A UNITED STATES DEPARTMENT OF COMMERCE PUBLICATION

NOAA FSYB-A 71-1

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Fishery Bulletin

U. S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

Vol. 71, No. 1 January 1973

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Seattle, Wash.

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National Oceanic and Atmospheric Administration

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Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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Seattle, Washington

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DISTRIBUTION OF MACROSCOPIC REMAINS OF RECENT ANIMALS FROM MARINE SEDIMENTS OFF MASSACHUSETTS

ROLAND L. WIGLEY[1] AND FREDERICK CHARLES STINTON[2]

ABSTRACT

Macroscopic animal remains are common constituents of bottom sediments on the continental shelf and upper continental slope south of Cape Cod, Mass. The largest quantities are in sandy deposits in the vicinity of Nantucket Shoals, where they form nearly 30% by volume of the total substrate. The smallest quantities are along the outer continental shelf and upper slope, where animal remains generally make up less than 1% of the substrate. Representatives of all three major realms of aquatic animals contribute to the prefossil skeleton assemblages; benthic forms are the principal components, nektonic forms are common, and planktonic forms are rare. The quantitatively dominant taxonomic groups present in the sediments are: echinoderms, mollusks, and teleosts.

Typical specimens of all groups represented in the samples are illustrated. Charts and graphs show the geographic and bathymetric distributions of the common species.

Durable remains of recently (up to several thousand years) deceased animals and plants constitute an important, but frequently overlooked, link between living organisms and their fossils. Reconstruction of the marine environment that existed in past geological ages can be better approximated when present-day marine populations and processes are well understood. A conventional approach used in paleobiological investigations is to equate the habits, ecological requirements, and functional morphology of fossil species with their living relatives (Ladd, 1957; and others). Consequently, a thorough knowledge of existing life is valuable to geological advancement. Events during the transitional phase between death and fossilization may strongly influence the dispersal, shape, and associated species of fossil remains. Frequently these events must be clearly understood to interpret fossil findings correctly and completely. It is in this context that the prefossil stage is considered to be significant in determining the history of life.

A series of samples collected from the ocean bottom off southeastern Massachusetts provide an insight into the composition and the geographic distribution of macrobenthic, nektonic, and planktonic animal skeletons—or portions thereof—that occur in continental shelf bottom sediments and that are available for fossilization. Thus the purpose of this report is to describe qualitatively and quantitatively the macroscopic animal remains (durable portions of recently dead animals) in the bottom sediments of this representative portion of the continental shelf in New England.

To avoid undue repetition of the words "dead," "deceased," "remains," and similar descriptive terms throughout this report, it must be emphasized at the outset that all samples of animal materials dealt with in this report are the remains of dead animals. Accounts of the living organisms obtained in these collections will be dealt with in other reports.

Previous studies of paleontological interest pertaining to prefossil marine animal remains are very diverse in subject. A few examples of these studies include such dissimilar topics as: the composition and distribution of mollusk shell remains (Habe, 1956; and others), biological alteration of bottom sediments (Schäfer, 1956; Rhoads, 1966; and others), comparison

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Manuscript accepted May 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

of the feeding habits and sediment types inhabited by epifaunal and infaunal benthic animals (Craig and Jones, 1966), catastrophism in the sea (Gunter, 1947; and others), position of pelecypod shells in different environments (Emery, 1968), burial of mollusk shells (Johnson, 1957), radiocarbon dating of relict oyster shells (Merrill, Emery, and Rubin, 1965), and other related subjects. Most of these studies are restricted to one specific topic. The present study, likewise, has a limited objective: to describe the species composition and distribution of macroscopic prefossil animal remains.

Literature pertaining to present-day mollusk remains in marine bottom deposits is relatively common; see references in Habe (1956), Schäfer (1956), Johnson (1957), Belyaev (1970), and others. In contrast, however, a paucity of reports dealing with prefossil fish remains became strikingly evident during our literature search. Research on this subject tends to be regionally oriented. For example, the study by Jensen (1905) deals with otoliths from an Arctic basin. David (1947) and Soutar (1967) described fish remains from off southern California, and Belyaev and Glikman (1970) describe selachian teeth from a broad expanse of the Pacific Ocean. A major exception to this regional basis is the report by Brongersma-Sanders (1949), which summarizes the earlier literature pertaining to fish remains (albeit mostly fossil) from many parts of the world.

Prefossil remains of marine organisms are more easily obtained than are those of most terrestrial or aerial forms. Macrobenthic and nektonic organisms are usually abundant on continental and insular shelves, and their skeletal components are massive compared with those of microplanktonic pelagic forms. As a result, the "fossil assemblages" (Craig, 1953) of the continental shelf are dominated by macroscopic organisms, as opposed to planktonic forms that make up the bulk of deep-sea fossils. Likewise, the prefossil material of organic origin on continental and insular shelves is generally of a larger size, and the macrofaunal components are considerably more abundant than they are in the deep sea.

MATERIALS AND METHODS

Samples were collected 11-20 June 1962, from the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) RV *Delaware* at 62 stations south of Martha's Vineyard, Mass. (Table 1; Figure 1). Stations were spaced at intervals of 16 km on a grid pattern having eight north-south transects at right angles to the depth contours. Quantitative bottom samples, including sediments and the constituent benthic fauna, were collected with a Smith-McIntyre grab sampler (Smith and McIntyre, 1954). This instrument effectively sampled a 0.1-m^2 area of bottom to a depth of about 10 to 17 cm. The volume of bottom material analyzed from individual samples averaged 8.9 liters. At sea, contents from the grab were washed on a 1-mm mesh sieving screen. Material remaining on the screen after washing was removed and preserved in a solution of neutral Formalin.[3] In the laboratory ashore.

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

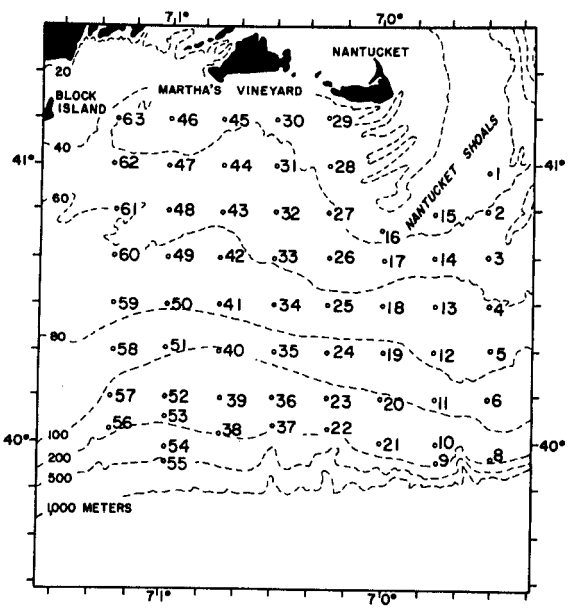

FIGURE 1.—Location of stations at which bottom samples were collected for determining the distribution of the remains of marine animals. Isobaths are indicated by dashed lines.

TABLE 1.—Station location, water depth, sediment type, and volume of bottom samples collected south of Martha's Vineyard, Mass., 11-20 June 1962.

Station number	Lat N	Long W	Water depth	Sediment type	Sample volume
			m		*liters*
1	40°58′	69°30′	46	Sand & gravel	2
2	40°51′	69°31′	46	Sand	4½
3	40°40′	69°31′	51	Sand	2¾
4	40°30′	69°29′	62	Sand	6¾
5	40°21′	69°30′	76	Sand	3¾
6	40°10′	69°31′	91	Sand	5¾
8	39°57′	69°30′	183	Sand	4¾
9	39°56′	69°45′	201	Sand	3¾
10	40°00′	69°45′	139	Silty sand	4¼
11	40°10′	69°45′	95	Silty sand	4¼
12	40°20′	69°46′	79	Sand	6¼
13	40°30′	69°45′	73	Sand	9¾
14	40°40′	69°45′	59	Sand	4½
15	40°50′	69°45′	37	Sand	6
16	40°46′	70°00′	38	Sand	2¾
17	40°39′	69°59′	49	Sand	4¾
18	40°30′	70°00′	73	Sand	11¾
19	40°20′	69°59′	91	Sand	7
20	40°10′	70°00′	117	Sand	¾
21	40°00′	70°00′	165	Sand	10¼
22	40°03′	70°15′	183	Silty sand	9¾
23	40°10′	70°15′	113	Silty sand	12¾
24	40°20′	70°15′	90	Silty sand	14¾
25	40°30′	70°15′	70	Sand	14
26	40°40′	70°15′	51	Sand	10
27	40°50′	70°15′	44	Sand	9¼
28	41°00′	70°15′	33	Sand	7¾
29	41°11′	70°16′	27	Sand	4¾
30	41°10′	70°30′	38	Sand	10
31	41°00′	70°30′	48	Sand	9¾
32	40°50′	70°30′	59	Sand	14¼
33	40°40′	70°30′	62	Silty sand	14¾
34	40°30′	70°30′	73	Sandy silt	13¾
35	40°20′	70°30′	97	Sandy silt	10¾
36	40°10′	70°30′	128	Silty sand	14¾
37	40°04′	70°29′	220	Sand	11½
38	40°02′	70°44′	194	Silty sand	5¾
39	40°10′	70°45′	132	Silty sand	14¾
40	40°20′	70°46′	106	Sand-silt-clay	14¾
41	40°30′	70°45′	79	Sandy silt	14¼
42	40°40′	70°45′	66	Silty sand	7½
43	40°50′	70°45′	55	Sand	9¾
44	41°00′	70°45′	51	Sand	7¾
45	41°10′	70°45′	38	Sand and gravel	5
46	41°10′	71°00′	40	Sand	6½
47	41°00′	71°00′	51	Sand and gravel	12¼
48	40°50′	71°00′	59	Sand	4¾
49	40°40′	71°00′	70	Sandy silt	14¾
50	40°30′	71°00′	84	Clayey silt	14
51	40°21′	71°00′	99	Sandy silt	14¾
52	40°10′	71°00′	146	Silty sand	4¾
53	40°06′	71°00′	179	Silty sand	11¾
54	39°59′	71°00′	366	Silt	11¾
55	39°56′	71°00′	567	Silt	10
56	40°03′	71°16′	183	Sand	10¾
57	40°10′	71°15′	110	Silty sand	7¾
58	40°20′	71°15′	91	Silty sand	14½
59	40°30′	71°15′	77	Silty sand	14¼
60	40°40′	71°15′	62	Sand	14½
61	40°50′	71°15′	62	Sand	12¾
62	41°01′	71°16′	48	Sand	¾
63	41°10′	71°15′	38	Sand	4¾

mineral matter and associated debris were removed by hand sorting, and the animals and animal remains were separated by species, identified, and counted. Only animal remains are considered in the present report.

Water depths at which samples were collected ranged from 27 to 567 m.

Sediment samples were collected at each station and at two localities equally spaced between stations along the cruise track. Of the 186 samples collected, 60 were analyzed in detail for particle size, and the remaining 126 were examined in the laboratory by field techniques. Names of the various sediment types are in accordance with the classification reported by Shepard (1954) and Emery (1960).

DESCRIPTION OF THE AREA

Three major physical features that have an important impact on the occurrence, distribution, and condition of the prefossil animal remains in this area are: physiography, bottom sediment composition, and hydrography. These features are briefly discussed below.

PHYSIOGRAPHY

The area studied is about 130 km square and extends across the continental shelf and the upper portion of the continental slope. Bottom configuration is moderately smooth; water depths increase gradually and rather uniformly from shore outward to the shelf break, which is at a depth of about 120 m. Beyond the shelf break, on the continental slope, the depth gradient is relatively steep, averaging 4°. Detailed bathymetric charts of this area having contour intervals of 1 fathom were published in 1967 by the U.S. Department of Commerce and U.S. Department of the Interior (Coast and Geodetic Survey, Bathymetric Maps numbers: 0708N-52 and 53; 0808N-51 and 52; and 0807N-51).

BOTTOM SEDIMENT COMPOSITION

Bottom sediments in the area are composed of relict glacial material—principally nonbiogenic sands and silts plus a few gravel patches

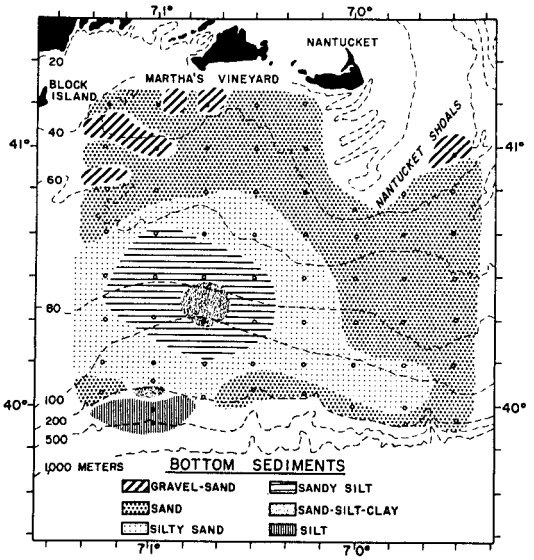

FIGURE 2.—Distribution of the various types of bottom sediments in the study area. Terminology is based on the classification reported by Shepard (1954) and Emery (1960).

of glacial erratics. Six major sediment types occur in the area (Figure 2). The terminology used is based on the standard Wentworth particle size classification (Twenhofel and Tyler, 1941; and others) and the nomenclature is that of Shepard (1954) and Emery (1960). Three types—sand, silty sand, and sandy silt—are distributed over a rather large area; the other three—gravel-sand, sand-silt-clay, and silt—have limited areal distributions. Sands cover more than half of the area. They occur mainly in shallow water (less than 60 to 80 m), except in the eastern sector and in a narrow (6 km) band parallel to the isobaths just below the outer periphery of the continental shelf. Sands and silts in the vicinity of the shelf break are primarily glauconitic. In shallow waters near Nantucket and Martha's Vineyard and in the vicinity of Nantucket Shoals, the sands are silt free and occasionally mixed with large quantities of shell. Mixtures of sand and gravel also occur in scattered patches in the shallower waters of the northwest sector and in Nantucket Shoals. Limonitic pellets and sand particles heavily stained with iron oxide are common in the northwest sector. Admixtures of silt occur with the sand over most of the remaining area.

A large (80 by 100 km) area of fine-grained sediments is situated in the southwestern sector. A relatively small circular area of sand-silt-clay near its center is surrounded by an inner band of sandy silt and an outer band of silty sand. Characteristically, the relatively large sand grains throughout the area of fine-textured sediments are frosted rounded quartz particles. Pyrite-filled foraminiferal tests occur in the eastern portion.

On the continental slope below the sand zone, the dominant sediment component is silt.

Additional information concerning sediments of this area and references to the geological literature were given by Uchupi (1963), Wigley and McIntyre (1964), Emery, Merrill, and Trumbull (1965), Emery (1966), Garrison and McMaster (1966), McMaster and Garrison (1966), and Wigley and Emery (1967).

HYDROGRAPHY

Within the area the water temperature regime is typically warm-temperate, although the boreal influence is seasonally significant. Surface temperatures are substantially higher than bottom temperatures; offshore surface waters are somewhat warmer than inshore waters throughout most of the year; temperatures of the entire water column change seasonally and to some extent from year to year. Most pertinent to the subject of this report are bottom water temperatures and nontidal currents.

A cell of cold (6.6°C in June 1962) bottom water extends in an east-west band from the New York region eastward to long 70°W (eastern Nantucket Island). This cell occurs at depths of about 40 to 80 m, which is roughly the midshelf region. At 300 to 600 m the bottom water temperatures are low and nearly constant throughout the year; they generally range between 4° and 7°C. Near the shelf break and upper continental slope the bottom temperatures are substantially higher, but also nearly constant; values range near 10° to 12°C throughout the year. Offshore shelf waters, especially in shallow sectors, may range from 3°C in Feb-

ruary-March to 14°C in September-November. Temperatures of inshore surface waters substantially exceed these values.

Nontidal movements of water masses on the continental shelf within the area are generally westward. Water in the Gulf of Maine and Nantucket Sound tends to flow southwesterly across Nantucket Shoals and into the area. Conversely, surface waters offshore beyond the continental shelf flow easterly. Authors who have published further information on the hydrography of the area include Bigelow (1927, 1933), Bumpus and Day (1957), Bumpus et al (1957), Day (1958), and Colton (1964, 1968, 1969).

ORDER OF DISCUSSION

The most common animal remains in the samples studied were echinoderms, mollusks, and fish. Considerably less common than the foregoing were remains of crustaceans and coelenterates. The order in which these groups are discussed below is according to the abundance of remains in each major group, namely, echinoderms, mollusks, fish, and crustaceans and coelenterates.

REMAINS OF ECHINODERMS

Echinoderms were the most numerous and quantitatively dominant group of animal remains occurring in the area. The sole contributors in this group were the echinoids. Spines and test fragments were rare to very abundant and were widely distributed. Presumably the skeletal fragments of asteroids and ophiuroids, of which living members of both groups are common in this region, were generally too small to be recovered using the 1-mm mesh screen. Of all macroscopic animals in the samples, the common sand dollar, *Echinarachnius parma* (discussed in the following subsection), was by far the leading component. Spines were the principal structures recovered from heart urchins and sea urchins. Some examples of typical echinoderm remains are illustrated in Figure 3.

The size of fragments of most organisms discussed in this section ranged from 1 mm (sand size) to 1 cm or more. The largest remains were tests of whole or nearly whole *E. parma*. Adult size of living members of this species (about 7 cm) is less than some of the other nonmolluskan species, but the comparatively strong, compact test is much more resistant to fracture. This durability, plus the enormous supply in the form of living individuals, contributed to the abundance of fragments of this species in the sediments. Counting the *E. parma* and other echinoids was impractical owing to the enormous numbers of small fragments, plus a gradation in size that precluded the separation of major fractions from minor ones. Occurrence of *Brisaster fragilis, Echinarachnius parma,* and *Strongylocentrotus drobachiensis* are listed by stations in Table 2.

ECHINARACHNIUS PARMA

Remains of *E. parma* were widespread (Table 2) and numerous. This species ranked first in volume and number of fragments of all organic remains in the study area; it occurred at 73% of the stations. It was most abundant in the vicinity of Nantucket Shoals (stations 2, 3, and 16). *E. parma* fragments made up nearly 30% (by volume) of the substrate near station 3. In deepwater areas in the vicinity of the middle and outer shelf, the density of fragments was low—occasionally less than 50/m^2 or about 0.01% by volume. (All animal remains combined generally formed less than 1% by volume of the substrates of the outer shelf and slope.)

The distribution of *E. parma* extended from the shallow inshore areas across the entire shelf to the upper portion of the continental slope (Figure 4). Surprisingly, it was rather sparse near the middle of the shelf. Fragments from inshore areas were different in size, color, and sphericity from those collected offshore. Test fragments from the inshore zone, which extends out to 50 or 70 m, were whitish, usually larger than 5 mm in greatest dimension, and had sharp and angular edges and apexes (Figure 3A). Fragments from depths of about 80 m or more were greenish-brown, commonly less than 5 mm long, and had rounded edges. In contrast to the fresh, new appearance of the test fragments

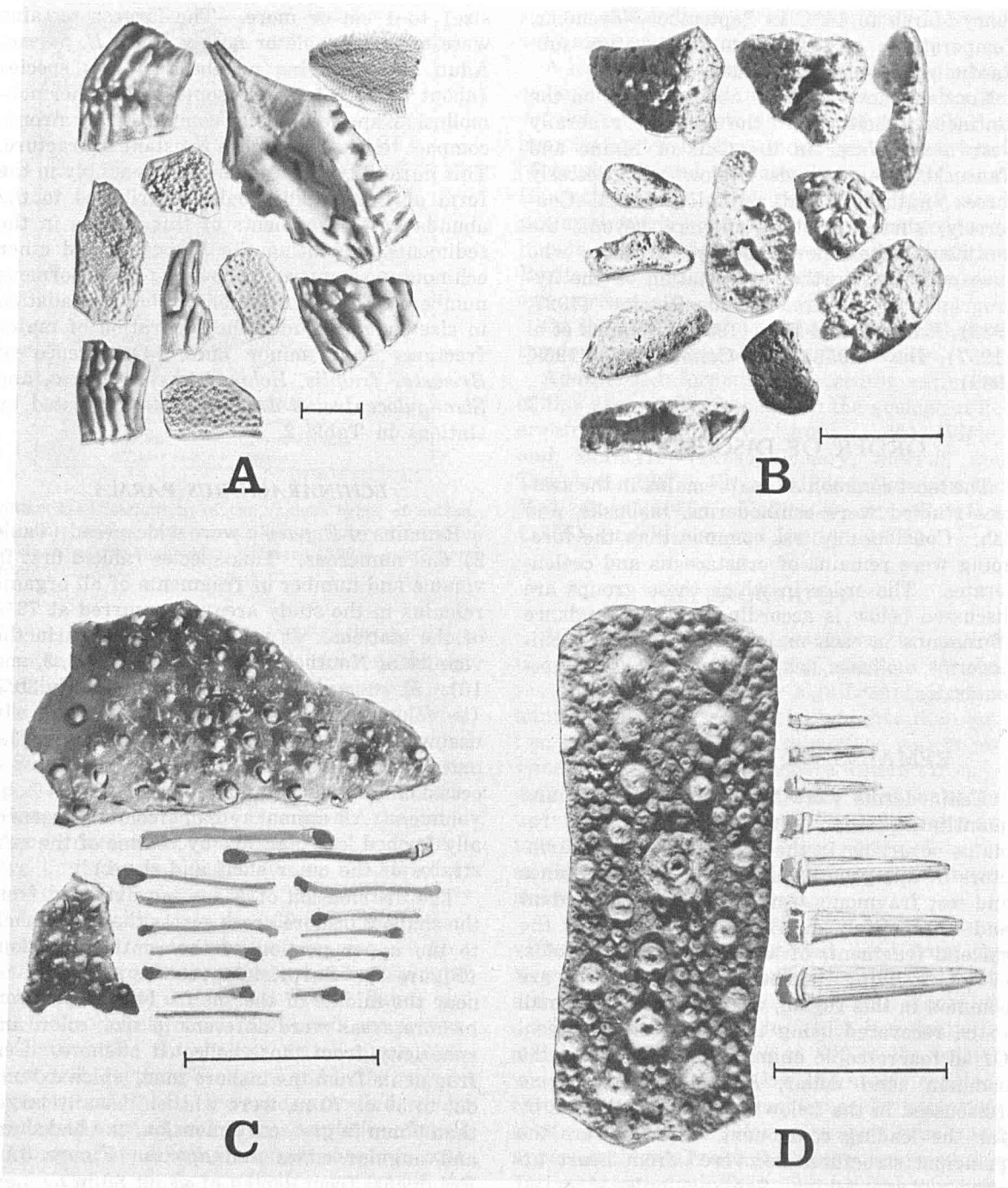

FIGURE 3.—Skeletal remains of echinoderms. A - *Echinarachnius parma*, test remains from shallow water; B - *E. parma*, test remains from deep water; C - *Brisaster fragilis*, test fragments and spines; D - *Strongylocentrotus drobachiensis*, test fragments and spines. Each scale bar is 5 mm.

TABLE 2.—Occurrence, by station, of the remains of three species of echinoderms. Present (+), absent (—).

Station number	*Echina rachnius parma*	*Brisaster fragilis*[1]	*Strongylo-centrotus drobachensis*
1	+	—	+
2	+	—	—
3	+	—	—
4	+	—	—
5	+	—	—
6	+	—	—
8	—	+	—
9	+	—	+
10	+	—	—
11	+	+	—
13	+	—	—
14	+	—	—
15	+	—	—
16	+	—	+
17	+	—	—
18	+	—	—
20	—	+	—
21	+	+	—
22	+	+	—
23	+	+	—
24	+	+	—
26	+	—	—
27	+	—	—
28	+	—	—
29	+	—	—
30	+	—	—
31	+	—	—
33	+	—	—
35	+	+	—
36	+	+	—
37	—	+	—
38	+	+	+
39	—	+	—
40	+	+	—
41	+	—	—
43	+	—	—
44	+	—	—
45	+	—	—
46	+	—	—
47	+	—	—
49	+	—	—
51	+	+	+
52	+	+	+
53	+	+	—
54	—	+	—
56	+	+	—
57	+	—	—
61	+	—	—
62	+	—	—
63	+	—	—

[1] May include some fragments of *Echinocardium* or *Schizaster*.

from the inshore zone, shells from deep water appeared old and worn (Figure 3B). The characteristics of specimens from the area between the two depth zones were intermediate.

OTHER SPECIES

Brisaster fragilis (Figure 3C) was distributed in a broad east-west band along the outer

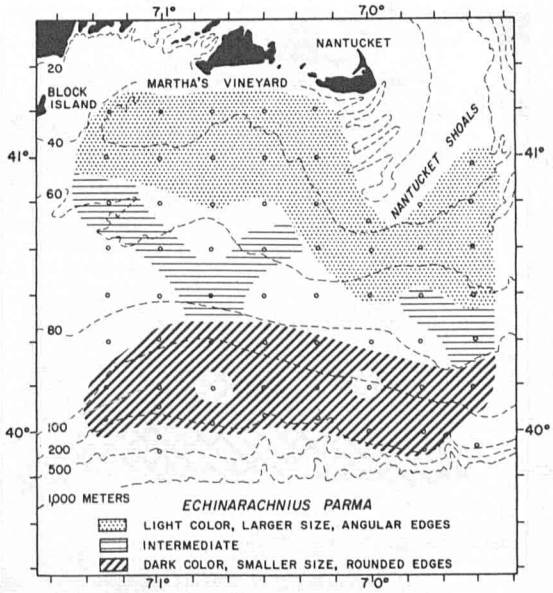

FIGURE 4.—Geographic distribution of remains of tests of *Echinarachnius parma*. Three categories of size, color, and sphericity are shown separately.

continental shelf and upper slope (Figure 5). The fragments were generally small and scattered. Even when all species are considered as a group, only a few spines or test fragments occurred in any one sample. Range in water depth for this echinoid was 90 to 366 m. Water depth range is compared with that of other species of echinoderms in Table 3 and illustrated in Figure 6.

The green sea urchin, *Strongylocentrotus drobachiensis* (Figure 3D), was represented chiefly by spines and less commonly by test fragments. The remains were rather widely scattered among six stations; two were in the

TABLE 3.—Bathymetric distribution of three species of echinoderms and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	*m*	*m*	
Brisaster fragilis[1]	90	366	155	18
Echinarachnius parma	27	201	84	45
Strongylocentrotus drobachiensis	38	201	121	6

[1] May include some spines of *Echinocardium* and *Schizaster*.

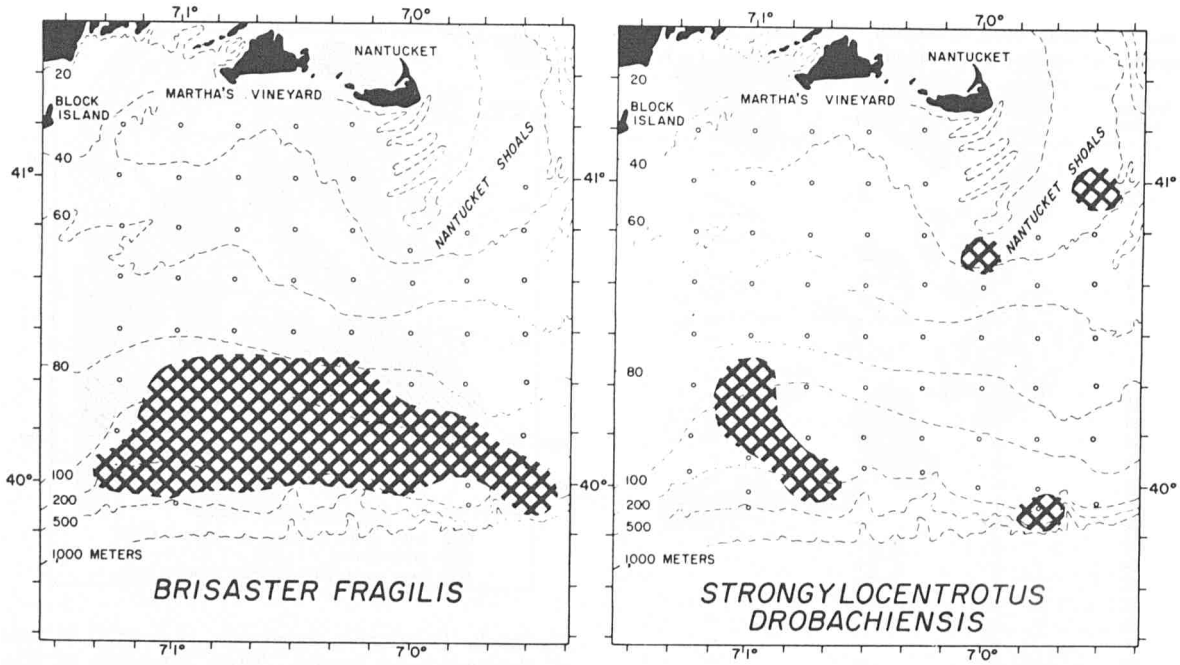

FIGURE 5.—Geographic distribution of skeletal remains of the echinoderms *Brisaster fragilis and Strongylocentrotus drobachiensis.*

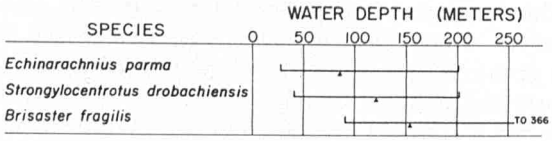

FIGURE 6.—Bathymetric range and mean depth of occurrence of echinoderm remains. (Mean values are listed in Table 3.)

shallow waters of Nantucket Shoals and the other four were in moderate to deep water near the shelf break (Figure 5). Bathymetric range at the locations where this species was found was from 38 to 201 m (Table 3, Figure 6).

REMAINS OF MOLLUSKS

Remains of mollusks were among the most common organic seabed constituents. In total abundance they ranked second; only the echinoderms were more plentiful. Four major groups of mollusks were represented in the material analyzed. Pelecypods were the most abundant molluscan group, gastropods ranked second, and the cephalopods and scaphopods were present in relatively small quantities. These groups are discussed below in the order of their abundance.

PELECYPODS

Pelecypod shells were abundant and conspicuous components of the prefossil animal remains. In addition to their relatively large size, often the color and texture of the shell surface contrasted sharply with the sediments in which they occurred. Size of the shells ranged from such large, robust species as *Spisula solidissima* (12 cm), *Arctica islandica* (10 cm), and *Placopecten magellanicus* (10 cm), to such small, fragile forms as *Thyasira gouldi, Nucula proxima, Bathyarca pectunculoides,* and others, all of which were 5 mm or less. A total of 57 species representing 40 genera were collected. Typical species are illustrated in Figure 7. Pelecypod remains were very widespread; they were collected at all stations except three (3, 47, and 62).

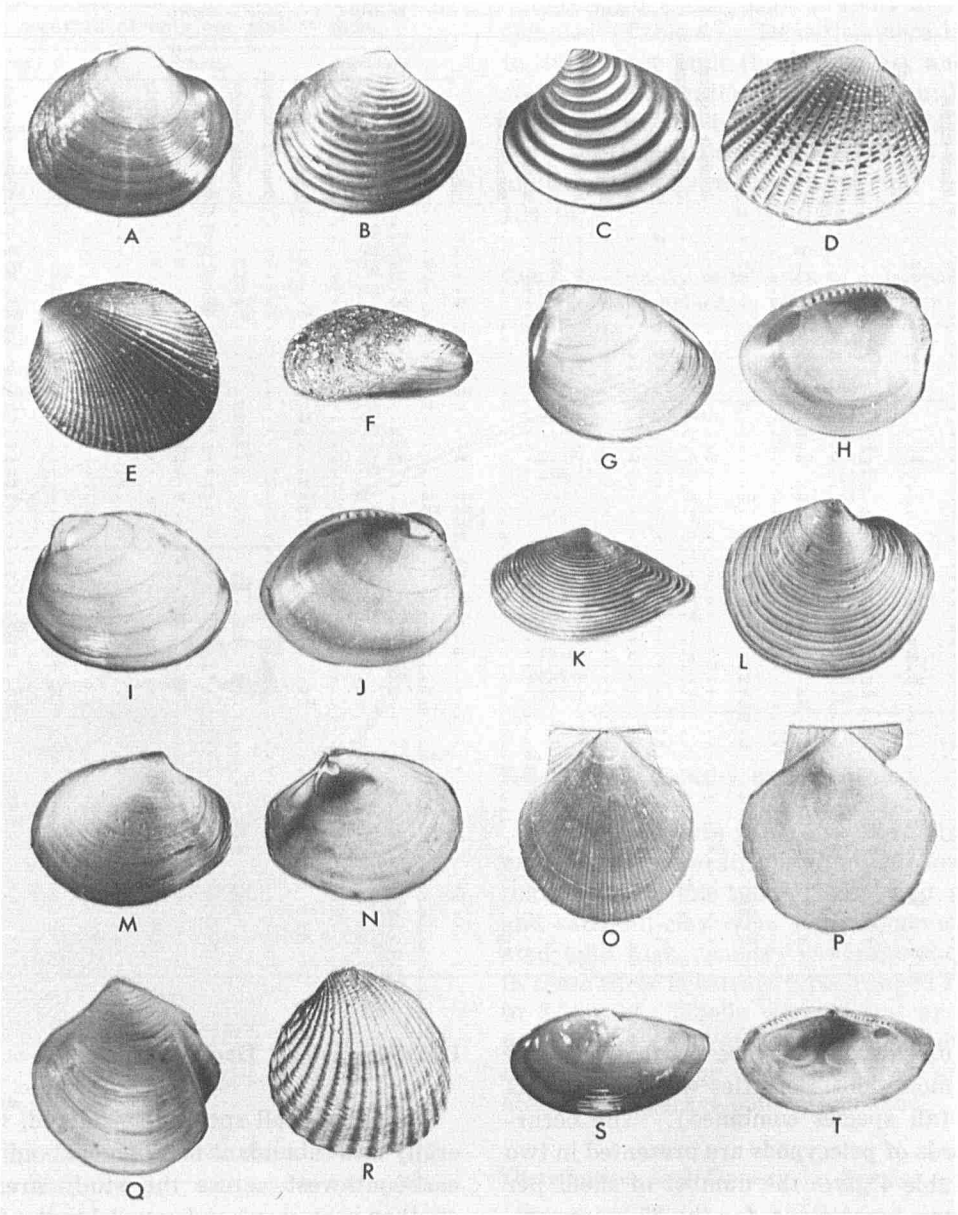

FIGURE 7.—Representative pelecypods from off southeastern Massachusetts. A - *Arctica islandica* (×0.7); B - *Astarte subequilatera* (×1); C - *Astarte undata* (×2); D - *Cerastoderma pinnulatum* (×2.6); E - *Crenella glandula* (×4); F - *Modiolus modiolus* (×0.7); G - *Nucula proxima* (×5); H - *Nucula proxima*, interior (×5); I - *Nucula tenuis* (×3.3); J - *Nucula tenuis*, interior (×3.3); K - *Nuculana acuta* (×4); L - *Phacoides filosus* (×2.6); M - *Periploma papyracea* (×2.6); N - *Periploma papyracea*, interior (×2.6); O - *Placopecten magellanicus*, left valve (×0.7); P - *Placopecten magellanicus*, right valve (×1); Q - *Thyasira trisinuata* (×3.3); R - *Venericardia borealis* (×1.3); S - *Yoldia sapotilla* (×2); T - *Yoldia sapotilla*, interior (×2).

Table 4.--Species and density (number per square meter), by station, of the common pelecypods.

Station number	Anomia aculeata	Arctica islandica	Astarte castanea	Astarte subequilatera	Astarte undata	Bathyarca pectunculoides	Cerastoderma pinnulatum	Crenella decussata	Crenella glandula	Cuspidaria perrostrata	Cyclopecten thalassinus	Ensis directus	Limatula subauriculata	Limopsis sulcata	Lyonsia hyalina	Mesodesma arctatum	Modiolus modiolus	Musculus niger	Nucula proxima	Nucula tenuis	Nuculana acuta	Pandora gouldiana	Periploma leanum	Periploma papyracea	Phacoides blakeensis	Phacoides filosus	Pitar morrhuana	Placopecten magellanicus	Spisula solidissima	Thyasira gouldi	Thyasira ovata	Thyasira plana	Thyasira trisinuata	Venericardia borealis	Yoldia sapotilla	Unidentified
1	20	-	150	-	-	-	-	-	10	-	-	-	-	-	-	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30
4	-	10	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	80	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	-	-	40	10	-	60
6	30	160	10	1,560	-	-	-	-	110	-	10	-	-	-	-	30	-	-	-	10	-	10	-	30	-	90	-	30	30	-	-	-	150	2,120	160	60
8	30	-	-	30	10	70	110	-	50	10	20	-	-	-	-	-	-	-	-	-	170	-	-	-	-	90	-	-	-	-	-	100	20	10	90	160
9	70	-	-	-	110	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	-	-
10	10	-	-	100	660	20	-	-	-	-	-	-	-	40	-	-	-	-	10	-	160	-	-	-	-	250	20	-	-	-	-	-	20	200	30	-
11	-	130	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	40	-	170	-	150	-	-	-	-	110	70	80	10
12	-	40	-	-	40	-	120	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	30	-	-	-	-	140	20	20	30
13	-	40	-	-	130	-	60	30	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	10	-	-	-	-	110	-	30	-
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
16	10	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	-	-	-	-	10
17	-	10	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-
18	-	760	-	-	10	-	10	70	20	-	-	-	-	-	-	-	-	-	50	10	-	-	-	-	-	10	-	30	-	-	-	-	230	-	50	-
19	-	20	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	80	-	70	-	40	-	-	-	-	50	-	50	-
20	-	-	-	-	50	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	80	-	-	-	-	-	-	60	160	-	-
21	-	-	-	50	280	-	30	-	-	-	-	-	10	-	-	-	-	-	-	-	550	-	-	-	-	190	-	10	-	-	-	-	10	150	160	10
22	40	-	-	290	40	10	120	-	-	10	-	-	10	-	-	-	-	-	40	-	760	-	-	-	-	240	-	10	-	-	-	-	40	70	90	-
23	-	-	-	-	170	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	40	10	-	10	-	-	-	-	10	120	-	-
24	-	70	-	-	10	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	20	-	-	-	-	50	-	-	80	20	20	-
25	-	2,080	-	-	-	-	60	-	110	-	-	-	-	-	-	-	-	-	250	40	-	30	-	30	-	-	-	30	-	-	-	-	1,160	-	350	-
26	-	40	-	-	30	-	10	-	-	-	-	-	-	-	-	-	-	-	1,360	230	-	-	-	40	-	-	-	-	-	-	-	-	70	-	40	-
27	-	50	-	-	10	-	50	-	-	-	-	-	-	-	-	-	-	-	1,360	250	-	-	-	90	-	10	-	-	-	-	-	-	-	-	360	-
28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	10
29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	-	-	-	20	-	20	-	-	-	-	-	-	-	-	-	-	-	90	-	-	-	-	-	-	-	20	-	-	-	-	-	-	120	30	10
31	-	-	-	-	30	-	30	-	-	-	-	-	-	-	-	-	-	-	60	-	-	-	20	20	-	20	20	-	-	-	-	-	10	-	50	-
32	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	140	-	-	-	-	-	-	130	-	90	-
33	-	870	-	-	-	-	140	-	10	-	-	-	-	-	-	-	-	-	90	20	-	-	-	10	20	-	-	30	-	-	-	-	330	10	90	-
34	-	220	-	-	-	-	140	-	30	-	-	-	-	-	-	-	-	-	10	-	-	-	-	10	-	-	-	20	-	-	-	-	40	-	70	-
35	-	430	30	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	30	-	90	-	70	-	-	-	-	220	110	60	-
36	-	-	-	10	40	10	20	-	-	-	-	-	-	-	-	-	-	-	-	-	120	10	-	-	-	50	-	-	-	-	-	-	10	20	30	-
37	-	-	-	20	70	-	170	-	-	-	-	-	-	-	-	-	-	-	10	10	360	-	-	-	240	-	-	-	-	-	-	-	80	30	160	-
38	-	-	-	-	160	150	90	-	10	10	-	-	-	-	-	-	-	-	-	-	150	-	-	-	90	-	-	-	-	-	-	20	-	130	60	-
39	-	-	-	100	10	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	250	-	-	-	-	110	-	10	-	-	-	-	-	30	-	-
40	-	20	-	-	390	-	30	-	30	-	-	-	-	-	-	-	-	-	-	20	50	50	-	60	80	-	-	90	-	-	-	10	920	1,340	210	-
41	-	190	-	-	-	-	30	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	490	-	-	-	20	-	-	-	-	430	-	210	-
42	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-
43	-	20	-	-	10	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44	-	-	50	-	-	-	30	-	10	-	-	30	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	30	-	-
45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46	-	-	-	-	20	-	10	-	-	-	-	-	-	-	-	-	60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	20
48	-	20	-	-	30	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	70	10	-
49	-	100	-	10	10	-	20	-	40	-	-	-	-	-	-	-	10	-	-	10	-	-	-	-	-	-	-	20	-	-	-	-	20	-	60	-
50	-	40	-	-	-	-	70	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	90	-	-	-	20	-	70	120	-	90	10	90	-
51	-	10	-	220	440	-	40	-	100	-	-	-	-	10	-	20	-	-	-	-	20	-	-	110	20	110	-	280	-	200	430	-	310	3,780	290	-
52	20	-	-	1,050	-	40	20	-	20	40	30	-	-	20	-	-	10	-	-	-	300	-	-	-	-	30	-	-	-	-	-	-	20	460	10	-
53	20	-	-	1,000	440	300	300	-	20	100	20	-	-	-	-	-	-	-	-	-	980	-	-	-	-	800	-	10	-	10	-	-	-	350	140	20
54	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-
55	-	-	-	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-
56	80	-	-	-	880	-	240	-	-	-	80	-	-	-	-	-	-	-	-	-	80	-	-	-	-	160	-	-	-	-	-	-	80	-	-	10
57	-	10	-	800	1,440	-	80	-	10	-	-	-	-	40	-	-	-	-	10	-	180	160	-	-	-	500	-	120	-	-	-	-	240	4,600	40	-
58	-	-	-	-	150	-	80	-	130	-	-	-	-	-	-	-	-	-	-	20	10	-	20	490	-	-	-	80	10	-	-	-	430	630	200	-
59	-	20	-	-	50	-	20	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	10	30	50	-	40	-	-	80	80	10
60	-	20	60	-	390	-	30	-	170	-	-	-	-	-	-	-	-	10	-	-	-	30	-	50	-	-	-	-	70	-	240	-	30	120	70	-
61	-	10	-	10	70	-	10	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	30	-	80	30	60	-
63	-	-	50	-		-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	10	-	-	-	-	140	-	-

Members of this group were by far the most abundant mollusks. Densities were as high as 8,230/m^2 (all species combined). The occurrence records of pelecypods are presented in two tables: Table 4 gives the number of shells per square meter, by stations, for the 35 more common species and Table 5 lists the number of shells per square meter for each of the 22 species that occurred at only one station. Each pelecypod shell was counted separately. No attempt was made to enumerate the left and right valves separately, because of the fragmentary nature of many specimens.

Distribution and Density

Pelecypods, all species considered, were generally most abundant in a band extending northeast-southwest across the study area and in another narrower band parallel to the depth contours near the shelf break (Figure 8). Densities were frequently less in the northwest, northeast, and south-central sections of the continental shelf and along the continental slope. As expected, the density of the group was strongly influenced by a relatively few species that were both abundant and widely distributed.

TABLE 5.—Species and density, by stations, of pelecypods that occurred at only one station each.

