the stimulus of lights-on entrains the rhythm of otolith growth to the photoperiods and thus is important for the formation of the otolith rings. The importance of this stimulus as a cue for the ring formation is supported by the experiment in which light and dark phases were reversed, where changes in phase of otolith growth started after the first stimulus of lights-on, but not lights-off, in the reversed cycle (Figure 4).

Since *T. nilotica*, as a typical diurnal fish, begins to feed immediately after lights-on, feeding was also expected to be one of the factors which control the daily rhythm of otolith growth. However, a difference of 6 h in daily feeding did not affect the phase of the rhythm. Therefore, feeding time is not critical for the formation of otolith rings when the fish is exposed to a 24-h photoperiod. Taubert and Coble (1977) also showed that the feeding cycle of 24 h did not cause the formation of daily rings on the otolith of *T. mossambica* held under constant light.

ACKNOWLEDGMENTS

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PREY OF THE STELLER SEA LION, *EUMETOPIAS JUBATUS*, IN THE GULF OF ALASKA

KENNETH W. PITCHER[1]

ABSTRACT

Stomach contents of 250 Steller sea lions, *Eumetopias jubatus*, collected in the Gulf of Alaska consisted by volume of 95.7% fishes, 4.2% cephalopods, <0.1% decapod crustaceans, <0.1% shelled-gastropods, and <0.1% mammals. The 10 top-ranked prey were walleye pollock, *Theragra chalcogramma*; squids, Gonatidae; Pacific herring, *Clupea harengus pallasi*; capelin, *Mallotus villosus*; Pacific cod, *Gadus macrocephalus*; salmon, *Oncorhynchus* spp.; octopus, *Octopus* sp.; sculpins, Cottidae; flatfishes, Pleuronectidae; and rockfishes, Scorpaenidae. Walleye pollock was the predominant prey, composing about 58% of the total volume and occurring in 67% of the stomachs with food. Predation on capelin and salmon appeared to be largely limited to spring and summer when these species were abundant in nearshore waters. Utilization of walleye pollock by sea lions appeared to have increased between 1958-60 and 1975-78, perhaps because of an increase in the relative abundance of walleye pollock. There was nearly complete overlap in the diet of sea lions and the harbor seal, *Phoca vitulina richardsi*. Potential competition may have been ameliorated by differences in distribution, differing diving capabilities, a more diverse diet for harbor seals and use of larger prey by sea lions.

The importance of knowledge of diets of marine mammals has become increasingly apparent with the recent emphasis in offshore oil and gas development and the resulting potential for reduction or change in composition of prey resulting from pollution (Evans and Rice 1974). These data are also needed by both fisheries and marine mammal managers, particularly since recent legislation (The Marine Mammal Protection Act of 1972; United States PL 92-522 and The Fishery Conservation and Management Act of 1976; PL 94-265) requires management based on ecosystem concerns.

Between 1975 and 1978 I studied prey utilization by the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska from Cape Suckling to Sanak Island (Figure 1). This area contains an estimated 110,000 to 140,000 sea lions, 10 breeding rookeries, and a mimimum of 50 hauling areas and is considered to be the center of abundance for the species (Calkins and Pitcher[2]).

Several prior studies of sea lion foods (Imler and Sarber 1947; Mathisen et al. 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966), although limited in geographic and seasonal coverage, provide a base for comparisons of prey use over time. Historical records of prey abundance (Pereyra and Ronholt[3]) provide valuable insight into prey utilization. The results of a concurrent study of harbor seal, *Phoca vitulina richardsi*, foods (Pitcher 1980) allowed me to compare prey utilization of these two resident pinnipeds with largely overlapping distributions.

METHODS

Between 1975 and 1978, 250 sea lions were collected by shooting from nearshore waters, rookeries, and hauling areas of the Gulf of Alaska (Table 1). Stomach contents were removed in the field, wrapped in muslin, and preserved in 10% Formalin.[4] In 15 cases, when large amounts of freshly eaten prey occurred, the prey were weighed, identified from external characteristics, and disposed of in the field. Volume (cubic centimeters) and weight (grams) of prey were assumed to be equal in these samples (Fiscus and

[1]Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[2]Calkins, D. G., and K. W. Pitcher. 1981. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Outer Continental Shelf Environmental Assessment Program Final Report. Juneau Project Office, P.O. Box 1808, Juneau, AK 99802.

[3]Pereyra, W. R., and L. L. Ronholt. 1976. Baseline studies of demersal resources of the northern Gulf of Alaska shelf and slope. U.S. Dep. Commer., NOAA Processed Rep. NMFS NWFC, 281 p.

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

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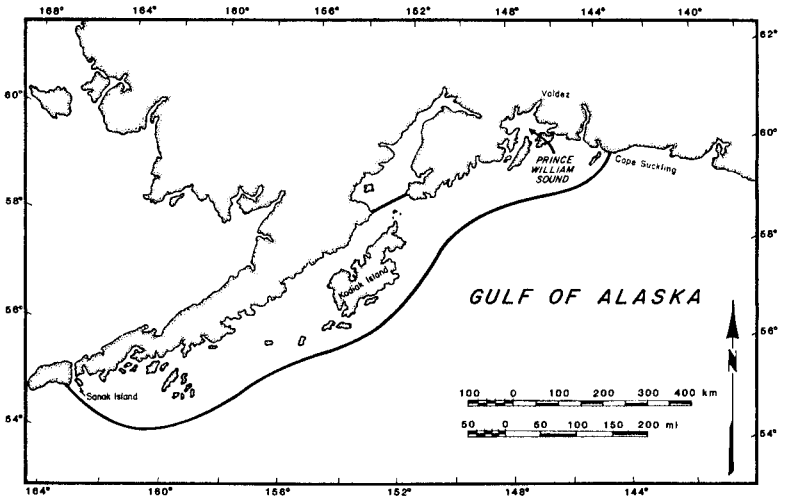

FIGURE 1.—Portion of the Gulf of Alaska where Steller sea lion prey utilization studies were conducted.

TABLE 1.—Comparison of seasonal and geographical distributions of 548 harbor seals and 250 Steller sea lions collected in the Gulf of Alaska. Numbers in the table are percentages of the samples taken during a particular season or in a geographical area.

Species	Winter	Spring	Summer	Fall	Northeastern Gulf of Alaska	Prince William Sound[1]	Kenai	Lower Cook Inlet	Kodiak	Alaska Peninsula
Harbor seals	21.7	44.3	13.3	20.7	5.7	35.8	10.9	6.8	36.7	4.2
Steller sea lions	28.4	35.2	6.0	30.4	4.4	37.2	17.2	0	34.4	6.8

[1]Includes 45 harbor seals from the Copper River Delta.

Baines 1966). For all other samples, volumes and occurrences of the various prey categories were determined in the laboratory. Prey identifications were based primarily on skeletal materials, particularly fish otoliths and cephalopod mandibles (beaks) (Fitch and Brownell 1968; Pinkas et al. 1971). Otoliths and other skeletal components from fish were identified to the lowest taxon possible by comparison with reference materials.

Food habit data were organized and examined as percentage of occurrence (number of stomachs in which a prey item occurred/total number of stomachs with food) and percentage of total volume (total volume of a prey item/total volume of all stomach contents). Confidence intervals for percentages of occurrence were calculated from tables presented by Rohlf and Sokal (1969). In the percent occurrence analysis, unimportant small but numerous organisms may be disproportionately evident (Perrin et al. 1973) as may species which have hard parts which resist digestion (Fiscus and Baines 1966). Volumetric analyses are distorting because various organisms are digested at different rates and because contents are at different stages of digestion when the collections are made (Perrin et al. 1973).

A combination rank index (CRI) was devised to integrate volumetric and occurrence data into a single indicator of prey use. Each prey category was ranked in descending order of percentage of occurrence and percentage of volume. The two rankings for each prey category were multiplied together to produce the CRI.

To compare sizes of walleye pollock, *Theragra chalcogramma*, eaten by Steller sea lions and harbor seals, random samples of walleye pollock otoliths recovered from stomachs were measured (total length). Fork lengths of the fish were then estimated, using a formula derived from regression analysis of otolith length and fish length (Frost and Lowry 1981). Estimated mean fork lengths are given in Table 2.

TABLE 2.—Estimated mean fork lengths based on otolith lengths, of walleye pollock eaten by Steller sea lions and harbor seals.

Item	Sea lions	Harbor seals
Otolith measurements, no.	2,030	2,180
Estimated mean fork length, cm	29.8	19.2
Standard deviation, cm	11.6	9.6
Range, cm	5.6-62.9	4.2-53.2

RESULTS AND DISCUSSION

Prey items were found in 153 of 250 sea lion stomachs examined. Fishes made up 95.7%, cephalopods 4.2%, decapod crustaceans <0.1%, shelled gastropods <0.1%, and mammals <0.1% of the volume of stomach contents (Table 3). Fishes included 14 species representing 11 families. Gadidae composed 59.7% of the total stomach contents and occurred in 82.4% of the stomachs with food. Walleye pollock was by far the dominant prey composing 58.3% of the total volume of stomach contents and occurring in 66.7% of the stomachs with food. Cephalopod remains occurred in 36.6% of stomachs with contents but made up only 4.2% of the total volume of stomach contents. This apparent disparity was probably the result of retention of cephalopod beaks in stomachs (Pitcher 1981) and the volumetric measurement was probably the most accurate measure of importance of cephalopods in the sea lion diet. Invertebrates other than cephalopods were found in 9.2% of the stomachs with food but composed <0.1% of total volume. Remains of two harbor seals were found in one stomach. Major prey were ranked (Table 4) using CRI.

TABLE 3.—Stomach contents of 153 Steller sea lions collected in the Gulf of Alaska.

Prey	Occurrence[1] No.	%[2]	95% C. I.[3]	Volume ml	%[4]
Gastropoda:					
Snails	2	1.3	0.1-4.5	20	<0.1
Cephalopoda	56	36.6	29.5-45.0	15,777	4.2
Octopus, *Octopus* sp.	20	13.1	8.2-19.2	250	<.1
Squids, Gonatidae	35	22.9	16.7-30.4	15,507	4.2
Unidentified cephalopods	1	.7	.1-4.5	20	<.1
Decapoda	11	7.2	3.6-12.2	130	<.1
Shrimps	8	5.2	2.2-9.7	100	<.1
Snow crab, *Chionoecetes* sp.	2	1.3	.1-4.5	20	<.1
Spider crab, *Hyas* sp.	1	.7	.1-4.5	10	<.1
Unidentified invertebrates	1	.7	.1-4.5	10	<.1
Rajidae:					
Skate, *Raja* sp.	1	.7	.1-4.5	960	.3
Clupeidae:					
Pacific herring, *Clupea h. pallasi*	16	10.5	5.8-15.8	76,920	20.6
Salmonidae:					
Salmon, *Oncorhynchus* spp.	6	3.9	1.5-8.4	19,160	5.1
Osmeridae:					
Capelin, *Mallotus villosus*	16	10.5	5.8-15.8	27,755	7.4
Gadidae	126	82.4	75.1-87.6	222,772	59.7
Saffron cod, *Eleginus gracilis*	2	1.3	.1-4.5	815	.2
Pacific cod, *Gadus macrocephalus*	19	12.4	7.4-18.1	3,471	.9
Pacific tomcod, *Microgadus proximus*	1	.7	.1-4.5	680	.2
Walleye pollock, *Theragra chalcogramma*	102	66.7	59.1-74.3	217,746	58.3
Unidentified gadid	2	1.3	.1-4.5	60	<.1
Zoarcidae:					
Eelpout, *Lycodes* sp.	1	.7	.1-4.5	10	<.1
Scorpaenidae:					
Rockfishes, *Sebastes* spp.	4	2.6	1.0-7.1	3,030	.8
Cottidae, sculpins	6	3.9	1.5-8.4	4,960	1.3
Agonidae:					
Sturgeon poacher, *Agonus acipenserinus*	1	.7	.1-4.5	60	<.1
Trichodontidae:					
Pacific sandfish, *Trichodon trichodon*	2	1.3	.1-4.5	300	<.1
Pleuronectidae, flatfishes	7	4.6	2.2-9.7	1,030	.3
Unidentified fishes	4	2.6	1.0-7.1	40	<.1
Harbor seal, *Phoca v. richardsi*	1	.7	.1-4.5	250	<.1
Total volume				373,184	

[1]Number of stomachs in which a prey item occurred.
[2]Number of occurrences/total number of stomachs with food (153).
[3]95% confidence interval.
[4]Total volume of a prey item/total volume of stomach contents.

TABLE 4.—Rankings by combination rank index (CRI, see Methods) of the 10 top-ranked prey of Steller sea lions collected in the Gulf of Alaska.

Rank	CRI	Prey	Percentage occurrence	Percentage volume
1	1	Walleye pollock	66.7	58.3
2	10	Squids	22.9	4.2
3	11	Pacific herring	10.5	20.6
4	16.5	Capelin	10.5	7.4
5	28	Pacific cod	12.4	.9
6	38	Salmon	3.9	5.1
7	51	Octopus	13.1	<.1
8	57	Sculpins	3.9	1.3
9	76	Flatfishes	4.6	.3
10	88	Rockfishes	2.6	.8

Predation on salmon, *Oncorhynchus* spp., and capelin, *Mallotus villosus*, appeared to be largely limited to spring and summer. Salmon occurred in 6 (12%) and capelin in 15 (30%) of 50 stomachs containing food collected from April through September. Salmon was not encountered and capelin was found only once (1%) in 103 stomachs containing food collected from October through March. This likely reflected seasonal, nearshore distribution associated with spawning in these species (Hart 1973; Jangaard 1974). I found a similar seasonal pattern of harbor seal predation on salmon and capelin in the Gulf of Alaska (Pitcher 1980).

Pacific herring, *Clupea harengus pallasi*, and squids were extensively used by sea lions in Prince William Sound but appeared to be relatively unimportant in other areas. Fifteen of 16 stomachs containing Pacific herring and 30 of 35 stomachs containing squids were from Prince William Sound both highly significant deviations (χ^2 = 12.30 and 16.61, $P<0.001$) from expected values based on the distribution of stomachs containing food (73 of 153 were from Prince William Sound). Harbor seals also appeared to utilize more squids and Pacific herring in Prince William Sound than in other areas of the gulf, which was attributed to differing water depths and bottom topography (Pitcher 1980).

Three studies of sea lion foods in which a total of 135 stomachs containing food were examined were conducted in the Gulf of Alaska between 1958 and 1960 (Mathisen et al. 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966). Major prey included shelled mollusks; cephalopods; Pacific sand lance, *Ammodytes hexapterus*; rockfishes; and smelts. Because geographic and seasonal composition of these samples and my collections were not strictly comparable (previous collections were nearly all near rookeries during the breeding season, while I sampled throughout much of the year at a wide range of locations) strict comparisons of the data are not possible. However, one major difference was apparent; walleye pollock, the predominant prey in my sample, was not found in the earlier studies. Concurrent with this apparent increase of walleye pollock in the sea lion diet has been an increase in walleye pollock abundance in the Gulf of Alaska. Between 1961 and 1973-75 walleye pollock increased from 5 to 45% by weight of total demersal fish stocks and was found to be the predominant species (Pereyra and Ronholt footnote 3).

One additional collection of seven sea lions was made in 1945 (Imler and Sarber 1947). Walleye pollock and flatfishes were the major foods.

Harbor seals and Steller sea lions are the only abundant pinnipeds resident in nearshore regions of the Gulf of Alaska. Food habit studies of both species were conducted concurrently; both sea lions and harbor seals (Pitcher 1980) frequently were collected on the same trips. This resulted in relatively comparable geographic and seasonal coverage (Table 1). Results of the two studies were similar (Table 5) with nearly complete overlap of principal prey. Spearman rank correlation analysis showed a significant positive correlation (r_S = 0.67, $P<0.01$) between the rankings of principal prey eaten by both sea lions and harbor seals. The percentage of cephalopods eaten by both predators was similar; however, sea lions ate more squids while harbor seals consumed more octopus. Walleye pollock was the top-ranked prey of both sea lions and harbor seals; however, the percentage of occurrence was nearly twice as high for sea lions (66.7%) as for harbor seals (34.9%). Eulachon, *Thaleicthys pacificus*, and Pacific sand lance were both evident components of the harbor seal diet (occurring in 8.2% and 7.1% of the stomachs, respectively) but were not recorded as food of sea lions during this study. Most eulachon occurrences were from harbor seals collected in freshwater and estuarine habitats of the Copper River Delta (Pitcher 1980) where no sea lions occurred.

Although use of prey by sea lions and harbor seals was similar, several factors may have ameliorated potential competition. Mean length of walleye pollock eaten by sea lions was significantly greater (t = 32.4, $P<0.001$) than for those eaten by harbor seals, based on otoliths recovered from stomachs (Table 2). This may indicate a tendency towards use of larger prey by sea lions. Although distribution of the two species often overlaps in the Gulf of Alaska, sea lions range farther offshore (Fiscus et al.[5]). In addition, harbor seals often use freshwater and estuarine habitats rarely used by sea lions in the Gulf of Alaska. Harbor seals can probably stay submerged for considerably longer periods than sea lions (R. Elsner[6]) which may allow them to more efficiently utilize cryptic and solitary prey such as octopus and flatfishes. Although use of principal prey between the two species was similar, harbor seals had a more diverse diet. They preyed upon a minimum of 31 species (Pitcher 1980) compared with 20 for sea lions. Both sea lions and harbor seals appeared to modify their diets according to prey availability. Several lines of evidence led to this hypothesis. Walleye pollock, the predominant prey of sea lions and harbor seals, was the most abundant species of demersal fish in the area. Similar seasonal and geographic variations in the diets of both species were found which probably reflected use of abundant and readily available prey at that time and location. There were apparent changes over time in the relative composition of the sea lion diet (primarily walleye pollock) which appeared to correlate with changes in prey abundance. Also, reports in the literature indicated use of different prey in other geographic regions (Spalding 1964; Fiscus and Baines 1966).

Four of the five, top-ranked prey of both sea lions and harbor seals (Table 5) were off-bottom schooling species. Many of the important prey reported in other studies of Steller sea lion foods also fit into this category and include Pacific herring; smelts;

[5]Fiscus, C. H., H. W. Braham, R. W. Mercer, R. D. Everitt, B. D. Krogman, P. D. McGuire, C. E. Peterson, R. M. Sonntag, and D. E. Withrow. 1976. Seasonal distribution and relative abundance of marine mammals in the Gulf of Alaska. *In* Environmental assessment of the Alaskan Continental Shelf, Vol. 1, p. 19-264. Principal investigators reports for October-December 1976. Environmental Research Laboratories, NOAA, Boulder, Colo.

[6]R. Elsner, Professor of Physiology, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. January 1980.

TABLE 5.—Comparative frequency of principal prey ($N \geq 4$) of 250 Steller sea lions and 548 harbor seals collected in the Gulf of Alaska between 1973 and 1978.

	Steller sea lion occurrence				Harbor seal occurrence[1]			
Prey	Rank	No.	%	95% C. I.[2]	Rank	No.	%	95% C. I.[2]
Walleye pollock	1	102	66.7	59.1-74.3	1	94	34.9	29.4-40.9
Squid	2	35	22.9	16.7-30.4	8	20	7.4	4.3-10.7
Octopus	3	20	13.1	8.2-19.2	2	77	28.6	23.8-34.7
Pacific cod	4	19	12.4	7.4-18.1	5	28	10.4	6.8-14.1
Pacific herring	5.5	16	10.5	5.8-15.8	4	29	10.8	7.6-15.3
Capelin	5.5	16	10.5	5.8-15.8	3	40	14.9	11.1-19.8
Shrimps	7	8	5.2	2.2-9.7	10	17	6.3	3.6-9.5
Flatfishes	8	7	4.6	2.2-9.7	6	23	8.6	6.0-13.0
Salmon	9.5	6	3.9	1.5-8.4	13	9	3.3	1.4-5.7
Sculpins	9.5	6	3.9	1.5-8.4	11.5	10	3.7	2.1-7.0
Rockfishes	11	4	2.6	1.0-7.1	17	4	1.5	0.2-3.4
Saffron cod	12.5	2	1.3	0.1-4.5	16	5	1.9	0.8-4.4
Pacific sandfish	12.5	2	1.3	0.1-4.5	11.5	10	3.7	2.1-7.0
Pacific tomcod	14.5	1	.7	0.1-4.5	14	7	2.6	1.4-5.7
Eelpouts	14.5	1	.7	0.1-4.5	15	6	2.2	0.8-4.4
Eulachon	16.5	0	.0	0.0-2.4	7	22	8.2	5.2-11.8
Pacific sand lance	16.5	0	.0	0.0-2.4	9	19	7.1	4.3-10.7
Others		16				31		
Stomachs with food		153				269		

[1]Pitcher (1980).
[2]95% confidence interval.

Pacific cod, *Gadus macrocephalus*; Pacific whiting, *Merluccius productus*; walleye pollock; rockfishes; and Pacific sand lance (Imler and Sarber 1947; Spalding 1964; Fiscus and Baines 1966). Use of this prey type may be important in minimizing foraging effort and conserving energy, compared with the energy expenditures of capturing more solitary species (Smith and Gaskin 1974; Pitcher 1980).

ACKNOWLEDGMENTS

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OFFSHORE DISTRIBUTION OF ALEWIFE, *ALOSA PSEUDOHARENGUS*, AND BLUEBACK HERRING, *ALOSA AESTIVALIS*, ALONG THE ATLANTIC COAST

RICHARD J. NEVES[1]

ABSTRACT

This study of the offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*, in the Atlantic Ocean was based on catch data collected over the 16-year period 1963-78 during bottom trawl surveys by the National Marine Fisheries Service and its predecessor agency. All catches of the two species were made where bottom water temperatures ranged from 2° to 17° C, and catches were most frequent at bottom temperatures between 4° and 7° C. Most catches of both species were made at stations where depth was less than 100 m. Chi-square analyses indicated that alewives were captured significantly more often than expected in the 56 to 110 m depth stratum and blueback herring in the 27 to 55 m stratum ($P < 0.01$). During summer and autumn, all catches of the two species were confined to the region north of latitude 40° north in three general areas: Nantucket Shoals, Georges Bank, and the perimeter of the Gulf of Maine (especially in autumn along the northwestern edge of the gulf). Winter catches were between latitude 40° and 43° north, and spring catches were distributed throughout the continental shelf area between Cape Hatteras, N.C., and Nova Scotia. Previous studies on juveniles, food of adults, and differences in time of capture during National Marine Fisheries Service surveys indicated that these species are vertical migrators, apparently following the diel movements of zooplankton in the water column.

The alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*, are anadromous clupeids that support substantial commercial fisheries during their spawning runs into rivers along the Atlantic coast. They are sympatric over most of their range and remarkably similar in external appearance; species separation is based primarily on eye size and the color of the abdominal peritoneum (Scott and Crossman 1973). Except for a description of some biological characteristics of these species from catches on Georges Bank (Netzel and Stanek 1966), virtually nothing has been written about the offshore biology or movements of these "river herring" (a term used by commercial fishermen for the two species combined).

The alewife, which ranges from North Carolina to the St. Lawrence River, Canada, spawns in rivers during spring. Spawning runs occur in a chronological south to north progression, from March through May. The significance of specific water temperatures for both upstream migration and spawning has been well documented for anadromous alewife populations (Cooper 1961; Dominy 1971; Saila et al. 1972; Kissil 1974; Richkus 1974; Tyus 1974). Adults migrate upstream and spawn in ponds, lakes, or slow-flowing stretches of rivers at water temperatures between 12° and 16° C (Bigelow and Schroeder 1953). Available evidence indicates that alewives home to their natal rivers to spawn (Belding 1921; Havey 1961; Thunberg 1971). The young remain in freshwater for several months, migrate downstream during summer and autumn, and generally spend 2 to 4 yr at sea, until sexually mature.

The behavioral response of alewives to changes in water temperature has received special research attention since the species invaded the Great Lakes (Colby 1973; Otto et al. 1976). Large, periodic die-offs in the Great Lakes have indicated a failure of this species to adjust completely to lake conditions. Hypotheses to explain these die-offs have alluded to differences between the lacustrine environment and the ancestral ocean, and their effect on the physiology of preadults (Smith 1968; Colby 1971; Stanley and Colby 1971); however, specific information on the marine phase of the alewife's life history is lacking.

The blueback herring ranges from northern Florida to Nova Scotia but is most abundant along the middle and south Atlantic coast. Its freshwa-

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ter life history is similar to that of the alewife, although its biology has not been as rigorously studied (Scherer 1972; Loesch and Lund 1977). Adults appear in rivers about 1 mo later than alewives and spawn over an extended period, at water temperatures between 21° and 24° C (Bigelow and Schroeder 1953). The young leave freshwater during their first year and remain in the ocean for 2 to 5 yr before returning to spawn.

This paper presents information on the offshore distribution and seasonal movements of these river herring, based on cruise and catch data collected during bottom-trawl surveys from 1963 to 1978 by U.S. research vessels between Cape Hatteras, N.C., and Nova Scotia, Canada.

METHODS

The National Marine Fisheries Service (NMFS) and its predecessor agency, the Bureau of Commercial Fisheries, have conducted bottom trawl surveys each autumn since 1963, using the RV *Albatross IV* and the RV *Delaware II*. The survey area, which extended from Nova Scotia to Cape Hatteras out to a depth of 366 m (Figure 1), was stratified into geographical zones based on depth and area. Coastal sampling stations were outside the 27 m depth contour. Middle Atlantic stations between New Jersey and Cape Hatteras were added during autumn 1967. A stratified, random sampling design was used in the surveys; trawl stations were allocated to strata in proportion to stratum area and randomly assigned within strata (Grosslein 1969). A standard No. 36 Yankee bottom trawl with a 1.25 cm stretched mesh cod end liner was towed at each station for 30 min at an average speed of 3.5 kn. Fall surveys were conducted 24 h/d between 3 September and 16 December 1963-78.

Bottom trawl surveys were conducted each spring during 1968-78 by U.S. vessels over the same geographical area (Figure 1). The No. 36 Yankee trawl was used from 1968 to 1972 and a larger No. 41 Yankee trawl from 1973 to 1978. Trawling procedures were the same as during autumn surveys, and stations were sampled between 4 March and 23 May. Spring and fall cruises were each conducted within an 8-wk period. A detailed description of NMFS bottom trawl surveys and survey procedures was provided by Flescher[2] and Grosslein.[3] All spring and autumn surveys and additional cruises during summer and winter are summarized in Table 1.

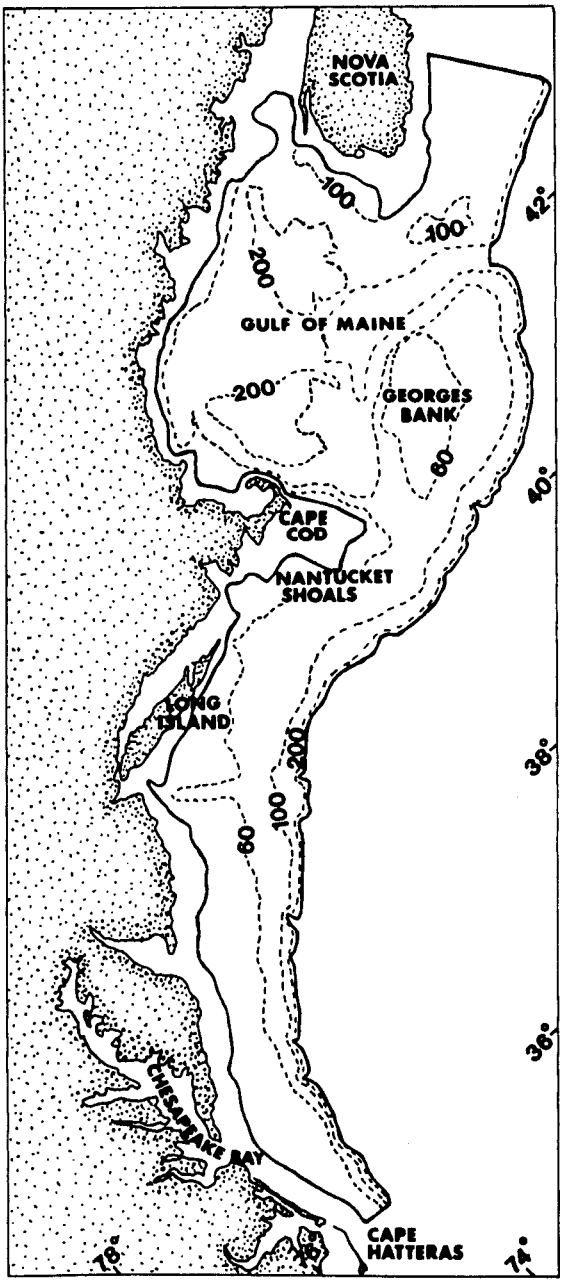

FIGURE 1.—National Marine Fisheries Service bottom trawl survey area, between depths of 27 and 366 m, Cape Hatteras, N.C., to Nova Scotia, western North Atlantic. Contour intervals are in meters (from Neves and Despres 1979).

[2]Flescher, D. 1976. Research vessel cruises, 1963-1975 National Marine Fisheries Service, Woods Hole, Massachusetts. NMFS, Woods Hole, Mass., Lab. Ref. No. 76-14, 30 p.

[3]Grosslein, M. D. 1969. Groundfish survey methods. NMFS, Woods Hole, Mass., Lab. Ref. No. 69-2, 34 p.

TABLE 1.—Summary of seasonal bottom trawl surveys conducted by U.S. research vessels between Cape Hatteras, N.C., and Nova Scotia, 1963-78.

Season	No. of surveys	No. of stations	Inclusive dates
Spring	11	3,097	4 Mar.-23 May
Summer	6	1,137	7 July-31 Aug.
Autumn	16	4,397	3 Sept.-16 Dec.
Winter	3	563	16 Jan.- 8 Apr.
Totals	36	9,194	

Pertinent survey station and catch data included date, location, time, depth, bottom and surface water temperatures, and number and length frequencies of river herring captured. Only catches of 10 or more alewives or blueback herring/trawl tow were used in this study. I plotted catch locations from all surveys (Table 1) by 10′ rectangles of latitude and longitude on depth contour maps according to month or season. Locations of catches during spring (March-May) and autumn (September-November) were plotted by month, although cruise direction and time schedules influenced date of sampling within the survey area. Surveys in summer (June-August) and winter (December-February) were grouped by season because sampling effort and catch frequency were lower during these seasons. Commercial catches reported to the International Commission for the Northwest Atlantic Fisheries (ICNAF[4]) by member nations from 1970 to 1978 were provided by Hodder.[5] These catch data were used to locate U.S. and foreign catches of river herring within each ICNAF division and were correlated with distribution patterns based on survey data. Surface and bottom temperatures (to the nearest 1° C) and depths were plotted for each trawl tow that collected 10 or more alewives or blueback herring.

[4]ICNAF was replaced by the Northwest Atlantic Fisheries Organization (NAFO) in January 1980.

[5]V. M. Hodder, ICNAF Office, Dartmouth, N.S., Canada B2Y 3Y9, pers. commun. July 1977, June 1980.

RESULTS

Bottom trawling at 9,194 stations during the 36 survey cruises yielded 37,313 alewives at 512 stations and 3,058 blueback herring at 96 stations within the survey area. The fish ranged from 6 to 35 cm fork length. Water temperatures recorded at approximately 95% of these collecting stations were used to plot catch frequency at 1° C intervals. Water temperatures at stations where alewives were collected ranged from 2° to 23° C at the surface (Figure 2) and from 3° to 17° C at the bottom (Figure 3). Surface temperatures at stations with blueback herring ranged from 2° to 20° C and

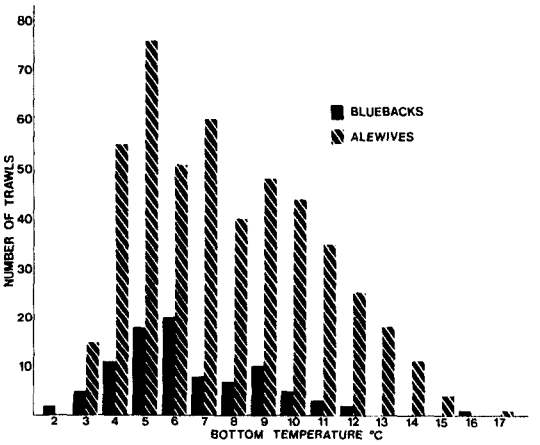

FIGURE 3.—Bottom temperatures at stations where alewives and blueback herring were collected during bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

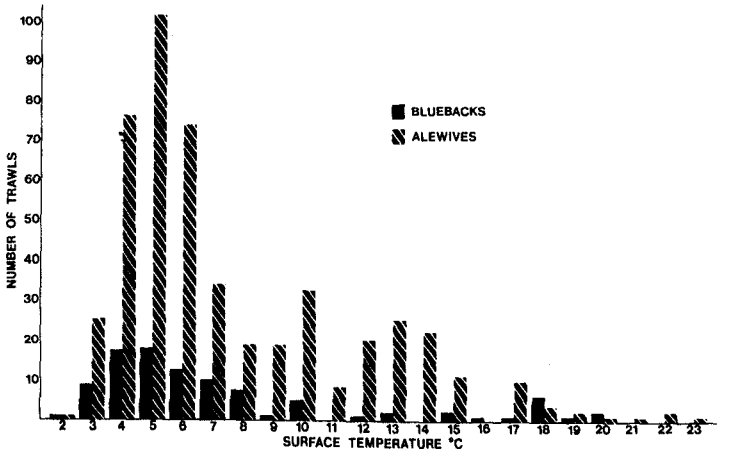

FIGURE 2.—Surface temperatures at stations where alewives and blueback herring were collected during bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

bottom temperatures from 2° to 16° C. Catches of each species were more frequent at stations where both surface and bottom temperatures were 4° to 10° C (Figures 2, 3).

Most stations with bottom temperatures <4° C occurred in the Gulf of Maine during early spring. Stations with bottom temperatures >15° C were mainly off the mid-Atlantic coast during late summer and early autumn. The apparent decline in occurrence of alewives and blueback herring as bottom temperatures increased was examined further by comparing catches with total sampling effort for each bottom temperature (range, 1°-23° C) at which trawls were fished (Table 2). Nearly all blueback herring were taken at water temperatures <13° C. Alewives were caught at temperatures from 3° to 17° C, and frequency of capture was highest at 4° C (Table 2).

Ocean depths at stations where river herring were caught ranged from 20 to 293 m, but most catches of alewives (77%) and blueback herring (83%) were made at stations <100 m deep (Figure 4). Since trawling effort during surveys was proportional to the area of each depth interval, the number of catches within these depth strata was amenable to chi-square analysis with correction for continuity (Zar 1974). A comparison between alewife and blueback herring catches at each depth interval and catches at all other depths combined indicated that both species were collected significantly more often than expected at depths <110 m (Table 3). Based on expected values, blueback herring were captured significantly more often in the 27-55 m depth stratum and alewives in the 56-110 m stratum ($P<0.01$).

TABLE 2.—Total sampling effort and percent of trawl tows with alewives or blueback herring at different bottom temperatures during bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

Bottom temp (° C)	Total trawl tows (no.)	Alewives (%)	Blueback herring (%)
1	9	0	0
2	87	0	2.3
3	243	6.2	2.1
4	589	9.3	1.9
5	1,064	7.1	1.7
6	1,040	4.9	1.9
7	1,018	5.9	.8
8	896	4.5	.8
9	806	6.0	1.2
10	699	6.3	.7
11	653	5.4	.5
12	523	4.8	.4
13	424	4.2	0
14	250	4.4	0
15	153	2.6	0
16	69	0	1.4
17	43	2.3	0
18	31	0	0
19	21	0	0
20	22	0	0
21	21	0	0
22	6	0	0
23	4	0	0

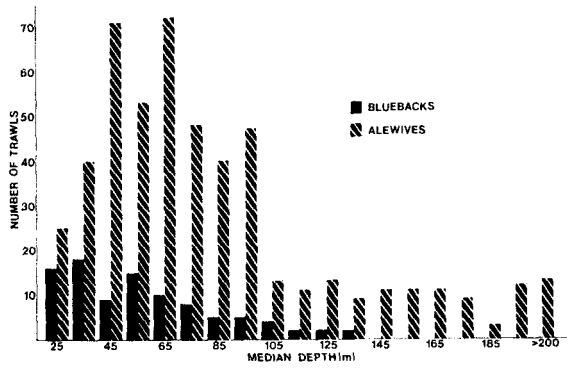

FIGURE 4.—Frequency of catches of alewives and blueback herring in relation to depth at trawling stations, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

Seasonal Distribution

Spring surveys were conducted primarily in March and April, accounting in part for the more frequent collections of alewives and blueback herring during these 2 mo (Figures 5, 6). During the spring, both species were widely distributed along the Middle Atlantic Bight, and mixed catches were common in this region. Alewife catches were also frequent between Cape Cod, Mass., and the western perimeter of Georges Bank (Figure 5). No spring catches of blueback herring were recorded for Georges Bank (Figure 6).

During the summer surveys of July and August, neither species was captured south of lat. 40° N; stations in the central Gulf of Maine were also unproductive (Figure 7). Alewives were collected most frequently on Georges Bank and south of

TABLE 3.—Depth intervals within the survey area and associated catches of alewives (A) and blueback herring (B) during complete bottom trawl surveys, 1967-78, Cape Hatteras, N.C., to Nova Scotia.

Depth interval (m)	Study area		Number of trawl tows with alewives or blueback herring					
			Observed		Expected		χ^2	
	km²	%	A	B	A	B	A	B
27-55	47,412	25.4	120	50	102	22	4.02	46.00**
56-110	55,009	29.5	194	33	118	26	68.45**	2.31
111-185	53,789	28.9	63	4	116	25	33.43**	23.59**
186-366	30,181	16.2	24	0	65	14	30.11**	15.52**
Totals	186,391	100.0	401	87	401	87		

**$P<0.01$.

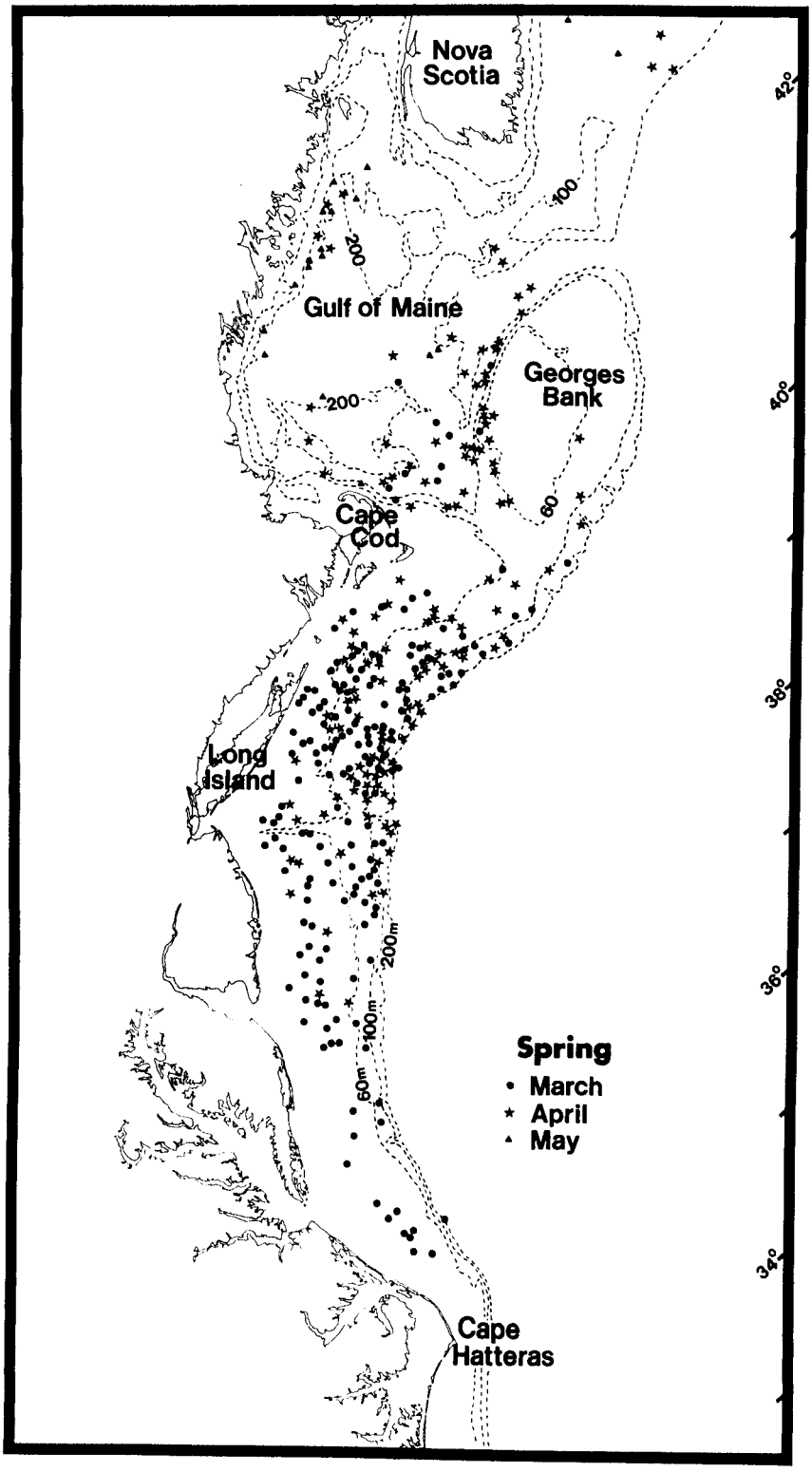

FIGURE 5.—Location of alewife catches during spring bottom trawl surveys, 1968-78, Cape Hatteras, N.C., to Nova Scotia.

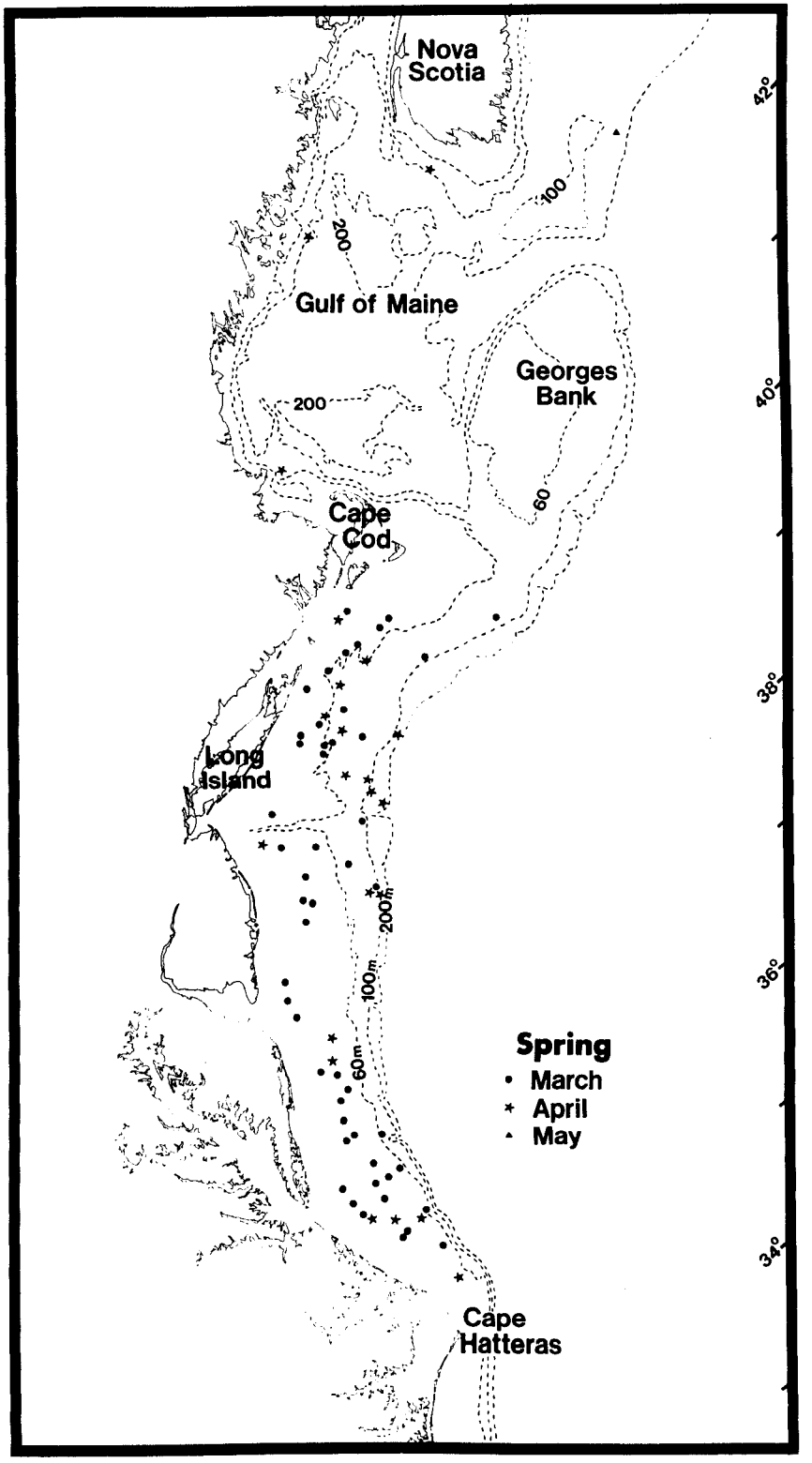

FIGURE 6.—Location of blueback herring catches during spring bottom trawl surveys, 1968-78, Cape Hatteras, N.C., to Nova Scotia.

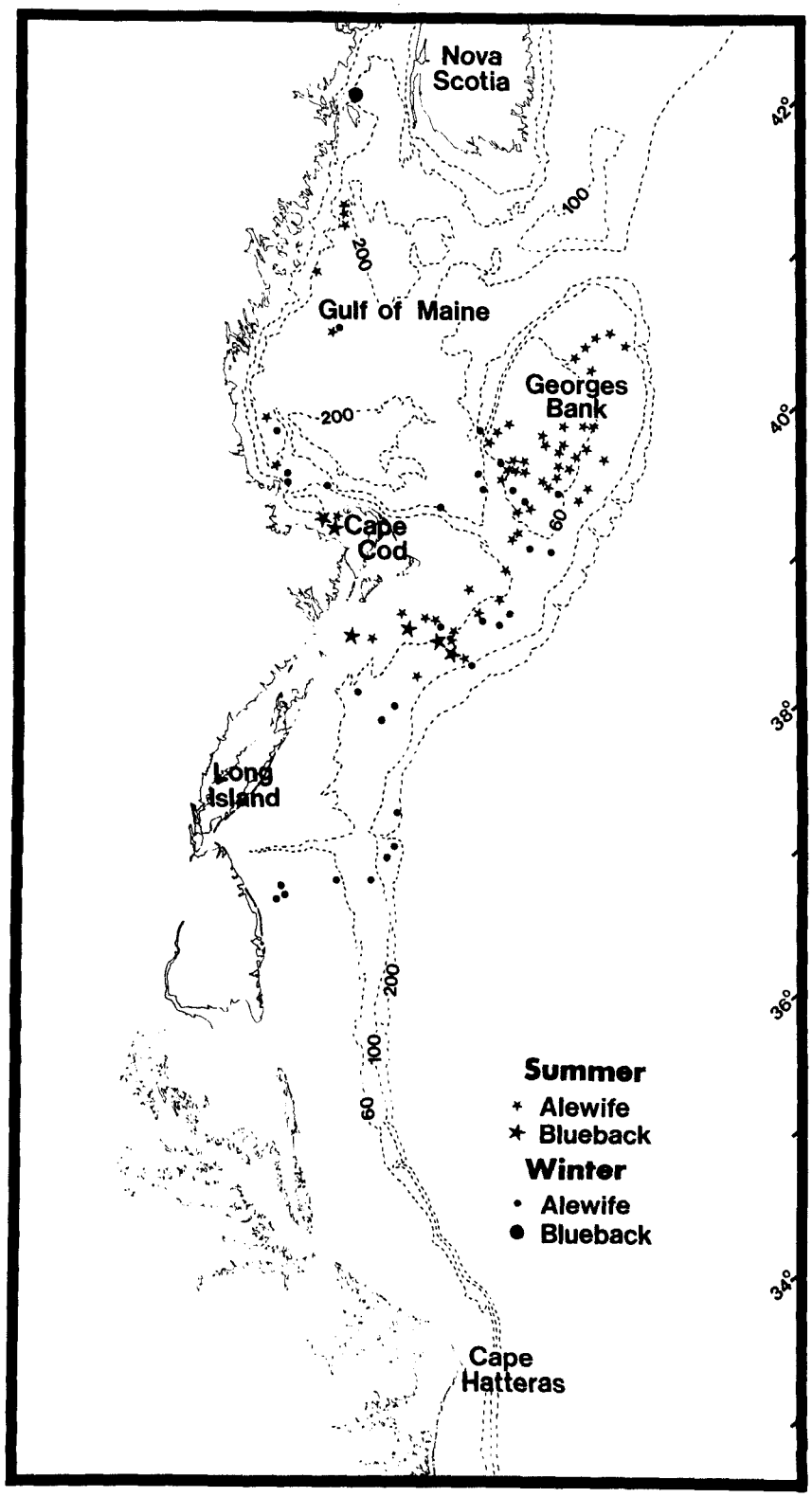

FIGURE 7.—Location of catches of alewives and blueback herring during summer and winter bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

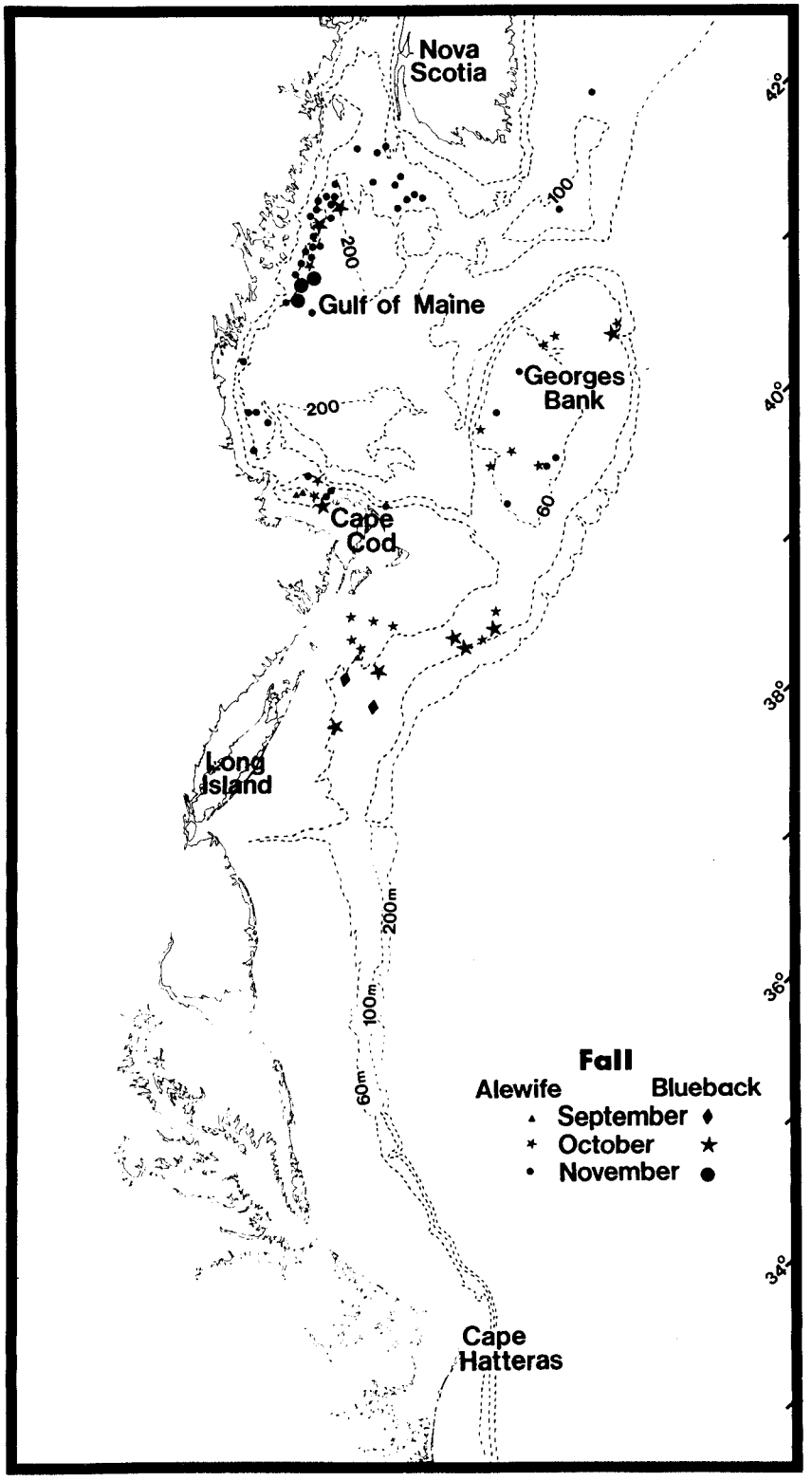

FIGURE 8.—Location of catches of alewives and blueback herring during fall bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

Nantucket Shoals; catch records of blueback herring were too infrequent to determine summer occurrence. Both species were rarely captured in water deeper than 100 m in summer.

During fall surveys, catches of river herring were less frequent than during the spring, even though more stations were sampled (Table 1). Distribution of catches was similar to that in summer, except that a concentration of both species was evident along the northwest perimeter of the Gulf of Maine (Figure 8). Catches of river herring were recorded at most stations in this region. In 12 yr of autumn bottom trawl surveys along the Atlantic coast, river herring were never collected offshore south of lat. 40° N.

The relatively small number of winter sampling stations was inadequate to define the wintering area for either species (Figure 7). The few winter catches were widely distributed, primarily from lat. 40° N (south of Long Island) to lat. 43° N (north of Cape Cod).

Commercial Catches

The time periods for major catches of river herring in ICNAF divisions by domestic (primarily inshore) and foreign (offshore) fisheries are summarized in Figure 9. Domestic catches in Subarea 5 resulted from both inshore and offshore fishing operations. The south to north progression in spawning runs is reflected in the time and location of commercial catches by the United States (Subareas 6 and 5) and Canada (Subarea 4), since most domestic catches occur during the upstream migration of anadromous stocks in each subdivision. The periods of principal foreign catches preceded or overlapped those of domestic catches in coastal waters. The year-round occurrence of river herring between Long Island and Georges Bank, as indicated by NMFS survey data, was corroborated by commercial catches in ICNAF divisions 5Zw and 5Ze (Figure 9).

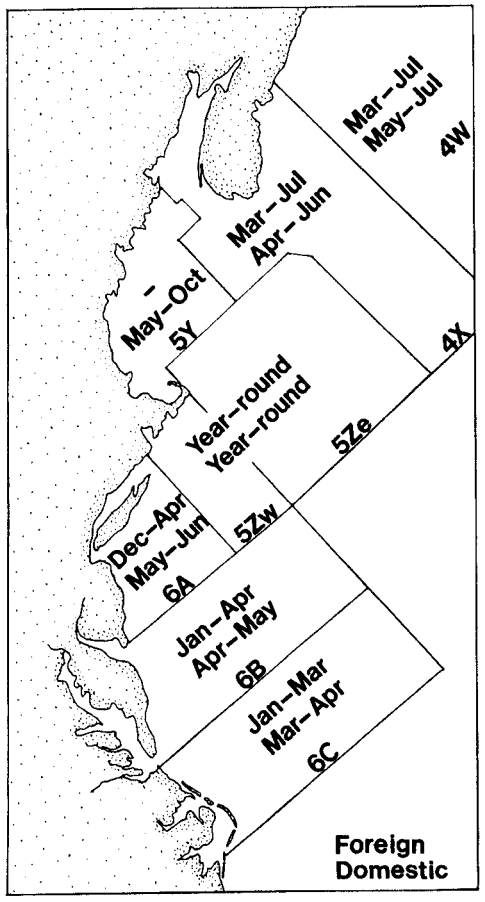

FIGURE 9.—Seasonal distribution of major catches of alewives and blueback herring in divisions of the International Commission for the Northwest Atlantic Fisheries, 1970-78, Cape Hatteras, N.C., to Nova Scotia. Within each division, the months for major catches are shown separately for foreign vessels (upper entry) and the domestic fishery (lower entry).

DISCUSSION

Offshore Distribution

Fish sampling during NMFS bottom trawl surveys covers a large area in a relatively short period and provides the most detailed, available records on offshore distribution of fishes and concurrent environmental conditions. As judged by the accumulated survey data, the seasonal offshore distribution of alewives and blueback herring resembles that of American shad, *Alosa sapidissima* (Neves and Despres 1979). River herring are widely distributed along the Middle Atlantic Bight during spring, appear to move north in the Nantucket Shoals, Georges Bank, and coastal Gulf of Maine areas during summer and early autumn, and then return south to the mid-Atlantic coast in winter and early spring. The extent of overwintering in deep water off the continental shelf is unknown. The similarities in seasonal distribution between American shad and river herring may be indicative of similar inshore and offshore migratory patterns. However, a determination of stock mixing and migratory routes is not possible, because no tagging studies have been conducted

comparable with those on other anadromous species (Merriman 1941; Raney et al. 1954; Talbot and Sykes 1958; Chapoton and Sykes 1961; Leggett and Whitney 1972).

If the water temperature regime recorded for oceanic occurrence of alewives and blueback herring (Figure 3) applies to all stocks of these species at sea, the migratory route of blueback herring populations returning to South Atlantic rivers would be similar to that proposed for American shad by Neves and Despres (1979). Prespawning adults returning to coastal waters from the ocean would encounter a thermal barrier south of Cape Hatteras, where offshore temperatures remain above 17.5° C throughout the year. Migration toward shore north of Cape Hatteras and then south along the coast would appear to be essential for successful homing to South Atlantic rivers.

A determination of oceanic location and migratory routes of river herring stocks has particular relevance to the commercial fishery, centered primarily in Virginia and North Carolina. Large catches of river herring were taken offshore by foreign fishing vessels in ICNAF Subarea 6 during the mid-1960's, and by 1969 foreign catches exceeded domestic catches (McHugh and Ginter 1978). The increase in high-seas catches, consisting of juveniles and adults, was accompanied by a marked decrease in inshore landings. This foreign fishing pressure, added to that of the domestic fishery, resulted in a drastic reduction of total annual catches (Table 4). Street and Davis[6] postulated that this decline reflected a reduction in stock size due to excessive harvest. The United States obtained certain limitations on foreign catches of river herring through bilateral negotiations during the mid-1970's, and after the implementation of the Fishery Conservation and Management Act of 1976 (PL 94-265), offshore catches of river herring by foreign vessels were virtually eliminated. Johnson et al.[7] reported that Virginia landings of river herring in 1978 increased 53% compared with those in 1977, but did not attribute this increase to good recruitment. River herring catches in North Carolina have continued to decline, and water quality degradation in several spawning areas may be creating additional problems (Street[8]). Future monitoring of stock abundance by coastal states should help resolve the question of whether stocks were seriously reduced by offshore fishing.

[6]Street, M. W., and J. Davis. 1976. Notes on the river herring fishery of SA6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. 76/VI/61, Serial No. 3848, 7 p.

TABLE 4.—Annual catches (metric tons round, fresh) of alewives and blueback herring (species combined) by domestic and foreign fisheries in three ICNAF subareas, 1966-78.

Year	ICNAF subarea 4	5	6	Total
1966	3,703	4,344	21,178	29,225
1967	2,978	9,285	23,182	35,445
1968	3,028	22,598	24,724	50,350
1969	1,655	26,185	34,732	62,572
1970	3,288	14,598	20,842	38,728
1971	10,938	14,618	21,213	46,769
1972	7,948	8,656	5,146	21,750
1973	8,859	5,865	11,202	25,926
1974	17,954	3,771	12,583	34,308
1975	5,683	5,019	9,553	20,255
1976	7,954	1,812	6,444	16,210
1977	7,744	1,765	4,586	14,095
1978	7,626	1,640	4,122	13,388

Depth Distribution

Frequency of alewife and blueback herring catches within the four depth strata indicated that these species occur primarily at water depths <110 m at sea. Both species are size-selective zooplankton feeders (Bigelow and Schroeder 1953; Hildebrand 1963; Brooks and Dodson 1965). My examination of the stomachs of 100 alewives and 75 blueback herring, collected in April 1978 during the spring survey, revealed calanoid copepods, mysids, and other zooplankters in that order of frequency and abundance in both species. The occurrence of major zooplankton concentrations in the Gulf of Maine at depths <100 m (Bigelow 1926; Whiteley 1948) may therefore influence the depth distribution of river herring.

The numerous catches of river herring in the northwestern Gulf of Maine during autumn were centered at about lat. 44° N, long. 68° W. Mean depth at these stations was 112 m (range, 64-179 m), and mean bottom temperature was 9.5° C (range, 8.0°-13.4° C). This apparent concentration of river herring is noteworthy, particularly since studies on zooplankton availability in this region are contradictory. From late summer to December, zooplankton is most abundant in the northern Gulf of Maine (Cohen[9]); however, Sherman (1970)

[7]Johnson, H. B., D. W. Crocker, B. F. Holland, Jr., J. W. Gilliken, D. L. Taylor, and M. W. Street. 1978. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. Annu. Rep. Anadromous Fish Proj. 1978, N.C.-Va. AFCS 9-2, 175 p.

[8]M. W. Street, N.C. Div. Mar. Fish. Morehead City, N.C. 28556, pers. commun. June 1980.

[9]Cohen, E. B. 1975. An overview of the plankton communities of the Gulf of Maine. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 106, Ser. No. 3599, 16 p.

recorded low volumes of zooplankton along the northern coast of Maine. Confirmation of river herring abundance in this region requires more extensive investigation.

The apparent difference in preferred depth distribution between the alewife and blueback herring (Table 3) may be related to the diagnostic character differences between these two species. The alewife has a slightly larger eye, an adaptation usually associated with an existence at greater depths (Marshall 1966). In addition, green wavelengths (ca. 500 mμ) penetrate waters of the continental shelf most effectively (Wald et al. 1957). Could the color of the dorsum, green in the alewife and blue in the blueback, be a countershading mechanism for reduced predation within the depth ranges most frequently occupied by each species? No direct evidence is available to support either the eye size or dorsal coloration postulates; however, the vertical segregation evidenced at sea has also been reported for juveniles in rivers (Loesch and Kriete[10]). Juvenile blueback herring occur in the upper levels of the river water column, and juvenile alewives frequent midwater depths.

Diel differences in catchability of river herring were examined by partitioning capture time (eastern standard time) during survey cruises (24 h/d) into day (0600-1800 h) and night (1800-0600 h). Chi-square analysis with correction for continuity on time of capture revealed that catches were made significantly more often ($P<0.01$) during the day than at night (Table 5). Alewives and blueback herring were apparently closer to the bottom during daylight, and thus more susceptible to bottom trawling gear. This diel difference in depth distribution has also been reported for juvenile river herring in estuaries (Warriner et al. 1969; Loesch et al.[11]) and adult alewives in the Great Lakes (Janssen and Brandt 1980).

I deduce from the above observations that river herring are vertical migrators like other schooling clupeids such as American shad and sea herring, *Clupea harengus* (Blaxter 1975; Neves and Despres 1979), which follow the diel movements of zooplankton in the water column. This reliance on zooplankton for food may partly account for the disjunct distribution of river herring in offshore waters during most seasons. Zooplankton distribution in the Gulf of Maine during summer and autumn is closely related to local and regional hydrography (Redfield 1941; Sherman 1970; Cohen footnote 9), and concentrations generally are along areas of current convergence and divergence (Zinkevich 1967). The waters around Georges Bank during the winter are nearly devoid of zooplankton, whereas sizeable neritic populations occur from Nantucket Shoals to southern Long Island (Clarke 1940; Grice and Hart 1962; Zinkevich 1967). Sette (1950) concluded that water temperature had a limiting rather than causal influence on the seasonal movements of the planktivorous Atlantic mackerel, *Scomber scombrus*. Similarly, Neves and Despres (1979) related American shad distribution to bottom temperatures and possibly seasonal shifts in zooplankton concentrations. Catches of river herring in specific areas along Georges Bank, the perimeter of the Gulf of Maine, and south of Nantucket Shoals may therefore be related to zooplankton abundance in these regions, although direct evidence is lacking.

TABLE 5.—Chi-square test comparing the number of day and night catches of alewives (A) and blueback herring (B) during U.S. bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

	Observed		Expected		χ^2	
Time	A	B	A	B	A	B
Day, 0600-1800 h	317	68	250	48		
Night, 1800-0600 h	183	28	250	48		
Total	500	96	500	96	35.4**	15.8**

**$P<0.01$.

Critical data on the oceanic life history of most anadromous fishes are lacking, and my synthesis of NMFS survey data and previous studies on the alewife and blueback herring should be considered tentative. Unanswered questions such as stock identification and mixing, and time and direction of migrations at sea during the year must await prescribed oceanic research.

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[10]Loesch, J. G., and W. H. Kriete, Jr. 1976. Biology and management of river herring and shad. Completion Rep. Anadromous Fish Proj. 1974-1976, Va. AFC 8-1 to 8-3, 226 p.

[11]Loesch, J. G., W. H. Kriete, Jr., H. B. Johnson, B. F. Holland, and M. W. Street. 1977. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. Annu. Rep. Anadromous Fish Proj. 1977, N.C.-Va. AFCS 9-1, 183 p.

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THE COMPLETE LARVAL DEVELOPMENT IN THE LABORATORY OF *MICROPANOPE SCULPTIPES* (CRUSTACEA, DECAPODA, XANTHIDAE) WITH A COMPARISON OF LARVAL CHARACTERS IN WESTERN ATLANTIC XANTHID GENERA[1]

BRYAN L. ANDRYSZAK[2] AND ROBERT H. GORE[3]

ABSTRACT

The larval development in the laboratory of *Micropanope sculptipes*, a western Atlantic deepwater xanthid crab which inhabits encrusted and coralline substrates, is completely described and illustrated. Development proceeds from a prezoeal stage of brief duration through four zoeal stages and one megalopa stage. Survival of larvae was poor under experimental conditions of diel illumination, 36‰ salinity, and temperatures of 20°, 25°, and 25°-30° C. Development to megalopa occurred only at 25° C. Morphological characteristics of *M. sculptipes* zoeae and megalopa are compared with larval characteristics of several other western Atlantic xanthid species.

Crabs of the family Xanthidae are both numerous and diverse with species inhabiting a great variety of marine and estuarine environments (Rathbun 1930). The genus *Micropanope* was erected by Stimpson in 1871 with the type-species *Micropanope sculptipes*. This genus consists of small (12 mm carapace width) xanthid crabs with a known range from the Bahamas and Florida Keys to Brazil and Bermuda in deeper offshore oceanic water (Rathbun 1930; Guinot 1967). *Micropanope* was originally noted to resemble *Pilumnus*, and to be allied with *Panopeus*, but was supposedly distinct in being a sublittoral to bathyal group and not littoral as was *Panopeus*. However, subsequent collections yielded *Micropanope* species which were more littoral in distribution and, through time, the genus was considered to be a heterogeneous mixture of several distinct generic groups which were yet to be defined (Guinot 1967). This author emended the genus *Micropanope* to contain only two western Atlantic species: viz. *M. sculptipes* Stimpson, the type-species, and *M. lobifrons* A. Milne Edwards. The remaining species within *Micropanope* sensu lato have either been placed by Guinot in several other genera, or await placement in genera yet to be named.

Larvae of many species of xanthid crabs from several different genera have been described based on laboratory rearing, but there have been no published descriptions of a complete larval development for any species of *Micropanope* sensu lato thus far. A study on the larval development of *M. barbadensis* Rathbun has recently been completed (Gore et al. 1981), but this species will ultimately be assigned to a separate, and as yet undefined, genus close to *Coralliope* (fide Guinot 1967). A knowledge of the larval morphology of *Micropanope*, when compared with larval characteristics of previously described xanthid species, especially those species once placed in the genus *Micropanope*, may be of some utility in recognizing the evolutionary relationships among such species within the Xanthidae. Accordingly, in this report we describe the complete larval development of *M. sculptipes* from hatching to megalopa stage based on specimens raised in the laboratory, and compare these larval and postlarval stages with those from other xanthid crabs in the western North Atlantic.

MATERIALS AND METHODS

A small (9.3 mm carapace width) ovigerous female *M. sculptipes* was collected 14 June 1978 by the crew of the Harbor Branch Foundation RV *Sea Diver* (cruise SD23, station #007), with a 20 ft (6.1 m) otter trawl. The trawl sample was taken off the

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coast of central eastern Florida between lat. 27°14.8′ N, long. 79°56.7′ W and lat. 27°15.1′ N, long. 79°58.0′ W from depths of 115.2-96.9 m. The specimen, collected from a substrate consisting of encrusted shell hash and *Oculina* coral, carried approximately 80 pale fuchsia eggs which darkened slightly before hatching on 20 June in the laboratory. After yielding larvae, this specimen was compared with specimens of *M. sculptipes* deposited in the National Museum of Natural History, Washington, D.C., which had been illustrated by Rathbun (1930: USNM 20719, 60777) and was found to agree in all important respects.

Three groups of 24 larvae were isolated, one each in 24 compartmented plastic boxes, and placed into controlled temperature units (CTU) at 20°, 25°, or 25°-30° C (±0.5° C) under diel illumination. Surf zone seawater (of 36‰) was filtered through glass wool fiber, stored in large Nalgene[4] bottles in the laboratory, and used to culture larvae.

Larvae received fresh seawater and were fed freshly hatched San Francisco brand *Artemia* nauplii daily. Molts and deaths of each larva and color notes of representative larval stages under refracted and reflected white light were recorded. Dead individuals and molts were preserved in 70% ethanol and were measured with a microscope fitted with an eyepiece micrometer. Measurements given are the arithmetic mean values of the number of specimens examined in each stage. Larvae were cleared in 50% lactic acid solution to which lignin pink stain was added to aid in drawing larval characters. Whole mounts (50×) and dissected appendages (drawn at 200× and checked for details at 400×) were mounted in CMCP mounting medium and drawn with Wild M5 and M20 microscopes equipped with camera lucidas.

The spent female and a complete series of larval stages are deposited in the United States National Museum, USNM 171393.

RESULTS OF REARING EXPERIMENT

Micropanope sculptipes larvae hatched as prezoeae of short, but not precisely determined, duration. They developed through four zoeal stages, after which metamorphosis to a megalopa occurred.

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

Figure 1 and Table 1 indicate that survival was poor and was apparently influenced by temperature. Most successful development occurred at 25° C; survival was notably lower at 20° C, and no larvae developed beyond first zoeae at 25°-30° C. Even at the "optimum" temperature of 25° C, 50% mortality occurred during the first zoeal stage and only one individual survived to the megalopa stage. At this temperature developmental duration was 26 d from hatching to megalopa; no crab stage was attained.

The duration of larval stages was variable. First stage zoeae generally required 6 or 7 d to successfully molt to second stage zoeae; however, one individual at 20° C required 15 d and another individual at 25° C persisted for 10 d before molting. These two zoeae did not survive beyond the second zoeal stage. Second and third zoeal stages generally remained as such 5 d before molting, although 20° C larvae took slightly longer than 25° C larvae. Fourth zoeal stages survived between 6 and 8 d before either molting or dying. The one fourth stage zoea at 25° C remained in stage 6 d before molting to megalopa.

Larval development was apparently regular and no larvae were observed to either skip a developmental stage or molt without developing into a more advanced stage. One zoea in the first stage at 25° C was grossly deformed when it molted to second stage at age 6 d and it died 7 d later without molting again. All other zoeae possessed similar morphological characters, so that temperature difference produced no variations. Many zoeae died during preecdysis or in ecdysis to the next larval stage. Five of the nine fourth stage zoeae died while attempting the molt to megalopae. Megalopal telsons, antennae, and chelipeds were observed beneath the transparent fourth zoeal exoskeletons of these specimens, indicating a terminal larval stage. No fifth zoeal stage larvae were observed.

The results of this study indicate that *M. sculptipes* larvae progress through four larval stages and thus are similar to the majority of xanthid species. Four zoeal stages have been considered characteristic in Xanthidae (Hyman 1925; Lebour 1928) and include many species, e.g., *Panopeus herbstii* (Costlow and Bookhout 1961a), *Eurypanopeus depressus* (Costlow and Bookhout 1961b), *Rhithropanopeus harrisii* (Chamberlain 1962), *Hexapanopeus angustifrons* (Costlow and Bookhout 1966), *Leptodius* [= *Pseudomedaeus*] *agassizii* (Costlow and Bookhout 1968), *Neopanope*

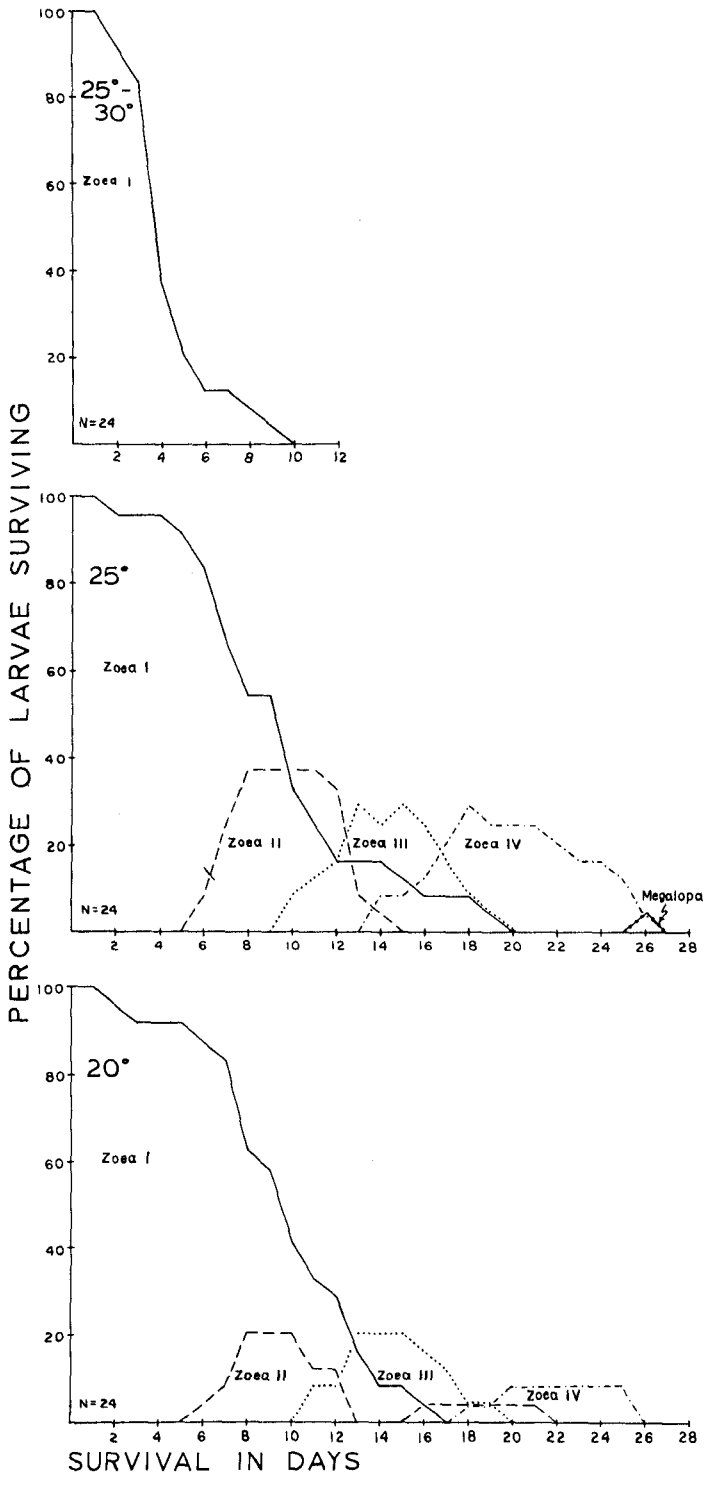

FIGURE 1.—*Micropanope sculptipes*. Percentage and duration of survival of larvae reared at three laboratory temperatures. N = number of larvae reared at each temperature in the series.

TABLE 1.—*Micropanope sculptipes*, relative duration of larval life in days at three temperatures. (Number of larvae started at each temperature = 24.)

Temp °C	Larval stage	Duration				Total no. molting to next stage
		Minimum	Mean	Mode	Maximum	
20	Zoea I	5	8	7	15	6
	Zoea II	4	—	5	5	5
	Zoea III	5	6	—	7	2
	Zoea IV	[1]6	—	—	[1]8	0
25	Zoea I	5	7	6	10	12
	Zoea II	4	—	5	5	9
	Zoea III	4	—	5	5	9
	Zoea IV	[1]1	6	6	[1]8	1
25-30	Did not survive beyond first zoeal stage					

[1]Died in stage without further molt.

texana (McMahan 1967), *N. sayi* and *N. packardii* (Costlow and Bookhout 1967), *Pilumnus dasypodus* (Sandifer 1974), and *P. sayi* (McDonald and Lang 1976). However, crabs of the genus *Menippe* develop through 5 or 6 zoeal stages prior to metamorphosis (e.g., Porter 1960; Ong and Costlow 1970; Scotto 1979), *Heterozius rotundifrons* and *Epixanthus dentatus* have two zoeal stages, and *Pilumnus lumpinus* has only one zoeal stage (Saba et al. 1978). The latter three species live in specialized and restricted habitats which may account for the differences in number of developmental stages. However, *Ozius truncatus* (four zoeal stages) and *Heteropanope (Pilumnopeus) serratifrons* (probably four zoeal stages) are also species which live in restricted habitats (Wear 1968), so other factors besides environment may influence developmental time. *Micropanope barbadensis* develops through either three or four zoeal stages (Gore et al. 1981), and the elimination of the "terminal" stage may be an adaptive response to food supply, nutritional deficiencies, or an inherited response from adult genotypes, according to several hypotheses considered by these authors.

It is therefore difficult to directly compare the duration of larval development for *M. sculptipes* (about 26 d at 25° C) with larval development times for other xanthid species. Species of *Menippe* (5 or 6 zoeal stages) required at least 17-21 d at 25° C to develop into megalopa (summarized by Scotto 1979). The duration of larval development seems to be largely dependent on temperature, and the experimental temperature conditions employed by different researchers may vary considerably for a number of reasons. Larval development time decreased for *Micropanope sculptipes* as temperature increased. This inverse relationship between temperature and duration of larval development is consistently observed for the larvae of different xanthid species (Costlow et al. 1962; Costlow and Bookhout 1971; Scotto 1979). Based on these data and at 25° C, we may postulate a planktonic development time on the order of 1 mo before metamorphosis to first crab in *M. sculptipes*.

LARVAL DESCRIPTION

First Zoea

Carapace length (anterior margin of orbit to median posterodorsal edge of carapace): 0.47 mm.

Number of specimens examined: 14.

Carapace (Figure 2A, B). Typically brachyuran, possessing rostral, dorsal, and 2 lateral spines. Eyes sessile. Rostrum straight, naked, sharply pointed, slightly shorter than carapace length. Dorsal spine about equal in length to carapace, curving gently posteriad, bearing a few scattered minute tubercles. Lateral spines short, naked, projecting perpendicular to sagittal plane. Carapace elliptical, naked except for 2 small dorsolateral setae originating midway between dorsal and lateral spines; mediodorsal knob [= "forehead protuberance" Yang 1967] naked.

Antennule (Figure 2C). Flabellate rod with 3 aesthetascs, 2 naked setae at tip.

Antenna (Figure 2D). Protopodite long, tapering to point; spirally arranged spines present along distal three-fourths length with spines larger, longer toward tip. Exopodite one-sixth to one-fifth protopodite length, naked throughout length, with 1 short apical spine, 1 long and 2 short apical nonplumose setae.

Mandibles (Figure 2E). Well-developed incisor and molar processes; no palp.

Maxillule (Figure 2F). Coxal endite with 7 stout, plumose setae. Basal endite with 5 denticulate spines, about 20 minute hairs on lateral surface. Endopodite two-segmented; proximal segment with 1 long, nonplumose seta; distal segment with 2 subterminal, 4 terminal, sparsely plumose setae.

Maxilla (Figure 2G). Coxal endite bilobed with 4 proximal, 3 distal plumose setae. Basal endite bilobed with 4 (occasionally 5) proximal and 4 distal plumose setae. Endopodite bilobed; 3 terminal sparsely plumose apical setae on proximal lobe, 5 terminal (appearing as 3 apical, 2 slightly lower) sparsely plumose setae on distal lobe; this setal formula holds for remainder of stages.

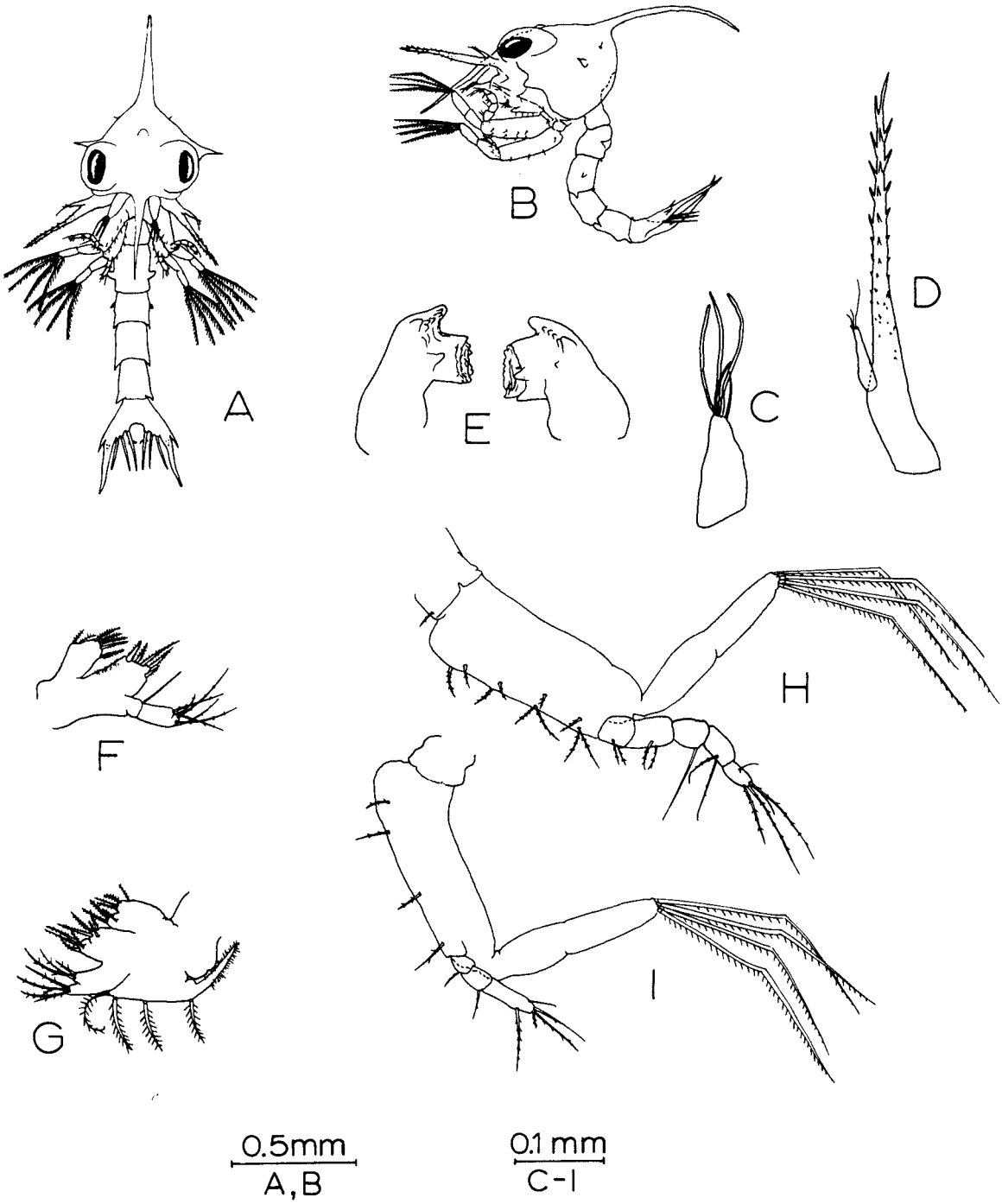

FIGURE 2.—*Micropanope sculptipes*, first zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

Scaphognathite with 4 marginal plumose setae and elongate sharp process bearing numerous minute hairs laterally.

Maxilliped 1 (Figure 2H). Coxopodite with 1 seta. Basipodite ventral margin with 10 sparsely plumose setae arranged (proximally to distally) 2, 2, 3, 3; this setal formula holds for remainder of stages. Endopodite five-segmented with proximal to distal segment setation of 2, 2, 1, 2, 4+I. (Roman numeral denotes dorsal seta.) Exopodite with 4 terminal natatory setae.

Maxilliped 2 (Figure 2I). Coxopodite without setae. Basipodite ventral margin with one row of 4 sparsely plumose setae; this setal formula holds for remainder of stages. Endopodite three-segmented with proximal to distal segment setation of 1, 1, 4+I. Exopodite with 4 terminal natatory setae.

Maxilliped 3 and Pereiopods. Not apparent.

Abdomen (Figure 2A, B). With five somites. Somite 1 unornamented; somite 2 with anteriorly curved lateral hooks; somite 3 with smaller posteriorly curved lateral hooks. Somites 3-5 with small posterolateral spines overlapping following somite. Somites 2-5 with pair of minute posterodorsal setae.

Telson (Figure 2A, B). Bifurcate; each furca smooth, possessing one larger lateral spine near its midlength and one smaller dorsal spine originating near apex of lateral spine. Inner telson margin with 3 pairs of articulated spines, each armed throughout length with minute spinules, center pair of spines with 2 longer interior spinules and 1 longer exterior spinule located at proximal one-third of spine. Inner telson margin with pronounced medial sinus.

Color. Zoea mainly colorless with exception of localized pigment concentrations. Dorsal area of orbit pale mint green, color fading into interorbital area; interorbital protuberance faint orange. Gastric region pale orange extending along gut through first two abdominal segments (this color not due to ingested *Artemia*); diffused pale mint green surrounds orange of gastric region. Mandible incisor and molar surfaces scarlet, blending into pale orange within mandible. First and second maxillipeds with diffuse pale orange at junction of basipodite and exopodite. Proximal region of telson furcae on either side of median telson sinus tinted with diffused pale orange.

Second Zoea

Carapace length: 0.61 mm.

Number of specimens examined: 10.

Carapace (Figure 3A, B). Eyes faceted, stalked. Rostrum base with small, lateral preorbital protuberances perpendicular to longitudinal axis. Dorsal spine usually with 2 small proximal setae, occasionally with a few small widely spaced setae and tubercles. Lateral spines with 2 to 4 minute dorsal tubercles. Carapace ventral margin with 3 or 4 fringing setae; mediodorsal knob now with 4 integumental sensillae arranged into rectangle on crest, one pair setae anterior and posterior to knob.

Antennule (Figure 3C). Four aesthetascs, 2 naked setae at tip.

Antenna (Figure 3D). Unchanged except for incipient endopodite primordium near exopodite base.

Mandibles (Figure 3E). As illustrated, without palp.

Maxillule (Figure 3F). Coxal endite unchanged from first zoea. Basal endite apex with 6 denticulate spines, 1 naked seta; lateral surface with 1 plumose seta, ≈20 minute hairs. Endopodite unchanged from first zoea. Protopodite now with 1 distal plumose seta.

Maxilla (Figure 3G). Coxal endite bilobed with 4 proximal, 4 distal plumose setae. Basal endite bilobed with 5 proximal, 4 distal plumose setae. Scaphognathite with 11 or 12 marginal plumose setae.

Maxilliped 1 (Figure 3H). Coxopodite with 1 (rarely 2) seta. Endopodite unchanged from first zoea. Exopodite with 6 terminal natatory setae.

Maxilliped 2 (Figure 3I). Coxopodite without setae. Endopodite three-segmented with proximal to distal segment setation of 1, 1, 4 or 5+I. Exopodite with 7 terminal natatory setae.

Maxilliped 3 and Pereiopods. Not apparent.

Abdomen (Figure 3A, B). With five somites. Somite 1 with 1 posterodorsal seta; somites 2-5 generally unchanged from first zoea, but posterolateral spines of somites 3-5 slightly longer relative to body size.

Telson (Figure 3A, B). Generally unchanged from first zoea. An additional minute lateral furcal spine may occasionally be present within the fork created by the major lateral spine where it originates from the furca. This spine (when present) may be readily apparent, reduced to a lump,

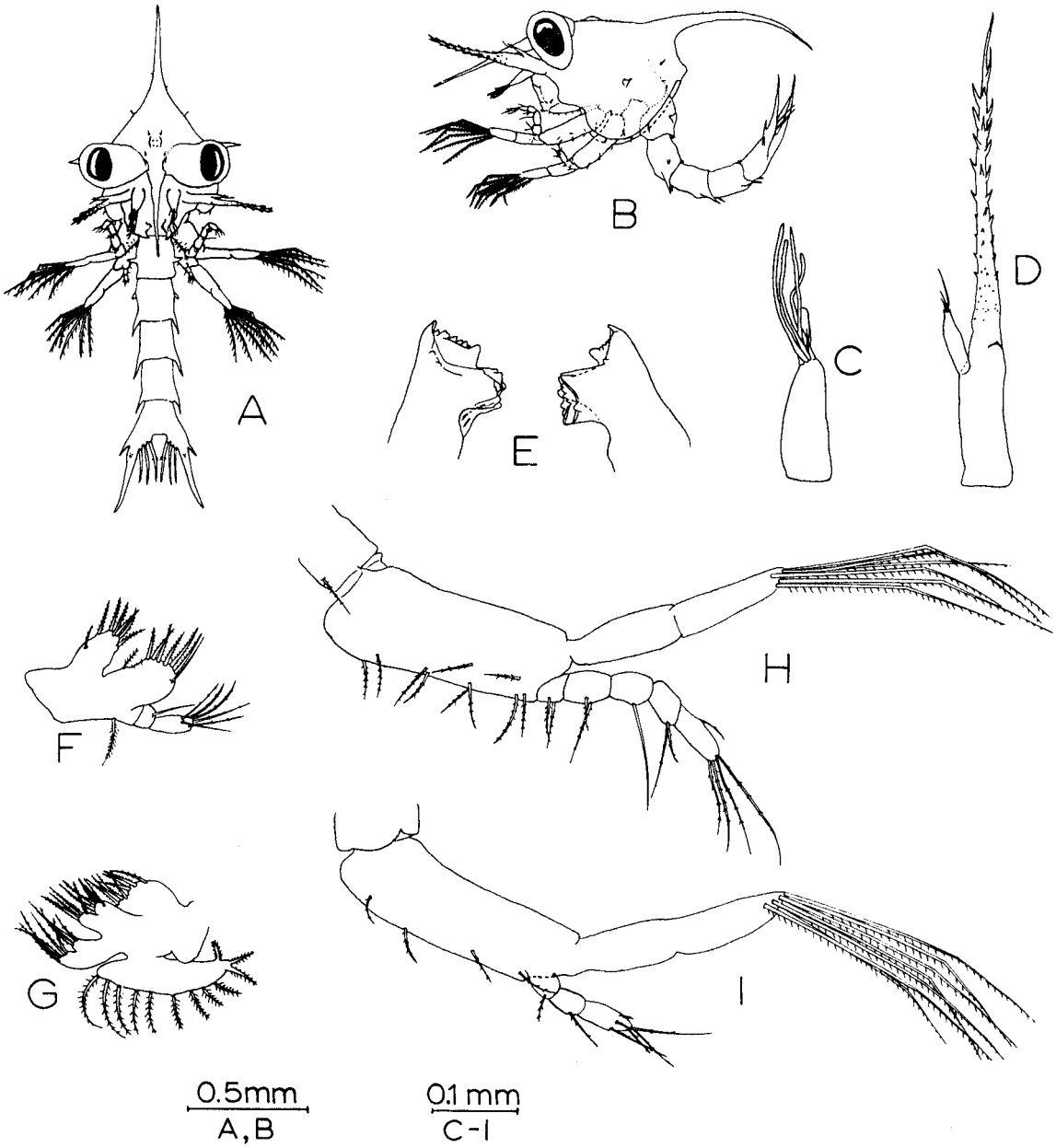

FIGURE 3.—*Micropanope sculptipes*, second zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

or present on one furca while absent from the other on the same individual.

Color. Similar to that of first zoea, but noticeably intensified. Pale orange highlights distal three-fourths of rostrum, dorsal spine, antennae, and antennules. Gut color more burnt orange, extending through abdominal somite 4. Mandibles most pronounced in burnt orange, outer surfaces scarlet.

Third Zoea

Carapace length: 0.76 mm.
Number of specimens examined: 8.

Carapace (Figure 4A, B). Rostrum preorbital protuberances pronounced, angular. Dorsal spine with 3 (occasionally 2 or 4) small, scattered proximal setae with some scattered distal setae and minute tubercles. Lateral spines with 3 or 4 minute dorsal tubercles. Carapace ventral margin with 2 or 3 setae. Mediodorsal knob with 2 or 3 additional smaller integumental sensillae located within rectangular region previously demarcated by 4 sensillae of second zoea; 6 setae anterior, 4 setae posterior to mediodorsal knob.

Antennule (Figure 4C). With 3 aesthetascs and 1 naked seta at tip, 1 subterminal budlike projection.

Antenna (Figure 4D). Similar to earlier stage, endopodite more developed, with pointed tip slightly exceeding exopodite length.

Mandibles (Figure 4E). As illustrated, without palp.

Maxillule (Figure 4F). Coxal endite with 8 thick, plumose setae. Basal endite with 5 pectinate spines, 3 long sparsely plumose setae, 1 subterminal plumose seta, almost no minute hairs. Endopodite as in first zoea. Protopodite with 1 distal plumose seta.

Maxilla (Figure 4G). Coxal endite bilobed with 5 proximal, 4 distal plumose setae. Basal endite bilobed with 5 proximal, 4 distal plumose setae. Endopodite as in first zoea except all setae naked. Scaphognathite with 17 to 20 marginal plumose setae.

Maxilliped 1 (Figure 4H). Coxopodite with 1 (rarely 2) seta. Five-segmented endopodite setation now 2, 2, 1, 2, 5+I. Exopodite with 8 terminal natatory setae.

Maxilliped 2 (Figure 4I). Coxopodite without setae. Three-segmented endopodite setation now 1, 1, 6. Exopodite with 9 terminal natatory setae.

Maxilliped 3. Present as small, unbranched lobe.

Pereiopods (Figure 4B). Apparent as small rudiments beneath carapace.

Abdomen (Figure 4A, B). Sixth somite present, lacking posterolateral spines and posterodorsal setae. Somite 1 with 2 or 3 posterodorsal setae; somites 2-5 as in second zoea, but with posterolateral spines of somites 3-5 progressively longer; somites 2-6 developing small pleopod buds; those of somite 6 barely apparent.

Telson (Figure 4A, B). Median sinus with 2 small plumose setae. Secondary minute lateral furcal spines may or may not be present as in second zoea.

Color. Rostrum, dorsal spine, antennules, antennae nearly colorless. Maxillipeds with pale orange spreading through much of basipodites. Mandibles slightly darker burnt orange. Orbits pale mint green blending into faint sky blue at interorbital region. Sky-blue stellate chromatophore at dorsal spine base. Vandyke-brown stellate chromatophore fringed in olive, mint green, sky blue at lateral spine bases. Pereiopod buds light orange. Gut burnt orange through somite 3, with small spots of pale orange highlighting pleopod buds on somites 3-5.

Fourth Zoea

Carapace length: 0.84 mm.
Number of specimens examined: 9.

Carapace (Figure 5A, B). Rostrum preorbital protuberances recurved into anteriorly directed hooks. Dorsal spine with 4 small proximal setae, few scattered minute tubercles. Lateral spines as in third zoea. Carapace ventral margin with 6-11 (usually 9) setae. Mediodorsal knob with 4 outer sensillae (arranged as rectangle) surrounding 4 smaller inner sensillae; 10 setae anterior, 4 setae posterior to knob.

Antennule (Figure 5C). Biramous. Endopodite half exopodite length, naked, pointed at tip. Exopodite two-segmented with 12 aesthetascs arranged proximally to distally (2, 6) (1, 3 apical) plus 1 naked seta at tip. Protopodite swollen proximoventrally, supporting 2 minute plumose setae.

Antenna (Figure 5D). Endopodite at least one-half protopodite length.

Mandibles (Figure 5E). As illustrated; palp present.

Maxillule (Figure 5F). Coxal endite with 11 or 12 setae (small proximal seta occasionally absent).

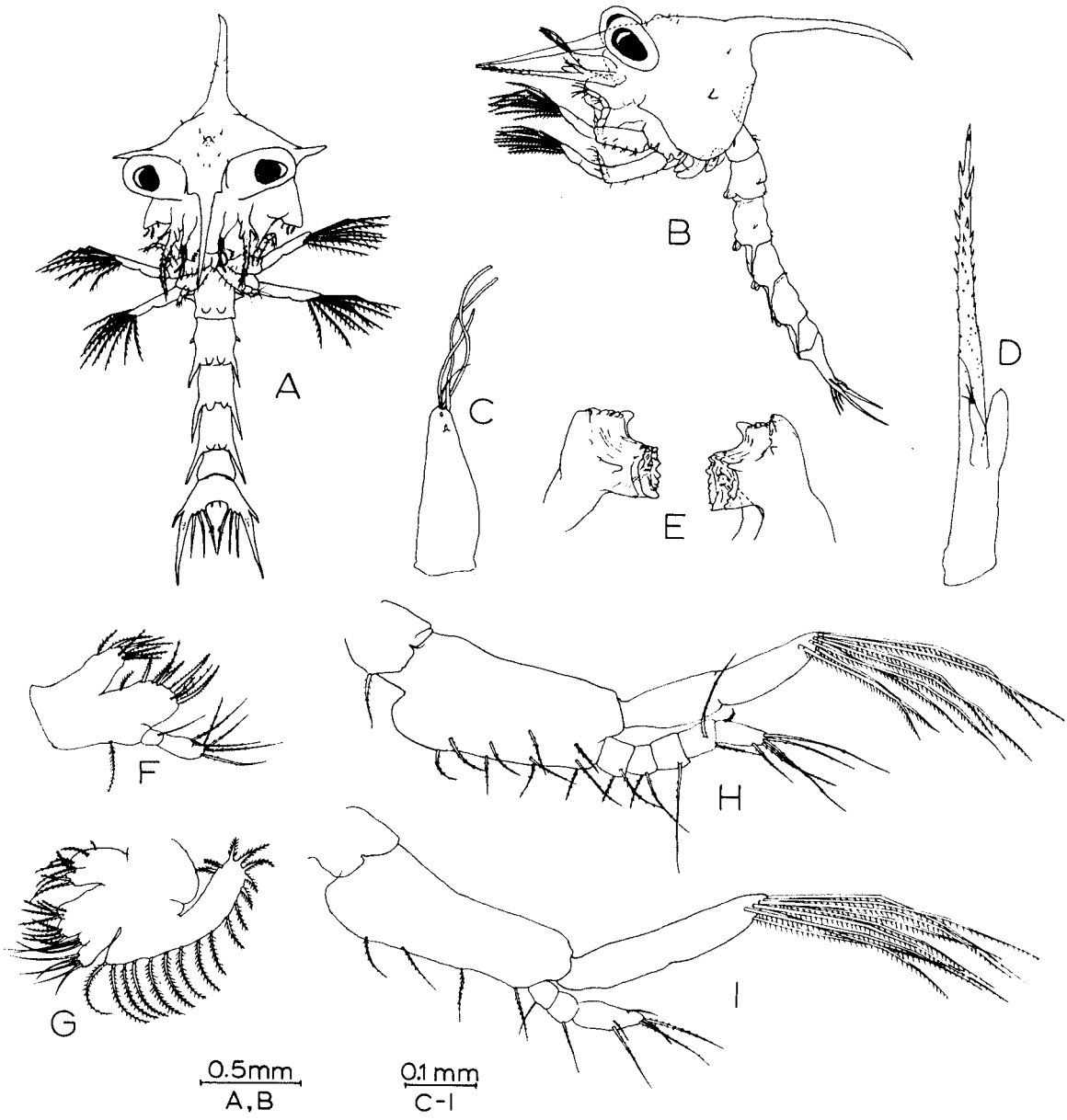

FIGURE 4.—*Micropanope sculptipes*, third zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

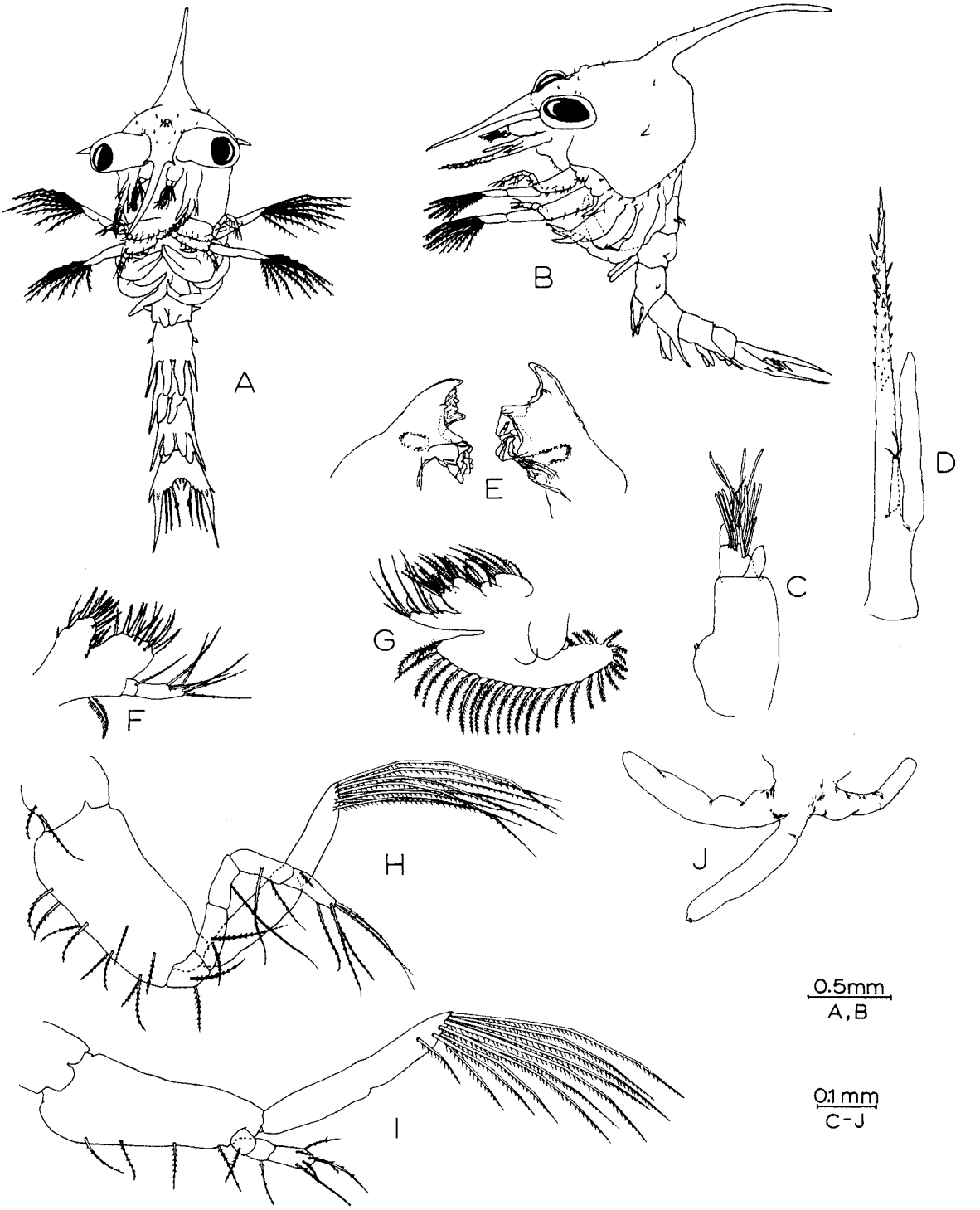

FIGURE 5.—*Micropanope sculptipes*, fourth zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2; J, maxilliped 3.

Basal endite with 7 denticulate spines, 5 or 6 sparsely plumose setae; few minute hairs. Endopodite and protopodites as in third zoea.

Maxilla (Figure 5G). Coxal endite bilobed with 6 proximal, 4 distal plumose setae. Basal endite bilobed with 6 proximal, 7 distal plumose setae, several minute lateral hairs on distal lobe. Scaphognathite with 25 to 30 (usually 28 or 29) marginal plumose setae.

Maxilliped 1 (Figure 5H). Coxopodite with 2 (rarely 1) setae. Endopodite as in third zoea. Exopodite with 9 terminal natatory setae.

Maxilliped 2 (Figure 5I). Coxopodite with no (rarely 1 very small) seta. Three-segmented endopodite setation 1, 1, 5+I (rarely 4+I). Exopodite with 11 terminal natatory setae.

Maxilliped 3 (Figure 5J). Greatly enlarged from third zoea, epipodite and endites well developed, not yet segmented.

Pereiopods (Figure 5A, B). Greatly enlarged from third zoea, with incipient segmentation and differentiation.

Abdomen (Figure 5A, B). Somite 1 with 3 posterodorsal setae, slight posterolateral projections. Somites 2-6 as in third zoea but pleopod buds enlarged and biramous on somites 2-5, small and uniramous on somite 6.

Telson (Figure 5A, B). Median sinus with 3 or 4 small plumose setae. Secondary minute lateral furcal spines may or may not be present as in second zoea.

Color. Rostrum, antennules, antennae pale orange. Maxilliped 1 and 2 basipodites proximally with prominent burnt-orange stellate chromatophores, diffused with pale mint green at basipodite-exopodite junction. Mandible incisor and molar surfaces fringed in dark Vandyke brown blending into scarlet and burnt orange. Orbits pale mint green. Sky-blue stellate chromatophore mixed with pale green and yellow at dorsal spine base. Lateral spines with burnt-orange and Vandyke-brown stellate chromatophores blending into mint green distally. Body (cephalothorax) generally pale yellow-orange mixed with faint mint green. Gastric region and gut burnt orange extending through abdominal somite 3. Abdominal somites 2-5 with paired patches of pale burnt orange lateral to pleopod bud origins, otherwise colorless. Telson entirely pale orange diffused with mint green in vicinity of lateral and dorsal furcal spines.

Megalopa

Carapace length (rostrum tip to median posterior margin) × greatest width: 1.25 mm × 1.20 mm.

Number of specimens examined: 1.

Carapace (Figure 6A-C). Slightly longer than wide, subrectangular, somewhat inflated. Frontal region produced, highly sculptured; rostrum prominent, acutely triangular, sharply rounded, becoming broader at base, recurving anteriad into prominent anterolateral horns; latter one-half rostrum length, each with a small lateral spine bearing 2 small apical setae near base, oriented perpendicular to longitudinal axis of horn. Four prominent plumose setae equal in length to rostrum project anteriorly between rostrum base and base of each horn. Several smaller setae scattered in interorbital, gastric, and cardiac regions. One small tubercle projecting near median posterodorsal margin. Numerous setae fringe posterior and ventrolateral margins.

Antennule (Figure 6D). Biramous; peduncle three-segmented; proximal article with 2 small plumose setae and 1 naked seta, penultimate article with 1 naked seta, ultimate article with 2 small lateral setae and 6 nearly terminal, long, naked setae (arranged as 3 on either side of segmented flagellum). Ventral ramus with 3 terminal, 1 slightly subterminal, naked setae; dorsal ramus with aesthetascs progressing distally as follows: (8), (6, +1 plumose seta opposite), (3 lateral, +3 nonplumose setae near tip).

Antenna (Figure 6E). Peduncle with 3 lateral setae, a distal lobe; setation (proximally to distally) on flagellar articles 1, 1, 0, 3, 4, 0, 0, 5. Articles 5 and 6 slightly constricted at midlength, may be partially segmented.

Mandibles, maxillule, maxilla, and *maxillipeds 1* and *2*. These were not dissected from the specimen to prevent the destruction of the only megalopa obtained.

Maxilliped 3 (Figure 6F). Coxopodite and epipodite not exposed for examination. Basipodite partially exposed with at least 16 short setae. Endopodite five-segmented, setation progressing distally 16, 14, 8, 12, 8 (5 lateral, 3 apical). Exopodite two-segmented; proximal segment with 3 lateral setae, distal segment with 1 subterminal seta and 6 long, plumose terminal setae.

Pereiopods (Figure 6A-C, 6G-I). All bear numerous setae. Chelipeds (Figure 6G) similar, equal;

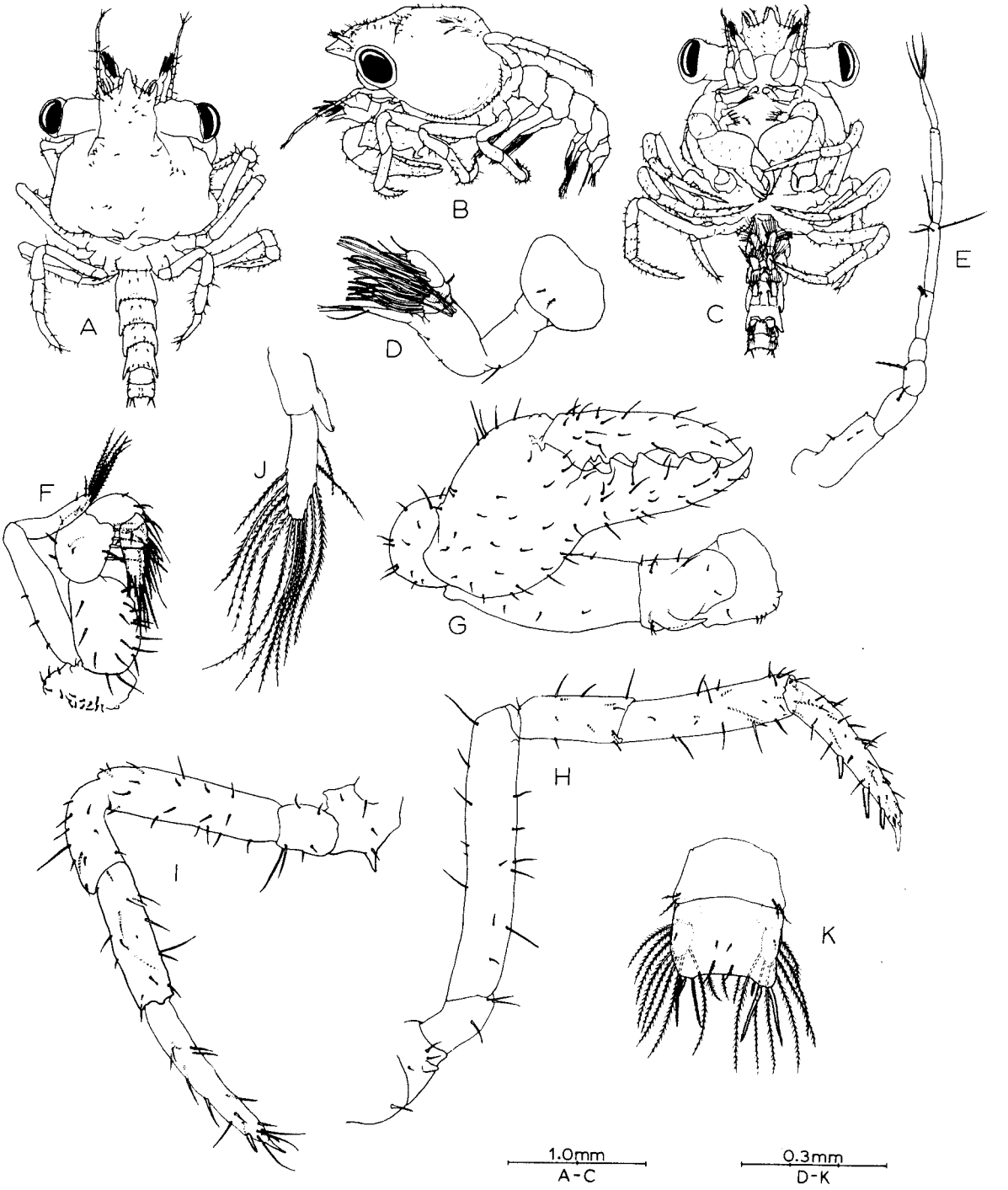

FIGURE 6.—*Micropanope sculptipes*, megalopa. A, dorsal view; B, lateral view; C, ventral view; D, antennule; E, antenna; F, maxilliped 3; G, cheliped; H, pereiopod 3; I, pereiopod 5; J, pleopod from abdominal somite 3; K, abdominal somite 6 with pleopods, telson.

coxa with small basal tubercle, ischium with large hooked spine and small dorsal tubercle. Bases of pereiopods 2-5 (Figure 6H, I) with small median spine; dactyls of pereiopods 2-4 with a row of 3 subterminal serrated spines, 1 terminal spine; dactylus of pereiopod 5 with 1 subterminal serrated spine, 3 long subterminal setae, 1 terminal spine.

Abdomen (Figure 6A-C). With 6 somites and telson. Lateral pleura of somites 2-5 slightly overlap following segment; lateral hooks of somites 2 and 3 absent. Numerous setae cover dorsal surfaces and posterodorsal margins of all somites. Pleopods biramous (Figure 6J) on somites 2-5, uniramous on somite 6 (Figure 6K); exopodites with plumose setae arranged (anteriorly to posteriorly) 15 or 16, 13 or 14, 13 or 14, 11, 7 or 8; endopodites of pleopods 2-5 with appendix interna consisting of 2 terminal curved hooks.

Telson (Figure 6K). Roughly rectangular with 2 pairs of dorsal setae. Lateral margins produced posteriorly, forming slightly extended lobes, each lobe bearing 3 serrated spines of variable length; posterior margin shallowly sinuous, with 3 plumose setae.

Color. The one megalopa died before color notes could be made.

DISCUSSION

Comparative Morphology of *Micropanope sculptipes* With Other Xanthid Larvae

The Xanthidae is a large and heterogeneous family containing many genera and numerous species. As a consequence, the larval stages of many such species from the Atlantic and Pacific Oceans have been studied over a long period (e.g., Lebour 1928; Aikawa 1929, 1937; Wear 1968; Saba et al. 1978). In the western Atlantic, larval development is reliably known either completely or in part for at least 10 genera and 15 species, in addition to several other genera and species which are less certain because identifications were based on planktonic material. As might be expected, there exist numerous characters, both shared and unshared, in the larval stages, so that comparison among the species and genera is often quite difficult. Readily observable morphological characters useful in distinguishing zoeae and megalopae of *M. sculptipes* from other western Atlantic xanthid species which may cooccur in the plankton include those of the rostral spine, antenna, anterodorsal carapace setae, abdominal spination, telsonal furcae spination, and armature on basal segments of the pereiopods.

Within the genus *Micropanope* (sensu lato), *M. sculptipes* exhibits extremely close morphological similarity (but not developmental similarity) with the larvae of *M. barbadensis* (Gore et al. 1981). Both species exhibit a type of antenna different from the four categories established by Aikawa (1929) necessitating the creation of a fifth category, Type E (Gore et al. 1981). This grouping contains those larvae (presently only the two species here considered) in which the antennal exopodite is from one-fourth to one-seventh total protopodite length. Other features allowing distinction between the two species include (in *M. sculptipes*) the unadorned rostral carapace spine, shorter lateral spines, unpaired lateral spines on the telsonal furcae, a less lunate telson, more distinct spination on the antennal protopodite, a single coxal seta on maxilliped 1, and the general distribution of fine hairs on the anterodorsal area of the carapace. The position and number of integumentary sensillae may prove to be of some value, but this feature in the genus has only been described for *M. sculptipes*. Gore et al. (1981) worked with molted carapaces in describing *M. barbadensis* and were unable to distinguish these sensory pits clearly.

A comparison of the larvae of *M. sculptipes* with those in other western Atlantic xanthid species is summarized in Table 2. The following differences appear salient. The preorbital rostral hooks of *M. sculptipes*, which are fully formed in the fourth zoeal stage, are similar to, yet larger than, those described for *Panopeus herbstii*. *Pseudomedaeus* [ex *Leptodius*] *agassizii* also possesses similar "secondary rostral spines," but these are much more prominent from its second through fourth zoeal stages. The rostrum of the other species noted (see Table 2) remains generally straight and unarmed throughout development.

The antenna of *M. sculptipes* consists of a spinous protopodite and has an exopodite which is one-sixth the protopodite length. The species in other genera possess an antennal protopodite which is either nonspinous or noticeably less spinous than that of *Micropanope*. The antennal exopodite of these xanthid zoeae fall into three general categories as described by Lebour (1928): equal to protopodite length or Type A (*Pilumnus sayi, P. dasypodus*); one-half to three-fourths protopodite length or Type B (*Menippe mercenaria, M.*

TABLE 2.—Comparison of morphologically important zoeal characters for distinguishing *Micropanope sculptipes* larvae from other western Atlantic species of Xanthidae based on descriptions and illustrations from different sources (only the first four zoeal stages of *Menippe mercenaria* and *M. nodifrons* are considered).

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
		First zoea			
Micropanope sculptipes	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 3/4 Exopodite: 1/6-1/5 protopodite length, 3 apical setae	None	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine
Neopanope sayi (Chamberlain 1961)	Straight, unarmed, 2× carapace length	Protopodite: unarmed Exopodite minute, apical seta	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Neopanope texana (McMahan 1967)	Straight, unarmed, ≈carapace length	Protopodite: unarmed Exopodite minute, apical seta	None	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Neopanope packardii (Costlow and Bookhout 1967)	Straight, unarmed, ≈carapace length	Protopodite: sparsely spinous tip Exopodite: minute spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Panopeus herbstii (Costlow and Bookhout 1961a)	Straight, unarmed, ≈carapace length	Protopodite: spinous tip Exopodite minute, apical spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Straight, unarmed, 1.5× carapace length	Protopodite: spinous distal 1/3 Exopodite minute, apical spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Straight, unarmed, 1.5× carapace length	Protopodite: unarmed Exopodite minute	None figured	Lateral hooks somites 2,3	Furca smooth
Rhithropanopeus harrisii (Chamberlain 1962)	Straight, unarmed, 2.5 × carapace length	Protopodite: minute spinules distal 1/4 Exopodite minute	None figured	Posterolateral spines somites 4, 5 prominant Lateral hooks somite 2	Furca smooth: 1 dorsal spine
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 1/2 Exopodite: 1/10 protopodite length, 2 apical setae	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines
Eurytium limosum (Kurata[1])	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 1/3 Exopodite minute, apical seta	None figured	Posterolateral spines somites 3-5 smooth, subequal Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine, 1 minute lateral seta
Pilumnus sayi (Kurata[1])	Unarmed, 1/3 carapace length	Protopodite: spinous distal 1/2 Exopodite = protopodite length, spinous distal 1/2, 2 mid-lateral spines	None figured	Posterodorsal margins somites 2-5 serrated Lateral hooks somites 2-5	Furca spinous: 1 dorsal spine, 2 lateral spines
Pilumnus dasypodus (Sandifer 1974)	Unarmed, 1/3 carapace length	Protopodite: spinous distal 1/2 Exopodite = protopodite length, spinous distal 1/2, 2 mid-lateral spines	None figured	Posterodorsal margins somites 3-5 serrated Lateral hooks somites 2,3	Furca spinous: 1 dorsal spine, 2 lateral spines
Menippe mercenaria (Porter 1960)	Straight, unarmed, ≈ carapace length	Protopodite: spinous distal 1/2-1/5 Exopodite: 3/4 protopodite length, apical spine 1/2-3/5 exopodite length	None figured	Dorsolateral spines somites 4, 5 Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine
Menippe nodifrons (Scotto 1979)	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 1/2-1/5 Exopodite: 3/4 protopodite length, apical spine 2/5 exopodite length	None	Dorsolateral spines somite 5 Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines

TABLE 2.—*Continued.*

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
		Second zoea			
Micropanope sculptipes	Small preorbital protuberances	Protopodite, exopodite unchanged[2]	4	Unchanged[2]	Furca smooth: 1 dorsal spine, 1 or 2 lateral spines
Neopanope sayi (Chamberlain 1961)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Neopanope texana (McMahan 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None	Unchanged[2]	Unchanged[2]
Neopanope packardii (Costlow and Bookhout 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Panopeus herbstii (Costlow and Bookhout 1961a)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks unchanged[2]	Unchanged[2]
Rhithropanopeus harrisii (Chamberlain 1962)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Secondary rostral spines	Protopodite: spinous distal 1/3 Exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Eurytium limosum (Kurata[1])	Unchanged[2]	Protopodite smooth, Exopodite unchanged[2]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus sayi (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[2]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus dasypodus (Sandifer 1974)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Menippe mercenaria (Porter 1960)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Posteroventral spines somites 3-5; otherwise unchanged[2]	Unchanged[2]; spines minute
Menippe nodifrons (Scotto 1979)	Unchanged[2]	Protopodite: unchanged[2] Exopodite: spine slightly longer	4	Posteroventral spines somites 3, 4; posteroventral tooth somite 5; otherwise unchanged[2]	Unchanged[2]; spines minute
		Third zoea			
Micropanope sculptipes	Angular preorbital protuberances	Protopodite: spinous distal 2/3 Exopodite unchanged[2]	10	Unchanged[2]	Unchanged[3]
Neopanope sayi (Chamberlain 1961)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Neopanope texana (McMahan 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None	Unchanged[2]	Unchanged[2]
Neopanope packardii (Costlow and Bookhout 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Panopeus herbstii (Costlow and Bookhout 1961a)	Small preorbital protuberances	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Unchanged[2]	Protopodite: spinous tip Exopodite miniscule	None figured	Unchanged[2]	Unchanged[2]
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[3]	Unchanged[2]
Rhithropanopeus harrisii (Chamberlain 1962)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Secondary rostral spines 1/3 rostrum length	Protopodite, exopodite unchanged[3]	None figured	Unchanged[2]	Unchanged[2]
Eurytium limosum (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[3]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus sayi (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[2]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus dasypodus (Sandifer 1974)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Menippe mercenaria (Porter 1960)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[3]	Unchanged[3]
Menippe nodifrons (Scotto 1979)	Unchanged[2]	Protopodite, exopodite unchanged[3]	4	Unchanged[3]	Unchanged[3]

TABLE 2.—*Continued.*

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
		Fourth zoea			
Micropanope sculptipes	Preorbital hooks	Protopodite: spinous distal 1/3 Exopodite unchanged[3]	14	Unchanged[2]	Unchanged[3]
Neopanope sayi (Chamberlain 1961)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Neopanope texana (McMahan 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None	Unchanged[2]	Unchanged[2]
Neopanope packardii (Costlow and Bookhout 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Panopeus herbstii (Costlow and Bookhout 1961a)	Small preorbital hooks	Protopodite: unchanged[2] Exopodite miniscule	None figured	Unchanged[2]	Unchanged[2]
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Unchanged[2]	Protopodite, exopodite unchanged[4]	None figured	Unchanged[2]	Unchanged[2]
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Unchanged[2]	Protopodite: unchanged[2] Exopodite miniscule	None figured	Unchanged[3]	Unchanged[2]
Rhithropanopeus harrisii (Chamberlain 1962)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Unchanged[4]	Protopodite, exopodite unchanged[3]	None figured	Unchanged[2]	Unchanged[2]
Eurytium limosum (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[3]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus sayi (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pilumnus dasypodus (Sandifer 1974)	Unchanged[2]	Protopodite, exopodite unchanged[2]	1(?) figured	Unchanged[2]	Unchanged[2]
Menippe mercenaria (Porter 1960)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[3]	Unchanged[3]
Menippe nodifrons (Scotto 1979)	Unchanged[2]	Protopodite, exopodite unchanged[2]	8	Posterolateral spines somites 3, 4, dorsolateral spines somite 5 longer	Unchanged[4]

[1]Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Unpubl. rep., 274 p. Univ. Georgia Mar. Inst., Sapelo Island.
[2]Character unchanged from first zoea.
[3]Character unchanged from second zoea.
[4]Character unchanged from third zoea.

nodifrons); minute or Type C (*Neopanope sayi, N. texana, N. packardii, Panopeus herbstii, Eurypanopeus depressus, Hexapanopeus angustifrons, Rhithropanopeus harrisii, Pseudomedaeus agassizii, Eurytium limosum*). The antennal exopodite of *Micropanope sculptipes* (Type E) is thus distinctive from other xanthid larvae both in its length relative to the protopodite length, and in armature. Although the antenna of *P. agassizii* closely resembles that of *M. sculptipes,* the protopodite is less spinous and the exopodite is one-tenth the protopodite length with two apical setae.

The anterodorsal carapace (anterior half of the dorsal carapace surface) setae of *M. sculptipes* zoeae first appear in the second stage (2), and number 10 and 14 in the third and fourth stages, respectively. Anterodorsal carapace setae are not described for most of the other xanthid species; one seta is illustrated in the fourth stage of *Pilumnus dasypodus*, and *Menippe nodifrons* develops 4 setae during its second and third stages and 8 setae in its fourth stage. These setae are present in stage II zoeae of *Micropanope barbadensis* (1-2), stage III (4), and stage IV (12-14).

Micropanope sculptipes zoeae have abdominal spination characteristics which consist of lateral hooks on the second and third abdominal somites, and smooth posterolateral spines on the third through fifth abdominal somites. The posterolateral spines increase in length with each succeeding zoeal stage. This pattern of abdominal spination is similar to that observed for most other xanthid species, but some species vary. *Hexapanopeus angustifrons* does not possess posterolateral spines in the first stage, but develops them in subsequent stages in a manner similar to *M. sculptipes*. *Rhithropanopeus harrisii* possesses lateral hooks only on the second somite and conspicuously long posterolateral spines on the fourth and fifth somites. *Pilumnus sayi* has serrated posterodorsal margins and lateral hooks on the second through fifth somites, and *P. dasypodus* has serrated posterodorsal margins on the third through fifth somites and lateral hooks on the

second and third somites. *Menippe mercenaria* and *M. nodifrons* possess lateral hooks on the second and third somites. *Menippe mercenaria* has a large pair of dorsolateral spines on the fourth and fifth somites, and develops posteroventral spines on the third through fifth somites in its second and subsequent zoeal stages. *Menippe nodifrons* has a large pair of dorsolateral spines only on the fifth somite, and develops posteroventral spines only on the third and fourth somites in its second and subsequent zoeal stages.

Spination of the zoeal telson furca is varied among xanthid species. *Micropanope sculptipes* first zoeae have smooth telson furcae with 1 dorsal and 1 lateral spine. Second and subsequent zoeal stages have furcae with 1 dorsal spine, and 1 or 2 lateral spines. *Neopanope sayi, N. texana, N. packardii, Eurypanopeus depressus*, and *Rhithropanopeus harrisii* have smooth telson furcae with only 1 dorsal spine. *Panopeus herbstii* and *Pseudomedaeus agassizii* have smooth telson furcae with 1 dorsal spine and 2 lateral spines. *Hexapanopeus angustifrons* has smooth telson furcae without dorsal or lateral spines. *Pilumnus sayi* and *P. dasypodus* have spinous telson furcae with 1 dorsal spine and 2 lateral spines. The telson furcae of *Menippe* are smooth and bear minute spines; *M. mercenaria* has 1 dorsal and 1 lateral furcal spines, and *M. nodifrons* has 1 dorsal and 2 lateral furcal spines.

Micropanope sculptipes megalopae may be quickly distinguished from those of *M. barbadensis*, because the latter is presently the only species within the genus which bears spines on the coxabases and ischia; in *M. sculptipes* only the bases are so armed.

Micropanope sculptipes may be separated from other xanthid megalopae by examining the frontal region ornamentation and telson structure (Table 3). The frontal region of *M. sculptipes* is ornamented with a prominent rostrum and lateral horns; each lateral horn has a small lateral spine near its base. Four long, plumose setae lay between the rostrum and each lateral horn. *Panopeus herbstii, Neopanope packardii*, and *Pseudomedaeus agassizii* have pointed, depressed rostrums. The lateral spines (horns) of *N. packardii* are short, and the frontal region is devoid of setae. *Panopeus herbstii* and *Pseudomedaeus agassizii* have conspicuous lateral spines with 1 seta and 2 setae, respectively, between the rostrum and each lateral spine. The remaining species discussed herein have rostrums which are reduced, broad, and generally rounded. The lateral spines of *Neopanope sayi* and *N. texana* are short and there are 5 setae and 2 setae, respectively, between the rostrum and each lateral spine. *Hexapanopeus angustifrons* and *Eurytium limosum* have prominent lateral horns which equal or exceed the rostrum length. Five setae and two setae are present between the rostrum and each lateral spine in *H. angustifrons* and *E. limosum*, respectively. No lateral horns are found in *Rhithropanopeus harrisii* or *Eurypanopeus depressus*; 2 setae are found lateral to the rostrum in the former species while no setae are present in the latter species. No lateral horns are found in *Pilumnus sayi* or *P. dasypodus*, and 3 setae are present on either side of the rostrum in both species. The rostrums of *Menippe mercenaria* and *M. nodifrons* are broad and have a distinct median cleft. No lateral horns or setae are present in *M. mercenaria*, but bluntly angular interorbital protuberances and a few small, scattered setae are found in the frontal region of *M. nodifrons*.

The telson of *Micropanope sculptipes* is rectangular with 2 pairs of dorsal setae, 3 serrated spines at each posterolateral angle, and 3 plumose setae along the shallow median telson sinus. Rectangular telsons are found in *E. depressus, H. angustifrons, Pseudomedaeus agassizii,* and *R. harrisii. Eurypanopeus depressus* has 3 short caudal setae with 2 longer setae on either side. *Hexapanopeus angustifrons* and *P. agassizii* have 2 to 4 short setae and 4 short setae, respectively, along the posterior telson margin. *Rhithropanopeus harrisii* has a few short setae along its posterior telson margin. Rounded (convex) posterior telson margins are found in *N. sayi, M. texana, N. packardii, Panopeus herbstii,* and *Eurytium limosum. Neopanope texana* has 3 pairs of dorsal telson setae and 3 setae along the posterior telson margin, and *N. packardii* has 8 stiff spines along its telson caudal margin. *Panopeus herbstii* has 3 to 6 stiff caudal telson spines. The telsons of *Pilumnus sayi* and *P. dasypodus* are posteriorly rounded; *P. dasypodus* has 2 dorsal and 2 ventral setae, and a posterior border which is generally unarmed. *Menippe mercenaria* has a rounded and somewhat truncated posterior telson margin. The telson of *M. nodifrons* is subquadrate with 5 setae along its posterior margin; other telson setation is variable.

Plesiomorphy and Larval Development

Scotto (1979) provided a detailed discussion of

TABLE 3.—Comparison of morphologically important megalopal characters for distinguishing *Micropanope sculptipes* from megalopae of other western Atlantic species of Xanthidae based on descriptions and illustrations from different sources.

Species (description source)	Frontal region	Telson
Micropanope sculptipes	Rostrum prominent, sharply rounded Lateral horns prominent, 1/2 rostrum length, small lateral spines bearing 2 apical setae 4 long, plumose setae between rostrum and each lateral spine	Rectangular, 2 pairs dorsal setae, 3 serrated spines at each outer corner, 3 plumose setae along shallow median sinus
Neopanope sayi (Chamberlain 1961)	Rostrum square, depressed into blunt bifid tooth Lateral spines blunt 5 short setae between rostrum and each lateral spine	Rounded posteriorly
Neopanope texana (McMahan 1967)	Rostrum blunt, depressed, notched Lateral spines small, pointed 2 short setae between rostrum and each lateral spine	Rounded posteriorly, 3 pairs dorsal setae, 3 posterior setae
Neopanope packardii (Costlow and Bookhout 1967)	Rostrum long, pointed, depressed Lateral spines short, pointed No frontal setae figured	Caudal margin with 8 stiff spines
Panopeus herbstii (Costlow and Bookhout 1961a)	Rostrum stoutly pointed, depressed Lateral spines stout, pointed slightly less than rostrum length 1 stout seta between rostrum and each lateral spine	Rounded posteriorly, 3-6 stiff caudal spines
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Rostrum blunt, broadly triangular, depressed No lateral spines or frontal setae	Rectangular, posterior margin with 3 short caudal setae, 2 longer setae on each side
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Rostrum broad, rounded, depressed Lateral horns prominent 5 short setae between rostrum and each lateral horn	Rectangular, posterior margin with 2-4 short setae
Rhithropanopeus harrisii (Chamberlain 1962)	Rostrum blunt, depressed bifid tooth No lateral spines 2 short setae on each side of rostrum	Rectangular, few short setae on posterior margin
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Rostrum pointed, depressed Lateral spines stout, pointed, slightly shorter than rostrum 2 small setae between rostrum and each lateral spine	Rectangular, 4 short setae on posterior margin
Eurytium limosum (Kurata[1])	Rostrum blunt, depressed bifid tooth Lateral horns prominent ≈rostrum length 3-4 setae between rostrum and each lateral horn, 1 outer lateral horn seta	Rounded posteriorly
Pilumnus sayi (Kurata[1])	Rostrum short, blunt, depressed No lateral spines 3 short setae on each side of rostrum	Rounded posteriorly
Pilumnus dasypodus (Sandifer 1974)	Rostrum broad, rounded, depressed No lateral spines or frontal setae	Rounded, 2 dorsal, 2 ventral setae; posterior border unarmed (rarely with 1, 2 small medial spines)
Menippe mercenaria (Kurata[1])	Rostrum broad, depressed, shallow median groove No lateral spines or frontal setae figured	Rounded, somewhat truncated posterior margin
Menippe nodifrons (Scotto 1979)	Rostrum strongly deflexed, blunt, rounded, distinct median cleft Interorbital prominences lateral to rostrum angular, blunt	Subquadrate, 5 setae on posterior margin, other setation variable

[1]Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Unpubl. rep., 274 p. Univ. Georgia Mar. Inst., Sapelo Island.

the importance of larval characters in determining phylogenetic relationships among brachyuran taxa, with special reference to the genus *Menippe*, and the families Xanthidae and Cancridae. Although Lebour (1928) enumerated several distinguishing morphological characters of xanthid larvae, including number of zoeal stages, carapacial armature, antennal morphology, abdominal morphology, and telson armature, Wear (1968, 1970) has shown that few of these are now valid. Even so, the larval characteristics of *Micropanope sculptipes* generally agree with Lebour's classical categorization of morphological characteristics of the Xanthidae. Moreover, the antennal structure of *M. sculptipes* differs in important respects, distinctive for the genus.

Hyman (1925) and Lebour (1928) divided the antennal morphology of xanthid larvae into two or three distinctive groups: antennal exopodite either minute, nearly equal to protopodite length, or about three-fourths protopodite length. Shorter antennal exopodites were considered indicative of evolutionarily more advanced species.

Aikawa (1929) recognized four types of antennae (A, B, C, D), also based on the relative length of the peduncle (= protopodite) to that of the exopodite. In Type A the protopodite and exopodite are nearly equal in length, a condition considered most primitive; in Type B the exopodite is one-half to three-fourths of the protopodite length, a type characteristic of most brachyuran zoeae; in Type C the exopodite is minute, these are the most highly developed. Type D antennae have a simple, inconspicuous spiny process which is shorter than either the rostrum or the antennule, and is considered to be a deviation.

The antennal exopodite of larval *M. sculptipes* is one-sixth to one-fifth the length of the protopodite, and therefore may be considered an intermediate form in the antennal classification schemes of Hyman (1925), Lebour (1928), and Aikawa (1929). The antennal configuration of *M. sculptipes* has been shown here to be distinctive from many other xanthid larvae, and it may be a general characteristic of the genus *Micropanope* (sensu lato). This contention is supported by a nearly identical antennal configuration for zoeae of *M. barbadensis*. However, similar antennal morphological characteristics are seen in the larvae of *Paramedaeus noelensis* and *Heterozius rotundifrons*. This similarity in antennal morphology allows establishment of a separate antennal classification typed "Group E" for larvae of the Xanthidae (Gore et al. 1981). Larvae in this grouping might be considered more advanced than most xanthids, although *P. noelensis* has four zoeal stages and is otherwise similar in development to other members of the family. *Heterozius* has two zoeal stages but, as noted by Wear (1968), may not belong in the Xanthidae.

Status of *Micropanope* in Family Xanthidae

Guinot (1967) discussed systematic relationships among adults of the Xanthidae and considered the genus *Micropanope* to be a mixture of several distinct generic groups which were intermediate between the genera *Panopeus* and *Pilumnus*. She concluded *Micropanope* to be more closely related to *Panopeus* than to *Pilumnus*.

A comparison of the overall larval morphology of *M. sculptipes* with *Panopeus herbstii* and *Pilumnus dasypodus* (Table 2) reveals a much closer similarity between larvae of *M. sculptipes* and *Panopeus herbstii* than between *M. sculptipes* and *Pilumnus dasypodus*. Examination of the antennal structure for these three species shows that the length of the antennal exopodite relative to that of the antennal protopodite for *M. sculptipes* (exopodite one-sixth protopodite length) is intermediate between the advanced state seen in *Panopeus herbstii* (exopodite minute) and the primitive state seen in *Pilumnus dasypodus* (exopodite equals protopodite length), being more similar to *Panopeus herbstii*. Assuming that the antennal exopodite relative length is an indicator of the degree of relative primitiveness among xanthid species (Lebour 1928; Aikawa 1929), it can be concluded on this larval character that *Micropanope* is evolutionarily more closely related to *Panopeus* than to *Pilumnus*. This finding supports the contentions of Guinot (1967), and the apparent alliance between both larvae and adults of *Micropanope* and *Panopeus* emphasizes the importance which larval taxonomy may have in determining systematic and possible evolutionary relationships within the complex family Xanthidae.

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ESTABLISHMENT OF NONINDIGENOUS RUNS OF SPRING CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN THE WIND RIVER DRAINAGE OF THE COLUMBIA RIVER, 1955-63

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ABSTRACT

In 1955, cooperating agencies of the Columbia River Fishery Development Program embarked upon a 9-year program to introduce nonindigenous spring chinook salmon, *Oncorhynchus tshawytscha*, into Wind River, a tributary of the Columbia River. The program consisted of: 1) construction of a fishway at an impassable falls on the lower Wind River, 2) transplantation of nonindigenous adult spring chinook salmon from the Columbia River to Carson National Fish Hatchery on the upper Wind River, and 3) rearing and release of juvenile spring chinook salmon into the Wind River. As a result of these activities, approximately 66,000 adult spring chinook salmon returned to Carson hatchery during 1959-79. Additional nonindigenous adult fish annually utilized natural spawning habitat of the Wind River drainage. Hatchery and naturally produced spring chinook salmon from the Wind River contributed to marine and freshwater commercial and sports fisheries. Through 1979, about 46.5 million spring chinook salmon eggs and 3.5 million juveniles were transplanted from Carson hatchery to other areas of the Pacific Northwest.

The Columbia River Basin produces the world's largest runs of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*; major runs of coho salmon, *O. kisutch*; and lesser runs of sockeye salmon, *O. nerka*, and chum salmon, *O. keta*. Since the 1938 completion of Bonneville Dam on the main-stem Columbia River at river mile 146.1 from the Pacific Ocean, the Columbia River Basin has been divided into upper and lower river fishery management units encompassing areas above and below Bonneville Dam, respectively. Chinook salmon produced in the upper river area, particularly the spring and summer runs,[3] provided the bulk of freshwater commercial catches which annually averaged approximately 29 million lb from 1866 to 1940, and peaked at more than 40 million lb/yr during 10 yr of that period (Beiningen[4]).

By the beginning of the 1940's, land and water developments in the upper Columbia Basin had eliminated or degraded major anadromous salmonid spawning and rearing areas. The resulting reduced production in combination with overfishing had a significant diminishing effect on salmon and steelhead runs originating in the upper basin (Chaney and Perry[5]).

In 1949 the U.S. Congress appropriated initial funds for a cooperative state-federal fishery development effort which soon came to be known as the Columbia River Fishery Development Program (CRFDP). This program is now administered by the Northwest Region Environmental and Technical Services Division, National Marine Fisheries Service, NOAA, Portland, Oreg. Operations are largely conducted via contract with the U.S. Fish and Wildlife Service and fishery management agencies of Oregon, Washington, and Idaho. The program has two primary components: protection and improvement of stream environments for anadromous salmonids, and hatchery production of salmon and steelhead to partially offset the loss of production from natural spawning and rearing areas.[6]

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[2]Northwest Resource Information Center, Inc., P.O. Box 427, Eagle, ID 83616.

[3]Distinct runs of adult chinook salmon enter the Columbia River from February through October of each year. Those entering the river in late February through May are classed as spring chinook salmon. Spring chinook salmon destined for upriver spawning areas generally enter the Columbia in late March through May with peak passage at Bonneville Dam in late April or early May. Chinook salmon entering the Columbia from late May through July are classed as summer chinook salmon and are all destined for spawning areas above Bonneville Dam (Chaney and Perry see footnote 5).

[4]Beiningen, K. T. 1976. Investigative reports of Columbia River fisheries project, Section E-Fish Runs. Prepared for Pacific Northwest Regional Commission, Vancouver, Wash., 65 p.

[5]Chaney, E., and L. E. Perry. 1976. Columbia Basin salmon and steelhead analysis. Prepared for Pacific Northwest Regional Commission, Vancouver, Wash., 74 p.

[6]Program activities to date include clearing of obstructions

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In 1955, CRFDP cooperating agencies initiated a 9-yr program to introduce spring chinook salmon into Wind River, which enters the Columbia River at river mile 155 in southwestern Washington (Figure 1). Historically, chinook salmon were blocked from all but a few miles of the lower Wind River by an impassable series of falls located 3.7 mi upstream from its confluence with the Columbia River. The upper Wind River drainage was believed to contain substantial spring chinook salmon spawning and rearing habitat and to have the potential for supporting a productive spring chinook salmon hatchery program. Approximately 35,000 spring chinook salmon eggs from Camas Creek, Idaho, were transferred to Carson National Fish Hatchery on upper Wind River in 1945. About 20,500 resulting fingerlings were marked and released into the Wind River in October 1946. In 1949, 21 adult spring chinook salmon were observed below Shipperd Falls. Four carcasses bearing the 1946 mark were subsequently recovered (Zimmer et al. 1963).

This report is a summary of the 1955-63 Wind River spring chinook salmon introduction program and results through 1979.

MAJOR ELEMENTS OF THE PROGRAM

The Wind River spring chinook salmon introduction program had three discrete, interrelated elements: 1) construction of a fishway at Shipperd Falls, 2) trapping nonindigenous adult spring chinook salmon from a heterogenous population passing Bonneville Dam on the main-stem Columbia River and transporting them to hatchery facilities on the upper Wind River, and 3) holding of transported adults to maturity, spawning the adults, and rearing the resulting progeny to migrant size for release into Wind River.

from about 2,000 mi of streams, construction of 87 fishways at natural barriers, installation of 570 screens at diversion ditches and canals, and construction or modernization of 22 salmon and steelhead hatcheries and 7 rearing ponds which annually produced an average of 98 million salmon (2.6 million lb) and 2.3 million steelhead (350,000 lb) during 1971-76. Wahle and Vreeland (1978) list numerous operational improvement studies also funded to complement artificial production throughout the basin.

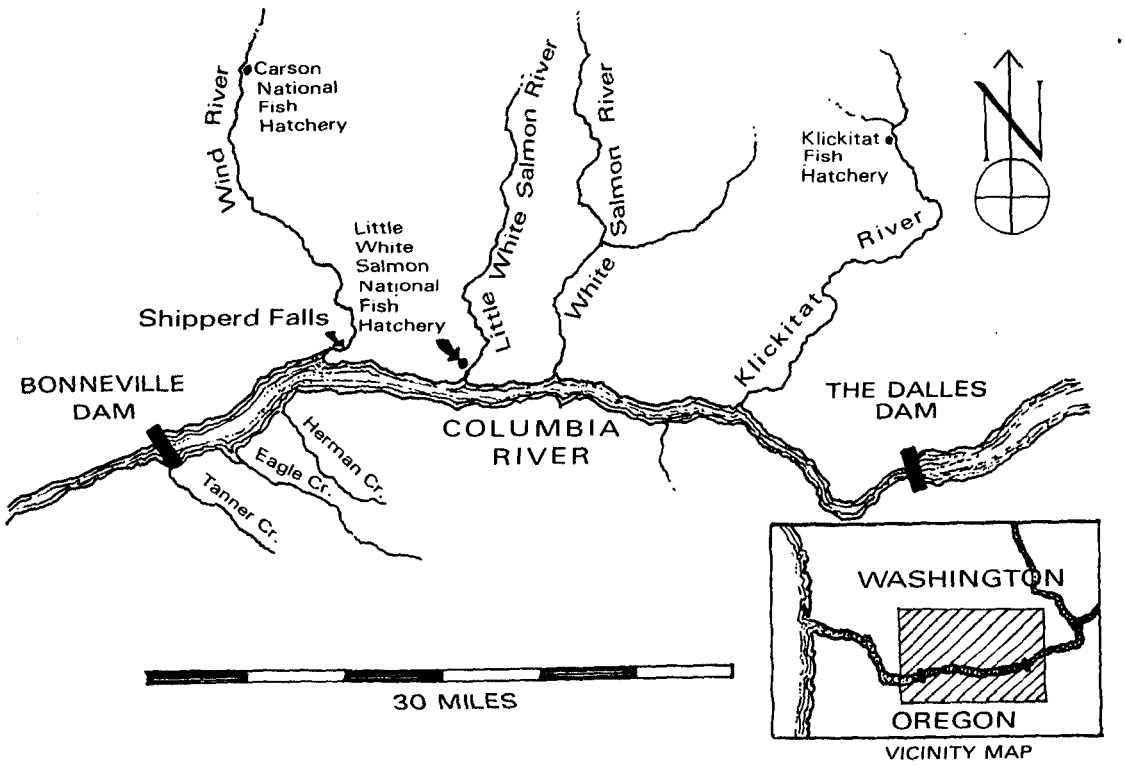

FIGURE 1.—Wind River and vicinity.

Shipperd Falls Fishway

Shipperd Falls is a series of falls ranging from 3 to 15 ft high with a collective total vertical drop of 44.8 ft. The falls are located 3.7 mi upstream from the Wind River's confluence with the Columbia River. Small numbers of steelhead reportedly were able to negotiate the falls during periods of high river flow during spring runoff (Bryant 1949). However, the falls apparently presented an impassable barrier to chinook salmon at all flows. No spring chinook salmon spawning habitat exists in the Wind River drainage below Shipperd Falls.

Construction of a fishway began in 1953 and was completed in 1956. A barrier dam was constructed across the stream to increase the height of the lowermost vertical drop of the falls to block upstream migrants and lead them to the fishway entrance. The fishway is of single slot vertical baffle design, commonly employed where integral pool regulation is not possible. Forty-five 9-ft long, 6-ft wide pools were constructed on a 1:9 slope providing 1-ft vertical rise from pool to pool. Total length of the fishway including entrance and exit facilities is about 454 ft with a vertical rise from downstream entrance to upstream exit of 44.8 ft. When complete the fishway provided fish passage at all stream flows (Figures 2, 3).

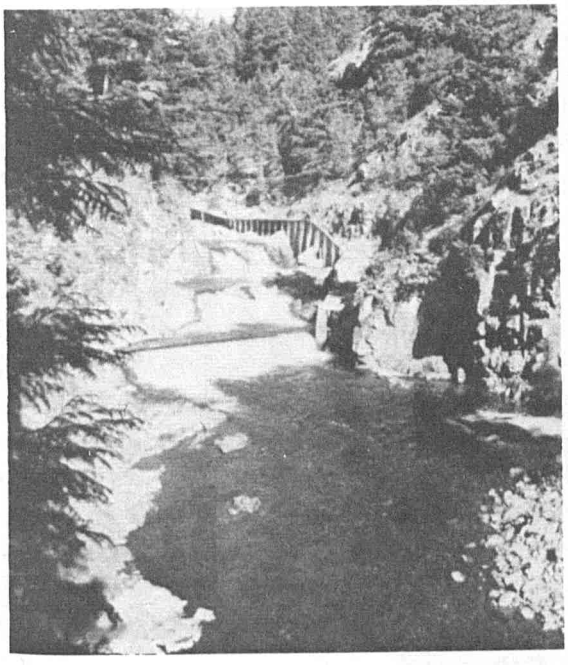

FIGURE 2.—Shipperd Falls and fishway.

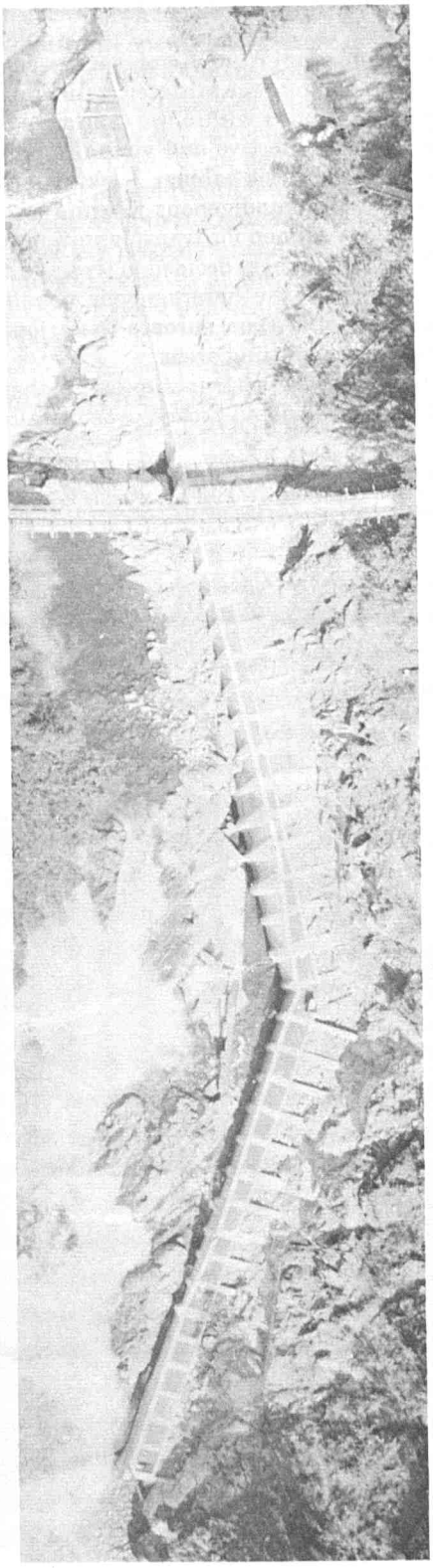

FIGURE 3.—Shipperd Falls and fishway.

Adult Trapping and Hauling

At the time the Wind River spring chinook salmon introduction was initiated, artificial propagation of all salmon within the Columbia Basin was generally ineffective and virtually nonexistent for spring chinook salmon. Lacking a convenient source of nonindigenous juvenile or adult spring chinook salmon for transplantation to the Wind River, researchers decided to trap adults for brood stock from the heterogenous population passing Bonneville Dam enroute to various upriver tributary spawning areas.

A specially designed trap similar to that described by Gunsolus and Eicher[7] was installed at the fishway on the north side of Bonneville Dam. The trap basically consisted of a hopper which was lowered into the fishway to intercept and collect upstream migrants. Once several adult spring chinook salmon had entered the hopper, it was raised from the fishway, positioned over and emptied into a 1,000-gal capacity tank truck previously filled with water from the fishway (Figure 4). This process was repeated until each truck held approximately 20 adult fish. During the loading operation, water in the truck tank was continually being drawn from the fishway, circulated through the tanks, and released to the forebay of the dam. Water in the tank was mechanically aerated during the approximately 1 h transportation time to Carson Hatchery. At the hatchery, the tank trucks were emptied into adult holding ponds. The fish were retained in water throughout the trapping and hauling operation.

[7] Gunsolus, R. T., and G. J. Eicher. 1962. Evaluation of fish passage facilities at the Pelton Project on the Deschutes River in Oregon. Oregon Department of Fish and Wildlife Research and Management Laboratory, 17330 SE Evelyn St., Clackamas, OR 97015, 133 p.

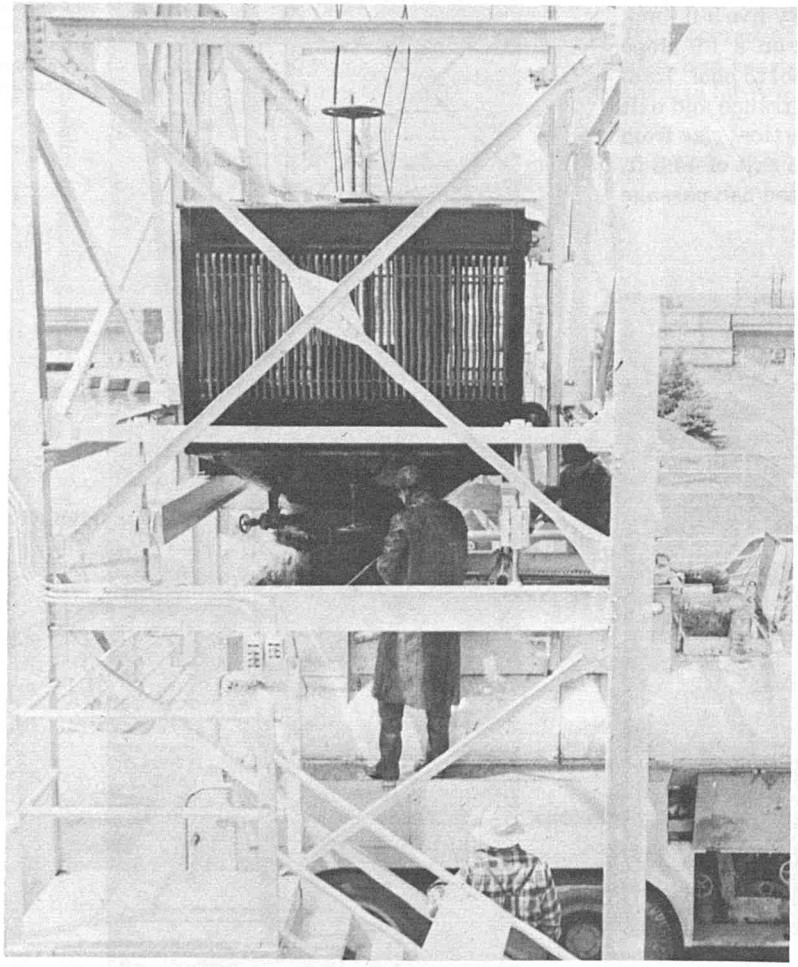

FIGURE 4.—Transfer of adult spring chinook from hopper of fishway to tank truck for transport to Carson Hatchery.

Zimmer et al. (1963) reported on adult mortalities resulting from trapping and hauling operations.

During 1955-63 a total of 4,239 adult spring chinook salmon were trapped at Bonneville Dam and hauled to Carson Hatchery. Table 1 displays trapping and related details for each year of that period.

Hatchery Operations

The adult spring chinook salmon trapped at Bonneville Dam in the spring of each year during 1955-63 were held in adult holding ponds at Carson Hatchery (Figure 5) until sexually mature and ready for spawning in late August and early September. Eggs taken were fertilized and incubated and the resulting juveniles reared for about 13 mo in hatchery raceways. Zimmer et al. (1963) provided details on hatchery facilities, water supply, fish cultural operations, disease, and diets.