Species	Station	Specimens
		No/m²
Abra longicallis	21	10
Aequipecten glyptus	10	10
Anadara ovalis	16	10
Axinopsis orbiculata	8	50
Bathyarca anomala	56	80
Crenella pectinula	33	20
Cuspidaria striata	8	20
Cyrtodaria siliqua	30	20
Liocyma fluctuosa	30	10
Macoma balthica	6	10
Modiolus demissus	46	10
Myonera limatula	8	10
Mytilus edulis	1	10
Nucula delphinodonta	11	10
Nuculana tenuisulcata	38	10
Panomya arctica	25	10
Periploma affinis	4	20
Siliqua costata	17	20
Solemya velum	4	10
Tellina agilis	29	10
Thracia conradi	13	40
Thracia myopsis	5	20

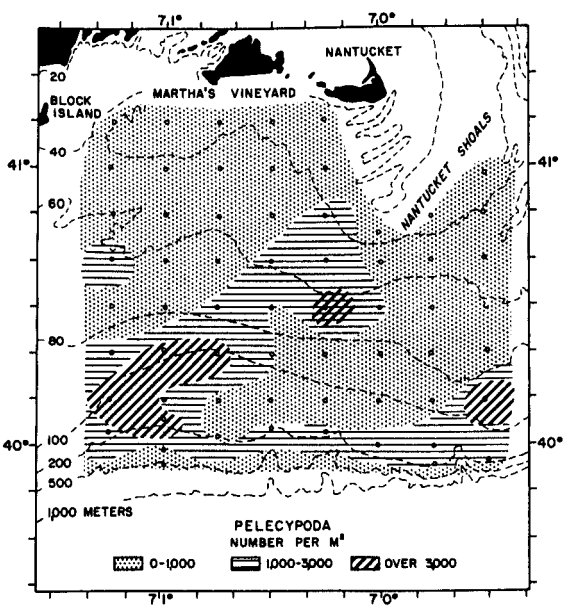

FIGURE 8.—Density distribution of pelecypod shells, all species combined.

Pelecypods were sparse (less than 50/m²) or absent at 8 stations, common (50 to 1,000/m²) at 32 stations, abundant (1,000 to 3,000/m²) at 16 stations, and very abundant (more than 3,000/m²) at 6 stations.

Pelecypod shells were present at all depths sampled (Table 6). Densities were lowest (30 to 40/m²) at both the shallowest and deepest stations; moderate (100 to 1,100/m²) between 30 and 89 m and between 200 and 249 m; high (greater than 1,100/m²) between 125 and 199 m; and highest (more than 2,000/m²) from 90 to 124 m.

TABLE 6.—Density distribution of pelecypod shells, all species combined, in relation to water depth.

Water depth class	Samples collected	Samples containing pelecypod shells	Mean number of shells
Meters	*Number*	*Percent*	*No/m²*
20-29	1	100	30
30-39	6	100	140
40-49	7	86	440
50-59	8	63	320
60-69	5	100	670
70-79	9	100	1,030
80-89	1	100	620
90-99	7	100	2,250
100-124	4	100	3,080
125-149	4	100	1,110
150-174	1	100	1,460
175-199	5	100	1,970
200-249	2	100	690
250-567	2	100	40

Relations of Density to Sediments

Pelecypods were generally more abundant in moderately fine-grained sediments than in either coarse or very fine types. Silty sand, sandy silt, and sand-silt-clay were most commonly associated with high density. Average shell density in these three substrate types ranged from 1,800 to 3,300/m². Shells were absent or sparse in gravel-sand substrates (average density 80/m²) and silts (average density 40/m²), and moderately low (average 650/m²) in sand.

Distribution and Density by Species

Geographic distributions of the 35 more common pelecypod species are illustrated in Figure 9. These charts are based on information listed in Table 4. No two species had identical distributions, but the distribution of a number of species in east-west bands across the study area suggests correlations with hydrographic features or bottom sediments, or both.

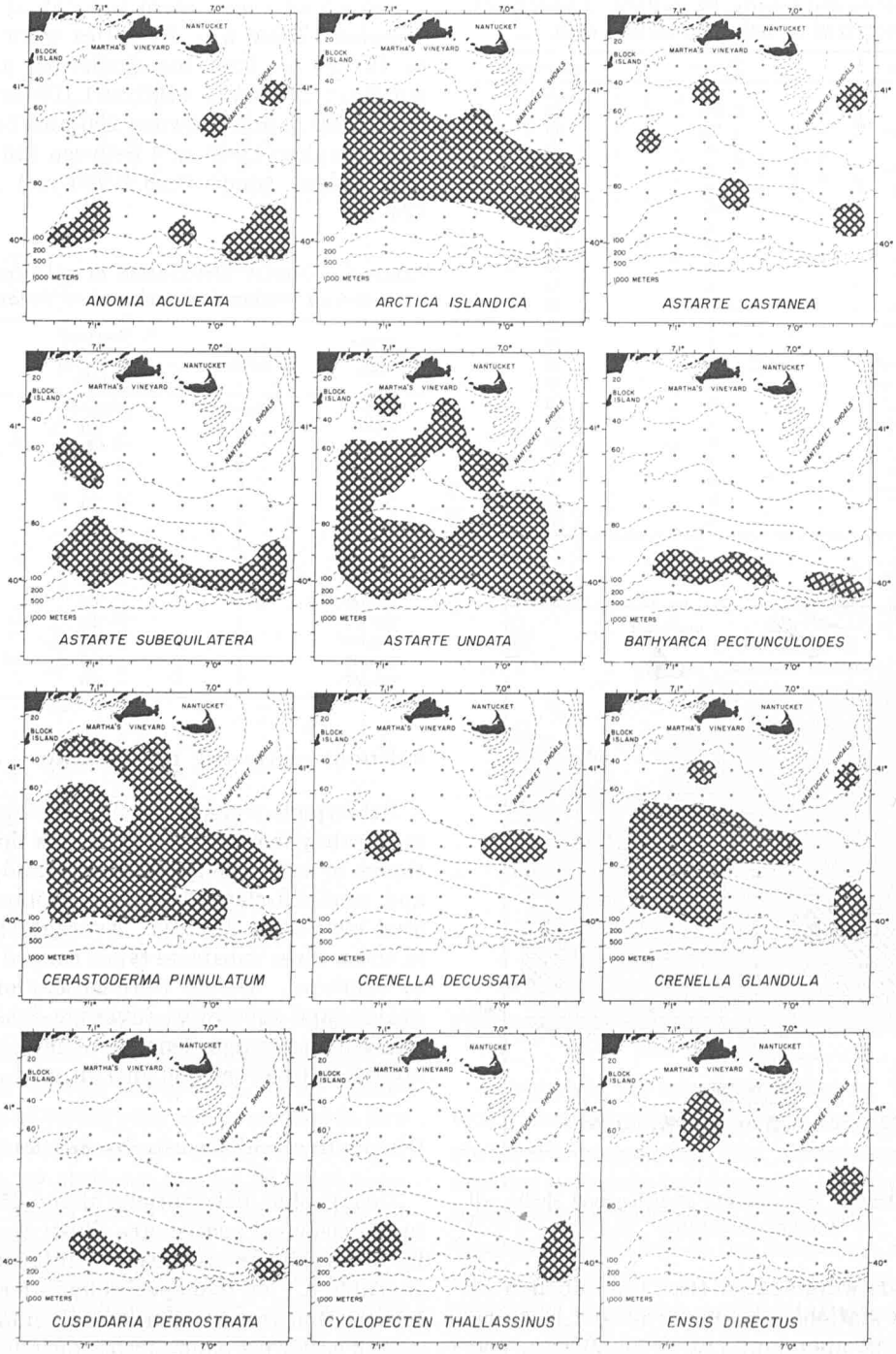

FIGURE 9.—Geographic distribution of the common pelecypods.

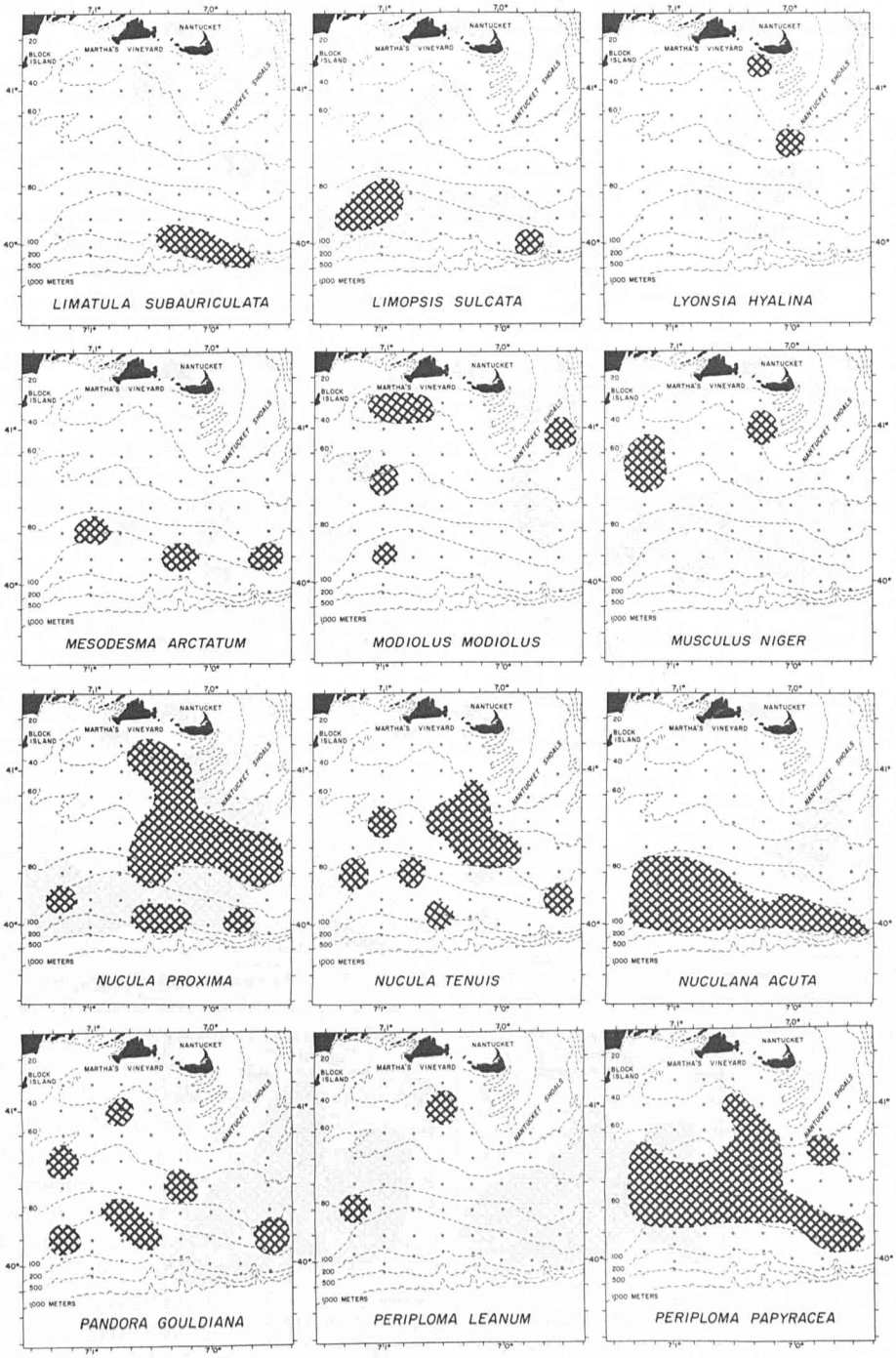

FIGURE 9.—Geographic distribution of the common pelecypods.—Continued.

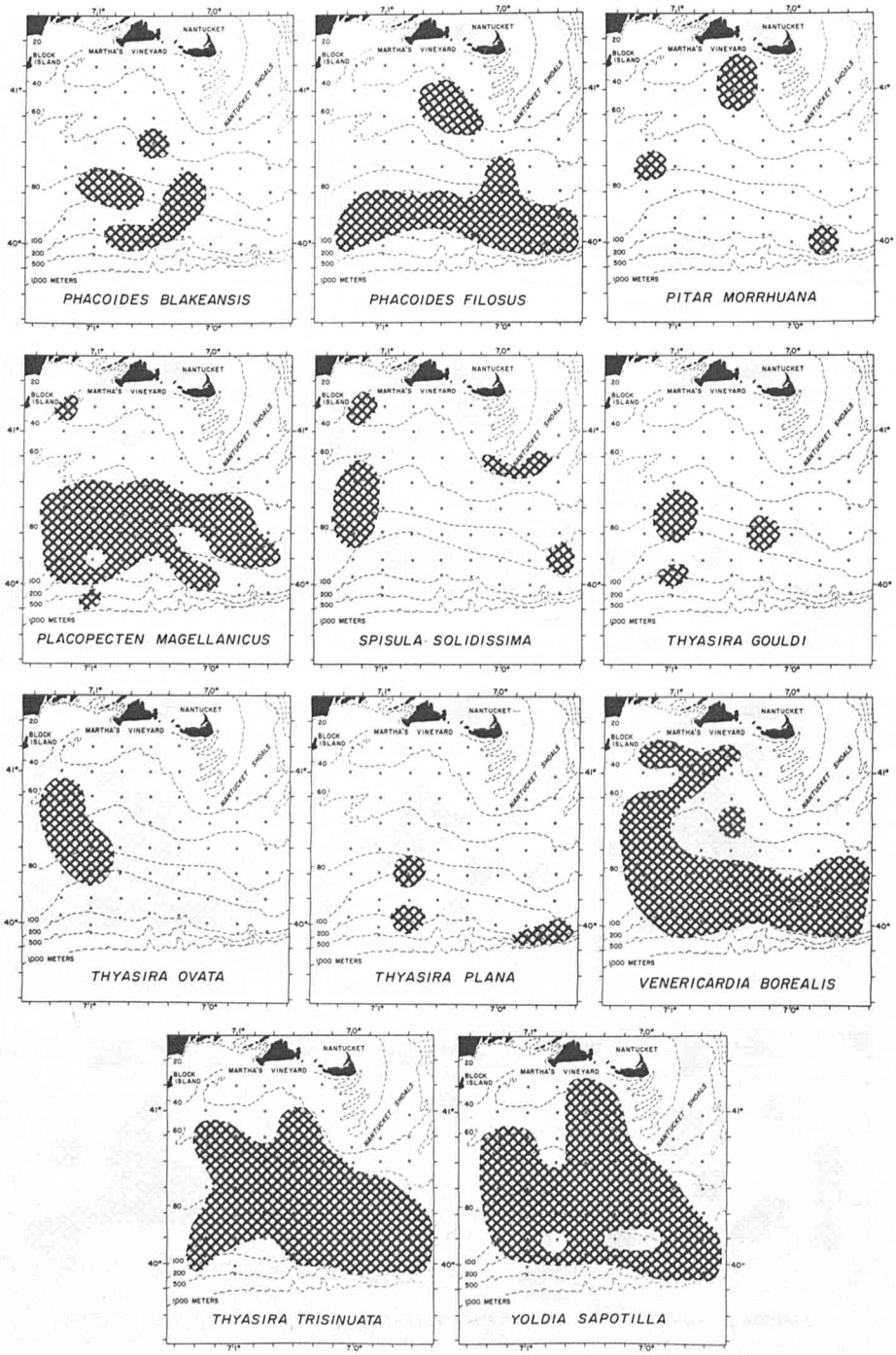

FIGURE 9.—Geographic distribution of the common pelecypods.—Continued.

The 10 most widely distributed species, in decreasing order, were: *Yoldia sapotilla, Cerastoderma pinnulatum, Astarte undata, Thyasira trisinuata, Venericardia borealis, Arctica islandica, Placopecten magellanicus, Phacoides filosus, Crenella glandula,* and *Nucula proxima.* All of these species inhabited rather broad east-west zones across the study area, except for *Nucula proxima,* which was absent in shallow water in the western sector. Its distribution was aligned in the north-south direction, and to some extent east-west.

Bathymetric distributions differed greatly among various pelecypod species. Depth range in which each species was found is listed in Table 7, and data for the most common species are plotted in Figure 10. Species dispersed over the widest depth range (38 to 567 m) were *Astarte undata* and *Placopecten magellanicus.* Depth ranges of 21 species were very narrow, but nearly all of these were based on few collections. Most of the species that occurred in two or more collections were taken over rather broad depth ranges.

Species found in shallow water (less than 50 m) were: *Anadara ovalis, Cyrtodaria siliqua, Liocyma fluctuosa, Lyonsia hyalina, Modiolus demissus, Mytilus edulis, Siliqua costata,* and *Tellina agilis.*

Species found in deep water (taken at depths greater than 200 m) were: *Anomia aculeata, Astarte subequilatera, A. undata, Cerastoderma pinnulatum, Limatula subauriculata, Nucula proxima, N. tenuis, Nuculana acuta, Phacoides blakeansis, P. filosus, Placopecten magellanicus, Thyasira plana, T. trisinuata, Venericardia borealis,* and *Yoldia sapotilla.*

Density of shells of individual pelecypod species ranged from 10/m² to 4,600/m² (Table 4). Densities tended to be high for the more widely distributed species and low for species with a restricted geographic distribution. Species found in greatest density were: *Venericardia borealis* —4,600/m², *Arctica islandica*—2,080/m², *Astarte subequilatera*—1,560/m², *Nucula proxima* —1,360/m², *Astarte undata*—1,440/m², and *Thyasira trisinuata*—1,160/m². All of these, except *Astarte subequilatera,* were among the 10 species with the widest geographic distribution. Among the species collected at 10 stations or less, few occurred in densities greater than

TABLE 7.—Bathymetric distributions of 57 species of pelecypods and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	m	m	
Abra longicallis	165	165	165	1
Aequipecten glyptus	139	139	139	1
Anadara ovalis	38	38	38	1
Anomia aculeata	38	201	139	10
Arctica islandica	44	110	75	27
Astarte castanea	38	97	64	6
Astarte subequilatera	62	366	152	15
Astarte undata	38	567	123	36
Axinopsis orbiculata	183	183	183	1
Bathyarca anomala	183	183	183	1
Bathyarca pectunculoides	128	194	164	7
Cerastoderma pinnulatum	38	220	96	38
Crenella decussata	73	84	77	3
Crenella glandula	46	194	99	20
Crenella pectinula	62	62	62	1
Cuspidaria perrostrata	146	194	177	5
Cuspidaria striata	183	183	183	1
Cyclopecten thallassinus	91	183	156	5
Cyrtodaria siliqua	38	38	38	1
Ensis directus	51	62	56	3
Limatula subauriculata	165	201	183	3
Limopsis sulcata	99	146	124	4
Liocyma fluctuosa	38	38	38	1
Lyonsia hyalina	27	49	38	2
Macoma balthica	91	91	91	1
Mesodesma arctatum	91	113	101	3
Modiolus demissus	40	40	40	1
Modiolus modiolus	38	146	68	5
Musculus niger	33	62	52	3
Myonera limatula	183	183	183	1
Mytilus edulis	46	46	46	1
Nucula delphinodonta	95	95	95	1
Nucula proxima	33	220	83	19
Nucula tenuis	44	220	88	10
Nuculana acuta	91	366	161	17
Nuculana tenuisulcata	194	194	194	1
Pandora gouldiana	51	110	88	7
Panomya arctica	70	70	70	1
Periploma affinis	62	62	62	1
Periploma leanum	48	91	70	2
Periploma papyracea	44	106	77	19
Phacoides blakeansis	62	220	126	7
Phacoides filosus	44	201	122	22
Pitar morrhuana	38	139	88	4
Placopecten magellanicus	38	567	116	25
Siliqua costata	49	49	49	1
Solemya velum	62	62	62	1
Spisula solidissima	37	91	62	7
Tellina agilis	27	27	27	1
Thracia conradi	73	73	73	1
Thracia myopsis	76	76	76	1
Thyasira gouldi	84	179	113	4
Thyasira ovata	62	99	77	5
Thyasira plana	106	201	171	4
Thyasira trisinuata	48	220	100	36
Venericardia borealis	38	366	116	33
Yoldia sapotilla	33	220	96	38

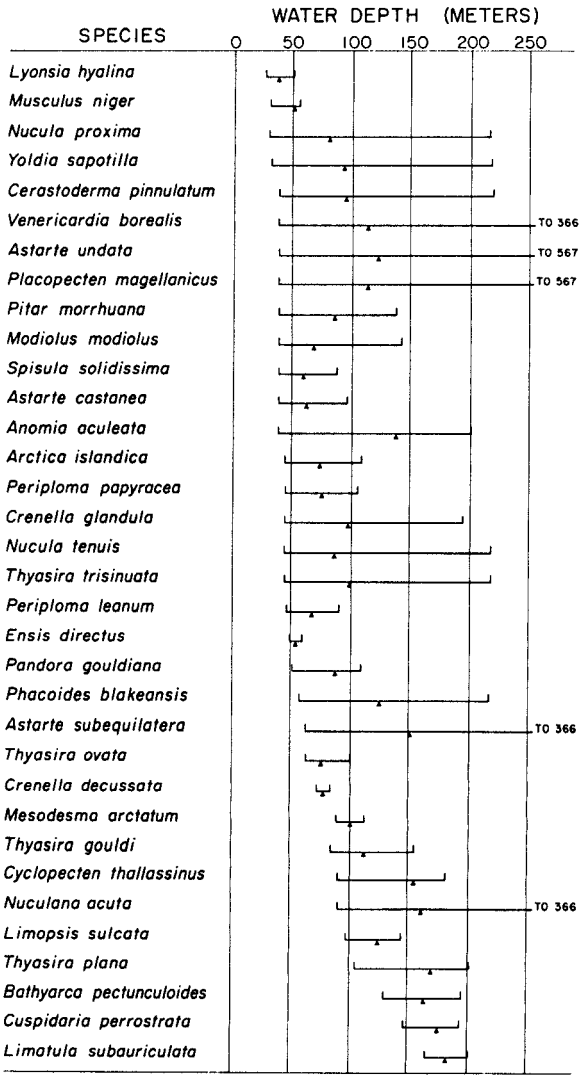

FIGURE 10.—Bathymetric range and mean depth of occurrence of the common pelecypods. (Observed values are listed in Table 7.)

500/m²; the maximum density for most of these species was less than 100/m².

Exceptions to the direct relation between high density and wide distribution were two types: (1) species widely distributed, but present in low density, such as *Cerastoderma pinnulatum, Crenella glandula, Placopecten magellanicus,* and *Yoldia sapotilla;* and (2) geographically restricted species of relatively high local densities, such as *Bathyarca pectunculoides* and *Thyasira ovata* (shells of these two species occurred at only seven and five stations each, but densities were as high as 300 and 430/m²).

Four patterns of geographic distribution revealed by these samples are: (1) Narrow band extending east-west across the area, such as: *Bathyarca pectunculoides, Crenella decussata, Cuspidaria perrostrata, Cyclopecten thallassinus, Limatula subauriculata, Mesodesma arctatum,* and *Nuculana acuta.* (2) Broad east-west band exemplified by: *Arctica islandica, Periploma papyracea, Placopecten magellanicus,* and *Thyasira trisinuata.* (3) Encircling distribution surrounding the center of the area, illustrated by *Astarte undata.* (4) Wide inshore-offshore distribution, as typified by: *Anomia aculeata, Cerastoderma pinnulatum, Crenella glandula, Nucula proxima, Venericardia borealis,* and *Yoldia sapotilla.*

Hydrographic conditions and the type of bottom sediments appear to have a substantial influence on the suitability of a habitat for some species of bivalves in this region. Unfortunately the common co-occurrence of fine-grained sediments in areas of low energy and relatively stable water temperature, as opposed to coarse sediments in high-energy and changeable water temperature does not lend itself to an evaluation of the specific conditions that limit the occurrence of the various species. Additionally, the presence of fossil shells invalidates a detailed evaluation of inferred habitat based on the presence of shell remains. For example, the shells of *Mesodesma arctatum* from depths of 91 to 113 m probably are remains of populations that inhabited nearshore areas during the rapid rise in sea level of the post-Pleistocene period. Radiocarbon age determinations for shells collected in this region at depths between 86 to 130 m, studied by Emery and Garrison (1967), range from 10,850 ± 150 to 14,850 ± 250 years before present.

Species that occurred in moderately deep waters and appeared to require a stenothermic habitat were: *Arctica islandica, Nuculana acuta, Thyasira plana,* and *Thyasira trisinuata* (Figure 9). Species that inhabited stenothermic

waters, but also showed special sediment requirements, were: *Bathyarca pectunculoides, Cuspidaria perrostrata, Limatula subauriculata,* and *Thyasira gouldi.* Conversely, those bivalves that occurred in eurythermic habitats (and coarse sediments) were: *Ensis directus, Lyonsia hyalina,* and *Musculus niger.*

Relations of pelecypod distributions with bottom sediments are discussed below.

Species-Sediment Relations

Shells from 89% of the 35 more common pelecypod species represented in the area were found in several different sediment types; only 11% were associated exclusively with one sediment type. All of the common species were primarily in sediments in which sand or silt was the chief constituent. Species frequently taken in sand sediments were: *Ensis directus, Limatula subauriculata, Lyonsia hyalina,* and *Musculus niger.* Species most commonly found in silty sand and sand were: *Bathyarca pectunculoides, Cuspidaria perrostrata, Cyclopecten thallasinus, Limopsis sulcata, Nucula proxima, N. tenuis, Nuculana acuta, Pandora gouldiana, Phacoides filosus, Pitar morrhuana, Spisula solidissima. Thyasira plana,* and *Venericardia borealis.* The only two species found mainly in sandy silt or silty sand were *Limopsis sulcata* and *Thyasira gouldi.* The absence of *Astarte undata* in the center of the area is probably due to the presence of fine-grained sediments there. All the remaining common species were collected from several different sediment types.

The presence of a narrow band of sand extending parallel to the depth contours near the outer margin of the shelf (Figure 2) appears to be a major feature affecting the distribution of many species having a narrow-band distribution (Figure 9).

GASTROPODS

Remains of gastropods formed an important component of organic origin, but compared with other mollusks they were far less common than pelecypods, but considerably more abundant than scaphopods and cephalopods. Gastropods were widely distributed throughout the area and ranged in density (all species combined) from 0 to slightly over 1,000/m^2. All remains were shells, except for one operculum of *Polinices duplicata.*

Forty-four species of gastropods were found in the samples. Some typical examples are shown in Figure 11. A large majority of specimens were small, less than 1 cm in shell height. Some of the smallest specimens, averaging between 2 and 5 mm, were *Alvania carinata, Cylichna alba, Retusa obtusa,* and larval forms, presumably of *Thais.* The larger species, averaging between 1 and 5 cm in greatest dimension, were: *Buccinum undatum, Colus pygmaeus, Crucibulum striatum, Crepidula fornicata,* and *Nassarius trivittatus.*

Gastropod occurrence records are listed in Tables 8 and 9. Table 8 gives the species-station record for the 24 more common species. Table 9 lists the occurrence record for species taken at only one station.

Distribution and Density

Gastropod shells (all species combined) were rather widely distributed throughout the area, occurring at 80% of the stations. Highest concentrations (250 to 1,050/m^2) were in the central part of the area in a lens-shaped patch at depths between 40 and 80 m (Figure 12).

Although gastropod shells were collected at all depths, the average concentration increased in each 10-m depth class from 20 m down to about 80 m (Table 10). Concentrations were lower in deeper water, except for a zone of greater density between 175 and 250 m. *Alvania carinata* and *Cylichna gouldi* made up the bulk of the gastropod remains in the shallowwater zone: *Mitrella zonalis,* a gastropod larva, and a variety of species accounted for the high abundance in the deepwater zone.

Relations of Density to Sediments

The density of gastropod shells as a group was related to sediment type only in a rather general way. No gastropod shells were found in the coarse sand or gravel-sand substrates. Concen-

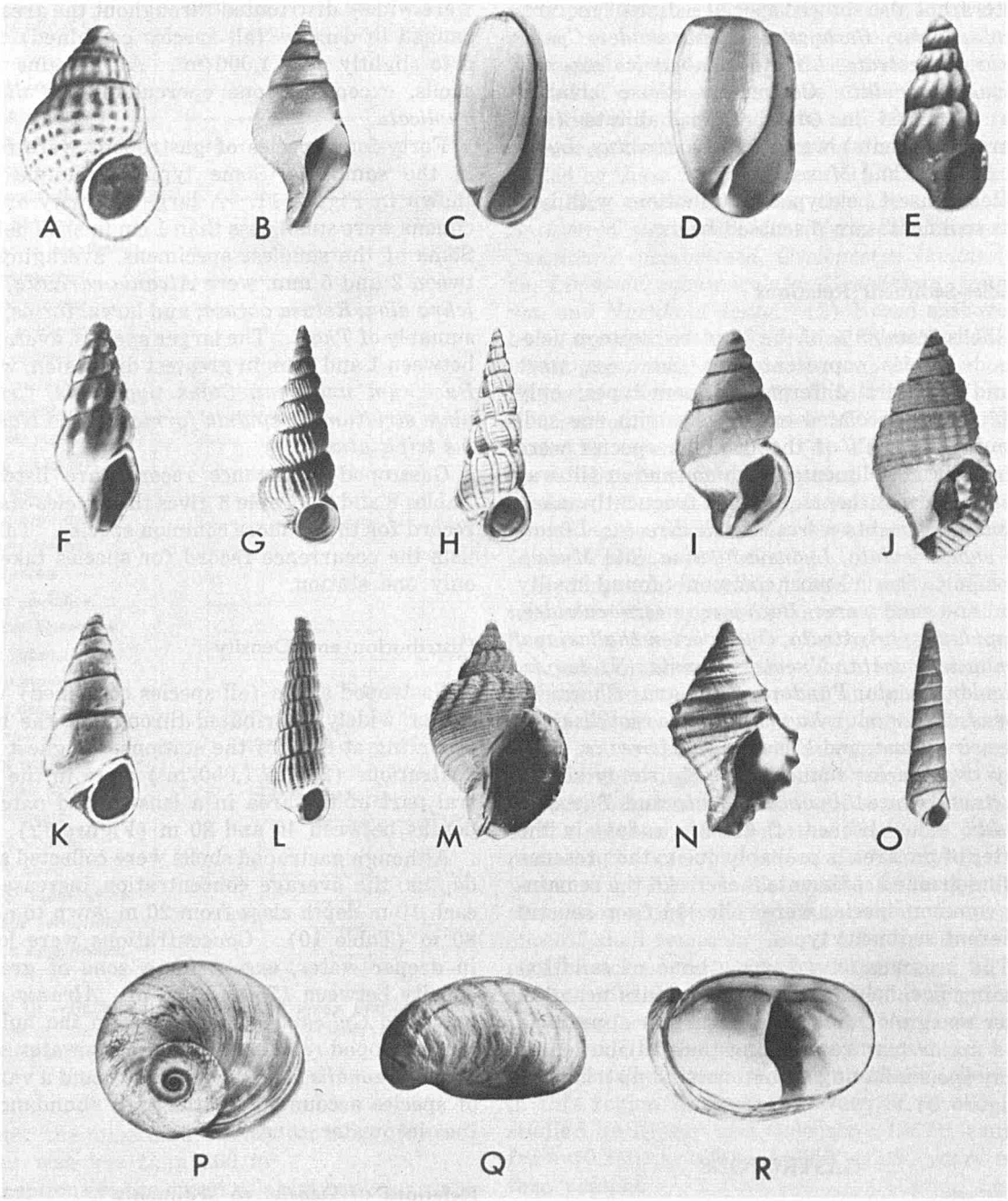

FIGURE 11.—Representative gastropods from off southeastern Massachusetts. A - *Alvania carinata* (×14); B - *Colus pygmaeus* (×1.5); C - *Cylichna alba* (×4); D - *Cylichna gouldi* (×11.7); E - *Drillia lissotropis* (×5.5); F - *Drillia* sp. (×4.7); G - *Epitonium dallianum* (×3); H - *Epitonium groenlandicum* (×0.8); I - *Mitrella zonalis* (×7); J - *Nassarius trivittatus* (×2.3); K - *Odostomia canaliculata* (×7); L - *Turbonilla interrupta* (×4.7); M - *Buccinum undatum* (×1); N - *Neptunea decemcostata* (×0.8); O - *Eulimella smithi* (×2.3); P - *Polinices duplicata* (×1); Q - *Crepidula fornicata* (×0.8); R - *Crepidula fornicata* (×0.8).

Table 8.--Species and density (number per square meter), by station, of the common gastropods.

Station number	Alvania carinata	Anachis costulata	Balcis intermedia	Buccinum undatum	Colus pygmaeus	Crepidula fornicata	Crucibulum striatum	Cylichna alba	Cylichna gouldi	Drillia lissotropis	Epitonium dallianum	Epitonium novangliae	Lunatia levicula	Mitrella zonalis	Mitrella sp.	Nassarius trivittatus	Odostomia canaliculata	Polinices duplicata	Rissoa sp.	Trochidae	Turbonilla interrupta	Turbonilla sp.	Gastropod larva	Unidentified
4	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	-	-	-
6	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-
8	20	-	20	-	-	-	-	20	-	-	-	10	-	50	-	-	10	-	-	-	-	-	-	-
9	-	30	-	-	-	-	-	-	-	10	40	-	-	-	-	4	-	-	-	-	50	-	10	-
10	-	-	10	-	-	-	-	-	-	-	10	-	-	20	-	-	-	-	-	10	40	10	-	-
11	60	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	20	-	-	-	-	20	-	-	20	-	-	-	-	-	-	-
13	-	-	-	-	60	-	-	-	10	-	-	-	-	-	-	-	10	-	30	-	-	-	-	-
14	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-
15	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	40	-	10	-	-	-	-	-	-
17	-	-	-	-	40	-	-	10	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-
18	200	-	-	-	10	-	-	-	100	-	-	-	-	40	-	-	30	-	-	-	10	-	10	20
19	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	10	-
20	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	10	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	-	-	-	-	-	-	10	-
22	-	-	-	-	-	-	-	10	-	-	10	-	-	10	-	-	10	-	-	-	10	-	20	-
23	20	-	-	-	-	-	-	-	-	20	-	-	-	10	-	-	-	-	-	-	50	-	10	-
24	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	630	-	-	-	10	-	-	-	410	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	-	-	-	-	-	-	-	-	530	-	-	-	-	-	-	20	-	-	-	-	-	10	-	-
27	-	-	-	-	-	10	-	-	70	-	-	-	-	-	-	130	-	-	-	-	-	-	-	-
28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-
30	-	-	-	-	20	-	-	-	10	-	-	-	-	-	-	50	-	10	-	-	-	-	-	-
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32	90	-	-	10	-	-	-	-	40	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-
33	600	-	-	-	10	-	-	-	150	-	-	-	-	20	-	10	-	-	-	-	-	-	-	-
34	40	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-
35	80	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	20	-
36	50	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	10	-	-	-	-	-	30	-
37	10	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	10	-	-	-	-	-	30	-
38	10	-	-	-	-	-	-	10	-	10	30	-	-	20	10	-	-	-	10	-	10	-	-	-
40	20	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-
41	-	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42	10	-	-	-	-	-	-	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
43	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	30	10	-	-	-	-	-	-	-
49	-	-	-	-	-	-	-	-	80	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-
51	10	-	-	-	-	-	-	-	-	-	10	-	-	10	-	-	-	-	-	-	-	-	-	10
52	-	-	10	10	-	-	10	-	-	-	30	-	-	-	-	-	20	-	-	-	10	-	-	-
53	10	-	-	-	-	-	-	10	-	-	20	-	-	30	10	-	-	-	-	-	-	-	-	10
54	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	30	-
55	-	10	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	40	-
56	-	-	-	-	-	-	-	-	-	10	-	-	-	10	-	-	-	-	-	-	20	-	-	-
57	-	-	10	-	-	-	-	-	-	-	50	-	-	-	-	-	10	10	-	-	-	-	-	-
58	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	-	-	10	-	-	-	-	-
61	10	-	-	-	10	-	-	30	10	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
62	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
63	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	20	-	-	-	-	-	-	-	-

trations were high in silty sand in some areas but were intermediate or low in other locations at similar depths. Densities of gastropod shells were high, intermediate, and low in sand, with no apparent correlation.

Distribution and Density by Species

The geographic distributions of the 24 most common forms of gastropods are shown in Figure 13. These charts are based on the data in

TABLE 9.—Species and density, by station, of gastropods that occurred at only one station each.

Species	Station	Specimens
		No/m²
Alvania janmayeni	55	20
Calliostoma occidentalis	23	20
Calliostoma sp.	53	10
Cavolina longirostris	51	10
Cavolina tridentata	53	20
Epitonium groenlandicum	52	10
Epitonium multistriatum	23	30
Eulimella smithi	37	10
Eulimella sp.	6	20
Eupleura caudata	29	10
Fossarus elegans	52	10
Lunatia heros	1	10
Mitrella lunata	27	10
Neptunea decemcostata	31	10
Odostomia gibbosa	1	40
Pseudorotella solida	38	40
Pyramidella sp.	21	10
Retusa obtusa	5	40
Solariella iris	9	30
Taranis cirrata	9	10
Turrtellopsis acicula	37	10

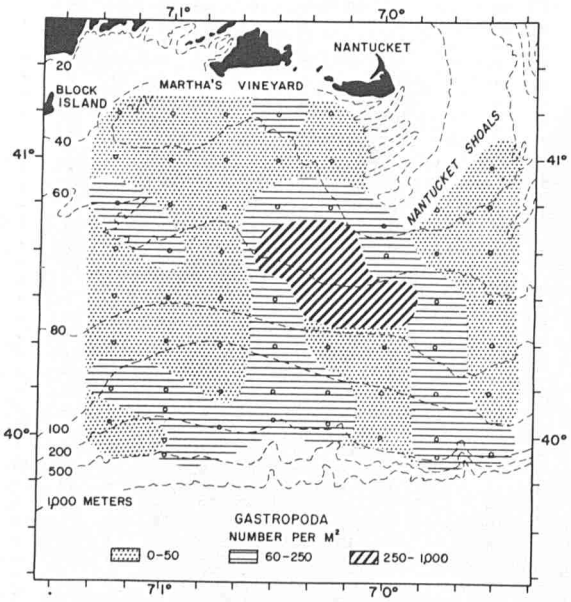

FIGURE 12.—Density distribution of gastropod shells, all species combined.

Table 8. Species with a wide geographic distribution were, in decreasing order: *Alvania carinata, Mitrella zonalis, Cylichna gouldi, Colus pygmaeus, Odostomia canaliculata, Epitonium dallianum, Cylichna alba, Nassarius trivittatus,* and *Turbonilla interrupta.*

TABLE 10.—Density distribution of gastropod shells, all species combined, in relation to water depth.

Water depth	Samples collected	Samples containing gastropod shells	Mean number of shells
Meters	*Number*	*Percent*	*No/m²*
20-29	1	100	10
30-39	6	83	35
40-49	7	71	84
50-59	8	63	96
60-69	5	100	190
70-79	9	89	221
80-89	1	0	0
90-99	7	100	51
100-124	4	100	72
125-149	4	75	80
150-174	1	100	60
175-199	5	100	102
200-249	2	100	140
250-567	2	100	65

Four patterns of geographical distribution are revealed: (1) The most common is a relatively narrow east-west band across the area in either shallow or deep water, typified by *Balcis intermedia, Crepidula fornicata, Drillia lissotropis, Epitonium dallianum,* and others. (2) Comparatively broad east-west bands across the area are illustrated by *Mitrella zonalis* and *Turbonilla interrupta.* (3) Peripherial occurrence around the fine-grained bottom sediments located in the center of the area is illustrated by *Cylichna alba, Odostomia canaliculata,* and to some extent by *Rissoa* sp. (4) Distribution in the central part of the area, a pattern nearly opposite that of peripheral distribution (pattern number 3), is illustrated by *Alvania carinata.*

Bathymetric range differed markedly among species. The minimum, maximum, and mean depth of occurrence for each species is listed in Table 11 and illustrated for the more common species in Figure 14. *Mitrella zonalis* was the only species taken over a wide range of water depths (62 to 567 m). Species that had a moderately wide depth range were: *Buccinum undatum, Cylichna alba, Epitonium novangliae, Odostomia canaliculata,* and *Rissoa* sp.

Species found in shallow water—those restricted to depths of 50 m or less—were: *Crepidula fornicata, Eupleura caudata, Lunatia her-*

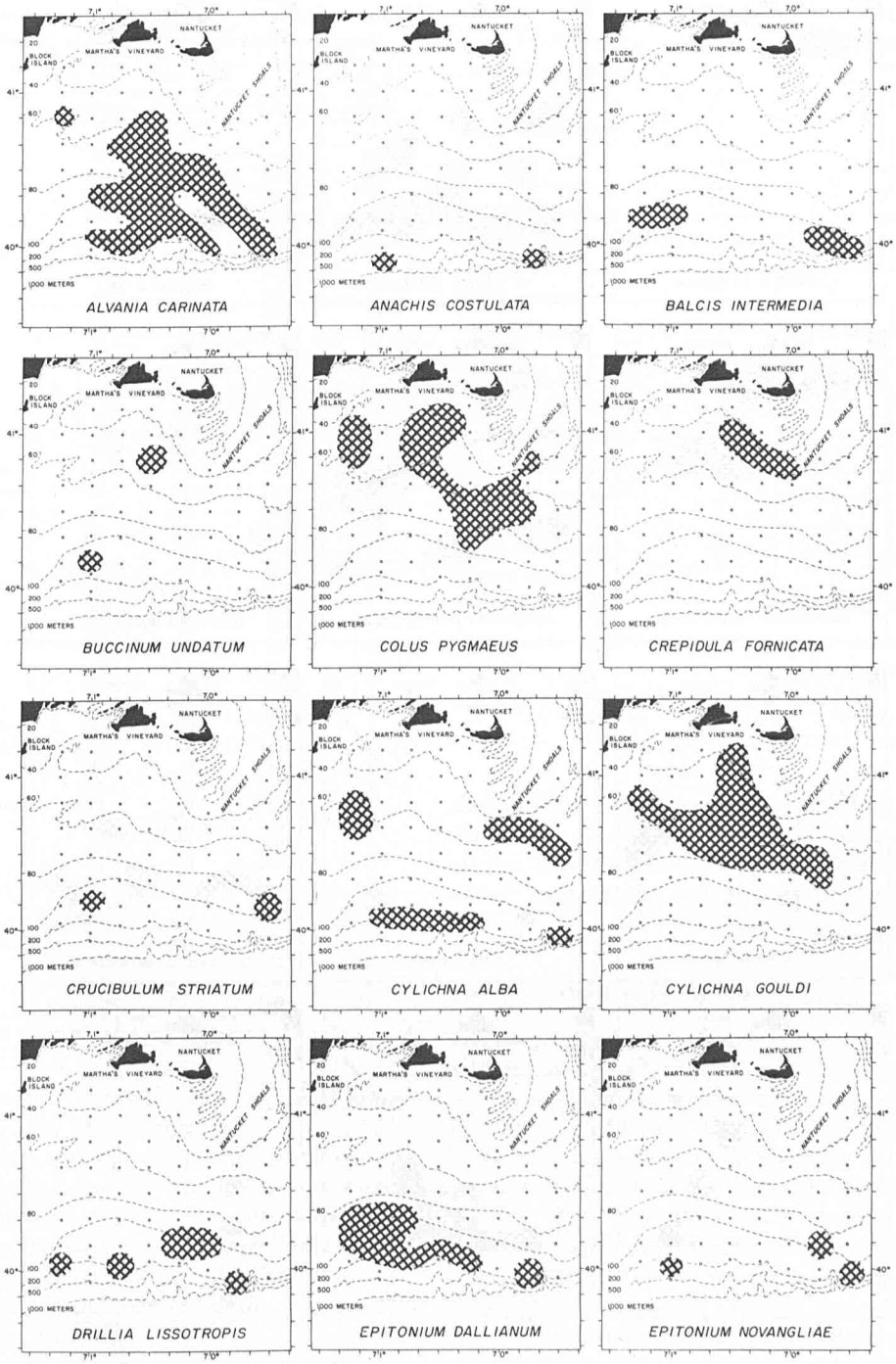

FIGURE 13.—Geographic distribution of the common gastropods.

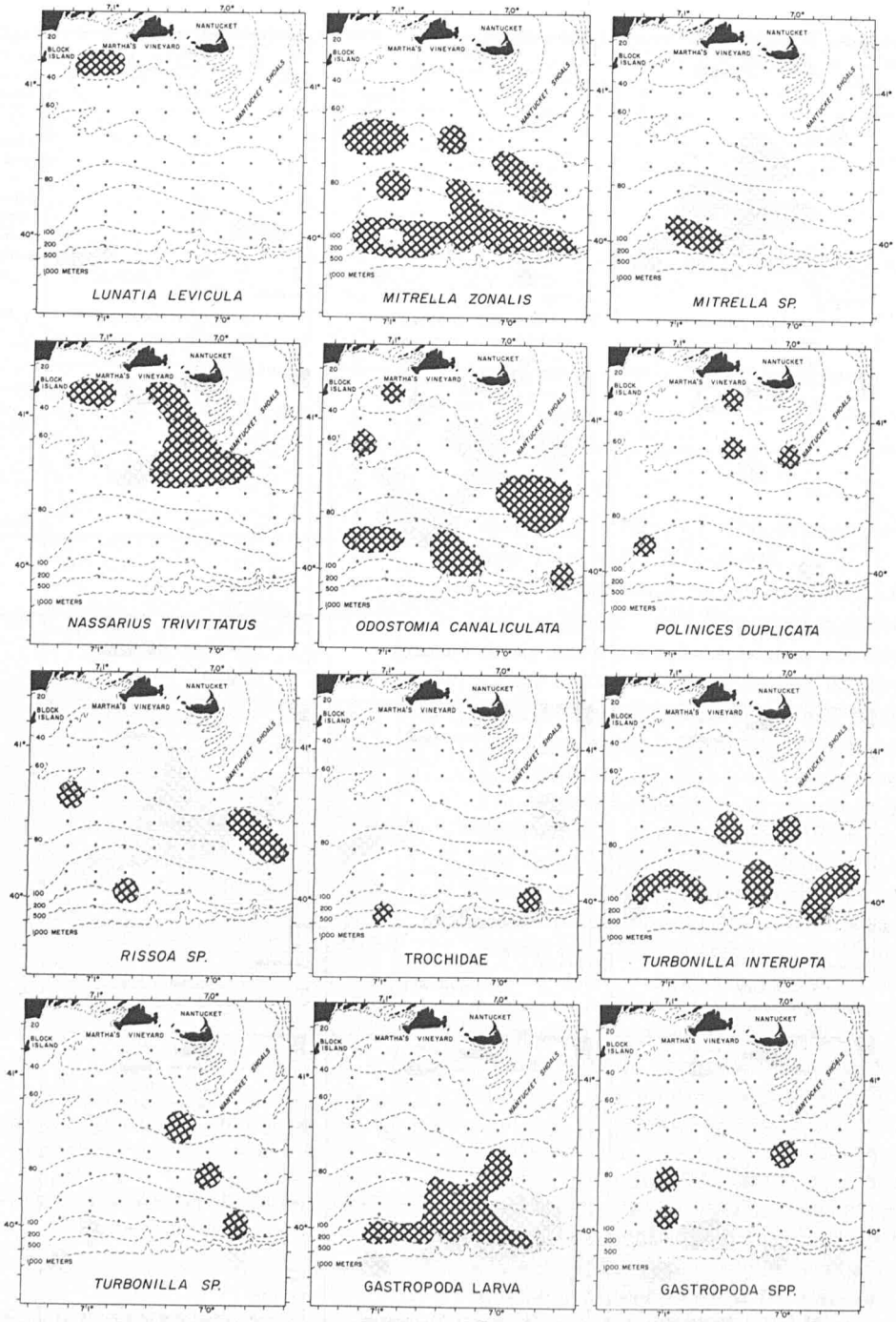

FIGURE 13.—Geographic distribution of the common gastropods.—Continued.

TABLE 11.—Bathymetric distributions of 44 gastropods and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	m	m	
Alvania carinata	59	220	112	19
Alvania janmayeni	567	567	567	1
Anachis costulata	201	567	384	2
Balcis intermedia	110	183	144	4
Buccinum undatum	59	146	102	2
Calliostoma occidentalis	113	113	113	1
Calliostoma sp.	179	179	179	1
Cavolina longirostris	99	99	99	1
Cavolina tridentata	179	179	179	1
Colus pygmaeus	37	90	58	13
Crepidula fornicata	38	48	43	3
Crucibulum striatum	91	146	118	2
Cylichna alba	49	220	125	10
Cylichna gouldi	38	79	63	15
Drillia lissotropis	113	201	162	5
Epitonium dallianum	91	201	143	11
Epitonium groenlandicum	146	146	146	1
Epitonium multistriatum	113	113	113	1
Epitonium novangliae	95	366	215	3
Eulimella smithi	220	220	220	1
Eulimella sp.	91	91	91	1
Eupleura caudata	27	27	27	1
Fossarus elegans	146	146	146	1
Lunatia heros	46	46	46	1
Lunatia levicula	38	40	39	2
Mitrella lunata	44	44	44	1
Mitrella zonalis	62	567	157	17
Mitrella sp.	179	194	186	2
Nassarius trivittatus	33	62	45	10
Neptunea decemcostata	48	48	48	1
Odostomia canaliculata	40	220	113	12
Odostomia gibbosa	46	46	46	1
Polinices duplicata	38	110	61	4
Pseudorotella solida Dall	194	194	194	1
Pyramidella sp.	165	165	165	1
Retusa obtusa	76	76	76	1
Rissoa sp.	62	194	101	4
Solariella iris	201	201	201	1
Solariella sp.	139	139	139	1
Taranis cirrata	201	201	201	1
Turbonilla interrupta	73	201	140	10
Turbonilla sp.	51	139	70	3
Turrtellopsis acicula	220	220	220	1
Gastropod larva[1]	73	567	200	11

[1] Only one species appeared to be represented—possibly a *Thais*.

os, *L. levicula*, *Mitrella lunata*, *Neptunea decemcostata*, and *Odostomia* sp.

Species taken only in deep water—those restricted to depths greater than 200 m—were: *Alvania janmayeni*, *Anachis costulata*, *Eulimella smithi*, *Taranis cirrata*, and *Turrtellopsis acicula*. All these species were taken at only one station, except *Anachis costulata*, which occurred at two stations.

Shells of individual species of gastropods generally occurred at low or moderately low densities. Only three were found in high or moderately high concentrations: *Alvania carinata* (630/m²), *Cylichna gouldi* (530/m²), and *Nassarius trivittatus* (130/m²). The density of other gastropods (41 species) was 60/m² or less.

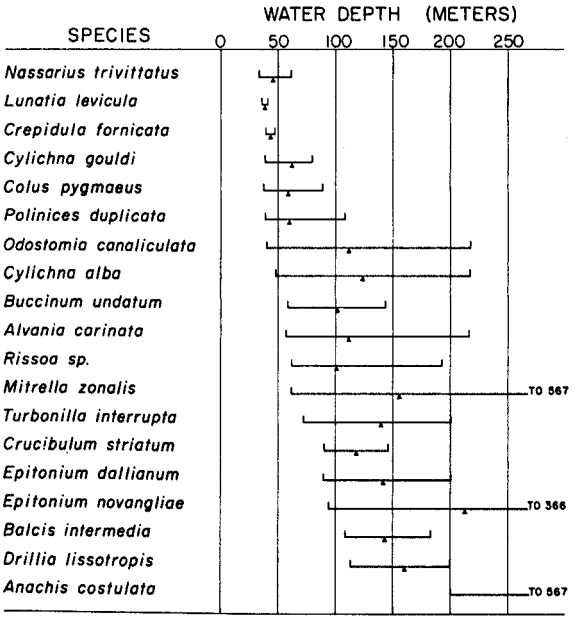

FIGURE 14.—Bathymetric range and mean depth of occurrence of the more common gastropod species. (Observed values are listed in Table 11).

Species-Sediment Relations

The majority of gastropod species occurred in sand and silty sand. None was in coarse sand or gravel-sand substrates, and none appeared to be restricted to silt. Widely distributed species generally occurred in a variety of sediment types ranging from medium sand to silt. A few species were associated with specific sediment types. Gastropods found chiefly in sand substrates were: *Colus pygmaeus*, *Crepidula fornicata*, *Cylichna alba*, *Lunatia levicula*, *Nassarius trivittatus*, and *Odostomia canaliculata*. The only species found principally in fine-grained sediments was *Epitonium dallianum;* it was mainly in silty sand.

CEPHALOPODS AND SCAPHOPODS

Remains of cephalopods and scaphopods were found in moderate to low densities, were small, and occurred in a relatively limited area. Only a few species of each group were represented in the samples. Illustrations of typical examples are shown in Figure 15.

Cephalopod remains consisted solely of beaks (jaws or mandibles) of Decapoda (squid). All were black and 4 to 6 mm long. The animals from which the beaks came were adults and probably rather small (less than about 10 cm in mantle length). Their uniformity in configuration and size suggests that only one or a few species are represented.

Scaphopod remains consisted only of shells or fragments of shells of a few species of the genus *Dentalium* (15 to 35 mm long) and one species of the genus *Cadulus* (mostly 10 to 13 mm long). Many *Dentalium* shells were inhabited by Sipunculida, whereas *Cadulus* shells were empty. Unbroken shells recovered from the samples included few of the thin-walled *Cadulus* but larger numbers of the thick-walled *Dentalium*.

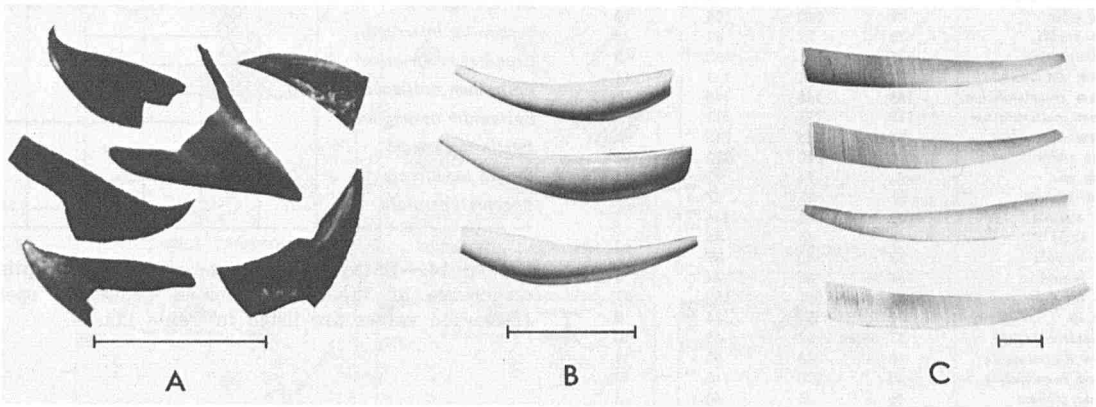

FIGURE 15.—Cephalopod mandibles and scaphopod shells from off southeastern Massachusetts. A - cephalopod beaks; B - shells of *Cadulus pandionis*; C - shells of *Dentalium* spp. Each scale bar is 5 mm.

TABLE 12.—Density of cephalopod beaks and scaphopod shells, by stations.

Station	Cephalopods[1]	Scaphopods	
		Cadulus pandionis	*Dentalium* spp.
	No/m²	*No/m²*	*No/m²*
5	10	--	--
6	--	--	--
8	40	--	20
9	--	80	--
10	10	10	--
11	10	--	--
21	30	--	20
22	--	20	20
23	20	--	110
36	20	--	--
37	40	110	--
51	--	--	40
53	20	60	10
54	130	10	--
55	110	--	--
56	10	--	--
57	--	--	10

[1] Remains of mandibles.

Distribution and Density

The distribution of cephalopod and scaphopod remains was somewhat limited geographically and densities were low. Quantitative occurrence records for both groups (Table 12), geographic distributions (Figures 16 and 17), and depth of water inhabited (Table 13), disclose that both groups occur primarily in deep water, only on the continental slope and outer part of the shelf.

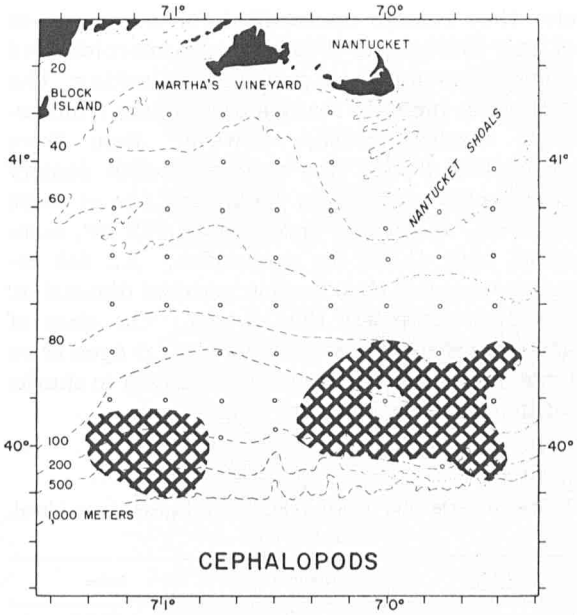

FIGURE 16.—Geographic distribution of cephalopod beaks.

Cephalopod beaks were present at 12 stations, at a depth range of 76 to 567 m. Their average density was 38/m², and maximum density 130/m². Highest densities were at the deepest stations sampled, stations 54 and 55, where water depths were 366 and 567 m.

Scaphopod shells were collected at 11 stations. *Cadulus pandionis* was present only on the continental slope at depths between 139 and 366 m. Average density at the six stations where it occurred was 41/m² and maximum density was 110/m². *Dentalium* spp. occurred along the continental shelf margin at depths of 91 to 183 m.

TABLE 13.—Bathymetric distribution of cephalopod beaks and scaphopod shells and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	*m*	*m*	
Cephalopods	76	567	201	12
Scaphopods				
Cadulus pandionis	139	366	213	6
Dentalium spp.	91	183	134	7

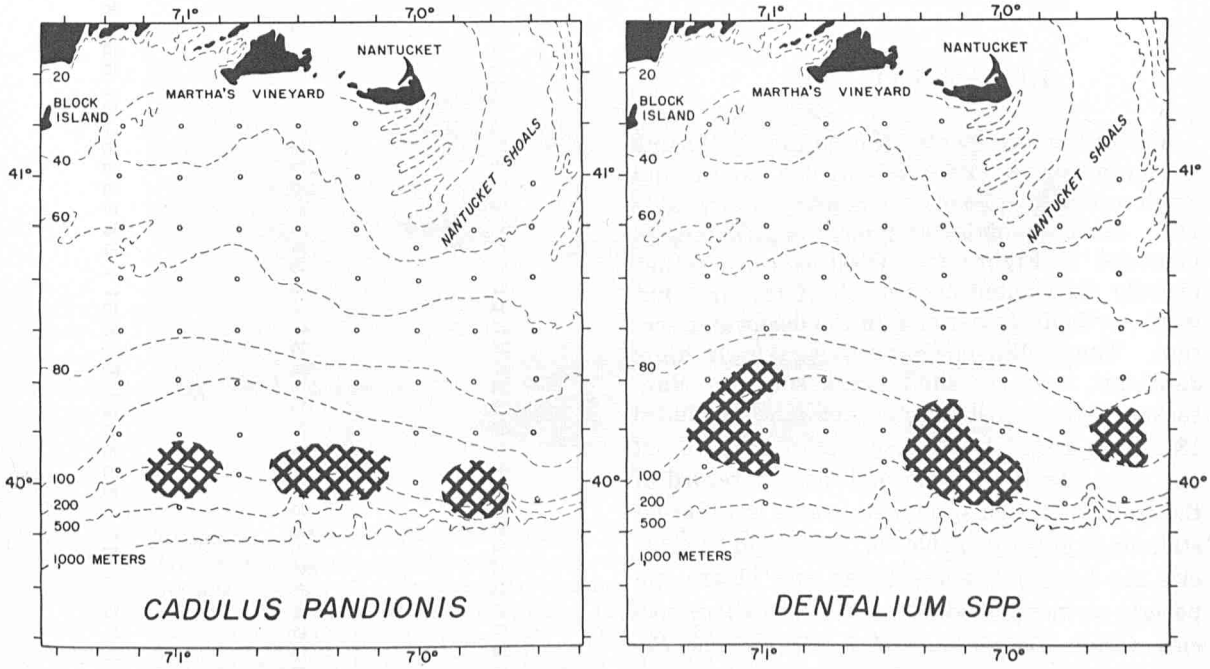

FIGURE 17.—Geographic distribution of shells of the scaphopods, *Cadulus pandionis* and *Dentalium* spp.

Average density at seven stations was 33/m², and maximum density was 110/m².

Relations with Sediments

The kinds of cephalopods that are abundant in this region are pelagic and their occurrence would not ordinarily be expected to be directly related to substrate composition. The fate of the remains of these animals that drop to the ocean floor may depend indirectly on sediment type because these species generally occur in deep or moderately deep water. Cephalopod remains were absent in coarse sand or gravel. Densities were moderate (10 to 40/m²) exclusively in silt.

Cadulus and *Dentalium* remains also were found only in fine-grained sediments; fine sand, silty sand, sandy silt, and silt. No areas of coarse sand, gravel, or mixtures of the two yielded scaphopod shells. A large majority were in areas where the sediments are fine sand and silty sand. *Cadulus* was densest in fine sand, and *Dentalium* in silty sand.

REMAINS OF FISH

Vertebrate remains in the bottom sediments were represented exclusively by fish otoliths and small numbers of bones, teeth, and scales (Table 14). Some examples of typical otoliths are illustrated in Figure 18. Otoliths were rather broadly distributed over much of the area but were particularly common in the deepwater section. The otolith density was strikingly high, 3,020/m², near the shelf break south of Nantucket Shoals. All samples combined included 18 genera and at least 26 species of fish; all but one were identified from otoliths. A record of the otoliths of each species recovered at different stations is given in Table 15. Eleven of the species are bottom-dwelling types, and 11 are epipelagic or mesopelagic (Table 16). Three species, *Merluccius albidus, M. bilinearis,* and *Peprilus triacanthus*, represented by otoliths range widely from the sea bottom to upper water levels; they remain unclassified for the purposes of this discussion. Clupeoids, scombroids, and other common pelagic groups were lacking. The collections included many more otoliths from pelagic species (1,288), however, than from groundfish (141); the average otolith density (based only on samples containing one or more otoliths), of pelagic species was 379/m², compared with 41/m² for groundfish. All fish remains were less than 2 cm in greatest dimension, and most were less than 3 mm. The sizes of fish from which these remains came ranged from lanternfish only a few centimeters long to sharks estimated to be 2 to 3 m long.

TABLE 14.—Density of fish remains[1], all species combined, by stations.

Station number	Otoliths	Bones
	No/m²	*No/m²*
4	10	--
5	10	--
6	30	--
8	3,020	--
9	1,250	--
10	360	10
11	10	20
12	10	--
13	--	10
16	--	10
17	10	--
18	--	10
20	20	--
21	760	10
22	2,200	10
23	170	40
24	--	10
25	--	30
27	30	10
31	10	--
33	10	--
34	10	10
35	40	10
36	30	10
37	1,460	80
38	1,270	--
39	150	10
40	20	10
41	20	20
50	--	60
51	50	10
52	50	--
53	830	--
54	870	40
55	580	--
56	1,380	--
57	60	10
58	10	--
59	10	--
61	10	--

[1] Scales occurred only at stations 11, 17, and 40 (10 to 20/m²) and teeth only at stations 53 and 54 (20 to 30/m²).

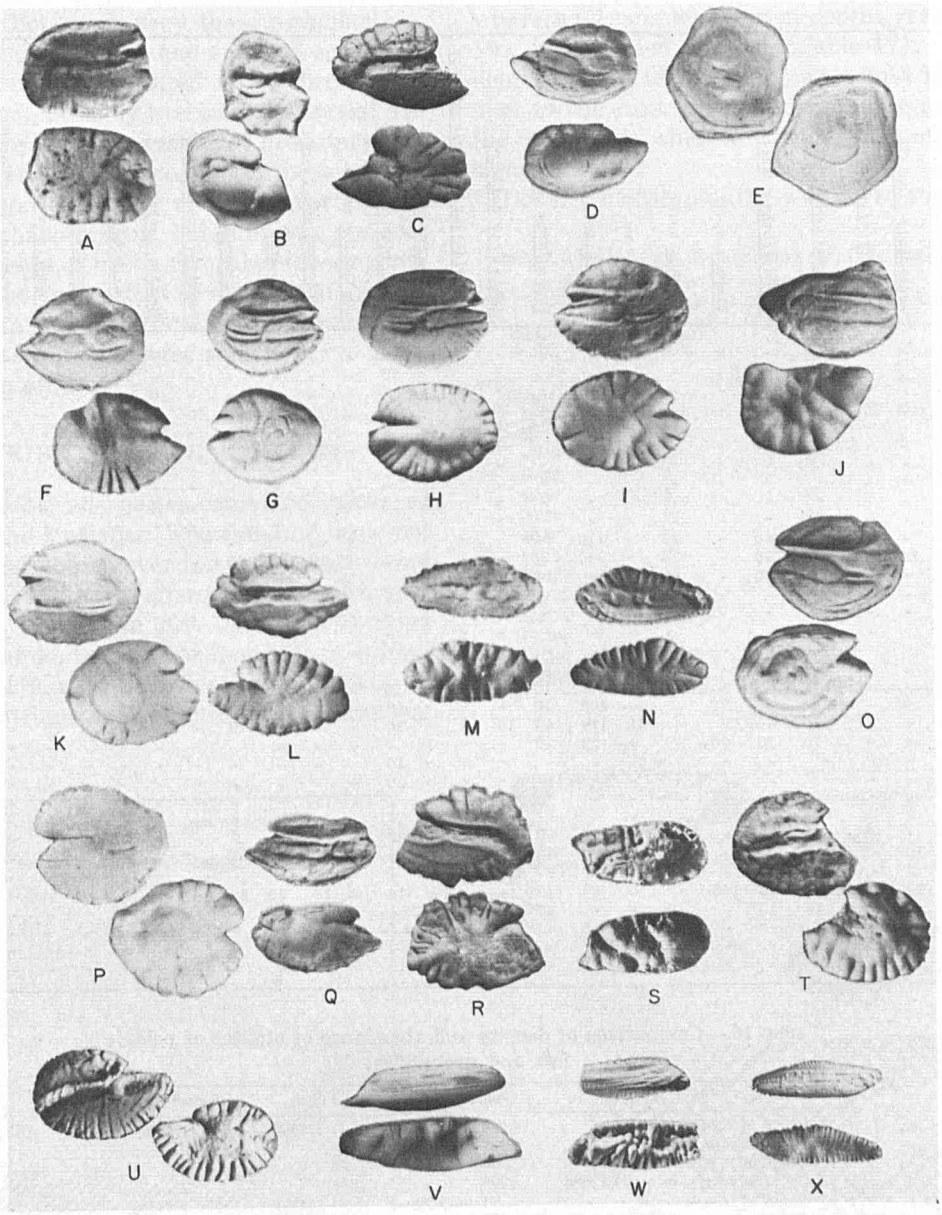

FIGURE 18.—Representative teleost otoliths from off southeastern Massachusetts. Inner face of otolith above, outer face below. A - Acanthuroidei sp.-1 (×10); B - *Benthosema glaciale* (×6.5); C - *Centropristis ocyurus* (×8); D - *Ceratoscopelus maderensis* (×4.5); E - *Citharichthys ?arctifrons* (×9); F - *Diaphus* sp.-1 (×2); G - *Diaphus* sp.-2 (×4.5); H - *Diaphus* sp.-3 (×4); I - *Diaphus* sp.-4 (×6.5); J - *Lepophidium cervinum* (×5.2); K - *Lobianchia dofleini* (×7); L - *Lopholatilus chamaeleonticeps* (×2.5); M - *Merluccius albidus* (×4.5); N - *Merluccius bilinearis* (×2); O - *Myctophum punctatum* (×4.5); P - *Myctophum* sp. (×6.5); Q - *?Notoscopelus* (×3.2); R - *Peprilus triacanthus* (×4.5); S - *Phycis chesteri* (×5.8); T - *Pomacanthus arcuatus* (×10); U - *"Stromateus"* (×5.8); V - *Urophycis chuss* (×2); W - *Urophycis ?floridanus* (×2); X - *Urophycis tenuis* (×1.3).

Table 15.--Species and density (number per square meter) of fish otoliths, by station.

Station number	Acanthuroidei sp.-1	Acanthuroidei sp.-2	Benthosema glaciale	Centropristis ocyurus	Ceratoscopelus maderensis	Citharichthys ?arctifrons	Diaphus sp.-1	Diaphus sp.-2	Diaphus sp.-3	Diaphus sp.-4	Lepophidium cervinum	Lobianchia dofleini	Lophotilus chamaeleonticeps	Merluccius albidus	Merluccius bilinearis	Merluccius sp.	Myctophum punctatum	Myctophum sp.	?Notoscopelus	Peprilus triacanthus	Phycis chesteri	Pomacanthus arcuatus	"Stromateus"	Urophycis chuss	Urophycis ?floridanus	Urophycis tenuis	Urophycis sp.	Unidentified fragments
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	+
8	-	-	40	20	2,160	130	-	180	-	270	40	10	-	-	40	-	-	120	-	10	-	-	-	-	-	-	-	-
9	-	-	-	-	650	-	-	30	-	440	10	10	-	-	-	-	10	80	-	-	10	-	-	-	-	10	-	-
10	-	-	-	-	220	20	-	-	-	30	50	-	-	-	20	-	10	10	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	-	-	-	-	520	40	-	20	-	110	40	-	-	-	-	-	10	20	-	-	-	-	-	-	-	-	-	-
22	-	-	10	-	1,480	110	-	20	-	330	80	-	-	-	60	-	10	70	10	-	-	-	-	10	-	10	-	-
23	-	-	-	-	40	50	-	-	-	-	30	-	10	-	-	20	-	-	-	-	-	-	-	10	10	-	-	-
27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	10	-	-	-	-	-
31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
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38	-	-	-	-	970	40	-	-	10	110	40	10	-	-	50	-	-	20	10	-	-	-	-	10	-	-	-	-
39	-	-	-	-	70	30	10	-	-	20	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	+
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59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 16.—Comparison of density and abundance of otoliths of pelagic fish and groundfish.

Item	Pelagic	Groundfish	Unclassified
Number of otoliths	1,288 (87%)	141 (10%)	41 (3%)
Average otolith density (per m²)			
Including all samples (62)	208	23	7
Only samples with otoliths (34)	379	41	12
Number of species	11 (44%)	11 (44%)	3 (12%)

IDENTIFICATION OF OTOLITHS

Otoliths of relatively deepwater teleosts form the major portion of all species dealt with here; littoral species rarely occurred in the samples. Myctophids (lanternfishes) contributed most of the otoliths. Many of these have been referred tentatively to various genera in this group, but specific determinations are not possible in the absence of suitable identified material for comparison. It is very likely that the species are already in ichthyological collections, but most

preserving fluids soon render the otoliths useless, if they do not destroy them completely.

Nearly all the otoliths had suffered some erosion that may have resulted from abrasion on the sea bottom, possibly preceded by partial dissolution in the digestive system of predatory animals and later by the reworking of bottom sediments by deposit-feeding benthic invertebrates such as polychaete worms, holothurians, starfish, and many others. One or several of these agents resulted in the destruction of the rostral area on all percoid otoliths. The outer rims of some merluccid otoliths were damaged sufficiently to make identification difficult.

DISTRIBUTION AND DENSITY

Fish remains, all species combined, occurred at 65% of the stations. The remains were not uniformly distributed over the area but occurred mainly in the southern, offshore sector (Figures 19 and 20). More than 90% of all fish remains were taken at depths greater than 150 m, whereas less than 1% came from depths less than 50 m. Only 36% of the samples collected at depths less than 100 m contained one or more otoliths, whereas all samples taken at depths greater than 100 m contained otoliths (Table 17). Highest densities, 500 to 3,030/m², were in a band parallel to the isobaths along the outer portion of the continental shelf and upper part of the continental slope.

Density of fish otoliths was correlated closely

TABLE 17.—Density distribution of fish otoliths in relation to water depth.

Water depth	Samples collected	Samples containing otoliths	Mean number of otoliths
Meters	*Number*	*Percent*	*No/m²*
20-29	1	0	0
30-39	6	0	0
40-49	7	43	7
50-59	8	0	0
60-69	5	60	6
70-79	9	56	7
80-89	1	0	0
90-99	7	71	20
100-124	4	100	70
125-149	4	100	142
150-174	1	100	740
175-199	5	100	1,724
200-249	2	100	1,365
250-567	2	100	735

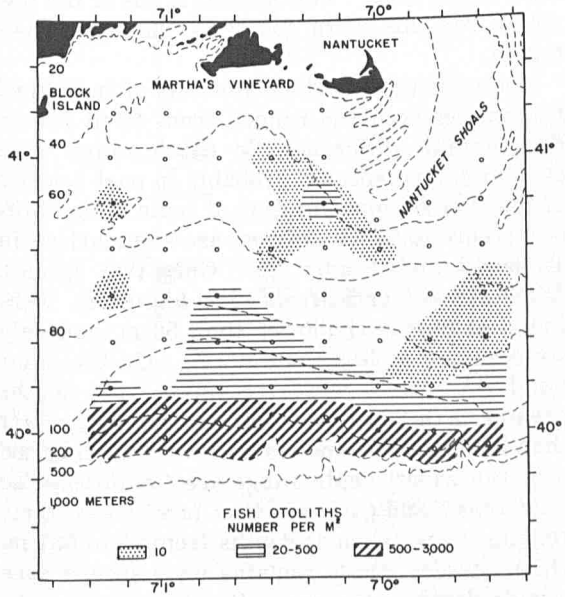


FIGURE 19.—Geographic distribution and density of fish otoliths, all species combined.

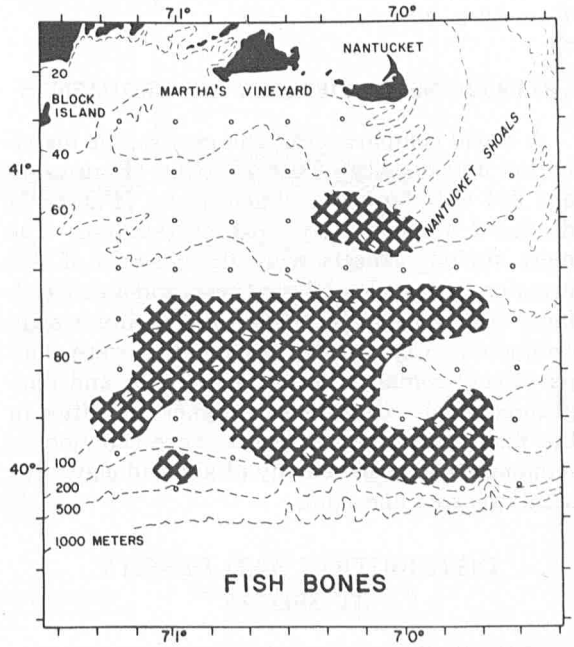


FIGURE 20.—Geographic distribution of fish bones.

with water depth (Table 17). Average densities ranged from 0 to 20/m² between 20 and 100 m and from 735 to 1,724/m² between 150 and 567 m.

Environmental features that contributed substantially to the observed correlations are the low energy environment combined with the relatively mild abrasive characteristics of the bottom sediments.

Densities of fish teeth, bones, and scales were low (80/m² or less). Teeth were recovered at only two stations (53 and 54), where water depths were 179 and 366 m; densities were 20 to 30/m². The teeth at station 53 were from the blue shark, *Prionace glauca,* a cosmopolitan species that commonly attains lengths of 2 to 3 m. Fish scales were found at three stations, at water depths of 49 to 106 m, and at densities of 10 to 20/m². Fish bones were detected at 22 stations (Figure 20). Vertebrae and rib bones were encountered most frequently but occasionally skeletal sections from the oral and branchial regions were taken. The small thin bones generally had a fresh appearance, whereas the larger thicker bones were often badly eroded and stained brown. Fish bones were collected at water depths from 38 to 366 m; densities ranged from 10 to 80/m².

RELATIONS OF DENSITY TO SEDIMENTS

A broad comparison of the geographic distribution and density of fish remains (Figures 19 and 20) with bottom sediment types (Figure 2) disclosed a moderately close correlation. The most obvious aspects were the absence of fish remains in gravel-sand mixtures, and an exceedingly low density in coarse and medium sand sediments. Conversely, fish remains were comparatively common in silt, sandy silt, and fine-grained sand. Otoliths had highest densities in the fine sand, whereas bones were common in sediments composed chiefly of silt and clay with admixtures of fine sand.

DISTRIBUTION AND DENSITY BY SPECIES

Of the 26 fish species whose remains were recovered from the bottom sediments, only six were abundant or moderately abundant; *Ceratoscopelus maderensis, Citharichthys ?arctifrons, Diaphus* sp.-4, *Lepophidium cervinum, Merluccius bilinearis,* and *Myctophum* sp. (Fish species represented by otoliths are listed by station in Table 15.) Each of these species occurred at eight or more stations, and maximum densities ranged from 60 to 2,160/m². Four of the six abundant species are pelagic forms (exceptions are *L. cervinum* and *M. bilinearis,* although *M. bilinearis* frequently is mesopelagic). The most common species was *Ceratoscopelus maderensis.* Otoliths of this species occurred at 19 stations and average density was 530/m².

Nearly all fish remains were collected in the southern half of the area. The geographic distribution of otoliths of different species is illustrated in Figure 21. With few exceptions, otoliths of individual species were geographically distributed in an east-west band across the area, roughly parallel to the depth contours. A major exception to this distribution was that for *M. bilinearis,* the most widely distributed species. It was found at 15 stations, most of which were located on the outer continental shelf, but a few otoliths occurred on the central and inner portions of the shelf. This species is one of the few whose remains were found in the inner-shelf region.

Water depths at which remains of individual fish species occurred ranged from 44 to 567 m. Considerable differences in depth range were evident among species, probably in part because of the sparse representation of some. Depth-of-occurrence data, by species, are summarized in Table 18 and Figure 22. Only two species, "*Stromateus*" and *Merluccius bilinearis,* were found at depths shallower than 50 m, and only six occurred at less than 100 m. On the other hand, 15 species were recovered from depths greater than 200 m, and 6 from depths greater than 360 m. The species that were distributed over the widest depth range are *Ceratoscopelus maderensis* and *Citharichthys ?arctifrons;* their remains were taken at depths from 95 to 567 m. Other species whose remains were spread over a wide depth range are: *Benthosema glaciale, Diaphus* sp.-2, *Diaphus* sp.-4, and *Lepophidium cervinum.* About 61% of the species were found

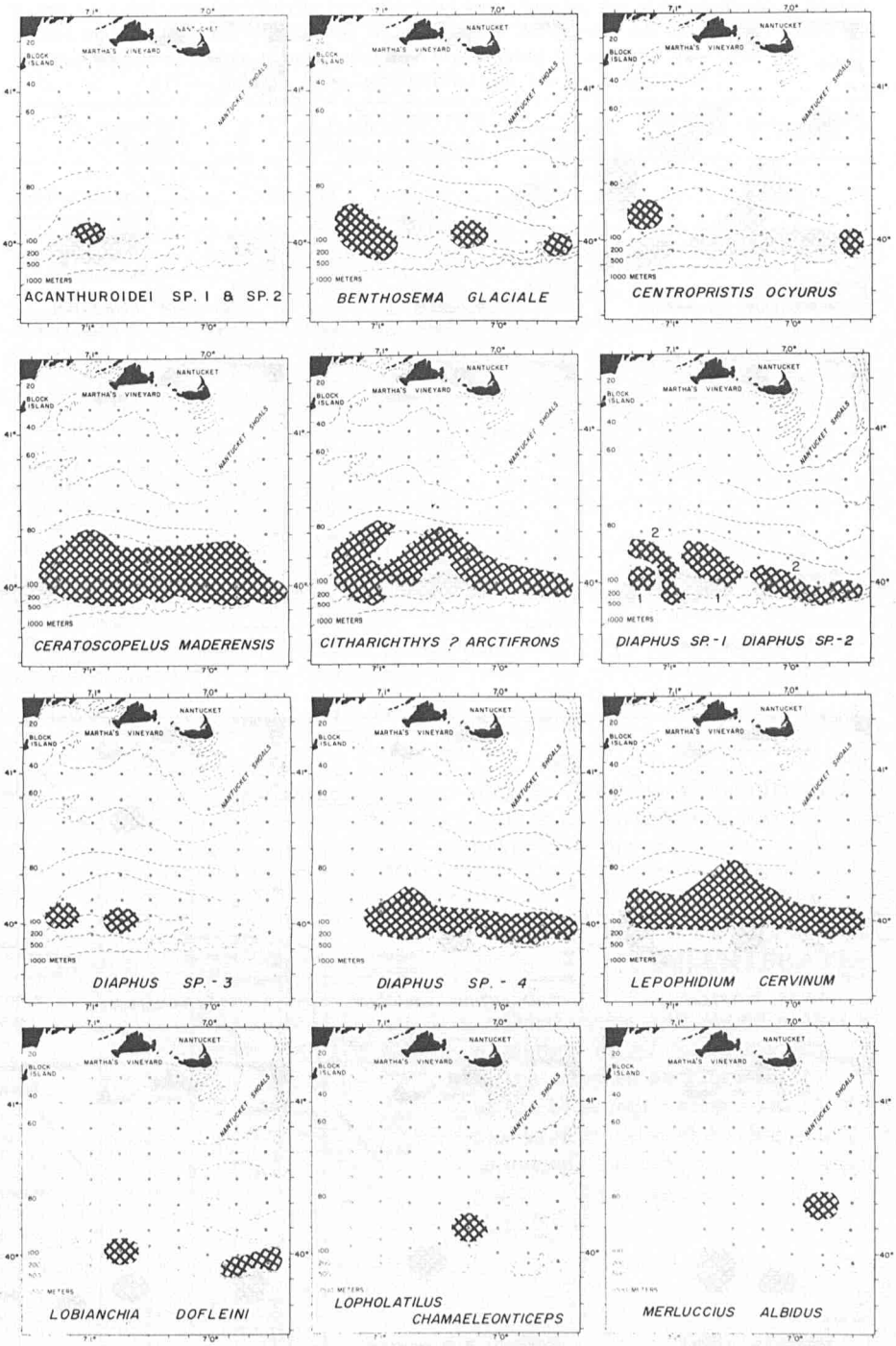


FIGURE 21.—Geographic distribution of fish otoliths, by species.

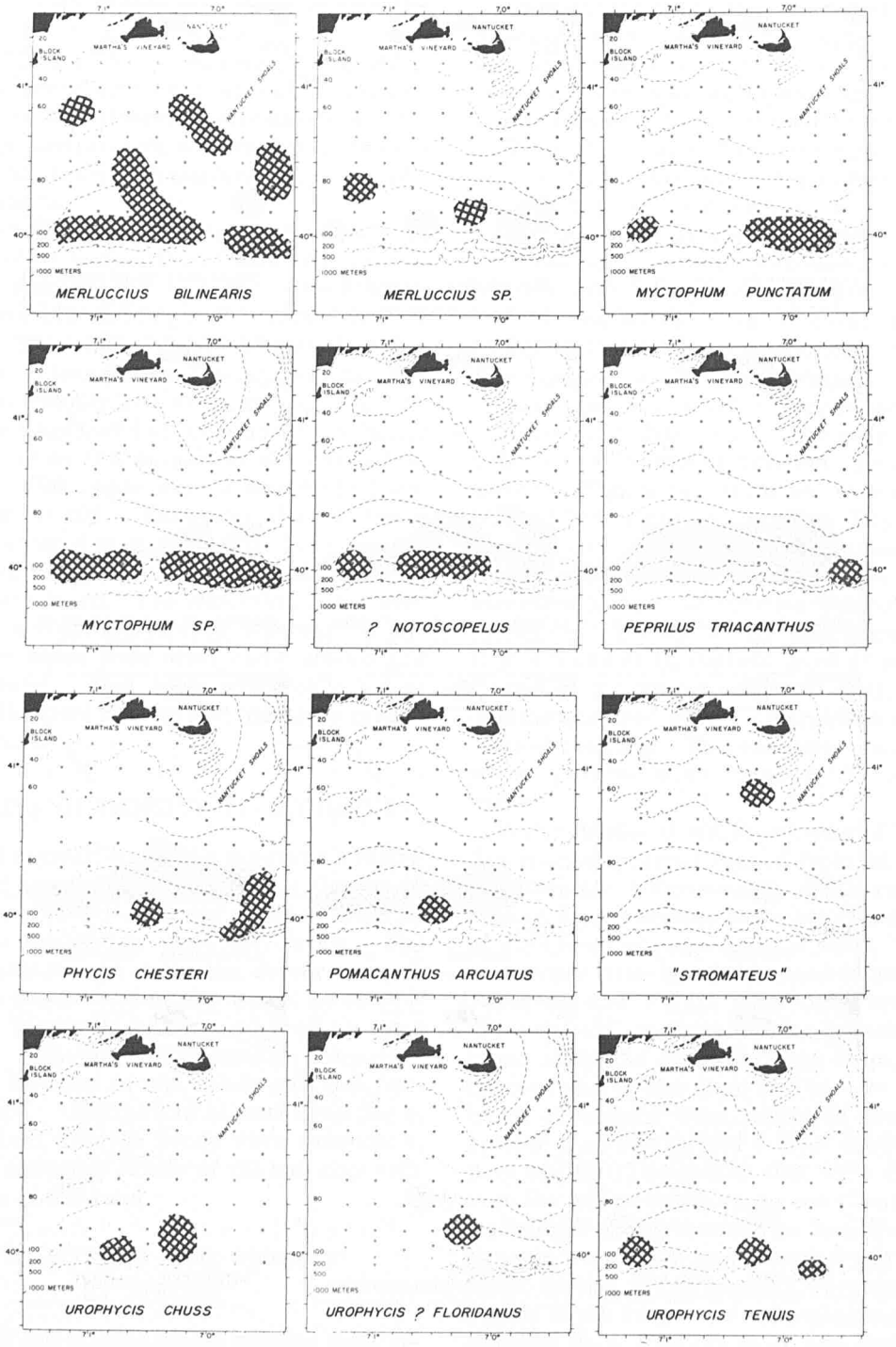
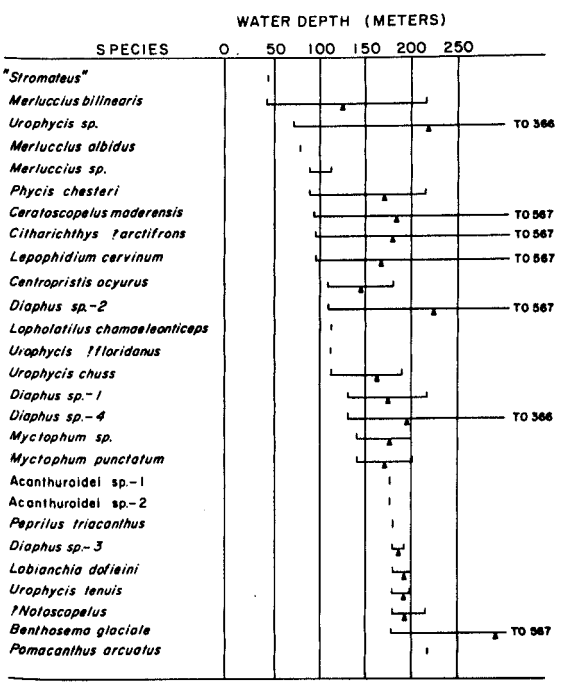


FIGURE 21.—Geographic distribution of fish otoliths, by species.—Continued.