During the 1955-63 transplantation program, about 8.5 million eggs were taken from adult female spring chinook salmon trapped at Bonneville Dam. In 1960-63, an additional 5.3 million eggs were taken from adult female spring chinook salmon returning to the hatchery as the result of releases of the progeny of the transplanted fish. Total juvenile releases at the hatchery from the 1955-63 brood years was about 10.6 million yearlings (Table 2).

EVALUATION OF THE RESULTS OF THE PROGRAM

Adult fish counts at Shipperd Falls fishway, returns to Carson National Fish Hatchery and

TABLE 1.—Adult spring chinook salmon trapped at Bonneville Dam and transferred to Carson National Fish Hatchery, 1955-63.

Year	Bonneville Dam spring chinook salmon count[1]	Period of trapping	No. days of trapping	Total trapping-period count[2]	Fish transferred to hatchery			
					Male[1]	Female	Total	Percent of trapping-period count
1955	171,596	19-22, 25, 27 April	6	28,007	161	356	517	1.85
1956	63,449	4-8 May	5	7,595	228	270	498	6.55
1957	136,440	22-26 April	5	8,111	192	234	426	5.25
1958	75,206	1-3, 5, 6 May	5	4,870	164	360	524	10.76
1959	61,133	27 April-1, 4, 11-15 May	11	10,740	94	90	184	1.71
1960	69,597	26 April-1 May	6	7,334	237	290	527	7.19
1961	98,695	17-22 April	6	1,993	252	293	545	27.30
1962	91,116	23-27 April, 3, 4, 7 May	8	13,067	212	267	479	3.67
1963	75,471	22-27 April	6	4,388	—	—	513	11.69

[1]Includes jacks.
[2]Washington shore fishway only.

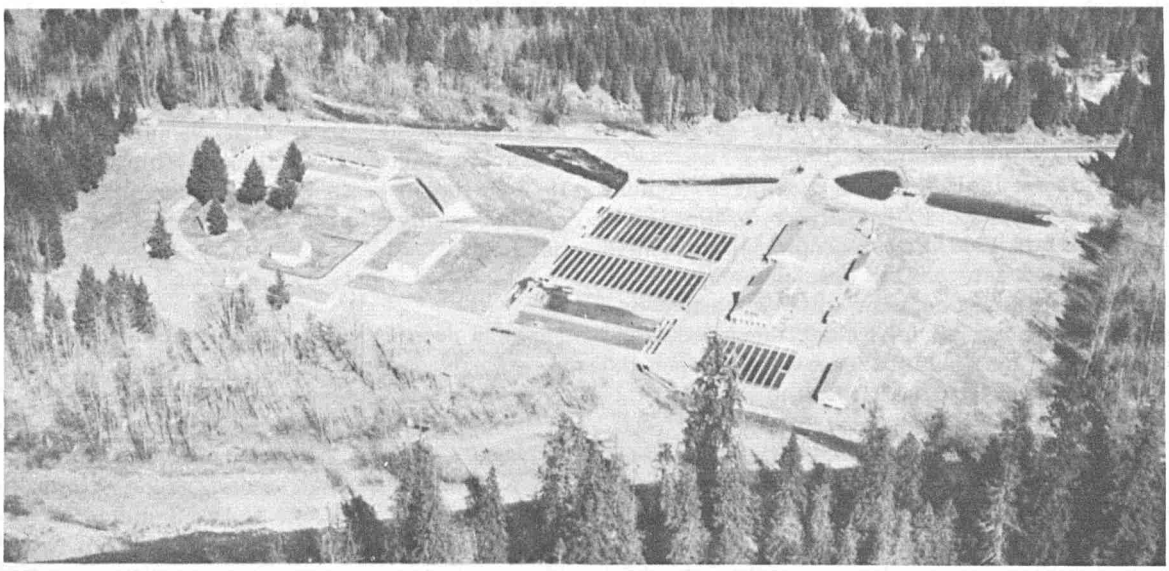

FIGURE 5.—Carson National Fish Hatchery.

TABLE 2.—Wind River Transplantation Program, 1955-79.

Year	Number adults hauled	Shipperd Falls adult count	Carson Hatchery returns[1]	Number fingerlings released at hatchery	Brood year
1955	517	—	—	—	—
1956	498	—	—	—	—
1957	426	—	—	967,000	1955
1958	524	—	—	623,000	1956
1959	184	—	107	733,000	1957
1960	527	854	552	1,016,000	1958
1961	545	1,032	609	261,000	1959
1962	479	2,515	1,718	[2]1,479,000	1960
1963	513	1,255	825	1,265,000	1961
1964	—	5,429	2,517	3,037,000	1962
1964	—	—	—	39,000	[3]1963
1965	—	2,284	1,474	[4]1,154,000	1963
1966	—	4,174	3,666	1,909,000	1964
1967	—	—	2,749	2,412,000	1965
1968	—	—	[5]663	1,613,000	1966
1969	—	—	1,609	1,535,000	1967
1970	—	—	3,120	757,000	1968
1971	—	—	4,250	1,178,000	1969
1972	—	—	6,641	1,409,000	1970
1973	—	—	2,189	1,541,000	1971
1974	—	—	1,563	2,001,000	1972
1975	—	—	4,905	2,000,000	1973
1975	—	—	—	197,000	[3]1974
1976	—	—	5,496	2,291,000	1974
1976	—	—	—	253,000	[3]1975
1977	—	—	2,975	2,813,000	1975
1978	—	—	2,976	2,836,000	1976
1979	—	—	2,541	1,792,000	1977

[1]After a sufficient number of adults had entered hatchery holding ponds, entrance to the hatchery was frequently blocked, forcing returning adults to spawn in Wind River and tributaries.
[2]First year released juveniles included progeny of nontransplanted adults.
[3]Time of release study.
[4]Included last juveniles from transplanted fish.
[5]Last year of possible returns resulting from first generation progeny of transplanted fish.

resulting juvenile releases, and Wind River spawning ground surveys provided the primary means of evaluating results of the Wind River spring chinook salmon introduction program. Secondary indicators were the amount of contribution to catches and a surplus of eggs and juveniles available from Carson hatchery for transplantation to other areas of the Northwest.

Shipperd Falls Counts

Counting of adult upstream migrant salmonids began at Shipperd Falls fishway in 1954 and terminated in 1966. Fish ascending the fishway were trapped in a confined area of the upstream exit facility, raised near the water surface by an electrically operated false floor, identified, and counted. An adjustable headgate was then opened, allowing the fish to exit from the fishway and continue upstream.

Frequency of counting varied with the number and rate of migration of spring chinook salmon through the fishway. Counting was intermittent during 1954-58, not conducted in 1959, and conducted throughout the time of spring chinook salmon migration in 1960-66. Spring chinook salmon counts ranged from 1 fish in 1957 to 5,429 fish in 1964 (Table 2).

Hatchery Returns-Juvenile Releases

Spring chinook salmon from any given brood year returned to Carson Hatchery as 3-yr-old precocious males (jacks) and 4-, 5-, and 6-yr-old adults. Table 3 contains age composition of spring chinook salmon from the 1963-73 broods that returned to the hatchery.

The first spring chinook salmon resulting from the transplantation program returned to Carson Hatchery in 1959: 99 jacks, 6 adult males, and 2 adult females. The first significant return, 522 spring chinook salmon in 1960, consisted of 331 adult females, 170 adult males, and 51 jacks.

Transplantation of brood stock from Bonneville Dam to Carson Hatchery terminated with the completion of 1963 trapping and hauling operations. Thereafter, hatchery brood stock consisted exclusively of adult fish returning as the result of juvenile releases at the hatchery.

From 1964 through 1979, about 49,000 spring chinook salmon returned to Carson Hatchery adult holding ponds. The annual average return during that period was about 3,100 spring chinook salmon. The peak return of 6,641 occurred in 1972 (Table 2).

Table 2 displays the number of juvenile spring chinook salmon released into the Wind River at Carson Hatchery 1956-79. Releases during 1956-61 (brood years 1954-59) were exclusively progeny of fish trapped at Bonneville Dam; 1962-65 releases (brood years 1960-63) were from a composite of adults transported and those returning to the hatchery from earlier juvenile releases. The approximately 26.6 million juveniles released 1966-79 (brood years 1964-77) were all progeny of adult spring chinook salmon returning to the hatchery.

TABLE 3.—Age composition of 1967-73 broods of spring chinook salmon returning to Carson National Fish Hatchery.

Brood year	3	4	5	6	Total
1967	0	2,580	2,470	0	5,050
1968	952	4,124	1,066	261	6,403
1969	50	1,022	261	0	1,333
1970	101	905	264	24	1,294
1971	384	4,630	5,025	0	10,039
1972	10	161	46	5	222
1973	288	2,907	2,360	12	5,567
Total	1,785	16,329	11,492	302	29,908
% of total	6	55	38	1	100

Spawning Ground Surveys

Achieving the production potential of natural habitat in upper Wind River and its tributaries was the companion goal to developing a self-sustaining spring chinook salmon hatchery program at Carson Hatchery. Annual spawning ground surveys for spring chinook salmon in the Wind River and selected tributaries began in 1959. Surveys were conducted in late August and early September; Table 4 contains data on the 1959-79 surveys. The largest number of spring chinook salmon observed during that period was 1,476 fish in 1962; the largest number of redds counted in the same period was 527 in 1964. Figure 6 illustrates the general distribution of spring chinook salmon spawners in Wind River and tributaries based upon composite data from several years' surveys.

TABLE 4.—Spawning ground surveys of Wind River spring chinook salmon, 1959-79.

	Above hatchery		Below hatchery		Totals	
Year	Fish	Redds	Fish	Redds	Fish	Redds
1959	—	—	24	—	24	—
1960	34	107	6	9	40	116
1961	23	62	8	12	31	74
1962	35	155	1,441	—	1,476	155
1963	—	—	—	—	—	—
1964	579	422	107	105	686	527
1965	—	—	—	—	—	—
1966	111	63	121	48	232	111
1967	—	—	—	—	—	—
1968	—	—	—	—	—	—
1969	—	—	—	—	—	—
1970	59	138	72	73	131	211
1971	839	308	391	52	1,230	360
1972	372	112	189	51	561	163
1973	79	56	17	8	96	64
1974	37	30	7	2	44	32
1975	25	16	12	9	37	25
1976	23	13	37	12	60	25
1977	26	29	16	9	42	38
1978	40	25	41	22	81	47
1979	—	—	—	—	—	—

Catch Contribution

In 1959 the first adult spring chinook salmon adults resulting from progeny of the transplantation program returned to Wind River. Small numbers of spring chinook salmon were reported caught by steelhead fishermen in 1959-61. In 1962 a spring chinook salmon sport fishery developed in the Columbia River at the mouth of the Wind River. Based upon Washington Department of Fisheries salmon creek census data submitted voluntarily by fishermen, catches during 1964 and

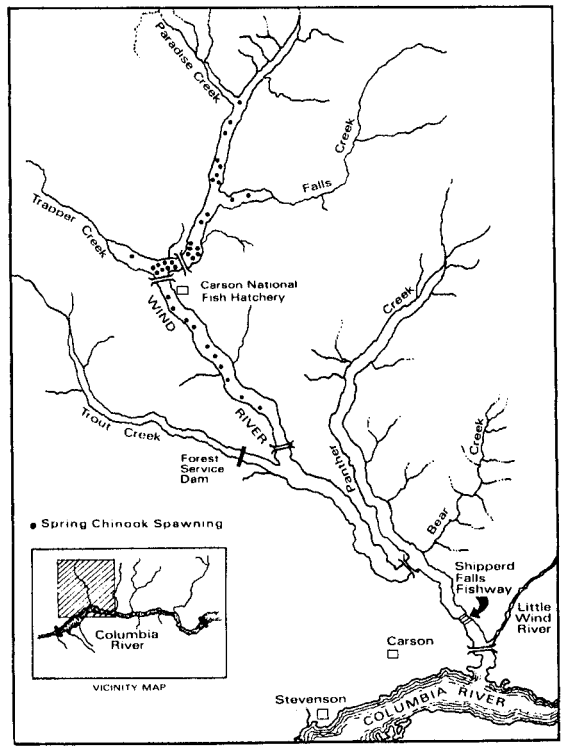

FIGURE 6.—Generalized distribution of naturally spawning chinook in the Wind River drainage. Stream widths exaggerated.

1965 were estimated at 592 fish and 363 fish, respectively (Nye and Ward 1968).

In 1966 an intensive creel census specially designed for small geographic areas[8] provided data to estimate the catch of Wind River spring chinook salmon at the confluence of the Wind and Columbia Rivers. Major features of the census program included: creel census of boat and shore fishermen twice daily 29 March-1 June, and hourly census of boat and shore fishermen for 6 weekend days and 10 weekdays, including number and species of fish caught and total hours fished. Total estimated catch for the period 29 March-1 June was 1,144 fish (Table 5). Based upon far less precise, voluntarily submitted creel census data, February-June 1964-75 Wind River spring chinook salmon sport catches ranged from 34 fish (1968) to 2,454 fish (1975) with an estimated catch of 362 spring chinook salmon in 1966 (Nye and Ward 1968; Nye et al. 1975, 1976).

[8]Donald D. Worlund, Northwest and Alaska Fisheries Center Fisheries Data and Management Systems, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

TABLE 5.—Estimates of sport catch of spring chinook salmon at the confluence of the Wind and Columbia Rivers, 29 March-1 June 1966.

Period ending	Boat	Shore	Total	Period ending	Boat	Shore	Total
17 April	69	10	79	15 May	40	28	68
24 April	269	61	330	22 May	35	7	42
1 May	271	63	334	29 May	2	1	3
8 May	239	49	288	Totals	925	219	1,144

TABLE 6.—Recovery data for marked spring chinook salmon of the 1971 brood from Carson National Fish Hatchery, 1973-76.

Area	Fishery	1973	1974	1975	1976	Total recoveries
Alaska	Troll	—	1	3	0	4
British Columbia	Troll	—	3	0	0	3
Washington:						
Cape Flattery	Troll	0	8	0	0	8
Quillayute		0	49	0	0	49
Split Rock		0	2	0	0	2
Grays Harbor		0	31	0	0	31
Columbia R.		0	17	0	10	27
Sekiu	Ocean sport	0	0	0	0	0
Neah Bay		0	9	0	0	9
LaPush		0	0	0	0	0
Westport		0	31	0	6	37
Ilwaco		12	25	0	0	37
Oregon:						
Astoria	Troll	0	2	4	0	6
Newport		0	3	0	0	3
Coos Bay		0	26	8	0	34
Bandon		0	0	1	0	1
Warrenton	Ocean sport	0	0	23	0	23
California:						
Crescent City	Troll	0	0	14	0	14
Eureka		0	15	9	0	24
	Sport	0	0	0	0	0
Columbia R.:						
Below Bonneville	Gill net	0	8	8	3	19
Above Bonneville		*0*	*0*	*0*	*0*	*0*
Below Bonneville	Sport	0	0	0	0	0
Above Bonneville[1]		—	—	—	—	—
Totals		12	230	70	19	331

[1]Not sampled.

In late March and early April 1972, 142,000 dorsal-right ventral marked 1970 brood Wind River spring chinook salmon juveniles were released at Carson Hatchery. From November 1971 to march 1972, 161,000 1970 brood juveniles bearing the same mark were released at two other hatcheries on nearby Klickitat and Little White Salmon Rivers. These releases were part of a Columbia River Fishery Development Program-funded marking and mark sampling program involving all spring chinook salmon rearing facilities in the Columbia River Basin. During 1972 and 1973, marks were sampled only at Washington, Oregon, and California ports. Beginning in 1974, the sampling program covered all significant Pacific coast marine and Columbia River recreational and commercial chinook salmon ports of landing from Pelican, Alaska, to Monterey, Calif. Sampling a total of 140 Wind-Klickitat-Little White Salmon-River marks, recoveries included Alaska 4, British Columbia 6, Washington 27, and California 5. Seventy-two marks were recovered in the main-stem Columbia River sport fishery and 26 in the main-stem Columbia River gill net commercial fishery.

In late March and early April 1973, about 142,000 1971 brood spring chinook salmon juveniles (average length 5½ in) bearing a distinctive adipose-right ventral mark were released from Carson Hatchery into Wind River. Table 6 contains 1973-76 mark recoveries in marine and Columbia River fisheries.

Wind River Spring Chinook Salmon Transfers

As a result of the Wind River spring chinook salmon introduction program, Carson National Fish Hatchery has become an important source of spring chinook salmon for transplantation to diverse areas within and outside the Columbia River Basin. About 46.5 million eggs and 3.5 million juveniles from adult returns to the hatchery were transferred to other areas during 1960-79 (Table 7).

These transfers contributed to the establishment of several spring chinook salmon runs, including hatchery runs to Leavenworth National Fish Hatchery on Washington's Icicle River, a tributary of the Wenatchee River, and to the Little White Salmon National Fish Hatchery on Washington's Little White Salmon River; naturally spawning runs were created in Fall Creek, tributary to Oregon's Willamette River, and in the Selway River, tributary to the Clearwater River in Idaho.

SUMMARY

In 1955, a 9-yr program was initiated to introduce nonindigenous spring chinook salmon into Wind River, a southwestern Washington tributary of the Columbia River. A fishway was constructed to provide chinook salmon passage over a heretofore impassable falls located at Wind River mile 3.7. During 1955-63, 4,239 adult spring chinook salmon were trapped from the heterogenous population passing over Bonneville Dam

TABLE 7.—Spring chinook salmon, eggs, and juveniles by brood year transported from Carson National Fish Hatchery, 1960-79.

Year	Transferred to	Number		Brood year
		Eggs	Juveniles	
1960	Klickitat Hatchery, Wash. (W.D.F.)[1]	35,000	—	1960
1961	Klickitat Hatchery	100,000	—	1961
1961	Warm Springs Creek, Oreg. (Warm Springs Indian Tribe)	—	75,313	1960
1961	Clearwater River, Idaho (I.F.&G.)	705,711	—	1961
1962	Klickitat Hatchery	899,339	—	1962
1962	Clearwater River	959,200	—	1962
1963	Clearwater River	1,000,000	—	1963
1964	Clearwater River	1,000,000	—	1964
1964	Klickitat Hatchery	121,500	—	1964
1965	Willard N.F.H.,[2] Wash. (U.S.F.&W.)	19,341	—	1965
1965	Clearwater River	634,942	—	1965
1966	Nat'l. Marine Fisheries Service, Seattle, Wash.	—	10,000 (50-70/lb)	1966
1966	Clearwater River	—	1,018,200 (50-70/lb)	1966
1967	Clearwater River	—	1,016,300 (50-70/lb)	1967
1968	Clearwater River	—	951,970 (50-70/lb)	1968
1968	Weyerhauser Corp., Oreg.	—	10,880 (125/lb)	1966
1968	Little White Salmon N.F.H., Wash. (U.S.F.&W.)	101,000	—	1968
1969	Kooskia N.F.H., Idaho (U.S.F.&W.)	255,300	—	1969
1969	Clearwater River	990,117	—	1969
1969	Warm Springs Creek	300,017	—	1969
1970	Little White Salmon N.F.H.	1,123,190	—	1970
1970	Leavenworth N.F.H., Wash. (U.S.F.&W.)	307,810	—	1970
1970	Willamette River, Oreg. (F.C.O.)	2,999,130	—	1970
1970	Willamette River	—	359,280 (462/lb)	1970
1971	Kooskia N.F.H.	1,532,020	—	1971
1971	Leavenworth N.F.H.	600,000	—	1971
1971	Southeast Alaska (A.F.&G.)	500,000	—	1971
1971	Clearwater River	2,423,080	—	1971
1972	Southeast Alaska	1,510,000	—	1972
1972	Leavenworth N.F.H.	600,860	—	1972
1972	Klickitat Hatchery	5,495,160	—	1972
1972	Willamette River	1,730,760	—	1972
1972	Little White Salmon N.F.H.	1,070,610	—	1972
1972	Kooskia N.F.H.	801,890	—	1972
1973	Little White Salmon N.F.H.	846,640	—	1973
1973	Eagle Creek N.F.H., Oreg. (U.S.F.&W.)	354,000	—	1973
1973	Leavenworth N.F.H.	747,000	—	1973
1974	Abernathy N.F.H., Oreg. (U.S.F.&W.)	113,000	—	1974
1974	Little White Salmon N.F.H.	300,000	—	1974
1975	Entiat N.F.H., Wash. (U.S.F.&W.)	1,000,000	—	1975
1975	Leavenworth N.F.H.	1,056,000	—	1975
1975	Leavenworth N.F.H.	1,243,000	—	1975
1975	Kooskia N.F.H.	300,000	—	1975
1975	Klickitat Hatchery	449,000	—	1975
1976	Kooskia N.F.H.	1,000,000	—	1976
1976	Entiat N.F.H.	721,000	—	1976
1976	Leavenworth N.F.H.	2,443,000	—	1976
1976	Winthrop N.F.H., Wash. (U.S.F.&W.)	473,000	—	1976
1976	Marion Forks Hatchery, Oreg. (F.C.O.)	744,000	—	1976
1977	Leavenworth N.F.H.	721,000	—	1977
1977	Leavenworth N.F.H.	1,171,000	—	1977
1978	Leavenworth N.F.H.	2,043,000	—	1978
1978	Leavenworth N.F.H.	250,000	—	1978
1979	Leavenworth N.F.H.	2,238,000	—	1979
1979	Leavenworth N.F.H.	315,000	—	1979
1979	Kooskia N.F.H.	200,000	—	1979
	Totals	46,543,617	3,441,943	

[1]Abbreviations: (W.D.F.) Washington Department of Fisheries, (I.F.&G.) Idaho Fish and Game Department, (U.S.F.&W.) U.S. Fish and Wildlife Service, (F.C.O.) Fish Commission of Oregon.
[2]N.F.H. - National Fish Hatchery.

at Columbia River mile 146.1 and transferred to Carson National Fish Hatchery on the upper Wind River. About 10.6 million yearling progeny of these fish were released into Wind River.

From 1959 to 1979, about 66,000 adult spring chinook salmon returned to Carson Hatchery. During that period about 37 million yearling progeny of the 1955-77 broods were released into Wind River. Surveys of natural spawning grounds during 1959-78 recorded a peak number of 1,476 spring chinook salmon in 1962 and 527 redds in 1964. A spring chinook salmon sport fishery developed within the Wind River drainage and at its confluence with the Columbia River at the mouth of the Wind. Marking and mark sampling programs indicated Wind River spring chinook

salmon contributed to marine commercial and recreational fisheries from Alaska to California, and to main-stem Columbia River fisheries. During 1960-79, about 46.5 million eggs and 3.5 million juveniles from spring chinook salmon introduced to Wind River were transplanted to other Pacific Northwest locations.

ACKNOWLEDGMENTS

Thanks to John Miller, U.S. Fish and Wildlife Service, for supplying the photograph of Carson National Fish Hatchery; to Steve Leek, U.S. Fish and Wildlife Service, for providing age composition data for spring chinook salmon returning to Carson Hatchery; to Mark Maher, National Marine Fisheries Service, for supplying engineering specifications of Shipperd Falls Fishway; and to R. Z. Smith, National Marine Fisheries Service, for salvaging the composite Shipperd Falls fishway photographs from the archives.

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ESTIMATED GROWTH OF SURFACE-SCHOOLING SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, FROM THE PAPUA NEW GUINEA REGION

J. W. J. WAŃKOWSKI[1]

ABSTRACT

The study was undertaken on length-frequency data collected from the Papua New Guinea pole-and-line fishery between June 1977 and December 1979.

Both skipjack and yellowfin tunas are recruited to all areas of the fishery at between 30 and 46 cm fork length. Skipjack tuna remain in the exploited phase up to an average 69 cm fork length and yellowfin tuna up to an average 85 cm fork length. Periods of time during which the greatest range of fork length occurred in the catch correspond with periods of low abundance, as inferred from catch per unit of effort indices. The estimated von Bertalanffy parameters are $k = 0.0429$ and $L_\infty = 74.8$ cm for skipjack tuna; and $k = 0.0243$ and $L_\infty = 180.9$ cm for yellowfin tuna (k on a monthly basis). Estimated growth over the observed range of modal values corresponds closely with that estimated from Papua New Guinea tagging data for skipjack tuna and from studies in other regions for yellowfin tuna.

Modal progressions indicate a 12-month periodicity in mass movement of yellowfin tuna stocks in northerly and southerly directions. The presence of two skipjack tuna spawning groups, one spawning during the northern summer and the other during the northern winter, is indicated by back calculation to date of birth of all length-frequency modes using an estimate of growth derived from the tag and recapture data.

With the recent expansion of surface fisheries for skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in the Pacific (Bour and Galenon 1979; Kearney[2]) the need for information on this resource is becoming increasingly important for rational management. One method that might provide the quantitative information necessary is that of estimating yield per recruit (Schaefer and Beverton 1963), for which an estimate of growth is necessary.

Three techniques of obtaining growth estimates are in common use: the analysis of tag and recapture data, the analysis of data from the examination of hard parts of the fish for growth marks, and the analysis of modal progressions in length-frequency distributions. All three techniques have been used, with varying success, throughout the world for both yellowfin and skipjack tunas. The results of these studies have recently been reviewed by Le Guen and Sakagawa (1973) and Josse et al. (1979). Both studies recalculated published growth estimates using standardized procedures and indicated that, since the variances of the estimates were so wide, calculated growth rates for each species were not dissimilar among geographical areas.

Studies of growth of tunas in the western Pacific have been few. Yabuta et al. (1960) investigated growth of longline-caught yellowfin tuna, Lewis[3] reported the results of aging studies of skipjack tuna using readings of "daily" growth increments on otoliths, and Josse et al. (1979) analyzed skipjack tuna growth from the results of tagging studies conducted in Papua New Guinea in 1971-74.

This paper presents the results of a program of length-frequency data collection carried out from June 1977 through December 1979 from the pole-and-line (baitboat) fishery operating in Papua New Guinea waters. The results are presented as length-frequency modal progressions from which an estimate of growth is compared with estimates available from published sources. Since the

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[2]Kearney, R. E. 1979. An overview of recent changes in the fisheries for highly migratory species in the western Pacific Ocean and projections on future developments. South Pac. Bur. Econ. Co-op., Fiji, SPEC (79)17, 99 p.

[3]Lewis, A. D. 1976. The relevance of data collected in Papua New Guinea to skipjack studies in the western Pacific. Unpubl. manuscr., 5 p. Kanudi Fisheries Research Laboratory, P.O. Box 2417, Konedobu, Papua New Guinea.

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fishery takes place on several adjacent fishing grounds, and length-frequency data are available separately for each ground, the movements of groups of fish through the fishery are investigated where possible. Finally the availability of an independent estimate of skipjack tuna growth, from the tagging data, makes possible the calculation of probable date of birth of the fish comprising each modal group, the results of which indicate possible stock structure in the Papua New Guinea region.

DATA COLLECTION

Although skipjack and yellowfin tunas are found throughout Papua New Guinea waters, the fishery (Figure 1) is centered on baiting grounds on the north coast of Manus Island, within the extensive lagoon systems around and to the east of the island of New Hanover, and in the barrier reef lagoons on the northwest coast of the large island of New Britain. During the period of the present study, these four areas were effectively separated on both a fishing fleet and geographical basis. Fleet A operated in the eastern Bismarck Sea (area 4, Figure 1), fleet B operated throughout both New Hanover fishing areas (2 and 3), and fleet C also operated from New Hanover, but at any one time fished either north (area 2) or south (area 3) of the baiting grounds. The Manus-based fishery (area 1) was exploited only occasionally and by few vessels.

Fifty-one Okinawan-type vessels (Tomiyama and Hibiya 1976) operated throughout the fishery in 1977, 47 in 1978, and 41 in 1979. Poor fishing conditions caused by the northwest monsoon season from December through February preclude intensive fishing in these areas, resulting in limited data being available for this period each year.

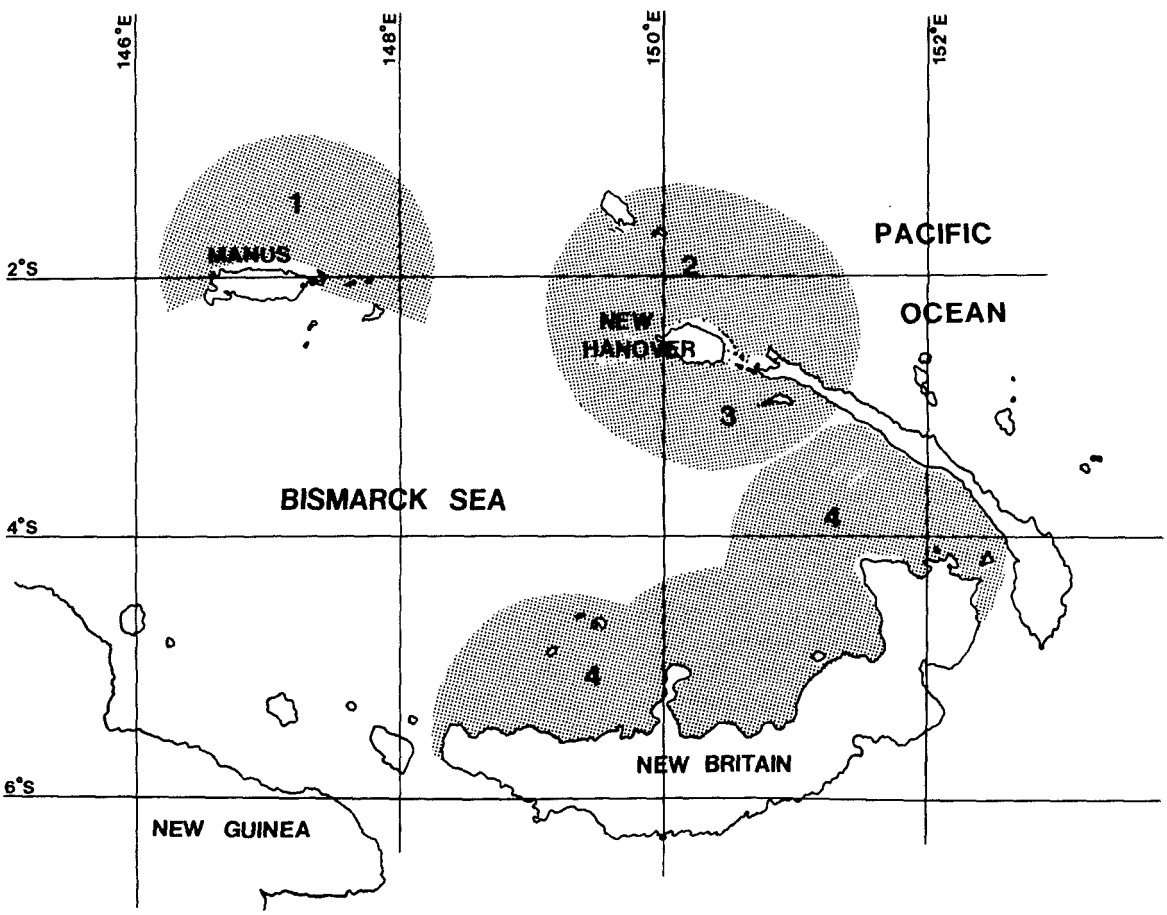

FIGURE 1.—Pole-and-line tuna fishing areas in the Papua New Guinea region (shaded): 1—north of Manus Island, 2—north of New Hanover Island, 3—south of New Hanover Island, 4—eastern Bismarck Sea.

Over the period of the study, 9.97% of the total catch consisted of yellowfin tuna, 89.83% skipjack tuna, and the remaining 0.20% other tunas and tunalike species. However, it should be noted that the proportion of yellowfin tuna in the catch is quite variable (Wańkowski 1980). The fishery since its inception in 1970 is described by Wańkowski (1980) while the 1978 and 1979 seasons are described in detail in Anonymous.[4, 5]

All vessels catch bait each day and the return to the baiting grounds is almost always accompanied by unloading the day's tuna catch onto one of the five motherships from which the fleets operate. From March 1978, length-frequency data were collected every day from each fishing area during unloading. The fork lengths (FL) of a sample of 10 skipjack and 5 yellowfin tunas from each vessel were measured to the nearest centimeter. This sample size was chosen since it represented an acceptable compromise between statistical and logistic requirements. The measurement of more than 15 fish/vessel proved impossible during busy periods of unloading, and it was considered more important to collect data from as large a number of vessels as possible than to increase sample size. Yellowfin tuna were measured only when sufficient numbers were present in individual catches to enable easy sampling, since the catches are rarely sorted by species.

During 1977, samples were measured on an ad hoc basis by Papua New Guinea Fisheries Division personnel during the course of their normal duties on board fleets operating in the Manus and eastern Bismarck Sea areas. The New Hanover fishery was sampled on a daily basis, but each sample was obtained from a small proportion of the total catch transhipped to a shore-based processing plant. It was therefore not possible in 1977 to differentiate between fish caught north or south of New Hanover.

During the 2½ yr of study, 106,933 skipjack tuna and 47,405 yellowfin tuna were measured.

DATA ANALYSIS

The length-frequency data were analyzed by area on a monthly basis. Individual monthly histograms were plotted by 1.0 cm FL interval for each of the four areas designated in Figure 1 and for the New Hanover area as a whole (areas 2 and 3, Figure 1). The separate data for north and south of New Hanover (areas 2 and 3, respectively) were obtained from fleet C only, while those for the New Hanover area as a whole were obtained only from fleet B. Monthly length-frequency distributions were therefore available separately for the Manus, New Hanover, and eastern Bismarck Sea areas.

Polymodal distributions were divided into successive unimodal distributions, using the method of "successive maxima" (Daget and Le Guen 1975). This method does not require the assumption of normality of distributions, but merely their symmetry in relation to the modal value. For samples with only one prominent mode and for the unimodal distributions resulting from the above analysis, the midpoint of the fork length interval of maximum frequency was taken as the modal length. Examples of length-frequency distributions and the resultant modal fork lengths are shown in Figure 2. Two conditions were attached to mode selection. The first was that model fork lengths were considered separate only if the midpoints of adjacent length intervals of maximum frequency were themselves separated by intervals of 3.0 cm or more. The second was that isolated peaks of only one 1.0 cm interval were not taken to represent modes (e.g., Figure 2: 1979, month 5, 61 cm).

Modal lengths were derived from all monthly samples where $n > 30$ fish (Figures 3, 4). However mean size of these monthly samples was 1,215 skipjack tuna and 578 yellowfin tuna. Only 19 (of 88) monthly skipjack tuna samples contained <400 fish and 1 <99; similarly, 21 (of 82) monthly yellowfin tuna samples contained <200 fish and 2 <49.

Because of the apparent large-scale migration between the relatively closely associated fishing areas, it was not possible to consider the results independently for each area. A serial succession of increasing modal lengths with time was designated a single group of fish distinguishable from other groups on the basis of size and progression with age. The progression which appeared to be most logical was used without taking into account the relative strength of each mode, major and minor modes being treated equally. As can be seen from Figures 3 and 4, the data does not naturally fall into conventional year-class or cohort structure. This absence of structural form, other than

[4]Anonymous. 1979. Fisheries research annual report for 1978. Dep. Primary Ind., Port Moresby, Papua New Guinea, 98 p.

[5]Anonymous. 1980. Fisheries research annual report for 1979. Dep. Primary Ind., Port Moresby, Papua New Guinea, 103 p.

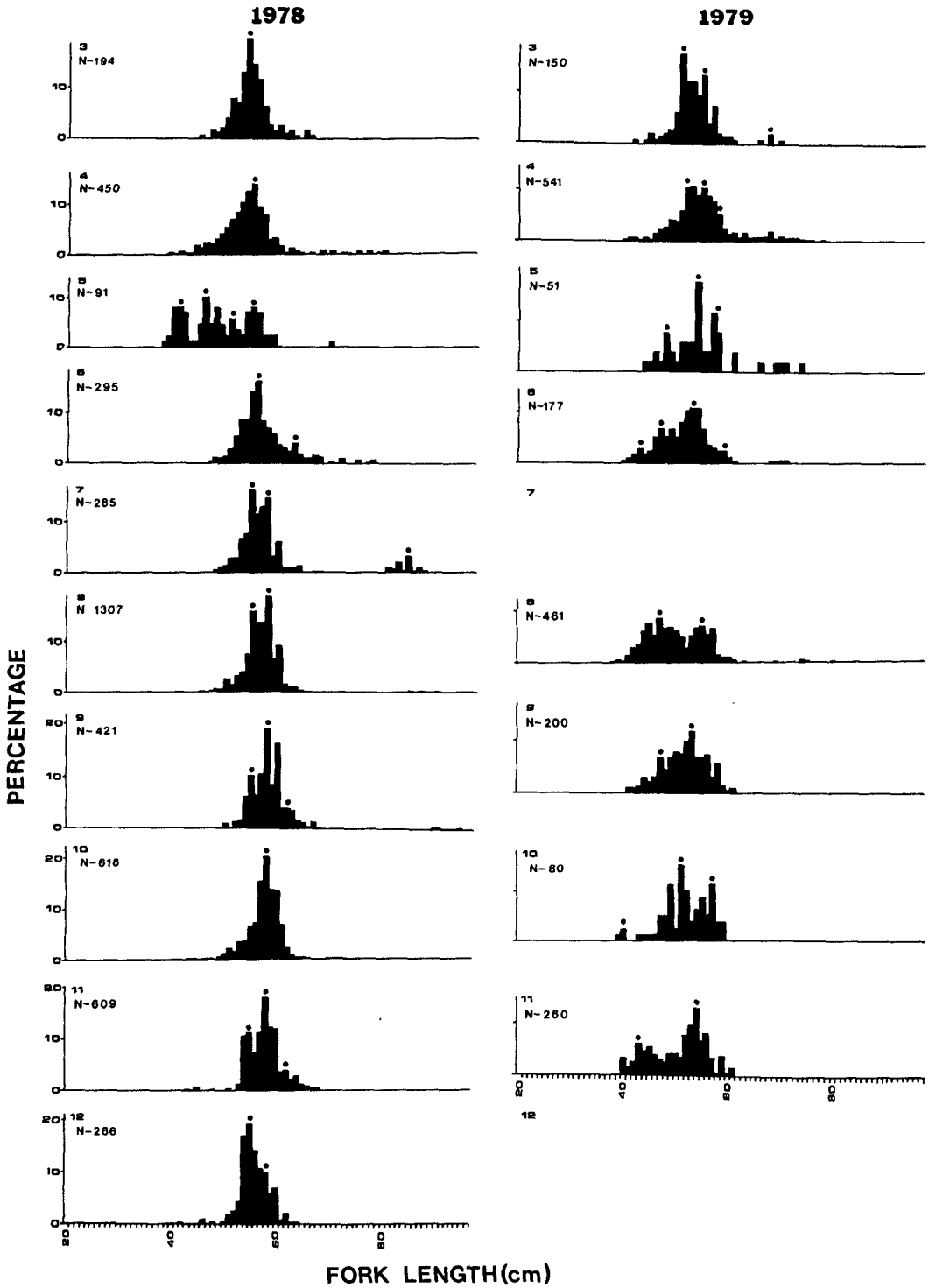

FIGURE 2.—Monthly length-frequency distributions of yellowfin tuna samples from the Papua New Guinea region from north of New Hanover (area 2) during 1978 and 1979. Modal fork lengths are indicated by dots. Note that data for July (month 7) and December (month 12) 1979 were not available.

modal progression, occurs whether the data are analyzed using all the modes as shown, or using the major mode of each monthly distribution only.

The von Bertalanffy growth function (Bertalanffy 1960) was used to describe growth. This function is usually expressed as

$$L_t = L_\infty [1 - \exp - k(t - t_0)]$$

where L_t = length at age t, L_∞ = asymptotic length, k = coefficient describing the rate of growth, and t_0 = theoretical age where L_t is zero. The Fabens' (1965) least squares procedure can be used to fit length data to the von Bertalanffy function, which then takes the form:

$$L_{t+\Delta t} = L_t + (L_\infty - L_t)(1 - \exp - k).$$

Although originally devised to fit tag return data, this procedure is equally applicable to length observations of untagged fish, and is especially useful since length at known age is not required. This procedure has been used by Rothschild (1967) and Joseph and Calkins (1969) to estimate growth of skipjack tuna from tagging data, and Le Guen and Sakagawa (1973) to estimate growth of yellowfin tuna from modal progression data.

In the present study, Fabens' (1965) procedure was used with monthly modal length data for individual groups of fish of unknown age. Estimates of L_∞ in centimeters and of k on a monthly basis were derived. Length-at-age information from published sources was used to fix the derived growth functions on a known time scale.

RESULTS

Recruitment and Exploited Size Range

Recruitment in this report refers to first entry into the fishery. Size at recruitment, as inferred from length-frequency samples, and the size range of both skipjack and yellowfin tunas exploited by the fishery varied throughout the duration of the study. The smallest size of fish of either species occurring in monthly samples was between 30 and 46 cm FL (Table 1), with the exception of a few yellowfin tuna <30 cm FL in July 1979. Skipjack tuna <46 cm and yellowfin tuna <54 cm FL were absent in February 1979. The maximum lengths of skipjack and yellowfin tunas were 74 and 96 cm FL, respectively (Table 1, Figure 5). However, few samples contained fish >69 and >85 cm FL, respectively. There were no consistent differences in size at recruitment, or in the size range exploited, among the four fishing areas.

TABLE 1.—Fork length range (centimeters) of skipjack and yellowfin tunas from all areas of the Papua New Guinea region combined, and corresponding catch per unit effort (CPUE) (metric tons per boat fishing day) and effort (number of fishing days). The fishing effort remained fairly constant from April to November of each year.

		Skipjack tuna		Yellowfin tuna		
Year	Month	Size range	CPUE	Size range	CPUE	Effort
1977	June	44-64	2.3		0.3	1,076
	July	43-65	3.0	39-92	.2	1,070
	Aug.	40-67	3.4	36-82	.4	1,093
	Sept.	38-65	1.7	37-80	.4	957
	Oct.	37-68	1.4	42-80	.4	966
	Nov.	36-68	1.7	36-77	.5	945
	Dec.	40-64	1.7	38-80	.6	579
1978	Mar.	31-69	2.2	41-80	1.4	471
	Apr.	33-69	2.4	30-80	.5	820
	May	33-69	4.6	35-81	.2	1,129
	June	40-69	4.4	34-81	.2	1,150
	July	43-69	4.4	41-88	.1	1,166
	Aug.	42-69	5.8	44-90	.3	1,168
	Sept.	40-69	6.1	46-96	.2	1,069
	Oct.	39-69	5.0	40-80	.3	1,271
	Nov.	42-68	5.0	31-80	.4	1,161
	Dec.	40-67	4.2	37-77	.4	423
1979	Feb.	46-59	5.0	54-72	.5	206
	Mar.	40-66	4.3	42-78	.4	351
	Apr.	34-65	5.5	40-78	.2	797
	May	33-68	3.3	35-80	.4	956
	June	40-70	3.5	32-83	.4	1,016
	July	40-74	2.9	24-83	.4	1,041
	Aug.	34-69	2.7	30-87	.2	922
	Sept.	33-69	2.0	31-84	.4	902
	Oct.	30-70	1.0	33-80	.6	719
	Nov.	30-70	1.1	31-90	.2	739
	Dec.	32-67	1.1	31-90	.4	276

Size at recruitment for yellowfin tuna was smaller than has been reported in the past for the eastern Pacific (Hennemuth 1961; Davidoff 1963; Anonymous[6,7]) or eastern Atlantic (Le Guen and Sakagawa 1973), where recruits are reportedly 40-60 cm and 60 cm FL, respectively, but similar to that recently reported for the eastern Pacific (Anonymous footnote 7) and for the western Indian Ocean (Marcille and Stequert 1976a). A similarity between skipjack tuna size at first recruitment in the western Pacific and western Indian Oceans is also apparent from a comparison of the results of the present study with those of Marcille and Stequert (1976b).

Suzuki (1971), Kikawa and Warashina (1972), Le Guen and Sakagawa (1973), Marcille and Stequert (1976b), and others have noted the extreme size-specificity of pole-and-line catches. In

[6]Anonymous. 1975. Annual report of the Inter-American Tropical Tuna Commission, 1974. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, Calif., 169 p.

[7]Anonymous. 1980. Annual report of the Inter-American Tropical Tuna Commission, 1979. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, Calif., 227 p.

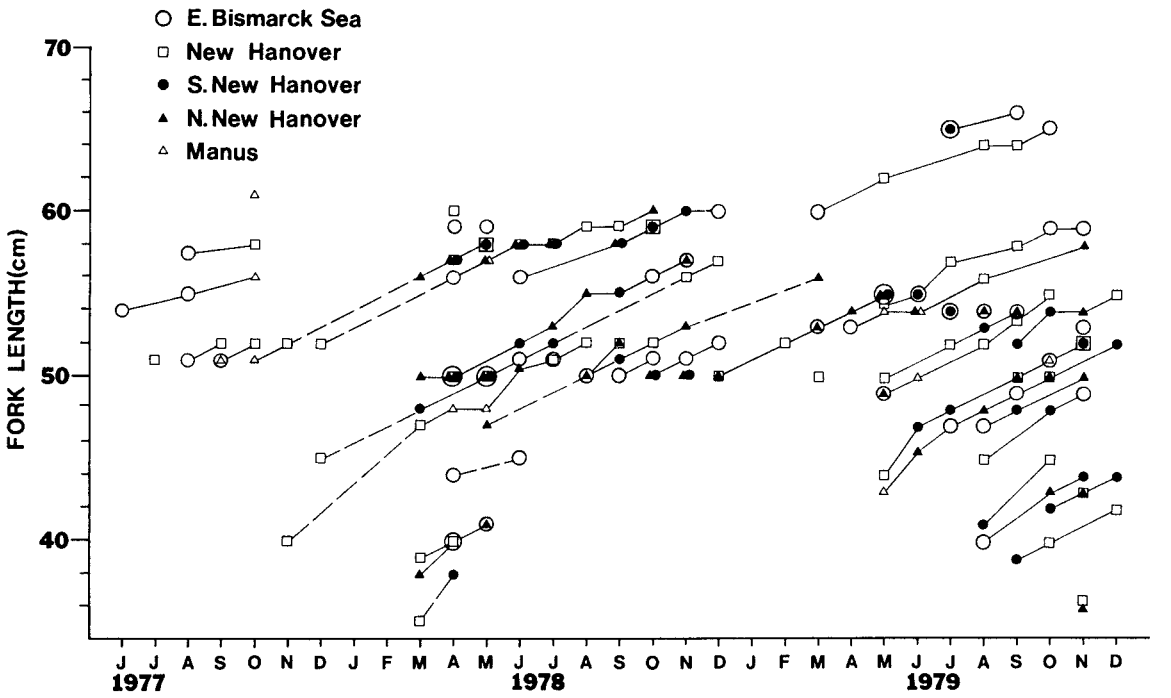

FIGURE 3.—Modal fork lengths of samples of skipjack tuna from all Papua New Guinea areas as a function of time (in months). Modal progressions are indicated by lines.

the Papua New Guinea fishery, observations have shown that vessels continually pursue and fish an individual school during periods of low catch per unit of effort (CPUE), thereby fishing few schools each day. However, during periods of high CPUE, vessels fish a large number of schools, taking fish from each school until they "go off the bite" and then moving on to a fresh school. Size-specificity of the catch, as a consequence of the fishing strategy adopted, would therefore be expected to be greatest during periods of high CPUE, vessels taking only a restricted size range of fish from each school (presumably those size classes most vulnerable to this method of fishing), and lowest during periods of low CPUE, during which a wider range of size classes would be represented in the catch.

Figures 3 and 4 show two periods, November 1977 to May 1978 and May 1979 through to the end of sampling in December 1979, during which a wide range of size classes appeared in the samples. These periods coincide with periods of relatively low skipjack tuna CPUE (Table 1). The situation is less clear for yellowfin tuna. However, since skipjack tuna composed 90% of the total catch on average, it is clear that skipjack tuna abundance would determine the adoption of a particular fishing strategy. This would therefore account for the yellowfin tuna size range, varying synchronously with that of skipjack tuna (Figures 3, 4), but independently of yellowfin tuna abundance (Table 1).

Observations from the fishing vessels during the course of the study confirmed that yellowfin tuna larger than the maximum size taken by the fishery and schools of very small skipjack tuna, both normally comparatively rare, were common throughout the fishery during late 1977 and from August to November 1979. There is therefore some indication that fishing strategy, determined by low apparent abundance, may not alone account for the appearance of small and large fish in the catch during these periods.

The results show that the timing of recruitment cannot be determined from the size composition of the landed catch. However, Ueyanagi (1970), Nishikawa et al. (1978), and Naganuma (1979) have demonstrated that skipjack tuna spawn throughout the year in the western Pacific, although in different geographical areas depending on season: a situation likely to result in continuous recruitment to the equatorial region. The re-

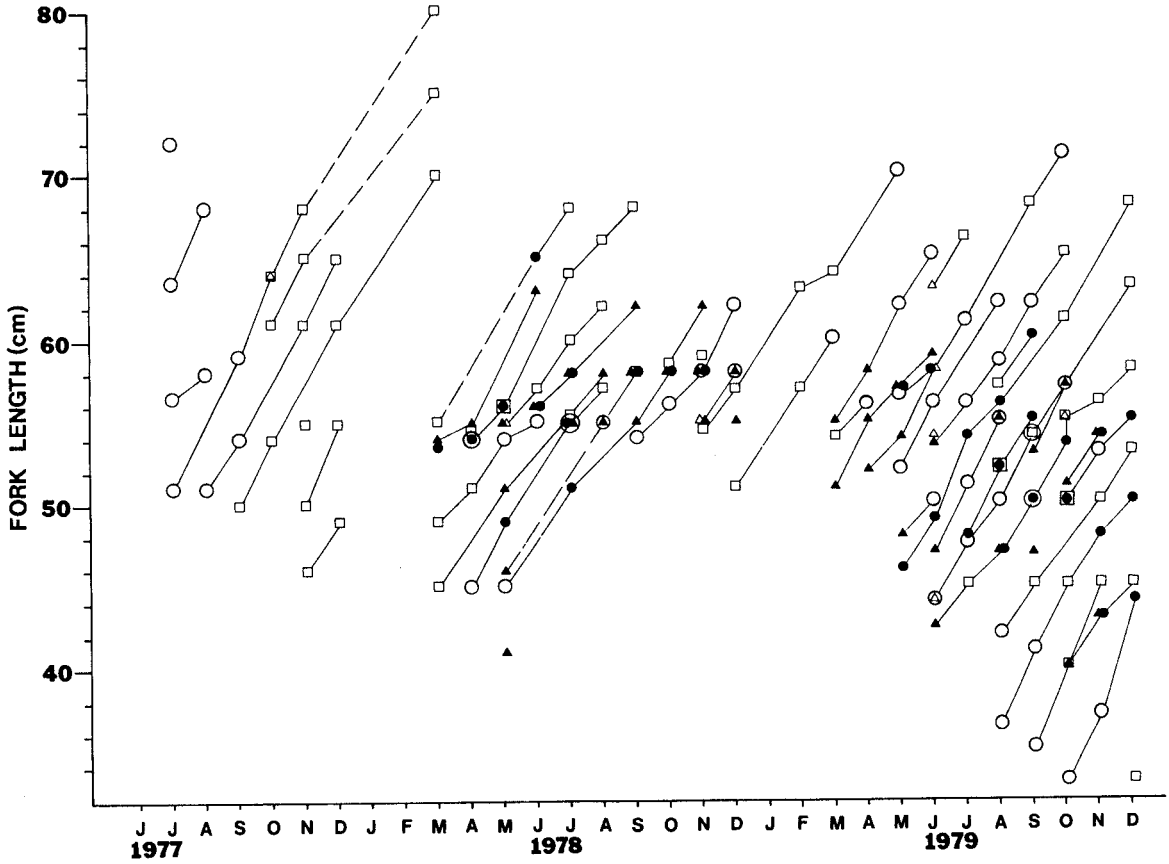

FIGURE 4.—Modal fork lengths of samples of yellowfin tuna from all Papua New Guinea areas as a function of time (in months). Modal progressions are indicated by lines. See Figure 3 for explanation of symbols.

sults of tagging studies in Papua New Guinea (Lewis 1980a, b, see footnote 8) indicate that skipjack tuna recruitment may be intermittent, and possibly dependent on periodic influxes from north and east of the area.

It has been suggested (Lewis 1980a, b, footnote 3; Anonymous[9]) that there are at least three partially mixing components to the skipjack tuna population in the western Pacific: one ranging from Japanese waters to the Equator, one centered on the Bismarck Sea and ranging to lat. 10° N, and the last extending south from the Bismarck Sea; and that these components are composed of separate spawning units, distinguishable on the basis of spawning periodicity with respect to northern and southern summers. The following analysis of data from the present study provides further evidence supporting this view.

Josse et al.'s (1979) estimates of the von Bertalanffy parameters (k = 0.94512 on an annual basis and L_∞ = 65.47 cm) for tagged skipjack tuna in the Papua New Guinea region were applied to the length-frequency modal data to estimate the dates of birth from all modal lengths available for skipjack tuna samples from the four areas. Josse et al.'s estimate is independent of the modal data, being derived from an earlier study using a different technique, and for this reason it is preferable (for present purposes) to the estimate derived in this report.

The frequency distribution of dates of birth is shown in Figure 6. The extremes of the range (pre-1975 and post-1977) are poorly represented; however, a 6-mo periodicity is indicated. Although

[8]Lewis, A. D. 1977. Tuna tagging in Papua New Guinea. Harvest, Papua New Guinea 4:13-17.

[9]Anonymous. 1976. Ad-hoc meeting of scientists to discuss skipjack fisheries developments and research requirements. Rep. meet., South Pac. Comm., Noumea, New Caledonia, 6-10 Dec. 1976, 27 p.

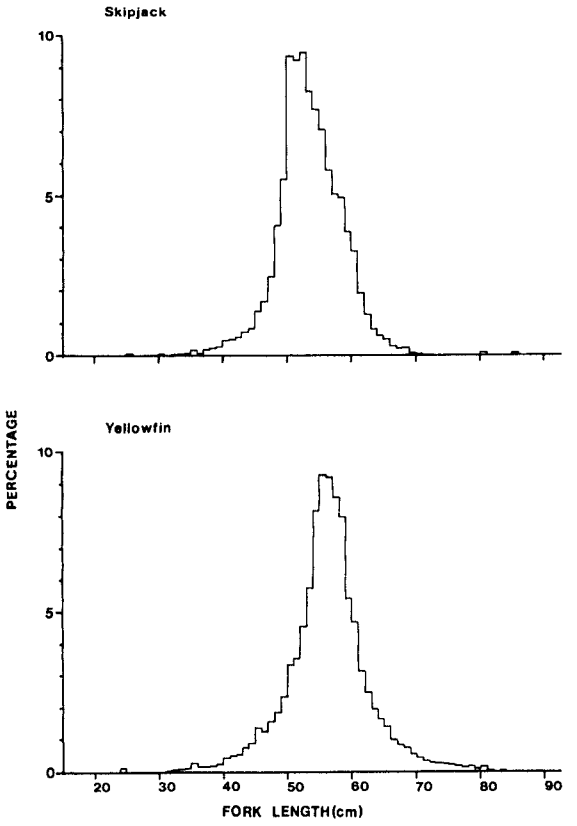

FIGURE 5.—Fork length-frequency distributions for skipjack (top) and yellowfin tunas (bottom) sampled during the study. Individual samples have been pooled for the four study areas in the Papua New Guinea region.

correspondence between 6-mo intervals and calculated peaks is not precise, considering the underlying assumption that all modal groups grew at identical rates, the observed correspondence is fairly good. The results indicate that the skipjack tuna stocks exploited by the Papua New Guinea fishery may exhibit two peaks in spawning activity, 6 mo apart.

Naganuma (1979), using gonad indices of skipjack tuna caught in the western Pacific, demonstrated the existence of two spawning groups: one spawning in southern waters in the southern summer (October-March) and the other in northern waters in the northern summer. Data for larval abundance in Papua New Guinea waters (Nishikawa et al. 1978) indicate almost identical peaks in spawning periodicity, although much continuous spawning in equatorial waters is also indicated. Spawning periodicity as determined from gonad indices and larval distribution there-

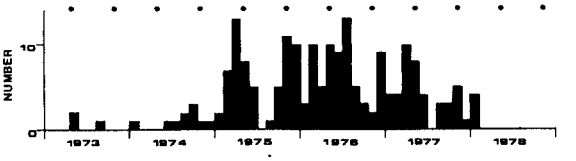

FIGURE 6.—Distribution of month of birth of skipjack tuna from the Papua New Guinea fishery calculated by the von Bertalanffy growth function, using an independent estimate of growth for all modal fork length data. Distribution is shown in one-tenths of 1 yr. Dots indicate 6-mo intervals.

fore corresponds to that determined from the results of the present study.

However, as is clear from the skipjack tuna modal data (Figure 3) and abundance (as inferred from skipjack tuna CPUE, Table 1), this possible 6-mo spawning periodicity did not result in semestral recruitment to the fishery in 1977-79. Lewis (1980a), however, reported that there were two groups of skipjack tuna present in the Bismarck Sea in 1972, apparently resulting from two periods of recruitment 6 mo or more apart. As 1972 was a year in which skipjack tuna abundance was exceedingly low, it might be expected that the consequences of possible large-scale periodic recruitment to the fishery would be more obvious then than during periods of relatively high abundance, as during the present study.

Yellowfin tuna show restricted spawning periods and semestral recruitment in many fisheries (Hennemuth 1961; Davidoff 1963; Matsumoto 1966; Le Guen et al. 1969; Richards 1969; Le Guen and Sakagawa 1973). That this is unlikely to have occurred in equatorial western Pacific waters during the period of the study is clear from Figure 4; the fairly continuous production of fish implied by the large number of modal groups passing through the fishery is unlikely to be the result of one or two short spawning periods. Although differential growth between elements resulting from a protracted spawning period might result in the observed spread in recruitment, the youth of the fish, as inferred from rate of growth estimates (Le Guen and Sakagawa 1973; present paper), would necessitate either early separation into groups of fish exhibiting different rates of growth or protracted spawning periods (perhaps continuous spawning activity).

Most identifiable groups of yellowfin tuna disappeared from the pole-and-line catch at between 62 and 71 cm FL (Figure 4). Kikawa and Warashina (1972) pointed out that the Japanese

long-range pole-and-line fisheries in the equatorial western Pacific take fish 30-100 cm FL (but mainly <70 cm), harvested well before they enter the deeper water longline fishery that exploits fish mainly >100 cm FL.

However, Wright (1980) indicated that a proportion of Japanese longline catches consist of yellowfin tuna of 70-100 cm FL which are discarded on capture owing to their unsuitability for the sashimi (raw fish) market that this fishery supplies. The equatorial western Pacific purse seine fishery exploits fish from 30 to 100 cm FL (Kikawa and Warashina 1972; Wańkowski and Witcombe[10]), about half the catch consisting of fish <100 cm. The absence of significant numbers of yellowfin tuna >70 cm in the Papua New Guinea pole-and-line catch (Figure 5) therefore indicates selectivity for smaller fish (confirmed by the absence of suitable gear, on Papua New Guinea-based vessels, for poling larger fish on board) and possible recruitment of 70-100 cm size class from the surface fishery into the longline fishery (yellowfin tuna in this region presumably spending less time at the surface with increasing age). However, that this size class of yellowfin tuna does not wholly enter deeper waters is indicated by observations of their presence in surface schools in late 1977 and late 1979, and by the fact that Japanese longliners set shallow lines when their target species is yellowfin tuna (Wright[11]).

A similar point of note is the low incidence of skipjack tuna >65 cm FL (Figure 5) in the catch. This is in contrast to the situation in the central and eastern regions of the Pacific where larger skipjack tuna are common (Rothschild 1965; Doumenge[12]), but is similar to that in the western Indian Ocean (Marcille and Stequert 1976b). Again, gear selectivity in the different regions might account for this difference. However, skipjack tuna >65 cm FL appear to compose a portion (discarded) of the longline catch in the equatorial western Pacific (Wright footnote 11). Barkeley et al. (1978) concluded that skipjack tuna >4.5 kg (about 60 cm FL) would be unable to inhabit the warm surface water of the tropics, unless they were able to make frequent incursions into cooler water, for example below a shallow thermocline.

Stock Movements

A stock is defined as the exploitable group of fish existing in a particular area at a particular time (Anonymous footnote 9). If it is assumed that a serial progression of length-frequency modes with time represents the progress of one group of fish through the fishery, then it should be possible to follow the movements of that group among the four fishing areas. While it is possible to do this, the analysis of skipjack tuna movements indicates only the complexity of the situation: groups of fish apparently moving freely and rapidly (often within 1 mo) between areas. No pattern nor periodic movement can be inferred from the present modal data. However, conclusions from Lewis (1980a, b, footnotes 3, 8) from the Papua New Guinea skipjack tuna tagging program are summarized below.

Skipjack tuna appear to be recruited from east of Papua New Guinea and from north of the Equator, and to move clockwise around the eastern and southern parts of the Bismarck Sea. Some fish appear to retrace this route up to 2 yr later, while others emigrate northward out of this area soon after recruitment. At least part of the stock, however, undergoes little translocation, remaining in one area for a considerable period of time. Most entries and exits appear to be through the northern Bismarck Sea between New Hanover and Manus. Some fish do not penetrate as far south as the eastern Bismarck Sea fishery, remaining in the New Hanover area only. While these results indicate extensive emigration and immigration, the skipjack tuna stocks cannot be considered purely transient since only a small portion of the tagged fish was recovered outside the Papua New Guinea region (although the variable distribution of fishing effort outside Papua New Guinea waters precludes definitive conclusions).

The present modal progressions indicate two types of movement of the yellowfin tuna: one commencing in the eastern Bismarck Sea, entering the area south of New Hanover and sometimes progressing to north of New Hanover (Figure 7, which shows those portions of the data in Figure 4, indicating movement of fish in the directions under discussion), and the reverse movement, indicated by the first appearance of a modal group to

[10]Wańkowski, J. W. J., and D. W. Witcombe. 1979. Fish associated with floating debris in the equatorial western Pacific purse-seine fishery. Unpbul. manuscr., 13 p. Kanudi Fisheries Research Laboratory, P.O. Box 2417, Konedobu, Papua New Guinea.

[11]Wright, A., Fisheries Biologist, Kavieng Fisheries Research Laboratory, P.O. Box 101, Kavieng, Papua New Guinea, pers. commun. 1979.

[12]Doumenge, F. 1973. The development of tuna and skipjack fisheries in French Polynesia and experience in live-bait technique. South Pac. Comm. Fish. Newsl. 10:27-30.

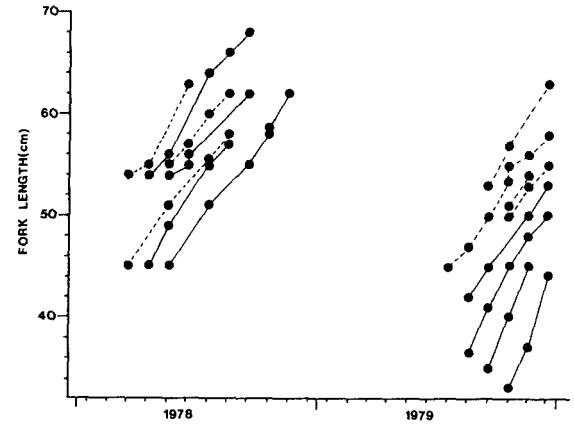

FIGURE 7.—Monthly modal progressions for yellowfin tuna in 1978 and 1979, showing apparent movement through the Papua New Guinea region from the eastern Bismarck Sea in a north and northwest direction through the New Hanover areas (line), and no apparent movement out of the area north of New Hanover (dashed line).

the north of New Hanover, or sometimes in the New Hanover area in general, and terminating in the eastern Bismarck Sea (Figure 8, which shows those portions of data in Figure 4, indicating the reverse movement of fish). A possible northward movement of yellowfin tuna recruited into the eastern Bismarck Sea in July and August 1977 is also indicated from the 1977 data (Figure 4).

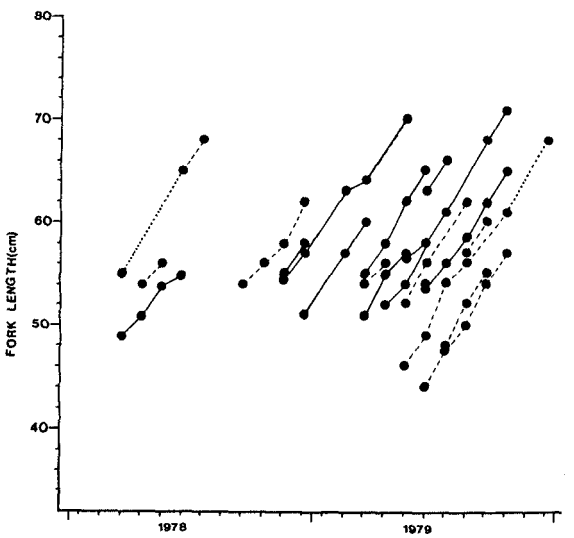

FIGURE 8.—Monthly modal progressions for yellowfin tuna in 1978 and 1979 showing apparent movement through the Papua New Guinea region from the New Hanover north area, south and southeast into the eastern Bismarck Sea area (line), and no apparent movement out of the Bismarck Sea (dashed line).

The periods of northward movement (of yellowfin tuna recruited to the eastern Bismarck Sea fishery in April and May 1978 and between August and October 1979) coincide with the appearance of small fish in the catch. However, since groups of fish of similar size appeared to move both north and south during 1978 and the first half of 1979, the direction of movement cannot be explained on the basis of size or age alone. During these periods of northward movement, all other groups of fish recruited to the fishery were restricted to the New Hanover area, almost exclusively to the north (Figure 4). These observations imply either a situation similar to that occurring in skipjack tuna where some fish penetrate no farther south than the New Hanover fishery or the northward movement of groups of fish that for some reason are not apparent in the Bismarck Sea catch. Groups of fish recruited at the same time as those moving in a southward direction (November 1978-June 1979) appeared to be restricted to the Bismarck Sea (Figure 4).

The results indicate extensive emigration and immigration of some of the yellowfin tuna stock, while other parts of the stock show little movement during their brief period of persistence in the fishery. The path taken appears similar to that shown by skipjack tuna stocks, and that proposed by Inoue (1969) for yellowfin tuna, not a surprising result in view of the geographical constraints of the region and the distribution of fishing effort. There is no evidence for emigration soon after recruitment, nor of source of recruitment, and groups of yellowfin tuna show mass movement either clockwise or anticlockwise through the Bismarck Sea with no indication of any retracing of their route.

Fundamental differences between the skipjack and yellowfin tuna stocks seem to lie in the long-term persistence of groups of skipjack tuna in the fishery (Figures 3, 4), probably an important function of their slower growth rate (Josse et al. 1979; present paper), while, in contrast, yellowfin tuna stocks remain in the exploitable size range for a few months only, since their faster growth rate (Le Guen and Sakagawa 1973; present paper) soon takes them out of the exploitable size range.

Estimated Length-At-Age

The von Bertalanffy parameters estimated from all data and all areas combined were $k = 0.0429$ and $L_\infty = 74.8$ cm for skipjack tuna, and $k = 0.0243$

and L_∞ = 180.9 cm for yellowfin tuna (k in both cases is estimated on a monthly basis). The calculated length-at-age curves are shown in Figures 9 and 10, which also include modal progression data fitted to the curve. Tables 2 and 3 list modal progressions used in the estimations. The mean square error was calculated from the formula:

$$\frac{\sqrt{\Sigma r^2}}{N}$$

where N is the number of pairs of observations and r a coefficient which is minimized in the curve fit.

$$r = \sqrt{\Sigma(\hat{L} - Li)^2}$$

where $\hat{L}$ is the length predicted by the particular curve and Li the observed length value. Since age at length data are unknown, r is not, strictly speaking, a true correlation coefficient. The mean square error was found to be 0.74 for the estimate of skipjack tuna growth and 2.01 for that of yellowfin tuna growth.

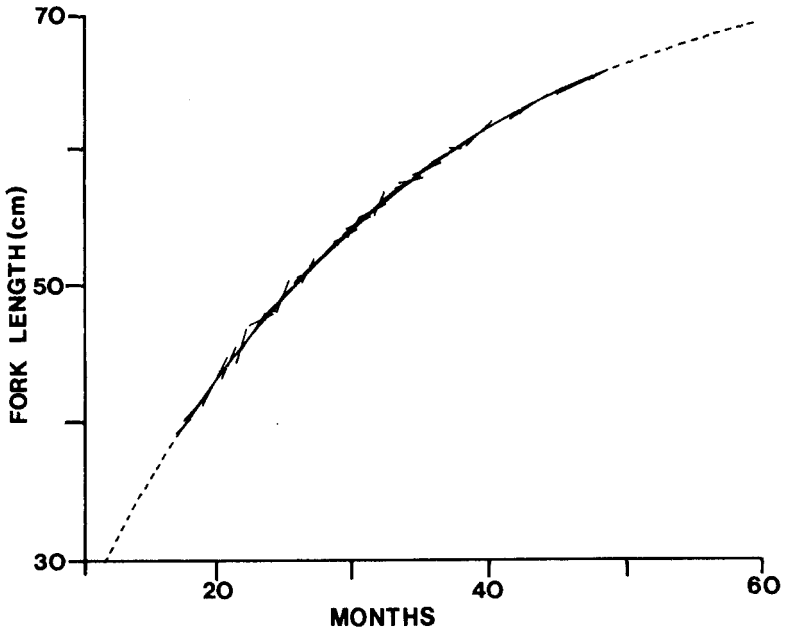

FIGURE 9.—Plot of length at age for skipjack tuna derived from all modal progressions for all Papua New Guinea areas combined, fitting the von Bertalanffy function by Fabens' (1965) procedure. Original modal data are shown fitted to the curve. The time scale is in elapsed months and does not indicate apparent age. Dashed line shows extrapolation beyond the range of observations.

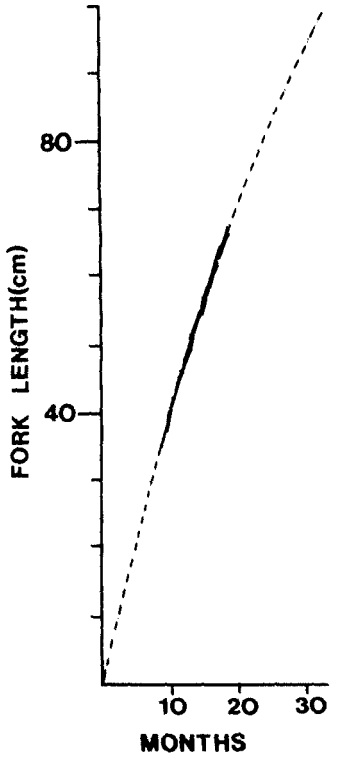

FIGURE 10.—Plot of length at age for yellowfin tuna derived from all modal progressions for all Papua New Guinea areas combined, fitting the von Bertalanffy function by Fabens' (1965) procedure. Original modal data are shown fitted to the curve. The time scale is in elapsed months and does not indicate apparent age. Dashed line shows extrapolation beyond the range of observations.

TABLE 2.—Modal progressions for skipjack tuna used to estimate fork length (centimers) at age. Modal progressions indicated by solid lines; $n = 83$.

Year	Month																				
1977	June		54																		
	July																				
	Aug.	57.5	55	51																	
	Sept.			52	51																
	Oct.	58	56		52	51															
	Nov.					52															
1978	Mar.	56				48	47								38	39					
	Apr.	57	56		50										40	40					
	May	58	57			50	48								41						
	June		58	56	52	51	50.5														
	July				53	52	51														
	Aug.		59				52	50	50												
	Sept.			58	55			51	52	50											
	Oct.		60	59	56			52		51	50										
	Nov.			60	57	56		53			51										
	Dec.			60		57					52	50									
1979	Jan.											52									
	Feb.											53									
	Mar.				60							54				53					
	Apr.											55	54.5	50	49	44	43				
	May				62								55	54	50	47	45.5				
	June												57		52	48	47				
	July			65										56	53		48	45			
	Aug.				64		47	41	40						54	50	49				
	Sept.			66		52	48			39			58			51	50	48			
	Oct.				65			45	43	40			59		55			49			
	Nov.					54	50		44	43				58		52	52				
	Dec.					55				44	42										

TABLE 3.—Modal progressions for yellowfin tuna used to estimate fork length (centimeters) at age. Modal progressions indicated by solid lines; $n = 105$.

Year	Month																				
1977	July	63.5	56.5	51																	
	Aug.	68	58		51																
	Sept.			59	54	50															
	Oct.			64		54	61														
	Nov.			68	61		65	50	46												
	Dec.				65	61		55	49												
1978	Jan.																				
	Feb.																				
	Mar.	54	49	45		70															
	Apr.	55	51		54		45														
	May		54	51	56		49	45	55												
	June	63	56						57	65											
	July		58	55.5	64		55	51	60	68											
	Aug.			58	66		57		62		55										
	Sept.		62		68			55			58	54									
	Oct.							58				56	58.5								
	Nov.											58	62	54.5	55						
	Dec.											62		57	58	51					
1979	Jan.													63		57					
	Feb.													64		60					
	Mar.	55	54	51										70							
	Apr.	58	56	55	52																
	May	62		57	54	46	48	52	56.5												
	June	65			58	49	50	56	58	44	47	53.5	63								
	July				61	54				46.5	51	56	66	45	48						
	Aug.					56		62		50	55	58.5		47	52	36.5	42	57			
	Sept.	53			68					54		62		50	55	41	45	60	35		
	Oct.	57	33	50	71	61	51			57		65		53.4		45			40		
	Nov.		37	53			54	43						56		48	50		45		
	Dec.		44	55		68		45		63				58		50	53				

DISCUSSION

The use of the von Bertalanffy function for estimating length-at-age implies that this function is a valid description of growth of skipjack and yellowfin tunas and that growth of all groups of each species is identical. Kearney (1978) has speculated that growth of skipjack tuna may be better represented by a number of linear stanzas, and an examination of the modal progression data indicates a disparity in growth rates among groups of fish. It should be noted that Knight

(1968), and others since, have pointed out the dangers of extrapolating the results beyond the range of observations on which they are based. However, provided that these limitations are recognized, and the results considered as representative of average growth of the stock, the length-at-age data are reasonable estimates of growth during the period of the study.

However, several qualifying comments must be made regarding these estimates. Length-frequency samples are subject to errors from two main sources: 1) Suzuki (1971) showed that samples obtained using a size-specific fishing technique are unlikely to be representative of the size class sampled. Fish at either extreme of the size range would be underrepresented: the mean length of modal groups is likely to be overestimated at the lower extreme and underestimated at the upper. 2) Josse et al. (1979) demonstrated that the modal progression method is sensitive to inadequate sampling: estimated growth rates vary widely if few landings are sampled. However, since daily landings from virtually every operating vessel were sampled, possible problems arising from the second source of error were minimized, if not eliminated entirely. The modal progression method itself is considered to be subjective (e.g., Joseph and Calkins 1969), both in view of the methods used to determine modal lengths and in connecting modal values to form serial progressions. However this technique has proved effective provided that the derived growth functions are considered estimates only.

Various studies on the growth of skipjack and yellowfin tunas have been conducted throughout the world, but few have been carried out in the western Pacific. Good estimates for the growth of medium-sized skipjack tuna are available from the Papua New Guinea tagging study. As Le Guen and Sakagawa (1973) pointed out, a comparison of the von Bertalanffy parameters k, L_∞, and t_0 often gives the misleading impression that growth is different in different regions. Two recent studies on yellowfin and skipjack tuna growth (Le Guen and Sakagawa 1973; Marcille and Stequert 1976b) compare these parameters from various regions and studies. In this paper, calculated growth curves from various studies in the Pacific Ocean are compared with those obtained by the present study. Such comparison requires the use of a common time base, in the form of apparent or estimated age, which may be achieved by fixing one common age at length for each species. In the absence of a reliable method for aging skipjack or yellowfin tuna it is necessary to estimate likely age at length by combining results obtained using several techniques.

Estimates of fork length of skipjack tuna at age 12 mo agree very closely. Batts (1972) and Cayre[13] used dorsal spine readings to obtain lengths of 40.6 and 40.7 cm for the western and eastern Atlantic. Yoshida (1971), using modal progression data from juveniles recovered from the stomachs of billfish, and Uchiyama and Struhsaker[14] from readings of sagittae, estimated lengths of 35.0 and 42.6 cm for the central Pacific. Finally Lewis (footnote 3), also reported in Josse et al. 1979) reported estimates from Papua New Guinea waters of between 40.0 and 45.0 cm, again from sagittal readings. In the present study an approximate average of these quoted figures was used: 40.0 cm at 12-mo age.

In comparing growth curves for skipjack tuna from different regions, only those from the Pacific have been used (Figure 11), since Josse et al. (1979) showed that, due to sample variability, no significant difference was detectable in growth among regions, nor between growth in the eastern and western Pacific as calculated from tagging studies. Underestimation (Josse et al. 1979) of growth of larger fish and their low L_∞ (65.47 cm) may account for the difference in slope of the two curves derived for Papua New Guinea skipjack tuna, and for the difference in the two values of k (Josse et al. 1979: $k = 0.9451$; present paper: $k = 0.5148$, both estimated on an annual basis).

Age at length estimates for yellowfin tuna obtained from scale readings and modal progression data show good agreement over the range of observed values only (Suzuki 1971; Le Guen and Sakagawa 1973), with the exception of the study by Yabuta et al. (1960) which appears to have underestimated growth rate. Estimates for age at length have been obtained for yellowfin tuna from the Atlantic from scale readings by Yang et al. (1969), whose observed fork lengths averaged 66.1 cm at 18-mo age, and by calculation from spawning and recruitment data (Le Guen et al. 1969). The latter study estimated fork length at 18 mo to

[13]Cayre, P. 1978. Determination de l'age de listao *Katsuwonus pelamis* L., debarques a Dakar. Int. Comm. Conserv. Atl. Tuna, Collect. Sci. Pap., SCR 78/50.

[14]Uchiyama, J. H., and P. Struhsaker. 1975. Age and growth of skipjack tuna, *Katsuwonus pelamis*, yellowfin tuna, *Thunnus albacares*, and albacore, *Thunnus alalunga*, as indicated by daily growth increments of sagittae. Int. Comm. Conserv. Atl. Tuna, SCRS 75/57.

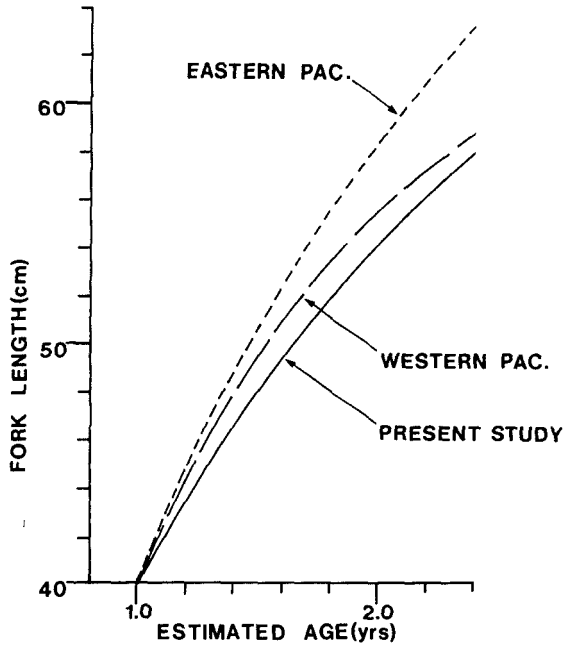

FIGURE 11.—Comparison of growth curves for skipjack tuna from the Pacific. Growth in the eastern Pacific (dashed line) was recalculated from various tagging studies by Josse et al. (1979); in the western Pacific from tagging (Josse et al. 1979, broken line) and modal progressions (present study, line). All are adjusted to a common base age of 12 mo at 40.0 cm FL. Data from Josse et al. (1979) were calculated by them using Tomlinson's (1971) least squares procedure.

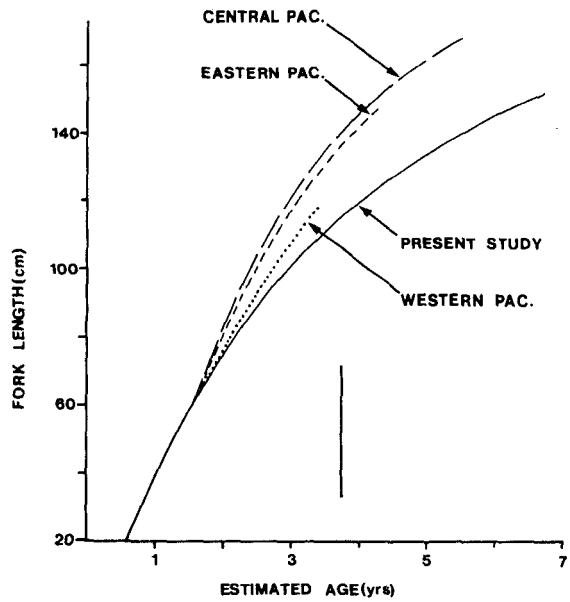

FIGURE 12.—Comparison of growth curves for yellowfin tuna from the Pacific. Eastern Pacific (Davidoff 1963, dashed line); central Pacific (Moore 1951, broken line); western Pacific (Yabuta et al. 1960, dotted line); and present study (line). All were recalculated using Fabens' (1965) least squares procedure. Vertical bar indicates limits of data used to derive the present curve; extrapolation beyond this range is for comparison purposes only.

be 60.0 cm, the value used in the present comparison.

Growth estimates of yellowfin tuna from the eastern Pacific (Davidoff 1963), central Pacific (Moore 1951), and western Pacific (Yabuta et al. 1960) were recalculated by Le Guen and Sakagawa (1973) using Fabens' (1965) method and are compared with the results of the present study (Figure 12). The recalculated lengths-at-age were in all cases similar to those obtained by the original authors. Although the above studies were carried out on large fish within the 47-170 cm FL range, their L_∞ values were only slightly higher (188.4-200.3 cm) than that obtained in the present study. The major difference lies in rate of growth, and, although extrapolation of the present results beyond 71 cm is dangerous, these results and those of Yabuta et al. (1960) imply that growth of yellowfin tuna in the western Pacific may be substantially slower than in the central and eastern Pacific. Marcille and Stequert (1976a) studied growth of pole-and-line caught yellowfin tuna of a similar length range (45-75 cm FL) in the equatorial western Indian Ocean. Their reported growth rate of 17-19 cm/6 mo for this size range of fish is similar to the results of the present study. A further possible explanation for this apparent disparity between growth in large and small yellowfin tuna may be simply that the von Bertalanffy function does not adequately describe yellowfin tuna growth, and that yellowfin tuna may undergo changes in growth pattern, due to movement into deeper water, for example.

A point of ecological importance is the great difference in growth rate between skipjack and yellowfin tunas of the same size. Yellowfin tuna grow to over 180 cm FL, over twice the length of skipjack tuna and almost 20 times the body weight. Studies on skipjack and yellowfin tunas' bioenergetics (Kitchell et al. 1978), although indicating a qualitative similarity between the two species, demonstrated that the metabolic rate of adult skipjack tuna, unlike that of yellowfin tuna and most other fishes, is independent of body weight. This may reflect the apparently less efficient hydrodynamics of skipjack tuna, a conse-

quence of the absence of a swim bladder and relatively small surface area of the pectoral fins, in comparison with yellowfin tuna.

Although over half of the tuna schools in Papua New Guinea waters are pure skipjack tuna (West and Wilson[15]), about 40% contain a mixture of yellowfin and skipjack tunas, and only about 5% are pure yellowfin tuna. Length-frequency sampling has demonstrated that yellowfin and skipjack tunas taken from any single mixed school comprise a similar size range, although observations indicate that larger yellowfin tuna (estimated to be in the 70-130 cm size range) are frequently present. Since yellowfin tuna grow so much faster than skipjack tuna, the yellowfin tuna members of a mixed school must, within a matter of a few weeks, outgrow their skipjack tuna counterparts. Such a situation would lead either to the break-up of the school as a consequence of divergence in size, or persistence of large-size yellowfin tuna in a school comprising mainly smaller skipjack tuna. Observations have indicated that the latter situation occurs during certain periods.

ACKNOWLEDGMENTS

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GROWTH, REPRODUCTION, AND FOOD HABITS OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, OFF CENTRAL CALIFORNIA

MILTON S. LOVE AND WILLIAM V. WESTPHAL[1]

ABSTRACT

We collected data on age-length and length-weight relationships, age at first maturity, spawning season, fecundity, and food habits of olive rockfish, *Sebastes serranoides*, off Diablo Cove, near Avila, California. Fish were aged from otoliths. Von Bertalanffy age-length parameters for females were $L_\infty = 51.9$, $k = 0.18$, and $t_0 = -1.57$; for males $L_\infty = 43.3$, $k = 0.27$, and $t_0 = -1.03$. Females grew at a faster rate than males beginning at the age where most males were mature. Age at first maturity ranged from 3 to 8 years, most fishes maturing by age 6. Olive rockfish spawned once per season, between December and March, with peak spawning in January. Fecundity ranged between 30,000 and 490,000 eggs. Small individuals preyed primarily on plankton, and larger ones concentrated on fishes, squids, and octopuses.

The rockfishes (Scorpaenidae: *Sebastes*) are an important constituent of many marine communities in the eastern North Pacific. Sixty-nine species are known to inhabit these waters (Lea and Fitch 1979) and members of the genus frequent virtually every habitat from intertidal regions to depths of well over 1,000 m.

Though these fishes were of some importance in commercial and sport fisheries in the past, population declines of more popular fishes have led to a steady increase in rockfish demand. Commercial rockfish catches in the Northeast Pacific exceeded 30,000 t in 1978 (Pacific Marine Fisheries Commission 1980) and in California, rockfishes are the most important sport fishes, by number, in party boat catches (Pinkas 1977).

Major, deeper water, commercially important species, such as Pacific ocean perch, *S. alutus* (Westrheim 1973; Gunderson 1977; Wishard et al. 1980); chilipepper, *S. goodei*, and bocaccio, *S. paucispinis* (Phillips 1964; Wilkins 1980; Wishard et al. 1980); and yellowtail rockfish, *S. flavidus* (Phillips 1964; Carlson and Haight 1972; Wishard et al. 1980) have received most attention from researchers. By contrast, with the exception of blue rockfish, *S. mystinus* (summarized in Miller and Geibel 1973), there are few papers on inshore rockfishes.

The olive rockfish, *Sebastes serranoides*, composes a major portion of the sport fish catch, both from party boats and private vessels, along southern and central California (Miller and Gotshall 1965; Wine and Hoban[2]; Maxwell and Schultze[3]). It lives in areas of reef and kelp, from Del Norte County, Calif., to San Benito Island, Baja California, Mexico, and is most abundant in depths of 5-100 m.

Olive rockfish are active, fast-swimming, streamlined predators, usually found in the water column, but occasionally hovering over or resting upon rocky substrates (Quast 1968a; Hobson and Chess 1976; Love and Ebeling 1978). Juvenile olive rockfish are primarily midwater feeders, preying upon zooplankton and small fishes, though some substrate feeding (on isopods, caprellid amphipods, etc.) has been noted (Quast 1968b; Hobson and Chess 1976; Love and Ebeling 1978). No data were available on the food habits of adults. Once they settle out of the plankton, individuals apparently grow to adulthood in a relatively small, circumscribed area (Love 1980) and reefs can be readily depleted of large individuals by overfishing. Off Santa Barbara, Calif., the diminishing sport catch of olive rockfish is now mostly of juvenile and subadult fish, younger than the age of first maturity (Love 1980). Yet, despite

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[2]Wine, V., and T. Hoban. 1976. Southern California independent sportfishing survey annual report July 1, 1975-June 30, 1976. Calif. Dep. Fish Game, 109 p.

[3]Maxwell, W. D., and D. L. Schultze. 1976. Southern California partyboat sampling study. Calif. Dep. Fish Game, Mar. Res. Adm. Rep. No. 76-3, 18 p.; 76-6, 18 p.; 76-9, 13 p.

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the importance and vulnerability of the olive rockfish, little was known about its life history.

METHODS

Specimens were collected between 1972 and 1977, at a group of shallow-water pinnacles, about 11 km west of Avila, Calif. (Figure 1). These pinnacles, at depths of 20-30 m, are situated 100-300 m offshore from Diablo Cove and North Cove, and rise to within 5-10 m of the surface. Brown algae (predominantly *Nereocyctis* sp.) grow on the shallower reefs during summer and fall. Sampling was sporadic until 1975, when, with a few exceptions, monthly collections were made through 1977.

Specimens were collected by hook and line and by pole spear (in about equal proportions), immediately placed on ice aboard the diving vessel, and then frozen for later examination ashore.

All specimens were measured (total and standard lengths—TL, SL) to the nearest millimeter and weighed to the nearest 0.1 g. Individuals larger than about 15 cm TL were sexed and their gonads weighed to the nearest 0.1 g.

Age Determination

Attempts to age rockfish have utilized various calcified structures (scales: Phillips 1964; Miller and Geibel 1973; otoliths: Chen 1971; Patten 1973; Westrheim and Harling[4]; vertebrae, opercles, otoliths, scales, anal pterygiophores, etc.: Six and Horton 1977), each with varying success. Otoliths and scales have been most useful, and in this study fish were aged with saccular otoliths. Sagittae were removed from 616 (320 female and 296 male) specimens. Otoliths were cleaned and stored in water. Often thick and difficult to read, otoliths from *S. serranoides* older than about 7 yr were immersed in clove oil for several months to increase their transparency. A chalky coating covering an occasional otolith was cleared away with a weak hydrochloric acid solution. Care was taken to prevent dissolving annuli at the otolith margins.

Otoliths were placed in a black-bottomed watchglass filled with water (or clove oil) and read under a dissecting microscope at a magnification of 10×. All otoliths were read twice, by the senior author, approximately 2 mo apart. Agreement between reading was highest (100%) in 0-yr fish, declining to 25% in 14-yr-olds (Table 1). If the readings did not agree, the otoliths were read again. The value of two coincident readings was accepted as the best estimate of age. If all three readings were different, the midreading was accepted. A few otoliths were rejected as unreadable due to fluctuations in readings of as much as 4 yr.

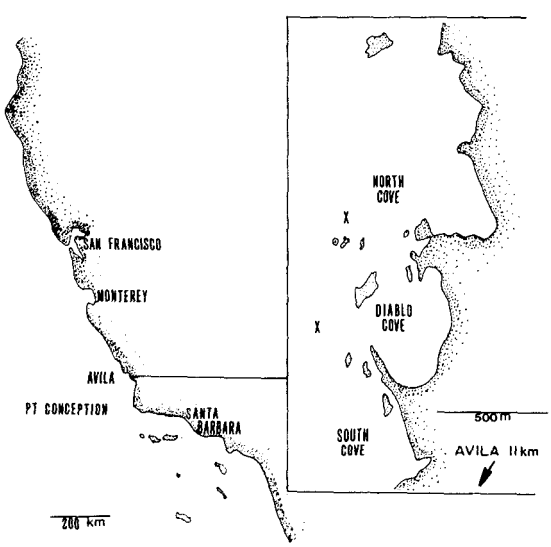

FIGURE 1.—Location of sampling sites (marked with an x) for olive rockfish off Diablo Cove, Calif.

TABLE 1.—Consistency (percent agreement) of duplicate readings from olive rockfish. The readings were made 2 mo apart by the same observer.

No. of zones	Otoliths (no.)	Percent	No. of zones	Otoliths (no.)	Percent
0	45	100	8	60	72
1	12	100	9	45	69
2	55	98	10	37	63
3	72	94	11	15	58
4	66	83	12	10	40
5	72	83	13	8	38
6	74	80	14	12	25
7	73	77			

Maturation and Reproduction

The gonads of mature olive rockfish undergo marked, yearly cyclical changes. Immediately after larvae are released spent ovaries are flaccid and reddish, purple, or gray. A resting period follows as the ovaries firm up, turning pink-red. Ovaries turn bright orange (very rarely cream-colored) and contain opaque eggs, during the mature phase, before fertilization. During the

[4]Westrheim, S. J., and W. R. Harling. 1975. Age-length relationships for 26 scorpaenids in the northeast Pacific Ocean. Can. Fish. Mar. Serv., Res. Dev., Tech. Rep 565, 12 p.

fertilized stage, the eggs are clear and turn gray as larvae develop in the ripe ovaries.

Mature males undergo a simpler cycle. Resting stage testes are small and brown, becoming larger and whitish brown as they develop. Fully developed testes are large, white, and delicate.

With this information, it was possible to determine when fish reproduced and when insemination occurred. Stages of gonad maturation (condition) in 1,056 adult olive rockfish, taken during 1972-77, were determined using the criteria of Westrheim (1975). A gonadosomatic index (gonad weight)/(total body weight) × 100 was computed to quantify changes in gonad size with season.

For fecundity estimates the ovaries of 83 mature fish captured in October and November were placed in modified Gilson's solution (100 ml 60% isopropanol, 880 ml freshwater, 15 ml 80% nitric acid, 18 ml glacial acetic acid, and 20 g mercuric chloride—Bagenal and Braum 1971) to harden the eggs and were periodically shaken to loosen them from ovarian tissue. Eggs were kept in the solution for about 2 mo, after which the fluid was poured off and replaced with water. Before eggs were counted, the ovaries were further broken up and repeatedly washed with water to remove remaining connective tissue. The eggs were placed in a larger beaker and water was then added until 2,000 ml of eggs and water had been obtained. The mixture was stirred magnetically until the eggs were homogeneously distributed throughout the water column, and a 5 ml subsample was drawn with a pipette. Three subsamples were taken.

Eggs in each subsample were counted, using a dissecting microscope, and the mean number per milliliter was calculated for the three subsamples. Fecundity was then estimated by back calculation.

Food Habits

Specimens were collected nearly every month between May 1975 and April 1977 by hook and line and pole spear (in about equal proportions), immediately placed on ice aboard the diving vessel, and frozen soon after for later examination ashore. A total of 591 specimens were collected, of which 374 (63.3%) had some food in their stomachs. We took precautions that only artificial lures were used and chumming or other disturbances were avoided, so that sampling method did not bias the stomach content composition.

Stomach contents were sorted taxonomically into 17 food items and the volume of each category was measured by liquid displacement. Food items were also grouped into three prey types (substrate oriented, nekton, and plankton) based on prey behavior and habitat. Nektonic prey included all nonlarval fish and squid. Substrate-oriented prey included all prey (except fish) that live on or about reef and plant surfaces; these may be motile, such as octopus, or attached, like algae.

To examine seasonal variation in diet within each size class of olive rockfish (except 10.1-20.0 cm which had too few specimens), food data was pooled by seasonal periods roughly corresponding to "upwelling" (March-August) and "oceanic" (September-February) oceanographic regimes off the Avila area (Bakun 1973).

RESULTS AND DISCUSSION

Age and Growth

There was no published work in aging olive rockfish (with the exception of a few fish mentioned in Burge and Schultz[5]), and the use of the otoliths in age studies had not been validated. To determine if the opaque and translucent zones were annular, we observed the development of the opaque zone on the edge of otoliths of fish from Avila, taken during a 5-yr period. The occurrence of a particular zone among most or all individuals during one part of the year would indicate that the zones were suitable for age determination (Williams and Bedford 1974; Dark 1975). Because the opaque zones become narrow and difficult to distinguish in older fish and the timing of zone deposition may be influenced by the species' age or state of maturity (Williams and Bedford 1974; Dark 1975), we limited sampling for otolith validity to 1- to 3-yr-old (immature) olive rockfish.

Data indicated that the opaque zone deposition was seasonal (Figure 2). The percentage of otoliths with opaque edges was low during fall and winter, but rose abruptly during late spring and peaked in summer months. Hence, the production of opaque zones coincides with the upwelling period along central California (Bakun 1973) and probably reflects increased feeding and growth. The percentage of opaque zones during the early spring may be underestimated as the newly deposited opaque material is quite thin. On the other hand,

[5]Burge, R. T., and S. A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 19, 433 p.

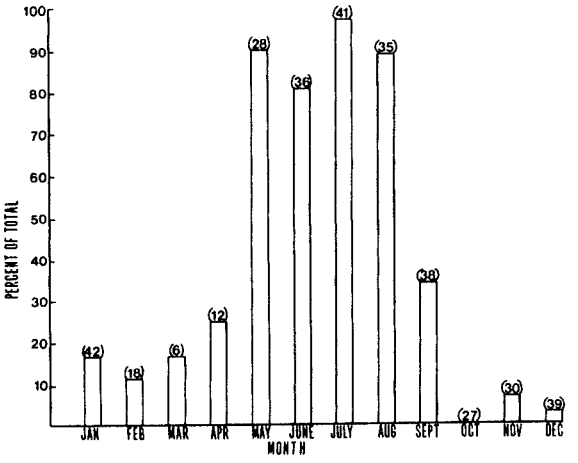

FIGURE 2.—Monthly percentages of 1- to 3-yr-old olive rockfish with opaque margins. Sample size is in parentheses.

the beginnings of the transparent zone during the fall are readily apparent.

Lengths at ages were estimated by direct observation of otolith annuli, back calculation of annuli, and through the von Bertalanffy growth curve model. In this model, the formula

$$L_t = L_\infty [1 - \exp -k(t - t_0)]$$

where L_t = length at time t
L_∞ = theoretical maximum length
k = constant expressing the rate of approach to L_∞
t_0 = theoretical age at which $L_t = 0$

was fitted to the direct observation age-length data.

We transformed the male and female von Bertalanffy growth equations to linear form (Allen 1976) and compared these by analysis of variance. Females were found to grow significantly faster than males ($F = 19.08$, $P < 0.01$), hence we have separated growth data by sex (Table 2).

Mean lengths at ages obtained by direct observations of annuli and as generated by the von Bertalanffy equations are plotted to age 14 (Figure 3). Through direct observation of annuli, we found

TABLE 2.—Parameters of the von Bertalanffy equation for olive rockfish off Diablo Canyon, Calif.

Sex	L_∞	SE	k	SE	t_0	SE
Females	51.90	0.93	0.18	0.01	−1.57	0.23
Males	43.30	.45	.27	.02	−1.03	.19

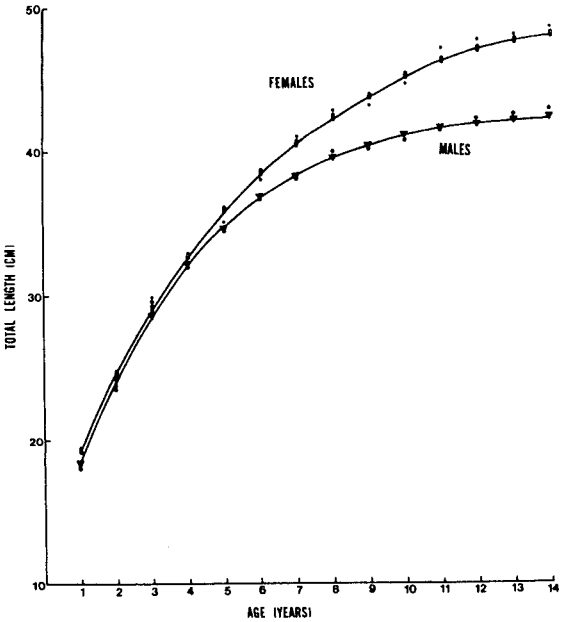

FIGURE 3.—Von Bertalanffy growth curves of female (circles) and male (triangles) olive rockfish. Also included are mean lengths at ages (females—stars, males—dots) computed from direct observation of otolith annuli. Based on 320 females and 296 males taken off Diablo Cove, 1972-77.

a few individuals to live to be as much as 25 yr. However, our samples of fishes older than about 14 yr were few, and older fish played little part in growth calculations. Back-calculated lengths (Tables 3, 4) were computed to age 12. Otoliths of fish older than 12 yr were often unusable for back calculations, because these fish laid down heavy layers of opaque material along the axis used to measure annuli, making measurements difficult.

All three measures of growth yielded similar results. Mean lengths at age for females and males were similar through age 4. Females outgrew males beginning at age 5, the age at which over 50% of the males were mature. Both male and female olive rockfish had k values (0.27 and 0.18, respectively) higher than most previously studied rockfish, indicating that the species reached maximum length relatively quickly. The k-values were similar (though slightly higher for both sexes) to those of *S. flavidus* (Fraidenburg 1980; Westrheim and Harling footnote 4), a closely related species.

Because few individuals older than 14 yr were captured, estimates of length at age of older fish produced by the von Bertalanffy equation may be inaccurate. Certainly the L_∞'s are too low, as

TABLE 3.—Mean back-calculated total length (centimeters) ± 95% confidence intervals at successive annuli for male olive rockfish captured off Avila during 1972-77.

Age-group	No. of fish	1	2	3	4	5	6	7	8	9	10	11	12
1	3	17.9±5.8											
2	24	18.5±1.0	22.8±0.6										
3	40	19.4±0.4	24.8±0.6	29.7±0.6									
4	34	18.7±0.6	24.9±0.8	29.5±0.6	33.0±0.6								
5	38	19.2±0.2	24.7±0.6	29.6±0.4	33.2±0.4	35.8±0.8							
6	33	19.1±0.8	24.2±0.8	29.0±0.8	32.7±0.6	35.0±0.6	36.7±0.6						
7	33	19.2±0.4	24.7±0.4	30.0±0.4	33.1±0.6	35.4±0.4	36.9±0.4	38.0±0.4					
8	27	18.7±0.6	24.1±0.6	30.4±0.8	33.4±0.6	36.0±0.6	37.2±0.6	38.3±0.6	39.4±0.6				
9	22	18.3±0.6	24.6±0.6	29.6±0.5	32.5±0.6	35.1±0.6	37.0±0.5	38.2±0.5	39.7±0.6	40.4±0.7			
10	14	17.8±0.1	22.8±0.3	28.6±1.2	32.4±1.0	35.9±1.0	36.3±1.2	38.1±0.4	38.0±1.1	39.4±1.1	41.1±1.3		
11	5	17.5±1.4	22.4±1.8	28.2±1.8	32.0±1.5	34.1±1.8	36.1±1.7	37.1±1.9	38.1±1.8	40.2±2.0	39.4±1.9	41.0±1.7	
12	9	18.1±1.5	22.5±1.4	29.0±1.3	32.6±1.7	35.0±1.5	36.5±1.4	37.4±1.4	38.5±0.5	39.3±1.5	41.4±1.5	40.8±1.4	40.9±1.6
Average		18.5	23.8	29.4	32.8	35.3	36.8	37.9	39.0	39.9	40.9	40.9	40.9

TABLE 4.—Mean back-calculated total length (centimeters) ± 95% confidence intervals at successive annuli for female olive rockfish captured off Avila during 1972-77.

Age-group	No. of fish	1	2	3	4	5	6	7	8	9	10	11	12
1	7	19.2±2.3											
2	24	18.1±0.8	24.0±0.8										
3	32	19.0±0.6	24.5±0.6	30.0±0.8									
4	31	19.4±0.6	24.9±0.8	29.8±0.8	33.7±0.8								
5	39	19.7±0.8	24.8±0.8	30.1±0.8	33.6±0.8	36.0±1.0							
6	35	19.1±0.6	24.4±0.8	28.7±1.0	32.6±1.0	35.2±1.0	37.9±1.0						
7	39	20.5±0.6	26.0±0.8	30.6±0.8	34.1±1.0	36.6±1.1	38.4±0.8	40.7±0.8					
8	32	19.6±0.1	24.8±0.3	31.0±0.5	35.1±0.3	37.1±0.3	39.3±0.4	41.9±0.5	42.6±0.2				
9	23	18.3±0.6	24.5±0.4	30.4±1.0	33.7±0.8	36.2±0.8	38.7±0.8	40.7±0.8	42.8±0.8	42.9±0.8			
10	23	20.3±0.2	26.3±1.3	31.0±1.3	34.6±0.9	36.1±1.3	38.1±1.1	40.1±1.2	41.7±1.4	42.8±1.2	43.9±1.1		
11	10	18.2±1.2	23.7±1.3	28.6±1.4	33.0±1.4	36.1±1.2	38.1±1.6	40.1±1.7	42.1±1.6	41.9±1.6	43.1±1.8	45.2±1.8	
12	4	18.2±1.4	24.0±1.6	28.3±1.8	33.3±1.6	35.4±1.9	38.3±2.0	40.3±2.1	41.9±1.6	41.6±2.1	42.9±1.6	45.1±1.8	45.6±1.9
Average		19.2	24.8	29.9	33.7	36.2	38.5	40.7	42.2	42.4	43.5	45.2	45.6

we did capture females to 61.9 cm and males to 50.2 cm.

No marked Lee's Phenomenon was noted, though it is found in other rockfishes (Chen 1971; Miller and Geibel 1973). A possible explanation is that fish older than age 12 were not used in back calculations, and since some members of the species live to at least 25 yr, the phenomenon may not be apparent until older fish are examined.

Length-Weight Relationships

A total of 312 males and 304 females were weighed and measured. The relationships between total length and weight seemed to fit the relationships $W = aL^b$, where W = weight in grams and L = total length in centimeters, and a and b are constants. The values of a and b were determined using $\log_{10}$ transformation and fitting the values to a straight line by least squares. Females tended to be heavier at a given length (analysis of variance, $F = 15.23$, $P < 0.01$) (Figures 4, 5). To test whether this difference was an artifact caused by the larger female gonads, we subtracted gonad weight from body weight, generated the length-weight relationships for each sex and tested these between sexes. Again, females were heavier at length (analysis of variance, $F = 10.18$, $P < 0.01$).

Maturation and Reproduction

Insemination and Birthing Season

Larval release occurred from December through March, peaking during January (Figure 6). Spent females were most prevalent during early spring, followed by a June peak in resting fish and a September-October peak in mature individuals. Fertilized fish were found from November through January. Ovary weights remained essentially constant during the spring and summer (Figure 7), averaging perhaps 0.3% of body weight, occasionally as little as 0.1%. Then, during the winter and spawning season, ripe ovaries averaged 13.8% of body weight (maximum 20.7%, minimum 2.3%).

Testes sizes (based on the gonad index) were relatively constant during spring and early summer, though they began to increase in size a month or two earlier than did the ovaries of females (Figure 7). During the constant period, they remained at minimum size, about 0.1% of body

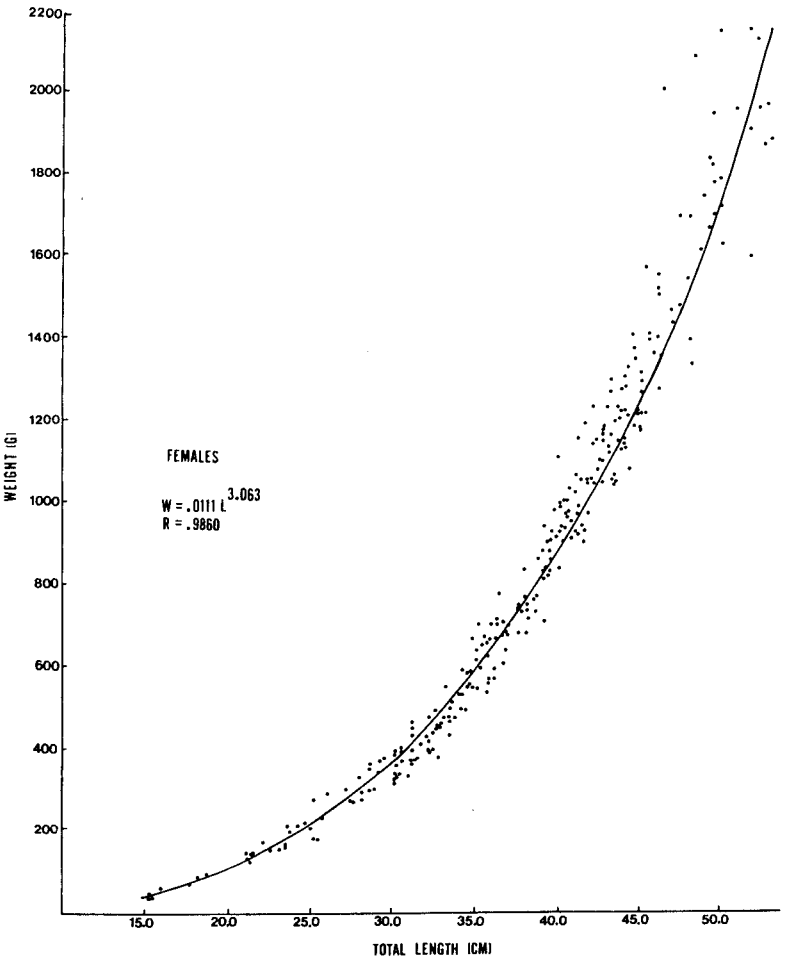

FIGURE 4.—Length-weight relationship based on 304 female olive rockfish sampled off Diablo Cove, 1972-77.

weight. They increased to 0.9-1.0% (maximum 2.2%) of body weight in late fall. It appeared that insemination occurred from October to December, perhaps peaking in November.

Moser (1967) found "a brood of advanced embryos or larvae and a series of ova undergoing vitellogenesis" in *S. chlorostictus*, *S. constellatus*, *S. eos*, *S. goodei*, *S. levis*, *S. ovalis*, *S. paucispinis*, and *S. rosaceus*, and stated that this offered direct evidence of multiple brood production. Similar findings for some of the above species were reported by MacGregor (1970), and Miller and Geibel (1973) noted that 1 of 648 *S. mystinus* examined showed multiple broods. We found no such evidence in olive rockfish, though females usually retained a few unexpelled eyed larvae, which appeared to be resorbed within a few months.

The evolution of reproductive isolating mechanisms in the genus *Sebastes* may not have included the restriction of random mating by seasonal isolation. It seems likely that the time from insemination to spawning is similar among closely related species. Rockfish species which mate over the same period, probably spawn at the same time during a later season. Olive rockfish and their presumed subgeneric congeners, *S. flavidus*, *S. mystinus*, and *S. melanops*, spawn and probably mate during the same seasons (Phillips 1964; Miller and Geibel 1973) as do other closely related rockfish species groups (e.g., *S. paucispinis-S. goodei*—Moser 1967) and other subgenera (*Sebastomus*—Chen 1971).

Instead, habitat isolation among some species (such as *S. chrysomelas-S. carnatus*—Larson 1977) may restrict interspecific mating. However, a number of species pairs (notably *S. paucispinis-S. goodei*) may aggregate together throughout the year. Even though closely related species mate in the same habitat, during the same season, hybrids

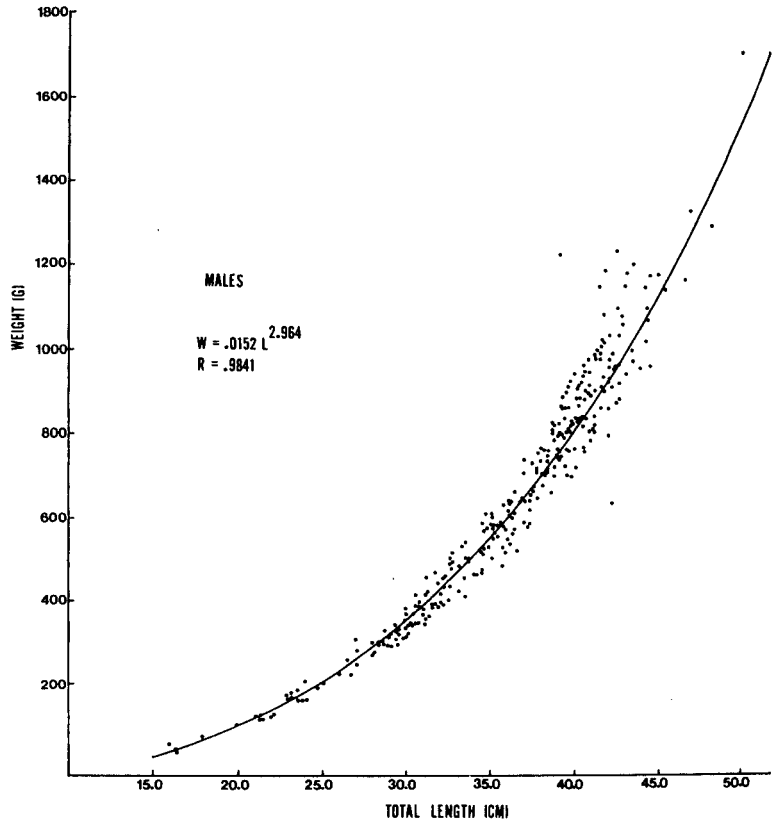

FIGURE 5.—Length-weight relationship based on 312 male olive rockfish sampled off Diablo Cove, 1972-77.

are very rare in California waters (the "hybrids" mentioned by Phillips (1964) are now recognized as distinct species), indicating that other anti-hybridization mechanisms are involved.

Though it is possible that extensive cross-specific mating occurs, and gametic or zygotic mortality prevents hybridization, it seems more likely that internal fertilization, necessitating close coordinated contact, has lent itself as a mechanism of mechanical and/or behavioral isolation. The copulatory organs of male *S. serranoides* are relatively small, thus a degree of closely coordinated movements is probably necessary to effect mating. Auditory, visual, and chemical cues may all play a part. It is known, for instance, that some rockfish species produce sounds (Hallacher 1974) and these may be used in species recognition. Deeper water species, living in relative darkness, may depend primarily on nonvisual recognition during mating season.

Size and Age at Maturity

It was often difficult to distinguish prereproductive female olive rockfish from mature late resting stage females (as noted by Westrheim 1975 and Gunderson 1977 in *S. alutus*). Females develop small orange ovaries 1 or 2 yr before they reproduce. During much of the year these "maturing" fish were easily distinguished from reproductive individuals by their consistently small, pale orange ovaries. However, during late spring and early summer, the ovaries of both reproductive and maturing fish are small and orange. Because mature and maturing females were not readily differentiated during late spring and early summer, females captured during this period were not included in this analysis.

There was considerable variation in size and age at first maturity (Figures 8, 9). A few fish were mature at 3 yr old (males 28.1-32.5 cm TL, females 31.1-33.6 cm TL). Yet not all males were mature before 7 yr and 39.0 cm TL, nor females before 8 yr and 37.0 cm TL. Over 50% of the females had spawned by 4 yr and 34.0 cm TL, while males were age 5 and 32.0 cm TL before reaching the 50% mark. In general, males first matured at a somewhat smaller size and somewhat later age than females.

Limbaugh (1955) reported that, off southern

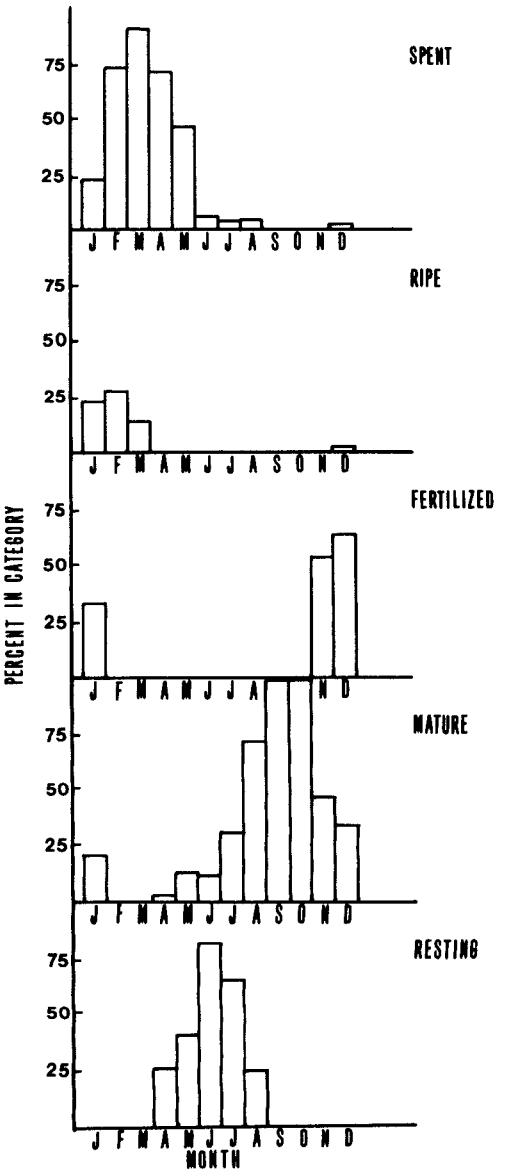

FIGURE 6.—Percent composition by month of five gonad condition stages for female olive rockfish taken off Diablo Cove, 1972-77. Resting refers to that period before egg development, vitellogenesis occurring during the maturing stage, which is terminated by the fertilized stage. Eyed larvae, which define ripe gonads, are extruded and the gonads are called spent.

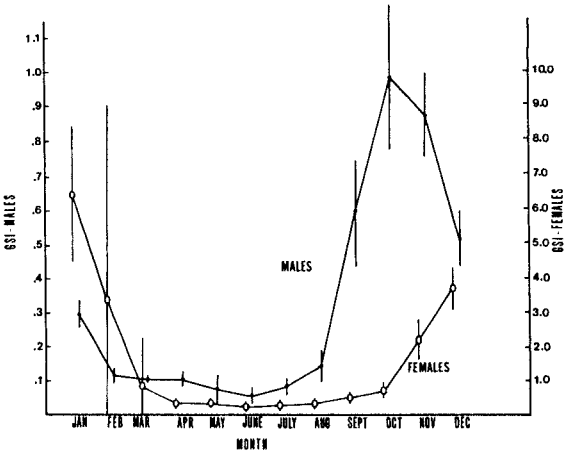

FIGURE 7.—Seasonal changes in the gonosomatic index (GSI—gonad weight as a percent of total body weight) of male and female olive rockfish. Vertical lines indicate 95% confidence intervals of the mean.

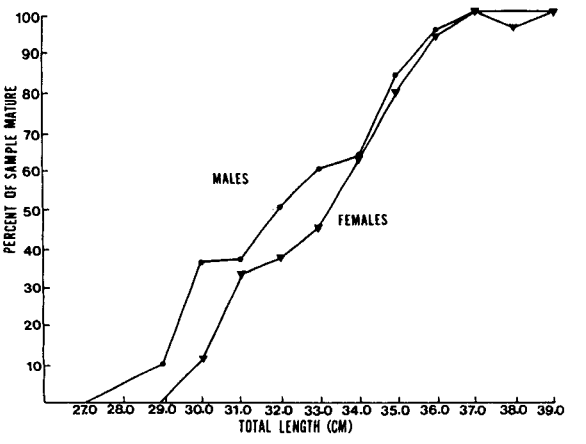

FIGURE 8.—Length-maturity relationship in 331 female and 318 male olive rockfish collected off Diablo Cove, 1972-77.

California, olive rockfish matured at 17-22 cm TL. This is considerably smaller than fishes taken off Diablo Cove. Unpublished data by Love (1978) indicated that olive rockfish off Santa Barbara (in southern California) mature at the same length as fishes farther north. It is possible that Limbaugh mistook prereproductive individuals, whose gonads do swell and color slightly, for mature fish.

Age of first maturity varies widely among rockfish species. At one extreme, *S. emphaeus* matures at 2-4 yr (Moulton 1975); *S. umbrosus*, *S. ensifer* (Chen 1971), and *S. jordani* (Phillips 1964) at 3 yr; while the others, *S. chlorostictus*, *S. rosenblatti*, and *S. constellatus* mature at about 10 yr (Chen 1971) and some stocks of *S. alutus* do not mature until 11 yr or later (Gunderson 1977). Modal period for first reproduction seems to be about 4-7 yr for most species (Phillips 1964; Patten 1973; Miller and Geibel 1973).

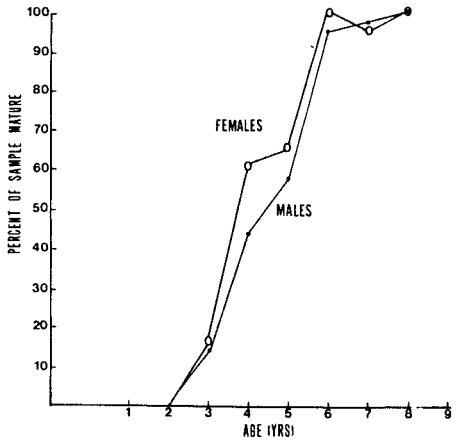

FIGURE 9.—Age-maturity relationship in 317 female and 302 male olive rockfish collected off Diablo Cove, 1972-77.

Fecundity

The nonlinear relation between fecundity and total length (Figure 10) was best described by the function $F = aL^b$, where F = number of eggs in thousands, L = total length in centimeters, and a and b = constants. The value of the parameters a and b were estimated by fitting the linear function $\log F = \log a + b \log L$ by least squares. Estimated fecundity ranged from 30,000 eggs for a 32.6 cm TL individual to about 490,000 for one 46.8 cm long.

Olive rockfish fecundity levels reflected the ranges determined for some other rockfish species, notably *S. flavidus* (Phillips 1964; Gunderson et al. 1980), *S. crameri*, *S. jordani*, and *S. entomelas* (Phillips 1964). They appear to be more fecund per body length than *S. alutus* (Gunderson 1977) and *S. goodei* (Phillips 1964; Gunderson et al. 1980) and less so than *S. elongatus*, *S. diploproa* (Phillips 1964), and *S. mystinus* (Miller and Geibel 1973). In all species studied, smaller individuals tend to carry fewer eggs. There is some evidence (MacGregor 1970) that smaller species also carry fewer eggs per body length.

Fish fecundity measurements, however, are tenuous at best and should only be looked upon as first approximations. Computations made before and after fertilization (Lisovenko 1956) or by differences in subsampling techniques (Gunderson 1977) may cause discrepancies between studies. Moreover the relationship between the number of maturing eggs in an ovary and viable larvae produced is unknown. Unfortunately, it is not practical to count larvae in the ovaries, as some may be lost during capture. Fecundity may also vary due to environmental factors (temperature—Rounsefell 1957 and food availability—Bagenal 1966) or genetic differences (Bagenal 1966).

Juveniles

Rockfish larvae are pelagic for a number of months, after which they settle into waters of various depths. The settling time and habitat of olive rockfish off Diablo Cove was determined from information based on underwater observations and young-of-the-year collected from 1974 to 1977. Though young *S. flavidus* closely resemble *S. serranoides*, and hence might be a source of confusion, they are rare in shallow waters off Diablo Cove (Berge and Schultz footnote 5). Based on spawning season and young-of-the-year sightings, olive rockfish probably spend 3-6 mo as pelagic larvae before settling out. Young-of-the-

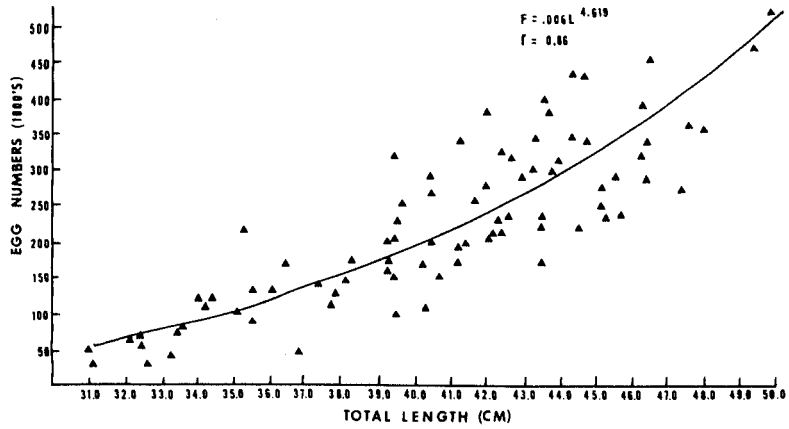

FIGURE 10.—Fecundity-total length relationship for 87 olive rockfish collected off Diablo Cove during October and November 1972-77.

year (of about 2-3 cm TL) first appeared inshore off Avila during March and April. At this stage, they were particularly common under the kelp canopy and over very shallow, protected rocky reefs (occasionally in the lower intertidal zone). Although they were not directly observed there, young-of-the-year probably also occur on reefs somewhat farther offshore (depth 20-50 m), since they were often found in the stomachs of resident rockfish in these habitats.

Food Habits

Olive rockfish were found to be primarily midwater predators of nekton (Table 5). Very important among its prey were small fishes, including blue rockfish; young olive rockfish; pipefish, *Syngnathus* sp.; shiner perch, *Cymatogaster aggregata*; kelp gunnel, *Ulvicola sanctaerosae*; northern anchovy, *Engraulis mordax*; topsmelt, *Atherinops affinis*; and cottids. Another important nektonic prey was the squid *Loligo opalescens*. Among planktonic prey, small crustaceans (particularly crab megalops larvae), tunicates (*Oikopleura* sp., *Doliolium* sp.), euphausids, fish larvae, and polychaetes were commonly eaten. Among substrate-oriented prey, octopus was the most important food item, followed by gammarid amphipods, isopod *Idothea* sp., and other small crustaceans.

As olive rockfish grow, their food habits change. Previous studies (Quast 1968b; Hobson and Chess 1976; Love and Ebeling 1978) have shown juvenile olive rockfish to be primarily midwater feeders, actively swimming after such forms as polychaetes, megalops larvae, mysids, and small fish. In the present study, though planktonic forms were important for individuals of all size classes, nektonic animals, primarily fish and squid, assumed dominance in the diet as the fish grew larger (Table 6). Plankton consumed by smaller individuals included a wide variety of small and large crustaceans, fish larvae, and polychaetes. For larger fish, plankton consumption was essentially limited to large items, such as euphausids, tunicates, and polychaetes. Nekton

TABLE 6.—Percentage occurrence of prey types in stomachs of four size classes (total length) of olive rockfish from Avila, Calif. Probabilities determined by 2 × 2 contingency G-test (Sokal and Rohlf 1969).

Size class (cm)	Stomachs with food (no.)	Plankton	Nekton	Substrate oriented
10.1-20.0	25	84.0*	16.0*	20.0
20.1-30.0	75	57.3*	40.0*	29.3
30.1-40.0	158	41.7**	56.5	22.0**
40.1-50.0	116	25.7	56.0	43.1

*$P \leq 0.05$, **$P \leq 0.01$.

TABLE 5.—Percentage total volume and frequency of occurrence of 17 food items in stomachs of olive rockfish off Avila, Calif. Olive rockfish are divided into 10.0 cm TL size groups. Food items are grouped by behavior and habitat.

	10.1-20.0 cm		20.1-30.0 cm		30.1-40.0 cm		40.1-50.0 cm		Total	
Food item by prey type	% vol	% freq	% vol	% freq	% vol	% freq	% vol	% freq	% vol	% freq
Primarily planktonic (sum)	(54.2)		(20.9)		(8.8)		(7.9)		(9.3)	
Small crustaceans, 0.5-5 mm:										
Zoea			.7	2.7	tr[1]	1.9			tr	1.3
Copepods	.8	24.0	1.2	4.0	tr	3.2	tr	1.7	tr	4.2
Megalops	4.8	28.0	9.6	33.3	.2	7.0	tr	3.4	.6	12.2
Large crustaceans, >10 mm:										
Euphausids			1.2	2.6	4.2	13.9	2.3	7.8	3.0	8.6
Small-medium sized, transparent										
Tunicates (salps, larvaceans)			.3	1.3	2.6	6.3	5.3	.9	4.0	5.7
Fish larvae	44.5	52.0	.9	6.6	.2	5.0	tr	1.7	.5	7.3
Polychaetes	4.1	16.0	7.0	28.0	1.6	22.8	.3	12.0	1.2	19.5
Primarily nektonic, 20-160 mm (sum)	(44.7)		(72.1)		(81.1)		(64.4)		(71.3)	
Fish	44.7	12.0	66.0	37.3	36.9	52.5	24.5	44.8	31.6	43.2
Squid			6.1	2.6	44.2	7.7	39.9	12.1	39.7	7.6
Primarily substrate oriented (sum)	(1.0)		(6.9)		(10.0)		(27.2)		(19.3)	
Free moving animals:										
Mysids			.9	4.0	tr	.6	tr	.9	tr	1.3
Isopods			.4	4.0	.3	6.0			.1	3.1
Gammaridean amphipods	1.0	20.0	2.2	18.6	.1	3.8	tr	.9	.2	6.8
Caprellid amphipods					tr	.6			tr	.2
Octopus			.7	2.6	9.3	12.0	27.2	37.9	18.6	16.7
Shrimp			.2	2.6					tr	.2
Algae			2.5	2.6	tr	1.9	tr	.9	.2	1.6
Pebbles					.3	1.3	tr	.9	.2	.8
Total volume of food consumed, ml	15.58		101.34		840.82		1,162.65		2,120.39	
Stomachs with food, no.	25		75		158		116		374	
Empty stomachs, %	22.0		33.0		38.3		39.3			

[1]Trace <0.05%.

feeding, though important in all size classes, increased to a peak for fish 30.1-40.0 cm long, then declined somewhat, as larger fish ate more substrate-oriented prey. Predators in the 20.1-30.0 cm size class had the smallest range of food items (Table 7), eating mostly fish. Range increased for larger predators, as their diets were supplemented by squid and octopus.

TABLE 7.—Food breadths (Bray and Ebeling 1975) based on proportionate item volumes for four size classes (total length) of olive rockfish from Avila, Calif. Maximum vol (%) is of the dominant item (Table 5).

Size class (cm)	Stomachs with food (no.)	Food items eaten (no.)	Breadth of diet	Maximum vol (%)	Dominant item
10.1-20.0	25	6	2.49	44.7	Fish
20.1-30.0	75	15	2.20	43.6	Fish
30.1-40.0	158	16	2.92	44.2	Squid
40.1-50.0	116	13	3.40	39.9	Squid

TABLE 8.—Seasonal variation in percentage frequency of occurrence of prey types in stomachs of three size classes (total length) of olive rockfish from Avila, Calif. Seasonal periods are explained in the text. Probabilities determined by 2 × 2 contingency G-test (Sokal and Rohlf 1969) on original frequencies.

Size class	Prey type	Seasonal period: Mar.-Aug.	Seasonal period: Sept.-Feb.
20.1-30.0 cm:			
Stomachs with food, no.		38	37
	Plankton, %	47.4	64.9
	Nekton, %	39.5	51.4
	Substrate oriented, %	31.6	21.6
30.1-40.0 cm:			
Stomachs with food, no.		71	87
	Plankton, %	42.3	46.0
	Nekton, %	70.4*	50.6
	Substrate oriented, %	19.7	23.0
40.1-50.0 cm:			
Stomachs with food, no.		63	53
	Plankton, %	30.2	22.6
	Nekton, %	66.7**	45.3
	Substrate oriented, %	39.7	45.3

*$P \leq 0.05$
**$P \leq 0.01$

Feeding on substrate-oriented forms, primarily gammarid amphipods and isopods, occurred occasionally in fish of the smaller size classes, but was much more frequent in larger fish, where foraging on octopus was important. Octopuses are normally secretive during daylight hours, but are often exposed during the night (D. Behrens[6]). Olive rockfish may feed at night on octopus—an example of a fish not adapted to benthic feeding, preying successfully on a bottom-dwelling form.

Food habits showed some seasonal variation. Nekton feeding significantly increased (in the 30.1-40.0 and 40.1-50.0 cm size classes) during the upwelling period (Table 8). Predation on both squid and young-of-the-year rockfish (which first appear in large numbers during April and May) increased during this period. Though juvenile rockfish were an important food item throughout the year, their importance decreased during fall and winter, probably because these growing juveniles become less vulnerable. Other prey, such as the northern anchovy, were of greater importance during the fall oceanic and winter Davidson Current periods. Tunicates and euphausids were eaten in far greater amounts during the upwelling season, particularly during April and May (an occurrence also noted off Carmel Bay, Calif., by Roberts 1979).

Limbaugh (1955) speculated that olive rockfish may replace kelp bass ecologically in central and northern California, where kelp bass decline in abundance. The two species are similar in appearance—having elongate, fusiform bodies, reduced or (in kelp bass) absent head spines, large mouths, and brownish bodies with light blotches along their back. In central and northern California, olive rockfish do, to a certain degree, assume the lifestyle of kelp bass. Olive rockfish live over high relief bottom and feed primarily on nekton, as do kelp bass. However, with the exception of octopus, olive rockfish rarely prey on the substrate-oriented food items, such as shrimp, algae, and hydroids, favored by kelp bass (Quast 1968b; Love and Ebeling 1978). In central California, olive rockfish and blue rockfish are the major midwater predators over inshore reefs. Though there is considerable overlap, blue rockfish feed primarily on relatively slow moving or drifting prey, such as tunicates, copepods, and chaetognaths (Gotshall et al. 1965; Hallacher 1977) while olive rockfish concentrate on more motile forms. Beginning in northern California, olive rockfish give way to midwater feeding yellowtail rockfish and black rockfish, *S. melanops* (Moulton 1977).

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[6]D. Behrens, Pacific Gas and Electric, Biological Laboratory, P.O. Box 117, Avila, CA 93424, pers. commun. November 1980.

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OVARIAN CYCLING FREQUENCY AND BATCH FECUNDITY IN THE QUEENFISH, *SERIPHUS POLITUS*: ATTRIBUTES REPRESENTATIVE OF SERIAL SPAWNING FISHES

E. E. DeMartini and Robert K. Fountain[1]

ABSTRACT

Egg production by *Seriphus politus* near San Diego in southern California was studied during 1978-79. Spawning frequency was estimated on the basis of incidence of females with hydrated eggs. Estimates of annual egg production were an order of magnitude greater than estimates based on conventional methods.

Seriphus politus spawns during March-August, and females mature at 10.0-10.5 cm standard length in their first spring or second summer following birth. Planktonic eggs are spawned between late afternoon and early evening. Spawning is asynchronous among females, but has monthly peaks in intensity during the waxing (first quarter) of the moon. Fecundity is proportional to size and is better correlated with weight than with length of female. Individuals spawn once a week on average, regardless of body size. Larger females begin spawning earlier in the season and continue spawning after the smallest females have ceased. Recruit spawners and the largest repeat spawners produce about 12 to 24 batches of eggs during their respective spawning seasons. The average-sized female spawns about 300,000 eggs in a year. Relative fecundity is an increasing function of body size. Larger females produce larger eggs, and all females produce larger eggs earlier in the season. Implications of these life-history attributes are discussed.

The croakers (family Sciaenidae) are a major component of the nearshore fish fauna of southern California (Frey 1971), yet little is known about their fecundity patterns or other details of their reproductive biology (Skogsberg 1939). Seven species of croakers occur off southern California (Miller and Lea 1972). General information on breeding seasonality and size at sexual maturity exists for white seabass, *Atractoscion nobilis* (Clark 1930); black croaker, *Cheilotrema saturnum* (Limbaugh 1961; Fitch and Lavenberg 1975); California corbina, *Menticirrhus undulatus* (Fitch and Lavenberg 1971; Frey 1971); and spotfin croaker, *Roncador stearnsi* (Frey 1971). The general seasonal nature of spawning is known for yellowfin croaker, *Umbrina roncador* (Frey 1971). Additional data on ovarian cycling exist only for white croaker, *Genyonemus lineatus*, and for queenfish, *Seriphus politus* (Goldberg 1976).

The queenfish is an abundant, small species that is a major component of the sport fish catch on piers in southern California (Frey 1971); the species moreover provides forage for several fishes important to the sport and commercial fisheries in the area (Young 1963; Feder et al. 1974). It is the purpose of this paper to document the fecundity and ovarian cycling patterns of queenfish and to relate these results to what we feel are some general reproductive characteristics of serial spawning fishes.

MATERIALS AND METHODS

Field Sampling

Fish were sampled at nearshore (5-20 m) depths, 0.5-3 km from shore, between San Clemente and Oceanside, Calif. (Figure 1), using a lampara net (560 m long × 25 m deep, mesh: 15 cm in wings to 1.25 cm in center bag), fished surface-to-bottom by a commercial vessel. Fish were caught at standard times of day (1-6 h after dawn) and night (1-6 h after sunset) on surveys conducted at fortnightly (September 1978-February 1979; September 1979) or weekly (March-August 1979) intervals. Six daytime and five nighttime net hauls were made each survey.

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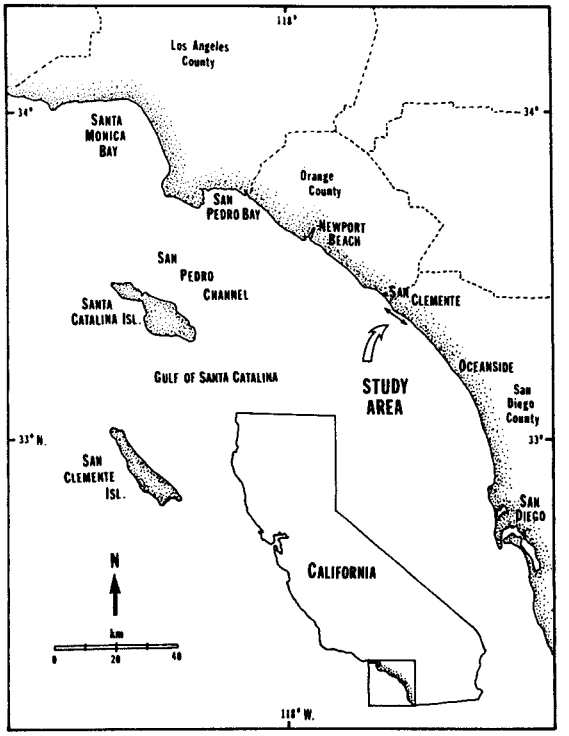

FIGURE 1.—Map of the study area.

Analysis of Fish and Ovaries

A maximum of two aliquots of 50 fish each were sacrificed from each net haul to determine size (standard length, SL, in millimeters) and sex composition. At most 15 females per 5 mm length class in each haul were measured and their ovaries excised and weighed (0.01 g) while fresh. Fresh (ovary-free) body weight (0.1 g) was recorded for subsampled, mature fish of a range of lengths. One or both ovaries of each mature pair were fixed and preserved in modified Gilson's fluid (Bagenal and Braum 1971) for 1-3 mo. Gonads were classified either as immature or mature according to several gross criteria (vascularization, oocyte appearance, Table 1) of Bagenal and Braum (1971). Gonad maturity also was estimated using a gonad index, $GI = W/SL^3 \times C$ (Moser 1967), where W = weight of both ovaries in grams, SL = standard length in millimeters, and the constant $C = 10^8$. The median diameter (random axis) was determined for oocytes present in the largest size-frequency mode in ripening ovaries (Stage 2, Table 1) of each of 10-15 fish from pooled monthly samples. Oocyte maturation size was inferred from a plot of median oocyte diameter versus gonad index (Higham and Nicholson 1964). For select ripe (Stage 3, Table 1) females, both ovaries were reweighed after Gilson's preservation, a tissue sample ($\bar{X} = 3.4 \pm 1.0\%$ (SE), range 1.0-7.2% of the weight of both ovaries) weighed, and the numbers of oocytes in the largest size-frequency mode estimated for both ovaries by gravimetric method (Bagenal and Braum 1971). Tissue samples from either ovary of a pair were used, as the right and left ovaries of *S. politus* are, on average, equivalent in weight (paired t-test, n = 20 ovary pairs, $0.4 > P > 0.3$) and in the size-frequency distribution of oocytes (Kolmogorov-Smirnov 2-sample test, n = 5 ovary pairs, $P > 0.1$). Tissue samples for fecundity analysis were taken from the anterior one-third of the ovary. For other select Stage 2 and 3 fish, the second ovary of a pair was fixed in 10% Formalin[2] for 2 wk, sectioned at 0.008 mm, stained with Harris' hematoxylin and eosin, and a slide mount examined at 60-240× to validate classification as nonhydrated or hydrated based on the gross ovarian characteristics listed in Table 1. The latter tissue samples were also taken from the anterior one-third of the ovary. No difference existed in the frequency distribution of oocyte maturation states within anterior, central, or posterior regions of the queenfish ovary (Smirnov 3-sample test, n = 5 ovary pairs, $P > 0.1$; Conover 1971).

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

TABLE 1.—Gross characteristics of various stages in the queenfish ovarian cycle.

Egg stages within the ovary		Gross appearance of ovary and oocytes
1	Vestigial (= immature or inactive)	Ovaries avascular; oocytes not visible to naked eye. Ovaries uniform whitish-yellow.
2	Nonhydrated (= ripening)	Ovaries vascular and oocytes visible to the naked eye. Oocytes uniformly small, opaque, and straw-yellow throughout entire ovary.
3	Hydrated (= ripe)	Many small, opaque oocytes plus a minority of large, hyaline oocytes present throughout ovary. The two egg types together produce a speckled, translucent-opaque appearance, yellowish-orange to orange, throughout ovary.
4	Ovulated (= running)	A band of small, opaque, straw-yellow oocytes present along dorsal ridge of ovary; many large, hyaline oocytes visible within lumen of ovary. Most of ovary uniform yellowish-orange or orange.
5	Residual (= spent)	Ovary slightly blood-shot and deflated (partially spent) to very blood-shot, completely collapsed and flaccid (totally spent). A small number of large, ovulated eggs usually visible in lumen of ovary. Most oocytes present are small and opaque.

RESULTS

Spawning Season and Gonad Maturation

Queenfish ovaries accelerate development in February when daylight lengthens beyond 10 h and nearshore water temperatures are 15°-16° C. Ovaries increase to their maximum relative weight in April-May and decline through August until a resting stage recurs in September (Figure 2A). During February-September, nearshore water temperatures in general increase to 17°-19° C, although aperiodic bouts of upwelling (13°-14° C water) occur (J. Reitzel[3]). Ovaries mature at a GI of 40, when the diameter of Gilson's fluid-fixed (nonhydrated) oocytes reaches 350 μm (Figure 3).

Body Size and Time of Spawning

The first sexual maturation of females begins at a length of 10-10.5 cm. The proportion of sexually active females increases with body size until, at a length of about 12 cm SL, virtually all females are spawning by midseason (Table 2). Larger females (>12 cm, age II and older, DeMartini et al.[4]) start spawning earlier and finish spawning later in the year than fish ≤12 cm SL (Table 2, Figure 4). Duration of spawning varies from 3 mo for first

[3]Reitzel, J. 1979. Physical/chemical oceanography. *In* Interim Report of the Marine Review Committee of the California Coastal Commission. Part II: Appendix of Technical Evidence in Support of the General Summary, March 12, 1979, p. 6-23. Unpubl. rep. Marine Review Committee Research Center, 533 Stevens Avenue, Suite E-36, Solana Beach, CA 92075.

[4]DeMartini, E. E., K. M. Plummer, and T. O. Moore. Age and growth of the queenfish (*Seriphus politus*), with back-calculated length-at-age estimates based on sections of otolith sagittae. Manuscr. in prep. Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106.

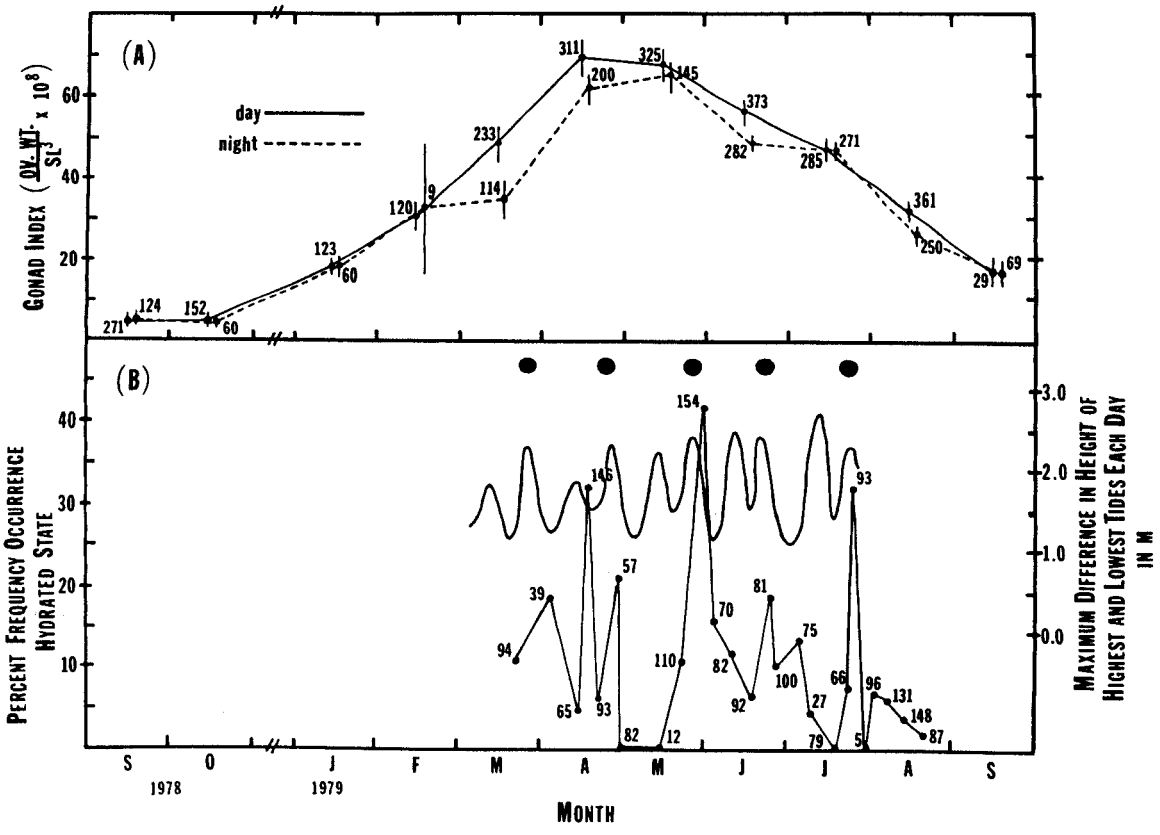

FIGURE 2.—(A) Mean gonad indices of female queenfish (of all body sizes) collected September 1978-September 1979. Indices of day and night sample fish plotted separately. Sample sizes and 95% confidence limits are indicated. (B) Percent frequency occurrence of adult female queenfish with ovaries containing oocytes in hydrated condition during March-August 1979. Fish are from daytime collections at 5-11 m depths. Noted are the numbers of sample fish, dates of new moon, and maximum range in heights of highest and lowest tides each day.

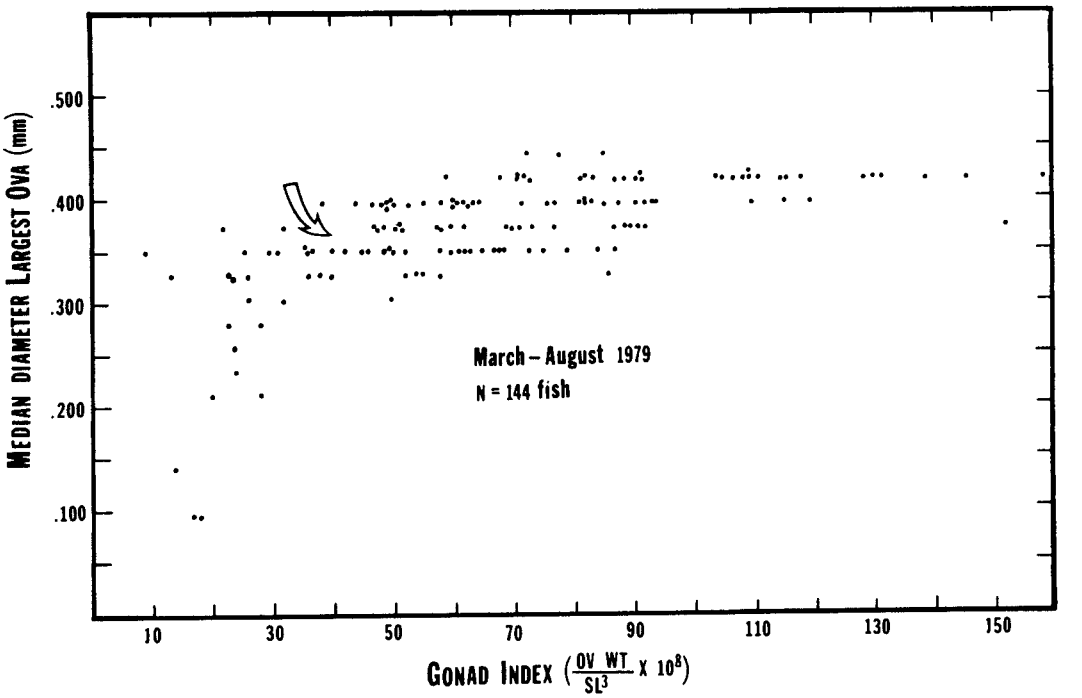

FIGURE 3.—Scattergraph of the median diameter (random axis) of the largest size-frequency mode of oocytes plotted against gonad index of the respective female queenfish. Asymptote (noted by arrow) occurs at an oocyte diameter of about 350 μm, corresponding to a gonad index of about 40.

TABLE 2.—Percent of female queenfish of various length classes[1] that were sexually mature during the 1979 spawning period.

Length class (cm SL)	Percent mature					
	Mar.	Apr.	May	June	July	Aug.
<10.5	0	0	<1	2	3	<1
10.6-11.0	14	63	68	58	22	3
11.1-11.5	18	95	93	92	53	9
11.6-12.0	48	97	100	94	85	12
12.1-12.5	82	98	100	100	96	73
12.6-13.0	90	100	100	98	99	97
13.1-13.5	100	100	100	98	100	100
>13.5	100	100	100	100	>97	>99

[1]An average of 90 female queenfish per length class were examined each month.

spawners to 6 mo in the largest fish. Relatively few females start spawning at age I. Of all sexually active (Stages 2-4, Table 1) females captured during the 1979 spawning season, 6 and 34% were <12 cm and <13.5 cm, respectively.

Ovarian Cycling

Monthly peaks in the proportion of females in ready-to-spawn condition occurred during the moon's first quarter (contingency chi square = 27.7; 3 df; $P<0.0005$; Siegel 1956). At such times from 19 to 42% of all the adult females in the day's samples had ovaries containing eggs in a hydrated state (Figure 2B).

Female *S. politus* begin hydrating oocytes after dawn and spawn between late afternoon and evening. No difference existed between the percent frequency occurrence of ready-to-spawn females in samples collected at different times during daylight hours; and no fish caught at any time during the night were ready to spawn (Table 3). These results were reexamined for subsample ovaries, using accepted histological criteria for distinguishing hydrated from non-

TABLE 3.—Frequency occurrence of mature female queenfish whose ovaries contained oocytes in a hydrated vs. a nonhydrated state in samples collected during various 6-h intervals on 25-28 June 1979.

Collection period	No. samples	No. fish containing		No. females examined
		Hydrated oocytes	Nonhydrated oocytes only	
0600-1200	3	10	90	100
1200-1800	4	15	66	81
1800-0000	5	0	81	81
0000-0600	5	0	84	84

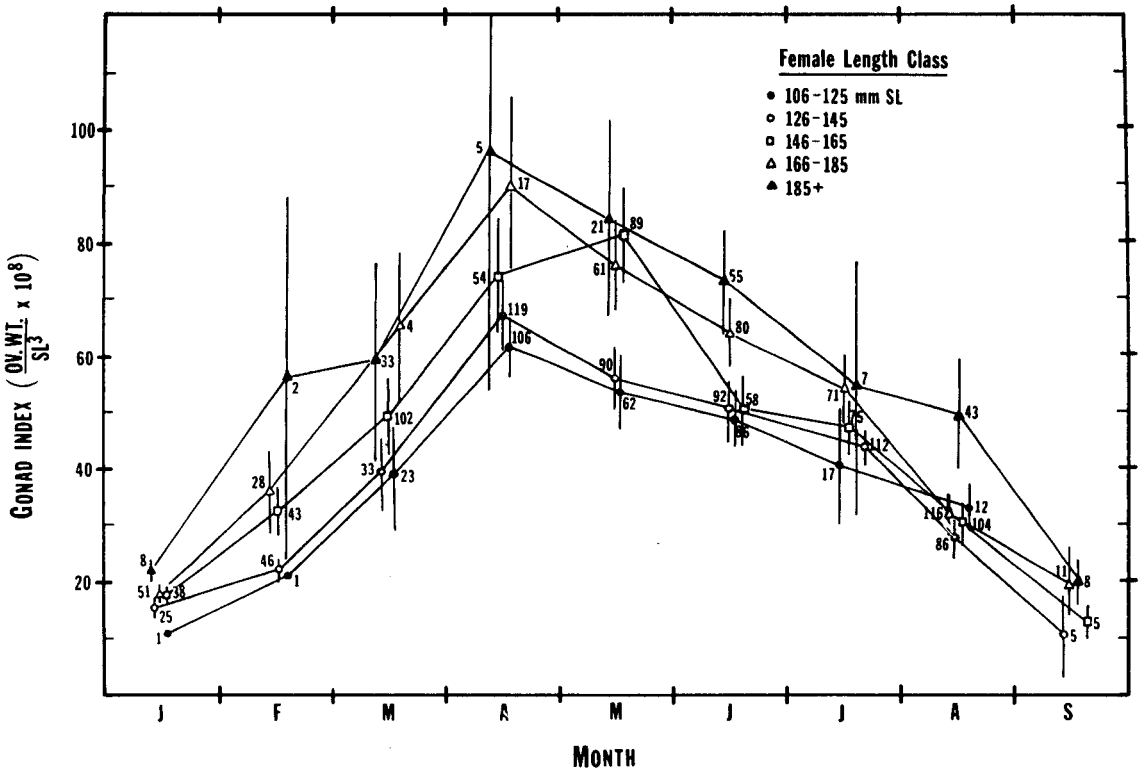

FIGURE 4.—Mean gonad indices of adult female queenfish of five length classes collected March-August 1979. Sample sizes and 95% confidence limits of means are indicated.

hydrated oocytes (Yamamoto and Yamazaki 1961; Yamamoto and Yoshioka 1964; Macer 1974; Htun-Han 1978), as illustrated in Figure 5. Histological results verified our conclusions based on the external appearance of ovaries (Table 4).

Spawning frequency thus can be inferred from the proportion of daytime sample fish whose ovarian eggs are in a hydrated state. Throughout the 1979 spawning season, an average of 13.6% of the females (of all sizes) present in daytime samples were in a ready-to-spawn condition (Table 5); thus females spawn on average every 7.4 d. Spawning frequency was similar for females of all body sizes (Table 5). Confidence intervals of these percent frequency occurrence data are necessarily asymmetrical, since female spawners are contagiously distributed among sample fish and, like hydrated-state females of the northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980), their sampling frequency is best described by the normal-log negative binomial distribution.

Sex Ratio

The breeding adult sex ratio of *S. politus* was 1.04 males to 1.00 females. The mean percentage of females among 16,794 adults was 49% with a 95% confidence interval of ±0.8%. The sex ratio was more skewed in favor of males in samples of fish containing one or more females in ready-to-spawn condition (Table 6).