TABLE 18.—Bathymetric distribution of teleost and selachian remains by species or higher taxon, and the number of stations at which each occurred. All entries are based on otoliths except *Prionace glauca*, which is represented by a tooth.
[P — pelagic, G — groundfish, and Un — unclassified.]

Species or higher taxon	Water depth			Number of stations	Environmental classification
	Minimum	Maximum	Mean		
	m	m	m		
Acanthuroidei sp.-1	179	179	179	1	G
Acanthuroidei sp.-2	179	179	179	1	G
Benthosema glaciale	183	567	296	5	P
Centropristis ocyurus	110	183	146	2	G
Ceratoscopelus maderensis	95	567	185	19	P
Citharichthys ?arctifrons	97	567	196	10	G
Diaphus sp.-1	132	220	176	3	P
Diaphus sp.-2	110	567	227	7	P
Diaphus sp.-3	183	194	188	2	P
Diaphus sp.-4	132	366	196	10	P
Lepophidium cervinum	97	366	169	17	G
Lobianchia dofleini	183	201	193	3	P
Lopholatilus chamaeleonticeps	113	113	113	1	G
Merluccius albidus	79	79	79	1	Un
Merluccius bilinearis	44	220	126	15	Un
Merluccius sp.	91	113	102	2	Un
Myctophum punctatum	139	201	174	5	P
Myctophum sp.	139	201	178	8	P
?Notoscopelus	183	220	195	4	P
Peprilus triacanthus	183	183	183	1	Un
Phycis chesteri	91	220	171	3	G
Pomacanthus arcuatus	220	220	220	1	G
Prionace glauca	179	179	179	1	Un
"*Stromateus*"	44	44	44	1	P
Urophycis chuss	113	194	163	3	G
Urophycis ?floridanus	113	113	113	1	G
Urophycis tenuis	183	201	189	3	G
Urophycis sp.	73	366	220	2	G



only in the general vicinity of the shelf break (100 to 220 m). None was restricted to a depth below 220 m.

REMAINS OF CRUSTACEANS AND COELENTERATES

Crustaceans and coelenterates were the least numerous of all taxonomic groups represented in the samples and formed only a small portion of the total macroscopic animal remains. These two groups differed markedly in geographic distribution, bathymetric distribution, and abundance. Thus, each is treated in a separate section below.

FIGURE 22.—Bathymetric range and mean depth of occurrence of fish species represented in the samples by otoliths. (Observed values are listed in Table 18.)

CRUSTACEANS

Remains of two groups of crustaceans—cirripedes and decapods—were present in the samples. Cirriped (barnacle) remains consisted of calcareous plates, primarily compartments (wall plates) plus a moderate proportion of opercular valves. Only balanomorph types were present, and generally the thicker, more durable portions were most numerous. Examples are illustrated in Figure 23. None of the chitinous parts of the skeleton, such as the covering of the appendages, was present. Decapod crustaceans were represented by anomuran (hermit) crabs and brachy-

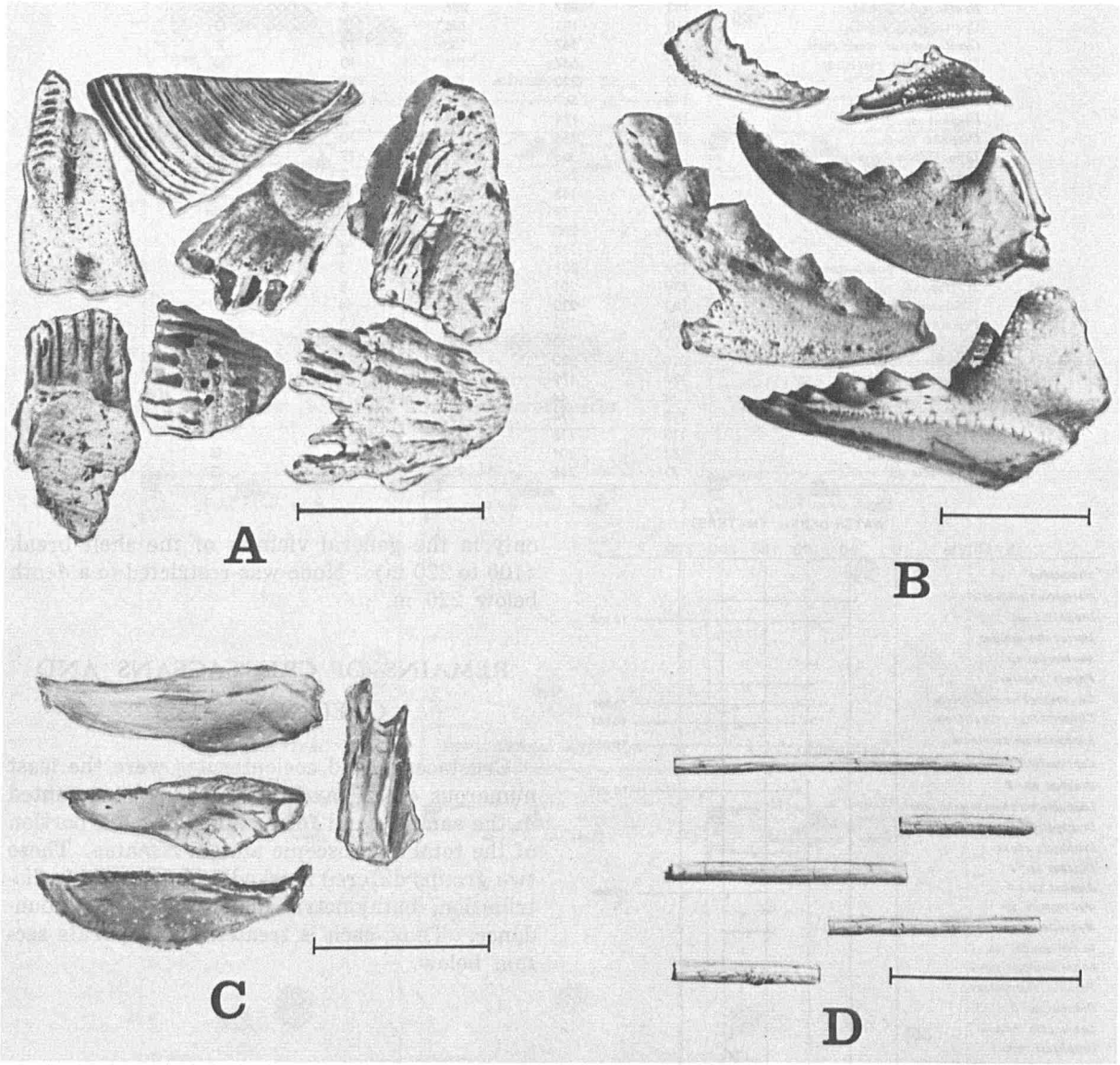


FIGURE 23.—Skeletal remains of crustaceans and coelenterates. A - cirripedes, scutum and compartments; B - anomuran and brachyuran, chelipod remains; C - *Flabellum*, corallite fragments; D - *Acanella* (?), axial skeleton remains. Each scale bar is 5 mm.

uran (true) crabs. Remains of the latter group consisted of the larger more massive and durable parts of the skeleton (mainly the carapace and chelipeds), and the anomuran remains consisted only of chelipeds. Occurrence records for both groups of crustaceans are included in Table 19; bathymetric data are given in Table 20. The geographic and bathymetric distributions are illustrated in Figures 24 and 25.

Remains of cirripedes (Figure 23A) were widely scattered over the area (Figure 24). The density of major fragments ranged from 10 to 90/m²; densities were substantially higher in shallow water than in deep water. The depth range was 27 to 567 m with the average depth at 123 m.

Remains of crustaceans carapaces and chelipeds were from anomuran and brachyuran crabs (Figure 23B). They were sparse to moderately dense and had a somewhat limited geographic distribution near the central part of the shelf (Figure 24) at depths from 51 to 113 m. Their distribution was much more restricted than that of cirripedes. Also, this part of the shelf is a low-energy region, as compared with the Nantucket Shoals and the shallow inshore areas where cirriped remains were prevalent.

TABLE 19.—Density of crustaceans and coelenterates, by station.

Station number	Crustaceans		Coelenterates	
	Cirripedes	Anomuran-brachyuran	*Flabellum*	*Acanella*(?)
	No/m²	*No/m²*	*No/m²*	*No/m²*
1	90	--	--	--
2	50	--	--	--
12	--	20	--	--
16	50	--	--	--
18	--	10	--	--
21	10	--	--	--
23	10	10	--	--
24	--	10	--	20
25	--	20	--	--
26	--	10	--	--
29	10	--	--	--
32	--	70	--	--
34	--	10	--	--
35	--	--	--	50
36	10	--	--	--
38	--	--	30	--
41	--	20	--	--
49	10	--	--	--
51	10	--	--	--
52	--	--	80	--
53	10	--	10	--
54	--	--	50	--
55	30	--	--	--
59	10	10	--	--
63	80	--	--	--

TABLE 20.—Bathymetric distribution of crustaceans and coelenterates, and the number of stations at which they occurred.

Group	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	*m*	*m*	
Crustaceans				
Cirripedes	27	567	123	13
Anomuran-brachyurans	51	113	76	10
Coelenterates				
Flabellum	146	366	221	4
Acanella (?)	90	97	94	2

COELENTERATES

Coelenterate remains were the rarest group of animals in the prefossil assemblage. They consisted solely of corals: *Flabellum alabastrum* (=*goodei* Verrill), a cup coral, and *Acanella* (?), a bush coral. Some examples of each kind are illustrated in Figure 23.

Flabellum, a solitary coral of the madreporian group, has a rather large (4 by 6 cm) polyp and a typical calcareous skeleton (corallite) with well-developed septae. Corallite remains contained a large proportion of septae and were commonly 4 to 8 mm long. This species occurred only in a limited area on the continental slope south of Martha's Vineyard (Figure 24) at depths of 146 to 366 m (Figure 25). Densities of fragments were as high as 80/m², but the average density at the locations where they occurred was about 40/m².

White calcareous rodlike structures about 0.5 mm in diameter and 0.5 to 1 cm in length (Figure 23D) were provisionally classified as *Acanella*, a colonial alcyonarian coral. The fragments appeared to be internodal portions of the axial skeletons. *Acanella normani* Verrill is not uncommon in the region. The multibranched colony of this species is composed of numerous slender, jointed segments. Total height of a full-grown colony is usually less than 30 cm. Remains of this coral were found at two stations near the center of the area (Figure 24) at depths of 90 to 97 m and in densities of 20 to 50/m².

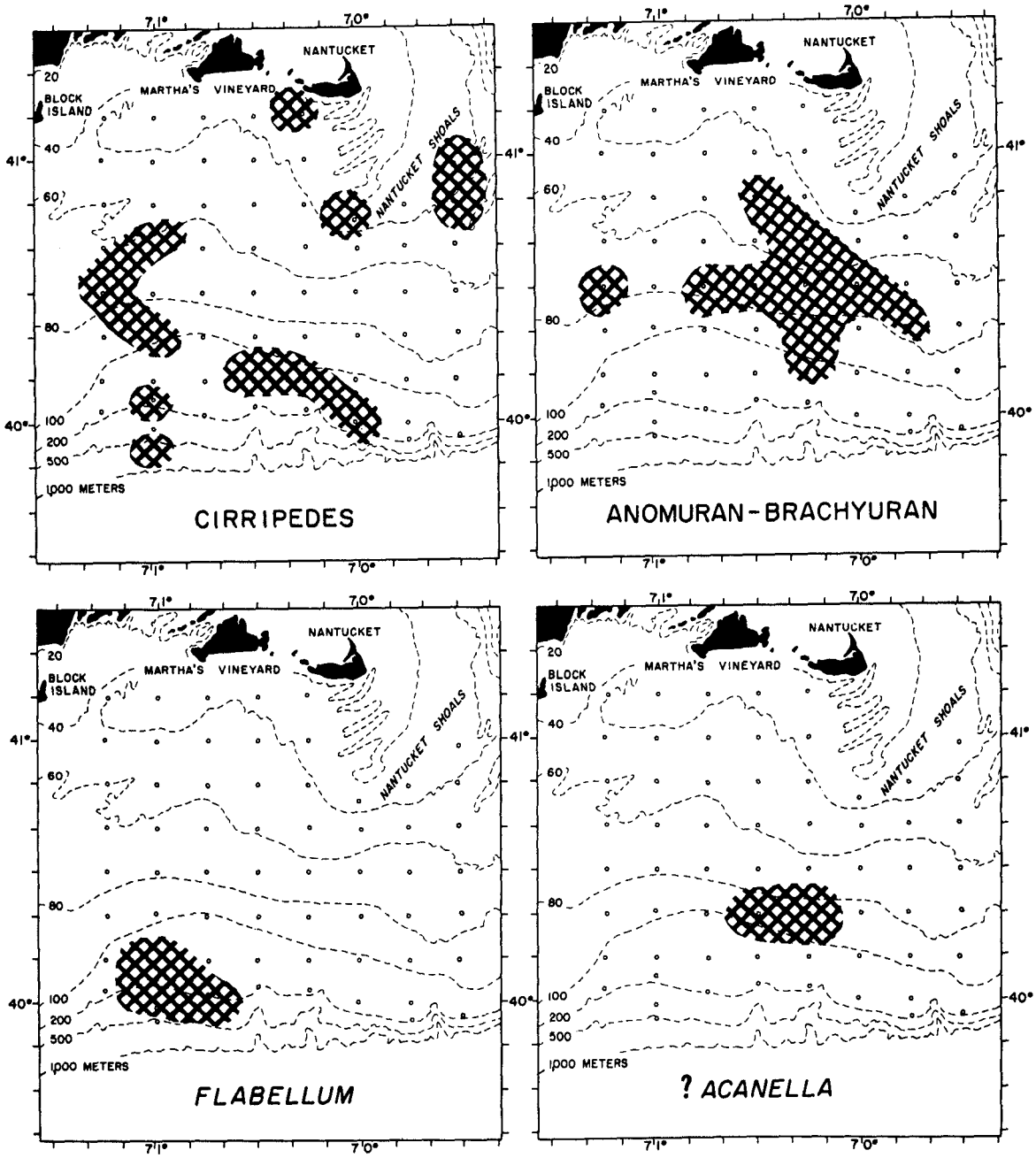


FIGURE 24.—Geographic distribution of skeletal remains of crustaceans and coelenterates.

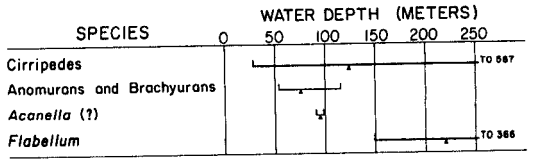


FIGURE 25.—Bathymetric distribution of skeletal remains of crustaceans and coelenterates.

COMPARATIVE DISTRIBUTION OF ALL TAXONOMIC GROUPS

The distribution of the principal animal remains in relation to each other, sediment type, and water depth, and, to a limited extent, their north-south geographical position on the continental shelf and slope are illustrated in Figure 26. This chart is a generalized profile of the study area with the inshore (north) section on the lefthand side and the offshore (south) section on the righthand side. Broad, diagonally striped bands indicate relatively high density, and narrow lines indicate low density. Animal groups whose centers of concentration were inshore in relatively shallow waters were cirripedes and *Echinarachnius parma*. The dominant midshelf and outer-shelf components were gastropods, pelecypods, and decapods. Pelecypods, scaphopods, *Brisaster*, and *Flabellum* were common along the outer portion of the continental shelf and upper portion of the continental slope. The chief components in deeper sections of the continental slope were fish otoliths and cephalopod mandibles.

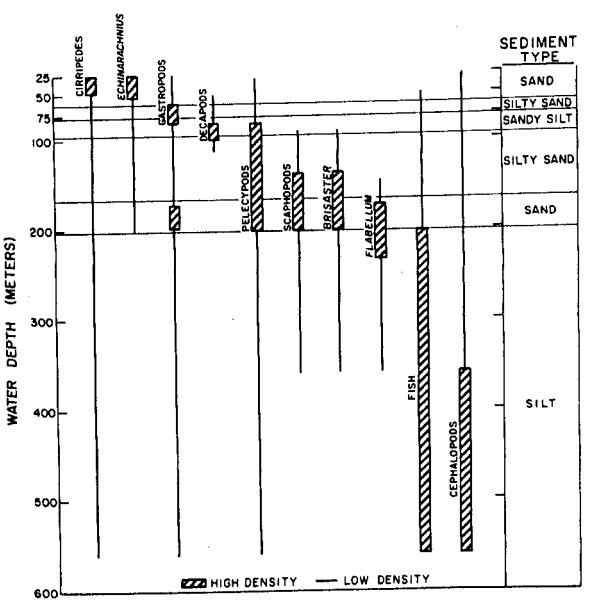


FIGURE 26.—Schematic diagram of the density distribution of macroscopic remains of the major animal groups represented in bottom sediments arranged according to water depth and sediment type (see text for details).

SUMMARY

Skeletal remains of deceased animals were common seabed components on the southern New England continental shelf and the upper part of the continental slope. In some sections, particularly in shallow water, skeletal remains constituted a substantial portion of the substrate volume—up to nearly 30% in the vicinity of Nantucket Shoals. Offshore, near the margin of the continental shelf and in the upper portion of the continental slope, macroscopic animal remains generally constituted less than 1% of the substrate.

Remains of benthic, pelagic, and nektonic organisms were present; benthic forms were dominant. Planktonic animals (represented only by pteropods) were sparse. Fish and cephalopods were the principal nektonic forms. They were rather abundant in the deeper waters, particularly on the outer portion of the continental shelf and on the continental slope.

The two animal groups that contributed the largest quantities of material to the substrate were echinoid echinoderms and pelecypod mollusks. Although remains of a wide variety of fish species were present, the quantity was moderate and the sizes small; consequently the volume of fish remains was rather small.

ECHINODERMS

The exceedingly abundant remains of echinoderms consisted exclusively of echinoids. Only one species—*Echinarachnius parma*—occurred in high densities and was the most abundant and widely distributed component of organic

origin in the sediments. Geographically it had a wide distribution, occurring at 72% of the stations. Depth range was 27 to 201 m. Size, shape, and color of *Echinarachnius* fragments differed markedly with water depth and sediment type. The *E. parma* fragments in the inshore localities were whitish, relatively large, and had angular edges and corners; in offshore localities, the fragments were light greenish-brown, smaller, and had rounded edges. Densities of echinoids other than *Echinarachnius* were low, and except for *Brisaster*, remains were found at only a few localities. Density of *Brisaster* remains were low but the remains were rather widely distributed along the outer portion of the continental shelf. Remains of *Strongylocentrotus drobachiensis* were sparse and widely scattered in both shallow and deep water.

MOLLUSKS

Pelecypods ranked first in diversity of forms (57 species) and second in volume of remains in the bottom sediments. They were present at all depths sampled, from 27 to 567 m, and were widely distributed geographically. Densities were high in a wide band extending from Nantucket Shoals southwestward across the area, and in a narrow band parallel to the isobaths near the shelf break. Pelecypods were very abundant (more than 3,000/m^2) at 6 stations, most of which were along the outer margin of the continental shelf; common to abundant (50 to 3,000/m^2) at 48 stations; and sparse (less than 50/m^2) or absent at 8 stations. In general, the species with the broadest geographic distributions occurred in highest densities. The six most abundant and widely distributed pelecypods were: *Venericardia borealis, Arctica islandica, Astarte subequilatera, A. undata, Nucula proxima,* and *Thyasira trisinuata.* Pelecypod shells were more abundant in moderately fine-textured sediments than in either the coarse or very fine sediments. Silty sand, sandy silt, and sand-silt-clay yielded the highest densities of pelecypod shells. Size of shells ranged from 10 to 12 cm (*Spisula, Arctica, Placopecten*) to less than 5 mm (*Thyasira, Nucula, Bathyarca*).

Gastropods ranked third in volume of skeletal material in the substrates. Shells of gastropods were distributed widely throughout the area, but highest densities were near the center. A total of 44 species were present, but only 2 were generally abundant—*Alvania carinata* and *Cylichna gouldi.* Shells were taken at all depths, and were particularly common between 60 and 80 m and moderately common between 175 and 250 m. Density was correlated in a general way with bottom sediments. High densities were in silty sand and sand sediments, whereas shells were absent in coarse sand and mixtures of sand and gravel. A large majority of gastropod shells was less than 1 cm in height.

Cephalopod remains, consisting entirely of beaks, were present at only 12 stations, all of which were from the outer portion of the continental shelf and upper part of the continental slope at depths between 76 and 567 m. Densities were generally less than 40/m^2 at the shallower depths, but ranged to 130/m^2 at a depth of 366 m and 11/m^2 at 567 m. Remains of this group ranged in size from 4 to 6 mm and were relatively fragile. They were recovered only from fine-textured sediments.

Distributions of scaphopods were rather limited geographically and densities were low. The two genera collected, *Cadulus* and *Dentalum,* were present at 11 stations, geographically limited to the deepwater areas on the outer portion of the continental shelf and the upper continental slope. The bathymetric range was 139 to 366 m for *Cadulus,* and 91 to 183 m for *Dentalium.* Sediments at the scaphopod localities were generally fine-grained, but *Cadulus* occurred in slightly coarser sediments than *Dentalium.* Densities at the stations where they occurred averaged about 30 to 40/m^2; maximum density for both genera was 11/m^2. *Cadulus* shells were 10 to 13 mm long, and *Dentalium* shells were 15 to 35 mm.

FISH

Fish were the only vertebrates in the samples. Otoliths were the main component and bones were moderately common, but teeth and scales were rare. Remains of 26 species were collected, nearly half of which were from epipelagic or mesopelagic forms. Myctophids were the most numerous and widely distributed, and they con-

tributed the greatest number of species. Thirty-six percent of the species and 87% of all otoliths were Myctophiformes. The six most abundant fish, based on otolith identifications, were: *Ceratoscopelus maderensis, Citharichthys ?arctifrons, Diaphus* sp.-4, *Lepophidium cervinum, Merluccius bilinearis,* and *Myctophum* sp. The estimated length of the fish whose remains were encountered ranged from a few centimeters to several meters. Remains of fish were at depths between 38 and 567 m, and an overwhelming majority was found at depths greater than 150 m. More than 90% of the otoliths were at depths below the 150-m isobath; bones were less common and more uniformly distributed, from 38 to 366 m. The remarkably high otolith density of 3,030/m^2 was found near the edge of the continental shelf south of Nantucket Shoals. Remains of most individual species were geographically distributed in east-west bands across the area, generally oriented parallel to the isobaths. Fish remains were absent in coarse-grained sediments, and most abundant in fine sands and silt-clay.

CRUSTACEANS AND COELENTERATES

Crustaceans and coelenterates were the only other nonmolluscan invertebrates, in addition to those previously described, that were present in the samples. The quantity of their remains was very small.

Crustaceans were generally sparse and rather widely distributed. Cirripedes consisted exclusively of shells of sessile forms; they were geographically scattered and were taken at all depths sampled. Cirripedes were only slightly more common in shallow water than in deep water. They were one of the few animal groups whose remains occurred in coarse-grained sediments. Fragments of skeletons of anomurans and brachyurans were encountered only in the midcontinental shelf in sediments primarily of silts and fine sands. They were collected between 51 and 113 m. Densities were low, from 10 to 70/m^2.

Remains of coelenterates occurred in low densities (10 to 80/m^2) and were geographically restricted to small areas in the south-central and southwestern sectors. Two genera—both corals—were represented, *Acanella* (?) (at 90 to 97 m) and *Flabellum* (between 146 and 366 m). Both kinds were restricted to fine-textured sediments.

ACKNOWLEDGMENTS

The staff members of the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Mass., who aided in collecting and processing the samples are: Harriett E. Murray, Samuel R. Nickerson, Ruth R. Stoddard, and Roger B. Theroux. Officers and crew of RV *Delaware* assisted in collecting the samples. Arthur S. Merrill, National Marine Fisheries Service; Earl Reed, Museum of Science, Springfield, Mass.; and Roger B. Theroux, National Marine Fisheries Service, identified mollusks; Malcolm R. Clarke, National Institute of Oceanography, Wormley, England, contributed information regarding cephalopods; and Richard H. Backus and James E. Craddock, Woods Hole Oceanographic Institution, Woods Hole, Mass., identified fish and provided reference specimens for otolith identification. K. O. Emery, Woods Hole Oceanographic Institution, Woods Hole, Mass., provided information on bottom sediments and suggestions for improving the manuscript.

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DEEP MAXIMA OF PHOTOSYNTHETIC CHLOROPHYLL IN THE PACIFIC OCEAN

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ABSTRACT

Data collected on several expeditions through the temperate and tropical Pacific Ocean show that during most of the year the maximum concentrations of chlorophyll occur below the surface, typically in a narrow layer near or below the depth of penetration of 1% of the surface light. The layer appears to be continuous across most of the Pacific although the depth and chlorophyll concentration vary regionally. The depth of the layer is more closely related to the depth of the nitrite maximum and to the position of the nutricline than to either light or density regimes. Productivity within the layer is low but positive, and contributes substantially to the total production of the water column. The maximum layer may be a seasonal phenomenon developing in the summer after the stabilization of the water column and mixing to the surface during the winter. Year to year fluctuations of depth and concentration of chlorophyll within the maximum layer may be related to large-scale meteorological fluctuations.

Doty and Capurro (1961) have tabulated the position, date, depth, and values of chlorophyll and productivity in the world's oceans. There are several thousands of these measurements in the Pacific. Most are in the Northern Hemisphere, and most are near land masses or islands (e.g., Hawaii, Luzon, Hokkaido, New Caledonia, New Zealand), along the equator, or north of lat 40°N. Of the values from the oceanic Pacific, between lat 50°N and 50°S, less than 10% of the chlorophyll values represent depths greater than 25 m; in the same region, over half of the productivity measurements were obtained at the sea surface. Koblenz-Mishke, Volkovinsky, and Kabanova (1970) have used these data and additional data available to them to estimate the plankton primary production of the Pacific, to construct tables and charts of its geographical variability, and to compare production in the Pacific with their estimates from other oceans. Their estimates of primary production, expressed in milligrams carbon per square meter of sea surface per day, represent production integrated through the water column. However, many of their production values are extrapolated from surface measurements, and, in large areas of the temperate gyres of the North and South Pacific, production is estimated from the available chlorophyll data, or from "oxygen or hydrogen saturation" values.

All values of total production in the water column are strongly dependent upon the assumed (usually) depth of zero productivity. This is traditionally taken to be the depth at which the light intensity has been reduced to 1% of the incident radiation, and this criterion has been used to divide the water column into a euphotic zone and an aphotic zone.

Evidence is accumulating that major concentrations of plant material in the ocean usually occur below the surface, typically within the thermocline and near the bottom of the euphotic zone. Maxima of chlorophyll or phytoplankton as deep as 100 m have been reported from the Indian Ocean (Yentsch, 1965), the Sargasso Sea (Menzel and Ryther, 1960), the Gulf of Mexico (Steele, 1964), and the Kuroshio and adjacent regions (Motoda and Marumo, 1963; Saijo, Iizuka, and Asaoka, 1969). Shallower maxima are characteristic of the California Current

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Manuscript accepted August 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

(Allen, 1939; Lorenzen, 1965, 1967). Initial results of the EASTROPAC survey (Love, 1970, 1971) indicate a chlorophyll maximum varying in depth between 50 and 100 m over large areas of the eastern tropical Pacific. Anderson (1969) has studied the chlorophyll maximum layer off the Oregon coast which is present between 50 and 75 m during the summer. The layer is continuous over a broad region in the Eastern Subarctic Pacific and maybe transpacific. Chlorophyll maxima have also been reported from the other major water masses of the Pacific (El-Sayed, 1970; Sorokin, 1970).

Different workers have attributed the existence of the maximum layer to different processes including the concentration of detrital chlorophyll in the pycnocline (Lorenzen, 1965), differential zooplankton grazing (Lorenzen, 1967), an increase in the chlorophyll/carbon ratio in plant cells, without an accumulation of cells (Steele, 1964), horizontal advection and layering of different water masses and plant populations (Sano, 1966), the sinking of active or senescent cells from shallower depth (Allen, 1932; Steele and Yentsch, 1960), and in situ production (Anderson, 1969). In short, the tendency has been to consider deep chlorophyll maximum layers as discrete and sporadic phenomena and to interpret them strictly according to local conditions.

The accuracy with which surface productivity reflects the productivity throughout the water column has been investigated by Koblenz-Mishke et al. (1970) by means of log-log scatter diagrams. There is a linear trend in their transformed data, but the spread of values around the regression line is broad. Lorenzen (1970) showed a significant linear regression, after transformation to logarithms, of total production on the concentration of surface chlorophyll. The regression, however, removes only half of the variability of the dependent variable, and the author advises that precise values of total production must depend upon direct measurements. He also cautions that extrapolations from surface values are based upon averages and will easily miss unexpected events.

There have been very few attempts to measure productivity in the deeper maximum layers. Anderson (1969) made one series of in situ measurements within the chlorophyll maximum layer off the Oregon coast. There was a peak in production within the layer and positive photosynthesis as deep as 90 m, the 0.1% light level. Implicit in most studies to date is the assumption that pigment concentrations below the level of 1% light are nonphotosynthetic and represent a loss of plant material from the "euphotic zone." The two extensive surveys from the Sargasso Sea and the eastern tropical Pacific both adjusted the depth of the lowest sample to the depth of 1% light, and rarely sampled below 100 m, even though the maximum pigment concentrations were frequently obtained from the deepest sample.

In the present paper, the authors have summarized a large amount of data accumulated over the past 8 years, all of which indicate that a deep chlorophyll maximum layer is a regular and continuous feature of much of the oceanic Pacific. It is frequently observed below the traditionally defined euphotic zone, yet it is dominated by photosynthetically active chlorophyll *a* which is present in concentrations as great as 10 times those at the surface. The development of this maximum layer appears not to be a localized process, but a widespread and regularly occurring phenomenon. Because of its limited vertical extent and great depth, the existence, extent and significance of this maximum layer has been overlooked by most previous surveys of chlorophyll and productivity. Evidence suggests that a better understanding of this layer will necessitate revision of existing estimates of total primary production in the ocean.

METHODS

Since 1964 we have been mapping and studying the subsurface chlorophyll maximum in the Pacific on a series of expeditions (Figure 1). In 1964 (URSA MAJOR Expedition: University of California, 1967) and 1966 (ZETES Expedition: University of California, 1970), chlorophyll pigments were determined with a D U Spectrophotometer; on other expeditions chlorophyll *a* and phaeophytin were assayed with a

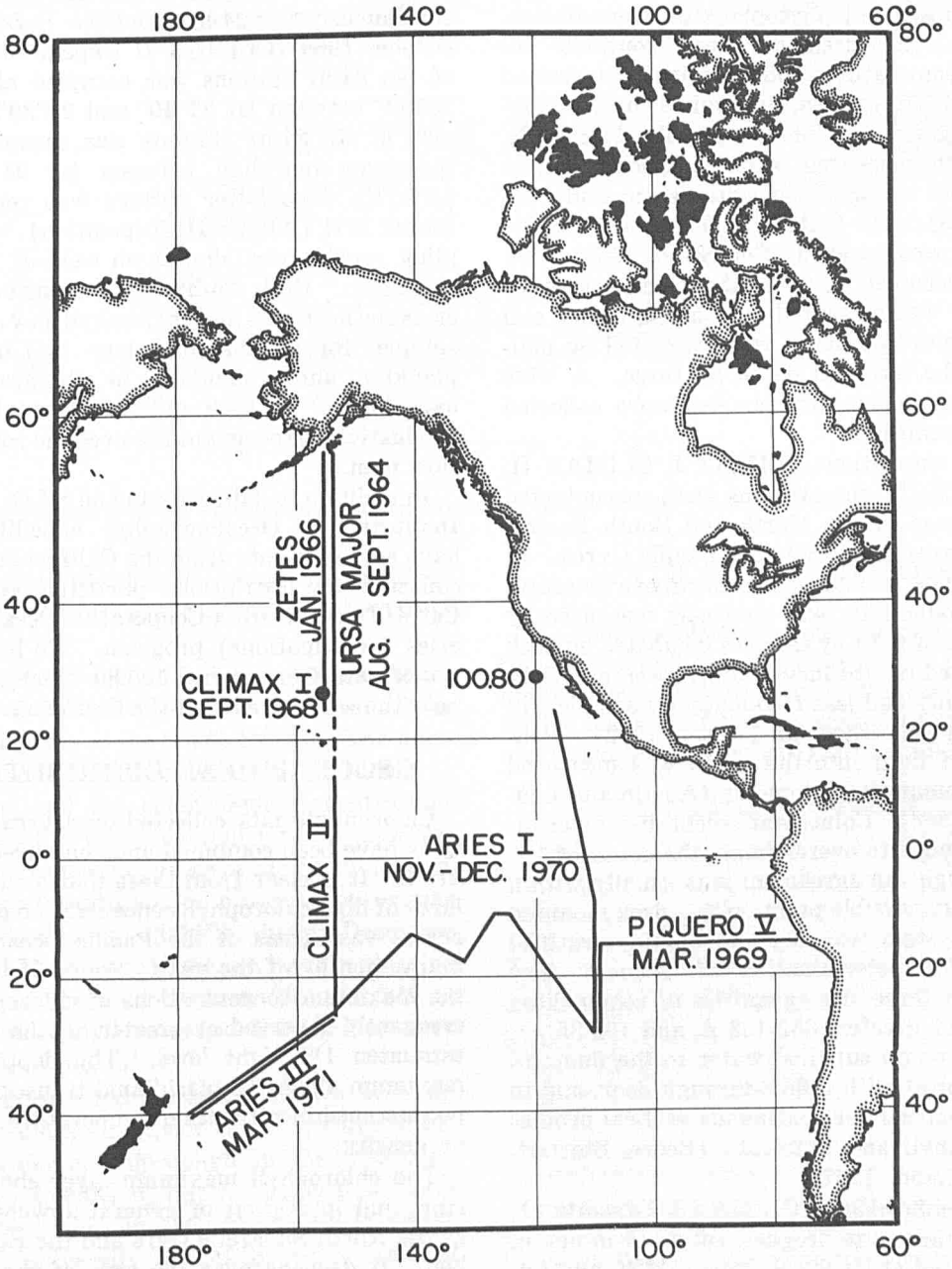

FIGURE 1.—Cruise tracks of seven expeditions from which chlorophyll data was obtained, and the location of Marine Life Research station 100.80 at which chlorophyll was sampled seasonally.

Turner Fluorometer.[2] Water samples from the same casts were preserved with neutral Formalin for subsequent phytoplankton enumeration. Additional measurements have routinely included temperature and salinity, determined with an STD; oxygen, determined by the Winkler procedure; and phosphate, silicate, nitrate, and nitrite, measured with the spectrophotometer or the autoanalyzer (Strickland and Parsons, 1968). On CLIMAX II and ARIES III ammonia was assayed (Solórzano, 1968). On stations occupied at noon, the transparency of the water was measured with a secchi disk and the compensation depth was estimated by multiplying the terminal depth by three. A wide variety of zooplankton samples were collected on all expeditions.

On the expeditions CLIMAX I, CLIMAX II, and ARIES III, observations were concentrated in two areas of the North and South Pacific, near the axes of the Central Pacific Gyres. In these regions, in addition to the above measurements, productivity was routinely measured by the uptake of C-14 by samples incubated on deck in simulated in situ incubators (Owen and Zeitzschel, 1970) and less frequently by samples incubated in situ (Steeman Nielsen, 1952). Penetration of light into the ocean was measured with a submarine photometer (Austin and Loudermilk, 1968). Coincident secchi disk determinations tended to overestimate the depth of 1% light, though the agreement was usually within 6 m. A submersible pump with a deck mounted filtering system was used to obtain stratified samples for determination of biomass (dry weight) of three size categories of zooplankton (333 μ and greater, 332-103 μ, and 102-35 μ). The same pump supplied water to the fluorometer, equipped with a flow-through door, and to the autoanalyzer for continuous vertical profiles of chlorophyll and nutrients (Beers, Stewart, and Strickland, 1967).

In September 1968 (CLIMAX I Expedition), a pair of parachute drogues, set at 10 m depth, were released at lat 27°N, long 155°W, and followed for 10 days, during which time they moved northwest approximately 150 miles. Physical, chemical, and biological properties were sampled continuously on a 24-hr schedule. In September-October 1969 (CLIMAX II Expedition), a grid of ten 24-hr stations was occupied along long 155°W between lat 27°10′ and 28°30′N, and a grid of six 24-hr stations was occupied along the same meridian between lat 24°40′ and 25°20′S. This latter pattern was repeated in March 1971 (ARIES III Expedition). The sampling routine was similar on each of these expeditions. Each 24-hr station included four casts for nutrients and chlorophyll, day and night samples for biomass of micro- and macrozooplankton, and a simulated in situ productivity experiment. In 1969 and 1971 a single in situ productivity experiment followed the routine station plan.

In addition to data collected on S.I.O. (Scripps Institution of Oceanography) expeditions, we have available data from the California Current collected by institutions participating in the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program. We have made use of data from station 100.80 which is located near the western edge of the California Current.

GEOGRAPHICAL DISTRIBUTION

Chlorophyll data collected on several expeditions have been combined and contoured in Figure 2. It is clear from these that a subsurface layer of high chlorophyll concentration is present across vast areas of the Pacific Ocean during many months of the year. South of lat 46°N, the maximum concentrations of chlorophyll are frequently observed at greater depths than the estimated 1% light level. The depth of the maximum along the meridianal transects shows no relationship with either temperature, salinity, or density.

The chlorophyll maximum layer shoals near land, and in regions of general upwelling such as the North Subarctic Gyre and the Equatorial belt. It deepens near the axes of the Central Pacific Gyres. The meridianal continuity of the layer is especially remarkable considering that it passes through three major epipelagic environments: the Subarctic, where it is likely to

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

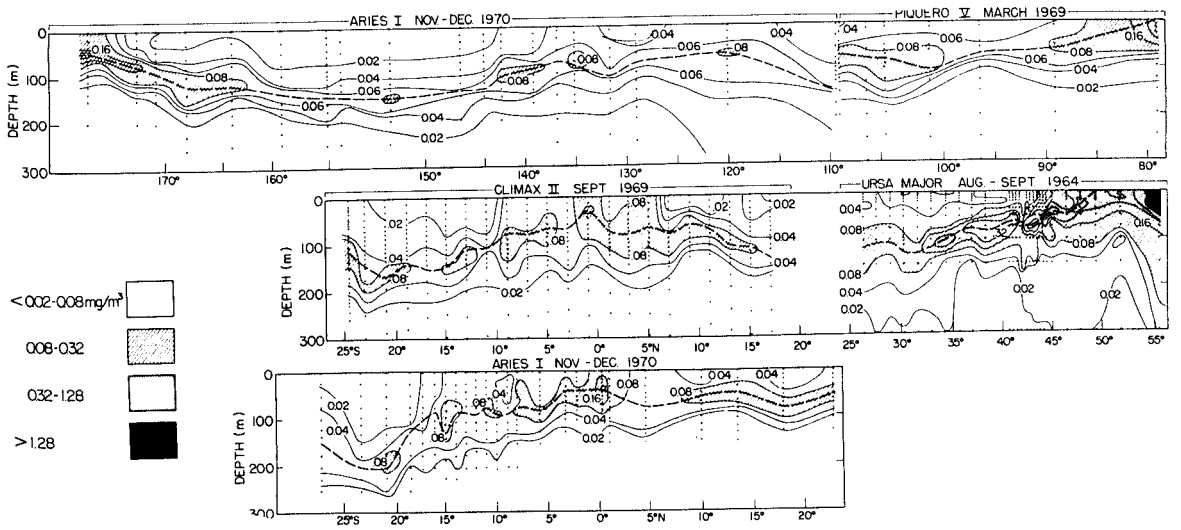

FIGURE 2.—Vertical sections of chlorophyll *a* concentrations in the Pacific Ocean; vertical exaggeration 5020.

be confluent with that discussed by Anderson (1969), the Central, and the Equatorial environments.

The east-west section indicates that the maximum layer is well developed over most of the middle latitudes of the South Pacific. The maximum layer in the South Central Gyre tends to be deeper, and the chlorophyll concentrations throughout the water column tend to be lower than in corresponding areas of the North Pacific. The greatest depth so far observed by us was at lat 20°09′S, long 118°18′W, during December (ARIES I Expedition) where a layer containing 0.05 mg/m³ occurred between 200 and 245 m depth; chlorophyll values at the surface were less than 0.01 mg/m³.

Portions of all three sections have been repeated by different expeditions. The depth and concentration of chlorophyll in the maximum layer vary somewhat, but the general features remain the same. In 1969, the Ocean Research Institute, University of Tokyo, ran a transect along long 155°W (Ocean Research Institute, University of Tokyo, 1970). The results of their chlorophyll measurements compare well with ours.

VERTICAL DISTRIBUTION

We have supplemented our discrete, quantitative chlorophyll samples with in vivo profiles of fluorescence which provide continuous, but qualitative pictures of the fine scale structure of the maximum layer (Figure 3). Although the major

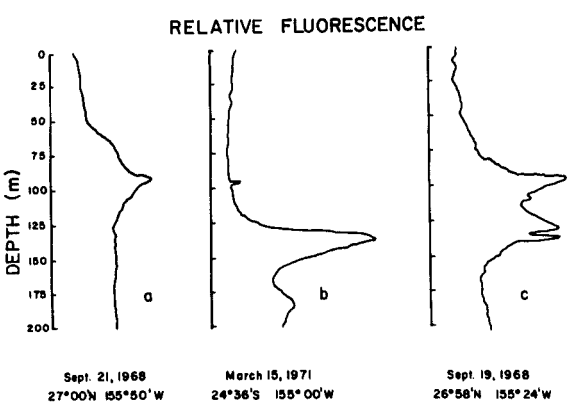

FIGURE 3.—Continuous vertical profiles of in vivo fluorescence of chlorophyll. a) a simple maximum layer in the North Central Pacific; surface chlorophyll concentration 0.02 mg/m³; b) a simple maximum layer in the South Central Pacific; surface chlorophyll concentration 0.01 mg/m³; c) a double maximum layer in the North Central Pacific; surface chlorophyll concentration 0.02 mg/m³.

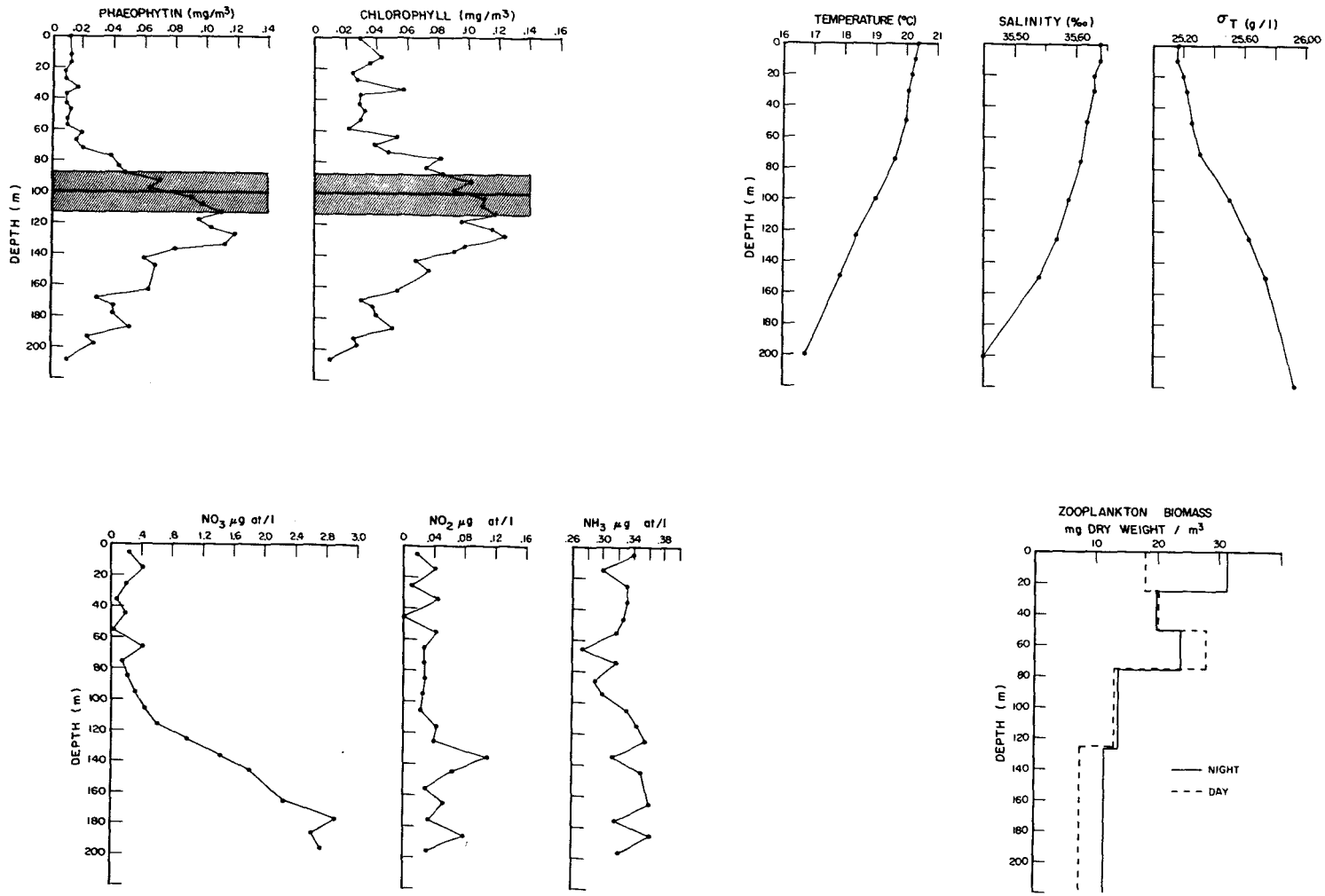

FIGURE 4.—Vertical profiles of chlorophyll, phaeophytin, and other physical, chemical, and biological properties observed in October 1969 in the vicinity of lat 25°S, long 155°W. Estimated depth of the 1% light level and 95% confidence interval indicated by horizontal bar and cross hatching.

accumulation of pigment generally occupies a layer 50-75 m thick, the core of the layer may be very abrupt. From closely spaced water samples (Table 1) we have found that the highest concentrations of chlorophyll may be contained in a layer less than 5 m thick and may exceed by 10% to 50% the concentrations in the adjacent samples. Occasionally maximum concentrations are found in more than one layer within the region of chlorophyll accumulation (Figure 3c, Table 1, 23 August 1967).

It is very difficult to sample such a narrow core with discrete water samplers. A routine cast, in which samples are usually spaced at least 15 m apart, is likely to miss the peak concentrations, and underestimate the chlorophyll content of the maximum layer. Moreover, because of the rapid vertical changes in chlorophyll concentration, slight variations in the position of the samples within the layer may appear as horizontal discontinuities of the layer. Discrete chlorophyll data, including those presented in this paper, must be interpreted accordingly.

SPECIES COMPOSITION

The numbers and species of diatoms in water samples collected on expeditions URSA MAJOR and ZETES have been enumerated (University of California, 1967, 1970; Venrick, 1969). The increase in chlorophyll concentration in the maximum layer is accompanied by a significant increase in the number of diatom cells. Furthermore, the maximum layer is composed of different assemblages of species within the Subarctic Pacific, the Transition Domain, and the Central Pacific (Venrick, 1971). In August, north of lat 40°N the species within the maximum layer were the same as those occupying the overlying water mass. South of lat 38°N, however, samples from the maximum layer were dominated by species which were not observed in shallower samples. During the winter when the maximum layer had been eroded by increased turbulence, the same species were present, but they were distributed randomly through the water column.

More recent studies were undertaken in 1968 at lat 26°57′N, long 155°10′W with a series of 19 replicate casts over a distance of 10.5 miles. Phytoplankton samples were collected from 25 m, 50 m, 75 m, and from the chlorophyll maximum layer at 125 m. A total of 80 species of diatoms were identified, of which 24, 36, and 37 were observed in the samples collected from 25 m, 50 m, and 75 m, respectively. A total of 64 spe-

TABLE 1.—Fine scale structure of the chlorophyll maximum layer.

URSA MAJOR		CLIMAX II			
2 Sept. 1964 lat 43°49′N, long 154°44′W		26 Aug. 1969 lat 27°09′N, long 155°18′W		23 Aug. 1969 lat 28°29′N, long 155°16′W	
Depth (m)	Chlorophyll *a* (mg/m³)	Depth (m)	Chlorophyll *a* (mg/m³)	Depth (m)	Chlorophyll *a* (mg/m³)
0	0.10	1	0.06	0	0.06
20	0.11	20	0.06	20	0.06
50	0.55	39	0.07	40	0.06
60	1.19	58	0.06	60	0.06
65	0.94	77	0.06	80	0.06
70	0.73	96	0.08	90	0.08
75	0.56	101	0.07	100	0.13
80	0.44	105	0.11	105	0.13
85	0.38	110	0.08	110	0.09
90	0.24	114	0.08	114	0.13
100	0.10	124	0.06	118	0.12
		141	0.02	122	0.10
				126	0.07
				130	0.07
				135	0.06
				140	0.04
				150	0.04
				165	0.03
				180	0.02
				200	0.02

cies were found at 125 m, and of these 64, 22 occurred only in samples from that depth. Thus, the chlorophyll maximum layer, which has a higher species diversity (as measured by the number of diatom species) and which may contain species not found at shallower depths appears to offer unique features as a biological habitat.

THE CENTRAL PACIFIC

Studies conducted on Expeditions CLIMAX I, CLIMAX II, and ARIES III near the axes of the North and South Central Pacific Gyres have provided us with a large amount of data concerning the vertical distribution of chlorophyll and productivity in the water column and their relationship with other physical, chemical, and biological parameters. Comparison with data collected over much wider areas on other expeditions leads us to believe that the relations observed in the Central Gyres may be pertinent to much of the oceanic Pacic.

The vertical distribution of chlorophyll and net production observed during these four studies have been summarized in Table 2. All studies show a well-defined subsurface accumulation of chlorophyll which varies in width from 50 to 75 m and contains maximum concentrations of chlorophyll in excess of 0.10 mg/m^3. The core of the layer always occurred below the depth penetrated by 1% of the surface radiation. In fact, more than half of the total chlorophyll within the water column was observed below this depth.

The rate of production per unit chlorophyll decreases with depth from a maximum at about 20 m, but this is partially offset by the increase in the amount of chlorophyll, and production rates as high as 0.13 mg C/m^3/hr have been observed in the maximum layer in the South Pacific. Our in situ experiments indicate that 7% to 20% of the total production in the water column occurs below the 1% light level. These are minimum values since our in situ studies did not reach the level of no productivity. The total rate of production throughout the water column is variable on rather small spatial and temporal scales, but appears to be considerably greater than maximum estimate of 100 mg C/m^2/day (8.3 mg C/m^2/hr) estimated by Koblentz-Mishke et al. (1970).

The vertical distribution of chlorophyll and several relevant properties are illustrated in Figure 4. Data points are mean values of observations made in replicate on six 24-hr stations in the South Central Pacific (CLIMAX II Expedition) and represent an area of 60 square miles and a time span of 6 days. Above 200 m there was an average of 12.35 mg chlorophyll per square meter sea surface. Of this, over half occurred below the estimated depth of 1% light. We estimated the light intensity at the core of the maximum layer to lie between 0.10% and 0.26% of incident radiation. The vertical distribution of phaeophytin is similar to that of chlorophyll.

The accumulation of both chlorophyll and phaeophytin occurs within the pycnocline. On a local scale, these layers may move up and down with the pycnocline, for instance in response to

TABLE 2.—Mean value and 95% confidence limits of the mean for data relative to the vertical distribution of light, chlorophyll *a*, and productivity at two stations in the North and South Central Pacific Ocean.

			Chlorophyll *a*					Productivity	
Position	Date	Depth of 1% light *m* (1)	Depth of maximum *m* (2)	Surface concentration *mg/m*^{3} (3)	Concentration at (2) *mg/m*^{3} (4)	Water column total 0-200 m *mg/m*^{2} (5)	% of (5) below (1) %	Total above (1) *mg C/m*^{2}*/hr*	Total below (1) *mg C/m*^{2}*/hr*
Lat 27°N, long 155°W	Sept. 1968	79 ± 5	104 ± 8	0.03 ± 0.01	0.16 ± 0.03	11.92 ± 2.62	73.5 ± 8.3	16.26 ± 2.25	
	Sept. 1969	73 ± 5	111 ± 9	0.09 ± 0.03	0.11 ± 0.02	11.67 ± 1.32	53.7 ± 4.6	31.74 ± 7.35	> 2.28
Lat 25°S, long 155°W	Oct. 1969	100 ± 13	122 ± 11	0.03 ± 0.01	0.13 ± 0.02	12.35 ± 3.22	58.5 ± 6.4	12.87 ± 9.08	> 3.28
	Mar. 1971	132 ± 14	140 ± 9	0.01 ± 0.00	0.11 ± 0.05	8.13 ± 1.47	58.3 ± 9.5	11.80	> 1.20

internal waves. However, on a wider scale, there appears to be no relationship between the depth of the maximum layer and any one isoline of temperature, salinity, or density.

Plant nutrients are present in very low concentrations in the upper 100 m. Phosphate values were less than 1.5 μg at./liter in the North Central Pacific and less than 0.2 μg at./liter in the South Central Pacific. Nitrate was less than 0.6 μg at./liter in the North and less than 0.8 μg at./liter in the South, while corresponding values of silicate ranged between 1 and 7 μg at./liter in the North and between 0 and 3 μg at./liter in the South. The concentrations of these three nutrients increase systematically and significantly at, or just below, the level of the chlorophyll maximum. Concentrations of ammonia are low and irregular throughout the upper 200 m, showing no pattern with depth. In contrast, high values of nitrite in the upper 200 m (occasionally as high as 4.5 μg at./liter) were observed only within or just below the chlorophyll maximum, and may indicate recent phytoplankton assimilation of nitrate-nitrogen (Vaccaro and Ryther, 1959). In all of our studies, the relationship between the vertical distributions of chlorophyll and nutrients was far more predictable than the relationship between chlorophyll and any of the physical properties.

We have found no evidence of any accumulation of zooplankton within the chlorophyll maximum layer. Total zooplankton biomass (animals greater than 35 μ) was greatest above the maximum layer during both day and night. This appears to be true for all size categories.

THE SEASONAL CYCLE

Seasonal samples from the western edge of the California Current (station 100.80 at lat 30°00′N, long 120°07′W) during 1969 demonstrate a seasonal change in the vertical distribution of chlorophyll *a* (Figure 5). We have evidence that this maximum layer is continuous with that observed within the Central Pacific Gyre and we expect their seasonal cycles to be comparable. For a short period in February, chlorophyll is essentially homogeneous through the upper 50 m. This corresponds in time to the maximum development of the mixed layer. When the water column begins to stratify in March, chlorophyll concentrations at the surface decrease abruptly and a subsurface maximum layer develops. As the summer progresses, the maximum decreases in concentration and the layer subsidies, reaching its maximum depth just prior to the breakdown of the density stratification in December. Figure 5b illustrates the lack of temporal relationship between the depth of the chlorophyll maximum and any one isopleth of density. This would seem to preclude the formation of the maximum layer from the accumulation of cells regulated solely by their physical density.

The vertical distribution of chlorophyll during August along long 155°W is presented in Figure 2. This may be compared with the

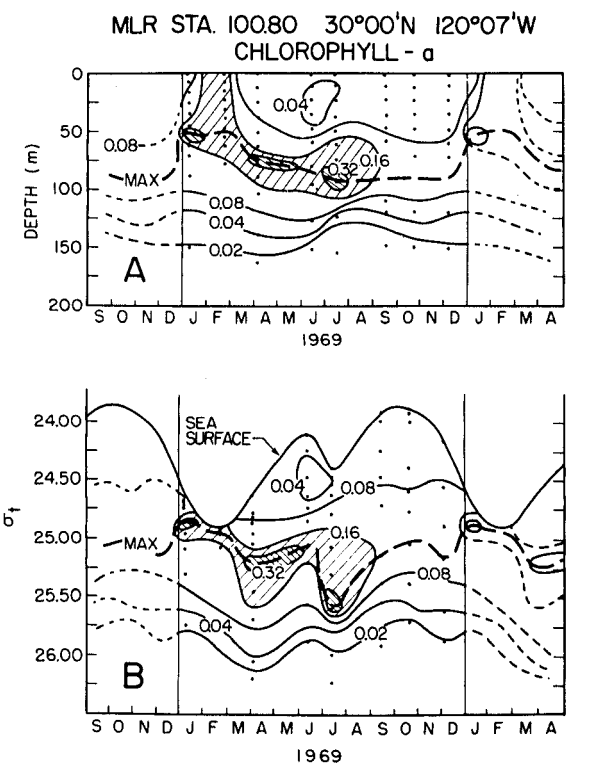

FIGURE 5.—Annual development of the subsurface chlorophyll maximum layer at lat 30°00′N, long 120°07′W. Chlorophyll *a* concentration is contoured with respect to depth (A) and density (B).

distribution along the same transect observed during January (ZETES Expedition) when a similar program of chlorophyll measurement was carried out. In January, north of lat 32°N, the mixed layer extends below 100 m. Concentrations of chlorophyll are uniform throughout this layer, decreasing abruptly below the mixed layer. Between lat 26°N and 32°N a weak chlorophyll maximum is still present near 120 m below the mixed layer which does not reach its greatest depth of 200 m until February (Robinson, 1951).

The evidence accumulated to date suggests that a subsurface concentration of plant material can persist only in the presence of a density gradient which isolates the layer from the effects of wind-driven turbulence. Thus, any seasonal fluctuations in the strength or depth of the pycnocline may be expected to affect the presence of the deep maximum layer. We can postulate with some assurance that in any environment in which the winter mixed layer regularly exceeds the depth of the chlorophyll maximum layer, the maximum layer must be a seasonal phenomenon. At any locality, the duration of the maximum layer will be determined by the duration of seasonal stratification of the water column and thus will be progressively shorter at higher latitudes.

This observation has important implications. Over most, if not all, of the ocean, the phytoplankton within the maximum layer do not represent a permanent loss to the epipelagic community. Neither need there be a balanced energy budget within the maximum layer. Sufficient energy may be produced and stored in a brief period prior to stratification of the water column or the depletion of nutrients from the surface waters to maintain the population within the maximum layer for considerable periods of time, even though photosynthesis may be depressed or absent.

LARGE-SCALE TEMPORAL FLUCTUATIONS

In the Central Gyre of the North Pacific we have recorded temporal fluctuations on a larger scale. In September 1969, the standing crop and productivity were higher and more variable throughout the water column than in the same month of the previous year. As a result, in 1969, the chlorophyll maximum layer was less sharply defined and was occasionally obscured by high chlorophyll concentrations in the overlying water. These fluctuations are of considerable interest. Namias (1971) has investigated the meteorological and oceanographic conditions accompanying a vast pool of abnormally warm water in the southern portions of the North Pacific during the summer and fall of 1968. He concludes:

> The abrupt and extensive anomalous warming of the southeastern quarter of the Pacific Ocean north of 20°N from May-June, 1968, appears to have been due largely to increased isolation and horizontal convergence of the surface layers of the sea and associated downwelling, ... These warming factors in the heat budget were associated with the development and maintenance of a strong and deep Pacific anticyclone in June which appears to have been persistently regenerated by an unusually strong mean jet around 40°N.

This period of stronger subsidence was accompanied by a clear sharpening of the maximum layer and by reduced standing crop of phytoplankton and productivity above the layer. The observations of Namias suggest that the generalized downwelling in the Central North Pacific anticyclone, which is an important factor inhibiting the vertical diffusion of nutrients into the euphotic zone, is also closely related to the depth and concentration of photosynthetic material below the mixed layer. Extrapolation leads us to expect to find similar chlorophyll maxima well developed in other large, persistent temperate gyres, such as the South Atlantic and the southern Indian Ocean.

DISCUSSION

It is evident that a deep chlorophyll maximum layer is a well-developed and consistent feature of the major gyres of both the North and South Pacific. In view of its geographic continuity, we must reevaluate the mechanisms postulated for its development, and seek a single explana-

tion to account for the presence of a chlorophyll maximum layer in very different environmental regimes. Of the numerous hypotheses which have been put forward, several may be relevant. The increase of chlorophyll with depth corresponds to an increase in the number of phytoplankton (diatom) cells, but this may be accentuated by an increase in the amount of chlorophyll per cell. Zooplankton have been shown to be concentrated above the maximum layer and differential grazing pressure may help to maintain the abrupt gradient at the top of the maximum layer. In situ production has been demonstrated within the maximum layer at very low light intensities, and this will contribute to the formation and maintenance of the layer.

The strong development of a deep maximum within the oligotrophic environments of the Central Gyres, the effect of fluctuations of the rate of downwelling on the depth of the maximum layer and the productivity in the overlying water, and the consistent relationship between the depth of the maximum layer and the depth of the nutricline and the nitrite maximum suggest that the nutrient regime may be a critical factor in the development and maintenance of the chlorophyll maximum layer. Our observations to date support the theory of Steele and Yentsch (1960) that depletion of nutrients above the summer thermocline leads to a reduction in the buoyancy of phytoplankton, and that a subsurface maximum results from the accumulation of impoverished cells at the top of the nutricline where the absorption of nutrients decreases the sinking velocity (Eppley, Holmes, and Strickland, 1967). The maximum layer may continue to subside slowly as the nutrients at the top of the nutricline are depleted, and thus it may be that the depth of the maximum layer is ultimately determined by the nutrient regime, rather than ambient light intensity. As long as the depth does not exceed the maximum depth of the winter mixed layer the cells will be returned to higher light levels during the winter. It may be that the chlorophyll maximum layer represents a senescent stage in the annual cycle of oceanic phytoplankton which is analogous to the formation of resting spores by many neritic species.

It is evident that the chlorophyll maximum layer, which may account for a major portion of the standing crop of plant material and for a substantial portion of the primary productivity, is not restricted to the traditionally defined "euphotic" zone, the zone above the 1% light level. There is no justification for limiting samples for chlorophyll or productivity measurements to this zone. These programs must be extended below the chlorophyll maximum layer. We expect this will result in a substantial increase in the estimates of total production within the water column.

ACKNOWLEDGMENTS

The work was supported in part by National Science Foundation Grant GB-12413 and in part by the Marine Life Research Program, the Scripps Institution of Oceanography's part of the California Cooperative Oceanic Fisheries Investigations, which are sponsored by the Marine Research Committee of the State of California, and by the National Science Foundation Grant GB-2861.

We thank Gary B. Smith for assistance in many phases of this program and members of the Scripps Institution of Oceanography Data Collection and Processing Group for the collection and processing of the hydrographic and chemical data. The seasonal data from station 100.80 was supplied by R. W. Owen and M. G. Kruse of the National Marine Fisheries Service.

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THE NAUPLIUS II, METANAUPLIUS, AND CALYPTOPIS STAGES OF *THYSANOPODA TRICUSPIDATA* MILNE-EDWARDS (EUPHAUSIACEA)

MARGARET D. KNIGHT[1]

ABSTRACT

A large, spinose metanauplius, a nauplius II, and calyptopis I, found in the Indian Ocean and Equatorial Pacific, are referred to *Thysanopoda tricuspidata*. The identifications are based on the distinctive morphological features shared by these larval stages and by the calyptopes II and III of *T. tricuspidata* identified by Sars (1885), and on the observed distribution of *T. tricuspidata* and the metanauplius in the Indian Ocean. Calyptopes II and III are redescribed to present the complete calyptopis phase of larval development in one account.

During a survey of euphausiids in the Indian Ocean (Brinton and Gopalakrishnan, in press), many specimens of a relatively large and very ornate metanauplius were found. There was conjecture that the curious, apparently undescribed form might be the larva of a species of the genus *Thysanopoda*, and it was sought for next in plankton from the Equatorial Pacific.

The metanauplius was found in these waters as were specimens of a seemingly related nauplius II and calyptopis I together with the calyptopis II, calyptopis III, furcilia, and juvenile stages of *Thysanopoda tricuspidata* identified by Sars (1885). When individuals of each of the larval stages were placed together, they appeared to form a natural developmental series; their relative size, the distinctive shape of developing eyes, telson, and carapace all suggested that the larvae were progressive stages of the same species. Evidence of their specific relationship was found in a detailed study of these features and of the morphology of larval appendages, and there seemed to be sufficient justification for referral of the three unidentified early stages to *T. tricuspidata*.

Redescriptions of the calyptopes II and III of *T. tricuspidata* are included in this paper with identification and description of the nauplius II, metanauplius, and calyptopis I, in order to present the complete calyptopis phase of the species in one account and to illustrate the setation of appendages more fully.

METHODS AND MATERIALS

Specimens of the metanauplius were observed in the standard collections, approximately 200-0 m depth, obtained during the International Indian Ocean Expedition (IIOE), 1962-65. About 100 metanauplii were removed for study. The distributions of *T. tricuspidata* and the metanauplius based on the data of Brinton and Gopalakrishnan are shown in Figure 9.

Selected samples taken during EQUAPAC Expedition by RV *Stranger* of the Scripps Institution of Oceanography in August-September 1956 between long 165°-175°W and lat 6°S-10°N by oblique tow in the top 200 m (Snyder and Fleminger, 1965) were sorted for the metanauplius and calyptopes. Positions of the samples yielding larvae and the developmental stages found in each sample are given in Table 1. The distribution of *T. tricuspidata* in the Pacific is described by Brinton (1962).

For measurement with an ocular micrometer, the larvae were straightened in a few drops of

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Manuscript accepted June 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

TABLE 1.—Location of samples collected by RV *Stranger* during EQUAPAC Expedition which contained larvae of *Thysanopoda tricuspidata* and the developmental stages found. Detailed station data for samples are given by Snyder and Fleminger (1965).

Station No.	Position		Sample (net)	Developmental stage				
	Lat	Long		Nauplius	Metanauplius	Calyptopis		
						I	II	III
15	5°59′N	166°40′W	45 cm	−	+	+	+	−
21	0°00′N	166°55′W	45 cm	−	+	−	−	−
25	4°00′S	167°03′W	45 cm	−	+	+	+	+
25	4°00′S	167°03′W	1 m	−	+	+	+	+
26	5°00′S	167°08′W	45 cm	+	+	+	+	+
26	5°00′S	167°08′W	1 m	+	+	−	+	+
28	5°58′S	175°02′W	45 cm	+	+	+	+	+
28	5°58′S	175°02′W	1 m	+	+	+	−	+
28	5°58′S	175°02′W	1 m	+	+	+	+	−
29	5°01′S	174°59′W	45 cm	−	+	−	+	+

2% formaldehyde in seawater on a slide. Total length (TL) was measured in dorsal view between center of anterior margin of carapace (excluding spines in metanauplius) or rostrum and distal point on posterior margin of telson excluding spines. Other measurements are explained by stage: nauplius II, width (W) at widest point in dorsal view; metanauplius, carapace length (CL) between midpoints of anterior and posterior margins excluding spines, carapace width (CW) at widest point between anterolateral margins excluding spines, both measured in dorsal view; calyptopes I and II, carapace length (CL) between midpoints of anterior and posterior margins measured in lateral view; calyptopis III, carapace length (CL) from rostrum to distal point on posterior margin measured in lateral view. The range (r) and mean (m) of each measurement and number (n) of specimens measured are given by stage.

Approximately equal numbers of the metanauplius stage from the Indian and Pacific Oceans were measured. The measurements given for nauplius II and calyptopes I-III, however, are based only on larvae from the Equatorial Pacific and, as calyptopis larvae of a single species have been shown to vary in size in different areas of the oceans (Mauchline and Fisher, 1969), it should be emphasized that the larvae measured for this study were collected during one season in one area of the Pacific. Measurements of some nauplius II and calyptopis stages sorted from Indian Ocean samples did fall well within the size ranges of Pacific larvae in equivalent developmental stages. Specimens of a nauplius I definitely referable to *T. tricuspidata* were not found.

For detailed study and dissection of appendages, larvae were placed in glycerine. Some were stained with Chlorazol Black E to clarify appendage setation. Fourteen nauplii and at least 20 individuals of each of the metanauplius and calyptopis stages I-III were examined in detail. At least 10 specimens of each stage were dissected for study of appendages. In a study of the larval development of *Nematoscelis difficilis* based on both larvae reared in the laboratory and larvae from the plankton, Gopalakrishnan (in press) found no variability in form or setation of appendages among individuals at the same stage of development. This also appears to be true of *T. tricuspidata* larvae, in the stages described, with respect to the mouthparts where setation is usually intact in preserved specimens. On antennules, however, the terminal setae, spines, and aesthetascs (sensory setae) were frequently broken; in calyptopis II, for instance, only 1 of 26 antennules examined had the third seta intact on the inner and outer flagella. An estimate of variability in the fragile setation in this species will require a detailed study of larvae either reared in the laboratory or collected specifically for the purpose.

Drawings of both whole larvae and appendages were prepared with the Wild M20[3] com-

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

pound microscope equipped with drawing attachment.

Nomenclature for description of appendages is based on that of Gurney (1942). For a review of the literature on larval development of the Euphausiacea and the nomenclature of their larval phases, the reader is referred to the papers by Gopalakrishnan (in press) and by Mauchline and Fisher (1969).

RESULTS

DESCRIPTION OF DEVELOPMENTAL STAGES

Nauplius II (Figure 1a, b)

Measurements: TL, r = 1.00-1.12 mm, m = 1.06 mm; W, r = 0.48-0.56 mm, m = 0.53 mm; n = 43.

Body oval, about 2 times as long as wide, anterior pointed, posterior truncate; posterior margin armed with 10 spines—3 pairs of posterolateral spines and 2 pairs of small to rudimentary medial terminal spines, posterolateral spine 1 (outer) is small, spines 2 and 3 are relatively large, only spine 3 (inner) bears spinules.

Antennule (Figure 4a) uniramous; with 2 terminal setae, 1 subterminal seta situated medioventrally, and small spiny prominences at base of each seta—that below largest terminal seta is like small lobe; spinules are distributed on surface as figured.

Antenna (Figure 5a) biramous; protopod may be constricted near middle and appear weakly segmented; endopod unsegmented with 3 terminal plumose setae, a rudiment of 4th terminal seta, 1 subterminal seta on inner margin, and rows of spinules at bases of setae; exopod with outer margin divided into about 10-11 segments (the segmentation was often indistinct in most distal and proximal parts of exopod), the 5 distal segments bear plumose setae—the terminal segment has 2 setae with a few spinules and the remaining 4 segments bear 1 seta each.

Mandible (Figure 6a) biramous and unsegmented; both rami bear 3 plumose setae with spinules at base of setae.

In well-developed nauplii nearing molt to metanauplius, the carapace of the metanauplius with its distinctive ornamentation could be seen inside the cuticle of the nauplius (Figure 1a), both the large long spines around the anterior margin which fold up and back around the body and the 4 large medial and smaller posterolateral spines on posterior margin may be visible and may be partially dissected out.

Metanauplius (Figure 1c, d)

Measurements: Equatorial Pacific larvae - TL, r = 1.36-1.50 mm, m = 1.43 mm; CL, r = 1.02-1.10 mm, m = 1.05 mm; CW, r = 0.60-0.70 mm, m = 0.64 mm; n = 39. Indian Ocean larvae - TL, r = 1.36-1.52 mm, m = 1.45; CL, r = 0.98-1.10 mm, m = 1.05 mm; CW, r = 0.61-0.68 mm, m = 0.65, n = 43.

Carapace with rounded frontal and anterolateral margins produced into long spines (the number of spines, counted in 25 individuals, ranged from 21 to 23 with 23 larvae having 22 spines), there may be tiny spines or "hairs" posterior to the posteriorly directed last large spine; posterolaterally deep winglike extensions of carapace curve ventrolaterally with margins produced into strong posteriorly directed spines which diminish in size around posterior margin where they are separated by small spines; the 4 large medial spines on posterior margin are usually relatively long and they project up dorsally away from body of larva. A faint outline of developing eyes is visible. Tail long and tapering with rounded posterolateral margins and median indentation, there is now a pair of lateral spines in addition to 3 pairs of posterolateral spines and 2 pairs of medial terminal spines, a small rudiment of one or both of inner (third) pair of terminal spines may be present.

In one well-developed metanauplius near molt, the telson of calyptopis I with invaginated terminal and lateral spines was visible beneath the cuticle (Figure 1e). As can be seen, posterolateral spine 3, although shorter than spine 2 in the metanauplius, is more deeply invaginated and longer than spine 2 in the developing calyptopis, and when extruded, it will have the greater relative length observed in the calyptopis stages of *T. tricuspidata.*

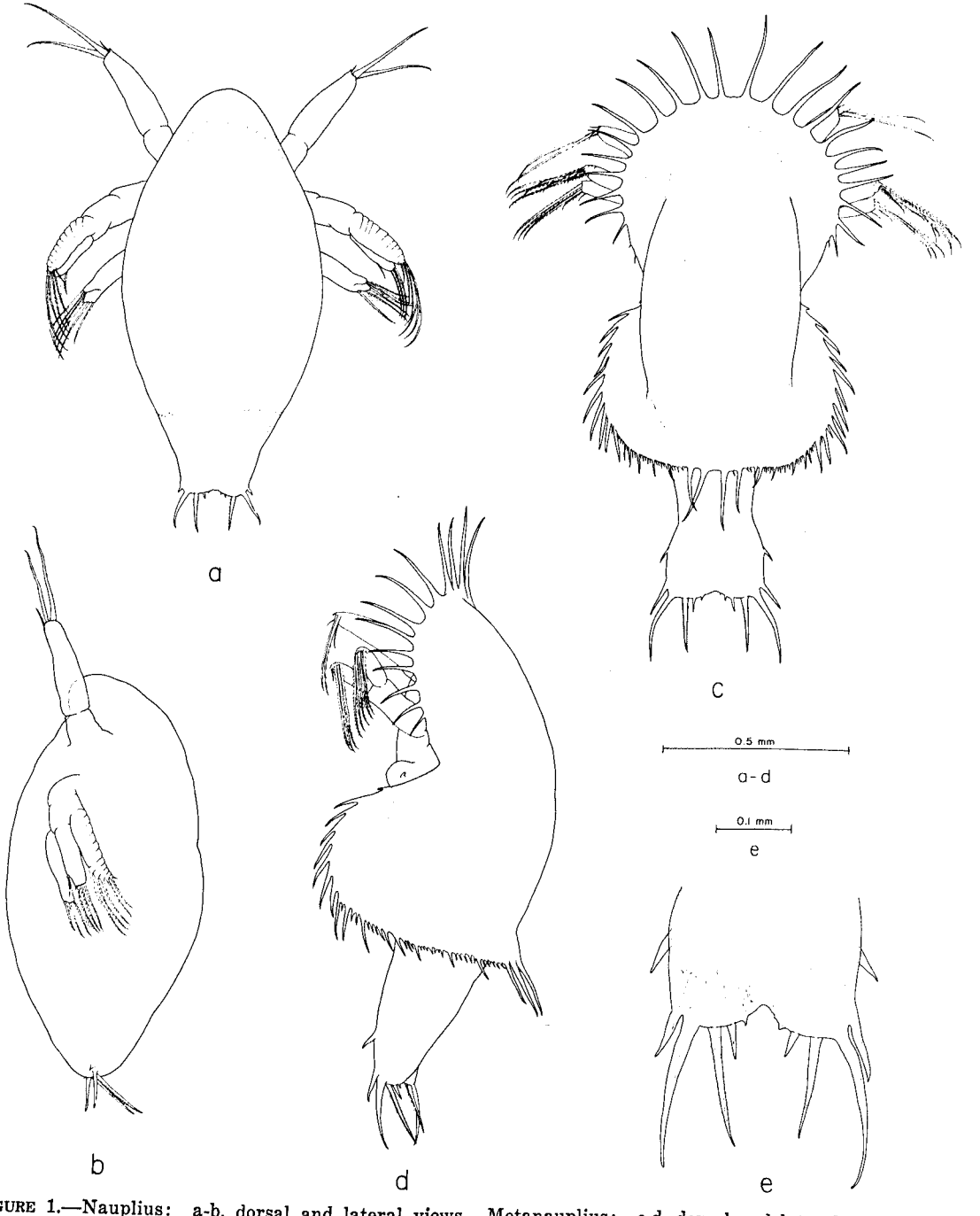
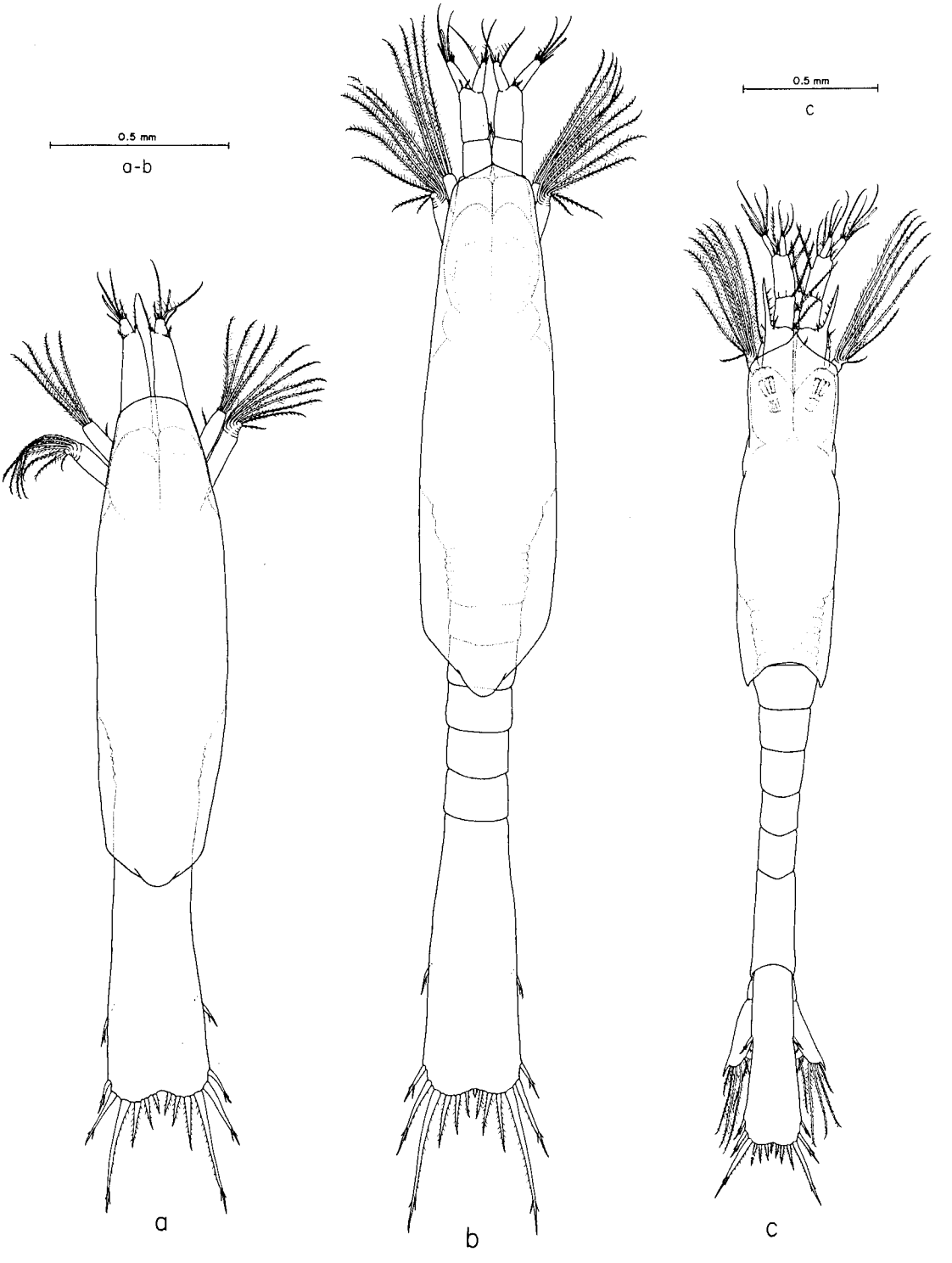


FIGURE 1.—Nauplius: a-b, dorsal and lateral views. Metanauplius: c-d, dorsal and lateral views; e, posterior enlarged showing invaginated spines of calyptopis I beneath cuticle.

FIGURE 2.—Calyptopis: a-c, stages I-III, dorsal views.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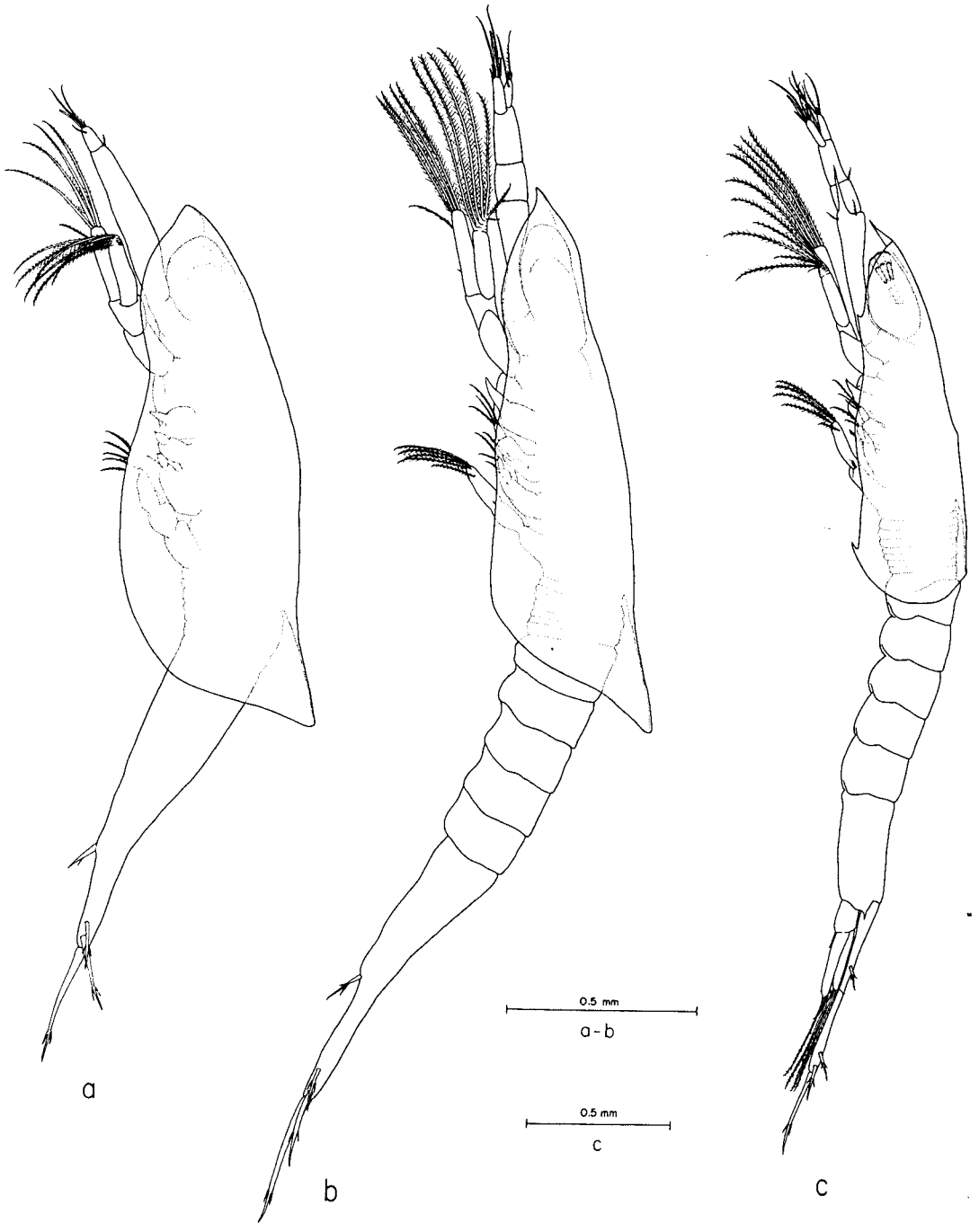

FIGURE 3.—Calyptopis: a-c, stages I-III, lateral views.

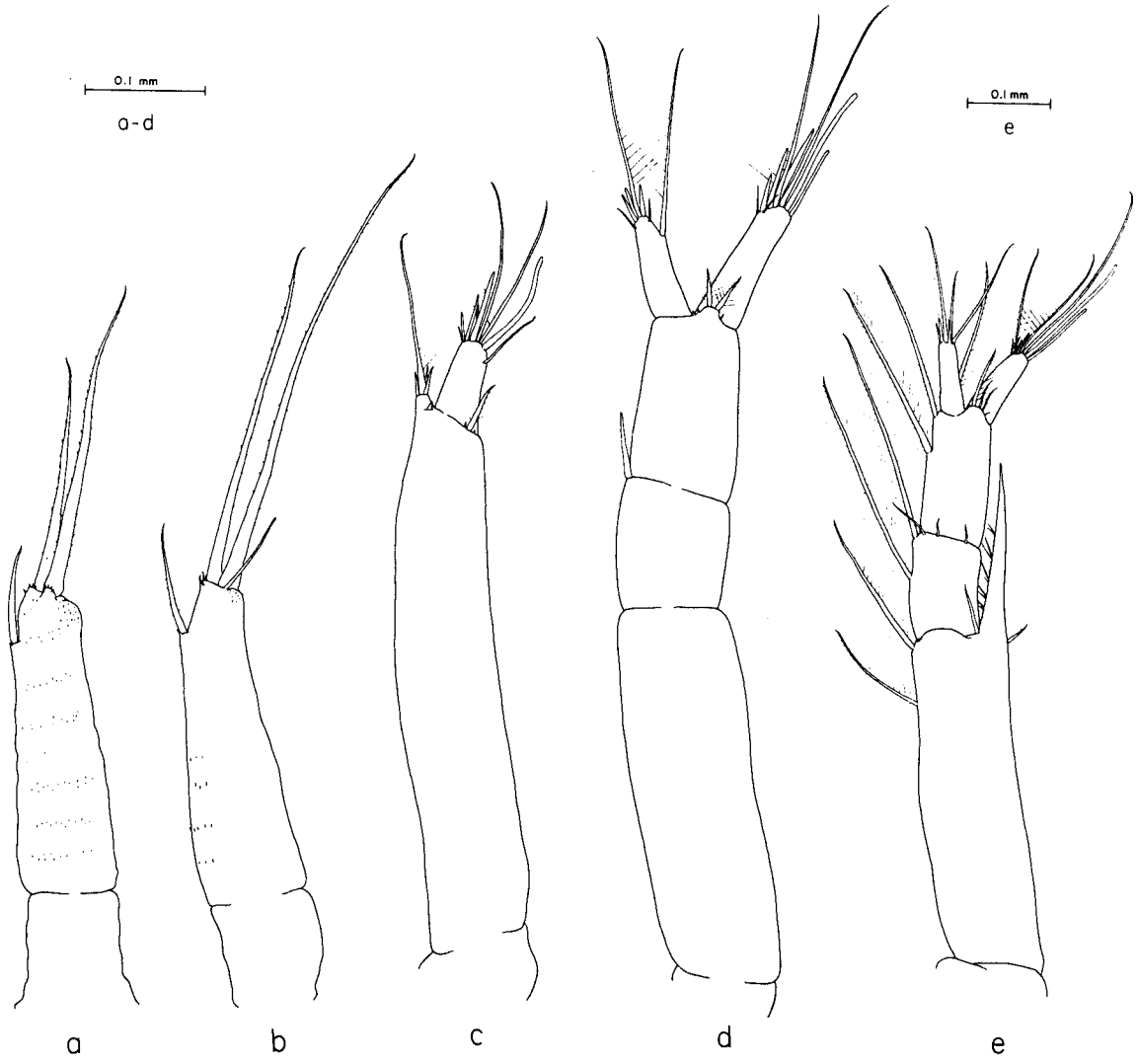

FIGURE 4.—Antennule, right, dorsal view: a, nauplius; b, metanauplius; c-e, calyptopes I-III.