Batch Fecundity

The number of eggs liable to be produced per spawning, i.e., the potential batch fecundity, was estimated for fish collected throughout the 1979 spawning season. The Gilson's fluid-fixed ovaries of daytime sample fish of a complete range of body sizes were used. Potential fecundity varied as the cube of standard length, and was proportional to body size in a consistent manner throughout the season (Figure 6). Bimonthly regressions of

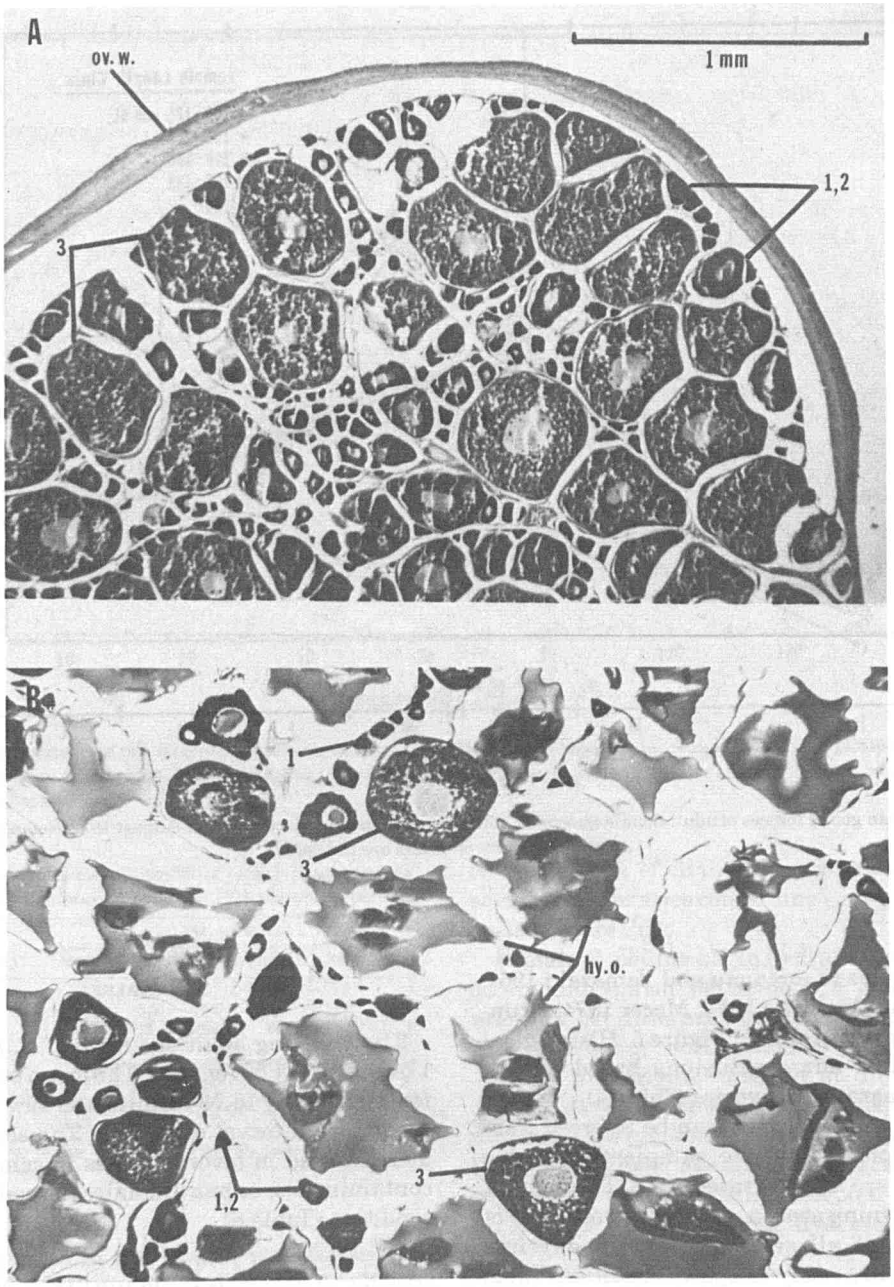

FIGURE 5.—Photomicrographs of transverse sections of (A) Stage 2 and (B) Stage 3 mature queenfish ovaries. Hyaline (hydrated) oocytes are still in their follicles in (B). Key for plate: hy.o. - hyaline oocyte; 1, 2 - Type 1 or Type 2 developing oocyte; 3 - Type 3 developing oocyte; ov.w. - ovarian wall. [See Goldberg (1976) for definitions and histological criteria distinguishing the stages of oocyte development in queenfish.]

TABLE 4.—Agreement between queenfish ovaries classified as hydrated or nonhydrated using external (gross) appearance and histological (microscopic) techniques.[1]

		Microscopic basis	
		Hydrated	Nonhydrated
Gross basis	Hydrated	49	2
	Nonhydrated	2	60

[1]n = 113 ovary pairs scored as (non)hydrated prior to fixation, staining, sectioning, and microscopic examination.

TABLE 5.—Frequency occurrence of queenfish ovaries in hydrated condition[1] as percent of all ovaries from adult sample fish[2] collected March-August 1979. The 95% confidence intervals on the percentage of hydrated females are indicated in parentheses.

Size group (cm SL)	No. sample fish	No. nonhydrated	No. hydrated	Mean[3] percent hydrated
10.5-12.5	342	294	48	14.0 (6.8, 28.8)
12.6-14.5	608	525	83	13.6 (7.9, 23.5)
14.6-16.5	519	462	57	11.0 (7.5, 16.1)
16.6-18.5	450	384	66	14.7 (6.8, 31.9)
>18.5	156	128	28	17.9 (9.0, 35.4)
All sizes	2,075	1,793	282	13.6 (8.2, 22.7)

[1]Classified based on gross characteristics of ovaries.
[2]Four net haul samples (daytime, 5-11 m) collected on 1 d cruise each week during 22 March-20 August 1979.
[3]Calculations based on normal-log negative binomial distribution (Zweifel and Smith in press).

fecundity on body size neither varied in slope (F = 1.49; 2,136 df; $P>0.25$) nor in intercept (F = 0.50; 2,138 df; $P>0.75$). Data were thus pooled over the entire 6-mo season and the general fecundity-length relation described by the best fit (R^2 = 0.664, n = 142, $P<0.01$) equation

$$\log_{10} F = 3.3809 \log_{10} SL - 3.1455$$

where F = batch fecundity
SL = standard length in millimeters.

Fecundity was better correlated (R^2 = 0.816, n = 42) with body weight (Figure 7) than with length of female (Figure 6), as described by the equation

$$\log_{10} F = 1.302 \log_{10} W + 1.968$$

where W = ovary-free weight in grams.

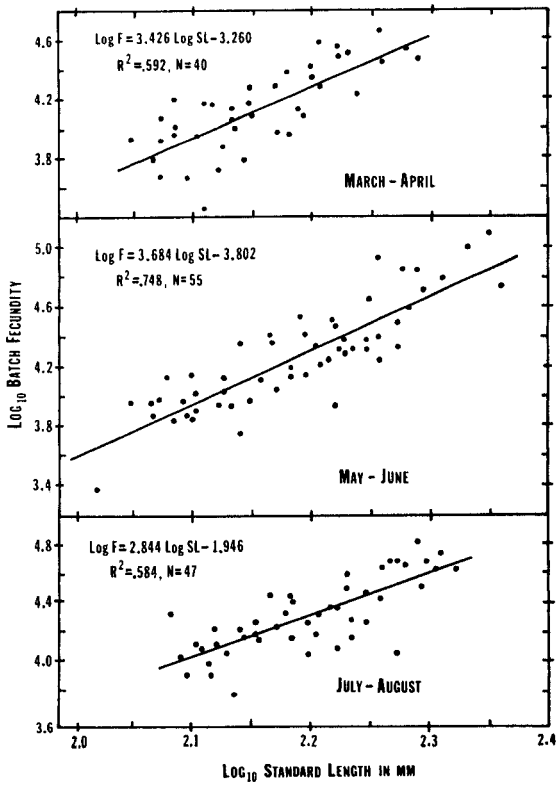

FIGURE 6.—Relation between the common logarithms of batch fecundity (as the number of hydrating oocytes) and length of queenfish collected during the first, middle, and latter third of the 1979 spawning season. Regression equations are least squares best fit.

The length-weight relation was tightly correlated (R^2 = 0.986, n = 175) according to the equation

$$\log_{10} W = 3.1105 \log_{10} SL - 5.0560.$$

The average-sized (14 cm, 42 g) female had a potential batch fecundity during 1979 of 12,000-13,000 eggs. Batch fecundities ranged from about 5,000 eggs in a 10.5 cm female to about 90,000 eggs in a 25 cm fish.

TABLE 6.—Relation between adult sex ratio (females/total adults) of samples and percent frequency occurrence of female queenfish containing hydrated[1] eggs.

			Percent of females containing		
Sex ratio class	Class mean	No. samples[2]	Hydrated[1] eggs	Nonhydrated[1] eggs only	No. adult females examined
0.22-0.50	0.37	46	15.2	84.8	1,003
.51- .74	0.61	19	13.4	86.6	649
.75- .98	0.84	13	10.9	89.1	384

[1]Classified based on external characteristics of ovaries.
[2]From four to six net haul samples (daytime, 5-11 m) examined each week during 22 March-20 August 1979.

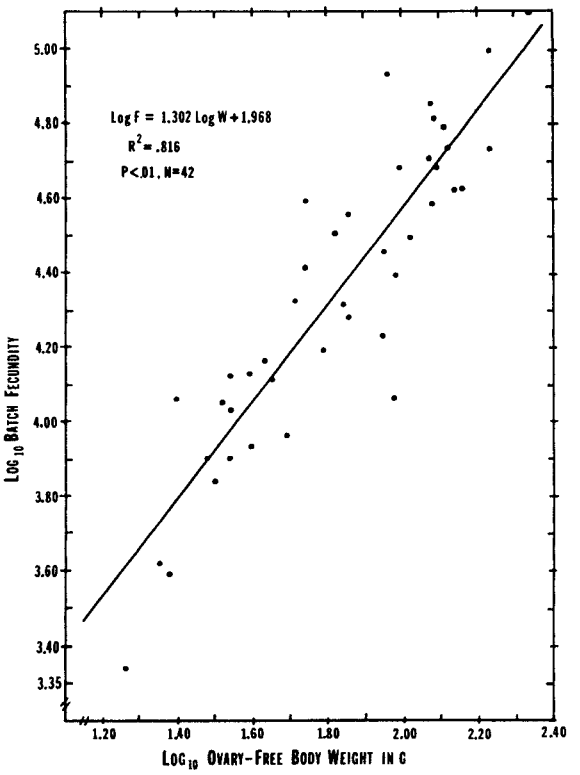

FIGURE 7.—Relation between the common logarithms of batch fecundity and ovary-free body weight of queenfish collected March-August 1979. Regression is the least squares best fit.

Residual Ova

Since not all of the eggs that are ripened and ovulated might be shed, we estimated the numbers of residual, ovulated eggs present in the ovaries of recently spawned, night sample fish. Numbers of residual ova were trivial (Table 7), indicating that females ovulate and shed virtually all of the eggs that undergo hydration.

Annual Egg Production

The spawning season of *S. politus* near San Diego lasts 3-6 mo, being longer for larger females (Table 2). Since batch fecundity is also proportional to female body size, annual egg production of individual fish ranges greatly. We estimate that a 10.5 cm female, spawning once every 7.4 d during May-July, produces about 60,000 eggs, whereas a 25 cm fish that spawns once every 7.4 d over a 6-mo period (March-August) produces nearly 2.3 million eggs. The relatively huge egg production by large *S. politus* thus reflects both greater numbers of spawnings over a longer season and larger batch fecundities.

TABLE 7.—Numbers of residual (ovulated but unspawned) eggs[1] present in spent (Stage 5) ovaries of queenfish. Numbers of residual eggs also expressed as percent of batch fecundity (estimated from standard length).

Item	No. residual ova	Batch fecundity	
		Estimated	Percent
Mean	25	25,500	0.1
Range	2-101	8,100-67,100	0.005- .6

[1]Based on examination of 16 females ($\bar{X}$ = 16.2 cm SL, range 12.1-22.0 cm) collected March-August 1979.

Relative Fecundity

The numbers of eggs produced per unit of body weight, i.e., "relative fecundity" (Nikolskii 1969), is an increasing function of body size in *S. politus* (Figures 4, 8). On a per spawning basis, larger females allocate relatively more energy to egg

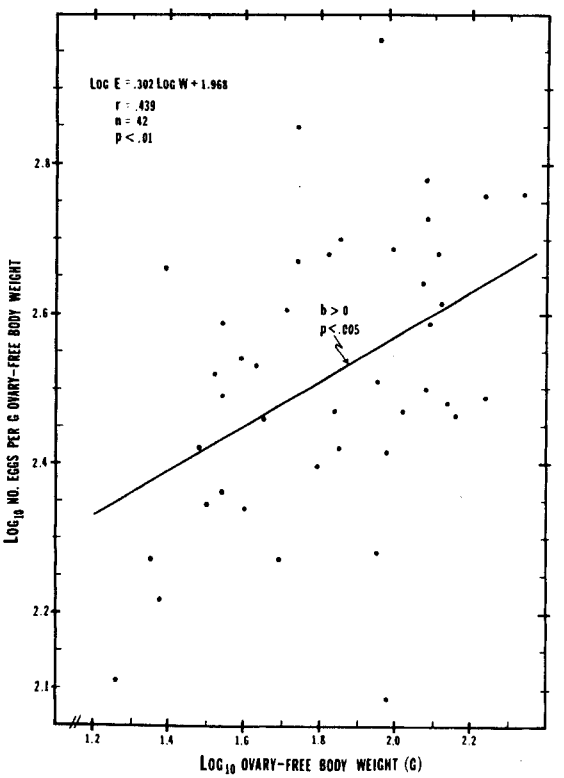

FIGURE 8.—Relation between relative fecundity (as the batch numbers of eggs per gram ovary-free body weight) and ovary-free body weight of queenfish collected March-August 1979. Transformation of raw data to common logarithms provided a tighter correlation (greater R^2) than untransformed data.

production than smaller females. The average 42 g fish produces 287 eggs/g of ovary-free body weight. Values range from an average 218 eggs/g to 494 eggs/g respectively (Figure 8) in a 10.5 cm and a 25 cm fish. Ripening (Stage 2, Table 1) ovaries compose 3.8% (for small fish <13.5 cm) and 4.2% (large fish >13.5 cm) of body weight. Ripe ovaries containing hydrated (Stage 3) oocytes made up an average 7.1% and 8.0% of the body weight of small and large *S. politus*, respectively. The average female produces about 4,570 eggs/g of Stage 3 ovary.

Egg Size

The Gilson's fluid-fixed, hydrated and non-hydrated oocytes of *S. politus* average 540 μm and 400 μm in diameter, respectively, and egg size in general declines as the spawning season progresses (Figure 9). Eggs fixed in Gilson's fluid are 85% the diameter of fresh eggs; thus actual egg size declined from about 685 to 580 μm between March and August 1979. Egg size also varied among different-sized females (Table 8). Throughout the season larger females generally produced larger eggs than did smaller females.

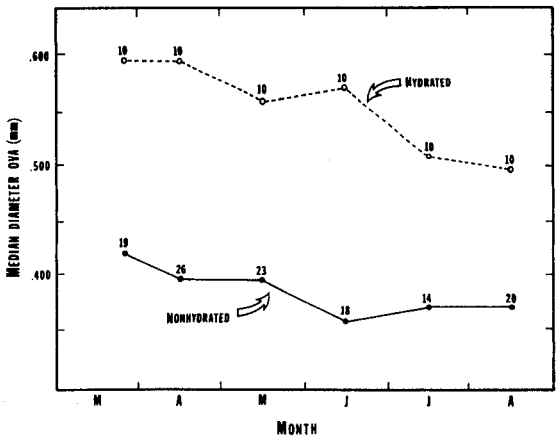

FIGURE 9.—Median diameters (random axis, Gilson's fixed) of the largest size-frequency class of oocytes present in subsampled queenfish of all body sizes collected March-August 1979. Data for fish with Stage 2 and Stage 3 ovaries are plotted separately. Numbers of sample fish are indicated.

TABLE 8.—Results of two-way analysis of variance of the effects of month and female size on the median diameter of the largest oocytes in ripening (Stage 2) ovaries of queenfish. Sample size = 417 fish.

Source of variation	df	*F*	*P*
Main effects	9	7.526	0.001
Month[1]	5	9.783	0.001
Female size[2]	4	3.833	0.005
Two-way interaction:			
Month × size	20	1.597	0.05
Explained	29	3.437	0.001
Residual	387	—	—
Total	416	—	—

[1]Spawning season partitioned into 6 mo: March, April, May, June, July, August 1979.
[2]Females divided into five length classes: 10.6-12.5, 12.6-14.5, 14.6-16.5, 16.6-18.5, >18.5 cm SL.

DISCUSSION

Size at Sexual Maturity

The smallest *S. politus* that contained ripe (Stage 3) eggs were 10.0-10.5 cm SL. At this size females are in their first spring or second summer following birth and average about 13 mo old (DeMartini et al. footnote 4). The onset of egg production by recruit spawners is variable, however; on average only 38% of the females this small contained mature eggs throughout the season, and >10% were generally immature at all lengths <13.5 cm (Table 2). A variable body size at first sexual maturity is a common feature of serial spawners and fishes in general (Nikolskii 1969).

Goldberg (1976) found no histological evidence of sexual maturity in female *S. politus* <14.8 cm SL among those he examined during November 1974-October 1975 from Santa Monica Bay, Calif., about 110 km upcoast of our study area. This might be due to geographic or annual variation in size at maturity, but more likely reflects chance error as only two fish <14.8 cm SL were among those examined (Goldberg[5]).

Body Size and Length of Spawning Season

Duration of the spawning season of repeat-spawning *S. politus* is in general about twice as long as the season for recruit spawners (Table 2). An earlier onset and later cessation of spawning by larger, older individuals is known for other serial spawning fishes of southern California, including northern anchovy (perhaps: see Hunter and Macewicz 1980); Pacific sardine, *Sardinops sagax caeruleus* (Clark 1934); jack mackerel, *Trachurus symmetricus* (Wine and Knaggs 1975); Pacific mackerel, *Scomber japonicus* (Knaggs and Parrish 1973); and California grunion, *Leuresthes*

[5]Stephen R. Goldberg, Department of Biology, Whittier College, Whittier, Calif., pers. commun. August 1978.

tenuis (Clark 1925). A protracted spawning season is generally characteristic of repeat spawners (Nikolskii 1969).

Temporal Patterns of Spawning

The peaks in spawning synchrony among female *S. politus* during the moon's first quarter are likely adaptive for several reasons. Spawning at dusk while the night sky is still fairly dark probably helps conceal adults and planktonic eggs from visual predators. Furthermore, tidal exchanges are minimal during the moon's first quarter (Figure 2B) and the conservation of planktonic eggs and larvae in nearshore areas may be facilitated. Juvenile and adult queenfish inhabit depths <20 m during most of the year (DeMartini and Larson[6]), and most queenfish larvae are found in water <30 m within 4-5 km of shore (Barnett et al.[7]).

Little data exist on the subseasonal spawning patterns of other temperate marine fishes. The data of Clark (1934) suggested monthly spawning peaks for Pacific sardine around times of the full moon. Farris (1963) later showed that no lunar spawning periodicity exists for Pacific sardine and jack mackerel off southern California, although diel and seasonal patterns occur in both species. Northern anchovies spawn between 2200 and 0400 h (Smith 1978, cited in Hunter and Goldberg 1980). A number of north Atlantic fishes have diel spawning periodicities (Simpson 1971). Lunar spawning intervals are known for several littoral fishes that spawn demersal eggs (e.g., California grunion, Clark 1925; mummichog, *Fundulus heteroclitus*, Taylor et al. 1979, Taylor and DiMichele 1980).

Sex Ratio of Spawning Fish

Although the overall adult sex ratio of *S. politus* was only slightly male biased, the male:female sex ratio averaged about 2:1 in groups of fish in which the highest proportion of ready-to-spawn females were present. Hunter and Goldberg (1980) noted the same phenomenon in spawning schools of the northern anchovy and other pelagic spawners. The skewed sex ratio in spawning schools of the queenfish, however, should not bias our estimates of female spawning frequency either for or against spawning females, as may be the case with northern anchovy (Hunter and Goldberg 1980; Hunter and Macewicz 1980), since queenfish were sampled within the entire water column over the total daytime onshore-offshore distribution of the species.

Egg Production and Fish Body Size

The batch fecundity of *S. politus* is proportional to length cubed and is better correlated with weight than with body length, both being general phenomena in fishes (Nikolskii 1969).

The low standing crop ovary weights (2-4% body weight) of *S. politus*, and of multiple-spawning fishes in general (e.g., 6% in the northern anchovy, Smith and Lasker 1978; 4.1-9.0% in the scaled sardine, *Harengula jaguana*, Martinez and Houde 1975), greatly underrepresent total egg production by serial spawners. We estimate that a 25 cm (253 g) *S. politus* with an annual egg production of about 2.2 million eggs (24 batches averaging 90,000 eggs, each egg an average 0.635 mm diameter and 0.134 mg fresh weight) expends the equivalent of 114% of its body weight in eggs in a year. This is not unexpectedly high, since, for example, females of one species of silverside, *Menidia audens*, produce about 6-8 times their body weight in eggs per year (Hubbs 1976). This is, however, considerably more than the seemingly great egg investments made by fishes in which females are single clutched and spawn large, benthic, adhesive eggs (e.g., 20% in the fourhorn sculpin, *Myoxocephalus quadricornis*, Westin 1968; 30% in the red Irish lord, *Hemilepidotus hemilepidotus*, DeMartini and Patten 1979; 34% in the plainfin midshipman, *Porichthys notatus*, DeMartini[8]). Doubtless the poorer survival of small, planktonic eggs and larvae (Ware 1975) necessitates the production of greater numbers of eggs. Partial overlap in the ripening of eggs in successive batches allows greater numbers of eggs of a given size to be produced per unit time, as

[6]E. E. DeMartini and R. J. Larson, Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106, unpubl. data.

[7]Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. Long term average spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS cooling system. A study submitted to the Marine Review Committee of the California Coastal Commission, July 22, 1980. Unpubl. rep., 32 p. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Suite D-57, Solana Beach, CA 92075.

[8]DeMartini, E. E. Variations in fecundity and growth among geographic populations of the plainfin midshipman, *Porichthys notatus*. Manuscr. in prep. Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106.

space within the female's body cavity must set an upper limit to the numbers of eggs of a given size that can be simultaneously ripened and shed.

Egg production in *S. politus* is not directly proportional to weight, as it is in many marine fishes (Bagenal 1967), but is instead an increasing function of body weight (Figure 8). Relative fecundity thus increases with body size in queenfish, as is also the case for northern anchovy (Hunter and Macewicz 1980) and two other offshore Pacific species, jack mackerel and the gonostomatid *Vinciguerria lucetia* (MacGregor 1976).

Spawning Frequency and Annual Fecundity

The 7-d ovarian cycling frequency of *S. politus* is similar to that of *Engraulis mordax* off southern California, the only other species for which analogous data now exists (Hunter and Goldberg 1980). Having first determined the degeneration rate of ovarian postovulatory follicles in laboratory fish, Hunter and Goldberg (1980) used data on the percent frequency occurrence of 1-d-old ovarian follicles in field sample fish to estimate that *E. mordax* spawns on average once every 6-8 d. Estimates of average spawning interval (5.3 d) based on relative incidence of northern anchovy females bearing hydrated oocytes and new postovulatory follicles were indistinguishable from estimates based on frequency occurrence of day 1 postovulatory follicles (Hunter and Goldberg 1980). Spawning frequency is unrelated to female body size in queenfish and the northern anchovy (Hunter and Macewicz 1980). Incidence of hydration provides accurate estimates of spawning frequency when, as with *E. mordax* and queenfish, an identifiable time of spawning exists, all ripe eggs are shed at this time, and sample fish can be collected accordingly.

Annual egg production is largely dependent on spawning frequency in multiple-spawning fishes. The 6- to 8-d spawning interval of *E. mordax* extrapolated over its 5-mo (January-May) peak spawning season (Lasker and Smith 1977), indicates that an individual northern anchovy ripens and sheds about 20 batches of eggs per year (Hunter and Macewicz 1980). At an average relative fecundity of 421 eggs/g (Hunter and Macewicz 1980), estimated annual egg production of the northern anchovy is over 8,000 eggs/g, or about 14 times greater than previous estimates of annual egg production inferred from standing crop fecundities (606 eggs/g, MacGregor 1968; 556 eggs/g, Norberg[9]). Similarly, our estimates of the annual egg production of *S. politus* range from 12 to 24 times the batch fecundity of recruit spawners (90-d season) and of the largest repeat spawners (180-d season), respectively. These data on the ovarian cycling frequencies of the queenfish and the northern anchovy indicate that prior studies of egg production in multiple-spawning marine fishes have in general underestimated annual egg production by at least an order of magnitude. This seems generally true whether the egg production estimate was based on standing crop fecundity (e.g., Simpson 1951; MacGregor 1957) or standing crop fecundity multiplied by the number of spawnings as inferred from the number of size classes of yolked eggs (e.g., Hickling and Rutenberg 1936; DeSilva 1973; but see Shackley and King 1977). Our queenfish data and Hunter and Goldberg's (1980) data for the northern anchovy illustrate that the spawning frequency (hence annual egg production) of serial-spawning fishes cannot usually be inferred from the number of size-frequency modes of ovarian eggs. It follows that many past estimates of the standing stocks of serial spawners that have inferred female abundance based on egg-larval abundances and female fecundities have greatly overestimated stock sizes.

Production Cycles, Timing of Reproduction, and Egg Size

The seasonality of phyto- and zooplankton production strongly influences the timing of reproduction of temperate marine fishes; in general spawning seasons in the temperate zone are timed so that planktonic offspring are exposed to peak food densities (Cushing 1975). The spawning season of the northern anchovy, a species with many reproductive attributes similar to those of queenfish, coincides with phytoplankton production at the start of the production cycle, yet precedes the disruption of prey patches that occurs due to subsequent upwelling (Lasker 1975, 1978). Queenfish larvae prey on copepodites and adult zooplankters (Barnett et al.[10]), and thus it would

[9]Norberg, R. H. 1975. Investigations on the fecundity of northern anchovy, jack mackerel, and Pacific mackerel. Unpubl. manuscr., 23 p. Calif. Dep. Fish Game, 350 Golden Shore, Long Beach, CA 90802.

[10]Barnett, A. M., P. D. Sertic, and R. Davis. 1980. Data summary of larval fish stomach analysis. A study submitted to the Marine Review Committee of the California Coastal Commission, September 7, 1980. Unpubl. rep., 22 p. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Suite D-57, Solana Beach, CA 92075.

seem that queenfish reproduction is timed to coincide with peak zooplankton densities later in the production cycle.

Further evidence for the controlling influence of planktonic production on the timing of reproduction by many fishes, including queenfish, comes from subseasonal variations in egg size. Blaxter and Hempel (1963) demonstrated that larval survival is related to hatchling size, which in turn is proportional to egg volume. The egg (hence larval) size of temperate spring-summer spawning species in general declines over the spawning season, whereas size of eggs of autumn-winter spawning species increases over the season (Ware 1975). These changes in egg size coincide with the planktonic production cycle as it affects the kinds, sizes, and quantities of zooplankton prey available for fish larvae. Larval growth and mortality rates (influenced by seasonally changing predator densities and water temperatures as well as densities of planktonic prey) may also elicit adaptive changes in egg size (Ware 1975). A scenario for spring-summer spawners like queenfish might be as follows: At low water temperatures in early spring, growth of fish larvae is slow, relatively few large (adult) zooplankton are available as food for larval fish, and larger hatchlings are better able to temporarily withstand starvation and to capture and ingest large zooplankton. Also, since survival is related to size of larvae (Ware 1975), larger fish larvae have a lower probability of being eaten. As spring becomes summer, water temperatures rise, larvae can grow faster as more zooplankton of a greater array of sizes become available, and it is then adaptive to spawn greater numbers of smaller eggs that subsequently hatch as smaller larvae (Ware 1975). A large number of spring-summer spawners in the temperate zone track the production cycle in this manner (Bagenal 1971). Serial spawning in regions of upwelling appears to be a tropical adaptation to a temperate production cycle of high amplitude that is highly variable in timing (Cushing 1975). Fishes like queenfish spawn on numerous occasions, perhaps so as to "hedge their bet" against unpredictable, and often poor, subseasonal conditions for planktonic propagules. Of course, serial spawning may also be influenced by the fecundity demands necessitated by small adult body size and high adult mortality rates.

We estimate that the spawned eggs of *S. politus* declined from about 685 to 580 μm in diameter over the interval from March to August 1979. This 15% decrease in diameter corresponds to a 39% decrease in volume, or 65% of the difference expressed as a percentage of the smaller volume. This is a reasonable value; for marine fishes with planktonic eggs, the median percentage difference in intraspecific egg volume is just over 100%, with a range from 4.5 to 403% (Bagenal 1971). Assuming that the chemical composition of yolk in queenfish eggs remains constant during the spawning season, the calorific value of individual eggs declined by about 39%. Since the relation between batch fecundity and female body size is constant throughout the spawning season (Figure 6), queenfish appear to allocate less energy to egg production later in the season by producing smaller eggs. *Engraulis mordax* likewise produces smaller (Smith and Lasker 1978) and perhaps fewer (Hunter[11]) eggs later in its spawning season. The availability of food for adults as well as larvae appears to determine the timing and intensity of spawning by northern anchovy (Hunter and Goldberg 1980) as well as queenfish and perhaps also influences egg size in these fishes.

SUMMARY

The queenfish is a serial spawner with a protracted spawning season. Spawning frequency, although generally asynchronous among females, can be estimated from the incidence of fish with hydrated eggs and averages about once per week for females of all adult sizes. Duration of the spawning season, however, is proportional to female body size, ranging from 3 mo (April-June) in recruit spawners (10.0-10.5 cm SL) to 6 mo (March-August) in repeat spawners (>13.5 cm). Larger females begin spawning earlier in the year and continue spawning after the smallest fish have ceased. Recruit spawners and the largest repeat spawners thus produce about 12 to 24 batches of eggs during their respective spawning seasons.

Batch fecundity is proportional to female body size and is better correlated with weight than with length of female. Batch fecundity ranges from about 5,000 eggs in 10.5 cm SL recruit spawners to about 90,000 eggs in the largest (25 cm) repeat spawners. The average (14 cm) fish produces about 12,000-13,000 eggs per batch. Almost all hydrated eggs are liberated at the time of spawning, which

[11]J. Roe Hunter, Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. August 1980.

occurs at dusk and has monthly peaks in intensity during the week of the moon's first quarter.

Annual egg production ranges from about 60,000 eggs to over 2.2 million eggs in the smallest recruit spawner and the largest repeat spawner, respectively. The average female produces about 300,000 eggs in a year. These estimates of annual egg production are an order of magnitude greater than usually would be inferred based on oocyte size class frequencies.

Relative fecundity of the queenfish is an increasing function of body size. Larger females produce larger eggs, and females of all adult sizes produce larger eggs earlier in the season.

As reflected by the general nature of its protracted, serial spawning activities and by the timing of subseasonal variations in its egg size and in the female size-to-egg size and egg number relationships, the queenfish closely resembles many or most small, planktonic spawners of warm temperate regions. We suggest that the reproductive dynamics of the queenfish typify the suite of reproductive adaptations characteristic of small, short-lived fishes that must cope with irregular (unpredictable) subseasonal variations in planktonic productivity.

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NOTES

SEASONAL SPAWNING CYCLE OF THE BLACK CROAKER, *CHEILOTREMA SATURNUM* (SCIAENIDAE)

Detailed information is lacking on the spawning cycle of the black croaker, *Cheilotrema saturnum*. Previous works (Eigenmann 1892; Skogsberg 1939; Limbaugh 1961; Fitch and Lavenberg 1975) have indicated spawning occurs in spring and summer. This report describes the histological changes occurring in the spawning cycle. Comparisons are made with the spawning cycles of two other sciaenid fishes (*Genyonemus lineatus* and *Seriphus politus*) which were studied by Goldberg (1976). *Cheilotrema saturnum* ranges from Magdalena Bay, Baja California, to Point Conception, Calif. (Miller and Lea 1976).

Methods

A total of 154 mature female *C. saturnum* were examined from collections made in January, March, July, September 1977 and 1978. Specimens were collected during heat treatment processes at the Scattergood Steam Plant (City of Los Angeles, Department of Water and Power, LADWP), El Segundo (lat. 33°50′ N, long. 118°30′ W), Los Angeles County, Calif. Steam generating plants periodically reverse the flow of cooling water in their intake and discharge pipes and raise the temperature to a level that will kill off entrapped organisms. Immediately after collection, fish were slit along the abdomen and placed in 10% Formalin.[1] Ovaries were embedded in paraffin; sections were cut at 8 μm and stained with iron hematoxylin. Body and ovary weights were measured on a torsion balance to the nearest 0.01 g. Standard lengths (SL) were measured to the nearest millimeter. Gonosomatic indices (GSI = ovary weight/fish weight × 100) were calculated from measurements made after preservation.

Results and Discussion

Ovaries were classified histologically into four stages (Table 1). Stage 1 (regressed or regressing ovary): the nonspawning condition consists principally of primary oocytes (<100 μm in diameter). Stage 2 (previtellogenic): slightly enlarged vacuolated oocytes (100-200 μm in diameter) predominate prior to onset of yolk deposition. Stage 3 (vitellogenic): yolk deposition in progress. Stage 4 (spawning): mature (ripe) oocytes (>300 μm) predominate.

Ovaries were regressed (Stage 1) during autumn and winter (Table 1, Figure 1). GSI values began to increase during winter and Stage 2 oocytes became common. In late spring enlarging follicles undergoing yolk deposition (vitellogenesis) were

TABLE 1. Monthly distribution of standard lengths and stages in *Cheilotrema saturnum* spawning cycle, January 1977-November 1978.

Month	*N*	Range (mm)	Stage 1 (%)	Stage 2 (%)	Stage 3 (%)	Stage 4 (%)
Jan.	6	160-240	100	0	0	0
Mar.	16	181-296	87	13	0	0
May	7	167-292	43	29	14	14
July	15	194-280	0	0	7	93
Sept.	6	160-232	83	0	0	17
Nov.	8	171-267	100	0	0	0
Jan.	16	166-283	100	0	0	0
Mar.	14	172-260	50	50	0	0
May	12	168-255	0	25	8	67
July	29	161-262	0	0	10	90
Sept.	11	165-231	64	9	0	27
Nov.	14	167-265	100	0	0	0

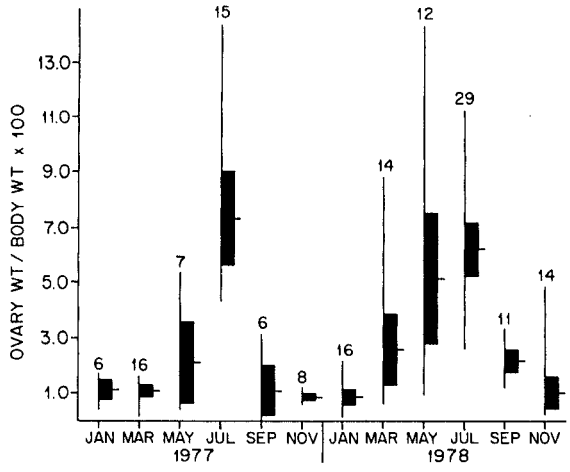

FIGURE 1.—Seasonal gonosomatic indices for *Cheilotrema saturnum*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval and sample size above each month.

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

present (Stage 3). Other fish examined at this time were in spawning condition (Stage 4) and contained ovaries with mature yolk-filled oocytes. The peak of spawning activity occurred in midsummer (July). Most spawning was completed by September as GSI values dropped and numbers of spawning females were fewer (Table 1). Atretic oocytes were common in September near the close of the spawning period when oocytes that failed to complete yolk deposition underwent resorption. They were observed in 67% of my combined 1977-78 September samples.

Rather than maturing and spawning one mode (size class) of eggs at a time, it seems that females reach spawning condition and then release batches of mature eggs throughout the spawning season. This is likely, as no summer females were observed with ovaries in postspawning (partly spent or spent) condition. Instead, *C. saturnum* oocyte development appears to be a continuous process during the spawning season, as ovaries at all times contained maturing and large numbers of mature oocytes. I have previously observed this pattern (Goldberg 1976) in *G. lineatus* and *S. politus*.

Postovulatory follicles (transitory remnants of the follicle wall from recently ovulated eggs) were seen in only 2% of my combined 1977-78 July samples. Ovaries containing these structures were in spawning condition. This low percentage is not unexpected in view of their rapid degeneration in teleost fishes (Yamamoto and Yoshioka 1964; Hunter and Goldberg 1980).

The spawning cycle of *C. saturnum* is similar to that of *S. politus*, namely, April-August (Goldberg 1976). Spawning in *G. lineatus* occurs November-April (Goldberg 1976) and is thus distinctly different from that of *C. saturnum* and *S. politus*. According to Feder et al. (1974) three other California sciaenids (*Atractoscion nobilis*, *Menticirrhus undulatus*, and *Roncador stearnsii*) are also summer spawners.

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POPULATION GROWTH AND CENSUSES OF THE NORTHERN ELEPHANT SEAL, *MIROUNGA ANGUSTIROSTRIS*, ON THE CALIFORNIA CHANNEL ISLANDS, 1958-78

The northern elephant seal, *Mirounga angustirostris*, has received considerable attention because of its dramatic recovery from near extinction in the late 19th century. Bartholomew and Hubbs (1960) reviewed the chronicle of the species from 1818 to 1960 and estimated the total population over its then known range at about 13,000 animals. Since 1960, a number of investigators have reported on the reestablishment of elephant seals on progressively northern islands and on the size of its breeding populations. Such information is now available for the islands of the Pacific coast of North America from Isla Natividad, Baja California,

northward to the Farallon Islands, Calif. (Bartholomew and Boolootian 1960; Radford et al. 1965; Rice et al. 1965; Carlisle and Aplin 1966, 1971; Carlisle 1973; Frey and Aplin 1970; Odell 1971, 1972, 1974; Le Boeuf et al. 1974; Le Boeuf and Mate 1978; Bonnell et al.[1]). By 1978 the total population was believed to have increased to an astounding 63,967 animals (Bonnell et al. footnote 1).

The northern elephant seal breeding population can be geographically divided into three subpopulations by centers of distribution (Figure 1): Baja California; California Channel Islands, including Islas Los Coronados, Baja California; and Central California (Gogan[2]).

One can trace a rapid increase in size of the California Channel Island subpopulation (hereinafter called the subpopulation) over the last nearly three decades. Rett (1952) reported seeing a single female on San Miguel Island in 1925. Bartholomew and Hubbs (1960) estimated that by 1957 the subpopulation contained 600 individuals. Births were first observed on San Miguel Island in 1958 and on San Nicolas Island in 1959, by which time the total subpopulation included an estimated 683 animals (Bartholomew and Boolootian 1960). By 1964, there were reportedly 2,158 elephant seals on three islands during the winter breeding season[3]: San Miguel (1,922), San Nicolas (197), and Santa Barbara (39) (Odell 1971). Based on cumulative data obtained during 4 yr of research, Bonnell et al. (footnote 1) estimated that by 1978 there were approximately 28,316 elephant seals in the subpopulation.

In this paper we report on counts of northern elephant seals conducted on all the California Channel Islands, including Islas Los Coronados, in February 1972. Using estimated pup production figures from this and other published censuses for the years 1958-78, we then assess rates of growth for each island within the subpopulation and for the subpopulation as a whole. The relative contributions of each island to the subpopulation total are also presented.

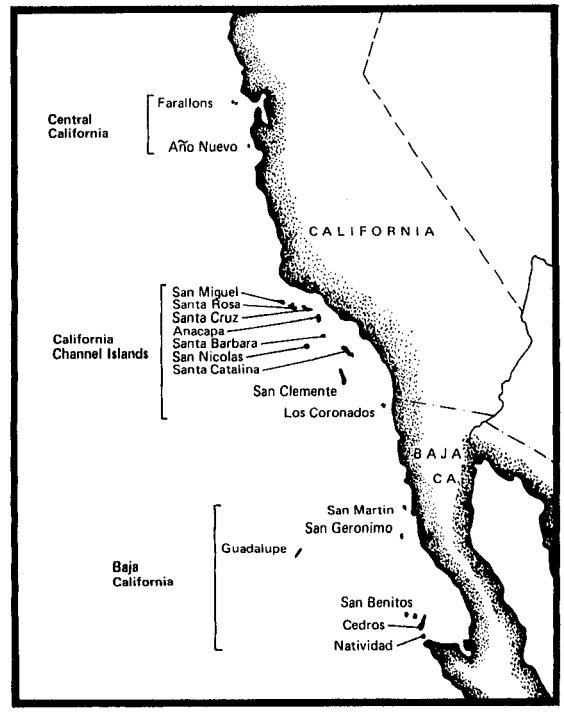

FIGURE 1.—Subdivision of the islands of California and northwestern Baja California into groups, corresponding with designated subpopulations of northern elephant seals (modified from Le Boeuf 1977; Gogan text footnote 2; Bonnell et al. text footnote 1).

Materials and Methods

On 8 February 1972, observers surveyed beaches of all California Channel Islands (except Islas Los Coronados) from U.S. Navy helicopters flying at an altitude of 150 m (500 ft) and a speed of 90 kn, taking large format (9 in × 9 in), near-vertical aerial photographs of all elephant seals seen. Counts of elephant seals were made from glossy black and white prints arranged into mosaics and handled in the manner described by Odell (1971). When possible, animals were differentiated as adult males, adult females, and pups. Counts on the Islas Los Coronados were made from the beach by swimmers dispatched from small boats anchored near shore. All counts represented minimum numbers in the population because an unquantified portion is always at sea (Le Boeuf 1972).

[1]Bonnell, M. L., B. J. Le Boeuf, M. O. Pierson, D. H. Dettman, G. D. Farrens, C. B. Heath, R. F. Gantt, and D. J. Larsen. 1980. Summary of marine mammal and seabird surveys of the Southern California Bight area 1975-1978. Vol. 3-Investigators' Reports, Part 1 - Pinnipeds of the Southern California Bight, 535 p. Univ. Calif., Santa Cruz, Calif., Final Report to the Bureau of Land Management, under Contract AA550-CT7-367.

[2]Gogan, P. J. P. 1977. A review of the population ecology of the northern elephant seal (*Mirounga angustirostris*). Processed Rep., 68 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

[3]For descriptions of seasonal fluctuations in numbers of northern elephant seals on land see Le Boeuf (1972) and Odell (1972).

Counts of suckling and weaned elephant seal pups from this and other censuses between 1958 and 1978 were assembled and compared. Because most pups remain on land until late February (Le Boeuf et al. 1972; Reiter et al. 1978) and are highly visible, they are easily counted during February surveys. We believe, therefore, that pup production estimates are the most accurate available means of assessing, from census data, trends in population numbers of elephant seals.

Total pup production estimates were extrapolated from pup counts (Odell 1974) by correcting for date of census using the equation:

$$\frac{Pi}{f} = Pt$$

where Pi = pups counted at time of census,
f = fraction of maximum pup numbers counted at time of census (Odell 1974, fig. 6),
Pt = estimated total number of pups born that year.

This calculation assumes that the temporal pattern of births on all Channel Island rookeries is not significantly different from that reported for San Nicolas Island (Odell 1974). Corrections are not made for neonatal mortality since rookery specific data are not available.

Three indices of population growth were calculated from both pup counts and estimated total pup production: RC = the relative contributions of each island expressed as a percentage of the total pup counts for each census year; $I\bar{r}$ = the estimated average annual rate of increase for each island; and $S\bar{r}$ = the estimated average annual rates of increase for the entire subpopulation. The average rates of increase ($\bar{r}$) were derived from the formula, $N_t = N_0 e^{\bar{r}t}$ where $\bar{r}$ carries no implication that the rate of increase is constant over the time interval, that the age distribution is constant, or that the resources are in superabundance (Caughley 1977). Thus, $\bar{r}$ can be used as a standardized means of comparing the rates of population increase from one census year to the next.

Results and Discussion

Results of the 1972 census are shown for each island, according to elephant seal age/sex class, in Table 1. All 1972 breeding season counts were greater than similar counts reported previously by Odell (1971) and Le Boeuf et al. (1975).

TABLE 1.—1972 breeding season census of northern elephant seals taken 8 February on the California Channel Islands, including Islas Los Coronados (see Figure 1). Unless otherwise noted, counts were made from aerial photographs.

Island	Adult males	Adult females	Total adults	Pups	Total animals
San Miguel	497	1,410	1,907	1,902	3,809
San Nicolas	103	305	408	399	807
Santa Barbara	4	39	43	26	69
Los Coronados[1]	6	27	33	6	39
San Clemente	0	20	20	0	20

[1]Land-based census.

Pup counts and the computed values they support for the indices RC, $I\bar{r}$, and $S\bar{r}$, are shown in Table 2 for the years between 1958 (San Miguel Island), 1959 (San Nicolas Island), or 1964 (Santa Barbara Island and Islas Los Coronados) and 1978. There was little difference in the indices that were calculated from actual pup counts and those from total pup production estimates (Table 2).

Although the California Channel Island elephant seal subpopulation as a whole and each of its component island colonies have continued to grow over the last 16-22 yr, the rates of increase and individual island contributions to the subpopulation have varied (Table 2).

Relative Island Contribution (RC)

In general the ranked island contributions relative to the total subpopulation pup counts from highest to lowest have been: San Miguel, San Nicolas, Santa Barbara, and Islas Los Coronados (Table 2). Consistent with that trend, in 1958-59 San Miguel Island contributed 55.9% and San Nicolas Island 44.1% of the known subpopulation. But by 1964, the San Miguel Island population had grown so fast that its pup population was an estimated 10 times greater than the San Nicolas Island population, accounting for 90% of the entire subpopulation. During the subsequent period, 1964 to 1972, the RC values decreased for San Miguel Island (81.5), increased for San Nicolas Island (17.1), and remained about the same for Santa Barbara Island (1.1). From 1972 to 1978 there was generally little change in the RC values for all islands.

Increases in numbers of elephant seals and RC values can reasonably be expected on San Miguel and San Nicolas Islands where there are remaining unused beaches suitable for breeding rookeries (Le Boeuf and Bonnell 1980). However,

TABLE 2.—Counts of northern elephant seal pups in the California Channel Islands subpopulation, including Islas Los Coronados (see Figure 1). Unless otherwise noted, counts were obtained from aerial photographs. Also presented are relative contributions by each island (*RC*) expressed as a percentage of the total pup count and average yearly rates of increase in pup production for each island ($I\bar{r}$) and for the Channel Islands subpopulation ($S\bar{r}$).

Island	Census date	Source	Pup counts		*RC*		$\bar{Ir}$		$S\bar{r}$	
San Miguel	14 Feb. 1958[1]	Bartholomew and Boolootian 1960	[2]80	(81)	[3]62.5	(55.9)				
San Nicolas	23 Jan. 1959[1]	Bartholomew and Boolootian 1960	48	(64)	37.5	(44.1)				
Santa Barbara	Not censused									
Los Coronados	Not censused									
		Total	128	(145)						
San Miguel	9 Feb. 1964	Odell 1971	796	(812)	90.0	(89.8)	[3]0.383	(0.384)		
San Nicolas	9 Feb. 1964		78	(80)	8.8	(8.9)	.081	(.037)		
Santa Barbara	9 Feb. 1964		12	(12)	1.2	(1.3)			[3]0.322	(0.305)
Los Coronados	12 Jan. 1964	Le Boeuf et al. 1975	0							
		Total	886	(904)						
San Miguel	8 Feb. 1972	This study	1,902	(1,941)	81.5	(81.5)	.109	(.109)		
San Nicolas	8 Feb. 1972		399	(407)	17.1	(17.1)	.204	(.203)		
Santa Barbara	8 Feb. 1972		26	(27)	1.1	(1.1)	.097	(.101)		
Los Coronados	8 Feb. 1972[4]		6	(6)	.3	(.3)				
		Total	2,333	(2,381)					.121	(.121)
San Miguel	27 Jan. 1978	Bonnell et al. text footnote 1	4,512	(5,013)	84.6	(84.2)	.144	(.158)		
San Nicolas	29 Jan. 1978		782	(850)	14.7	(14.3)	.112	(.123)		
Santa Barbara	29 Jan. 1978		37	(40)	.7	(.7)	.059	(.066)		
Los Coronados	29 Jan. 1978			[5](45)		(.8)		(.336)	.138	(.153)
		Total	5,331	(5,948)						

[1]The 1958 and 1959 census data averaged and treated as a single census year.
[2]Actual counts, followed in parentheses by total pup production estimates which were corrected for times when less than maximum pup numbers can be counted.
[3]Values calculated from actual pup counts, followed in parentheses by values calculated from total pup production estimates.
[4]Land based census.
[5]Only estimated value reported (Bonnell et al. text footnote 1).

the fact that there is apparently little suitable space available for new elephant seal rookeries on Santa Barbara Island and Islas Los Coronados (Le Boeuf et al. 1975; Bonnell et al. footnote 1) suggests that the numbers on those islands have stabilized and that there will be a concommitant decline in their *RC* values in future years.

Estimated Average Annual Rate of Increase by Island ($I\bar{r}$)

The $I\bar{r}$ values peaked between 1958 and 1964 on San Miguel Island and between 1964 and 1972 on San Nicolas and Santa Barbara Islands. Data presented suggest that numbers on Islas Los Coronados probably increased most rapidly between 1972 and 1978. This suggestion is supported by results of a more detailed study of those islands which provide data for intermediate years during this period (Le Boeuf et al. 1975).

Generally for each island, periods of high annual increase in population have been followed by periods of decreasing $I\bar{r}$ values. Such trends in reduction of growth rate can be expected to continue until such time as each island's elephant seal numbers reach stability, a pattern of population growth characteristic of other large marine and terrestial mammals (Fowler[4]). The increase from 1972 to 1978 on San Miguel Island is not surprising for an island where space does not appear to be a limiting factor, and similar increases might yet occur on the other islands where suitable breeding space is available. High rates of increase might also occur on new rookeries as northern elephant seals begin to colonize such areas as San Clemente Island and the mainland (Le Boeuf and Panken 1977; Le Boeuf and Mate 1978). But it is highly unlikely that any of the presently colonized California Channel Islands will ever experience growth periods that will exceed the largest $I\bar{r}$ values presented in Table 2.

Estimated Average Annual Rate of Increase in the Subpopulation ($S\bar{r}$)

The most rapid growth in the Channel Island subpopulation as a whole apparently occurred between 1958 and 1964. During this period, $S\bar{r}$ values reached 0.384 then dropped to 0.121 for 1964-72 and 0.153 for 1972-78. The extremely high rate of increase observed from 1958 to 1964 was proba-

[4]Fowler, C. W. 1978. Appendix C. Non-linearity in population dynamics with special reference to large mammals. *In* C. W. Fowler, W. T. Bunderson, M. B. Cherry, R. J. Ryel, and B. B. Steel. Comparative population dynamics of large mammals: a search of management criteria, p. 174-220. Report to U.S. Marine Mammal Commission, Wash., D.C. (Available Natl. Tech. Inf. Serv., Springfield, VA 22161 as PB80-178627.)

bly the result of recruitment both from the Baja subpopulation and from within the California Channel Island subpopulation (Chapman in press; Gogan footnote 2).

Although the Channel Islands subpopulation as a whole may continue to grow, it is likely that future $S\bar{r}$ values will eventually follow the decreasing trend towards stability which was described above for $I\bar{r}$ values (Fowler footnote 4).

Other California Channel Islands

Breeding colonies were not observed on any of the remaining Channel Islands during the 1972 censuses. The small numbers of animals seen on San Clemente Island included no pups, although there is a more recent indication that breeding/pupping sometimes occurs there. A single female with a pup was observed on San Clemente Island in January 1977 (Le Boeuf and Mate 1978). However, no pups were observed there during the 1978 breeding season surveys from land by Cohen.[5]

Anacapa Island may not offer suitable habitat for elephant seals because of its high cliffs and rocky coastline. The beaches on San Clemente Island are near a naval shore bombardment range and frequent bombing may have prevented the animals from establishing a breeding colony there. However, reasons for the absence of elephant seals on Santa Cruz, Santa Rosa, and Catalina Islands, all of which have some beaches which appear suitable, are not known, although human disturbance may be an important factor (Kenyon[6]).

Acknowledgments

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[5]Robert H. Cohen, Naval Ocean Systems Center, San Diego, CA 92152, pers. commun. March 1978.

[6]Kenyon, K. W. 1973. Human disturbance of marine birds and marine mammals in wilderness areas of Baja California, Mexico, 10-17 February 1973. Unpubl. manuscr., 16 p. U.S. Dep. Inter., Bur. Sport Fish. Wildl., Div. Wildl. Res., Mar. Mammal Substation, Seattle, Wash. (Available Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.)

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GROWTH CHARACTERISTICS OF YOUNG-OF-THE-YEAR WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN JOHN DAY RESERVOIR ON THE COLUMBIA RIVER, 1979

The walleye, *Stizostedion vitreum vitreum*, is becoming increasingly abundant in many of the large reservoirs of the Columbia River (Durbin[1]). Although the origin of this species in the Columbia River system is not entirely clear, Durbin (footnote 1) reported that walleye was introduced into the upper Clark Fork River, Idaho (a tributary of the Columbia River drainage), in the late 1940's (Figure 1). The large impoundments of the Columbia River, with turbid water conditions occurring through most of the spring and early summer, are providing walleye with suitable habitat. Scott and Crossman (1973) reported that walleye, throughout its range, reaches its greatest abundance in large turbid lakes and slow moving rivers.

[1]Durbin, K. 1977. News column. Oreg. Dep. Fish Wildl., Portland.

The increase in walleye population has generated considerable interest among sport fishermen throughout the Columbia River area (Harbour 1980). Because of its value as a game fish, some envision a significant new fishery similar to the historic fisheries of the Great Lakes region. Fisheries managers responsible for the survival of juvenile salmon, *Oncorhynchus* spp., and steelhead, *Salmo gairdneri*, are viewing the increase in walleye population with alarm, fearing that because of its highly piscivorous habits, it may become a significant salmonid predator.

Turbine intake gatewells at major dams in the Columbia River system are sampled each year to monitor the juvenile salmonid migrations (Raymond 1979). John Day Dam, a large hydroelectric project on the Columbia River, was completed in 1968 and created a reservoir (Lake Umatilla) 122 km long (Figure 1). Juvenile walleye was first observed in the gatewells at John Day Dam in 1973, and small numbers continued to be taken through 1978. In 1979, a large increase in the number of young-of-the-year walleye in the gatewells at John Day Dam was observed.

Information yielded by monitoring these young-of-the-year walleye in John Day Reservoir is presented in this paper. A comparison between growth of walleye in this reservoir and walleye populations from other areas is also given.

Methods

A large dip net, similar to that described by Bentley and Raymond (1968), was used to collect juvenile walleye from the turbine intake gatewells at John Day Dam. Young walleye were captured incidentally to the juvenile salmonid monitoring operation at the dam. A sample consisted of a 24-h composite catch removed daily from the gatewell via the dip net. Sampling extended from 1 March through 18 December 1979. All fish taken were measured for total length (TL) to the nearest millimeter and weighed to the nearest 0.1 g. Age was determined from scale samples taken in the manner described by Eschmeyer (1950). Scales were removed and examined from all specimens ≥100 mm TL to confirm that they were in fact young-of-the-year fish.

Results and Discussion

In 1979, the number of walleye entering the turbine intake gatewells at John Day Dam in-

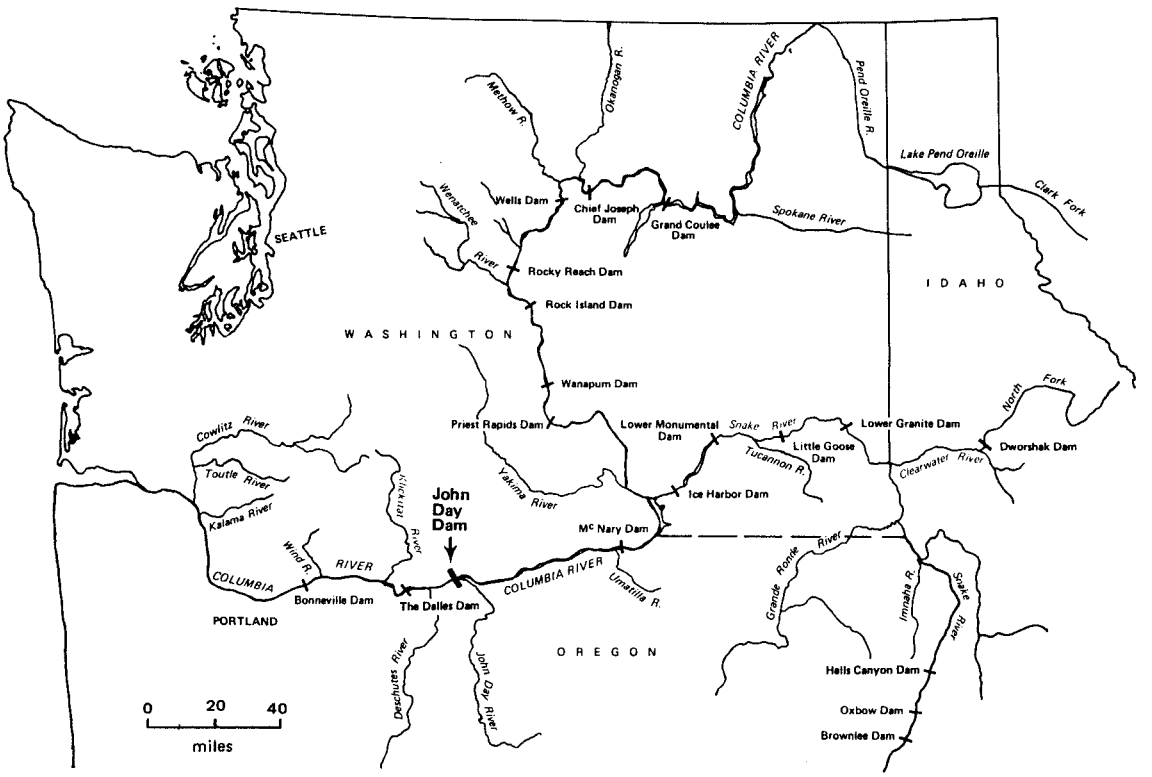

FIGURE 1.—Columbia River drainage.

creased significantly. From 1973 through 1978 fewer than 15 juvenile walleye were taken per year, whereas in 1979, several hundred were taken with similar fishing effort. Early in the season, an exact count was not possible because many of the small fish (<40 mm TL) fell through the mesh of the net [12.7 mm (½ in) stretched measure]. In 1979, young-of-the-year walleye was first taken in the gatewells in July and continued to be taken until sampling was suspended in mid-December.

Walleye normally spawns at water temperatures between 5.6° and 11.1° C (Scott and Crossman 1973). Hatching occurs in 21 d at water temperatures of 10°-12.8° C (Niemuth et al. 1972). Water temperatures at John Day Dam rose from 6.2° to 13.8° C during April and May 1979. At these temperatures one would expect hatching to extend through May, producing fry in the 40 mm class by early July.

Water temperatures in John Day Reservoir during the summer were near optimum for excellent growth of juvenile walleye. Huh et al. (1976) reported the growth of young-of-the-year walleye to be temperature dependent, with optimum growth occurring at 22° C. Water temperatures in John Day Reservoir fluctuated between 19° and 21° C for a 10-wk period extending from early July through September.

Total length of juvenile walleye increased an average of 11 mm/wk from July to October (Figure 2). This compares very favorably to the 13 mm/wk reported by Wolfert (1977) for walleye in Lake Erie. Mean length of young-of-the-year walleye in John Day Reservoir at the end of the 1979 growing season was 226 mm. Average weight by this time was 87.4 g (0.19 lb). Total length at the end of the growing season was only slightly less than reported for walleye in Lake Erie (Wolfert 1977) and considerably greater than lengths reported in Lake Gogebic, Mich. (Eschmeyer 1950); Red Lake, Minn. (Smith and Pycha 1960); and Oneida Lake, N.Y. (Forney 1966). Growth of young-of-the-year walleye in John Day Reservoir slowed steadily in November with declining water temperatures.

The presence of a larger number of walleye in the gatewell samples during 1979 indicates that the abundance of juvenile walleye appears to be increasing. The potential impact on salmonid

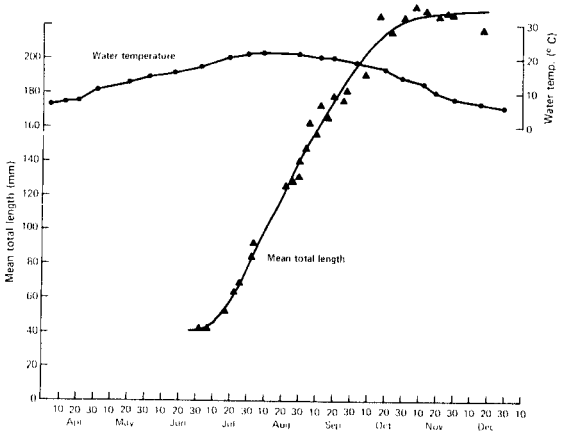

FIGURE 2.—First year growth of walleye and water temperature at John Day Dam on the Columbia river, 1979. Growth curve fitted by inspection (171 fish represented). Each point on the growth curve is the arithmetic mean of 3 to 12 specimens.

populations by the increasing abundance of walleye indicates a continuing need for monitoring walleye in this section of the Columbia River system.

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EFFECTS OF TEMPERATURE AND SALINITY ON EGG HATCHING AND LARVAL SURVIVAL OF RED DRUM, *SCIAENOPS OCELLATA*[1]

The red drum, *Sciaenops ocellata*, is a sciaenid fish distributed along the eastern coast of North America from Massachusetts to southern Florida and along the gulf coast at least as far south as Tampico, Mexico (Hildebrand and Schroeder 1928; Simmons and Breuer 1962). Spawning occurs in late summer through fall outside estuaries in nearshore coastal waters, and the young red drum is carried into the estuaries by tides and currents (Pearson 1929; Mansueti 1960). Late larvae and early juveniles have been collected in the shallow water of tidal flats and sea grass beds. The early planktonic stages, the eggs and yolk-sac larvae, have not been identified from field collections but have recently been described, based on specimens from laboratory-spawned red drum (Holt et al. 1981).

Temporal fluctuations in abundance of red drum result in annual variation in sport and commercial catches (Matlock and Weaver 1979). Variations in environmental factors such as temperature and salinity could affect egg incubation and larval survival, and ultimately year-class strength. Juveniles and adults are euryhaline and are found naturally in freshwater, in brackish

[1]University of Texas Marine Science Institute Contribution No. 466.

water estuaries, and most abundantly in salinities of 20-35‰ (Simmons and Breuer 1962). A wide temperature range of 2°-33° C can be tolerated as long as the temperature change is gradual (Gunter and Hildebrand 1951; Simmons and Breuer 1962). Little is known about the upper and lower limits of temperature and salinity and their effects on survival of eggs and early larval stages, or on early development and growth.

The objective of this study was to determine the optimum temperatures and salinities for hatching and growth of red drum eggs and larvae. Similar work on temperature and salinity effects on survival and development have been detailed for other marine species (Alderdice and Forrester 1971; Alderdice and Velsen 1971; May 1975).

Methods

Eggs were obtained from laboratory spawnings induced by manipulations of temperature and photoperiod to simulate natural seasonal changes (Arnold et al. 1977). Brood tank temperatures ranged from 24° to 26° C and salinities from 26 to 32‰. The most successful method for rearing larvae under our experimental conditions was the following: 1) Hatching at a density of 50-100 eggs in a 100 ml beaker with 10 ppm erythromycin; 2) feeding sequentially the dinoflagellate *Prorocentrum micans* (500/ml, day 2) and the rotifer *Brachionus plicatilis* (50-100/ml, day 3); 3) transferring larvae after 3-4 h feeding on rotifers to a Nitex[2] holding chamber in a 1 l beaker; 4) feeding *Artemia salina* nauplii to larvae (2/ml, beginning on day 7).

Water was changed every fourth day. The holding chambers were made from a cylinder of 300 μm Nitex net glued to a plastic Petri dish; the dish forming the bottom and the Nitex net the sides of the container. Air was introduced into the beaker outside the holding chamber to avoid producing turbulence and bubbles within the chamber. Test salinities were made with filtered seawater (1 μm) diluted with deionized water or concentrated with artificial sea salts (Instant Ocean). Temperatures were maintained within 0.5° C and illumination from fluorescent room lamps was continuous. Percentage hatch, percentage survival of the larvae to 24 h and 14 d, and standard length (millimeters) of 14-d-old larvae were measured to determine the influence of temperature and salinity. Analyses were conducted on the arc sine transformation of the percentages. Two-way factorial analysis of variance was used to test for significant differences among eggs and larvae reared at 12 salinity-temperature conditions.

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

Results

Results of initial tests of the influence of different temperature-salinity combinations on hatching and survial of red drum showed poor hatching rates at low salinity (10‰) over all temperatures except 25° C. Red drum eggs floated in 25‰ or greater salinity and sank to the bottom in lower salinities. High temperatures (30° and 35° C) and high salinities were associated with poor survival of the yolk-sac larvae. Based on these results four salinities (15, 20, 25, and 30‰) and three temperatures (20°, 25°, and 30° C) were used to determine conditions for optimum survival and growth of red drum eggs and larvae. The ranges of salinity and temperature selected are representative of conditions occurring in coastal waters during the normal spawning period.

TABLE 1.—Percentage hatch and larval survival of red drum for each salinity-temperature condition tested. Initially each replicate contained 50-100 eggs.

Salinity (‰)	Temp (° C)	Hatch (%) Replicates								Mean		24-h-old larvae (%) Replicates					Mean
15	20	100	95	91	79	94	100	100	97	96	95	93	100	100	97	98	97
	25	87	58	3	10	84	80	100	100	65	87	28	98	95	94	93	83
	30	89	50	72	64	61	79	100	100	77	89	22	84	98	1	1	49
20	20	100	96	94	85	98	92	100	100	96	97	96	100	100	98	97	98
	25	86	98	34	74	92	88	100	100	84	86	98	100	100	100	99	97
	30	90	71	94	72	57	56	100	100	80	90	55	86	83	25	83	70
25	20	100	98	84	87	96	98	100	100	95	97	96	100	100	98	97	98
	25	100	98	95	89	98	97	100	100	97	100	98	100	100	99	100	100
	30	96	100	96	80	96	100	100	100	96	79	72	98	100	94	95	90
30	20	100	98	91	94	94	100	100	100	97	98	98	100	100	100	98	99
	25	100	100	100	100	98	98	100	100	100	100	98	100	100	100	100	100
	30	100	100	91	100	98	100	100	100	99	82	79	100	100	96	98	93

The best conditions for hatching and 24-h larval survival were 30‰ salinity and 25° C (Table 1). Analysis of variance of the hatching data showed temperature (T) and the temperature-salinity interaction ($T \times S$) effects to be of borderline significance ($0.10 > P > 0.05$); only salinity was significant ($P < 0.05$) (Table 2). A pattern of decrease in percent hatch with increase in temperature at the lower salinities (15 and 20‰), but not at the higher salinities (Table 1), is indicative of the $T \times S$ interaction. Hatching was significantly greater at the two higher salinities than at lower salinities (Table 3).

Survival of larval red drum to 24 h was influenced by both temperature and salinity. Poorest survival was at 30° C and 15‰ (Table 3).

Temperature was associated with significant differences in survival of 2-wk-old larvae (Table 2). The lowest temperature (20° C) resulted in reduced survival rate. The effect of temperature on larval growth rate was pronounced; growth at 20° C was much slower than at 25° or 30° C (Table 4). Salinity had little influence on growth.

TABLE 3.—Mean percentage hatch, 24-h survival, and 2-wk survival of red drum over all conditions. Individual means were compared using Duncan's multiple range test. Any two means connected by the same line were not significantly different ($P < 0.05$).

Item	15‰	20‰	25‰	30‰	20° C	25° C	30° C
% hatch	76.46	86.54	96.17	98.42	96.09	86.47	87.87
% 24-h survival	64.57	75.19	81.79	84.20	98.04	94.71	75.42
% 2-wk survival	6.00	4.17	5.42	4.92	0.37	8.00	7.00

TABLE 4.—Standard length (millimeters) of red drum larvae that survived 2 wk.

Salinity (‰)	20° C			25° C			30° C		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
15	2.80		1	4.90	1.137	18	6.20	1.316	38
20	3.35	0.212	2	4.60	1.046	34	5.80	1.500	17
25	3.20		1	4.70	1.078	27	7.00	1.794	29
30	3.55	.071	2	4.75	.937	30	6.80	2.019	13

Discussion

Salinity was important for hatching and 24-h survival but not for 2-wk survival. Red drum eggs developed successfully to feeding larvae at salinities of 10-40‰ at 25° C; at other temperatures the salinity range for 75% hatch was reduced to 15-30‰. In low salinities, eggs sank to the bottom; as Fonds (1979) explained for the common sole, *Solea solea*, crowding and possible respiratory stress contributed to reduced survival under these conditions. In natural populations high mortality of eggs developing on the bottom would be expected.

Red drum eggs may have been acclimated to the higher salinities since salinities for best hatching were very near the salinities of the maturation and spawning tanks (26-30‰). Solemdal (1967) reported that the osmotic concentration of the ovarian fluid affected the buoyancy of flounder eggs and that both could be changed experimentally. Kinne and Kinne (1962) found that the salinity of the water in which the parents lived affected the response of developing cyprinodont fish to salinity. Differences in response were explained as being primarily nongenetic adaptations to the spawning salinity (Kinne 1962). Conversely, May (1975) found salinity tolerance of *Bairdiella icistia* eggs was not affected by acclimation of the parent fish to low salinity and suggested that salinity responses determined for eggs accurately predict reaction to different salinities in nature.

Temperature became increasingly important as the larvae developed. Apparently contradictory results showed low temperature (20° C) to be superior for 24-h survival, but inferior for 2-wk survival and growth. With low temperature, development and probably metabolism were slowed to the extent that growth and even mortality were delayed. The time spent in the yolk-sac stage is temperature dependent; ranging from 40 h at 30° C to 85 h at 20° C (Holt et al. 1981). Blaxter (1969) cautioned that high yolk-sac utilization efficiency may result from low activity which becomes a liability when it is reflected in

TABLE 2.—Analysis of variance of percent hatch and survival of red drum eggs and larvae subjected to various temperature-salinity conditions.

	% hatch				24-h-old larvae				2-wk-old larvae			
Source	df	MS	F	P	df	MS	F	P	df	MS	F	P
Temperature (T)	2	459.94	2.44	0.09	2	3,090.70	16.43	0.00	2	450.69	20.66	0.00
Salinity (S)	3	1,634.80	8.67	0	3	1,386.77	7.37	0	3	4.56	.21	.89
$T \times S$	6	400.18	2.12	.06	6	352.40	1.87	.10	6	6.54	.30	.92
Error	84	188.41			60	188.12			12	21.82		

low feeding activity. This was clearly the case with the few fish that survived 2 wk in 20° C. These larvae were inactive, were not seen catching prey, and they grew very slowly. Larvae raised at higher temperatures actively attacked and ate prey as soon as it was introduced to the chamber.

Based on these results we hypothesize that red drum spawning success and subsequent year-class strength will be adversely affected by the early onset of low water temperatures. Red drum is a fall spawner and the young must survive and grow at the winter temperatures found in low-temperate estuaries; bay water temperatures often fall below 20° C in November and average 15°-17° C in December in Texas (Martinez 1975). The results indicate that for the first week or so the larvae are stenothermal. The ability to find and catch prey when the yolk sac has been absorbed is a critical phase in larval survival (May 1974). Once temperature in the coastal water declines to 20° C red drum larvae that have reached the critical phase may not be able to find and catch prey. An early reduction in nearshore water temperatures could result in an unsuccessful red drum reproductive effort for that year. Indirect evidence implicates the importance of temperature to reproductive success in that our laboratory-reared red drum stop spawning when the temperature drops below 20° C. This phenomenon may account for the earlier spawning of red drum in its more northerly range (Mansueti 1960) and prolonged spawning in warmer regions (Jannke[3]).

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MARINE FISHERIES OF DELAWARE[1,2]

J. L. McHUGH[3]

ABSTRACT

Delaware is almost in the geographical center of the Middle Atlantic Bight. The fisheries harvest endemic species, more or less restricted to the area, boreal species that migrate south in winter, and warmwater species that come north in summer. About 85 species have been recorded in commercial and recreational fisheries. Some have produced substantial catches, and the total commercial catch reached a peak in 1953 at nearly 167,000 metric tons. Production of commercial fisheries has since dropped to a low of only 305 metric tons in 1968, a drop of 99.8%, and has remained not much higher than that level ever since. Most of this decline was caused by the decline of the dominant menhaden fishery to zero in 1967, but drops in food finfishes and food shellfishes have been substantial also. The history has been one of boom or bust since the beginning, but superimposed upon this has been a gradual decline in almost all species. Several fisheries, notably purse seine, otter trawl, clam dredge, haul seine, and pound net, have ceased altogether.

The recreational fisheries have been growing in numbers of fishermen and in catches. Comparing food finfishes only, because industrial fisheries have no counterpart in the recreational fishery, and shellfishes have never been compared adequately, the recreational fisheries may now be taking three times as much as the commercial.

The boom and bust characteristic of the commercial fisheries has been caused by the widely fluctuating and uncertain nature of the major species, menhaden, blue crab, weakfish, croaker, and spot. Others, like surf clam, oyster, alewives, horseshoe crab, sturgeon, shad, and hard clam, have declined from overfishing, adverse changes in the inshore environment, or both. Some, like blue crab and weakfish, are fairly abundant at present, and weakfish is taken mostly by recreational fishermen. Others, like menhaden, have succumbed to heavy fishing of younger fish farther south. Menhaden vessels are now refrigerated, and can stay out longer and travel farther, which reduces the number of plants needed. Menhaden are still taken in Delaware Bay, but landed elsewhere.

The oceanographic regime is highly variable and not conducive to regular movements of northern or southern species into the area. These fisheries probably would be highly variable even if other changes had not also intervened. Maintaining them at fairly high levels will require cooperation from other states, cooperation which has not been forthcoming up to now. The State-Federal Fishery Management Board may help to improve interstate cooperation. The shellfisheries are more likely to survive, but to do so they will require enlightened management. The popular food fishes are likely to continue to decline as commercial species and become largely recreational. Some attention to the balance between commercial and recreational fisheries probably should be given soon.

The marine fisheries of the State of Delaware in many respects characterize the marine fisheries of the Middle Atlantic Bight region (New York to Virginia) as a whole. Delaware Bay is in the geographical center (lat. 39° N) of the section of coast from Cape Cod, Mass. (lat. 42° N), to Cape Hatteras, N.C. (lat. 36° N), and its marine fisheries have relied on three general classes of marine resource: 1) endemic species, more or less restricted to the region, or at least restricted in their migrations, such as surf clam, *Spisula solidissima*, and American oyster, *Crassostrea virginica*; 2) boreal species that migrate seasonally into the region in winter, such as Atlantic cod, *Gadus morhua*, or silver hake, *Merluccius bilinearis*; and 3) temperate water species that migrate north in summer, like Atlantic croaker, *Micropogonias undulatus*, or weakfish, *Cynoscion regalis*. Delaware is far enough south so that it does not usually get large quantities of boreal species, but it does on occasion have large numbers of southern species in the area.

June and Reintjes (1957), with respect to the fisheries of New Jersey, Delaware, and Maryland, noted that this area more or less marks the center of geographical distribution of migratory fish stocks which range between Cape Cod and Cape Hatteras. They pointed out that it is the southern

[1]The studies on which this paper is based were supported in part by grants from the New York Sea Grant Institute.
[2]Contribution No. 292 of the Marine Sciences Research Center of the State University of New York, Stony Brook, N.Y.
[3]Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794.

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limit of such species as the Atlantic cod; haddock, *Melanogrammus aeglefinus*; American lobster, *Homarus americanus*; and others which come down from the north, and the northern edge of the range of black drum, *Pogonias cromis*; red drum, *Sciaenops ocellatus*; spot, *Leiostomus xanthurus*; and other southern species. They also noted that it is one of the most productive coastal regions in North America, which in 1953 produced over 662 million lb (300,300 t (metric tons)) of fishes and shellfishes, with an estimated value of $11.5 million to fishermen, and was capable of producing a great deal more. We could not reproduce these figures exactly from the 1953 statistics, but they were not far off. Total fishes were about 815 million lb (369,700 t), worth $12.7 million to fishermen, and the total commercial catch for the three States, including shellfishes, was about 891 million lb (404,200 t) worth about $31 million. By 1977 this had dropped to a commercial catch of 150 million lb (68,040 t) of fishes, 93 million lb (42,200 t) of shellfishes, for a total of only 243 million lb (110,200 t) worth about $70.5 million to fishermen. To this should be added 149 million lb (67,600 t) of fishes and 24.7 million lb (11,200 t) of shellfishes caught by recreational fishermen in 1974. These figures are not comparable with the recreational catch in 1953, which was presumably for the outer coast only, and did not include shellfishes. Nevertheless, it is fairly obvious that the recreational catch was larger in 1974. In 1947 dollars the two values were almost identical, $38.7 and $38.9 million. This is not consistent with the view that these fisheries were underexploited in 1953.

Reintjes and Roithmayer (1960) extended these studies for another 4 yr (1954-57 inclusive) and concluded that the region supports large populations of resident species and seasonal concentrations of migratory fishes. They concluded that production of fishes and shellfishes in the area appeared to be the highest per unit area in the Western Hemisphere, and that the fisheries generally were underexploited and underutilized. Using Rounsefell and Everhart's (1953) criteria, they found that of resident benthic species, such as summer flounder, *Paralichthys dentatus*; black sea bass, *Centropristis striata*; butterfish, *Peprilus triacanthus*; and scup, *Stenotomus chrysops*; only black sea bass appeared to be exploited at the maximum. Sedentary benthic species included surf clam and sea scallop, *Placopecten magellanicus*, and these and ocean quahog, *Arctica islandica*, and others were not overtaxed at that time. Migratory coastal species, like Atlantic menhaden, *Brevoortia tyrannus*; croaker; Atlantic cod; silver hake; weakfish; spot; red hake, *Urophycis chuss*; and bluefish, *Pomatomus saltatrix*, fluctuated widely and created greater instability in the fisheries than any other component of the total resource. Finally, migratory pelagic species like tuna, *Thunnus* sp.; sharks, Class Chondrichthyes; round herring, *Etrumeus teres*; sand lance, *Ammodytes* sp.; squids, *Loligo* sp. and *Illex* sp.; and others, were all abundant but in 1957 unexploited.

Perlmutter (1959) on the other hand, considering the fisheries of a wider area, from New York to Virginia inclusive, concluded that of the five major species other than menhaden and alewives—namely croaker, weakfish, scup, summer flounder, and black sea bass—only black sea bass appeared not to have declined in abundance. Thus, the picture is not entirely clear, and previous authors have not agreed. It must be pointed out, however, that those authors were not looking at precisely the same set of fisheries.

Eight fish and shellfish species have produced commercial landings >1,000 t (2,204,000 lb) in Delaware at some time in the recorded history of commercial fisheries in the State (Table 1). Another 10 species have at one time or another yielded commercial landings between about 1,000 and 100 t (2.2 million and 220,000 lb). Altogether, in recorded history from 1880 to 1978 inclusive (Pileggi and Thompson 1978), about 85 aquatic species or groups of species have been recorded in commercial or recreational marine fishery landings in Delaware. All species or groups of species are listed in Tables 1 and 2. Major species are discussed later in descending order of maximum annual landed weight.

The commercial fisheries of Delaware have been substantial in their time, peaking at nearly 167,000 t (370 million lb) in 1953 (Figure 1), but falling off after 1962 to a low of only 305 t (673,000 lb) by 1968. This was once the fourth largest State along the Atlantic coast in total landings. By far the most important species in terms of weight was menhaden, which reached a peak of 164,000 t (>360 million lb) in 1953 (Figure 2). Setting aside menhaden, which in most years made up the bulk of the catch, and the horseshoe crab, *Limulus polyphemus*, total food finfishes emerge as declining steadily since landings were first recorded (Figure 3), beginning in 1887 with a total of nearly

TABLE 1.—Maximum domestic commercial landings by species in the State of Delaware since 1880 and year of maximum landings. Species arranged in decreasing order of maximum landings. Weights in metric tons.

Species	Maximum landings and year	Secondary peak and year	Species	Maximum landings and year	Secondary peak and year
Atlantic menhaden, *Brevoortia tyrannus*	163,679 (1953)		American lobster, *Homarus americanus*	18 (1887, 1888)	14 (1971)
Surf clam, *Spisula solidissima*	3,962 (1970)				
Blue crab, *Callinectes sapidus*	2,233 (1957)		Suckers, family Catostomidae	16 (1897)	
American oyster, *Crassostrea virginica*	1,969 (1954)		Northern kingfish, *Menticirrhus saxatilis*	15 (1956)	
Weakfish, *Cynoscion regalis*	1,457 (1889)		Atlantic mackerel, *Scomber scombrus*	14 (1967)	
Alewife, *Alosa pseudoharengus*, *A. aestivalis*	1,449 (1930)		Terrapin, *Malaclemys* sp.	14 (1880)	
			Red crab, *Geryon quinquedens*	12 (1977)	
Horseshoe crab, *Limulus polyphemus*	1,352 (1908)	907 (1976)	Mussel, *Mytilus edulis*	10 (1932)	
Atlantic sturgeon, *Acipenser oxyrhynchus*	1,281 (1887)		Squids, *Loligo opalescens*, *Illex illecebrosus*	10 (1952)	
American shad, *Alosa sapidissima*	735 (1897)				
Atlantic croaker, *Micropogonias undulatus*	510 (1930)	303 (1955)	Atlantic herring, *Clupea harengus*	9 (1948)	
Hard clam, *Mercenaria mercenaria*	414 (1951)		King mackerel, *Scomberomorus cavalla*	8 (1951)	
Spot, *Leisotomus xanthurus*	294 (1880)	103 (1955)	Unclassified flounders	5 (1977)	
Striped bass, *Morone saxatilis*	266 (1973)		American plaice, *Hippoglossoides platessoides*	4 (1947)	
Mullet, *Mugil cephalus*	264 (1931)				
American eel, *Anguilla rostrata*	198 (1887)		Northern puffer, *Sphoeroides maculatus*	3 (1963)	
Conchs, *Busycon* spp.	189 (1976)		Unclassified sharks	3 (1955)	
White perch, *Morone americana*	181 (1897)		Sheepshead, *Archosargus probatocephalus*	3 (1880)	
Common carp, *Cyprinus carpio*	98 (1904)		Minnows, family Cyprinidae	2 (1957)	
Summer flounder, *Paralichthys dentatus*	95 (1958)		Silver perch, *Bairdiella chrysoura*	2 (1939)	
Red hake, *Urophycis chuss*	92 (1947)		Grayfish, *Squalus acanthias*, *Mustelus canis*	2 (1975)	
Silver hake, *Merluccius bilinearis*	92 (1947)				
Black sea bass, *Centropristis striata*	82 (1975)		Red drum, *Sciaenops oscellatus*	1 (1926)	
Scup, *Stenotomus chrysops*	71 (1949)		Yellowtail flounder, *Limanda ferruginea*	1 (1930)	
Catfish and bullheads, family Ictaluridae	68 (1908)		Hickory shad, *Alosa mediocris*	1 (1948)	
			Black bass, *Micropterus* spp.	1 (1908)	
Yellow perch, *Perca flavescens*	68 (1880)	22 (1930)	Gizzard shad, *Dorosoma cepedianum*	1 (1932)	
Black drum, *Pogonias cromis*	62 (1880)	14 (1956)	Frogs, *Rana* spp.	1 (1908, 1926)	
Snapper turtle, *Chelydra serpentina*, *Macrochelys temminckii*	60 (1955)		Unclassified food fishes	1 (1977)	
			White hake, *Urophycis tenuis*	[1] (1976)	
Atlantic cod, *Gadus morhua*	59 (1944)		Shrimp, *Palaemonetes vulgaris* or *Crangon septemspinosus*	[1] (1887, 1888)	
Tautog, *Tautoga onitis*	34 (1930)				
Bluefish, *Pomatomus saltatrix*	32 (1931)	29 (1949)	Soft clam, *Mya arenaria*	[1] (1887, 1888)	
Butterfish, *Peprilus triacanthus*	31 (1949)				
Unclassified industrial fishes	27 (1958)		Sunfish, family Centrarchidae	[1] (1901)	
Winter flounder, *Pseudopleuronectes americanus*	23 (1966)		Atlantic bonito, *Sarda sarda*	[1] (1935, 1953)	
Jonah crab, *Cancer borealis*	20 (1977)				
Pike or pickerel, *Esox* spp.	19 (1897)		Conger eel, *Conger oceanicus*	[1] (1935)	

[1] One-half t or less.

TABLE 2.—Species reported as caught by recreational fishermen in Delaware waters and not included in Table 1.

Species	Species	Species	Species
Skates, family Rajidae	Dolphin, *Coryphaena* sp.	Yellowfin tuna, *T. albacares*	Wahoo, *Acanthocybium solanderi*
Stingray, *Dasyatis* sp.	Pigfish, *Orthopristis chrysoptera*	Albacore, *T. alalunga*	White marlin, *Tetrapturus albidus*
Lizardfish, *Synodus* sp.		Little tunny, *Euthynnus alletteratus*	
Oyster toadfish, *Opsanus tau*	Tunas, *Thunnus* spp.		Searobins, *Prionotus* spp.
Goosefish, *Lophius americanus*	Bluefin tuna, *T. thynnus*	Spanish mackerel, *Scomberomorus maculatus*	Spiny boxfish?, *Lactophrys* sp.?
Amberjack, *Seriola* sp.	Blackfin tuna, *T. atlanticus*		

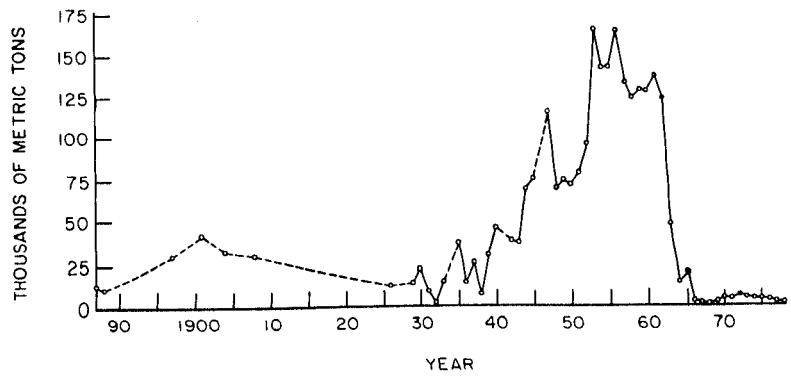

FIGURE 1.—Total commercial landings, all species, in Delaware, 1887-1978. When years were missing, points were joined by broken lines.

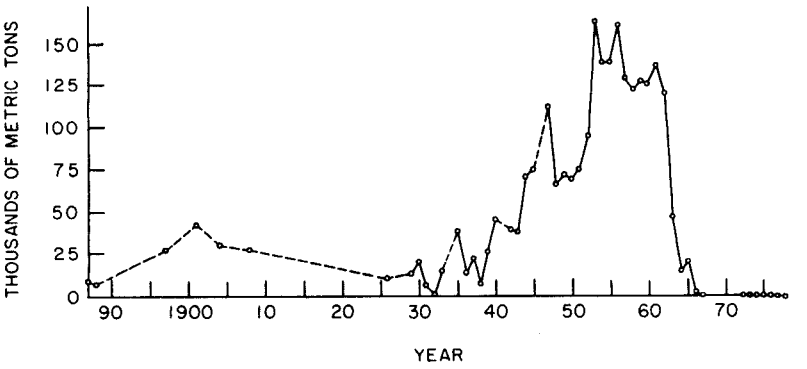

FIGURE 2.—Total landings of industrial fishes and shellfishes in Delaware, 1887-1978.

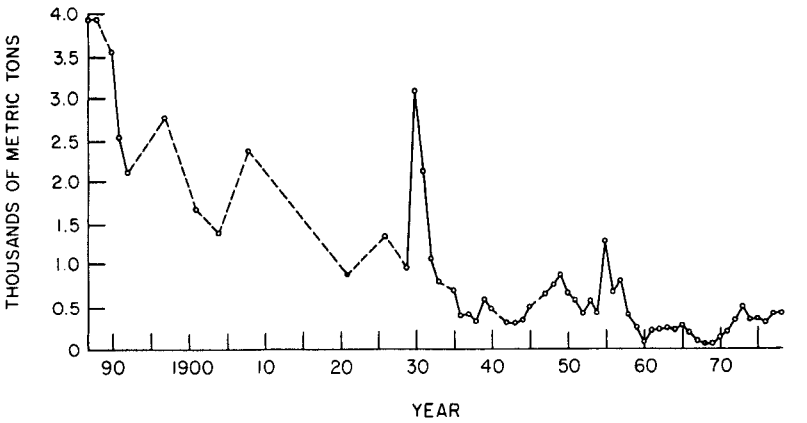

FIGURE 3.—Total commercial landings of food finfishes in Delaware, 1887-1978.

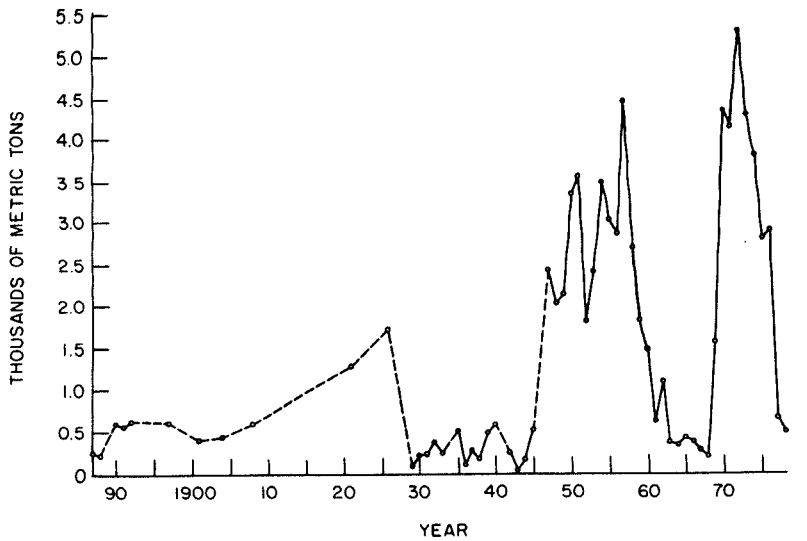

FIGURE 4.—Total commercial landings of food shellfishes in Delaware, 1887-1978.

4,000 t (9 million lb), falling by 1969 to a low of 65 t (143,000 lb), then rising to 418 t (921,000 lb) by 1977. This was a decline from peak to valley of about 98.4%. Species that contributed mainly to this drop were Atlantic sturgeon, *Acipenser oxyrhynchus*; American shad, *Alosa sapidissima*; alewife, *A. pseudoharengus* and *A. aestivalis*; and white perch, *Morone americana*, all anadromous species. Later croaker, weakfish, spot, and striped bass, *Morone saxatilis*, also dropped substantially, all species with a close coastal or anadromous life history. The drop was not all caused by a reduction in abundance of these species, since effort in most fisheries was dropping too.

The shellfishes had quite a different history (Figure 4), peaking in 1926 at about 1,800 t (nearly 4 million lb), in 1957 at 4,500 t (nearly 10 million lb), and in 1972 at 5,400 t (nearly 12 million lb). This was interspersed with lows of <54 t (120,000 lb) in 1943, 232 t (512,000 lb) in 1968, and 685 t (1,511,000 lb) in 1977, drops of 94.3, 94.8, and 87.2%, respectively. These represent three periods in the history of the shellfisheries of Delaware, oyster peaking in 1926, blue crab, *Callinectes sapidus*, in 1957, and surf clam rising briefly in the early 1970's.

The history of Delaware's commercial fisheries has been one of boom and bust since the beginning. The causes have been the wide fluctuations in availability, referred to already, associated with species at the limits of their geographic ranges, plus overexploitation and degraded habitat. The menhaden industry harvested its last fish with purse seines in 1966, the food finfish industry has declined fairly steadily, and the shellfish industry has had at least three major ups and downs in the last 50 yr. Several fisheries have ceased completely. What are the prospects for the future of Delaware's fisheries?

INDUSTRIAL FISHERIES

Industrial fisheries have consisted mostly of menhaden, with lesser amounts of horseshoe crab from time to time. The industrial fisheries were relatively small until 1944, when they rose above 100 million lb for the first time. They remained fairly large until 1963, and quickly collapsed after that. The last purse seine catch landed in Delaware was in 1966. Menhaden are still caught in Delaware waters but are landed elsewhere. Prior to the mid-1940's the fishery was not well developed, probably because the Pacific sardine, *Sardinops sagax*, industry on the west coast was more efficient and was able to supply most of the markets. After 1945, the decline of the Pacific sardine industry and the growth of the broiler industry in the east opened up new markets, and the menhaden industry on the east coast prospered, especially after 1952. By 1963, declining recruitment, probably associated with heavy fishing farther south, affected the supply of fish to northern waters, and the last plant in Delaware closed at the end of the 1966 season.

A small reduction plant operated on horseshoe crab for a few years from 1930 to 1944. A small number was taken after 1966, probably for bait. The greatest landings recorded were about 500,000 lb in 1935. The decrease was largely caused by a reduction in demand, although horseshoe crab now may be less abundant than before (Daiber[4]). This conclusion, however, is largely intuitive.

FOOD FINFISHES

Landings of food finfishes in Delaware have been declining since the first record in 1887. There have been temporary increases, such as in 1930-31 and 1955, but for the most part it has been steadily downward (Figure 3). The anadromous species were the first to be affected. Sturgeon was first, dropping from a high of nearly 1,300 t (3 million lb) in 1887 to only 15 t (34,000 lb) by 1908. This was reflected also in the price, which was less than a cent a pound, on the average, in 1887, but had risen to over 20¢/lb by 1908. Shad was not far behind, dropping from about 800 t (1.4 million lb) in 1890 to 18 t (39,000 lb) in 1931, while the price rose from <4¢ to about 18¢/lb. Alewife catches reached their peak later, at about 1,450 t (3.2 million lb) in 1930. By 1938 they had dropped to 21 t (47,000 lb), and never exceeded 60 t (150,000 lb) after that. White perch, another anadromous species, produced the greatest landings in 1897 at about 180 t (297,000 lb), and by 1940 was down to 7 t (16,000 lb).

Coastal fishes were equally temporary. Weakfish was the most important species, with total landings of about 1,500 t in 1889 (3,212,000 lb), later fluctuating several times, and finally dropping to a low of only 2 t (5,000 lb) in 1968.

[4]Franklin C. Daiber, Professor of Marine Biology and Biological Sciences, College of Marine Studies, University of Delaware, Newark, DE 19711, pers. commun. December 1979.

Croaker produced 500 t (>1 million lb) in 1930 and was down to nothing in 1961 for over a decade. Spot produced almost 300 t (649,000 lb) in 1880 and was highly variable after that, dropping to nothing in 1961 for over a decade, then showing up again in 1975. Spot is salted down for personal use by local fishermen, and some parts of the catch are not reported. Striped bass was never a large commercial producer in Delaware, and in fact reached its peak in 1973 at about 265 t (586,000 lb).

FOOD SHELLFISHES

Landings of shellfishes, minus seed oysters, which appear later as market oysters, and horseshoe crabs, which are used to make meal or as bait, have an interesting history. The principal species are only four: American oyster, blue crab, surf clam, and hard clam, *Mercenaria mercenaria*. The total take of these species has been highly variable, fluctuating from almost nothing to nearly 5,500 t (12 million lb), with different species making up most of the landings at each peak. Almost the entire peak in 1926 was made up of American oyster (Figure 4), 1,554 t (3,426,000 lb). In 1951 and 1957 the major species was blue crab, with American oyster second. Blue crab landings peaked in 1951 and 1957 at 2,260 t (nearly 5 million lb). The peak in 1972 was caused mostly by landings of 3,879 t (8,551,000 lb) of surf clam.

American oyster was relatively high in the early days, dropped to a low of only 22 t (48,000 lb) in 1943, peaked again from 1947 to 1958 with a maximum of 1,968 t (4,340,000 lb) in 1954, reached an all-time low of 15 t (33,000 lb) in 1961, and since has come back partially, reaching a high of 230 t (509,000 lb) in 1972. Blue crab dropped to a low in 1968, and since have risen to 1,655 t (3,650,000 lb) in 1976. Surf clam did not appear in landings until 1956, rose to a peak of 773 t (1,705,000 lb) in 1959, dropped to nothing in 1963, showed up again in 1969, peaked in 1970 at 3,962 t (8,734,000 lb), and dropped again to nothing in 1976. Hard clam built up to a peak of 414 t (912,000 lb) in 1951 and dropped to a low of 15 t (34,000 lb) in 1975. The only one of the four that appears to be reasonably healthy at the present time is the blue crab, but judging from past fluctuations blue crab can not be depended upon to maintain a healthy fishery, even if adequate management measures were in effect. Blue crab is near the northern limit of its range in Delaware, and probably can be expected to fluctuate widely for that reason.

RECREATIONAL FISHERIES

The recreational fisheries of Delaware, like marine recreational fisheries almost everywhere, are not well known. It can safely be assumed that they are growing, if the national surveys are a criterion, for catches have risen from 80,741 t (178 million lb) of food finfishes in 1960 to 121,564 t (about 268 million lb) in 1974. The rate of rise may have been greater than this, for in 1965 the estimated catch dropped to 58,060 t (128 million lb). These catches, however, are for the area from New York to Cape Hatteras, except for 1974, which did not include any part of the North Carolina coast. Only in 1974 was an estimate made of the Delaware catch, at about 2,903 t (6.4 million lb) of food finfishes, plus 1,814 t (about 4.0 million lb) of shellfishes. This consisted of 1,723 t (about 3.8 million lb) of weakfish, 227 t (about 500,000 lb) of bluefish, 84 t (185,000 lb) of sharks, 69 t (153,000 lb) of summer flounder, 227 t (500,000 lb) of other fishes; 998 t (2.2 million lb) of hard clam, 816 t (1.8 million lb) of soft clam, *Mya arenaria*, and a small amount of other shellfishes. If these figures are at all realistic, the food finfish catch of recreational fishermen in Delaware is substantially higher than the commercial catch.

This is confirmed by figures contained in sportfishing surveys conducted in 1953, 1954, and 1955. Using average weights of fishes from the 1970 saltwater angling survey (Deuel 1973), it was estimated that recreational fishermen caught 1,814 t (nearly 4 million lb) of fishes in 1955, which compared with 1,225 t (about 2.7 million lb) of the same species in the commercial catch. Estimates of recreational catches covered a period of only about 3 mo, whereas the commercial catch covered the entire year. Consequently, it is probably a conservative estimate that recreational fishermen took at least twice as much as commercial fishermen.

Later estimates made the discrepancy even greater, and this is not surprising, for the numbers of anglers were increasing also (Deuel 1973). Miller (1978) estimated that the recreational catch in 1977 was about 5.8 million fishes, plus considerable quantities of blue crab and hard clam. By weight, this would be perhaps 3,402 t (7.5 million lb), which was three times as great as the

commercial catch, and possibly more. This report also gave estimated landings by recreational fishermen for other years, 2.4 million fishes in 1968 and 1.9 million in 1973. Using the same average annual weights these amounted to roughly 1,542 t (3.4 million lb) and 1,225 t (2.7 million lb), respectively. This was 21 times and 2.3 times the commercial catch of finfishes, respectively. These are probably not very accurate, but it is clear that sportfishermen in Delaware caught more fishes than commerical fishermen.

THE OCEANOGRAPHIC REGIME

Parr (1933) found that through alternate development and breakdown of temperature barriers at Cape Cod-Nantucket Shoals and Cape Hatteras, the shallow water belt along the Middle Atlantic coast is in open-temperature continuity with the waters north of Cape Cod in winter and with waters south of Cape Hatteras in summer, being barred in opposite directions during these seasons. Temperatures in the Cape Cod region develop slowly in winter, early spring, and late fall, but show violent fluctuations in summer. In the Cape Hatteras region the opposite succession of conditions prevails, with relatively smooth temperature changes in summer, but with violent fluctuations in winter, early spring, and late fall. Winter invasions of fishes from the north are quantitatively poor and not very penetrating, but visitors from south of Cape Hatteras are usually complete. In the Delaware Bay region these changes are at a maximum, and Delaware Bay has the greatest difference between maximum and minimum temperature whether at the 5 percentile (Figure 5) or the 95 percentile (Figure 6) level. This means that the temperature regime is less variable to the north and south of Delaware, and presumably the effect on migrations is less. The data from which Figures 5 and 6 were taken are from Waters (1967). This shows for a period of over 100 yr the 5 percentile and 95 percentile isotherms of surface water temperatures along the Atlantic coast of North America. The temperature rises rapidly in spring and falls almost as rapidly in fall, and also varies considerably from time to time. For example, the 70° F isotherm penetrates only to Virginia in cool years (Figure 5), but rises as far north as Cape Cod in warm years (Figure 6) in summer. Similarly, in winter the 42° F isotherm comes as far south as Cape Hatteras in cold years, whereas in warm years it barely reaches Cape Cod.

This means that Delaware is in a region of rather highly variable water temperature, which will influence how far north southern species will come in summer, and how far south boreal species will come in winter. This is obviously not a favorable oceanographic regime for highly predictable fisheries, even if their numbers did not fluctuate greatly from time to time.

FISHES AND SHELLFISHES

Menhaden

Although it undoubtedly was abundant in the Delaware area, menhaden did not support a major commercial fishery in the early days. Along many parts of the coast it was originally used mainly as fertilizer, applied directly to agricultural land.

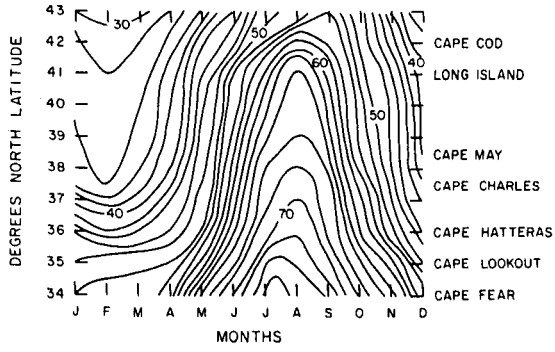

FIGURE 5.—Surface temperatures along the Middle Atlantic coast, 5 percentiles, by months and degrees latitude.

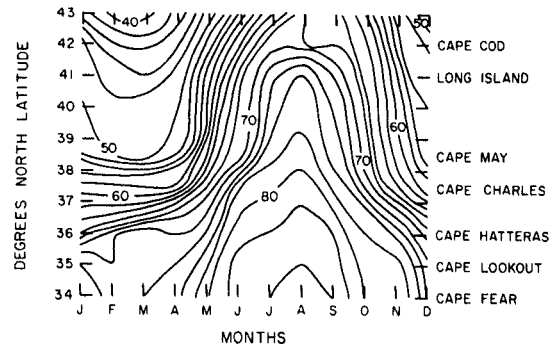

FIGURE 6.—Surface temperatures along the Middle Atlantic coast, 95 percentiles, by months and degrees latitude.

Most, if not all, of this harvest probably was not recorded in commercial landings. In 1880 (Collins 1887), 10 t (23,000 lb) of the total reported catch of 237 t (522,999 lb) landed in Delaware were used as human food. Modern usage of the resource is as raw material for production of oil, meal, and soluble proteins. Menhaden now is used only indirectly as a commercial food product, by incorporating meal and solubles in diets for poultry and livestock. The oil is used in a variety of products from paint to cosmetics.

By 1887 and 1888 a menhaden industry had developed in Delaware. Two factories were in operation at Lewes, employing 88 men ashore. Fishing vessels were powered by steam; 5 vessels and 107 fishermen operated in 1887, 4 vessels and 84 fishermen in 1888. Most of the catch at that time was made in gill nets but haul seines took about 27% of the total catch. The catch produced 878,206 l (232,000 gal) of oil and 3,000 tons of scrap (fish meal) in 1887; 582,455 l (153,870 gal) and 1,800 tons in 1888.

The method of recording landings and industrial production of menhaden used in the 1880's produced some inconsistent figures. It is obvious that landings of 100 t (220,399 lb) reported for Delaware in 1887 could not produce 878,206 l (232,300 gal) of oil and 3,000 tons of scrap. The discrepancy was caused by the method of allocating raw materials and processed products. The fishing vessels were registered in Connecticut and their catch was reported in their State of origin. The plants at Lewes, Del., were also built and owned by Connecticut interests, but their production was credited to Delaware, the State in which they were located.

Menhaden landings in Delaware can be estimated by using figures on menhaden production for the State. These are given, for the most part, in numbers of fish rather than in weight, a peculiar method of accounting for the greatest weight of fish landed, especially as we know that they were not counted. Menhaden were weighed by filling a bucket which held half a ton. In 1901 weight was given in numbers of fish, but it was also said that 1.67 fish weighed 1 lb, which was equivalent to 3,000 fish/ton. This conversion factor was used to calculate weight of fish in 1904 and earlier. In 1908 and thereafter, total landings for Delaware were given in pounds.

This peculiar way of handling menhaden could be quite misleading. For example, in Chesapeake Bay, the average weight of menhaden in the purse seine catch was about 3 or 4 fish to the pound, and probably is more now. In North Carolina it must be even greater. These are averages, and they will vary considerably from spring to fall, and with relative numbers of the different ages of fish. Thus, it is much more logical to quote menhaden landings by weight, since that is the way they are measured. A menhaden catch in Chesapeake Bay will contain considerably greater numbers of fish than one of the same weight in Delaware or farther north.

Menhaden landings in Delaware were fairly large in the early 1900's but fell to a low point in 1932 (Figure 7). This low point was partly caused by the depression, which reduced demand and prices, but also by the great overproduction of whale oil in 1931, which saturated world markets. The Pacific sardine fishery was also beginning about 1915, and the menhaden fishery did not develop fully until the late 1940's, when the Pacific sardine fishery began to collapse. The rise of the broiler industry, especially in the Delmarva Peninsula, also created favorable market condi-

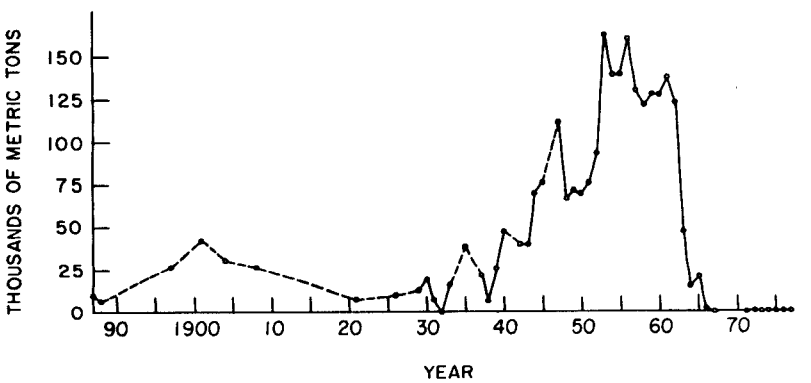

FIGURE 7.—Commercial landings of Atlantic menhaden in Delaware, 1887-1977.

tions. Catches were at a peak from 1953 to 1962, averaging 136,828 t (301,649,000 lb), after which they sharply declined, and the purse seine fishery, which was the dominant gear used until then, ended after the 1966 season. During this period Delaware was the most important State along the Atlantic coast in 1952 in menhaden landings, second in importance from 1953 to 1958, and second again in 1960 and 1961.

Surf Clam

Next to menhaden, surf clam produced the greatest weight of landings in Delaware, 3,962 t (8.7 million lb) in 1970. This was weight of meats only, equivalent to 28,123 t (about 62 million lb), live weight. This was not only the most recent fishery in Delaware, having produced the first small catch in 1956 (Figure 8), but also was relatively short lived. The fishery developed quickly but dropped to nothing by 1963, redeveloped in 1969, and produced its last catch in 1975. Figures on landings, however, do not tell the whole story. According to Daiber (footnote 4), a processing plant has been situated at Lewes for approximately 20 yr. At first, dredge boats landed directly at the plant, then as they fished farther away they landed the catch at other ports and surf clams were trucked to Lewes. More recently, vessels became larger, and when they worked near the mouth of Delaware Bay they landed at the docks of the former menhaden plants and surf clams were trucked the short distance to the processing plant. The vessels are now landing in New Jersey, and surf clams are trucked in, for the plant is still operating.

The fishery in the vicinity of Delaware was merely a phase of the fishery as a whole, which began off Long Island, N.Y., during the Second World War, and gradually shifted down the coast as ground after ground was overexploited. The peak was reached in 1974, off Virginia, and catches declined substantially after that. The Mid-Atlantic Council is now trying to manage the resource, along with ocean quahog.

Blue Crab

A small fishery for blue crab has existed in Delaware waters since the early days. Landings were not very large until after the Second World War, then shot up to 2,000 t (>4 million lb) in 1950 and 1951 (Figure 9). They dropped sharply in 1952, then rose gradually to nearly 2,265 t (5 million lb) in 1957, then dropped off to about 90 t (200,000 lb) by 1968. Subsequently, they have risen again and in 1975 and 1976 were 1,590 t (>3.5 million lb). The decline in 1977 probably was caused by an extremely cold winter.

Blue crab is abundant north to Chesapeake Bay, where it supports a major fishery. From Delaware north it appears spasmodically, sometime existing in great abundance, sometimes almost disappearing. It extends north to Cape Cod, and occasionally appears in the Gulf of Maine. The great variations in availability from Delaware Bay north are probably explained on the basis of environmental fluctuations, the major element of which is probably winter temperature. This is characteristic of a species near the northern limits of its range.

During the 1960's, however, it has been suggested that the intensive use of DDT in control of

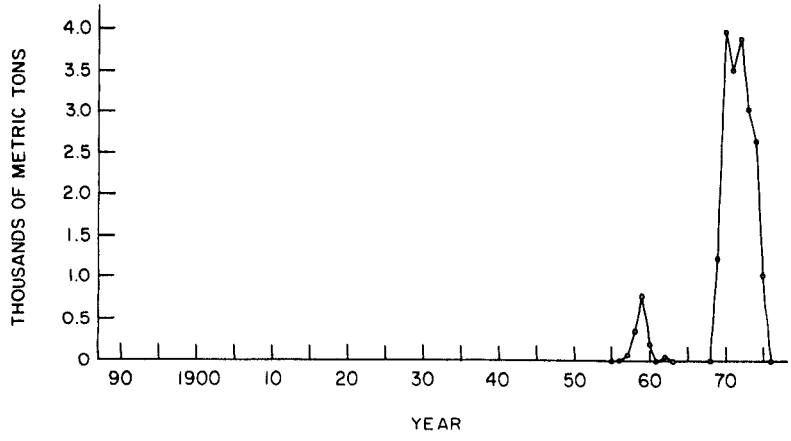

FIGURE 8.—Commercial landings of surf clam in Delaware, 1956-1975.

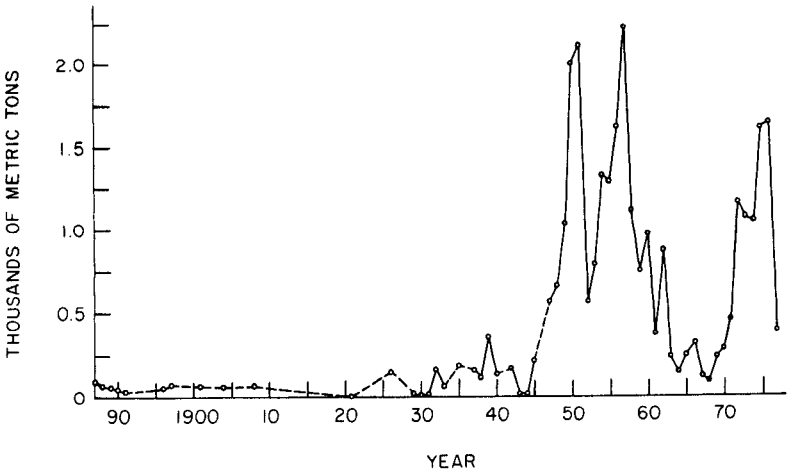

FIGURE 9.—Commercial landings of blue crab in Delaware, 1887-1977.

mosquitoes on coastal marshlands may have been a factor. It is suggestive in that blue crab has returned in great abundance to Delaware, New Jersey, New York, and even farther north. On the other hand, its abundance is obviously affected adversely by cold winters, such as the winter of 1976-77, which killed many of the blue crabs in New York waters. It is expected that blue crab will continue to be highly variable in abundance from Delaware north. At present, however, it is the most important fishery in the area.

Blue crab is an important predator of hard clam wherever it is abundant. In areas where extensive hard clam fisheries exist, or where the potential for hard clam production is high, it might be well to encourage fisheries for blue crab, and to place no limits on the catch, because there is an established and valuable fishery for hard clam, and the two may not be able to coexist in abundance.

American Oyster

The American oyster industry in Delaware was rather small for most of its history, taking most of its harvest from naturally producing grounds in the State. Prior to 1929 its history is not clear because landings were available for only 14 of the 49 yr. It appears that it peaked somewhere between 1912 and 1926 (Figure 10), then dropped off to low levels until after the Second World War. For about 12 yr, from 1947 to 1958, it fluctuated from about 900 to 1,800 t (2 to 4 million lb), then dropped abruptly, and since then has been <225 t (500,000 lb) except for 1 yr. Poor management, followed by disease, were the principal causes, according to Daiber (footnote 4).

Price (1978) has noted that in the late 1800's, Delaware Bay as a whole (New Jersey and Delaware) produced about 10,423 t (23 million lb)

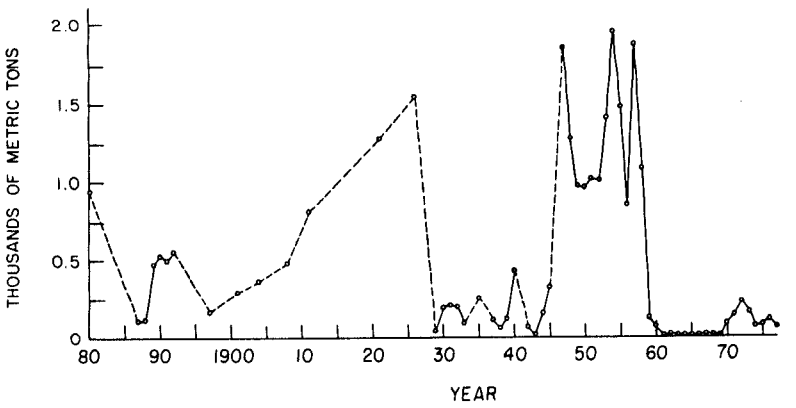

FIGURE 10.—Commercial landings of American oyster in Delaware, 1880-1977.

of American oysters, and had substantial shad, sturgeon, and other fisheries. A variety of factors, including improper management of shellfish beds (harvesting without replenishing equal quantities of shell stock), development of the watershed with attendant siltation, heavy industrialization of the Delaware River, industrial effluents and oil spills, mosquito control by ditching wetlands and spraying, and closure of harvesting areas caused by sewage contamination, caused American oyster production to decline to 4,082 t (9 million lb) by 1954. By 1960 the American oyster industry suffered a catastrophic collapse caused by the pathogen MSX (*Minchinia nelsoni*). In Delaware, the value of American oyster landings declined from almost $3 million to <$40,000 from 1954 to 1961. The fishery has not been reestablished to date (Maurer et al. 1971).

Gunter (1975) claimed that American oyster production in Delaware Bay as a whole (Delaware and New Jersey) has declined in two vast steps, from about 6,500 t (14,247,000 lb) from 1880 to 1931, to 3,600 t (7,951,000 lb) from 1932 to 1957, to 390 t (859,000 lb) from 1959 to 1970. He pointed out that the two declines each occurred 3 yr after diversions of Delaware River water to New York City in 1929 and 1953. He did not offer other data to substantiate cause and effect.

Weakfish

There is little question that weakfish was the "money" fish of the Delaware fishery. It has fluctuated widely in abundance from time to time, but has held up well, and may now be as abundant or more so, than it ever was. Although the record of commercial landings from 1880 to 1977 is in general downward (Figure 11), this is a popular sport fish, and recreational catches in recent years, if they are at all accurate, suggest that the catch remains at over 1,360 t (3 million lb). The resource obviously fluctuates widely in abundance for environmental reasons, of which more will be said later. It was relatively abundant in the 1950's and very low in abundance in the 1960's. The decline of the commercial fishery was probably a combination of these natural fluctuations and an increasing catch by the recreational fishery. The estimated catch by sport fishermen in 1974 was 1,724 t (about 3.8 million lb). Assuming a much smaller recreational catch in the 1880's, this compares favorably or even exceeds earlier catches. Some also have suggested that the decline in abundance of weakfish after the Second World War may have been caused by widespread use of DDT on salt marshes (Joseph 1972).

The gradual decline in the take of weakfish by commercial fishermen probably contributed to the virtual collapse of the commercial fisheries generally in Delaware. Sturgeon, shad, and croaker, the other major contributors to the inshore fishery, had already been reduced in abundance much earlier, and with weakfish virtually gone, there was little else to attract commercial fishermen. This probably was hastened by recreational fishermen, who discovered an old law some time in the 1960's that prohibited trawling in Delaware Bay and applied pressure to have it observed. New Jersey fishermen have not been allowed to trawl in the Bay for many years.

Alewives

Except for a brief period in the early 1930's, alewives were a relatively small and declining resource in Delaware (Figure 12). Catches declined fairly steadily, until by the 1960's they were almost zero. The brief increase in alewife landings in the early 1930's may have been caused by the

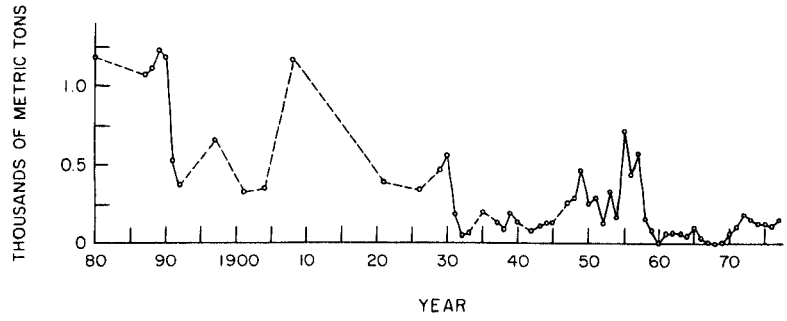

FIGURE 11.—Commercial landings of weakfish in Delaware, 1880-1977.

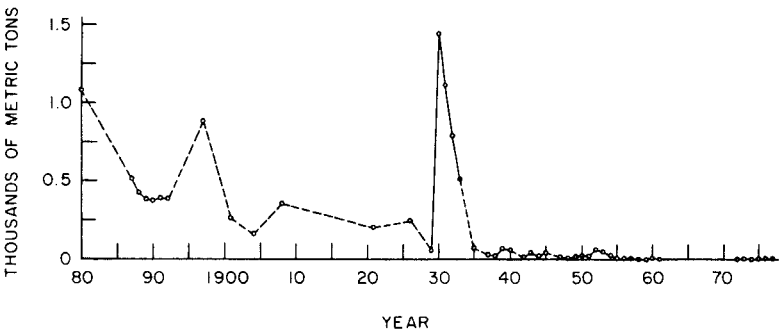

FIGURE 12.—Commercial landings of alewife in Delaware, 1880-1977.

depression, which created markets for a few years for cheap fish.

Establishment of water powered mills on all the tidal creeks, with their associated dams, may have contributed to the decline in landings, preventing spawning above the dams.

Sturgeon

Sturgeon was still fairly abundant in Delaware in the 1880's (Figure 13), producing 1,300 t (nearly 3 million lb). By the 1900's, however, they had declined to a low level, and yielded 45 t (<100,000 lb) annually thereafter. It is a tribute to the viability of the sturgeon that it has continued to produce small catches, despite its vulnerability. Fishermen in the early days may have contributed deliberately to the decline of the sturgeon stocks, by destroying them because they damaged nets. The great demand and high prices for caviar also undoubtedly had an effect.

Shad

Shad declined in landings much as sturgeon did in the early days, producing relatively small catches after about 1908 (Figure 14). In Delaware it produced somewhat increased catches in the mid-1940's, early 1950's, and early 1960's, but not as great during the days of the Second World War as in New Jersey, New York, and Connecticut. Like all anadromous species, shad was particularly vulnerable to adverse changes in the environment of rivers, but changing human tastes,

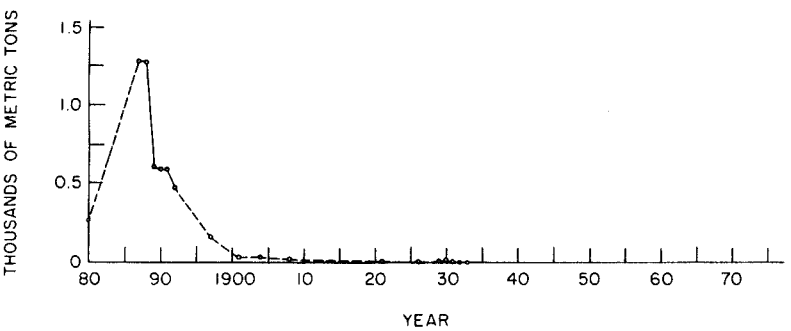

FIGURE 13.—Commercial landings of Atlantic sturgeon in Delaware, 1880-1932.

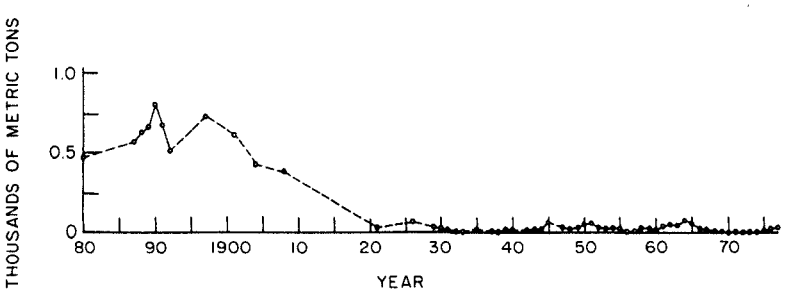

FIGURE 14.—Commercial landings of American shad in Delaware, 1880-1977.

highly seasonal demand, and the growing ease of trucking or flying shad from the south, where runs are much earlier, probably also played a part, as they did in New York (Medeiros 1974). Recreational fishing for shad in the Delaware River is growing (Grucela 1978) in landings and effort. The Delaware River stock is in good condition as compared with other rivers in the area.

Croaker

Croaker appeared later than weakfish in Delaware (Figure 15), reaching its peak in 1930 with about 500 t (slightly over 1 million lb). Thereafter it fell off irregularly, producing no catches after 1960 until 1975. Croaker, like weakfish, is a southern fish, and comes north of Chesapeake Bay only when conditions are particularly favorable, or when populations are high. Thus its abundance is likely to remain quite variable. The complete absence of croaker as a commercial resource during the 1960's and early 1970's may also have been caused by extensive use of DDT in estuaries, enhanced also by the stresses of living at the northern extreme of its range. Recovery in the mid-1970's may have been a delayed response to banning the use of this compound for mosquito control.

Hard Clam

Hard clam did not figure prominently in the catch in Delaware until after the Second World War (Figure 16) when stabilization of Indian River Inlet raised the salinity in the bay behind, and improved the environment for hard clam. It did not remain high for very long, however, and fell irregularly but steadily after 1951, when the maximum catch was about 414 t (912,000 lb) to 17 t (38,000 lb) in 1977, a drop of nearly 96%. It is probable that the decline was caused by a combination of overharvesting and pollution, which closed certain areas to clamming. Recreational clamming also is popular in Delaware (Miller 1978).

Spot

Spot is reported to have produced 295 t (650,000 lb) in Delaware in 1880, but was not reported again in catches until 1904 (Figure 17). This species is often caught by fishermen for their own

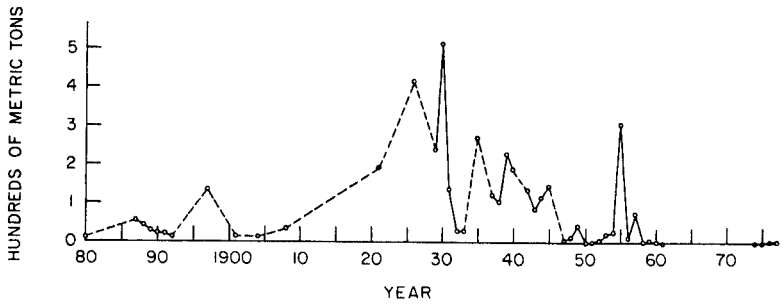

FIGURE 15.—Commercial landings of Atlantic croaker in Delaware, 1880-1977.

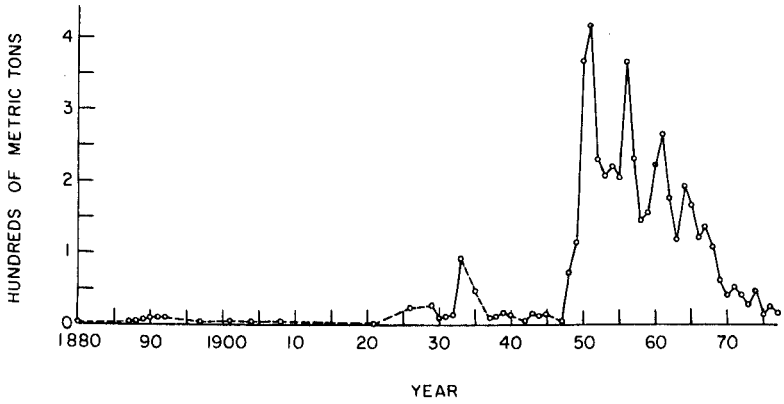

FIGURE 16.—Commercial landings of hard clam in Delaware, 1880-1977.

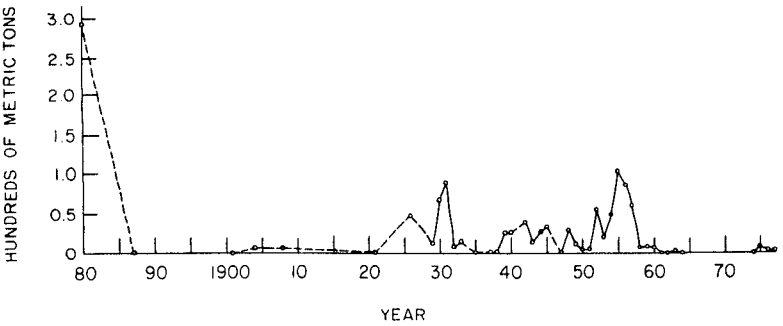

FIGURE 17.—Commercial landings of spot in Delaware, 1880-1977.

use, and is salted down for winter consumption. Such fish are not normally recorded in the catch. Existing records show that it reached a peak in 1931 and again in 1955, then fell off to nothing after 1963 until 1975. It is possible that spot also was affected by DDT in that period. Spot is an inshore species and, like croaker and other species, is near the northern limit of its range, thus is subjected sometimes to great stress when winter temperatures are low.

Striped Bass

Striped bass catches parallel those along other sections of the coast, declining to a low in the 1930's, then building up to a peak in the early 1970's, with rather wide fluctuations in between (Figure 18). There is little doubt that abundance has increased since the 1930's, but it is too early to say whether the recent decline is large enough to be of concern or simply reflects another temporary low in abundance. Striped bass probably once spawned in the Delaware River from Marcus Hook to below Wilmington where the river waters are normally between 1 and 5‰ in salinity. These waters are presently heavily polluted.

Regulation of the striped bass fishery has become a social-political matter, as the resource has grown in popularity as a sport fish. Recently, the Congress has allocated considerable sums for striped bass biological research, probably too late to do much good. If past history repeats itself, the resource will recover before the research produces much new knowledge. The State-Federal Fishery Management Board is putting together a coordinated coastwise research and management program, which may be of benefit if the states can get together on a uniform management program in the face of conflicting pressures. We will have to wait and see whether the past 50 yr have produced any accumulated wisdom that can be applied effectively.

Mullet

Mullet, *Mugil cephalus*, produced maximum landings in 1931 and fell off to low levels thereafter (Figure 19). Mullet may not have caught on as a popular fish in Delaware, and its brief upswing in the early 1930's may have been in response to the depression. There must be additional causes, however, for mullet has not been recorded in commercial catches since the early 1960's.

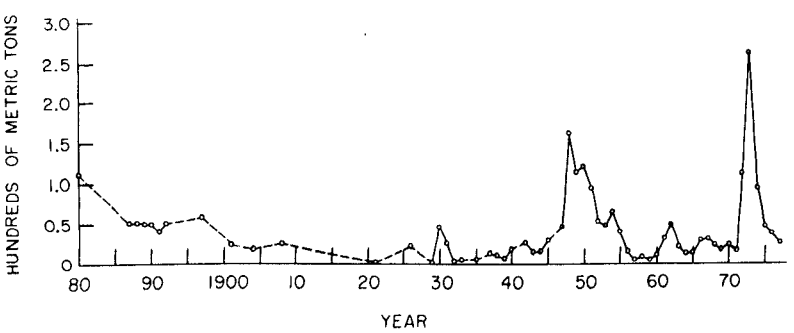

FIGURE 18.—Commercial landings of striped bass in Delaware, 1880-1977.

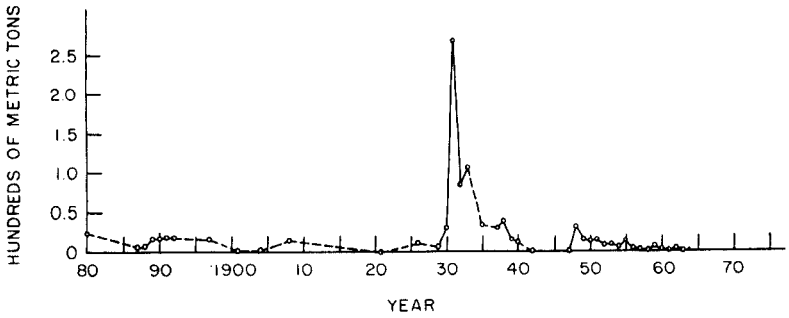

FIGURE 19.—Commercial landings of mullet in Delaware, 1880-1962.

American Eel

American eel, *Anguilla rostrata*, fell off to an all-time low in commercial landings in the 1940's, and since has built up slowly (Figure 20). Although it may have been affected by deterioration of the rivers, it does not spawn there, thus would not be affected as seriously as sturgeon, shad, or alewife. It is probably underexploited, and the recent modest size in landings in the last 30 yr may have been caused by increased markets in Europe and elsewhere.

White Perch

White perch has fallen off rather steadily since the 1880's, with major short rises in production in 1930, late 1940's, and 1958 (Figure 21). These fluctuations were probably caused by temporary upsurges in abundance caused by unusually good year classes. The decline in weakfish production generally has to be related to the decline in commercial fishing. There is no indication that the resource is in poor condition.

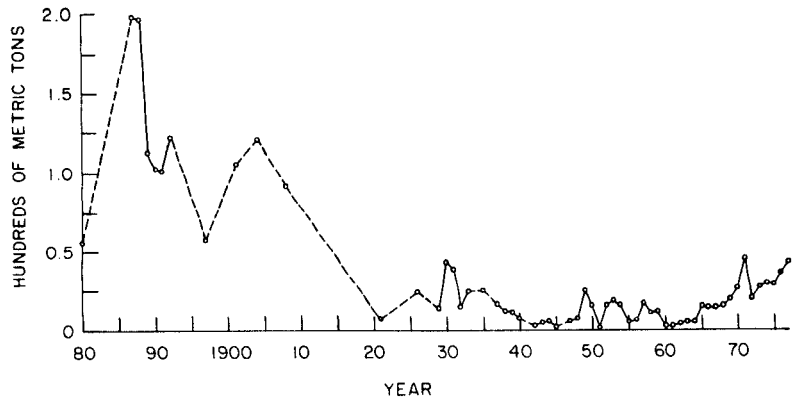

FIGURE 20.—Commercial landings of American eel in Delaware, 1880-1977.

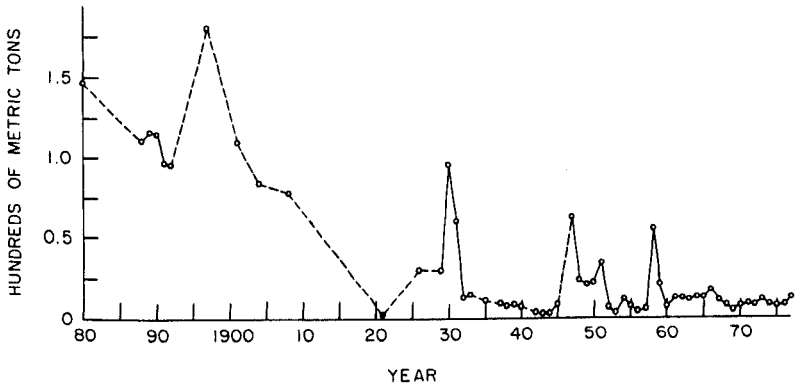

FIGURE 21.—Commercial landings of white perch in Delaware, 1880-1977.

FISHING GEARS

The principal gears used in Delaware were purse seines, gill nets, haul seines, pots, lines, and otter trawls. Except for otter trawls, these were mostly inshore gears, and took sturgeon, shad, alewife, weakfish, croaker, striped bass, and other anadromous or coastal species.

Purse Seines

Purse seines landed by far the greatest amounts of fishes in Delaware. The peak (Figure 22) was reached in 1953 at 165,000 t (somewhat over 360 million lb), the third largest of any state on the Atlantic coast, exceeded only by Virginia and New Jersey. Delaware led the states in menhaden landings in 1944-47, 1949, and 1952 and was second in 1950 and 1958. The fishery peaked temporarily in the 1940's, as did many fisheries toward the end of the war, but major landings were from 1953 to 1962, the decade of prosperity. The fishery collapsed soon after, and the last landings with purse seines were in 1966. Prior to the Second World War, the purse seine fishery was relatively small.

The purse seine fishery was directed at menhaden, and no other fishes were credited to this gear, although very small numbers of other species may have been taken occasionally. The collapse of this fishery was caused primarily by a reduction in abundance following the 1962 fishing year. The purse seine fishery in Virginia had been increasing in intensity during this period, and by 1963 relatively few fish survived the Virginia and North Carolina fisheries to migrate farther north. The effect was felt at all points north of Chesapeake Bay. Probably the only way of preserving the purse seine fisheries to the north, except on those rare occasions when large year classes or reduction in effort allowed some fish to migrate farther north, would have been to prohibit fishing south of Delaware or to place a minimum size on fishing to the south. Either alternative would be virtually impossible because southern fishermen would be certain to oppose it. The effect of such a law, if it could have been passed before a large industry developed in Chesapeake Bay and southward, would have been interesting to observe. It is possible, although of course not certain, that the decline might not have been as great.

Gill Nets

Four kinds of gill nets have been used in Delaware: drift, stake, anchor, and runaround. Drift gill nets were further broken down at times into shad, sturgeon, and other. For practical purposes, these can be broken down into fixed nets, drift nets, and runaround nets. Generally speaking, drift nets were set in slower waters farther downstream and took large quantities of weakfish and

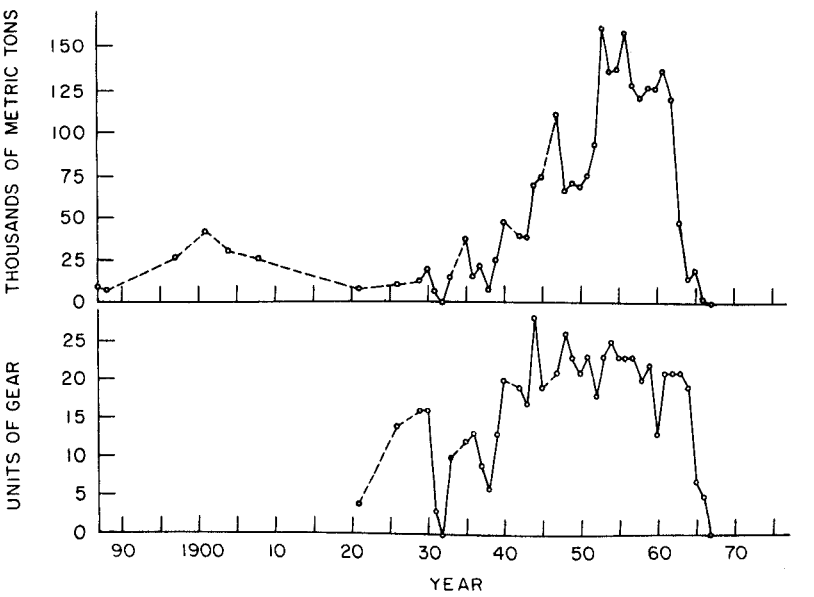

FIGURE 22.—Commercial landings by purse seines in Delaware, 1887-1966, and numbers of units of gear licensed.

croaker, among other fishes. Fixed nets were set for the most part farther upstream and took anadromous and freshwater species. Runaround nets also took mostly marine species, mullet when it was plentiful, but also weakfish, croaker, spot, and other fishes.

Landings from gill nets have declined rather steadily since the 1880's (Figure 23). The numbers of gill nets fell rather sharply to a low in the early 1940's, but have risen slowly since then. In general, numbers of gill nets have paralleled the catch, but whether they have remained about the same size is not known. Recent catches have been somewhat better than usual, as species like weakfish, striped bass, and certain others have shown up in increasing numbers off the coast.

In the beginning the greatest catch was sturgeon, making up >50% of the catch in 1887 and 1888. Sturgeon lost importance as time went on, dropping to seventh in importance by 1926, and was not a major species thereafter. American shad soon became first, but also dropped off fairly early, regaining first place in the mid-1930's, and holding this position almost every year until about 1951. Shad then dropped off again, regained first place in 1958, and was first until 1965 except for 1 yr. Since then it has fallen off to fourth or fifth place. Alewives ranked third in the early days, then slowly fell off, although in 1932 they ranked first. They are now relatively minor, and in several years in the late 1930's and early 1940's, and from 1958 to 1972, were caught in only 2 yr. Croaker became first in 1926 and retained that rank in most years until after 1945. Weakfish has fluctuated, but in general has increased in abundance, ranking second or third in most years since 1929, although it fell off in the early 1950's and again in the 1960's. In the 1970's it has ranked first most of the time. Striped bass has increased until recently, ranking first or second in 1958, and, except for a period of 5 yr in the late 1950's, has remained first or second until recently.

Other species have been prominent in landings occasionally, but have not remained among the primary species for long. Among these is mullet, first to third from 1931 to 1940, but absent from catches in most years since then. White perch ranked third to fifth until 1904, and did not regain this rank until 1960. Spot was second to fourth from 1939 to 1948, and again from 1952 to 1960,

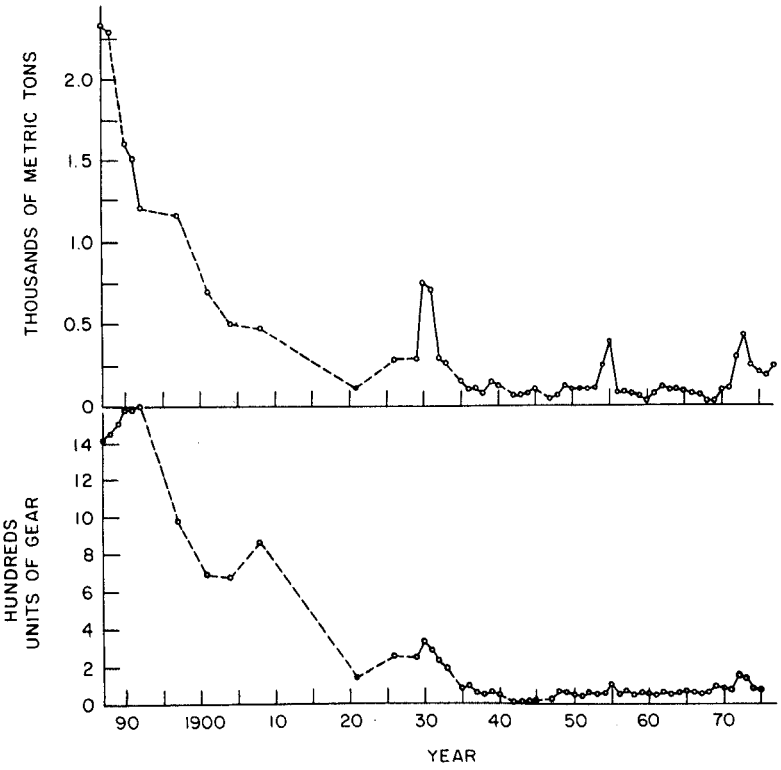

FIGURE 23.—Commercial landings by gill nets in Delaware, 1887-1977, and numbers of units of gear licensed.

even ranking first in 1956 and 1957. During the whole period gill net catches dropped from 22,700 t (>5 million lb) in 1887 to 45 t (<100,000 lb) in 1960, 1968, and 1969, then rose to 450 t (almost 1 million lb) in 1973. For most of the period, shad, weakfish, striped bass, and croaker, all relatively high-priced fishes, kept the fishery going, although until very recently, with decreasing numbers of fishes. It is difficult to escape the fact that the declining supply of weakfish was the primary reason for the decline of the gill net fisheries (Figure 11).

Haul Seines

Haul seines were a fairly important gear in the early days, reaching peak landings of 2,000 t (>4.4 million lb) in 1930 (Figure 24), but slowly and somewhat irregularly declining in production until the last net ceased operating in 1971 after landing <0.5 t (only 1,000 lb) of fishes. Weakfish again was the most important species most of the time, being exceeded by alewives in 1897, and in 1930 to 1933 inclusive. It is clear that weakfish was the mainstay of the haul seine fishery, and when it was gone the fishery did not survive for long. Haul-seining, however, has always been a part-time operation in spring according to Daiber (footnote 4).

Croaker also was important for a time, especially in 1926, 1929, and 1930, 1935 to 1942, 1945, 1955, and 1957. Shad was important from 1887 to 1904, white perch from 1887 to 1908. Striped bass was important in the 1880's and 1890's, showed up again from 1942 to 1951; common carp, *Cyprinus carpio*, was fairly important in 1897 to 1930, again in 1935 and 1950, 1951, and 1957; spot was important in 1926 and 1942; and mullet in 1948.

Pots

Pots were used for various species in Delaware, primarily for American eel, lobster, and blue crab. Later, considerable quantities of sea bass and conch, *Busycon* sp., were taken. Most of the catch, however, was blue crab, which peaked in 1957 and in 1975 (Figure 25). Obviously this fluctuation in blue crab abundance was real, dropping from 1,450 t (about 3.2 million lb) in 1957 to 110 t (<250,000 lb) in 1968, then climbing rather rapidly to 1,632 t (nearly 3.6 million lb) by 1975. This is the largest fishery in Delaware at present, but it is unlikely, in view of the variable nature of the resource, to remain high for long. Being near

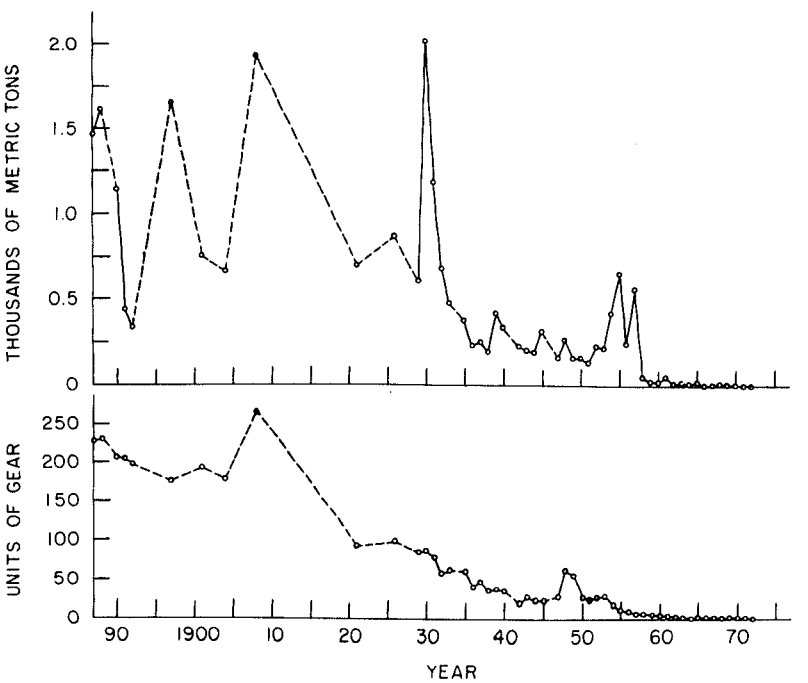

FIGURE 24.—Commercial landings by haul seines in Delaware, 1887-1971, and numbers of units of gear licensed.

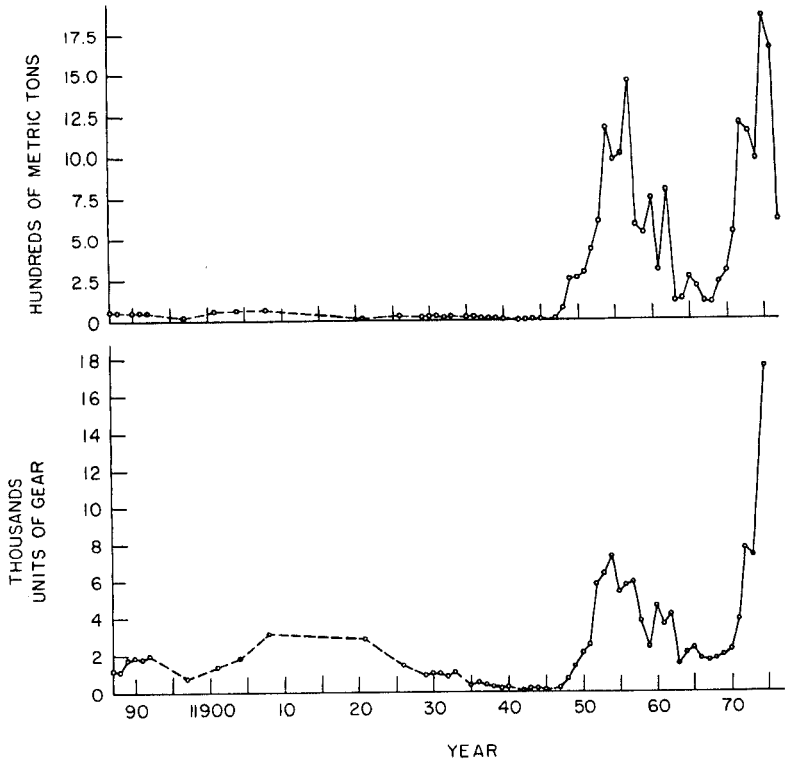

FIGURE 25.—Commercial landings by pots in Delaware, 1887-1977, and numbers of units of gear licensed.

the northern limit of its usual range, the blue crab is likely to be variable in abundance in Delaware.

Lines

Various kinds of line also were fished in Delaware from time to time. In addition to handlines, trawl lines, trotlines with baits, and longlines with hooks have been fished from time to time. From 1887 to 1926 inclusive, the kinds of line were not specified. In all years but one, however, weakfish was the largest catch. In 1926 crab made up about 85% of the catch, probably on trotlines with baits. From 1929 on, weakfish was an important, but variable component of the catch; tautog, *Tautoga onitis*, was important for a few years in the early 1930's; and croaker was an important, but variable component of the catch from 1930 to 1944. Striped bass was important from 1943 to 1945 and rose to first or second in rank in the 1970's. Trawl lines and later trotlines with hooks took almost exclusively cod, the first from 1929 to 1944, the second from 1960 to 1971. Trotlines with baits took blue crab in 1929, 1935, 1939 to 1951, and 1955 to 1960. Handlines were the only ones that have persisted, and their catches were almost entirely weakfish and striped bass in the 1970's (Figure 26). Once again, weakfish appears to have been the mainstay of the handline fishery.

Otter Trawl

The otter trawl fishery was relatively short lived in Delaware. It began in 1935, did not make catches again until 1940, reached its peak in 1948, and was over at the end of the 1966 season (Figure 27). It was an inshore fishery for the most part, taking mostly weakfish, summer flounder, scup, white perch, croaker, red hake, spot, butterfish, silver hake, striped bass, and squids. Over half the accumulated catch was weakfish, which substantiates the importance of this species to the fisheries of Delaware. The other main species, in the sense that they supported the fishery to the end, were summer flounder, butterfish, and striped bass. In the 1960's, recreational fishermen found an old law that prohibited trawling in Delaware Bay and put on pressure to enforce it. As already mentioned, this, with the decline in weakfish, was the final blow to the trawl fishery.

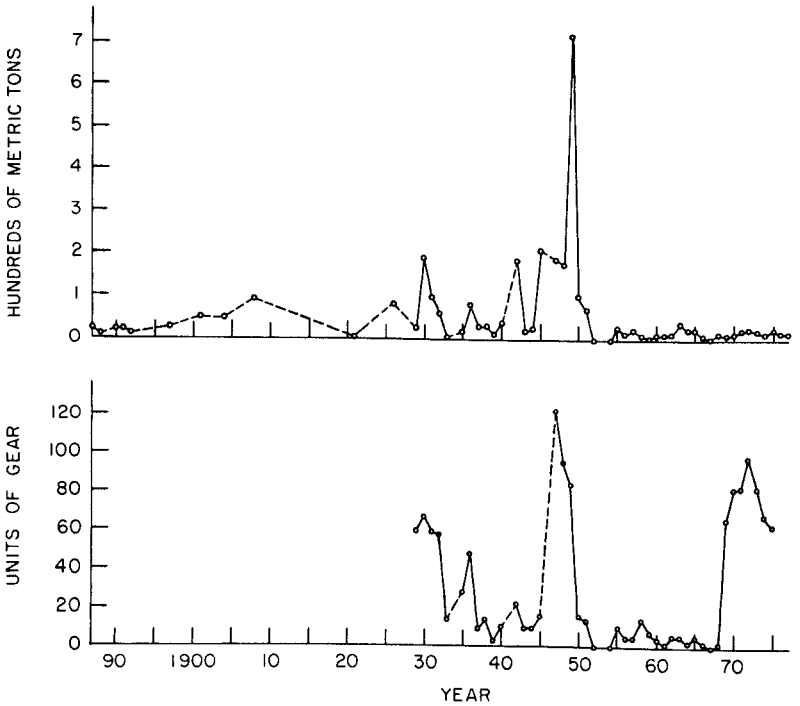

FIGURE 26.—Commercial landings by lines in Delaware, 1887-1977, and numbers of units of gear licensed.

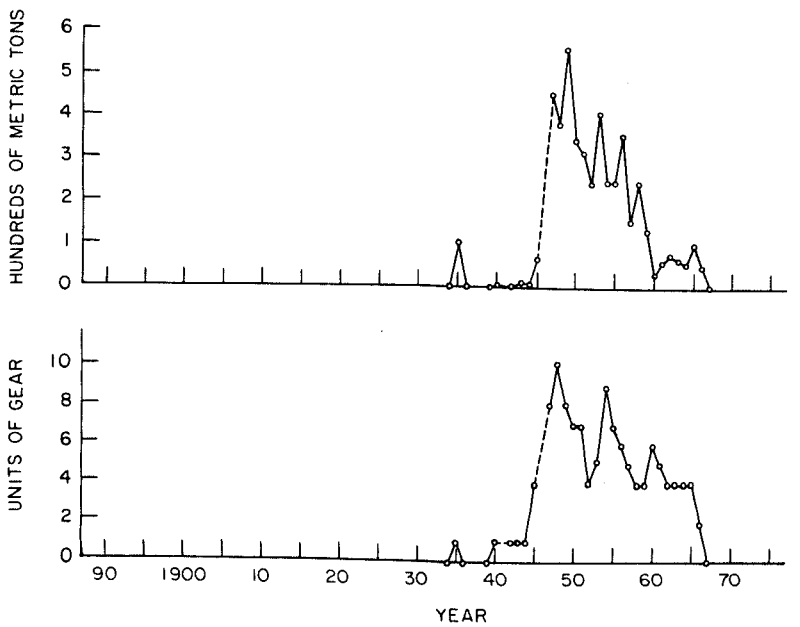

FIGURE 27.—Commercial landings by otter trawls in Delaware, 1935-66, and numbers of units of gear licensed.

Pound Net

Pound nets were not as important in Delaware as they were along most of the coast. They were used in Delaware mostly to catch horseshoe crab for manufacture into meal (Figure 28). Only 13.5% of the catch was fishes, and these were mostly alewife, white perch, carp, and catfish or bullheads (Family Ictaluridae). When horseshoe crab was no longer taken, pound nets quickly ceased operation. The last net was fished in 1938. In 1956 and 1957 pound nets were set again, but the catch was insignificant.

Oyster Dredges

Dredges were the main gear used to harvest oysters in Delaware, and they apparently took fair numbers prior to 1929 (Figure 29). There followed about a 15-yr period in which the catch was very

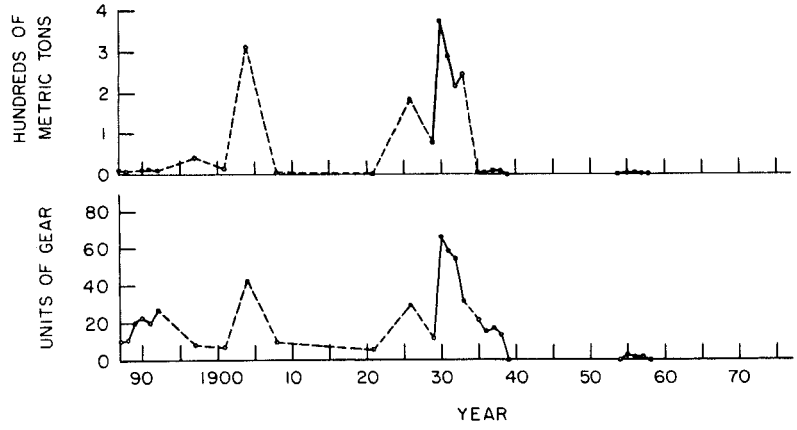

FIGURE 28.—Commercial landings by pound nets in Delaware, 1887-1957, and numbers of units of gear licensed.

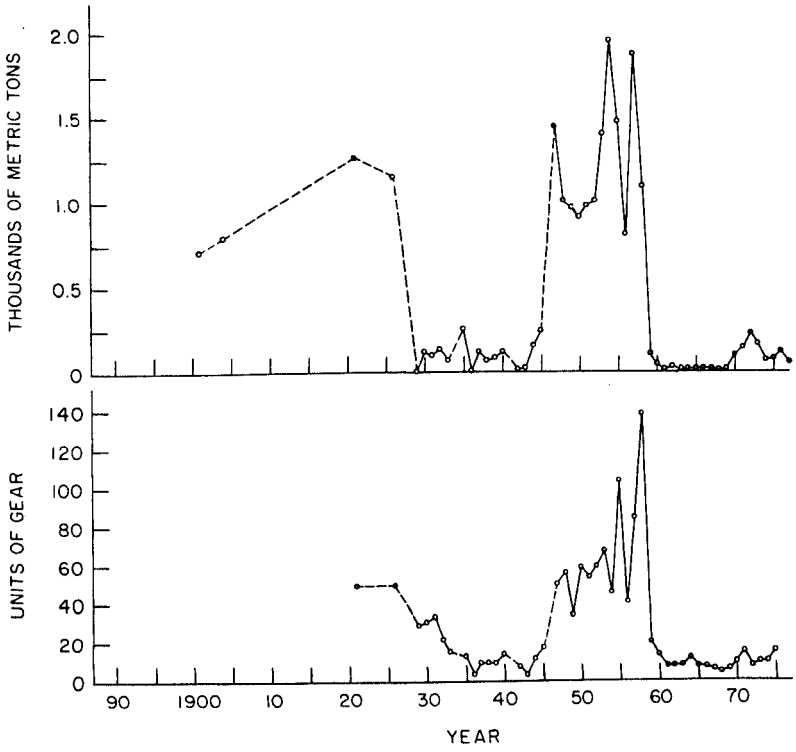

FIGURE 29.—Commercial landings by oyster dredges in Delaware, 1901-77, and numbers of units of gear licensed.

low, followed by the decade 1947 to 1958 when the industry was at its peak. After 1958 the industry almost collapsed, and it has not recovered. The harvest of oyster by tongs was much smaller, but somewhat similar through 1947. After 1947 there was no resurgence.