Antennule (Figure 4b) now with 3 terminal processes, there is a small seta or sensory filament in place of spiny lobe; surface spinules appear to be organized into fewer simpler rows.

Antenna (Figure 5b) with protopod segmented into coxa and basis, there are a few spinules on inner distal margin of each; endopod with 4 terminal setae—1 seta is relatively short, and 2 setae on inner margin—the proximal seta is short to rudimentary; exopod with 5 short terminal segments but without proximal segmentation of outer margin seen in nauplius, the setation is unchanged although there may be a spinous rudiment of third seta on terminal segment.

Mandible (Figure 6b) reduced to rounded lobe bearing pointed lateral process.

Maxillule, maxilla, and maxilliped are represented only be rounded prominences. In specimens nearing molt, the rudimentary spines on endopod and endites of developing maxillules and

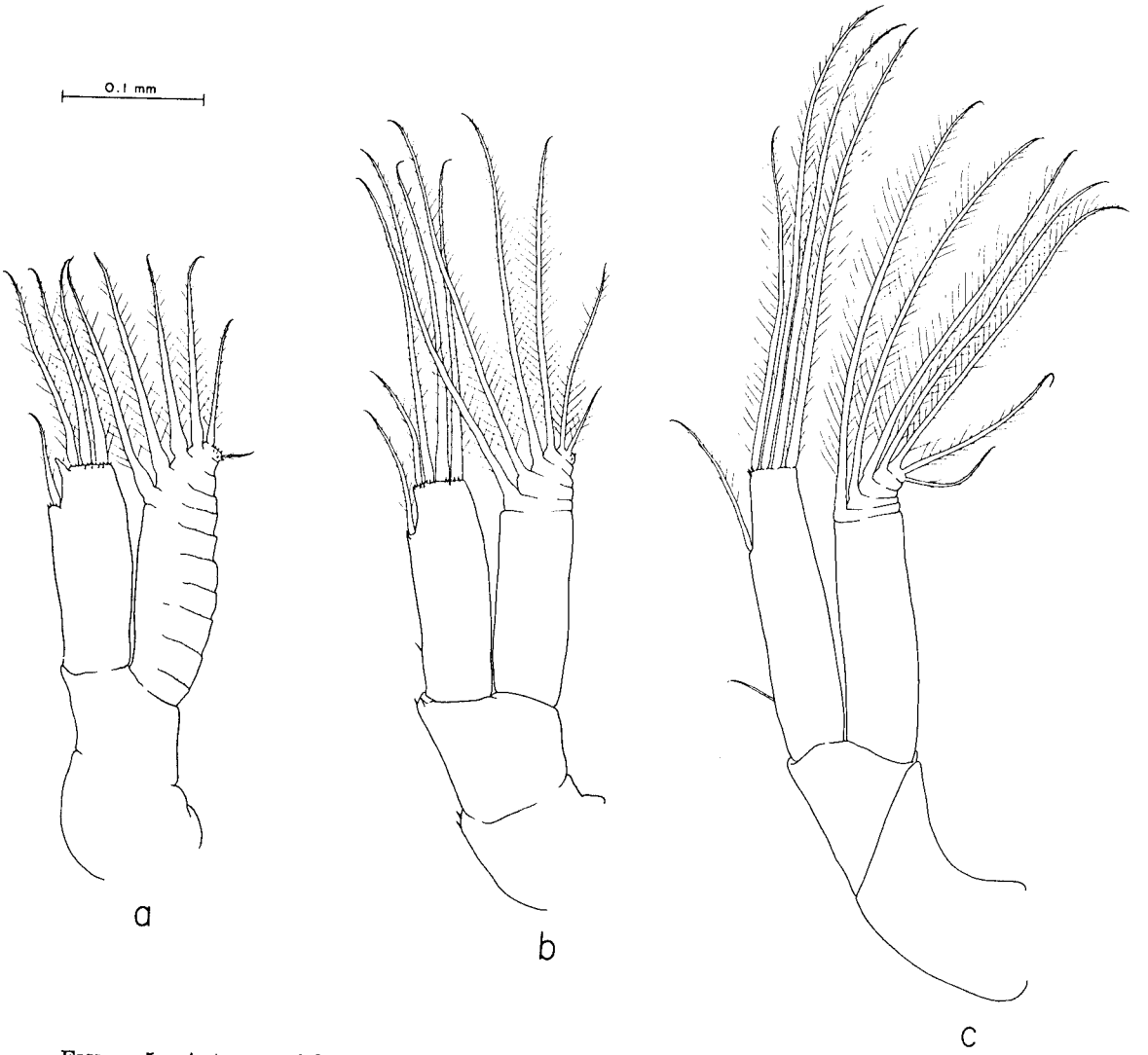

FIGURE 5.—Antenna, right, anterior view: a, nauplius; b, metanauplius; c, calyptopis I.

maxillae and setae of biramous maxilliped of calyptopis I may be seen through the cuticle. Figure 7a and d show such a maxillule and maxilla dissected from a metanauplius providing evidence of its relationship with the calyptopis I described.

Calyptopis I (Figures 2a, 3a)

Measurements: TL, r = 1.90-2.16 mm, m = 2.07 mm; CL, r = 1.38-1.48 mm, m = 1.44 mm; n = 34.

Carapace long and slender, without spines, anterior margin forming narrow hood over developing eyes, posterior margin pointed and curving dorsally. Abdomen unsegmented, telson with a pair of lateral spines, 3 pairs of posterolateral spines, and 3 pairs of medial terminal spines, posterolateral spine 3 is now longest; posterior margin curves in medially.

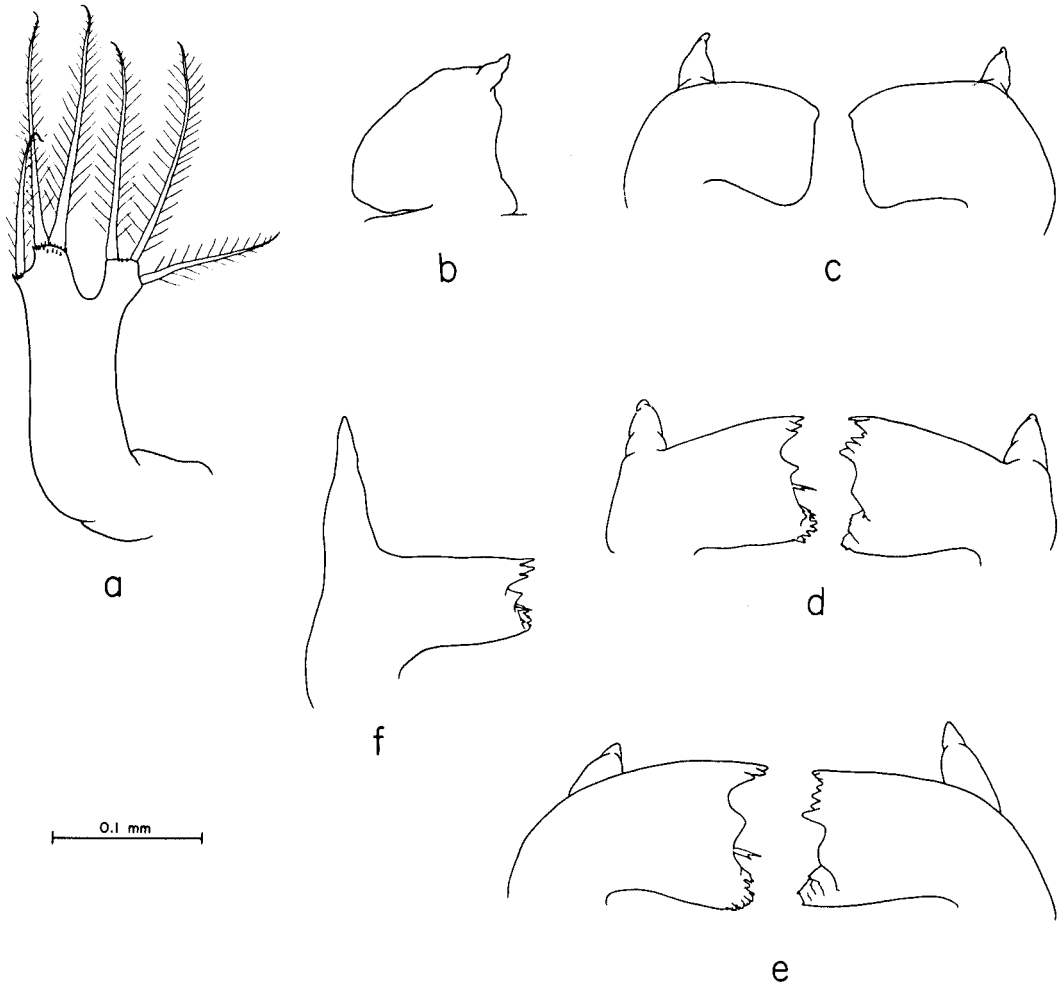

FIGURE 6.—Mandible: a, nauplius, right, anterior view; b, metanauplius, left, posterior view. Mandibles, posterior view: c-e, calyptopes I-III; f, right mandible of calyptopis II rotated to show relative length of triangular lateral process.

Antennule (Figure 4c) 2-segmented; protopod long and slender with small terminal segment forming outer flagellum which bears about 9 terminal processes including 2 long setae, 2 aesthetascs (one of these is situated slightly subterminally on outer margin), and about 5 spinous processes of varying sizes; there is rudiment of inner flagellum bearing 1 long seta and 3 spinous processes; a small spine is situated at base of inner ramus, and there is 1 seta and 1 or 2 small spines dorsally on distal margin of protopod at base of outer flagellum.

Antenna (Figure 5c) now with form found in calyptopis stages I-III; endopod with 4 long terminal setae and 2 setae on inner margin, proximal seta still relatively short; exopod with 7 plumose setae, the terminal segment now bears 3 setae; coxa and basis without spinules.

Mandibles (Figure 6c) rudimentary, with large lateral process, medial margins smooth except for 1 small incisor tooth on each mandible.

Maxillule (Figure 7b) armed only with rudimentary small spines; endopod of 1 segment with 3 spines; exopod a very small lobe bearing

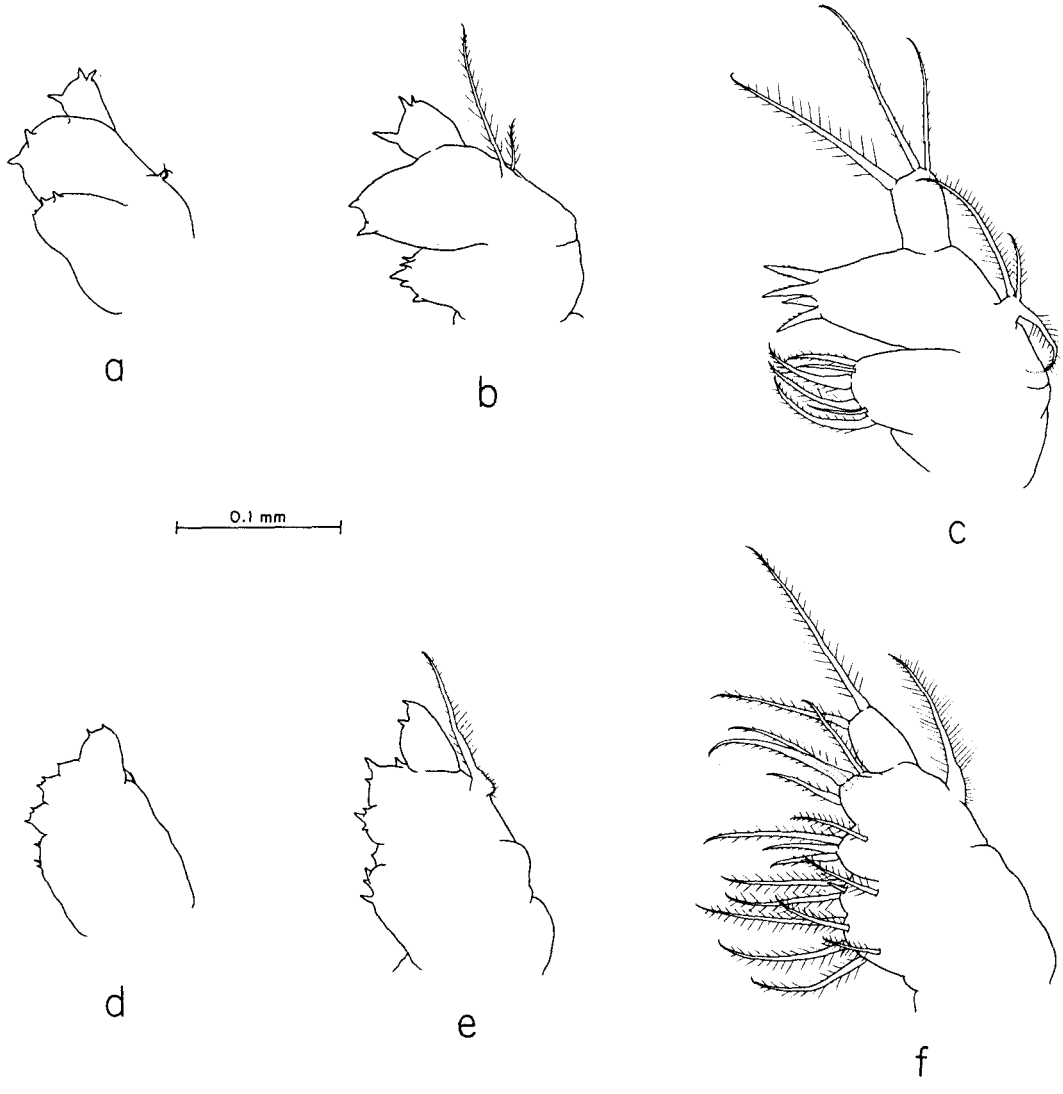

FIGURE 7.—Maxillule, left, posterior view: a, developing appendage of calyptopis I dissected from metanauplius; b-c, calyptopes I and II. Maxilla, left, posterior view: d, developing appendage of calyptopis I dissected from metanauplius; e-f, calyptopes I and II.

2 plumose setae; basal endite with 2 spines, there may be a tiny third spine between large spines; coxal endite with about 5 spines.

Maxilla (Figure 7e) with rudimentary setation except for 1 plumose seta arising from small finely setose lobe on lateral margin and representing exopod; endopod of 1 segment with 2 spines; medial lobes of endites discernible with small spines on medial margin.

Maxilliped (Figure 8a) biramous; exopod with 4 terminal plumose setae and 1 subterminal seta on outer margin, also a small stout seta at base of exopod near articulation with basis; endopod of 2 segments, terminal segment with 4 setae distally, 3 terminal and 1 subterminal; there are a few weak setae and rudiments of setae on medial margins of both coxa and basis and of proximal segment of endopod.

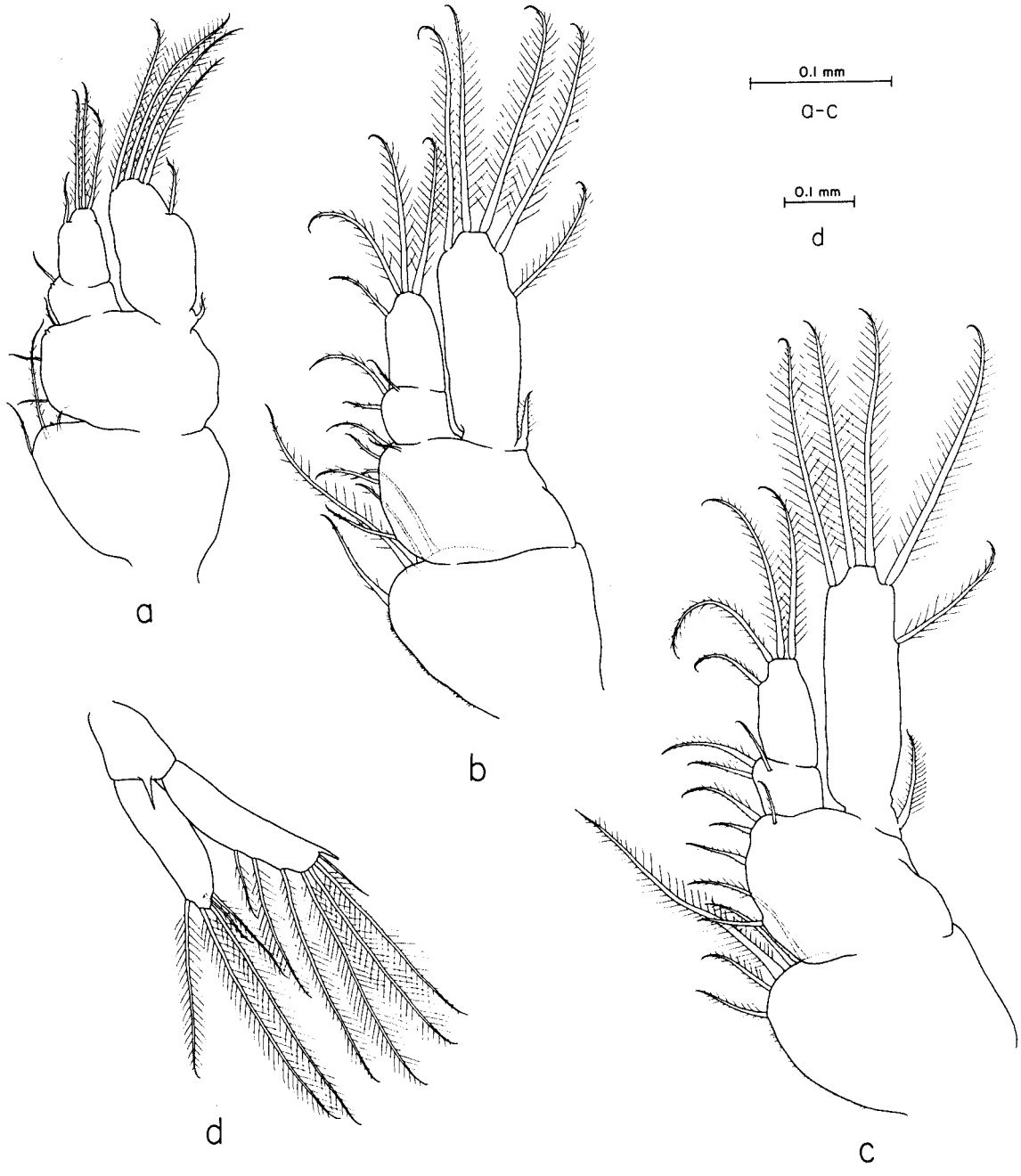

FIGURE 8.—Maxilliped, left, posterior view: a-c, calyptopes I-III. Uropod, left, ventral view: d, calyptopis III.

Calyptopis II (Figures 2b, 3b)

Measurements: TL, r = 2.50-2.74 mm, m = 2.63 mm; CL, r = 1.42-1.54 mm, m = 1.49 mm; n = 18.

Carapace with frontal margin produced into small triangular spine and posterior margin more pointed than in preceding stage; developing eyes may contain some pigment. Thoracic segments forming; abdomen segmented, sixth segment not separate from telson; posterior margin of telson with small median 7th terminal spine.

Antennule (Figure 4d) with protopod divided into 3 peduncular segments, there is stout seta distally on inner margin of second segment and a small dorsal lobe bearing 2 setae and a few small spines on distal margin of third segment at base of outer flagellum; outer flagellum with about 9 terminal processes including 2 setae, 2 aesthetascs, and about 4-6 spinous processes; inner ramus with about 6 terminal processes including 1 seta and usually 5 spines, there is 1 subterminal seta on inner margin.

Antenna as in calyptopis I.

Mandibles (Figure 6d) asymmetrical, now differentiated into incisor and molar areas, right mandible with slender articulated spine with spinule situated near molar area; right mandible rotated in Figure 6f to show relative length of lateral process.

Maxillule (Figure 7c) with setae and spines fully formed; endopod of 1 segment with 3 setae; exopod with 3 plumose setae; basal endite with 4 stout spines armed with spinules; coxal endite with 6 setae—2 are small smooth setae, 4 are setose and the largest bears strong spinules distally.

Maxilla (Figure 7f) with full setation; endopod of 1 segment with 2 setae; exopod represented by a single plumose seta on small setose lobe; basal endite with 3 medial lobes, coxal endite bilobed, lobes 1-5 with setation of 5-4-4-3-1 progressing distally, 1 seta on each of lobes 1-3 is situated on posterior face of maxilla, 1 marginal seta on lobe 2 is quite small.

Maxilliped (Figure 8b) now with full medial setation; coxa with 4 plumose setae, 1 seta is relatively long; basis with 5 setae; proximal segment of endopod with 3 setae; 1 distal seta on basis and 1 distal seta on first segment of endopod are situated slightly submarginally on posterior face, both are small and frequently difficult to locate; setation of exopod and terminal segment of endopod is unchanged.

Calyptopis III (Figures 2c, 3c)

Measurements: TL, r = 2.90-3.40 mm, m = 3.14 mm; CL, r = 1.30-1.42 mm, m = 1.35 mm; n = 34.

Larva now appears more slender for its length; carapace considerably altered, still forming narrow hood over eyes but in other respects more like carapace of furcilia, frontal margin produced into small triangular rostrum, lateral margins with small anterolateral spine below eye and large posterolateral denticle, posterior dorsal margin no longer tapering to point but indented medially. Eye with 7 well-developed facets arranged in a circle of 6 with seventh central facet, and ommatidia with pigment. Thoracic segmentation more distinct. Abdomen with 6 segments, there is dorsal ridge or fold around segment 1 and segment 6 carries biramous uropods. Setation of telson unchanged.

Antennule (Figure 4e) with distal lateral margin of basal peduncular segment produced into strong lateral spine which extends to or beyond midpoint of distal segment of peduncle; there are about 5 groups of 2 setae each along inner margin of this spine with spinules between 3 distal groups and a seta at base of spine on both outer and inner margins; basal segment of peduncle dorsoventrally flattened; the peduncular segments bear plumose setae along medial margins with 2-2-3 setae on segments 1-3 respectively, there are 3 small setae around distal margin of segment 2, and 3 setae and setules on dorsal lobe below outer ramus on distal margin of segment 3; outer flagellum with 2 aesthetascs, 3 setae, and about 4 small spines; inner flagellum with 3 terminal setae and about 3 spinous processes.

Antenna as in calyptopis I.

Mandibles (Figure 6e) similar to calyptopis II, medial teeth somewhat flattened.

Maxillule and maxilla as in calyptopis II.

Maxilliped (Figure 8c) with 5 setae on medial margin of coxa; there is no other change in setation.

No rudiment of the second thoracic appendage was observed.

Uropod (Figure 8d) biramous; protopod with stout ventral spine; exopod produced into posterolateral spine and bearing 7 plumose setae around posterior and medial margins, the seta near posterolateral spine is relatively small; endopod with 5 distal plumose setae, 1 seta is situated submarginally and projects dorsally.

IDENTIFICATION OF EARLY STAGES

The morphological evidence on which the identification of the larval series is based may be summarized as follows: 1) the nauplius II is linked to the metanauplius by dissection of the spinose carapace of the metanauplius from well-developed nauplii; 2) the metanauplius and calyptopes I-III are related by the setation of mouthparts, particularly the endopods of maxillule and maxilla; 3) the third calyptopis is identified with the larva described by Sars (1885) by the long and slender body, the distinctive 7-facetted eyes, and the setation of the exopod and 1-segmented endopod of the maxillule which bear 3 setae each.

There is additional evidence to support the identification of the metanauplius in the way in which the observed distribution of the larva corresponds with that of *T. tricuspidata* in the Indian Ocean as shown in Figure 9, and in the occurrence of the larvae within the range of *T. tricuspidata* in the Pacific.

DISCUSSION

The only description of *T. tricuspidata* larvae found which deals with the calyptopis stages is that of Sars (1885); other authors referring to larvae of the species (i.e., Tattersall, 1936; Gurney, 1947; Lebour, 1950; Pillai, 1957) discuss the furcilia stages only. Sars provides some details of setation with his general descriptions and figures the mandible, maxillule, maxilla, and maxilliped of the third calyptopis (1885, Plate 21, Figures 13-16). The mouthparts of the calyptopis III described in this study agree with those figured by Sars in the dentition of left mandible, in segmentation and setation of endopod and exopod of maxillule, in rudimentary exopod of maxilla, and in setation of exopod and terminal segment of endopod of maxilliped. The carapace of Sars' calyptopis III appears to be indented medially on the posterior margin rather than pointed as in calyptopis II, but it is not figured with a lateral denticle.

The descriptions of larvae of other species of the genus *Thysanopoda* are also almost entirely limited to the furcilia phase; only two exceptions were found. Einarsson (1945) described the calyptopes II and III of *T. acutifrons* and Lebour (1950) the calyptopis III of *T. cristata,* but figures of the appendages and the details of setation are not given.

The described larvae of *T. acutifrons* are larger than those of *T. tricuspidata* in equivalent stages; calyptopes II and III measure 3.4 and 3.8 mm in total length respectively while *T. tricuspidata* averages 2.6 and 3.1 mm (Sars' specimens measured 2.5 and 3.5 mm). The carapace of the third calyptopis of *T. acutifrons* is like that of the second calyptopis with "characteristic pointed end," and the lateral denticle is sometimes discernible although very small. Einarsson notes that the maxillule has a palp of 2 segments and an inner lobe with 7 bristles. Frost (1939) figures the appendages of the first furcilia of *T. acutifrons* showing the maxillule with 6 setae on the endopod and 4 setae on the exopod, and the endopod of the maxilla with 3 setae. This setation is probably also found on the calyptopis III of the species she describes. [Einarsson (1945) suggested that, based on the shape of the eye, Frost's larvae may instead belong to *T. microphthalma;* he notes, however, that the species are otherwise alike in development.]

Lebour (1950) describes and figures the carapace of the calyptopis III of *T. cristata* as long and "pointed behind," noting that the larva closely resembles the calyptopis III of *T. acutifrons* described by Einarsson. It is also very large, measuring 4.2 mm in length. Gurney (1947), in his description of the first furcilia

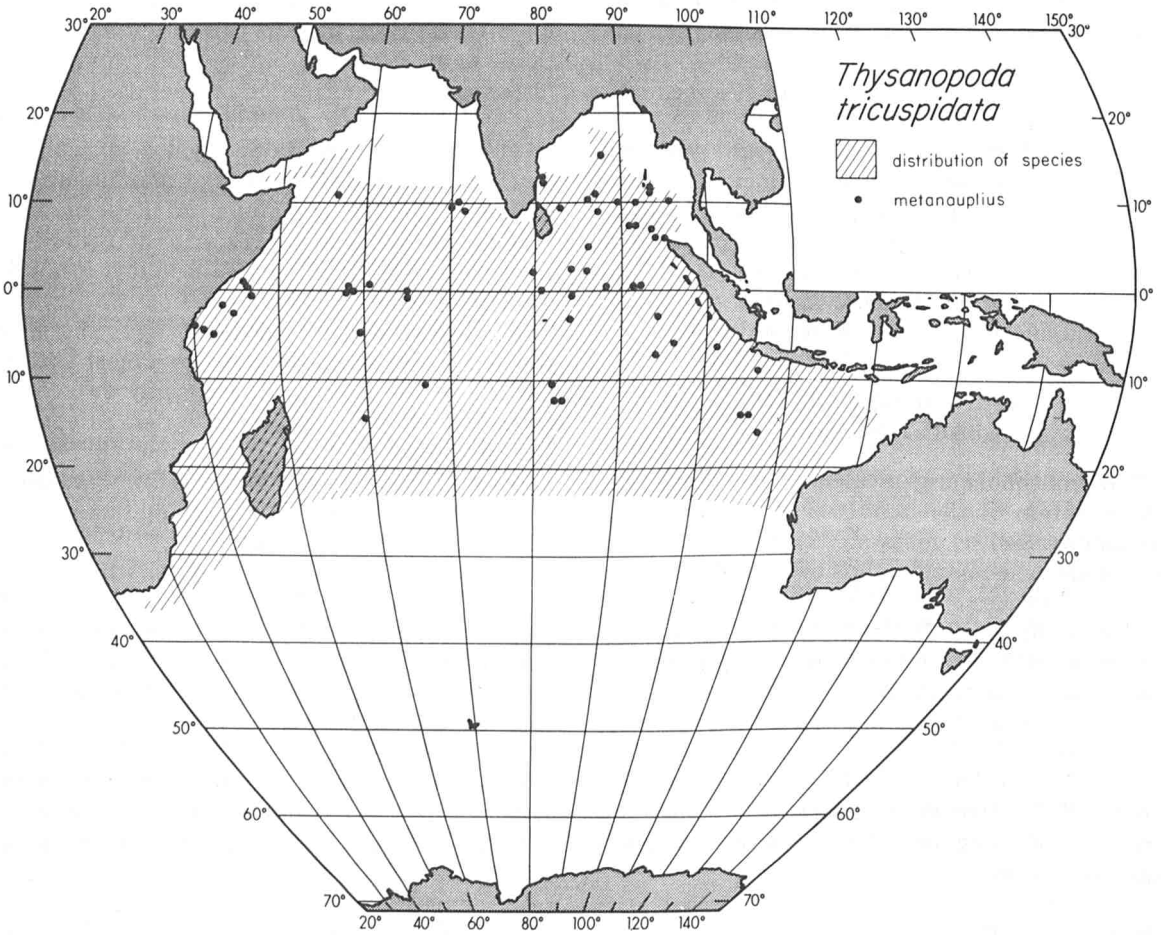

FIGURE 9.—The distribution of *Thysanopoda tricuspidata* and the metanauplius larva in the Indian Ocean based on the analyses of Brinton and Gopalakrishnan (in press).

of *T. cristata*, notes that the maxillule has an endopod of 2 segments, and again it seems likely that this is also found in the third calyptopis.

Both *T. acutifrons* and *T. cristata*, then, differ from *T. tricuspidata* in length of described stages, in shape of carapace in calyptopis III, and probably in details of segmentation and setation of maxillule and maxilla at least.

Calyptopes I and II of *T. monacantha* (identified by E. Brinton) were dissected to compare the endopods of the maxillule and maxilla with those of calyptopes I and II of *T. tricuspidata*. The calyptopis I had full setation of mouthparts and, in both stages, the maxillule, like that of Frost's furcilia, had an endopod of 2 segments with 6 setae and exopod with 4 setae, and there were 3 setae on the endopod of the maxilla. In fact, more setae were found on all of the mouthparts of the *T. monacantha* larvae with the exception of the endopod and exopod of the maxilliped which were like those of the *T. tricuspidata* calyptopes.

Information in these few accounts from the literature and from personal observation suggest that *T. tricuspidata* larvae may prove to differ from larvae of other species of the genus

in many respects. The partial segmentation of antennal exopod in the nauplius II and the form and armature of carapace and telson of the metanauplius may be distinctive, the rudimentary setation of mouthparts in calyptopis I appears to be unusual—indeed the larva seems ill-equipped to feed, there seems to be a reduction in dentition of mandibles and in numbers of setae on mouthparts in calyptopes II and III, and the carapace of calyptopis III is transitional between the usual calyptopis and furcilia forms. In addition, the larvae are known to deviate from trends within the genus in development of abdominal pleopods during the furcilia phase. According to Lebour (1950), *T. tricuspidata* is the most variable in pleopod succession of any *Thysanopoda* species, indeed of any euphausiid known and, as it has been demonstrated that there is a correlation between a more rigidly defined number of furciliar stages and a more oceanic distribution within the genus *Thysanopoda* (Mauchline and Fisher, 1969), such variability in the oceanic species *T. tricuspidata* is surprising.

Although there is too little information available at this time for speculation as to the significance of the unusual morphological features observed in this study, the details found in the literature did support the identification of the larvae in that the combination of setation of endopod and exopod of the maxillule and endopod of the maxilla of *T. tricuspidata* calyptopes was not noted or figured in descriptions of the larvae either of other species of *Thysanopoda* or of other genera of the family.

ACKNOWLEDGMENTS

I wish to thank E. Brinton for his assistance and criticism of the manuscript, and we both wish it to be known that the plankton sorting staff at the Indian Ocean Biological Centre first identified the unique metanauplius as a euphausiid.

This work was supported by the Marine Life Research Program, the Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigations, a project sponsored by the Marine Research Committee of the State of California, and by the Oceanography Section, National Science Foundation, NSF Grant GA-31783.

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THE LARVAL STAGES OF THE DEEP SEA RED CRAB, *GERYON QUINQUEDENS* SMITH, REARED UNDER LABORATORY CONDITIONS (DECAPODA: BRACHYRHYNCHA)

HERBERT C. PERKINS[1]

ABSTRACT

A prezoeal stage, four zoeal stages, and one megalopa stage were obtained from eggs of *Geryon quinquedens* Smith hatched in the laboratory. Each zoeal stage and the megalopa are discussed and illustrated.

The commercial potential and abundance of the deep sea red crab, *Geryon quinquedens* Smith, are discussed by Schroeder (1959), McRae (1961), and Holmsen (1968). The red crab is obviously an important constituent of the deep-water benthic fauna found on the continental shelf off New England and the middle Atlantic states, and its larvae should therefore occur in considerable numbers in the plankton of that region. Knowledge of the larval stages of this species is apparently totally lacking. Brattegard and Sankarankutty (1967) have described the prezoea and the first zoea of *Geryon tridens* Kröyer from Norway, but I can find no other reference to the larval stages of this genus.

It is the purpose of this paper to describe the larval stages of *Geryon quinquedens* so that they may be identified in plankton collections and thus facilitate the understanding of the early life history of this species and hopefully to shed light on its apparently tenuous taxonomic status within the Brachyrhyncha.

METHODS AND MATERIALS

In February 1971, several berried females of *Geryon quinquedens* were captured in 300 fm of water (bottom temperature was 5.9°C) in the Baltimore Canyon area of the continental shelf (lat 37°56′N, long 73°55′W) off Delaware Bay. Three of the berried crabs were returned to the Boothbay Harbor Laboratory and maintained in shallow tanks at temperatures that ranged from 5° to 12°C. On 29 April 1971, one of the females died and some of her eggs were removed and placed in beakers of filtered seawater. Temperature in the beakers was 15°C; prezoeae were observed the next day and on 1 May first zoeae were apparent. On 10 May, another female's eggs started hatching in one of the tanks. Water temperature in this tank was 10°C. A prezoea stage was noted in the tank also but lasted less than 1 hr. First zoeae from each of these batches were maintained separately in beakers containing 1,000 ml of filtered seawater and 50,000 units of penicillin plus a small amount of streptomycin (some larvae were raised without the antibiotics with no differences noted). Newly hatched *Artemia* nauplii obtained from California eggs were given as food. Small amounts of algae (*Dunaliella*) were also added to sustain the *Artemia* nauplii. Water and food were changed every other day. At the start the zoeae were maintained at a constant temperature of 15°C, but fouling organisms grew on many of the zoeae and it was necessary to maintain them at room temperature (18°-21°C) to accelerate development. Salinity ranged 30 to 31‰ during the study. Zoeae were also put into compartmented plastic trays, one to a compartment, and were maintained as those in the beakers. The zoeae in the compartments were used for the developmental studies. When a zoea molted in a

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Manuscript accepted July 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

compartment it was preserved, along with its molt, the following day.

Measurements of the larvae were made with an ocular micrometer and are given in millimeters; drawings were made with the aid of a camera lucida. Ten individuals, of each stage, and their molts were examined and measured for the developmental series. Carapace length measurements were made from the anterior edge of the carapace (posterior edge of eye sockets) to the posterior margin, along the midline. Total length represents the distance from the tip of the rostral spine to the tip of the telson along the curves of the dorsal midline. The setae on some appendages have been shortened or deleted in some of the illustrations to ensure clarity, but are given full descriptions in the text.

RESULTS

A prezoea stage of short duration, four zoeal stages, and a megalopa stage were obtained. The prezoeae measured about 2.8 mm in total length. The following are the average number of days from one stage to the next at temperatures of 18° to 21°C; first stage zoea to second, 7 days; second to third, 6; third to fourth, 5; fourth to megalopa, 7; and megalopa to first crab, 14. Two abnormalities were observed; a first stage zoea with the protopodite of one antenna forked from the base, and a second stage zoea with the large lateral spine on one side of the telson forked from its base. The larvae are usually light reddish brown in gross appearance. Some individuals are quite light in appearance but both phases exhibit numerous melanophores scattered over the entire body, particularly on the cephalothorax and along the outer margins of the abdomen. Small melanophores are often scattered on the basipodite on the maxillipeds.

DESCRIPTION OF THE LARVAE

ZOEA I (Figure 1A)

Carapace length 0.83 mm (0.81-0.86); total length 3.71 mm (3.67-3.73). Carapace with rostral, lateral, and dorsal spines. Rostral spine strongly depressed; slightly longer than antennae and nearly three quarters the length of the dorsal spine. Lateral spines flexed slightly ventrad, broad based, and nearly as long as the rostral spine. Width of the carapace from tip to tip of lateral spines about half the total length of the body. Dorsal spine long and curved slightly posteriad; its length about one-third the total length of the body. A short slender seta is present on each side of the carapace, in line with the posterior margin of the dorsal spine's base. The eyes are not stalked. Abdomen with five somites and the telson (Figure 2H). Abdominal somites two through five with lateral spines (fifth somite in some individuals without spines); those on second somite fairly blunt and directed somewhat anteriad; spines on somites three through five sharper and hooked posteriad, decreasing in size posterially. Posterior lateral margin of somites three through five produced into long, sharp spines. Second somite with two setae on middorsal surface; somites three through five with two setae each on posterodorsal margin. Telson bifurcate with three pairs of setae on the inner side. Each furca with two lateral spines, one long and strong, the other much smaller, and a small dorsal spine. Antennule (Figure 2B) with four unequal aesthetes and a small seta terminally. The antenna (Figure 2A) bears a long protopodite with a row of spinules on the outer margins; the exopodite is about half the length of the protopodite and terminates in a spine and one seta. Mandible (Figure 2C) with two large teeth anteriorly, a medial blade, and a toothed edge posteriorly. The maxillule (Figure 2D) bears a two-segmented endopodite, the short proximal segment bears one long plumose seta, the distal segment with six long plumose setae, two of which are subterminal; the basal and coxal endites each bear six spinous setae. The scaphognathite of the maxilla (Figure 2E) has seven marginal plumose setae and a plumose apical tip; the endopodite is bilobed with five spinous setae on the distal lobe and three on the proximal; basal and coxal endites each bilobed with 5 + 5 and 3 + 3 spinous setae respectively. There is a suggestion of two segments in the exopodite of the first maxilliped (Figure 2F) which bears four, one-jointed, natatory setae terminally; endopodite

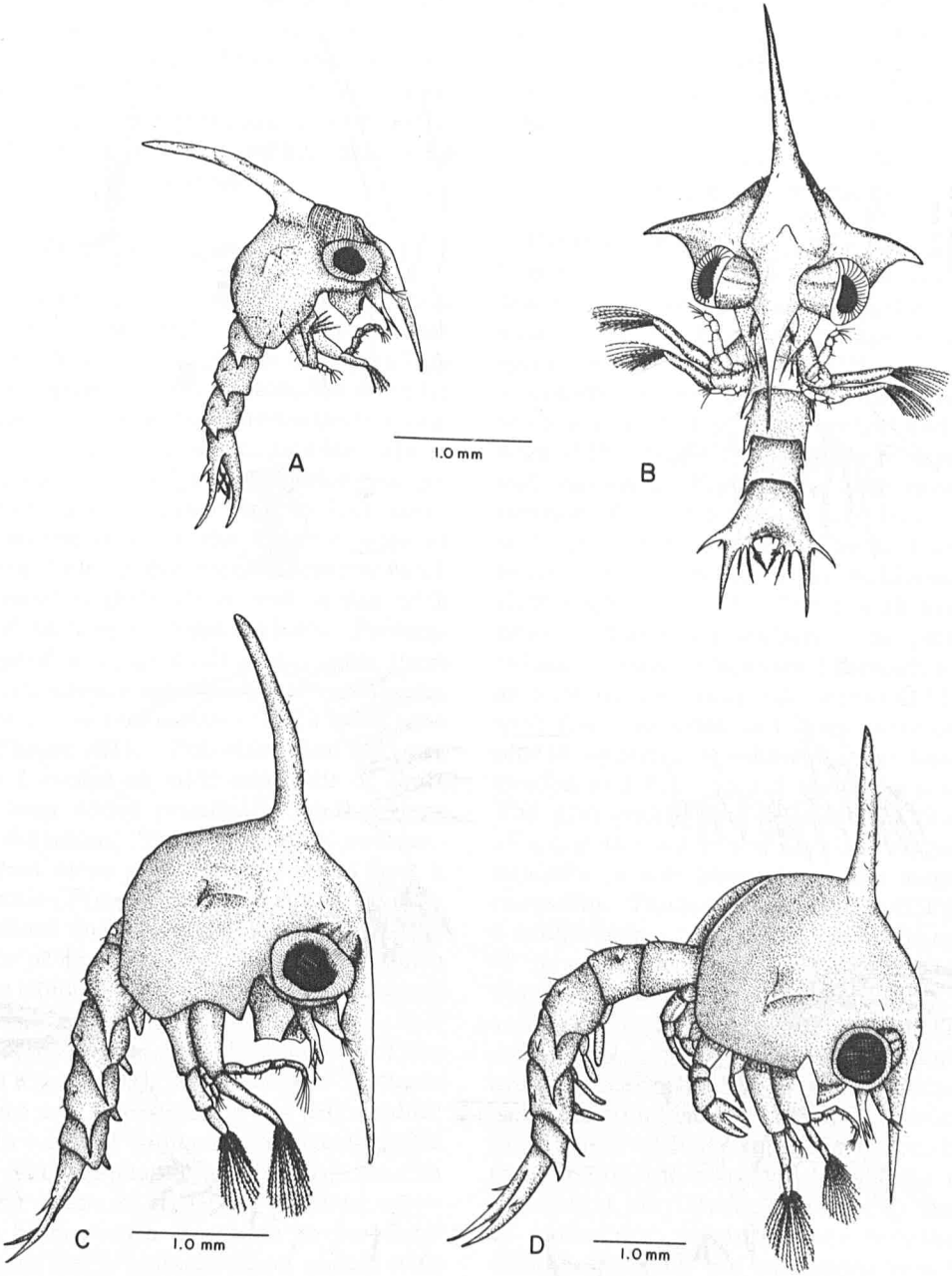

FIGURE 1.—*Geryon quinquedens.* A. Zoea I, B. Zoea II, C. Zoea III, D. Zoea IV.

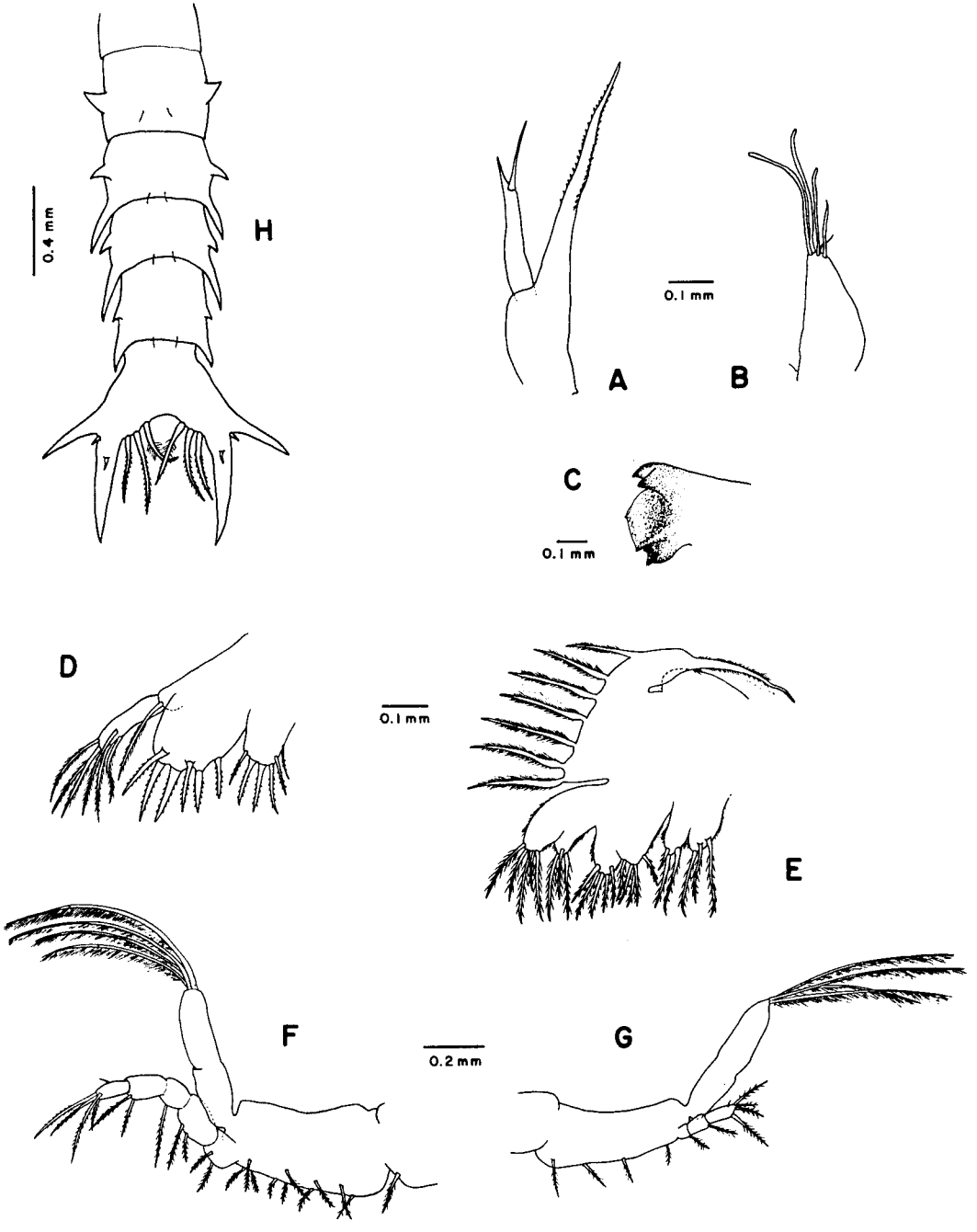

FIGURE 2.—*Geryon quinquedens*, Zoea I. A. antenna, B. antennule, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. dorsal view of abdomen and telson.

five-segmented with 2, 2, 1, 2, 5 setae on the segments (proximally to distally); basipodite with 10 setae, coxa with 1 seta. The exopodite of the second maxilliped (Figure 2G) bears four, one-jointed natatory setae terminally; endopodite three-segmented with 1, 1, 5 setae; basipodite with four setae; coxa naked.

ZOEA II (Figure 1B)

Carapace length 1.07 mm (1.00-1.13), total length 4.97 mm (4.89-5.02). Spines on carapace as in Zoea I. The rostral spine is nearly as long as the dorsal spine. Width of carapace from tip to tip of lateral spines about four-tenths the total length of the body. A short, slender seta is present at each side of the posterior margin of the dorsal spine's base. One to four small setae are scattered along the anterior edge of the proximal half of the dorsal spine; a small seta is present slightly above and in line with the base of each eye. Eyes stalked. Posteroventral edge of carapace finely serrate with three of four short, slender setae on the inner margin. Abdomen with five free somites (sixth fused with telson) (Figure 3H). Spination and setation as in Zoea I except an additional pair of short setae has been added proximally on the inner margin of the telson. The spines on the abdomen are somewhat more pronounced than in Zoea I. The antennule (Figure 3A) bears four aesthetes, plus one short and one long setae terminally. Protopodite of the antenna (Figure 3B) as in Zoea I; the exopodite terminates in two unequal setae and the endopodite is evident as a bud. Mandible as in Figure 3C. Endopodite of the maxillule (Figure 3D) as in Zoea I; a single, long plumose seta is present on the protopodite; basal endite with 12 spinous setae, coxal endite with 11. The scaphognathite of the maxilla (Figure 3E) bears 22 marginal plumose setae; endopodite bilobed with five setae on the distal lobe, three on the proximal; basal endite with seven setae on the distal lobe, five on proximal; coxal endite with four setae on each lobe. The two-segmented exopodite of the first maxilliped (Figure 3F) now bears 10 or 11 articulated natatory setae terminally; endopodite, basipodite, and coxa as in Zoea I. The exopodite of the second maxilliped (Figure 3G) bears 11 articulated natatory setae; endopodite, basipodite, and coxa as in Zoea I. The third maxillipeds, chelipeds, and pereiopods are evident as minute buds.

ZOEA III (Figure 1C)

Carapace length 1.42 mm (1.35-1.48); total length 6.13 mm (5.75-6.48). The lateral spines are more ventrally flexed and the number of small setae on the anterior edge of the dorsal spine has increased from the previous stage. There are 15 small setae along the inner margin of each side of the posteroventral and posterior edge of the carapace. Abdomen with six somites and the telson (Figure 4I). The spination and setation of somites two through five is the same as in the previous stage. The first somite now bears two small setae on the middorsal surface; sixth segment naked. Telson with five pairs of setae on the inner portion. The pleopods are evident as buds on somites 2 through 5; uropods as buds on the sixth. Antennule (Figure 4A) with four aesthetes and three setae terminally, plus three aesthetes subterminally; basal portion swollen and the endopod occurs as a small bud. The protopodite and exopodite of the antenna (Figure 4B) as in the previous stage; the endopodite is now about the same length as the exopodite. The mandible (Figure 4C) now bears a simple palp, evident as a bud. The endopodite of the maxillule (Figure 4D) has five or six long plumose setae on the distal segments; the basal and coxal endites each bear about 17 spinous setae. The scaphognathite of the maxilla (Figure 4E) bears about 31 marginal plumose setae; endopodite and basal endite as in previous stage; coxal endite with five spinous setae on distal lobe, and nine on the proximal lobe. The exopodite of the first maxilliped (Figure 4F) bears about 14 articulated natatory setae terminally; the distal segment of the endopodite now bears six setae; setation of other segments as in the previous stages, as is that of the basipodite; coxa with three setae. The exopodite of the second maxilliped (Figure 4G) bears about 14 articulated natatory setae; setation of endopodital segments as in the previous stages; basipodite with

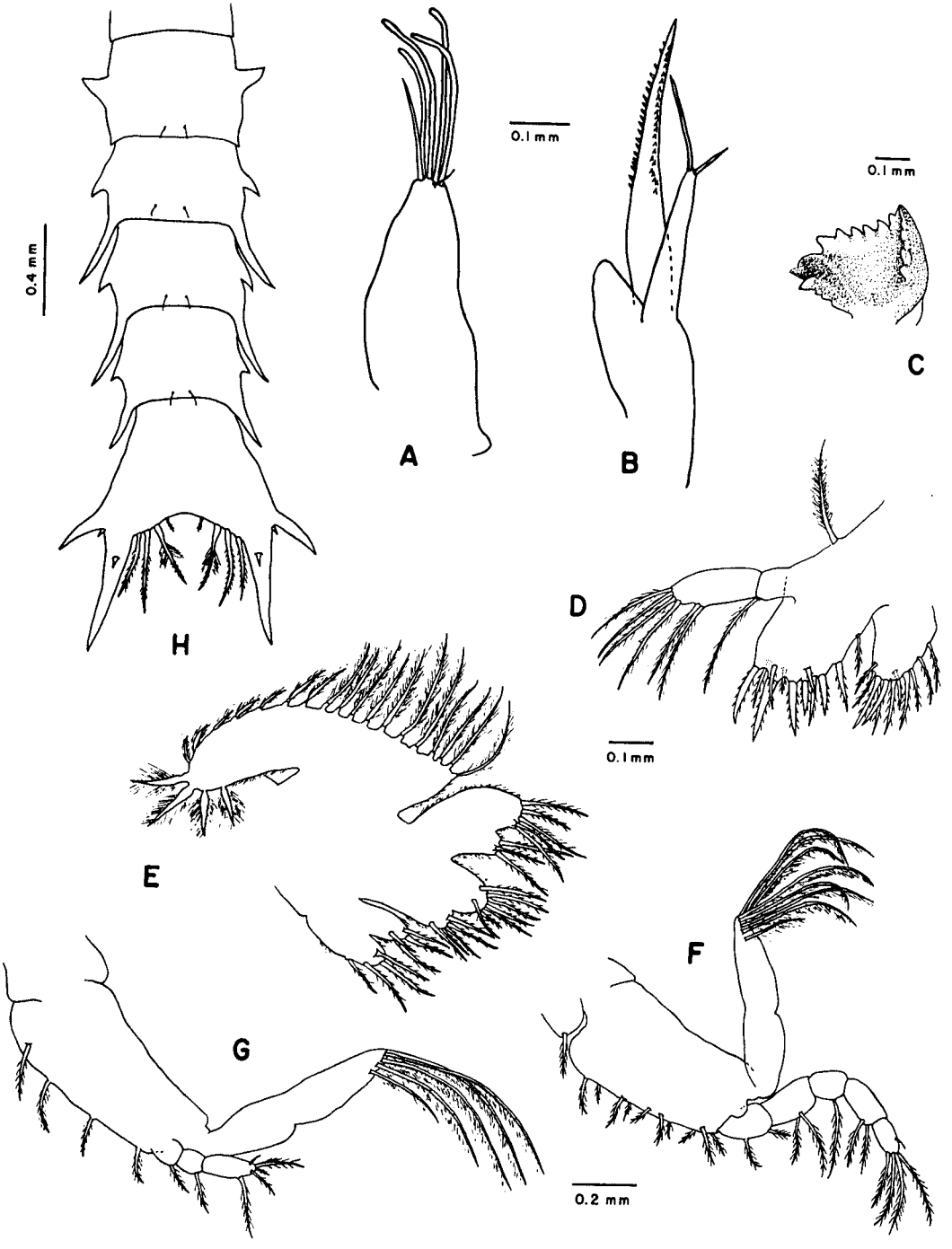

FIGURE 3.—*Geryon quinquedens*, Zoea II. A. antennule, B. antenna, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. dorsal view of abdomen and telson.

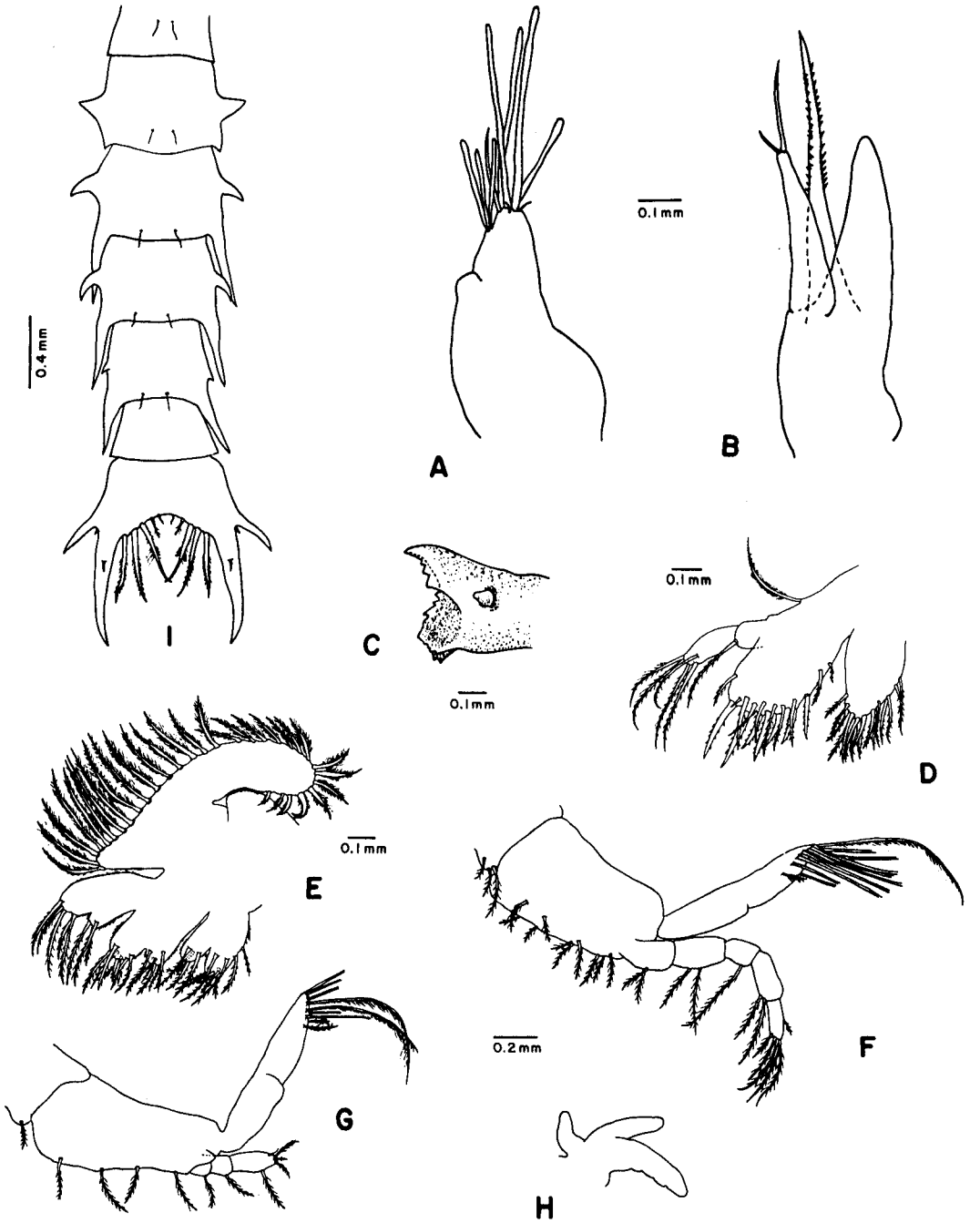

FIGURE 4.—*Geryon quinquedens*, Zoea III. A. antennule, B. antenna, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. third maxilliped, I. dorsal view of abdomen and telson.

three or four setae; coxa with one seta. The rudimentary third maxilliped as in Figure 4H. Chelipeds and pereiopods about twice as large as in previous stage.

ZOEA IV (Figure 1D)

Carapace length 1.94 mm (1.89-1.97); total length 8.31 mm (7.62-8.95). There is an indication that the considerable range in total and dorsal spine length is due to the nearness of a particular animal to its next molt. In some individuals a relatively short, blunt dorsal spine was observed; these individuals showed the greatest total length, while on shorter individuals a relatively long, slender dorsal spine was observed. Dorsal spine from 20 to 30% of the total length, with small setae scattered along its entire anterior edge; rostral spine usually as long or longer than the dorsal spine. Lateral spines flexed ventrally; carapace width, from tip to tip of lateral spines, about one-third of the total length of the body. A few additional setae occur between the anterior edge of the dorsal spine and the base of the rostral spine; 20 to 25 slender setae mid-ventrally to posteriorly on the inner margin of the carapace. Abdomen with six somites and the telson (Figure 5I). The blunt lateral spines on the second somite now directed slightly posteriad; spines on other somites more pronounced than in the previous stage. The first somite bears four setae on the middorsal surface; the second somite with two setae anterior and four setae posterior to the midline; the third somite with two setae middorsally and two on the posterodorsal margin; somites 4 and 5 each with a pair of setae on the posterodorsal margin, sixth somite naked; telson as in previous stage but with the proximal setae on the inner portion larger; pleopods and uropods considerably enlarged from the previous stage. Antennule (Figure 5A) with four aesthetes and two setae terminally, one group of six aesthetes and another of two subterminally; bud of endopod enlarged from previous stage; basal portion with five setae. Antenna (Figure 5B) as in previous stage but with the endopodite considerably enlarged and longer than the protopodite. Mandibular palp (Figure 5C) simple and much enlarged from the previous stage. The endopodite of the maxillule (Figure 5D) the same as in the previous stages; basal endite with about 22 spinous setae, coxal endite with 17. Scaphognathite of the maxilla (Figure 5E) with about 54 marginal plumose setae; endopodite the same as in the previous stages; distal lobe of the basal endite with 12 spinous setae, proximal lobe with nine; coxal endite as in the previous stage. The exopodite of the first maxilliped (Figure 5F) bears 17 setae; endopodite and basipodite as in the previous stage; coxa with six setae. The exopodite of the second maxilliped (Figure 5G) with 19 setae; the terminal segment of the endopodite with six setae, other segments as in the previous stages; basipodite with three setae; coxa with one. Exopodite of the third maxilliped (Figure 5H) with slight articulation; endopodite faintly five-segmented, the two distal segments each with one spine. Chelipeds and pereiopods considerably enlarged from previous stage.

MEGALOPA (Figures 6A and 7A)

Carapace length 3.16 mm (3.02-3.26); total length 6.46 mm (6.32-6.60). Rostrum one-fifth the length of the carapace, strongly depressed and bifid at the tip; a medial groove present from interorbital position nearly to the distal end of the rostrum. Eye stalks with a few small setae on the anterior and dorsal surfaces. A carina is present on each side of the mesogastric midline (highest points on carapace) and another prominence is present in the cardiac region of the carapace; hepatic and branchial lobes rounded; setation sparse, occurring along the margins of the rostrum, a few in the postorbital region, and a few tufts on the mesogastric prominences; numerous setae are present along the mid-ventral to posterior margin of the carapace. Abdomen with six somites and the telson; setation sparse and as figured; pleopods with about 28 long natatory setae each (Figure 7D); uropods with about 15 each (Figure 7H). The peduncle of the antennule (Figure 6B) is three-segmented, the proximal segment with one plumose seta, the middle segment with five setae subterminally, and the distal segment has two setae; inner

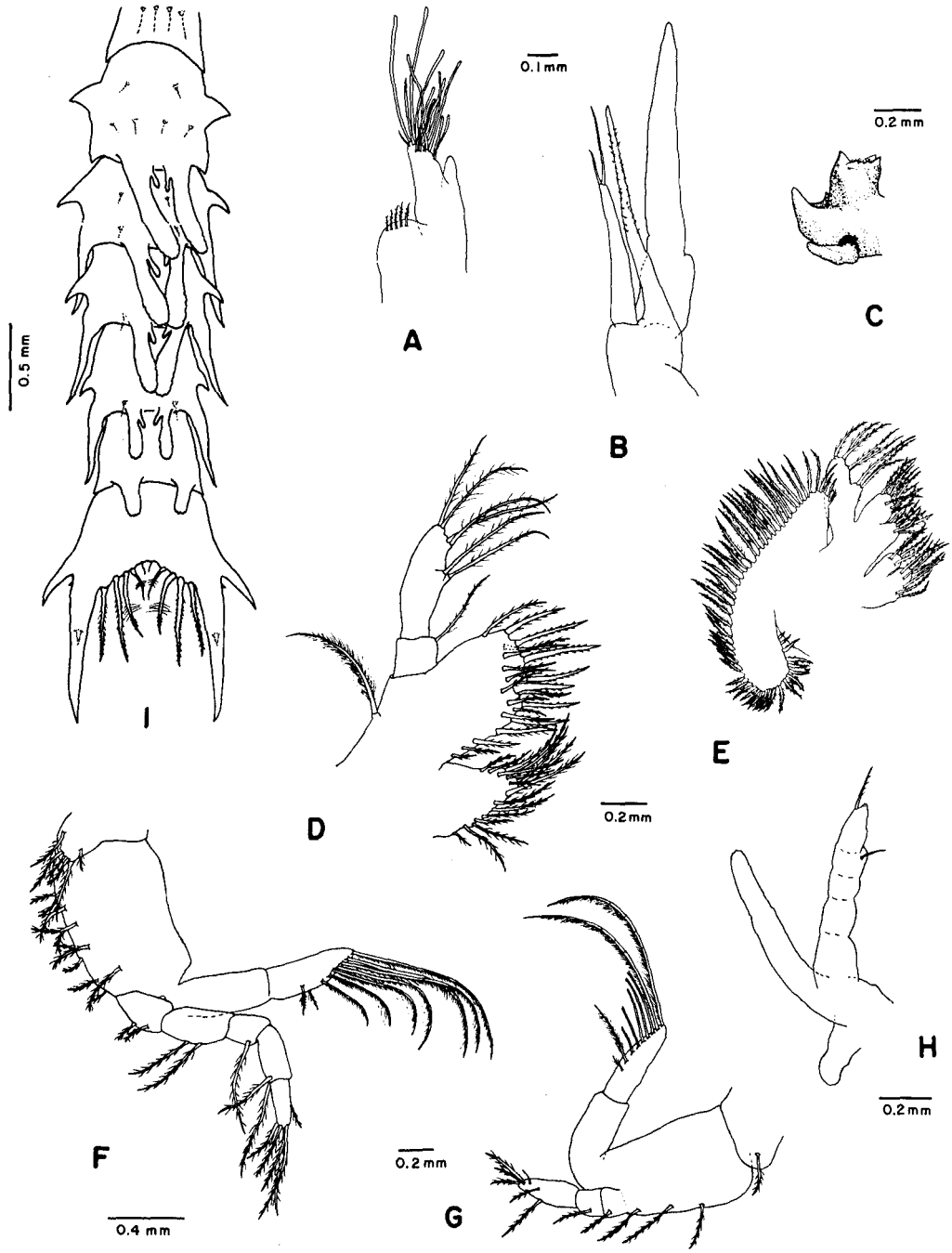

FIGURE 5.—*Geryon quinquedens*, Zoea IV. A. antennule, B. antenna, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. third maxilliped, I. ventral view of abdomen and telson.

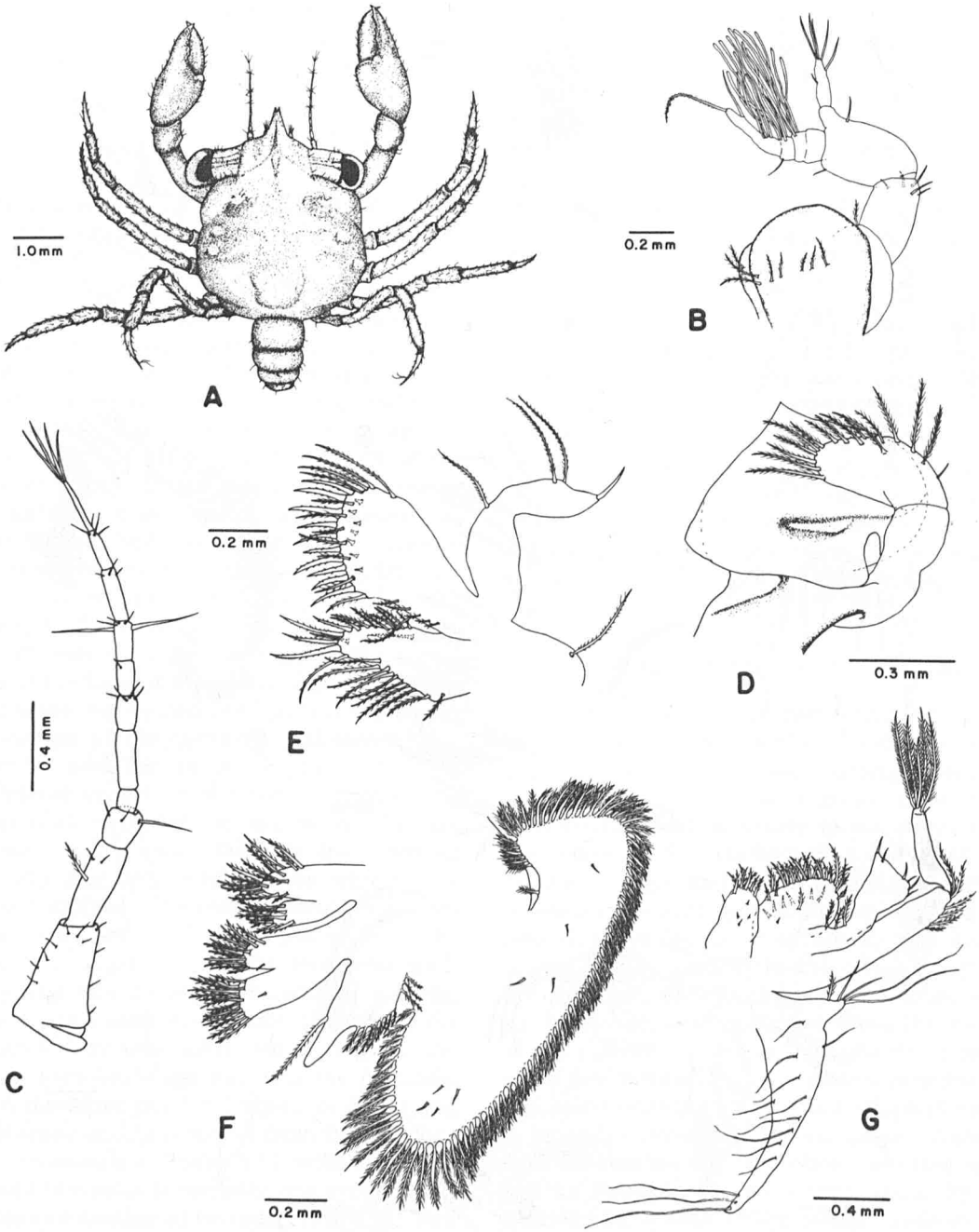

FIGURE 6.—*Geryon quinquedens*, megalopa. A. dorsal view, B. antennule, C. antenna, D. mandible, E. maxillule, F. maxilla, G. first maxilliped.

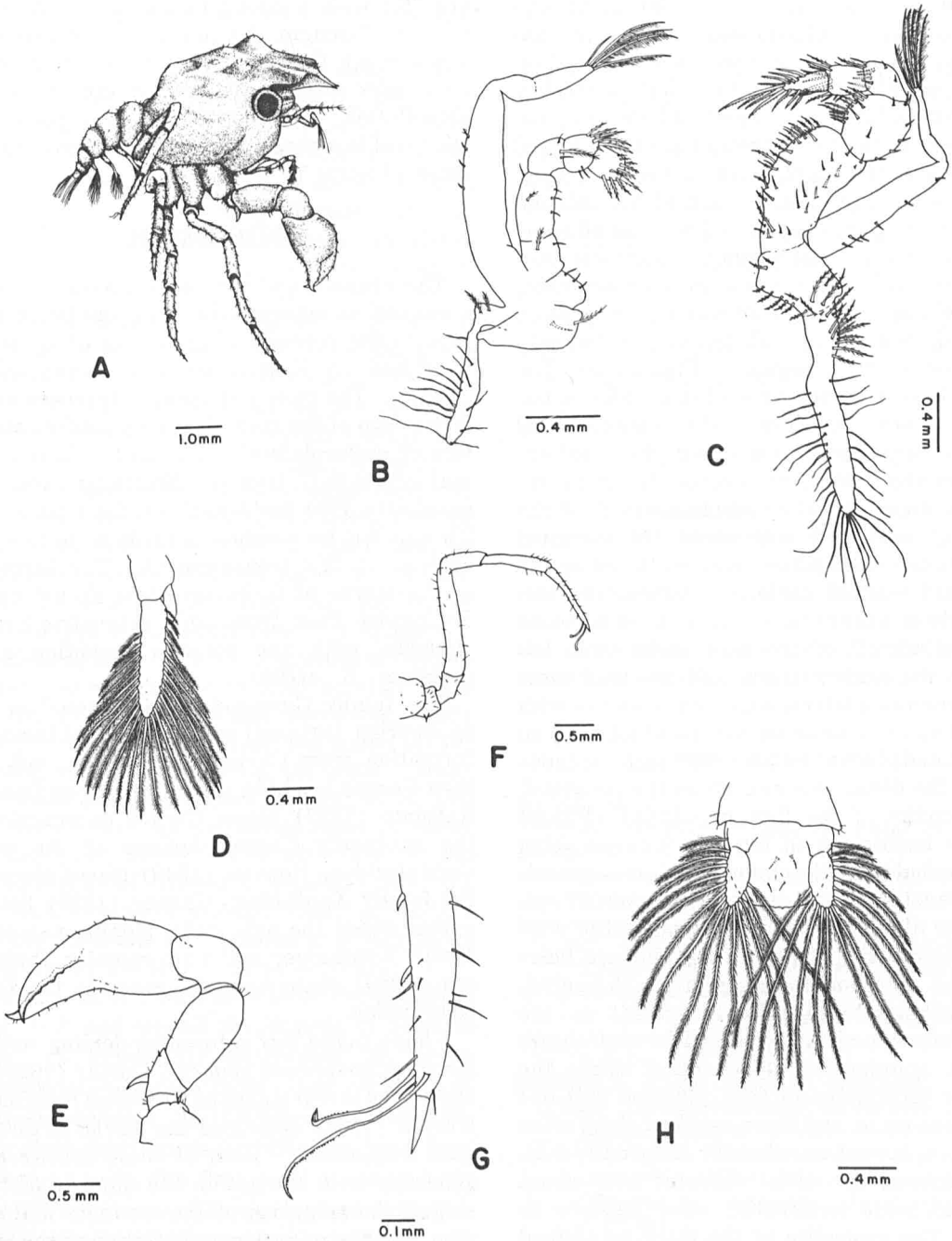

FIGURE 7.—*Geryon quinquedens*, megalopa. A. lateral view, B. second maxilliped, C. third maxilliped, D. pleopod of second abdominal somite, E. cheliped, F. last pereiopod, G. dactyl of last pereiopod, H. ventral view of telson and uropods.

flagellum two-segmented with four setae terminally and two subterminally; outer flagellum with four segments; proximal segment naked, the antepenultimate segments with six aesthetes, penultimate with five aesthetes and one seta, distal segment with five aesthetes near its base and one seta subterminally, terminating in a long, plumose seta. The basal portion of the antenna (Figure 6C) is two-segmented with small setae scattered on the distal segment; peduncle two-segmented with three setae on each segment; the flagellum is eight-segmented, the setation as figured. Mandibular palp two-segmented with 16 setae on the distal segment (Figure 6D). The endopodite of the maxillule (Figure 6E) is unsegmented, has one lateral and two subterminal setae, and terminates in a spine; the basal endite bears about 35 spinous setae; the coxal endite with about 25. The scaphognathite of the maxilla (Figure 6F) with about 100 marginal plumose setae, with a few setae scattered on the dorsal and ventral surfaces; endopodite produced into a narrow lobe, with three setae on the distal margin of the base, eight setae laterally on the same margin, and one long setae on the proximate lateral edge; basal endite with about 14 spinous setae on the distal lobe, 11 on the proximal; coxal endite with eight spinous setae on the distal lobe and 16 on the proximal. The exopodite of the first maxilliped (Figure 6G) now terminates in but five plumose setae and one naked seta; the endopodite is unsegmented and bladelike; basal endite with about 37 spinous setae along the margin; coxal endite with 12; epipodite with about 16 nonplumose hairs and 1 seta; setation of other portions as figured. A well-developed epipodite is present on the second maxilliped (Figure 7B) and bears about 14 nonplumose hairs and 2 setae; the exopodite terminates in four plumose and one nonplumose setae, and there are four short setae on the outer lateral margin; the endopodite with four segments, the distal segment with about 13 spinous setae terminally; other setation as figured. The exopodite of the third maxilliped (Figure 7C) terminates in six plumose setae; the endopodite is five-segmented, its spination and setation variable as is that of the epipodite and is approximately as figured. Chelipeds (Figure 7E) with a strong hooked spine on ventral portion of ischum. Spines on coxa of pereiopods one through three and another blunt spine subterminally on the posterior margin of the same articulation, decreasing in size posteriorly. Dactyl of last pereiopod with two curved, toothed setae (Figure 7F and G).

DISCUSSION

The prezoea and first zoea stages of *Geryon quinquedens* appear to be quite similar in structure to the corresponding stages of *G. tridens* described by Brattegard and Sankarankutty (1967). The most trenchant differences are the larger size of the zoea of *G. quinquedens* and the lack of posterolateral spines on the fifth abdominal somite in *G. tridens*. Brattegard and Sankarankutty give the length of the first zoea as 2.0 mm but no mention is made as to how they arrived at this measurement. The large size of the larvae of *G. quinquedens* should help to distinguish them from other sympatric Brachyrhyncha, with the possible exception of its congener, *G. affinis*.

The family Geryonidae was erected in 1930 by Beurlen (original reference not obtained, information from Christiansen, 1969), but since then *Geryon* has been placed in various families: Rathbun (1937) places *Geryon quinquedens* in the subfamily Carcinoplacinae of the family Goneplacidae; Bouvier (1940) placed *Geryon* in the family Xanthidae; Gurney (1939) lists the genus under the subfamily Menippinae of the family Xanthidae; and more recently Christiansen (1969) reassigned the genus to the family Geryonidae.

I have found few references dealing with the larvae of goneplacid genera. Lebour (1928) discussed the larval stages of *Gonoplax rhomboides;* Kurata (1968) described the larvae of *Carcinoplax longimanus*. Both of these species agree generally with *Geryon* in the number of larval stages, the spination of the carapace and abdomen, and the spination and setation of the telson. The relative length of the exopodite to the protopodite of the antenna in *Geryon* is apparently similar to that in *Carcinoplax* but different from that in *Gonoplax*. Megalopa of both *Gonoplax*

and *Carcinoplax* bear spines on the carapace, while megalopa of *Geryon* do not.

The exopodite of the antenna in zoeae of *Geryon quinquedens* is about one-half the length of the protopodite; in *Gonoplax* (Lebour, 1928) the exopodite is about the same length as the protopodite, and bears two short setae medially, rather than terminally as in *Geryon*. On the basis of the relative length of these two structures, *Geryon* would not align with *Gonoplax* in Lebour's key to the zoeae. The configuration and relative length of the antennal exopodite and protopodite in *Geryon* are more like those of *Cancer* (Poole, 1966), some portunids (Lebour, 1928; Roberts, 1969) and certain grapsids (Diaz and Ewald, 1968). Boyden (1943) and Leone (1951) discuss the serological relationships of *Geryon quinquedens* to other members of the Brachyura. Each found *Geryon* to be closer to the Xanthidae than to other families tested, with certain affinities noted to the Cancridae and Portunidae. However, neither of these workers tested other members of the Goneplacidae against *Geryon*. The zoeae of *Geryon quinquedens* are similar to most xanthid zoeae (Lebour, 1928; Costlow and Bookhout, 1968) in the number of zoeal stages, the spines on the carapace, and the armature of the telson. However, there are differences in the latter two characters within the Xanthidae alone (Costlow and Bookhout, 1966). The structure of the zoeal antennae of *Geryon* is decidedly different from the antennae of xanthid zoeae; in xanthid zoeae the exopodite of the antenna is very short in relation to the length of protopodite.

The number of terminal setae on the exopodite of the first and second maxillipeds of Zoea II through IV apparently distinguish the larvae of *Geryon quinquedens* from other members of the Brachyrhyncha. In this group the exopodite of the first maxillipeds consistently bear four terminal setae in the first zoeal stage and six in the second stage. The same number is usually associated with the second maxilliped. *G. quinquedens* bears 4 setae in the first stage and 10 or 11 in the second. Knight (1968) reports that the raninid species, *Raninoides benedicti* Rathbun, has nine setae on the exopodite of the second maxilliped (six on the first) of Zoea II. Only members of the rather diverse and remote Anomura apparently bear as many terminal setae on the maxillipeds of stages subsequent to Zoea I as does *G. quinquedens*. The lithodid species, *Cryptolithodes typicus* Brandt, bears four setae on the exopodite of the first maxilliped in the first zoeal stage and eight in the second stage (Hart, 1965). The porcellanid genera *Polyonyx* (Knight, 1966; Gore, 1968), *Pachycheles*, and *Petrolisthes* (Greenwood, 1965) bear from 11 to 14 terminal setae on the exopodite of the first maxillipeds in Zoea II. All bear four setae on this structure in Zoea I.

ACKNOWLEDGMENTS

I wish to thank James A. Rollins for making the drawings of the larval stages (Figures 1, 6A, and 7A), Warren Rathjen for supplying me with the female crabs, Mary Elizabeth Joralemon and Margaret S. Kelly for assistance in rearing the crab larvae, and Gareth W. Coffin for his reproductions of the illustrations.

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THE SYSTEMATIC STATUS OF *MERLUCCIUS* IN THE TROPICAL WESTERN ATLANTIC OCEAN INCLUDING THE GULF OF MEXICO

CHARLES KARNELLA[1]

ABSTRACT

Several morphometric and meristic characters are used to compare populations of *Merluccius* from the Gulf of Mexico and Atlantic Ocean. Both populations are shown to have similar values for all characters studied. As a result *M. magnoculus* Ginsburg is relegated to the synonymy of *M. albidus* (Mitchill).

Geographical variation is noted in many of the characters investigated.

The widely distributed gadoid fish genus *Merluccius* contains an indeterminate number of commercially fished species. There are 11 nominal species (Grinols and Tillman, 1970), known variously in the United States as either whiting or hake. The object of this paper is to determine the number of species living in the tropical western Atlantic (including the Gulf of Mexico and Caribbean). Ginsburg (1954) recognized three species from the western North Atlantic. One of these, *M. bilinearis* (Mitchill), is distinct from the other two nominal forms in having more gill rakers on the first arch (15-22 vs. 9-12). This species will not be considered further as it does not occur south of Cape Fear, N.C. *M. magnoculus* Ginsburg was described as new mainly on the basis of its having a longer head and shorter paired fins than its closest relative, *M. albidus* (Mitchill). *M. albidus* is found in the tropical western Atlantic, although not exclusively so, as it is known to occur sympatrically with *M. bilinearis* in the north. Ginsburg further noted that *M. magnoculus* and *M. albidus* were also moderately to slightly divergent in the following characters: maxillary length, snout length, eye diameter, and number of first dorsal, second dorsal, pectoral, and anal fin rays. Moreover, *M. magnoculus* was confined to the Gulf of Mexico while *M. albidus* occurred off the eastern coast of North America from Georges Bank to the Tortugas off the west coast of Florida. The lack of comparative material of equivalent size from the Gulf, the doubtful systematic status of two specimens from Savannah, Ga., and of a single specimen from off Cape Canaveral, Fla., make uncertain Ginsburg's tentative assignation of these specimens to *M. albidus*. Difficulty in identifying subsequent material from the Gulf of Mexico and Caribbean has necessitated a reassessment of the taxonomic status of *M. albidus* and *M. magnoculus*, especially since the stated differences between the two are slight and there is at least some overlap in all characters used to separate them.

Throughout the body of this paper the Atlantic population is taken to include specimens from the Caribbean also.

MATERIAL

A total of 253 specimens was examined; 86 from the Gulf of Mexico and 167 from along the eastern coast of the Americas, lat 41°30′N south to lat 7°26′N (Figure 1). This total included Ginsburg's material whenever possible. How-

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Manuscript accepted July 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

ever, some of his specimens were in poor state of preservation and too fragile to be handled. The list of specimens is as follows:

ATLANTIC OCEAN AND CARIBBEAN SEA

U.S. National Museum (USNM): 25769-1 specimen; 26049-1; 26073-1; 31630-1; 31677-1; 31686-1; 31739-1; 31741-1; 31822-1; 31842-2; 31844-1; 31863-2; 32791-1; 33032-1; 44264-1; 45920-1; 155475-2; 159214-1; 159230-1; 186294-5; 186299-1; 186302-1; 190356-1; 205223-1; 205224-1; 205230-1; 205231-1; 205233-1; 205235-1; 205237-4; 205240-2; 205241-1; 205242-1; 205243-1; 205244-1; 205245-1; 205246-1; 250247-1; 205248-1; 205249-1; 205251-1; 205252-1; 205253-1; 205255-1; 205257-2; 205259-1; 205260-1; 205262-1; 205263-2; 206190-1; 206191-1; 206192-2; 206194-1; 206195-7; 206196-1; 206197-1; 206198-1; 206199-1; 206200-1; 206201-2; 206202-5; 206203-4; 206204-1; 206205-30; 206207-2; 206208-5; 207187-3; 207188-1; 207189-1.

University of Miami Marine Laboratory (UMML): 3418-2 specimens; 3696-2; 4431-2; 22957-2; 29224-5; 29506-4; 29508-1.

Museum of Comparative Zoology (MCZ): 37754-2 specimens; 38086-3; 38130-3; 38324-1; 38333-1; 38338-2; 38350-1; 38395-1; 38399-2.

GULF OF MEXICO

U.S. National Museum (USNM): 92045-2 specimens; 157757-1; 157758-2; 157759-5; 157760-5; 157761-4; 157762-2; 157763-10; 186331-2; 187134-5; 187136-1; 205225-1; 205226-1; 205227-2; 205228-1; 205229-3; 205232-3; 205234-2; 205236-1; 205238-1; 205239-1; 205250-1; 205254-3; 205256-1; 205258-1; 205261-1; 206187-1; 206188-2; 206189-2; 206193-4; 206206-3; 207153-2; 207190-1.

University of Miami Marine Laboratory (UMML): 29507-9 specimens.

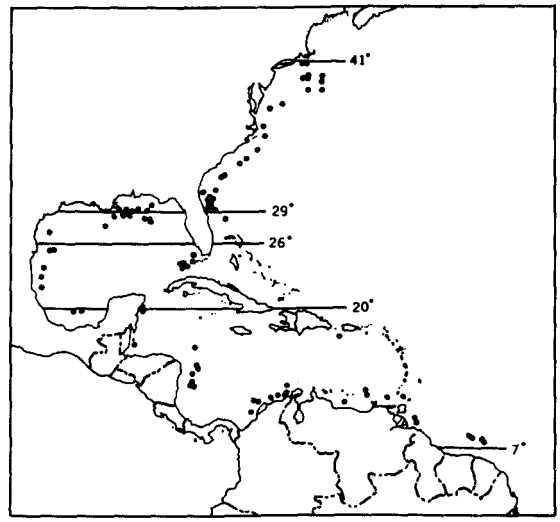

FIGURE 1.—Distribution of samples, western North Atlantic Ocean; equator to lat 45°N.

METHODS

All counts and measurements were made as described in Ginsburg (1954), so that the data from both studies would be directly comparable. The median fin rays, except the caudal, pectoral rays on both sides, and gill rakers of the outer arch on both sides were counted on all specimens that were not damaged. Total vertebral counts were made on selected specimens. Standard length, head length, snout length, maxillary length, eye diameter, pectoral fin length, and pelvic fin length were measured on all specimens when possible.