Maurer et al. (1971) made a survey of the oyster industry in Delaware Bay in 1968 and 1969. They found that Delaware Bay beds were badly depleted, but certain rivers in the vicinity showed potential as seed areas. One planted bed showed promise, suggesting that with proper management Delaware Bay could be rehabilitated and again produce oysters. The incidence of *Minchinia nelsoni* probably always was lower in the rivers than in the bay, and incidence on Delaware Bay beds was not as high as in the mid-1960's.

The hoped for increase had not occurred up to 1978, suggesting that no one was willing to take the risks, or had tried and failed. The present poor condition of oyster beds in Delaware Bay is caused by *M. nelsoni*, aggravated by general degradation of the environment. It is possible, but not certain, that with proper care the grounds could be restored to production.

Clam Dredges

Dredges were used to harvest hard clam and surf clam in Delaware. The first hard clam taken by dredge was recorded in 1901, but substantial numbers were not taken until 1929, when 360 t (nearly 800,000 lb) were caught (Figure 30). Catches dropped to much lower levels in 1931 and 1932, and remained fairly low until after the Second World War. This probably was at least partly caused by stabilization of Indian River Inlet, which raised the salinity in the Delaware Bay, and proved favorable for hard clam. Landings have been quite variable since, and the last hard clam listed as taken by this gear was in 1969.

Another short-lived fishery was dredging for surf clam, which began in 1956 and produced moderate catches until 1962, then ceased. Landings again were reported in 1969, peaked at 3,800 t (>8 million lb) in 1970, remained fairly high until 1974, but ceased in 1976. The fluctuations largely reflected where the boats were operating, as discussed earlier in the surf clam section.

Crab Dredges

Blue crab was first recorded as caught by dredges in Delaware in 1932. Catches were relatively small until the 1950's, when 1,700 t (>3.5 million lb) were recorded in 1950 and 1951 (Figure 31). Catches then dropped sharply, peaked again in 1957 at 770 t (about 1.7 million lb), and dropped to a very low level from 1964 to 1973, after which they picked up again but at a lower level.

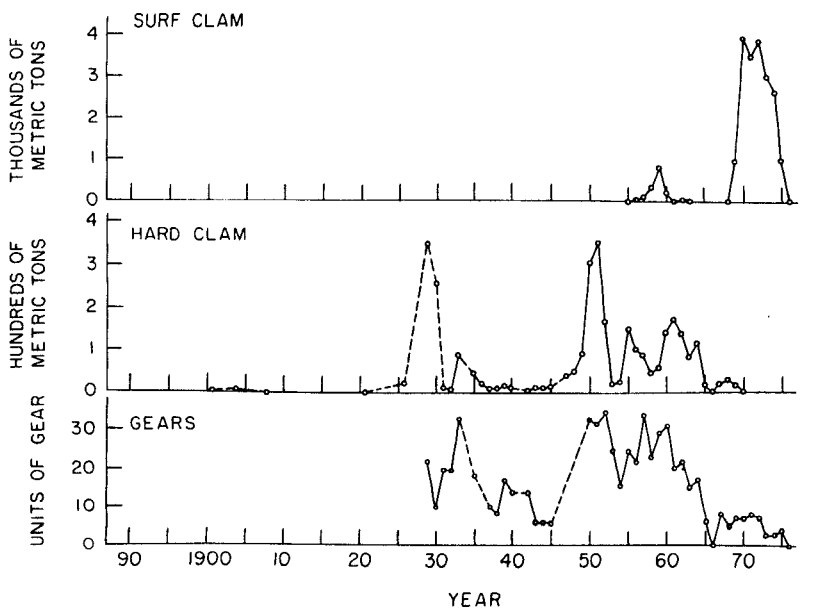

FIGURE 30.—Commercial landings by hard clam dredges in Delaware, 1901-69, and by surf clam dredges 1956-75, and numbers of units of gear licensed.

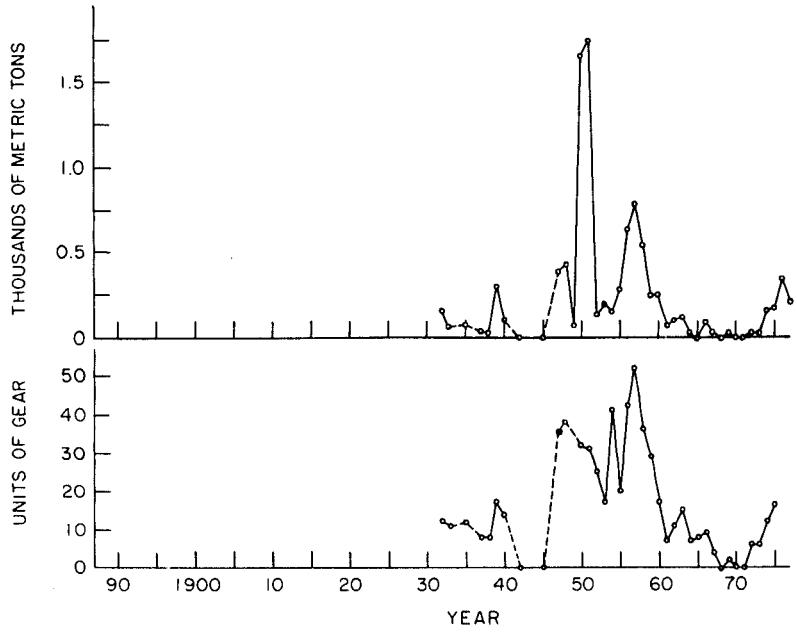

FIGURE 31.—Commercial landings by crab dredges in Delaware, 1932-77, and numbers of units of gear licensed.

Blue crab is highly variable in abundance in Delaware, and can not be expected to support a steady fishery.

Fyke Nets

Fyke nets were much more important in Delaware in the early days, reaching a low point in 1947, and fluctuating, more or less according to the abundance of fishes later (Figure 32). A low point in landings was reached in the 1940's, followed by peaks in 1955, 1964, and 1977, each at lower levels. Species composition of the catch has varied—catfish; white perch; American eel; sea bass; striped bass; alewife; flounders; yellow perch, *Perca flavescens*; and turtles making up most of the catch at various times.

Rakes

Most of the catch by rakes has been hard clam. Catches were insignificant in 1929 and 1930, and

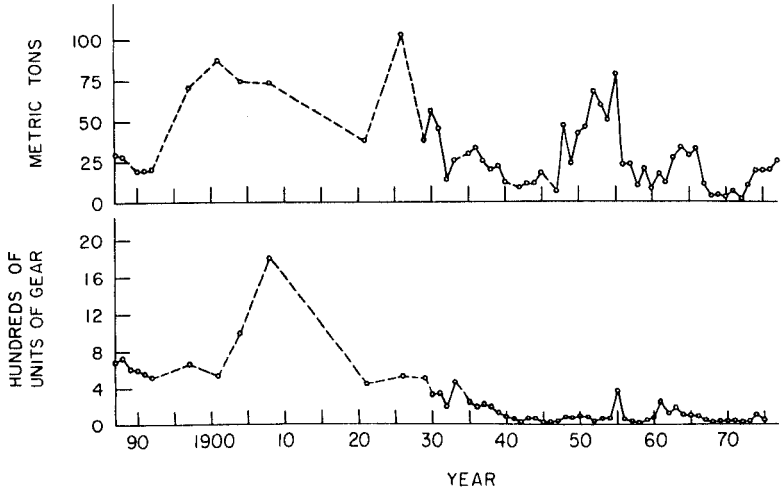

FIGURE 32.—Commercial landings by fyke nets in Delaware, 1887-1977, and numbers of units of gear licensed.

harvesting did not begin again until 1948 (Figure 33). Catches rose to a peak in 1953 at 215 t (about 474,000 lb), fell off to almost nothing by 1955, followed by an all-time high in 1956 of >300 t (683,000 lb). Subsequently, they have fallen off to 9 t (<20,000 lb) by 1977.

CONCLUSIONS

This history of the Delaware fisheries illustrates clearly the transient nature of marine resources generally in the Middle Atlantic Bight region, especially when effective controls on fishing are lacking. All of the major species in the region, with the possible exception of surf clam, are freshwater, anadromous, or coastal migratory species, and all have shown major fluctuations in abundance or availability. All are much less abundant in the region than formerly, and in nearly every case this can be attributed to overfishing. This, and the great variability in the supply of many of the major species, has led to a decline in the commercial fisheries, and a gradual takeover by recreational fishermen. Several major fisheries, e.g., purse seine, surf clam dredge, haul seine, otter trawl, and pound net fisheries, have ceased altogether.

Degradation of the coastal environment also has taken a toll, although this cannot be documented clearly. However, it is fairly clear that dams and pollution of coastal streams have affected spawning of anadromous species, and these have suffered most. Mitigation of pollution and clearing of obstructions from waterways should improve the situation.

The future is uncertain. Many of the species cannot be helped very much unless cooperation with other states is improved. This is underway through the State-Federal Fishery Management Board, but it is too early yet to tell how much this will improve the situation. Menhaden is unlikely to come back unless effective steps can be taken to increase mesh size or otherwise reduce the catch of small fishes in Virginia and North Carolina. Even if that unlikely alternative is accomplished, it probably would be difficult or impossible to reestablish a reduction plant because environmental laws in Delaware would prevent it. Weakfish was the principal mainstay of the food fish industries in Delaware, and its present value to recreational fishermen in the State makes it unlikely that a commercial fishery will start again. The other species are even less likely to support major commercial fisheries.

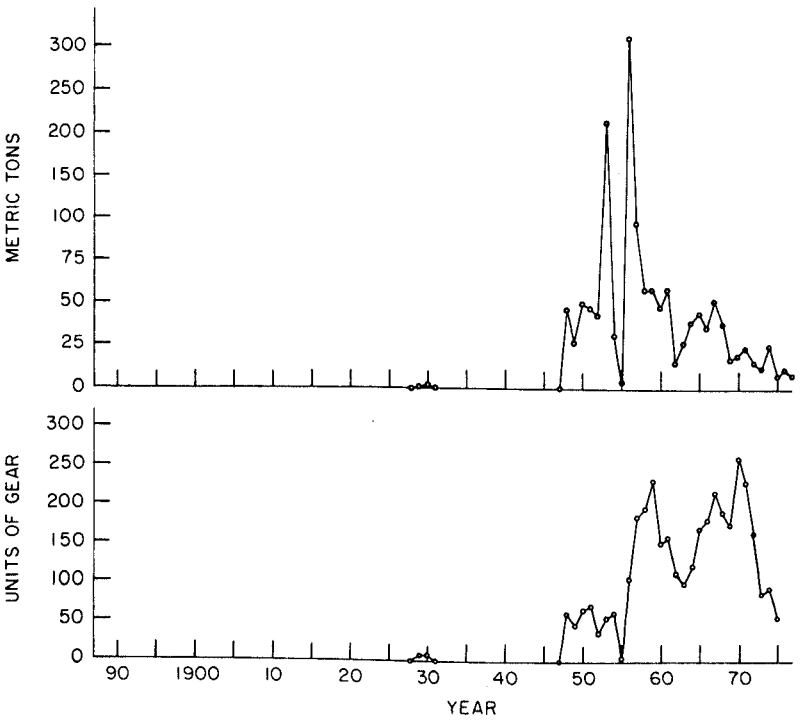

FIGURE 33.—Commercial landings by rakes in Delaware, 1929-77, and numbers of units of gear licensed.

The remaining species are shellfishes, mainly surf clam, blue crab, American oyster, and hard clam. The future of the surf clam resource will depend upon how successful the Mid-Atlantic Council can be in developing adequate enforcement measures, and on the ability of the states to develop parallel management plans. Blue crab will probably continue to be highly variable in production, but should be able to support a fairly prosperous fishery at times. Oysters might be able to come back from their present reduced level if adequate attention is paid to modern methods of culture. Hard clam probably can support a modest fishery if the environment of the coastal bays can be preserved and enhanced.

As a whole, it appears that the commercial fisheries of Delaware will remain small, and that they will be largely shellfisheries. Recreational fishing probably will continue to take increasing numbers of the total catch of finfishes. Whether the recreational fisheries can be managed to maintain the yield will depend upon how the states can cope with this problem.

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ASSIMILATION EFFICIENCY AND NITROGEN EXCRETION OF A FILTER-FEEDING PLANKTIVORE, THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE)

EDWARD G. DURBIN AND ANN G. DURBIN[1]

ABSTRACT

Experiments were carried out at 20° C with adult Atlantic menhaden, *Brevoortia tyrannus*, to follow the time course of changes in feces elimination rate, assimilation efficiency, nitrogen excretion rate, and oxygen:nitrogen ratios during and after a 7-hour period of feeding on the diatom *Ditylum brightwelli*. Assimilation efficiency for wild zooplankton dominated by *Acartia tonsa* is also reported.

The elimination of a meal was exponential (mean = 0.366/hour) and thus meals of different size reached the same stage of digestion at the same time. Changes in stomach contents and evacuation rates with time were calculated using the model of Elliott and Persson. These corresponded closely with observed changes in feces elimination rates following a meal. Assimilation, as indicated by the patterns of nitrogen excretion, and the elimination of a meal were rapid: 50% of the exogenous nitrogen excretion occurred within 1 or 2 hours after 50% of the meal was ingested; 50% of the feces were eliminated within a mean of 5.7 hours after the midpoint of feeding.

Mean carbon, nitrogen, and caloric assimilation efficiencies for *D. brightwelli* were 86.4, 92.4, and 89.5%; for zooplankton these were 86.7, 91.3, and 87.7%, respectively. Assimilation efficiencies decreased when fecal elimination rates declined below 0.3 mg dry weight/g dry weight per hour. This resulted in lower assimilation at the beginning and end of each experiment, and a slight decrease in the overall assimilation efficiency in low ration experiments, where the fecal elimination rates were also low.

Nitrogen excretion consisted of 69.6% ammonia and 30.4% dissolved organic nitrogen. The mean excretion rate of fish unfed for 36 hours (10.72 μg nitrogen/g dry weight per hour) increased as much as 17-fold when the fish were digesting and assimilating the food. Exogenous nitrogen excretion was a constant proportion of the ingested and the assimilated rations (61.6 and 65.5%, respectively).

Oxygen:nitrogen ratios indicated that Atlantic menhaden use protein as a metabolic fuel at all times. The mean oxygen:nitrogen (28.2) of fish unfed for 36 hours decreased to values as low as 5.0 during feeding.

In the development of an energy budget for fish it is necessary to determine the proportion of the ingested ration which is lost in the feces and the excretory products. The remainder represents physiologically useful energy available for growth and metabolism.

Here we examine digestion rates, assimilation efficiency, nitrogen excretion rates, and oxygen:nitrogen (O:N) ratios of adult Atlantic menhaden, *Brevoortia tyrannus*, a filter-feeding planktivore. Since Atlantic menhaden normally feed for a prolonged period each day, the experiments were designed to permit observations on the fish before, during, and after a 7-h feeding period during which food was made available at a constant rate. This study is part of a larger effort to determine the energy budget of Atlantic menhaden in Narragansett Bay, R.I.

METHODS

All experiments were carried out on a school of 12 Atlantic menhaden, with a mean wet weight of 302 g, dry weight of 101 g, and fork length of 26 cm. Experiments were carried out during 26 July-9 September 1977 at a temperature of 20.0±1.0° C and a salinity of 31‰. Details of the procedures used for maintenance of the fish and for carrying out the experiments are given in Durbin et al. (1981).

Before an experiment the tank was thoroughly cleaned and the inflowing water was filtered through a GAF[2] polypropylene bag filter of nominal 5 μm pore size. The fish were deprived of food for 36 h to eliminate the remains of the previous meal. The experiment began with a measurement of the excretion rate of the unfed fish between 0600

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

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and 0800 h. Plankton was then siphoned into the tank at a constant rate over a 7-h period from about 0800 to 1500 h. At intervals prior to, during, and for about 20 h after the feeding period, respiration rates and voluntary swimming speeds were measured (Durbin et al. 1981), and samples of the tank water were collected for determination of ammonia and dissolved organic nitrogen (DON) excretion rates. Feces were periodically siphoned from the tank during the feeding period and for 41 h thereafter for the determination of assimilation efficiency. The tank was briefly flushed with filtered seawater at the end of the feeding period to reduce the ammonia concentration. Control measurements on the tank and tank water with and without plankton, demonstrated that these did not measurably effect ammonia or dissolved oxygen concentrations during the experiments.

Seven experiments were carried out using cultures of the solitary diatom *Ditylum brightwelli*, and three using Narragansett Bay zooplankton consisting mainly of adult *Acartia tonsa* and a small number of unidentified crab zoeas. Details of the culturing and processing of the *D. brightwelli* during experiments are given in Durbin et al. (1981). Narragansett Bay zooplankton were collected with 0.5 m diameter, 300 μm mesh nets on the day before an experiment and maintained alive in 1.2 m diameter tanks overnight.

During each experiment the plankton was concentrated into seven equal batches of about 18 l. Each batch was then siphoned into the tank over a 1-h period, providing an approximately constant input of food over the 7-h period without greatly changing the volume of the tank (1,400 l). Each batch of phytoplankton was subsampled for determination of C and N (Durbin et al. 1981). Each hourly batch of zooplankton was concentrated onto a 100 μm mesh and weighed just before use. A subsample of this was removed for determination of the dry weight:wet weight ratio, C and N content (Hewlett-Packard Model 185B CHN Analyzer), ash (combustion at 475° C for 4 h), caloric (Parr adiabatic bomb calorimeter), and chitin (Windell 1966) content. The remaining sample was dispersed in about 18 l of water and siphoned into the tank. By changing the concentration of plankton in the batches, we obtained different concentrations of food in the tank and different ration sizes. Turbulence produced by the swimming of the fish kept the water and plankton in the tank well mixed at all times.

Feces settled to the bottom of the tank, and were collected at 1-6 h intervals depending on the rate at which they were eliminated. Feces were gently siphoned into a plastic bucket and allowed to settle; the water was then aspirated off, and the feces were briefly rinsed with a little distilled water and transferred to preweighed aluminum dishes. Fecal pellets formed cohesive, cylindrical rods; the loss of material during collection and concentration was nominal. These dishes were then freeze-dried and reweighed to determine the dry weight of the feces. Each sample of feces was subsequently analyzed for carbon and nitrogen (3 replicates), ash (4-8 replicates), and calories (4 replicates). Each sample of feces from the phytoplankton experiments was also analyzed in triplicate for particulate silicon (Durbin 1977).

Samples for dissolved nitrogen analysis were siphoned from the tank into a clean, acid washed container, and then filtered through prerinsed glass fiber filters. The sampling interval was 1-4 h, depending on the excretion rate. All determinations were carried out in triplicate.

Ammonia determinations were carried out immediately with a modification of the method of Solorzano (1969), using 10 ml samples which were incubated in the dark for 4 h for color development. The range of values for 3 replicates was <0.1 μM of ammonia.

Total dissolved nitrogen was determined using the alkaline persulphate method of D'Elia et al. (1977). Nitrate formed during digestion of the samples was determined using a Technicon AutoAnalyzer II. At the same time, nitrate, nitrite, and ammonia concentrations were also determined on noncombusted subsamples using the AutoAnalyzer. These concentrations were subtracted from the total dissolved nitrogen determined from the persulphate digestion to give a measure of DON. Ammonia concentrations of the samples which had been frozen were always very similar to the concentrations determined from fresh samples immediately after collection. The range of values for three replicates of each measurement of total dissolved N was ≤ 0.5 μM N.

Excretion rates of the nonfeeding fish were low, and thus changes in total dissolved nitrogen concentration in the tank water were small. Although the ammonia excretion rate could always be satisfactorily determined, the greater errors inherent in the DON determination made it impossible to accurately measure DON excretion except during and soon after feeding, when the N excretion rates were high. During feeding the increase in NH_3

and DON concentrations in the tank was approximately linear, and linear regressions were calculated to estimate the excretion rates. The ratio of the DON:NH_3 regression slopes was similar in all experiments (overall means $\Delta DON/\Delta NH_3$ = 0.437, σ = 0.088). We assumed that this average value would provide the best estimate of DON excretion in both feeding and nonfeeding fish, and therefore multiplied the observed NH_3-N excretion rates by 0.437 to calculate DON-N excretion.

The Atlantic menhaden did not excrete any measurable quantities of nitrate, nitrite, or dissolved silicon. The latter was measured because of the large amounts of particulate silicon in the phytoplankton used as food. Nitrate, nitrite, and silicate were determined in triplicate on selected samples using methods described in Strickland and Parsons (1972).

Assimilation efficiency was calculated in two ways: by calculating the overall assimilation efficiency of C, N, and calories, and by following the time course of changes in the assimilation efficiency during each experiment. Both methods were based on the assumption that all of the feces were quantitatively collected.

The overall assimilation of C, N, or calories was determined by subtracting the total amount of each of these constituents that remained in the feces, from the amount in the food for each experiment. The C assimilation efficiency (percent), for example, was calculated:

$$\text{C assimilation} = \frac{C_{food} - C_{feces}}{C_{food}}(100). \quad (1)$$

In the second method, assimilation was calculated separately for each sample of feces. Since silicon (Si) was not absorbed by the fish, the Si content of each sample of feces was used to calculate the quantity of food (C, N, calories) which corresponded to each fecal sample. This was done by using the C:Si, N:Si, and calories:Si ratios of the food for each experiment, which were calculated from the measurements of the C, N, and calories in the food, and the total Si content of the feces. The assimilation efficiency was then determined in a manner analagous to Equation (1), using the back-calculated amount of C, N, and calories in the food which corresponded to each fecal sample, and the actual amount of C, N, and calories remaining in the sample.

The assumptions that all of the feces were collected quantitatively, and that Si was not absorbed by the fish, were verified in a phytoplankton experiment in which Si was used as a tracer. Subsamples of the phytoplankton were centrifuged and the Si content of the freeze-dried pellets then determined. This gave an estimate of 1.87 g for the total Si in the ration, which was very similar to that actually collected in the feces, 1.98 g.

A small but unknown amount of seawater remained interstitially within the pellets of both the phytoplankton and the feces, the salt content of which may have contributed to the estimates of ash content (Table 1). Because of this it was not possible to use ash content as a tracer to calculate assimilation efficiency. However, it should be noted that since the calculations of assimilation were based on direct measurements of C, N, and Si in the food and feces, they were not affected by the presence of trace amounts of seawater in the samples.

Nitrogen excretion and feces elimination by Atlantic menhaden are reported per gram dry weight, as micrograms N per gram dry weight per hour and milligrams per gram dry weight hour, respectively. It should be noted that measurements of oxygen consumption by the Atlantic menhaden during these experiments were reported in Durbin et al. (1981) as milligrams O_2 per gram wet weight per hour, to conform to the usual manner of reporting respiration rates in the literature.

RESULTS

The chemical composition of Atlantic menhaden, zooplankton, and *D. brightwelli* differed considerably (Table 1). Atlantic menhaden contained more C and calories, and less ash, per gram dry weight than the plankton, and were intermediate in N content between *D. brightwelli* and zooplankton. The composition of the fecal pellets was considerably altered from that of the food (Table 1). Atlantic menhaden assimilated N more efficiently than C, causing the C:N ratios of the fecal pellets to be higher than in the food.

The total dry weight of plankton fed to the 12 fish in each experiment ranged from 7.20 to 17.67 g of zooplankton, and 9.60 to 94.79 g of phytoplankton (Table 2). However, since the chemical composition of Atlantic menhaden differs from that of the plankton, the food rations are equivalent to different percentages of Atlantic menhaden dry weight, C, N, and calories. For example, the phytoplankton rations represented from 0.79% to

TABLE 1.—Chemical composition (mean ± σ) of *Brevoortia tyrannus*, plankton food organisms, and *B. tyrannus* fecal pellets.

Item	Dry wt as % of wet wt	Percent of dry weight					C:N	kcal/g dry wt	kcal/g ash-free dry wt
		Carbon	Nitrogen	Chitin	Silicon	Ash[1]			
B. tyrannus[2]	33.4±1.80	56.61±3.18	8.03±0.78	—	—	10.94±1.40	7.05	6.238±0.481	7.002±0.450
Zooplankton[3] mostly *Acartia tonsa*	10.86±0.20	40.05±2.34	10.91± .86	5.42±0.69	—	19.96±3.81	3.67	4.278± .161	5.348± .059
Chitin	—	39.37± .89	5.88± .17	—	—	—	6.70	—	—
Phytoplankton[4]: *Ditylum brightwelli*	—	18.52± .19	3.04± .05	—	9.28±0.16	55.24± .37	6.09	1.872± .072	4.179± .160
Fecal pellets[5]:									
Zooplankton	—	10.34±1.20	1.85± .34	—	—	72.3±2.14	5.59	1.013± .037	3.666± .297
Phytoplankton	—	9.29±1.34	.80± .11	—	25.7±7.35	74.6±1.20	11.61	.715± .042	2.818± .111

[1]May be an overestimate for plankton and fecal pellets; see text.
[2]Dry weight was determined on experimental fish; other constituents estimated from measurements on Atlantic menhaden collected from Narragansett Bay, R.I. (Durbin et al. unpubl. manuscr.).
[3]Mean ± σ of Experiments 1-3.
[4]*D. brightwelli* from Experiment 7; mean ± σ of four replicate determinations.
[5]Mean ± σ from Experiments 1-3 (zooplankton) and 4-10 (phytoplankton).

TABLE 2.—Food rations fed to 12 Atlantic menhaden.

Food type	Experiment no.	Duration of feeding (h)	Feeding rate[1] (mg food/g dry wt fish per h)	Food rations[2]				
				Dry weight[1]		Carbon (% of fish)	Nitrogen (% of fish)	kcal (% of fish)
				g	% of fish			
Zooplankton mostly *Acartia tonsa*	1	5.6	2.61	17.67	1.46	0.97	1.81	0.96
	2	8.1	1.19	11.58	.96	.71	1.39	.68
	3	3.8	1.55	7.20	.59	.42	.82	.41
Phytoplankton *Ditylum brightwelli*	6	7.1	10.99	94.79	7.80	2.56	3.01	2.35
	4	7.3	9.79	86.93	7.15	2.35	2.60	2.15
	5	7.0	7.93	67.46	5.55	1.82	2.13	1.67
	9	6.7	3.39	27.64	2.27	.75	.75	.68
	7	6.8	2.51	20.76	1.71	.56	.61	.51
	8	6.9	1.84	15.43	1.27	.42	.42	.38
	10	6.9	1.14	9.60	.79	.26	.29	.24

[1]Dry weight of zooplankton was measured in each experiment. Phytoplankton dry weight was estimated from C measurements in each experiment, and the conversion factor milligram C = 0.1852 (mg dry wt) (Table 1).
[2]Based on 12 fish = 1,212 g dry weight, 686.1 g C, 97.3 g N, and 7,560 kcal.

7.8% of the Atlantic menhaden dry weight, but only 0.26% to 2.56% of the estimated carbon content of the fish.

Each of the 12 fish was assumed to have obtained the same proportion (1/12) of the plankton added to the tank. This appeared reasonable since they were of similar size and swam at the same average speed during feeding (Durbin et al. 1981), and thus filtered similar volumes of water.

In the zooplankton experiments the duration of the feeding period was variable because of a problem caused by crab zoeas present in low numbers in the plankton. It was apparent that the sharp, 5 mm spines of these zoeas irritated the gill rakers of the Atlantic menhaden, because in three of four experiments attempted, the fish fed normally at first, then stopped feeding and began shaking their heads and repeatedly flaring their gill rakers. They stopped this unusual behavior as soon as the zoeas were washed out of the tank with filtered seawater. The fish were not satiated, since trial experiments demonstrated that once the zoeas were removed, the fish would feed readily on salmon food. The number of zoeas was least in Experiment 2, and in this instance the fish fed in their normal manner for as long as zooplankton was made available, 8.1 h. Because of these problems, only total assimilation efficiency will be reported from the zooplankton experiments.

Feces Elimination

In the phytoplankton experiments, feces began to appear about 2.4 h after the beginning of feeding (Table 3, column 2). The rate of elimination continually increased during the feeding period. The peak rates increased with increasing meal size, and occurred during the first 1 or 2 h following feeding (Figures 1, 2, 3). The elimination of feces began an approximately exponential decline 2 or 3 h after the end of feeding (Figure 1). With the exception of Experiment 6, these rates were all similar (overall $\bar{X}$ = 36.6%/h, or 38.1%/h if Experiment 6 is excluded) (Table 3, column 8). The exponential period lasted until about 14 h after the end of feeding, after which elimination continued at a low, nearly constant rate for the next 27 h (Figures 2, 3).

One consequence of the exponential elimination of the feces was that different sized rations

TABLE 3.—Feces elimination and nitrogen excretion of a school of 12 Atlantic menhaden, in relation to a 7-h period of feeding on the diatom *Ditylum brightwelli*, where time t_0 = the beginning, $t_{0.5}$ = the midpoint, and t_1 the end of the feeding period. At $t_{0.5}$, 50% of the ration has been ingested. Column numbers, in parentheses, are for text reference.

	Elapsed time (h)						
	After t_0	After $t_{0.5}$		After t_1			
Experiment no. (1)	Elimination begins (2)	50% Si eliminated (3)	50% N excreted (4)	90% Si eliminated (5)	90% N excreted (6)	Elimination rate ≥0.3 mg/g per h (7)	Exponential decline in elimination rate (per h) after t_1 (8)
6	2.0	5.5	2.3	10.0	2.9	13	−0.275
4	2.0	5.8	1.9	6.6	1.3	10	− .363
5	1.4	5.7	1.3	7.5	2.8	10	− .344
9	3.9	5.8	1.1	8.9	3.3	6	− .372
7	2.5	5.3	1.0	6.6	5.3	6	− .406
8	2.2	6.1	1.0	7.7	.7	7	− .392
10	2.6	6.0	1.5	7.0	.8	5	− .409
Mean ± σ	2.4 ± 0.8	5.7 ± 0.3	1.4 ± 0.5	7.8 ± 1.3	2.4 ± 1.6		−.366 ± .046

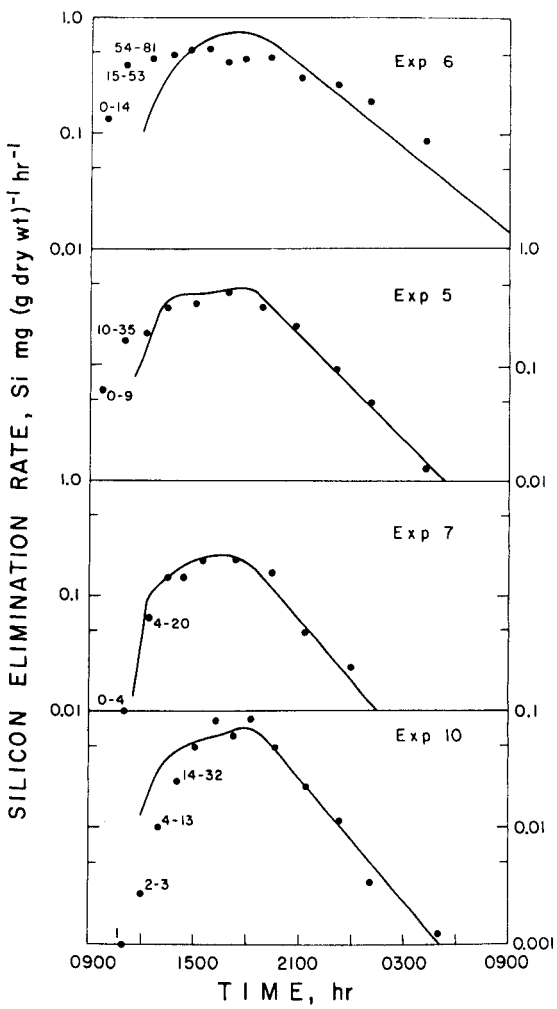

FIGURE 1.—Silicon elimination rate (circles) of a school of 12 *Brevoortia tyrannus*, during and after a 7-h (0800-1500 h) period of feeding on the diatom *Ditylum brightwelli*. Curve representing the calculated stomach evacuation rate is fitted to the feces elimination data; further explanation in text. Numbers refer to the elapsed time (minutes) in the feeding period when food corresponding to the fecal sample was ingested.

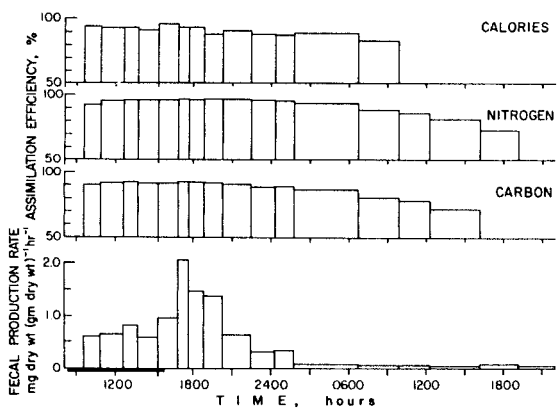

FIGURE 2.—Experiment 4 (high ration, Table 4). Changes in the fecal elimination rate of 12 *Brevoortia tyrannus*, and carbon, nitrogen, and caloric assimilation efficiency during and after a 7-h period of feeding (dark line on the *x*-axis) on *Ditylum brightwelli*.

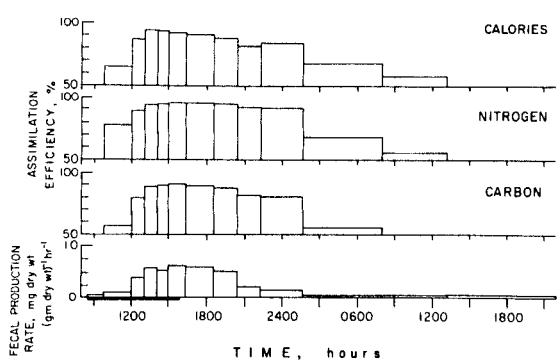

FIGURE 3.—Experiment 7 (low ration, Table 4). Symbols are as in Figure 2.

reached the same stage of elimination (i.e., 50%, 90%) at about the same time (Table 3, columns 3, 5).

Particulate Si in the feces was used to trace the passage of phytoplankton through the gut, since Si was not digested by the fish. Elimination of the experimental meal was rapid; 50% of the Si from the food was recovered in the fecal pellets within an average of 5.7 h after the midpoint of the feeding period (the time at which 50% of the food had been ingested) (Figure 4; Table 3, column 3). Because of the exponential decline in feces production following feeding, Si from the second half of the ration was egested more slowly, particularly the final 10%. Ninety percent of the Si in the food was recovered within a mean of 7.8 h after the end of feeding (Figure 4; Table 3, column 5) and a mean of 94.3% was recovered by 10 h after the end of feeding. Much of the fecal material eliminated during the next 31 h appeared to have sloughed from the gut since the C:Si ratios were higher in these samples. The amount of Si released during the interval between 14 and 41 h after the end of feeding was small, corresponding on the average to the food ingested during the final 10 min of the 7-h feeding period.

Assimilation Efficiency

The assimilation efficiency was high and similar for both phytoplankton and zooplankton (Table 4, columns 3, 4, 7). In the phytoplankton experiments, there was a slight positive trend between assimilation and increasing meal size, except in the largest ration experiment. In this experiment, assimilation appeared to be reduced.

It is not known whether Atlantic menhaden are able to digest chitin. The chitin content of the

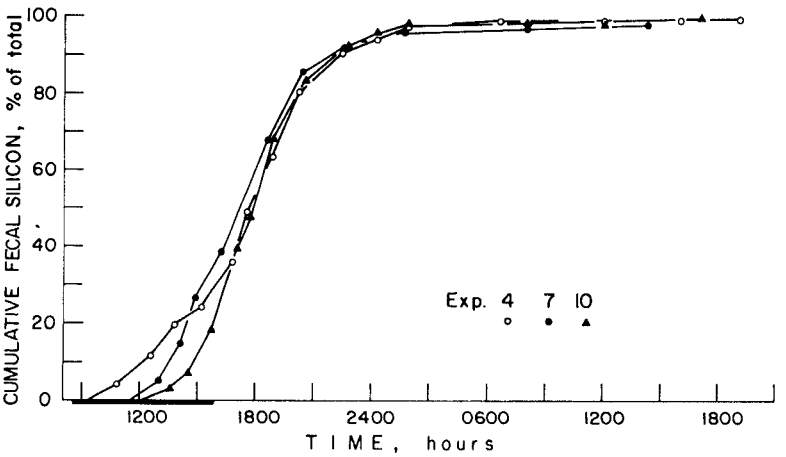

FIGURE 4.—Cumulative fecal silicon eliminated by 12 *Brevoortia tyrannus* in Experiments 4, 7, and 10 during and after the 7-h feeding period.

TABLE 4.—Assimilation efficiency of *Brevoortia tyrannus*, and the percentage of the total feces which were eliminated at a rate ≤0.3 mg/g dry weight per h. A) Overall assimilation efficiency. B) Assimilation during the period when fecal production was ≥0.3 mg/g dry weight per h. C) Calculated assimilation after subtraction of the chitin C and N from the total. Column numbers, in parentheses, are for text reference.

			Assimilation efficiency (%)						
			Carbon			Nitrogen			
Food type (1)	Experiment no. (2)	kcal A (3)	A (4)	B (5)	C (6)	A (7)	B (8)	C (9)	% of total elimination ≤0.3 mg/g per h (10)
Zooplankton	1	89.01	86.55	—	91.79	90.23	—	93.25	—
mostly	2	88.19	87.09	—	91.10	91.78	—	94.01	—
Acartia	3	85.80	86.39	—	91.39	91.88	—	94.72	—
tonsa	Mean ± σ	87.67 ± 1.67	86.68 ± 0.37		91.43 ± 0.35	91.30 ± 0.93		93.99 ± 0.74	
Phytoplankton	6	89.76	86.86	87.23	—	92.48	92.57	—	10.81
Ditylum	4	92.20	91.08	91.49	—	95.28	95.53	—	7.50
brightwelli	5	—	89.39	89.91	—	94.47	94.81	—	9.02
	9	—	86.99	89.15	—	92.66	94.15	—	43.04
	7	86.67	83.90	87.84	—	91.64	93.37	—	28.11
	8	—	84.43	87.55	—	90.22	92.49	—	35.08
	10	—	81.84	86.43	—	90.08	92.38	—	66.06
	Mean ± σ	89.54 ± 2.77	86.36 ± 3.22	88.51 ± 1.76		92.40 ± 1.97	93.61 ± 1.25		

zooplankton food (Table 1) was measured gravimetrically, but it was not possible to obtain an accurate measurement of chitin in the feces because of their very high ash content. However, if it is assumed that chitin (39.37% C and 5.88% N by weight) was not assimilated by Atlantic menhaden, and the chitin C and N are then subtracted from the total C and N in the food and the feces, the calculated assimilation efficiency for zooplankton would be increased slightly, to 91.43% (C) and 93.99% (N) (Table 4, columns 6, 9).

Changes in assimilation efficiency within experiments followed the general trend of the elimination of feces (Figures 2, 3). During feeding, assimilation efficiency increased from initial low values to a peak, which was sustained for several hours after the end of feeding and thereafter declined. The peak assimilation was reached sooner, and remained elevated for longer, in the high ration experiments (Figures 2, 3). With the two smallest rations, assimilation was still ascending when the feeding period was terminated.

Assimilation remained high as long as the fecal elimination rate exceeded about 0.3 mg/g dry weight per h (Figure 5). At lower elimination rates, assimilation declined precipitously. The reduced assimilation efficiencies at the beginning and near the end of feces production were associated with the presence of a mucuslike material which the fish released with the feces when the elimination rate was low. This material resulted in high C:Si and N:Si ratios in these feces. Any such input of C and N to the feces other than from the food would reduce the calculated assimilation efficiency. With the smaller meal sizes a greater proportion of the feces were eliminated at a low rate (Table 4, column 10), and the materials produced by the digestive tract of the fish constituted a significant fraction of the total fecal material. This reduced the apparent overall assimilation efficiency (Table 4, columns 3, 4, 7). If the feces produced at low rates (<0.3 mg/g dry weight per h) are excluded from the calculation, the dependence of assimilation efficiency on ration size is reduced (Table 4, columns 5, 8).

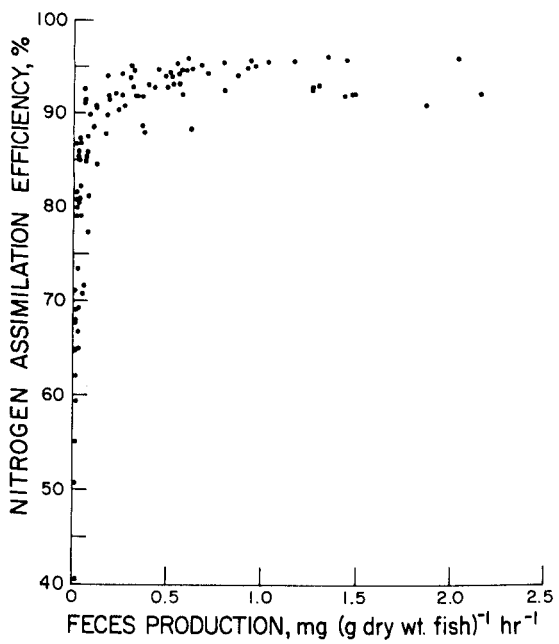

FIGURE 5.—Relationship between fecal elimination rate of *Brevoortia tyrannus* and the assimilation efficiency for nitrogen.

Nitrogen Excretion

When the fish were not feeding, their excretion rates were low and changes in the concentration of ammonia and DON in the tank were small. However, during feeding the excretion of the fish increased rapidly, and produced a rapid and nearly linear increase in the ammonia and DON concentrations (Figure 6). Excretion declined soon after the fish stopped feeding (Figure 7).

The mean ratio between DON and NH_3 excreted during the feeding period in all experiments was:

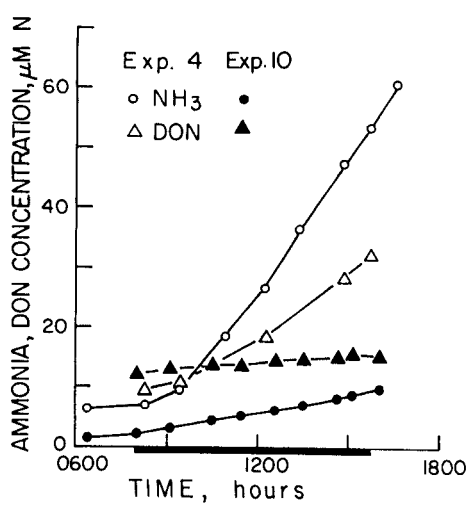

FIGURE 6.—Changes in ammonia and dissolved organic nitrogen concentration in the tank water due to excretion by 12 *Brevoortia tyrannus* during and after feeding. A high ration (Exp. 4) and a low ration (Exp. 10) experiment are illustrated.

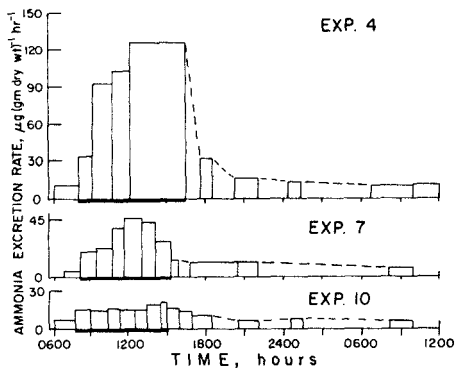

FIGURE 7.—Ammonia excretion rates of *Brevoortia tyrannus* before, during, and after a 7-h period of feeding on three ration sizes of *Ditylum brightwelli*.

$$\bar{X}\,\frac{\text{DON}-\text{N}}{\text{NH}_3-\text{N}} = 0.437, \quad \sigma = 0.088. \qquad (2)$$

Thus 30.4% of the total N excretion was in the form of DON, and 69.6% was in the form of ammonia.

The mean ±95% confidence limits of the ammonia excretion rate of fish unfed for 36 h (corresponding to measurement no. 1 in Durbin et al. 1981) was 7.46±2.54 µg NH_3-N/g dry weight per h. Using Equation (2), the total excretion was calculated to be 10.72±3.65 µg total N/g dry weight per h.

The amount of exogenous N excretion (that derived from the food) was calculated by subtracting the basal N excretion (10.72 µg N/g dry weight per h) from the total during the period of elevated excretion. Excretion rates were considered to have returned to basal when they reached the upper 95% confidence limit on the mean prefeeding rate, 14.4 µg N/g dry weight per h. Assimilation and N excretion did not lag far behind ingestion of the food. The time required for 50% of the exogenous N excretion to occur was only 1 or 2 h after 50% of the food was ingested ($\bar{X}$ = 1.4 h, Figure 8; Table 3, column 4). This indicates that all of the N ingested during the first 5.6 h of feeding (80% of the total) was assimilated during the feeding period.

The immediate decline in excretion rate after the fish stopped feeding was in accord with the decline in the elimination rate. In spite of this decline, 90% of the total exogenous excretion was completed within a mean of 2.4 h after the end of feeding (Figure 8; Table 3, column 6). The digestion and assimilation of *D. brightwelli* is therefore much more rapid than its complete elimination

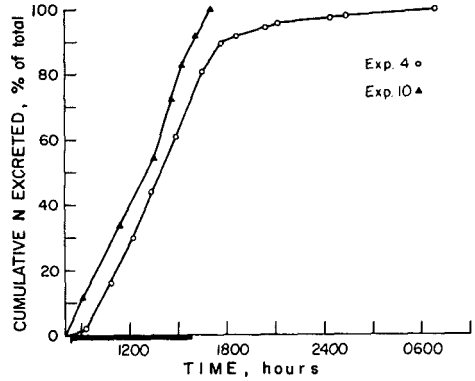

FIGURE 8.—Cumulative total exogenous nitrogen excreted by 12 *Brevoortia tyrannus* during and after feeding on *Ditylum brightwelli*. A high ration (Exp. 4) and a low ration (Exp. 10) experiment are illustrated.

from the gut (i.e., compare Table 3, columns 4, 6 with columns 3, 5).

The total exogenous N excreted (E_N, milligrams/gram dry weight) increased linearly with both the total N ingested in the ration (R_N, milligrams) (Figure 9) and the N assimilated from the ration (pR_N, milligrams). The least squares linear regressions were:

$$E_N = 0.616R_N - 0.020 \qquad (3)$$
$$r = 0.99$$

$$E_N = 0.655pR_N - 0.016 \qquad (4)$$
$$r = 0.99$$

where p is the assimilation efficiency for N. These regressions indicate that approximately 61.6% of

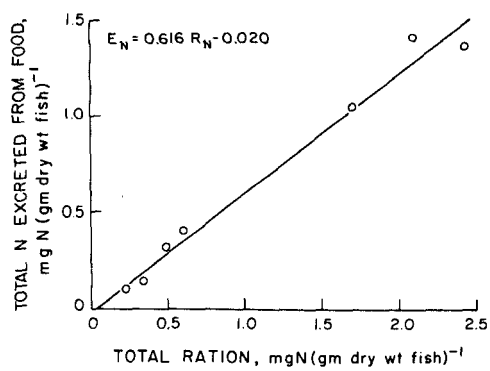

FIGURE 9.—Total exogenous nitrogen excreted by *Brevoortia tyrannus*, as a function of the amount of nitrogen ingested from *Ditylum brightwelli*. The least squares linear regression is shown.

the N in the ingested ration, and 65.5% of the N in the assimilated ration, were excreted.

If the total basal N excreted per day (0.257 mg N/g dry weight per d) is incorporated into Equations (3) and (4), the relationship between the total N excreted per day and the ingested N ration becomes:

$$E_N = 0.616R_N + 0.237 \text{ mg N/g dry weight per d} \quad (5)$$
$$r = 0.99$$

and the relationship between total daily N excretion and the assimilated N ration becomes (Figure 10):

$$E_N = 0.655pR_N + 0.241 \text{ mg N/g dry weight per d} \quad (6)$$
$$r = 0.99.$$

Equation (6) can be used to calculate, on a daily basis, the efficiency with which Atlantic menhaden retain N for growth as a function of N in the ration. This is analagous to calculating the net growth efficiency K_2:

$$K_2 = \frac{G}{pR} \quad (7)$$

where G = growth, grams/day
p = assimilation efficiency
R = ration, grams/day.

In the present case, growth in N (G_N, milligrams N/gram dry weight per day) will be equal to the N in the assimilated ration (pR_N) minus the total amount of N excreted per day (E_N total):

$$G_N = pR_N - E_N \quad (8)$$

$$= pR_N - (0.655\,pR_N + 0.241) \text{ mg N/g dry weight per d} \quad (9)$$

$$= 0.345\,pR_N - 0.241 \text{ mg N/g dry weight per d} \quad (10)$$

and

$$K_2 = \frac{0.345\,pR_N - 0.241}{pR_N} \quad (11)$$

K_2 calculated from Equation (11) for different assimilated ration sizes is shown in Figure 11. At an assimilated ration of 0.70 mg N/g dry weight per d there would be no net gain or loss of N. If Atlantic menhaden are composed of 8.03% N by weight (Table 1), this maintenance ration would correspond to 0.87% of their body N per day. The amount of N provided in the four lowest ration experiments was less than this daily maintenance requirement. The asymptotic value of K_2 at high ration levels was 0.345 (Figure 11). For K_2 = 0.20 and 0.30, the Atlantic menhaden would have to assimilate 1.66 and 5.36 mg N (2.1 and 6.7% of their body N, respectively) per day, with resultant growth rates of 0.42 and 2.01% of body N per day.

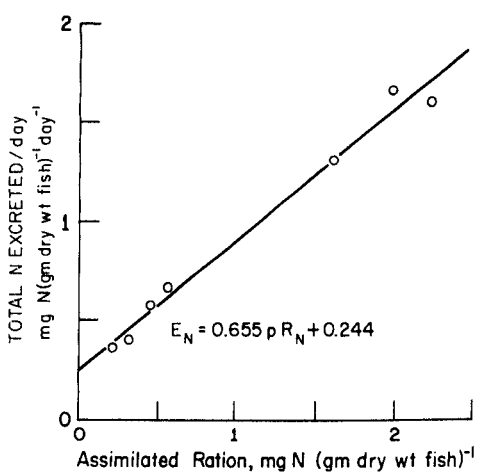

FIGURE 10.—Relationship between the amount of nitrogen assimilated from the daily ration, and the total daily nitrogen excretion by *Brevoortia tyrannus*.

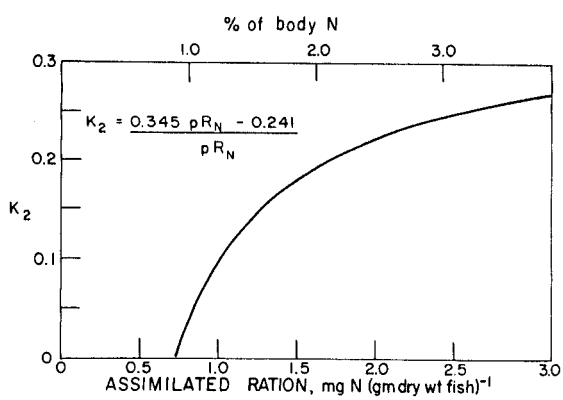

FIGURE 11.—Calculated efficiency of the utilization of nitrogen for growth by *Brevoortia tyrannus*, as a function of the nitrogen content of the assimilated ration.

Oxygen:Nitrogen Ratios

The ratio of O_2 consumed to N excreted (by atoms) has been used to give an indication of the type of food the fish are metabolizing. The O:N ratio during the combustion of protein is about 7.4 (Kutty 1972), while the ratio for carbohydrate is infinity, and for fat is about 415 (Ikeda 1977).

The change in the O:N ratio with time is shown for four phytoplankton experiments (Figure 12). The mean O:N for all initial prefeeding measurements in the phytoplankton experiments was 28.2, σ = 9.8. There was a slight increase of the O:N immediately after the beginning of feeding in most of the experiments. This was because the increase in the voluntary swimming speed of the fish during feeding produced an immediate increase in O_2 consumption, whereas N excretion increased more gradually. Swimming speeds and respiration rates during feeding in the three high ration experiments (nos. 4, 5, 6) averaged about 41.3 cm/s and 0.48 mg O_2/g wet weight per h, respectively. In these experiments, the O:N ratios declined to very low levels (between 5 and 10) soon after the initiation of feeding and remained at these low levels for the rest of the feeding period (Figure 12). In the four smaller ration experiments, the swimming speed during feeding ranged between 29.3 and 36.5 cm/s and O_2 consumption between 0.221 and 0.354 mg O_2/g wet weight per h.

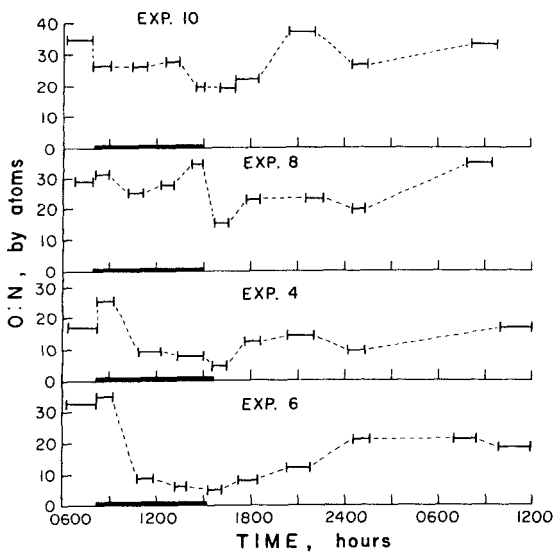

FIGURE 12.—O:N ratios of *Brevoortia tyrannus* before, during, and after feeding on *Ditylum brightwelli*. Oxygen data are from Durbin et al. (1981).

The decline in the O:N ratios during feeding was much less than in the high ration experiments. Swimming speeds and O_2 consumption rates of nonfeeding fish averaged about 12.2 cm/s and 0.10 mg O_2/g wet weight per h, respectively.

In all of the experiments, the lowest O:N ratio occurred immediately following feeding. This was because after the plankton was gone the fish immediately reduced their voluntary swimming speed and O_2 consumption, whereas their ammonia excretion remained high. Following this the O:N ratio gradually increased to the high prefeeding values.

DISCUSSION

Elimination of Food From the Gut

There has been some controversy concerning whether digestion rates and elimination rates are linear or exponential (Fänge and Grove 1979). In the linear model, a constant amount (g) is evacuated per unit time and therefore the instantaneous evacuation rate continually changes. In the exponential model, a constant proportion of the food present in the stomach is evacuated per unit time; thus, while the exponential rate remains constant, the actual amount of food (g) evacuated per unit time continually decreases.

In some studies the linear model has been explicitly used, by fitting a linear regression through the data points representing the food remaining in the stomach vs. time (e.g., Swenson and Smith 1973; Bagge 1977). In other studies the time to 100% evacuation of the stomach has been determined (e.g., Hunt 1960; Molnar and Tölg 1962; Edwards 1971; Jobling et al. 1977). Here there is usually an implicit assumption that evacuation is a linear process. Several recent careful studies, however, have found that gastric evacuation was clearly a curvilinear process which was closely approximated by an exponential curve (Brett and Higgs 1970; Tyler 1970; Elliott 1972; Elliott and Persson 1978). Beamish (1972) also concluded that evacuation is exponential over a major part of the digestion period, but that it may deviate at the beginning and near the end of digestion. In the initial stages this may occur if there is a lag between the ingestion of a meal, and the beginning of gastric evacuation. The final stages of evacuation are obviously not exponential, since completely empty stomachs are frequently seen in fishes.

With the Atlantic menhaden the exponential model seems appropriate since fecal elimination rates showed an exponential decline after the fish stopped feeding. This exponential fecal elimination rate (R'), determined from the decrease in fecal silicon elimination rate with time, is different from the exponential rate of gastric (stomach) evacuation (R), which is the factor measured in most studies. However, if the time required for food to travel the length of the intestine is constant, then the estimate of R' based on measurements of fecal elimination will be the same as R determined directly from measurements of the decline in stomach contents with time. In order to more fully investigate this, and to understand the patterns of change in feces elimination by Atlantic menhaden, especially during feeding, we have fit the data to a modified version of a model proposed by Elliott and Persson (1978). This theoretical model was then compared with our observed elimination rate data. A good agreement between the two would indicate that stomach evacuation is exponential, that R' is a good estimator of R, and that stomach evacuation is the principal factor governing the fecal elimination rate. Such an analysis may also serve to indicate whether systematic deviations between predicted and observed data occur as ration size changes.

The model of Elliott and Persson (1978) assumes that the fish feed at a constant rate, and that the gastric evacuation rate R is exponential. Thus the rate of change in stomach content (S) is given by:

$$(dS/dt) = F - RS. \tag{12}$$

The actual amount of food (S_t, milligrams/gram dry weight) present in the stomach after t hours is given by:

$$S_t = S_0 e^{-Rt} + \frac{F}{R}(1 - e^{-Rt}) \tag{13}$$

where S_0 is the initial amount of food in the stomach and F is the amount of food consumed per hour. As $F \to 0$, $S_t \to S_0 e^{-Rt}$. The amount of food (SE_t, milligrams/gram dry weight) which has been evacuated from the stomach by time t is simply:

$$SE_t = C_t - S_t \tag{14}$$

where C_t is the total amount of food (milligrams/gram dry weight) consumed in t hours. Thus SE_t and C_t are cumulative quantities measured since the onset of feeding, whereas S_t is the instantaneous amount present in the stomach at time t. For the present analysis we assumed that $R' = R$, and substituted R' into Equation (13). From values of R', F, and C_t for each experiment we then calculated S_t and SE_t for hourly intervals during and after feeding. All calculations were in terms of silicon, since this was not digested by the fish.

Curves illustrating C_t, S_t, and SE_t for the 12 fish are shown in Figure 13 for Experiment 7. The value of R' was 0.406/h and F was 0.241 mg Si/g dry weight per h. Since the ingestion rate was constant, C_t increased linearly with time. The amount of Si present in the stomach (S_t) increased curvilinearly during the feeding period, then declined exponentially after feeding stopped. The cumulative Si evacuated (SE_t) increased sigmoidally, with the inflection point at the time the fish stopped feeding. While most of the Si had been evacuated from the stomach within 5 h after the end of feeding, small amounts continued to be evacuated for many hours as the evacuation rates declined exponentially to very low levels.

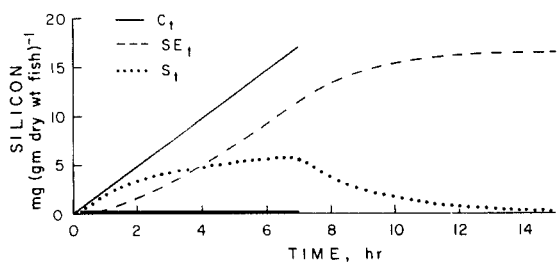

FIGURE 13.—Experiment 7. Cumulative ingestion of silicon (C_t), and model calculations of the instantaneous amounts of silicon present in the stomach (S_t) and the cumulative amounts of silicon which have been evacuated from the stomach (SE_t) during and after a 7-h feeding period.

The time lag between the ingestion of a particle and its elimination in the feces is the digestive tract residence time for that particle. Similarly the stomach residence time is the time lag between the ingestion and the gastric evacuation of a particle. The total digestive tract residence time was determined by subtracting the time required for the fish to ingest a given amount of Si, from the observed time when that same amount of Si was eliminated in the feces. The gastric residence time was similarly calculated from the observed feeding rate and the predicted values of SE_t. In each experiment the calculated gastric residence time followed a pattern similar to the digestive tract residence time (Figure 14). The two curves were

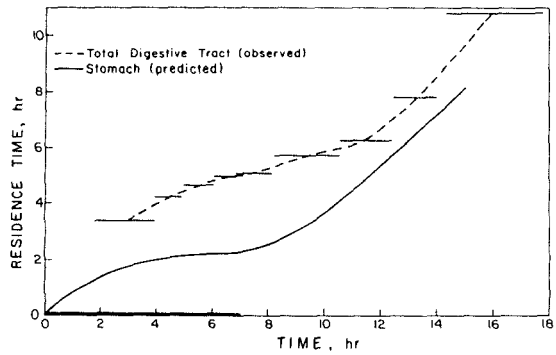

FIGURE 14.—Experiment 7. Changes in the digestive tract residence time of silicon (measured) and the stomach residence time of silicon (calculated) during and following a 7-h feeding period.

offset by the time required for Si to travel the length of the intestine; in the example shown, about 2 h.

Figure 14 demonstrates that particles eaten at the beginning of a feeding period have the shortest residence times. Residence time increases asymptotically during feeding, and then exponentially once the fish have stopped feeding. At the end of feeding the observed digestive tract residence time ranged between 5 and 6 h in all but the largest ration experiment, in which the residence time was only 4.5 h.

This model provides a quantitative explanation of the earlier observations by Noble (1973) and D. J. W. Moriarty and C. M. Moriarty (1973) that during continuous feeding, small food particles ingested early in the feeding period travel through the stomach more quickly than particles eaten later. In addition, observations that food particles eaten during continuous feeding will pass through the stomach more rapidly than when they are eaten as a single meal (i.e., Laurence 1971; Noble 1973) are also consistent with this model, since residence time remains short as long as feeding continues, but increases rapidly after the fish stop feeding.

Finally, the observed fecal elimination rates by the Atlantic menhaden (milligrams Si/gram dry weight per hour) were compared with the predicted gastric evacuation rates (milligrams Si/gram dry weight per hour) calculated from the model. Since the two curves were offset in time by the travel time of particles in the intestine, a comparison of the two is facilitated by lagging the stomach evacuation curve by the amount of the intestinal travel time. This time lag was graphically determined for each experiment by overlaying the curve of stomach evacuation on the curve of feces elimination rate such that the periods of exponential decline coincided. These lag times were quite similar for all experiments (overall mean $\pm\sigma$ = 2.17 ± 0.18 h). These values agree well with the average time for the first appearance of feces after the onset of feeding (2.4 h).

These plots of the observed fecal elimination rates and the predicted gastric evacuation rates (Figure 1) showed that in general there was good agreement between the two. There were, however, some systematic deviations with change in ration size. At high food rations, the observed elimination rates of the first fecal samples were higher than predicted by the model, indicating that these passed through the digestive tract more rapidly than predicted. In contrast, at the lowest rations the initial elimination rates were lower than predicted. Since the presence of food directly stimulates gastric motility and the secretion of digestive enzymes (Fänge and Grove 1979), it may be that the larger rations have a greater stimulatory effect on the digestive tract than small rations. It should be noted, however, that these deviations observed in the first two or three fecal samples represent food ingested quite early during the feeding period (Figure 1). Subsequent samples more closely followed the model.

The largest ration experiment (no. 6) also deviated from the model during the postfeeding period. The model predicts that if the exponential evacuation rate is <1 (i.e., in the present case = 0.366), food will continuously accumulate in the stomach during feeding (Figure 13). The largest amount of material in grams is therefore evacuated at the end of the feeding period (Figure 13), and the maximum fecal elimination rates should occur during the postfeeding period (because of the time required for material to travel through the intestine). However, in Experiment 6, the elimination rates quickly rose to high levels, but then declined and leveled off during the postfeeding period without reaching the maximum rates predicted by the model (Figure 1). This implies that stomach evacuation was also lower than the model would predict during the last 2 or 3 h of feeding. A possible explanation is that after the Atlantic menhaden had fed for several hours at this high rate, the amount of food may have accumulated in the stomach to an extent which exceeded the maximum physical capacity of the fish to process the material, which caused the gastric evacuation rate to level off. It was interesting that

assimilation efficiency in this experiment was also somewhat reduced. However, even with this high feeding rate, the behavior of the Atlantic menhaden did not change significantly during the course of the feeding period, and the fish gave no indication of approaching satiation (Durbin et al. 1981).

In summary we conclude that the calculated gastric evacuation by Atlantic menhaden calculated from Elliott and Persson's (1978) model agrees well with our experimental measurements of elimination rates following a meal. The calculated lag between the gastric evacuation of a particle and its elimination in the feces was similar for all ration sizes and also agreed well with the estimates of the time of the beginning of fecal elimination (Table 3, column 2). These results indicate that R' should be a good estimator of R. However, the stomach evacuation rates of Atlantic menhaden need to be determined directly, both in order to verify the model predictions, and to explore the reasons for the systematic deviations of the observed elimination from that predicted as food ration size changes.

Finally, with regard to methods employed for the study of fish digestion, present results with Atlantic menhaden indicate that when digestion is an exponential process, measurements of the time to "100% evacuation" are of limited value. This is because they cannot be used to determine the exponential evacuation rate R. The evacuation of the final portion of a meal is extremely protracted and may even be nonexponential. With Atlantic menhaden, for example, the food eliminated between 8 and 41 h after the end of feeding corresponded on average to the food ingested during the final 35 min of feeding; feces eliminated during hours 14-41 corresponded to the final 10 min of feeding. This makes selection of an end point, to be taken as 100%, quite difficult and arbitrary. If the final stages are nonexponential, then obviously the estimate of R would be biased. The final problem is computational: in an exponential process, the stage of 100% digestion is mathematically never reached, and it is necessary to approximate 100% with another value, such as 98, 99, or 99.9%. Although the choice of any of these values would be purely arbitrary, each provides a very different estimate of the value of R.

Assimilation Efficiency

The Atlantic menhaden was very efficient at absorbing N, C, and calories from both phytoplankton and zooplankton food. These high assimilation efficiencies are in general agreement with those reported for carnivorous fish (Gerking 1955; Menzel 1960; Pandian 1967; Beamish 1972; Kelso 1972). Few studies have examined the assimilation efficiency of herbivorous fishes. C. M. Moriarty and D. J. W. Moriarty (1973) and D. J. W. Moriarty and C. M. Moriarty (1973) found that the maximum mean C assimilation of *Tilapia nilotica* varied according to food type, being highest for the diatom *Nitzschia* (79%), somewhat lower for two bluegreen algae, *Microcystis* (70%) and *Anabaena* (75%), and least for the green alga *Chlorella* (49%). The average maximum C assimilation of *Haplochromis nigripinnis* for *Microcystis* was 71%. Menzel (1959) reported that *Holacanthus bermudensis* assimilated 85% (range 82-91%) of the N and 77.7% (range 72-84%) of the calories from two macroalgae, *Monostroma* and *Enteromorpha*. Plant materials described from the gut contents of Atlantic menhaden are planktonic and resuspended benthic diatoms, and detrital particles presumably derived from marsh grasses (Peck 1894; Darnell 1958; Peters and Kjelson 1975; Jeffries 1975). The high assimilation efficiency for *D. brightwelli* indicates that Atlantic menhaden should have high assimilation efficiency for other diatoms also. The ability of Atlantic menhaden to assimilate detrital material has not been experimentally determined. Planktonic green and bluegreen algae are much less important in the marine environment than in freshwater; moreover they are generally too small to be filtered by Atlantic menhaden (Durbin and Durbin 1975) and are not a significant food. Thus the comparatively low assimilation efficiency which has been reported for some freshwater herbivores fed green and bluegreen algae is not relevant to Atlantic menhaden or to most other marine phytoplankton-feeding fishes, which eat mainly diatoms and dinoflagellates (i.e., see Durbin 1979 and references therein).

Ration size has generally been shown to have little or no effect on assimilation efficiency (Gerking 1955; Pandian 1967; Beamish 1972; Kelso 1972; Solomon and Brafield 1972), although Elliott (1976) found that assimilation in brown trout, *Salmo trutta*, decreased as ration level increased.

Our results show a slight increase in assimilation efficiency with increasing meal size. This effect, as well as the changes in assimilation efficiency during the course of a feeding period, may have two possible causes: 1) the addition to the fecal pellets of significant quantities of materials

secreted by the gut, resulting in lower apparent assimilation efficiencies; and 2) a possible lag in the secretion of digestive enzymes after a period of fasting, which would cause assimilation to be initially low. The latter effect was observed by D. J. W. Moriarty and C. M. Moriarty (1973), who found that in *Tilapia* a period of about 4 h was required for the secretion of stomach enzymes, and hence assimilation efficiency, to reach high values. We have no measures of temporal changes in stomach enzymes for the Atlantic menhaden. While explanation 2 may have contributed to the initial low assimilation efficiency at the beginning of feeding, it would not explain the decline in assimilation towards the end of feces elimination, since this food was presumably digested at the end of the feeding period when stomach enzymes should have been maximal. Visual observations of the organic material surrounding the feces at low fecal production rates provided support for the first explanation, and would be consistent with the reduced assimilation efficiency observed at both the beginning and end of feces production.

The reason for the reduced assimilation efficiency at the highest ration level is unclear. If the maximum capacity of the digestive tract was reached, the assimilatory processes may have become saturated, causing a reduction in assimilation efficiency.

However, the supply rate of plankton in the highest ration experiment exceeded the concentration of diatoms which Atlantic menhaden would normally be expected to encounter on its summer feeding grounds in Narragansett Bay (Durbin and Durbin 1981). Thus Atlantic menhaden probably does not ordinarily feed at such high rates for prolonged periods in nature. Therefore, the slight decline in assimilation efficiency at the high feeding rate of Experiment 6 may not have much ecological significance. We conclude that overall, the effect of meal size on the assimilation efficiency of Atlantic menhaden is small. Because of the very rapid digestion rates and high assimilation efficiencies of Atlantic menhaden, this planktivore appears to be adapted to process efficiently large amounts of food continuously.

Nitrogen Excretion

In most teleosts ammonia is the principal end product of protein catabolism, and is the major component of N excretion; other N compounds excreted include urea, creatine, creatinine, and trimethylamine oxide (Watts and Watts 1974). In Atlantic menhaden the percent of total N excreted as ammonia (69.6%) appears to be similar to that observed in other species (Smith 1929; Atherton and Aitken 1970; McCarthy and Whitledge 1972).

Nitrogen excretion by Atlantic menhaden changed according to whether or not the fish were feeding, the rate at which they fed, and the time since the last meal. Previous studies have also found that N excretion increases as a result of feeding (Brett and Zala 1975; Elliott 1976; Savitz et al. 1977). These studies differed from the present study, however, in the timing of the peak of N excretion and the subsequent return to endogenous rates. Fingerling sockeye salmon, *Oncorhynchus nerka*, at 15° C showed a peak ammonia excretion rate about 4 h after a meal and did not return to a basal rate until about 16 h after feeding (Brett and Zala 1975). Similarly, N excretion rates of brown trout at 17° C did not return to baseline until about 12-20 h after feeding (Elliott 1976) and largemouth bass, *Micropterus salmoides*, at 21°-23° C took 1 or 2 d (Savitz et al. 1977). In contrast, when Atlantic menhaden fed continuously for 7 h, the excretion rate remained high throughout the feeding period and lagged only 1 or 2 h behind ingestion of the food. The return to baseline was also rapid, with 90% of the exogenous N excretion occurring within a mean of 2.4 h following the end of feeding.

The Atlantic menhaden excreted a constant proportion of N in its ration (61.6% of the ingested and 65.5% of the assimilated ration). Savitz et al. (1977) also found a linear relationship between ingestion and N excretion in largemouth bass, although in that case only 40% of the ingested N was excreted. Gerking (1971) reported that in bluegill there was a linear relationship between the amount of N consumed and the amount retained for growth, which implied that the relationship between the amount of N ingested and that excreted was also linear. Additional studies are needed to determine the extent to which the proportion of N excreted by different species varies. Factors which may be expected to affect this proportion are the nutritional requirements of the fish, which may change seasonally, relative to the chemical composition of the food.

Oxygen:Nitrogen Ratios

The chemical composition of Atlantic menhaden compared with that of plankton indicates that the

fish conserve C and calories relative to N and ash from its food. Exogenous N in excess of body requirements is excreted. The O:N ratios indicate that proteins are used as a metabolic fuel by both feeding and nonfeeding Atlantic menhaden with subsequent excretion of N. This is consistent with results from other teleosts (Watts and Watts 1974). If an O:N ratio of 7.4 indicates that pure protein is being burned, then the mean value of 28.2 in fish unfed for 36 h indicates that 7.4/28.2 = 26.2% of the O_2 consumed is being used for protein catabolism. The increase in O:N ratios immediately after the beginning of feeding indicates that the fish are metabolizing proportionally more carbohydrate or lipid to support the increased swimming speed until significant quantities of food have been assimilated and become available as an energy source. During the feeding period of the three high ration experiments, the O:N ratios declined to or below that associated with the combustion of pure protein. The decline in the O:N ratios during feeding can be caused by two processes, which can act simultaneously: the fish are obtaining a large proportion of their energy directly from the breakdown of the C skeletons of amino acids absorbed from the food, with subsequent excretion of the N; and the proportions of the various amino acids taken in the food are being balanced to meet the requirements of protein synthesis; excess α-amino acids are excreted (Watts and Watts 1974). While it is impossible to separate the two processes in the present experiments, O:N ratios below 7.4 are an indication that both are occurring.

Kutty (1978) has calculated the ammonia quotient (AQ = NH_3 excreted/O_2 consumed) from the data of Brett and Zala (1975), from which O:N ratios can be determined. In that study the fish were fed a single meal over a brief time interval, and the peaks in O_2 consumption and N excretion were separated by several hours. However, the trend in the O:N ratios was similar to the present study, in that they declined from high values ($\approx$ 40.0) in the unfed fish to a minimum of about 8.3 during the digestion and assimilation of the food, then gradually increased to the prefeeding level.

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TAXONOMIC STATUS AND BIOLOGY OF THE BIGEYE THRESHER, *ALOPIAS SUPERCILIOSUS*

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ABSTRACT

This paper reviews the life history, taxonomic status, abundance, distribution and habitat, reproduction, feeding habits, scientific and economic importance, and literature of the bigeye thresher, *Alopias superciliosus*; and presents new information on morphometrics, vertebral counts, tooth counts, denticles, size, age, and growth from 22 specimens. We found *A. profundus* is a junior synonym of *A. superciliosus*, and we have extended the geographic range of the latter to the Mediterranean Sea and New Zealand. *Alopias superciliosus* is a wide-ranging, circumtropical species between the latitudinal limits of 40° north and 40° south.

Thresher sharks (family Alopiidae, genus *Alopias*), instantly recognizable by their tremendously elongated caudal fins (the upper lobe of the caudal fin about as long as the rest of the shark), have been known since antiquity. According to Salviani (1554), Aristotle was familiar with thresher sharks and described their behavior. Bonnaterre (1788) proposed the first valid specific name for a thresher, *Squalus vulpinus* (the common thresher), while Rafinesque (1809) proposed the genus *Alopias* for the same species, which he termed *Alopias macrourus*. More recently Tortonese (1938), Bigelow and Schroeder (1948), and Bass et al. (1975) reviewed the systematics of the genus *Alopias*.

Lowe (1839) described new fishes from Madeira in the eastern Atlantic. Among these was a very brief diagnosis of a new thresher, *Alopecias superciliosus*, which he characterized as follows: "At once distinguished from the only other known species of the genus, *Carcharias vulpes*, Cuv., by the enormous eye and its prominent brow. I have at present only seen a single young example."

This shark, the bigeye thresher, was not mentioned by name in the literature until Fowler (1936) erroneously synonymized it with *Alopias vulpinus* (Bonnaterre 1788). The species was apparently overlooked in the reviews of Dumeril (1865), Günther (1870), Garman (1913), White (1937), and Tortonese (1938). Bigelow and Schroeder (1948) resurrected Lowe's species and gave the first detailed diagnosis and description of *Alopias superciliosus*, based on Floridian and Cuban specimens. Earlier, Grey (1928), Nakamura (1935), and Springer (1943) reported specimens of the bigeye thresher under different scientific names, but all of these writers overlooked Lowe's obscure account. More recently, Cadenat (1956), Strasburg (1958), Fitch and Craig (1964), Kato et al. (1967), Telles (1970), Bass et al. (1975), and Stillwell and Casey (1976) have presented descriptive accounts as well as morphometric, meristic, and other quantitative data on the species.

Thresher sharks are peculiar in that their elongated tails are the only known structure in sharks, other than jaws and teeth and the armed rostrum of sawsharks (Pristiophoridae), that function in killing or immobilizing prey (Springer 1961). An Indo-Pacific orectoloboid, the zebra shark, *Stegostoma fasciatum* (family Stegostomatidae), also has a greatly elongated caudal fin, but is not known to use it as a weapon.

Bigeye threshers are noteworthy in having enormous, dorsally facing eyes and unique head grooves, structures which may reflect specialized habits of the species that differ from the other two species of thresher shark.

The impression gained in most of the taxonomic literature is that *A. superciliosus* is a widespread but rare species. However, the works of Gubanov (1972), Guitart Manday (1975), and Stillwell and Casey (1976) indicate that it can be locally abundant and of importance in pelagic longline fisheries of the west-central Atlantic and northwestern Indian Ocean.

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The purpose of this paper is to bring together the widely scattered information on *A. superciliosus*, summarize its life history, and correct certain inconsistencies in the literature. We present morphometric, meristic, and other quantitative data, including descriptive accounts of specimens from Florida and the central Pacific, compare the bigeye thresher with other species of threshers, and discuss its taxonomic history.

MATERIAL

1. SHG-A2 (S. H. Gruber, private collection); adult female, 356 cm TL (total length), weight 140 kg; Straits of Florida several kilometers east of Miami Beach, Fla.; captured on 29 June 1977 by sport fishermen on a hook baited with squid at 30 m depth in water about 400 m deep. The specimen was photographed, measured, and dissected, and two early fetuses, both eyes, skin patch, and the tail were saved. The jaws were used in a taxidermist's mount and were not available, but the teeth were photographed before the fish was mounted. The fetuses are males, 207 and 213 mm TL.

2. SHG-A7; adult male, 356 cm TL; Straits of Florida several kilometers east of Pompano Beach, Fla.; captured at 1000 h e.d.t. on 4 July 1979 by commercial longliner at 40 m in water about 400 m deep. The specimen was photographed, measured, and dissected. Head, jaws, vertebral column (precaudal), tail, and claspers were saved. The spiral valve was sent to M. Dailey, Long Beach, Calif., for parasite investigation. One eye was sent to G. Hughes, Canberra City, Australia, for retinal study.

3. SHG-A5; adult female, 320 cm TL; Straits of Florida several kilometers east of Miami Beach, Fla.; captured on a longline at 40 m at 2200 h e.s.t., 14 March 1979. The water depth was 350 m. The head was removed, dissected, and saved with the jaws intact.

4. SHG-A6; subadult female, 306 cm TL; caught on same set as no. 3 above.

5. SHG-A3; subadult male, 291 cm TL; Straits of Florida, 35 km east of Palm Beach, Fla.; captured on 24 July 1979 by commercial longliner at 30 m in water about 120 m deep. The specimen was photographed, measured, and dissected, and the jaws, vertebrae, and head saved.

6. SHG-A4; immature male, 150 cm TL; east of Hatteras, N.C.; captured on a longline on 6 May 1979. The specimen was photographed and measured. No parts were saved as the whole shark was used in taxidermy.

7. *Shoyo Maru* voyage 13, SM-9-II-64-3; Nankai Regional Fisheries Laboratory, Japan; immature female, 279 cm TL, weight 62 kg; eastern Central Pacific, lat. 0°38′ N, long. 124°23′ W; captured on a longline on 9 February 1964. The specimen was photographed, measured, and dissected by Susumu Kato[3]; skin, jaws, reproductive organs, eyes, nasal sac, and parasites saved.

8. LJVC-0355 (L. J. V. Compagno, private collection), *Shoyo Maru* voyage 13, SM-11-II-6493; immature female, 287 cm TL, weight 59 kg; eastern Central Pacific, lat. 3°16′ S, long. 128°18′W; captured on a longline on 11 February 1964. The specimen was measured and preserved intact by Susumu Kato (footnote 3), later photographed and dissected by Compagno; skin, jaws, cranium, eyes, vertebral column, and fins saved.

9. *Shoyo Maru* voyage 16, SHO-16-2; 461 cm TL; Mediterranean Sea, lat. 36°39′ N, long. 17°51′ E; captured on a longline on 2 December 1966. Specimen measured by Izumi Nakamura[4] and data presented to Susumu Kato (footnote 3).

10. *Shoyo Maru* voyage 16, SHO-16-22; 2 individuals, 343 and 347 cm TL; lat. 13°36.4′ N, long. 75°34.2′ W; captured on a longline on 4 February 1967. Specimen measured by Izumi Nakamura (footnote 4) and data presented to Susumu Kato (footnote 3).

11. LACM-F-89; no length or sex data; Odawara, Japan, 1968; jaws only, teeth counted by Bruce Welton[5].

12. CAS (California Academy of Science, San Francisco, Calif.) Acc. 1963-X: 7; adult male, 372 cm TL; off San Clemente Is., southern California, 23 July 1963; partly dissected and preserved, jaws dried; previously reported by Fitch and Craig (1964).

13. LACM-F-88; male, presumably adult, 378 cm TL; 25 km ESE of east end of Santa Catalina Is., Calif., 30 June 1967; jaws only, teeth counted by Bruce Welton (footnote 5).

14. LACM-F-90; immature female, ca. 305 cm TL; southern California, probably Santa Mon-

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[4]Izumi Nakamura, Fisheries Research Station, Kyoto University, Maizuru, Kyoto 625, Japan.

[5]Bruce Welton, Department of Paleontology, Los Angeles Museum of Natural History, 900 Exposition Boulevard, Los Angeles, CA 90007.

ica Bay area, 26 October 1966; jaws only, teeth counted by Bruce Welton (footnote 5).

15. Several other examples are listed in the tables on tooth counts but were not otherwise measured or seen.

DISTINCTIVE CHARACTERS

Alopias superciliosus (Figures 1-4) can be immediately distinguished from other threshers by its unique head shape, with lateral grooves

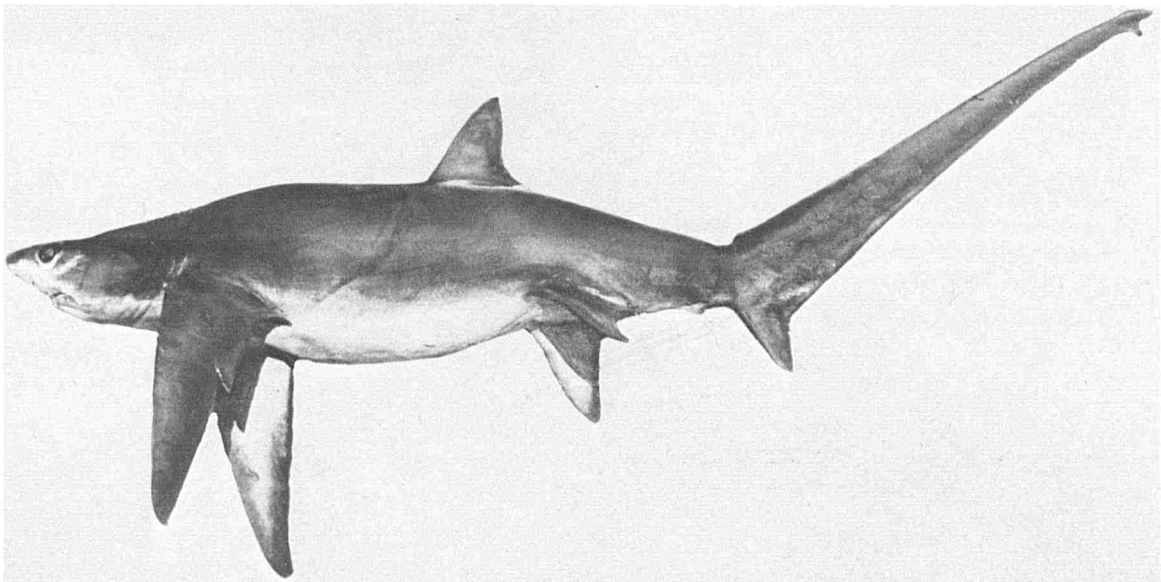

FIGURE 1.—Lateral view of a 356 cm TL, 140 kg female *Alopias superciliosus* (SHG-A2) taken off Miami Beach, Fla. Detailed measurements of this shark are given in Table 1, column 1. The characteristic head grooves are not clearly shown because of the slightly ventral angle of the photograph. Photo: S. Gruber.

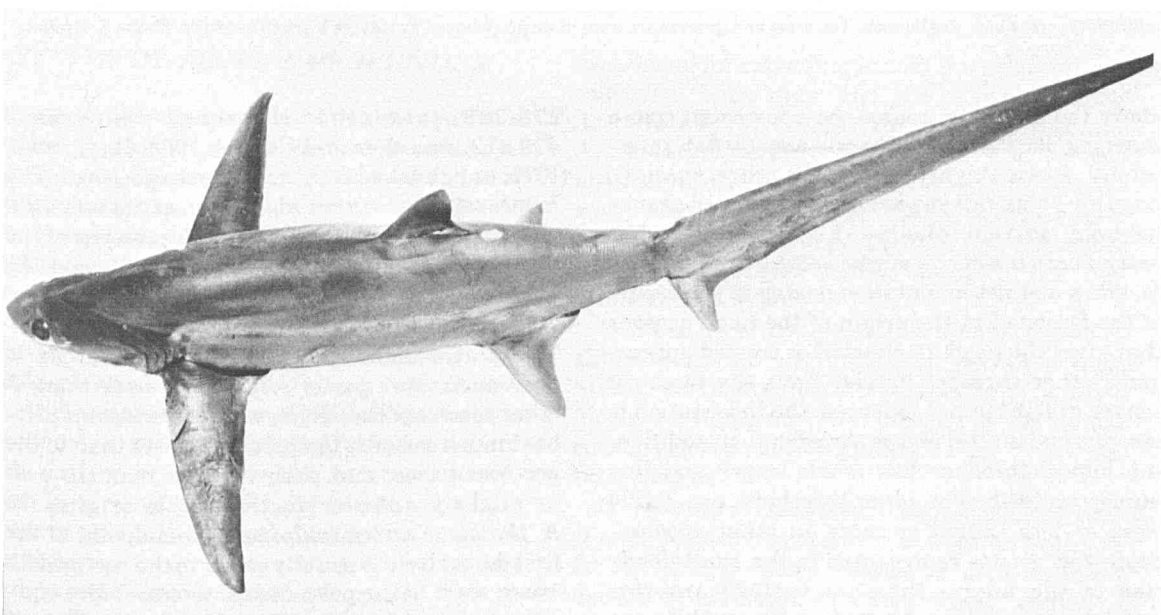

FIGURE 2.—Dorsal view of *Alopias superciliosus* (SHG-A2). The head grooves and upward-looking eyes are more easily seen in this photograph. Photo: S. Gruber.

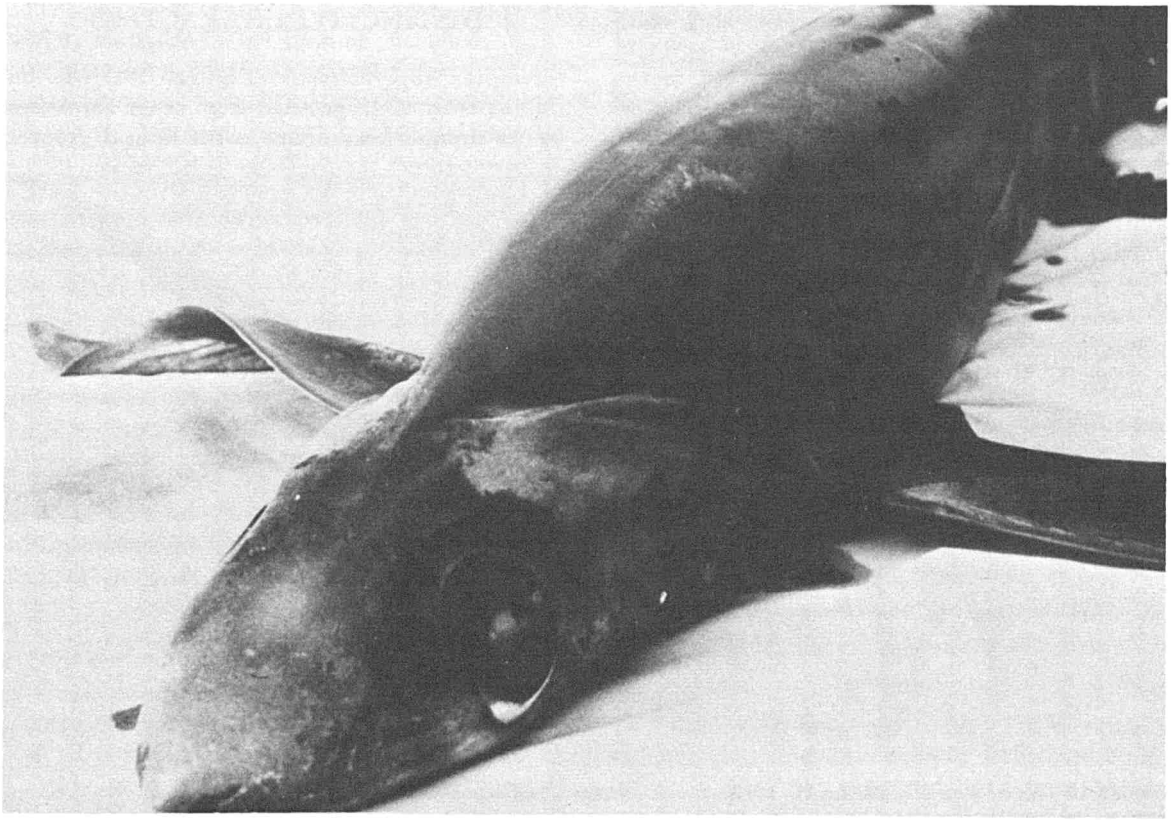

FIGURE 3.—Three-quarter lateral view of the head of a 159 cm TL immature male *Alopias superciliosus* (SHG-A4) showing the head grooves and massive "crest" composed of the epaxial musculature. The characteristic large eyes, bulbous snout and flattened interorbital space can also be seen. The crest and grooves are even more pronounced in mature bigeye threshers. Photo: S. Gruber.

above the branchial region, bulbous snout (more tapering in other threshers), nearly flat interorbital space (highly arched in other species), huge eyes with lids shaped like an inverted pear or keyhole (in individuals >1,300 mm TL) that extend onto the dorsal surface of the head (Figure 4), and a distinct indentation or step in the profile of the forehead at the origin of the head grooves that gives the head a helmeted or crested appearance (other thresher species have the forehead convex or flat but not indented; the indentation is less marked in fetal bigeye threshers). In addition, the bigeye thresher has much larger and less numerous teeth than other threshers, e.g., 24/24 rows or less (32/29 or more in other species). Tooth row groups represented in the adult dentition of the bigeye thresher include anterior and lateroposterior teeth only, without the symphysial or intermediate teeth found in other species. The bigeye thresher has fewer vertebrae, 278-308, than other threshers, which have 339-472 (Springer and Garrick 1964; Bass et al., 1975; unpublished data on all three species). In the monospondylous precaudal region of the vertebral column, the vertebral calcification patterns of the bigeye thresher are simpler than in other species, with fewer radii in the intermedialia and no fusion of their bases (extensively fused in *A. pelagicus*). The first dorsal fin of the bigeye thresher is positioned more posteriorly on the back than in other species of threshers, with the midpoint of its base much closer to the pelvic fin bases than to the pectoral bases, and with its free rear tip over or slightly anterior to the pelvic origins. In *A. pelagicus* and *A. vulpinus* the midpoint of the first dorsal base is usually closer to the pectoral fin bases than to the pelvic bases (occasionally equidistant between pectoral and pelvic bases), and the free rear tip of the first dorsal is far anterior to the pelvic origins.

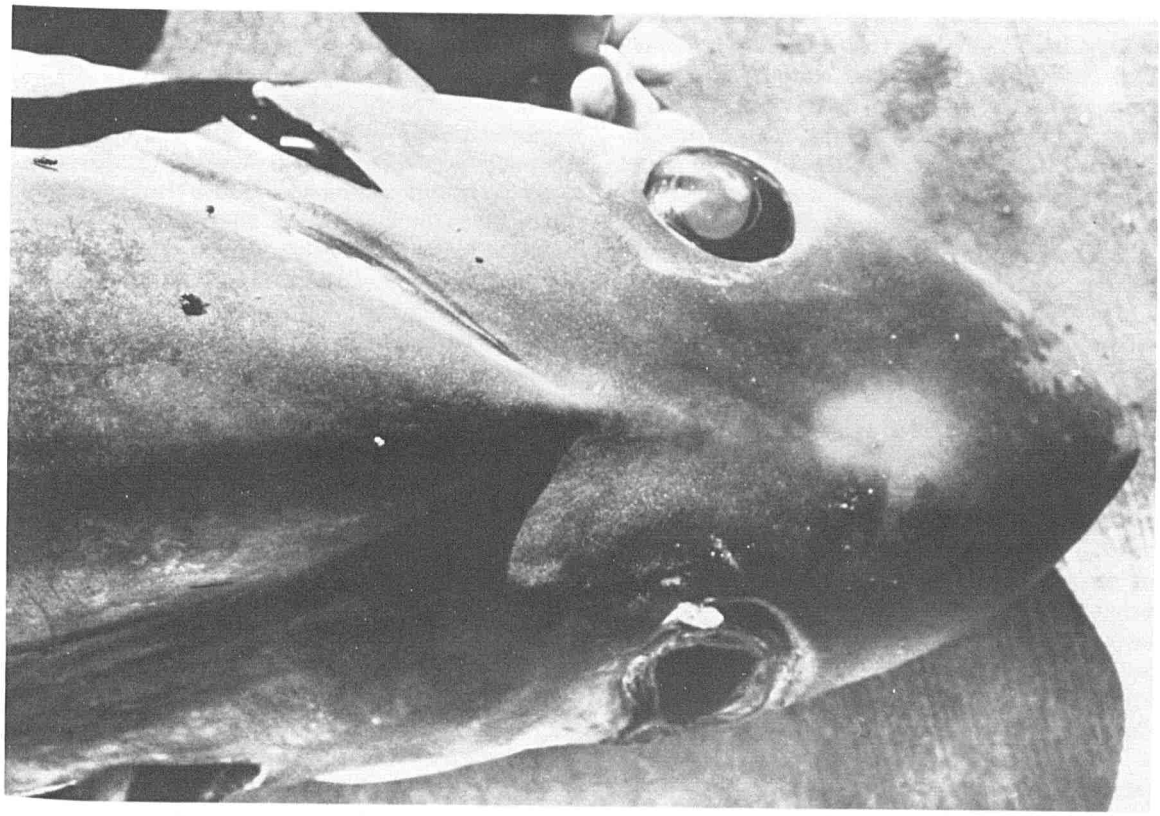

FIGURE 4.—Dorsal view of the head of a 356 cm TL male *Alopias superciliosus* (SHG-A7) showing the head grooves and upward looking eyes. (The lens of the right eye has been removed.) Photo: S. Spielman.

STATUS OF *ALOPIAS PROFUNDUS*

Nakamura (1935) described two new species of thresher sharks, *A. profundus* and *A. pelagicus*, from Taiwan. The thresher sharks were collected at a fish market and capture data were unavailable. Nakamura thought that one of these species lived near the sea bottom and so named it *A. profundus*. He was evidently unaware of Lowe's account of *A. superciliosus*, and only compared his new species with each other. Nakamura concluded that there was insufficient evidence in the literature to determine if either of his two species was equivalent to the wide-ranging "*Alopias vulpes*" (= *A. vulpinus*), and gave this reason as justification in naming *A. profundus* and *A. pelagicus*.

Fowler (1941) listed both Nakamura's species as questionable synonyms of *A. vulpinus* but Bigelow and Schroeder (1948) recognized them as distinct. They noted that *Alopias* can be divided into two groups, one including *A. profundus* and *A. superciliosus*, both with the free rear tip of the first dorsal fin extending to over the pelvic origins and with huge eyes; and the other including *A. vulpinus*, *A. pelagicus*, and the dubious *A. caudatus*, having the first dorsal rear tip well anterior to the pelvic origins and with smaller eyes. Using Nakamura's (1935) account as a source for *A. profundus*, Bigelow and Schroeder (1948) distinguished the two species in the "bigeye" group as follows:

1) "Rear tip of 2nd dorsal terminates considerably anterior to origin of anal; pelvics a little higher vertically than 1st dorsal and a little larger in area; anterior margin of 1st dorsal strongly convex; no lower precaudal pit." *Alopias superciliosus*.

2) "Rear tip of 2nd dorsal terminating over base of anal; pelvics less than 1/2 as high vertically as 1st dorsal and much smaller in area; anterior margin of 1st dorsal only very weakly convex; a precaudal pit below as well as above." *Alopias profundus*.

Several writers, following Bigelow and Schroed-

er (1948), including Teng (1962), Matsubara (1963), Chen (1963), Garrick and Schultz (1963), Fitch and Craig (1964), and Kato et al. (1967), recognized *A. profundus* as distinct, though Kato et al. suggested that it might be identical to *A. superciliosus*. Bass et al. (1975) synonymized *A. profundus* and *A. superciliosus* because the relative positions of anal and second dorsal fins, relative sizes of first dorsal and pelvic fins, and absence of a lower precaudal pit were, in their opinion, "...highly variable and probably invalid as diagnostic characters," but they did not discuss the matter further. Our analysis of the characters supposedly separating *A. profundus* and *A. superciliosus* leads us to concur with Bass et al. in synonymizing these species.

We have taken Nakamura's (1935) original measurements of *A. profundus* and converted them to precaudal proportions for comparison with other bigeye thresher (Table 1) and find that most of them fall within the range for other specimens identified as *A. superciliosus*. The differences listed by Bigelow and Schroeder (1948) for *A. profundus* and *A. superciliosus* appear to be based on ontogenetic changes and individual variation in a single species, or, in the case of the pelvic

TABLE 1.—Measurements of 13 specimens of *Alopias superciliosus* from the Atlantic, Indian, and Pacific Oceans. All values are proportional to precaudal length (given as unity) except rows 1 and 2 which are in centimeters as indicated.

Item	Original SG-A2 Western North Atlantic Female	Original SG-A7 Western North Atlantic Male	Stillwell and Casey (1975) Western North Atlantic Female	Original SG-A3 Western North Atlantic Male	Original SG-A4 Western North Atlantic Male	Bigelow and Schroeder (1948) Western North Atlantic Male	Telles (1975) Eastern North Atlantic Male	Bass et al. (1975) Western Indian Male	Nakamura (1935) Western North Pacific Female	Strasburg et al. (1958) Central North Pacific Male	Original SM-9-11-64-3 Eastern Central Pacific Female	Original LJVC 0355 Eastern Central Pacific Female	Fitch and Craig (1964) Eastern North Pacific Male
Total length, cm	356	356	340	290.8	159	130	269	363	332	328	279	287	381
Precaudal length, cm	201	199.4	190	150.4	84.5	. 66	152	198	170	167.4	139	144	208
Snout to													
Mouth	085	089	087	094	123	118	079	078	—	061	099	097	076
Eye	080	087	074	096	109	—	—	062	—	—	078	079	—
Pectoral origin	269	286	287	316	328	333	252	265	300	309	320	306	—
Pelvic origin	697	701	702	735	734	716	692	729	729	744	770	716	740
Anal origin	876	930	926	939	976	938	921	—	929	957	—	—	952
1st dorsal origin	535	586	569	603	621	612	562	557	588	595	612	597	600
2d dorsal origin	866	853	874	916	911	903	—	—	894	902	906	903	918
Internarial	027	028	029	031	034	035	—	027	—	029	031	029	026
Mouth:													
Width	070	069	082	076	078	086	086	069	—	082	079	087	072
Height	042	050	051	062	046	051	—	048	—	047	043	046	050
Gills, length:													
1st	045	040	—	—	038	057	—	040	—	049	051	043	057
3d	050	047	—	044	047	055	—	051	—	057	056	048	057
5th	035	046	—	043	050	037	—	045	—	047	045	045	054
Eye (orbit):													
Horizontal	030	029	031	034	047	055	033	031	028	039	034	042	029
Vertical	050	051	048	049	058	—	042	—	044	—	049	050	045
1st dorsal:													
Base	119	117	—	137	101	124	110	112	—	131	122	120	107
Height	129	130	147	144	107	102	128	121	163	147	150	133	152
2d dorsal:													
Base	010	015	—	012	012	018	—	018	—	016	012	015	019
Height	007	—	014	009	009	014	—	007	—	012	010	009	014
Pectoral, anterior margin	343	328	387	380	398	375	356	348	362	393	403	389	324
Pelvic fin:													
Base	164	121	—	169	169	122	—	—	—	—	176	156	155
Height	—	—	—	135	118	—	—	—	—	—	126	128	138
Anal fin:													
Base	017	019	—	016	018	018	018	013	—	025	022	019	022
Height	025	025	—	020	018	020	029	026	—	029	025	031	019
Caudal fin:													
Dorsal lobe	851	792	—	912	905	964	823	864	—	957	1.007	993	839
Ventral lobe	119	118	—	135	132	124	—	127	—	—	137	125	125
Trunk-at-pectoral:													
Height	192	208	—	194	178	178	196	—	—	—	187	181	219
Width	149	135	—	154	160	145	111	—	—	—	151	149	166
Interspace:													
1D-2D	189	171	200	176	189	174	—	—	—	—	191	184	—
2D-caudal	097	072	086	—	—	090	—	128	—	090	094	077	101
Anal-caudal	080	—	052	—	—	037	036	057	—	053	075	054	056

fins, possible misinterpretation of the actual size of these fins in *A. profundus*.

The relative positions of the anal and second dorsal fins vary. The account and illustration of a 130 cm TL *A. superciliosus* from Cuba in Bigelow and Schroeder (1948, figure 5) shows the free rear tip of the second dorsal fin terminating anterior to the anal origin by a distance about equal to the second dorsal base. Nakamura's (1935) illustration of an adult *A. profundus* (pl. 1, figure 1) indicates that the dorsal rear tip extends posterior to the anal base, but his illustration of a fetal *A. profundus* (pl. 2, figure 3) shows that it is about opposite the anal origin. Cadenat (1956, figure 3B-C) illustrated two fetuses of *A. superciliosus* from Senegal, one with the rear tip over the rear end of the anal base and the other with it over the middle of the anal base. Bass et al. (1975, figure 19) pictured a South African specimen of *A. superciliosus* with the tip about over the anal origin. Our 356 cm TL specimen (SHG-A2) from Florida also had the rear tip about opposite the anal origin, but her two fetuses have the rear tip slightly anterior to the anal fin origin. Two specimens from the eastern Central Pacific (SM-9-II-64-3 and LJVC-0355), respectively, had the tip anterior to the anal origin and over the first third of the anal base.

Accounts of bigeye threshers such as those of Springer (1943), Bigelow and Schroeder (1948), Cadenat (1956), Fitch and Craig (1964), Kato et al. (1967), Telles (1970), and Bass et al. (1975), and the specimens examined by us show the pelvic fins to be very large and about the size of the first dorsal fin, but Nakamura's (1935, pl. 1, figure 1) line drawing of an adult female *A. profundus* shows a minute pelvic fin, less than one-fourth of the area of the first dorsal fin. Curiously, the pelvic fins in Nakamura's (pl. 2, figures 3, 4) drawings of a 71 cm fetus of *A. profundus* have the proportions of other bigeye threshers and are about as large in area as the first dorsal fin. Yet Nakamura described the pelvic fins of both adults and fetuses in the same words, "ventral fins moderate" (p. 2, 5). In the absence of pelvic fin measurements in Nakamura's account, we suspect that the unusually small pelvic fins pictured in his adult *A. profundus* may be erroneous and are perhaps due to the difficulties of accurately drawing a large shark, without special techniques and perhaps under trying circumstances (i.e., in a fish market). The drawing of the fetal *A. profundus* seems more accurate and may reflect the writer's ability to study and draw it in his laboratory. Possibly the large adult specimen of *A. pelagicus* sketched by Nakamura (pl. 1, figure 2) was also drawn with undersized pelvics, at least in comparison with the photograph of a specimen by Bass et al. (1975, figure 17), and with photographs and specimens of *A. pelagicus* seen by Compagno. The fetal specimen of "*A. pelagicus*" illustrated by Nakamura (1935, pl. 3) is of no help here as it appears to be a specimen of *A. vulpinus* (unlike the adult).

The supposed differences in the contour of the anterior margin of the first dorsal fin are probably size-related, the contour becoming straighter with increase in size. The adult *A. profundus* pictured by Nakamura (1935) has a nearly straight anterior margin, while in the fetal specimen it is strongly convex. This applies likewise to the 356 cm TL Miami specimen (SHG-A2) of *A. superciliosus* and to the two fetuses taken from her. This change also occurs in *A. vulpinus* (compare the juvenile pictured in Bigelow and Schroeder [1948] with the adult in Bass et al. [1975]) and *A. pelagicus*, as well as some other lamnoid sharks, such as *Isurus oxyrinchus* (Garrick 1967, figure 6).

The lower precaudal pit appears to be variably present or absent in bigeye threshers, as suggested by Bass et al. (1975). The lower pit was present in possibly all of the three adults of *A. profundus*, 332-366 cm TL, studied by Nakamura (1935), though it is not specifically mentioned in his account of a fetal *A. profundus* and not shown in his illustration (pl. 2, figure 1). It was also present in a 372 cm TL adult male from California (CAS-1963-X: 7) studied by Fitch and Craig (1964) but absent in all our Miami specimens and absent in two specimens from the eastern Central Pacific (SM-9-II-64-3 and LJVC-0355). We suspect that the lower precaudal pit is present only in some adult or subadult bigeye threshers, as it has not occurred so far in fetal or very small, free-living specimens. The upper precaudal pit is less well-marked in small specimens than in large subadults and adults.

DESCRIPTIVE NOTES

Proportional measurements of 13 bigeye threshers, including 6 reported by us, are given as proportion of precaudal length in Table 1, rather than total length, as the tail length is apparently quite variable relative to body length. Writers

have previously used precaudal length (Fitch and Craig 1964), total length (Bigelow and Schroeder 1948), and fork length (Stillwell and Casey 1976).

The prominent horizontal head grooves (Figures 3, 4) that are characteristic of *A. superciliosus* are present in all specimens we examined, but are better developed in the large subadults and adults than in the two fetuses taken from SHG-A2. The grooves were not indicated in a 130 cm TL, free-living specimen figured by Bigelow and Schroeder (1948); but we suspect that they were overlooked on this shark although we were not able to examine it. Fitch and Craig (1964) first called attention to these grooves in *A. superciliosus* and noted that similar grooves are also found in teleosts, in the swift, mesopelagic louvars (*Louvarus*) and escolars (*Lepidocybium*). They speculated that the grooves might aid in hydrodynamic flow, thus enabling the bigeye thresher to maneuver more rapidly. Head grooves are absent or poorly developed in other species of threshers.

Another characteristic of the bigeye thresher, at least at sizes above 130 cm TL, are the huge, vertically elongated, fleshy orbits, which are expanded onto the dorsal surface of the head and provide the shark with a dorsal, binocular visual field (Figures 4, 5). The eyes, head grooves, and bulbous, elongated snout of *A. superciliosus* give its head a unique, upward-looking, crested or helmeted appearance. The eyelids (Figure 5) apparently change shape with growth, as our two fetuses, and a 130 cm specimen in Bigelow and Schroeder (1948) have relatively enormous, circular lids without the anteroposterior shortening seen in larger individuals such as the 161 cm immature female pictured by Bass et al. (1975). This change in lid shape is also seen though to a lesser degree in *A. pelagicus*, in which fetuses and small, free-living specimens have circular eyelids and adults more vertically oval lids (Compagno unpubl. obs.).

COLOR

The bigeye thresher is often described as gray (Cadenat 1956; Garrick and Schultz 1963; Bass et al. 1975). Bigelow and Schroeder (1948) stated that the bigeye thresher is "Dark mouse gray above and hardly paler below...," but we suggest that this coloration is true for preserved material and not living or freshly killed specimens. Nakamura (1935) noted that a freshly killed bigeye thresher

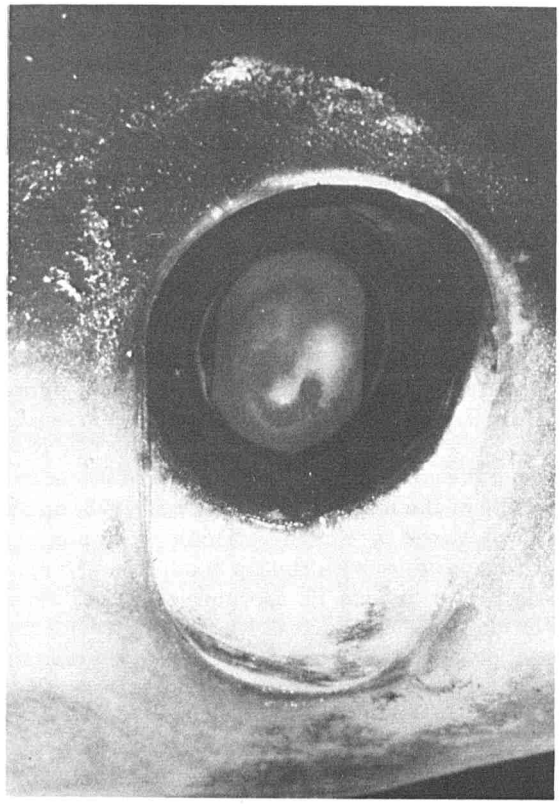

FIGURE 5.—Lateral view of the left eye of *Alopias superciliosus* (SHG-A7) showing the keyhole shape which may be an adaptation for increasing the dorsal binocular fields. The vertical distance between upper and lower eyelid is 101.5 mm. Photo: S. Spielman.

is purple above, and we observed a violet to purplish cast above fading to creamy white below on the body of the 356 cm TL Miami specimen (SHG-A2). S. Kato and I. Nakamura[6] stated that fresh Central Pacific and eastern Atlantic bigeye threshers are purple-brown or gray-brown dorsally, white, grayish or whitish brown below. In the Miami and Central Pacific specimens a metallic silver or silver blue-green sheen was present on the sides at the level of the gills and on the flanks, as in *A. pelagicus* (Bass et al. 1975) and *A. vulpinus* (Compagno unpubl. data). The ventral surface of the paired fins and the caudal fin is oulined in dark gray.

VERTEBRAE

Vertebral counts have been used as an important character in teleost systematics for many

[6]Susumu Kato (see footnote 3) and Izumi Nakamura (see footnote 4), pers. commun. to L. J. V. Compagno, 1978.

years (i.e., Bailey and Gosline 1955) but their importance in shark systematics was recognized only with the surveys by Springer (1964) and Springer and Garrick (1964). We have compiled available vertebral counts for *A. superciliosus* (Table 2), which includes five of our specimens. The counts indicate that bigeye threshers of the eastern Pacific and Indian Ocean have slightly higher caudal and probably higher total vertebral counts than bigeye threshers from the western North Atlantic. Considerable variation is found in caudal counts in *A. vulpinus* from California (230-254, $n = 8$; Compagno unpubl. data) so that larger samples of vertebral counts of *A. superciliosus* from different regions will be needed to confirm possible population differences.

Vertebrae from the monospondylous precaudal region (centra 30-35) were radiographed in a bigeye thresher (LJVC-0355), in longitudinal view to show the calcification pattern. As with most other lamnoid sharks the dorsal, ventral, and lateral spaces of the intermedialia, between the diagonal uncalcified areas of the basalia, are composed of longitudinal calcified plates or radii that are distally bifurcated and interleaved with cartilage (terminology follows Ridewood 1921). In *A. superciliosus* these radii are fewer and less branched than in either *A. vulpinus* or *A. pelagicus*, and are not basally fused into a solid mass as in *A. pelagicus* (Figure 6).

DENTITION

Another quantitative character often used in shark systematics is the number of tooth rows in each jaw. We give dental formulas for 22 bigeye

TABLE 2.—Vertebral counts of *Alopias superciliosus*.

Number[1]	Size cm (TL)	Maturity	Sex	Locality[1]	Counts[1] MP	DP	PC	DC	TC	Source
—	—	—	—	WNA, New York	—	—	102	190±3	295±3	Springer and Garrick (1964)
GH-A6	340	Adult	Male	WNA, Florida			100	203	303	Original
SHG-A2	356	Adult	Female	WNA, Florida	—	—	102	196	298	Original
SHG-A3	241	Subadult	Male	WNA, Florida	—	—	—	191	—	Original
SHG-A7	356	Adult	Male	WNA, Florida	—	—	102	175	[2]278	Original
UMML-8861	—	Fetus	—	WNA, Florida	—	—	102	180	282	Springer and Garrick (1964)
UMML-8861	—	Fetus	—	WNA, Florida	—	—	102	187	289	Springer and Garrick (1964)
MCZ-36155	63	Fetus	Male	WNA, Cuba	—	—	102	181	283	Springer and Garrick (1964)
USNM-197700	369	Adult	Female	ENP, California	—	—	100	204	304	Springer and Garrick (1964)
LJVC-0355	287	Immature	Female	ECP	66	39	105	196	301	Original
—	161	Immature	Male	SWI, S. Africa	—	—	106	202	308	Bass et al. (1975)
—	363	Adult	Male	SWI, S. Africa	—	—	98	—	—	Bass et al. (1975)

[1]Abbreviations: NUMBER: GH, Hubbell collection; LJVC, L. J. V. Compagno collection; MCZ, Museum of Comparative Zoology, Harvard; SHG, Gruber Collection; UMML, University of Miami Marine Laboratory; USNM, United States National Museum of Natural History, Smithsonian Institution. LOCALITY: ECP, eastern-Central Pacific; ENP, eastern North Pacific; SWI, southwestern Indian Ocean; WNA, western North Atlantic. COUNTS: DC, displospondylous caudal centra; DP, diplospondylous precaudal centra; MP, monospondylous precaudal centra; PC, precaudal (MP + DP) centra; TC, total (MP + DP + DC or PC + DC) centra.
[2]Tail of SHG-A7 noticeably shorter; <49% of the total length.

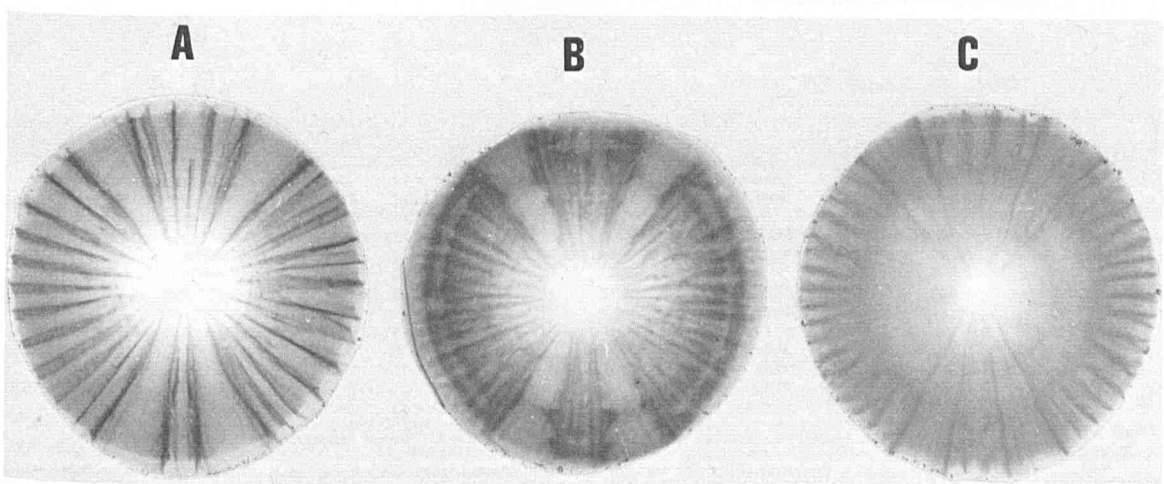

FIGURE 6.—Radiographs in transverse view of the monospondylous vertebral centra of all three *Alopias* species: A, *A. superciliosus*; B, *A. vulpinus*; C, *A. pelagicus*. Note the more simple pattern in *A. superciliosus*. Photo: L. Compagno.

threshers in Table 3, in the form A + B/C + D, where A and B are the numbers of rows in the upper left and right jaw halves, and C and D the numbers in the lower left and right jaw halves. Also presented are total tooth row counts, in the form Ab/Cd, where Ab is the total number of upper rows and Cd the total lower rows. For dental formulas of 10 bigeye threshers the ranges, means, and standard deviations are 11-12 (11.7±0.5) + 10-12 (11.5±0.7)/10-12 (10.8±0.8) + 10-12 (10.7±0.7). For the same number of total counts the ranges, means, and standard deviations are 20-24 (23.2±1.1)/20-24 (21.5±1.4).

Using Applegate's (1965) and Compagno's (1970) terminology for tooth row groups, the dentition of the bigeye thresher can be divided into two rows of anteriors (A) at either side of the symphysis and 8-10 rows of lateroposteriors (LP) on either side and postlateral to them (in both upper and lower jaws, Figure 7). An expanded formula for the bigeye thresher is:

LP9-10 + A2 + A2 + LP8-10/LP8-10
+ A2 + A2 + LP8-10 (Figure 8).

Anterior teeth of threshers differ from lateral and posterior teeth in having narrower crowns relative to their height and more erect cusps, but they are less well differentiated in *Alopias* than in lamnids, odontaspidids, mitsukurinids, and pseudocarchariids. The lateroposterior teeth of the bigeye thresher vary towards the dental band (gradient monognathic heterodonty), becoming smaller, lower relative to width, more oblique-cusped, more convex along the premedial edge, and more deeply notched in the postlateral edge, with the postlateral blade tending to change into cusplets on the more postlateral rows. Posterior teeth are not well differentiated from laterals in the bigeye thresher and are not separated out in the expanded formula; upper intermediate teeth and upper and lower symphyseal teeth are absent.

Teeth in the upper jaw are not markedly different in shape from lowers, but are slightly larger. All teeth are compressed, sharp-edged, and bladelike, and have narrow-based cusps.

Bass et al. (1975) suggested that in *A. superciliosus* the teeth of females are somewhat broader than those of males, reflecting gynandric or sexual heterodonty (dental sexual dimorphism; see Compagno 1970). Comparison of the jaws of an adult female with those of a large adult male (Figures 9, 10) shows that males have teeth (especially the anteriors and more premedial lateroposteriors) with higher, more flexed cusps than females. Gruber and Hubbell[7] (unpubl. data) have examined a number of jaws from male and female

[7]Gordon Hubbell, Director, Candron Park Zoo, Miami, FL 33149.

TABLE 3.—Dental formulas of *Alopias superciliosus*.

Number[1]	Size cm (TL)	Maturity	Sex	Locality[1]	Formula	Total	Source
MCZ-	—	—	—	WNA, Cuba	11 + 11/10 + 10	22/20	Bigelow and Schroeder (1948)
SHG-A2	356	Adult	Female	WNA, Florida	12 + 12/12 + 12	24/24	Original
SHG-A3	290	Subadult	Male	WNA, Florida	12 + 12/11 + 11	24/22	Original
SHG-A4	159	Immature	Male	WNA, North Carolina	12 + 12/11 + 11	24/22	Original
SHG-A5	320	Subadult	Female	WNA, Florida	12 + 11/11 + 11	23/22	Original
SHG-A6	306	Subadult	Female	WNA, Florida	11 + 11/10 + 11	22/21	Original
SHG-A7	356	Mature	Male	WNA, Florida	12 + 12/11 + 10	24/21	Original
GH-A1	—	—	—	WNA, Caribbean	12 + 12/12 + 12	24/24	G. Hubbell (pers. commun.)
GH-A2	381	Mature	Female	WNA, Florida	11 + 11/11 + 11	22/22	G. Hubbell (pers. commun.)
GH-A3	312	Subadult	Female	WNA, Florida	11 + 12/10 + 11	23/21	G. Hubbell (pers. commun.)
GH-A4	342	Mature	Male	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
GH-A5	—	—	—	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
GH-A6	340	Mature	Male	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
MBP-	269	Adult	Male	ENA, Portugal	12 + 12/10 + 10	24/20	Telles[2] (1970)
CBAT-	—	—	—	ESA, Angola	11 + 10/11 + 10	21/21	Telles[2] (1970)
—	400	Adult	Female	ENA, Senegal	10 + 8/ 9 + 8	—	Cadenat[3] (1956)
—	161	Immature	Female	SWI, S. Africa	12 + 11/11 + 11	24/22	Bass et al. (1975)
LACM-F-89	—	—	—	WNP, Japan	12 + 11/11 + 11	23/22	B. Welton (pers. commun.)
CAS-1963-X	372	Adult	Male	ENP, California	11 + 11/10 + 10	22/20	Original[4]
LACM-F-88	378	Adult (?)	Male	ENP, California	12 + 12/10 + 11	24/21	B. Welton (pers. commun.)
LACM-F-90	305	Immature	Female	ENP, California	12 + 12/11 + 11	24/22	B. Welton (pers. commun.)
LJVC-0355	287	Immature	Female	ECP	12 + 12/12 + 11	24/23	Original

[1]Abbreviations: CAS, California Academy of Sciences, San Francisco, Calif.; CBAT, Centro Biologia Aquatica Tropica, Lisbon; GH-A, Gordon Hubbell, *Alopias* jaw collection; LACM, Los Angeles County Museum of Natural History, California; LJVC, L. J. V. Compagno collection; MBP, Museu Bocage, Portugal; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts; SHG-A, Samuel H. Gruber, *Alopias* collection. WNA, western North Atlantic; ENA, eastern North Atlantic; ESA, eastern South Atlantic; SWI, southwestern Indian; WNP, western North Pacific; ENP, eastern North Pacific; ECP, eastern Central Pacific.
[2]We doubt that this was a mature adult.
[3]Cadenat (1956) mentioned that 1 or 2 teeth were missing on each side of this specimen.
[4]Fitch and Craig (1964) give 9 + 10/10 + 10 for this specimen, but we found that they apparently missed 3 rows of upper teeth.

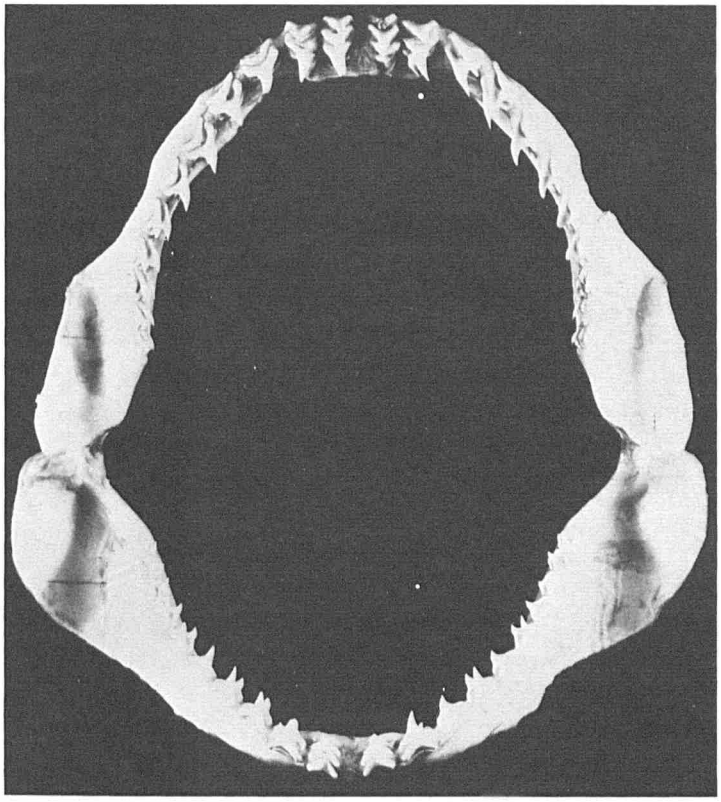

FIGURE 7.—Jaws of 372 cm TL male *Alopias superciliosus* (CAS-Acc. 1963-x: 7). Note the elongated, flexed cusps on the anterior and some lateral teeth which are characteristic of males and shown in detail in Figure 10. Photo: L. Compagno.

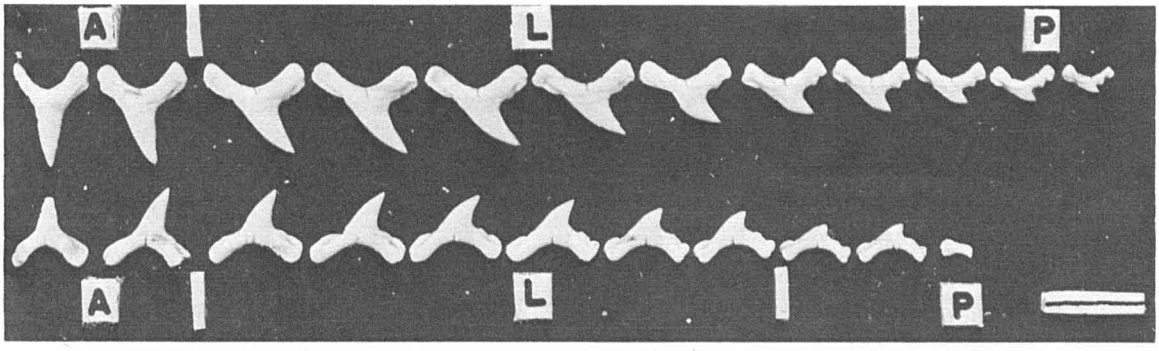

FIGURE 8.—Tooth set from the right side of the jaw of a 278 cm TL female *Alopias superciliosus* (LJVC-0355). A, anterior teeth; L, lateral teeth; P, posterior teeth. Scale mark at lower right is 1 cm. Photo: L. Compagno.

bigeye threshers and have documented this sexual heterodonty. Gynandric heterodonty is found in other sharks (see for example Springer 1964; Springer 1966), and in its ordinary form (teeth larger, more erect, and with larger cusps and often less well developed cusplets in males than in females) may aid the male in holding the female during courtship and copulation (Gruber and Myrberg 1977).

DENTICLES

Samples of skin from the back below the first dorsal fin were removed from three species of threshers (*A. superciliosus*, *A. pelagicus*, and *A. vulpinus*), dried, and examined under the scanning electron microscope to show the structure of their dermal denticles. The lateral trunk denticles of all three species are similar in

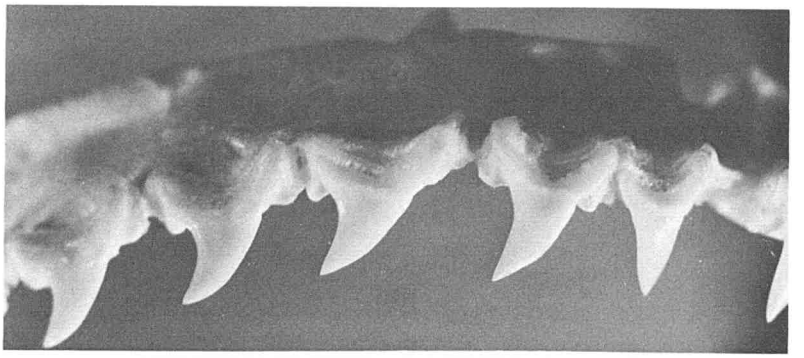

FIGURE 9.—Upper right anterior teeth 1 through 5 of a 381 cm TL female *Alopias superciliosus* (GH-A2) showing that the typical female shape is broader, less sinuous and somewhat flatter than its male counterpart. The cusp height of the 3d anterior tooth was 1.20 cm. Photo: F. Karrenburg.

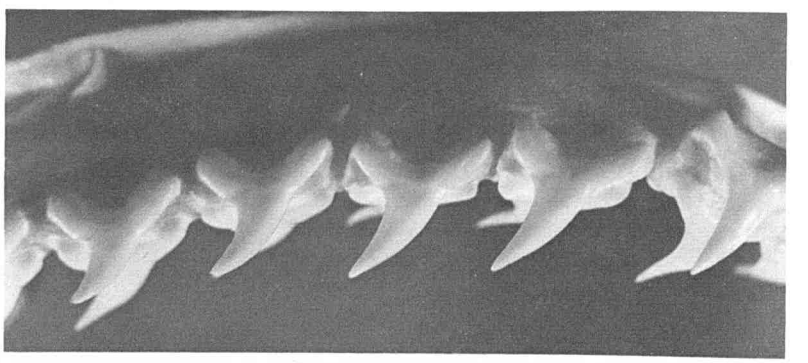

FIGURE 10.—Upper right anterior teeth 1-5 of a 342 cm TL male *Alopias superciliosus* (GH-A4). These elongate, narrrow flexed cusps are typical of males and when compared with the female above one can clearly see the gynandric heterodonty in this species. The cusp height of the third anterior tooth was 1.45 cm. Photo: F. Karrenburg.

having an oval or nearly circular crown with a strong medial ridge and posterior cusp, a pair of weaker lateral ridges, and variably developed lateral cusps (Figure 11). The crowns of these denticles are connected to their bases (buried in the skin) by tall, broad pedicles. The specimen of *A. pelagicus* examined has smaller denticles with less prominent lateral cusps than the two specimens of *A. superciliosus* and three *A. vulpinus* examined.

SIZE

The bigeye thresher grows to a large size as an adult; the heaviest reliably reported was a 284.5 kg female from Cuba (Guitart Manday 1975). Grey (1928) stated that one from New Zealand weighed 640 lb (290 kg). Using the length-weight equation for bigeye threshers given in Guitart Manday (1975)

$$W = 0.1825 \times 10^{-5} L^{3.448534} \text{ or}$$
$$L = 3.448534\,(W/1.825 \times 10^{-6})^{1/2}, \qquad (1)$$

where W is weight in kilograms and L is precaudal length in centimeters; the weight of Guitart Manday's largest bigeye thresher corresponds to a precaudal length of 237 cm and a total length of about 452 cm, while that of Grey's 290 kg bigeye thresher corresponds to a precaudal length of 240 cm and a total length of about 458 cm. Total lengths for these specimens were estimated by averaging the ratio of dorsal caudal and precaudal lengths for 10 specimens of large subadult and adult threshers in Table 1, 270-460 cm TL, which gives $L_{\text{caudal}} = 0.908 \pm 0.079$ SD.$L_{\text{precaudal}}$.

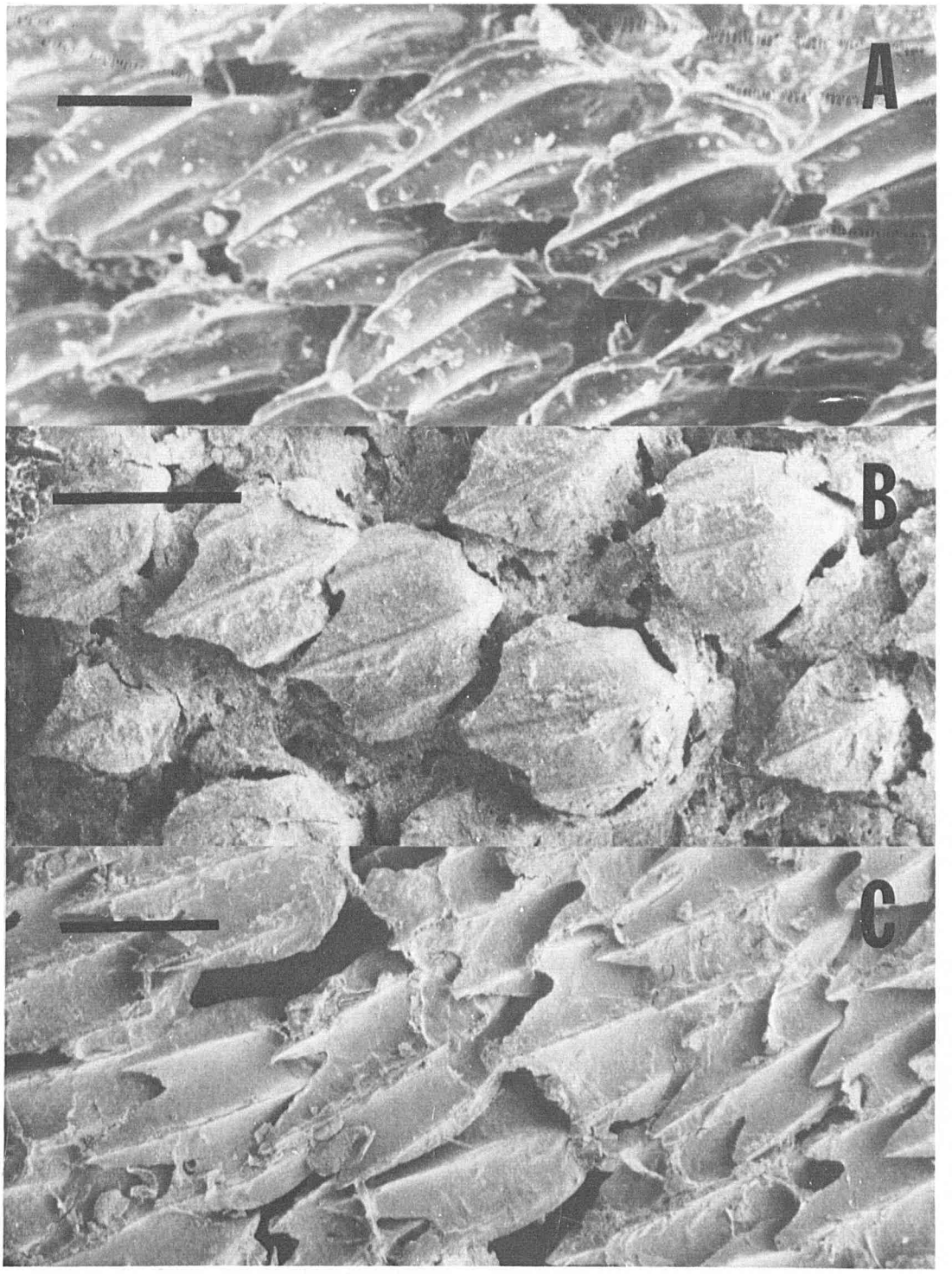

FIGURE 11.—Scanning electron micrographs of thresher lateral trunk denticles. Scale lines (black horizontal bars) equal to 0.1 mm. A, *Alopias superciliosus*, SHG-A2, 356 cm TL adult female. B, *A. pelagicus*, LJVC-0414, 192 cm TL immature male. C, *A. vulpinus*, LJVC-0234, 206 cm TL immature female. Photos: S. Gruber, L. Compagno.

Caudal lengths are variable in the sample mentioned, so that adding and subtracting one standard deviation from the average ratio of caudal to precaudal lengths gives $L_{caudal} = 0.829$ or 0.987 $L_{precaudal}$. Total length given as $L_{total} = L_{precaudal} + 0.908$ (0.829 or 0.987) $L_{precaudal}$. Using the minimum and maximum ratios of caudal to precaudal lengths, Guitart Manday's largest bigeye thresher was estimated to be 434-471 cm long, and Grey's 439-477 cm long.

A bigeye thresher (SHO-16-2) reported by I. Nakamura (pers. commun. to S. Kato[8]) had a precaudal length of 227.2 cm, a dorsal caudal length of 233.5 cm, and a total length (precaudal + dorsal caudal lengths) of 460.7 cm; using Guitart Manday's equation, its precaudal length corresponds to a weight of about 245 kg. Stillwell and Casey (1977) and Cadenat (1956) also measured bigeye threshers of about 4 m TL. However, most adults, especially males, fall below 350 cm TL.

Bigelow and Schroeder (1948) reported a 5.5 m TL bigeye thresher from Cuba, apparently based on data associated with a set of jaws in the collection of Museum of Comparative Zoology, Harvard. It is likely, as Bass et al. (1975) pointed out, that this figure considerably overestimates the maximum size of this shark. The tooth size from Bigelow and Schroeder's (1948) "5.5 m" specimen corresponds almost perfectly to that of a 363 cm TL shark examined by Bass et al. (1975), so that, in the absence of contrary data, the total length of Bigelow and Schroeder's largest specimen should be revised downward to about 360 cm.

The average size of adult females of *A. superciliosus* is larger than males. Guitart Manday (1975) stated that females are always the largest bigeye threshers caught on longlines, many exceeding 250 kg, and averaging 203.8 kg in a sample of eight adults; but males are much smaller, averaging 185.3 kg in a sample of four adults. Stillwell and Casey (1976) reported that 25 females ranged up to 399 cm TL, while the 15 males they examined never exceeded 352 cm TL. However, the mean length of females was only 5 cm greater than that of males. This similarity in average total length resembles a condition noted by Springer (1960) for certain carcharhinid and sphyrnid sharks, in which a small percentage of females in a population grow to a much larger size than most of their sex and species.

[8]Susumu Kato (see footnote 3), pers. commun. to L. J. V. Compagno, 1978.

The longest known adult male bigeye thresher shark was 378 cm TL (LACM-F-88),[9] from off California, and the smallest was 270 cm, from off Portugal (Telles 1970). The longest known adult females are the two of 399 cm TL and about 400 cm TL reported by Stillwell and Casey (1976) and Cadenat (1956) from the western North Atlantic and Senegal, and the shortest two of 355-356 cm from the western North Atlantic (Stillwell and Casey 1976; specimen from Miami, Fla.). The heaviest bigeye thresher reported (Guitart Manday 1975), was a female, presumably mature, and probably over 4.3 m TL (see above).

The smallest free-living bigeye thresher reported to date is a 130 cm TL immature male from off Cuba (Bigelow and Schroeder 1948). Guitart Manday (1975) reported a 144 cm TL free-living individual that weighed 6.7 kg, while Stillwell and Casey (1976) captured a 155 cm TL immature male. We report here a specimen from North Carolina of 159 cm TL. Bigelow and Schroeder (1948) and Osipov (in Gubanov 1979) suggested that parturition occurs in *A. superciliosus* when the fetus attains 64 cm TL, but Cadenat (1956), Nakamura (1935), and Gubanov (1979) reported fetuses respectively at 68, 73, and 100 cm long. Bass et al. (1975) suggested that the most likely size at birth is 100-103 cm TL. Gubanov noted the possibility that larger females might give birth to larger offspring, a possible explanation of the discrepancy of size at birth given by various authors.

Based on available data, the maximum accurately measured total length for *A. superciliosus* is 4.61 m, and weight, 284.5 kg, with total lengths of 4.7-4.8 m and weights of 290+ kg not unlikely. Apparently this species averages smaller in size than at least some populations of *A. vulpinus*, in which females in the western North Atlantic reach 479-549 cm TL; the maximum size for *A. vulpinus* may be over 609 cm TL (Bigelow and Schroeder 1948; Bass et al. 1975).

AGE AND GROWTH

The age of a bigeye thresher has never been determined by standard methods such as analysis of vertebral rings. However, age and growth in other shark species have been investigated by several techniques (i.e., Petersen method, tagging, growth in captivity) and found generally to

[9]Grey's (1928) 4 m bigeye thresher appears to be a male in the published photograph, but the article does not mention the sex.

conform to the von Bertalanffy (1938) model (Wass 1973; Stevens 1975). Holden (1974, 1977) has shown that it is possible, as a first approximation, to obtain parameters for a von Bertalanffy growth curve independently of field data. Using a modification of von Bertalanffy's (1938) basic equation, Holden (1974) rearranged the formula as follows:

$$l_{t+T} - l_t = (L_{max} - l_t)(1 - e^{-KT}) \qquad (2)$$

where l_t = length at fertilization
l_{t+T} = length at birth
T = gestation period
L_{max} = maximum observed size
K = growth constant.

We have evaluated these parameters from data given in the literature, and solution of this equation, including generation of the growth curve, was accomplished with computer programs written by Allen (1966).

If Stillwell and Casey (1976) are correct in their assertion in that males mature at 300 cm TL compared with 350 cm TL for females, then time to maturity can be estimated from Figure 12. Assuming parturition in the bigeye thresher at 100 cm (lower curve, Figure 12), then males mature in a little over 3.5 yr while females become sexually active (i.e., reach 350 cm TL) between their fifth and sixth year. Bigeye threshers measuring 4 m TL would be about 10 yr old and the biggest members of this species (480 cm) would be at least 20 yr old.

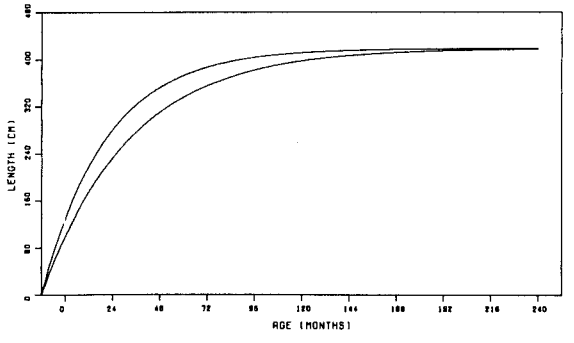

FIGURE 12.—Von Bertalanffy-type growth curve for *Alopias superciliosus*. The curve is based on parameters of: maximum total length of 420 cm; length at birth 100, 130 cm TL and gestation period of 12 months. The lower and upper curves represent a growth rate in sharks born at 100 and 130 cm TL, respectively. If this model is correct, males mature in approximately 3½ yr compared to 4½ yr for females. The largest of these sharks would be between 10 and 20 yr of age.

It should be reemphasized that this curve is but a first approximation since the assumptions of the von Bertalanffy model may not actually be satisfied by growth of the bigeye thresher. Thus this curve cannot substitute for field data and must be validated by independent methods.

No previous attempts have been made to determine the age of a bigeye thresher. We stained a few vertebral centra of the bigeye thresher LJVC-0355—287 cm TL female—from the monospondylous precaudal region (centra 30-31, 33, as counted from the head) using the alizarin technique of LaMarca (1966) and the silver nitrate technique of Stevens (1975), to demonstrate growth rings on the inner surfaces of the calcified double cones. This technique revealed a central clear area surrounded by at least eight dark rings concentric with and interspaced by lighter rings (Figure 13). The clear area is about 14.1 mm across, and the double cone 25.2 mm in horizontal diameter in centrum 33. It is not known if the dark rings are annual (added once a year), but presumably the central clear area represents the maximum size of the fetal vertebral centrum.

A comparison of Figure 12 with the data given in Figure 13 shows that if the rings are annual, the von Bertalanffy model considerably underestimates rate of growth in the bigeye thresher. However, we are not aware of any published work showing that growth rings in the centrum of warm-water sharks are annual. Several temperate water elasmobranchs lay down annual growth rings but the (temperate water) basking shark, *Cetorhinus maximus*, forms a pair of rings each year (Tanaka and Mizue 1979). So in the absence of some confirming data giving the interval between ring formation, we cannot estimate the age of the bigeye thresher by counting circuli in the vertebral centrum.

Beside the length-weight relations developed by Guitart Manday (1975) and Stillwell and Casey (1976), the only other growth data are deductions made by Stillwell and Casey concerning allometry. Based on measurements from 12 adult bigeye threshers (8 males, 4 females) they concluded that head, eye, and mouth dimensions become proportionally shorter as growth proceeds. In contrast, the height of the first dorsal, interspaces between fins, and clasper length all increase. Some differences between males and females in proportional growth were noted in their study.

Data from several sources (Nakamura 1935; Springer 1943; Bigelow and Schroeder 1948;

FIGURE 13.—Centrum 33 from a 287 cm TL, 59 kg female *Alopias superciliosus* (LJVC-0355) treated with the silver nitrate technique of Stevens (1975). This method intensifies the calcified growth rings as shown, for easy visualization. At least 8 and probably 11 dark rings surround a central clear area of 14.1 mm. The external diameter of centrum 33 is 25.2 mm. Photo: L. Compagno.

Cadenat 1956; Bass et al. 1975), but primarily Stillwell and Casey (1976), indicate that males mature at about 300 cm TL, while females mature at a larger size, probably 350 cm TL. To these data are added the observation that all males over 307 cm TL examined by Stillwell and Casey had calcified, elongate claspers, and mature sperm in the epididymis. They noted that a smaller male of 289 cm TL had nearly mature testes.

In contrast, of 13 females examined by Stillwell and Casey (1976), only those over 350 cm TL possessed mature ova and enlarged ovaries. These data support earlier studies indicating that mature (pregnant) females are all larger than about 350 cm TL. Guitart Manday (1975) noted that only the largest females captured in the Cuban fishery were pregnant. Finally, the size of our pregnant female (356 cm TL) agrees with the concept of female maturity at about 350 cm TL.

ABUNDANCE, DISTRIBUTION, AND HABITAT

The early literature on the bigeye thresher seemed to indicate that it is a widely distributed but rare, subtropical to tropical pelagic shark inhabiting relatively deep water. For example, Telles (1970) believed that only 20 bigeye threshers had ever been recorded. Nakamura (1935), Bigelow and Schroeder (1948), Cadenat (1956), and others suggested that *A. superciliosus* was a deepwater species, and Springer (1963) reported that it never approached to within a few hundred meters of the surface. More recent data based on longline catches point to localized concentrations of this species in considerable numbers, especially in the western North-Central Atlantic from off the north coast of Cuba and off North Carolina (Guitart Manday 1975; Stillwell and Casey 1976), and in the northwestern Indian Ocean (Osipov 1968; Gubanov 1972). Enough occur off Cuba to have yielded a total commercial catch for 1975 of 3,400 kg (Guitart Manday[10]). In the western Central Atlantic the species occurs north at least to off New York (Schwartz and Burgess 1975; Stillwell and Casey 1976) and apparently is relatively eurythermic. In the western North Atlantic bigeye threshers are usually caught in waters with the surface temperature from 16° to 25° C, and with longlines fished at a depth from slightly below the surface to 65 m depth where the temperature falls to 14° C (Stillwell and Casey 1976).

The bigeye thresher may be able to maintain body temperatures higher than ambient water temperature (Carey et al. 1971), which may equip it for incursions into colder water. However, like the shortfin mako, *Isurus oxyrinchus*, which is also partly homeothermic, the bigeye thresher is apparently a species preferring warm temperate to tropical waters. From available distributional data the bigeye thresher does not occur in cold temperate waters and apparently has a narrower temperature and latitudinal range than either the blue shark, *Prionace glauca*, or the great white shark, *Carcharodon carcharias*, both of which range from cold temperate seas into the tropics.

[10]Dario Guitart Manday, Institute of Oceanology, Academy of Science of Cuba, Havana, Cuba, pers. commun. to S. H. Gruber, 24 January 1978.

Alopias superciliosus is both neritic and pelagic. Kato et al. (1967) and S. Kato (footnote 8) noted that the bigeye thresher is commonly caught on high-seas longlines far from land, but capture data in Cadenat (1956), Strasburg (1958), Fitch and Craig (1964), Osipov (1968), Guitart Manday (1975), and Stillwell and Casey (1976) indicate that concentrations of the species commonly occur near land and that it occasionally enters coastal and even shallow waters. It also occurs near the bottom in relatively deep water (Nakamura 1935; Fitch and Craig 1964), has been captured at the surface offshore (the Miami specimen), and is known to range to a depth of about 500 m. Prey items taken from stomachs of the bigeye thresher include both midwater and benthic species indicating the habitats visited by the shark (see below for details).

Figure 14 is a map of the known distribution of *A. superciliosus*, including approximate numbers collected. The range as presently known includes the western North Atlantic from off New York to Florida, the Bahamas, Cuba, and the Caribbean to at least Venezuela (Springer 1943; Bigelow and Schroeder 1948; Fitch and Craig 1964; Mago L. 1970; Schwartz and Burgess 1975; Stillwell and Casey 1976; Compagno 1978). It occurs in the western South Atlantic from off southern Brazil (Sadowsky and Amorim 1977); the eastern Atlantic from off Portugal, Madeira, Senegal, possibly Guinea or Sierra Leone, Angola, and the Mediterranean (Lowe 1840; Cadenat 1956, 1961; Williams 1968; Telles 1970; and authors' specimens); the western Indian Ocean from off South Africa, Madagascar, and the Arabian Sea (Fourmanoir 1963; Osipov 1968; Gubanov 1972; Bass et al. 1975); the western Pacific from off Taiwan, possibly Japan, New Caledonia, and New Zealand (Grey 1928; Nakamura 1935; Fourmanoir and Rancurel 1972; and authors' specimens); the central Pacific, north and south of the Hawaiian Islands and between Panama and the Marquesas Islands (Strasburg 1958; S. Kato footnote 8); and the eastern Pacific from off southern California (Fitch and Craig 1964) and in the Gulf of California (Applegate et al. 1979).

REPRODUCTION

Intrauterine development in thresher sharks is ovoviviparous. As in the lamnids and odontaspidids, fetal bigeye threshers are apparently

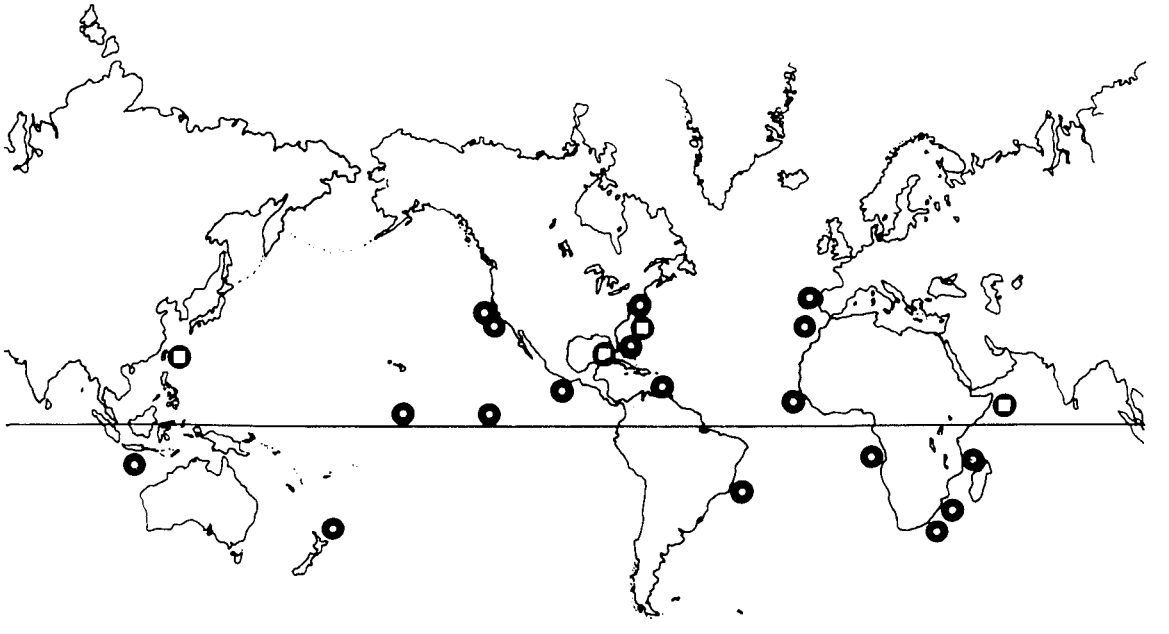

FIGURE 14.—Distribution of *Alopias superciliosus*. The 16 filled circles represent stations where fewer than 10 bigeye threshers were collected. The four filled squares show stations where this shark has been taken in commercial numbers. Several more Bahamian locales reported by the U.S. National Marine Fisheries Service were not included because the scale on the map is too coarse. This chart does not include much of the Soviet or Japanese longline catch, but extends the known distributon of *A. superciliosus* to the Mediterranean and New Zealand.

ovophagous. Horny infertile eggs are deposited in each oviduct and the embryo consumes these as development proceeds (Cadenat 1956; Gubanov 1972). Figures 15 and 16 show the embryos and the infertile eggs removed from the oviducts of specimen SHG-A2. Curiously, Gubanov (1979) claimed that the eggs of the bigeye thresher differ considerably from those of the common thresher. However, the eggs shown in our Figure 11b appear almost exactly like those shown in Gubanov's figure 1. Yet the eggs shown in Gubanov's figure 1 were said to be characteristic of the common thresher only. A possible explanation of this discrepancy is that Gubanov's figures 1 and 2 actually represent nutritive and fertile eggs, which might be similar in both species.

Most sharks do not acquire functional teeth until they reach a size close to that at parturition. However, both of our immature fetuses (Figure 15) had fully functional teeth, which is quite unusual among sharks. Perhaps the early formation of teeth aids the fetal bigeye thresher in cannabalizing potential siblings. Yet, fetal pelagic thresher *A. pelagicus* does not acquire functional teeth until it reaches considerably larger size than our two bigeye thresher fetuses.

As is often the case in odontaspidids and lamnids, the bigeye and other threshers produce only two well-developed offspring per pregnancy. While Guitart Manday (1975) mentioned one or two embryos in each oviduct the usual number is a single fetus in each oviduct (Nakamura 1935;

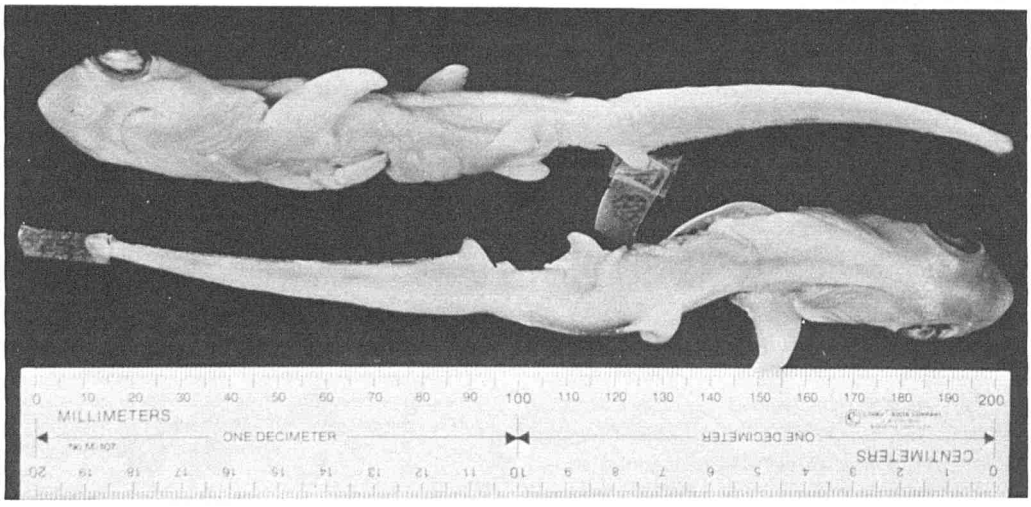

FIGURE 15.—Embryos removed from the specimen shown in Figures 1 and 2. As shown, they are approximately 206 mm TL and are probably in the first trimester of development. Photo: S. Gruber.

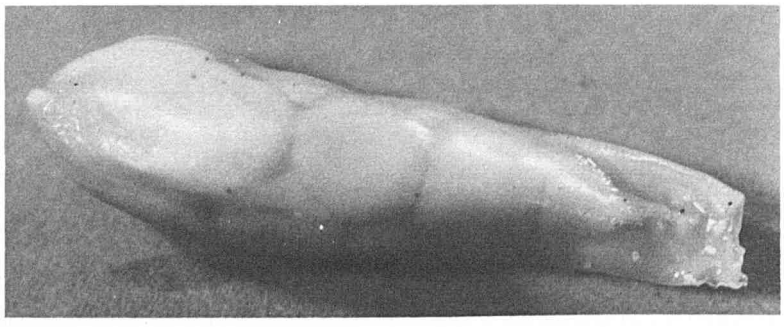

FIGURE 16.—Infertile, horny eggs of *Alopias superciliosus* (SHG-A2) found in the oviducts along with the embryos. Thresher embryos are thought to consume the nutritive, yolk-filled eggs during development (ovophagy). Photo: F. Karrenburg.

Springer 1943; Cadenat 1956; etc.). Since the gestation period is probably 12 mo (Holden 1974), the reproductive capacity of this shark may be said to be relatively low.

Guitart Manday (1975) reported that most large females throughout the year contained embryos. If the reproductive pattern is similar to that of the common thresher (Gubanov 1972, 1979), then mating occurs throughout the year. Not enough data are available for the bigeye thresher to demonstrate seasonality. However, most of the large females examined have been pregnant.

FOOD

Stomach contents of bigeye threshers have been reported in only three studies: Fitch and Craig (1964) obtained some 5 kg of Pacific whiting, *Merluccius productus*, a benthic teleost, from the stomach of their specimen; Bass et al. (1975) reported that a bigeye thresher captured in the protective shark nets along the beach at Durban (hardly deep water) had recently eaten another elasmobranch, perhaps also fouled in the net; Stillwell and Casey (1976) examined the stomachs of 35 bigeye threshers and found over 50% to have food remains—squid was the most common food, composing some 66% of the stomach contents. Other prey included remains of pelagic teleosts, such as scombrids, alepisaurids, clupeids, and istiophorids.

Stomach contents recovered from one of our specimens (SHG-A2) consisted of several eye lenses and two pairs of squid beaks. These were identified by Gilbert Voss[11] as ommastrephid remains, probably from the genus *Illex*. Voss mentioned that *Illex* made up 75-80% of the cephalopod diet of the swordfish, *Xiphias gladius*, caught in the Florida Current.

The food of the bigeye thresher thus consists of small to moderate benthic and pelagic teleost fish, crustaceans, and cephalopds, and as presently known, is restricted to a few species.

PREY CATCHING

According to Springer (1961) the upper caudal lobe of *Alopias* (along with the armed rostrum of the pristiophorids *Pristiophorus* and *Pliotrema*) are the only structures of modern sharks functioning specifically for killing prey (jaws and teeth being used for other purposes in addition to feeding). However, it has not been universally accepted that the tail of thresher sharks is actually used in feeding. In an interesting discussion of this controversy, Lineweaver and Backus (1969) noted that the ichthyologists J. T. Nichols and C. M. Breder doubted that the tail was sufficiently rigid or muscular to kill prey.

Grossly overdeveloped appendages such as the claw of the male fiddler crab, *Uca* sp., often evolve along with elaborate courtship signals, and it is possible that the elongated tail of *Alopias* evolved in the context of a social or species recognition signal. However, field observations support Springer's (1961) concept of the thresher's tail as an offensive weapon for prey capture. One of the first such observations is that of Blake-Knox (1866), who claimed that a common thresher, *A. vulpinus*, used its caudal fin to kill a loon and then consumed the bird. Coles (1915) reported common threshers as feeding in shallow water by throwing fish into their mouth with their caudal fins. Allen (1923) gave a similar detailed description of the feeding behavior of a common thresher. Grey (1928) observed common threshers following baits trolled from a sport fishing boat and striking at the bait with their tails.

Recently, indirect but compelling observations from longline fisheries confirm that threshers use their tail in feeding. Gubanov (1972) reported that 97% of all three thresher species captured were foul-hooked in the upper caudal. This agrees with Stillwell and Casey (1976), who noted that several bigeye threshers were tail-hooked and that two or more baits were often recovered from a captured bigeye thresher's stomach. This suggested to Stillwell and Casey as well as to Gubanov that the live baits were dislodged from the hooks probably by blows from the thresher's caudal fin.

EXPERIMENTAL STUDIES

The bigeye thresher has occasionally been the subject of study unrelated to fishery, natural history, or taxonomic observation. Carey et al. (1971) measured the muscle temperature of a number of freshly captured sharks and teleosts and concluded that, among others, the bigeye thresher is warm-bodied. They described a single vascular heat exchanger which probably makes the storage of heat possible in this species.

[11]Gilbert Voss, Professor of Biology and Living Resources, RSMAS, University of Miami, Miami, FL 33149, pers. commun. to S. H. Gruber, December 1979.

Okada et al. (1969) removed the brain from *A. superciliosus* and compared it with the brains of a number of other sharks in an effort to discern a common structural pattern which might be related to ecology or predatory behavior. They concluded that brain morphology correlates with ecology and behavior rather than with taxonomic similarity since distantly related shark species sharing similar behavior and habitat shared in the development of a number of homologous brain structures. According to Okada et al. the optic tectum of *A. superciliosus* is well developed compared with that of the common thresher and mako, *Isurus*. Perhaps most noteworthy was the size of the cerebellum, which was even larger than the telencephalon. The reverse is usually found (Figure 17). The brain of a 3 m *A. superciliosus* weighed approximately 30 g, some one-third heavier than that of a 3.6 m *A. vulpinus*. The heavier brain of *A. superciliosus* reflects the prominence of the optic lobes. Speculations as to the significance of these structures would be premature because of the paucity of physiological data on shark brains.

Two further studies have used the bigeye thresher as a laboratory subject. Bundschuh and Ballester (1971) tested the serum of 10 shark species including the bigeye thresher for antibodies against human saliva, erythrocytes, and serum. Natural antibodies against human proteins were reported, although the significance of these antibodies was unclear. Finally, Gabeva and Kovaleva (1976) described morphological changes associated with spermatogenesis in the bigeye thresher, and the role of the follicular epithelium of the testes in the process.

The dearth of experimental studies on the bigeye thresher points to the difficulty of obtaining fresh material for detailed analysis. Because of this and because the bigeye thresher has never been kept in captivity, it does not ordinarily make a suitable subject for experimental or detailed study.

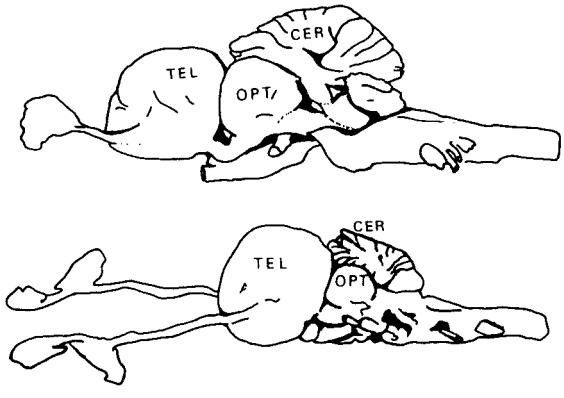

FIGURE 17.—Lateral views of the brains of *Alopias superciliosus* (upper) and *Carcharhinus* sp. (lower) after Okada et al. (1969). Brains have been sketched with telencephalon (TEL) the same size. Note that the optic tectum (OPT) and cerebellum (CER) are relatively much larger in the bigeye thresher.

PARASITOLOGY

The known parasite fauna of the bigeye thresher has been given in five papers: three on gut cestodes and two on external copepods. Dailey (1969) erected the order Litobothridea to include some unusual tapeworms he found in massive infections of the spiral valve of two bigeye threshers collected in southern California. Two worms, *Litobothrium alopias* and *L. coniformis*, were described as new species. Kurochkin and Slankis (1973) further described *L. daileyi* and *Renyxa amplifica* from the spiral valve of bigeye threshers also from the Pacific Ocean. Thus, it would appear that this group of cestodes has evolved along with the Alopiidae and may be restricted to that family. Finally, Heinz and Dailey (1974) reported two cestodes from the stomach of the bigeye thresher: *Sphyriocephalus viridis* and *S. pelorosoma*, the latter a new species.

The only other parasites reported from the bigeye thresher were two new species of copepods: *Pagina tunica* and *Bariaka alopiae*. *Pagina tunicata* was removed from the body surface while *B. alopiae* was taken from the gills (Cressey 1964, 1966). Cressey collected the type-specimen of *B. alopiae* from bigeye threshers captured off Madagascar and South America at stations separated by almost 20,000 km. Because of this great distance Cressey speculated that *B. alopiae* has a specific affinity for the bigeye thresher.

These few species probably do not represent a complete catalogue of parasites infecting the bigeye thresher, but rather are noteworthy examples. If the bigeye thresher is similar to other shark species, it harbors a diverse assemblage of macroparasites including cestodes, nematodes, leeches, copepods, and amphipods.

COMMERCIAL IMPORTANCE

Commercial exploitation of threshers, especially the bigeye thresher, follows two fishery

patterns. The first, exemplified by methods of the Japanese and Soviet high-seas pelagic fleet, involves highly mobile longline fishing vessels which actively seek out concentrations of predatory fish associated with small-scale oceanographic processes, such as plankton concentrations, and local circulation patterns (Osipov 1968; Gubanov 1972). While tunas are the major objective of these fisheries, sharks and billfishes are an important bycatch.

Osipov (1968) noted that, in the northwestern Indian Ocean, local circulation patterns produce distinct areas of plankton and fish concentrations in which one or two predatory species predominate. These associations are dynamic both in species composition and time. Thus the concentration of any species in such an area is both spatially and temporally discontinuous and falls off rapidly outside the enrichment cells. As a consequence, fishing vessels must move continuously in the wake of fish schools as concentrations form and disperse.

Osipov (1968) identified three such areas in the Indian Ocean off the Republic of Somalia. In one of these plankton-enriched areas carcharhinid sharks predominated, while the bigeye thresher was the most plentiful shark in another. Taken overall, however, the bigeye thresher amounted to only 12% of the total shark catch. Thus, while the distribution of *A. superciliosus* on the high seas is patchy, they make up a reasonable proportion (over 10%) of the shark catch, at least seasonally.

The bigeye thresher is also commercially important in the short-range pelagic fishery operating off the northwestern coast of Cuba (Guitart Manday 1975, footnote 10). However, the pattern of distribution is quite different from that in the Indian Ocean. Longlines are set year round in the Cuban fishery and 11 shark species are caught in commercially exploitable numbers. Of 11 species, the bigeye thresher is the third most abundant and amounted to some 20% by weight of the total 1973 shark catch. The Cubans have been fishing this species more effectively in recent years and have doubled their catch between 1971 and 1975.

Seasonal distribution is also evident in the Cuban catch records (Guitart Manday 1975). The poorest catches are in March-June. The catch of bigeye threshers gradually increases over the summer and peaks in the fall around September-October, to decline again in the winter.

Bigeye threshers occasionally enter the market when they are caught by sport and commercial anglers fishing for swordfish off southeastern Florida. Since both species are caught at night near the surface in the Florida Current it is not surprising to see several bigeye threshers each year captured by commercial longliners or during the swordfish tourneys. Incidentally, many of these animals are foul-hooked as described above, perhaps reflecting a preference to attack bait with their caudal fins. However, in this fishery the hook is usually attached to a nylon monofilament leader specifically to avoid catching sharks. Thus the low incidence of mouth hooked bigeye threshers could reflect losses due to biting through the leader.

Finally, this species has been captured a few times in gill nets set at moderate depth, to 160 m (Fitch and Craig 1964; Telles 1970; Bass et al. 1975).

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IMPAIRMENT OF THE CHEMOSENSORY ANTENNULAR FLICKING RESPONSE IN THE DUNGENESS CRAB, *CANCER MAGISTER*, BY PETROLEUM HYDROCARBONS

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ABSTRACT

After exposing Dungeness crabs in a continuous-flow system to seawater contaminated with Prudhoe Bay crude oil (0.27 parts per million), we observed the behavior of crabs presented with a clam extract. In response to seawater solutions of clam extract, Dungeness crabs change antennular orientation and increase antennular flicking rate. After 24-hour exposure and with oil still present, the proportion of crabs showing the changes in antennular behavior indicating detection of chemical food cues was significantly reduced. In contrast, the proportion showing chelae probing was not. Within 1 hour after return to clean water the antennular response recovered. Such rapid recovery indicates that the chemosensory impairment probably did not derive from structural damage to sensory cells but does not indicate which of several other possibilities was the most likely mechanism. By impairing the chemosensory antennular flicking response of Dungeness crabs, petroleum hydrocarbons could cause crabs some difficulty in finding food.

For marine organisms, disruption of chemoreception by oil is viewed as both likely and of important ecological consequence (Blumer 1969; Olla et al. 1980). Chemosensory disruption by various petroleum hydrocarbons and oil fractions has been reported in snails (Jacobson and Boylan 1973; Hyland and Miller 1979), lobsters (Atema and Stein 1974), and in shore crabs (Takahashi and Kittredge 1973). In some of these early studies the exposure regime was not well defined and did not always compare well with the length and level of exposure likely to be encountered in oil spills. Here we report on the ability of the Dungeness crab, *Cancer magister* Dana, to detect and respond to a food extract after 24-h exposure to seawater contaminated with Prudhoe Bay crude oil in a continuously flowing seawater system.

The antennules of many decapod crustaceans are a site for chemoreception of water-borne chemical cues (Hazlett 1971a). Antennular flicking may be analogous to sniffing in vertebrates (Fuzessery 1978) and enhances the ability of crustaceans to detect changes in their chemical environment (Schmitt and Ache 1979). Behavioral observations of antennular flicking rate indicate that detection of a clam extract occurs at 10^{-15} g/l in the blue crab, *Callinectes sapidus* (Pearson and Olla 1977), and at 10^{-10} g/l in the Dungeness crab (Pearson et al. 1979).

To determine whether exposure to petroleum hydrocarbons impaired this acute detection ability, we exposed Dungeness crabs to oil-contaminated seawater for 24 h, presented them with a clam extract in the presence of the oil-contaminated seawater, and recorded the percentages of crabs showing the changes in antennular behavior indicative of detection and of those showing the chelae probing indicative of food searching. At 24 h and 48 h after stopping the flow of oil-contaminated seawater, we retested the crabs to determine the time necessary for recovery of detection ability. Because this first experiment indicated rapid recovery, we performed a similar second experiment in which we presented the clam extract to Dungeness crabs 1 h after stopping the flow of contaminated seawater.

MATERIALS AND METHODS

Animal Collection and Maintenance

Dungeness crabs trapped in the Strait of Juan de Fuca, Wash., were held under the conditions described by Pearson et al. (1979). Seawater temperatures during the two experiments were 8.9 (±2.7 SD)° C (n = 16) and 9.2 (±0.5)° C (n =

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16); salinities, 31.8 (±0.4)‰ (n = 5) and 32.0 (±0.0)‰ (n = 4); and dissolved oxygen 7.6 (±0.7) mg/l (n = 16) and 8.0 (±0.3) mg/l (n = 9). Clumps of the blue mussel, *Mytilus edulis*, and the littleneck clam, *Protothaca staminea*, provided an ad libitum diet.

Experimental Apparatus

We coupled the oil delivery system developed by Vanderhorst et al. (1977), and used extensively by Anderson et al. (1979, 1980), to the chemosensory testing apparatus of Pearson et al. (1979). Seawater contaminated with Prudhoe Bay crude oil was delivered to 20 of the 40 chemosensory testing chambers from dripper arms situated along manifolds connected to the oil delivery system. Contaminated water entered each exposure chamber at 0.1 l/min while clean water entered at 0.9 l/min. Control chambers received clean water at 1.0 l/min. Seawater entered each chamber through a glass funnel connected to a slotted inlet tube within the chamber. Teflon[3] tubes carried seawater solutions of the clam extract to the funnels from burets calibrated to deliver 20 ml within 15 s. Previous dye studies of Pearson et al. (1979) showed that the maximum concentration of an introduced solution within a chamber occurs 10 s after introduction and is 0.011 (±0.003) times the concentration of the introduced solution.

The delivery system produced oil-contaminated seawater that was largely a water-soluble fraction with some finely dispersed droplets. The chemical composition of this oil-contaminated seawater has been well characterized by Bean et al. (1978) and reported by Anderson et al. (1980). Here we sampled seawater in the testing chambers by the resin column absorption technique of Bean et al. (1978) and analyzed the samples by infrared (IR) spectrophotometry. The data of Bean et al. and Anderson et al. show the correlations between the values determined by IR and the concentration of specific hydrocarbons determined by other methods for the same system. To determine how rapidly hydrocarbon concentrations dropped after stopping the flow of oil-contaminated water in the second experiment, we supplemented IR analyses with analyses for monoaromatic hydrocarbons by a helium gas partitioning technique modified from McAuliffe (1971).

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

Experimental Solutions

The experimental solutions were seawater solutions of freeze-dried clam extract (FDCE) of littleneck clam prepared following Pearson et al. (1979). Stock solutions averaging 1.89 (±0.12) g FDCE/l (n = 6) for the first experiment and 2.06 (±0.22) g FDCE/l (n = 5) for the second were refrigerated and used within 5 d. A 10^{-6} dilution of the stock FDCE solution was made 1 h before testing with seawater freshly filtered through a 0.4 μm membrane. An aliquot of the filtered seawater used for dilution was used as the control solution. All solutions were held in a water bath at ambient seawater temperature.

Procedures

After the oil delivery system had been operating for several days and the hydrocarbon concentrations measured, a single Dungeness crab was added to each of the 20 exposure and 20 control chambers. Chemosensory testing was synchronized to begin and end within either a rising or falling tide and after 24-h exposure to oil-contaminated seawater. In the first experiment, the FDCE solutions were presented with oil-contaminated seawater still flowing through the chambers. Each crab was presented with either one of two dilutions of FDCE or a control of filtered seawater. After correction for dilution within a chamber, these FDCE concentrations were 10^{-2} and 10^{-8} g/l. The choice of dilution and the order of presentation were randomized except that active crabs and those with retracted antennules were passed over. The observer did not know the identity of any solution. An individual crab was observed for 60 s prior to introduction of experimental solution, and the antennular flicking rate and other behavior recorded. The observer depressed a switch of an event counter for each flick of one antennule. The solution (20 ml) was then introduced and observation continued for another 60 s from onset of introduction.

The criteria of Pearson et al. (1979) were used to score the behavior. Detection was indicated when a crab abruptly changed antennular orientation and increased antennular flicking rate so that the ratio of the rate after solution introduction to that before was 1.50 or higher. Previous observations indicate that the a priori probability that such an increase in antennular flicking is spontaneous, rather than in response to the solution, is $<5\%$

(Pearson et al. 1979). The onset of food searching was indicated when a crab probed the substrate with its chelae or exhibited the capture response described by Pearson et al. (1979).

To examine recovery of detection ability, we stopped the flow of oil-contaminated water after the first presentation of FDCE. Clean seawater then entered the chambers at 0.9 l/min. After 24 h and 48 h both exposed and control crabs were again presented with experimental solutions and their behavior observed and scored.

Because the first experiment indicated rapid recovery, we wished to see if such recovery was quick as 1 h and, therefore, repeated the exposure phase of the first experiment. Instead of presenting FDCE with oil-contaminated water still present, we turned off the contaminated water and presented the FDCE 1 h later. The start and finish of exposure for individual crabs was staggered to achieve this 1-h clearance of oil from the chambers.

Statistical Analysis

The experiments were run until 28-33 crabs had been tested under each experimental condition. The numbers of crabs detecting and not detecting the various experimental solutions were totaled for exposed and control conditions. Although data is presented as the percentage of crabs detecting the FDCE, chi-square analysis was done on 2 × 2 contingency tables of the number of crabs detecting or not detecting under control or exposed conditions. Data for crabs showing chelae probing were treated similarly.

RESULTS

Hydrocarbon Concentrations

During the first experiment, where the clam extract was presented in the presence of oil-contaminated seawater, the total hydrocarbon concentrations by IR analyses were 0.27 (±0.04) ppm (n = 22) during the 24-h exposure and 0.013 (±0.004) ppm (n = 6) 24 h after the oil-contaminated water was stopped. During the second experiment, where the clam extract was presented 1 h after stopping the oil-contaminated seawater, the total hydrocarbon concentration by IR averaged 0.34 (±0.07) ppm (n = 10). Also, in the second experiment after 1 h the concentration of monoaromatic hydrocarbons (Table 1) fell to 0.008 times the exposure level.

TABLE 1.—The concentrations (parts per billion) of monoaromatic hydrocarbons in the testing chambers. Determined by helium gas partitioning, n = 4.

	Hydrocarbon concentrations			
	During 24 h of continuous flow		1 h after flow stopped	
Hydrocarbon	$\bar{X}$	SD	$\bar{X}$	SD
Benzene	50.1	10.8	0.13	0.24
Toluene	85.0	12.7	.16	.31
Ethylbenzene	13.8	2.8	.74	.95
m- plus *p*-Xylene	38.0	5.2	.94	1.36
o-Xylene	19.5	3.4	.90	1.22
Total trimethylbenzenes	40.6	11.9	<.01	
Total	247.0	34.7	1.98	3.76

Impairment and Recovery of Chemosensory Detection

After 24-h exposure to and still in the presence of oil-contaminated seawater, the percentage of exposed crabs detecting the clam extract was about half that of control crabs (Table 2). In contrast, the percentage of crabs probing with chelae did not differ significantly between control and exposed conditions (Table 3). Of the exposed crabs that probed the substrate with their chelae after presentation of 10^{-2} g FDCE/l, 48% (n = 25) did so without the normally preceding increase in the antennular flicking rate to above the criterion ratio of 1.50. One control crab (3%, n = 31) probed with the chelae without the normal increase in the antennular flicking rate. For crabs showing chelae probing, the antennular flicking rate ratio was significantly higher for control individuals (median = 2.36, range = 1.46-17.50, n = 31) than for exposed individuals (median = 1.56, range = 0.76-6.82, n = 25; median test, χ^2 = 9.19, df = 1, P = 0.998). Previously, no Dungeness crab (n = 89) presented with high levels of clam extract (10^{-3} to 10^{-6} g/l) showed chelae probing without first increasing the antennular flicking rate (Pearson et al. 1979).

Recovery of detection ability occurred rapidly. In the first experiment the percentage of crabs detecting FDCE at both levels did not differ between control and exposed conditions for both 24 h and 48 h (Table 2). In the second experiment, where the FDCE was presented 1 h after the flow of oil-contaminated seawater was stopped, again the percentage of crabs detecting did not differ significantly between control and exposed conditions (Table 4).

Whereas the antennular response to the clam extract was reduced under exposure and recovered after return to clean water, the basic rate of

TABLE 2.—Percentage of Dungeness crabs detecting the clam extract (FDCE) after exposure to continuously flowing seawater contaminated with Prudhoe Bay crude oil.

FDCE (g/l)	Treatment	After 24-h exposure				After 24 h in clean water				After 48 h in clean water			
		No. tested	Detecting (%)	χ^2	P	No. tested	Detecting (%)	χ^2	P	No. tested	Detecting (%)	χ^2	P
10^{-2}	Control	32	97	16.0	0.999	37	95	1.18	0.723	31	97	1.96	0.838
	Exposed	30	53			31	87			31	87		
10^{-8}	Control	34	32	3.46	.937	38	42	.05	.177	31	36	1.06	.697
	Exposed	31	13			33	39			31	48		
Control	Control	18	17	.40	.473	17	35	.13	.282	16	40	1.97	.840
	Exposed	20	25			22	41			17	18		

TABLE 3.—Percentage of Dungeness crabs probing with the chelae upon presentation of a clam extract (FDCE) after exposure to continuously flowing seawater contaminated with Prudhoe Bay crude oil.

FDCE (g/l)	Treatment	After 24-h exposure				After 24 h in clean water				After 48 h in clean water			
		No. tested	Probing (%)	χ^2	P	No. tested	Probing (%)	χ^2	P	No. tested	Probing (%)	χ^2	P
10^{-2}	Control	32	97	2.18	0.860	37	84	0.114	0.265	31	84	2.20	0.862
	Exposed	30	87			31	81			31	68		
10^{-8}	Control	34	6	.329	.434	38	5	.395	.470	31	0	1.02	.687
	Exposed	31	10			33	9			31	3		
Control	Control	18	0	.924	.664	17	0	.793	.627	16	6	1.10	.705
	Exposed	20	5			22	4			17	0		

TABLE 4.—Percentage of Dungeness crabs responding to a clam extract (FDCE) presented in clean water 1 h after 24-h exposure to oil-contaminated seawater.

FDCE (g/l)	Treatment	No. tested	Crabs detecting			Crabs chelae probing		
			%	χ^2	P	%	χ^2	P
10^{-2}	Control	28	96	0.002	0.040	89	0.952	0.671
	Exposed	30	97			80		
10^{-8}	Control	33	42	.551	.542	0	1.118	.710
	Exposed	30	33			3		
Control	Control	19	37	.681	.591	0		
	Exposed	13	23			0		

antennular flicking was not affected by exposure. The antennular flicking rate during the minute before introduction of the clam extract did not vary under exposure, control or recovery conditions over both experiments (median test, $\chi^2 = 2.62$, df = 7, $P = 0.08$). The overall grand median flicking rate was 33 flicks/min ($n = 653$). The median antennular flicking rate for resting Dungeness crabs was previously found to be 30 flicks/min (Pearson et al. 1979).

DISCUSSION

Whereas our exposure regime was low, brief, and well-characterized compared with most of the oil effects studies to date, we must clarify the circumstances to which our exposure is applicable. We exposed Dungeness crabs for 24 h to oil-contaminated seawater (0.27 ppm total hydrocarbons by IR) in which dissolved monoaromatic hydrocarbons (0.247 ppm) predominated. Our system produced this oil-contaminated seawater by continuous mixing of fresh oil with flowing seawater (9° C) followed by separation of floating oil and diversion of nonfloating mixture to the exposure chambers (Vanderhorst et al. 1977).

For a study of its kind we believe our exposure regime to be the best characterized to date, but the exposure regime is not representative of all, or perhaps even most, oil spill situations. Concentrations of total oil in the water ranging from 0.1 to 1.0 and lasting several days have indeed been reported (Grahl-Nielsen 1978; Calder and Boehm in press), but in such cases detection of substantial amounts of alkane (saturate) hydrocarbons indicated that an unknown but substantial amount of oil was emulsified, i.e., present as droplets. Because only 2% of the total hydrocarbons in our oil-contaminated seawater were saturates (Anderson et al. 1980), our exposure regime did not mimic situations where emulsified oil and high proportions of saturate hydrocarbons exist. The chemosensory effects of emulsified oil remain to be studied. Our results are most applicable to situations where dissolved monoaromatic hydrocarbons predominate in the water column.

When oil is spilled, monoaromatic hydrocarbons usually do not attain high concentrations in the water column but rather are rapidly lost by evaporation (McAuliffe 1977a, b). During the last 3 d of a 21-d platform spill in the Gulf of Mexico McAuliffe et al. (1975) measured total low molecular weight (C_1-C_9) hydrocarbons in the water column using a gas equilibration method similar

to ours and found concentrations ranging from 0.002 to 0.010 ppm at 5 and 10 m. Near-surface concentrations ranged from a maximum of 0.200 ppm near the platform (230 m) to 0.002 ppm at a distance (1.5 km). About half these C_1-C_9 hydrocarbons, i.e., 0.100 ppm, were the monoaromatics predominating in our oil-contaminated seawater. During four 10.5-barrel experimental spills concentrations of C_2-C_{10} aromatic hydrocarbons ranged from 0.002 to 0.050 ppm at 1.5 m within 20 min after the spill and were not detectable after 1 h (McAuliffe 1977b). Because the low temperature (9° C) of our seawater and perhaps other system properties slow evaporative loss, our system produced oil-contaminated seawater with a monoaromatic concentration 2.5 to 5 times higher than those reported in the water column during spills. While our higher concentration has not been reported, it is conceivable that subsurface leakage of fresh oil from pipelines or sunken vessels into cold water could produce exposures similar to ours.

One example of how cold temperature and other hydrographic conditions may combine to prevent evaporative loss and allow monoaromatic concentrations more persistent and higher than those cited above for oil spills is found in Valdez Arm, Alaska. Because of the stratification of the water column typical of a fjord, effluent from the oil tanker ballast water treatment facility at Valdez does not mix uniformly but instead is confined to a lens near the bottom. The treatment facility releases about 4.5×10^7 l (12×10^6 gal) daily (Lysyj et al. 1979) with average concentrations of monoaromatic hydrocarbons between 5.1 and 6.4 ppm (Lysyj et al. 1979, 1981; Rice et al. 1981). The distribution of monoaromatics in the receiving body was studied by Lysyj et al. (1981) who found the monoaromatics trapped within a narrow (10 m) zone of maximum concentration that spread horizontally 2 to 3 km in a thin pancake shape. Depth of the pancake varied with season from 50 to 65 m and approached the bottom. A monoaromatic concentration of 0.021 ppm was found 2 m off the bottom, and the maximum monoaromatic concentration observed was 0.127 ppm, half of the exposure concentration used here. Our exposure regime then may be most applicable to situations where there is chronic release of monoaromatic hydrocarbons under hydrographic conditions, e.g., low temperatures and stratification of the water column, that prevent evaporative loss.

The observed chemosensory impairment under oil exposure could have derived from several possible mechanisms, structural damage to chemoreceptor cells, anesthesia of chemoreceptors or other neurons, masking of food cue odor by oil, oil-induced changes in motivation, or coating or matting of the sensory hairs of the antennule by oil. The rapid recovery of the antennular flicking response eliminates only direct structural damage to the chemoreceptor cells as a possibility. Cellular damage would have required a recovery period of days whereas other mechanisms, such as masking or anesthesia, would have been rapidly reversible upon return to clean seawater (Johnson 1977). Anesthesia of the chemoreceptor or higher level neurons remains possible because our oil-contaminated seawater contained several aromatic and saturate hydrocarbons known to produce anesthesia or reversible narcosis in barnacle larvae (Crisp et al. 1967). Dungeness crabs do detect the water-soluble fraction of Prudhoe Bay crude oil at 10^{-4} ppm (Pearson et al. 1980) so that masking of the clam extract by the odor of oil was also possible. Odor masking by oil was also suggested by Atema and Stein (1974) as one possible mechanism behind a longer food finding time in the northern lobster, *Homarus americanus*. A change in feeding motivation was also suggested by Atema and Stein, but the observation in our first experiment of no difference between exposed and control conditions in the proportion of Dungeness crabs showing the chelae probing indicative of food searching argues against a change in motivation having occurred here. Antennular flicking enhances the ability of crustaceans to detect changes in the chemical milieu by splaying out the sensory hairs and increasing the passage of stimulative chemicals to the sensory neurons (Schmitt and Ache 1979), and oil might impair chemosensory function by slowing the passage of stimulating chemicals through coating or matting of the sensory hairs. Because our system produced oil-contaminated seawater with only 2% saturate hydrocarbons (Anderson et al. 1980) and thus little oil existed as emulsified droplets rather than dissolved hydrocarbons, we feel that in our system coating of the sensory hairs was not as likely as one of the other mechanisms. In a spill like the *Amoco Cadiz* where large amounts of oil are emulsified by turbulence (Calder and Boehm in press) physical blockage of chemical cues by the coating of sensory hairs is a possibility that needs study. Whereas

our behavioral results indicate direct structural damage to chemosensory cells was unlikely, which of the other mechanisms actually produced the observed chemosensory impairment remains an open question.

Decapod crustaceans have two chemoreceptor systems, one seated in the antennules and another in the dactyls, chelae, and mouth parts (Luther 1930; Case and Gwilliam 1961; Levandowsky and Hodgson 1965; Hazlett 1968, 1971a, b). The observation that after presentation with a clam extract a significant proportion of exposed crabs showed chelae probing without the normally preceding increase in antennular flicking suggests that 24-h exposure to our oil-contaminated seawater depressed the functioning of the antennular system in Dungeness crabs while, at least as far as we can determine, not significantly affecting the dactyl chemoreceptor system. Perhaps longer exposure would have affected the dactyl system.

The practical implication that needs further investigation is how the observed impairment of the chemosensory antennular flicking response would affect food foraging by the Dungeness crab. Whereas the exact role of the antennules in food finding is not fully understood, abundant evidence exists for the involvement of the antennules in food searching. Upon water-borne chemical stimulation, increases in antennular flicking rate precede food searching behaviors in the Dungeness crab (Pearson et al. 1979) and the blue crab (Pearson and Olla 1977). Because the electrophysiological work of Schmitt and Ache (1979) demonstrated that antennular flicking enhances perception of changes in the chemical milieu, increased flicking would presumably further enhance detection of rapid chemical changes. In the spiny lobster, *Panulirus argus*, chemical stimulation of the antennules usually initiated feeding behavior although chemical-tactile stimulation of the dactyl was more effective (Maynard and Sallee 1970). In hermit crabs intact antennules were necessary to sustain feeding behavior when contact with food is not direct and immediate (Hazlett 1968). Ablation of the antennules impaired the ability of the pelagic shrimp, *Acetes sibogae australis*, to follow food scent trails although antennular ablation did not prevent the detection of scent trails (Hamner and Hamner 1977). The ablation experiments of Reeder and Ache (1980) showed that chemosensory input from the lateral aesthetasc hair tufts of the antennules triggers food searching by *P. argus* and guides the spiny lobster to a distant odor source. Our observation of an impaired chemosensory antennular flicking response coupled with the good evidence of antennular involvement in food finding indicated that difficulty in finding food in the presence of petroleum hydrocarbons is a possibility for Dungeness crabs. If the antennular chemoreceptor system is as critical to successful guidance to distant odor sources in the Dungeness crab as the results of Reeder and Ache (1980) showed it is for the spiny lobster, then we particularly need to investigate whether entry to baited traps is affected when dissolved aromatic or other hydrocarbons are present.

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REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE SAND SEATROUT, *CYNOSCION ARENARIUS*[1,2]

PHILIP A. SHLOSSMAN AND MARK E. CHITTENDEN, JR.[3]

ABSTRACT

Cynoscion arenarius females mature at 140-180 mm total length as they approach age I. Spawning occurs from early March through September, but concentrates in a distinct spring period (March-May) and a distinct late summer period (August-September). Spawning occurs in the inshore Gulf of Mexico and coincides with the periodicity of onshore winds and surface currents which probably transport eggs or larvae to estuarine and inshore gulf nurseries. Estuarine nurseries may be most important to late summer spawned groups. The main gulf nursery in the northwestern area is in waters shallower than 18 m. Both spawned groups leave estuarine nurseries in fall to overwinter in the gulf. Late summer spawned groups return to estuaries in midspring but reenter the gulf in August to spawn. Fish average 210-280 mm total length at age I but some were 300 mm. Predicted sizes of late summer fish were 425 mm total length at age II and 574 mm at age III. The largest trawled specimen was 342 mm total length and 99.5% were less than 280 mm. No more than three spawned groups or two year classes occurred at any one time. The typical maximum life span is 1-2 years based on trawl data and possibly as much as 2-3 years for other gear. Total annual mortality rate was 99.79% based on trawling data and appears no lower than 80-90% if maximum lifespan typically is as great as 3 years. *Cynoscion arenarius* can be aged using scales. Total weight-total length, girth-total length, and standard length-total length regressions are presented. Temporal isolation of the two spawned groups produced each year suggests they may be separate populations or species. The life history and population dynamics of *C. arenarius* appear similar to *C. regalis* along the Atlantic coast south of Cape Hatteras, North Carolina. The latter taxon shows zoogeographic change at Cape Hatteras, which needs management consideration.

The sand seatrout, *Cynoscion arenarius* (Ginsburg), is endemic to the Gulf of Mexico (gulf) and ranges from southwest Florida (Roessler 1970) to the Bay of Campeche (Hildebrand 1955). It is one of the most abundant fishes in estuaries and the shallow gulf (Gunter 1945; Christmas and Waller 1973) and is a major component of the industrial fishery landings and shrimp bycatch (Roithmayr 1965; Gutherz et al. 1975).

The life history of *C. arenarius* is essentially undescribed despite its abundance. Food habits have been studied (Darnell 1958; Diener et al. 1974; Moffett et al. 1979), and general material appears in many faunal studies including Franks et al. (1972), Gallaway and Strawn (1974), and Chittenden and McEachran (1976). Much of this information is misleading, however, because the complex life history of this species has not been recognized. Literature on the possibly conspecific *C. regalis* might apply to *C. arenarius*, but their taxonomic status is still in doubt (Mohsin 1973; Weinstein and Yerger 1976). We have referred to *C. arenarius* herein as a species separate from *C. regalis* following Bailey et al. (1970).

This paper describes spawning seasonality, periodicity, and areas, seasonal distribution and movements, age determination, growth, mortality, and total weight-total length, girth-total length, and standard length-total length relations.

METHODS

Sand seatrout were collected monthly along a transect in the gulf off Freeport, Tex. (Figure 1), from October 1977 through September 1979 aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Stations were occupied at depths of 4.5, 7, 9, 14-15, 18, 22, 27, 37, and 46 m. One or two tows were made at each depth (two tows after October 1978), except

[1]Based on a thesis submitted by the senior author in partial fulfillment of the requirements for the MS degree, Texas A&M University.

[2]Technical article TA 16254 from the Texas Agricultural Experiment Station.

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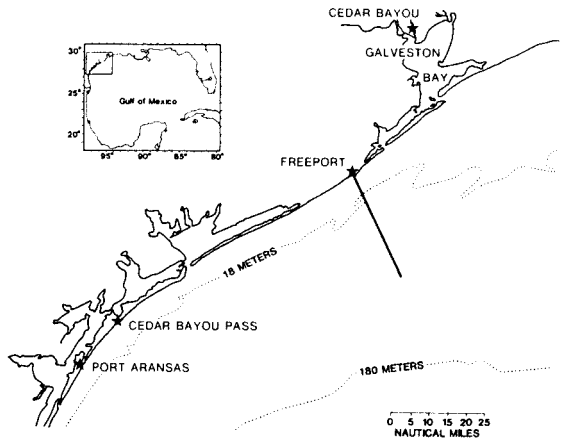

FIGURE 1.—Location of sampling area. Cedar Bayou Pass near Port Aransas is the study location of Simmons and Hoese (1959).

that 8-12 tows were made at 14-15 m and about 24 tows usually were made at 22 m. The 22 m depth primarily was occupied after October 1978.

Cynoscion spp. were culled from the catch, fixed in 10% Formalin,[4] and stored in 70% ethanol before analysis. *Cynoscion arenarius* was separated from *C. nothus* primarily by comparing the anal fin base to the eye width following DeVries (1979). Total length (TL) was measured on all fish. All specimens captured from October 1977 through December 1978, except as noted, were processed and scales were taken to determine age, standard length (SL), girth (G) at the anterior origin of the dorsal fin, total weight (TW), sex, ovary weight (GW) to the nearest 0.1 g, and gonad maturity stage. In June and early December 1978, 300 specimens were randomly selected except that all fish >120 mm TL were processed in June 1978. Scales were taken above the lateral line below the second dorsal fin following procedures for *C. regalis* (Perlmutter et al. 1956), and cellulose acetate impressions were examined using a scale projector. Females and immature fish were assigned gonad maturity stages (Table 1) slightly modified from Kesteven's system (Bagenal and Baum 1971).

Findings based on collections off Freeport were verified by the following materials. Fish were captured from February through December 1977 and in March, June, and July 1978 off Port Aransas, Tex., aboard the Texas Parks and Wildlife Department (TPWD) RV *Western Gulf* using a 13.7 m otter trawl with a 5.1 cm stretched mesh cod end. Stations usually were occupied at 11 m at night, at 7, 15, and 18-24 m during the day; and also at night at 20-22, 29-31, and 38 m from May through October 1977. Additional monthly day collections were made in Galveston Bay, Tex., aboard the TPWD RV *Drum II* from December 1977 through July 1979 using a 6 m otter trawl with a 3.8 cm stretched mesh cod end or a 3 m otter trawl with a 2.5 cm stretched mesh cod end. Finally, collections from July 1978 through July 1979 in Cedar Bayou, Tex., using a 3 m otter trawl with a 2.5 cm stretched mesh cod end were made available by Pridgeon.[5]

TABLE 1.—Description of gonad maturity stages assigned to *Cynoscion arenarius*.

Stage and name	Description
1 Immature	Gonads barely visible or not visible, sexes indistinguishable.
2 Maturing virgin	Gonads very small, sexes distinguished only with magnification.
3 Early developing	Sexes visually distinguished, ovaries occupy <25% of body cavity, individual eggs not visible to the naked eye.
4 Late developing	Ovaries occupy 25-50% of body cavity, eggs clearly visible to naked eye, no translucent eggs.
5 Gravid	Ovaries occupy at least 50% of body cavity, up to 50% of the eggs translucent.
6 Ripe	Ovaries occupy at least 50% of body cavity, >50% of the eggs translucent.
7 Spawning/spent	Ovaries flaccid and at least partly empty, no opaque eggs.
8 Resting	Ovaries fit same description as those in Stage 3, but fish are large enough and were collected at a time when they could already have spawned.

Spawned groups and their year class identities were indicated by specifying the season and year when they hatched, e.g., spring 1978. Spawning periodicities and group identities assume that a total length of 30 mm at 1 mo of age for *C. regalis* (Welsh and Breder 1923) applies to *C. arenarius*. Hatching dates of 1 April and 1 September were assigned to spring and late summer spawned groups to estimate growth and ages.

MATURATION AND SPAWNING PERIODICITY

Results

Cynoscion arenarius matures at 140-180 mm TL as they approach age I and spawn. Gonad devel-

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

[5]B. Pridgeon, Graduate Research Assistant, Texas A&M University, College Station, TX 77843, pers. commun. December 1979.

opment was distinct at 140-200 mm TL as most specimens entered the early developing stage (Figure 2). Fish began to enter the late developing, gravid, or ripe stages at 180 mm TL. These data are supported by regressions of ovary weight on total length (Table 2, Figure 3) in which extrapolated x-intercepts were 120-170 mm TL in the March-September spawning period. Age compositions and sizes presented later indicate that *C. arenarius* matures to first spawn at 12 mo.

Sand seatrout spawn from early March through September. The collections off Freeport of fish 45-55 mm TL in mid-May 1978, 25-80 mm TL in mid-May 1979, and 60-120 mm TL in June and July of 1978 and 1979 (Figure 4) indicate that spawning began in early March and continued through May. This is supported by the collections of: 1) fish 50-75 mm TL off Port Aransas in late May and late June of 1977 and 1978 (Figure 5), 2) fish 50-80 mm TL in Galveston Bay in May 1978 and 1979 (Figure 6), and 3) fish 20-70 mm TL at Cedar Bayou in the period 1 May-2 July 1979 (Figure 7). Spawning also occurred in August and September; because a distinct group of fish 25-60 mm TL were collected off Freeport in late September 1979 (Figure 4), and fish 65-130 mm TL collected in early December of 1977 and 1978 were too small to represent spring spawning. This is supported by the collections of: 1) fish 25-50 mm TL at Cedar Bayou in September 1978 (Figure 7), 2) fish 70-120 mm TL in Galveston Bay in December 1977 and 50-80 mm TL in September-December 1978 (Figure 6), and 3) fish 70-150 mm TL off Port Aransas in February and December 1977 (Figure 5). Spawning did not occur from October through February, because no fish 25-60 mm TL were collected from November through April in the gulf (Figures 4, 5), in Galveston Bay (Figure 6), or at Cedar Bayou (Figure 7).

Gonad maturity and weight data suggest that females spawned from February or March through September in agreement with length frequencies. Two gravid females were collected in mid-February 1978 and late developing, gravid, or ripe stage fish from March through July 1978 and in September 1978 (Figure 8). No spawning occurred from October through December, because all fish then were in resting, maturing virgin, or early developing stages. Gonad size increased during February (Figure 3), reached a peak in April and May, and rapidly declined through July. Increased

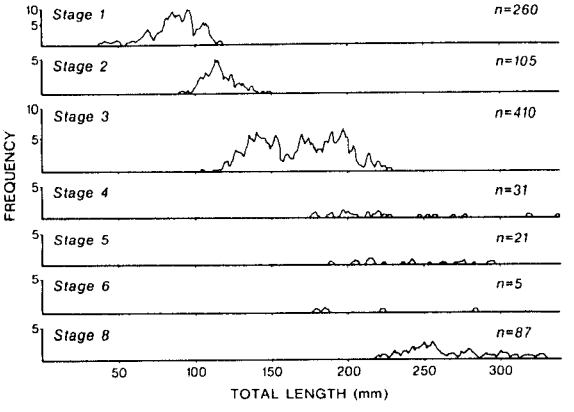

FIGURE 2.—Length frequencies (moving averages of three) of immature and female *Cynoscion arenarius* in maturity stages 1 through 8. Maturity stages are described in Table 1. No stage 7 fish were caught.

TABLE 2.—Analysis for regressions of gonad weight (grams) on total length (millimeters) for female *Cynoscion arenarius* each month, October 1977-December 1978. All regressions are significant at $\alpha = 0.05$.

Date	n	r^2	Equation
October 1977	75	0.759	$GW = -2.4537 + 0.0139\,TL$
November 1977	66	.801	$GW = -1.9946 + .0117\,TL$
December 1977	56	.828	$GW = -1.7127 + .0113\,TL$
February 1978	12	.353	$GW = -4.9977 + .0330\,TL$
March 1978	152	.503	$GW = -6.4522 + .0479\,TL$
April 1978	16	.702	$GW = -13.4576 + .0896\,TL$
May 1978	14	.579	$GW = -27.0498 + .1592\,TL$
June 1978	8	.696	$GW = -4.8433 + .0423\,TL$
July 1978	84	.436	$GW = -1.2198 + .0106\,TL$
September 1978	100	.498	$GW = -3.7836 + .0252\,TL$
October 1978	21	.250	$GW = -1.8382 + .0110\,TL$
December 1978	45	.673	$GW = -1.1223 + .0079\,TL$

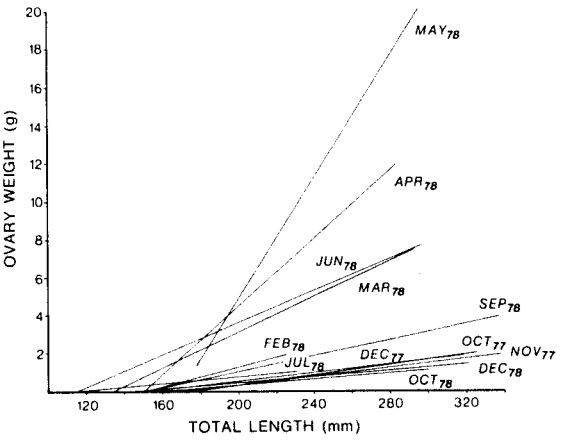

FIGURE 3.—Monthly ovary weight-total length regressions for *Cynoscion arenarius*. The length of each line shows the observed size range. X-intercepts indicate total length at which gonad development begins in what would be a curvilinear regression if smaller lengths were available.

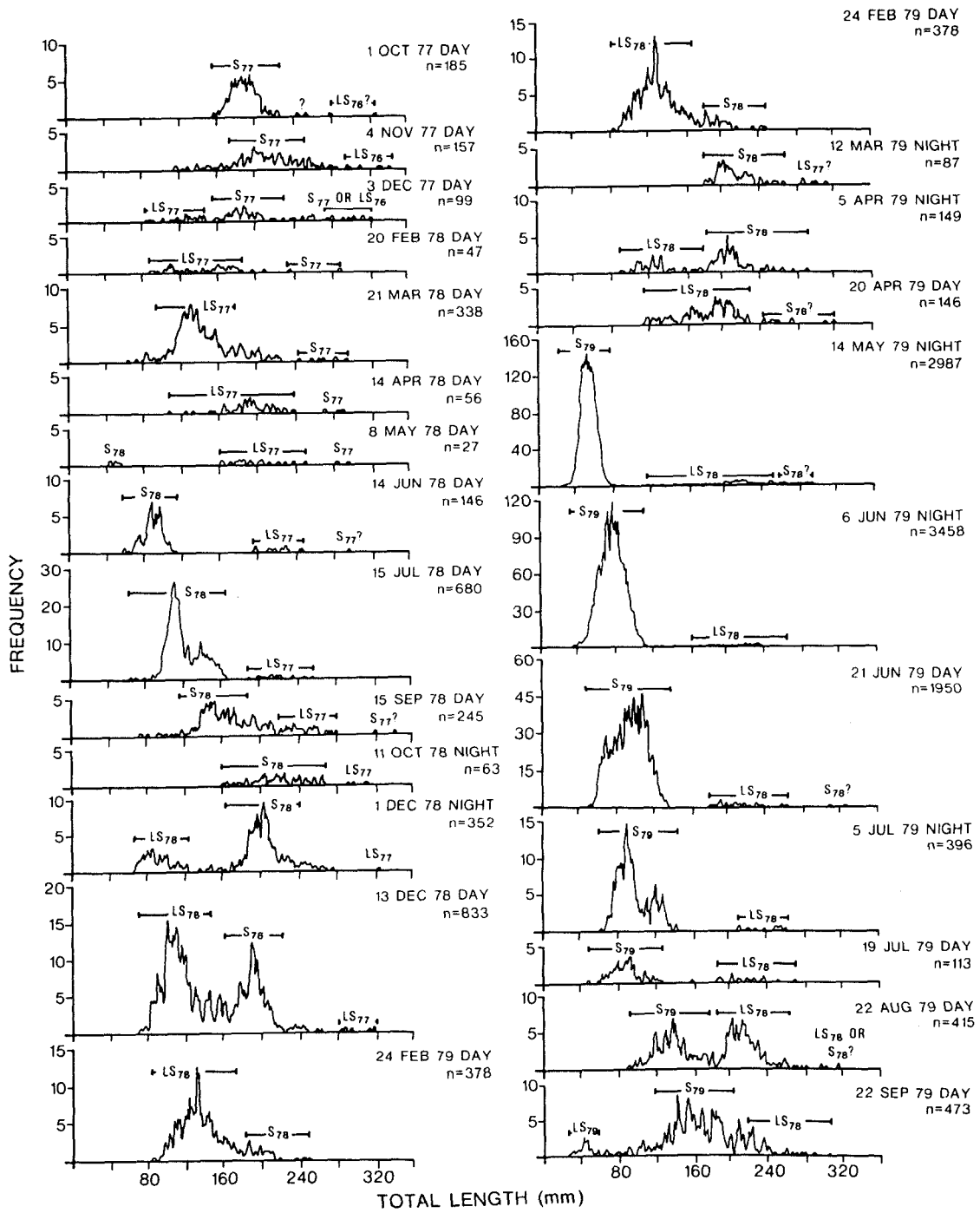

FIGURE 4.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured off Freeport, Tex. Spawned group identity (S = spring; LS = late summer) is often not clear where spawned groups meet.

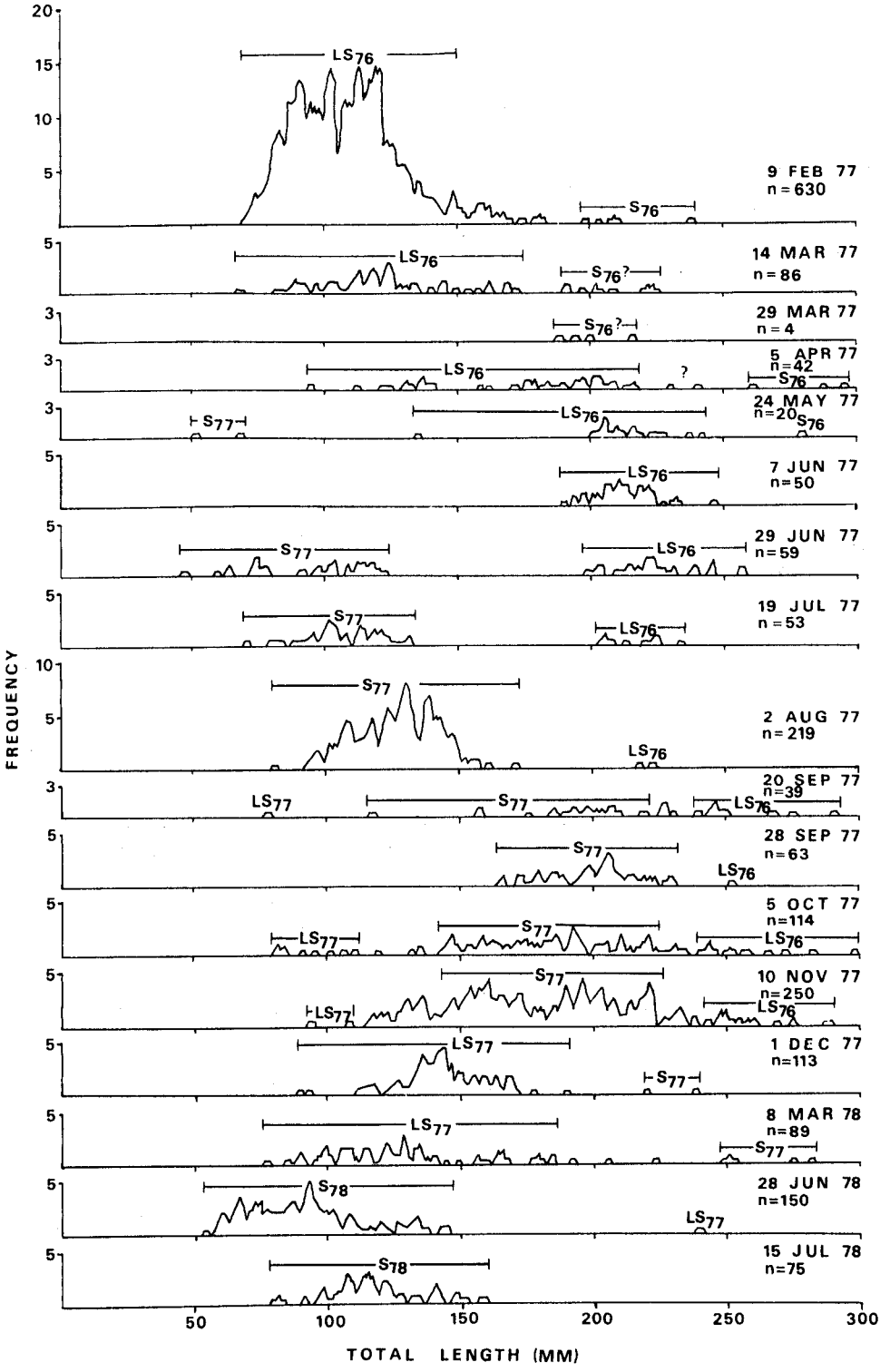

FIGURE 5.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured off Port Aransas, Tex. Spawned group identity (S = spring; LS = late summer) is often not clear where spawned groups meet.

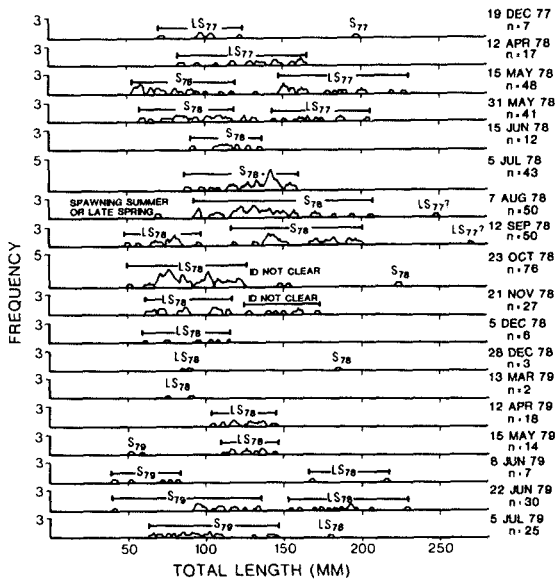

FIGURE 6.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured in Galveston Bay, Tex. Spawned group identity (S = spring; LS = late summer; ID = identity) is often not clear where spawned groups meet. No fish were captured in February and March 1978 and February 1979.

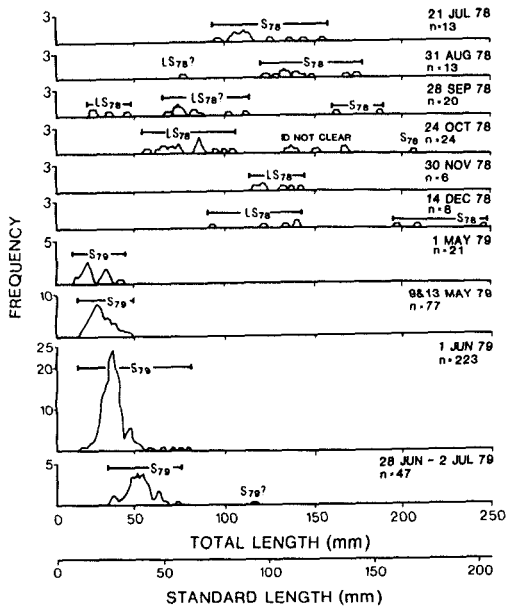

FIGURE 7.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured in Cedar Bayou, Tex. Spawned group identity (S = spring; LS = late summer; ID = identity) is often not clear where spawned groups meet. No fish were captured from January through April 1979.

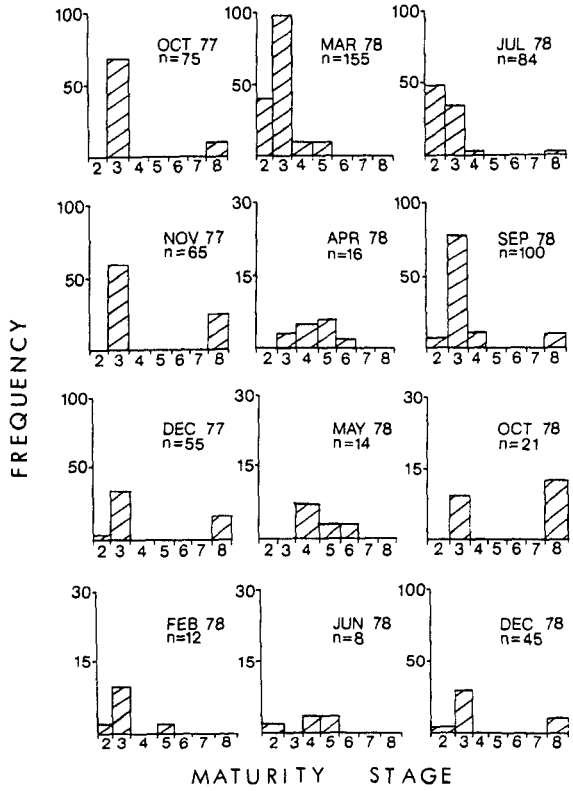

FIGURE 8.—Monthly maturity stages of female *Cynoscion arenarius*. Maturity stages are described in Table 1.

gonad size in mid-September might reflect August-early September spawning.

Although *C. arenarius* spawns over a broad time period, spawning primarily occurs during two discrete periods, a spring spawn from early March through May and a late summer spawn in August and September. Spring spawned fish formed length-frequency modes readily followed in the periods: 1) May-December 1978 and May-September 1979 off Freeport (Figure 4), 2) May-September 1977 and June-July 1978 off Port Aransas (Figure 5), 3) May-September 1978 and May-July 1979 in Galveston Bay (Figure 6), and 4) July-December 1978 and May-July 1979 at Cedar Bayou (Figure 7). Late summer spawned fish formed less distinct modes readily followed in the periods: 1) December 1977-July 1978 and December 1978-August 1979 off Freeport (Figure 4), 2) February-July 1977 off Port Aransas (Figure 5), 3) December 1977-May 1978 and November 1978-May 1979 in Galveston Bay (Figure 6), and 4) September-December 1978 at Cedar Bayou (Figure 7). Little spawning occurred in June and July,

because few fish 25-60 mm TL were captured from late June through August in the gulf (Figures 4, 5), in Galveston Bay (Figure 6), or at Cedar Bayou (Figure 7).

Discussion

Our findings on *C. arenarius* spawning agree with the limited literature. The small size at maturity agrees with Gunter's (1945) capture of a ripe male only 157 mm TL. The broad March-September spawning period found agrees with many studies, including Franks et al. (1972), Gallaway and Strawn (1974), and Moffett et al. (1979). The fact that spawning occurs in distinct spring and late summer peaks has not been recognized clearly but is supported by: 1) the midsummer lull in spawning that Margraf (1978) noted; 2) the late winter-early spring and early fall spawnings that Juneau (1975) observed; and 3) the distinct modes, one formed in spring and one formed in late summer, in size data of Gunter (1945:76), Christmas and Waller (1973, fig. 8), Gallaway and Strawn (1974, table 24), Swingle and Bland (1974:41), Moffett (1975, fig. 19), and Landry (1977, fig. 23, 24). Multiple spawning peaks also have been reported for other *Cynoscion* spp. such as *C. nothus* (DeVries and Chittenden[6]) and *C. regalis* (Daiber 1957 and Harmic 1958 cited in Thomas 1971; Massmann et al. 1958; Merriner 1976).

SPAWNING AREAS, EARLY NURSERIES, AND MOVEMENTS

Results

Sand seatrout of both spring and late summer groups spawn in the inshore gulf. Spawning and nursery areas of spring spawned groups are indicated by distinct size gradients in length frequencies for May-August 1979 (Figure 9B): 1) an estuarine gradient in which the smallest fish were in the upper estuary at Cedar Bayou while larger ones were in Galveston Bay and at 4.5 m in the gulf, 2) a gradient in the gulf in which the smallest fish were at 7-15 m and sizes increased in deeper water, and 3) another gradient in the gulf in which the smallest fish were at 7-15 m but sizes increased in shallower water. Length frequencies from Cedar Bayou, Galveston Bay, and the gulf off Freeport indicate growth continued in May-August 1979 (Figures 4, 6, 7). Therefore, the first size gradient indicates dispersion of larger juveniles down the estuary. The latter two size gradients indicate outward dispersion of larger young and/or eggs and larvae from spawning grounds near 7-15 m in the gulf to deeper and shallower water. Late summer spawned groups also use inshore gulf spawning grounds as indicated by locations of mature fish at spawning time.

Capture locations of mature and ripe adults at spawning time also suggest an inshore gulf spawning area. Many fish of the late summer 1978 group reached age I and entered the gulf in August 1979 (Figure 4), presumably to spawn near the 7-22 m depths where they were captured; none were captured at 4.5 or 55-100 m (Chittenden unpubl. data), but the 27-46 m depth range was not occupied in that cruise. Five ripe stage fish were captured in April and May 1978 at 14-46 m in the gulf. However, it is not clear how far these fish traveled before spawning.

Discussion

The estuarine size gradient that we found could reflect spawning grounds in the upper estuary, or most probably, spawning grounds that encompass the inshore gulf and/or lower estuary. This gradient probably does not reflect an upper estuarine spawning ground, because the early life history of *C. arenarius* is much like that of the Atlantic croaker, *Micropogonias undulatus*. The Atlantic croaker exhibits egg and/or larval transport to the upper estuary from spawning grounds in the sea (Wallace 1940; Haven 1957) and well-documented estuarine size gradients (Gunter 1945; Haven 1957; Reid and Hoese 1958). Moreover, a similar early life history has been suggested for other Sciaenidae, especially *C. regalis* (many references in Wilk 1979).

Our explanation for the estuarine size gradient conflicts with the size pattern in the gulf. The latter pattern suggests outward dispersal of young and/or transport of eggs and larvae from spawning grounds near 7-15 m. The direction of movement suggested by the estuarine gradient, however, is opposed to the direction of movement suggested by the gulf gradient in which sizes increase inshore. We offer no simple explanation for the apparent dichotomy except that it might reflect: possibly separate estuarine and gulf spawning grounds which might involve temporal

[6]DeVries, D. A., and M. E. Chittenden, Jr. In prep. Spawning, age determination, and population dynamics of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico.

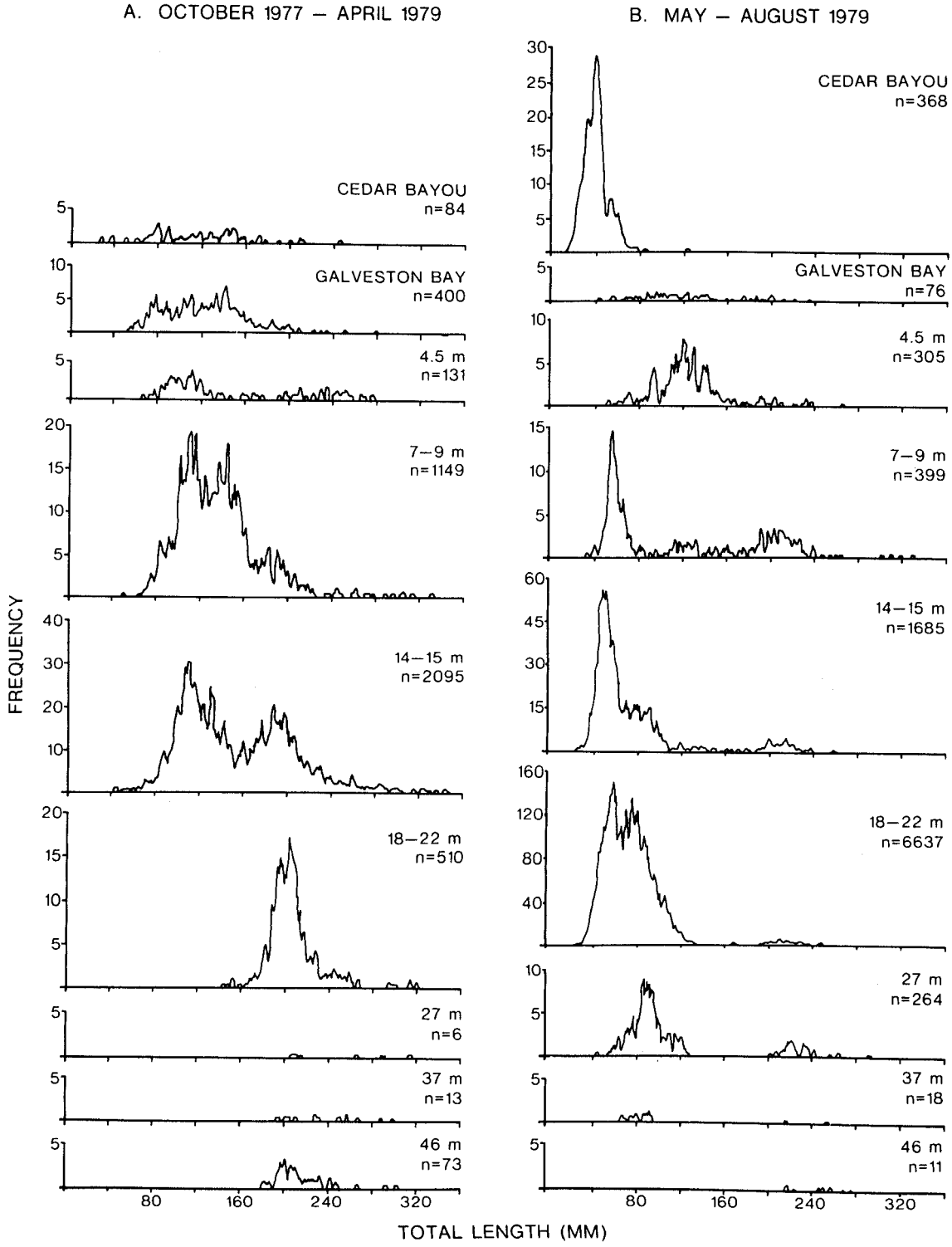

FIGURE 9.—Length frequencies (moving averages of three) of *Cynoscion arenarius* collected at each depth off Freeport and in Galveston Bay and Cedar Bayou, Tex. A. October 1977-April 1979. B. May-August 1979.

differences in spawning, and as noted shortly, the unusual flooding near Galveston Bay during spring 1979 and current transport phenomena which are strongly wind-driven in the gulf and its estuaries. Under nonflood conditions a single gradient of increasing size extended from the upper estuary out to at least 22 m in the gulf (Figure 9A), which suggests that the dichotomous condition in May-August 1979 (Figure 9B) was an exception caused by flooding.

Our data suggest that *C. arenarius* spawns in the shallow inshore gulf, but the extent of its spawning grounds is not yet clear and could vary seasonally. Other workers also have reported evidence of gulf spawning (Gunter 1945; Moffett et al. 1979). Perry (1970) and Franks et al. (1972) captured running ripe *C. arenarius* in the gulf during February and March at 73-91 m (about 105 km offshore) which could indicate spawning offshore in deep water; but the distance these fish traveled before spawning is not clear. Reid (1955), Hoese (1965), and Copeland and Bechtel (1974) reported spawning in estuaries, but they presented little evidence. However, Harmic (1958) found that the closely related *C. regalis* spawned within Delaware Bay.

Clear delineation of the spawning grounds requires understanding how this species passes from spawning grounds to nurseries. The spring and late summer spawning periods of *C. arenarius* coincide with periods of rising sea level in the northern gulf in response to prevailing onshore winds and surface currents (Collier and Hedgpeth 1950; Marmer 1954). Spawning probably is timed to take advantage of this seasonal phenomenon to transport eggs and/or larvae from inshore gulf spawning grounds to estuarine and gulf nurseries as our size composition data indicate. The bayward movement of postlarvae that Simmons and Hoese (1959) reported on incoming tides could be enhanced by rising sea levels and prevailing onshore winds and currents. However, spawning also coincides with seasonal rainfall peaks (Collier and Hedgpeth 1950) which could modify estuarine transport phenomena. Currents and tides in the nearshore northern gulf and its shallow estuaries are influenced greatly by wind and flooding (Collier and Hedgpeth 1950; Smith 1975). Therefore, spawned group strength of *C. arenarius* and its spatial distribution may be influenced greatly by short-term wind and rainfall patterns that affect current transport and, thereby, survival of the eggs and/or larvae as Nelson et al. (1977) reported for Atlantic menhaden, *Brevoortia tyrannus*.

NURSERIES AND LATER MOVEMENTS

Results

Spring and late summer spawned groups use both estuarine and inshore gulf nurseries in their early life, although estuaries may be most important for late summer fish. Recently hatched spring fish were abundant in 1977-79 from May through July in the inshore gulf, in Galveston Bay, and Cedar Bayou (Figures 4-7). Few recently hatched late summer fish were in the inshore gulf in September-November of 1977-78 (Figures 4, 5), but they were common then in Galveston Bay and Cedar Bayou (Figures 6, 7) and were abundant in the gulf in December (Figures 4, 5).

The main nursery of *C. arenarius* in the northwestern gulf lies in water <18 m. Fish >160 mm TL occurred throughout the 4.5-46 m depth range (Figure 9A). However, fish <160 mm TL only occurred in <18 m except in May-August 1979 when recently hatched spring 1979 fish were abundant to 27 m and present to 37 m (Figure 9B). The Gulf nursery probably expands or contracts depending on spawned group strength and factors that determine dispersal of the young. For example, the great abundance of small fish in the gulf during May-August 1979 might be due to increased spawned group strength and/or heavy flooding in the Galveston Bay area in that spring (Barris 1979).

Fish that use estuarine nurseries in their early life enter the gulf during mid and late fall to overwinter. Spring fish grew in the gulf from May through September-October 1977 and 1978 (Figures 4, 5), but thereafter showed no growth or decreased sizes through December. This pattern indicates movement from estuaries to the gulf with the larger fish preceding smaller ones, assuming continued growth in that period. Many recently hatched late summer fish entered the gulf during December 1977 and 1978 (Figures 4, 5), because few were in the gulf before then. Few were in Galveston Bay or Cedar Bayou from December through March (Figures 6, 7), although they were abundant in the gulf.

Late summer spawned groups return to estuaries during midspring after overwintering in the gulf. Although abundant in the gulf in the February-April periods of 1977-79 (Figures 4, 5),

few late summer fish were in the gulf in the following May-July period except in 1977 off Port Aransas. Most must have returned to estuaries in midspring and remained there until they returned to the gulf to spawn in August (Figure 4). Late summer fish were captured in Galveston Bay in May-July (Figure 6), but not in large numbers which may reflect a habitat change by these larger fish or avoidance of the small trawls used there. Sizes of the late summer fish in the gulf remained stable or decreased in July-August 1978 and 1979 (Figure 4). This is similar to the pattern noted in the fall for spring spawned fish and suggests a similar gradual dispersal of the late summer groups to the gulf.

Movements of spring spawned groups as they reach age I are not clear. We captured few age I fish in the spring or following summer except in March and April 1979 in the gulf (Figure 4). Most apparently die after spawning, but our data do not clarify movements of the survivors.

Cynoscion arenarius exhibits little diel variation in size composition. The two spawned groups off Freeport during December 1978 and in April, June, and July 1979 showed little day-night size variation (Figure 4). Some differences—e.g., December 1978—probably reflect growth or movements in the 2-wk period between collections.

Discussion

Our findings on the nurseries and later movements of *C. arenarius* agree with the limited literature, although the complex life history of this species has not been recognized. The fact that the young occur in both estuaries and the inshore gulf has been reported (Gunter 1945; Miller 1965; Christmas and Waller 1973), but these workers did not recognize separate spring and late summer spawned groups nor possible differences in their nurseries. Our finding that *C. arenarius* move in fall from estuaries to overwinter in the gulf has been reported by many workers including Gunter (1938, 1945), Chambers and Sparks (1959), Perret and Caillouet (1974), and Ogren and Brusher (1977) who based their findings only on apparent change in abundance without recognizing size composition changes, or the differences between spring and late summer spawned groups. Movement of "mature" *C. arenarius* in the period April-May from the gulf to estuaries has been reported (Simmons 1950-51 cited in Guest and Gunter 1958; Simmons and Hoese 1959). These might have been late summer fish in agreement with our findings, but these workers did not recognize different spawned groups. Data of Perret and Caillouet (1974, fig. 6), however, show return of late summer fish to Vermillion Bay, La., in April and May. The absence of diel size variation in *C. arenarius* contrasts with its presence in *C. nothus* (DeVries and Chittenden footnote 6).

GROWTH AND AGE DETERMINATION BY LENGTH FREQUENCY

Results

No more than two year classes of *C. arenarius* occurred in any 1 mo in the gulf, in Galveston Bay, or in Cedar Bayou (Figures 4-7). Only one year class was captured from February through April, except possibly in March 1979 off Freeport. Two year classes usually were present in the gulf and in Galveston Bay from May through December—but no more than three spawned groups.

Cynoscion arenarius averages 210-280 mm TL at age I depending on spawned group. Spring fish averaged 160-190 mm TL at 6 mo and 220-280 mm at age I (Figure 10), although many were 200 mm or more at 6 mo and some were 300 mm at age I (Shlossman 1980, tables 1, 2). Late summer fish were slightly smaller, averaging 120-150 mm TL at 6 mo and 210-250 mm at age I (Figure 10), although many were 175 mm or more at 6 mo and some were 300 mm at age I (Shlossman 1980, tables 1, 2). Mean sizes predicted by regression (Figure 10) were 250 mm TL at age I, 425 mm at age II, and 574 mm at age III for late summer fish. Predictions for spring fish were 260 mm TL at age I, 301 mm at age II, and 160 mm at age III. Predictions for spring fish are unrealistic at age III and probably too low at age II, because the simple polynomial regression used describes growth as a parabola.

Growth generally was greatest in warmer months and least in colder months. Both spring and late summer spawned fish grew slowest (5-10 mm TL/30 d) in winter (Figure 11). Spring fish grew fastest (35 mm TL/30 d) from May through October; much variation occurred, however, and zero increments in summer and mid to late fall reflect movement of larger fish from estuaries to the gulf, not lack of growth. Late summer fish grew rapidly in spring; decreased increments in late spring and early summer may reflect movement of larger fish from estuaries to the gulf.

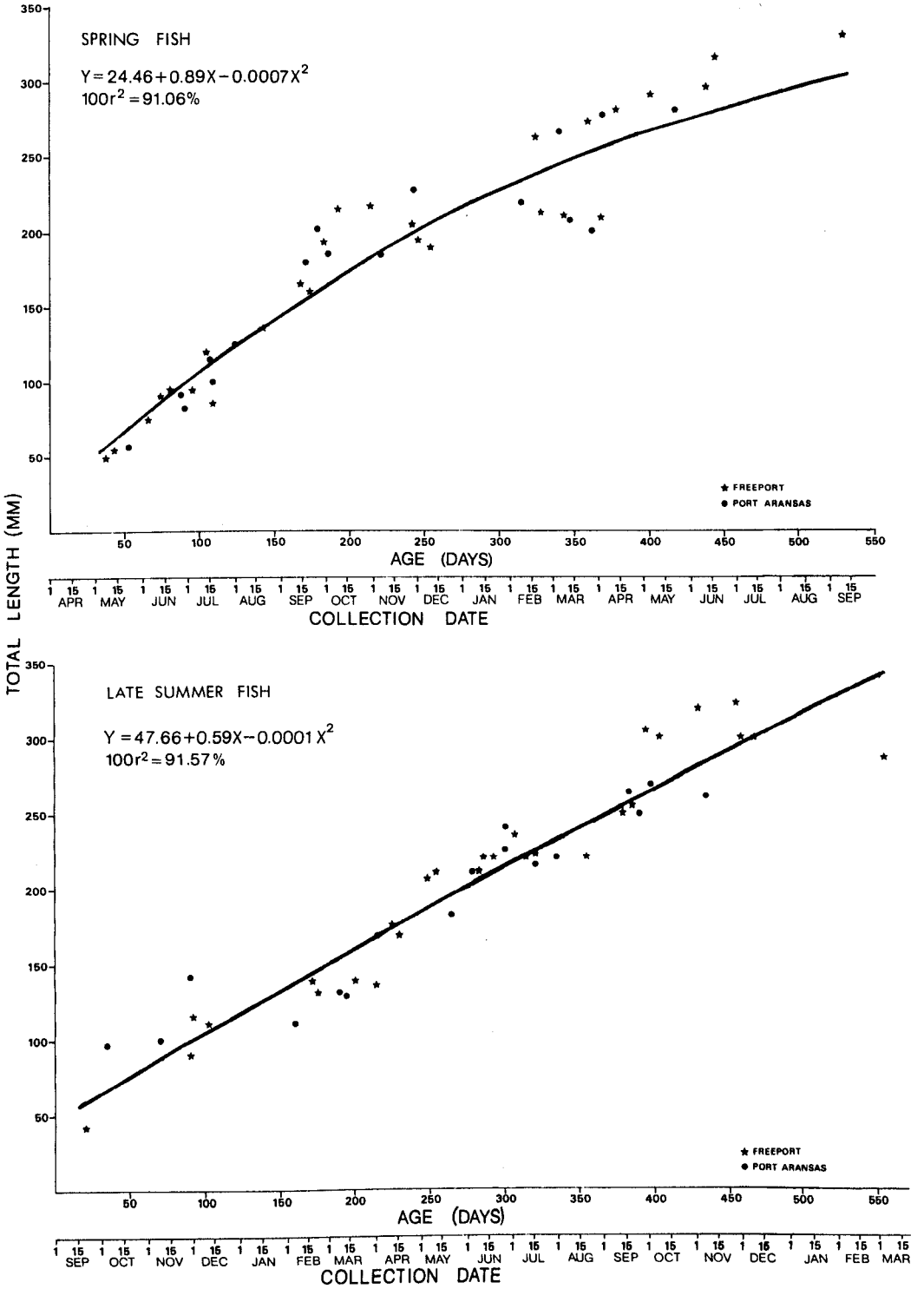

FIGURE 10.—Observed and predicted sizes at age of *Cynoscion arenarius* from the gulf off Freeport and Port Aransas, Tex., for spring spawned fish and late summer spawned fish. Modal sizes (Shlossman 1980, tables 1, 2) were regressed on ages after assigned hatching dates. Regression was significant at $\alpha = 0.01$.

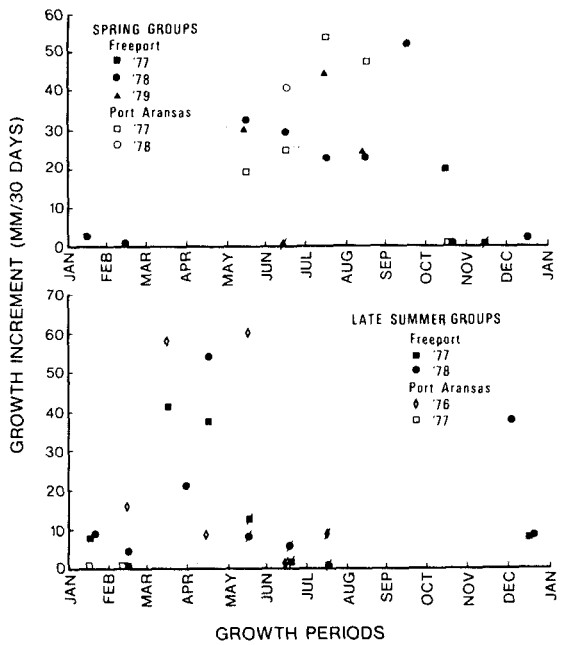

FIGURE 11.—Monthly growth increments of *Cynoscion arenarius* for spring and late summer groups from the Gulf of Mexico. Unadjusted well-defined increment data of Shlossman (1980, tables 1, 2) were converted to growth per 30 d. Increments with a diagonal (/) reflect movement, not necessarily low growth. Negative increments were rounded to zero.

Female *C. arenarius* reach larger sizes than males. All fish >300 mm TL (n = 13) and 88% examined >250 mm (n = 80) were female.

Discussion

Our findings on *C. arenarius* growth agree with the limited literature. Our average growth estimates—210-280 mm TL at age I depending upon the spawned group—agree with data of Perret and Caillouet (1974, fig. 6), but slightly exceed data of Swingle and Bland (1974:41) and estimates of Hoese et al. (1968), McEachron et al. (1977), and Chittenden (1977). Decreased growth in winter agrees with observations of Gunter (1945) and Hoese et al. (1968). Seasonal growth is similar to that of *C. nothus* (DeVries and Chittenden footnote 6), *C. nebulosus* (Pearson 1929; Tabb 1961), and *C. regalis* (Welsh and Breder 1923; Hildebrand and Cable 1934; Merriner 1973). However, *C. arenarius* is larger at age I than its three congeners in the western North Atlantic: 1) *C. nothus*, 130-190 mm SL = 158-229 mm TL (DeVries and Chittenden footnote 6); 2) *C. regalis*, 143-180 mm SL = 173-218 TL (Taylor 1916 in Merriner 1973; Perlmutter et al. 1956; Merriner 1973); and 3) *C. nebulosus*, 116-165 mm SL = 144-201 mm TL (Pearson 1929; Moody 1950; Klima and Tabb 1959; Moffett 1961; Tabb 1961). Our findings that females grow larger than males has been reported (Franks et al. 1972), and similar differences occur in *C. nebulosus* (Pearson 1929; Klima and Tabb 1959; Tabb 1961).

AGE DETERMINATION USING SCALES

General Basis

Cynoscion arenarius can be aged using scales. Annuli were identified using standard criteria (Tesch 1971) and procedures for *C. nebulosus*, *C. nothus*, and *C. regalis* (Klima and Tabb 1959; Tabb 1961; Merriner 1973; DeVries and Chittenden footnote 6). Characters used to identify annuli included: 1) a clear zone between bands of circuli in the anterior field (Figures 12, 13), 2) a band of crowded circuli adjacent to a band of more widely spaced circuli (Figure 12), 3) secondary radii radiating from a clear zone or changed spacing between circuli (Figures 12, 13), 4) cutting over of circuli (Figures 12, 13), and 5) appearance of these characters on all or most scales. Marks identified as false annuli: 1) appeared on only a few scales from a fish, 2) had secondary radii not accompanied by a clear zone or changed spacing of circuli, 3) had a clear zone or changed spacing between circuli not accompanied by other characters, and 4) lacked distinct cutting over. False annuli were common, as Merriner (1973) found for age 0 and age I *C. regalis*.

Results

Few fish had scales with an annulus. Only 159 of 1,602 fish (10%) examined had one annulus and only 6 fish (0.4%) had two annuli. This finding that 10% had one annulus is not consistent with the 99% annual mortality rate reported later. However, the sample aged was biased by arbitrary selection of large fish. Moreover, the annulus primarily forms at 0.5-0.75 yr which is before annual mortality is complete.

The first annulus forms from April through November, although spring and late summer spawned fish may form annuli at different times. Marginal increments in late summer fish were smallest in spring and early summer (Figure 14),

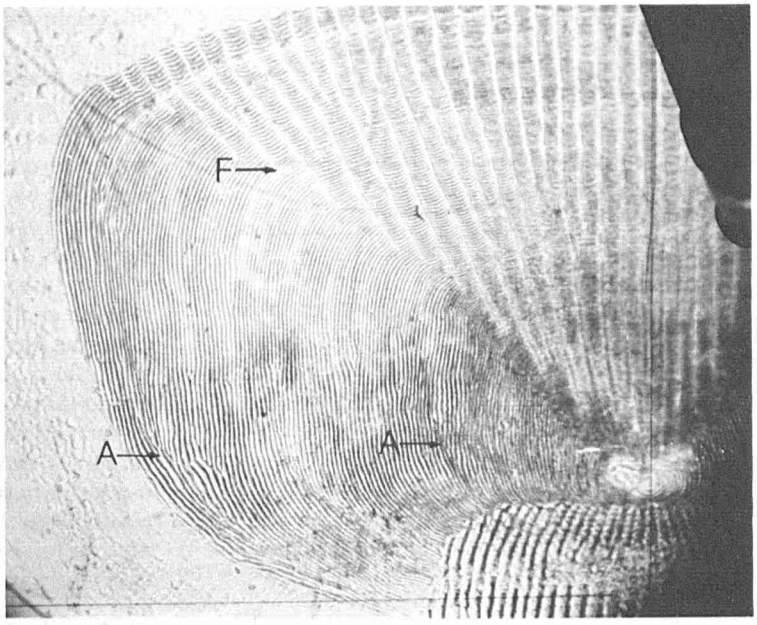

FIGURE 12.—Scale from a spring spawned 338 mm TL *Cynoscion arenarius* captured in September showing two annuli (A). The first annulus shows cutting over in the lateral field and changed spacing of circuli associated with secondary radii in the anterior field. The second annulus shows cutting over in the lateral field and a clear zone between circuli in the anterior field. A false annulus (F) had a few secondary radii but lacked changed spacing between circuli or a clear zone and distinct cutting over and was absent on most scales.

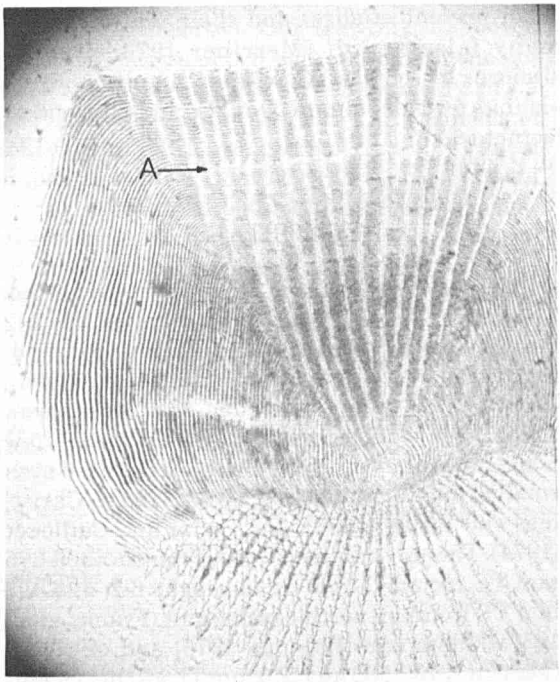

FIGURE 13.—Scale from a late summer spawned 300 mm TL *Cynoscion arenarius* captured in December showing one annulus (A). Note the cutting over in the lateral field and secondary radii in conjunction with a clear zone between circuli in the anterior field.

so that their first annulus primarily formed from April through July. Marginal increments in spring fish were smallest in late summer and fall, so that their first annulus formed primarily from September (possibly August) through November. Therefore, both spring and late summer fish primarily formed their first annulus at about 0.5-0.75 yr of age.

Fish with one annulus were 136-329 mm TL. The percentage having a first annulus increased with size: 1) 8% at 150-199 mm TL (n = 518), 2) 24% at 200-249 mm (n = 268), 3) 52% at 250-299 mm (n = 77), and 4) 71% at 300 mm and greater (n = 14). Fish with two annuli were 265-338 mm TL.

Back-calculated lengths were smaller than lengths at age determined from length frequencies. Lengths at annulus formation for spring fish using Jones' (1958, equation 2) formula were 81-257 mm TL, and the mean was 162 mm with 95% confidence limits of 154-171 mm. Back-calculated lengths at annulus formation for late summer fish were 96-255 mm TL, and the mean was 178 mm with 95% confidence limits of 169-186 mm. These data support analyses of marginal increments that indicate the first annulus primarily forms at 0.5-0.75 yr, because lengths at age I determined from length frequencies were 220-280 mm TL for spring fish and 210-250 mm for late summer fish. The back-calculated size range of 81-257 mm TL for spring fish agrees with their sizes at age 0 during summer and early fall (Figures 4, 5). Similarly, the back-calculated size range of 96-255 mm TL for late summer fish agrees

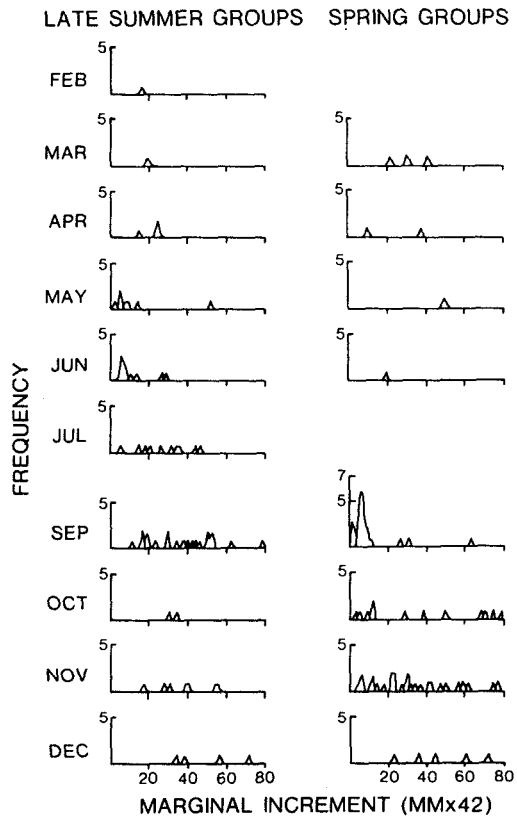

FIGURE 14.—Monthly marginal increments for *Cynoscion arenarius* with one mark.

with their sizes at age 0 in spring and early summer (Figures 4, 5).

Repeated examination suggests that age determination was consistent. We found 86% agreement in a second reading of scales from 361 fish 120-338 mm TL, including all fish initially determined to have an annulus. Disagreement occurred primarily when the scales had a mark close to the margin or had one annulus and one false annulus.

Discussion

Scales can be used to age *C. arenarius*, but length-frequency analysis is simpler and at least as accurate except possibly with fish much older than those we caught. Separate spring and late summer spawning periods complicate age determination. Age, growth, and mortality estimates should be based on individual spawned groups to avoid misinterpretation. Valid estimates require assignment of individuals to correct spawned groups; and that requires length-frequency analysis, because annulus formation occurs over a broad time period in both spring and late summer groups. Exact age determination may be impossible for the apparently few fish older than say, age II or III. Their ages probably would not be distinct in length frequencies and a spawned group probably could not be assigned.

Causes of annulus formation in *C. arenarius* are not clear, although temporary growth cessation may be associated with movements between estuaries and the gulf and/or gonad development. Annulus formation in late summer fish coincides with their spring movement to estuaries and gonad development. Similarly, annulus formation in spring fish coincides with fall movements from estuaries. However, many spring fish use only gulf nurseries in their early life which might minimize mark formation in those fish. False annulus formation might be associated with movements between estuaries and the gulf. *Cynoscion arenarius* and *C. regalis* are similar in that both migrate between the sea and estuaries (Welsh and Breder 1923; present studies) and their scales exhibit many false annuli (Merriner 1973; present studies). In contrast, *C. nothus*, a gulf resident, exhibits few false annuli (DeVries and Chittenden footnote 6).

MAXIMUM SIZE, LIFESPAN, AND MORTALITY

Cynoscion arenarius is small and short lived. The largest of the 13,780 fish we captured was 342 mm TL, although few exceeded 300 mm. Our findings agree with Gunter (1945), Hildebrand (1954), Perry (1970), and Chittenden and McEachran (1976) who captured fish to 377 mm TL but few >300 mm. Many other studies have reported even smaller maxima including Miller (1965), Christmas and Waller (1973), and Perret and Caillouet (1974). The only published records much >300-375 mm TL include a few trawl-caught fish 425-497 mm TL from the north-central gulf (Franks et al. 1972; Adkins and Bowman 1976) and off Texas (Mohsin 1973), 590 and 540 mm TL gill net caught fish from northwestern Florida (Vick 1964; Trent and Pristas 1977), and fish as large as 483 and 503 mm TL captured in Galveston Bay, Tex., by commercial and recreational fishermen, respectively (Heffernan et al.[7]). The latter study gave size data

[7]Heffernan, T. L., A. W. Green, L. W. McEachron, M. G. Weixelman, P. C. Hammerschmidt, and R. A. Harrington. 1976. Survey of finfish harvest in selected Texas

from fisheries whose gear was biased seriously to capture large fish about 12 mo and older. However, even these fish averaged only 280 mm TL in recreational catches and 343 mm in commercial catches; and few were >330 mm and 406 mm TL, respectively.

The maximum lifespan of *C. arenarius* typically is 1-2 yr at most for trawl-caught fish and possibly as much as 2-3 yr for other gear. In the period October 1977-April 1979, 90% of the 3,988 fish that we captured off Freeport were <215 mm TL (Figure 15), 99% were <280 mm, and 99.5% were <300 mm. Similarly, of the 2,073 fish collected off Port Aransas during February 1977-July 1978 (Figure 15), 90% were <210 mm TL, 99% were <260 mm, and 99.5% were <275 mm. A t_L value of 1-2 yr at most is reasonable for the Beverton-Holt model parameter (Gulland 1969) for trawl-caught *C. arenarius* because fish >260-300 mm TL made up <0.5-1.0% of our catch. This is about the average size at age I (210-280 mm TL), which many individuals exceed, and approaches the maximum sizes usually reported. Our trawling, moreover, shows the scarcity of fish with more than one annulus, a disappearance of all fish by 14-18½ mo of age (Table 3), and agrees with Chittenden and McEachran's (1976) suggestion that the typical lifespan is no more than 1-2 yr. Even recreational and commercial gear seriously selective for larger sizes (references cited above) catch fish whose typical maximum age appears to be only 2-3 yr, at most, because mean sizes at these ages predicted by polynomial regression were 431 mm TL at age II and 574 mm at age III for late summer fish and a probably unrealistically low 301 mm at age II for spring fish.

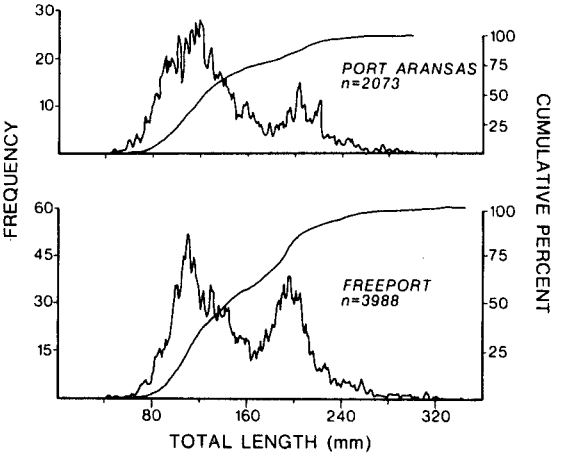

FIGURE 15.—Length frequency (moving average of three) and cumulative percentage of all *Cynoscion arenarius* collected in the Gulf of Mexico off Freeport, Tex., October 1977-April 1979 and off Port Aransas, Tex., February 1977-July 1978.

Sand seatrout has a total annual mortality rate that approaches 100% and has a best estimate of 99.79% based on trawling data. Time-specific values of total annual mortality ($1 - S$) were calculated for each individual month from the expression $S = N_t/N_o$ where S = rate of survival and N_o and N_t are the number of fish collected from consecutive spring or late summer groups. Of the 20 mo when collections were made off Freeport, only one spring group was present in 14 mo and only one late summer group was present in 17 mo (Figure 4). Of the 14 mo when collections were made off Port Aransas, only one spring group was present in 13 mo and only one late summer group was

bays. Tex. Parks Wildl. Dep., Coastal Fish Branch, Proj. Rep. 2-231-R-1, 116 p.

TABLE 3.—Periods of time, sizes, and ages when spawned groups of *Cynoscion arenarius* were last captured off Freeport and Port Aransas, Tex.

Spawned group and location	Disappeared in the period	TL (mm)	Age (mo)	Comments
Spring 1976:				
Port Aransas	5 Apr.-28 May 1977	260-295	12-14	Few specimens ever captured
Late summer 1976:				
Freeport	4 Nov.-3 Dec. 1977	275-340	14-15	Few specimens ever captured
Port Aransas	10 Nov. 1977	240-285	14-15	
Spring 1976:				
Freeport	14 June-15 Sept. 1978	295-340	14½-17½	Few captured after December 1977
Port Aransas	8 Mar. 1978	250-280	11-12	Few captured after November 1977
Late summer 1977:				
Freeport	13 Dec. 1978-12 Mar. 1979	280-320	15½-18½	Few captured after September 1978
Port Aransas	28 June 1978	240	11	
Spring 1978:				
Freeport	21 June 1978	305-325	14½	Few captured after April 1979
Port Aransas	15 July 1978	80-150	4½	Still being recruited when last collection was made
Last summer 1978:				
Freeport	22 Sept. 1979	205-305	13	Still abundant when last collection was made; sizes not distinct

present in 11 mo (Figure 5). The apparent values of $1 - S$ were 100% within each month when N_t was zero. In six other months the youngest group in the ratio N_t/N_o was incompletely recruited off Freeport, so that the following mortality rates would be underestimates: 1) June 1978, 99.2%, spring fish; September 1978, 98.9%, spring fish; 2) May 1979, 99.5%, spring fish; June 1979, 99.9%, spring fish; August 1979, 99.0%, spring fish; and 3) December 1978, 98.8%, late summer fish. Because the youngest spawned group in the ratio strongly showed incomplete recruitment, realistic mortality estimates were not possible for the following months: 1) spring groups, May 1977, Port Aransas; 2) late summer groups, September, October, and November 1977, Port Aransas; 3) spring groups, May 1978, Freeport; and 4) late summer groups, December 1977, September 1979, Freeport. Following the first procedure of Robson and Chapman (1961), we calculated an average value of $1 - S$ = 99.79% by pooling identifiable N_o and N_t values from each month except the seven in which the youngest spawned group strongly showed incomplete recruitment.

Our observed estimates agree with the theory (Royce 1972:238) that the total annual mortality rate is about 90% if the lifespan is about 2 yr and approaches 100% if 1 yr. Our high mortality estimates are consistent with maximum sizes and length frequencies in many published faunal studies based on trawling in estuarine and gulf waters. Theoretical values that $1 - S$ = 80-90% based on lifespans of 2-3 yr appear to be lowest tenable values even if the data include recreational or trammel/gill net caught fish.

TOTAL WEIGHT-, GIRTH-, AND STANDARD LENGTH-TOTAL LENGTH RELATIONS

Total weight-total length, girth-total length, and standard length-total length relationships are presented in Table 4. Regressions of total weight on total length were significantly different in elevation between sexes (F = 5.38; 1, 1,501 df; α = 0.05) but not in slope (F = 2.41; 1, 1,500 df; α = 0.05). Calculated slopes significantly exceeded β = 3.0 at α = 0.5 (data pooled, t = 18.85; males, t = 15.10; females, t = 14.85).

GENERAL DISCUSSION

The fact that *C. arenarius* produces two distinct, major spawned groups each year may be important to its systematic status, management, and to understanding its population fluctuations.

The temporal separation of the spawned groups implies reproductive isolation, the extent of which remains to be determined. The existence of the two spawned groups—and their systematic status—must be considered in resolving the status of *C. arenarius*. Ginsburg (1929), Mohsin (1973), and Weinstein and Yerger (1976) did not indicate the spawned groups studied. The two spawned groups may be separate populations or, possibly, separate species. That should be determined and considered in management because fishing could affect them differently.

The production of two major spawned groups each year would minimize year to year population fluctuations even though *C. arenarius* is short lived and little more than an annual crop. As DeVries and Chittenden (footnote 6) noted for *C. nothus*, each spawned group buffers population stability as a multiple year class structure buffers longer lived species. Ricker reproduction curves (Ricker 1954, 1975) might be useful to simulate fluctuations of multiple spawned-group stocks.

Many aspects of the life history and population dynamics of *C. arenarius* differ from *C. regalis* in the Middle Atlantic Bight north of Cape Hatteras, but *C. arenarius* appears similar to *C. regalis* south of Cape Hatteras. In general, it appears that for *C. arenarius*: 1) spawning lasts from March through September but mainly occurs in two peaks, a spring period (March-May) and a late summer period (August-September); 2) maturity is reached at 140-180 mm TL as they approach age I and spawn; 3) maximum size typically is 350-375 mm TL, but most fish are much smaller so that *C. arenarius* is not a major commercial food fish; 4) maximum age typically is 1-2 yr, or 3 yr at most; 5) total annual mortality rate is 80-90% or more, our best estimate being 99%, and 6) fish reach 210-280 mm TL at age I.

The life history of *C. regalis* in the Middle Atlantic Bight is more difficult to enumerate, because it makes north-south and onshore-offshore migrations (Pearson 1932; Nesbit 1954; Wilk 1979). Moreover, at least two intermixing populations may occur there (Nesbit 1954; Perlmutter et al. 1956; Seguin 1960), although stocks remain undefined (Joseph 1972; Merriner 1973; Wilk 1979). However, it appears that *C. regalis* north of Cape Hatteras 1) spawn from May to August with one peak period about April-June (statements of sev-

TABLE 4.—Total weight-total length, total length-girth, and standard length-total length regressions for *C. arenarius* with supporting statistics. All regressions were significant at $\alpha = 0.05$. Measurements are grams and millimeters.

Equation	n	TL range	$100r^2$	Residual MS	Corrected total SSx	Corrected total SSy	$\bar{X}$	$\bar{Y}$
$\log_{10} TW = -5.6609 + 3.2572 \log_{10} TL$ (males)	851	—	97.7	0.0027	9.52	103.35	2.2096	1.5359
$\log_{10} TW = -5.6325 + 3.2420 \log_{10} TL$ (females)	653	—	98.4	0.0025	9.48	101.32	2.2346	1.1612
$\log_{10} TW = -5.4698 + 3.1715 \log_{10} TL$ (males, females, immatures)	1,776	40-338	98.5	0.0032	38.67	394.07	2.1780	1.4379
$G = 1.197 + 0.512\ TL$	1,776	40-338	97.0	20.20	1,220,591 (G)		159.2	82.7
$TL = 2.269 + 1.897\ G$	1,776	40-338	97.0	74.80	4,519,719 (*TL*)		82.7	159.2
$SL = -6.49 + 0.85\ TL$	1,776	40-338	99.7	4.56	3,369,130 (*SL*)		159.2	128.8
$TL = 8.01 + 1.17\ SL$	1,776	40-338	99.7	6.30	4,641,233 (*TL*)		128.8	159.2

eral workers including Welsh and Breder 1923; Hildebrand and Schroeder 1928; Nesbit 1954) or with two peak periods about June and July (Daiber 1957 and Harmic 1958 cited in Thomas 1971); 2) mature at 160-230 mm TL (130-190 mm SL) and spawn at age I throughout their range (Merriner 1976), the validity of which might be reexamined for the New York Bight, because females in Delaware Bay first spawn at age III-IV when fish average 280-330 mm TL (Welsh and Breder 1923); 3) more or less commonly reached maximum weights of 4.54-7.72 kg (10-17 lb) or more (Welsh and Breder 1923; Wilk 1979), maximum lengths of about 400-600 mm TL or more (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Nesbit 1954; Perlmutter et al. 1956), and average long enough to support important commercial food fisheries (Nesbit 1954; Perlmutter et al. 1956; Joseph 1972; Merriner 1973); 4) commonly reach or once reached ages of 3-7 yr (Welsh and Breder 1923; Nesbit 1954; Perlmutter et al. 1956; Massmann 1963; Wilk 1979), although Massmann (1963) described a long-term reduction in size and presumably age composition in Chesapeake Bay; 5) have total annual mortality rates of 48-73% (Nesbit 1954; Massmann 1963; Merriner 1973) which agree with theoretical estimates of 48-68% for lifespans of 4-7 yr assuming negative exponential survivorship; and 6) reach 170-220 mm TL (143-180 mm SL) at age I (Thomas 1971, table 13; Merriner 1973, table 2.23), although reported growth varies and ages may be questionable (Merriner 1973; Wilk 1979).

Although less has been published from south of Cape Hatteras, it appears that those *C. regalis* generally 1) spawn from March through August with a peak about March-June (Hildebrand and Cable 1934; Mahood 1974; Merriner 1976), although a second smaller peak may occur in July-August (Merriner 1976); 2) mature at 160-230 mm TL and spawn at age I throughout their range (Merriner 1976); 3) are much smaller than more northern fish, because few have been reported much >350-375 mm TL (unpubl. data of Anderson from 1930 to 1932 in Mahood 1974, fig. 11; Wolff 1972; Hoese 1973; Mahood 1974; Wenner[8]); 4) commonly reach ages of only 2-3 yr (Wolff 1972; Merriner 1973: data from Morehead City, N.C., fig. 2.7) although age IV fish were common in Pamlico Sound at Hatteras, N.C. (Merriner 1973, fig. 2.7); 5) have total annual mortality rates of 48-73% (Merriner 1973), which might be too low if maximum age typically is 2-3 yr; and 6) average 180-195 mm TL (150-160 mm SL) at age I (Merriner 1973, table 2.11).

The preceding comparisons indicate typical maximum sizes and ages of *C. regalis* differ north and south of Cape Hatteras, and this suggests different total annual mortality rates. New York Bight fish might be older at maturity than fish south of Cape Hatteras, although Merriner (1976) felt they matured at age I throughout their range. Although *C. regalis* migrates north-south and stocks need study, tagging (Nesbit 1954) indicated that North Carolina does not contribute much to New York Bight catches at least. Therefore, movements should not affect the basic conclusion of zoogeographic change in population dynamics at Cape Hatteras. Large *C. regalis* do appear near Cape Hatteras at times as Pearson (1932) and Merriner (1973, fig. 2.7, data from Hatteras) observed, but these may be from northern stocks that had moved south (Pearson 1932).

Zoogeographic changes in the life history and population dynamics of *C. regalis* support the suggestion (White and Chittenden 1977) that species widely distributed along the east coast of the United States may show marked change in life

[8]E. Wenner, Assistant Marine Scientist, South Carolina Department of Wildlife and Marine Resources, P.O. Box 12559, Charleston, SC 29400, pers. commun. August 1980.

history and population dynamics at Cape Hatteras. This phenomenon needs to be considered in management; because given rates of fishing, for example, would more strongly affect stocks north of Cape Hatteras.

In contrast to the zoogeographic differences within *C. regalis*, the life history and population dynamics of *C. arenarius* appear similar to *C. regalis* south of Cape Hatteras. Reproduction is similar in age at maturation, age at first spawning, and the spawning period. The bimodal spawning periodicity in *C. arenarius* differs, at first glance, from that of *C. regalis* south of Cape Hatteras, but this has been recognized only recently for *C. arenarius* and may exist in southern *C. regalis* (Merriner 1976). Differences in typical maximum sizes and ages are small, if real, and this suggests mortality rates more similar than present data indicate. The similarity of the life history and population dynamics of *C. arenarius* to that of *C. regalis* south of Cape Hatteras is consistent with Weinstein and Yerger's (1976) suggestion that they may be one species.

Finally, the population dynamics of *C. arenarius*, including its short lifespan, high mortality rate, and rapid turnover of biomass, are similar to those of *C. nothus* (DeVries and Chittenden footnote 6) and Atlantic croaker of the Carolinean Province (White and Chittenden 1977; Chittenden 1977). This supports the suggestion (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the gulf have evolved towards a common pattern of population dynamics. Moreover, Chittenden's (1977) simulations on Atlantic croaker could serve as a first approximation of the effects of harvesting *C. arenarius*, and *C. regalis*, south of Cape Hatteras.

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MOVEMENTS AND ACTIVITIES OF THE ATLANTIC BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, NEAR SARASOTA, FLORIDA

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ABSTRACT

A tagging-observation program was conducted to study the behavioral ecology of Atlantic bottlenose dolphins near Sarasota, Florida. Forty-seven bottlenose dolphins (24 males, 23 females) were captured, tagged, and released a total of 90 times from 29 January 1975 through 25 July 1976. Tagged animals were identified during regular boat surveys, and information was collected on all individuals and groups encountered. A total of 997 tagged or marked bottlenose dolphins were sighted. A population of bottlenose dolphins was identified in an estuarine-nearshore area extending about 40 km to the south from Tampa Bay and up to 3 km into the Gulf of Mexico. Social organization was characterized by small dynamic groups that appeared to be subunits of a larger socially interacting herd. Average group size of 688 groups was 4.8 bottlenose dolphins (standard error = 0.16). Bottlenose dolphins concentrated in different areas seasonally, possibly in response to distribution changes of important prey species. Feeding strategies of the bottlenose dolphins apparently varied according to available water depth and differed from strategies of pelagic small cetaceans. Calving apparently occurred from spring to early fall.

Until the 1970's, information on the natural history of free-ranging small cetaceans consisted primarily of chance observations (e.g., Norris and Prescott 1961). Increased interest and application of new technology have now greatly expanded our knowledge. Long-term studies of the behavior and ecology of dolphins have been conducted by researchers using boats, submersibles, aircraft, and towers or cliff-top vantage points (see review by Norris and Dohl 1980a). Biotelemetry and newly developed tagging techniques have been used extensively to gather information on delphinid movements, activities, and herd structure (Norris and Pryor 1970; Evans et al. 1971; Perrin 1975; Leatherwood and Evans 1979; Norris and Dohl 1980b). Natural marks that identify individuals have also been used as the basis for field studies of dolphins (Würsig and Würsig 1977, 1979; Shane and Schmidly[5]) as well as whales (Pike 1953; Payne 1976; Katona et al. 1979; Balcomb and Goebel[6]). Unfortunately, in most studies of free-ranging cetaceans, the age, size, and sex of herd members was usually unknown, and consequently few details about herd structure and social dynamics were collected.

The research reported here was an 18-mo tagging-observation study to collect data on movements, home range, herd structure, and habitat use of the bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Fla. (lat. 27°25′ N, long. 80°40′ W). This area was chosen for several reasons: bottlenose dolphins were present throughout the year in areas where channels and islands limited their movements to predictable routes (Irvine and Wells 1972); because the area was used by many boaters, discrete use of an observation boat was not likely to affect the bottlenose dolphins' behavior; and mild weather and sheltered waters made year-round observations feasible. The study was intended to provide insights into the ecology of bottlenose dolphins in a bay-estuarine environment. This report is a revision and reanalysis of parts of Irvine et al.[7]; Wells et al. (1980)

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[5]Shane, S. H., and D. J. Schmidly. 1978. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-283 393, 130 p.

[6]Balcomb, K. C., III, and C.A. Goebel. 1976. A killer whale study in Puget Sound. Final Report to the National Marine Fisheries Service, Contract No. NASO-6-35330. Unpubl. rep.

[7]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. Appendix A, A study of the activities and movements of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-298 042, 54 p.

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present an in-depth analysis of social behavior data from the same study.

METHODS

Study Area

The study area included inshore and coastal waters up to 3 km off the coast, extending about 40 km south from the southern edge of Tampa Bay, Fla. This area is characterized by bays and grass flats 1-4 m deep, and is protected by a series of barrier islands separated by narrow passes (Figure 1). Inshore waters, defined here as the waters between the barrier islands and the mainland, were generally protected from heavy winds and ocean swells. The Intracoastal Waterway (ICW), a boat channel between the barrier islands and the mainland, is maintained by dredging to depths of at least 2 or 3 m. Depths in the Gulf of Mexico increase gradually; the 10 m contour is about 3 km offshore (N.O.S. Chart No. 11425).

Data Collection and Analysis

We captured bottlenose dolphins using the seine net technique described by Asper (1975). We recorded the length and sex of all captured animals and then marked them with combinations of spaghetti tags, fiber glass "visual" tags, freeze brands, roto tags, and radio tags, using methods developed and tested on other small cetaceans (Norris and Pryor 1970; Evans et al. 1972). The radio tags were modified dolphin transmitters, model PT 219, of the Ocean Applied Research Corporation (OAR[8]). Transmitter signals were received on an OAR model 210 Auto-

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

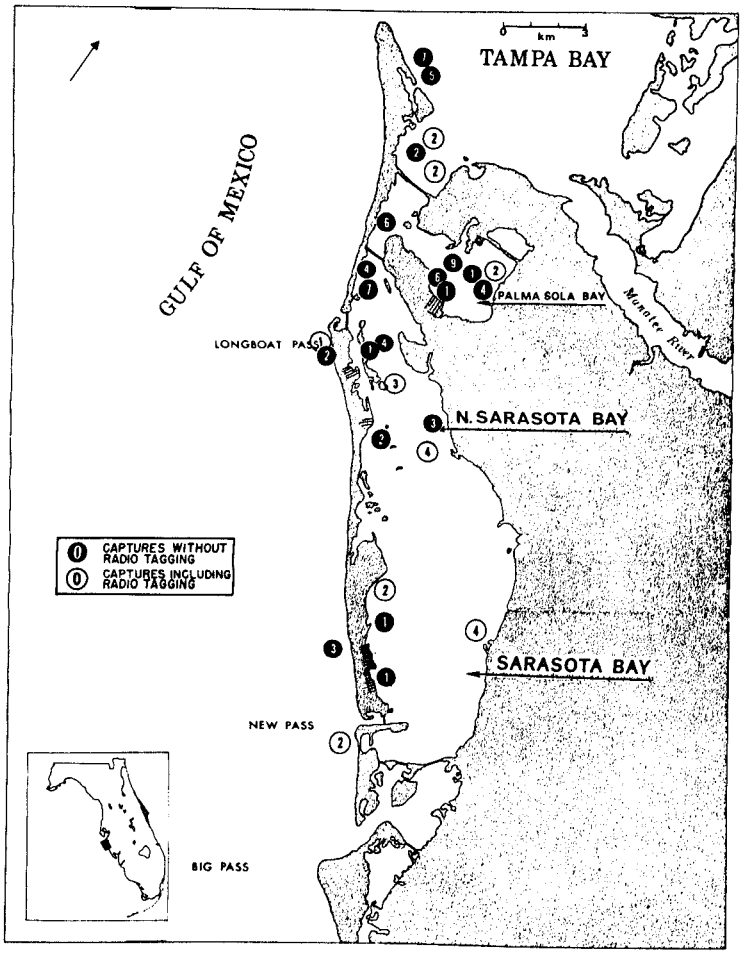

FIGURE 1.—The study area, located south of Tampa Bay near Sarasota (lat. 27°25′ N; long. 80°40′ W), Fla. The encircled numbers indicate numbers of bottlenose dolphins captured at each site.

matic Direction Finder. The tags and marking techniques used in the study were described and evaluated by Irvine et al. (footnote 7).

The boat used as a tagging platform and for surveys and radio tracking was a 7.3 m Wellcraft "Fisherman," equipped with a 3 m tuna tower. During captures, the boat was camouflaged with canvas and netting and towed to the capture site to lessen chances that tagged bottlenose dolphins might later recognize the motor sounds or visually identify the boat, and avoid it during surveys.

Radio-tagged bottlenose dolphins were usually tracked continuously for 24-48 h after installation of the radio transmitter and then relocated and tracked intermittently during the remaining life of the transmitter. As reported by Martin et al. (1971), the radio tags transmitted only when the antenna was at the surface, enabling us to measure dive times by timing the intervals between transmissions. Tracking was generally conducted from a distance and at anchor, to lessen possible influences of the tracking boat on the bottlenose dolphins' movements. Locations of radio tagged animals were determined at night by triangulation and during the day by triangulation or occasional sightings.

Boat surveys were conducted during periods when bottlenose dolphins were not being radio tracked. Surveys were conducted at least twice a week and were concentrated in northern inshore areas (Figure 2). Surveys were extended to include the Gulf of Mexico and southern inshore areas when time was allowed. Survey routes were influenced by tide and wind but were usually confined to channels or other areas >1 m deep (Figure 2).

During boat surveys and tracking trips, all dolphins sighted were counted, and tagged or marked individuals were identified if possible. Groups containing several recognizable animals were usually observed for longer periods to verify identities and associations. The distribution of sightings was therefore influenced by boat channels and by the length of time that groups were followed.

The location and direction of movement of all bottlenose dolphins sighted were noted on charts, and notes on each encounter were entered on data sheets. To correct for repeated sightings of known individuals during the same survey, we based distribution and herd size analyses on sightings more than 1 h apart. Associations between recognizable bottlenose dolphins were compiled as one sighting per group per day, but were retabulated each time the composition of a group changed. For "seasonal" analysis, the year was divided into quarters based on the beginning of field activities (29 January 1975) as follows: February, March, and April (spring); May, June, and July (summer); August, September, and October (fall); and November, December, and January (winter).

Population units were difficult to define because sea conditions and local topography usually limited sightings to nearby animals. Consequently, all bottlenose dolphins sighted within about 100 m of the boat were defined as a group. The smallest group of bottlenose dolphins observed to be closely associating and engaging in similar activities was labeled a primary group. Combinations of primary groups were labeled secondary groups. A "herd" was defined as an aggregation of bottlenose dolphins that more or less regularly occupied a given area and interacted socially with each other to a markedly greater extent than with bottlenose dolphins in adjacent areas. This definition of a herd was based on observed social interactions or associations over an extended period of time. At any given time, the members of the herd were distributed among a number of primary and secondary groups. Herds sighted during aerial surveys (e.g., Leatherwood et al. 1978) have been defined, by necessity, by proximity of animals sighted, and are probably most comparable to our definitions of primary and secondary groups.

RESULTS AND DISCUSSION

Forty-seven bottlenose dolphins (24 males, 23 females) were captured or recaptured for tagging a total of 90 times between 29 January 1975 through 25 July 1976. Ten dolphins (designated RT-1 to RT-10) were fitted with radio tags and radio tracked for up to 22 d. The total of 3,331 bottlenose dolphins sighted (Figure 3) included 2,373 during surveys (730.2 h), 529 during radio tracks (245.3 h), and 429 during capture efforts (150.8 h). Of the 997 marked bottlenose dolphins that were sighted, 781 were tagged and identifiable, 129 were tagged but unidentifiable, and 87 (distributed among 12 dolphins) were identifiable by distinctive natural marks (usually dorsal fin shape). Numerous sightings from close range suggested that tagged bottlenose dolphins did not attempt to avoid the tagging-observation boat.

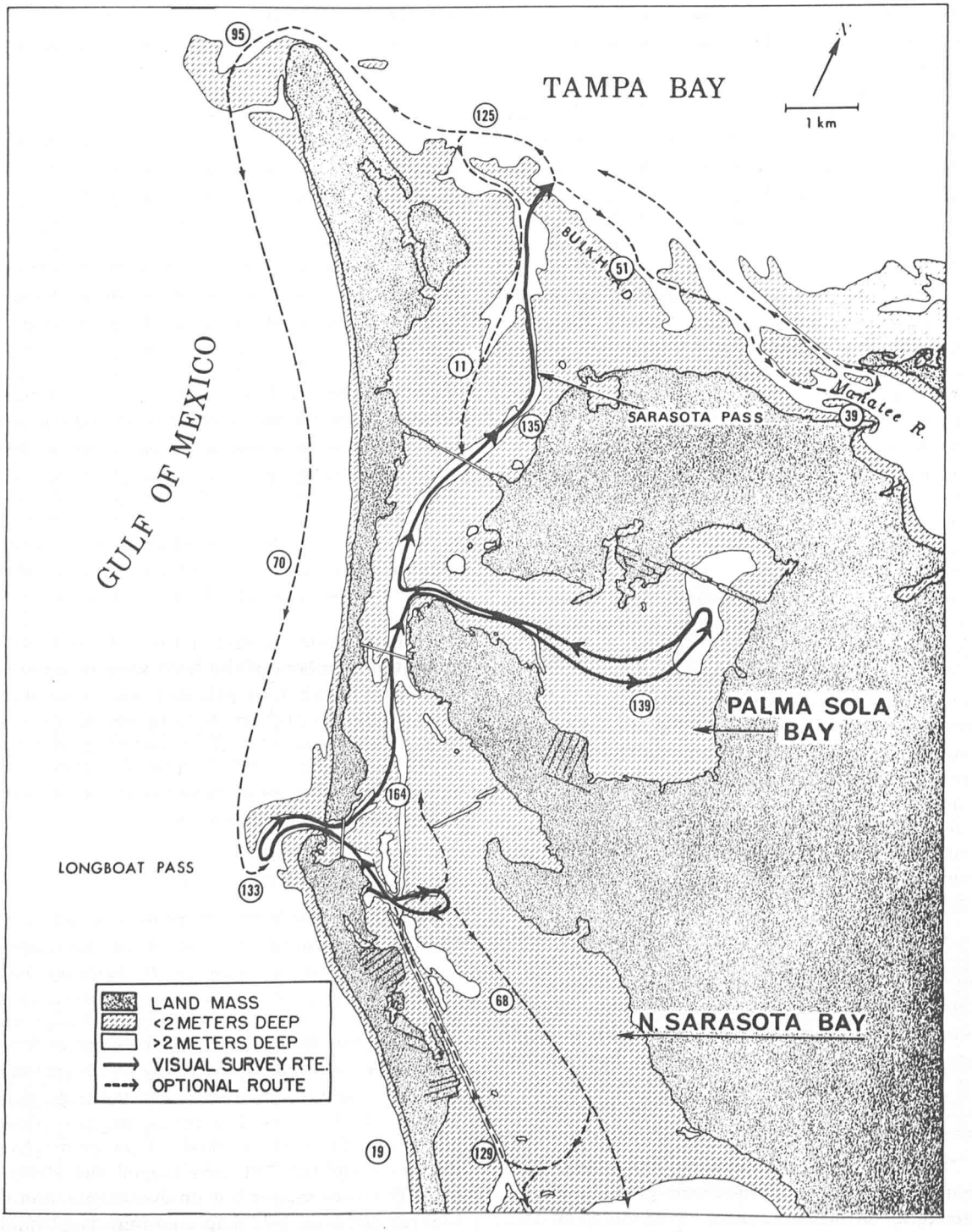

FIGURE 2.—Northern part of the study area with numerals indicating number of surveys along specific routes. Solid lines indicate usual routes. Dashed lines indicate optional routes taken when weather and time permitted. Tagged bottlenose dolphins often traveled north to the edge of Tampa (solid line route) before turning east or west (dashed line) or returning south.

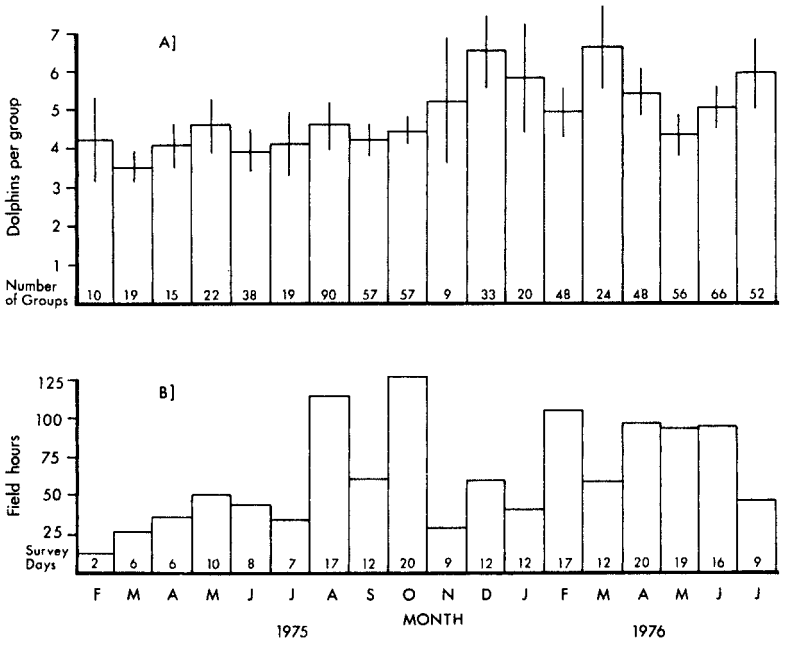

FIGURE 3.—Compilation of bottlenose dolphin sighting data by month, from boat surveys: A) Average number of dolphins sighted per group with standard error (vertical lines) and numbers of groups sighted (numerals) for each month. B) Number of field hours and boat survey days (numerals).

Home Range

Resightings of tagged bottlenose dolphins suggest that at least some were year-round residents of the study area (Figure 4). We recaptured 11 of the 12 animals tagged in 1970-71 by Irvine and Wells (1972) and identified them by freezebrands, tag scars, or dorsal fin shape—strongly implying that some bottlenose dolphins may remain in the area for several years. The existence of resident bottlenose dolphins has previously been widely proposed (Caldwell 1955; Caldwell and Golley 1965; Norris and Pryor 1970; Saayman et al. 1972; Saayman et al. 1973; Würsig and Würsig 1977, 1979; Würsig 1978; Saayman and Tayler 1979; Norris and Dohl 1980b; Shane and Schmidly footnote 5).

The home range of the bottlenose dolphins in the study area appeared to extend south from the southern edge of Tampa Bay to Big Pass (Figure 5; see also Wells et al. 1980), and to include inshore areas and waters up to 1 km into the Gulf of Mexico. No tagged bottlenose dolphins were observed more than 1 km offshore; however, survey trips rarely extended farther than 3 km offshore. At their apparent northern boundary, tagged animals terminated northerly movements at the edge of Tampa Bay by turning either east or west (Figure 2). Groups containing identifiable naturally marked bottlenose dolphins, apparently

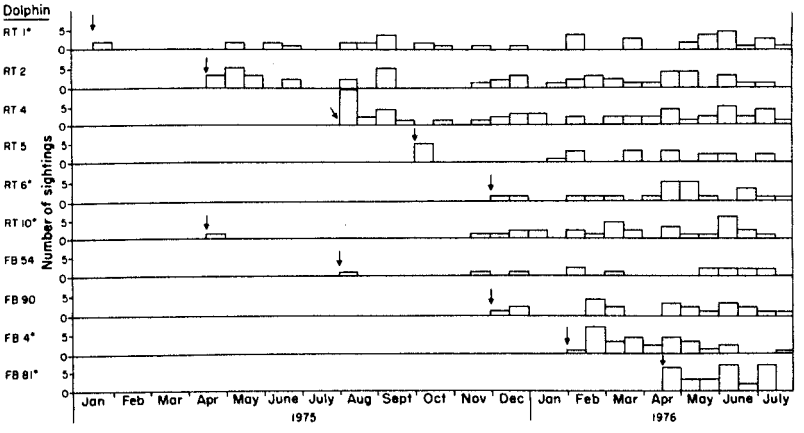

FIGURE 4.—Total biweekly sightings of selected tagged bottlenose dolphins; one sighting per day included. Twenty-three of these sightings were reported by other observers. Arrows indicate capture dates. Sighting locations of dolphins marked with an asterisk are shown in Figure 5.

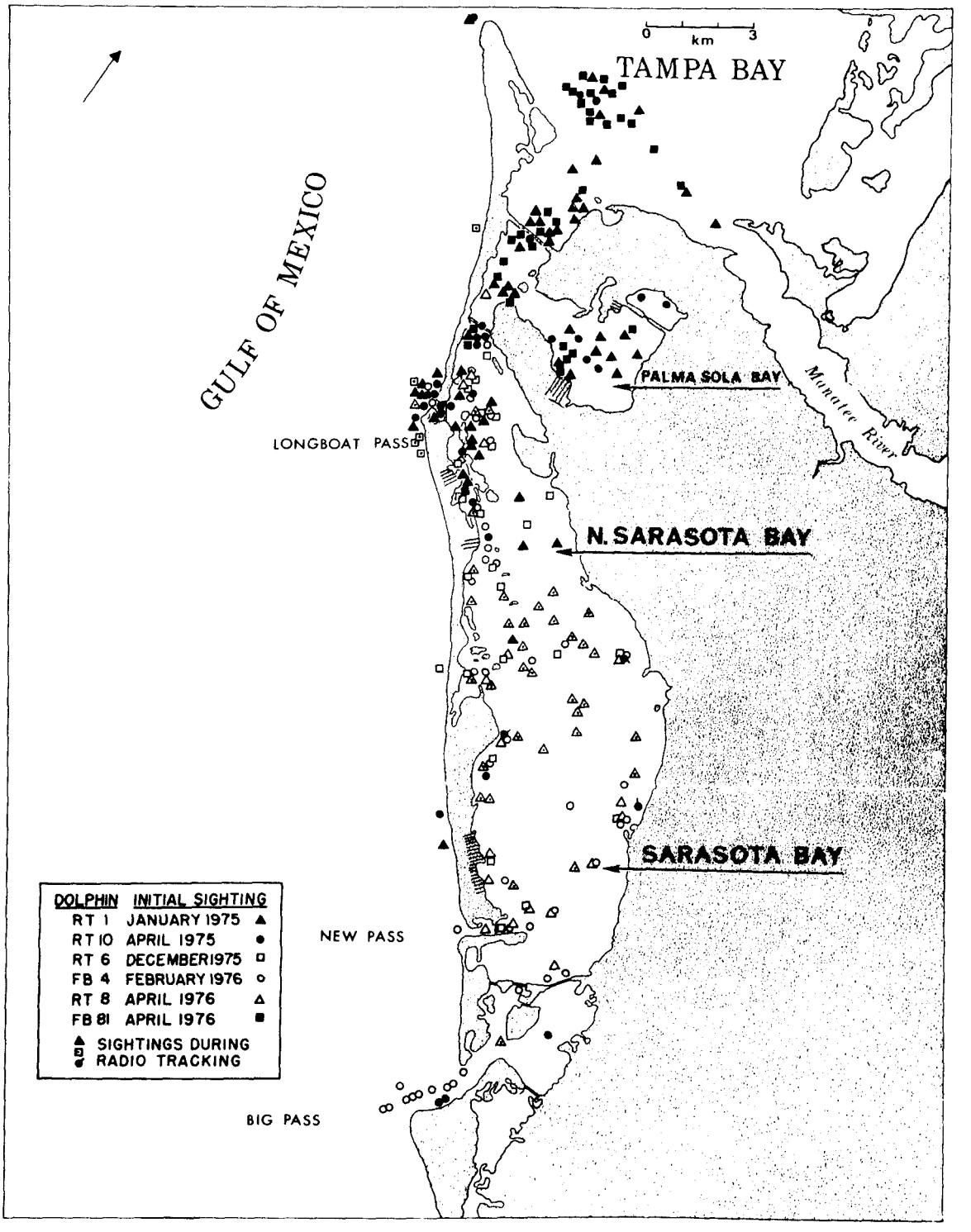

FIGURE 5.—Locations of accumulated sightings of six marked bottlenose dolphins. Sightings of these dolphins were selected to demonstrate generalized use of northern or southern parts of the study area by some animals. The home range of all tagged bottlenose dolphins in the study area extended from approximately southern Tampa Bay to Big Pass.

not belonging to the study herd, occasionally moved along the southern edge of Tampa Bay, but rarely approached tagged bottlenose dolphins and were never observed moving south in the ICW. The only tagged bottlenose dolphins known to have left the study area were two radio-tagged animals that left briefly (one moved 15 km north, the other 10 km south) on the first night after tagging. Both returned within 10 h.

The home range boundary cues used by the animals are unknown. At Tampa Bay, bottlenose dolphins might have used acoustic or visual cues associated with the sharp dropoff at the edge of Tampa Bay. Bottlenose dolphins may use landmarks to limit movements in Golfo San Jose, Argentina (Würsig and Würsig 1979), although known individuals also disappeared from the study area for 6 mo, were resighted 300 km away and then were rediscovered back in the study area 9 mo later (Würsig and Würsig 1977). Long-range movements by some group members but not by others have not been reported elsewhere; however, most studies of bottlenose dolphin home range have been conducted in restricted geographical areas with relatively few identifiable animals (see review by Norris and Dohl 1980a).

Movements and Activities

Movement patterns were similar throughout the northern part of the study area. Slow moving groups of up to six animals often spent several hours over grass flats 1-3 m deep, particularly west of the ICW north of Sarasota Pass and east of the ICW in northern Sarasota Bay (Figure 2).These groups were usually dispersed and dynamic; individuals often approached each other only occasionally, but all usually moved in the same general direction. The pace of individuals quickened at irregular intervals when apparent feeding occurred. Typically, a group of bottlenose dolphins was found in one part of the study area for several survey days, before it moved to another area, but locations and intragroup associations were generally not predictable.

Group members often converged and used channels to move between areas, usually at speeds of 2-5 km/h, although occasionally small groups in tight formation moved along the ICW at speeds exceeding 5 km/h. North-south movements of up to 30 km in a day have been observed but were not typical.

Bottlenose dolphin distribution, and perhaps abundance, differed seasonally within the home range (Figure 6). In winter, bottlenose dolphins were most abundant in passes and along the gulf shore, whereas during the warmer months relatively higher numbers were sighted in the channels and bays inshore of the barrier islands. These localized changes in bottlenose dolphin distribution may reflect changes in the distribution of food resources, or possibly seasonal changes in abundance of sharks (Wells et al. 1980).

Unlike the habitat of pelagic cetaceans, which theoretically does not restrict horizontal and vertical movements, the shallowness of many parts of our study area restricted vertical movements and thereby dictated bottlenose dolphin travel routes and influenced the structure of swimming groups. Bottlenose dolphins were only occasionally observed crossing areas <1 m deep. Bottlenose dolphins have partly beached themselves in Georgia marshes while pursuing fish (Hoese 1971), and other dolphins have been observed feeding in estimated depths of <50 cm (A. B. Irvine pers. obs.; J. S. Leatherwood[9]).

The habitat used by the bottlenose dolphins reported here appears most like that of the humpback dolphin, *Sousa* sp., observed from cliffs in South Africa (Saayman et al. 1972; Tayler and Saayman 1972; Saayman and Tayler 1973, 1979; Saayman et al. 1973) and bottlenose dolphins observed in a bay in Argentina (Würsig and Würsig 1977, 1979; Würsig 1978). In these areas, the animals also usually moved in small groups and fed individually. Although most bottlenose dolphin sightings in our study area were east of the barrier islands, tagged animals were also periodically observed near shore in the Gulf of Mexico. Bottlenose dolphins are found from well offshore into extreme shallows in the Gulf of Mexico (Leatherwood 1975; Leatherwood et al. 1978; Odell and Reynolds[10])—suggesting a distribution that is similar to that of bottlenose dolphins studied in South Africa (Saayman et al. 1972; Tayler and Saayman 1972; Saayman and Tayler 1973, 1979; Saayman et al. 1973).

Movements of bottlenose dolphins with the tides were suggested by True (1885), Gunter (1942), Irvine and Wells (1972), Würsig and Würsig

[9]S. Leatherwood, research biologist, Hubbs-Sea World Research Institute, San Diego, CA 92109, pers. commun. March 1980.

[10]Odell, D. K., and J. E. Reynolds. 1980. III, Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, on the west coast of Florida. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB 80-197 650, 47 p.

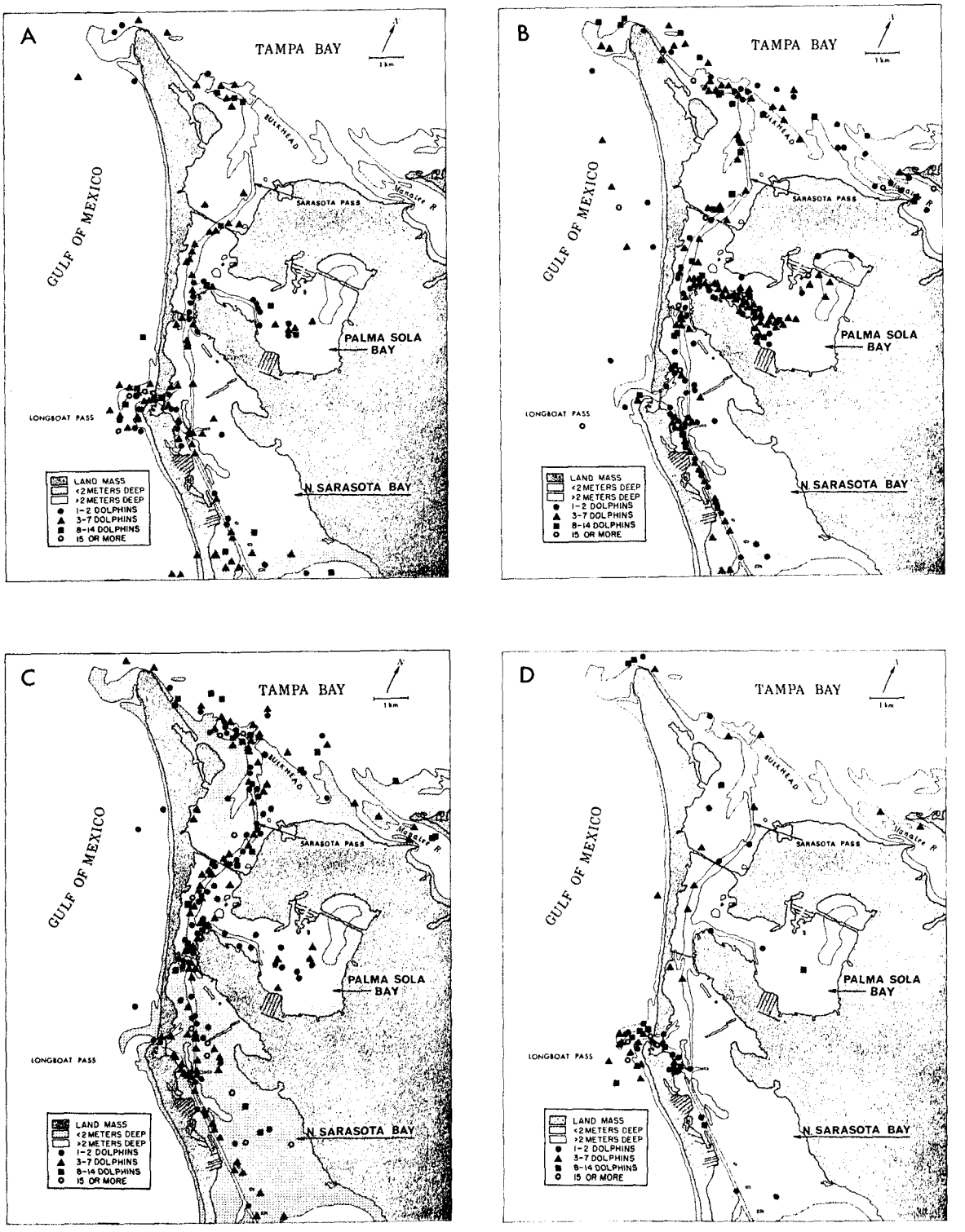

FIGURE 6.—Locations of bottlenose dolphins sighted during 3-mo periods: A) February, March, and April 1975 and 1976; B) May, June, and July 1975 and 1976; C) August, September, and October 1975; D) January, November, and December 1975, and January 1976.

(1979); however, Shane (1980) reported more movements against than with the tidal current, and Leatherwood (1979) reported seeing no relation between the bottlenose dolphin movements and tide. As indicated in Figure 7, considerably more bottlenose dolphins in our study were moving with than against the tidal currents, although the numbers of groups moving with and against the currents were almost equal. This observation suggests that larger groups of animals more often moved with the tide. The data were not analyzed statistically because a large number of animals seen were in the "milling" category, moving across the current or in irregular patterns.

The tidal current in the study area varied with physiography, but was strongest in narrow channels and passes, at times exceding 5 km/h. In Palma Sola Bay, a shallow bay with one access channel, bottlenose dolphins more often moved against than with a sometimes strong current. The animals rarely reversed direction in the Palma Sola Bay channel but often swam near the sides of the channel possibly because current velocity was reduced there.

Movement and activity patterns were not influenced by other environmental conditions in any recognizable way. Possible sun orientation, as reported for the common dolphin, *Delphinus delphis*, by Pilleri and Knuckey (1968) and Evans (1971), was not observed, although the restrictions of movements dictated by area physiography may have masked such effects. We did not detect the distinctive day-night dive interval patterns noted for other dolphin species by Evans (1971, 1974, 1975), Leatherwood and Evans (1979), Leatherwood and Ljungblad (1979), Norris and Dohl (1980b), and Würsig (in press, see footnote 11).

Social Structure

Available evidence suggests that the study area was occupied by a single discrete social unit or "herd." Groups containing naturally marked bottlenose dolphins that were seemingly not a part of this herd were repeatedly observed north, west, and south of the study area. These observations suggest that the bottlenose dolphin population on Florida's west coast may be composed of a number of distinct herds inhabiting limited geographical areas. Overlapping home ranges have also been proposed for coastal bottlenose dolphins off southern California (Leatherwood and Reeves 1978).

The uneven dispersal of sightings of bottlenose dolphins of different age and sex classes within the

[11] Würsig, B. 1976. Radio tracking of dusky porpoises (*Lagenorhynchus obscurus*) in the South Atlantic, a preliminary analysis. ACMRR Scientific Consultation on Marine Mammals, Bergen, Norway, 21 p.

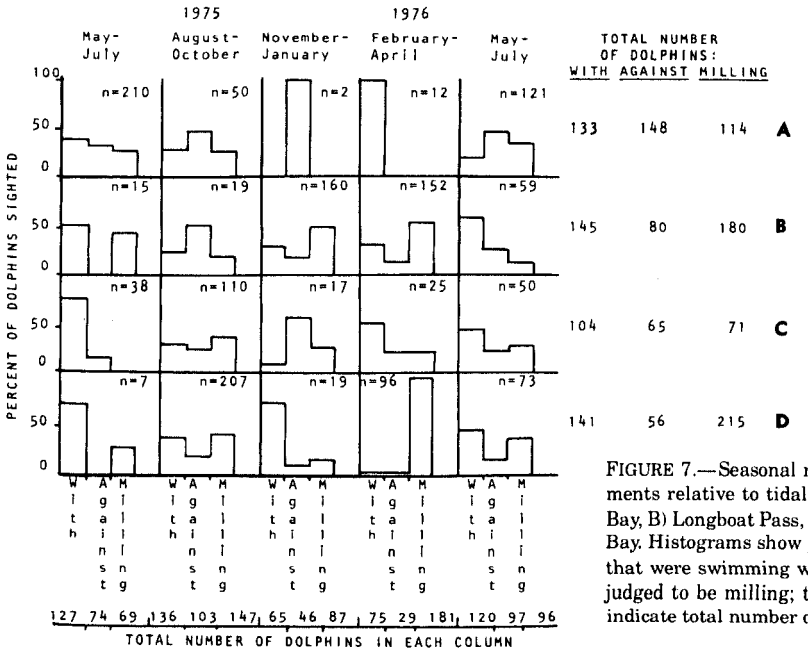

FIGURE 7.—Seasonal relationship of bottlenose dolphin movements relative to tidal flow in selected areas. A) Palma Sola Bay, B) Longboat Pass, C) Sarasota Pass, and D) North Sarasota Bay. Histograms show percent of dolphins sighted in each area that were swimming with the current, against the current, or judged to be milling; the numbers in each category and area indicate total number of dolphins seen.

study area suggested the presence of several "subherds" (Figure 5). The bulk of the tag sightings in the southern part of the study area were of the same subadult male groups, whereas cow-calf pairs were more commonly sighted in the north (Wells et al. 1980). However, some identifiable bottlenose dolphins were sighted in all parts of the study area and were associated with as many as 20 other tagged animals. Overall, we interpret the resightings of tagged animals to indicate that different age and sex classes may have favored different areas, but that social relationships were still maintained among members of the entire herd.

Bottlenose dolphins from adjacent areas that occasionally approached animals from the study herd remained for only a few minutes, and social interactions between the different groups were not observed. Various species of macropods, primates, and ungulates have similar social organizations; subgroups join to form discrete social units ("mobs," "troops," or "herds") that exhibit spatial fidelity and have little interaction with conspecifics outside the social unit (see review by Wilson 1975).

The size of the herd within the study area was difficult to determine. Boat survey results were variable, and information on bottlenose dolphin migration was unavailable. However, the lack of sightings from outside the study area, the observed movements of visually and radio-tagged dolphins, and an increase in tag sightings as the number of tags installed increased (Table 1) all suggested that the captures involved a discrete population of bottlenose dolphins. Assuming a constant population size with no emigration or immigration, we estimated that the local population contained 102 bottlenose dolphins (95% confidence limits = 90-117), using a Lincoln Index (Overton 1971) and a basis of 35 survey days (165 h), from 9 May through 9 July 1976 (Table 1). Until more data are available about this assumption, however, our population estimate must be viewed with caution.

Assuming that the group home range was 85 km^2 (Wells et al. 1980), the estimated population size suggests a density of 1.3 bottlenose dolphins/km^2. Aerial surveys indicate densities of 0.23-0.68 bottlenose dolphin/km^2 in other coastal areas of the southeastern United States (see review by Leatherwood 1979). Monthly mean bottlenose dolphin densities derived from surface survey data of Shane (1980) were 1.5-5.1 bottlenose dolphins/km^2 near Port Aransas, Tex., whereas aerial density estimates at the same area were 2.6 bottlenose dolphins/km^2 (Barham et al. 1980). The reasons for the large discrepancies between aerial and surface survey density estimates are unclear. Some animals may be counted more than once from boats, or perhaps observers in rapidly moving aircraft do not see all bottlenose dolphin groups. In any case, the differences in density estimates suggest that population estimates of bottlenose dolphins in Florida based on aerial and surface surveys may not be directly comparable.

It is not known whether the study herd remained intact throughout the year or changed composition seasonally. Tagged bottlenose dolphins that were not sighted for long periods (see Figure 4) may have lost their identifying tags, or may have left the study area, as did some bottlenose dolphins in Argentina (Würsig and Würsig 1977).

Fewer than 15% of the field sightings were of solitary bottlenose dolphins, which is an indication of the high degree of gregariousness of free-ranging bottlenose dolphins (Figure 8). Average group size (n = 688 groups) varied from 2 to 6 about an overall mean of 4.8 bottlenose dolphins/group (SE = 0.16; Figures 3A, 8). During summer 1975 and early summer 1976, groups of >40 unmarked bottlenose dolphins, probably from adjacent herds, were observed <1 km offshore in the Gulf of Mexico and within 1 km of the northern

TABLE 1.—Sightings of marked and unmarked dolphins and population size estimates, during periods from December 1975 to July 1976.

Item	17 Dec.-13 Feb.	15 Feb.-17 Mar.	20 Mar.-14 Apr.	17 Apr.-6 May	9 May-6 June	12 June-9 July
A) Number of marked dolphins	19	[1]20.75	24	[1]27.83	37	38
B) Total number of dolphins sighted	261	176	49	200	226	[2]415
C) Number of marked dolphins sighted	38	49	10	67	103	132
D) C/B	0.15	0.28	0.20	0.34	0.46	0.32
E) Estimated population size	130	74	118	83	81	119
F) 95% confidence limits	91-179	55-98	55-221	65-106	67-99	100-142

[1]Tagged dolphins were found dead on 5 March and 3 May 1976; population estimates are adjusted to account for survey days after these animals were dead.
[2]Includes 95 unmarked dolphins (in 5 groups) sighted on the periphery of the study area.

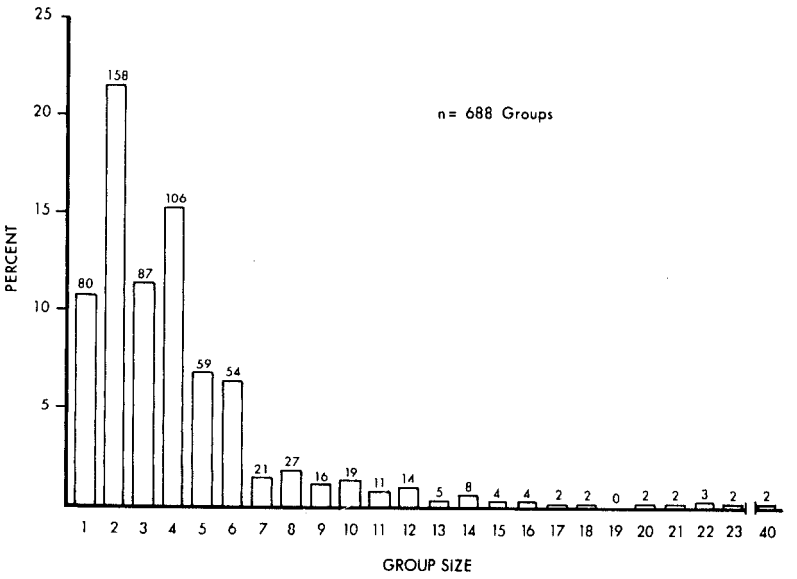

FIGURE 8.—Group size-frequency distribution. Groups were defined as all animals within about 100 m of the survey boat. Numerals indicate the number of groups in each size category.

limit of the study area in Tampa Bay. However, group size-frequency distributions did not vary significantly by month ($P>0.60$; chi-square) or season ($P>0.90$; chi-square). Group sizes were not normally distributed (Kolmogorov-Smirnov test; $P>0.05$) during 11 of the 18 mo of field activity (518 sightings), even after square root transformations (Sokal and Rohlf 1969). The lack of significant monthly trends in herd size was corroborated ($P\leq 0.35$) by a Kruskal-Wallis nonparametric analysis of variance test (Sokal and Rohlf 1969).

Social Interactions

Applying the body length-maturity relationship of Sergeant et al. (1973) we categorized each tagged bottlenose dolphin as adult or subadult. The frequencies of interactions between bottlenose dolphins of various age and sex categories are summarized in Figure 9. Adult males (246-268 cm long) associated primarily with females, apparently preferring females without calves, and were rarely observed with subadult males (210-237 cm). Subadult males were most often seen together. Adult females (235-250 cm) were sighted most often with other females. Subadult females (207-234 cm) were also frequently associated with adult females. An adult female nicknamed "Killer" (240 cm long) was usually sighted with subadult males or four adult females. Details of these observed associations are also discussed by Wells (1978) and Wells et al. (1980).

Sexually segregated groups were sighted on a number of occasions in our study and have been reported in other studies (Evans and Bastian 1969; D. K. Caldwell and M. C. Caldwell 1972; Irvine and Wells 1972; Tayler and Saayman 1972; Mead 1975; Norris and Dohl 1980a). Tavolga (1966) noted four subgroups in her detailed study of a captive colony of bottlenose dolphins at Marineland of Florida: a single adult male, adult females, subadults (mostly males), and juveniles. Miyazaki and Nishiwaki (1978) classified groups of the striped dolphin, *Stenella coeruleoalba*, into juvenile, mature mating, and mature nonmating schools, but did not report if sexual isolation occurred. Tayler and Saayman (1972) reported on the basis of five captures that subadult male bottlenose dolphins off South Africa are rarely found with "bulls" or in exclusively subadult male groups, but that captive subadult males do closely associate with bulls.

Our observations suggest that subadult males rarely interacted with bulls, but largely formed stable primary groups among themselves. Subadult males were never captured with adult males (28 captures). We observed apparent homosexual interactions within a primary group of four known subadult males during February to July 1976, but cannot verify if it is a year-round behavior. Behaviors were classified as homosexual only when an extruded penis or an apparent copulatory attempt was observed.

"Killer's" frequent association with subadult males is difficult to explain. Inasmuch as she was

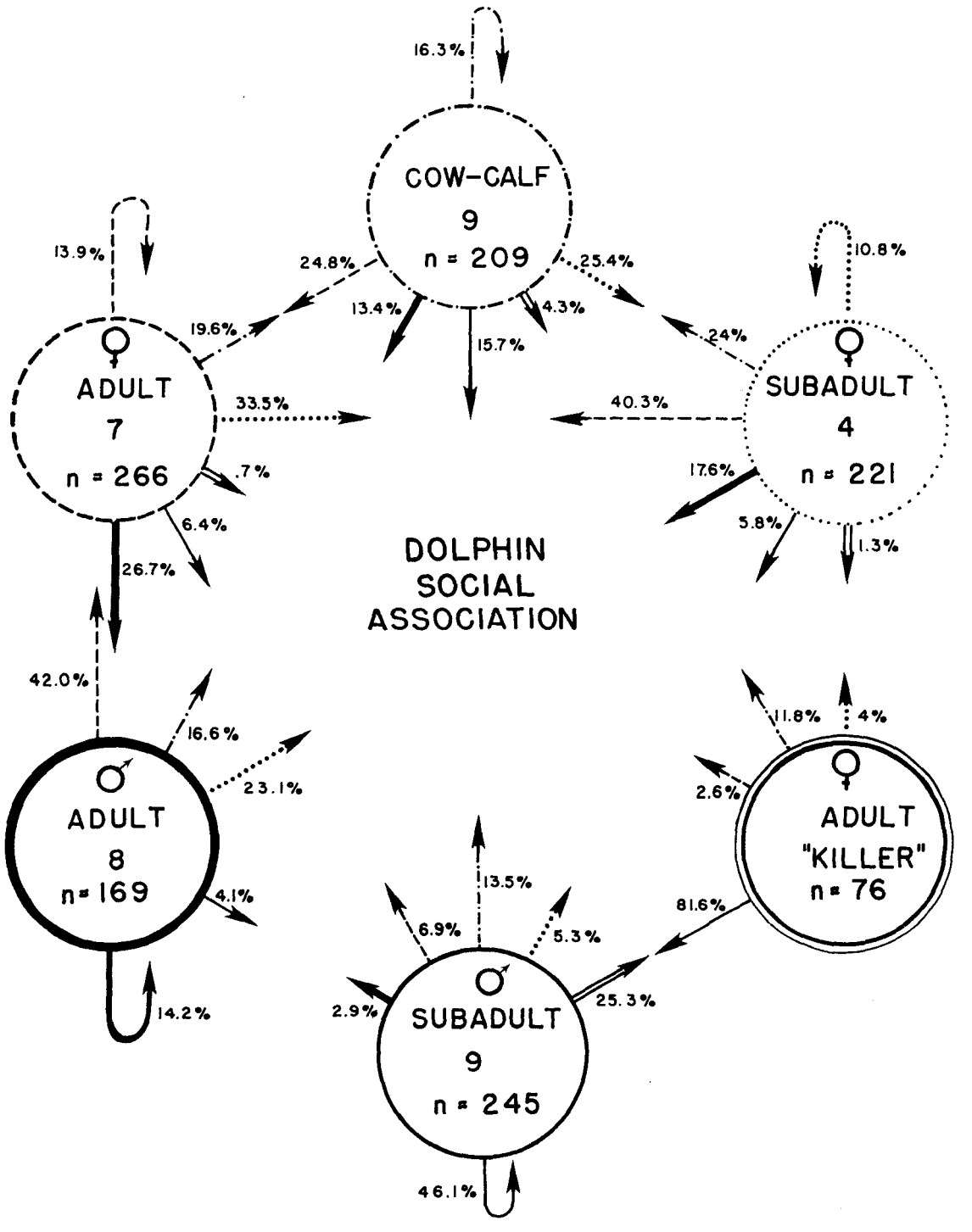

FIGURE 9.—Component social interactions among age-sex classes of known bottlenose dolphins. Sex and length were determined when the animals were captured. Age classes are based on body length-maturity data from Sergeant et al. (1973). Number of individuals is presented under each age-class. n = number of observations. Adult female "Killer" was a dolphin that had an atypical association pattern (see text).

captured and sexed several times, error in sex determination is not likely. She was occasionally seen with the same group of subadult males that had been observed engaging in homosexual activities, and on one occasion she appeared to engage in sexual activities with at least one member of that group.

The associations of longest duration involved cows and calves, although relatively prolonged aggregations of subadult males and frequent associations of adult males with adult females were noted in the spring. One calf was observed during 30 of 32 sightings of the apparent mother over a period of 15 mo, and another calf was observed with its mother on all of 20 sightings during a 9-mo period. We did not observe straying of calves, as has been noted in captivity (see review by M. C. Caldwell and D. K. Caldwell 1972) and inferred for free-ranging bottlenose dolphins in Argentina (Würsig 1978) and the Gulf of Mexico (Leatherwood[12]).

When pursued during capture attempts, calves stayed close beside their fleeing mothers, apparently being partly pulled along in the suction created by the mother's movement through the water (Norris and Prescott 1961; Norris and Dohl 1980a; Leatherwood footnote 12). While the mother was being tagged, calves remained close to the stretcher, often emitting underwater whistles audible in air. A calf released outside the net quickly became tangled in the net while attempting to return inside, where its mother was trapped. When a cow was released before her calf was freed, she invariably patroled outside the net until the calf was released. On one occasion a loud whistle from a bottlenose dolphin calf being tagged brought the mother rapidly to within 5 m of the capture net from a point about 75 m away. Apparently similar behaviors have been observed for *Stenella* sp. involved in the purse seine fishery for yellowfin tuna, *Thunnus albacares* (W. F. Perrin[13]). Close approaches by large male killer whales, *Orcinus orca*, to the outside of an enclosure containing a killer whale calf have also been observed by A. B. Irvine in Puget Sound.

Dolphins being pursued by the capture boat fled as a close-knit group often in a line abreast formation. As with bottlenose dolphins off California (Norris and Prescott 1961; Norris and Dohl 1980a) and off Louisiana (Leatherwood and Platter[14]), some bottlenose dolphins recognized the capture boat and began fleeing rapidly 400 m or more ahead of the boat. The bottlenose dolphins apparently associated the sound of the boat's engine with past captures, since naturally marked animals not previously subjected to our capture attempts did not flee. When part of a bottlenose dolphin group was encircled, the remaining members did not temporarily remain nearby, as has been reported for *Steno bredanensis* (Evans 1967), common dolphins (Pilleri and Knuckey 1968), the dusky dolphin, *Lagenorhynchus obscurus* (Würsig and Würsig 1980), and killer whales (Balcomb and Goebel footnote 6). We often observed and sometimes recaptured dolphins near earlier capture sites, suggesting that capture areas were not avoided.

Behaviors associated with the formation and maintenance of intragroup associations are not well understood. Studies of captive animals have indicated that dominance, exerted by combinations of physical posturing, aggression, and vocalization, may be important in the establishment and maintenance of social hierarchies (Tavolga 1966; M. C. Caldwell and D. K. Caldwell 1967, 1972; Evans and Bastian 1969). Most studies of captive dolphins, however, have been of <15 dolphins, often interspecifically mixed, and confined in a tank. The dominance hierarchies and social structure described for captive groups may therefore not represent the social organization of free-ranging bottlenose dolphins. For instance, the concept of microterritories suggested for captives (M. C. Caldwell and D. K. Caldwell 1972; Tayler and Saayman 1972) and presumably maintained by dominance relationships is probably not relevant to the study of wild bottlenose dolphins, which move constantly and change companions often. The small "family unit" concept proposed by McBride and Kritzler (1951) is also not compatible with our observations of dynamic group membership. Evans and Bastian (1969) proposed that the spatial consideration of primary importance to

[12]Leatherwood, S. 1977. Some preliminary impressions on the numbers and social behavior of free swimming bottlenosed dolphin calves (*Tursiops truncatus*) in the northern Gulf of Mexico. *In* S. H. Ridgway and K. W. Benirschke (editors), Breeding dolphins, present status, suggestions for the future, p. 143-167. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-273 673.

[13]W. F. Perrin, fishery biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, pers. commun. March 1980.

[14]Leatherwood, S., and M. F. Platter. 1975. Aerial assessment of bottlenosed dolphins off Alabama, Mississippi, and Louisiana. *In* D. K. Odell, D. B. Siniff, and G. H. Waring (editors), *Tursiops truncatus* Assessment Workshop, p. 49-86. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PD-291-161.

free-ranging bottlenose dolphins may be inter-individual distances and ease of access to the surface for breathing. The size of the herd home range of *Tursiops truncatus*, the frequently changing group compositions, and the number of bottlenose dolphins apparently residing in the study area suggest that the social organization is very complex.

Food Resources and Feeding Behavior

Striped mullet, *Mugil cephalus*, one of the four most common fish species in the Gulf of Mexico (Gunter 1941), is thought to be the mainstay of the diet of bottlenose dolphins (Gunter 1942; D. K. Caldwell and M. C. Caldwell 1972). Seasonal movements and ranges of tagged striped mullet have been determined in several areas of the gulf coast (Idyll and Sutton 1952; Broadhead and Mefford 1956; de Sylva et al. 1956; Ingle et al. 1962). Usually, the fish remained within 32 km of the capture location, but there is little documentation of daily movements. Local commercial fishermen reported that striped mullet spawn in the Gulf of Mexico in November and remain there until spring. Bottlenose dolphin movements from inshore to gulf waters in November thus appear to be similar to those of their primary prey.

Reports by Futch (1966) and local commercial fishermen indicated that the fish movements, and therefore bottlenose dolphin feeding activities, may also be influenced by the tides. Apparently striped mullet are often found in small groups on the shallow banks of bays and estuaries during the flood tide, and gather into larger schools in deeper water as the tide begins to ebb. Dolphin movements and feeding activities cannot be directly correlated with fish distributions in our study area, but such correlations have been reported for nearshore groups of bottlenose dolphins (Würsig and Würsig 1979) and humpback dolphins (Saayman and Tayler 1979).

We surveyed potential food resources of the bottlenose dolphin by interviewing and occasionally accompanying commercial fishermen in the study area. Although striped mullet were most commonly caught, significant numbers of pinfish, *Lagodon rhomboides*; sheepshead, *Archosargus probatocephalus*; and crevalle jack, *Caranx hippos*, were also taken in the same areas. According to fishermen, local dolphins prefer striped mullet, but when striped mullet are not plentiful will eat any available fish, including the hardhead catfish, *Arius felis*, which they swallow after detaching the head. Opportunistic feeding by bottlenose dolphins has also been noted in other areas (D. K. Caldwell and M. C. Caldwell 1972; Leatherwood 1975).

The use of radio tracking data to indicate feeding behavior has been proposed for the harbor porpoise, *Phocoena phocoena* (Gaskin et al. 1975), and small pelagic cetaceans (see reviews by Leatherwood and Evans 1979). Observations of apparent feeding by tagged and untagged bottlenose dolphins in our study area, however, suggested that respiratory intervals interpreted from breaks in transmitter signals were not a valid criterion to indicate foraging for this species. We believe that the long dives associated with foraging for pelagic species are not typical in the shallow habitat of our study area, and therefore transmitted dive times were relatively uniform. Dive intervals ranged from a few seconds to 4 min 25 s, but no relations between dive intervals and time of day were detectable. Lengths of hourly dives averaged 30-40 s, but varied with location and individual bottlenose dolphin.

Feeding strategies of bottlenose dolphins appear to vary with prey abundance and depth. Large compact groups of feeding bottlenose dolphins were seen in the Gulf of Mexico, although the dispersed foraging pattern reported for common dolphins (Evans 1971, 1974, 1975) and the spinner dolphin, *S. longirostris* (Norris and Dohl 1980b), was also evident. When foraging through shallow bays and grass flats, bottlenose dolphins typically formed slow-moving, dispersed groups. Humpback dolphins off South Africa (Saayman and Tayler 1973, 1979) and bottlenose dolphins off Argentina (Würsig and Würsig 1979) also forage close to shore in small groups. Dispersed feeding would be especially effective if the dolphins stayed in acoustic contact, then responded to certain signals by converging on a concentration of fish discovered by one or more individuals. This type of convergence on food sources has been proposed for dusky dolphins (Würsig and Würsig 1980). We did not observe dolphins rapidly converging on fish schools in shallow areas, but group members did occasionally move to an area where a single dolphin had paused to feed.

Shallow-water feeding was often characterized by a rapid erratic chase that ended in a sudden tight spin or pinwheel—the process lasting 1-5 s and covering 5-20 m. Fish sometimes leaped ahead of the approaching bottlenose dolphin and

were sometimes briefly observed in the bottlenose dolphin's mouth at the end of the chase. Similar behavior by feeding bottlenose dolphins has been described by Leatherwood (1975), Shane and Schmidly (footnote 5), and Shane (1980). The upside down feeding behavior reported for bottlenose dolphins (Leatherwood 1975) and humpback dolphins (Saayman and Tayler 1979) was occasionally observed. Obvious herding of fish as has been reported for several small cetaceans in nearshore areas (D. K. Caldwell and M. C. Caldwell 1972; Saayman et al. 1972; Tayler and Saayman 1972; Saayman et al. 1973; Leatherwood 1975; Saayman and Tayler 1979; Shane and Schmidly footnote 5) was not observed.

In the Gulf of Mexico (at depths of 3-6 m), rapid convergence by bottlenose dolphins within a radius of about 200 m was observed on several occasions. The bottlenose dolphins dove and remained submerged for 30-90 s in an area where no fish were obvious. Then a number of bottlenose dolphins surfaced almost simultaneously in a confined area amid large numbers of jumping striped mullet, some of which were captured in midair. Although cooperative feeding cannot be confirmed, at the very least the bottlenose dolphins were feeding on the same school of fish, and we suspect they may have herded the school at the surface in an organized way. This behavior differs somewhat from other accounts of cooperative feeding (see review by Norris and Dohl 1980a) because the fish school remained at the surface only briefly, after which the bottlenose dolphins milled in the area for 1-3 min before gradually dispersing into small groups. On one occasion, a sequence of rapid convergence on a concentrated fish school, brief intense feedings, and then dispersal into small groups was repeated three times within 45 min by 20-30 bottlenose dolphins.

Concentrated feeding at more productive areas may optimize food availability for flocking birds in the Mojave Desert (Cody 1971), and a similar strategy has been suggested for common dolphins (Evans 1971, 1974, 1975) and spinner dolphins (Norris and Dohl 1980a). These pelagic cetaceans may feed intensively, primarily after dusk and before dawn, in productive areas of the deep scattering layer before moving on. Theoretically, if the dolphins do not return to the same site for some time, the food source will replenish. In contrast, bottlenose dolphins in our study area may exert an almost constant pressure on available food resources. Inshore regions of the study area and the waters along the Gulf beaches were often traversed several times in a single day by different groups of foraging bottlenose dolphins. Evidence from captives and anecdotal accounts from commercial fishermen indicate that bottlenose dolphins also feed at night. Bottlenose dolphins may feed on different ecotypes in different geographic areas (Walker[15]), and presumably *T. truncatus* in coastal Florida have prey and feeding strategies different from bottlenose dolphins in pelagic habitats. Habitat differences are therefore important to any generalized concept of cetacean behavior and herd function. Because ecological variables influence social behavior and therefore the structure of small-cetacean herds (see reviews by Norris and Dohl 1980a; Wells et al. 1980), studies of adjacent inshore and offshore populations of bottlenose dolphins could do much to elucidate the influence of habitat on cetacean behavior.

Reproduction and Growth

Calves were defined as noticeably smaller bottlenose dolphins closely associating with a single larger animal and composed 8.2% of the bottlenose dolphins sighted. Extensive observations of tagged cow-calf pairs suggest that the above definition was generally applicable. Ten calves ($\bar{X}$ = 171 cm; SE = 9) represented 19% of all captures and recaptures. The relative number of calf sightings per month varied significantly ($P<0.0005$; chi-square contingency tables) from August 1975 to July 1976. It is not clear from the sighting data if the calves were produced during a bimodal breeding season with peaks in late spring and early fall, as suggested by Harrison and Ridgway (1971), or during a continuous breeding season with increases in activity during spring and fall. Many small cetaceans copulate throughout the year, and evidence for discrete breeding seasons is still contradictory (see review by Saayman and Tayler 1979).

Growth measurements were obtained from the repeated captures of calves and the recapture of a young individual originally captured in 1970 (Irvine and Wells 1972). Two calves were captured several times during the study; one grew from 172 to 183 cm in 13 mo, and the other from 189 to 198

[15]Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Natl. Mar. Fish. Serv. Admin. Rep. LJ 81 03C. Unpubl. rep.

cm in 7 mo. A young bottlenose dolphin with a deformed jaw originally captured in 1970 grew from 185 to 219 cm in 5.3 yr.

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MAXIMUM YIELD ESTIMATES FOR THE PACIFIC THREAD HERRING, *OPISTHONEMA* SPP., FISHERY IN COSTA RICA

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ABSTRACT

Linear and exponential surplus production models were applied to annual 1969-79 catch per unit effort and effort data obtained from the Costa Rican Pacific thread herring fishery. Effort was estimated as the number of calendar days at sea and standardized to account for presumed increases in fishing power and "real" fishing time (time spent searching for fish) after 1973. Independent regression analyses were performed using standardized and unstandardized effort estimates. In addition, values of the independent variable were estimated both as simple annual effort and as a moving 2-year average of effort. All regressions were statistically significant, but the best fit was obtained with standardized average effort and the exponential model. The "best" estimates of maximum equilibrium yield and effort (Y_s = 6,430 t; f_s = 1,036 days or 1,096 standard days) indicated that the resource was overexploited in 1974-75, 6 years after fishing began. In 1976-77 catch remained at approximately Y_s levels while effort remained above f_s. Catch and observed effort declined dramatically during 1978-79 although standardized effort remained slightly above 1,100 standard days. Future management of the resource may require limited catch and/or effort. The validity of the model is discussed primarily in terms of the nonindependence of the X and Y variables.

Thread herring (genus *Opisthonema*) are schooling pelagic clupeids which inhabit tropical and subtropical coastal waters of the western Atlantic and eastern Pacific Oceans. According to Berry and Barrett (1963), three Pacific species (*Opisthonema libertate*, *O. bulleri*, and *O. medirastre*) are found in continental waters between northern Mexico and Peru while a fourth species (*O. berlangai*) is limited to the Galapagos Islands. These authors differentiated individual species on the basis of the number of gill rakers, a meristic character which was found to be positively related to standard length. The most abundant Atlantic species (*O. oglinum*) is distributed from southern Brazil to the Gulf of Maine.

Thread herring school in nearshore waters (Klima 1971; Magnusson 1971) and are planktivorous feeders. Fuss et al. (1969) observed copepods and larval pelecypods, gastropods, and barnacles in the stomachs of Atlantic thread herring. Peterson (1956) reported mostly phytoplankton from Pacific thread herring stomachs collected in Costa Rica. The presence of fine sediments in the stomachs of Atlantic thread herring indicated that these fish may spend some time feeding on the bottom.

Atlantic thread herring spawn during April-August in the eastern Gulf of Mexico. Fuss et al. (1969) reported a maximum mean gonad index in June, and Houde (1976) collected eggs when surface seawater temperature ranged from 22.5° to 30° C. Most eggs and larvae were collected within 50 km of the coast. Based on the histological examination of reproductive tissue, Paez Barrera[3] reported peak spawning for *O. libertate* in Mexico during June and July at water temperatures of 25°-29° C. Peterson (1956) collected small individuals (<60 mm SL, standard length) in the Gulf of Nicoya, Costa Rica, during all months of the years 1952-54. His observations indicated that spawning may have been continuous. Furthermore, nearly all collections of adults included some individuals which were sexually mature. Continuous recruitment on the Pacific coast of Costa Rica was also implied by the presence of a predominant size group at 18-20 cm SL in most

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[3]Paez Barrera, F. 1976. Desarrollo gonadal, madurez, desove y fecundidad de sardina crinuda, *Opisthonema libertate* (Gunther) de la zona de Mazatlán, basados en el análisis histológico de la gónada. Mem. del Simp. sobre Recursos Masivos de México, Ensenada, B.C., 28-30 de Septiembre de 1976, p. 207-255.

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monthly length-frequency distributions compiled from commercial landings by the Costa Rican Ministry of Agriculture during 1975-77.

Attempts to determine the age and growth of *Opisthonema* spp. based on apparent scale annuli and length-frequency analyses have not produced very satisfactory results, presumably since growth rates and recruitment are more or less continuous throughout the year. Reintjes[4] reported that few Atlantic thread herring live beyond age 4, and Sokolov and Wong[5] speculated that there were three adult year classes of *O. libertate* within the harvestable size range (5-26 cm SL) in the Gulf of California. Paez Barrera (footnote 3) reported a minimum length at maturity of 13-14 cm SL for *O. libertate* in Mexico. Houde (1976) reported that age 1 Atlantic thread herring measured approximately 13 cm SL. Length-frequency distributions for *Opisthonema* spp. sampled from commercial landings in Costa Rica were commonly characterized by a single predominant size group at 18-20 cm SL, but occasionally included a second group at 12-16 cm SL.

Although he presented no information for *Opisthonema*, Beverton (1963) indicated that most clupeid and engraulid species are short lived (5 yr or less) and are generally characterized by high growth and mortality rates. Furthermore, these fish mature at relatively early ages (age at maturity/maximum age = 0.30-0.37) and grow very little after maturing (length at maturity/maximum length = 0.65-0.80) compared with other taxonomic groups. High mortality rates (Z = 0.5-3.0) can be largely attributed to the active predation on these fish by man, birds, and other fish. Highly variable recruitment has contributed to the decline of many stocks of small pelagic fishes for which recruitment appears to be independent of spawning stock size over a wide range of stock sizes (Murphy 1977).

The most important thread herring fisheries are conducted on the Pacific coast of Central and South America. Most of the 1972-77 catch of Pacific thread herring was landed in Ecuador (Table 1) where landings increased by 700% during this 6-yr period. Panama and Mexico accounted for <10% of the total reported landings in 1976 and 1977. Thread herring are harvested with the Pacific sardine, *Sardinops sagax*, in Mexico and are utilized both for human consumption and for fish meal. Thread herring are harvested incidentally to the anchoveta, *Centengraulis mysticetus*, in the Gulf of Panama and reduced to meal. Thread herring fisheries do not presently exist in any of the remaining Central American countries except Costa Rica where, by law, the total production is canned for human consumption.

TABLE 1.—Annual 1972-77 landings (thousand metric tons) of Pacific thread herring in Ecuador, Panama, and Mexico. Sources: FAO Yearbook of Fishery Statistics (1979) and Instituto Nacional de Pesca, Mexico.

Country	1972	1973	1974	1975	1976	1977
Ecuador	552	950	1,100	1,750	2,250	3,830
Panama	143	205	367	201	166	234
Mexico	18	36	22	32	35	65
Total	713	1,191	1,489	1,983	2,451	4,129

Thread herring have been harvested on the Pacific coast of Costa Rica since 1968. The fleet expanded steadily from a single vessel in 1968-69 to nine vessels in 1975. At present the fleet consists of 10 vessels, although only half the fleet may be active at any one time. Most of the fish landed during 1968-73 were harvested in the outer Gulf of Nicoya (Figure 1) and from coastal waters immediately to the south. Purse seiners and trawlers have been prohibited from fishing in the interior of the Gulf of Nicoya since 1975. The fishery expanded as far south as Golfo Dulce near the Panamanian border in 1972. Total catch reached a maximum of 7,500 t in 1975 and declined to about 5,000 t in 1978 and 1979, while total catch per day at sea peaked in 1971 (Figure 2). Catch in the Gulf of Nicoya peaked at 5,000 t in 1972 (Figure 3) and at 2,800 t in Golfo Dulce during 1975 (Figure 4).

The thread herring resource supports a small but important industry in Costa Rica. Landings in 1978 accounted for 36% of all fish and shellfish landed by the domestic fleet and $76,635 in ex-vessel revenue. Most of the herring canned in Costa Rica is sold domestically. A small quantity (9% in 1977) is exported to other Central American countries. There are three canning plants in the country, two in Puntarenas and one in Golfito. Eight of the existing 10 vessels are based in Puntarenas.

The objective of this study was to determine, from historical catch and effort data compiled by

[4]Reintjes, J. W. 1979. A review of the clupeoid and carangid fishery resources in the western central Atlantic. Interregional Project for the Development of Fisheries in the Western Central Atlantic (WECAF), 49 p.

[5]Sokolov, V. A., and M. I. Wong. 1973. Informe científico de las investigaciones sobre los peces pelágicos del Golfo de California (sardina crinuda y anchoveta) en 1971. Inst. Nac. Pesca, Inf. Cién. 2, 41 p.

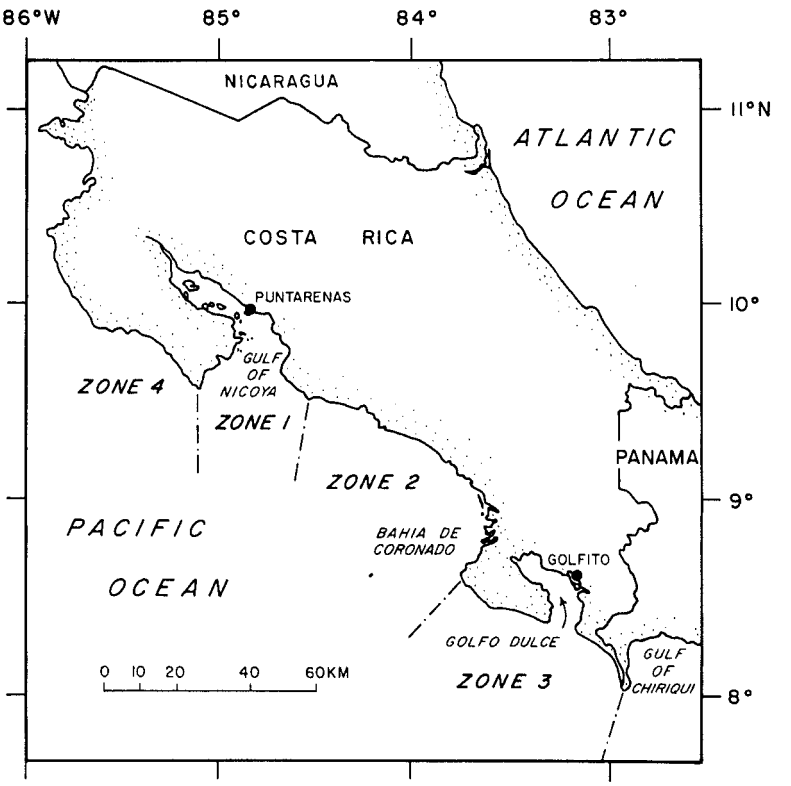

FIGURE 1.—Map of Costa Rica showing four thread herring fishing zones and two principal ports on the Pacific coast.

the Costa Rican Ministry of Agriculture, the maximum equilibrium yield which this resource will support and the amount of fishing effort required to achieve complete utilization. The methodology and the simplifying assumptions used in this study were necessary given the scarcity of biological information, the absence of species-specific catch data, and the nature of available effort statistics, and illustrate some of the problems which impede stock assessments in developing countries.

DEFINITION OF THE UNIT STOCK

Three species of *Opisthonema* are harvested on the Pacific coast of Costa Rica. Species identifica-

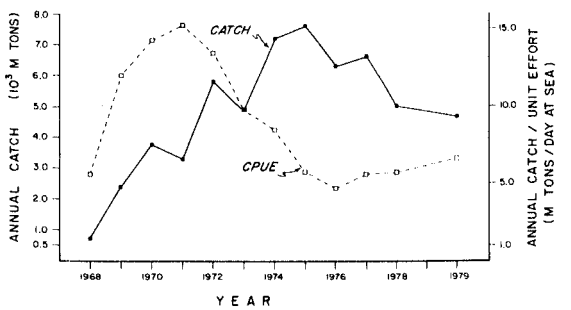

FIGURE 2.—Annual 1968-79 catch and catch per unit effort for three species of thread herring captured on the Pacific coast of Costa Rica (all zones). Catch and effort data were compiled from sales receipts.

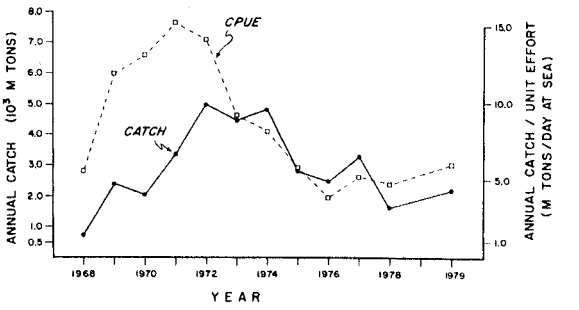

FIGURE 3.—Annual 1968-79 catch and catch per unit effort data for three species of thread herring captured in the Gulf of Nicoya, Costa Rica (zone 1). Catch and effort data were compiled from captain's reports and verified from sales receipts.

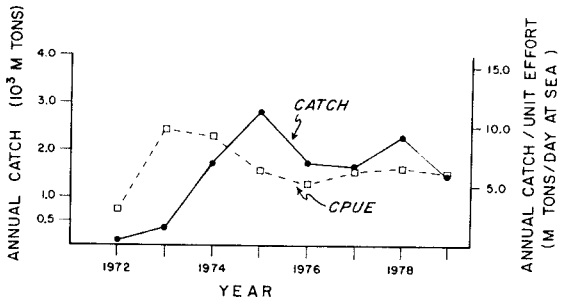

FIGURE 4.—Annual 1972-79 catch and catch per unit effort data for three species of thread herring captured in the Golfo Dulce area of Costa Rica (zone 3). Catch and effort were compiled from captain's reports and verified from sales receipts.

tion is based on the relation between the number of gill rakers and standard length (Berry and Barrett 1963). Over 3,000 specimens of thread herring collected from commercial catches by the Costa Rican Ministry of Agriculture during the period April 1975 to December 1977 were separated into two groups based on external coloration and morphological features. One group ("blue sardines") consisted of fish which more easily lost their scales and which were characterized by a blue dorsal coloration and more shallow, elongated bodies. These fish were predominantly *O. bulleri*. The second group ("green sardines") consisted primarily of *O. medirastre* and *O. libertate*. Fish in this group retained their scales, had deeper bodies, and a greener dorsal coloration. The second group was more abundant than the first, accounting for more than 90% of the fish sampled from commercial landings except during February-July 1977 when blue sardines made up 25-63% of the samples. Since the sampling procedures used were not strictly random and exact species identifications were not attempted, it can only be concluded that *O. medirastre* and *O. libertate* appeared to be the predominant species in the catch during most of the sampling period.

In the absence of species-specific catch and effort information all three species were, for the purposes of analysis, assumed to compose a single unit stock confined to Costa Rican coastal waters. The degree to which the different species shared common growth or natural mortality rates was not known, nor was it certain whether they school together and were thus exploited with the same intensity in the same areas. Although commercial fishermen in Costa Rica have observed that *O. libertate* and *O. medirastre* intermingle in the same schools, *O. bulleri* are rarely captured together with the other two species and apparently do not school with them. Berry and Barrett (1963) reported that the size ranges of all three coastal Pacific species collected in Central and South America were nearly equal, an observation that was generally confirmed in samples taken from commercial catches in Costa Rica and which indicated that all three species were equally susceptible to capture over the same size range. All three species harvested in Costa Rica during 1975-77 reached a maximum size of about 24 cm SL.

The assumption of a single geographic stock in Costa Rican waters was largely an arbitrary one since there was no information available concerning the migratory behavior of the Pacific species. Klima (1971) reported that Atlantic thread herring, *O. oglinum*, in the northeastern Gulf of Mexico seldom are found in depths >100 m and are most common in depths <40 m. Similar observations have been reported for Pacific thread herring in Central America (Magnusson 1971). Kinnear and Fuss (1971) reported seasonal north-south migrations of *O. oglinum* on the west coast of Florida in response to changes in surface water temperatures. A southerly fall migration of 6-7 mi/d has been observed for *O. oglinum* between North Carolina and Florida (Pristas and Cheek 1973). Since seawater temperatures along the Pacific coast of Central America presumably are more constant, such directed migration may not occur.

Despite the fact that the three coastal Pacific species of *Opisthonema* are distributed continuously from the Gulf of California to Peru (Berry and Barrett 1963), there is some justification for treating the Costa Rican thread herring resource as a single geographic unit stock since there are no fisheries for thread herring in any of the other Central American countries except Panama. In Panama, *Opisthonema* spp. are harvested only in the Gulf of Panama and not in the intervening coastal waters of western Panama between the Gulf and the Costa Rican border.

METHODS

Estimation of Catch and Effort Statistics

Total annual catch and effort data were compiled from sales receipts obtained from the canning companies in Puntarenas and Golfito (Table 2). Catch data were reliable since the entire catch in Costa Rican waters was harvested by Costa

TABLE 2.—Annual 1968-79 catch, effort, catch per unit effort, and average effort statistics for three species of thread herring captured on the Pacific coast of Costa Rica. Catch and effort data were compiled from sales receipts. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Year	C_t Catch (t)	f_t Effort (d at sea)	$\bar{f}$ Average effort $=\frac{1}{2}(f_t+f_{t-1})$ (d at sea)	C_t/f_t (t/d)
1968	726	130	65	5.59
1969	2,400	200	165	12.00
1970	3,765	264	232	14.26
1971	3,323	217	240	15.31
1972	5,822	431	324	13.51
1973	4,886	501	466	9.75
1974	7,193	844	672	8.52
1975	7,592	1,304	1,074	5.82
1976	6,330	1,350	1,327	4.69
1977	6,619	1,176	1,263	5.63
1978	5,034	884	1,030	5.70
1979	4,654	753	818	6.18

Rican vessels and sold for canning in these two ports. Effort was estimated from sales receipts as the number of calendar days at sea and recorded as the difference between the dates of departure and arrival in port. One day at sea was considered to include only 12 daylight hours since no fishing was conducted at night. Effort measurements included any daylight time spent in transit to and from port, time actually spent setting and retrieving the net, time spent searching for schools of fish, and any time lost for vessel repairs or other activities unrelated to the capture of fish.

Some information on the division of total effort was available from Ministry of Agriculture biologists who observed vessel activities during five fishing trips in the Gulf of Nicoya during August and September 1980 (Table 3). During a total of 95 h absent from port, 60 h (63%) were spent searching for fish, 23 h in setting and retrieving the net, and 12 h were lost in transit and other activities unrelated to fishing. An average of 8.6 h were spent working per calendar day. The fourth trip was the most productive trip in terms of catch per day, catch per hour search, and catch per total hours, but the first and second trips were the most productive in terms of catch per hour fishing. These observations tended to confirm the assumption that search time was the most significant component of total effort and indicated that catch per day, the index of CPUE (catch per unit effort) used in this assessment, compared more closely to catch per hour search than to catch per hour fishing with the net. Although these observations were recorded for a very short period of time and did not represent average fishing conditions for the entire fishery during that time, they do give an idea of how time at sea was apportioned for vessels fishing close to Puntarenas during trips of 2-3 d duration in 1980 when catches were poor.

The original 1974-79 effort data (Table 2) were adjusted to account for a presumed increase in the proportion of a 12-h day spent searching for fish as stock abundance declined and an improved capture efficiency associated with the construction of larger, more powerful vessels using larger nets. In the absence of reliable information on the decline in resource availability or increased vessel fishing power, the standardization procedures which were applied were very approximate, but served in some degree to counteract the probable underestimation of real fishing effort during the later years of the fishery as measured simply by the number of days at sea. The year 1974 was selected as the critical year to initiate effort standardization since it was in 1974 that the fleet, in response to declining yields in the Gulf of Nicoya, expanded operations in earnest to more distant fishing grounds (Table 4) and increased in size from five active vessels to seven. The fleet continued to exploit more distant fishing grounds during subsequent years and expanded to nine active vessels in 1975-77. Most of the larger vessels were first

TABLE 3.—Detailed catch and effort information recorded by observers aboard thread herring vessels fishing in the Gulf of Nicoya, Costa Rica, during August and September 1980. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Trip	Days[1]	Hours	H/d	Sets	Catch[2] (t)	Search time (%)	Catch per unit effort			
							t/d	t/h search	t/fishing h	t/total h
1	2	22.7	11.4	2	32.0	66	16.0	2.2	4.7	1.4
2	2	16.5	8.2	6	19.0	47	9.5	2.4	5.4	1.2
3	3	27.7	9.2	6	12.0	76	4.0	.6	2.9	.4
4	[3]1	11.9	11.9	4	22.5	39	22.5	4.9	4.0	1.9
5	3	15.9	[4]5.3	6	2.5	74	.8	.2	.8	.2
All	11	94.7	8.6	24	88.0	63	8.0	1.5	3.8	.9

[1]Calendar days absent from port.
[2]Estimated by captain.
[3]Two days were spent tuna fishing.
[4]Trip terminated early morning of day 3 due to equipment failure.

TABLE 4.—Distribution of reported 1968-79 fishing effort for thread herring among the three principal fishing zones on the Pacific coast of Costa Rica and percent of total effort expended in zones two and three. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Year	Effort (d at sea) Zone 1	Zone 2	Zone 3	% total effort in zones 2-3[1]
1968	130	0	0	0.0
1969	200	0	0	0.0
1970	154	110	0	41.7
1971	217	0	0	0.0
1972	351	45	35	18.6
1973	458	8	35	8.6
1974	584	64	187	29.7
1975	490	344	451	61.0
1976	628	359	334	51.3
1977	622	251	270	44.3
1978	339	188	349	60.7
1979	371	125	255	50.5

[1]Total effort includes a small amount of fishing in zone 4 which is not shown in this table.

registered in 1973 or later (Table 5). At least one of the newer vessels was equipped with directional sonar equipment, an addition which greatly aids in the location of schools.

TABLE 5.—Characteristics of purse seine vessels and gear which constituted the Costa Rican thread herring fleet in 1979. Vessels are ranked according to net tonnage and fall roughly into two groups according to size, horsepower, and the size of the net used by each vessel. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Vessel	Year registered	Net tonnage (t)	Length (m)	Capacity (t)	Horse-power	Net size (m)
			Group 1			
1	1975	20	13.7	—	150	—
2	1971	30	15.2	27	180	324 × 32
3	1971	33	17.1	33	125	324 × 32
4	1973	35	17.7	30	180	324 × 32
5	1971	40	15.2	38	40	324 × 32
[1]6	1973	40	18.9	45	228	360 × 45
			Group 2			
7	1973	42	24.4	60	500	450 × 36
8	1973	51	24.4	70	420	450 × 36
9	1973	56	26.5	120	360	504 × 36
10	1977	70	22.9	70	240	—
11	1975	75	22.9	60	330	486 × 54

[1]This vessel was lost at sea in October 1979.

Original 1974-79 effort data were adjusted (Table 6) to account for increased search time by increasing observed effort in five 5% annual increments beginning in 1975 and by a constant 25% annual increment to account for increased fishing power beginning in 1974. The first adjustment was based on the presumption that no more than 5 h in an average 12-h day (or 50% of the total fishing time after deducting 2 h for travel to and from port) were spent searching for fish in the early years of the fishery when fishing was concentrated primarily in the Gulf of Nicoya (Table 4), whereas 9 out of 12 h (75%) may have been spent searching for fish in 1979, assuming that the fish were less abundant and that vessels which travelled longer distances to and from fishing grounds in zones two and three devoted most of their daylight transit time to searching. This last assumption has in fact been confirmed by vessel captains. Observations made aboard vessels fishing near Puntarenas in 1980 during only 11 d (Table 3) showed that 63% of the daylight hours were devoted to searching. Since catch data originally collected for individual vessels and trips were no longer available when this assessment was conducted, the relative fishing power of individual vessels and the factors affecting vessel performance could not be determined.

Yield Analyses

Maximum equilibrium yield (Y_s) and its corresponding effort (f_s) were estimated by applying the linear and exponential forms of the surplus production model to annual catch and effort data compiled during 1969-79. These data were collected beginning in 1968 when fishing began and represented fishing activity during an initial period of high CPUE and low effort, an intermediate period when larger vessels were built and

TABLE 6.—Annual 1974-79 catch, adjusted effort and adjusted catch per unit effort (CPUE) statistics for three species of thread herring captured on the Pacific coast of Costa Rica. Original effort data were adjusted to account for a presumed 25% annual increase in vessel fishing power beginning in 1974 and an additional 5% annual increment to account for a presumed increase in search time per day at sea beginning in 1975.

Year	Catch C_t (t)	Original effort f_t (d at sea)	Correction factor x_t	Adjusted effort $x_t f_t$ (standard d)	Adjusted CPUE $C_t/x_t f_t$ (t/standard d)	Average effort $\frac{1}{2}(x_t f_t + x_{t-1} f_{t-1})$ (standard d)
1974	7,193	844	1.25	[1]1,055	6.82	778
1975	7,592	1,304	1.30	1,695	4.48	1,375
1976	6,330	1,350	1.35	1,822	3.47	1,758
1977	6,619	1,176	1.40	1,646	4.02	1,734
1978	5,034	884	1.45	1,282	3.93	1,464
1979	4,654	753	1.50	1,130	4.12	1,206

[1]$x_t f_t$ in 1973 was 1.0(501 d) = 501 d.

the fleet expanded to new fishing grounds in response to declining CPUE and a later period characterized by diminished total production and severely reduced CPUE throughout the entire geographic range of the fishery. Estimates of maximum equilibrium yield and the amount of fishing effort required to produce that yield could serve as "starting points" for management strategies intended to conserve the Costa Rican thread herring resource and achieve maximum social and economic benefits from the fishery.

The linear surplus production model was first outlined by Graham (1935) and further developed by Schaefer (1954). These authors postulated that under equilibrium conditions the instantaneous rate of surplus production from a given population at any time (t) is directly proportional to the biomass (B_t) of the population at that time and to the difference between the theoretical maximum biomass (B_∞) and B_t and inversely proportional to B_∞, i.e.

$$\frac{dB}{dt} = \frac{kB_t(B_\infty - B_t)}{B_\infty} \tag{1}$$

where k = the instantaneous rate of increase in stock size at densities approaching zero.

Moreover, when the biomass which exceeds an equilibrium level (B_E) is being removed at the same rate as it is produced, the surplus production (dB/dt) is converted into an annual equilibrium yield (Y_E) according to the following expression:

$$\frac{dB}{dt} = Y_E = F_E B_E \tag{2}$$

where F_E = rate of fishing which maintains the population at B_E.

If we assume that the rate of fishing (or instantaneous rate of fishing mortality) at equilibrium is proportional to the fishing intensity (or effort) then

$$F_E = qf_E \tag{3}$$

where f_E = fishing effort under equilibrium conditions

q = the coefficient of "catchability," i.e., the vulnerability of the population to fishing.

From Equations (1) and (2), at equilibrium

$$\frac{dB}{dt} = Y_E = F_E B_E = \frac{kB_E(B_\infty - B_E)}{B_\infty}. \tag{4}$$

Substituting Y_E/F_E for B_E in Equation (4)

$$Y_E B_E = F_E B_\infty - \frac{B_\infty}{k} F_E{}^2 \tag{5}$$

and from Equation (3)

$$Y_E = qB_\infty f_E - \frac{q^2 B_\infty}{k} f_E{}^2 \tag{6}$$

which defines a parabola in which Y_E is a function of f_E.

Dividing both sides of Equation (6) by f_E yields a linear relationship $Y_E/f_E = a + bf_E$ where the intercept $a = qB_\infty$ and the slope $b = q^2B_\infty/k$. The effort f_s which corresponds to the maximum equilibrium catch Y_s is determined from the relationship

$$\frac{dY_E}{df_E} = a - 2bf_E = 0. \tag{7}$$

Therefore

$$f_E - f_s = \frac{a}{2b}. \tag{8}$$

Substituting Equation (8) in Equation (6), the maximum equilibrium yield Y_s determined from the regression function is

$$Y_E = Y_s = \frac{a^2}{4b}. \tag{9}$$

Thus, when Equation (3) is valid, estimates of maximum equilibrium yield and associated effort

can be obtained from CPUE and effort data compiled from a unit stock fishery under equilibrium conditions even when the catchability coefficient (q) is unknown.

Since catch and CPUE will usually be related to effort within a single year and during several preceding years, Gulland (1969) has argued that the abundance of a particular year class which has been in the fishery for x years would be influenced by the fishing mortalities during those x years and proposed that the total CPUE for all ages during any given year would be related to some weighted mean of fishing effort in those x years. According to Gulland (1969), if this mean is taken over a period of time equal to the mean duration of life in the exploited phase, then the relation between CPUE and this mean effort $\bar{f}$ will approximate that between CPUE and effort in the steady state.

An exponential form of the surplus production model was developed by Fox (1970) to express the nonlinear relationship between CPUE and effort statistics. The exponential surplus production model was based on the assumption that the rate of population increase was best described by the Gompertz growth function rather than the logistic growth function assumed by the linear form of the model. For the exponential model, under equilibrium conditions

$$\frac{dB}{dt} = kB_E(\log_e B_\infty - \log_e B_E) \tag{10}$$

and the annual equilibrium yield (Y_E) is therefore

$$\frac{dB}{dt} = Y_E = kB_E(\log_e B_\infty - \log_e B_E). \tag{11}$$

Since CPUE ($Y/f = U$) is defined to be proportional to population biomass

$$B_E = \frac{1}{q}\left(\frac{Y_E}{f_E}\right) = \frac{U_E}{q}, \tag{12}$$

Equation (11) can be rewritten as

$$\frac{dB}{dt} = Y_E = \frac{U_E}{q} k\left(\log_e \frac{U_\infty}{q} - \log_e \frac{U_E}{q}\right). \tag{13}$$

Collecting terms and dividing through by U_E ($= Y_E/f_E$)

$$f_E = \frac{k}{q}(\log_e U_\infty - \log_e U_E) \tag{14}$$

or

$$\log_e U_E = \log_e U_\infty - \left(\frac{q}{k}\right) f_E \tag{15}$$

which is equivalent to

$$U_E = U_\infty e^{-bf_E}. \tag{16}$$

Multiplying Equation (16) by the fishing effort at equilibrium (f_E)

$$Y_E = f_E U_\infty e^{-bf_E}. \tag{17}$$

Therefore, the effort (f_s) which produces maximum equilibrium yield (Y_s) is determined from the relationship

$$\frac{dY_E}{df_E} = -bf_E U_\infty e^{-bf_E} + U_\infty e^{-bf_E} = 0 \tag{18}$$

and

$$f_s = \frac{1}{b}. \tag{19}$$

Since $bf_s = 1$, CPUE at f_s (U_s) is

$$U_s = U_\infty e^{-bf_s} = \frac{U_\infty}{e} \tag{20}$$

and the maximum equilibrium yield (Y_s) is given by

$$Y_s = f_s U_s = \frac{U_\infty}{be}. \tag{21}$$

Y_S and f_S were estimated from linear and exponential regressions of CPUE vs. effort when the effort corresponding to a given year's catch was set equal to effort applied during the same year (f_t), or an average of the effort applied buring the same year and the previous year ($\bar{f}$). For the purposes of calculating average effort, it was assumed that thread herring exploited in Costa Rican waters were recruited to the fishery at age 1 and remained in the exploitable size range for 3 yr. Effort was therefore averaged for a 2-yr period according to the procedure described by Gulland (1969) on the presumption that the mean duration of life in the exploitable size range was 2 yr. This assumption was generally supported by age and growth observations for species of this genus (Houde 1976; Sokolov and Wong footnote 5; Paez Barrera footnote 3; Reintjes footnote 4) but needs to be confirmed by specific growth studies.

A total of eight pairs of Y_S and f_S estimates were obtained from both the original and standardized data sets (Table 7). Analysis of the variance due to random error after regression was evaluated by calculating F-statistics. All regressions were performed for 1969-79 data since the 1968 catch was extremely low relative to the amount of effort expended (Table 3), suggesting that the single vessel which was in operation that year was not performing to its full capacity. For each model, predicted yield values for f_E = average observed effort and f_E = average standardized effort were plotted and compared with actual annual 1969-79 yields. Values of equilibrium yield (Y_E) predicted by each model for given values of equilibrium effort (f_E) were calculated according to

$$Y_E = af_E - bf_E{}^2 \quad (22)$$

for the linear model, and

$$Y_E = af_E e^{-bf_E} \quad (23)$$

for the exponential model.

RESULTS AND DISCUSSION

The results (Table 7) indicated a range of Y_S and f_S estimates depending on the model, the form of the independent variable (f_t or $\bar{f}$), and whether or not effort was standardized. For all cases, Y_S ranged from 6,290 to 7,890 t. A wider range of Y_S estimates was predicted by the linear model (6,700-7,890 t) as compared with the exponential model (6,290-6,730 t). Observed f_S estimates ranged from 888 to 1,067 d and standardized f_S estimates ranged from 1,041 to 1,117 standard days. Given the range of options which were tested, these ranges were not extreme. All regressions were statistically significant at >99% confidence levels.

Based on the "goodness of fit" as evaluated by the F-statistic, $\bar{f}$ produced a better fit than f_t in all cases, as did the exponential model as opposed to the linear model and the standardization of effort. The improved fit of the exponential model to CPUE vs. average observed and average standardized effort graphically was quite obvious (Figures 5, 6). Examining the independent effects on maximum equilibrium yield estimates produced by the standardization of effort data and the use of two different models, it was apparent that within each model standardization of the 1974-79 data increased Y_S, especially in the case of the linear model whereas use of the exponential model decreased Y_S estimates for both the standardized and observed data, but more significantly with the standardized data. Furthermore, the choice of f_t or $\bar{f}$ as the independent variable had very little effect on the magnitude of these changes. Looking at the

TABLE 7.—Summary of maximum equilibrium yield (Y_S), the amount of fishing effort which produces maximum equilibrium yield (f_S), and Y_S/f_S estimates for the Costa Rican thread herring fishery as derived from linear and exponential surplus production models applied to 1969-79 catch per unit effort and effort data. Linear and exponential regressions were repeated using effort data collected during the same year (f_t) and average effort over a 2-yr period ($\bar{f}$) as well as observed and adjusted effort estimates (see Tables 2, 6). Analyses of variance (F-tests) indicated that all regressions were statistically significant at 99% confidence levels.

Model	Effort	Y-intercept a	Slope × 10^3 b	Y_S[1] (t)	f_S (d at sea)	Y_S/f_S (t/d)	F-statistic
Linear	f_t observed	15.21	−8.317	6,950	914	7.60	41.4
	$\bar{f}$ observed	15.09	−8.494	6,700	888	7.54	61.5
	f_t adjusted	14.81	−6.952	7,890	[2]1,065	[2]7.41	58.4
	$\bar{f}$ adjusted	14.51	−6.969	7,550	[2]1,041	[2]7.25	64.8
Exponential	f_t observed	16.61	− .937	6,520	1,067	6.11	54.2
	$\bar{f}$ observed	16.50	− .965	6,290	1,036	6.07	114.7
	f_t adjusted	16.39	− .895	6,730	[2]1,117	[2]6.02	79.2
	$\bar{f}$ adjusted	15.96	− .912	6,430	[2]1,096	[2]5.87	138.8

[1]Rounded off to the nearest 10 t.
[2]Effort expressed in standard days at sea.

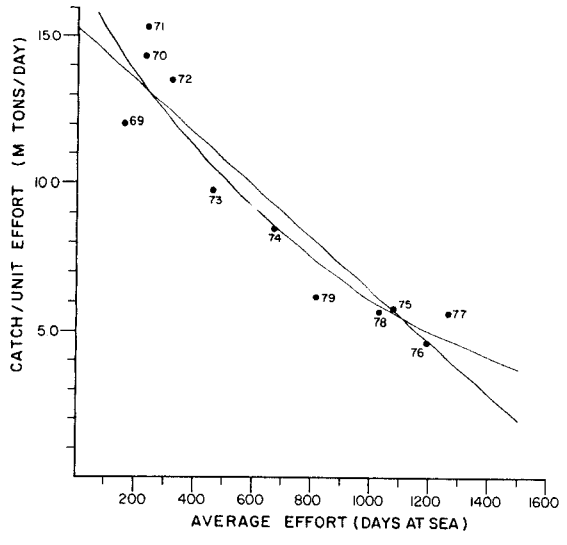

FIGURE 5.—Linear and exponential regressions of annual 1969-79 catch per unit effort versus observed effort averaged over a 2-yr period for three species of thread herring captured on the Pacific coast of Costa Rica.

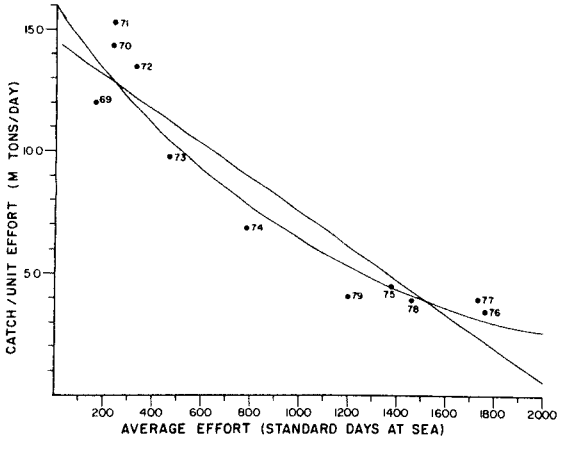

FIGURE 6.—Linear and exponential regressions of annual 1969-79 catch per unit effort versus standardized effort averaged over a 2-yr period for three species of thread herring captured on the Pacific coast of Costa Rica. Effort was standardized to account for improved capture efficiency and reduced resource availability after 1973 (see text).

effects on effort at Y_s, the exponential model produced higher f_s estimates, but only significantly with observed effort data.

Using "goodness of fit" as the only criterion, the most acceptable Y_s estimate was 6,430 t. This Y_s was surpassed by 760 t in 1974 and by 1,160 t in 1975. Catch remained at this maximum equilibrium level in 1976 and 1977, but declined to the pre-1974 level in 1978 and 1979. In fact, all the yield analyses except the linear model as applied to standardized CPUE and effort data indicated overfishing in 1974 and 1975.

According to the "best" unadjusted f_s estimate (1,036 d), fishing effort in 1975 abruptly exceeded—by 20%—the level which produced the maximum equilibrium catch and remained excessive in 1976 and 1977. Observed effort declined dramatically after 1977. Using standardized effort as a guide, the most acceptable f_s estimate (1,096 standard days) was exceeded by an average annual amount of 57% during 1975-77. Assuming that the standardization procedure was accurate, "real" effort remained slightly above 1,100 standard days in 1978 and 1979 even though catches were considerably below the estimated Y_s of 6,430 t. The exponential model predicted that the maximum equilibrium yield would be maintained when CPUE was 6.1 t/d or 5.9-6.0 t/standard day. The linear model predicted considerably higher Y_s/f_s values.

A comparison of the predicted yield curves for both models—as applied only to average observed and standardized effort—with actual 1969-79 catches (Figures 7, 8) revealed a closer overall agreement between catch and predicted yields for the exponential model even though the linear model produced a closer agreement for certain

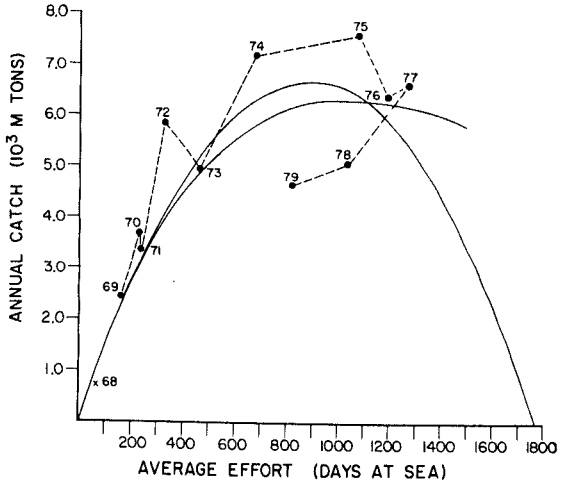

FIGURE 7.—Costa Rican thread herring yield curve predicted by the exponential and linear surplus production models and annual 1968-79 catch and average observed effort data.

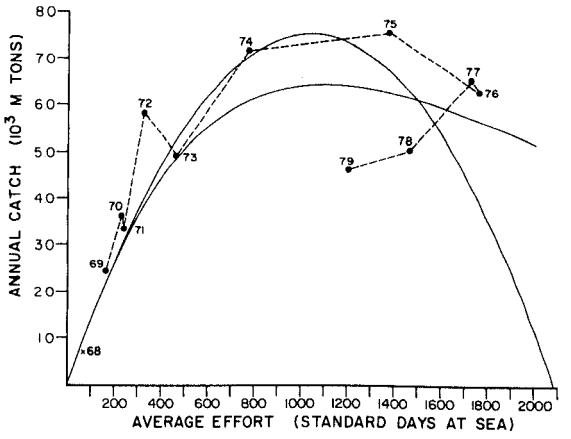

FIGURE 8.—Costa Rican thread herring yield curves predicted by the exponential and linear surplus production models and annual 1968-79 catch and average standardized effort data.

years. Catches in 1972, 1974, and 1975 were considerably greater than Y_E values estimated by the exponential model. The linear model predicted actual yields more accurately through 1975, especially when effort data were standardized, but deviated substantially in 1976 and 1977.

The general tendency toward increasing effort ceased in 1978 and 1979 when substantially lower catches were taken with less effort (Figures 7, 8). Linear and exponential models were fit to 1969-77 data, using average effort only, since it appeared that a closer agreement between observed and predicted yields might be obtained if data for the last 2 yr were eliminated. This was not the case. Y_s estimates increased by 280-360 t and f_s estimates by about 50 d (Table 8), corresponding to a slight shift upwards and to the right in the predicted yield curves, but no statistical improvement in fit could be demonstrated. Yield analyses therefore were quite robust since approximately the same results were obtained from the two data sets.

TABLE 8.—Estimates of maximum equilibrium yield (Y_s), the corresponding amount of fishing effort (f_s) and Y_s/f_s estimates for the Costa Rican thread herring fishery as derived from linear and exponential surplus production models for 1969-76. Only average observed and adjusted effort data were used.

Model	Effort	Y_s[1] (t)	f_s (d at sea)	Y_s/f_s (t/d)	F-statistic
Linear	Observed	7,050	930	7.58	54.7
	Adjusted	7,910	[2]1,090	7.26	49.1
Exponential	Observed	6,570	1,075	6.11	124.8
	Adjusted	6,780	[2]1,149	5.90	138.2

[1]Rounded off to the nearest 10 t.
[2]Effort expressed in standard days at sea.

Evaluation of the Model

A fundamental assumption of the surplus production yield model is that surplus population growth that is harvested by the fishery is at any point in time a function of population biomass. Under the assumption that fishing mortality is directly related to fishing effort by a constant proportionality factor, changes in the rate of population growth can also be related to fishing effort. Thus, the model assumes equilibrium conditions, i.e., that changes in population size—as estimated by CPUE—will remain in equilibrium with a given fishing effort. For developing fisheries in which effort is continually increasing, this equilibrium seldom has an opportunity to become established. Even in cases where effort does stabilize, variations in population size (and therefore, yields) can be expected, especially if recruitment is highly variable and bears little relation to spawning stock size. The problem is further exacerbated if there is a significant delay between spawning and recruitment since the model assumes that the response of equilibrium yield to changes in population size is immediate. In fact, yield in any given year will seldom be related to population size during the same year.

For the Pacific thread herring, the presumed lag time between spawning and recruitment was small (1 yr?) and correction procedures were not employed. The relationship between recruitment and stock size for *Opisthonema* spp. was not known, but the fact that the Costa Rican thread herring population declined without major interruptions once the fishery began suggests that recruitment fluctuations were not extreme. If recruitment had varied significantly as stock size declined, the reduction in CPUE with increasing effort (Figures 5, 6) would not have been so uniform and the model would not have fit the data nearly so well.

A major problem which is common to all surplus production yield analyses is the nonindependence of X and Y variables when CPUE is plotted as a function of effort. As pointed out by Sissenwine (1978), the relationship between X and its reciprocal is hyperbolic. Therefore, CPUE vs. effort relationships are inherently biased. Following Gulland's (1969) procedure for averaging effort in the independent variable, not only does the model

more closely approximate equilibrium conditions, but the replacement of f_t by $\bar{f}$ reduces the interdependence of the two variables. However, as demonstrated by Roff and Fairbairn (1980), temporal trends in effort such as those observed for the Costa Rican thread herring fishery produce correlations between f_t and $\bar{f}$ since both are increasing (or decreasing). This autocorrelation in the independent variable in turn indicates a spurious correlation between CPUE and average effort. In the examples examined by those authors, the degree of autocorrelation between f_t and $\bar{f}$ increased when shorter time periods were used to calculate $\bar{f}$. Furthermore, for periods of 2 or 3 yr, there was a significant correlation between f_t and $\bar{f}$ even in the absence of trends in f_t over time.

In the present assessment, since there were definite trends in both standardized and unstandardized effort and since effort was averaged over only a 2-yr period, the nonindependence of the variables in the regression analyses could not have been significantly reduced. In fact, an examination of the deviations between observed and predicted CPUE for both models as applied to average observed and standardized effort (Figure 9) revealed considerable time trends. These trends were more obvious after effort standardization. Clearly, the variables in the regression analyses were not independent. Strictly speaking, therefore, the F-test used to evaluate the degree of fit was not valid since it assumes that Y observations are independent and normally distributed with common variance. Residual mean squares for the individual regression analyses, however, assume nothing about the distributive properties of the error term in the regression model. Although they cannot be used to evaluate the statistical significance of fit, they did confirm that better fits were obtained with average effort, the exponential model and standardized effort.

A second problem which was not addressed was the assumption that fishing mortality remained directly proportional to fishing effort (Equation (3)) as population size diminished. Thread herring may remain vulnerable to capture even at low stock sizes since they congregate in schools at the surface, i.e., the same fishing mortality may be exerted even with reduced effort. If fishing mortality and effort do not remain directly proportional, the surplus production model is not appropriate for predicting maximum equilibrium yields. There was no way to evaluate this possible source of error.

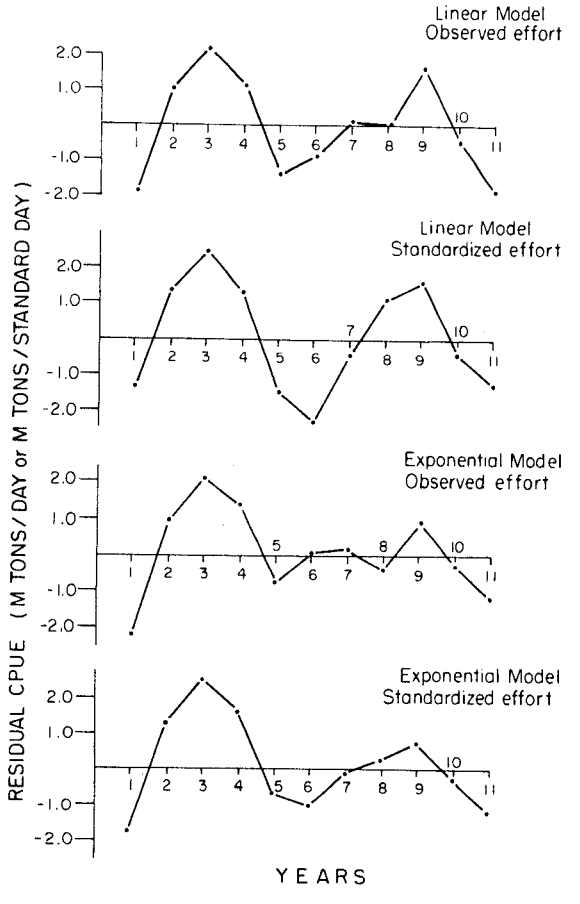

FIGURE 9.—Residual (observed-predicted) 1969-79 catch per unit effort values for the linear and exponential yield models arranged in chronological sequence.

Despite these problems, the surplus production model provided a clear analytical interpretation of the data. The range of Y_s and f_s estimates was not extreme, although the linear model applied to standardized data produced higher Y_s estimates than the other analyses. While there was no basis for assessing how "correct" the standardization procedure was, it did result in higher Y_s and f_s estimates for both the linear and exponential models and improved the least squares fit to the data, especially for the exponential model. Clearly, some adjustment in observed effort was called for. Acceptable estimates of Y_s and f_s were obtained from a fairly short time series of catch and effort data (11 yr). The success of this assessment was due in part to the reliability of the catch and effort data provided by the canning companies to the Ministry of Agriculture, and the fact that data

were available from the beginning of the fishery as well as from the period characterized by diminishing yields.

Management Implications

This assessment of the Costa Rican thread herring resource indicated that a maximum equilibrium yield of approximately 6,430 t was surpassed in 1974-75, leading to stock depletion and reduced catches in subsequent years. Declining catches during 1976-79 were certainly due only in part to reduced effort. Effort increased dramatically after 1973 and remained in excess of f_s (1,036 d) during 1975-77. "Real" effort may have remained slightly above optimum even in 1978 and 1979 when catch declined to about 5,000 t.

Management thus far has been self imposed by the industry in response to rapidly declining CPUE. Economic returns have presumably suffered at least as much as biomass yields. To protect the resource, Costa Rican Government regulation would only be necessary if effort again approached 1,000 d at sea or if catch exceeded 6,500 t. Regulation of effort should concentrate on "real" effort, not merely the number of days vessels spend at sea. It would be important, therefore, to maintain effort at some level below 1,000 d if fishing power were suddenly increased, say, by the use of aircraft to spot schools of fish. Since real effort is not easily measured, a catch quota might be a more practical management strategy. Given the small number of vessels in the fishery, allocation of vessel quotas would be feasible. A reduction in the number of vessels, however, would more effectively maintain acceptable economic returns for the industry. Maximum economic returns would presumably be achieved at some effort level below f_s.

Once an exploited population is depleted, biomass can be restored to a level which supports maximum equilibrium yield by reducing the harvest of adults, thus reducing adult mortality and stimulating increased recruitment. Catch should be maintained at reduced levels for a period of time equal to the delay between spawning and recruitment. As a general policy, fishing at below Y_s also protects to some extent against additional stock depletion due to poor recruitment. For the Costa Rican thread herring population, some increase in stock size (and therefore CPUE) following overfishing in 1974-75 should have been noticeable after a year or two of reduced catches such as occurred in 1978-79. The observed increase in CPUE since 1976 (Table 2, Figure 2) was small and may not have been "real" since standardized CPUE stabilized after 1976 (Table 6). However, catch and effort data available for the first 5 mo of 1980 (Table 9) showed a continued low CPUE when compared with the same period in 1979.

TABLE 9.—Observed catch, effort, and CPUE data compiled from sales receipts for the first 5 mo of 1979 and 1980 for thread herring captured on the Pacific coast of Costa Rica. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Period	Catch (t)	Effort (d at sea)	CPUE (t/d at sea)
Jan.-May 1979	2,270	330	6.88
Jan.-May 1980	1,860	340	5.47

Unit stock identification is an important area requiring further research. Although thread herring on the Pacific coast of Central America may not be highly migratory, it seems likely that there is some mixing across national boundaries. The rapid decline in population size in Costa Rican waters—as inferred from reduced CPUE estimates—would not have been possible, however, if there had been a significant influx of fish from other areas along the Central American coastline. The Panamanian thread herring fishery is only active in the Gulf of Panama, although thread herring were detected acoustically in the Gulf of Chiriqui (see Figure 1) and off Guatemala, El Salvador, and Nicaragua during a 1970 survey (Magnusson 1971). If the same stock is presently being exploited in Costa Rican and Panamanian waters, stock assessment and resource management should be a joint activity of both countries. The possibility also exists that more than one stock is present in Costa Rican waters, either geographically or taxonomically. Clearly, the assumption that the three species which currently make up the catch can be treated as a single unit stock needs to be confirmed with additional ecological and life history information. In the meantime, efforts should be made to determine the species composition of landings, and to compile catch and effort data by species.

SUMMARY

1. Catch and effort data were compiled for three species of Pacific thread herring harvested in Costa Rican waters during 1968-79. Effort was estimated as the number of calendar days at sea. Data were available from the beginning of the

fishery and from a period of diminishing and declining yields.

2. Effort data were standardized to account for a presumed 25% increase in capture efficiency beginning in 1974 when larger, more powerful vessels with larger nets first entered the fishery and for a presumed 5% annual increment in the proportion of time spent searching for fish as stock size declined beginning in 1975.

3. Estimates of maximum equilibrium yield (Y_s) were obtained by fitting linear and exponential forms of the surplus production model to plots of catch per unit effort (CPUE) vs. effort. Eight yield analyses were performed using observed and standardized effort to calculate CPUE and a moving 2-yr average of observed and standardized effort as well as simple annual observed and standardized effort as the independent variable.

4. All regression analyses were statistically significant at the 99% confidence level. The standardization and averaging of effort data, and the use of the exponential model improved the degree of statistical fit. The predicted yield curves fit observed catch data fairly well.

5. Y_s estimates ranged from 6,290 to 7,890 t, observed f_s ranged from 888 to 1,067 d and standardized f_s ranged from 1,041 to 1,117 standard days. The best fit to the data was obtained with the exponential model applied to standardized CPUE vs. average standardized effort data. This analysis produced a Y_s estimate of 6,430 t and a f_s estimate of 1,096 standard days. The best estimate of unstandardized effort was 1,036 d.

6. The "best" Y_s estimate was exceeded by 760 t in 1974 and by 1,160 t in 1975. Overfishing probably contributed to catches of 5,000 t and lower in 1978-79. Observed effort abruptly exceeded f_s in 1975 by 20%, remained above 1,000 d in 1976 and 1977, and then declined dramatically in 1978-79. Standardized effort remained slightly above standardized f_s even in 1978 and 1979.

7. Attempts to reduce the dependence of the CPUE and effort variables in the regression analyses by averaging effort were of doubtful value since there was a trend toward increasing effort as the fishery developed and since only 2 yr were used to average effort. Thus, significant autocorrelations between f_s and $\bar{f}$ could not be avoided. Obvious time trends in the deviations between predicted and observed CPUE provided evidence for the nonindependence of the variables in the regression analyses. This problem, however, was not believed to have seriously altered the results of the assessment.

8. The industry should be encouraged to either maintain effort below 1,000 d at sea or annual catch below 6,500 t as was done in 1978 and 1979. If regulations are necessary, a catch quota may prove to be more feasible since it could fairly easily be allocated to individual vessels and since effort limitations must consider "real" changes in fishing effort which are difficult to quantify. On the other hand, a reduction in the number of vessels would improve economic returns for the fishing vessels which remain in the fishery.

9. Unit stock identification is an important area requiring further research. The inferred rapid reduction in stock abundance in Costa Rican waters suggests that there was little net immigration of thread herring from neighboring countries, but the degree to which the stock (or stocks) exploited by the Costa Rican fleet may also be exploited elsewhere (Panama, in particular) needs to be clarified.

ACKNOWLEDGMENTS

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DIEL-DEPTH DISTRIBUTION OF SUMMER ICHTHYOPLANKTON IN THE MIDDLE ATLANTIC BIGHT

ARTHUR W. KENDALL, JR.[1] AND N. A. NAPLIN[2]

ABSTRACT

A series of discrete depth plankton tows made every 3 h over a 72-h period off Ocean City, Maryland, in July 1974 allowed analysis of the diel-depth distribution of ichthyoplankton. Overall egg and larval densities averaged 5.6 eggs/m^3 and 6.3 larvae/m^3. Seven species of eggs made up over 90% of those caught with *Merluccius bilinearis* eggs accounting for 45.9% of the eggs taken. Over 16 species of fish larvae were identified, of which *Urophycis* sp., *Pomatomus saltatrix*, and *Citharichthys arctifrons* were the most abundant. The fish eggs were concentrated near the surface and their age distribution at different times of day provided information about diel spawning times, spawning depth, and embryonic mortality. Larvae of all species moved to shallower depths at night. The actual depth distribution and extent of vertical movements varied among the species. The surface and the thermocline were the primary water column features to which diel movements were related.

Studies of the diel vertical distribution of early stages of fish contribute to knowledge of several phases of their life history. For eggs, diel and depth differences in age distribution can be used to estimate time of day and depth of spawning and hatching, rate of embryonic development, and to some extent egg mortality. For larvae, a large body of literature has confirmed the conclusions of the early work by Russell (1926) and Bridger (1956) that most species exhibit diel vertical migrations. Although the depth ranges differ, most species move to shallower depths at night. In some species, e.g., herring, *Clupea h. harengus*, (Seliverstov 1974) and yellowtail flounder, *Limanda ferruginea*, (Smith et al. 1978) the extent of movement increases as the larvae grow. Speculation about causes of vertical migration has centered around diel feeding behavior and predator avoidance. Most larval fishes are visual feeders on zooplankters, which undertake vertical migrations similar to those of larval fish. In addition, Zaret and Suffern (1976) concluded that vertical migration patterns occur in prey species that are vulnerable to visually dependent predators; thus, larvae may reduce predation by moving to deeper water during the day.

Aside from understanding the biological consequences of vertical distribution of larval fishes, the effect this distribution has on results of broad-scale ichthyoplankton surveys is critical. During most such surveys, samples are taken at more-or-less random times during a 24-h day at stations that are separated by tens of kilometers. Depending on the sampling procedures, the diel spawning and embryonic developmental cycle and the diel vertical distribution of larvae may affect interpretation of catches from surveys (Ahlstrom 1959; Miller et al. 1963). If sampling fails to include the entire depth range of the taxa sought, errors in abundance estimates will be made.

METHODS

After making several trial tows at varying distances from shore between Sandy Hook, N.J., and Ocean City, Md., we located a concentration of fish larvae 95 km off Ocean City (lat. 38°32′ N, long. 73°52′ W) in 57 m of water (Figure 1). Earlier studies (Kendall and Walford 1979) indicated that larvae of bluefish, *Pomatomus saltatrix*, which were among those found here, occurred primarily near the surface, above the thermocline. To track the concentration of larvae we deployed a parachute drogue with a lighted staff buoy and the parachute centered at 5-10 m in the layer above the thermocline which was present from 10 to 30

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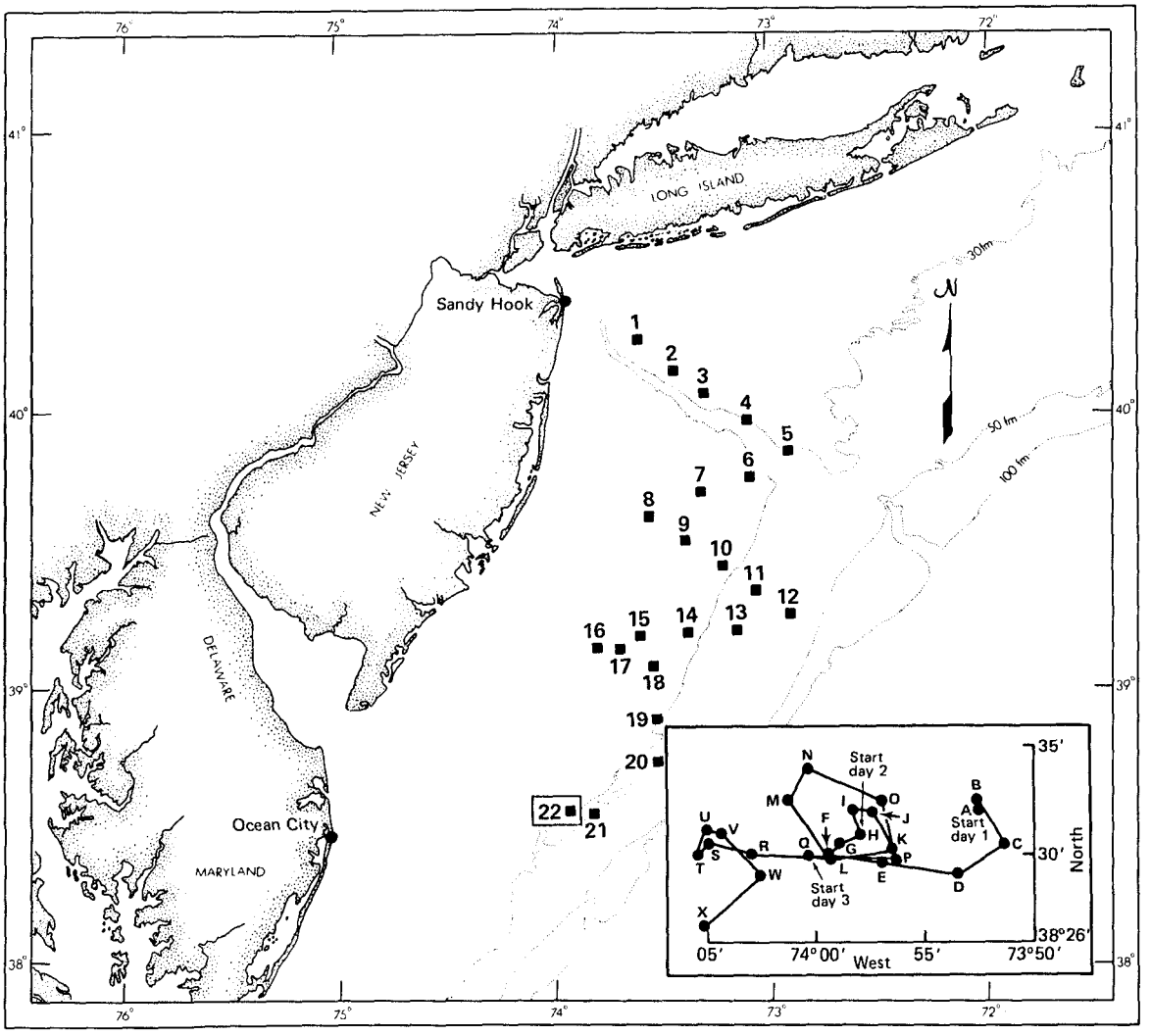

FIGURE 1.—Search (squares) and drogue stations (inset) during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

m. Plankton was sampled near the drogue at 3-h intervals for 72 h starting at 0600 (e.s.t.) on 18 July 1974. We used 20 cm bongo nets equipped with General Oceanics[3] flowmeters and 0.505 mm mesh nets. This mesh size may have caused extrusion of smaller larvae and eggs. Two or four nets were fished simultaneously at discrete depths. A Braincon 6-ft (1.82 m) V-fin depressor was used and wire stops held the nets at predetermined places on the wire.

Before each tow, temperature profiles were obtained with expendable bathythermographs and surface salinity samples were taken. Before every other haul salinity samples from the sampling depths and 50 m were obtained. Salinities were determined on shore with a Beckman RS 7B induction salinometer.

Nominal plankton sampling depths were: surface, 2, 4, 6, 15, and 30 m. Every 3 h a haul was made at 0, 4, 15, and 30 m (first experiment). During the second half of the 72-h period, on every other haul a second haul was made in a similar manner immediately after the first one with the

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

nets fishing at 2 and 6 m (second experiment). The depth stratum from 30 m to the bottom (57 m) was not sampled, and some larvae probably occurred in this area. Bendix bathykymographs on the wire near the subsurface nets checked the actual sampling depths on each haul. During each haul we placed the nets on the wire as it was paid out; the vessel maintained minimal headway to keep the nets from tangling around the wire. Once the nets were on the wire, the vessel speed was increased to 5 kn (9.3 km/h). Hauls lasted 15 min from the time the surface net started to fish to when it was brought out of the water. At the end of the 15 min, the ship was set adrift and the nets were hauled in as quickly as possible. Since the nets had no opening-closing devices, this procedure minimized contamination of the deeper nets by organisms in shallower water. Such contamination was considered inconsequential since the horizontal towing distance was a nominal 2,325 m, and maximum towing distance in shallower layers for the 30 m net was judged to be 75 m (3.2% of the haul); however, it may have accounted for some of the predominantly shallow-caught larvae found in the deeper nets. Samples were preserved in 5% seawater buffered Formalin. The bongo nets provided paired samples that we designated port and starboard. All starboard net samples and one of the four or six port net samples from each sampling time were brought ashore. All fish eggs and larvae were removed from the plankton samples, identified, and counted.

Selected samples of Atlantic whiting,[4] *Merluccius bilinearis*; Gulf Stream flounder, *Citharichthys arctifrons*; and snake eel, *Pisodonophis cruentifer*, eggs were staged (categorized according to developmental stage), based on divisions of the embryonic period used by Naplin and Obenchain (1980). Although many of the early stage eggs had ruptured yolks, these were considered intact prior to sampling. As has been noted in other species (Leis 1977), until the blastoderm completely covers the yolk sac, yolk breakage occurs easily and is likely to happen during sampling. Some middle stages, too, were ruptured, but we cannot determine whether they ruptured during sampling or whether they were already dead when collected. As most of the embryos looked normal and undeteriorated other than having a ruptured yolk, these also were considered to have been alive when sampled.

Atlantic whiting eggs were initially staged at all depths for the first day of sampling (39 samples at eight time periods). Predominant stages at a particular time of day were the same regardless of depth, indicating that stages were not stratified with depth. As 95% of the eggs were taken in the surface and 4 m samples, only the surface samples were staged at each time period for the remaining 2 d of sampling. Gulf Stream flounder eggs were staged at all depths for the first day of sampling, and snake eel eggs, which occurred in fewer numbers, were staged at all depths for all 3 d of sampling.

Stokes' law for determining the settling velocity of a particle has been used to estimate the rising velocity of planktonic eggs (English 1961). Stokes' law, applied to this problem states that

$$V = \frac{2}{9} g \frac{[d_1 - d_2]}{\mu} r^2$$

where V = velocity
d_1 = density of egg
d_2 = density of liquid
g = acceleration of gravity
r = radius of egg
μ = dynamic viscosity of liquid.

All values are expressed in the centimeter-gram-second system. Although no measurements of specific gravity of eggs for species discussed here are available, values for other planktonic eggs have ranged from 1.021 for pleuronectid eggs (English 1961) and for eggs of the gadid *Theragra chalcogramma* (Kanoh 1954) to 1.0287 for *Argentina silus* eggs (Schmidt 1906, quoted by Breder and Rosen 1966). We used the 1.021 value in our calculations because a value >1.022 would not permit eggs to float in the upper 10 m where the eggs we took were abundant.

Bluefish larvae from all samples were measured and those from a subset of 28 samples were used for gut content analysis. From each of these samples, 10 fish representing the sample size distribution were examined for gut contents. The number and types of food organisms in the foregut, midgut, and hindgut were noted. Atlantic whiting and Gulf Stream flounder larvae were also measured.

[4]The common name Atlantic whiting is used in this paper for *Merluccius bilinearis* to avoid confusion with hakes (*Urophycis* spp.). Recently the common name of *M. productus* has been changed from Pacific hake to Pacific whiting. We suggest that fish of the genus *Merluccius* be recognized as whitings, a name in common use on the east coast already.

The average volume of water filtered during the hauls was 82.9 m^3 (range 58.6-109.2 m^3). All numbers of eggs and larvae were adjusted to numbers per 100 cubic meters. Using UCLA BMD computer program 02V (Dixon 1973), analyses of variance were performed for several species after the data had been transformed to $\log_{10}(X + 1)$ to normalize the distribution and homogenize the variances, which were proportional to the means before transformation. The factorial design of the first experiment had the following factors: three 24-h days, four sampling depths (0, 4, 15, 30 m), and day and night. Each factor combination had three replicates. Because the cruise was in midsummer, by sampling every 3 h, three tows were taken each night and five each day. To equalize the number of day and night tows for the analyses of variance, only the first, third, and fifth daytime tows were used. We performed similar analyses on the data associated with the second experiment when collections were also made at the 2 and 6 m depths. For these data the factors were: three times of day (evening—1800 h; night—0000 h; and day—0600 h and 1200 h), and six depths (0, 2, 4, 6, 15, 30 m). Each of these factor combinations had two replicates.

RESULTS

The drogue drifted about 11 nmi (20.4 km) to the west-southwest of its original position during the 72-h sampling period. Three circular patterns that corresponded to a diurnal tidal cycle were evident within the overall drift (Figure 1). During the first half of the experiments the wind was generally southerly at 5-25 kn (9.3-46.3 km/h). The skies were cloudy and a thundersquall occurred around 0300 h on the first night. Around 2100 h on the second night there was another thundersquall, and at 0300 h the wind shifted to north-northwest at 20 kn (37.0 km/h) and the skies cleared. The wind diminished during the third day and by 2100 h it had shifted to southeast at only 2 kn (3.7 km/h). The sky remained clear. The sun rose at 0545 h and set at 2016 h during the experiments. The new moon rose and set during twilight or daylight hours throughout the sampling period, so there was no moonlight at night.

The water column represented three water types characteristic of the continental shelf of the Middle Atlantic Bight. Coastal water above the thermocline at 8 m was isothermal at 22.2°-22.8° C and had salinities of <33.6‰ (Figure 2). Below

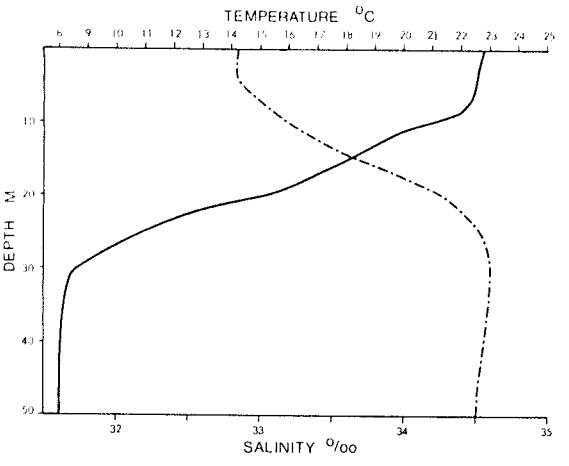

FIGURE 2.—Mean temperature (line) and salinity (dashed line) profiles at drogue stations during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

the thermocline, where temperatures dropped from 21.5° C at 10 m to 8.5° C at 30 m and salinities exceeded 33.6‰, was shelf edge water (Wright and Parker 1976). Near the bottom, where temperatures were <10° C and salinities were 34.5-34.6‰, the water was part of the cool pool that occurs over the middle of the shelf off the Middle Atlantic Bight in summer (Bowman and Wunderlich 1977). The diversity of ichthyoplankton collected was probably due in part to our sampling in these three water types.

A total of 61,534 eggs (an overall arithmetic mean of 562 eggs/100 m^3), most of which were identified to species, were taken during the experiments (Table 1). Most numerous were Atlantic whiting and Gulf Stream flounder. Butterfish, *Peprilus triacanthus*; fourspot flounder, *Hippoglossina oblonga*; hakes, *Urophycis* spp.; snake eel; and cunner, *Tautogolabrus adspersus*, eggs were also taken in significant numbers. No bluefish eggs were taken during the cruise.

Throughout the cruise, egg numbers of all species decreased with depth. Data from the second experiment was similar to that from the first, and showed that the catches at 6 m more closely resembled those at the surface and 4 m than those at 10 and 30 m. These findings indicate that the planktonic eggs of all species taken behave in much the same way in the water column, and have similar specific gravities.

A total of 68,840 larvae (an overall mean of 629 larvae/100 m^3), of which most were identified to

TABLE 1.—Numbers and relative abundance of fish eggs and larvae at the drogue stations during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Taxon	Eggs			Larvae		
	Total number	Mean no./ 100 m³	% of total	Total number	Mean no./ 100 m³	% of total
Hakes, *Urophycis* spp.	2,988	27	4.9	15,972	146	23.2
Bluefish, *Pomatomus saltatrix*				15,202	139	22.1
Gulf Stream flounder, *Citharichthys arctifrons*	17,311	158	28.1	13,568	124	19.7
Frigate mackerel, *Auxis* sp.				5,904	54	8.6
Butterfish, *Peprilus triacanthus*	4,497	41	7.3	5,445	50	7.9
Fourspot flounder, *Hippoglossina oblonga*	3,898	36	6.3	5,062	46	7.4
Atlantic whiting, *Merluccius bilinearis*	28,243	258	45.9	3,281	30	4.8
Smallmouth flounder, *Etropus microstomus*				1,000	9.1	1.5
Atlantic bonita, *Sarda sarda*	114	1.0	.2	764	7.0	1.1
Searobins, *Prionotus* spp.				445	4.1	.6
Cusk eels, Ophidiidae				183	1.7	.3
Cunner, *Tautogolabrus adspersus*	2,397	22	3.9	152	1.4	.2
Yellowtail flounder, *Limanda ferruginea*				151	1.4	.2
Eels, Anguilliformes				98	.9	.1
Goosefish, *Lophius americanus*				63	.6	.1
Witch flounder, *Glyptocephalus cynoglossus*				42	.4	.1
Snake eel, *Pisodonophis cruentifer*	2,058	19	3.3			
Miscellaneous[1]	28	.3		1,508	13.8	2.2
Total	61,534	562	99.9	68,840	629	100.1

[1]Animals that were too mutilated to be identified or too sparse for meaningful analysis.

species, were taken during the experiments (Table 1). Hakes, bluefish, and Gulf Stream flounder were most abundant, and frigate mackerel (*Auxis* sp.), butterfish, fourspot flounder, Atlantic whiting, and smallmouth flounder, *Etropus microstomus*, were taken in substantial numbers.

Bluefish

An overall mean catch of 139 larvae/100 m³ was made placing bluefish second to hakes in abundance. A highly significant difference occurred in the catches among the 3 d, with more larvae caught on day 2 than on the other 2 d (Table 2). More larvae were taken in the surface and 4 m nets than at other depths, with more taken at the surface at night than during the day (Figures 3, 4). Both day and night catches at 15 and 30 m were so small that they may have been a result of contamination of the nets as they passed through shallower water. During the second experiment, the larvae were concentrated at 2 m at night and 6 m at other times (Table 2).

The vertical-diel migration of these larvae is clearly seen by comparing the proportions of larvae in the 0 and 4 m tows at each time of day sampled (Figure 4). The proportion in the surface tow was lowest at midday (1200 h) when it was 4% of the total catch. It increased steadily to 49% of the catch at midnight (0000 h) when it started to decline again, reaching 17% by midmorning (0900 h). Thus the larvae appear to be varying their depth distribution continuously on a diel cycle, concentrating near 4 m during midday and at the surface at night.

The percentage of the larvae with food in their guts also showed a marked diel pattern (Figure 4). The maximum proportions of larvae with food in their guts were taken from 0600 to 1200 h when 86-90% of the guts contained food. At 1500 and 1800 h, 70% of the larvae contained food. By 2100 h the proportion had dropped to 22% and during the night (0000 and 0300 h) none of the larvae had food in their guts.

Most of the food consisted of various life stages of copepods, including nauplii, copepodites, and adults. Cladocerans and invertebrate eggs were also present in small numbers. It also appeared that smaller larvae had higher proportions of nauplii while larger larvae had higher proportions of adult copepods and cladocerans although too few fish were examined for detailed analysis.

Several factors indicate that food passes through the gut fairly rapidly. Few fish had any food particles in the foregut. At 0600 h about twice as many larvae had food in the midgut as had food in the hindgut. Later in the day about equal numbers of larvae contained food in the midgut and in the hindgut. At no time did more hindguts than midguts contain food.

The mean lengths of bluefish larvae were compared among the tows. The mean length for all tows was 4.33 mm (Table 3). We found no significant difference in mean lengths among the 3 d of sampling, between day and night sampling, or among the six sampling depths. Larger larvae

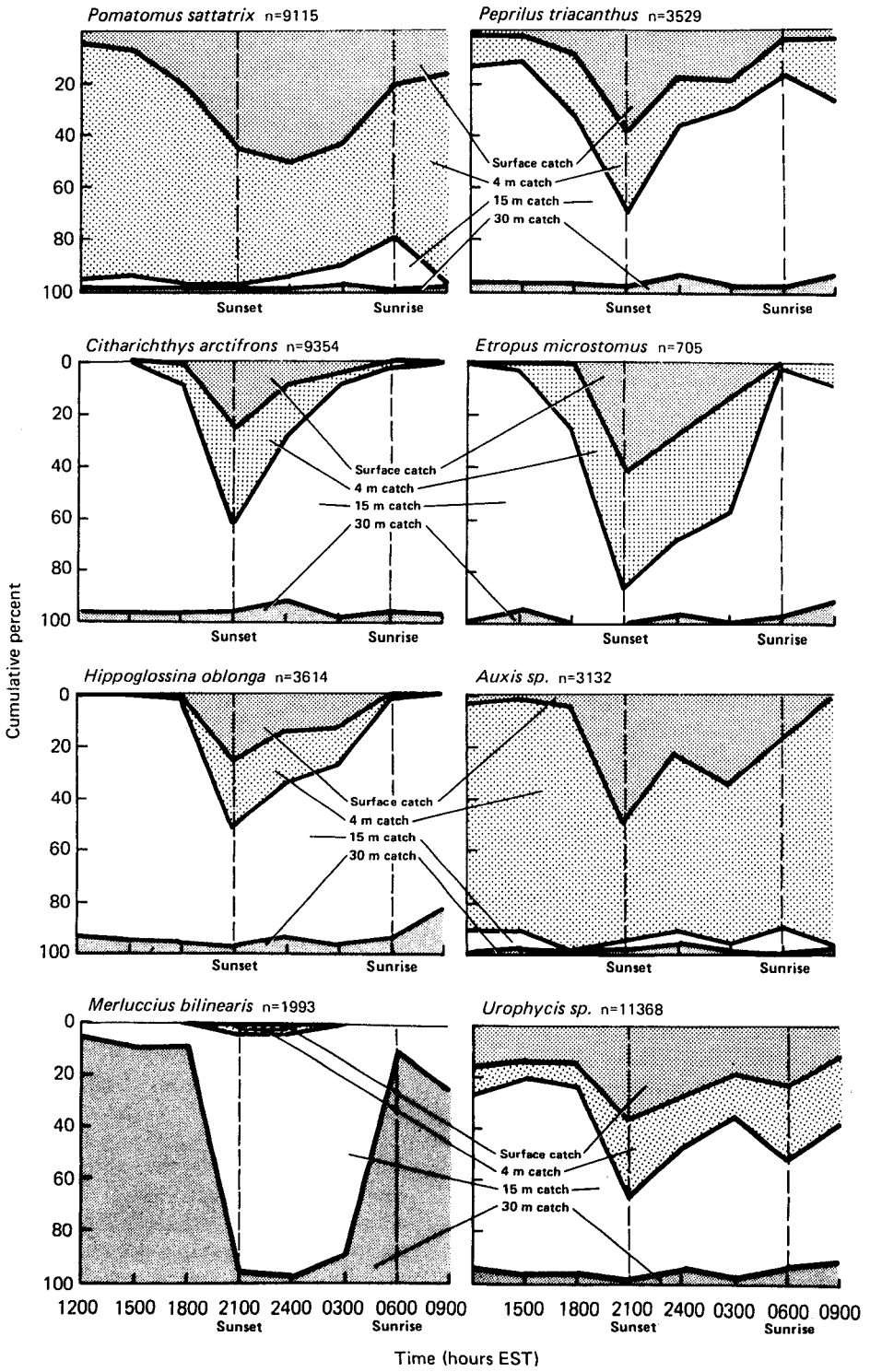

FIGURE 3.—Mean proportions of larvae of eight species of fish at four depths over a 24-h cycle from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 2.—Transformed ($\log_{10} X + 1$) mean numbers of larvae per 100 m^3 and *F*-values from analysis of variance for eight species of fish taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Item	Bluefish	Atlantic whiting	Gulf Stream flounder	Butterfish	Fourspot flounder	Hakes	Frigate mackerel	Smallmouth flounder
Experiment 1: depths = 0, 4, 15, 30 m; times = day, night; days = 1, 2, 3								
Means:								
Overall	1.550	0.786	1.311	1.315	1.088	1.904	1.056	0.524
Day	1.497	.692	1.105	1.222	.799	1.885	.880	.392
Night	1.603	.880	1.518	1.408	1.378	1.923	1.233	.656
Day 1	1.289	.819	1.215	1.334	1.024	1.945	.793	.199
Day 2	1.717	.879	1.287	1.287	1.006	1.859	1.238	.538
Day 3	1.644	.660	1.432	1.325	1.235	1.907	1.138	.835
Depths:								
0	1.847	.150	.835	1.087	.791	2.005	1.222	.445
4	2.375	.266	1.075	1.400	.846	1.916	1.870	.658
15	1.210	1.404	2.193	1.391	1.849	2.378	.728	.801
30	.768	1.323	1.143	.843	.867	1.318	.405	.191
F-values								
Days	12.32**	3.77*	1.32	.09	3.33*	.43	11.45**	25.40**
Day-night (diel)	1.99	7.89**	13.72**	3.80	51.63**	.26	19.74**	13.22**
Depth	88.13**	99.32**	29.19**	24.14**	39.88**	33.74**	64.43**	13.31**
Days/Day-night	1.35	3.49*	.40	.20	.72	.54	2.53	5.58**
Days/Depth	1.02	.13	1.20	1.06	3.65**	1.10	2.06	2.70*
Day-night/Depth	6.96**	4.88**	13.49**	5.70**	29.57**	2.85*	6.89**	13.16**
Days/Day-night/Depth	1.72	.30	.81	.42	1.36	1.89	1.31	1.80
Experiment 2: depths = 0, 2, 4, 6, 15, 30 m; times = 1800, 0000, 0600-1200 h								
Means:								
Overall	1.954	.523	1.280	1.348	1.073	1.909	1.422	.740
Times:								
1800	1.945	.524	1.388	1.570	0.818	1.810	1.521	1.019
0000	1.965	.591	1.612	1.375	1.458	1.892	1.598	.638
0600-1200	1.952	.453	.840	1.100	.942	2.023	1.146	.563
Depths:								
0	1.839	.064	.633	.884	.459	1.946	.941	.361
2	2.295	.115	1.308	1.362	1.223	2.000	2.026	.958
4	2.471	.244	.994	1.410	.615	1.847	1.931	.731
6	2.628	.244	1.154	1.552	1.043	2.016	2.179	.809
15	1.552	1.117	2.260	2.065	2.176	2.388	.984	1.288
30	.939	1.351	1.331	.817	.920	1.254	.468	.294
F-values								
Time of day	.02	.74	10.36**	12.02**	10.46**	2.25	7.69**	5.92
Depth	30.85**	2.48	9.73**	22.90**	16.80**	13.32**	33.32**	6.90**
Time/Depth	2.63*	8.54**	4.49**	5.08**	3.17*	1.27	3.89**	4.80**

*P = 0.05; **P = 0.01.

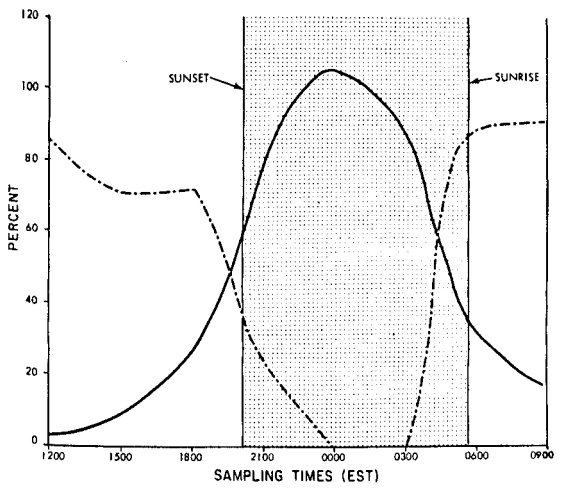

FIGURE 4.—Mean percentage (surface/4 m) of bluefish larvae in the 4 m tow relative to those in the 0 m tow (line) and percentage of bluefish larvae with food in their guts (dashed line) by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 3.—Mean standard lengths (millimeters) of bluefish larvae taken at various times of day and depths during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day 1		Day 2		Day 3		All times
	Day	Night	Day	Night	Day	Night	
0	5.30	4.38	4.57	4.25	4.87	4.69	4.57
2			4.38	4.45	4.60	4.85	4.59
4	4.38	4.52	3.89	4.45	4.27	4.63	4.22
6			4.27	4.42	4.25	4.79	4.33
15	4.65	4.45	4.49	4.42	4.31	4.71	4.47
30	4.57	4.61	4.45	4.35	4.25	4.50	4.45
	Day 1 - 5.00		Day 2 - 4.18		Day 3 - 4.46		
	Day - 4.25		Night - 4.54		Overall - 4.33		

showed no increased net avoidance during daylight, nor any difference in depth distribution with size. The apparent lack of larval growth over the 72-h sampling period may be related to the difference between the drift of bluefish larvae and that of our drogue.

Since bluefish egg incubation takes about 48 h

at temperatures near 22° C (Salekhova 1959; Deuel et al. 1966) and bluefish larvae hatch at about 3.0 mm, the larvae we caught averaging 4.3 mm were probably several days old. Apparently bluefish spawned rather steadily over a period of several days somewhere "upstream" from our drogue a few days prior to our experiment, and the larvae drifted continuously through our sampling area. Alternate hypotheses that the larvae did not grow during the experiment, or that larvae >4.3 mm avoided the nets, do not seem as tenable.

Atlantic Whiting

Atlantic whiting eggs were the most numerous among the species taken, with an overall mean of 258 eggs/100 m^3 taken during the cruise. All three primary factors (depth, time of day, and days) showed significant differences: egg number decreased with increasing depth (Figure 5), more eggs were taken at night than during the day, and significantly fewer eggs were taken on the second sampling day than on the other two (Table 4).

The uneven distribution of various developmental stages over time allows separation of eggs into distinct groups or batches whose development can be traced from spawning through hatching (Table 5). At each sampling time, eggs from two distinct batches were taken which apparently represented the daily spawning products of adults in the area. Very early stages appeared daily in the afternoons from about 1500 to 1800 h. These eggs continued developing throughout the next day and began hatching at 0300 h the second day after being spawned. After 0900 h, virtually all eggs had hatched. Therefore, the total incubation time at the surface temperature we observed, 22.2°-23.2° C (mean = 22.7° C), was about 39 h.

TABLE 4.—Transformed ($\log_{10} X + 1$) mean numbers of eggs per 100 m^3 and F-values from analysis of variance for six species of fish taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Item	Atlantic whiting	Gulf Stream flounder	Butterfish	Fourspot flounder	Hakes	Snake eel
Experiment 1: depths = 0, 4, 15, 30 m; times = day, night; days = 1, 2, 3						
Means:						
Overall	1.971	2.059	1.180	1.228	1.056	0.907
Day	1.892	1.996	1.052	1.259	.985	.864
Night	2.051	2.122	1.307	1.197	1.128	.950
Day 1	2.058	1.888	1.090	.944	1.053	.831
Day 2	1.867	2.110	1.255	1.336	.998	.861
Day 3	1.988	2.179	1.194	1.403	1.119	1.029
Depths:						
0	2.640	2.251	1.575	1.677	1.521	1.271
4	2.606	2.205	1.670	1.685	1.582	1.494
15	1.552	1.887	.950	.755	.700	.650
30	1.086	1.893	.524	.973	.423	.212
F-values						
Days	4.19*	14.76**	.76	31.87**	.62	5.88**
Day-night (diel)	8.46**	7.62**	5.36*	1.49	2.59	2.92
Depth	201.63**	18.31**	24.13**	106.64**	43.33**	132.38**
Days/Day-night	1.11	2.21	2.26	.32	3.29*	3.19
Days/Depth	.19	4.46**	.43	2.13	1.08	2.58*
Day-night/Depth	1.08	2.84*	.19	.58	.28	3.58*
Days/Day-night/Depth	.52	.19	.25	.66	.74	3.35**
Experiment 2: depths = 0, 2, 4, 6, 15, 30 m; times = 1800, 0000, 0600-1200 h						
Means:						
Overall	2.142	2.217	1.366	1.548	1.250	1.166
Times:						
1800	2.141	2.165	1.598	1.546	1.146	1.163
0000	2.225	2.348	1.595	1.514	1.336	1.107
0600-1200	2.061	2.138	.904	1.584	1.267	1.228
Depths:						
0	2.561	2.331	1.591	1.831	1.510	1.109
2	2.537	2.405	1.691	1.822	1.563	1.680
4	2.537	2.295	1.601	1.848	1.655	1.544
6	2.590	2.382	1.783	1.815	1.645	1.624
15	1.554	2.007	1.088	1.010	.764	.875
30	1.076	1.882	.440	.963	.361	.165
F-values						
Time of day	4.30*	8.68**	27.96**	.27	3.53	.75
Depth	139.11**	15.77**	23.07**	21.53**	57.70**	35.30**
Time/Depth	3.52*	1.67	2.00	.56	2.91*	1.41

*P = 0.05; **P = 0.01.

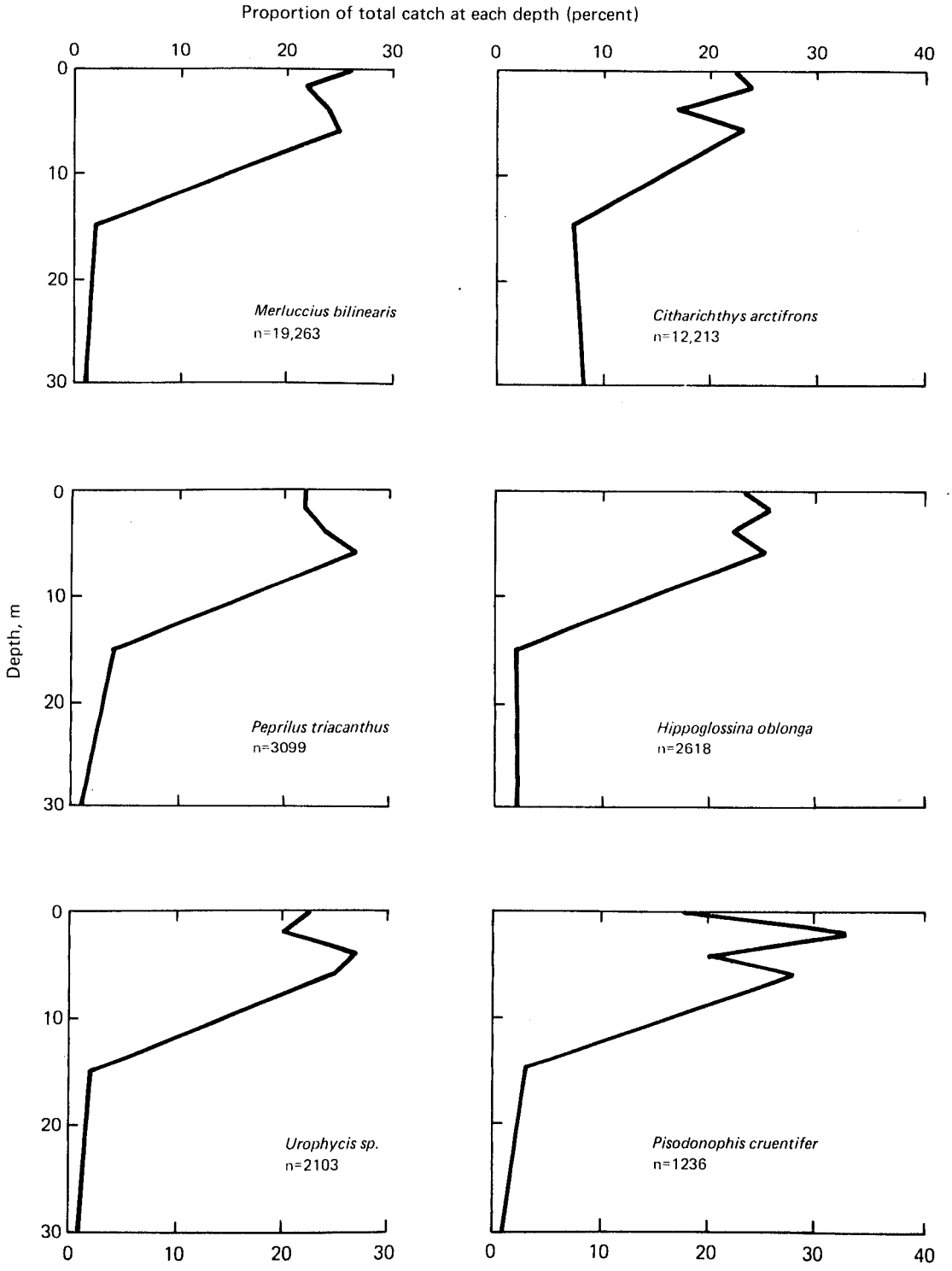

FIGURE 5.—Depth distribution of planktonic eggs of six species of fish collected during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 5.—Stages of Atlantic whiting eggs taken in surface samples during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight. Roman numerals refer to batch numbers that were assigned to eggs.

Stage	Drogue station: Time:	A 0600	B 0900	C 1200	D 1500	E 1800	F 2100	G 2400	H 0300	I 0600	J 0900	K 1200	L 1500	M 1800	N 2100	O 2400	P 0300	Q 0600	R 0900	S 1200	T 1500	U 1800	V 2100	W 2400	X 0300
Precell	III			1	49	26	6				IV	3	44	2				V	3	28	1				
2 cell					13	3	4						11	3							17				
4 cell					1		6						3								2				
8 cell							1														1	2			
16 cell	II					5	1														3	22			
Cell stage					5	28	7						15	53	5	22					11	22	4	1	
Early blastula		9	1		1	58	23	4	5	2				37	13	15	12	4	1		1	177	14	24	3
Blastodermal cap		7	1	1	1	32	161	19	5	5				16	121	29			1			63	183	28	94
Early germ ring		9	4	1		8	39	345	22	19					10	142	18	8				2	12	182	93
Germ ring ½ down		58	5	1	1		1	59	89	17	3					2	95	25	8	3			1	4	554
Germ ring ¾ down		46	21	2					283	15	5	1				1	54	42					1		198
Blastopore almost closed		28	31						176	25	16						3	11							9
Early middle		106	71	26					23	401	36	8					1	85	19	18	4				
Middle middle		54	164	51	19	1				40	380	23	3	1				1	107	12	25	2			
Late middle		1	37	137	44	9	1				42	79	29	2					7	155	67	19	1		
Early late				45	15	11					1	5	30	5						13	34	15	2		
Tail ⅝ around yolk	I	1		8	148	31	11	3				5	70	41	4						261	66	8	7	6
Tail ¾ around yolk		1		2	23	124	42	7					4	105	32	4	1				12	200	56	14	8
Tail ⅞ around yolk		8				10	170	47	4		1			4	98	13	6					6	160	99	35
Full circle		29	7				6	86	26	28					3	22	10	3					3	116	57
Tail 1⅛ around yolk		58	38	3				13	86	47	6	1			1		17	8	6					2	57
Abnormal late		6	2			20	14	21	4	5			1	2	1	30	14	16		2		2	9	12	7
Total		421	382	278	320	366	493	604	723	604	490	125	210	271	288	280	231	203	149	206	466	599	454	489	1,121

Kuntz and Radcliffe (1917) found that development in the laboratory required "not over" 43 h, but did not give temperature data.

During the cruise, all the eggs collected were spawned on 5 different days. Those spawned during the afternoon of the first sampling day (batch III) were the only ones sampled from spawning to hatching.

Batches of developing embryos spent roughly 3 h in each of the developmental stages listed in Table 5, except for the very early cell stages. From these data we derived a timetable of embryonic development (Table 6). Blastopore closure occurred about 12 h after spawning. Eggs were in middle stages of development, i.e., between blastopore closure and first appearance of the tail bud, for about 9 h. Hatching occurred about 15 h after tail bud formation.

The numbers of eggs in each batch are plotted according to developmental stage and time of day in Figure 6. Number of eggs taken varied widely from tow to tow; hence, we could not estimate mortality within any batch. In most tows, however, several obviously malformed late stages occurred in which embryos usually had ruptured yolks and shortened, rather wide tails. We assume that the condition of these embryos was not due to handling. These embryos, which composed up to 5.2% of an egg batch (Table 7), would probably not have survived to hatch.

The numbers of eggs taken at different times of day vary as batches are spawned and as they hatch (Figure 7). Because the eggs are spawned during only one period of the day (1500-1800 h), we would expect the maximum numbers of eggs to occur at

TABLE 6.—Timetable of development of Atlantic whiting eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage
Day 1:		
1500	0	Precell
1800	3	Cell stage
2100	6	Early blastula
2400	9	Blastodermal cap
0300	12	Early germ ring
0600	15	Germ ring ½-¾ down
0900	18	Early middle
Day 2:		
1200	21	Middle middle
1500	24	Late middle
1800	27	Tail ⅝ around yolk
2100	30	Tail ¾ around yolk
2400	33	Tail ⅞ around yolk
0300	36	Full circle
0600	39	Tail 1⅛ around yolk—hatching
0900	42	Tail 1⅛ around yolk—hatching

about 1800 h; however, we found egg density to increase until 0300 h. The downward slope on the right side of the curves primarily reflects embryonic mortality, although hatching accounts for the decrease during the latest developmental stages. The fact that the egg batches reached their peak abundance later than expected probably reflects the influence of local currents on distribution of spawning adults and eggs.

Determining the time and depth at which eggs were spawned provides information about adult spawning behavior. We have shown that newly spawned eggs appear in the afternoon and early evening. The depth at which spawning occurs can be estimated from knowing the depth at which the very early stage eggs were collected. Atlantic whiting eggs are planktonic, tending to rise toward the surface at a rate which, aside from turbulence of the water, depends on their specific gravity and that of the surrounding water. Estimating the rate of rise of the eggs in the water column enables us to calculate the depth at which

TABLE 7.—Percentage of abnormal Atlantic whiting embryos in each spawning batch from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Batch	Total no. eggs	No. abnormal late stages	Minimum mortality (%)
I	153	8	5.2
II	2,012	64	3.2
III	3,224	64	2.0
IV	2,624	32	1.2
V	1,760	—	—

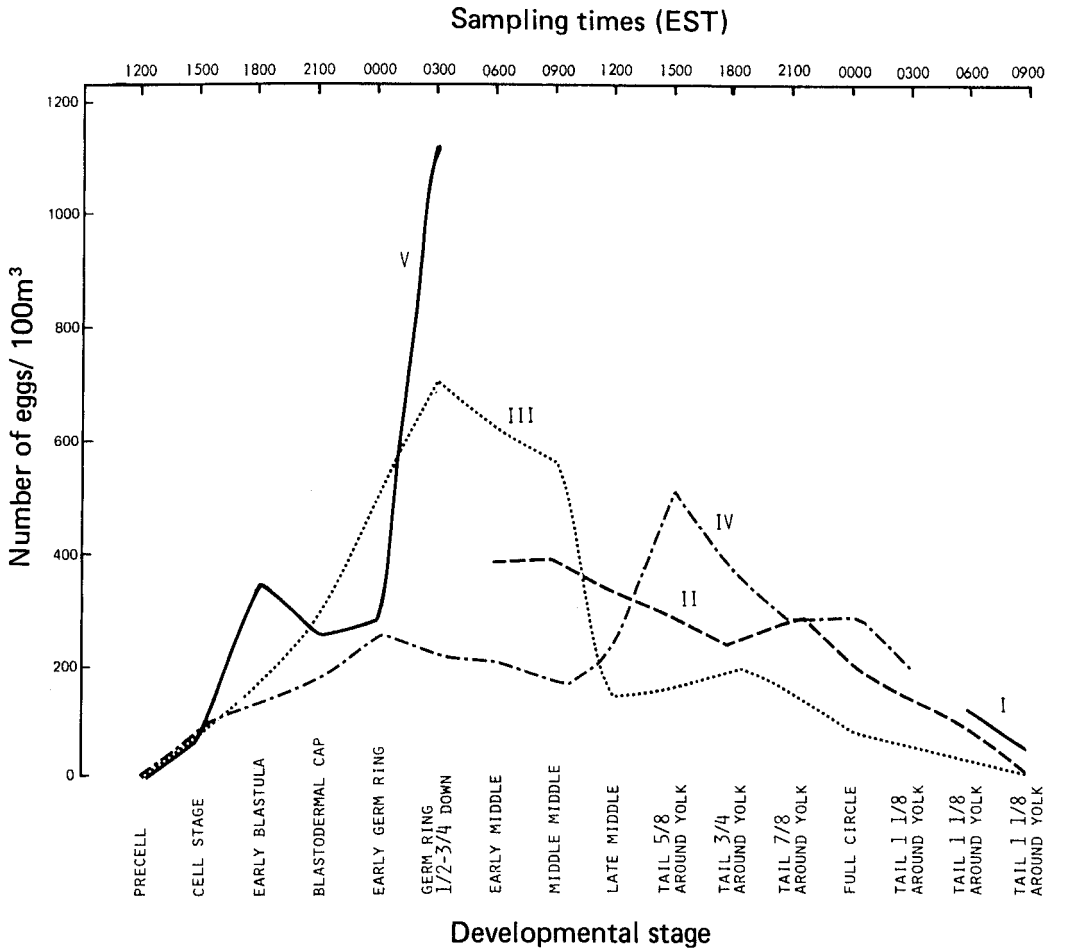

FIGURE 6.—Numbers of Atlantic whiting eggs in the five batches taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by developmental stage and time of day.

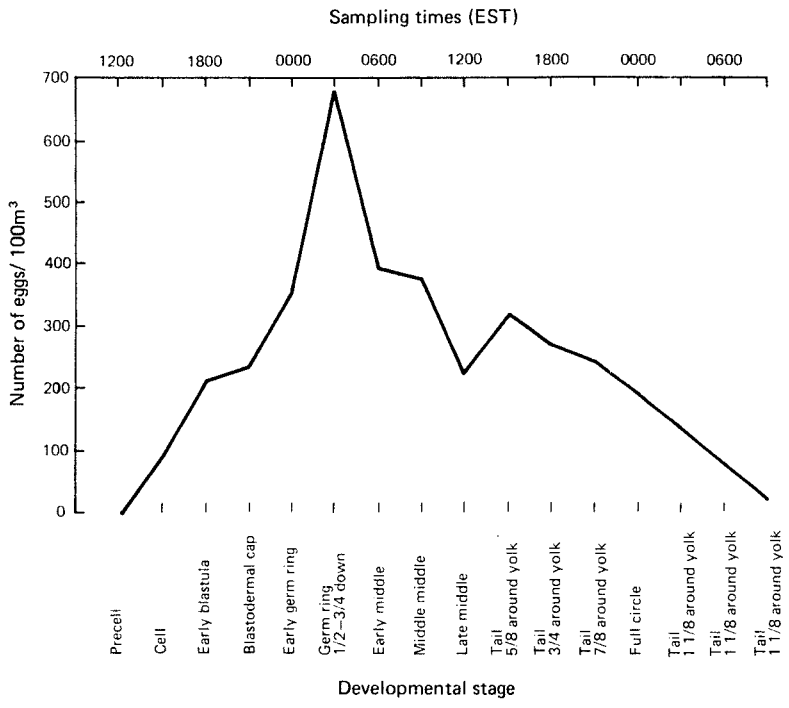

FIGURE 7.—Average number of Atlantic whiting eggs from spawning to hatching plotted by developmental stage and time of day, based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

the eggs were spawned. According to Stokes' law, Atlantic whiting eggs would have a rising velocity of 1.18 m/h or about 3.5 m during the 3-h interval between samples. Based on this and the fact that newly spawned eggs were taken primarily in the 0 and 4 m nets, the adults were spawning in the upper 10 m of the water column.

An overall mean of 30 Atlantic whiting larvae/ 100 m^3 was taken during the cruise. The numbers of larvae showed significant differences for all three primary factors (depth, time of day, and days) (Table 2). In general, the number of larvae caught increased with increasing depth (Figure 3). Significant numbers of larvae may have occurred below our 30 m sampling depth. A comparison of the numbers of larvae taken in the 15 and 30 m tows at various times of day (Figure 8) shows that more larvae were caught at 30 m during the day, while at night many more larvae were taken at 15 m. In general, more larvae were caught at night; however, on day 3 more were taken in the daytime. The larvae either avoided the nets more effectively in the daytime or more larvae migrated upward into the range of the nets at night.

Figure 9 shows the average lengths of larvae caught at 15 m and at 30 m. During the daytime, the 4.5 mm larvae were at 15 m while 6.5-9.2 mm larvae stayed at 30 m. At night, large larvae (6-9 mm) were at both 15 and 30 m, probably mixing with the small larvae, some of which may have sunk between 1800 and 0000 h, based on the decrease in mean length at 30 m and the increase in mean length at 15 m.

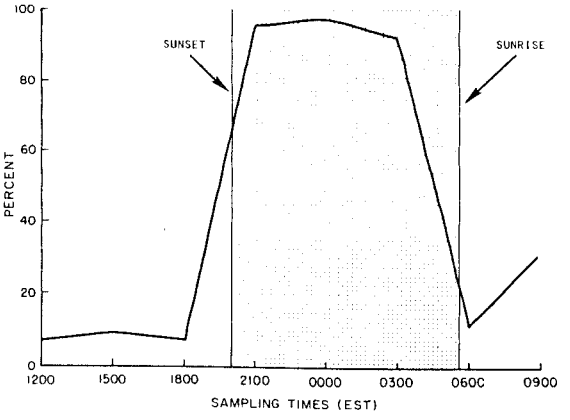

FIGURE 8.—Mean percentage of Atlantic whiting larvae at 15 m relative to larvae at 30 m by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

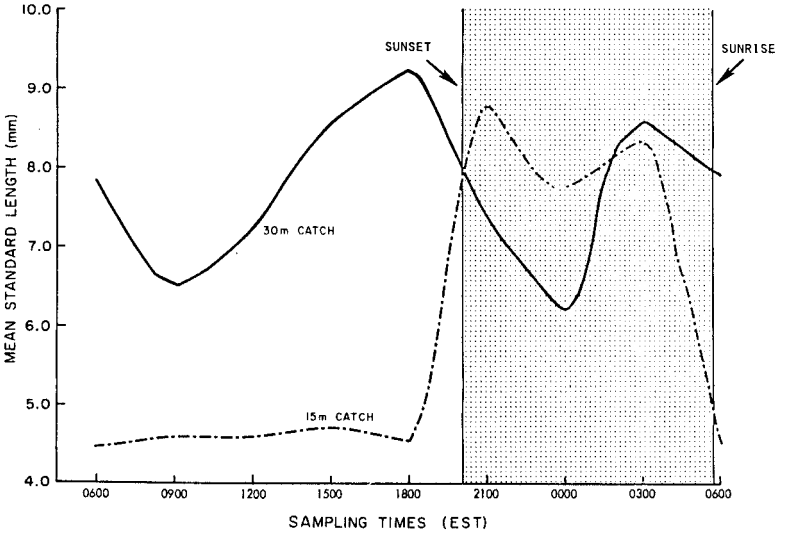

FIGURE 9.—Mean standard lengths (millimeters) of Atlantic whiting larvae taken at 15 and 30 m by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

We caught very few hatchlings (<3.0 mm [Kuntz and Radcliffe 1917]), as they appear to have been extruded from the 0.505 mm mesh net. Therefore, we could not detect a pulse in the numbers of very small larvae corresponding to the daily time of hatching or shortly thereafter. Significantly fewer larvae of all sizes were taken on day 3.

Gulf Stream Flounder

Gulf Stream flounder eggs have not been fully described in the literature, although Richardson and Joseph (1973) described eggs stripped from Gulf Stream flounder that were approaching spawning condition. The very small larvae are so similar to those of smallmouth flounder, *Etropus microstomus*, that the eggs also may be virtually indistinguishable from that species. In fact, eggs from our samples are identical to those described as smallmouth flounder eggs by Scherer and Bourne (1979), who did not provide adequate means of distinguishing the two species.

We have identified eggs from the plankton that we consider to be Gulf Stream and/or smallmouth flounder eggs based on egg and oil globule diameter and late embryonic characteristics. We assume that such eggs taken during this cruise are Gulf Stream flounder eggs for three reasons. First, Gulf Stream flounder occurs mainly at depths >46 m while smallmouth flounder is most common in water <27 m (Richardson and Joseph 1973); our samples were from an area where the water was 57 m deep. Second, smallmouth flounder larvae occur farther south than Gulf Stream flounder; our sampling location was in an area of peak Gulf Stream flounder abundance, but north of the area of maximum smallmouth flounder concentration (Smith et al. 1975). Finally, Gulf Stream flounder larvae occurred in markedly greater numbers in our samples than did smallmouth flounder larvae (19.7% as opposed to 1.5% of the total catch).

Gulf Stream flounder averaged 158 eggs/100 m^3 during the cruise. The catches were significantly different for all three primary factors (depth, time of day, and day) (Table 3). Fewer eggs were taken with increasing depth (Figure 5), though comparable numbers were taken at 15 and 30 m; more eggs were taken at night; and the total number of eggs increased with each day of sampling. More eggs were taken on each succeeding day at all depths except 30 m, where the number decreased with time.

Gulf Stream flounder eggs showed patterns of developmental stages that changed with both time and depth. Table 8 shows stages of eggs summed over all depths at each sampling time. The eggs were more difficult to separate into batches than Atlantic whiting eggs, but batches were defined in which eggs could be traced from spawning through hatching in succeeding samples. Usually three distinct groups of developmental stages were apparent at each sampling time. Precell stages were taken in the afternoon from 1500 to 2100 h. These eggs required about 3

TABLE 8.—Stages of Gulf Stream flounder eggs taken on day 1 during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974. Roman numerals refer to batch numbers that were assigned to the eggs.

Stage / Drogue station: / Time:	A 0600	B 0900	C 1200	D 1500	E 1800	F 2100	G 2400	H 0300
Precell	IV	1		25	19	5	V	2
2 cell				11	17	8	3	1
4 cell			2	2	15	15	1	
8 cell				2		4	12	
16 cell	2		3			11	1	
Cell stage	11	III 3			2	4	19	4
Early blastula	15	8	6	17	6	18	33	13
Blastodermal cap	86	84	43	17	38	18	41	32
Early germ ring	56	104	83	88	58	25	20	16
Germ ring ½ down	6	13	27	38	37	19	14	3
Germ ring ¾ down	7	9	4	12	17	21	10	3
Blastopore almost closed	9	II 3	6	7	10	8	20	
Early middle	22	15	5	4	4	19	38	8
Middle middle	16	13	8	6	6	6	19	20
Late middle	13	34	9	9	4	2	12	14
Early late	21	21	18	7	4	1	10	8
Tail ½ around yolk	5	11	1	7	4	1	1	2
Tail ⅝ around yolk	18	14	8	25	17	21	7	10
Tail ¾ around yolk	9	8	16	12	14	27	8	8
Tail ⅞ around yolk	11	I 6	7	15	15	16	32	10
Full circle	5	8	5	3	4	2	4	4
Total	312	355	251	307	291	251	305	158

full days to hatch; hatching occurred primarily in near-surface water beginning around 0900 h the morning of the fourth day after spawning.

Staging the eggs also revealed that they were stratified with depth, with early stages being taken in the deeper nets (Figure 10). Precell stages were taken primarily at 30 m, while eggs with several cell divisions and early blastula and blastodermal cap stages were taken mainly at 15 m. From 0900 to 1200 h the morning after spawning, early germ ring stages gradually shifted from 4 m to the surface. After 1200 h, the later stages were found at all depths sampled, but were concentrated at the surface and 4 m.

By using Stokes' law for calculating the rising velocity of the eggs, which have an average diameter of 0.70 mm, we estimated when the eggs were spawned and how old they were when sampled. If eggs were spawned on the bottom (57 m), they required 7 h to rise to 30 m and another 5.8 h to reach 15 m. As several precell and cell stage eggs appeared from 1500 to 1800 h in the 30 m net, the eggs were probably spawned between 0800 and 1100 h. Table 9 is a timetable for development of Gulf Stream flounder eggs based on the stages of eggs in Table 8 and on egg rising velocities calculated from Stokes' law.

The overlap between batches of the Gulf Stream flounder eggs as compared with the clearly defined batches of Atlantic whiting eggs may be related to two factors. First, the incubation time of Gulf Stream flounder is about twice that of Atlantic whiting eggs; therefore, eggs from twice as many batches are present in the plankton at once. Second, because Gulf Stream flounder spawns on the bottom, the eggs were subjected to turbulence and mixing by the time they were

TABLE 9.—Timetable of development of Gulf Stream flounder eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage	Depth mainly taken (m)
Day 1:			
1500	7	Precell—cell stage	30
1800	10	Precell—cell stage	30
2100	13	Cell stage—early blastula	15
2400	16	Early blastula—blastodermal cap	15
0300	19	Blastodermal cap	15
0600	22	Blastodermal cap	15
0900	25	Early germ ring	4
1200	28	Early germ ring	4
Day 2:			
1500	31	Early germ ring	0-4
1800	34	Migrating germ ring	0-4
2100	37	Migrating germ ring	0-4
2400	40	Early middle	0-4
0300	43	Middle middle	0-4
0600	46	Middle middle	0-4
0900	49	Late middle	0-4
1200	52	Early late	0-4
Day 3:			
1500	55	Tail ⅝ around yolk	0-4
1800	58	Tail ⅝ around yolk	0-4
2100	61	Tail ¾ around yolk	0-4
2400	64	Tail ⅞ around yolk	0-4
0300	67	Tail ⅞ around yolk	0-4
0600	70	Tail ⅞ around yolk	0-4
0900	73	Full circle	0-4
1200+	76+	Hatching	0-4

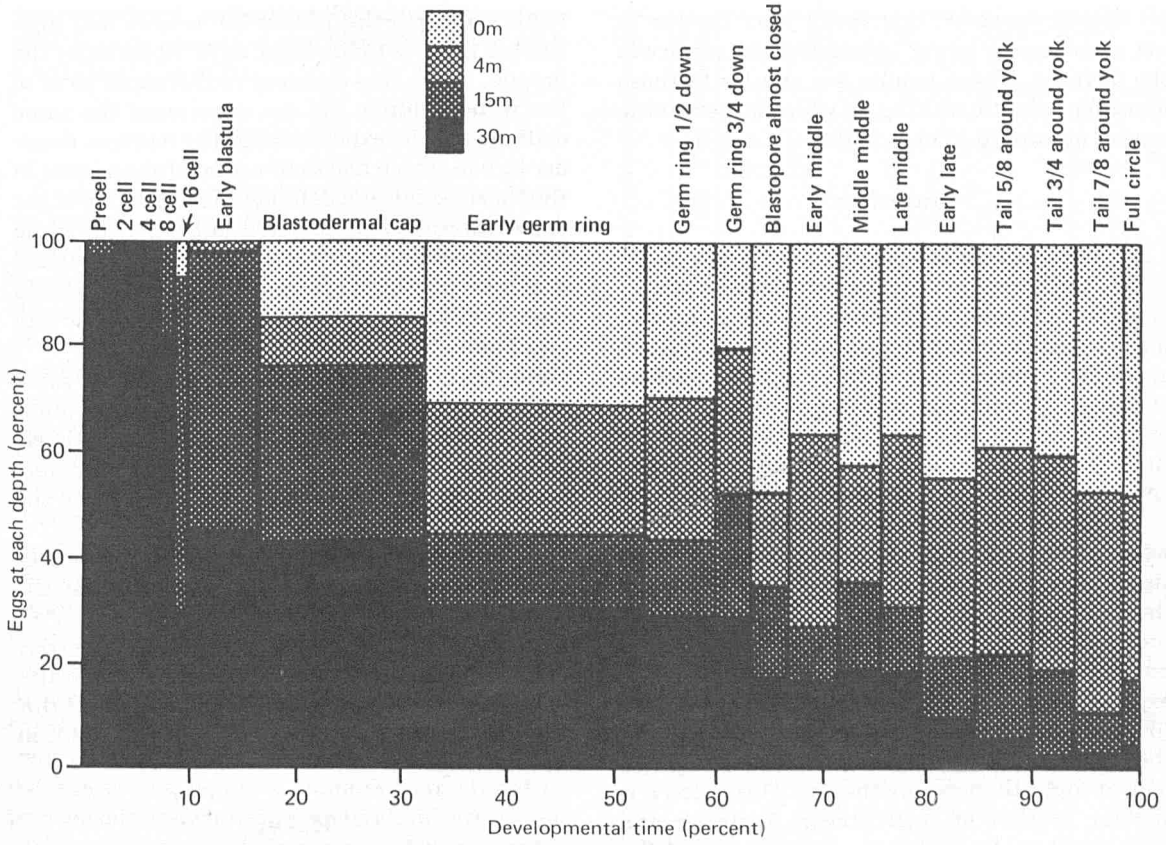

FIGURE 10.—Percentage of Gulf Stream flounder eggs at each depth plotted by age and stage based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

sampled, while Atlantic whiting eggs were collected from depths near where they were spawned.

An overall mean of 124 Gulf Stream flounder larvae/100 m^3 was taken during the cruise (Table 1). More larvae were taken at night than during the day and more were caught at 15 m than at the other depths sampled (Figure 3). The diel-depth interaction was significant in that Gulf Stream flounder, like fourspot flounder, were relatively more abundant at 0 and 4 m at night and at 15 and 30 m during the day, indicating a vertical migration upward at night (Table 2). Gulf Stream flounder larvae are concentrated in the thermocline during the day, but at least some move toward the surface at night.

From the second experiment, it appears that the movement toward the surface may occur in early evening because catches in the 2 m tow were high at 1800 h, while the 15 m tow took more larvae at other times (0000, 0600, and 1200 h). There was no significant difference in catches over the 3 d of the experiment, nor in the mean standard lengths, which ranged from 4.33 to 4.57 mm.

Smaller larvae were taken from 0 to 4 m during the day, while larger larvae were taken from 6 to 30 m (Table 10). At night, it seems that some of the larger larvae spread upward and were caught at

TABLE 10.—Mean standard lengths (millimeters) of Gulf Stream flounder larvae at six depths during day and night from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day			Night		
	Mean	SE	No.	Mean	SE	No.
0	3.31	0.267	12	4.10	0.278	114
2	3.55	.285	64	3.82	.370	55
4	4.03	.688	55	4.00	.217	185
6	5.93	2.188	27	4.04	.317	38
15	4.74	.172	328	5.22	.321	135
30	5.69	.414	177	4.40	.128	93

all depths; however, this result may be due to net avoidance by larger larvae near the surface in the daytime. These results are similar to those found for Atlantic whiting, in which larger larvae spread upward to 15 m at night.

Butterfish

An overall mean of 41 eggs/100 m^3 was caught during the cruise, making butterfish eggs third in abundance (Table 1). Fewer eggs were caught at the greatest sampling depths though the eggs at 4 m slightly outnumbered those at the surface (Table 4). In addition, more eggs were taken at night, which could reflect an evening spawning time. No significant differences in the number of eggs taken from day to day was evident.

An overall mean of 50 butterfish larvae/100 m^3 was taken during the cruise. There were no significant differences in numbers of larvae over the 3 d or during day as opposed to night (Table 2), indicating that we were probably sampling a uniform concentration of larvae throughout the experiment. In general, more larvae were taken at 15 m, but the diel-depth interaction indicated that the larvae were more abundant in the 0 and 4 m nets at night than during the day. This pattern is similar to that of Gulf Stream flounder and fourspot flounder indicating that some of the larvae that spend the day in the thermocline move toward the surface at night (Figure 3). The second experiment indicated that the 2 m catches were highest at 1800 h while the 15 m catches were high at all other times.

Fourspot Flounder

Fourspot flounder eggs ranked fourth in abundance, with a mean of 36 eggs/100 m^3 taken during the cruise (Table 1). Fewer eggs were taken at the greatest sampling depths though similar numbers were taken at 0 and 4 m and at 15 and 30 m (Figure 5, Table 4). No significant differences between day and night catches were evident.

An overall mean of 46 fourspot flounder larvae/100 m^3 was taken. The catches were significantly different for all three primary factors, i.e., more were caught at night than in the daytime, more were caught on day 3 than on the first 2 d, and the 15 m tow took more than the other three (Table 2). The interaction between days and depth was significant because on day 2 the surface and 4 m tows had high catches relative to the other days, while on day 3 the 15 and 30 m tows had high catches relative to the other days. Apparently the drogue, which was centered in the upper 10 m of the water column, did not experience the same drift during the experiment as the fourspot flounder larvae, which had their center of abundance in the thermocline at a depth of 15 m. The day-night depth interactions indicated migration by some larvae toward the surface at night since the 0 and 4 m tows had high catches at night while the 15 and 30 m tows had high catches during the day (see Figure 3).

Results of the second experiment show the same pattern in that more larvae were caught at night and the 15 m tow had high catches at all times. However, the 0, 2, 4, and 6 m tows had relatively higher catches at night than during either of the day periods.

These results indicate that fourspot flounder larvae occur mainly in the upper part of the thermocline where temperatures are above 10° C. Those larvae that move from 15 m during the day to near the surface at night, pass from 18° C water to 22° C water. The salinity also changes over this depth range from about 33.6‰ at 14 m to 32.8‰ at the surface.

Hakes

The species of hake (*Urophycis*) eggs and larvae in our samples could not be determined because of overlapping meristic characters and spawning seasons, so more than one species may be represented. An overall mean of 27 eggs/100 m^3 was taken, making hake eggs fifth in abundance. Slightly more eggs were taken at 4 m than at the surface (Figure 5), but otherwise egg numbers decreased with increasing depth (Table 4). No significant differences between day and night catches were evident, indicating that the daily spawning time was prolonged, or that we were possibly sampling more than one species with somewhat different spawning times. Egg concentration in the area of the drogue remained fairly constant. There were no significant differences among the 3 sampling days.

An overall mean of 146 larvae/100 m^3 was taken, making hakes the most abundant larvae caught (Table 1). In general, they were most abundant at 15 m (Table 2), but more were taken in the 0 and 4 m nets at night, and more in the 15 and 30 m nets during the day (Figure 3). During the second experiment, the time-depth interaction

was significant, indicating that during the three time periods examined, the larvae moved to shallower depths at night.

Snake Eel

Snake eel eggs ranked sixth in abundance, with an overall mean of 19 eggs/100 m^3. Fewer eggs were taken in the deeper tows, though slightly more eggs occurred at 4 m than at the surface (Figure 5). No significant difference between day and night egg catches was apparent (Table 4). However, at all depths except 15 m, more eggs usually were taken at night. At 15 m, more eggs were caught in the daytime. Significantly more eggs were caught on each succeeding day of the cruise.

The numbers of eggs in various stages taken during the cruise are shown in Table 11. Because the eggs were not stratified with depth, and because relatively few eggs were taken at each depth, we combined the eggs from the four depths sampled during the first experiment. The eggs are divided into seven batches that were spawned on the 3 d of sampling and the preceding 4 d. Where some ambiguity as to the boundary between older batches exists, replicate samples were staged to provide better definition of individual batches. At each sampling time, four groups of developmental stages were present. Spawning began at 2100 h each day, and was restricted to a relatively short period of time. Most eggs had hatched by 2100 h 4 d after being spawned. These data for development times have been used in a description of embryonic stages in this species (Naplin and Obenchain 1980).

The numbers of eggs in each batch are plotted according to developmental stage and time of day in Figure 11, from which the duration of each stage can be readily determined. For example, complete epiboly required about 12 h and took place from 0900 until 2100 h the day after the eggs were spawned. Table 12 is the corresponding complete developmental timetable for the snake eel. The regular fluctuations in egg number apparent in Figure 11 are even more clearly displayed in Figure 12, which depicts the total number of snake eel eggs over time. The fluctuations occurred on a 12-h cycle, and are possibly the result of tidal periodicity in spawning. As sampling progressed, the vessel gradually drifted into an area of more concentrated spawning, which was somewhat west of and closer to the 30-fathom (54.9 m) line

TABLE 11.—Stages of snake eel eggs taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974. Roman numerals refer to batch numbers that were assigned to the eggs.

Stage	Drogue station:	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
	Time:	0600	0900	1200	1500	1800	2100	2400	0300	0600	0900	1200	1500	1800	2100	2400	0300	0600	0900	1200	1500	1800	2100	2400	0300
Precell or unfertilized							2								11								3		
2 cell							5								11								6		
Cell stage								1								2								5	
Early blastula							V	2							VI	7	2	1					VII	6	1
Blastodermal cap		16	2						8	12	2	1					14	19	2						64
Early germ ring			32	6	1						45	1							27	2					
Germ ring ½ down	IV			12	3							19	9							14	7	5			
Germ ring ¾ down				1	6	5							15	4							5	5			
Blastopore almost closed						7	3	1					3	20	3							6	8		1
Early and middle middle		7	3			2	21	14	8	11	2	1			30	19	6	11	8	1			15	35	22
Late middle		2	4	1			2		2	11	15			1			3	4	24	10				1	
Early late				6	2	2		1				11					2			7	5				
Tail ⅝ around yolk	III			1	1	1	10	2	4	2	1	2	5	10	10					1	13	16	29	6	3
Tail ¾ around yolk		2	1			1		5		2	5			4	8	10	4		1	1			8	27	14
Tail ⅞ around yolk	II	1							1	7		1	2				2	12	3	2					2
Full circle				1	2	6	1	1	3	1	1	1	2	2		1		3	3		2	2	3	2	6
Tail 1⅛ around yolk		2				3	2			2			2	3	4	2				1	3	2	7	7	3
Tail 1¼ around yolk		1	1			1	1	1	1	2	1				4	2	3				1	1	7	6	12
Tail 1⅜ around yolk	I			1		1			2	2	1			1		2				3	1	1		1	1
Tail 1½ around yolk						2					1														2
Dead					1	1										1			2					2	
Total		30	44	29	16	32	47	28	29	52	74	37	36	45	81	46	36	50	70	43	37	38	87	97	131

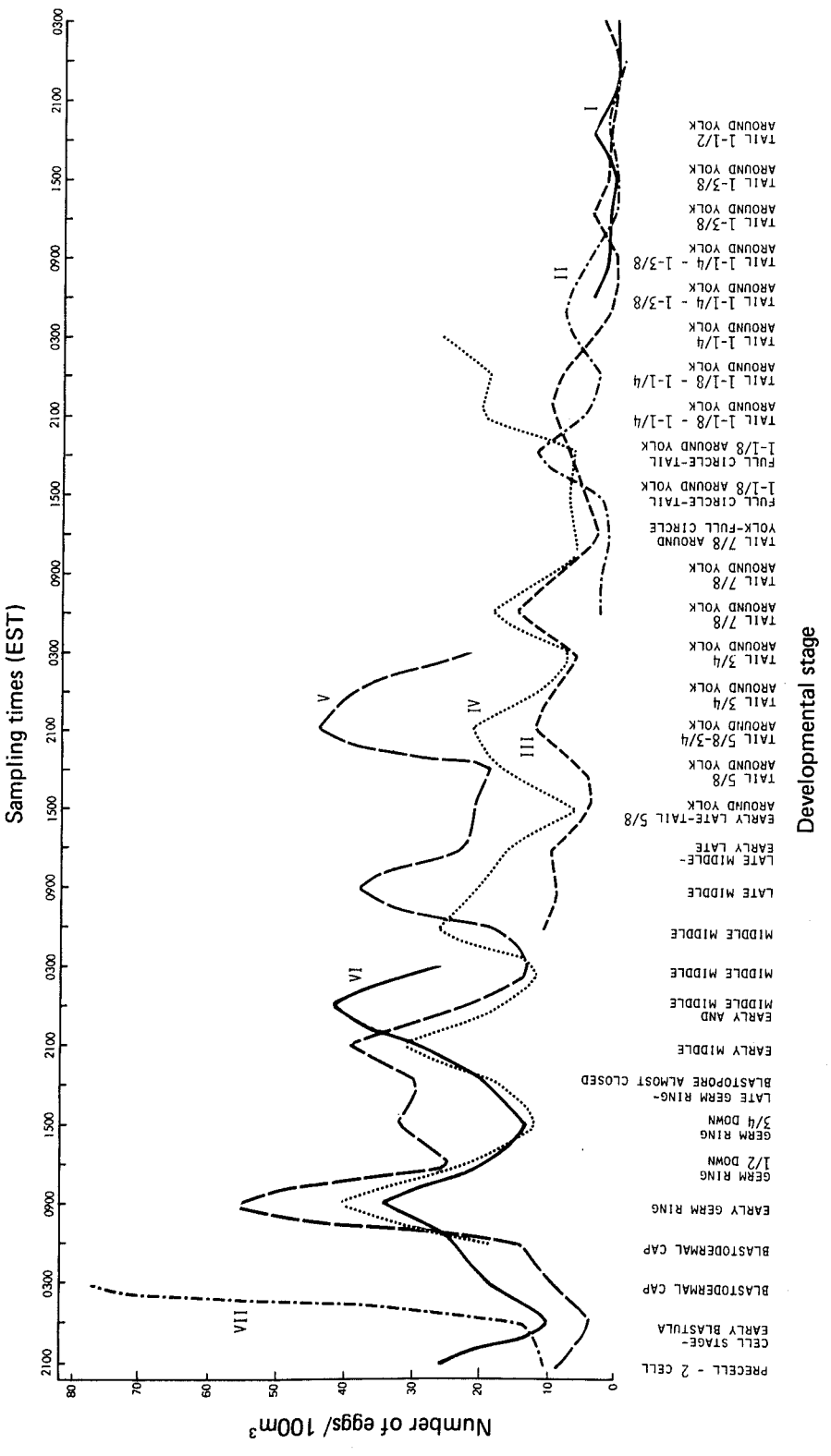

FIGURE 11.—Numbers of snake eel eggs in the seven batches taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by developmental stage and time of day.

TABLE 12.—Timetable of development of snake eel eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage
Day 1:		
2100	0	Precell—2 cell
2400	3	Cell stage—early blastula
0300	6	Blastodermal cap
0600	9	Blastodermal cap
0900	12	Early germ ring
1200	15	Germ ring ½ down
1500	18	Germ ring ¾ down
1800	21	Late germ ring—blastopore almost closed
Day 2:		
2100	24	Early middle
2400	27	Early and middle middle
0300	30	Middle middle
0600	33	Middle middle
0900	36	Late middle
1200	39	Late middle—early late
1500	42	Early late—tail ⅝ around yolk
1800	45	Tail ⅝ around yolk
Day 3:		
2100	48	Tail ⅝-¾ around yolk
2400	51	Tail ¾ around yolk
0300	54	Tail ¾ around yolk
0600	57	Tail ⅞ around yolk
0900	60	Tail ⅞ around yolk
1200	63	Tail ⅞ around yolk—full circle
1500	66	Full circle—tail 1⅛ around yolk
1800	69	Full circle—tail 1⅛ around yolk
Day 4:		
2100	72	Tail 1⅛-1¼ around yolk
2400	75	Tail 1⅛-1¼ around yolk
0300	78	Tail 1¼ around yolk
0600	81	Tail 1¼-1⅜ around yolk
0900	84	Tail 1¼-1⅜ around yolk
1200	87	Tail 1⅜ around yolk
1500	90	Tail 1⅜ around yolk
1800	93	Tail 1½ around yolk
2100	96	Hatching

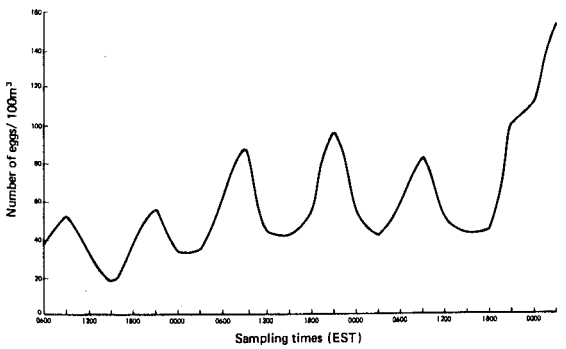

FIGURE 12.—Number of snake eel eggs during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by time of day.

than the original sampling site. Because more eggs were taken each day, it was not possible to estimate the total size of any one batch.

A rough estimate of egg mortality within individual batches based on numbers of eggs at different times during their development and at corresponding points of the tidal cycle is approximately 0.5 to 0.6%/h, totaling 48 to 57.6% over the 96 h development time.

Applying Stokes' law to snake eel eggs results in an overall time of only 2.1 h required for eggs to rise from the bottom to the surface. The rapid rising velocity of the eggs is a result of their large diameter ($\overline{X}$ = 2.60 mm). Slightly more time would be required for eggs to rise to the surface if their density is somewhat greater immediately after spawning. In any case, if Stokes' law still holds for eggs of this size, it is inadequate for determining the depth of spawning for snake eel although from behavior of the adults it is likely to occur on or near the bottom.

Few snake eel larvae were caught during the cruise.

Frigate Mackerel

No frigate mackerel eggs were taken during the cruise. Due to nomenclatural confusion, the species of *Auxis* larvae in our collections cannot be determined. However, only one type of larva appears to be represented, and an overall mean of 54 larvae/100 m^3 was caught during the cruise. There were highly significant differences in days, diel, and depth factors (Table 2), indicating that we were not sampling a uniformly distributed population during the experiments. The larvae were more abundant at night than during the day, and more were caught on the second day than on the first or third. Larvae were most abundant overall in the 4 m tow, and more were taken at the surface during day than at night. Catches at 15 and 30 m were so small in both day and night tows that contamination of the nets in shallower water as they passed through the water column could account for them (Figure 3). In the second experiment, the 2 m tow caught most fish at 1800 h, while the 6 m tow caught more at other times. Thus *Auxis* larvae were mostly in the upper 6 m of the water column above the thermocline and were found closer to the surface during the evening.

Smallmouth Flounder

Smallmouth flounder eggs have not been described. Based on the similarity of the early larvae, however, it is likely that they closely resemble Gulf Stream flounder eggs. In view of

the relative proportions of larvae of the two species taken during the cruise, eggs with characteristics of smallmouth flounder and Gulf Stream flounder were assumed to be of the latter species.

An overall mean of 9.1 smallmouth flounder larvae/100 m^3 was taken during the cruise. In general, the 15 m tow caught most of the larvae; however, more larvae were taken at 15 and 30 m in the daytime, while more were caught at 0 and 4 m at night (Figure 3). The larvae moved toward the surface at night and were also more abundant at all depths at night. More larvae were taken on each succeeding day of the experiment (Table 2).

We found little difference in mean length during day tows at all depths, and although the larvae caught at night at 30 m were larger than those caught at other depths, only two were taken (Table 13). The mean lengths of the larvae taken each day remained virtually constant from 3.58 to 3.61 mm. Evidently the drogue gradually drifted into an area of higher larval concentration, resulting in the increasing number of larvae taken each succeeding day.

TABLE 13.—Mean standard lengths (millimeters) of smallmouth flounder larvae at six depths during day and night from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day			Night		
	Mean	SE	No.	Mean	SE	No.
0	—	—	—	3.65	0.102	87
2	3.73	0.515	38	3.41	.410	52
4	4.14	.390	15	3.63	.078	135
6	4.48	.765	8	3.60	.350	40
15	3.42	.098	200	4.06	.298	78
30	4.13	.932	13	5.30	.300	2

DISCUSSION

The two major techniques applied to the egg data, i.e., analyses of variance of egg numbers based on a factorial experimental design and staging the eggs, tend to complement each other. The former technique is used to point out significant variation in the data that may be clarified and elaborated by staging selected egg samples. For example, significant differences in egg number at various times of day revealed by factorial analysis can be accounted for by the daily spawning and hatching cycles revealed by staging the eggs. In our experiments, analysis of variance demonstrated significant changes in egg numbers over four sampling depths, over 3 d, and in the daytime and at night. Egg staging provided us with developmental timetables, and time of day and depth of spawning and hatching. Spawning and developmental characteristics of the three species whose eggs were staged are summarized in Table 14. Atlantic whiting and snake eel eggs were distributed homogeneously by stage over all depths sampled, whereas Gulf Stream flounder eggs were stratified by stage to some extent. Stage stratification of Gulf Stream flounder eggs indicated that spawning probably occurred on the bottom, and rising velocity calculations for these eggs support that conclusion. The rising velocity for Atlantic whiting eggs narrowed the possible spawning depth to the upper 10 m of the water. Fluctuations in egg numbers that appeared to be tide induced could indicate that the bottom-dwelling snake eel spawns on the bottom during a particular time of the tidal current cycle.

In a study of haddock eggs, Walford (1938) found that the eggs were spawned on the bottom and had a tendency to rise. Because egg stages were homogeneously distributed with respect to depth, he concluded that the eggs could adjust their specific gravity within limits to match that of the ambient water. Most planktonic eggs probably possess some capacity to adjust their densities (Walford 1938). However, because a definite age stratification with depth appeared for the Gulf Stream flounder eggs, we can conclude that in this case the eggs rise in the water column more rapidly than they adjust their density to the ambient water.

Spawning and hatching times for the three species were staggered throughout the day, with no two species having similar schedules. Atlantic whiting and snake eel spawned in the afternoon and evening, and while Atlantic whiting eggs hatched in the morning, snake eel eggs hatched at about the same time of day they were spawned.

TABLE 14.—Summary of local characteristics of distribution of spawning and development determined by staging eggs of Atlantic whiting, Gulf Stream flounder, and snake eel, based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Characteristic	Atlantic whiting	Gulf Stream flounder	Snake eel
Stage vs. depth	Same stage at all depths	Earliest stages - deepest	Same stage at all depths
Spawning depth	Upper 10 m	Bottom (57 m)	Bottom
Spawning time, h	1500-1800	0800-1100	2100
Hatching time, h	0300-0800	1200-1500	1500-2100
Incubation time	1.5 d (39 h)	3 d (72 h)	4 d (96 h)
No. stages/samples	Usually 2	Usually 3	4

Gulf Stream flounder spawned in the morning and the eggs hatched around noon. The progression from precell to hatching stages in all of these species allowed construction of detailed developmental timetables. Ahlstrom (1943) found spawning to occur during only a few hours of the day, and that plankton samples contained discrete batches of eggs spawned on different days. He also determined developmental times from this information. Ferraro (1980) reported on daily spawning times of a number of species. All fish investigated spawn during limited times of day, mainly at some time between noon and midnight.

For species that spawn on a regular diel basis, the number of predominant stages at any time about equals the number of days the eggs require to hatch (Table 14). Therefore, longer incubation times mean that more days of spawning are represented at any one time, making the separation of eggs into discrete spawning batches more difficult. Atlantic whiting eggs, with a short incubation time and spawned in the upper 10 m of water, were readily separated into discrete batches. Theoretically, snake eel eggs with a development time of 96 h would be more difficult to separate into batches than Gulf Stream flounder eggs with a development time of only 72 h. This was not the case, probably because of the depth stratification of the Gulf Stream flounder eggs and their longer daily spawning period compared with the homogeneous depth distribution of snake eel eggs and their very short daily spawning period.

Among the eight most abundant types of larvae collected during this study, all were more abundant closer to the sea surface at night. Two general patterns were seen: bluefish and frigate mackerel larvae were mostly above the thermocline (most abundant at 6 m) and some migrated to the surface at night; the other six species were most abundant below the thermocline at 15 m during the day but some larvae of each species migrated to waters above the thermocline at night. Within these two patterns, specific variations occurred. No two species showed the same combination of significant F-values for the factors tested and their interactions. We remained in a body of water where factors affecting larval abundance were so constant for three of the species that no significant differences were seen in the catches over the 3-d study. The two species most closely associated with the surface (bluefish and frigate mackerel) showed the greatest fluctuations in abundance over the 3 d, indicating that in following the drogue, we moved to areas where variation in factors affected larval abundance occurred. In such areas where water movement varies considerably with depth, a drogue can be expected to track only uniform patches of those organisms whose depth ranges are similar to that of the drogue. Four species were collected in significantly larger numbers at night than during the day. This may have resulted from increased avoidance by larvae during daylight. However, significantly more Atlantic whiting larvae were taken during day than at night. Some of these differences may thus reflect differences in vertical distribution on a diel cycle. If the larvae were more concentrated during day than at night at one or more of the levels sampled, they would appear more abundant during the day, although their overall abundance in the water column would not actually be different. Significant portions of the larval population of species that were abundant in our deeper nets may have occurred below the depths we sampled.

This study, as have others (e.g., Miller et al. 1963), points out the necessity of sampling the entire water column, at least over continental shelves, during ichthyoplankton surveys. This is accomplished in the many recent surveys which employ oblique or vertical plankton tows. In other sampling designs significant portions of the populations can be either undersampled or oversampled depending on their depth distribution and the time of day of sampling. The implications of this study regarding effects of time of day on numbers of fish eggs in the water column due to diel spawning and embryonic developmental cycles need to be considered in analyzing results of ichthyoplankton surveys.

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We extend our appreciation to the many members of the staff of Sandy Hook Laboratory for their help at sea and in the laboratory in gathering and processing the samples on which this paper is based. Special thanks are due to W. G. Smith and Jack Colton who reviewed drafts of the manuscript.

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RESPONSES OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE TO PREDATION BY A BITING PLANKTIVORE, *AMPHIPRION PERCULA*

P. W. WEBB[1]

ABSTRACT

Responses of northern anchovy larvae, ranging from 0.29 to 1.2 cm total length, to attacks by a biting planktivore, the clown fish, were recorded on video tape. Schlieren optics were used to simultaneously view an opaque predator and transparent prey. All fish were reared, and experiments performed, at 20° C. The percentage of larvae responding to attacks increased from about 9% for 0.29 cm larvae to 80% for 1.2 cm larvae. Of these larvae responding to attack, 26 ± 10% attempted to escape too late and were caught. This proportion was not related to larval size. The direction of larval escape paths to the initial orientation of the body was not related to larval size, but escape distances traveled and mean escape speeds increased with size from 1.0 cm and 4.0 cm/s respectively for larvae 0.29 cm total length to 3.5 cm and 8.2 cm/s in larvae 1.2 cm total length. Larval performance was not maximal except during rare chases which occurred in 7% of attacks by the predator.

Escape maneuvers in vertebrates are initiated by the magnifying retinal image of an approaching object, called the looming effect, and calculated as the rate of change of the angle subtended by the predator as seen by the prey. In the present study, apparent looming thresholds for larval avoidance responses were calculated at the start of the response, and differ from the true response because there must be a finite time difference between the stimulus exceeding the response threshold and the motor response itself (response latency). Maximum likelihood mean apparent looming thresholds were calculated for log-transformed data, assuming nonresponding prey had apparent looming thresholds greater than the maximum actually observed. These mean apparent looming thresholds decreased with larval length from approximately 32 rads/s at 0.29 cm to 1.7 rads/s at 1.2 cm. The most important feature of the larval avoidance response was that an escape attempt should be made appropriately timed to an attack.

The method could be used to examine larval fish responses in other interactions where predation events take place over a small distance. Examples are attacks by biting juvenile and adult fish, and other planktonic invertebrate predators. Effects of larval density and alternate prey species could also be evaluated.

Predation and starvation are believed to be the dominant factors contributing to the extensive mortality of fish eggs and larvae (Blaxter 1969; Hunter 1977, in press; Hunter and Kimbrell 1981). Following Hjort's critical period concept concerned with the importance of first-feeding success to larval survival (Hjort 1914), most attention has concentrated on feeding behavior and food consumption (e.g., Hunter 1972, in press; Arthur 1976; Lasker 1978). Fish eggs and larvae are also extremely vulnerable to a wide variety of fish and invertebrate predators. A few experimental studies have determined feeding rates for invertebrate predators on eggs and larvae in the laboratory (Lillelund and Lasker 1971; Theilacker and Lasker 1974; von Westernhagen and Rosenthal 1976) and rates of egg cannibalism by fish in the field (Hunter and Kimbrell 1981). I know of no studies that have examined responses of larvae to a fish predator.

Northern anchovy, *Engraulis mordax*, larvae are exposed to a wide range of juveniles and adults of fish and consequently to a range of feeding habits on a continuum from filter-feeding to biting (e.g., Leong and O'Connell 1969). The purpose of the experiment described here was to develop a method to study responses of northern anchovy larvae to attacks by fish, and to determine how avoidance responses and larval vulnerability to capture change during early development. A biting fish planktivore was used as a predator in an attempt to complement studies relating to filter-feeding predators, often crudely simulated by towed plankton nets (e.g., Webb and Corolla 1981).

METHODS

Northern anchovy larvae were reared from eggs

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as described by Hunter (1976). Eggs were spawned from five groups of adults taken from laboratory stocks on five occasions during spring 1980 (Table 1.) Eggs were transferred to noncirculated filtered sea water in 400 l black fiber glass tanks. Food for larvae was the dinoflagellate *Gymnodinium splendens* for 2- to 5-d-old larvae, and the rotifer *Brachionus plicatilis* for older larvae. Water temperature was maintained at 20° C. Larvae were held under constant illumination of 2,000 lx at the water surface, provided by standard room fluorescent lights.

Observations were made on predation of eggs and 10 groups of larvae of different total lengths, ranging from 0.29 to 1.2 cm (Table 1). Lengths were based on measurements of a subsample from each group at the time they were used for experiments. Observations were concentrated on early larvae because this is the period of greatest morphogenesis (O'Connell 1981) and maturation of response systems (Kimmel 1972; Webb and Corolla 1981).

TABLE 1.—Total length of subsample ($\bar{X} \pm 2$ SE; $N = 10$) of northern anchovy larvae populations used in predation experiments with a model predator, the clown fish. Data are also given on spawnings.

Total length at test (cm)		Group	Date spawned (1980)	Date tested
Eggs[1]		C	13 Mar.	13 Mar.
Larvae	0.287 ± 0.015	C	13 Mar.	14 Mar.
	.322 ± 0.008	E	4 Apr.	5 Apr.
	.391 ± 0.020	E	4 Apr.	6 Apr.
	.399 ± 0.010	E	4 Apr.	7 Apr.
	.417 ± 0.011	E	4 Apr.	8 Apr.
	.421 ± 0.011	B	28 Feb.	4 Mar.
	.626 ± 0.050	B	28 Feb.	12 Mar.
	.867 ± 0.053	D	27 Mar.	14 Apr.
	.953 ± 0.090	A	7 Feb.	29 Feb.
	1.166 ± 0.095	A	7 Feb.	18 Mar.

[1]Eggs were 0.135 ± 0.005 cm long × 0.069 ± 0.003 cm wide.

Attempts to obtain natural predators of uniform and suitable size were not successful. Therefore a mimic for biting predators was used. This model was the clown fish, *Amphiprion percula*, cultured from eggs. The fish were held in 40 l polypropylene tanks at 20° C and under constant illumination. The fish were fed daily on a diet of Tetramin[2] and northern anchovy eggs and larvae. The predator was readily available at uniform sizes throughout the duration of the experiment. The clown fish were 4.4 ± 0.2 cm total length (TL) and mass was 1.58 ± 0.17 g. The maximum depth was 1.8 ± 0.2 cm, and maximum width 0.6 ± 0.1 cm, both located 1.3 ± 0.1 cm from the nose (data are $\bar{X} \pm 2$ SE; $N = 10$).

Interactions between the model predator and northern anchovy eggs and larvae were observed using schlieren optics (Holder and North 1963). Briefly, a vertical collimated light beam was produced by a high intensity monochromatic point source at the focus of a concave mirror (focal length 140 cm) attached to the ceiling. A second mirror, with the same focal length, was located at the floor and focused the light on a black spot on a glass plate.

The observation arena was a cylindrical tank, located in the light beam. It was 35 cm in diameter and 10 cm deep and had a plate-glass bottom. The tank contained a central cylinder, 26.5 cm in diameter and 5 cm deep, which supported a circular plate-glass lid. The lid and the bottom were parallel to each other and normal to the light beam. Discontinuities in refractive index (i.e., larvae in the water) deflected the light from the focus spot on the glass plate, and were seen as bright objects against a dark background. Opaque objects (i.e., the predator) were seen as black silhouettes.

The clown fish were starved for 5 d to ensure uniform high motivation. This was necessary because northern anchovy larvae grow rapidly and loss of a day required starting new batches, particularly for young larvae. Individual clown fish were placed in the observation arena and left for 24 h. After this period, up to 100 northern anchovy eggs and larvae were introduced through a side port in the central cylinder. After 10 to 30 min, the predator began feeding on the prey distributed through the tank. The reason for the delay in the onset of feeding is not known. Behavior was recorded on video tape. Experiments were performed at 20° C.

The video tape was manually advanced to analyze images frame by frame (framing rate = 60 Hz). The following observations were made: the number of attacks by clown fish, escape attempts by prey, escape success of the prey, catch success of the predator, and the number of predator errors. The prey escape angle, distance traveled, and mean speed during an escape attempt were measured.

Animals from a wide range of taxa, including fish, show avoidance responses to approaching, presumably threatening objects (see Gibson 1980). The image of such an object on the retina expands rapidly and this magnification in time is called the "looming effect." It is measured as the rate of

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

change of the angle, α, subtended by the approaching object measured at the prey's eye (Dill 1974a, b). The looming effect is greater as the speed of an approaching object increases, as the object gets closer, and for larger objects. The threshold was calculated at the start of an escape attempt by the larvae, after Dill (1974a),

$$\frac{d\alpha}{dt} = \frac{4\,U\,S_h}{4(D+d)^2 + {S_h}^2} \quad (1)$$

where U = predator speed at the time of the prey response,
Sh = predator shape; mean of maximum depth and width of the clown fish,
D = distance between the predator's nose and the prey when the prey responded,
d = posterior distance of the predator's maximum depth and width from its nose.

Here, $d\alpha/dt$ at the start of the response by the larvae is called the apparent looming threshold (ALT). This is because the true threshold must occur prior to the observed motor response because there is a finite delay in the nervous system between receipt of the stimulus and the start of the motor response. The value of this response latency, or reaction time, is unknown for northern anchovy larvae.

RESULTS

Clown fish fed discontinuously on eggs and larvae, feeding intensely on prey in one location and then swimming around the tank before feeding again. Thus the clown fish did not attack prey as encountered, and often ignored nearest prey between feeding bouts. The clown fish were continuously active, swimming mainly by paddling movements of the pectoral fins supplemented with caudal fin beats. The mean speed was 3.2 ± 0.5 cm/s ($\bar{X} \pm 2$ SE; $N = 100$; range 0.5 to 9.1 cm/s).

Attacks were made on individual larva. Orientation by the clown fish prior to a strike could not be distinguished with confidence from normal swimming. Prey that did not attempt to escape were always caught, with the exception of eggs and the smallest larvae tested. Thus 12% of strikes on eggs and 3% of strikes on nonresponding 0.29 cm larvae were not successful. Predator failures are presumed due to predator error, which has been reported as 8% for largemouth bass, *Micropterus salmoides*, (Nyberg 1971) and 34% for chain pickerel, *Esox niger* (Rand and Lauder 1981). Larvae that made an avoidance response to an attack by clown fish were rarely pursued because clown fish usually attacked another larva. Eight chases were observed in 113 escape attempts by northern anchovy larvae. One escape each was observed for larvae in the 0.626 and 1.166 cm TL groups and two in each of the 0.399, 0.867, and 0.953 cm groups.

Larval responses to attacks by clown fish were characteristic startle responses, followed by a short period of sprint swimming. The startle response consisted of a C-start form of a fast start and a turn (Eaton et al. 1977). The sprint was a period of swimming at constant speed for <1 s (see Hoar and Randall (1978) for definitions). Together, these two components constitute a swimming burst (Webb and Corolla 1981).

The proportion of larvae responding to attacks increased with size, from approximately 9% for 0.29 cm larvae to 80% for 1.2 cm larvae (Figure 1A). The proportion of larvae escaping an attack similarly increased with size, but at a lower rate than the proportion making an escape attempt (Figure 1B). This was because $26 \pm 10\%$ ($N = 10$ groups of larvae) of larvae showing an escape response were eaten anyway, before a chase began. These larvae were defined as attempting to escape too late. This proportion of escaping larvae caught

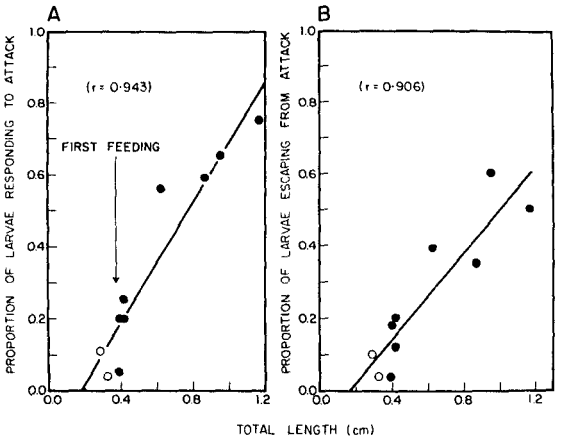

FIGURE 1.—Relationships between (A) the proportion of northern anchovy larvae responding to an attack by clown fish and (B) the proportion escaping an attack, both as functions of the total length. Circles are for prefeeding yolk-sac larvae.

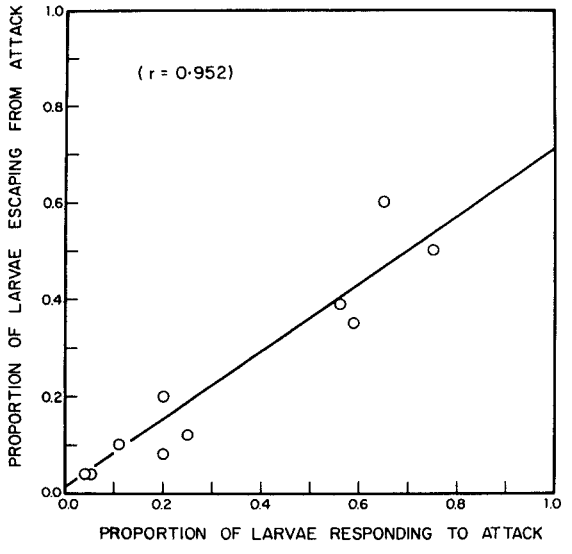

FIGURE 2.—The relationship between the proportion of northern anchovy larvae responding to an attack and the proportion escaping an attack by clown fish.

by the clown fish was not correlated with larval size.

The proportion of larvae attempting to escape was therefore related to the proportion escaping (Figure 2). Using functional regression analysis (see Ricker 1979), the relationship was found to be linear, and gave a value of 30% of larvae attempting to escape being captured. This is within the expected range obtained from observations on each group of larvae.

The startle response included a turn. The angle of the prey escape path relative to the predator strike path showed no particular relationship with larval length (Figure 3A), but this was primarily due to the large angles measured for the 0.391, 0.399, and 0.421 cm larvae. Without these data, the escape angle would have increased with larval length, implying larger larvae were better at avoiding the predator's strike path. However, larvae in the three length classes with large angles did not differ from others in any obvious way, and therefore the data cannot be rejected.

However, the distance traveled in an escape swimming burst increased with larval total length (Figure 3B). Using regression analysis (type II) the relationship was best described by a power function, but r^2 values were relatively low. Mean escape speeds in an escape swimming burst also increased with larval size (Figure 4). These speeds were normally about half the mean burst speeds

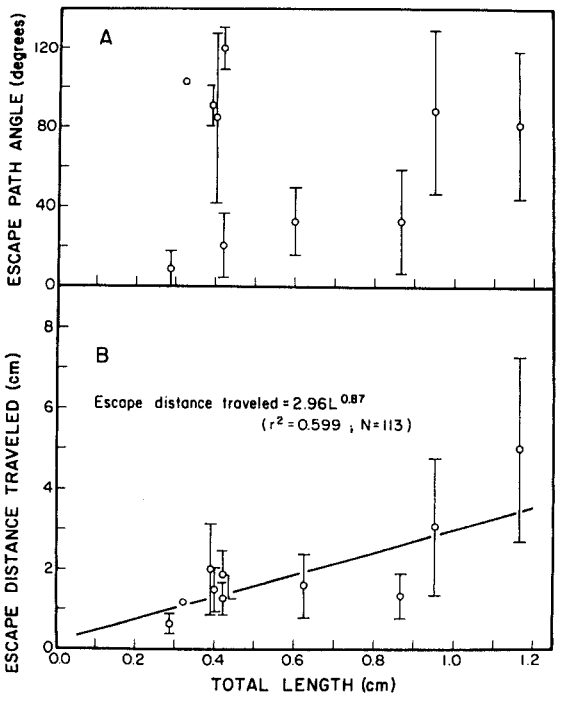

FIGURE 3.—The relationship between (A) the angle of the prey escape path to the predator's strike path and (B) escape distance traveled both as functions of total length of northern anchovy larvae attacked by clown fish. Vertical bars show ±2 SE.

obtained in a forced swimming burst (Webb and Corolla 1981), but escape speeds comparable with the forced maximum were seen during chases.

Analysis of ALT's for larval escape responses is somewhat complex. These ALT's were assumed to be distributed in the population like any other character. However, not all larvae responded. Since nonrespondants were eaten before responding they were assumed to have higher ALT's than larvae showing escape responses. Therefore, the true distribution of ALT's in the population is not known as values above some observed level are missing. Such a population is said to be censored, and since values are missing from one end of the distribution only, it is said to be singly censored. Cohen (1961) has described methods to calculate the maximum likelihood mean and variance of such censored samples. However, before this can be done, the nature of the ALT distribution must be considered.

The nature of the distribution of ALT's in the population was evaluated using probit analysis, developed to examine related problems in toxicology (Sprague 1969). ALT values were ranked and

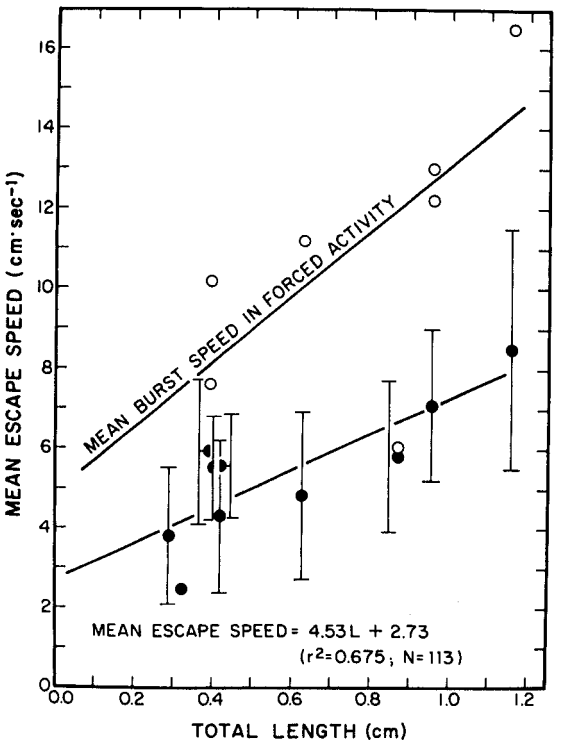

FIGURE 4.—The relationship (dots) between mean escape speed and total length of northern anchovy larvae attacked by clown fish. Vertical bars are ±2 SE. Circles show mean escape speeds during chases. The line for mean burst speeds was taken from Webb and Corolla (1981).

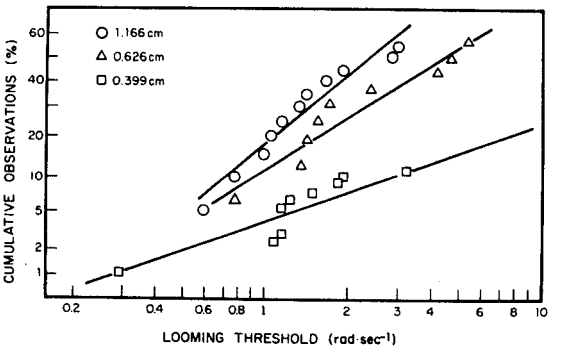

FIGURE 5.—Representative relationships between cumulative number of startle responses, expressed as percentages of total attacks (probit scale) and the logarithm of ALT's for northern anchovy larvae of three different total lengths.

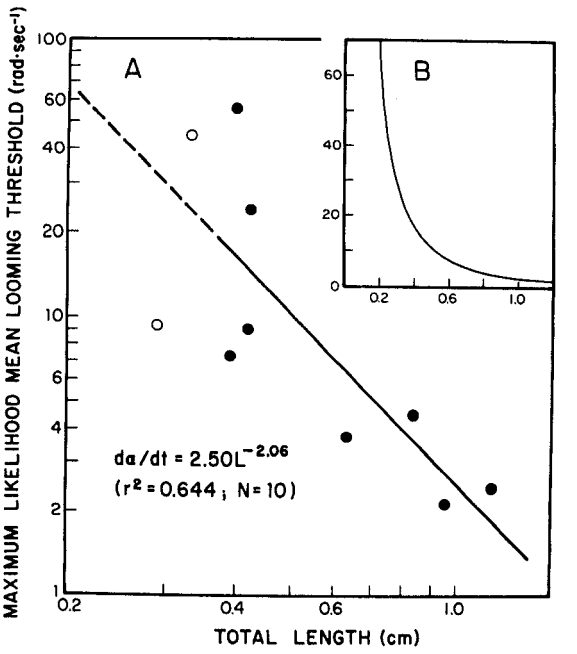

FIGURE 6.—The relationship between the maximum likelihood mean ALT and total length of northern anchovy larvae attacked by clown fish. The relationship is shown for logarithmic coordinates in (A) and for arithmetic coordinates in the inset (B). Circles are for prefeeding yolk-sac larvae.

the cumulative percentage of observations was plotted on a probit scale against these values. A logarithmic transformation of ALT values linearized the relationship to the greatest extent (Figure 5) implying ALT's were log-normally distributed in the population. Some curvature remained after this transformation, probably due to decision errors (Treisman 1975) and individual variability in response latencies. Thus ALT values were assumed to be log-normally distributed in the larval populations sampled, and maximum likelihood means and variances were calculated for a type I singly censored sample (Table 2) as described by Cohen (1961). Resulting mean ALT's are shown as a function of total length in Figure 6.

The most important result from this analysis was that ALT's decreased rapidly with increasing size, and hence development, tending towards a plateau for larger larvae and presumably for adults. The relationship was best described by a power function with a negative exponent (see Figure 6) but such a description should be treated with caution. This is because the ALT distributions were severely censored, with a resulting large variance about each mean. In addition, the residual curvature in the transformed data could influence mean ALT values, but this would not alter the general shape of the inverse relationship between ALT's and larval size.

TABLE 2.—Parameters used in the calculation of maximum likelihood values of the population mean $d\alpha/dt$ ($\hat{\mu}$) and variance ($\hat{\sigma}^2$) for northern anchovy larvae responses to clown fish predators, using the method of Cohen (1961). Logarithm-transformed data for $d\alpha/dt$ were used in these calculations. $\hat{\lambda}$ taken from tables in Cohen (1961); $h = (N-n)/N$, $\hat{\gamma} = S^2/(\bar{X} - X_0)^2$, $\hat{\mu} = \bar{X} + \hat{\gamma}(\bar{X} - X_0)$, and $\hat{\sigma}^2 = S^2 + \hat{\gamma}(\bar{X} - X_0)^2$.

Length (cm)	Sample mean $\bar{X}$ (log rad/s)	Sample variance S^2	Sample range $(\bar{X} - X_0)$	h	$\hat{\gamma}$	$\hat{\lambda}$	$\hat{\mu}$ (log rads/s)	$\hat{\sigma}^2$	N
0.29	0.12	0.03	0.24	0.91	0.56	3.60	0.97	0.23	63
.32	.34	.19	.31	.96	2.00	4.31	1.65	.59	45
.39	−.64	.41	−.64	.93	.99	4.18	.86	.95	56
.40	.10	.08	.52	.87	.30	3.16	1.75	.93	79
.42	.17	.11	.36	.75	.87	2.23	.96	.39	32
.42	−.05	.07	.41	.91	.42	3.53	1.39	.65	45
.63	.33	.08	.44	.45	.47	.76	.65	.22	36
.83	−.08	.41	.63	.50	.40	.96	.58	.36	34
.95	−.12	.45	.30	.41	.47	.72	.33	.46	40
1.17	.14	.44	.42	.42	.46	.83	.39	.12	32

DISCUSSION

These experiments were performed to examine responses of northern anchovy larvae to attacks by biting (i.e., nonfilter-feeding) fish planktivores such as juvenile fish preying on zooplankters. The nature of the predator is relatively unimportant. Inexperienced larvae are likely to respond to an attack in the same way because in all cases failure to do so is terminal. The other alternative is that prey have specific predator images to which they respond, which seems improbable.

One objective was to evaluate an experimental technique that could be easily repeated and applied further (e.g., to problems of larval vulnerability and starvation interactions, effects of alternate prey species, prey density, and other questions affecting larval predation mortality). For this reason it was considered important initially to use a predator that was readily available at a uniform size. Natural fish predators could not be obtained in good condition and in a reasonable size range for the period of the experiment. Clown fish were found to be an excellent substitute.

However, experiments were performed at 20° C which is at the upper extreme of the temperature range of northern anchovy, but this probably had a small effect on the observations. The energy required for the short periods of high level activity in an escape swimming burst is undoubtedly derived mainly from anaerobic metabolism, which is known to be less dependent on temperature than aerobic metabolism (see, e.g., Bennett 1980). Experimental data on burst swimming performance are only available for rainbow trout and these data confirm the small effect of temperature in the range of 10° to 25° C (Webb 1978).

Two primary measures of response to attack were obtained, the proportion of larvae showing a startle response and the apparent looming threshold for that response. The proportion of larvae responding to attack increased linearly with length (Figure 1). This result is surprising. Kimmel (1972) has shown that several days are required for the Mauthner cell, which initiates the startle response, to extend caudally. The eyes are not functional before first feeding, so they could not initiate a startle response (O'Connell 1981). Neuromasts are present from hatching but if they were involved in stimulating a startle response, very high percentages of early larvae should show responses to attack. These developmental events suggest a rapid increase in percent response to attack would be expected in the yolk-sac stages, approaching maximum response levels at about first feeding, as found for responses to electric shock stimuli (Webb and Corolla 1981).

However, development rates are likely to vary widely in a population of larvae. It is for this reason that food is first added on the second day after hatching in spite of the fact that the mean time to first feeding is about 4 d (Hunter 1976). The percentage of yolk-sac larvae responding to attack was quite small and was probably due to early maturation (most likely of the visual system) of the most rapidly developing individuals.

The ALT changed with larval size, decreasing rapidly as larvae grew in length. This decline could have been due to improved acuity in the visual system and/or maturation of neural pathways processing visual information. This later could include shorter response latencies with age. The changes in ALT may be the basis for the increasing proportion of avoidance responses in larger larvae.

The only other measurement of looming thresholds for fish are those of Dill (1974a, b) for postlarval zebra danio, *Brachydanio rerio*, in re-

sponse to attacks by largemouth bass and to silhouettes. These data are not fully comparable with those obtained here for several reasons. First, the mean depth plus width was used to characterize the shape of the clown fish. Dill (1974a) used only width, citing reports that fish are more sensitive to horizontal movement than to vertical movement (Cronly-Dillon 1964; Jacobson and Gaze 1964). In contrast, operant conditioning experiments show that fish are particularly sensitive to apices (e.g., Hinde 1970; Baerends 1971) which occur at the dorsal and ventral margins of laterally compressed bodies. In the absence of definitive experiments relating shape to looming response thresholds, the mean value of depth plus width was considered most appropriate. Use of the mean value of depth and width would give larger values of $d\alpha/dt$ than use of depth alone (Equation (1)).

Second, the distance between the nose and the maximum depth and width of the predator was added to the reaction distance separating the predator and prey. This assumes that the prey either has depth vision or sees the equivalent of a silhouette of the predator. The inclusion of this term would reduce values of $d\alpha/dt$ compared with Dill's method.

The ALT values for postlarval zebra danios (2.0 cm long) was 0.43 rad/s. Northern anchovy larvae of the same size would be expected to have a mean value of about 0.6 rad/s from the relationship in Figure 6.

The overall function of the startle response is to avoid predators. How effective is it? The clown fish rarely pursued escaping larvae, although when they did so, the larvae were easily caught. In these experiments, chases may have been rare because larval densities were high. However, observations on adult piscivores attacking single prey show that chases are also rare with pike, *Esox* (Neill and Cullen 1974; Webb and Skadsen 1980), largemouth bass (Nyberg 1971; P. W. Webb unpubl. obs.), and rock bass, *Ambloplites rupestris* (P. W. Webb unpubl. obs.). Presumably the cost of pursuit is large relative to the benefits of capturing small prey particularly where there are alternative prey. In a normal planktonic assemblage, alternate prey could be important in reducing vulnerability of larval northern anchovy, especially in the presence of more opaque forms and those with more strongly pigmented eyes (Zaret and Kerfoot 1975).

Unfortunately, there are no field observations on larval responses to predation, and the likelihood of making the requisite field observations is remote. Nevertheless, the response of a prey to an attack is an obvious indicator of the prey's awareness and the possible difficulty of capture. The reluctance of many predators to attack responding prey, as noted above, together with the behavior of the clown fish observed in these experiments, imply that the startle response is an effective deterrent. Thus, it is most important that the larvae respond, but initially maximum swimming speeds are not required. Indeed the latter would be energetically more costly. Larvae clearly behave appropriately with a submaximal evasion (Figure 4), except when maximum performance becomes desirable in the rare event of a chase. Nevertheless, timing of the escape attempt must be accurate as 24 to 30% of the larvae attempted a response too late to escape capture.

Larval looming response thresholds will not only be important in escaping biting predators, but also other predation threats. Webb and Corolla (1981) discussed relationships between burst swimming performance of northern anchovy larvae and escape probabilities from plankton nets as a crude analogy with filter-feeding predators. While swimming performance could explain a large part of net avoidance, other factors were involved. Webb and Corolla suggested that declining response thresholds with experience would be important so that larger larvae responded earlier to an impending collision. The inverse relation between ALT with larval total length suggests that such changes occur. Presumably, similar thresholds or size relations would apply to larger predators. Then the reaction distance to a net moving, for example, at a given towing speed would be expected to be greater for larger northern anchovy larvae. This would contribute significantly to the size-dependent sampling bias of such nets.

This work has attempted to evaluate a method for quantifying responses of a fish larva to attacks by a predator as one step in studying the neglected aspect of predation on larval mortality. The advantages of the method are the visualization of both opaque and transparent individuals of small size and continuously recording their behavior. The disadvantages are that the space viewed must be small and hence only small predators can be used, and filtering predators are excluded. However, predation could be studied for particular feeders (e.g., biting fish and chaetognaths) arthropods (e.g., copepods and euphausids), and less discriminating feeders such as thaliaceans and

cnidarians. These are abundant in the plankton. In addition, effects of 1) larval density, 2) alternate prey in mixed planktonic assemblages, and 3) effects of starvation on larval vulnerability to predation could be studied.

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GULF OF MEXICO SHRIMP PRODUCTION: A FOOD WEB HYPOTHESIS[1]

R. WARREN FLINT AND NANCY N. RABALAIS[2]

ABSTRACT

The desire to better understand the dynamics of commercial shrimp populations which support an important regional fishery on the south Texas outer continental shelf stimulated us to investigate an extensive data base for links in the various ecosystem components that related to these dynamics. A correlational model was developed that suggested relationships between pelagic and benthic components of the south Texas marine ecosystem. Utilizing tracers, such as nickel concentrations in biota, sediment, and water, we identified pathways of natural transfer between zooplankton, the benthos, and coastal shrimp populations. These results stimulated us to develop a theoretical food web for the shrimp populations, focusing on transfer of carbon. The results of this exercise indicated that the majority of primary production (approximately 80%) is diverted to the benthos. Furthermore, it appeared that the secondary production of benthic infauna was not sufficient to alone support the coastal shrimp populations. We concluded that at least part of their nutrition was derived from the detritus pool which was maintained by the excessive amount of primary production diverted to the benthos. The evidence presented here suggests that the marine ecosystem in the coastal waters of south Texas functions differently than other ecosystems studied in recent years and pinpoints the need for a better understanding of the basis upon which our marine living resources are supported, in order to predict not only fishery yields but also effects of environmental disturbance.

The commercial shrimp fishery in the U.S. waters of the Gulf of Mexico is one of the most productive fisheries the United States pursues. This fishery provides better than 20% of the gross dollar value for the total U.S. harvest (U.S. National Marine Fisheries Service 1976) and represents the largest fishery in terms of weight harvested and effort expended along the gulf coast. For example, from a coastal area of Texas covering 10,000 km^2, an average of 5.7×10^6 kg/yr of brown shrimp, *Penaeus aztecus*, was landed in 1975-76, which represented an annual value of $18 million. A decline in this fishery could cause economic loss, at least on a regional scale.

Research emphasis on the populations of penaeid shrimp that support the commercial fishery in the northwestern Gulf of Mexico has been directed towards laboratory behavioral studies, migratory habits, and the development of models relating harvest to environmental factors and management strategies. Although the data derived from these studies contribute to our understanding of the natural fluctuations that occur in the fishery, they do not provide adequate information about where the penaeid populations fit into the trophic structure of the marine ecosystem and how these populations function. Due to this lack of knowledge, environmental managers would not be able to predict with confidence how a major perturbation in the Gulf of Mexico would affect the shrimp populations.

For years information has been accumulating on primary production, zooplankton biomass, and the distribution of benthic fauna in important marine fishery areas. Attempts to quantify links between these components have been provided by Steele (1974) for the North Sea ecosystem and by Mills and Fournier (1979) for the Scotian shelf. Arntz (1980) more recently attempted to relate benthic production with that of commercially important demersal fishes in the Baltic Sea. With the completion of a 3-yr multidisciplinary environmental study of the south Texas continental shelf (Flint and Rabalais 1981), one more fishing area has been characterized.

The Texas shelf ecosystem is a dynamic system driven by a complex aggregation of meteorologic and oceanographic events. Superimposed upon these phenomena are influences from local rivers and estuaries as well as from distant points such as the Mississippi River and the deep oceanic waters of the gulf basin (Flint and Rabalais 1981). The shallower waters of the Texas shelf are biologically a critical part of this ecosystem because of

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their larger standing crops of phytoplankton, zooplankton, and benthos (Flint and Rabalais 1981) which are capable of supporting the large shrimp fishery yield in these waters.

Based upon a desire to better understand the characteristics of an important resource of the Texas continental shelf, we used the south Texas environmental study data as well as information from the published literature to develop a model of the trophic relationships supporting the brown shrimp fishery. This analysis provided insight into the general structure of marine ecosystems which support fisheries. It also provided the necessary data to judge whether the generalization of Dickie (1972) and Mills (1975)—that despite geographic differences most coastal ecosystems with productive fisheries have similarly constructed food webs—is well founded or not.

METHODS

A multidisciplinary research program (1975-77) was conducted on the south Texas outer continental shelf (STOCS) at 25 stations (Figure 1). The study included water mass characterization, pelagic primary and secondary production as described by floral and faunal biomass, and benthic productivity as described by macroinvertebrate infaunal and epifaunal densities as well as demersal fish densities and biomass. The study, summarized by Flint and Rabalais (1981), provided a data base depicting the general characteristics of a marine subtidal area with important natural resources.

The focus of the results presented in this paper is on data collected from a "Reference Station" (Figure 1) which we consider representative of Statis-

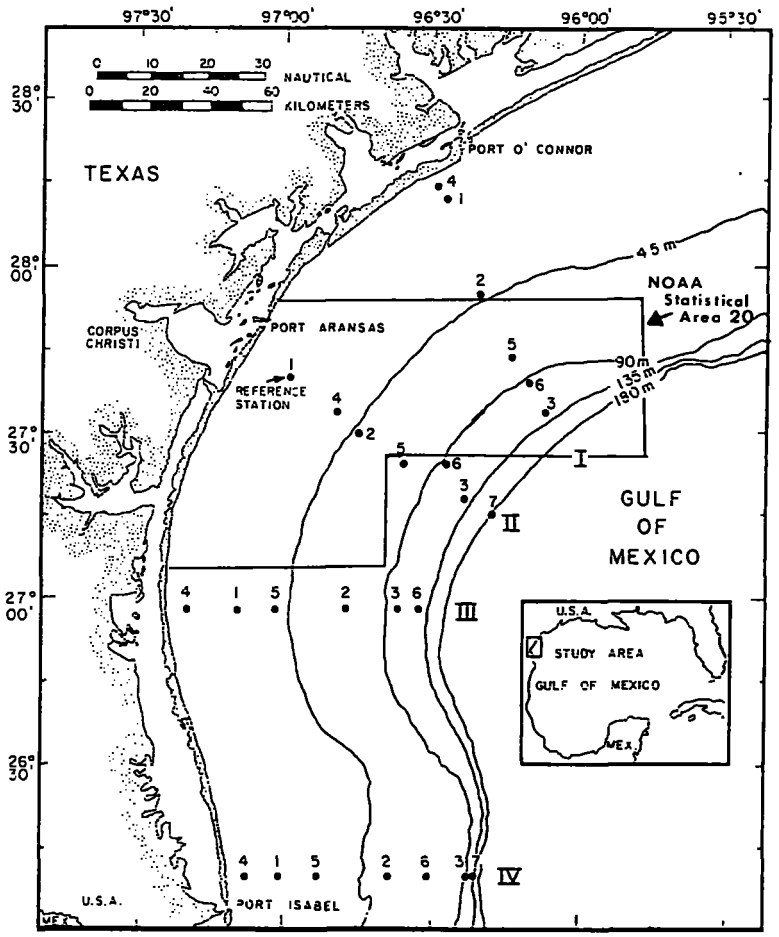

FIGURE 1.—Map of the south Texas continental shelf with location of sampling sites for 1975-77 environmental study. NOAA shrimp catch Statistical Area 20 is superimposed along with the Reference Station representing the source of data used in the text.

tical Area 20, the shrimp landing reporting region (U.S. National Marine Fisheries Service 1978) most closely associated with the STOCS study area. As mentioned previously, the shallower waters of the south Texas shelf are more productive, and the maximum yield of the brown shrimp fishery is within the depth range of this station (Grant and Griffin 1979). This site was characterized by one of the largest data bases of all 25 stations. Water column variables were sampled monthly during 9 mo in 1976 and 1977, and benthic variables were sampled monthly during 9 mo in 1976 and seasonally (winter, spring, and fall) in 1977. Details of sampling procedures are available in Flint and Rabalais.[3]

The STOCS data base contained adequate data on various biotic and abiotic components to allow for an integrated investigation of ecosystem relationships, with the shrimp populations as the ultimate focus of this exercise. Our approach was twofold. In the first step, we evaluated all variables in relation to one another using a correlation matrix. These comparisons included components within the pelagic environment, within the benthic environment, and between the two environments. Variables considered were similar to those listed in table 3 of Flint and Rabalais (1981). We looked for relative changes in population densities and biomass of biota that might be expected to be associated, such as phytoplankton and zooplankton or brown shrimp and benthic macroinfauna. Also, tracers, such as hydrocarbons and trace metals, identified relationships between components of the ecosystem based on organism body burdens and concentrations of the tracers in water samples and sediments.

Bivariate Pearson correlation coefficients were used (Sokal and Rohlf 1969). All correlation coefficients, either positive or negative, were evaluated for their biological meaning. Those suspected of ecosystem relationships were put in a two-by-two correlation matrix, within which the number of significant correlations ($P<0.01$) had to be more than 5% of the total for us to conclude that they were not chance produced (Bernstein et al. 1978).

The goal of this first step was to develop a correlational model of relationships in the data that suggested patterns in trophic coupling between shrimp populations and other biotic components. The patterns derived in step one prompted us to develop biomass estimates for the related components. The goal of the second step was to develop a theoretical model of energy flow in a trophic web which included penaeid shrimp as our central focus. Data from the STOCS Reference Station were used to estimate floral and faunal biomass as follows.

Chlorophyll *a* was measured according to standard techniques (Strickland and Parsons 1968). Biomass of zooplankton was determined from oblique (surface to near bottom to surface) tow samples taken with a 1 m net of 223 μm mesh. Neuston biomass was determined from samples collected in a 505 μm mesh neuston net towed in surface waters for 15 min. Zooplankton and neuston data were originally reported as ash-free dry weights but were converted to wet weights using a conversion factor of 0.15 for crustaceans (Lie 1968). Microplankton samples were collected in a 50 l Niskin bottle at the surface and at one-half the depth of the photic zone. Wet weight biomass was estimated by measuring volume displacement and assuming that a cell density of 1 μ^3 equalled 10^{-6} μg wet weight.

Benthic macroinfauna (>0.5 mm) samples were taken with a 0.1 m Smith-McIntyre grab. Estimates of benthic infaunal biomass (Table 1) in the south Texas shelf area ranged between 0.5 g/m^2

[3]Flint, R. W., and N. N. Rabalais (editors). 1980. Environmental studies, south Texas outer continental shelf, 1975-1977. Vol. III. Final report to the Bureau of Land Management, Department of the Interior, Wash., D.C. Contract AA551-CT8-51, 648 p.

TABLE 1.—Comparison of abundance and biomass of macrobenthos from the northwestern Atlantic Ocean and northwestern Gulf of Mexico.

Atlantic Ocean[1]			Gulf of Mexico				
Depth	Density (no./m^2)	Wet weight (g/m^2)	Depth	Density[1] (no./m^2)	Wet weight[1] (g/m^2)	Density[2] (no./m^2)	Wet weight[3] (g/m^2)
30	26,060	7.69	12			1,536	0.63
40	7,390	2.44	16	1,373	0.74		
			30	14,623	4.09	675	0.28
Average	16,725	5.07		7,998	2.42	1,106	0.46

[1]*Measures from Rowe et al. (1974).*
[2]Measures from the South Texas Outer Continental Shelf Study, 1975-77.
[3]Wet weight calculated from densities of organisms using the density to wet weight ratio of the respective values from Rowe et al. (1974).

(STOCS study) and 2.4 g/m^2 (Rowe et al. 1974). Since the data from Rowe et al. (1974) were based on a single sampling effort and the measures from the south Texas study were based on 12 separate sampling periods, we biased our infaunal biomass estimates towards the STOCS data and derived a biomass figure from a regression between total density and total biomass of infaunal samples (Table 1). Epifaunal invertebrates and demersal fish were sampled in 15-min bottom tows with a 10.7 m Texas box otter trawl with a 25 mm stretched mesh cod end. Wet weights were determined directly from the trawl samples.

Because biomass measurements were made on the penaeid shrimp during only one season in the whole STOCS study, we felt the data were not sufficient to completely characterize the biomass levels for the shrimp. Thus, shrimp biomass data were taken from Gulf Coast Annual Shrimp Landing Reports (U.S. National Marine Fisheries Service 1976, 1978). The shrimp fishery yields, however, did not represent the total production of shrimp in the coastal gulf waters. Therefore, for our model we estimated the biomass of shrimp populations that was not reflected by the catch statistics. A survival curve for the shrimp population was calculated (Figure 2), based upon a total population egg production rate of 10^{11} [based on a mean of 800,000 eggs/adult female >140 mm total length and a 1:1 sex ratio (Pérez Farfante 1969)] with a survival rate for the hatch of 1%. This resulted in a recruitment rate of 10^5 juveniles to the population (Figure 2). The three additional data points on the curve were determined by splitting the shrimp biomass from the catch statistics (shaded area) into three size classes and calculating the number of shrimp of mean size within each of these classes. The curve was then extrapolated from recruitment through each of these data points with the mean size at emigration from the bays indicated (Figure 2).

The results of this two-step exercise provided information to estimate production and develop an energy flow model for the components of the south Texas shelf food web according to the ideas of Steele (1974) and Mills and Fournier (1979). Primary production estimates on an annual basis were calculated from chlorophyll *a* measurements according to the methods of Ryther and Yentsch (1957). A turnover ratio of 7 was used to convert macrozooplankton standing stocks to annual production (Steele 1974). Certain factors, such as tows failing to reach the bottom and net clogging causing <100% efficiency, contribute known biases to zooplankton sampling methods (Hopkins 1963; Wiebe and Holland 1968; Fasham 1978). Because of this and the fact that the water column was usually homogeneous in the shallow waters at the Reference Station (Flint and Rabalais 1981), we doubled the zooplankton production estimates. A turnover ratio of 10 was used for the microzooplankton standing stocks because we assumed a

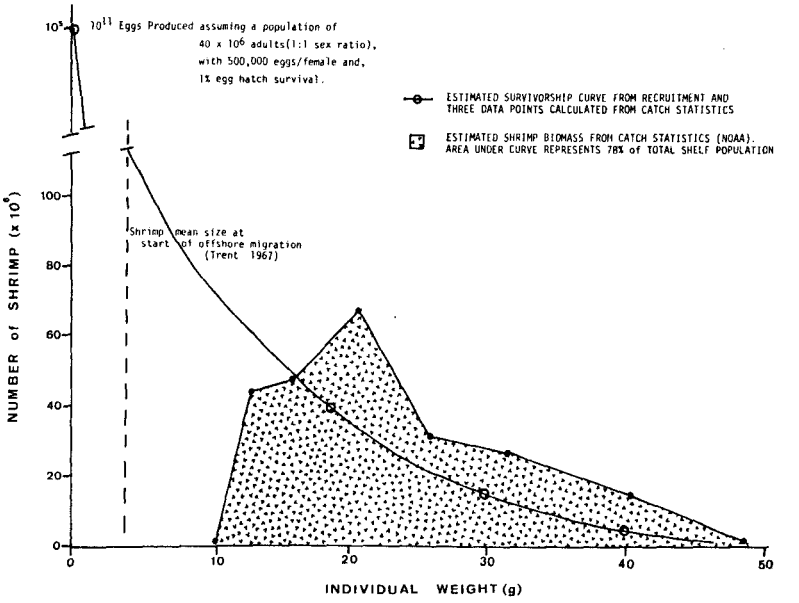

FIGURE 2.—Plot of the reported shrimp (*Penaeus aztecus*) fishery yield according to size class (shaded area) along with an estimated survivorship curve (solid line) for the south Texas continental shelf from NOAA Statistical Area 20 (see Figure 1).

larger ratio for the smaller sized microplankton as found by Droop and Scott (1978) and Mills and Fournier (1979). Benthos standing stocks were converted to annual production using a turnover ratio of 4.5 (Nichols 1977; Arntz 1980). A conversion for heads-on weight (1.61) and a turnover ratio of 0.8 (E. Klima[4]) were used to determine annual production from estimated shrimp standing stocks. A 6% conversion between wet weight and carbon content of metazoans (G. T. Rowe[5]) was used to determine carbon equivalents of annual production estimates.

RESULTS

Correlational Model

Significant correlation coefficients identified in the bivariate correlation analysis along with relationships in the data that suggested patterns in trophic coupling were used to develop the model illustrated in Figure 3. There was a relationship between the water column fauna, in this case zooplankton, and the sediment detritus pool as evidenced by the correlations between zooplankton nickel body burdens and sediment nickel concentrations as well as several zooplankton hydrocarbon body burden variables and hydrocarbons observed in the sediment (Figure 3). The analysis further indicated that primary producer biomass, represented by bottom water chlorophyll *a* concentrations, was related to density changes in benthic macroinfauna, potentially through the detritus pool (Figure 3). Relationships also existed between sediment hydrocarbon concentrations and bacterial density, indicating another potential link through the detritus pool.

Within the benthos, meiofaunal and macroinfaunal densities were correlated to bacterial densities, and macroinfaunal densities were correlated with meiofaunal densities (Figure 3). The constant ratio of benthic faunal densities to bacteria and not organic carbon (Figure 3) suggested

[4]E. Klima, Director, Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 U Street, Galveston, TX 77550, pers. commun. August 1980.

[5]G. T. Rowe, Research Scientist, Brookhaven National Laboratory, Upton, Long Island, NY 11973, pers. commun. June 1980.

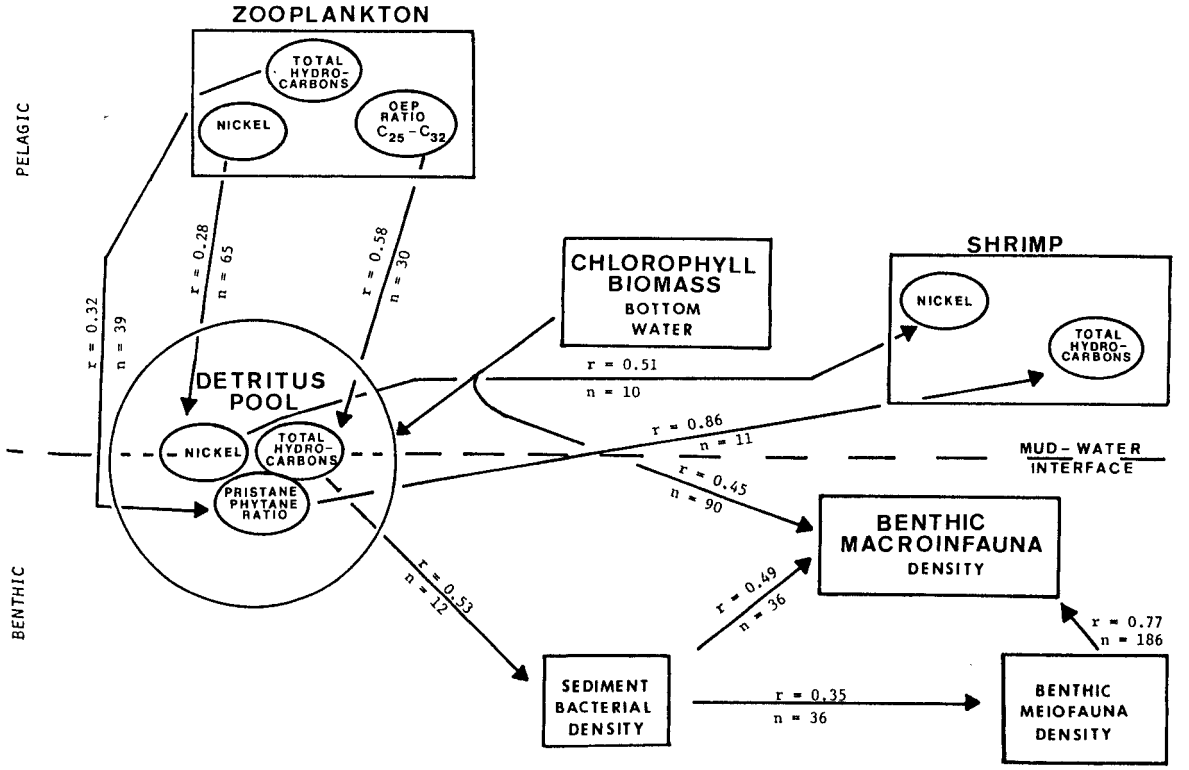

FIGURE 3.—Schematic representation of significant ($P<0.01$) correlation coefficients (r) found between south Texas continental shelf environmental variables measured for 1976-77. Sample size (n) is also shown for each correlation.

bacteria as a food source. The meiofauna-macrofauna correlation completed the trophic web between the sediment inhabitants.

Finally, densities of shrimp on the Texas shelf were tied to the sediment detritus pool by correlations between shrimp body burdens of nickel and total hydrocarbons and sediment nickel concentrations and a sediment hydrocarbon variable (Figure 3). The correlations between zooplankton nickel body burdens, nickel concentrations in the sediment, and shrimp nickel body burdens (Figure 3) allowed us to propose a trophic coupling hypothesis for the shelf shrimp populations that included both pelagic and benthic components.

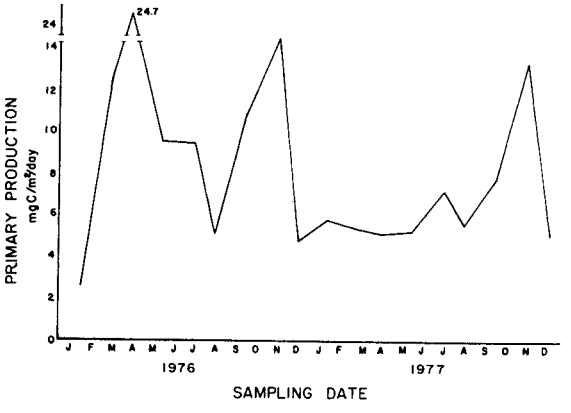

FIGURE 4.—The 2-yr cycle of primary production (carbon fixation) for Texas coastal waters between 1976 and 1977. Primary production calculated according to methods of Ryther and Yentsch (1957) using chlorophyll *a* measurements.

Trophic Web

Primary production for Texas inner shelf waters, determined from the Reference Station chlorophyll *a* measurements, was bimodal annually with peaks usually occurring in spring and fall (Figure 4). Since the spring peak in biomass for 1977 was not measured and presumably missed by the timing of our sampling, the estimate of 103 g C/m^2 per yr representing the amount of carbon fixed in the primary level of the trophic web (Figure 5) was probably low.

Macrozooplankton biomass on the Texas shelf averaged 3.57 g/m^2 wet weight (Table 2). From this amount, annual production of macrozooplankton was estimated to be 24.98 g/m^2 per yr. In conversion for sampling bias, the production estimate was doubled to 49.96 g/m^2 per yr. The carbon equivalent of zooplankton production was estimated to be 3 g C/m^2 per yr. Similarly converted biomass data from the neuston component of the planktonic community added 0.2 g C/m^2 per yr (Table 2) to the macrozooplankton portion of the trophic web (Figure 5). Standing stock of microzooplankton was 0.47 g/m^2 wet weight which converted to an annual production of 0.9 g C/m^2

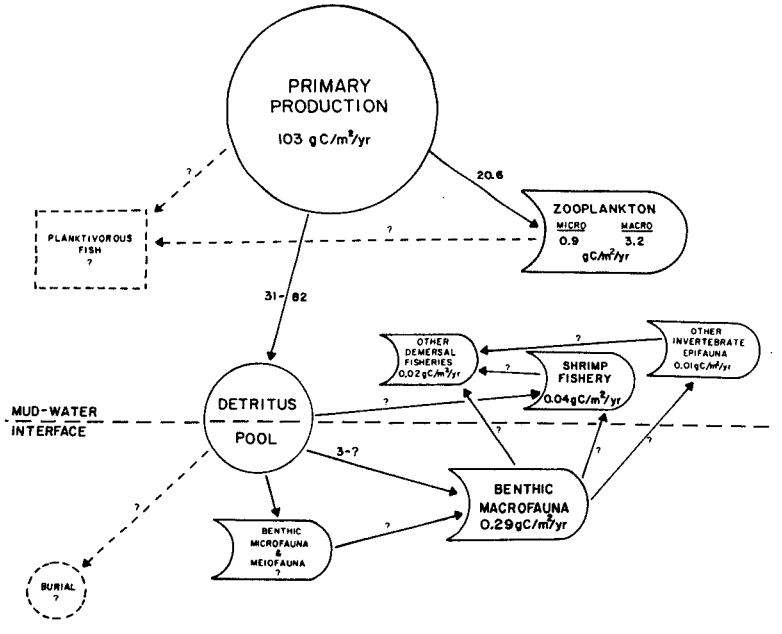

FIGURE 5.—Theoretical model of an annual production and energy flow food web for the south Texas continental shelf. All material flows represent gram C/square meter per year.

TABLE 2.—Procedures for calculating the amount of annual production for zooplankton components.

Macroplankton:							
Zooplankton biomass (wet weight)	3.57 g/m²	assume → TR = [1]7	24.98 g/m² per yr	sampling → bias conversion	49.96 g/m² per yr	assume carbon → equivalent = 6% wet weight[2]	3.0 g C/m² per yr
Neuston biomass (wet weight)	0.16 g/m²	assume → TR = [1]7	1.13 g/m² per yr	sampling → bias conversion	3.40 g/m² per yr	assume carbon → equivalent = 6% wet weight[2]	0.2 g C/m² per yr
Microplankton: biomass (wet weight)	0.47 g/m²	assume → TR = [3]10	4.65 g/m² per yr	sampling → bias conversion	13.96 g/m² per yr	assume carbon → equivalent = 6% wet weight[2]	0.9 g C/m² per yr
						Total	4.1 g C/m² per yr

[1]Turnover ratio (TR) for zooplankton from Steele (1974).
[2]Assume carbon equivalent equal to 6% wet weight for metazoans (G. T. Rowe pers. commun).
[3]Assume higher turnover ratio for microplankton than TR = 7 from Steele (1974).

per yr (Table 2). The estimated total production for the zooplankton components of the food web on the inner Texas shelf was 4.1 g C/m² per yr (Table 2, Figure 5).

If we assume a minimum transfer efficiency of 20% between primary producers and zooplankton as suggested by Steele (1974), which is more conservative than the 27-32% suggested by Mills and Fournier (1979), then 20.6 g C/m² per yr (Figure 5) would be required to support these fauna and 82 g C/m² per yr of primary production would remain. With the exception of a small proportion of this 82 g C/m² per yr, which may support pelagic planktivorous fish, we believe that the majority of the primary production is directed elsewhere.

We derived a biomass figure for the benthic macroinfauna of 1.1 g/m² which we then converted to an annual production of 0.29 g C/m² per yr (Figure 5). From shrimp catch statistics, we estimated shrimp production at 0.03 g C/m² per yr. Based on the hypothesized survival curve (Figure 2), the estimate of shrimp production from catch statistics was found to represent 78% of the actual shelf population production as indicated by the shaded area under the curve. Therefore, with the additional 22% of unharvested shrimp biomass, the annual shrimp production was 0.04 g C/m² per yr (Figure 5). Additional data from the STOCS study indicated that demersal fish and invertebrate epifauna composed 0.02 and 0.01 g C/m² per yr production, respectively (Figure 5). The combination of these amounts with the shrimp production estimates accounted for 0.07 g C/m² per yr produced by fauna living in the bottom waters. Comparing this trophic level with the infaunal production (0.29 g C/m² per yr) and assuming a 10% transfer efficiency, benthic infaunal production appears to be an insufficient food source to solely support the demersal component of the inner shelf food web.

DISCUSSION

Research emphasis on the populations of shrimp that are fished in the gulf has been directed towards migratory habits (e.g., Inglis 1960; Klima 1964; Kutkuhn 1966; Trent 1967), dockside catch statistics (e.g., Gunter 1962; Caillouet and Patella 1978; U.S. National Marine Fisheries Service 1978), the development of models relating fishery harvest to environmental factors such as freshwater inflow (e.g., Hildebrand and Gunter 1952; Martin et al. 1980), and natural history (e.g., Heegard 1953; Iversen and Idyll 1960; St. Amant et al. 1966). Other studies have focused on behavior under laboratory conditions (e.g., Aldrich et al. 1968; Lakshmi et al. 1976). More recently, simulation of the shrimp fishery emphasizing different management strategies has been attempted by Grant and Griffin (1979). These studies, however, fail to pinpoint which factors maintain the shrimp production which supports a thriving fishery. Sources and pathways of nutrition and ramifications of interruption of this flow still remain to be determined.

Other recent studies on important fishery areas (Steele 1974; Mills and Fournier 1979; Arntz 1980) point out the need to understand the general structure of marine ecosystems and the trophic webs which support species important to fisheries. Our study consolidates information on primary production, secondary production, and abundance of benthic animals into a theoretical model of the northwestern gulf shrimp fishery food web.

The Texas shelf supports large phytoplankton biomasses with high annual production, especially in inner shelf waters where plankton are most abundant (Figure 6). Spring blooms in phytoplankton biomass are correlated with riverine inputs and nutrient maxima (Flint and Rabalais 1981). The patterns of inner shelf phyto-

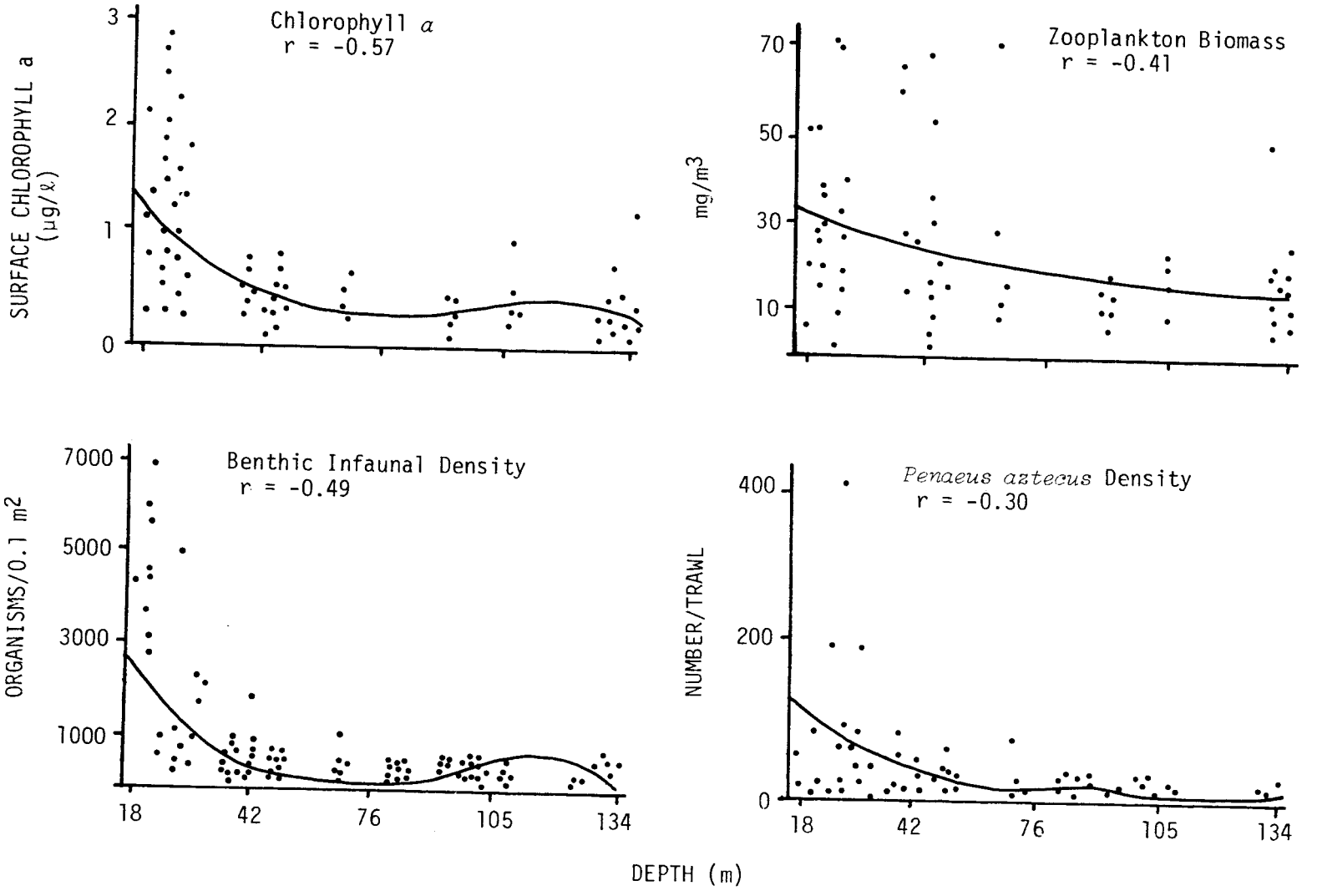

FIGURE 6.—Chlorophyll *a*, zooplankton biomass, benthic infaunal density, and shrimp (*Penaeus aztecus*) density for the south Texas continental shelf study 1976-77. Best fit fourth order polynomial regression lines are presented along with the significant ($P<0.05$) correlation coefficients (r) (from Flint and Rabalais 1981).

plankton productivity are paralleled by zooplankton biomass (Figure 6) with peaks in shallow waters and decreases in an offshore direction. Likewise, both infaunal and epifaunal (represented by *P. aztecus*) benthic organisms are more numerous along the inner shelf (Figure 6) where general productivity is greatest in response to larger food supplies, greater habitat heterogeneity, and nutrients. These productive shallow waters are critical to the shrimp fishery populations. Greatest shrimp harvests for this part of the Gulf of Mexico are recorded for these shallow waters (Grant and Griffin 1979).

Although our estimate of primary production (103 g C/m^2 per yr) may be low because one spring bloom (1977) was missed by sampling frequency, this value is similar to values reported for other fish-producing areas. Mills and Fournier (1979) reported 102 and 128 g C/m^2 per yr for the Scotian shelf and slope, respectively, and Steele (1974) reported 90 g C/m^2 per yr for the North Sea ecosystem. With the exception of a small portion which may support pelagic planktivorous fish, we believe that the majority of the northwestern gulf primary production is directed to the bottom. The amount of pelagic fish production supported by primary production on the Texas inner shelf is unknown; however, the amount of zooplankton biomass measured is not sufficient to support large populations of pelagic planktivorous fish. As indicated by the lack of a commercial fishery, the planktivorous fish that primary production could support represent small standing stocks in this area of the Gulf of Mexico. Thus, almost 80% of the total primary production biomass remains and presumably much of this reaches the bottom in coastal waters.

Further evidence for this conclusion is shown by the phytoplankton biomass distributions in the water column (Figure 7). The bottom waters support equal or greater biomass of primary producers than the surface or middepth waters as

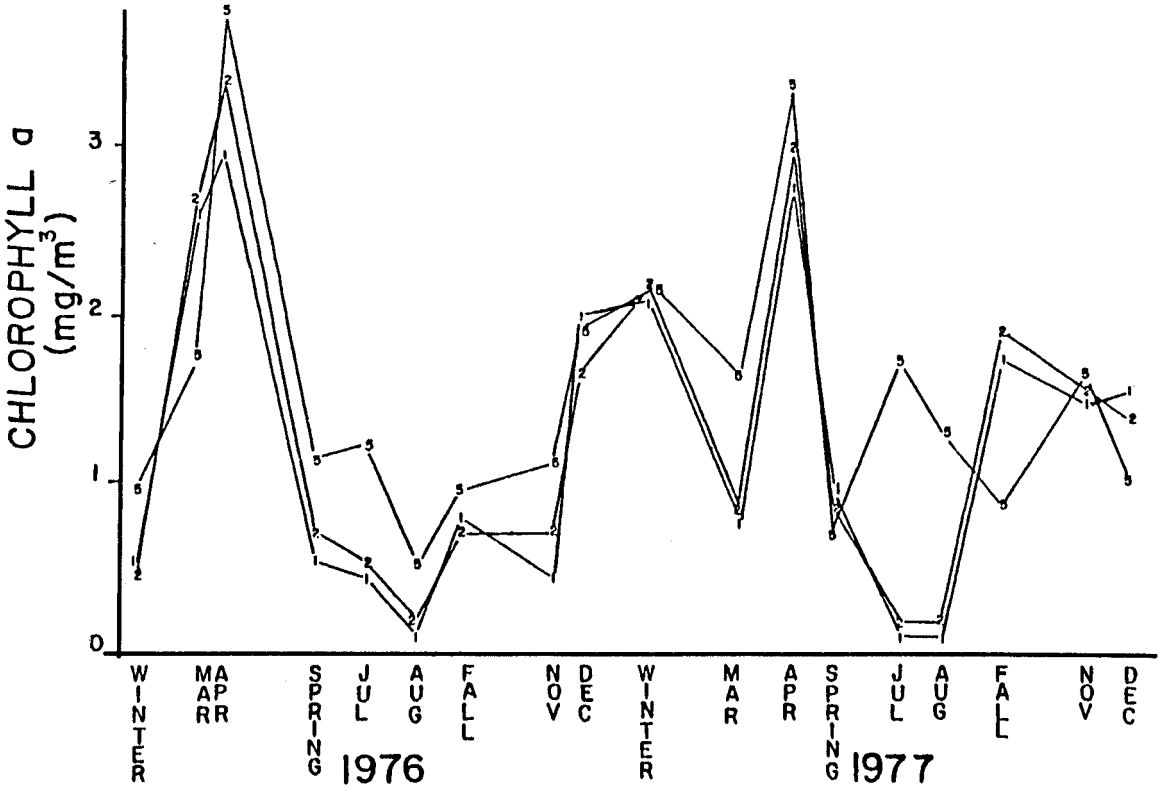

FIGURE 7.—Plot of surface (1), one-half the depth of the photic zone (2), and bottom (5) water chlorophyll *a* concentrations for the south Texas continental shelf environmental study between 1976 and 1977 at the Reference Station in Figure 1 (from Kamykowski, D.L., and S. Milton. 1980. Phytoplankton and productivity. *In* R. W. Flint and N. N. Rabalais (editors), Environmental studies, south Texas outer continental shelf, 1975-1977, Vol. III, p. 231-284. Final report to the Bureau of Land Management, Wash., D.C. Contract AA551-CT8-51).

shown by the chlorophyll *a* concentrations in the water column (Figure 7). These increases with depth indicate that much of what is produced in the pelagic zone reaches the bottom and accumulates.

The lack of stratification of the water column on the inner shelf during most of the year makes this conclusion reasonable. The water column is almost always well mixed in shallower waters <30 m depth (Flint and Rabalais 1981, figure 4), allowing for a direct transport of photic zone primary production to the bottom. This characteristic is also ideal for processes related to benthic-pelagic coupling, which we suspect are important in this coastal ecosystem.

Because mixing in the shallow shelf waters results in a relatively homogeneous water column, it is reasonable to propose a trophic coupling hypothesis for shrimp which includes both pelagic and benthic components. The relationships based on nickel tracers (zooplankton→sediment→shrimp) support this scheme. Also, zooplankton fecal pellets are a major input to the marine detritus pool (Cushing 1966; Steele 1974). Under the hydrographic conditions present, the discrimination between pelagic and benthic parts of the ecosystem is decreased and the potential for trophic coupling between the sea floor and overlying waters becomes more meaningful.

A key question about shrimp production concerns the component(s) of the benthic community from which shrimp derive their nutrition. Several studies have attempted to determine the role of benthic infauna as a food source for commercially important demersal species. Boesch (in press) found alterations in macrobenthic communities that resulted in reductions in populations which were dominant food items for demersal fishes and invertebrates. However, the contribution of energy flow to higher trophic levels from these populations and whether the larger fish and invertebrates were severely affected were unknown. Additional observations such as those of McIntyre et al. (1970) on molluscan siphon cropping by a commercially important fish species, and Arntz (1980) on changes in benthic infaunal biomass directly associated with demersal fish predation, implicate the benthos as important food items for species of commercial value.

Based upon our theoretical model of production estimates and energy flow for the south Texas coastal environment, benthic infaunal production appears to be an insufficient food source to solely support the demersal component of the inner shelf food web. If we assume a minimum 10% transfer efficiency for the infaunal biomass produced, which is 0.29 g C/m^2 per yr, this trophic level could not support the 0.07 g C/m^2 per yr of total production by fish, shrimp, and other invertebrates, nor the 0.04 g C/m^2 per yr annual production of *P. aztecus*. Our calculations do not include meiofauna production. Even if this component were known, there probably would still not be enough carbon production by fauna in the benthos to directly support all higher trophic levels in the bottom waters. In addition, the correlation analysis did not identify any significant correlations between shrimp densities and densities of fauna inhabiting the sediment.

The correlations between shrimp body burdens and tracers in the sediment, however, provide evidence for another means of shrimp gaining nutrition, the detritus pool. These correlations support conclusions from other studies (Cook and Lindner 1970; Caillouet et al. 1976) that shrimp rely upon food provided by the marine detritus pool for at least some of their nutrition. Condry et al. (1972) observed that brown shrimp ate dead diatoms and algal mat material in an estuarine habitat. Moriarty (1977) recorded microbial feeding by shrimp from detritus substrates, and Foulds and Mann (1978) found evidence that crustaceans are able to digest cellulose. The dependence of these populations on the detritus pool is a reasonable conclusion.

Another potential contribution to the detritus pool comes from the discards—small shrimp, fish, and other invertebrates—from the methods of harvest employed by the shrimp fishery. According to Bryan and Cody,[6] approximately 116 million kg of catch-associated organisms are discarded annually on the shelf off south Texas. Most of this material eventually reaches the bottom and becomes an additional source of food for scavengers, such as shrimp, to supplement the food sources from the benthic habitat.

The theoretical food web we propose for the penaeid shrimp fishery of the shallow nearshore waters of the south Texas continental shelf is in contrast to the food web described by Steele (1974) for the North Sea ecosystem and its related

[6]Bryan, C. E., and T. J. Cody. 1975. Discarding of shrimp and associated organisms on the Texas brown shrimp (*Penaeus aztecus*) grounds. Final Rep. to Texas Parks and Wildlife Department PL88-309, Project 2-276R, 38 p.

fisheries. Whereas we propose a detrital-based food web dependent on about 80% of the primary producer biomass being directed to the bottom, Steele (1974) indicated that only 30% of the primary production reached the benthos in the North Sea. On the other hand, Mills and Fournier (1979) observed that the majority of primary production was diverted to the bottom on the Scotian shelf. This primary production, however, was not adequate to satisfy the requirements of the benthic or pelagic food chains. The importance of herbivorous zooplankton and secondary consumers, such as ctenophores and chaetognaths, was emphasized by Mills and Fournier as elements potentially characterizing the structure of energy transfer in the Scotian shelf ecosystem. From the evidence available, the inner shelf ecosystem of the northwestern Gulf of Mexico, with its food webs leading to commercially important penaeid shrimp, appears different in structure from other areas with major commercial fisheries. The concept that food webs leading to these fishery populations are similarly constructed is not supported by our study, which only further points out what Mills and Fournier (1979) emphasized—detailed regional studies are needed before predictive models can be developed for these fisheries.

Our theoretical model of the trophic structure supporting the penaeid populations in the northwestern Gulf of Mexico is an approach to the detailed regional studies that are necessary. Much still needs to be done to define the pathways of nutrition and the implications of these pathways being interrupted by major environmental disturbances. Research on shrimp migratory patterns, behavior, response to environmental factors, and fishery statistics alone will not provide adequate information about the functioning of an ecosystem with respect to the trophic structure supporting a commercial fishery. Our study pinpoints some of the potential pathways of energy flow. The need for research to define the functioning of the ecosystem of which penaeid shrimps are a part cannot be overemphasized.

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FEEDING SELECTIVITY OF DOVER SOLE, *MICROSTOMUS PACIFICUS*, OFF OREGON

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ABSTRACT

Factors influencing the selection of food by Dover sole were investigated by analyzing stomach contents of fish and serially sectioned box core samples for benthic invertebrates from two areas of high Dover sole abundance on the central Oregon continental shelf. At both locations (119 and 426 m depth), polychaetes and ophiuroids were more important than molluscs and crustaceans as food in terms of frequency of occurrence, weights, and numbers. Polychaetes and ophiuroids were generally positively selected at both locations; i.e., they were more common in fish stomachs than in box core samples. Molluscs were generally negatively selected at both locations. Crustaceans were positively selected at 426 m and consumed nonselectively at 119 m. The box core samples may, however, underestimate crustaceans and hence give artificially high values of electivity.

Significant changes in frequency of occurrence of principal prey taxa with fish size were observed for 27 principal prey taxa at 119 m and 7 prey taxa at 426 m. These changes indicate that composition of fish diet varies with fish size.

At the 119 m station, the larger the fish size at which a significant difference in prey frequency occurred, the larger the increase in electivity across the size interval. This implies increased selectivity by large fish. Body size of a prey taxon was positively correlated with fish length at which significant difference in prey frequency occurred: larger fish consumed larger prey. Mean depth of a prey taxon within the sediment was also positively correlated with the length of fish at which a significant increase in prey frequency occurred: larger fish consumed prey found deeper in sediment.

Few size-related changes in diet were found at the 426 m location. Environmental abundance of a preferred taxon, polychaetes, was lower at 426 m than at 119 m. Dover sole may therefore change feeding strategy from that of a specialized predator, whose feeding habits vary with its body size where polychaetes are abundant, to that of a generalist consuming more types and sizes where few polychaetes are available. Vertical distribution of prey within the sediment at 426 m was shallower than at 119 m; thus the advantage afforded large fish in removing deeply buried prey may be eliminated. Implications of results are discussed in terms of optimal foraging strategy.

The Dover sole, *Microstomus pacificus*, is a prominent member of the deepwater continental shelf community off Oregon (Pearcy 1978) and makes the largest contribution to total biomass of flatfishes landed commercially off the coast of Oregon (Demory et al.[3]). Yet the published literature on the trophic role of this species in deepwater continental shelf assemblages is sparse. Hagerman (1952) listed "small bivalves...scaphopods ...sipunculids, polychaetes (*Nereis* sp.), nematodes, echinoids (sea urchins), ophiuroids (brittle stars),...gastropods (*Thais* sp.),...at times... shrimp and other crustacean forms" as principal prey animals off California. Pearcy and Hancock (1978) included a list of 35 common polychaete species or taxa, 7 crustacean species or taxa, 9 mollusc species or taxa, and 2 echinoderm taxa consumed by Dover sole collected on the central Oregon continental shelf.

Although selectivity has long been considered an important aspect in resource partitioning within and among species, few studies have included a survey of available food items on which to base and compare feeding habit descriptions of benthic fishes. Early work by Steven (1930) described prey available and consumed by demersal fishes in the English Channel. Later, Jones (1952) related the Cumberland coast bottom fauna and food of flatfishes. More recently, Arntz (1978) described the benthic food web of the western Baltic, including food selection by the two most common demersal fish species found there (the cod, *Gadus*

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[3]Demory, R. L., M. J. Hosie, N. TenEyck, and B. O. Forsberg. 1976. Groundfish surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl. Inf. Rep. 76-9, 7 p.

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morhua, and the dab, *Limanda limanda*). Levings (1974) investigated seasonal changes in feeding and particle selection by winter flounder, *Pseudopleuronectes americanus*, and Moore and Moore (1976) studied various factors influencing the selection of food by the flounder *Platichthys flesus*. In North Pacific demersal communities, however, even the qualitative aspects of selectivity and the role of selectivity in trophic dynamics have yet to be estimated.

The objectives of this study are to: 1) describe the food habits of the Dover sole in an area of an active commercial fishery for this species off Oregon, 2) determine if the species is a selective feeder, and 3) determine how feeding habits are related to location of fish capture, size of fish, and size and depth of prey in the sediment.

METHODS AND MATERIALS

Samples of demersal fishes and benthic invertebrates were taken on the central continental shelf off Oregon in locations of high Dover sole abundance (Demory et al. footnote 3; Tyler[4]) (Figure 1). Station SG29 (lat. 44°05.0′ N, long. 124°35.0′ W) was located in Heceta Swale, the region east of Heceta Bank. The mean sampling depth was 119 m; the sediment is silty sand (Maloney 1965). Station SG10 (lat. 43°49.3′ N, long. 124°50.0′ W) was located south of Heceta Bank. The mean sampling depth was 426 m. The sediment is glauconitic sand; however, sediment distribution is patchy in this area (Bertrand 1971). Samples were taken over a limited area and time interval to reduce large-scale spatial and temporal variability (SG29: 41.6 km^2, 44 h; SG10: 34.21 km^2, 27 h; day and night 20-24 June 1976).

Benthic infauna was sampled at each station by two box corers: a 0.1 m^2 Bouma box corer (Bouma 1969) and a modified 0.25 m^2 Hessler-USNEL box corer (Hessler and Jumars 1974). The Hessler-USNEL box corer is designed to reduce pressure waves which often blow away small surface invertebrates before corer impact. Box cores provide the largest, deepest, and least disturbed sample of consistent surface area when compared with other commonly used sediment samplers (Word[5]). In <45 min after retrieval of the core, core samples were extruded in 0.1 m^2 boxes and sectioned at 1 cm intervals for the first 10 cm, 2 cm intervals for the next 10 cm, and 4 cm intervals for the remainder of the core. These sections were then washed onto a 1 mm aperture sieve screen, and washed invertebrate samples were preserved in 4% unbuffered formaldehyde.

Beam trawl tows to sample Dover sole were made in the immediate area of box core sampling. A beam trawl with an effective trawling width of 2.72 m (Carey and Heyomoto 1972) and 3.8 cm stretched mesh lined with 1.3 cm mesh netting was towed at 3 kn for 30 min per haul at SG29 and 20 min at SG10. Fish were preserved in 8% (unbuffered) formaldehyde as soon as possible after the trawl was brought aboard. The body cavities of fish >12 cm were slit to allow rapid formaldehyde penetration into the coelom.

A total of four 0.1 m^2 box cores, eight 0.25 m^2 box cores, and 15 successful beam trawl tows were made at SG29. At SG10, nine 0.1 m^2 box cores and 10 successful beam trawl tows were made.

In the laboratory, invertebrates from box cores were transferred to 70% isopropyl alcohol, sorted into major taxa, and identified to species whenever possible. Dover sole were measured (standard length) and stomachs (from esophagus to constriction before pyloric caeca) were removed and transferred to 70% isopropyl alcohol. A total of 202 stomachs from SG29 and 63 stomachs from SG10 were processed. Stomach contents were sorted into phyla and identified to species whenever possible. Total lengths of polychaetes, aplacophorans, and scaphopods were measured. Gastropod and pelecypod measurements were made along the longest axis and included shells. Crustaceans were measured from base of rostrum to point of flexure of abdomen. Since ophiuroids occurred as pieces, a single measurement of ophiuroid volume per stomach was made.

Dry weights of prey items were estimated using conversion factors. Shells, tubes, massive paleal setae (in the case of the polychaete *Pectinaria californiensis*), and posterior scutes (in the case of the polychaete *Sternaspis fossor*) were removed before individual items of known length were dried (36 h, 65° C). Items were weighed using an electrobalance or Mettler[6] balance. Regression curves were fitted to sets of length-weight points

[4]A. V. Tyler, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, pers. commun. June 1976.

[5]Word, J. Q. 1977. An evaluation of benthic invertebrate sampling devices for investigating feeding habits of fish. *In* C. A. Simenstad and S. J. Lipovsky (editors), Proc. 1st Pac. NW. Tech. Workshop. Fish food habits studies, p. 43-55. Washington Sea Grant, Seattle. WSG-WO-77-2.

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

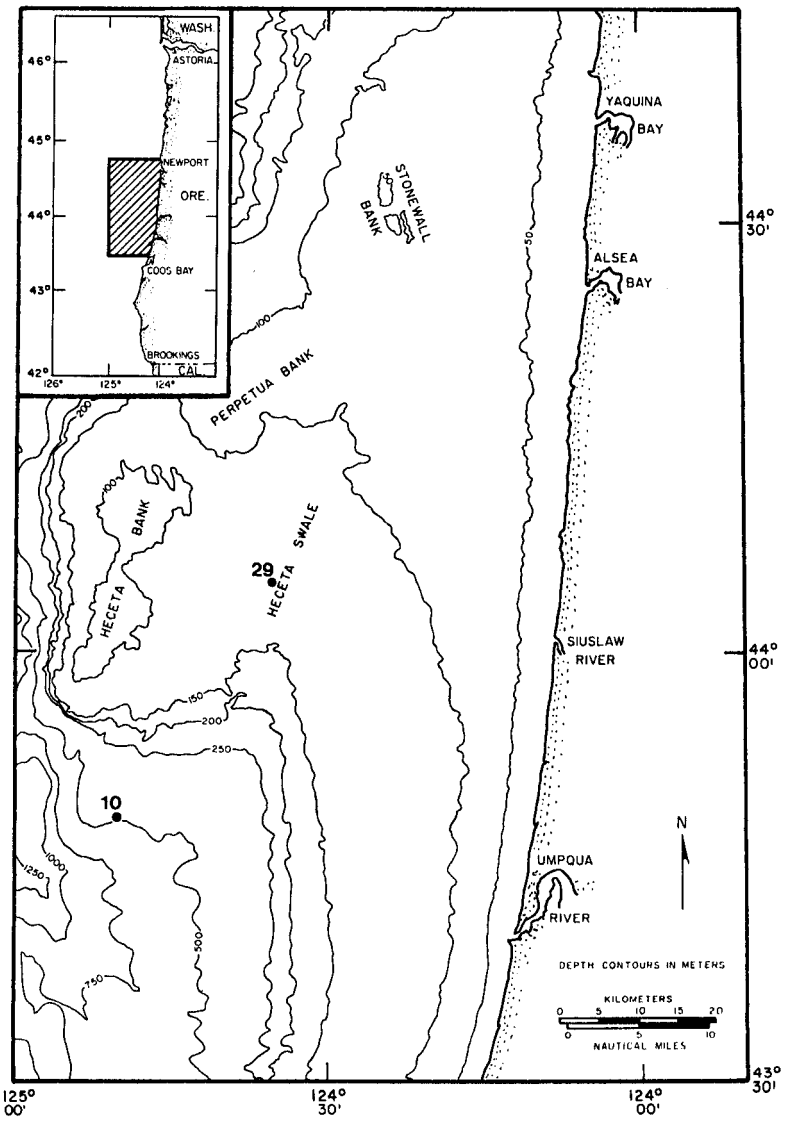

FIGURE 1.—Location of sampling stations on the central continental shelf off Oregon.

for gastropods, pelecypods, amphipods, cumaceans, and "noncylindrical" polychaetes (*Sternaspis fossor*); otherwise, a simple milligram per centimeter conversion factor was calculated for polychaetes, aplacophorans, and scaphopods. For each prey taxon, at least 10% of the total number consumed or 20 individuals were dried and weighed. Although formaldehyde and particularly alcohol are known to leach out organic material from biological specimens and to reduce the weight of the organisms (Thorson 1957; Howmiller 1972), these estimates were assumed to be adequate for estimating relative importance of prey taxa biomass. Dry weights of ophiuroids overestimate the food value of these animals compared with soft-bodied polychaetes. Therefore, ash-free dry weight estimations were made for all groups from conversion factors found in the literature and previous laboratory work for shell-free or tube-free weights (Richardson et al.[7]; Ruff[8]).

[7]Richardson, M. D., A. G. Carey, Jr., and W. H. Colgate. 1977. The effects of dredged material disposed on benthic assemblages off the mouth of the Columbia River. *In* Final report, Department of the Army Corps of Engineers, p. 59. Contracts DACW 57-75-C0137 and DACW 57-76-C-0092.

[8]R. E. Ruff, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1978.

RESULTS

Feeding Habits of Dover Sole

Dover sole off the Oregon coast in midsummer fed most often on polychaetes, although a surprisingly large proportion of the diet consisted of ophiuroids (Table 1). At station SG29, polychaetes occurred in 97.3% of stomachs examined, and composed 43% of the total ash-free dry weight of stomach contents examined. Ophiuroids occurred in 63.0% of the stomachs, made up 41% of the ash-free dry weight of stomach contents at that location. At station SG10, polychaetes occurred in 83.6% of the stomachs examined and constituted 11% of total ash-free dry weight of stomach contents examined, while ophiuroids occurred in 80% of those stomachs, composing 84% of ash-free dry weight of the diet at SG10; otherwise, crustaceans and molluscs made up <6% of biomass consumed.

The largest proportion of polychaete biomass consumed was derived from *Pectinaria californiensis* and members of the families Glyceridae (SG29: *Glycera capitata*, SG10: *Glycinde picta*),

TABLE 1.—Percentage of frequency of occurrence, numerical abundance, dry weight, and ash-free dry weight that polychaetes, molluscs, crustaceans, and ophiuroids composed in Dover sole stomachs at SG29 and SG10.

	Percent frequency of occurrence		Percentage of numerical total[1]		Percentage of total dry weight		Percentage of total ash-free dry weight	
Taxon	SG29	SG10	SG29	SG10	SG29	SG10	SG29	SG10
Polychaeta	97.3	83.6	84.7	57.7	22.3	3.6	42.7	10.5
Mollusca	68.6	69.1	9.1	15.4	6.0	1.0	14.5	3.5
Gastropoda	8.0	20.0	.4	2.3	.3	.3		
Pelecypoda	61.2	50.9	7.2	9.9	5.2	.5		
Scaphopoda	12.2	16.4	.7	1.5	.3	.1		
Aplacaphora	16.9	14.5	.7	1.7	.2	.1		
Crustacea	62.2	83.6	6.2	26.9	.9	.8	1.5	2.1
Miscellaneous[2]	15.3	18.2	.7	2.0	.5	.2		
Cumacea	26.6	47.3	1.5	5.5	.1	.2		
Amphipoda	48.9	76.4	3.9	19.4	.3	.4		
Ophiuroidea	63.0	80.0			70.8	94.6	41.4	84.0

[1]Ophiuroids excluded from total, since this organism was nearly always found as uncountable fragments of arms.
[2]Includes Ostracoda, Copepoda, Pericarida, and Eucarida.

TABLE 2.—Frequency of occurrence of polychaete families in Dover sole, and percentage composition of polychaetes found in stomachs on numerical and dry weight bases at SG29 and SG10.

	Percent frequency of occurrence		Percentage of numerical total of polychaetes		Percentage of total dry weight of polychaetes	
Family	SG29	SG10	SG29	SG10	SG29	SG10
Ampharetidae	19.1	34.5	2.0	8.5	1.5	2.5
Apistobranchidae	18.1	1.8	1.3	.2	.1	.1
Arenicolidae	.5	0	.1	0	<.1	.1
Capitellidae	52.7	30.9	7.7	7.6	1.8	1.7
Chaetopteridae	2.7	0	<.1	0	<.1	0
Cirratulidae	26.1	18.2	2.1	5.0	.6	1.6
Cossuridae	33.5	0	4.4	0	.2	0
Flabelligeridae	5.9	3.6	.4	.9	3.6	2.4
Glyceridae	43.6	18.2	3.7	4.0	11.3	14.1
Goniadidae	3.2	14.5	.2	1.2	.8	6.5
Lumbrineridae	81.4	23.6	19.2	4.3	4.5	1.6
Magelonidae	6.4	5.5	.3	.7	.4	1.0
Maldanidae	39.9	21.8	4.3	4.0	4.5	3.2
Nephtyidae	34.6	60.0	3.4	24.6	.5	2.8
Nereidae	1.1	0	<.1	0	<.1	0
Onuphidae	13.8	3.6	.9	.7	3.7	.5
Opheliidae	1.6	25.5	<.1	5.2	.5	7.4
Orbiniidae	4.3	0.0	.2	0	<.1	0
Oweniidae	56.9	14.5	8.8	1.7	.8	.1
Paraonidae	78.7	45.5	24.1	14.7	4.0	5.5
Pectinaridae	11.7	18.2	1.1	3.1	20.9	29.2
Phyllodocidae	17.0	7.3	1.1	2.8	.1	.6
Polynoidae	.5	0	<.1	0	<.1	0
Sabellidae	.5	3.6	<.1	.5	<.1	.1
Sigalionidae	23.9	29.1	1.6	4.0	.3	2.6
Sphaerodoridae	.5	0	<.1	0	<.1	0
Spionidae	51.6	9.1	5.9	1.4	4.7	1.4
Sternaspidae	32.4	5.5	2.1	.9	12.1	4.5
Syllidae	6.9	7.3	.3	.7	<.1	0
Terebellidae	31.9	16.4	3.8	3.1	22.7	10.5

Terebellidae (SG29: *Pista disjuncta*), Sternaspidae (SG29: *Sternaspis fossor*), and Opheliidae (SG10: *Travisia foetida*). Most frequently consumed polychaete species were generally smaller bodied, including lumbrinerid (primarily at SG29), nephtyd (primarily at SG10), paraonid, and capitellid polychaetes (Table 2). Principal prey species are listed in Tables 3 (SG29) and 4 (SG10).

Pelecypods were the most frequently consumed molluscs, constituting most of the mollusc biomass eaten (Table 1). *Macoma* spp., *Adontorhina cyclia*, and *Axinopsida serricata* were most important at SG29 and *Crenella decussata, Huxleyia munita*, and *Odontogena borealis* were common at SG10. Among crustaceans, amphipods (SG29: *Harpiniopsis excavata, H. fulgens*; SG10: *Melphidippa amorita, Ampelisca macrocephala, Nicipe tumida*) occurred more frequently and in larger numbers than cumaceans, and were consumed more often than molluscs at the deeper station.

Changes in Diet with Predator Length

A chi-square test (Tyler[9]) was used to determine the dependency of diet on fish size, based on differences in frequency of occurrence of prey items consumed by predators belonging to different length intervals. The chi-square test showed many size-related variations in the diet of Dover sole taken at SG29 but few in the diet at SG10. At

[9]Tyler, A. V. 1969. Computer programs for analysis of feeding heterogeneities related to predator body size. Fish. Res. Board Can. Tech. Rep. 121, 49 p.

TABLE 3.—SG29: Changes in selectivity with fish size considered by principal prey taxa. Range of fish size is divided to maximize heterogeneity between size intervals for each principal prey taxon as described in text.

	Taxon	For fish ≤ length (cm)	Ivlev index of electivity	Chi-square value	Significance[1]	For fish ≥ length (cm)	Ivlev index of electivity	Chi-square value	Significance[1]
1	Polychaeta:								
2	Ampharetidae[2]	31	0.45	8.646	***	31	−0.33	2.060	NS
3	Apistobranchidae: *Apistobranchus ornatus*	21	−1.00	.688	NS	21	.59	7.286	**
4	Capitellidae: *Decamastus gracilis*	29	−.05	1.957	NS	29	.15	2.086	NS
5	Cirratulidae: *Tharyx* spp.[3]					11	−.13	3.034	NS
6	Cossuridae: *Cossura* sp.	29	.52	11.762	***	29	.72	42.421	***
7	Glyceridae: *Glycera capitata*	37	−.12	1.781	NS	37	.55	18.297	***
8	*Glycinde picta*					11	.69	11.073	***
9	Lumbrineridae: *Lumbrineris latreilli*					11	.68	149.112	***
10	*Ninoe gemmea*	32	−.76	33.946	***	32	−.20	1.858	NS
11	Maldanidae[2]	33	−.64	206.469	***	33	−.18	12.331	***
12	Nephtyidae: *Nephtys* sp.	33	.67	25.046	***	33	.54	7.781	**
13	Onuphidae: *Nothria* spp.[4]	35	−.62	17.607	***	35	.50	10.411	***
14	Oweniidae: *Myriochele heeri*	33	.15	.540	NS	33	−.48	5.548	*
15	*M. oculata*	33	−.17	17.364	***	33	−.60	37.979	***
16	Paraonidae[2]	21	.42	15.575	***	21	.60	179.784	***
17	*Aedicira antennata*[5]	24							
18	*Aricidea ramosa*	21	.66	22.164	***	21	.73	86.711	***
19	*Paraonis gracilis*[5]	21							
20	Pectinaridae: *Pectinaria californiensis*	34	−.38	.851	NS	34	.91	59.486	***
21	Phyllodocidae: *Anaitides groenlandica*[6]	29	.28	.127	NS	29	.66	5.983	*
22	Sigalionidae[2]	24	.77	2.343	NS	24	.93	21.043	***
23	Spionidae: *Prionospio* spp.[3]					11	.12	.144	NS
24	*Spiophanes* spp.[3]	26	−.35	9.185	***	26	.08	.129	NS
25	*S. berkeleyorum*	27	−.47	17.738	***	27	−.19	5.501	*
26	Sternaspidae: *Sternaspis fossor*	21	−1.00	2.775	NS	21	.22	1.613	NS
27	Terebellidae: *Pista cristata*	35	.19	0.625	NS	35	.79	66.159	***
28	*Terebellides stroemii*	28	−.70	13.772	***	28	−.13	1.180	NS
	Mollusca:								
29	Pelecypoda (unidentifiable, nonprincipal)[7]					11	−.81	668.332	***
30	"A-type"[8]	33	−.55	195.445	***	33	−.95	137.863	***
31	*Macoma* spp.[3]					11	−.47	50.222	***
32	Scaphopoda	28	−.86	80.797	***	28	−.68	70.064	***
33	Aplacophora					11	.09	.002	NS
	Crustacea:								
34	Cumacea: *Eudorella pacifica*	35	−.07	.859	NS	35	−.72	8.243	***
35	Ampnipoda: *Harpiniopsis excavata*[9]					11			
36	*H. fulgens*[9]	36	.38	6.935	**	36	−.01	.001	NS
37	Ophiuroidea[10]	28	.92	37.430	***	28	.93	41.757	***

[1]NS = not significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.
[2]All members of family pooled.
[3]All members of genus pooled (species identifications not possible).
[4]Members of two species pooled based on taxonomic uncertainty (*Nothria elegans* and *N. iridescens*).
[5]No members of this genus present in box core.
[6]All members of genus pooled (species identifications tentative or uncertain).
[7]All nonprincipal or unidentifiable pelecypods found in fish compared with all pelecypods found in box core.
[8]*Axinopsida serricata* and *Adontorhina cyclia* pooled.
[9]No members of this genus present in box cores, value for *Harpiniopsis fulgens* represents all Phoxocephalidae, pooled.
[10]Based on frequency of occurrence in fish compared with numbers of ophiuroids found in box core.

TABLE 4.—SG10: Changes in selectivity with fish size considered by principal prey taxon. Range of fish size is divided to maximize heterogeneity between size intervals for each principal prey taxon as described in text.

Taxon	For fish >length (cm)	Ivlev index of electivity	Chi-square value	Significance[1]
Polychaeta:				
Ampharetidae[2]	24	0.57	11.875	***
Capitellidae: *Decamastus gracilis*[3]	24	−.22	4.777	*
Cirratulidae: *Tharyx* sp.[4]	24	.89	11.436	***
Glyceridae: *Glycinde* sp.	28	.59	3.320	NS
Lumbrineridae: *Lumbrineris* sp.[4]	24	.77	8.518	***
Maldanidae[2]	24	−.32	5.788	*
Nephtyidae: *Nephtys* sp.	24	.98	91.741	***
Opheliidae: *Travisia* sp.[4]	24	.91	15.763	***
Paraonidae[2]	24	.45	13.691	***
Pectinaridae: *Pectinaria californiensis*[5]	24	.41	1.823	NS
Sigalionidae[2]	24	.68	6.778	**
Mollusca:				
Pelecypoda (unidentifiable, nonprincipal)	24	−.35	14.176	***
Huxleyia munita	24	−.84	110.067	***
Crenella decussata	24	−.78	171.609	***
Odontogena borealis	25	−.81	61.853	***
Gastropoda: pteropoda[6]	24			
Scaphopoda	24	−.39	5.516	*
Aplacophora	26	.28	.756	NS
Crustacea:				
Amphipoda: *Melphidippa amorita*[6]				
Nicipe tumida[6]				
Metopa sp.				
Ampelisca macrocephala	24	.77	8.518	***
Cumacea: *Campylaspis* sp.[4]	24	.79	14.800	***
Ophiuroidea[7]	24	.25	3.764	NS

[1]NS = not significant; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.
[2]All members of the same family pooled.
[3]Positive identification of species difficult for this species, pooled with *Mediomastus californiensis*.
[4]Species not found in box core, calculation based on numbers of representatives of same genus.
[5]Species pooled with *Pectinaria belgica*.
[6]No representative of genus in box core—no electivity values calculated.
[7]Based on frequency of occurrence in fish compared with numbers of ophiuroids found in box core.

SG29, out of 35 principal prey taxa (taxa occurring in at least 10% of stomachs containing food), 27 showed significant changes in frequency of occurrence. Five types of prey frequency patterns were apparent for these 27 prey over the size range of fish sampled, 11-42 cm. Examples are shown in Figure 2.

The first prey pattern, typified by the polychaete *Decamastus gracilis* (I), reflects prey which occurred at low frequencies in diets of small-sized fish (11-20 cm) and at increasing frequency in diets in intermediate-sized fish (21-30 cm), and which remained approximately constant at that same frequency in the diets of large-sized fish (30-42 cm) (Figure 2). Other taxa for which this pattern existed include the Ophiuroidea; polychaetes *Aedicira antennata, Spiophanes berkeleyorum*, the Sigalionidae, *Ninoe gemmea, Spiophanes* sp.; and the Scaphopoda, many of which are sessile or motile outside of tubes and surface feeders.

The second prey pattern describes taxa which occurred at relatively high frequency in diets of small-sized fish and occurred at decreased frequency in diets of intermediate- and large-sized fish; e.g., the small tubed polychaetes *Myriochele oculata* (II) and *M. heeri*, the amphipod *Harpiniopsis fulgens*, and small ampharetid polychaetes. The cumacean *Eudorella pacifica*, pelecypod group *Adontorhina cyclia-Axinopsida serricata*, and polychaete *Nephtys* sp. also occurred often in diets of intermediate-sized fish, but occurred at low frequency in diets of large-sized fish.

The third prey pattern is depicted by a hump-shaped curve, in which case a prey taxon occurred at low frequencies in diets of small- and large-sized fish but at relatively high frequencies in diets of intermediate-sized fish. Many principal prey taxa belong to this category, including the polychaetes *Anaitides groenlandica* (III), *Aricidea ramosa, Sternaspis fossor, Paraonis gracilis, Apistobranchus ornatus, Cossura* sp., and *Terebellides stroemii*.

The fourth prey pattern reflects increasing prey frequency with increasing fish size. Prey taxa following this pattern included many larger tubed, surface and subsurface feeding polychaetes: *Nothria elegans* (IV), *Pectinaria californiensis, Glycera capitata, Pista cristata*, and the Maldanidae.

The fifth prey pattern includes prey whose frequency of occurrence in diets did not change significantly over the entire size range of fish sampled; e.g., polychaetes *Lumbrineris latreilli* (V),

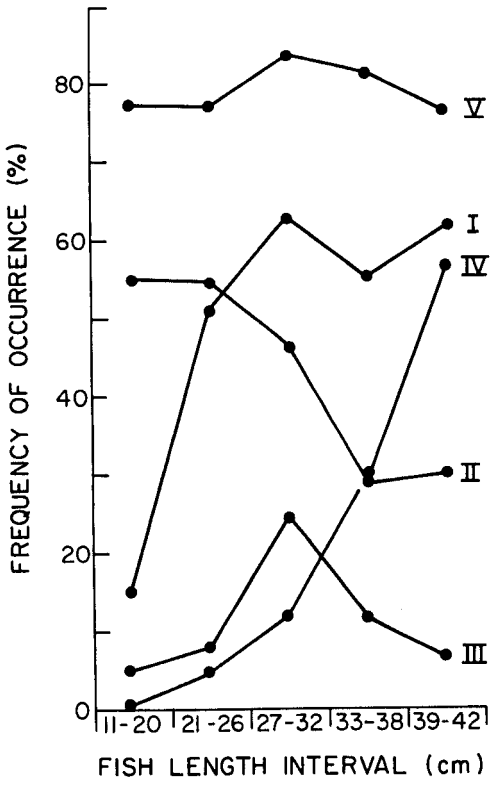

FIGURE 2.—Five patterns of change in the frequency of occurrence of prey for different sizes of Dover sole at SG29. Curve shape I typified by *Decamastus gracilis*, shape II by *Myriochele oculata*, shape III by *Anaitides groenlandica*, and shape IV by *Nothria elegans*.

Glycinde picta, *Prionospio* sp., *Tharyx* sp., the amphipod *Harpiniopsis excavata*, the Aplacophora, unidentifiable Pelecypoda, and *Macoma* sp.

At SG10, 19 out of the 26 principal prey species showed no significant change in frequency of occurrence over the range of fish sampled (24-43 cm). The frequency of occurrence of *Melphidippa amorita*, an amphipod, increased significantly in fishes 32 cm or longer. Occurrence of two amphipod taxa, *Nicipe tumida* and *Metopa* sp., decreased significantly in fish 32-33 cm or larger. In the case of the four remaining taxa, the series of chi-square tests produced intervals across which frequency of occurrence changed gradually, rather than defining a well-marked break in frequency at one particular length. *Glycinde picta*, a tubeless, subsurface deposit feeding polychaete, increased in frequency in fish 28-29 cm or longer. *Odontogena borealis*, a small bivalve, increased over the 25-32 cm fish size interval. Aplacophorans increased in frequency in 26-27 cm fish and longer, and Ophiuroidea increased in the 30-32 cm interval.

Selectivity

A chi-square test of 2×2 contingency tables was used to test the null hypothesis that the relative abundance of a taxon among items consumed is dependent on the relative abundance of the taxon in the environment. Ivlev's (1961) index of electivity

$$E = (r_i - p_i)/(r_i + p_i),$$

where r_i = percentage of ration composed of a given prey taxon i and p_i = percentage of food complex in environment composed of prey taxon i, was used to determine whether selection was positive or negative. Overall trends in selectivity by major taxa for all fish from each station are shown in Table 5. Ophiuroids were the most highly selected food taxon at SG29. The calculations of electivity indices and chi-square values for this taxon were based on number of occurrences rather than number of individuals consumed, and hence underestimated the importance of ophiuroids. Ophiuroids were removed from the data sets for subsequent calculations so that estimations for other taxa were unbiased by this representation. Polychaetes were selected food of fish at both locations. Chi-square values were larger for polychaetes than any other positively selected taxon. Molluscs, especially pelecypods and

TABLE 5.—Summary of selectivity considered by major taxa at stations SG29 and SG10 for Dover sole of all sizes.

Station	Taxon	Ivlev index of electivity	Chi-square value	Significance[1]
SG29	Polychaeta	0.13	243.451	***
	Mollusca:			
	Pelecypoda	−.49	248.739	***
	Gastropoda	−.43	6.015	**
	Scaphopoda	−.75	112.448	***
	Aplacophora	.09	.105	NS
	Crustacea:			
	Amphipoda	.08	.839	NS
	Cumacea	−.10	.766	NS
	Ophiuroidea	.92	40.724	***
SG10	Polychaeta	.33	117.446	***
	Mollusca:			
	Pelecypoda	−.72	425.683	***
	Gastropoda	.50	4.061	*
	Scaphopoda	−.39	4.602	*
	Aplacophora	.28	1.039	NS
	Crustacea:			
	Amphipoda	.69	79.629	***
	Cumacea	.67	20.771	***
	Ophiuroidea	.25	3.764	NS

[1]NS = not significant; ***$P<0.001$; **$P<0.01$; *$P<0.05$.

scaphopods, were the least often selected food at both locations. Aplacophoran molluscs, however, were neither significantly selected nor rejected. At SG29, the numerical proportions of crustaceans (amphipods and cumaceans) in stomachs and box core samples were nearly equal. At SG10, however, these crustaceans appeared highly selected.

Among polychaetes at SG29, the most highly selected prey species were *Glycinde picta* and *Lumbrineris latreilli* (in fish of all sizes, i.e., >11 cm), Sigalionidae (especially in fish >21 cm), *Aricidea ramosa* (in fish of all sizes, but especially those >21 cm), *Cossura* sp. (in fish of all sizes, but especially those >29 cm), *Pectinaria californiensis* (in fish >34 cm), and *Pista cristata* (in fish >35 cm) (Table 3). No principal mollusc taxa were selected, with the exception of aplacophorans, which appeared to be neither significantly selected nor ignored. The cumacean *Eudorella pacifica* was negatively selected by fish >34 cm. The phoxocephalid amphipod species *Harpiniopsis excavata* and *H. fulgens* were not present in box cores, indicating high selectivity by fish or inadequate box core sampling. If values for all phoxocephalids were pooled, it appeared that the family was selected positively by fish <36 cm.

Changes in electivity related to fish size and prey taxa are shown in Figure 3. Values of E were calculated for each principal prey taxon found at SG29 within three fish size intervals (11-21, 22-31, and 32-42 cm). The patterns of changes in electivity with fish size are similar to the patterns found for changes in frequency of occurrence of prey with fish size in Figure 2. In one pattern, electivity of a prey taxon was low by small fish, higher by intermediate fish, and remained constant by large fish relative to intermediate values (Figure 3A). Taxa belonging to this category included the polychaetes *Anaitides groenlandica* (21), *Sternaspis fossor* (26), *Prionospio* spp. (23), *Spiophanes* spp. (24), and *Terebellides stroemii* (28); and the Scaphopoda (32). In the second pattern (Figure 3B), electivity of prey taxa decreased with fish size. Taxa in this category included the polychaetes *Myriochele oculata* (15), *M. heeri* (14), and Ampharetidae (2); phoxocephalid amphipods; the cumacean *Eudorella pacifica* (34); and the combined pelecypod group *Adontorhina cyclia-Axinopsida serricata* (30). In the third category (Figure 3C), electivity was highest by intermediate-sized fish, and lower for larger and smaller fish. Taxa following this pattern included the polychaetes *Cossura* sp. (6), *Tharyx* sp. (5), and *Apistobranchus ornatus* (3). In the fourth

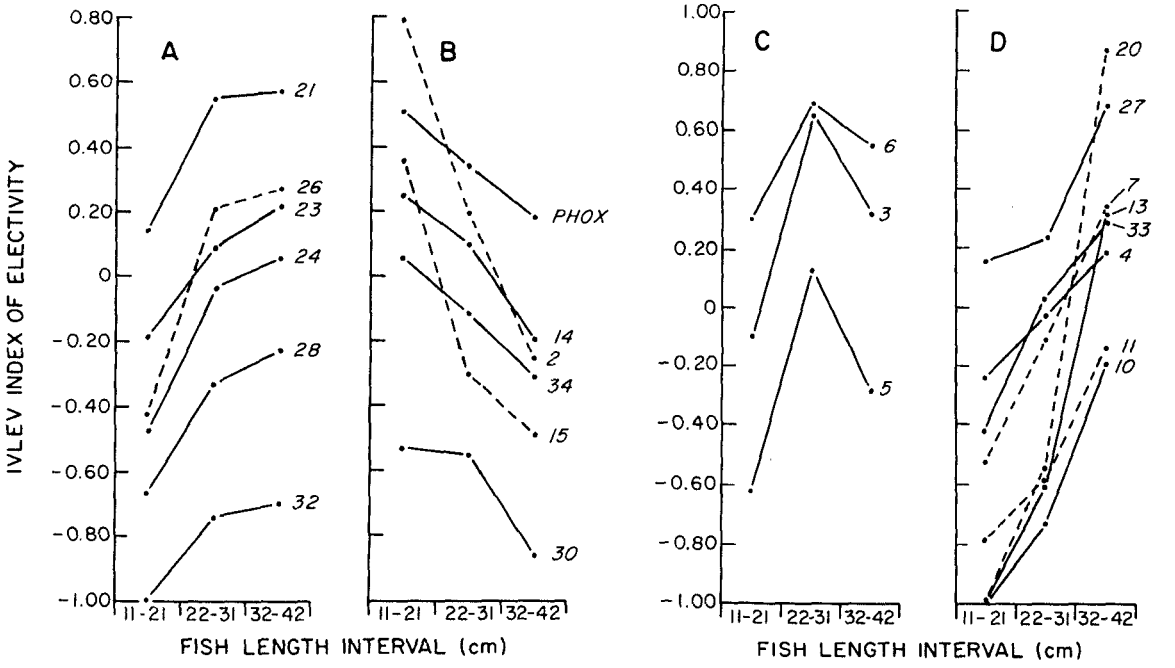

FIGURE 3.—Changes in Ivlev indices of electivity with fish length at SG29. Numbers designate taxa of prey in Table 3. Phox = Phoxocephalidae. Taxa with similar patterns of change are grouped as Figures A, B, C, and D.

category (Figure 3D), electivity increased among all three size categories of fish. This pattern existed for the large-bodied, tubed polychaetes *Pectinaria californiensis* (20), *Pista cristata* (27), *Nothria* sp. (13), and Maldanidae (11), the large-bodied, tubeless polychaete *Glycera capitata* (7); two small-bodied, tubeless polychaetes *Decamastus gracilis* (4) and *Ninoe gemmea* (10); and the aplacophoran molluscs (33). In a fifth pattern (not shown), electivity of a prey taxon did not change significantly with fish size. The polychaetes *Lumbrineris latreilli*, *Glycinde picta*, the Paraonidae, and the Sigalionidae followed this pattern, as did the molluscan genus *Macoma*. Taxa belonging to each category of electivity patterns were not necessarily identical to taxa belonging to each analogous category of frequency of occurrence patterns, since the index of electivity of a prey taxon was based on proportion of numerical abundances of the prey taxon in the diet, rather than on frequency of occurrence.

Among polychaetes at SG10, the most highly selected prey taxa were *Nephtys* sp. and *Tharyx* sp. by fish of all sizes (Table 4). No specimens of *Travisia foetida* or *Lumbrineris latreilli* were found in the core samples so the values shown in Table 4 were based on pooling of the taxa at the generic level. Once again, all principal molluscan taxa were negatively selected, with the exception of aplacophorans (no significant selection) and pteropods, which were not found in core samples. If values for all cumaceans of genus *Campylaspis* were pooled, the taxon appeared positively selected; however, no species common to both fish and box core were found. In the case of amphipods, three of the four principal taxa were not represented in box core samples. The fourth, *Ampelisca macrocephala*, appeared positively selected based on these samples.

Merely because a taxon is positively selected does not mean it plays an especially important role in diet. For example, frequency of occurrence, biomass contribution, and numerical abundance of gastropods in diets of fish at SG10 were small compared with other taxa. Yet this taxon was positively selected (Table 5). Conversely, even though a taxon is negatively selected, it may still play an important role in diets. Positive selection may also be an artifact of the environmental sampling device. Crustaceans appear highly selected at SG10 (Table 5), but this may be partly due to the inefficiency of the box corer in sampling motile epifauna relative to infauna.

A significant positive correlation was found between prey size (weight/length) of 16 prey and the length of fish at which that prey began to significantly increase in frequency ($r = 0.540$, $P < 0.05$) (Figure 4). Large prey were consumed by large fish. Prey which decreased in frequency were generally small-bodied polychaetes (Ampharetidae, *Nephtys* sp., *Myriochele heeri*, *M. oculata*), amphipods, and cumaceans. In the case of the five prey taxa which showed no significant change in frequency in fish of different sizes (Aplacophora, *Glycinde picta*, *Prionospio* sp., *Tharyx* sp., and *Lumbrineris latreilli*) some other criteria for inclusion in diet may have been more important than size.

When prey frequency increased with increased size of Dover sole at SG29, predator selectivity also appeared to increase. From the iterative chi-square tests described earlier, a fish length was found which divided the total fish size range into (usually) two length intervals of statistically homogeneous prey frequency for each prey taxon. A value of E was calculated for each interval, and the difference in values between the two intervals was determined for each applicable prey taxon. This difference was then plotted against the fish

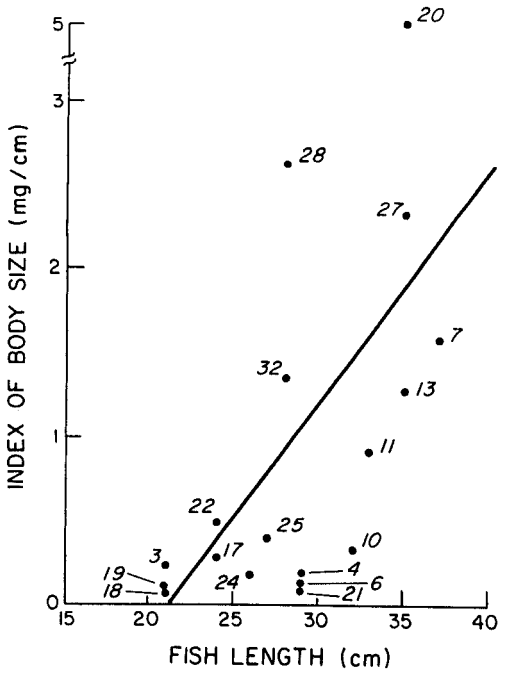

FIGURE 4.—Body size of prey vs. fish length at which frequency of prey increased significantly. Numbers designate prey taxa (see Table 3).

length which separated the two intervals of statistical homogeneity for that prey. (Prey species which were not present over the entire range of fish sampled were not included, e.g., *Apistobranchus ornatus* and *Sternapis fossor*.) For example, the value of E for the polychaete *Glycera capitata* for fish <37 cm was −0.12. For fish 37 cm or larger, the value of E rose to 0.55; the difference, 0.67, was associated with a division point of 37 cm. Although the resulting relationship (Figure 5) may not be amenable to tests of statistical significance, a positive trend exists. Prey which showed an increase in frequency in larger fishes also showed a greater increase in electivity by these larger fish.

Nonparametric ranking statistics were used to test the possible effects of prey mobility, feeding method, and protective structures (polychaete tubes) on size-related increases in prey frequency. The rank for each prey was determined by the fish length at which the prey showed a significant increase in frequency (Table 3). For each test, prey were assigned to categories based on characteristics as described in published literature (Barnes 1968; Smith and Carlton 1975; Jumars and Fauchald 1977) or as described by workers familiar with local fauna (Jones et al.[10]). A lack of difference between summed ranks for each category would imply that the distributions of different prey types (motile, discretely motile, or sessile, in this example) were the same over all fish sizes at which any prey frequency increased; e.g., a prey taxon which was found at higher frequency in fish >21 cm was just as likely to be motile or sessile as one which was found at higher frequencies in fish 35 cm or longer.

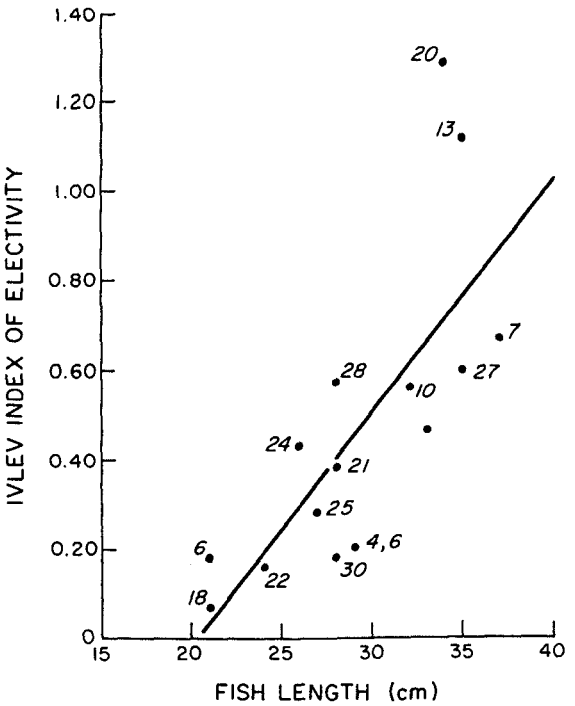

FIGURE 5.—Increase in the Ivlev electivity of prey vs. length of fish at which frequency of that prey increased significantly. Numbers designate prey taxa (see Table 3).

The results of these nonparametric tests (Table 6) show that no one motility type predominated in prey taxa frequent in either small or large fish sizes. Feeding locale, a possible indicator of exposure of a taxon to predation at the sediment surface, was not significant in explaining size-related variations in prey frequency. Feeding type, which is related to both degree of exposure and motility, also showed no trend when ranked over fish lengths. The only statistically significant relationship appeared when ranks for 11 tubed polychaetes were compared with ranks for 7 untubed polychaetes. Tubed taxa generally had a higher rank than untubed taxa. This implied that large fish selected tubed more often than untubed polychaetes. However, three of the four polychaete taxa which decreased in frequency in larger fish (Table 3) have tubes. Thus, the presence or absence of tubes in polychaetes did not always appear to be an important criterion for variation in prey frequency with fish size.

[10]H. Jones, G. Bilyard, and K. Jefferts, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1978.

TABLE 6.—Results of nonparametric tests of effects of prey characteristics on fish size related increases of prey frequency. Prey are ranked by fish size at which prey frequency increased.

Test and categories	Value of test statistic	Critical value for significance[1]
Prey motility:		
Motile	[2]H = 0.029	χ^2 = 5.991
Discretely motile	NS	df = 2
Sessile		
Feeding mechanism:		
Tentaculate	[2]H = 3.508	χ^2 = 5.991
Burrowing (deposit feeder)	NS	df = 2
Carnivorous (raptorial)		
Protective structures:		
Tubed polychaetes	[3]U_S = 58	U_S = 58
Untubed polychaetes	*[1]	n_1 = 11, n_2 = 7
Feeding locale:		
Surface	[3]U_S = 57	U_S = 72
Subsurface	NS	n_1 = 11, n_2 = 9

[1]Significant at 95% confidence level.
[2]H: result from Kruskal-Wallis test (3 categories) (Sokal and Rohlf 1969).
[3]U_S: result from Wilcoxson two sample test (2 categories) (Sokal and Rohlf 1969).

The mean depth of a prey taxon within the sediment was significantly related to fish size at which frequency of that prey increased (Figure 6, $r = 0.542$, $P < 0.05$). Prey which were important to large fish were usually found deeper in the sediment. Prey occurring frequently in small fish were found near the sediment surface. Prey which occurred at statistically equal frequencies for all-sized fish were generally found within the top 4 cm of the core sample, e.g., *Lumbrineris latreilli*, which was consumed in large numbers by fish of all sizes. Prey which decreased in occurrence in larger fish were often concentrated near the surface, with a mean depth distribution of 2 cm. Although the relationship between depth of prey in sediment and index of body prey was not significant (Figure 7) ($r = 0.220$), few large-bodied principal prey taxa had a mean depth in the sediment <4 cm.

At SG10, few prey taxa changed significantly in frequency of occurrence over the range of fish sizes sampled. The mean depth of a taxon within the sediment was rarely >4 cm, and usually <3 cm, regardless of prey body size. The depth range of all

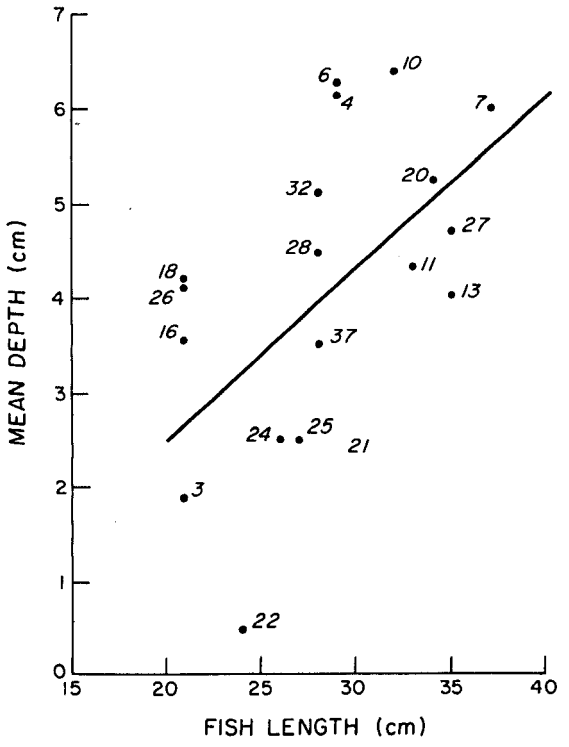

FIGURE 6.—Mean depth of prey in the sediment vs. fish length at which frequency of prey increased significantly. Numbers designate prey taxa (see Table 3).

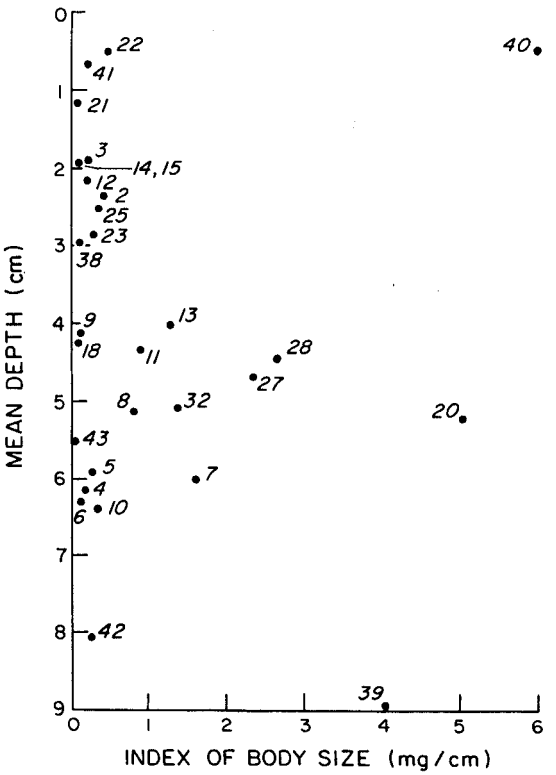

FIGURE 7.—Mean depth of prey in the sediment vs. index of prey body size. Numbers designate prey taxa (see Table 3. Nonprincipal prey: 38 = *Aricidea neosuecica*, 39 = *Laonice cirrata*, 40 = *Pherusa papillata*, 41 = *Polydora socialis*, 42 = *Spiochaetopterus costarum*, 43 = *Haploscoloplos elongatus*).

invertebrates at this station was generally shallower than at SG29.

Prey Abundance Patterns

Prey abundance also varied with location. Although the total density of individuals per square meter was slightly higher at SG10 than SG29, the density of polychaetes, a preferred taxon, averaged 886 individuals/m^2 at SG29 and only 397 individuals/m^2 at SG10 (Table 7). Most principal polychaete taxa were found in lower densities at SG10 than SG29. The density of pelecypod molluscs, a negatively selected (avoided) taxon, was several times higher at SG10 than SG29, 861 and 297 individuals/m^2, respectively.

DISCUSSION

How similar is the Dover sole to the hypothetical

TABLE 7.—Major taxon composition of 19 box core[1] samples containing 154 species taken at SG29 (119 m deep) and 8 box core samples containing 97 species taken at SG10 (426 m deep).

Taxon	SG29		SG10		Bertrand 1971[2]
	No./m²	Percent	No./m²	Percent	
Polychaetes	*886.4*	*65.5*	*396.8*	*26.9*	30.1%
Molluscs	*388.5*	*28.7*	*928.5*	*62.9*	
Pelecypods	296.6	21.9	861.1	58.3	59.2%
Gastropods	14.2	1.0	7.9	.5	1.2%
Scaphopods	66.0	4.9	45.6	3.1	1.2%
Aplacophorans	8.4	10.6	13.9	.9	0%
Other	3.3	.2			
Crustacea	*73.5*	*5.4*	*61.5*	*4.2*	4.4%
Amphipods	45.9	3.4	45.6	3.1	
Cumaceans	25.9	1.9	15.9	1.1	
Other	1.7	.1			
Echinoderms	*.8*	*<.1*	*51.6*	*3.5*	2.3%
Ophiuroids	.8	<.1	47.6	3.2	
Miscellaneous	3.3	.2	9.6	2.0	.9%
Individuals	1,352.5 n = 1,619		1,476.2 n = 744		343

[1]Effective sampling area is 0.063 m².
[2]Values found for the same location.

optimal forager that 1) prefers more profitable prey, i.e., prey whose ratio of food value to predator search and handling time is highest, 2) feeds more selectively when profitable prey are common, and 3) ignores unprofitable prey whose addition to the diet lowers the net energy intake per time spent searching and handling (Pyke et al. 1977; Krebs 1978)?

The Dover sole is not a simple opportunistic feeder, consuming all available prey in proportion to their occurrence in the environment. Since the percentage contribution of a major taxon in the diet and in the environment (as reflected by box core samples) was often significantly different, the Dover sole can be termed a selective feeder. For example, polychaetes and ophiuroids played a more important role in the diet than molluscs and crustaceans, despite the fact that polychaetes and ophiuroids were not always most abundant in box core samples. Moreover, trends in selectivity of major taxa were qualitatively similar at both locations despite different abundances of prey. Polychaetes and ophiuroids were always positively selected, occurring more often in the diet than in the environment. Even though density of pelecypod molluscs at SG10 was three times greater than at SG29, the contribution of molluscs to total diet was lower at SG10 than SG29. This general consistency of diet between these two locations in the face of varying abundances of prey, species composition, depth of benthic macrofauna within the sediment, and depth of the station itself does not support a hypothesis of the Dover sole as a simple opportunistic feeder.

The most profitable prey for a Dover sole in terms of food value (gram-calorie per gram dry weight) are first, molluscs and crustaceans; second, polychaetes; and third, ophiuroids (Brawn et al. 1968; Cummins and Wuycheck 1971; Tyler 1973). However, most observations of calories per gram dry weight were made for shell-free molluscs while polychaete weights included tubes. This is probably why values for *Lumbrineris fragilis*, an untubed polychaete, are comparable with those for pelecypods (= 4,500 g cal/g dry weight) and greater than those for amphipods (e.g., 4,050 g cal/g dry weight), while those for tubed polychaetes (e.g., *Pherusa plumosa, Pectinaria hyperborea*) are lower (2,200-3,500 g cal/dry weight). Ophiuroids generally have lowest food values (2,100 g cal/g dry weight) of the four major prey taxa consumed (Brawn et al. 1968; Cummins and Wuycheck 1971). Thus, an optimal diet based only on maximum caloric value per gram of food ingested would consist principally of crustaceans, followed by molluscs and polychaetes, and lastly of ophiuroids. However, observed diets of all sizes of Dover sole consisted primarily of ophiuroids and polychaetes, with relatively few molluscs and crustaceans. Thus, food value alone does not explain the diet of Dover sole.

The second factor determining profitability of prey, the relative expense of acquiring and digesting different prey, may play a more important role than food value in structuring the diet of Dover sole. Although no quantitative observations of feeding behavior in terms of search and handling costs have been made, some inferences can be made based on knowledge of environmental conditions and morphological features. Crustaceans were not major components of the diet, perhaps because 1) crustaceans such as amphipods may be difficult to detect in dim or turbid bottom water, 2) energy expended in pursuit of agile swimming prey may be greater than that derived from their digestion, or 3) jaw morphology may make capture of swimming crustacea difficult (Yazdani 1969, based on *Microstomus kitt*).

Molluscs may also require expenses in acquisition or digestion beyond their energetic benefits. They may be more difficult to detect and less efficiently digested than polychaetes and ophiuroids. Because the shell is not digested, digestion of molluscs such as pelecypods must take place slowly through the apertures of the shell. Calcium from the shell may also raise pH in the gut, thereby reducing efficiency of gastric enzymes. The optimal pH level for enzymes found in the stomachs of

plaice, *Pleuronectes platessa*, lies between 1.5 and 2.5; and stomach enzyme activity in plaice may cease at pH levels above 5.5 (Bayliss 1935). However, optimal pH levels in Dover sole stomachs and effects of food on local pH levels are unknown.

Relatively indigestible, low caloric ophiuroid arms were surprisingly abundant in the stomachs of Dover sole. Rae (1956) reported frequent occurrences (up to 30% of stomachs sampled) of ophiuroids in the guts of lemon sole, *Microstomus kitt*. Ophiuroids may be easy to capture and readily available. Alternatively, they could provide some required nutrient unavailable in other food sources. Finally, different rates of stomach evacuation and digestion could affect our results. The importance of ophiuroids may be easily overestimated because ophiuroids may remain in the stomach longer than the soft-bodied polychaetes, small molluscs, or crustaceans. Their arms were frequently tangled in a bulky, inflexible mass which may move slowly through the digestive tract. If a stomach contained only one or two food items, ophiuroid arms were usually present. Less digestible food items in the diet of fishes often have slower gastric evacuation rates (Fänge and Grove 1979). This would result in a longer "residence time" for ophiuroids than other prey taxa and suggests that the diet of Dover sole is principally composed of polychaetes. De Groot (1971) categorized *M. pacificus* as a polychaete-mollusc-(echinoderm) feeder, characterized by a small esophagus and stomach and complicated intestinal loop, an adaptation characteristic of flatfishes which feed on polychaetes which are often contaminated with indigestible items, e.g., tubes.

On first inspection, it appears that Dover sole do not feed more selectively on energetically more profitable prey when these prey types are more common. For example, the value of E of polychaetes at SG29 was lower than at SG10 (0.13 vs. 0.33, Table 5) while the abundance of polychaetes at SG29 was higher than at SG10 (886 vs. 396/m^2; 66% vs. 27% of the total numbers of benthic animals in the box cores (Table 7)). However, the frequency of occurrence of principal prey often changed with fish size at SG29, indicating prey selection, whereas most prey species occurred at statistically equal frequencies over the entire size range of fish sampled at SG10.

These size-related changes in selectivity at the two locations may be related to availability or energetic advantage of the prey. Prey body size was significantly correlated with size of fish at which a prey increased in importance in diet at SG29 (Figure 4). Large fish were apparently more successful than small fish at capturing large prey. Small fish may be limited to smaller, slower moving or weaker prey by mouth size or body strength. These predator-prey size relationships are consistent with those observed by Schoener (1971) for *Anolis* lizards: as predator size increased, average prey size increased. Ross (1978) also reported that mean size of prey increased with fish size for the leopard sea robin *Prionotus scitulis*, >90 mm.

Depth of prey in sediment is also significantly correlated with size of fish at which a prey species begins to occur more significantly (SG29; Figure 6). Although prey depth and prey body size were not statistically correlated, the small-bodied prey found deep in the sediment were usually not the same species which increased in frequency in larger fish. Thus, large fish apparently are physically capable of extracting large-bodied, deeply buried prey from sediment while smaller fish are not. Learning as well as extraction capability may be important in successful extraction of large polychaetes.

Since the distribution of prey species was shallower at SG10 than at SG29, the physical advantage afforded large fish in the exploitation of prey buried deep in the sediments may be eliminated at SG10. When depths of species common to both stations were compared, nearly all species were found closer to the surface at SG10, although the differences are not often statistically significant because of small sample size at SG10.

Two potential instances of increased selectivity in the face of increased abundance of a profitable or preferred prey are suggested in this study. First, the abundance of polychaetes, a preferred taxon, was lower at SG10 than SG29 (Table 7). Few significant changes in the frequency of occurrence of prey occurred with fish size at SG10 where large fish may have had to consume any polychaete encountered, regardless of size and/or location, to meet their energetic requirements. In other words, the energetic advantage arising from size-selective specialization may disappear as abundance of preferred food items decreases, as found for bluegills by Werner and Hall (1974).

Second, size-related availability results in differing effective prey densities to larger vs. smaller fish at SG29. As fish size increases, a wider range of prey may become available and so prey densities are effectively higher for larger fish. Selectivity increases with fish size (Figure 5). Since body size

of prey is also correlated with fish size, it can again be concluded that selectivity increases with an increase in densities of profitable prey.

Even though large fish at SG29 strongly selected large-bodied prey, some small-bodied prey showed no statistically significant change in frequency over the entire size range of fish. These small prey may still be "profitable" to capture by large fish. Large fish at SG29 generally consumed a wider variety of prey than small fish. The number of large-sized prey species which increased in frequency with fish size was greater than the number of small-sized species which decreased with fish length. Thus, although large-size fish consumed large-sized prey more often than small fish, they also consumed a larger range of prey sizes than did small fish.

SUMMARY

1. Dover sole off the Oregon coast in midsummer of 1976 were polychaete-ophiuroid-mollusc feeders, according to analysis of stomach contents. Polychaetes and ophiuroids were more important than molluscs and crustaceans as food in terms of frequency of occurrence, weight, and numbers.

2. Dover sole were selective feeders. Polychaetes and ophiuroids were positively selected and composed higher proportions of fish diets than of box core samples from the same location. Molluscs were not generally selected. Crustaceans were selected (SG29) or nonselectively consumed (SG10).

3. Dependency of diet on fish size varied with location. Dover sole sampled in a region of high polychaete abundance (SG29) showed size-related changes in diet. Dover sole sampled in a region of relatively low polychaete abundance (SG10) showed few size-related changes in diet.

4. When size-related changes in diet were observed, prey body size was positively correlated with predator length at which the prey taxon showed a significant increase in frequency of occurrence.

5. Consumption of polychaetes by Dover sole was a function of depth of prey taxon within the sediment and size of the fish consuming the prey. The mean depth of a prey taxon within the sediment was positively correlated with the predator length at which the prey taxon showed a significant increase in frequency of occurrence (SG29). Where polychaetes were distributed closer to the surface, few size-related changes were observed.

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CEPHALOPODS IN THE DIET OF THE SWORDFISH, *XIPHIAS GLADIUS*, FROM THE FLORIDA STRAITS

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ABSTRACT

An analysis was conducted on the cephalopod remains from the stomachs of 65 swordfish, *Xiphias gladius*, from the Florida Straits. Results indicated that cephalopods contribute a large proportion of the total ration of food items, accounting for over 90% of total weight of contents in 69% of the stomachs. Of these, ommastrephid squid of the genus *Illex* represented the single most important prey items. In total, 15 species of cephalopods were encountered, consisting of 13 teuthoids and 2 octopods. This previously unrecognized diversity confirmed the earlier postulated opportunistic feeding strategy of *X. gladius*. Cephalopod, fish, and crustacean remains are reported in terms of frequency of occurrence and biomass. Analysis of the vertical distribution of cephalopod prey indicated that swordfish feeding is most concentrated in epipelagic and upper mesopelagic waters. Comparisons with feeding studies on billfishes from the western North Atlantic indicated that istiophorids may rely more heavily on finfish prey than squid in contrast with the present findings for *X. gladius*. Also, octopods may contribute a greater proportion of the cephalopod component of total ration in the istiophorids than in *X. gladius*.

Analysis of stomach contents of many marine teleosts, mammals, and birds (Bouxin and Le Gendre 1936; Clarke 1966; Rancurel 1970, 1976; Dragovich and Potthoff 1972; Imber 1973, 1975; Perrin et al. 1973; Clarke and MacLeod 1970, 1976; Mercer 1974) coupled with estimates of cephalopod biomass (Voss 1973) suggest a key role of cephalopods in oceanic food webs. Nevertheless, few thorough studies have been conducted that have analyzed cephalopod remains, both qualitatively and quantitatively (see Voss 1953; Rees and Maul 1956; Jolley 1977; Matthews et al. 1977; Morejohn et al. 1978). Oceanic vertebrates are often more efficient collectors of cephalopods than available oceanographic gear (Clarke 1966). Therefore, information from stomach content analyses can supplement and refine existing knowledge of the biology of both prey and predator.

Cephalopods represent a major element in the diet of the swordfish, *Xiphias gladius* Linnaeus (Maksimov 1969). Yet, investigations of swordfish diet, commencing with Fleming (1828), yield little data concerning the trophic relationship between this predator and cephalopod mollusks. Acquisition of 65 swordfish stomachs allowed investigation of feeding ecology with emphasis on aspects of the biology and systematics of cephalopod prey.

HISTORICAL RESUMÉ

The feeding ecology of *X. gladius* is poorly understood, not only because of a general paucity of studies concerning xiphiid predation, but perhaps more importantly, from a lack of studies by invertebrate specialists dealing with invertebrates consumed by swordfish (e.g., mollusks, crustaceans). In contrast, stomach content analyses made by ichthyologists have provided reasonably good specific-level diagnoses of fish remains. A brief summary of studies that contain information on cephalopod remains from *X. gladius* stomachs is provided here.

Goode (1883) cited Fleming's (1828) report of the remains of *Sepiae* from a swordfish stomach. Goode also noted the occurrence of squid mandibles and speculated they were from the loliginid squid, *Loligo Pealii* (= *L. pealei*). In addition, Goode observed that stomach contents of swordfish from the western Atlantic were "...for the most part of the common schooling species of fishes." Rich (1947) noted a set of large beaks ("perhaps *Architeuthis*") from a *Xiphias* harpooned on the northern Georges Banks. Bigelow and Schroeder (1953) noted a specimen of *Ilex* (= *Illex*) from the stomach of a swordfish harpooned off Halifax, Nova Scotia, and commented that squid may, at times, form the chief component of the swordfish diet. Yabe et al. (1959) reported squid (mantle length 20-40 mm) and

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squid fragments (mantles and beaks) from several swordfish stomachs. They did not assign these cephalopod remains to more specific taxa. Several specimens contained "octopus jaws." Their study demonstrated ontogenetic changes in prey selection, with adult Pacific swordfish feeding principally on squid. Tibbo et al. (1961) examined stomachs of 39 swordfish from Nantucket Shoals and Sable Island Bank, finding fish and the squid *Illex illecebrosus*. In 14 of those swordfish (Sable Island Bank specimens), 22 squid were included among 564 food items.

De Sylva (1962) analyzed stomachs of seven female swordfish caught in April to May off northern Chile. Of the five specimens containing food remains, 24 squid *Dosidicus gigas* were found. These findings led de Sylva to believe that most swordfish feeding takes place near the surface. Cavaliere (1963) reported swordfish diets from the Straits of Messina and adjacent waters during spring and summer. Cephalopods were found in 80% of the stomachs with *I. coindetii*, *L. todarus* (= *Todarodes sagittatus* ?), and *Todarodes sagittatus* being most common. Guitart-Manday (1964), reporting on an unspecified number of swordfish taken during February and March near Cuba, found teuthoids, including *Thysanoteuthis rhombus* and a single octopod, constituting approximately 30% of the diet by number of items. Scott and Tibbo (1968), utilizing volumetric analysis, examined stomach contents of 514 swordfish from the western North Atlantic between Virginia and Sable Island Banks. They reported that, from March to October, swordfish feed on *I. illecebrosus*, as well as on a variety of fishes. Scott and Tibbo also noted the occurrence of the squid *Ommastrephes*. Interestingly, they reported the infrequent occurrence of the octopod, *Bathypolypus arcticus*, a benthic inhabitant of the continental shelf.

Maksimov (1969) examined stomach contents from 502 swordfish from the tropical Atlantic. Frequency of occurrence and average size of food items were reported. Cephalopods were a major component of the diet in all areas sampled. The following organisms were represented: *Loligo* sp., *Ommastrephes* sp. (3 undetermined spp.), and an undetermined species of sepioid. Ovchinnikov (1970) noted cephalopod and fish remains by percentage from swordfish taken near Cuba. They are identical to those reported by Guitart-Manday (1964) and probably are an uncited repetition of the same data. Beckett (1974) reported swordfish diets from the northwest Atlantic. He indicated that swordfish over deep water usually feed on vertically migrating species including squids, however, no further taxonomic breakdown was given.

MATERIALS AND METHODS

Food remains from the stomachs of 65 specimens of *X. gladius* from the Straits of Florida were examined. Samples were obtained from three sources: sportfishing tournaments in Miami and Ft. Lauderdale, Fla. (38 specimens), commercial longliners (23 specimens), and other sources (4 specimens). Collection data are given in Appendix Table 1.

Tournament swordfish specimens were measured and weighed at dockside. Weights of longline specimens were estimated using fork length-weight relationships for both males and females (Southeast Fisheries Center[2]). Stomachs were removed and the contents fixed in 10% Formalin.[3] Following fixation, samples were transferred to 70% ethyl alcohol for storage.

Analysis of individual stomachs was conducted as follows. Contents were separated into squid, fish, and other invertebrate components. Total weights were taken for each group. Remains of intact squid were further analyzed for individual weight, dorsal mantle length, sex, state of maturity, and general condition. Based on available morphological features, squid were assigned to the lowest possible taxa. Because of the poor condition of many squid, numerous systematic characters often were destroyed or unrecognizable. Most species-specific diagnoses of teuthoid cephalopods are based on external, soft-tissue characters. It is just those features that are subject to the intial effects of digestion. As a result, identifications were based on a composite of less frequently utilized morphological features that are more resistant to digestive enzymes. These included gladius and spermatophore morphology, internal anatomy, dermal cartilage, mantle musculature, photophore number and distribution, salient beak characters, and radulae. The potential utility of such characters to predator-

[2]Southeast Fisheries Center. 1981. Report of the ICCAT Inter-sessional Workshop on Billfish. Natl. Mar. Fish. Serv., Southeast Fish. Cent., Miami, Fla., Doc. 8, 16 p. Unpubl. manuscr.

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

prey studies by nonteuthologists has prompted the writers to begin work on a guide to identification of cephalopod remains from predatory species.

Buccal masses were dissected from identified squid remains and retained for future examination of mandibles. Estimates of the number of cephalopods were based solely on soft-tissue remains. Unassociated hard structures such as free mandibles, lenses, and gladii often were encountered in large numbers suggesting extended residence within the stomach. Therefore, inventories of those remains were not utilized in determining total numbers of cephalopod prey.

An attempt was made to assess the vertical migratory behavior of swordfish based on known bathymetric distribution of their squid prey. Other aspects of swordfish feeding ecology were examined using fishing depth and hookup time, as well as sex and size of swordfish specimens.

RESULTS

Tables 1 and 2 present frequencies and biomasses of prey in stomachs of 65 swordfish. Cephalopods were the most important component, both in numbers and weight. Fish remains were of secondary importance, followed by crustaceans (shrimp). Figures 1-3 depict frequency of occurrence of each group. Cephalopods composed over 90% of the contents by weight in 68% of the stomachs examined. Only 9% of the stomachs contained <50% cephalopod remains. Fish remains accounted for >50% of contents in only 11% of the stomachs. Fish remains were ≤10% of total remains in 69% of all stomachs. Shrimp remains were found in only 9% of the stomachs, accounting for 8% by weight in one stomach and <3% in all other instances. Weights of stomach contents are conservative because swordfish are known to occasionally regurgitate or even evert their stomach when captured (Tibbo et al. 1961).

Cephalopod remains were found to include the following species:

Class: Cephalopoda Cuvier 1798
- Subclass: Coleoidea Bather 1888
  - Order: Teuthoidea Naef 1916
    - Suborder: Oegopsida Orbigny 1845
      - Family: Enoploteuthidae Pfeffer 1900
        - Subfamily: Ancistrocheirinae Pfeffer 1912
          - Genus: *Ancistrocheirus* Gray 1849
            - Species: *A. lesueuri* (Orbigny 1839)
      - Family: Onychoteuthidae Gray 1849
        - Genus: *Onychoteuthis* Lichtenstein 1818
          - Species: *O. banksii* (Leach 1817)
      - Family: Lepidoteuthidae Naef 1912
        - Genus: *Tetronychoteuthis* Pfeffer 1900
          - Species: *T. massyae* Pfeffer 1912
      - Family: Architeuthidae Pfeffer 1900
        - Genus: *Architeuthis* Steenstrup 1857
          - Species: *Architeuthis* sp.
      - Family: Histioteuthidae Verrill 1881
        - Genus: *Histioteuthis* Orbigny 1841
          - Species: *H. dofleini* (Pfeffer 1912)
            Histioteuthis sp.
      - Family: Ctenopterygidae Grimpe 1922
        - Genus: *Ctenopteryx* Appellöf 1899
          - Species: *C. sicula* (Verany 1851)
      - Family: Ommastrephidae Steenstrup 1857
        - Subfamily: Ommastrephinae Steenstrup 1857
          - Genus: *Ommastrephes* Orbigny 1835
            - Species: *O. pteropus* Steenstrup 1855
          - Genus: *Ornithoteuthis* Okada 1927
            - Species: *O. antillarum* (Adam 1957)
        - Subfamily: Illicinae Posselt 1890
          - Genus: *Illex* Steenstrup 1880
            - Species: *I. coindetii* ? (Verany 1837)
              I. oxygonius Roper, Lu, and Mangold 1969
              I. illecebrosus ? Lesueur 1821
      - Family: Thysanoteuthidae Keferstein 1866
        - Genus: *Thysanoteuthis* Troschel 1857
          - Species: *T. rhombus* Troschel 1857
      - Family: Cranchiidae Prosch 1849
        - Subfamily: Cranchiinae Prosch 1849
          - Genus: *Cranchia* Leach 1817
            - Species: *C. scabra* Leach 1817
- Order: Octopoda Leach 1818
  - Suborder: Incirrata Grimpe 1916
    - Family: Bolitaenidae Chun 1911
      - Genus: *Japetella* Hoyle 1885
        - Species: *J. diaphana* Hoyle 1885

Family: Argonautidae Naef 1912
Genus: *Argonauta* Linnaeus 1758
Species: *Argonauta* sp.

Octopod remains were limited to a single occurrence of each of two species, both taken from the same stomach. Remaining cephalopods consisted of squid of the suborder Oegopsida. Of these, the genus *Illex* was predominant (Figure 4). *Histioteuthis* was second most common based on number of individuals, followed by equal numbers of *Ommastrephes pteropus* and *Onychoteuthis banksii*. Following these, in decreasing frequency of occurrence were *Thysanoteuthis rhombus* and *Cranchia scabra*. There were single records of *Ornithoteuthis antillarum*, *Tetronychoteuthis massyae*, *Ancistrocheirus lesueuri*, *Ctenopteryx sicula*, and *Architeuthis* sp. Because *Ommastrephes pteropus* and *Thysanoteuthis rhombus* reach large sizes, their contribution to prey biomass was more important than reflected by number of individuals.

Comparison of prey composition and quantity relative to swordfish sex, size, capture method, hookup time, and time of year did not reveal any correlations.

TABLE 1.—Diversity and abundance (number of individuals) of cephalopod remains in the stomach contents of *Xiphias gladius*.

	Order Teuthoidea												Order Octopoda		Other cephalopod remains				
Fish no.[1]	*Illex* spp.[2]	*Ommastrephes pteropus*	*Ornithoteuthis antillarum*	*Ancistrocheirus lesueuri*	*Onychoteuthis banksii*	*Tetronychoteuthis massyae*	*Architeuthis* sp.	*Histioteuthis dofleini*	*Histioteuthis* sp.[3]	*Ctenopteryx sicula*	*Thysanoteuthis rhombus*	*Cranchia scabra*	*Japetella diaphana*	*Argonauta* sp.	Soft-tissue fragments	Buccal masses[4]	Mandibles[4]	Gladii (Ommastrephidae)[4]	Lenses[4]	Total
1	15				1										1					17
2	7														2+	1	42	18+	32	9+
3	10																1			10
4	2														5+		32	19+		7+
5	3	1													2+		40			6+
6	13	1															14			14
7	1																			1
8	27	1			1		1								5+	5	23	2	4	35+
9	28														2+					30+
10	1														2+					3+
11	1																23			1
12	2															6	19			2
13	1														1+		8			2+
14															2+	2	2			2+
15	1	1														4	4		3	2
16	2														1+	1	6			3+
17															1+	1	66	14+		1+
18		1													4+	4				5+
19	15										1				2+	2				18+
20	8														5+		46	25	29	13+
21									1							5	4	5	6	1
22															13+	3		10	24	13+
23	13														1				17	14
24	9																			9
25	14														6+		11		11	20+
26	12																			12
27	2							1							16+	6		16	15	19+
28	5				3											5	63	53	78	8
29																			51	0
30															13+	4	35	34	12	13+
31	10														19+		16	18	31	29+
32	5														4+	7	8	7+		9+
33															1					1
34	2														7+	2	25	6+		9+
35	13	1													9+	8	96	25+		23+
36					2										2+			13	24	4+
37															1+	1	12	6	3	1+
38	17																			17
39	7														3+				4	10+
40	10														4+		42	15	41	14+
41															1+		38	22	12	1+
42															9+	8	23	18		9+
43	1														4+	3	2	10	13	5+

TABLE 1.—*Continued*.

Fish no.[1]	Order Teuthoidea: *Illex* spp.[2]	*Ommastrephes pteropus*	*Ornithoteuthis antillarum*	*Ancistrocheirus lesueuri*	*Onychoteuthis banksii*	*Tetronychoteuthis massyae*	*Architeuthis* sp.	*Histioteuthis dofleini*	*Histioteuthis* sp.[3]	*Ctenopteryx sicula*	*Thysanoteuthis rhombus*	*Cranchia scabra*	Order Octopoda: *Japetella diaphana*	*Argonauta* sp.	Other cephalopod remains: Soft-tissue fragments	Buccal masses[4]	Mandibles[4]	Gladii (Ommastrephidae)[4]	Lenses[4]	Total
44	1										1				3+	1	4	4		5+
45	1										1				4+	3	18	13	16	5+
46															10+	7	16	22	19	10+
47															8+	2		2	5	8+
48	7														4+	10		4	12	11+
49	2														6+	1	20	10+	44	8+
50	6														2+	3	4	2	1	8+
51															9+	2	12	18	13	9+
52	6														1					7
53	1																			1
54	4														3+					7+
55	1											1								2
56			1																	1
57						1				1		1								3
58								1					1	1						3
59		1																		1
60	4								4						1+		8			9+
61								1												1
62	4														1+	2	22	12		5+
63	8																56	28		8
64	7														2+	2	5	8	13	9+
65				1					1						1+		2	2		3+

[1]See Appendix Table 1.
[2]Includes *I. coindetii*, *I. illecebrosus*, and *I. oxygonius* (see Discussion).
[3]May include more than one species.
[4]Not included in total cephalopods (see Materials and Methods).

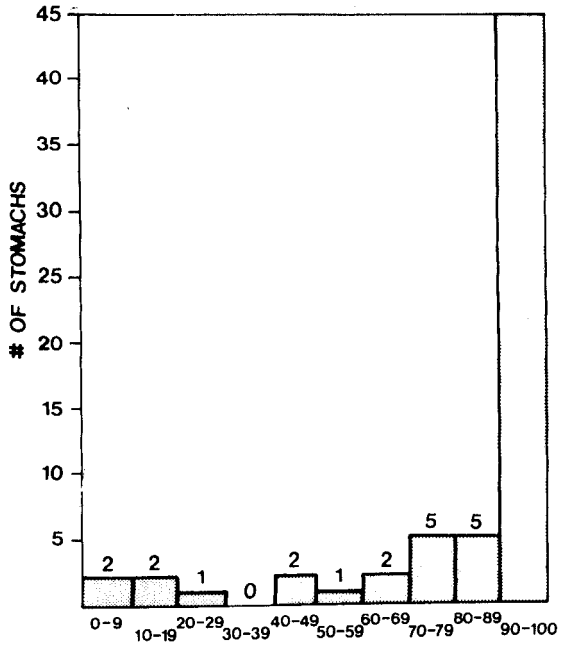

FIGURE 1.—Cephalopod remains as percent of total stomach contents by weight.

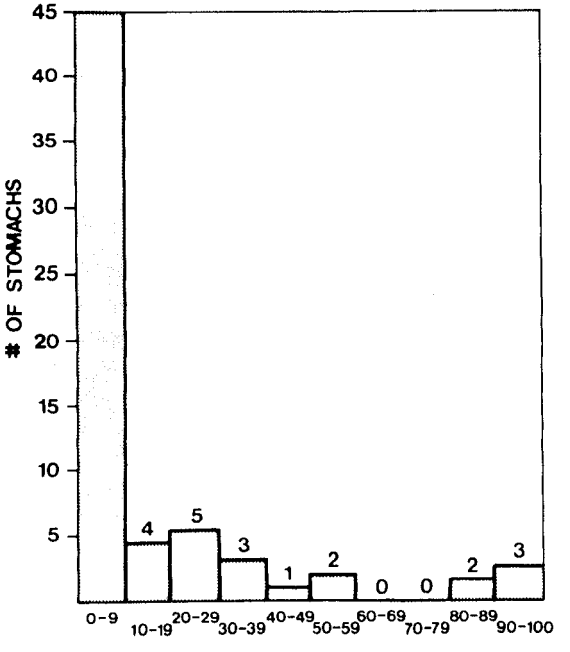

FIGURE 2.—Fish remains as percent of total stomach contents by weight.

TABLE 2.—Weights (grams) of cephalopod, fish, and other invertebrate remains in the stomach contents of *Xiphias gladius*.

	Order Teuthoidea												Order Octopoda		Total			Percent of total			
Fish no.[1]	*Illex* spp.[2]	*Ommastrephes pteropus*	*Ornithoteuthis antillarum*	*Ancistrocheirus lesueuri*	*Onychoteuthis banksii*	*Tetronychoteuthis massyae*	*Architeuthis* sp.	*Histioteuthis dofleini*	*Histioteuthis* sp.[3]	*Ctenopteryx sicula*	*Thysanoteuthis rhombus*	*Cranchia scabra*	*Japetella diaphana*	*Argonauta* sp.	Cephalopods	Fish	Other invertebrates (shrimp)	Cephalopods[4]	Fish	Other invertebrates (shrimp)	Total of all components
1	1,033				36										1,088	1	0	>99	<1	0	1,089
2	421														477	24	1	95	4	<1	502
3	1,062														1,062	0	0	100	0	0	1,062
4	88														213	0	0	100	0	0	213
5	178	334													614	0	0	100	0	0	614
6	1,316	319													1,635	0	0	100	0	0	1,635
7	73														73	10	0	88	12	0	83
8	3,023	155			70		107								3,730	72	0	98	2	0	3,802
9	2,726														2,812	0	0	100	0	0	2,812
10	61														145	0	4	97	0	3	149
11	177														177	1	0	>99	<1	0	178
12	155														155	0	0	100	0	0	155
13	80														141	0	0	100	0	0	141
14															141	20	0	88	12	0	161
15	49	475													524	0	0	100	0	0	524
16	263														263	0	23	92	0	8	286
17															4	88	1	4	>95	<1	93
18		661													859	77	0	92	8	0	936
19	2,471										75				2,642	214	0	93	7	0	2,856
20	811														994	75	0	93	7	0	1,069
21									2						15	61	0	20	80	0	76
22															795	0	11	98	0	2	806
23	1,059														1,091	0	0	100	0	0	1,091
24	1,131														1,131	0	0	100	0	0	1,131
25	1,517														1,993	93	0	96	4	0	2,086
26	1,553														1,553	0	0	100	0	0	1,553
27	178							45							223	0	0	100	0	0	223
28	395				2										397	0	0	100	0	0	397
29															—	0	0	100	0	0	—
30															505	0	0	100	0	0	505
31	689														1,328	162	0	89	11	0	1,490
32	387														531	39	0	93	7	0	570
33															36	319	0	10	90	0	355
34	80														362	445	0	45	55	0	807
35	1,090	375													1,871	11	0	99	1	0	1,882
36					2										140	725	0	16	84	0	865
37															24	10	0	71	29	0	34
38	1,273														1,273	0	0	100	0	0	1,273
39	572														715	26	0	96	4	0	741
40	569														644	21	0	97	3	0	665
41															78	0	0	100	0	0	78
42															419	388	0	52	48	0	807
43	114														163	0	0	100	0	0	163
44	108										487				675	287	0	70	30	0	962
45	98										6				161	44	0	79	21	0	205
46															408	116	0	78	22	0	524
47															426	76	0	85	15	0	502
48	644														678	0	0	100	0	0	678
49	226														574	21	0	96	4	0	595
50	627														650	0	0	100	0	0	650
51															389	242	0	62	38	0	631
52	768														838	0	0	100	0	0	838
53	151														151	73	0	77	23	0	224
54	684														789	200	0	80	20	0	989
55	93											7			100	0	0	100	0	0	100
56			12												12	0	0	100	0	0	12
57						15				85		5			105	0	0	100	0	0	105
58								1					2	1	4	992	2	<1	>99	<1	998
59		146													146	73	0	67	33	0	219
60	379								235						679	0	0	100	0	0	679
61								164							164	0	0	100	0	0	164
62	446														468	34	0	93	7	0	502
63	617														628	0	0	100	0	0	628
64	600														713	0	0	100	0	0	713
65				26					209						391	420	0	48	52	0	811

[1] See Appendix Table 1.
[2] Includes *I. coindetii*, *I. illecebrosus*, and *I. oxygonius* (see Discussion).
[3] May include more than one species.
[4] Includes weights of fragments.

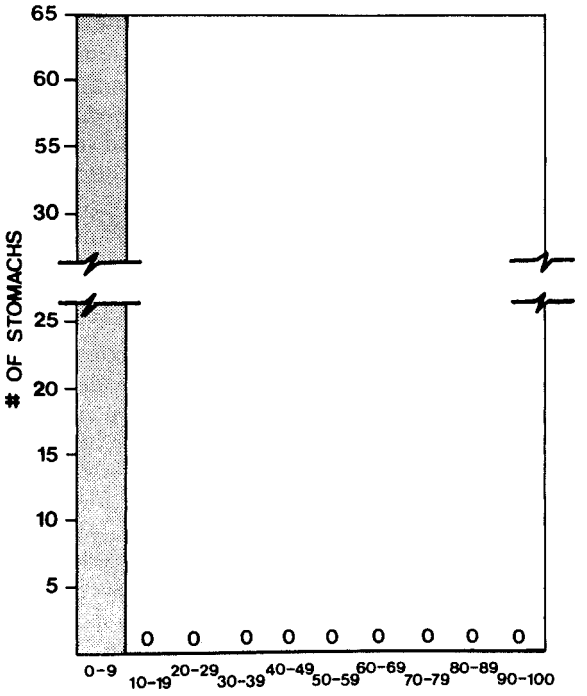

FIGURE 3.—Shrimp remains as percent of total stomach contents by weight.

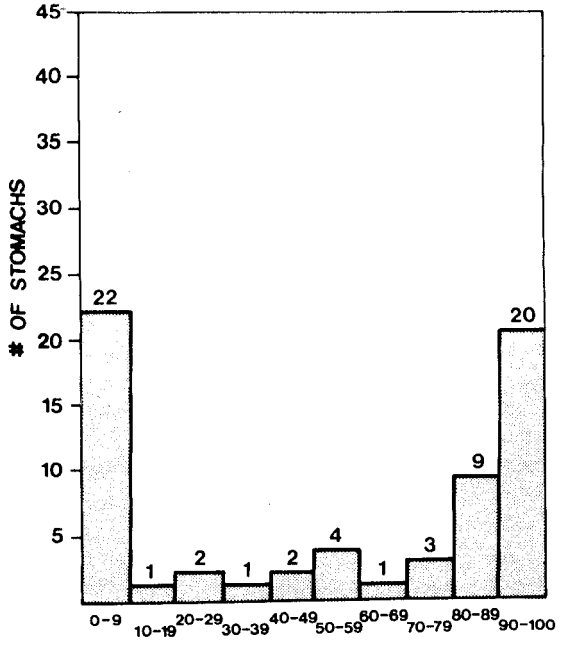

FIGURE 4.—*Illex* spp. remains as percent of total stomach contents by weight.

DISCUSSION

Swordfish in the Straits of Florida demonstrate a clear predilection for cephalopods as prey, specifically squids. Furthermore, the genus *Illex* constitutes the single most important component in the diet. At present, there are three nominal species of *Illex* known from the western North Atlantic: *I. illecebrosus*, *I. coindetii*, and *I. oxygonius*. A recent revision (Roper et al. 1969) attempted to stabilize the systematic positions of these taxa. However, the same authors reemphasized systematic and distributional complexities of this polytypic genus, especially in the tropical western Atlantic which includes the present study area. Numerous specimens examined in this work had the specific characters assigned to their nominal species, however, systematic problems appear to be most acute in the *I. illecebrosus-I. coindetii* complex. Because of the tenuous systematic and distributional aspects, as well as the poor condition of much of the material, the writers thought it best to deal with the group at the generic level rather than possibly adding to the underlying systematic and zoogeographic confusion.

Many teuthoids aggregate for feeding or reproduction (see Clarke 1966). The cephalopod prey in this study included such aggregating squid as *Illex* spp., *Ommastrephes pteropus*, *Thysanoteuthis rhombus*, *Onychoteuthis banksii*, and *Histioteuthis* sp. Additionally, *Ornithoteuthis antillarum* and *Tetronychoteuthis massyae* probably behave similarly. Heavy swordfish predation upon aggregating or schooling cephalopods is similar to reported predation on schooling fishes (Goode 1883; Tibbo et al. 1961). Tibbo et al. (1961) and Scott and Tibbo (1968) noted the use of the bill by swordfish to wound or kill prey. They suggested that swordfish slash laterally with their bills, while ascending or descending through a school of prey. The present material contained numerous decapitated squid and more frequently, oblique slash marks on mantles thus supporting the postulated foraging behavior. Furthermore, this concurs with the known horizontal orientation of the pelagic squids listed above. Ommastrephids and *Thysanoteuthis* have muscular mantles and are powerful swimmers. Swimming ability of swordfish does not appear to be a limiting factor in the selection of cephalopod prey, as indicated by the predominance of these organisms in the diet of *X. gladius*.

In the tropics, swordfish undergo daily vertical migrations, rising to feed near the surface at night and returning to deeper waters by day (Beardsley 1978). The full extent of these vertical migrations is poorly known. Cephalopods also exhibit vertical distributions and diel migrations of considerable range (Voss 1967; Clarke and Lu 1974, 1975; Lu and Clark 1975a, b; Roper and Young 1975; Herring 1977). While these works provide some data on bathymetric distribution suggesting general patterns of vertical migration, the actual distributions of most cephalopod species remain poorly known. At the familial level, all but three of the cephalopods encountered in this work may occur from the surface to depths between 500 and 1,000 m. Histioteuthids are found from near the surface to about 2,500 m. Cranchiids range, in general, from the surface to about 3,000 m, but the only species found in swordfish stomachs, *Cranchia scabra*, is confined to the upper several hundred meters of the water column (N. Voss[4]). Thore (1949) stated that adults of *Japetella diaphana* are found in 330-3,000 m of water, while younger animals are concentrated at depths of 100-330 m. Bathymetric ranges of all cephalopod species considered here encompass the upper 500 m of water. While it remains possible that swordfish forage at greater depths, it appears that most feeding is concentrated in epipelagic and upper mesopelagic waters.

This analysis of the cephalopod component of the swordfish diet supports earlier observations (Scott and Tibbo 1968), suggesting the opportunistic nature of *X. gladius* predation. Based on the data presented here, prey composition is independent of season, fish size, or sex. Rather, stomach contents appear to reflect the diversity and relative abundance of potential prey.

Voss (1953) examined stomach contents of 241 sailfish, *Istiophorus americanus* (= *I. platypterus*), from Florida waters. Of 461 identified prey, 83% were fish, including members of at least 20 families. A total of 78 cephalopods, including 27 octopods, were found. Voss identified the octopod specimens as *Argonauta argo*, *Argonauta* sp., and *Grimpoteuthis*?. Of the 49 teuthoids recovered, all were considered *Sthenoteuthis bartrami* (= *Ommastrephes bartrami*), but probably were *O. pteropus*. Maksimov (1971) examined stomachs of sailfish from the tropical Atlantic. Teuthoids and octopods predominated as food. Over 61% of sailfish stomachs from Brazil contained squid and 50% contained octopods. Sailfish taken off Barbados contained squid, but no octopods. Jolley (1977) examined 778 sailfish from off southeast Florida and found scombrid fish to be the most important prey followed by cephalopods. Jolley found 27% of all stomachs examined to be empty.

Krumholz and de Sylva (1958) reported on the stomach contents of white marlin, *Tetrapterus albidus*, taken near Bimini, Bahamas. Nine stomachs contained cephalopods, arthropods, and fish. Squid and octopods were the most abundant items, accounting for 41% and 18%, respectively, by frequency of occurrence. An additional 41 stomachs were empty. De Sylva and Davis (1963) examined stomachs of 55 white marlin from the Middle Atlantic Bight. Round herring, *Etrumeus teres*, and *Loligo pealei* were the chief components of the diet. Ovchinnikov (1970) investigated diets of white marlin in the tropical Atlantic, noting *Loligo pealei* as the most important prey.

Krumholz and de Sylva (1958) also reported on 14 blue marlin stomachs of which 10 contained food. Fish were more important than cephalopods by frequency of occurrence. Cephalopod remains consisted of the pelagic octopods *Argonauta argo* and *Ocythoe tuberculata*, which together constituted 17% of the total number of prey. Voss and Erdman (1959) reported finding a large specimen of the squid *Thysanoteuthis rhombus* in the stomach of a blue marlin caught off San Juan, Puerto Rico. Ovchinnikov (1970) investigated stomachs of blue marlin. These fish contained teuthoids and less frequently sepioids. Fish were more important than cephalopods in the diet of blue marlin.

Two observations are apparent from comparisons of diets of istiophorids and swordfish. First, fish appear to be more important in diets of istiophorids, with cephalopods of secondary importance. The opposite is true for swordfish. Second, octopods may be a more important component of the cephalopod prey of istiophorids than of swordfish.

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APPENDIX TABLE 1.—Swordfish collection data.

Fish no.	Date landed	Sex[1]	Lower jaw fork length (cm)	Weight (kg)	Method of capture[2]	Hookup time (e.s.t)	Fish no.	Date landed	Sex[1]	Lower jaw fork length (cm)	Weight (kg)	Method of capture[2]	Hookup time (e.s.t)
1	17 June 1978	M	138	30	R	—	34	20 July 1978	M	170	72	R	0400
2	17 June 1978	M	142	35	R	—	35	20 July 1978	M	178	77	R	2238
3	21 June 1978	M	142	29	R	0006	36	21 July 1978	M	134	30	R	0320
4	21 June 1978	M	155	45	R	0152	37	21 July 1978	M	156	47	R	0220
5	21 June 1978	M	167	62	R	0300	38	21 July 1978	M	169	59	R	2200
6	21 June 1978	M	176	69	R	0045	39	21 July 1978	M	170	65	R	2230
7	21 June 1978	M	196	102	R	0500	40	21 July 1978	M	174	74	R	0147
8	21 June 1978	F	205	120	R	2300	41	21 July 1978	F	211	136	R	0255
9	21 June 1978	M	206	101	R	0050	42	27 July 1978	M	153	[3]45	LL	—
10	22 June 1978	M	134	29	R	0315	43	27 July 1978	M	199	[3]101	LL	—
11	22 June 1978	M	142	35	R	2230	44	13 Sept. 1978	M	138	[3]33	LL	—
12	22 June 1978	M	151	41	R	0400	45	29 Sept. 1978	M	101	[3]13	LL	—
13	23 June 1978	M	189	80	R	0246	46	29 Sept. 1978	M	165	[3]57	LL	—
14	23 June 1978	F	214	126	R	0435	47	29 Sept. 1978	M	235?	[4]166	LL	—
15	24 June 1978	M	147	41	R	0530	48	30 Sept. 1978	F	106	[3]12	LL	—
16	24 June 1978	M	193	92	R	2400	49	30 Sept. 1978	M	169	[3]61	LL	—
17	24 June 1978	M	206	112	R	0430	50	5 Oct. 1978	F	102	[3]11	LL	—
18	24 June 1978	F	207	105	R	—	51	5 Oct. 1978	M	143	[3]37	LL	—
19	24 June 1978	F	209	118	R	—	52	5 Oct. 1978	M	150	[3]42	LL	—
20	17 July 1978	M	141	36	R	0150	53	6 Feb. 1979	F	121	[3]19	LL	—
21	17 July 1978	M	160	52	R	0243	54	7 Mar. 1979	F	241	[4]203	LL	—
22	17 July 1978	M	175	64	R	2312	55	10 Apr. 1979	M	126	[3]25	LL	—
23	17 July 1978	M	181	77	R	2345	56	10 Apr. 1979	F	131	[3]25	LL	—
24	17 July 1978	M	186	72	R	2304	57	10 Apr. 1979	F	132	[3]26	LL	—
25	17 July 1978	F	213	143	R	2207	58	10 Apr. 1979	M	157	[3]49	LL	—
26	18 July 1978	—	118	20	R	0345	59	10 Apr. 1979	M	163	[3]55	LL	—
27	18 July 1978	M	158	50	R	2251	60	11 Apr. 1979	M	165	[3]57	LL	—
28	18 July 1978	M	200	110	R	—	61	6 June 1979	M	155	[3]47	LL	—
29	18 July 1978	M	209	115	R	2400	62	29 Sept. 1979	F	106	[3]12	LL	—
30	18 July 1978	M	214	125	R	0315	63	29 Sept. 1979	M	174	[3]67	LL	—
31	18 July 1978	M	218	114	R	2300	64	5 Oct. 1979	M	124	[3]24	LL	—
32	20 July 1978	M	132	27	R	0112	65	—	—	—	—	—	—
33	20 July 1978	M	140	39	R	0410							

[1]M = Male, F = Female.
[2]R = Rod and reel, LL = Longline.
[3]Weight computed from weight/length formulas according to sex (Southeast Fisheries Center text footnote 3).
[4]Weight computed from dressed weight/whole weight formula (South Atlantic Fishery Management Council. 1980. Draft Swordfish Management Plan. Unpubl. manuscr.)

TROPHIC RELATIONSHIPS AMONG DEMERSAL FISHES IN A COASTAL AREA OF THE GULF OF MAINE[1]

JOHN S. HACUNDA[2]

ABSTRACT

Food resource utilization was investigated among eight demersal fish species (longhorn sculpin, *Myoxocephalus octodecemspinosus*; winter flounder, *Pseudopleuronectes americanus*; windowpane, *Scopthalmus aquosus*; yellowtail flounder, *Limanda ferruginea*; little skate, *Raja erinacea*; Atlantic cod, *Gadus morhua*; red hake, *Urophycis chuss*; ocean pout, *Macrozoarces americanus*) over a 13-month period in an area of Johns Bay, Maine. Despite the dominance of polychaetes and mollusks in the benthos, crustaceans composed the major prey group in all predators. There was considerable trophic similarity among the fishes and the amphipods *Unciola* sp. and *Leptocheirus pinguis* were the most important prey in seven of the eight predators. The results indicate that resource partitioning by prey size is related to different mouth morphologies for closely related species (winter flounder, yellowtail flounder, windowpane), and that unrelated species with similar mouth morphologies may overlap in prey size use (longhorn sculpin, Atlantic cod).

Recent studies have revealed the complexity of feeding relations among marine organisms (Isaacs 1972; Lange and Hurley 1975). The concept of unstructured food webs necessitates a detailed knowledge of the food habits of component species in order to establish their trophic connections and to determine energy flow pathways through the ecosystem. Fish food habit studies are helpful in deciphering some of the higher level trophic relations in an ecosystem. From a practical standpoint, information on the quantity and quality of food consumed by fish is needed for estimating fish production (Paloheimo and Dickie 1970; Mills and Fournier 1979). In addition, knowledge of the feeding ecology of noncommercial, as well as commercial species, is essential for implementing a multispecies approach to fishery management (Gulland 1977; Larkin 1978).

Studies of the food habits of fish communities in the marine environment are becoming increasingly popular. Most of the early effort was centered on freshwater fish communities (e.g., Nilsson 1967; Keast 1970; Zaret and Rand 1971), but there is now a growing literature on marine systems (e.g., Tyler 1972; Hobson and Chess 1976; Kislalioglu and Gibson 1977; Langton and Bowman 1980; Hunter[3]). These fish population studies are part of a broader area of research in modern ecology concerned with the question of how closely related species coexist in communities. Patterns of resource utilization by cooccurring species have been studied to assess interspecific competition and gain insight into community organization (see review by Schoener 1974).

The purpose of the present study is to examine feeding relationships among demersal fishes in a coastal area of the Gulf of Maine. Specifically, the objectives are 1) to determine quantitatively the principal prey species of the demersal fishes, 2) to examine food resource division and interrelationships among the predator species, and 3) to compare predator diets with food resources potentially available in the benthic infauna.

METHODS

I made monthly trawl collections of demersal fishes in Johns Bay, Maine, from April 1978 through April 1979. A 5.5 m otter trawl was used during the initial 3 mo of sampling. For the remainder of the study I used a 9.1 m otter trawl. The trawl had a 50.8 mm #15 nylon mesh with a 38.1 mm cod end. Trawls were made in approximately

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[3]Hunter, M. 1979. Food resource partitioning by demersal fishes from the vicinity of Kodiak Island, Alaska. *In* S. J. Lipovsky and C. A. Simenstad (editors), Fish food habits studies (Proc. 2d Pac. NW. Tech. Workshop), p. 179-186. Wash. Sea Grant Publ. WSG-WO-79-1.

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30 m of water along the eastern side of Johns Bay (Figure 1). Two or three 15-min trawls were made during each sampling trip to obtain a sufficient number of fish. I measured temperature and salinity at the surface (1 m and at a depth of 30 m) using a Beckman[4] RS5-3 salinometer.

Immediately after capture I sorted the trawl catch by species. Total length (TL to nearest millimeter), weight (to nearest gram), sex, and maturity determinations were made for each specimen. By cutting at the esophagus and pyloric constriction stomachs were removed from a maximum of 20 specimens (>15 cm TL) of each species (a subsample of the total size range), fixed in 10% Formalin, later preserved in 70% isopropanol, and then, contents were sorted and identified to the lowest possible taxon. Prey items were damp dried on bibulous paper, and the number of individuals and total wet weight (to nearest 0.01 g) of each prey category were recorded. Total weight included shell weight for mollusks, crustaceans, and echinoderms.

I determined the contribution of different prey categories to the diet of a fish species by three methods: 1) the percentage weight of a prey category (pooled) to the weight of the total stomach contents, 2) the percentage abundance of individuals of a prey category to the total number of individual prey in the stomachs, and 3) the percentage frequency of occurrence of the number of stomachs in which a prey category occurred to the total number of stomachs examined. Berg (1979) discussed the limitations of using any single measure to evaluate the importance of a food taxon. Therefore, an index of relative importance, modified from Pinkas et al. (1971), has been calculated since it incorporates all three measures and gives a better assessment of the dietary importance of a prey group. The formula used is as follows: $IRI = (N + W)F$, where N = numerical percentage, W = weight percentage, F = percentage frequency of occurrence, and IRI = index of relative importance. The original formulation proposed by Pinkas et al. (1971) used volumetric percentage instead of percentage weight.

I calculated niche overlap using the formula proposed by Pianka (1973):

$$A_{ij} = \frac{[\Sigma p_{ih} p_{jh}]}{[\Sigma p^2_{ih}\ \Sigma p^2_{jh}]}$$

where A_{ij} is the overlap of species j on species i; p_{ih} is the proportion (percentage weight) of a particular food h ($h = 1\ldots,s$) in the diet of species i; and p_{jh} is the proportion of the same food h in the diet of species j. Values for the overlap index may vary between 0, if no overlap occurs, and 1 for complete overlap. A value >0.3 is significant and ones >0.7 are considered high (Keast 1978).

The division of principal prey among the predators was examined by means of a partition plot. I defined principal prey as those with an IRI >100 because this emphasized the major food sources of each predator. Principal prey accounted for 73.3-94.7% by number of the food items in predator diets. The partition plot facilitates the calculation of the percentage reoccurrence of prey in more than one predator, which is empirically defined as the number of reoccurrences observed divided by the total number of reoccurrences possible in the plot, multiplied by 100 (Tyler 1972). One reoccurrence is defined as the presence of a prey in two

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

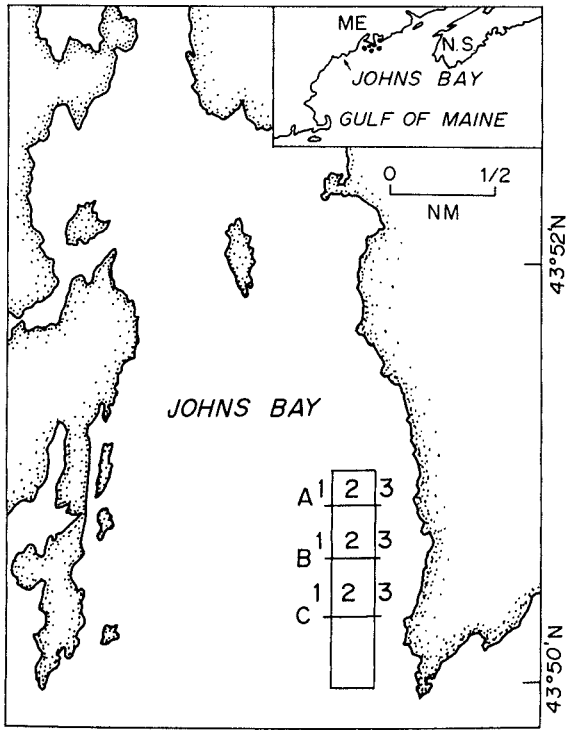

FIGURE 1.—Location of trawling area (closed box) and benthic sampling sites (transects A-C, stations 1-3) in Johns Bay, Maine.

predators. The total number of reoccurrences possible is obtained by the number of predators minus one, multiplied by the number of prey. The percentage reoccurrence of principal prey was calculated a second way by modifying the above procedure and ranking the principal prey in each predator's diet in terms of relative importance (e.g., first = 4 points, second = 3 points, third = 2 points, fourth = 1 point, each additional principal prey = ½ point). In this case, points are totaled for principal prey that are shared by two or more predators, and this value is divided by the total points possible if complete overlap occurred for all principal prey in all predators, the result being multiplied by 100 to give a percentage.

I made length measurements of crustacean prey species for several predators according to the procedure used by Ross (1977). A sample ($N \leq 25$) of each principal prey species was measured for several specimens of each predator. Measurements were made to the nearest millimeter along the axis of greatest dimension. Mouth measurements of fish species were also taken to compare prey size with mouth morphology. Upper jaw length was the distance from the posterior end of the maxillary to the tip of the snout. Mouth width was the distance between the posterior edges of the maxillaries with the mouth fully closed.

I collected benthic samples in September using a ponar grab. A series of three transects was established along the trawl tract (Figure 1). Three stations at different depths were sampled along each transect. Each ponar grab sampled a 0.05 m^2 area. Samples were washed through a 0.5 mm sieve and then fixed in 10% Formalin. I analyzed grab samples in the same manner as the stomach contents.

RESULTS

Abundance of Fishes

Twenty species of fish were collected during the 13-mo sampling period. The most abundant species were the longhorn sculpin, *Myoxocephalus octodecemspinosus*, and the winter flounder, *Pseudopleuronectes americanus*. The fish community showed the greatest diversity and abundance during summer. From January to March the fish fauna was limited and no fish at all were taken in the February sample.

The fish community can be broken down into different temporal components (Tyler 1971). "Regulars" were those species present on nearly every sampling date and included the longhorn sculpin; winter flounder; yellowtail flounder, *Limanda ferruginea*; and the Atlantic cod, *Gadus morhua*. "Summer periodics" were those species found in samples taken during the warmer months: the windowpane, *Scopthalmus aquosus*; ocean pout, *Macrozoarces americanus*; red hake, *Urophycis chuss*; and little skate, *Raja erinacea*. There was no corresponding "winter periodics" group. "Occasionals" were fish that occurred in low numbers at infrequent intervals: the sea raven, *Hemitripterus americanus*; the winter skate, *R. ocellata*; thorny skate, *R. radiata*; American plaice, *Hippoglossoides platessoides*; fourspotted flounder, *Paralichthys oblongus*; witch flounder, *Glyptocephalus cynoglossus*; cunner, *Tautogolabrus adspersus*; silver hake, *Merluccius bilinearis*; white hake, *Urophycis tenuis*; alligatorfish, *Aspidophoroides monopterygius*; moustache sculpin, *Triglops murrayi*; and sand lance, *Ammodytes* sp.

Foods

I examined the foods of the eight most abundant species (longhorn sculpin, winter flounder, windowpane, yellowtail flounder, ocean pout, little skate, Atlantic cod, and red hake). The diet for each species for the entire sampling period is summarized in Tables 1-8.

Longhorn Sculpin

Sixty-three prey taxa were identified in the 299 longhorn sculpin stomachs. Crustaceans were the most important prey group, making up 58.4% of the diet by weight and 95.8% of the diet by number (Table 1). Amphipods were most heavily preyed upon, especially *Unciola* sp. and *Leptocheirus pinguis*, which had the two highest indices of relative importance. Decapods were next in importance, with the sand shrimp, *Crangon septemspinosa*, and rock crab, *Cancer irroratus*, constituting 18.2% of the diet by weight. Mysids, principally *Mysis mixta*, were also significant food items. Pisces were the second major prey group and made up 25.2% of the diet by weight. Larval Atlantic herring, *Clupea harengus harengus*, were important fish prey. Other phyla (Porifera, Polychaeta, Mollusca) formed a minor portion of the diet.

TABLE 1.—Stomach contents of 299 longhorn sculpins ranging from 15.8 to 32.2 cm TL (mean 21.1 ± 3.4 cm) and 21 to 380 g (mean 101 ± 52 g). Twenty-four stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Porifera total	0.00	0.02	0.33	0
Polychaeta total	2.92	1.08	19.40	78
Mollusca total	.34	.61	7.69	7
Crustacea total	58.42	95.84	88.63	13,672
Mysidacea total	3.55	10.26	29.10	402
Neomysis americana	1.23	4.11	7.69	41
Mysis mixta	1.79	4.80	14.72	97
Other Mysidacea	.53	1.35		
Cumacea total	.04	.32	4.01	1
Isopoda total	1.50	2.55	13.38	54
Edotea montosa	.17	1.96	8.70	19
Cirolana sp.	1.33	.59	5.35	10
Amphipoda total	25.66	78.94	82.61	8,641
Unciola sp.	10.58	46.64	64.55	3,694
Leptocheirus pinguis	10.21	16.94	40.47	1,099
Aeginella longicornis	1.12	6.22	25.08	184
Erichthonius rubricornis	.20	3.09	14.72	48
Hippomedon serratus	.30	1.32	8.36	14
Monoculodes sp.	.13	.95	10.70	12
Other Amphipoda	3.12	3.78		
Decapoda total	27.67	3.77	30.77	967
Crangon septemspinosa	10.05	2.06	14.72	178
Cancer irroratus	8.15	.71	6.69	59
Other Decapoda	9.47	1.00		
Pisces total	25.19	2.45	18.39	508
Clupea h. harengus	11.04	2.01	10.03	131
Other Pisces	14.15	.44		
Remains	11.16			
Detritus	1.97			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

TABLE 2.—Stomach contents of 201 winter flounder ranging from 15.2 to 42.6 cm (mean 24.0 ± 6.0 cm) and 29 to 1,120 g (mean 209 ± 187 g). Fifty-seven stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Nemertea total	0.16	0.05	0.50	0
Algae total	12.67	0	2.49	32
Polychaeta total	18.26	8.11	53.73	1,417
Phyllodoce sp.	.28	2.19	20.90	52
Melinna cristata	2.16	2.19	4.48	19
Maldanidae	.69	.80	9.95	15
Lumbrineris fragilis	2.79	.53	6.97	23
Pherusa affinis	5.03	.42	5.47	30
Other Polychaeta	7.31	1.98		
Mollusca total	6.09	3.13	24.88	229
Bivalvia total	5.13	2.60	22.89	177
Cerastoderma pinnulatum	4.21	1.87	17.91	109
Other Bivalvia	.92	.73		
Gastropoda total	.96	.53	3.98	6
Crustacea total	32.50	86.72	70.65	8,422
Cumacea total	1.02	3.99	27.36	137
Diastylis quadrispinosa	.50	1.87	14.43	34
Other Cumacea	.52	2.12		
Isopoda total	.20	.58	6.97	5
Edotea montosa	.15	.47	5.97	4
Other Isopoda	.05	.11		
Amphipoda total	25.74	81.96	69.65	7,502
Ampelisca agassizi	.49	7.09	9.45	72
Leptocheirus pinguis	9.18	16.24	32.34	822
Corophium sp.	.11	1.77	10.95	21
Erichthonius rubricornis	.01	1.37	13.44	17
Unciola sp.	10.17	44.30	56.22	3,062
Pontogeneia inermis	.29	.76	4.98	5
Aeginella longicornis	2.86	6.94	16.92	166
Other Amphipoda	2.63	3.49		
Decapoda total	5.53	.18	3.98	23
Echinodermata total	.50	1.98	24.38	62
Ophiuroidea total	.39	1.87		52
Amphipholis squamata	.16	.92	11.94	13
Other Ophiuroidea	.23	.95		
Asteroidea total	0	.03	.50	0
Echinoidea total	.11	.08	1.49	0
Remains	15.03			
Detritus	14.81			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Winter Flounder

Sixty-six prey taxa were identified from the 201 winter flounder stomachs. Crustaceans were the major prey group for the winter flounder (Table 2). Amphipods accounted for the largest percentage of the diet by weight (25.7%). *Unciola* sp., *Leptocheirus pinguis*, and *Aeginella longicornis* were the principal amphipods consumed. Cumaceans, isopods, and decapods were of minor importance. After crustaceans, polychaetes were the next major prey group, making up 18.3% of the diet by weight. Polychaete identification was often difficult due to partial digestion or incomplete animals and this obscured the importance of some species. *Melinna cristata, Lumbrineris fragilis, Pherusa affinis*, and *Phyllodoce* sp. were the principal polychaetes consumed. Mollusks were of little importance, but one species, the bivalve *Cerastoderma pinnulatum*, was preyed on significantly and constituted 4.2% of the diet by weight. Algae made up 12.7% of the diet. Echinoderms accounted for only a small fraction of the stomach contents.

Windowpane

The windowpane had a specialized diet and only seven prey taxa were found in the 37 stomachs. Crustaceans were by far the most important prey group, constituting 79.3% of the diet by weight and 99.0% of the diet by number (Table 3). Mysids, principally *Mysis mixta*, were the main component of the crustacean prey. *Mysis mixta* accounted for 72.4% of the diet by weight. Pisces, namely *Clupea h. harengus*, were secondary in importance and made up 20.3% of the diet by weight. Polychaetes composed a negligible portion of the diet.

Yellowtail Flounder

The 60 yellowtail flounder stomachs analyzed contained 39 prey taxa. Crustacea accounted for

TABLE 3.—Stomach contents of 37 windowpane ranging from 21.0 to 33.6 cm (mean 27.3±3.3 cm) and 90 to 482 g (mean 244±90 g). Eight stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Polychaeta total	0.13	0.06	2.70	1
Crustacea total	79.27	98.99	75.68	13,490
Mysidacea total	78.78	98.74	75.68	13,434
Neomysis americana	1.16	2.46	8.11	29
Mysis mixta	72.41	94.65	59.46	9,933
Other Mysidacea	5.21	1.63		
Amphipoda total	.26	.19	8.11	4
Decapod total	.23	.06	2.70	1
Pisces *Clupea h. harengus*	20.25	0.94	2.70	57
Remains	0.36			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

almost half the diet by weight (48.5%) and almost the entire diet by number (95.1%) (Table 4). Amphipods were the most important crustaceans consumed, followed by mysids, cumaceans, and decapods. *Unciola* sp. was the principal amphipod prey, making up 28.7% of the diet by weight and 82.0% of the diet by number. The amphipod *Leptocheirus pinguis* and mysid *Mysis mixta* were also important. After crustacea, polychaetes (10.2% of the diet by weight) and mollusks (5.2% of the diet by weight) were the next largest dietary components. The bivalve *Cerastoderma pinnulatum* was a significant prey item. Other prey groups (Nemertea, Echinodermata, Pisces) were of minor importance.

TABLE 4.—Stomach contents of 60 yellowtail flounder ranging from 19.0 to 42.0 cm (mean 30.9±7.2 cm) and 42-670 g (mean 280±174 g). Fourteen stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Nemertea total	3.50	0.00	1.67	6
Polychaeta total	10.15	2.38	35.00	438
Phyllodoce sp.	.32	.40	10.00	7
Nephtys sp.	2.64	.04	3.33	9
Glycera sp.	.23	.18	5.00	2
Maldanidae	.87	.44	11.67	15
Other Polychaeta	6.09	1.32		
Mollusca total	5.19	2.33	36.67	276
Bivalvia total	5.19	2.29	36.67	274
Nucula proxima	1.46	.63	5.00	10
Cerastoderma pinnulatum	3.41	1.44	26.67	129
Other Bivalvia	.32	0.22		
Gastropoda total	0	.04	1.67	0
Crustacea total	48.50	95.07	68.33	9,810
Cumacea total	.45	1.57	21.67	44
Diastylis quadrispinosa	.23	.36	8.33	5
Other Cumacea	.22	1.21		
Amphipoda total	33.58	85.78	63.33	7,559
Leptocheirus pinguis	1.73	.99	25.00	68
Unciola sp.	28.66	82.01	53.33	5,903
Hippomedon serratus	.27	.49	11.67	9
Monoculodes sp.	.41	.72	13.33	15
Other Amphipoda	2.51	1.57		
Mysidacea total	12.51	7.27	3.33	66
Mysis mixta	12.19	7.18	3.33	65
Other Mysidacea	.32	.09		
Decapoda *Crangon septemspinosa*	1.59	.13	5.00	9
Isopoda total	.37	.32	8.33	6
Echinodermata total	.05	.13	6.67	1
Pisces total	.05	.04	1.67	0
Remains	16.38			
Detritus	16.20			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Ocean Pout

Twenty-seven prey taxa were found in the 46 ocean pout stomachs. A comparison of the relative contributions of echinoderms and crustaceans to the diet showed that echinoderms were the most important prey group in terms of percent weight (20.6% vs. 13.7%), while crustaceans had a greater *IRI* (7,382 vs. 974) (Table 5). Amphipods and, to a lesser extent, cumaceans were the principal crustacean orders present in the ocean pout diet. The amphipods *Unciola* sp. and *Leptocheirus pinguis* and the cumacean *Diastylis quadrispinosa* were significant prey. Principal echinoderm prey were the sea urchin, *Strongylocentrotus droebachiensis*; the sand dollar, *Echinarachnius parma*; and

TABLE 5.—Stomach contents of 46 ocean pout ranging from 18.2 to 49.0 cm (mean 34.3±5.9 cm) and 24 to 660 g (mean 214±11.8 g). Five stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Polychaeta total	1.41	0.27	19.57	33
Mollusca total	9.78	12.11	45.65	999
Gastropoda total	.21	.45	13.04	9
Bivalvia total	9.57	11.66	39.13	831
Placopecten magellanicus	4.57	.81	4.35	23
Cerastoderma pinnulatum	3.85	4.88	21.74	190
Mya arenaria	.91	5.33	8.70	54
Other Bivalvia	.24	.64		
Crustacea total	13.65	83.37	76.09	7,382
Mysidacea total	.14	.27	4.35	2
Cumacea total	2.12	18.78	41.30	863
Diastylis quadrispinosa	1.86	15.90	26.09	463
Other Cumacea	.26	2.88		
Isopoda *Edotea montosa*	.02	.36	6.52	2
Amphipoda total	10.29	63.32	71.74	5,281
Leptocheirus pinguis	1.15	2.71	17.39	67
Unciola sp,	8.00	57.99	58.70	3,874
Pontogenia inermis	.09	.91	6.52	7
Aeginella longicornis	.07	.54	6.52	4
Other Amphipoda	.98	1.17		
Decapoda total	1.08	.64	10.87	19
Echinodermata total	20.63	4.25	39.13	974
Echinoidea total	19.81	1.35	23.91	506
Strongylocentrotus drobachiensus	1.78	.99	15.22	42
Echinarachnius parma	18.03	.36	10.87	200
Ophiuroidea total	.82	2.90	26.09	97
Amphipholis squamata	.40	2.18	15.22	39
Other Ophiuroidea	.42	.72		
Detritus	47.55			
Remains	6.99			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

the brittle star, *Amphipholis squamata*. Mollusca constituted 9.8% of the diet by weight. The sea scallop, *Placopecten magellanicus*; the soft-shell clam, *Mya arenaria*; and the cockle, *Cerastoderma pinnulatum*, were noteworthy. Polychaetes formed a small portion of the diet. A large amount of bottom sediment and organic material was found in the stomachs examined.

Little Skate

Thirty-one prey taxa were found in the 33 little skate stomachs. The little skate fed primarily on crustaceans (Table 6). The decapods were the most important group, making up 50.7% of the diet by weight. *Crangon septemspinosa* and *Cancer irroratus* were principal prey species. Amphipods were next in importance with *L. pinguis, Unciola* sp., and *Monoculodes* sp. as significant prey items. The remaining crustacean groups did not constitute a substantial part of the diet. Polychaetes were the next major prey group, accounting for 10.1% of the diet by weight. Porifera, Nematoda, and Pisces were of minor importance.

TABLE 6.—Stomach contents of 33 little skates ranging from 25.6 to 55.2 cm (mean 39.6 ± 10.1 cm) and 71 to 1,194 g (mean 496 ± 346 g). There were no empty stomachs. *IRI* = index of relative importance (see text).

Taxon	Percentage			*IRI*
	Weight	Number	Frequency[1]	
Porifera total	0.15	0.00	3.03	0
Nematoda total	.08	4.17	15.15	64
Polychaeta total	10.14	.17	36.36	375
Crustacea total	66.89	94.78	96.97	15,677
Mysidacea total	.19	1.22		
Mysis mixta	.13	.70	6.06	5
Other Mysidacea	.06	.52		
Cumacea total	.08	1.22	15.15	20
Amphipoda total	15.80	70.78	84.85	7,347
Ampelisca agassizi	.06	1.04	9.09	10
Leptocheirus pinguis	5.01	24.17	66.67	1,946
Unciola sp.	1.37	12.52	51.52	716
Pontogenia inermis	.08	1.57	12.12	20
Anonyx sarsi	2.38	3.13	9.09	50
Monoculodes sp.	2.42	24.52	57.58	1,551
Other Amphipoda	4.48	3.83		
Decapoda total	50.71	21.39	78.79	5,680
Crangon septemspinosa	18.51	9.22	57.58	1,596
Cancer irroratus	22.68	9.39	36.36	1,166
Other Decapoda	9.52	2.78		
Isopoda total	.11	.17	3.03	1
Pisces total	.67	.87	15.15	23
Detritus	1.60			
Remains	20.47			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Atlantic Cod

The 75 Atlantic cod stomachs contained a total of 30 prey taxa. Crustaceans were the major prey group, accounting for 40.3% of the diet by weight and 98.5% of the diet by number (Table 7). Amphipods, especially *Unciola* sp. and *L. pinguis*, were most heavily preyed upon. The decapods made up 18.2% of the diet by weight, with *Crangon septemspinosa* and *Cancer irroratus* as principal prey. The mysids, notably *Mysis mixta*, were next in importance. Cumaceans and isopods made up a negligible portion of the diet. Pisces were the next major group and constituted 14.6% of the diet by weight. Other phyla (Nematoda, Polychaeta, Mollusca, and Echinodermata) were of little importance. A large amount of unidentifiable remains (40.9% of the diet by weight) was found in the stomachs examined.

TABLE 7.—Stomach contents of 75 Atlantic cod ranging from 15.0 to 53.6 cm (mean 22.5 ± 5.5 cm) and 27 to 1,555 g (mean 128 ± 195 g). Ten stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			*IRI*
	Weight	Number	Frequency[1]	
Nematoda total	0.00	0.35	4.00	1
Polychaeta total	1.06	.35	12.00	17
Mollusca total	.02	.43	1.33	1
Crustacea total	40.27	98.45	84.00	11,652
Mysidacea total	4.00	8.46	38.67	481
Mysis mixta	2.45	7.42	25.33	250
Other Mysidacea	1.55	1.04		
Cumacea total	.07	1.04	5.33	6
Isopoda total	1.01	.43	5.33	8
Cirolana polita	1.01	.35	4.00	5
Other Isopoda	.00	.08		
Amphipoda total	16.98	85.85	72.00	7,404
Ampelisca agassizi	.51	10.01	2.67	28
Leptocheirus pinguis	2.44	3.80	21.33	133
Unciola sp.	11.16	66.01	58.67	4,528
Pontogenia inermis	.12	1.21	10.67	14
Hippomedon serratus	.45	1.55	12.00	24
Aeginella longicornis	.05	.69	6.67	5
Other Amphipoda	2.25	2.58		
Decapoda total	18.21	2.67	24.00	501
Crangon septemspinosa	9.06	1.55	13.33	141
Cancer irroratus	6.07	.26	4.00	25
Other Decapoda	3.08	.86		
Echinodermata total	1.94	.17	1.33	3
Pisces total	14.61	.26	5.33	79
Detritus	1.17			
Remains	40.94			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Red Hake

Twenty-four prey taxa were found in the 30 red hake stomachs. The red hake fed principally upon crustaceans, and this group accounted for 72.4% of the diet by weight (Table 8). Amphipods were the most important order with *L. pinguis, Unciola* sp., and *Ampelisca agassizi* as significant prey items. Decapods were also heavily preyed upon and

Crangon septemspinosa was a principal prey species. Mysids, cumaceans, and isopods were of minor importance. Other groups (Algae, Porifera, Polychaeta, Mollusca) constituted a small portion of the diet.

TABLE 8.—Stomach contents of 30 red hake ranging from 15.0 to 40.1 cm (mean 25.6 ± 6.1 cm) and 22 to 392 g (mean 121 ± 86 g). Three stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Algae total	1.60	0.00	3.33	5
Porifera total	.16	0.00	3.33	1
Polychaeta total	3.35	.63	20.00	80
Crustacea total	72.36	99.36	86.67	14,884
Mysidacea total	.24	.31	3.33	2
Cumacea total	.16	2.19	13.33	31
Isopoda total	3.19	.94	10.00	41
Cirolana polita	2.96	.63	6.67	24
Other Isopoda	.23	.31		
Amphipoda total	31.87	87.46	80.00	9,546
Ampelisca agassizi	2.48	28.53	10.00	310
Leptocheirus pinguis	13.98	26.65	50.00	2,031
Unciola sp.	6.71	21.94	60.00	1,719
Hippomedon serratus	1.44	4.08	13.33	74
Aeginella longicornis	.32	2.19	16.67	42
Other Amphipoda	6.94	4.07		
Decapoda total	36.90	8.46	40.00	1,815
Crangon septemspinosa	28.67	7.21	26.67	957
Other Decapoda	8.23	1.25		
Mollusca total	.16	0.00	3.33	1
Detritus	.88			
Remains	21.49			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Dietary Overlap

The fish community in Johns Bay showed a considerable degree of food overlap (Table 9). Eight species-pairs had overlap values >0.50. This is a reflection of the dominance of crustaceans in the diets of the predators examined. The greatest dietary overlap occurred between the Atlantic cod and longhorn sculpin. In addition, high dietary overlaps occurred among the Atlantic cod, red hake, longhorn sculpin, little skate, winter flounder, and yellowtail flounder, a consequence of the dependence of these predators on amphipod and decapod prey.

Although over 100 prey taxa were found during the study, only 13 were classified as principal prey. In the partition plot predators that share principal prey are generally arranged adjacent to one another (Table 10). Difficulty in identifying digested organisms necessitated using the broad classification of Polychaeta in this partition plot. Generally, predators consumed 4 or 5 principal prey, and the percentage reoccurrence of principal

TABLE 9.—A summary of the predator feeding habits and food overlap in fishes from Johns Bay, Maine. Species pairs with overlaps 0.50 or greater are in italics.

Predator number	Predator species	Feeding habits	Predator species						
			2	3	4	5	6	7	8
1	Longhorn sculpin	Crustaceans and fish	*0.74*	*0.59*	*0.63*	0.43	0.43	0.19	0.18
2	Atlantic cod	Crustaceans and fish		*.57*	*.62*	*.60*	.34	.05	.13
3	Little skate	Crustaceans, particularly decapods			*.68*	.13	.19	.05	.01
4	Red hake	Crustaceans				.27	.36	.11	.01
5	Yellowtail flounder	Crustaceans and polychaetes					*.51*	.38	.36
6	Winter flounder	Crustaceans and polychaetes						.27	.01
7	Ocean pout	Mollusks, echinoderms, and crustaceans							.01
8	Windowpane	Specialist on mysids							

TABLE 10.—Partition plot of principal prey for demersal fishes in Johns Bay, Maine. Numbers listed are index of relative importance values for principal prey. Prey classifiction: (I) Infaunal, (E) Epifaunal, (N) Nektonic.

Prey	Longhorn sculpin	Atlantic cod	Red hake	Little skate	Winter flounder	Yellowtail flounder	Ocean pout	Windowpane
Unciola (I)	[1]3,694	[1]4,528	1,719	716	[1]3,062	[1]5,903	[1]3,874	—
Leptocheirus (I)	1,099	133	[1]2,031	[1]1,946	822	—	—	—
Crangon (E)	178	141	957	1,596	—	—	—	—
Polychaeta (I)	—	—	—	375	1,417	438	—	—
Cerastoderma (I)	—	—	—	—	109	129	190	—
Aeginella (E)	184	—	—	—	166	—	—	—
Mysis (N)	—	250	—	—	—	—	—	[1]9,933
Monoculodes (I)	—	—	—	1,551	—	—	—	—
Ampelisca (I)	—	—	310	—	—	—	—	—
Diastylis (I)	—	—	—	—	—	—	463	—
Cancer (E)	—	—	—	1,166	—	—	—	—
Echinarachnius (E)	—	—	—	—	—	—	200	—
Clupea (N)	131	—	—	—	—	—	—	—

[1]Indicates most important principal prey of prey of predator.

prey in more than one predator was 20% (19/96) by Tyler's (1972) method and 57% (65.5/116) by the ranked principal prey method.

Prey Size and Predator Mouth Morphology

Resource partitioning by prey size was examined for several predators by means of length-frequency distributions of crustacean prey. Crustaceans were analyzed because of their importance as a food group and because their hard external skeletons permitted reliable measurements.

A comparison of three flounder species showed that the winter flounder consumed the smallest prey (Figure 2). The majority of the winter flounder prey ranged between 4 and 10 mm long ($\overline{X} \pm 95\%$ CL = 6.8 ± 0.6). The yellowtail flounder prey lengths were bimodally distributed. In one group most prey ranged between 5 and 10 mm, while in the second they were between 14 and 17 mm ($\overline{X} \pm 95\%$ CL = 10.8 ± 1.3). The windowpane utilized the largest prey, with most ranging between 13 and 17 mm ($\overline{X} \pm 95\%$ CL = 14.4 ± 0.7).

The longhorn sculpin and Atlantic cod, were two other important crustacean predators examined. Longhorn sculpin prey showed a wide range in size (1-30 mm) (Figure 3). The largest proportion of longhorn sculpin prey was between 5 and 15 mm long ($\overline{X} \pm 95\%$ CL = 11.1 ± 0.7). The distribution of cod prey sizes was similar to that of the longhorn sculpin. Most of the cod prey were between 4 and 13 mm long ($\overline{X} \pm 95\%$ CL = 9.0 ± 0.7).

Data on mouth measurements are presented in Table 11. The basic mouth shape is given as the ratio of the mean mouth width to mean upper jaw

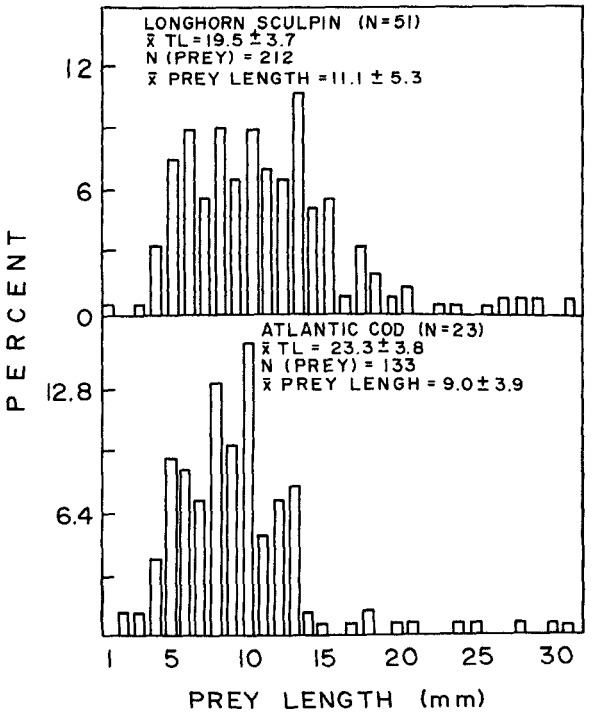

FIGURE 2.—Prey size distributions for winter flounder, yellowtail flounder, and windowpane.

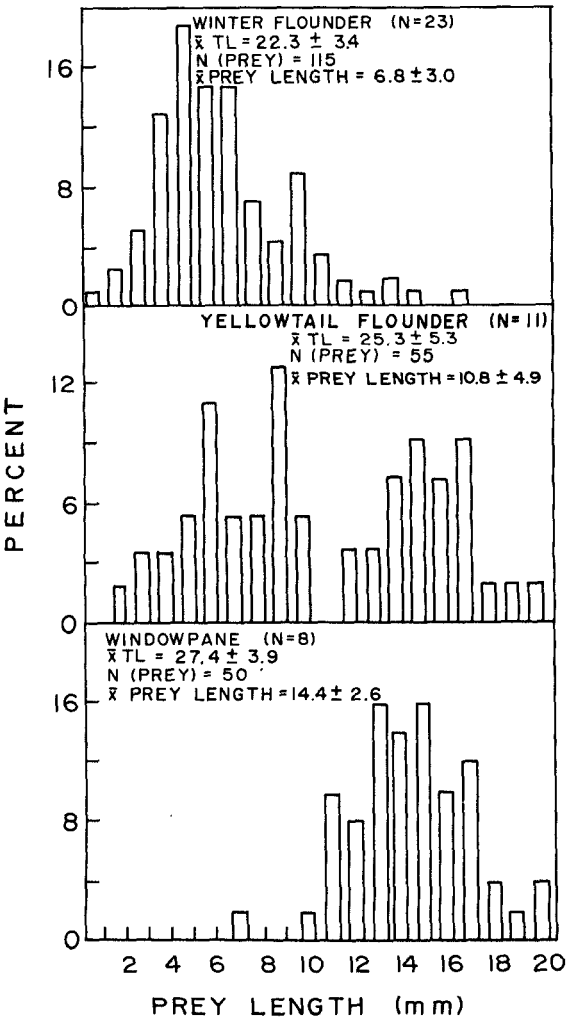

FIGURE 3.—Prey size distributions for longhorn sculpin and Atlantic cod.

TABLE 11.—Mouth dimensions of fish species.

Species	N	TL (cm) $\bar{X}\pm$SD	Upper jaw length (% TL) $\bar{X}\pm$SD	Mouth width (% TL) $\bar{X}\pm$SD	$\bar{X}$ mouth width ÷ $\bar{X}$ upper jaw length
Winter flounder	30	25.5±5.3	4.9±0.32	4.3±0.38	0.87
Yellowtail flounder	6	30.7±8.2	5.0± .39	3.8± .47	.76
Windowpane	17	24.7±4.5	9.2± .44	4.0± .80	.43
Longhorn sculpin	19	22.1±3.3	15.1± .69	16.9±1.67	1.12
Atlantic cod	3	24.5±3.1	11.7± .75	10.5± .62	1.11

length. The flounders had different ratios (windowpane 0.43, yellowtail flounder 0.76, winter flounder 0.87). The longhorn sculpin (1.12) and the Atlantic cod (1.11) had similar mouth shapes.

Benthos Analysis

A summary of the species composition by numbers and weights for the benthic samples is given in Tables 12 and 13. The sediment at stations A-1, A-2, B-1, and C-1 was silty sand, and remaining stations were sand. A total of 55 species were identified. The polychaetes were the dominant group and constituted 51.4% (by number) of the organisms present. Crustaceans (34.1%) and mollusks (12.8%) were next in abundance. The remaining groups (sipunculids(?), nematodes, echinoderms) accounted for only 1.7% of the total number of individuals. The most abundant species were the polychaetes *Prionospio steenstrupi, Exogone hebes, Tharyx acutus, Lumbrineris fragilis*; the crustaceans *Unciola* sp. and *Ampelisca agassizi*; and the mollusk *Nucula proxima*. In terms of biomass (percentage wet weight) mollusks (41.2%) were the most important group followed by polychaetes (41.0%) and crustaceans (8.8%). The biomass was dominated by the mollusk *N. proxima* (34.6%) and to a lesser extent by the polychaetes *L. fragilis, Sternaspis scutata*, and *P. steenstrupi*, and the crustaceans *A. agassizi* and *Unciola* sp.

DISCUSSION

Recent studies of temperate, coastal marine fish communities have suggested that there is considerable division of food resources among predators (Tyler 1972; Kislalioglu and Gibson 1977). Tyler (1972) examined the food utilization among demersal fishes in Passamaquoddy Bay, New Brunswick, and found relatively little overlap among diets based on the percentage reoccurrence of principal prey among predators (16% summer community; 24% winter community). In Johns Bay the percentage reoccurrence of principal prey among demersal fishes was 20% which is within the range (10-24%) that Tyler calculated for other marine communities. However, assessing dietary overlap by means of the method proposed by Tyler may be misleading because all principal prey are weighted equally in the calculation (see Methods). For example, although the percentage reoccurrence of principal prey of the fishes in Johns Bay suggests considerable resource division, a closer examination of the data reveals that seven of the eight predators rely primarily on two prey types, *Unciola* and *Leptocheirus* (Table 10). If the principal prey items in each predator's diet are weighted in terms of relative importance a more accurate evaluation of dietary overlap may be determined from the partition plot. For the demersal fishes in Johns Bay the percentage reoccurrence of ranked principal prey is 57%, which indicates that predators rely on many of the same major food sources. This conclusion is supported by the food overlap values that were obtained using Pianka's (1973) formula (Table 9).

There is insufficient information provided in Tyler's (1972) paper to evaluate the relative importance of his principal prey; however, a study by Kislalioglu and Gibson (1977) provided another source of data. These authors calculated a 14.7% reoccurrence of principal prey for shallow-water fishes from three habitats in Loch Etive, western Scotland. Food resource partitioning, however, is not as dramatic as this value would indicate because of the inclusion of five pelagic fishes in the calculation. Moreover, almost all the demersal species (13 out of 15) in Loch Etive were primarily dependent on amphipods as their most important food source (based on a points method of stomach content analysis), and among these fishes 25.7% had significant dietary overlap in terms of the proportion of different amphipod species utilized. If the percentage reoccurrence of principal prey is recalculated using weighted principal prey, the result is 56%.[5] Trophic similarity is especially evident for the fishes from the open sand-shell mud habitat (which corresponds to the habitat examined in Johns Bay) where there was significant overlap in amphipod species consumed between four of the five species examined. In Loch

[5]Resource division is not strictly comparable to Johns Bay because of the differing degrees of principal prey subdivision which may affect the result of the calculation.

TABLE 12.—Summary of the numbers of live invertebrates identified in nine benthic samples (0.05 m^2) taken from Johns Bay, Maine, in September 1978 (N = number; % = percent number). See Figure 1 for locations of transects.

Taxon	Station A-1	Station A-2	Station A-3	Station B-1	Station B-2	Station B-3	Station C-1	Station C-2	Station C-3	Total N	Total %
Mollusca:											
Nucula proxima	16	7	36	9	72	—	68	—	—	208	9.85
Mya arenaria	3	9	2	1	7	1	—	—	—	23	1.09
Cerastoderma pinnulatum	—	—	—	—	3	1	—	2	3	9	.43
Thyasira gouldi	—	—	5	1	2	—	—	—	—	8	.38
Crenella grandula	—	—	4	—	4	—	—	—	—	8	.38
Astarte undata	—	—	1	—	4	—	—	—	—	5	.24
Margarites sp.	—	—	—	—	—	—	—	—	2	2	.09
Nuculana tenuisculcata	—	1	—	—	—	—	—	—	—	1	.04
Yoldia sp.	—	—	—	1	—	—	—	—	—	1	.04
Unidentified bivalves	1	3	—	1	1	—	—	—	—	6	.28
									Total	271	12.82
Crustacea:											
Unciola sp.	—	—	—	—	—	114	2	72	190	378	17.90
Ampelisca agassizi	—	3	259	—	37	—	—	—	—	299	14.16
Aeginella longicornis	—	—	1	1	2	1	—	—	—	5	.24
Hippomedon propinquus	—	—	3	—	—	—	1	—	1	5	.24
Monoculodes sp.	—	—	—	1	1	1	—	—	—	3	.14
Petalosarsia declivis	—	—	—	—	—	—	—	1	2	3	.14
Edotea montosa	—	—	—	1	—	1	—	—	—	2	.09
Hippomedon sp.	—	1	—	—	1	—	—	—	—	2	.09
Harpinia propinqua	—	—	2	—	—	—	—	—	—	2	.09
Anonyx liljeborgi	—	—	2	—	—	—	—	—	—	2	.09
Eudorella sp.	—	—	—	1	—	—	—	—	1	2	.09
Corophium sp.	—	—	—	—	—	1	—	—	1	2	.09
Protomedeia fasciata	—	—	—	—	—	1	—	—	1	2	.09
Ampelisca macrocephala	—	—	—	—	—	—	1	1	—	2	.09
Erichthonius rubricornis	—	—	—	—	—	—	—	1	—	1	.05
Diastylis sp.	—	1	—	—	—	—	—	—	—	1	.05
D. sculpta	—	—	—	—	—	—	—	1	—	1	.05
D. quadrispinosa	—	—	1	—	—	—	—	—	—	1	.05
Leptocheirus pinguis	—	—	—	—	—	1	—	—	—	1	.05
Cyathura polita	—	—	—	—	—	—	—	—	1	1	.05
Unidentified amphipods	—	—	—	—	—	4	2	—	—	6	.28
									Total	721	34.12
Polychaeta:											
Prionospio steenstrupi	1	—	19	5	458	—	30	—	—	513	24.29
Exogone hebes	—	—	—	—	1	64	—	8	78	151	7.15
Tharyx acutus	—	14	6	7	9	12	5	2	12	67	3.17
Lumbrineris fragilis	12	16	8	3	18	—	7	—	—	64	3.03
Aricidea catherinae	14	11	—	7	—	4	2	1	16	55	2.60
Clymenella torquata	—	—	1	—	4	19	1	—	23	48	2.27
Phyllodoce mucosa	3	5	—	4	9	2	—	—	4	27	1.28
Scoloplos sp.	7	1	2	11	—	—	3	—	—	24	1.14
Ammotrypane aulogaster	—	1	5	—	15	—	—	—	—	21	.99
Scolecolepides viridis	18	—	—	—	—	—	—	—	—	18	.85
Nephtys sp.	—	3	—	—	3	—	3	4	—	13	.62
N. incisa	1	1	2	4	2	—	1	—	1	12	.57
Scalibregma inflatum	—	1	1	1	3	—	3	—	—	9	.43
Flabelligeridae	2	—	—	1	—	1	2	1	—	7	.33
Amphitrite affinis	—	—	—	—	—	3	—	—	3	6	.28
Nereis virens	—	—	—	1	4	—	—	—	—	5	.24
Phyllodoce sp.	—	—	4	—	—	—	—	—	—	4	.19
Melinna cristata	—	—	2	—	—	—	2	—	—	4	.19
Polynoidae	—	2	—	—	2	—	—	—	—	4	.19
Maldanidae	—	—	—	—	4	—	—	—	—	4	.19
Terebellides stroemi	—	—	1	—	—	—	—	—	—	1	.05
Phyllodoce maculata	—	—	—	—	1	—	—	—	—	1	.05
Sabellidae	—	—	—	—	—	1	—	—	—	1	.05
Pherusa affinis	—	—	—	—	—	—	—	—	1	1	.05
Nereis sp.	—	—	—	—	—	—	—	—	1	1	.05
Paraonis sp.	—	—	—	—	—	—	—	—	1	1	.05
Spiophanes bombyx	—	—	—	—	—	—	—	—	1	1	.05
Ampharete acutifrons	—	—	—	—	—	—	1	—	—	1	.05
Sternaspis scutata	1	5	2	2	5	—	3	2	—	20	.95
									Total	1,084	51.35
Sipuncula(?)	11	—	3	—	—	—	—	—	2	16	.76
Nematoda	—	—	—	—	—	6	—	—	11	17	.80
Echinodermata											
Amphipholis squamata	—	—	—	—	—	1	—	—	—	1	.05
Echinarachnius parma	—	—	—	—	—	—	—	—	1	1	.05
									Total	2	.10
									Grand total	2,111	99.95

TABLE 13.—Summary of the weights of live invertebrates identified in nine benthic samples ($0.05m^2$) taken from Johns Bay, Maine in September 1978 (Wt = weight in grams; % = percent weight; tr = <0.01 gram) See Figure 1 for location of transects.

Taxon	Station A-1	A-2	A-3	Station B-1	B-2	B-3	Station C-1	C-2	C-3	Total Wt	%
Mollusca:											
Nucula proxima	0.30	0.12	0.54	0.19	1.49	—	1.92	—	—	4.56	34.60
Mya arenaria	.03	.08	.02	.01	.14	tr	—	—	—	.28	2.12
Margarites sp.	—	—	—	—	—	—	—	—	0.14	.14	1.06
Thyasira gouldi	—	—	.03	.01	.02	—	—	—	—	.06	.46
Astarte undata	—	—	.01	—	.05	—	—	—	—	.06	.46
Crenella glandula	—	—	.02	—	.03	—	—	—	—	.05	.38
Yoldia sp.	—	—	—	.05	—	—	—	—	—	.05	.38
Nuculana tenuisculcata	—	.02	—	—	—	—	—	—	—	.02	.15
Cerastoderma pinnulatum	—	—	—	—	.03	tr	—	0.04	.04	.11	.83
Unidentified bivalves	.01	.07	—	tr	.02	—	—	—	—	.10	.76
									Total	5.43	41.20
Crustacea:											
Ampelisca agassizi	—	.01	.48	—	.05	—	—	—	—	.54	4.10
Unciola sp.	—	—	—	—	—	0.13	tr	.07	.26	.46	3.49
Monoculodes sp.	—	—	—	.01	.01	.01	—	—	—	.03	.23
Hippomedon sp.	—	.01	—	—	.02	—	—	—	tr	.03	.23
Ampelisca macrocephala	—	—	—	—	—	—	tr	.02	—	.02	.15
Hippomedon propinquus	—	—	.02	—	—	—	—	—	—	.02	.15
Leptocheirus pinguis	—	—	—	—	—	.01	—	—	—	.01	.08
Edotea montosa	—	—	—	.01	—	tr	—	—	—	.01	.08
Aeginella longicornis	—	—	tr	tr	tr	tr	—	—	—	tr	—
Erichthonius rubricornis	—	—	—	—	—	—	—	tr	—	tr	—
Harpinia propinqua	—	—	tr	—	—	—	—	—	—	tr	—
Corophium sp.	—	—	—	—	—	tr	—	—	tr	tr	—
Anonyx liljeborgi	—	—	tr	—	—	—	—	—	—	tr	—
Protomedeia fasciata	—	—	—	—	—	tr	—	—	tr	tr	—
Diastylis sp.	—	tr	—	—	—	—	—	—	—	tr	—
D. sculpta	—	—	tr	—	—	—	—	tr	—	tr	—
D. quadrispinosa	—	—	tr	—	—	—	—	—	—	tr	—
Eudorella sp.	—	—	—	tr	—	—	—	—	tr	tr	—
Petalosarsia declivis	—	—	—	—	—	—	—	tr	tr	tr	—
Cyathura polita	—	—	—	—	—	—	—	—	tr	tr	—
Unidentified amphipods	—	—	—	—	—	.03	.01	—	—	.04	.30
									Total	1.16	8.81
Polychaeta:											
Lumbrineris fragilis	.02	.12	.40	.02	.49	—	.11	—	—	1.16	8.80
Sternaspis scutata	.01	.11	.05	—	.22	—	.25	—	—	.64	4.86
Prionospio steenstrupi	tr	—	.01	tr	.48	—	.03	—	—	.52	3.95
Nephtys sp.	—	.01	—	.02	.04	—	.01	.24	.03	.35	2.66
Clymenella torquata	—	—	.03	—	.01	.11	tr	—	.15	.30	2.28
Maldanidae	—	.10	.07	—	.03	—	—	.08	—	.28	2.12
Tharyx acutus	.03	.04	.01	.03	.03	.03	.03	tr	.01	.21	1.59
N. incisa	tr	.01	.10	.03	.01	—	.03	—	.02	.20	1.52
Scoloplos sp.	.02	.02	.02	.05	.01	—	.02	—	—	.14	1.06
Scolecolepides viridis	.03	—	—	—	.11	—	—	—	—	.14	1.06
Aricidea catherinae	.02	.02	—	—	—	.01	.01	tr	.01	.07	.53
Scalibregma inflatum	—	tr	.02	—	.03	—	—	—	tr	.05	.38
Exogone hebes	—	—	—	—	tr	.02	—	.01	.03	.06	.46
Pherusa affinis	—	—	—	—	—	—	—	—	.06	.06	.46
Melinna cristata	—	—	.02	—	—	—	.03	—	—	.05	.38
Amphitrite affinis	—	—	—	—	—	.01	—	—	.03	.04	.30
Paraonis sp.	—	—	—	—	—	—	—	—	.04	.04	.30
Ammotrypane aulogaster	—	tr	tr	—	.04	—	—	—	—	.04	.30
Flabelligeridae	.01	—	—	tr	—	tr	tr	.01	—	.02	.15
Terebellides stroemi	—	—	.02	—	—	—	—	—	—	.02	.15
Sabellidae	—	—	—	—	—	.02	—	—	—	.02	.15
Ampharetes acutifrons	—	—	—	—	—	—	.02	—	—	.02	.15
Phyllodoce mucosa	tr	.01	—	tr	tr	tr	—	tr	tr	.01	.08
Phyllodoce sp.	—	—	.01	—	—	—	—	—	—	.01	.08
Polynoidae	—	.01	—	—	—	—	—	—	—	.01	.08
Phyllodoce maculata	—	—	—	—	tr	—	—	—	—	tr	—
Nereis virens	—	—	—	tr	tr	—	—	—	—	tr	—
Nereis sp.	—	—	—	—	—	—	—	—	tr	tr	—
Spiophanes bombyx	—	—	—	—	—	—	—	—	tr	tr	—
Unident. polychaetes	—	.24	.08	—	.15	.07	.18	.09	.13	.94	7.13
									Total	5.40	40.98
Nemertea:	—	.05	—	—	.25	—	.70	—	—	1.00	7.59
Sipuncula(?):	.12	—	—	—	.04	—	.03	—	—	.19	1.44
Nematoda:	—	—	—	—	—	tr	—	tr	—	tr	—
Echinodermata:											
Amphipholis squamata	—	—	—	—	—	tr	—	—	tr	tr	—
									Grand total	13.18	100.00

Etive as in Johns Bay, use of an unweighted percentage reoccurrence of principal prey to evaluate dietary overlap gives an exaggerated picture of partitioning of prey types.

Trophic partitioning by prey size was apparent for the three flounder species examined from Johns Bay (Figure 2). Keast and Webb (1966) have stressed the importance of mouth morphology and body form in channeling predators towards distinct prey. The small-mouthed winter flounder selected small crustaceans, mainly amphipods, and the larger mouthed windowpane concentrated on larger prey, primarily mysids. The yellowtail flounder had a mouth size intermediate between the other two flounder species and it fed on prey from both size ranges. Ross (1977) noticed a similar segregation of prey sizes by searobins as spatial overlap increased. Resource partitioning by prey size was at a minimum between the Atlantic cod and longhorn sculpin (Figure 3). Both of these species had a similar mouth shape and ingested prey of the same size range. The similarity of prey size utilization is reflected in the high food overlap value (0.74) for these two species. Hespenheide (1975) observed a strong correlation between prey size overlap and prey type overlap for cohabiting birds.

An analysis of the benthic infauna was made to determine potentially available food and selectivity of prey by the demersal fishes (Tables 12, 13). Availability depends not only on prey abundance, but also on the interactions of other factors, including prey size, microdistribution, capture success, and speed of movement (Griffiths 1975). Although polychaetes and mollusks dominated in the bottom sediments, crustaceans were the preferred food of the demersal fishes. Generally, predators consumed prey that were active either at the sediment surface or in the upper few centimeters of the bottom sediments. Some abundant food items, such as *Nucula proxima, Prionospio steenstrupi*, and *Exogone hebes* were not important dietary constituents. The small size of *P. steenstrupi* and *E. hebes* probably limits their selection by predators. Predation on *N. proxima* may be low because the feeding structures of some predators prevent extensive burrowing in the sediment or because of this bivalve's low caloric value. Optimal feeding strategy predicts that animals should feed on prey that give the maximum energy yield per unit time and this will govern the degree of palatability of a prey item (Schoener 1971; Emlen 1973).

Recent work by Virnstein (1977) in Chesapeake Bay concluded that infaunal densities in soft-bottom communities are predator controlled. The cropping pressure of the demersal predators checks the population growth of many prolific benthic invertebrates. The benthos in Johns Bay is subject to varying amounts of predation pressure throughout the year. During the winter, the fish community in Johns Bay was very depauperate and it is likely that many fishes moved into warmer water offshore (Edwards 1964). Many of these demersal fishes show a decrease in feeding rate as temperature drops (Tyler[6]) and the winter flounder ceased feeding during the cold months. Because of the reduced abundance and lowered metabolism of the fishes, predation on the benthos was probably at a minimum during the winter. During the warmer months there was an influx of fish species into the bay and an increase in fish diversity and abundance. Environmental conditions are favorable at this time and the food supply may be abundant enough to support the expanded fish community without competitive interactions.

The demersal fishes in Johns Bay occupy the same habitat and there is considerable spatial overlap in their foraging zones. Active predators (e.g., Atlantic cod, red hake) forage over a wider area than sedentary predators (e.g., longhorn sculpin, ocean pout). These wide-ranging species may feed in the foraging zones of several sedentary individuals. My data suggest that the benthic fishes partition food resources by selecting prey from different depth strata (microhabitats) in the environment. Predators may choose either infaunal, epifaunal, or nektonic organisms and the proportion of these prey types in the diet is a reflection of preferred foraging strata (Table 14). At one extreme are predators that feed largely on nektonic prey (e.g., windowpane), while other fishes are strongly dependent on bottom-dwelling organisms (e.g., yellowtail flounder).

The trophic similarity of the demersal fishes in this coastal community suggests that in a food-limited environment many of these predators would experience intense competition. However, establishing food limitation is a difficult task because information is lacking both on benthic production rates and the food rations required by the

[6]Tyler, A. V. 1971. Monthly changes in stomach contents of demersal fishes in Passamaquoddy Bay, N.B. Fish. Res. Board Can., Tech. Rep. 288, 114 p.

TABLE 14.—Numerical percentage of prey types in predator diets.

Predator	Nekton	Epifauna	Infauna
Windowpane	100.0	0.0	0.0
Little skate	2.1	21.4	76.5
Longhorn sculpin	12.7	10.0	77.3
Atlantic cod	8.7	3.5	87.8
Red hake	.3	10.7	89.0
Winter flounder	0	9.1	90.9
Yellowtail flounder	7.3	.3	92.4
Ocean pout	0.3	5.0	94.7

fishes. Another factor to consider is the multidimensional aspect of resource partitioning. Previous studies of fish assemblages have suggested that subtle differences of resource use along complimentary dimensions offer a possible means of reducing interspecific competition (Werner 1977; Ross 1977; Keast 1978). There is evidence that time (e.g., daily and seasonal activity patterns) and space (e.g., foraging pattern) are additional dimensions of importance influencing food utilization by the demersal fish community in Johns Bay. However, unraveling the confounding effects of resource use along several dimensions depends upon more detailed study of these cohabiting fishes as well as increased sophistication of techniques for community analysis (Pianka 1980).

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THE EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON LABORATORY GROWTH OF JUVENILE *SEBASTES DIPLOPROA* AND A COMPARISON WITH GROWTH IN THE FIELD

Growth rates of fishes may act as sensitive indicators of environmental conditions. Variations in food supply, temperature, photoperiod, and other physical and biotic conditions may be reflected in the pattern of growth in a given species, yet the effect may vary depending upon the ontogenetic stage studied. Young stages, for example, generally tolerate and prefer higher temperatures than adults, both in the laboratory (Ferguson 1958; McCauley and Read 1973) and in the field (Brandt 1980); thermal optima for growth may similarly be higher. The present study examines the effects of temperature and photoperiod on growth rate in juveniles of the splitnose rockfish, *Sebastes diploproa*, in the laboratory and compares these growth rates with growth in the field. Adults of this species are benthic at depths of 200-500 m in the northeastern Pacific Ocean. *Sebastes* larvae are pelagic (Ahlstrom 1961), and prejuveniles of this species remain pelagic for about 1 yr, reaching maximum sizes near 55 mm standard length (SL) prior to migrating to the benthic habitat (Boehlert 1977). The thermal regime of the surface waters (13°-22° C) differs greatly from that in the adult habitat (6°-8° C; Reid et al. 1958), suggesting that temperature is an important factor in the life history of this species.

Materials and Methods

Prejuveniles were collected from under drifting kelp by dip net 8-18 km offshore from San Diego, Calif. (lat. 32°52′ N, long. 117°20′ W), and brought to the laboratory. Animals were initially maintained under ambient temperature and photoperiod, but these were changed at 0.5° C and 15 min/d, respectively, until reaching the two photoperiods and three temperatures of acclimation (12 light:12 dark, 16L:8D; 10°, 15°, and 20° C). Fish for the 12L:12D experiments were collected 17 March 1976 at 15.5° C; those for the 16L:8D experiments were collected 14 and 21 May 1976 at 17.7° and 17.6° C, respectively. When acclimation conditions were reached, standard lengths of all fish in each treatment were recorded. During the experiments fish were fed to satiation once daily on a mixture of Trout Chow,[1] ground squid, and frozen brine shrimp. An average of 26 fish were used for each experiment; the range of initial lengths was 30-55 mm SL.

Individual fish were not marked or tagged; individual growth rates were estimated by assuming that rank of individuals in length did not change during the experiment. This allowed determination of the size dependence of growth rate, subject to some unmeasured error if rank of individuals changed enough to affect estimated growth rate. These data were fit by photoperiod to quadratic response surface models using stepwise multiple regression (Nie et al. 1975) in the form

$$G = a + b_1 L_i + b_2 T + b_{11} L_i^2 + b_{22} T^2 + b_{12} L_i T$$

where G = growth rate (millimeters standard length per day), L_i = initial standard length (millimeters), T = temperature of acclimation (degrees Celsius), a = constant, and b_n = regression coefficients.

To compare the growth rates measured in the laboratory with growth of fish in the field, several specimens were collected for analysis of age using daily growth increments on the otoliths. Fish collected for age determination were taken to the laboratory alive where the otoliths were removed and stored dry in vials. Otoliths were processed for age determination as described in Taubert and Coble (1977). Briefly, otoliths (sagittae) were placed on slides with histological mounting medium and ground in sagittal sections. Small otoliths were ground on only one side whereas otoliths from fish >25 mm SL were removed from the slide, remounted, and ground on the other side. After the final grinding cover slips were placed over the otoliths. Each otolith was assigned a random number and read three times at least a week apart at 800 to 1,000 magnifications. If the range of three independent readings was not within 10% of the mean, the otolith readings were rejected.

Results

Mean laboratory growth rates were dependent upon temperature and photoperiod (Table 1). Comparison of mean daily growth rates, however, is confounded by the effects of initial length. At 16L:8D, growth rate was positively correlated with initial length at 10° C ($r = 0.78$) but negatively correlated at both 15° and 20° C ($r = -0.99$ in both cases, Figure 1A). At 12L:12D, growth rates were negatively correlated with initial length at 10° C ($r = -0.97$) and at 15° C ($r = -0.94$) but positively correlated with initial length at 20° C ($r = 0.42$, Figure 1B). In the latter experiment, however, the length range was not as complete as in the other experiments (Table 1).

The relationship of growth to temperature and initial length are more easily interpreted with the multiple regression models. Regression coefficients for the growth response models were all significant with the exception of the length squared term (Table 2). Effects of temperature were similar at both photoperiods; growth increased to some optimum temperature and then declined (Figure 2A, B), as indicated by the negative value of the regression coefficient for temperature squared, b_{22} (Table 2). The apparent temperatures of optimum growth increased slightly with length at 12L:12D but decreased with length at 16L:8D (Figure 2A, B). Initial length showed a clear relationship with growth at 12L:12D (Figure 2B). At all temperatures, growth decreased with increasing length; zero growth, observed in the 10° C experiment at the largest sizes (Table 1), is predicted by the model at sizes >50 mm SL within the range of temperatures studied. At 16L:8D, the growth response to initial length is more complex. At approximately 10.5° C the model predicts a

TABLE 1.—Length-frequency distributions at the start and end of the growth experiments for laboratory acclimated prejuvenile *Sebastes diploproa* at two photoperiods and three temperatures. N = number of fish in the experiment, $\bar{X}$ = mean standard length (millimeters), Δ = change in the sum of lengths (millimeters) between start and end of each experiment, t = duration of the experiment in days.

	12L:12D						16L:8D					
	10°		15°		20°		10°		15°		20°	
SL (mm)	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End
30	1		4		2		1		2			
31	2		3		1		1		1		1	
32	2		4		2						1	
33	4		5		3							
34	4		4		2						3	
35	4		4	1	6	1	3		3			
36	3		2		3	2		1	1			
37					3	2						
38	3				4	4		1				
39	2	3		1	1	3						
40	3	3		2		6						3
41	1	7	2		1	2		2	1			
42	2	4		7		2	1		1			1
43	1	6		4		2	1	1				1
44	1	3	1	5		1	3					
45				5		2	1			1		
46		6	1	1			4		2	1	3	
47				2		1	2			2	2	
48			1	1			1		2		4	
49		1		1			1	1	2	1	1	
50	1						1	2	2	2	2	2
51	2	3		1					2			3
52			1					2	1		2	3
53								1		1		3
54	1			1				2			1	1
55	1	2						2		1		2
56								1		2		1
57								2		1		
58								1		3		
59										2		
60								1		3		
N	38	38	32	32	28	28	20	20	20	20	20	20
$\bar{X}$	38.3	43.9	35.2	44.0	35.1	40.1	42.7	50.6	42.8	54.2	44.8	49.7
Δ	213		281		140		158		228		97	
t	54		54		53		53		54		51	
Growth (mm/d)	.105		.164		.093		.150		.211		.096	

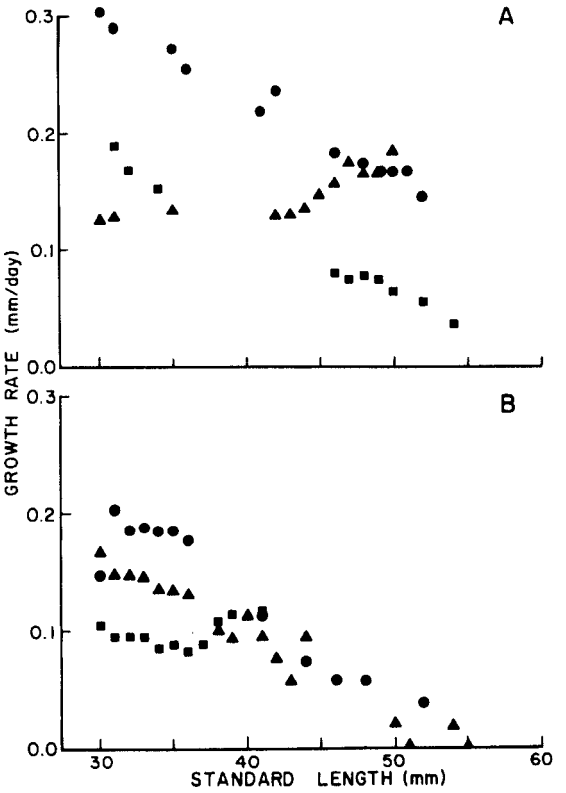

FIGURE 1.—Relationship of initial fish length with measured growth rates during A) 16L:8D experiments, B) 12L:12D experiments. Triangles represent values for fish acclimated to 10° C; dots, 15° C; squares, 20° C.

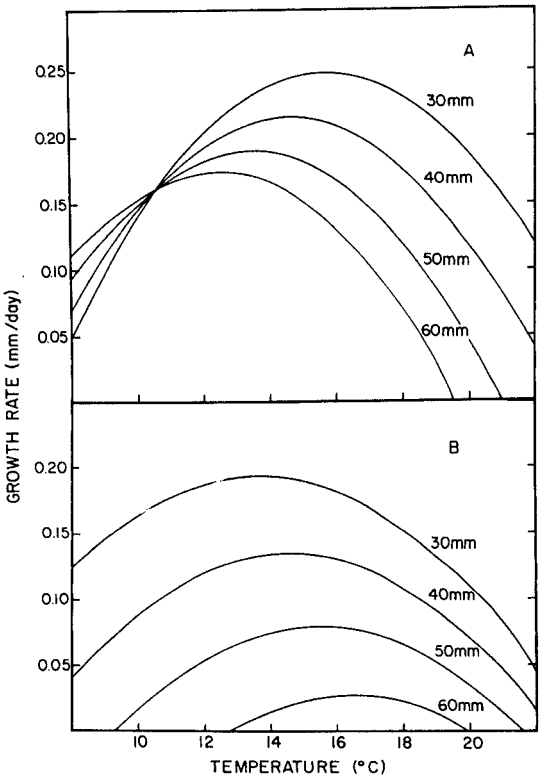

FIGURE 2.—Growth response surfaces for given isopleths of initial standard length as predicted by the multiple regression models. A) 16L:8D experiments, B) 12L:12D experiments.

nodal point where fish of all initial lengths are characterized by the same growth rate (Figure 2A). Below that temperature, growth increases with increasing length, whereas at higher temperatures, it decreases with increasing length. The response of growth to photoperiod indicates a generally positive relationship (Figure 2A, B), with faster growth under most conditions at 16L:8D. Growth with length at all temperatures at 12L:12D and at higher temperatures at 16L:8D decreases with length, suggesting a temperature-dependent asymptote for growth. For low temperatures at 16L:8D, however, growth increases with length and no asymptote is apparent.

TABLE 2.—Coefficients and related statistics for the growth response models for laboratory growth in *Sebastes diploproa*. Multiple correlation coefficients (R) were 0.919 and 0.933 for 12L:12D and 16L:8D, respectively.

	12L:12D (N = 98)			16L:8D (N = 60)		
Item	Value	SE	P	Value	SE	P
a	0.1378	0.0729	0.062	−0.8090	0.0919	0.001
b_1	−.0112	.0016	.001	.0080	.0018	.001
b_2	.0459	.0073	.001	.1264	.0087	.001
b_{22}	−.0021	.0002	.001	−.0033	.0003	.001
b_{12}	.0004	.0001	.003	−.0007	.0001	.001

Growth of fish collected in the field was determined from daily growth increments. Otoliths from 53 specimens were processed as described. Due to broken or unclear otoliths, loss of material from the margin during grinding, or failure to meet the criterion of consistency in age from the three readings, 21 ages were determined. These 21 fish were collected in April (6), August (2), September (3), October (1), and December (9) from 1973 through 1978. Thus a variety of surface temperatures and thermal histories were experienced by these fish. Fish ranged from 9.0 to 42.7 mm SL; the age ranged from 43 to 205 d. The resultant pattern of growth in the field was linear over the size range studied (Figure 3). The growth rates for these specimens, averaged over the

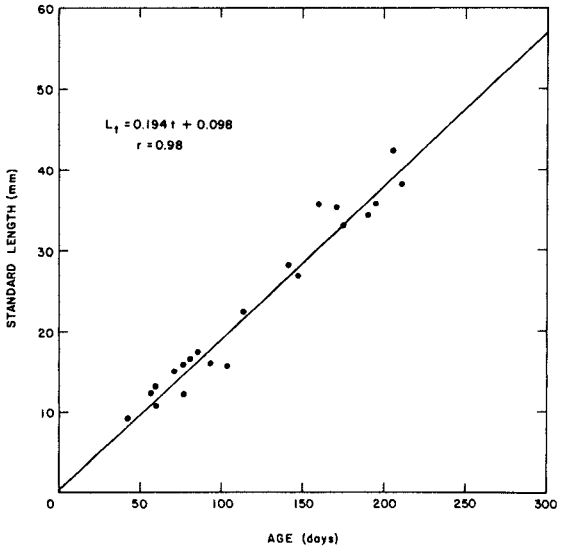

FIGURE 3.—Age at length for field-captured prejuvenile *Sebastes diploproa* as determined by analysis of daily growth increments on otoliths. L_t = length at time t (days).

lifetime of each fish, ranged from 0.154 to 0.225 mm SL/d, with the mean value indicated by the slope of the line, 0.194 mm SL/d. These rates were similar to predicted laboratory growth rates under a variety of temperature and initial length conditions at 16L:8D (Figure 2A) but only to the smallest fish between 10° and 18° C at 12L:12D (Figure 2B). *Sebastes diploproa* apparently grows more slowly in the field than pelagic juvenile *S. melanostomus* of similar size, the only other species of *Sebastes* whose growth has been estimated using daily growth increments (Moser and Ahlstrom 1978).

Discussion

Fish growth generally reaches a maximum at some optimum temperature and decreases at temperatures above and below this level (Brown 1957; Brett 1979), approaching zero near lethal temperatures. Upper lethal temperatures (critical thermal maxima) for prejuvenile *S. diploproa* range from 26° to 30° C, depending upon the temperature of acclimation (Boehlert 1981), and prejuveniles tolerate surface temperatures up to 23° C. The optimum temperature for growth of juvenile *S. diploproa* depends upon both photoperiod and fish length. The growth models suggest optimum temperatures for growth which increase with length at 12L:12D from 13.8° C at 30 mm SL to 15.7° C at 50 mm SL (Figure 2B) and decrease with length at 16L:8D from 16.0° C at 30 mm to 13.8° C at 50 mm SL (Figure 2A). These temperatures clearly exceed those experienced by later benthic juveniles and adults.

Longer photoperiod enhanced growth at nearly all conditions of fish length and temperature (Table 1; Figures 1, 2). Increased growth with longer photoperiod has been observed in green sunfish (Gross et al. 1965), plaice and sole (Fonds 1979), and Baltic salmon parr (Lundqvist 1980). Brown (1946b), however, observed lower growth rate of brown trout in long photoperiods. As the fish in the present experiments were fed to satiation only once daily, it is reasonable to assume that rations under both photoperiods were similar. Surface prejuvenile *S. diploproa* acclimated to short photoperiods have greater standard metabolic rates than those acclimated to long photoperiods at the same acclimation temperatures (Boehlert 1978). Thus the enhanced growth in the longer photoperiod may be related to a greater scope for growth (Elliot 1976) due to lower standard metabolic rates.

The dependence of growth on fish size in the present study is interesting in relation to the life history of this species. Other investigators have observed both increases and decreases in the size range of fishes at the beginning and end of growth experiments. Brown (1946a) described the "size hierarchy effect," which apparently results from development of a peck order with larger fish dominant (Stringer and Hoar 1955). No dominance or peck order with respect to feeding was apparent in the experiments with *S. diploproa*, and in four of six experiments, growth rate decreased with increasing size (Figure 1), as is predicted by the growth models (Figure 2). Laboratory and field growth rates were similar for fish at approximately the same lengths, but it is uncertain whether the decreased growth apparent with increasing length observed in the laboratory occurs in the field. The largest specimen from the field successfully aged using daily growth increments on the otoliths was 42.7 mm SL, below the size at which significantly decreased growth rates occured in the laboratory (Figure 1). If an asymptote does exist in the field, it fits well with the largest pelagic prejuvenile captured in the field (59 mm SL; Boehlert 1977) and with the maximum size after growth in the present study (60 mm SL, Table 1).

The parturition season for *S. diploproa* off California is February through July (Phillips 1964), with possible limited year-round spawning (Boehlert 1977). This results in poorly defined year classes and length-frequency distributions, yet a size threshold and distinct season exist for migration from the surface to the benthic habitat (Boehlert 1977, 1978). Zamakhaev (1964) suggested that size discrepancy within an age-group may be minimized through compensatory growth. The observed pattern of reduced growth at sizes >40 mm SL may serve as a variant on the phenomenon of compensatory growth, consolidating the 0-group fish at sizes near 50 mm SL prior to the migration, which occurs from May through September (Boehlert 1978). At the onset of migration, the oldest and largest fish would migrate first, as observed in sockeye salmon (Foerster 1937) and Atlantic salmon (Elson 1957). Smaller fish would continue rapid growth, and as they reached the size threshold, would also migrate.

Initiation of the surface-to-benthic migration of juvenile *S. diploproa* may be dependent upon photoperiod or rate of change of photoperiod subject to an endogenous program which depends upon a size threshold (Boehlert 1978, 1981). The temperature change between surface and benthic habitats is about 12° C, suggesting that temperature is an important consideration in the migration. Although there is no change in critical thermal maximum for juvenile *S. diploproa* acclimated to the same temperature but different photoperiods (Boehlert 1981), prejuveniles from the field are metabolically preadapted for the lower temperatures during the migratory season (Boehlert 1978). The size dependence of growth in the present experiments suggests a downward shift in the temperature of optimum growth with increasing size in 16L:8D but not in 12L:12D. Photoperiod may thus interact with size, resulting in an ontogenetic change in thermal requirements.

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A CORRELATION BETWEEN ANNUAL CATCHES OF DUNGENESS CRAB, *CANCER MAGISTER*, ALONG THE WEST COAST OF NORTH AMERICA AND MEAN ANNUAL SUNSPOT NUMBER

A recent paper by Driver (1978) described the prediction of shrimp landings off northwest England based on sunspot activity. Stimulated by this work, we examined the relationship between the Dungeness crab, *Cancer magister*, commercial fishery off the west coast of North America and mean annual sunspot number. The Dungeness crab is commercially important and its fluctuating catch has made it the subject of numerous papers (Reed 1969; Peterson 1973; Botsford and Wickham 1975, 1978), some of which noted a distinct rhythm in annual catch. Moreover, Dungeness crab catch statistics are particularly favorable for this study, as it has been estimated that almost every legal crab within the species' range is taken during the commercial season (Pacific Marine Fisheries Commission 1965) and hence there was no need to factor fishing effort into the computations.

Catch statistics were provided by the Pacific Marine Fisheries Commission and comprise commercial landings made in Alaska, British Columbia, Washington, Oregon, and California from 1955 (the earliest year for which complete records were available) to 1980. We utilized the mean annual sunspot values in Waldmeier (1961, 1978) with additional data supplied by Adkins[1] and Eddy.[2] Data were plotted (Figure 1) and correlation coefficients and associated values generated by linear regression (Table 1) for two complete cycles, 1955-64 and 1965-75.

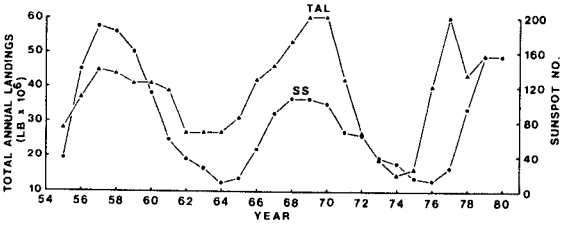

FIGURE 1.—Total annual landings of Dungeness crabs off the west coast of North America (TAL) and mean annual sunspot number (SS) for the period 1955 through 1980.

TABLE 1.—The correlation between commercial Dungeness crab catch and mean annual sunspot number off the west coast of North America.

Period	*r*	df	*f*-ratio	*P*
1955-64	0.90	1, 8	35.3	<0.001
1965-75	.87	1, 9	29.3	<.001

Dungeness crab catches and sunspot numbers both varied in approximately 11-yr cycles and the cycle periods for the two were strongly correlated

[1]J. Adkins, Solar Observer, Mt. Wilson and Las Canpanis Observatory, 813 Santa Barbara Street, Pasadena, Calif., pers. commun. August 1980.
[2]J. Eddy, High Altitude Observatory, National Center for Atmospheric Research, Boulder, CO 80307, pers. commun. March 1981.

(1955-64, r = 0.90; 1965-75, r = 0.87) as the peak catches of 1957, 1969, and 1970 closely corresponded to sunspot maxima years 1957, 1968, and 1969. However, the amplitude of the two phenomena appeared to be asynchronous. The very high sunspot peak of 1957 saw a considerably lower peak crab catch than did the relatively low sunspot peak of 1969.

Woelke[3] suggested that Dungeness crab landings were influenced by water temperature during the crabs' larval stage about 4 yr before, with temperatures at that time being inversely correlated to landings. We analyzed the relationships between crab catches and the sunspot numbers of 4 and 5 yr previous. Correlation coefficients were generated for two crab catch cycles (cycle 1 = 1955-64; cycle 2 = 1965-74). The highest correlation (cycle 1, r = 0.82; cycle 2, r = 0.95) was between Dungeness crab catches and the sunspot number of 5 yr before (Figure 2, Table 2). The correlation was strongly negative. That is, high sunspot number in a particular year seemed to be a predictor of relatively low crab catches 5 yr hence.

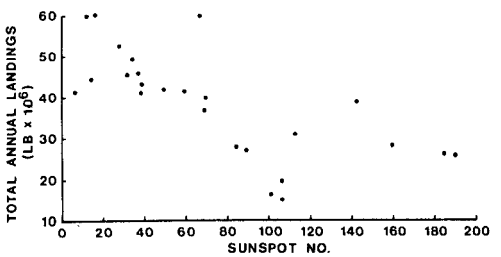

FIGURE 2.—Mean annual sunspot numbers (SS) of the years 1950-69 plotted against total annual landings of Dungeness crabs (TAL) 5 yr later (1955-74).

TABLE 2.—The correlation between commercial Dungeness crab catches and the mean annual sunspot number 5 yr previous (cycle 1 = sunspots of 1950-59, crab landings 1955-64; cycle 2 = sunspots of 1960-69, crab landings 1965-74).

Period	r	df	f-ratio	P
Cycle 1	0.82	1, 8	16.7	<0.01
Cycle 2	.95	1, 9	87.6	<.001
Cycles 1 and 2	.69	1, 23	20.8	<.01

A number of factors may be involved in the cyclical *C. magister* catches. Upwelling, by influencing food density, may have an effect (Peterson 1973). Water temperature and salinity, as well as current pattern may influence larval survival (Lough 1976). Botsford and Wickham (1975) felt that density-dependent biotic factors, such as cannibalism, might play a part.

However, as Eddy (1979) stated, in discussing sunspot studies, "We start into the deep waters of uncertainty not from rocks but from the sand, and with statistics our only lifeline." Sunspots, relatively dark areas about 2000°K cooler than their surroundings, have been noted for more than 1,500 yr (Herman and Goldberg 1978). In the past 200 yr, sunspot activity has been correlated to many planetary processes. Statistical correlations have been made between sunspots and both climatological and biological phenomena (Gnevyshev and Ol' 1977; Pittock 1978). However, increased sunspot activity brings about only slight changes in both magnetic fields and incident radiation levels and, unfortunately, there exists no completely acceptable hypothesis which explains how these slight alterations act on the various processes.

Thus, whether sunspot activity somehow influences any of the above (including crab catches) is unknown. The work of Southward et al. (1975) suggests that an array of events, including intertidal barnacle, *Chthalamus* sp., numbers, hake and cod trawl catches and pilchard egg densities are correlated, in 11-yr cycles, to sunspot number. There is the strong suggestion in this work that sea surface temperature (also strongly correlated to sunspot activity) may be responsible for the cyclical events. Hence, sunspot activity may be linked to biotic events through the agencies of another level of phenomena (in this case temperature).

Whether the crab catch and sunspot cycles remain congruent will have to be seen. Other correlations of this nature have proven spurious with time. If the pattern holds, however, annual sunspot number may be a useful predictor of Dungeness crab catch, delineating periods of catch maxima and minima and perhaps predicting catch amplitude, i.e., how many crabs will be taken.

Acknowledgments

We would like to thank J. Eddy and P. Gilman for enlightening discussions on solar activity, S. Penn and K. Zerba for the illustrations, and S. Warschaw and J. Schulz for typing the manuscript.

[3]Woelke, C. E. 1971. Some relationships between temperature and Pacific Northwest shellfish. Proc. 51st Annu. Conf., Western Assoc. Game Fish Comm., p. 132-135.

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FECUNDITY OF THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, IN NEWFOUNDLAND WATERS

In lobster (genus *Homarus*) fisheries generally, current minimum legal size limits are below the size at 50% female maturity and fishing mortality rates are very high (Anonymous 1979). Under such conditions, widespread recruitment overfishing appears to be a distinct possibility. Conventional yield per recruit assessment models are not totally adequate when dealing with lobsters and this has led to the development of models which are much more species oriented (Caddy 1977, 1979; Ennis and Akenhead 1978). A feature of these models which resulted from concern with recruitment overfishing is provision for assessing the effect on population fecundity of changes in size limit and fishing mortality. In addition to size-maturity information, such assessments require data on fecundity.

Unfortunately, the general applicability of size-fecundity relationships for the American lobster, *Homarus americanus*, which are available from the literature, is suspect. Saila et al. (1969) concluded that the methodology used by Herrick (1911) resulted in quite substantial overestimates of egg numbers. The size-fecundity relationship Saila et al. (1969) presented was based on samples obtained from three widely separated areas; however, Squires (1970) and Squires et al. (1974) suggested that size-fecundity relationships for American lobsters in different areas could be quite different. Squires' (1970) methodology was similar to that of Herrick but he found that his estimates varied from actual counts by $<2\%$, an error factor comparable with that reported by Saila et al. (1969) and Perkins (1971) using electronic counters. Aiken and Waddy (1980) suggested that standardized egg counts from different areas would clarify the question of geographic variation in American lobster fecundity and concluded that Herrick's estimates should not be dismissed until the results of these or other, more explicit studies are available.

This paper presents new fecundity data for a Newfoundland area as a contribution to the literature on the subject and provides comparisons with published size-fecundity relationships.

Materials and Methods

Ovigerous females were included in samples ob-

tained during spring (near the end of the incubation period) trap fishing in the area of Arnold's Cove, Placentia Bay, on the southeast coast of Newfoundland in 1969, and in the areas of Ship Harbour and Paradise in Placentia Bay in 1970 (Figure 1). Portions of the samples (up to 50 American lobsters) were usually held in floating wooden boxes (about 100-lb capacity) for several days before being subjected to detailed biological examination. Carapace lengths (millimeters) were recorded and the abdomens of ovigerous specimens with attached egg masses were preserved individually in 10% Formalin.[1] Loss of eggs over the holding period cannot be discounted, but it is felt that such losses were minimal.

Eggs were removed from the pleopods, washed on a screen of fine-meshed plankton netting to remove the larger pieces of connective tissue and other material, and then left to soak in freshwater overnight. After soaking, the eggs were spread thinly over very shallow pans to dry at room temperature until they were quite hard (usually after about 24 h) and could withstand being rubbed over a fine-meshed screen to remove the remaining connective tissue. After drying and final cleaning, the weight of the egg sample was obtained (to the nearest 0.0001 g). A subsample, representing approximately 1/30 of the whole sample (as determined by weighing), was weighed and the eggs counted manually. The number of eggs in the whole sample was then calculated.

To determine the error associated with this method, total numbers for 11 samples were determined by actual counts for comparison with the estimated total numbers for the same samples. The error ranged from −3.6% to 0.04% and for the 11 sets of counts totaled the error was 0.54%.

Carapace length and fecundity data were log (base 10) transformed and the linearized version of the power curve was fitted to each set. The linear relationships thus derived were compared by analysis of covariance.

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

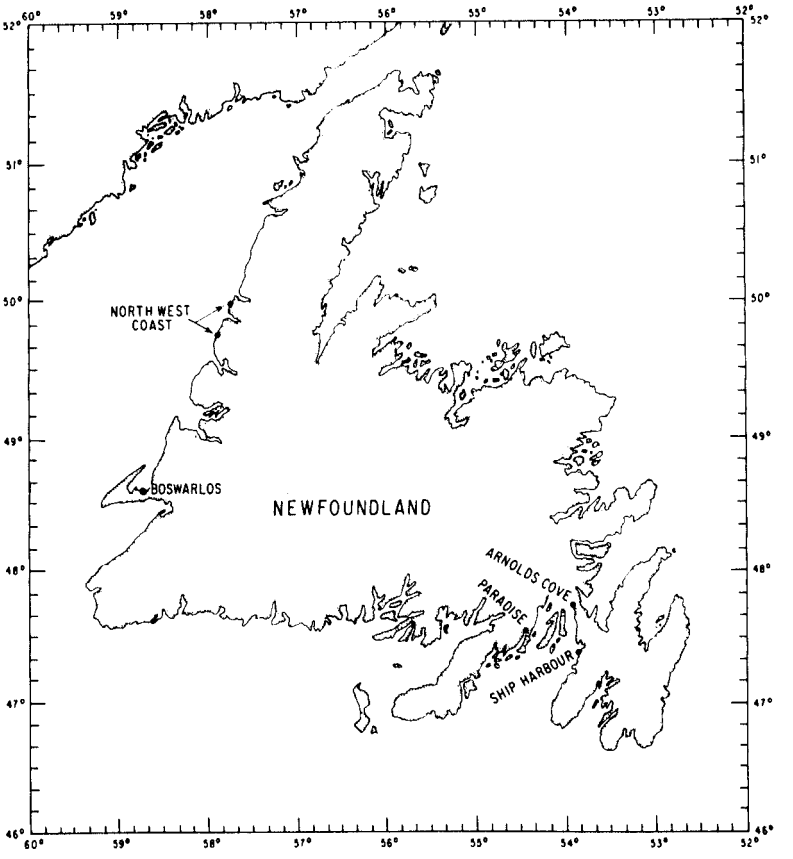

FIGURE 1.—Map of Newfoundland showing places mentioned in the text.

Results and Discussion

Curvilinear size-fecundity relationships derived from log-log (base 10) regression analysis for spring-caught (April-June) samples are presented for three areas in Placentia Bay, along with the same relationships obtained from reanalysis of the data presented by Squires (1970) and Squires et al. (1974) for two Newfoundland west coast areas (Figure 2, Table 1). The methodology of Squires (1970) and Squires et al. (1974) was similar to that used here except that the estimates were determined volumetrically instead of by weighing. These estimates varied from actual counts by <2% which is within the range of error determined in this study. For this reason the following statistical comparisons between the Placentia Bay and west coast samples are considered valid.

An F_{MAX} test on the log-transformed data demonstrated significantly different ($P<0.01$) residual variances among the five samples. Various combinations of the log-log relationships were compared by analysis of covariance. In all comparisons between relationships for Placentia Bay and the comparison between the two relationships for the west coast, residual variances were similar. However, in all comparisons between one of the Placentia Bay and one of the west coast relationships, residual variances were significantly different (Table 2). Two of the four sets of relationships with similar residual variances had significantly different slopes, the other two had similar slopes but significantly different means. There was wide variation in fecundity at size and the samples differed in size composition (Table 3). Significant differences in these relationships may result in large part from differences in sample size and size composition.

Samples with at least six specimens in the same 5 mm size group were compared by analysis of variance. There is some size-related variation in fecundity within each 5 mm size group. This could confound a comparison if, in the samples being compared, there is clustering of specimens at opposite ends of the size range. Upon examination it was found that for each sample compared in Table 4 the specimens were fairly well distributed throughout the 5 mm size range and it is assumed that size-related variation does not invalidate

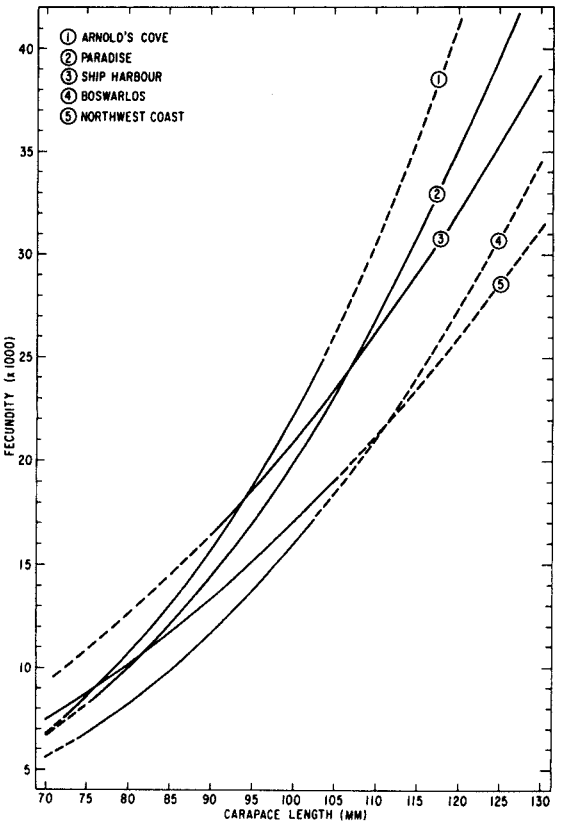

FIGURE 2.—Carapace length-fecundity relationships for American lobsters from three areas in Placentia Bay, Newfoundland and two areas on the west coast of Newfoundland. Dashed lines indicate extrapolations beyond the data.

TABLE 1.—Regression equations from which the curvilinear relationships shown in Figure 1 were derived.

Sample	N	Carapace length range (mm)	Regression equation	r
Arnold's Cove	43	72-104	$\log_{10} F = 3.3471 \log_{10} CL - 2.3437$	0.88
Paradise	72	75-139	$\log_{10} F = 3.0984 \log_{10} CL - 1.8963$	.94
Ship Harbour	68	89-159	$\log_{10} F = 2.3188 \log_{10} CL - 0.3117$	.89
Boswarlos	75	74-103	$\log_{10} F = 2.9387 \log_{10} CL - 1.6747$	.58
Northwest coast	63	70-107	$\log_{10} F = 2.3161 \log_{10} CL - 0.3998$	.60

TABLE 2.—Results of analyses of covariance of size-fecundity relationships presented in Figure 1.

Relationships compared	Mean squares F	Mean squares P	Slopes F	Slopes P	Means F	Means P
Arnold's Cove vs. Ship Hr.	1.29	>0.20	9.44	<0.01		
Arnold's Cove vs. Paradise	1.27	>.20	.57	.542	6.29	0.013
Paradise vs. Ship Hr.	1.02	>.50	15.86	<.001		
Arnold's Cove vs. Boswarlos	3.08	<.001				
Arnold's Cove vs. NW coast	3.48	<.001				
Boswarlos vs. NW coast	1.13	>.50	.98	.674	15.08	<.0001
Paradise vs. Boswarlos	2.42	<.001				
Paradise vs. NW coast	2.73	<.001				
Ship Hr. vs. NW coast	2.69	<.001				
Ship Hr. vs. Boswarlos	2.38	<.001				

TABLE 3.—Summary of fecundity data on which relationships shown in Figure 1 are based.

Carapace length	Arnold's Cove			Paradise			Ship Harbour			Boswarlos			Northwest coast		
	N	$\bar{X}$	Range	*N*	$\bar{X}$	Range	*N*	$\bar{X}$	Range	*N*	$\bar{X}$	Range	*N*	$\bar{X}$	Range
66- 70													1	4,700	
71- 75	3	9,096	8,293-10,115	1	6,756					4	8,000	7,000- 9,300	4	10,075	9,100-11,500
76- 80	4	9,375	7,299-11,423	12	9,716	7,727-12,535				37	8,178	4,600-11,800	14	10,236	6,800-15,100
81- 85	12	11,821	9,894-13,479	16	11,391	7,112-15,704				21	8,414	3,500-12,800	21	11,214	6,700-16,100
86- 90	11	14,393	9,836-19,909	9	13,156	10,245-16,992	1	13,773		8	10,850	7,800-15,300	8	13,887	9,400-18,800
91- 95	8	18,085	15,833-20,858	8	16,445	11,248-20,767	6	17,348	12,703-22,555	3	13,667	13,000-14,000	7	13,500	6,900-22,100
96-100	3	21,432	16,414-29,888	8	19,697	14,304-24,421	4	20,291	12,926-24,875	1	19,200		5	20,240	16,700-23,900
101-105	2	23,379	22,535-24,223	4	26,213	24,477-27,530	4	22,544	21,351-25,216	1	22,800		2	12,500	10,700-14,300
106-110				3	24,920	20,477-30,099	5	26,266	22,548-28,878				1	26,000	
111-115				3	29,462	25,516-33,660	6	32,559	27,894-36,896						
116-120				2	38,536	34,621-42,450	12	32,247	24,135-43,116						
121-125				2	39,778	32,887-46,669	6	32,018	19,915-38,601						
126-130				1	36,337		4	40,794	34,078-45,443						
131-135				2	42,591	41,645-43,537	6	43,467	37,882-49,681						
136-140				1	42,837		5	46,038	40,638-55,937						
141-145							4	44,511	36,395-57,457						
146-150							2	47,904	47,716-48,092						
151-155							2	56,986	52,399-61,573						
156-160							1	56,995							

these comparisons. All comparisons between Placentia Bay samples showed no significant differences (Table 4). For the comparisons between the two west coast samples and between samples from each of the two areas, there were significant differences for some size groups but not for others. The relationships shown in Figure 2 indicate that American lobsters in Placentia Bay are more fecund than those on the west coast. This observation is supported by the analysis of covariance and to a lesser extent by the analysis of variance.

Data for the three Placentia Bay areas were combined as were data for the two west coast areas. The curvilinear relationships derived from log-log regression analysis were plotted with those available from the literature for other areas (Figure 3). Substantial differences in size-fecundity relationships between some of these areas are apparent.

Perkins (1971) reported substantial egg loss during incubation (36% between October and June) for American lobsters from the offshore canyon areas of the northeast United States. This should not be a significant factor in the above comparisons, however, since in all cases samples were ob-

TABLE 4.—Results of analyses of variance of fecundity data for different size groups from the various samples.

Samples compared	Size groups (mm)			
	76-80	81-85	86-90	91-95
Arnold's Cove vs. Paradise	—	NSD	NSD	NSD
Arnold's Cove vs. Ship Hr.	—	—	—	NSD
Paradise vs. Ship Hr.	—	—	—	NSD
Arnold's Cove vs. Boswarlos	—	**	*	—
Arnold's Cove vs. NW coast	—	NSD	NSD	NSD
Paradise vs. Boswarlos	*	**	NSD	—
Paradise vs. NW coast	NSD	NSD	NSD	NSD
Ship Hr. vs NW coast	—	—	—	NSD
Boswarlos vs. NW coast	**	**	NSD	—

NSD = no significant difference $P \geq 0.05$, $^{*}0.01 < P < 0.05$, $^{**}P < 0.01$.

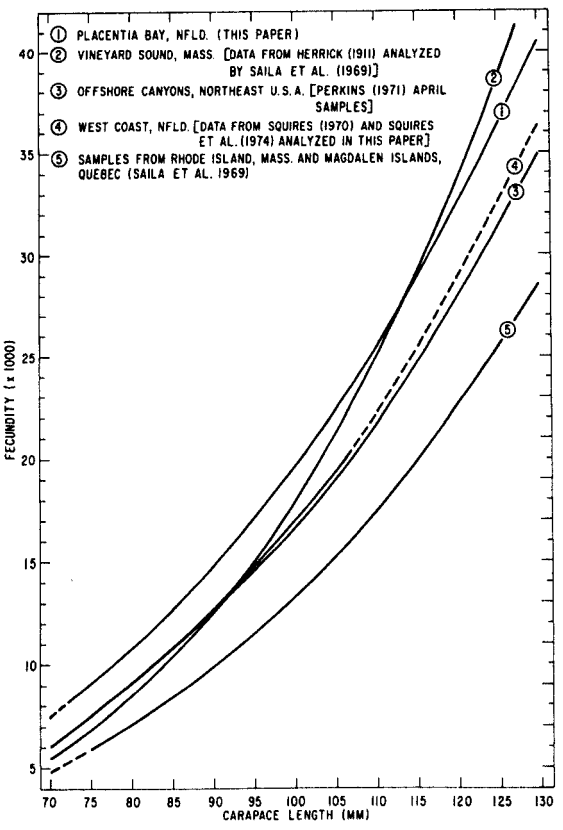

FIGURE 3.—Carapace length-fecundity relationships for American lobsters from two Newfoundland areas and those available for the literature for other areas. Dashed lines indicate extrapolations beyond the data.

tained during late spring-early summer towards the end of the incubation period.

Fecundity values calculated from the relationships in Figure 2 range from 4,800 to 7,450 at 70 mm carapace length and from 25,400 to 38,300 at 125 mm. The relationship of Saila et al. (1969) gives the lowest values over the entire range of sizes considered. This relationship is suspect, however, since it is based on samples obtained from three widely separated areas. Over most of the size range considered the relationship for Placentia Bay gives higher estimates than those from the relationship derived by Saila et al. (1969) from Herrick's (1911) data, indicating that Herrick's data should not be discounted as Saila et al. (1969) suggested.

Definitive statistical comparisons of size-fecundity relationships for American lobsters from different areas would require large samples which adequately cover a wide range of sizes. Even with such samples comparisons could be somewhat confounded by geographic variation in size at first maturity, which, for certain areas, would preclude direct comparison of fecundity at smaller sizes. In addition, samples would have to be taken at approximately the same stage in the incubation period by the same method of capture and be subjected to similar handling and procedures for determining egg numbers. These requirements are unlikely to be met in the foreseeable future. However, as tenuous as the comparisons presented here may be, they do suggest substantial geographic variation in size-fecundity relationships for American lobsters.

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MORTALITY OF SEABIRDS IN HIGH-SEAS SALMON GILL NETS[1]

Since 1952, the Japanese have operated a large salmon driftnet fishery in the northern North Pacific Ocean and Bering Sea. This fishery is divided into two components: the high-seas mothership fleet, which consists of several processing ships and their numerous, smaller catcher boats that remain at sea during the entire fishing season, and the land-based fleet, which consists of independent fishing boats that catch and store their own fish and return to Japan at more fre-

[1]Contribution No. 224 of the Point Reyes Bird Observatory.

quent intervals (Sanger 1976; Fredin et al.[2]). A similar fishery in the North Atlantic between 1965 and 1976 was responsible for the deaths of large numbers of the thick-billed murre, *Uria lomvia*, and significant reductions in its breeding populations (Tull et al. 1972). Recent work in the North Pacific and Bering Sea by Sano (1978) and King et al. (1979) indicated that large numbers of seabirds are killed annually in the Japanese salmon fishery also.

Previous estimates of seabird mortality resulting from the Japanese high-seas and land-based gill net fisheries were based on data gathered from research nets only (e.g., Sano 1978; King et al. 1979). These nets include both smaller and larger mesh sizes than nets used in the commercial fishery. We wished to investigate if mesh size influenced bird mortality rates, and if so, to reassess the impact of gill net fisheries on seabird mortality. Since previous estimates of the total bird catch were based on data averaged over broad regions, we also investigated the geographic variation in catch rates to determine whether in some areas they could potentially be having an important impact on local bird populations.

[2]Fredin, R. A., R. L. Major, R. G. Bakkala, and G. K. Tanonaka. 1977. Pacific salmon and the high seas salmon fisheries of Japan. Processed Rep., 324 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

Methods

We participated in cruises aboard Japanese research vessels during 1978 and 1979 as shown in Figure 1. The *Oshoro Maru* and *Hokusei Maru* deployed research nets and the *Hoyo Maru No. 67* deployed a small series of research nets between two extensive spans of commercial nets. Research and commercial nets differ significantly only in the variety of mesh sizes used. In this study the mesh sizes in the research nets ranged 37 to 233

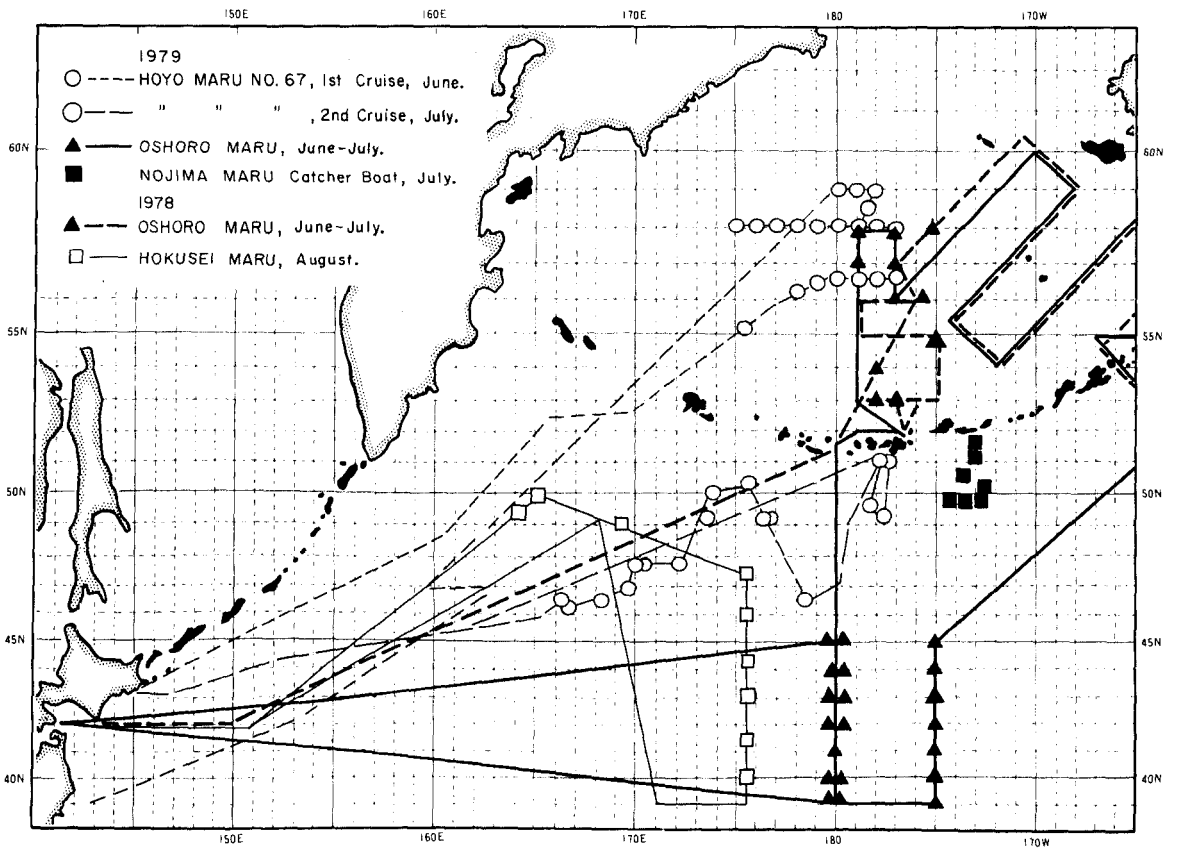

FIGURE 1.—Cruise tracks (lines) and net setting stations (symbols) where observations were made in 1978 and 1979.

mm but the commercial nets were limited to meshes ranging 110 to 130 mm. In 1979 we also obtained some data from commercial catcher boats of the mother ship *Nojima Maru*, but these were used only in determining geographical differences in catch rates. Nets were set at 16:30 h and hauled at 02:30 h on *Hoyo Maru No. 67*, similarly to commercial boats; on other cruises deployment and retrieval were at 18:00 h and 03:00 h. Nets consisted of panels, called tans, 50 m by 6 m deep that were sewn together in series, with floats attached to the topline and lead weights attached to the bottom line of each panel. The stretched mesh thus hung vertically like a curtain from the sea surface down to a depth of 6 m. A commercial net was usually about 15 km long, while those on our vessels were about 6.5 km (130 tans). A commercial fleet of 45 catcher boats (plus a mother ship) deployed its nets in parallel lines on a grid, each net about 5 nmi from neighboring ones. For several sets in the central Bering Sea, *Hoyo Maru No. 67* fished within the configuration of a commercial fleet. A complete review of the Japanese drift gill net fishery is contained in Fredin et al. (footnote 2).

On all cruises except that of the *Nojima Maru* catcher boats, we noted entangled birds as the nets were being retrieved. Carcasses from the first cruise of *Hoyo Maru No. 67* were saved by Jones, frozen, shipped to the United States, and, along with those from *Nojima Maru*, were later identified by Ainley; those from other cruises were identified immediately by Ainley and DeGange. On most sets the mesh size and the depth at which birds were entangled were recorded.

Using data from the *Hoyo Maru No. 67* and the *Nojima Maru* catcher boats (see Figure 1), we compared catch rates to distance south of the Aleutian Islands. Data from *Oshoro Maru* and *Hokusei Maru* were not used because they did not use commercial nets. However, a comparison of catch rates to the distance north of the Aleutians used data exclusively from *Oshoro Maru* because we had no data from commercial nets close enough to the islands. The shape of the regression curve would not be affected but the asymptotes would be displaced downward due to the low catch rates of the research nets used.

On two cruises in 1979, Ainley and DeGange censused seabirds that occurred within 300 m of one forequarter of the ship whenever we steamed at 9-12 kn during daylight; birds circling or following the ship were ignored. Distance traveled during a given time period (a transect) multiplied by the 300 m transect width provided an estimate of ocean area surveyed. Area divided into the number of birds counted resulted in an index of bird density per square kilometer. For 16 sets on the July cruise of *Hoyo Maru No. 67* and 5 sets on the 1979 cruise of *Oshoro Maru*, densities of netable seabird species (i.e., those caught during the cruises) were correlated to the number caught per tan (110-130 mm mesh only) at each set. Density indices at netting areas were averages of the counts immediately before arrival at and another after departure from the netting site. Only five of *Oshoro Maru*'s sets were used because other studies took her far away from netting areas at very low speed before transits at cruising speeds began. We equilibrated our estimates of bird density based on simultaneous but independent counts made aboard *Oshoro Maru*, 25-27 July 1979.

In the following discussions oceanographic regions are approximate because they are based on geographic locality as shown in Favorite et al. (1976), and not on sophisticated oceanographic measurements taken at the time of bird observations. Hourly sea-surface temperatures, however, did aid somewhat in confirming the boundaries between certain domains.

Results and Discussion

Species Observed

We recorded 31 species of seabirds during our at-sea observations but only 15 of these were caught in the nets (Table 1). For certain species, their pelagic distribution was reflected in the gill net catch by statistically significant correlations ($P < 0.05$) between density estimates and number of birds caught. For example, in the Bering Sea and in Western Subarctic waters south of the Aleutians, the short-tailed shearwater greatly outnumbered the sooty shearwater, both in density and in the gill nets, but farther south to just north of the Subarctic Front their numerical importance in the catch and in the censuses was reversed. Several other species also showed differences in their distributions, for example, ancient murrelet and crested auklet.

A bird's foraging methods influenced its susceptibility to being caught (Table 2). Of the 13 species we observed that feed beneath the sea surface by diving or pursuit plunging (see Ainley 1977 for

TABLE 1.—Density indices ±SD and number caught per tan ($\times 10^{-3}$) in parentheses for netable seabird species in different oceanographic areas; the number of ½-h transects are shown below each area name.

Species	Transitional Domain (27)	W. Subarctic Gyre (36)	Alaskan Stream (24)	Bering Gyre (97)	Bering Current (8)
Laysan albatross,	0.1±0.1	0.1±0.1	0.1±0.1		0.1±0.2
Diomedea immutabilis	(2.0)	(1.0)			
Northern fulmar,	3.2±5.6	1.8±1.4	.8±0.4	.3±.3	.6±.3
Fulmarus glacialis		(3.0)			
Flesh-footed shearwater,[1]	.1				
Puffinus carneipes	(0.3)				
Sooty shearwater, [1,2]	.4±.8	.1			
P. griseus	(18.0)	(2.0)	(.2)		
Short-tailed shearwater, [1,2]		11.7±15.6	10.0±13.5	.8±1.2	5.5±1.9
P. tenuirostris	(0.6)	(17.0)	(66.)	(3.0)	(60.0)
Fork-tailed storm-petrel,	1.9±1.8	3.1±2.8	2.6±1.1	1.5±1.0	2.3±1.2
Oceanodroma furcata		(8.0)		(.6)	(2.0)
Common murre,[1]		.1		.1	
Uria aalge				(.3)	
Thick-billed murre,[1,2]		.1±.2	.2±.4	.1±0.2	.5±.2
U. lomvia		(2.0)	(5.0)	(4.0)	(12.0)
Ancient murrelet,[1]				.1±.4	.8±.8
Synthliboramphus antiquus				(1.0)	(2.0)
Parakeet auklet,[1]			.1	.1	
Cyclorrhynchus psittaculus			(0.2)		
Cassin's auklet,[1]					
Ptychoramphus aleuticus			(.2)		
Least auklet,[1]			.2±.6	3.3±4.3	1.2±1.6
Aethia pusilla		(1.0)			
Crested auklet,[1]			.1	.7±1.6	.7±.8
A. cristatella		(2.0)	(1.0)		
Rhinoceros auklet,[1]	.1±.2				
Cerorhinca moncerata			(0.2)		
Horned puffin,[1]	.2±.2	.4±.5	.3±.4	.4±.5	3.9±2.4
Fratercula corniculata	(.6)	(5.0)	(3.0)	(2.0)	(2.0)
Tufted puffin,[1]	.2±.2	.4±.5	.3±.4	.4±.5	3.9±2.4
Lunda cirrhata	(3.0)	(8.0)	(18.0)	(7.0)	(6.0)

[1]Species that feed principally beneath the sea surface by diving or pursuit plunging.
[2]For correlation between density index and catch rate, $P < 0.05$; Spearman's rank correlation.

TABLE 2.—The number of individuals by species caught in net meshes of various sizes (stretched).[1]

Species	Mesh size (mm)																
	37	42	48	55	63	72	82	93	106	112-115	118-121	130	138	157	179	204	233
Laysan albatross		2								2	1						
Northern fulmar										9			1				
Flesh-footed shearwater														1			
Short-tailed shearwater			1			1		1	14	106	11	15		1			
Sooty shearwater		1			1		3	4	2	23	12	4	3	3	2	2	
Fork-tailed storm-petrel							1			11							
Common murre										1							
Thick-billed murre							2		1	25	2	1	1	1	1		
Ancient murrelet							1	1			1						
Cassin's auklet								1									
Horned puffin							1			8			2				
Tufted puffin								4	2	42	4	1	3	1		2	
Least auklet										1							
Crested auklet							1			2	1						
Total	0	3	1	0	1	1	9	11	19	230	32	21	10	7	3	4	0
Tans set	162	162	489	495	495	495	495	495	495	7,303	3,035	674	495	495	155	162	27
Birds/tans set	0.00	0.019	0.002	0.00	0.002	0.002	0.018	0.022	0.038	0.031	0.011	0.031	0.020	0.014	0.019	0.025	0.00
$\bar{X}$ catch rate			[2]0.003				[3]0.020				[4]0.026				[3]0.018		

[1]Does not include thick-billed murre of *Hoyo Maru* set 17 or ancient murrelets of set 20; net retrieval was not observed.
[2]Significantly fewer than the other three classes ($P<0.01$; Sokal and Rohlf 1969:608).
[3]No significant difference in catch rates ($P>0.05$).
[4]Significantly higher than the other three classes ($P<0.05$).

definitions), all were entangled at least once and were also entangled deeper in the nets than just the upper meter (Good and Ainley unpubl. data). Only 3 (17%) of the other 18 species we observed at sea were caught in the nets. Almost all of these feed at the surface by scavenging, dipping, or by shallow plunges; the 3 caught were the most abundant scavengers of the area: laysan albatross, northern fulmar, and fork-tailed storm-petrel. Direct observations of their behavior and examina-

tion of their stomach contents (Good and Ainley unpubl. data) indicated that entanglement occurred as they attempted to eat fish caught in the net. A much smaller percentage (ca. 5%) of shearwaters (pursuit plungers) were caught while eating entangled fish, but probably none of the diving species (murres, puffins, etc.) scavenged from the nets (confirmed by stomach contents).

Rates of Entanglement

We tabulated birds by the mesh size in which they were entangled (Table 2). Catches in 112-115 mm meshes were combined as were those in 118-121 mm meshes. Not included were birds caught by commercial boats because we were not sure that all specimens reached us. Catch rates for six mesh sizes <82 mm were negligible, but rates for 106-138 mm meshes, including those used in the commercial salmon fishery (121-138 mm) (Fredin et al. footnote 2) were statistically greater than for the other categories. In 157-233 mm meshes, with or without the 233 mm mesh—no birds caught and only 27 tans set—the rate was similar to that for 82-93 mm meshes. Based on those results, we excluded from further analysis birds caught with ≤82 mm meshes.

The number of birds caught per tan was directly proportional to the density of netable species present at the netting locality ($r = 0.7154$, $P<0.01$, t-test). The correlation was improved ($r = 0.7604$) when catch rates were adjusted for the actual amount of time the nets were deployed (i.e., birds/tan per hour deployed). The correlation would probably be improved even more if density indices were adjusted for the detectability of birds. For instance, tufted puffins on the water in the outer third of the 300 m count zone would probably not have been seen, especially in rough seas. The difficulty in detecting puffins might account for the lack of correlation between density indices and catch rates in Table 1, where significant correlations existed for more easily observed species.

The facts that bird densities differed geographically (or oceanographically; Table 1) and that catch rates were proportional to bird density led us to look for geographic differences in catch rates. In the northern North Pacific, the mean number of birds caught per tan increased with latitude. Rates were lowest, varying 0.00-0.03 bird/tan, between lat. 39° and 43° N (Subarctic Front and the Transitional Domain); were slightly higher, 0.03-0.08, between lat. 44° and 48° N (Western Subarctic Domain); and were highest, 0.04-0.51, between lat. 49° and 51° N (Alaskan Stream). In that part of the Bering Sea sampled, the number of birds caught per tan increased with decreasing latitude. In the central Bering Sea (Bering Sea Gyre) catch rates were low, ranging 0.01-0.05, and were higher at the gyre periphery. Farther south in the extreme periphery of the gyre, the Bering Current, catch rates ranged 0.04-0.16. These rates were consistent with the relative differences in bird densities in these oceanographic regions (Table 1). Greater bird densities in the Alaskan Stream and Bering Current were due to the more productive waters there and to closer proximity to the Aleutian Islands where murres, puffins, and several other netable species breed. In fact, as a direct function of distance, within 200 nmi of the Aleutians catch rates varied logarithmically ($P<0.01$; Figure 2). Rates were especially high within 50-75 nmi of the islands, where most of the murres and puffins in net samples were breeding adults (based on the presence of incubation patches). Most of those caught in the Bering and Western Subarctic Gyres and Transitional Domains were immature.

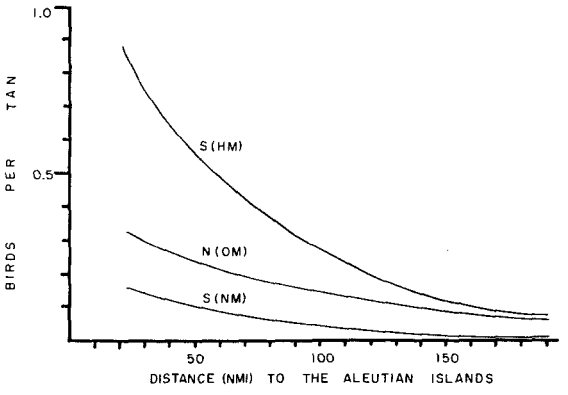

FIGURE 2.—Logarithmic relationships between bird catch rates and distance to the Aleutian Islands within 200 nmi, 1979: S(HM) = *Hoyo Maru* stations south of the islands ($r = 0.9167$, $P < 0.01$; $y = 0.74 - 0.13 \ln x$), S(NM) = Nojima Maru stations south of the islands ($r = 0.9186$, $P < 0.01$; $y = 0.36 - 0.07 \ln x$), and N(OM) = *Oshoro Maru* stations north of the islands ($r = 0.9869$, $P < 0.01$; $y = 0.74 - 0.13 \ln x$); see Figure 1 for station localities.

Overall Seabird Mortality

The above estimates of catch rates, if applied to the commercial fishery, are minimal for two

reasons: most could be increased by >30% to account for the higher catch rates of nets with commercial size meshes (Table 2), and our estimates of commercial catch rates did not account for birds that dropped from the net before its retrieval. On the July cruise of *Hoyo Maru No. 67*, 3 shearwaters (of 6 caught) and 1 puffin (of 12 caught) dropped from the net when it was stretched taut in the retrieval process. On that cruise, 13% of the dead birds would not have been counted if only figures on the number of dead birds reaching the deck had been used as in other estimates of catch rates. Similarly, on cruises of the *Hokusei Maru* in 1978 and that part of the *Oshoro Maru* cruise south of the Aleutian Islands in 1979, 1 of 9 (11%) and 3 of 66 birds (5%), respectively, dropped out during net retrieval.

A valuable result of this study is the more realistic estimate of bird catch rates, compared with previous estimates (Sano 1978; King et al. 1979; Japanese Fishery Agency 1977 in DeGange[3]; DeGange footnote 3). Prior estimates agreed but were too low because they were based on research gear and the assumption that catch rates were the same regardless of mesh size, and they did not give enough attention to geographic differences in catch rates. They derived an overall mean value for birds caught per tan fished which dilutes considerably the high catch rates in certain areas. DeGange's (footnote 3) analysis, representative of earlier mortality estimates, derived a total of about 112,500 birds caught annually in the mothership fishery. We propose that a figure of 205,000, an increase of about 82%, is more realistic (Table 3). If our estimate were increased by an additional 30% to adjust for the high catch rates of commercial meshes, the resultant figure of 266,500 birds is 136% higher.

The demonstration that bird catch rates increase logarithmically as distance to the Aleutian Islands decreases, and are generally higher in productive waters, is especially important. More observations are needed on catch rates in commercial nets to clarify the critical distance, but fishing at some distance within 50-75 nmi of the islands would severely reduce breeding populations of certain diving birds. This is precisely what happened when a salmon gill net fishery off Greenland was concentrated too near to murre breeding sites (Tull et al. 1972). In that fishery, 88% of the estimated 350,000-500,000 thick-billed murres caught per year were entangled in nets set <30 nmi from the coast. Other species, however, showed different distance-to-coast relationships; for example, 36% of the black guillemot, *Cepphus grylle*, were entangled <12 nmi from the coast, 80% of the greater shearwater, *Puffinus gravis*, were caught between 12 and 30 nmi, and 75% of the dovekie, *Plautus alle*, were caught between 12 and 60 nmi (50% at 30-60 nmi; Christensen and Lear (1976)).

In the North Pacific where the salmon driftnet fishery is much larger than the one in Greenland was, it is likely that gill netting has also been concentrated near bird breeding sites. In a sample of years for which data on the number of tans fished were available to us (n = 12 during 1955-69 International North Pacific Fisheries Commission[4]), 44.4% of effort east of long. 170° E, or several million tans annually, was concentrated in the six 2° × 5° blocks (24 total blocks fished in that area) containing the western Aleutians. Such concentration of effort, coupled with marked geographic differences in bird catch rates, indicates the limitations in estimating the total seabird kill by using statistics averaged over broad areas as attempted by King et al. (1979). Their estimate of 5.0 million birds killed by the entire mothership fishery between 1952 and 1974, based on an average annual mortality of 250,000, is extremely low and should be at least doubled. After all, in the fishing area east of long. 170° E alone, we estimate that at least 4.1 million birds were killed in just the 12 yr mentioned above.

[3]DeGange, A. R. 1978. Observations on the mortality of seabirds in Japanese salmon gill nets made from the OSHORO MARU and HOKUSEI MARU, summer 1978. Unpubl. Rep., 37 p. U.S. Fish Wildl. Serv., Off. Biol. Serv., Anchorage, Alaska.

TABLE 3.—A comparison of bird catch in the 1978 mothership salmon fishery using two methods of catch rate estimation; the DeGange (text footnote 3) method is typical of all previous types of estimation.

		Bird per tan		Total birds caught		
2° N × 5° E Block	Tans fished[1]	DeGange	This report	DeGange	This report	Percent increase
50-165	34600	0.036	0.130	1,246	4,498	260
52-165	45800	.036	.130	1,649	5,954	260
48-170	250600	.040	.130	10,024	32,578	220
50-170	939500	.084	.130	78,918	122,135	60
52-170	281500	.053	.130	14,920	36,596	140
54-170	103400	.053	.038	5,480	3,929	−30
56-170	8900	.035	.038	312	338	10

[1]Source of data: International North Pacific Fisheries Commission (text footnote 4).

[4]International North Pacific Fisheries Commission. 1955-79. Catch statistics of Japanese mothership gillnet and land-based driftnet fisheries. Int. North Pac. Fish. Comm. Doc.

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HISTOCHEMICAL INDICATIONS OF LIVER GLYCOGEN IN SAMPLES OF EMACIATED AND ROBUST LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

On the basis of histological criteria (O'Connell 1976), 8% of northern anchovy, *Engraulis mordax*, larvae from special net tows taken in the Southern California Bight in March 1977 were found to be in starving condition (O'Connell 1980). Almost three-quarters of the larvae that showed signs of starvation were concentrated in 4 of the 64 net tow samples. The present report compares the amount of glycogen in livers of additional larvae drawn from these four samples to that in the livers of larvae from samples taken in the same area, which contained robust larvae almost exclusively.

Glycogen, which is stored in the liver and transformed to glucose as needed to maintain an adequate blood sugar level, is the most immediately available of the three energy sources, glycogen, lipid, and protein (Love 1974). It is known to virtually disappear from the livers of many teleosts after only a few days of starvation (Black et al. 1966; Inui and Ohshima 1966; Bellamy 1968), but fish generally live long beyond the depletion of liver glycogen, maintaining the blood sugar level by gluconeogenesis (Love 1974; Cowey and Sargent 1979). However, there are also teleosts in which liver glycogen does not decline sharply at the onset of starvation, although gluconeogenesis does increase (Cowey and Sargent 1979). Thus abundance of liver glycogen cannot be considered a dependable indicator of starvation in teleosts, at least not for adult stages.

Postyolk-sac larval stages, which first exhibit stained liver glycogen about the time yolk is depleted, are more likely to show a drop in liver glycogen at onset of starvation. First feeding northern anchovy larvae die after only a few days of starvation (O'Connell 1976), indicating that reserves are limited. Lipid reserves, for example, are known to be negligible in early postyolk-sac herring and plaice larvae (Ehrlich 1974), and even at the relatively large size of 35 mm SL northern anchovy larvae survive starvation conditions for only 2 wk, on the average, during which time lipid reserves are severely depleted (Hunter 1976). Presumably liver glycogen declines sharply before lipid reserves are depleted in these early stages.

The estimates of glycogen reserves in the works cited above, and in many others, are derived from weight-based biochemical determinations, which

is not a feasible approach for small larvae already preserved as part of plankton samples at sea. A histochemical approach is feasible, however, and we elected the periodic acid-Schiff (PAS) procedure, which has largely superseded other histochemical tests for glycogen (Davenport 1960).

Cardell et al. (1973) showed good correlation of PAS staining reactions with biochemical determinations of liver glycogen for the rat. Glycogen decreased from about 9% of liver wet weight to 0.7% after 1 d of fasting and to 0.4% after 3 d. At the start of the experiment all hepatocytes had dense masses of intensely stained glycogen. As the fasting period lengthened to 2 and 3 or more days, the masses decreased in size, number, density, and stain intensity, and the number of cells showing glycogen decreased markedly. Presumably such differences in staining reaction in livers of northern anchovy larvae would be an indication of differences in glycogen reserves.

Materials and Methods

In the laboratory, 49 larvae in the size range 3.5-11 mm SL were selected by random dipping from about half of the 37 nearshore net tow samples that showed larvae of generally good histological condition from the March 1977 cruise (O'Connell 1980). Forty-one larvae were selected, also by random dipping, from three of the four nearshore tows containing abundant larvae in generally poor histological condition. An additional dozen larvae were selected from three of the offshore tows.

All larvae had been fixed at time of capture in Bouin's fluid and stored in 70% ethyl alcohol. They were subsequently dehydrated in *n*-butyl alcohol, embedded in paraffin, sectioned sagittally and stained by the PAS method (Preece 1965). We did not subject the material used in this study to diastase digestion tests but feel confident that the red coloration in the livers indicates glycogen. Glycogen gives one of the stronger reactions to the PAS stain (Lillie and Fullmer 1976), and Cardell et al. (1973) established with diastase controls that the PAS-positive material in the livers of rats was glycogen. The diastase test essentially distinguishes between glycogen and mucins (Preece 1965), some of which show strong PAS reactions, but these occur primarily in the integument and epithelia of the digestive tract and various glands of animals (Lillie and Fullmer 1976).

After staining, slides were randomized with their identities concealed and then rated by microscope examination. Each of two observers rated each specimen as High, Medium, or Low, depending on the degree and extent of red coloration in the liver. The Low grade was assigned when livers showed virtually no red color, the High grade when color was strong and widespread. The Medium grade was assigned when color was light and scattered, or irregular. The two readers disagreed on a little >12% of the larvae but never by more than one grading step. These differences were reconciled by reexamination and discussion.

No attempt was made to characterize the specimens stained by the PAS procedure as robust or emaciated on the basis of histological factors per se. There was the possibility that the PAS procedure would be less precise and consistent than the previously used hematoxylin and eosin stain in demonstrating cell and tissue components other than polysaccharides.

Study of material from the sea samples was preceded by analysis of 99 specimens from groups of larvae that were fed or starved in the laboratory. Fixation, staining, and microscope analysis were exactly as outlined above, except that the laboratory material was held in 70% ethyl alcohol for only a few days before dehydration and embedding. Reader disagreement was 9% on the laboratory material.

The larvae obtained from laboratory containers ranged from 5- to 26-d-old. The rotifer *Brachionus plicatilis* was introduced into containers as food at a density of 40 to 60/ml when the larvae were 3-d-old and maintained above 30/ml by additions as needed. The smaller *Gymnodinium splendens* was included as a starting food at the outset, but was not afterwards maintained. Northern anchovy larvae require *Brachionus* at densities of at least 10 to 20/ml to survive and grow well in laboratory containers for the first weeks of life (Theilacker and McMaster 1971).

Food was withheld from two containers, and specimens from these were sacrificed on the first and second day after yolk exhaustion. Starvation at more advanced ages was accomplished by removing the food from selected containers 2 to 4 d before the larvae were sacrificed. Food was removed with a siphon filter devised by P. Paloma for the purpose. A typical air-driven aquarium siphon was enclosed in an 8.89 cm (3.5 in) diameter perforated plastic cylinder covered by nylon netting with 0.333 mm mesh openings, which allowed food organisms but not fish larvae to pass

towards the siphon. The outflow tube of the siphon recurved after passing through the top stopper of the cylinder and terminated in a small perforated cylinder above the water surface. Inside the small cylinder the outflow tube opened into a bag of nylon netting with 0.024 mm mesh openings, which removed food organisms and allowed water to return to the rearing container by dropping onto a small glass plate at the water surface.

Operating at a flow rate of 3 l/h in containers of 12.6 l capacity, the filter reduced *Brachionus* populations ranging from 40 to 100/ml at the start to 7/ml in 1 d, 3/ml in 2 d, and considerably < 1/ml in 3 d. It reduced populations of *Gymnodinium* at about the same rate. At the filtering rate of 3 l/hr, larvae close to the submerged barrier cylinder did not appear to be disturbed.

Results

Laboratory material showed good association between food treatment and PAS glycogen rating over the entire length range involved, 3 to 15 mm SL. The larvae were divided into two groups, those smaller than the median (6.4 mm SL) and those larger than the median. For both size groups, as for all larvae pooled, the majority of High ratings occurred in the "fed" category and the majority of Low ratings occurred in the "starved" category (Table 1). It is noteworthy that only 4 larvae among the 45 from starvation treatments received High ratings. Three of these were from the oldest age group, 26 d (starved 3 d), and were in fact three of the four largest larvae in the entire starved contingent. Examples of stained liver sections representing High, Medium, and Low glycogen ratings are shown in Figure 1.

Larvae from the laboratory trials were fixed in Bouin's solution, as described earlier, to be comparable to the Bouin-fixed sea samples, but a few other fixatives were tested as a matter of perspective. Gendre's solution (Preece 1965) gave somewhat better results than Bouin's, but 10% alcoholic Formalin,[1] which is theoretically a better fixative for preserving glycogen (Davenport 1960; Preece 1965), gave the best results. Some specimens fixed in alcoholic Formalin from fed containers had most hepatocytes solidly filled with deep red color (Figure 1). Presumably more of the glycogen present in the livers at termination was retained with this fixation. However, integrity of cells and tissues of the larvae was not well preserved in alocholic Formalin.

High, Medium, and Low ratings for the ocean-caught larvae (Figure 2) reflect essentially the same levels of staining intensity as for laboratory material. Ocean samples show an appreciably higher proportion of Medium ratings than the laboratory material, but nevertheless exhibit some association between glycogen rating and histological characterization of the samples from which the larvae were drawn (Table 2). However, the association occurs only among the smaller larvae, as indicated by comparing the distributions for larvae smaller and larger than the median, 6.9 mm SL. The smaller larvae show a relatively good proportion of High ratings for robust samples and of Low ratings for emaciated samples. The larger larvae do not exhibit this association.

Significance of the various distributions described above is indicated by X^2 values (Table 3) calculated for each of the six pairs of columns (treated as 2 × 3 contingency tables) from Table 1 and 2. All three X^2 values for the laboratory material clearly reject the null hypothesis, i.e., that there is no association between the two classifications, food treatment and liver glycogen rating. For the ocean material the null hypothesis is rejected only for small larvae, indicating

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

TABLE 1.—Distribution of High, Medium, and Low glycogen ratings, based on PAS staining intensity in livers of northern anchovy larvae fed or starved in the laboratory.

	≤6.4 mm SL		>6.4 mm SL		Pooled	
Glycogen rating	Fed	Starved	Fed	Starved	Fed	Starved
High	14	1	25	3	39	4
Medium	2	7	3	4	5	11
Low	8	18	2	12	10	30

TABLE 2.—Distribution of High, Medium, and Low glycogen ratings, based on PAS staining intensity in livers of northern anchovy larvae from ocean samples showing either generally robust condition or generally emaciated condition. Condition of samples is based on a previous histological study of other specimens from the same collection.

	≤6.9 mm SL		>6.9 mm SL		Pooled	
Glycogen rating	Robust	Emac.	Robust	Emac.	Robust	Emac.
High	7	2	9	8	16	10
Medium	17	5	7	10	24	15
Low	4	10	5	6	9	16

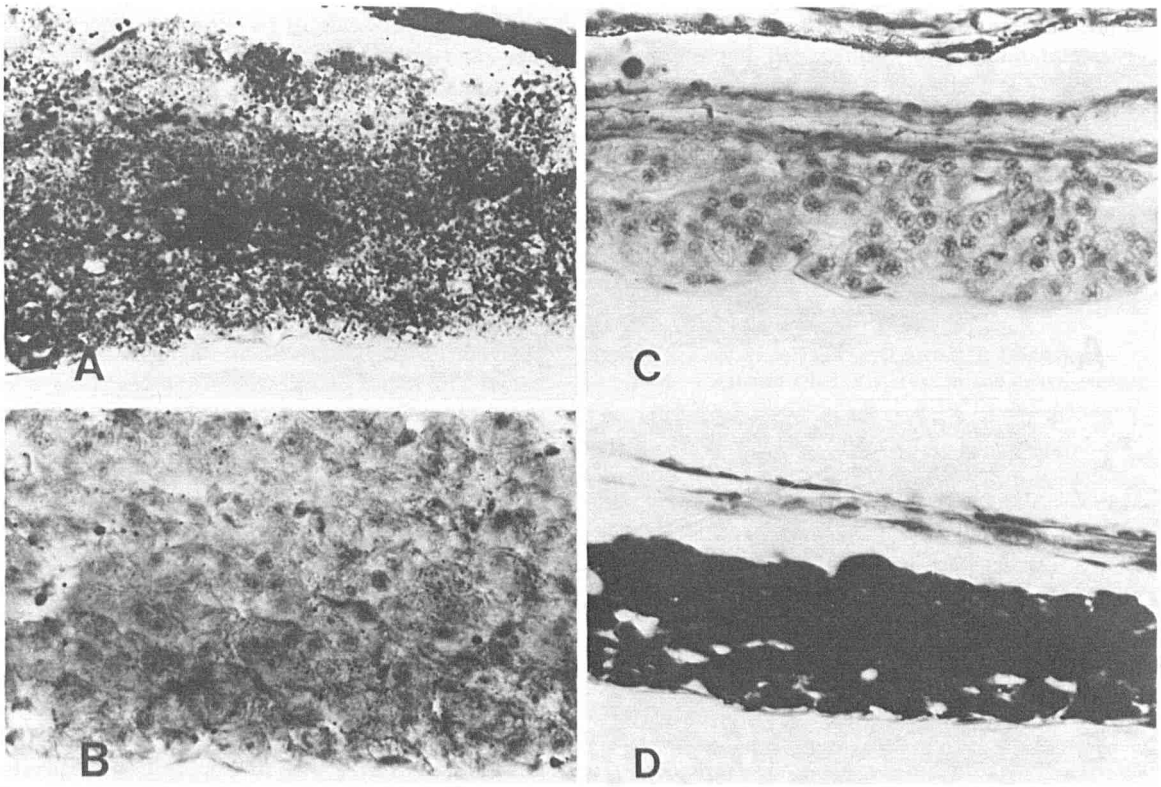

FIGURE 1.—Sagittal sections of livers of northern anchovy larvae from the laboratory, showing the three grades based on intensity of the PAS staining reaction. Except for the nuclei, and occasional portions of other organs, black and the darker shades of grey represent PAS-positive red material presumed to be glycogen. All photomicrographs were taken and processed in the same way. All were taken at 787 ×. A. 5.5 mm larva, fed, graded High. B. 5.0 mm larva, starved, graded Medium. C. 6.1 mm larva, starved, graded Low. D. 5.2 mm larva, fed, graded High. The first three were fixed in Bouin's fluid, but the fourth was fixed in 10% alcoholic Formalin and showed a very intense staining reaction.

TABLE 3.—X^2 and mean contingency square (X^2/n) values for the association between PAS glycogen rating and food treatment for the arrays of larvae shown in Table 1 (laboratory) and Table 2 (ocean). Each set of values is for a 2 × 3 contingency table with (n) larvae and 2 df. In each group, small larvae are those below, and large larvae those above, the median standard length.

Contingency set	n	X^2	P	X^2/n
Laboratory:				
Small larvae	50	17.84	0.001	0.36
Large larvae	49	23.28	.001	.48
Pooled	99	40.13	.001	.41
Ocean:				
Small larvae	43	9.74	.01	.22
Large larvae	43	.47	NS	.01
Pooled	86	4.73	NS	.05

that only for the lower part of the length range is there a meaningful association between treatment (histological characterization of the samples from which larvae were drawn) and liver glycogen rating. As already mentioned, the relevant association is High ratings with samples of generally robust histological condition, and Low ratings with samples of generally emaciated condition. The mean square contingency values (X^2/n) indicate the extent to which the association for small larvae from the ocean is weaker than those from the laboratory.

The dozen larvae from the offshore samples, not included in the above analysis of inshore larvae, showed relatively high liver glycogen ratings. They were almost equally divided among three tows, each of which was taken between 0300 and 0400 h on a different day and contained larvae in a different part of the size range. There were no Low liver glycogen ratings among them. Ratings were largely Medium for the small to medium standard lengths (3.4-7.8 mm) and High for the largest larvae (8.0-9.2 mm). These High ratings, moreover, represent the most intensely PAS

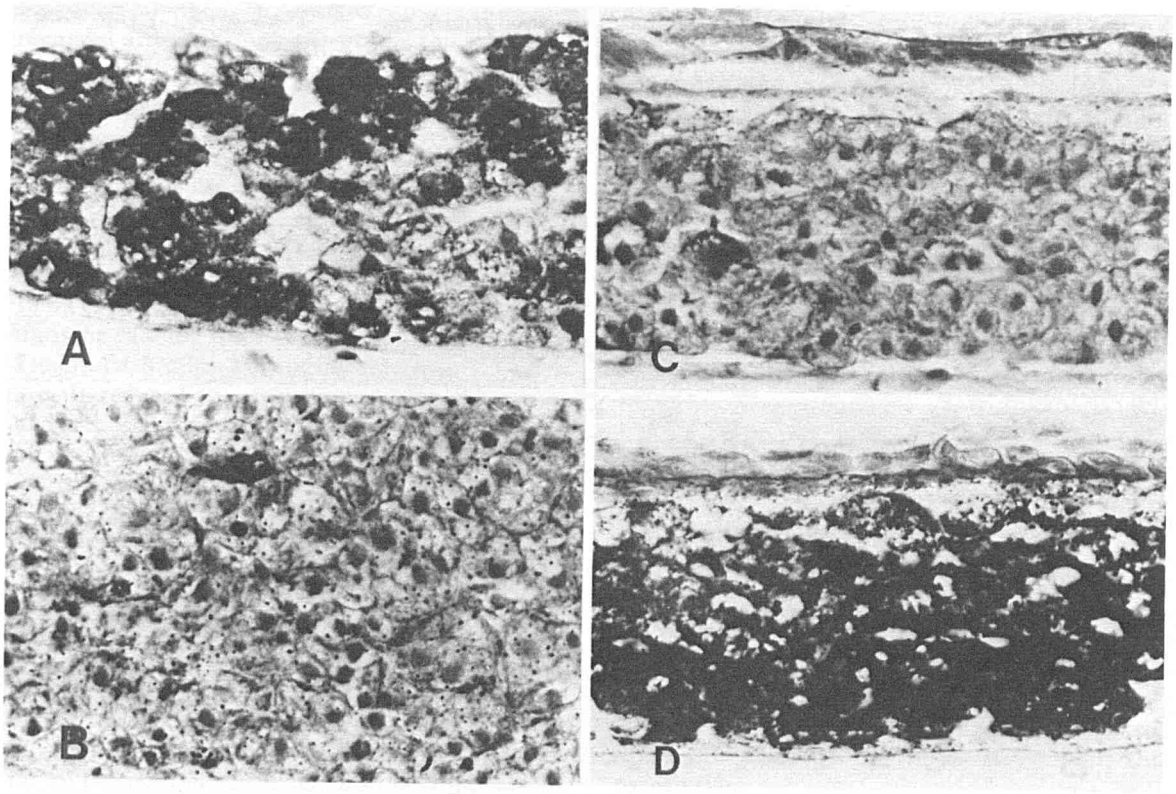

FIGURE 2.—Sagittal sections of livers of anchovy larvae from ocean samples, showing the three grades based on intensity of the PAS staining reaction. Darker shades represent PAS positive red material. Photomicrographs were taken and processed in the same way as those in Figure 1. All were taken at 787 ×. A. 6.2 mm larva, robust sample, graded High. B. 6.3 mm larva, emaciated sample, graded Medium. C. 6.0 mm larva, emaciated sample, graded Low. D. 9.2 mm larva, robust sample, graded High. Whereas the first three are from inshore samples, the fourth is from an offshore sample that produced the most intense staining reactions of all ocean samples.

stained livers in the entire set of ocean specimens (Figure 2).

Discussion

This study was undertaken to determine whether a histochemical test for glycogen in the liver would indicate the occurrence of starvation among northern anchovy larvae from the sea. The results show that variation in glycogen concentration was lower, on the average, for larvae from sea samples classified in a previous histological study (O'Connell 1980) as generally emaciated, than for larvae from samples classified as generally robust. However, the difference was not as strong as it was for larvae that were fed or starved in the laboratory.

Glycogen stored in the livers of fishes can be severely reduced by sustained swimming activity at moderate levels (Miller et al. 1959; Pritchard et al. 1971) or by starvation (Love 1974). It may also undergo some change relative to daily cycles of feeding and nonfeeding. There is no reason to believe that undue exercise was involved in the present case, and the data do not indicate a relation between glycogen rating and hour of capture. Starvation therefore seems the most likely explanation of the low levels shown by certain samples studied here, and this is supported by the relation of glycogen level to plankton volume, a not unreasonable index of food availability in the sea. For those sea samples characterized as emaciated and showing low liver glycogen reserves, the plankton volumes were among the lowest volumes obtained on the March 1977 cruise (O'Connell 1980). These low plankton volumes can be assumed to represent reduced but not essentially nonexistent food, as does

the starvation treatment in the laboratory. This difference might account for the greater proportion of Medium ratings in the ocean samples, robust as well as emaciated. In any event, a moderate proportion of Medium glycogen ratings for the ocean samples is not inconsistent with the earlier histological assessments. The emaciated samples, for example, contained only 60% larvae showing histological signs of moderate to severe emaciation or starvation (O'Connell 1980).

The apparently higher level of liver glycogen among larvae from offshore samples further indicates that food availability is an important factor governing liver glycogen reserves. The plankton volumes for all offshore samples averaged considerably higher than the plankton volumes for inshore samples (O'Connell 1980). Moveover, the particular offshore sample that produced the larvae with the most intense PAS indications of liver glycogen had the second highest plankton volume of the entire 1977 cruise.

The fact that the association of glycogen reserves and histological condition is evident for only the smaller larvae from the sea might mean that as larvae become larger, they can better tolerate fluctuations in the plankton regime. There was a hint of this also in the laboratory results. Marine fish larvae in general select progressively larger prey and also a broader size range of prey as they grow, and engraulids tend to increase maximum prey size markedly between 8 and 12 mm SL (Hunter in press). Thus a reduction in any part of the crustacean plankton community, but particularly among the smaller organisms, could be detrimental primarily to the smaller larvae.

The PAS staining procedure appears, then, to be capable of demonstrating the presence of starvation effects in a larval fish population. On balance, it is a more readable indicator than the comprehensive histological analysis, but it also provides less information. The level of liver glycogen reflects the status of only the first line of energy reserve, whereas histological analysis, with more varied indications, is more sensitive to the extent of emaciation that has been sustained by the larva. Perhaps both approaches can be applied to the same larva, but if so, the histological indications should be interpreted cautiously. Our impression is that tissues of larvae can be moderately distorted and degraded by the PAS procedure regardless of feeding history or fixative. On the other hand, the histochemical test might provide a sufficient characterization of the condition of larval fish samples for some purposes, especially if fixation is optimized for the preservation of glycogen.

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Page 565, right column, second paragraph, line 4, correct to read:

ues reached 0.305 then dropped to 0.121 for 1964-

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