RESULTS AND DISCUSSION

Inspection of the counts and measurements indicates that the Gulf and Atlantic populations are similar in all characters studied. Within each area there are local differences in most of the characters; however, these differences are minor. The Gulf and Atlantic populations have identical or nearly identical ranges for all characters investigated, and the average values for both are generally only slightly divergent.

Differences in the relative head length and the

relative length of the paired fins were the main criteria used by Ginsburg (1954) for recognizing the Gulf population as a distinct species, *M. magnoculus*. These differences, however, were minor. More importantly the material used in his study did not adequately represent either the Atlantic or Gulf population. Thirty of thirty-eight specimens from the Atlantic were taken off Long Island, N.Y., and all 32 of the specimens from the Gulf of Mexico came from north of lat 26°N. Ginsburg was not able to make a valid comparison of the Atlantic and Gulf populations with the limited material available to him.

HEAD LENGTH

Ginsburg (1954) listed the range of head length taken as a percent of standard length as 27.3-31.3 for *M. albidus* and 29.6-31.3 for *M. magnoculus* but gave no mean values. Average values calculated from the data in Table 8 in Ginsburg (1954) are 28.7 for *M. albidus* and 30.6 for *M. magnoculus*. The specimens from the Atlantic and Caribbean populations examined in this study, had a range of 26.4-32.9 and a mean of 29.0, while the Gulf population had a range of 27.3-31.3 with a mean of 29.7. As can be seen from Table 1 the head length expressed as a percent of standard length is fairly uniform over the entire geographic area represented in this study.

TABLE 1.—Head length as a percent of standard length for the Atlantic and Gulf populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	27.9-31.8	29.8
21°-41°N	114	26.4-32.9	28.7
7°-41°N	162	26.4-32.9	29.0
Gulf			
19°-25°N	42	27.3-31.2	29.4
26°-29°N	43	28.6-31.3	30.0
19°-29°N	85	27.3-31.3	29.7

Although the Gulf population does have a slightly larger head, degree of difference between the two populations reported by Ginsburg is unsupported by the present data. The two populations are not separable on the basis of relative length.

Ginsburg also stated that growth of the head was allometric. The present data indicate that growth of the head is isometric (see Figure 2).

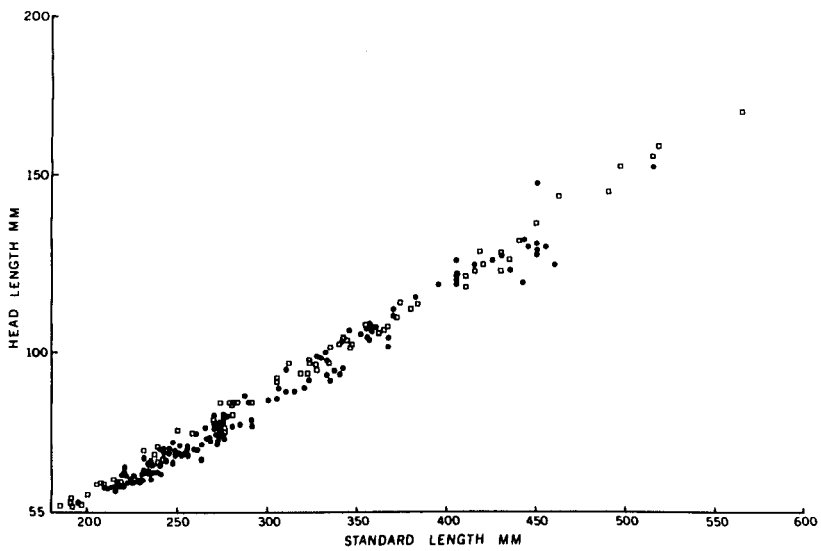

FIGURE 2.—Gulf (squares) and Atlantic (circles) populations: relation of head length to standard length.

PAIRED FIN LENGTH

Ginsburg (1954) reported the range of pectoral fin length taken as a percent of standard length to be 18.0-21.5 and 15.5-19.0 for *M. albidus* and *M. magnoculus*, respectively. The Atlantic specimens examined in the study have a similar maximum value to that of *M. albidus* (21.7, see Table 2) but the minimum value obtained, 13.7, is much lower. The minimum value obtained from the Gulf population, 13.7, is somewhat lower than the minimum value recorded for *M. magnoculus*, while the maximum value obtained, 19.4, is similar to that given by Ginsburg for *M. magnoculus*. Average values calculated from the data in Table 10 in Ginsburg (1954) are 19.8 for *M. albidus* and 17.0 for *M. magnoculus*. These compare fairly well with the values obtained for the Atlantic and Gulf populations 18.3 and 16.8, respectively.

TABLE 2.—Pectoral fin length as a percent of standard length for the Atlantic and Gulf populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	13.7-19.5	17.3
21°-41°N	113	15.8-21.7	18.8
7°-41°N	161	13.7-21.7	18.3
Gulf			
19°-25°N	41	13.7-19.2	17.2
26°-29°N	42	13.8-19.4	16.4
19°-29°N	83	13.7-19.4	16.8

The range of values for the pelvic fin length expressed as a percent of standard length is 12.8-19.2 with an average value of 15.6 for the Atlantic population and 11.6-17.0 with a mean of 14.3 for the Gulf population (Table 3). Ginsburg also reported a range of 13.5-19.5 for *M. albidus* and 12.0-16.0 for *M. magnoculus*, and the averages computed from data contained in his Table 9 are 16.6 and 14.0 for *M. albidus* and *M. magnoculus*, respectively.

The present data indicate that the Gulf population does have proportionally smaller paired fins than the Atlantic population, however, the differences are much smaller than indicated by Ginsburg. The relative length of the paired fins is similar in both populations and is clearly of no value in separating the two.

TABLE 3.—Pelvic fin length as a percent of standard length for the Gulf and Atlantic populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	12.8-19.2	14.7
21°-41°N	114	12.8-17.7	15.9
7°-41°N	162	12.8-19.2	15.6
Gulf			
19°-25°N	41	12.7-17.0	15.1
26°-29°N	43	11.6-16.2	13.6
19°-29°N	84	11.6-17.0	14.3

Ginsburg (1954) stated that the growth of the pelvic fin was allometric and that the relative pectoral fin length changed little if any with growth. To compensate for this he arranged his material into several size classes and compared similar sizes for both populations. However, he gave no average standard length for the classes, and it is impossible to determine if the size composition of the classes he compared was similar. Figure 3 indicates that growth of the pectoral fin is allometric and not isometric as reported by Ginsburg (1954). The pelvic fin does undergo allometric growth as stated by Ginsburg (see Figure 4).

Since the material examined from both areas is not of the same size composition (the average standard length of the specimens from the Atlantic population is 283 mm while the average standard length of the specimens from the Gulf population is 323 mm) at least some of the difference in paired fin length is due to allometric growth.

Figures 3 and 4 indicate that for some of the Gulf material the paired fins are relatively smaller than in other specimens of similar sizes. The majority of specimens with the smaller fins were collected north of lat 26°N. Most of the specimens with the higher values were collected north of lat 21°N in the Atlantic. Many specimens examined from the northern Gulf have fins of the same size as specimens from the southern Gulf and Atlantic populations. Hence, not all of the northern Gulf material can be distinguished by relative fin size.

The paired fins are poor characters to use in *Merluccius* because they are generally damaged to some degree. It is often impossible to determine if the fine ends of the rays are broken off.

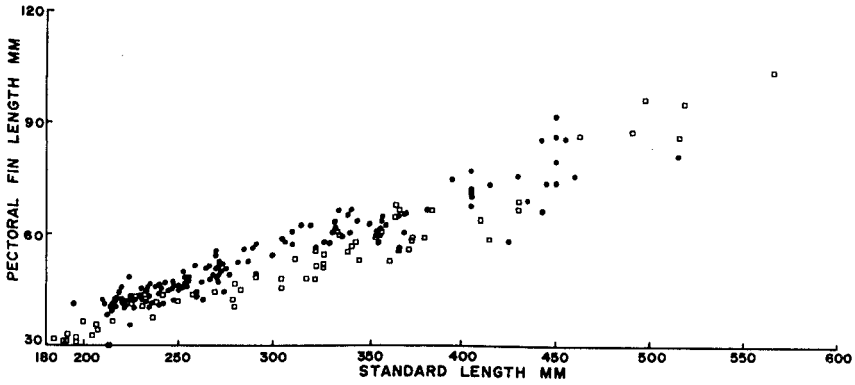

FIGURE 3.—Gulf (squares) and Atlantic (circles) populations: relation of pectoral fin length to standard length.

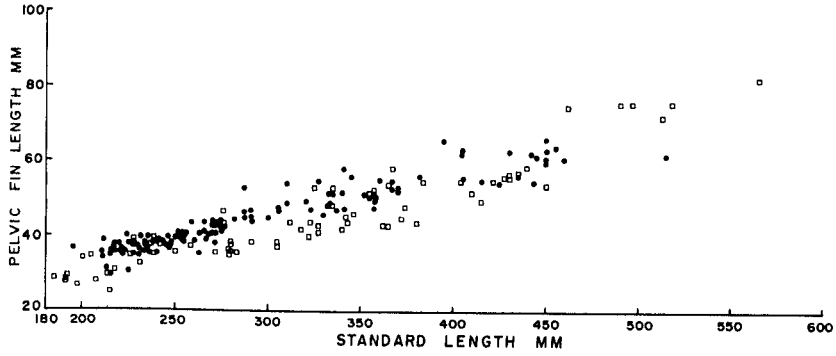

FIGURE 4.—Gulf (squares) and Atlantic (circles) populations: relation of pelvic fin length to a standard length.

Although the proportion and degree of damaged fins should be the same for both populations, a slight error will be introduced, and values presented for these measurements should be considered only as approximations of the real values.

EYE DIAMETER, SNOUT LENGTH, AND MAXILLARY LENGTH

The values obtained for these characters were similar in the Atlantic and Gulf populations, with the Gulf population having a slightly larger average value for all three characters (Tables 4, 5, 6); these values agree well with those of Ginsburg (1954).

All differences in these characters reported by Ginsburg (1954) may be explained by his limited material. Material from other areas examined in the present investigation indicate there are no differences between the two populations in any of the above characters (Figures 5, 6, 7).

TABLE 4.—Eye diameter as a percent of standard length for the Gulf and Atlantic populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	4.6-8.4	5.6
21°-41°N	114	4.8-8.4	5.9
7°-41°N	162	4.6-8.4	5.9
Gulf			
19°-25°N	42	5.2-7.0	6.0
26°-29°N	43	4.8-7.1	6.1
19°-29°N	85	4.8-7.1	6.0

TABLE 5.—Snout length as a percent of standard length for the Gulf and Atlantic populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	44	8.8-10.7	9.7
21°-41°N	114	8.1-11.1	9.2
7°-41°N	158	8.1-11.1	9.4
Gulf			
19°-25°N	42	8.7-11.2	9.8
26°-29°N	43	9.2-10.8	10.2
19°-29°N	85	8.7-11.2	10.0

TABLE 6.—Maxillary length as a percent of standard length for the Gulf and Atlantic populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	13.6-16.8	15.0
21°-41°N	114	13.3-17.7	14.4
7°-41°N	162	13.3-17.7	14.6
Gulf			
19°-25°N	42	13.6-15.9	15.0
26°-29°N	43	14.7-16.2	15.3
19°-29°N	85	13.6-16.2	15.2

Eye diameter is quite variable and several workers have noted that there are big eyed and small eyed forms in the Caribbean and Gulf of Mexico (D. M. Cohen, National Systematics Laboratory, National Marine Fisheries Service, NOAA, Washington, DC 20560, pers. comm.). Figure 5 indicates that the eye size is quite variable and there is no division between the big eyed and small eyed forms.

Eye size does not appear to be related to sex. Females (73 specimens) with small, intermediate, and large eyes were noted. Only two males were found, both with eyes of intermediate size.

MERISTIC CHARACTERS

Values obtained for meristic characters (Tables 7, 8, 9, 10, 11) are in agreement with those given by Ginsburg (1954) for both pop-

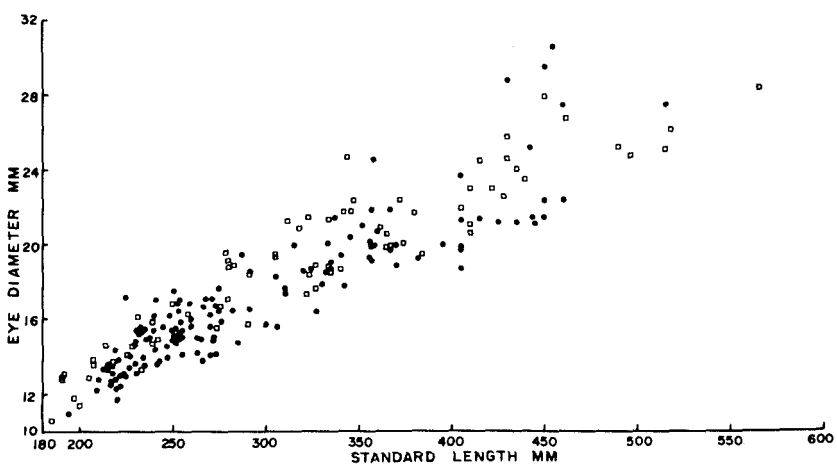

FIGURE 5.—Gulf (squares) and Atlantic (circles) populations: relation of eye diameter to standard length.

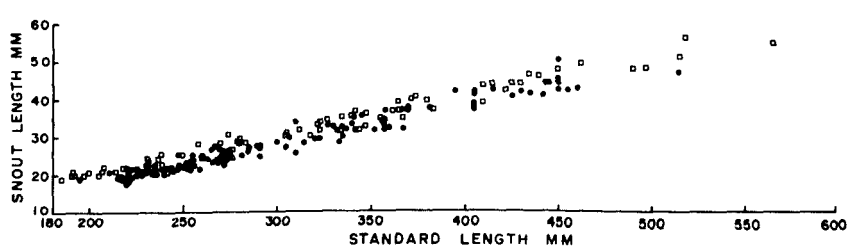

FIGURE 6.—Gulf (squares) and Atlantic (circles) populations: relation of snout length to standard length.

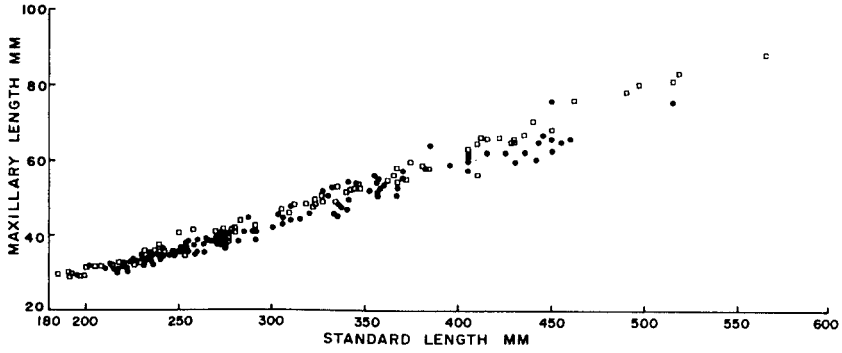

FIGURE 7.—Gulf (squares) and Atlantic (circles) populations: relation of maxillary length to standard length.

TABLE 7.—Frequency distribution of the number of gill rakers on the first gill arch for the Gulf and Atlantic populations.

Population	Number of gill rakers					
	8	9	10	11	12	Mean
Atlantic						
7°-20°N	3	22	46	24	3	10.0
21°-41°N	1	14	157	56	3	10.2
7°-41°N	4	36	203	80	6	10.1
Gulf						
19°-25°N	2	21	54	5	--	9.8
26°-29°N	4	13	63	8	--	9.9
19°-29°N	6	34	117	13	--	9.8

TABLE 8.—Frequency distribution of the number of first dorsal rays for the Gulf and Atlantic populations.

Population	Number of first dorsal rays				
	10	11	12	13	Mean
Atlantic					
7°-20°N	--	14	32	3	11.8
21°-41°N	3	63	49	1	11.4
7°-41°N	3	77	81	4	11.5
Gulf					
19°-25°N	--	16	24	2	11.7
26°-29°N	--	4	32	8	12.1
19°-29°N	--	20	56	10	11.9

ulations. However, for all characters but the number of first dorsal rays there was an increase in the range of one to three elements. In general, the average values computed from data presented in Ginsburg (1954) for *M. albidus* and *M. magnoculus* agree well with the average values calculated for the Atlantic and Gulf populations respectively.

Total vertebral counts for the Atlantic and Gulf populations were similar in both ranges and averages (Table 12). Geographic variation in most meristic characters is slight. Vertebral elements, pectoral fin rays, and anal fin rays are more variable than other meristic characters examined.

The ranges for all meristic characters studied are identical or nearly so for both the Gulf and Atlantic populations. For all characters there is a difference of less than one element in the average value between the two populations. Within each population there is variation in some or all of the meristic characters studied. The

TABLE 9.—Frequency distribution of the number of second dorsal rays for the Gulf and Atlantic populations.

Population	Number of second dorsal rays							
	35	36	37	38	39	40	41	Mean
Atlantic								
7°-20°N	2	14	20	8	3	--	--	36.9
21°-41°N	--	3	22	42	39	9	1	38.3
7°-41°N	2	17	42	50	42	9	1	37.9
Gulf								
19°-25°N	--	6	14	12	8	2	--	37.7
26°-29°N	--	2	10	12	14	5	1	38.3
19°-29°N	--	8	24	24	22	7	1	38.0

TABLE 10.—Frequency distribution of the number of anal rays for the Gulf and Atlantic populations.

Population	Number of anal rays								
	35	36	37	38	39	40	41	42	Mean
Atlantic									
7°-20°N	2	6	22	15	2	--	--	--	37.2
21°-41°N	1	8	42	32	28	2	2	--	37.8
7°-41°N	3	14	64	47	30	2	2	--	37.6
Gulf									
19°-25°N	2	9	12	7	6	4	2	--	37.6
26°-29°N	--	2	2	7	13	15	4	1	39.2
19°-29°N	2	11	14	14	19	19	6	1	38.4

TABLE 11.—Frequency distribution of the number of pectoral rays for the Gulf and Atlantic populations.

Population	Number of pectoral rays						
	12	13	14	15	16	17	Mean
Atlantic							
7°-20°N	6	24	57	6	2	--	13.7
21°-41°N	--	1	28	124	72	4	15.2
7°-41°N	6	25	85	130	74	4	14.8
Gulf							
19°-25°N	--	13	27	25	15	2	14.6
26°-29°N	6	42	28	11	--	--	13.5
19°-29°N	6	55	55	36	15	2	14.0

northern Gulf population has a slightly higher average value than the southern Gulf population for all meristic characters except pectoral fin rays and vertebrae. The southern Gulf has on the average a greater number of pectoral fin rays and vertebrae (Tables 7, 8, 9, 10, 11, 12). In the Atlantic the more southerly populations have fewer vertebrae, pectoral rays, second dorsal rays, and anal rays and more first dorsal rays than the northern populations.

Material collected between lat 7° and 20°N in the Atlantic has on the average between two and three (2.5) fewer vertebrae than the material collected north of lat 21°N. There is very little overlap in the range of vertebrae in the northern and southern Atlantic populations. Only 1 of 41 specimens from south of lat 20°N has more than 53 vertebrae and only 13 of 87 specimens north of lat 20°N have less than 54 vertebrae (Table 12). However, the relatively few specimens collected between lat 16° and 20°N may not be representative of the population residing there due to sampling error and hence, not represent the true range of vertebrae for that population.

CONCLUSIONS

The above data suggest that there is but a single species of *Merluccius* in the tropical western Atlantic, including the Caribbean and Gulf of Mexico. The Gulf population as a whole cannot be distinguished from the Atlantic population by means of any of the characters examined. For all of the characters examined differences between both populations are small. Within each area there are local differences in most of the characters; however, these differences are minor. The Gulf and Atlantic populations have identical

TABLE 12.—Frequency distribution of the number of vertebrae for the Gulf and Atlantic populations.

Population	Number of vertebrae							
	50	51	52	53	54	55	56	Mean
Atlantic								
7°-20°N	6	7	19	8	1	--	--	51.8
21°-41°N	--	--	--	13	41	31	2	54.3
7°-41°N	6	7	19	21	42	31	2	53.5
Gulf								
19°-25°N	--	1	5	14	10	2	1	53.3
26°-29°N	--	1	15	9	4	1	--	52.6
19°-29°N	--	2	20	23	14	3	1	53.0

or nearly identical ranges for all characters investigated, and the average values for both are generally only slightly divergent.

The northern Gulf population is, in many characters, divergent from the northern Atlantic population, which led Ginsburg (1954) to describe this population as a distinct species. However, the northern Gulf population is also somewhat divergent from the southern Gulf and Atlantic populations and, in both cases, the divergence is clearly not great enough to warrant recognition at the specific level. Furthermore, the amount of overlap in all characters is of such magnitude that individuals of the northern Gulf population cannot always be distinguished from individuals from other areas. Hence, *M. magnoculus* Ginsburg should be considered a junior synonym of *M. albidus* (Mitchill).

ACKNOWLEDGMENTS

Daniel M. Cohen and Bruce B. Collette of the National Systematics Laboratory, National Marine Fisheries Service, NOAA reviewed the manuscript and made valuable suggestions for improving it. I thank them for their advice and guidance throughout this study. The Southeast Fisheries Center, Pascagoula Laboratory, National Marine Fisheries Service provided the bulk of the material from the Gulf of Mexico and Caribbean; special thanks are due Bennie A Rohr. Tomio Iwamoto of the University of Miami searched through the University of Miami Marine Laboratory and Tropical Atlantic Biological Laboratory collections to find valuable material. Myvanwy M. Dick provided material from the Museum of Comparative Zoology. Keiko H. Moore of the National Marine Fisheries Service prepared the figures. My especial thanks go to George E. Clipper of the National Marine Fisheries Service for his help and many valuable suggestions.

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REGIONAL DISTRIBUTION OF THYROID STIMULATING HORMONE ACTIVITY IN THE PITUITARY GLAND OF THE ATLANTIC STINGRAY, *DASYATIS SABINA*

RODNEY G. JACKSON AND MARTIN SAGE[1]

ABSTRACT

The possibility that the elasmobranch pituitary contains thyroid stimulating hormone (TSH) activity was investigated by measuring the increase in the release of thyroxine from thyroid glands of the Atlantic stingray, *Dasyatis sabina*, incubated with homogenates of various pituitary regions. The ventral lobe of the pars distalis contained most of the TSH activity, with lesser amounts in the neurointermediate lobe. Histological techniques were not sensitive enough to detect changes in the thyroid associated with the increase in thyroxine release. It is concluded that the elasmobranch pituitary contains TSH activity but its functional significance remains to be determined.

Few studies have been conducted to examine the functional relationship between the pituitary and the thyroid gland of elasmobranchs. Dodd and Goddard (unpublished but cited by Dent and Dodd, 1961) hypophysectomized adult dogfish, *Scyliorhinus caniculus*, but found no histological changes in the thyroid after 2 years, whereas Vivien (1964) found that after decapitation of *Scyliorhinus* embryos the thyroid failed to complete its differentiation. The latter result is, of course, open to several interpretations since decapitation removes more than the pituitary. Injection of homoplastic pituitary homogenates into *Scyliorhinus* resulted in histological signs of stimulation of the thyroid gland (Vivien, 1941; Olivereau, 1954). Unfortunately, histological methods of assessing thyroid activity are frequently both insensitive (Sage and Robins, 1970) and unreliable (Swift, 1960).

Ferguson, Dodd, Hunter, and Dodd (unpublished data summarized by Dodd et al. (1963)) using the McKenzie mouse assay found thyroid stimulating hormone (TSH) activity in all parts of the *S. caniculus* pituitary, most of it being in the ventral lobe. However, the highest activity found was much less than that found in the posterior lobe of the mouse pituitary, which presumably does not contain TSH. Their results could be interpreted as suggesting that the small amount of TSH activity found in the dogfish pituitary was of no significance. The interpretation of assays of lower vertebrate TSH on mammalian assay systems is further complicated by the probability of phylogenetic specificity of hormone action. It is known that teleost TSH is relatively inactive on the mammalian thyroid (Fontaine, 1969); similarly it is possible that if there is an elasmobranch TSH it may have low activity on mammalian tissues. In a recent review Gorbman (1969) states that "definite proof of a TSH-like principle in elasmobranch pituitaries remains to be provided." In an attempt to elucidate this problem we investigated the stimulatory effects of homogenates of the different regions of the pituitary of *Dasyatis sabina* on thyroxine release from the animal's own thyroid gland in vitro. This technique eliminates the problem of phylogenetic specificity, and, by measuring thyroxine release, avoids the problems of interpretation associated with histological assessment of thyroid activity.

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Manuscript accepted May 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

MATERIALS AND METHODS

ANIMALS

Dasyatis sabina (Lesueur) were collected in otter trawls. In the fall and winter stingrays are most abundant in the shallow waters in the Gulf of Mexico adjacent to Port Aransas, Tex. In late spring the stingrays migrate into the bays behind the line of barrier islands where they were caught during the summer (Sage et al., 1972).

INCUBATION TECHNIQUE

Animals were killed by cutting across the hind brain. The compact thyroid is located ventral to the anterior end of the ventral aorta. The thyroid was removed and divided into experimental and control halves, and further divided where necessary so that no piece of tissue was larger than 5 mg. Preliminary experiments indicated that the elasmobranch thyroid was slow in responding to stimulation. Thyroid tissue was therefore incubated for 3 days in 2 ml of elasmobranch saline (Nicoll and Bern, 1964). Antibiotics were added (Bakke et al., 1957) in order to inhibit bacterial growth which might result in the breakdown of the thyroxine released into the medium. The addition of antibiotics does not interfere with the ability of thyroid glands to respond to TSH (Bakke et al., 1957; Sage, 1968a). The incubation flasks were gassed with 95% oxygen and 5% carbon dioxide and shaken at 120 strokes/min at 30°C. This temperature is within the normal environmental range of *D. sabina*. Modification of the incubation medium by the addition of 0.5 mg/ml lactalbumin hydrolysate was found to increase control rates but reduce the variability of the response and was used in later experiments as described in the text.

Homogenates of whole pituitaries or various regions of the stingray pituitary were made in a glass homogenizer and added to the incubation media at a concentration of one pituitary gland or region per thyroid gland. The homogenates were added immediately prior to gassing and adding of the thyroid tissue.

THYROXINE ANALYSIS

At the end of the 3-day incubation period thyroid tissue was removed for histological examination, and the incubation media was centrifuged at 10,000 rcf for 10 min to remove cell debris. Incubations were then stored below 0°C until analyzed. Thyroxine was isolated by ion exchange chromatography (Galton and Pitt-Rivers, 1959). The catalytic effect of iodine in reducing ceric ions was used to quantify thyroxine iodine (Pileggi et al., 1961; Pileggi and Kessler, 1968). Oxford Laboratories' (San Mateo, Calif.) kit[2] of reagents was used in the determinations. The results were converted to rates of thyroxine release per unit thyroid weight per incubation, and the responses of treated halves of the gland were then expressed as a percentage of the matched control incubated halves. Additives to the incubation media were routinely analyzed but were invariably devoid of thyroxine.

HISTOLOGICAL METHODS

At the end of the incubation period, thyroid tissue was removed and fixed in mercuric formol (90 parts saturated mercuric chloride to 10 parts formaldehyde solution). Sections were cut in polyester wax and stained with hematoxylin and light green. The image of the thyroid follicles was projected onto a sheet of paper, and a planimeter was used to determine the percentage of the area of follicle occupied by epithelium.

Unstained thyroid sections were used for interferometric determinations of mass per unit area of the colloid (Bromage and Sage, 1968; Sage, 1968b). Such methods are very sensitive in detecting changes in thyroid activity in both teleosts (Bromage and Sage, 1968) and mammals (Sage and Robins, 1970).

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

RESULTS

A preliminary study was carried out to determine responsiveness of the thyroid to homogenates of the various regions of pituitary and to control material. The results (Table 1) indicated that the addition of large amounts of protein or protein hydrolysate resulted in a stimulation of the gland, thus suggesting an inadequate culture medium. The medium was therefore modified by the addition of 0.5 mg lactalbumin hydrolysate/ml, and the response to various regions of the pituitary reexamined (Table 2). TSH activity was greatest in the ventral lobe of the proximal pars distalis, but significant activity was also found in the neurointermediate lobe. The latter is not due to the presence of thyroxine in this pituitary lobe since the thyroxine content of the homogenates was undetectable. In this respect the elasmobranch is unlike the mammal where the neural lobe does concentrate thyroxine (see review by Pitt-Rivers and Tata, 1959).

Histological methods have previously been used to assay the state of thyroid activity. In order to determine whether such techniques would detect stimulation resulting from incubation of thyroids with whole pituitary homogenates, interferometric measurements on the colloid were made together with a determination of the percentage of the follicular area occupied by epithelium. Neither technique was sensitive enough to detect the stimulation observed by measuring changes in the release of thyroxine (Table 3).

TABLE 1.—Percentage increase in release of thyroxine from *Dasyatis* thyroid tissue produced by adding homogenates of various regions of the *Dasystis* pituitary or lactalbumin hydrolysate to a medium containing salts, urea, and glucose.

Item	*N*	Mean ± SE
Rostral pars distalis (1 lobe/thyroid)	7	43 ± 22
Neurointermediate lobe (1 lobe/thyroid)	8	*31 ± 9
Proximal pars distalis:		
Dorsal lobe (1 lobe/thyroid)	6	40 ± 18
Ventral lobe (1 lobe/thyroid)	7	47 ± 27
Lactalbumin hydrolysate (2 mg/thyroid)	5	35 ± 24

* Significantly differs from zero, $P<0.01$.

TABLE 2.—Percentage increase in the release of thyroxine from *Dasyatis* thyroid tissue produced by adding homogenates of various regions of the *Dasyatis* pituitary to a medium containing salts, urea, glucose plus lactalbumin hydrolysate.

Item	*N*	Mean ± SE
Rostral pars distalis	9	30 ± 19
Neurointermediate lobe	9	*55 ± 20
Proximal pars distalis:		
Dorsal lobe	9	19 ± 15
Ventral lobe	9	**123 ± 40

* Significantly differs from zero, $P<0.05$.
** Significantly differs from zero, $P<0.02$.

TABLE 3.—A comparison of the effectiveness of various techniques for determining the response of *Dasyatis* thyroid glands to 3-day stimulation in vitro by homogenates of whole *Dasyatis* pituitaries (1 pituitary/thyroid).

Item	*N*	Mean percentage of control values ± SE
Increase in release of thyroxine	12	*51 ± 16
Increase in area of follicles occupied by epithelium	7	4.4 ± 5.1
Decrease in interferometric measure of dry wt/unit area of colloid	12	63 ± 38

* Significantly differs from zero, $P<0.01$.

DISCUSSION

The present work confirms the unpublished but frequently quoted work of Ferguson et al. (Dodd et al., 1963) in that there is TSH activity in the elasmobranch pituitary and that the greatest concentration is found in the ventral lobe where gonadotropic activity has also been found (Dodd, Evennett, and Goddard, 1960). The finding of lesser amounts of TSH activity in the neurointermediate lobe is in agreement with the finding of Goddard and Dodd (unpublished but quoted by Dodd et al., 1960). However, their suggestion that the activity is due to a thyrotropin releasing factor cannot explain the present results obtained in vitro with thyroid tissue. The nature of the neurointermediate thyroid stimulating substance is unknown. Dodd et al. (1963) reported that it is heat stable, whereas the activity of the dogfish ventral lobe is not. However, it is not possible to argue that the activity in the neurointermediate lobe is nonprotein since all the activity present in the frog (*Rana temporaria*) pituitary is heat stable and some at least of this is presumed to be the protein TSH.

The comparison of techniques for the demonstration of TSH activity of the pituitary homogenates on the thyroid clearly indicates the inadequacy of histological methods. In spite of a highly significant increase in the release of thyroxine there was no change observed in the follicular epithelium nor in measurements on the colloid weight per unit area. This method is capable of detecting the response of teleost thyroid follicles to a 24-hr incubation with mammalian TSH (Bromage and Sage, 1968).

While the results of incubations of thyroid with pituitary homogenates indicate TSH activity is present in the pituitary, they do not indicate whether it is of functional significance. An obvious followup to these experiments would be the removal of the ventral lobe and the measurement of blood thyroxine levels. However, removal of the ventral lobe in this species has not so far been possible due to the close association of this region with the carotid anastomosis.

Furthermore, the analysis of thyroxine in elasmobranch blood by the present methods is difficult due to unknown factors in the blood which interfere with thyroxine analysis. From this study we conclude that TSH activity is present in the elasmobranch pituitary and that most of this activity is in the ventral lobe. However the functional significance of this activity remains to be determined.

ACKNOWLEDGMENTS

We are indebted to Mr. J. Thompson and his staff at the Marine Science Institute, especially Boat Captains E. Wingfield and J. Shanklin for help in collecting Atlantic stingrays. We also thank Dr. V. de Vlaming and L. C. Sage for their comments on the manuscript. Supported by NSF grant GB 22995.

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EFFECT OF DRYING AND DESOLVENTIZING ON THE FUNCTIONAL PROPERTIES OF FISH PROTEIN CONCENTRATE (FPC)

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ABSTRACT

Experiments were performed to determine the effects of drying and steam desolventizing on the functional properties of fish protein concentrate (FPC). The FPC's were produced by a room temperature extraction of either red hake or menhaden with azeotropic isopropyl alcohol. FPC's thus produced contained about 36% soluble protein and, when dried at ambient temperature and pressure, showed very little loss in protein solubility. Drying the extracted wet solids at 40° to 50°, 60° to 70°, 90° to 100°, or 140° to 150°C for 30 or 120 min produced decreased protein solubility, i.e., 30.7% (40° to 50°C) to 12.5% (100° to 120°C). Emulsion stability of an FPC-water-oil system was satisfactory with all samples except those dried at 140° to 150°C.

Desolventizing dry solids or alcohol wet solids by steam stripping produced a dramatic loss in soluble protein and emulsion stability. There was also a significant darkening in color of the FPC's desolventized as wet solids as compared to FPC's desolventized as dry solids.

Food protein additives are used because of their nutritional and/or functional properties. Functional properties include solubility, dispersibility, water holding capacity, and emulsifying capacity (Johnson, 1969, 1970). FPC (fish protein concentrate) can have a range of functional properties depending upon the processing methods used. It is necessary, however, to control certain processing parameters in order to retain functionality.

Extraction of fish with IPA (isopropyl alcohol) at 20° to 30°C produces an FPC with better functional properties than extraction at 50°C (Dubrow, 1971). Similar results have been obtained by extracting chicken protein with IPA (Toledo, 1970).[2] Although low temperature extracted FPC retains a certain degree of protein solubility and emulsifying capacity, these properties may be lost during subsequent drying and desolventizing of the wet solids. Drying and desolventizing is necessary to reduce the residual IPA to 250 ppm to meet FDA (Food and Drug Administration) regulations (Federal Register, 1967). The purpose of the present studies, therefore, was to determine the effect of time and temperature of drying and desolventizing on the functional properties of FPC.

EXPERIMENT I: EFFECT OF TIME AND TEMPERATURE OF DRYING ON FUNCTIONAL PROPERTIES

MATERIALS AND METHODS

Preparation of Samples

Whole red hake (*Urophycis chuss*) were obtained from Block Island off the coast of Pt. Judith, R.I. They were iced on board the fishing vessel and then frozen at dockside. The extraction process consisted of a five-stage crosscurrent batch extraction at 22° to 27°C. The solvent to raw fish ratio was 2:1 w/w. Each

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Manuscript accepted July 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

extraction stage was limited to 10 to 15 min followed by centrifugation of the solids from liquid. Under these conditions of extraction, the residual lipid in the FPC is reduced to less than 0.5%. Approximately 10 lb. from the last stage centrifuged wet solids were used for drying experiments.

To dry the wet solids, approximately 454 g of wet solids were placed in an aluminum foil dish and spread evenly to a depth of about 6.5 mm. Thermocouples were inserted into the bed of solids for temperature recording. The sample was then placed into a vacuum oven and subjected to drying temperatures of (1) 40° to 50°C, (2) 60° to 70°C, (3) 90° to 100°C, (4) 110° to 120°C, or (5) 140° to 150°C for either 30 or 120 min. Residence time was from the time the sample reached temperature. The sample, after drying, was milled in a Wiley mill[3] and passed through a 40-mesh screen. The samples were then placed into polyethylene bags for storage and subsequent analysis. A control was dried overnight at ambient temperature and pressure.

Methods of Analysis

The following properties were determined:

Salt soluble protein.—Two grams of FPC were added to 50 ml of cold 5% NaCl (in 0.02 M $NaHCO_3$) and magnetically stirred for 3 hr (Dubrow, 1971). The slurry was filtered through Whatman #1 filter paper. The filtrate was analyzed for nitrogen by Kjeldahl method (Horwitz, 1965). Protein was calculated as N $\times$ 6.25.

Emulsion stability.—Two grams of FPC were blended (Waring blender, Model #1083) in a pint-size jar with 20 ml of 5% NaCl (in 0.02 M $NaHCO_3$) for 3 min at low speed. Twenty ml of corn oil were added to the blender and the entire mixture blended for 1.5 min at low speed. Ten ml portions of the mix were then poured into three graduated test tubes. The tubes were placed in a water bath (at about 98°C) for 30 min and were then cooled in an ice water bath. Since FPC is more lipophylic than hydrophylic, measurements were taken of the volume of water separated. If oil separated at the same time, measurements were also taken of this phase. Emulsion stability was calculated as the percentage of water (total) that separated from the system.

Residual isopropyl alcohol.—Residual IPA was determined according to the method of Smith and Brown (1969).

Total volatiles.—Total volatiles were determined by placing a weighed sample in a 103°C oven overnight; cooling in a dessicator and reweighing.

RESULTS AND DISCUSSION

Table 1 shows the results of drying temperature and time upon the protein solubility of the FPC solids. The wet solids, prior to drying, had about 36.6% soluble protein. In comparison, wet solids produced by extraction at 70° to 80°C prior to drying contained only 3% soluble protein. Drying overnight under ambient conditions resulted in very little loss in solubility (36.4%). Vacuum drying at 40° to 50°C showed a 15-18% decrease in soluble protein over the ambient dried sample. Variable and unexplainable results were obtained by drying at 60° to 70°C: the soluble nitrogen was less after 30 min drying than after 120 min. Increasing the drying temperature to 90° to 100°C or to 110° to 120°C produced a further decrease in protein solubility. Drying at 140° to 150°C resulted in about a 65% decrease in solubility from the starting wet solids.

The emulsifying stability of the dried FPC's produced under the various conditions of drying, showed that all treatments, except the FPC's dried at 140° to 150°C formed stable oil: water emulsions (Table 1). Separation of oil and water occurred with the FPC's dried at 140° to 150°C.

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

TABLE 1.—Effect of drying temperature and time on the salt soluble protein and emulsifying capacity of FPC.

Temperature	Time	Kjeldahl soluble nitrogen[1]	Soluble protein (N × 6.25)		Emulsifying capacity
°C	hr	mg N/ml	% dry wt	$\bar{x}$	% water separated
Wet solids	--	1.17 ± 0.08	36.56	36.56	
Ambient	16.0	2.10 ± 0.04	36.43	36.43	0
40-50	0.5	1.80 ± 0.08	31.33		0
	2.0	1.76 ± 0.08	29.99	30.66	0
60-70	0.5	1.44 ± 0.03	24.06		0
	2.0	1.81 ± 0.11	31.46	27.76	0
90-100	0.5	1.76 ± 0.09	28.92		0
	2.0	1.62 ± 0.10	26.88	27.90	0
110-120	0.5	1.31 ± 0.04	21.64		0
	2.0	1.29 ± 0.03	21.42	21.53	--
140-150	0.5	0.84 ± 0.01	13.55		100
	1.0	0.77 ± 0.01	12.19		100
	2.0	0.73 ± 0.02	11.70	12.48	100

[1] Mean ± standard deviation.

The effects of drying times and temperatures on the residual IPA and total volatiles are shown in Table 2. The sample of FPC dried overnight, under ambient conditions, had a residual IPA content of 2.0%. The samples dried at 40° to 50°C averaged 2.76% IPA; 60° to 70°C averaged 2.62%; 90° to 100°C averaged 2.53%; 110° to 120°C averaged 2.42%; and 140° to 150° averaged 1.45%. Retention of alcohol residues of about 1 to 2% has been obtained even under prolonged drying for up to 4 hr at 70° to 80°C.

TABLE 2.—Effect of drying temperature and time on the total volatile and residual isopropyl alcohol contents of FPC.

Temperature	Time	Total volatiles	Residual isopropyl alcohol[1]	
°C	hr	%	%	
Wet solids		50.00		
Ambient	16	9.94	2.00 ± 0.09	
40-50	0.5	10.25	2.47 ± 0.09	2.76
	2.0	8.30	3.05 ± 0.17	
60-70	0.5	6.50	2.85 ± 0.13	2.62
	2.0	10.10	2.40 ± 0.14	
90-100	0.5	4.90	2.75 ± 0.19	2.53
	2.0	5.85	2.32 ± 0.13	
110-120	0.5	5.40	2.55 ± 0.06	2.42
	2.0	5.90	2.30 ± 0.14	
140-150	0.5	3.20	1.50 ± 0.14	1.45
	2.0	2.45	1.40 ± 0.18	

[1] Mean ± standard deviation and mean of the two groups combined.

In general, the total volatile content of the FPC's ranged from 5 to 10% except those dried at 140° to 150°C, which contained from 2.4 to 3.2% volatiles.

EXPERIMENT II: EFFECT OF DESOLVENTIZING ON FUNCTIONAL PROPERTIES

The results obtained from the drying tests were used to set up the second phase—desolventizing. Thus, the solids dried at ambient temperatures, which yielded the least loss in protein solubility, were used to steam desolventize. Also, the effect of desolventizing wet solids was determined. In this phase, whole menhaden (*Brevoortia tyrannus*) were used for solvent extraction because previous observations had shown this species to be subject to greater color differences than red hake.

MATERIALS AND METHODS

Preparation of Samples

Twenty pounds of whole menhaden were extracted with IPA by the same manner as described for hake in Experiment I. After extraction, one-half of the wet solids were dried at ambient temperature and pressure overnight

and were then steam desolventized. The other half was desolventized as wet solids.

Desolventizing consisted of placing approximately 454 g of either wet solids or dry solids in an autoclave and steaming (exhaust vent open) at 2 to 3 psi for 0, 5, or 10 min. Time of exposure was determined from the time when the autoclave reached pressure, which took about 2 min. After stripping, the sample was dried overnight at ambient conditions and then milled through a 40-mesh screen.

Methods of Analysis

Tests for soluble protein, emulsion stability, residual IPA, and total volatiles were as reported in the experiments on drying. Color of the samples was determined by reflectance analysis (Dubrow, 1971), using a Beckman DB Spectrophotometer with reflectance attachment. Reflectograms were obtained by scanning from 700 mμ to 390 mμ.. Analysis of color was also determined on a Hunter Color Meter, Model D25.

RESULTS AND DISCUSSION

Desolventizing Wet Solids

Table 3 shows the effect of steam desolventizing wet solids on the salt soluble proteins, emulsion stability, color, residual IPA, and total volatiles.

The protein solubility of FPC's decreased from 32.3% in the nonsteamed solids to between 8.6 and 10.5% in the steamed solids. The loss in solubility occurred during the come-up period as evidenced by the low soluble protein content of the solids from the 0 min treatment.

The loss in protein solubility was also accompanied by a loss in emulsion stability. All treatments resulted in a separation of phases; emulsion, water, and solids. About 20 to 25% of the water separated from the mixture.

The effect of steaming to remove IPA showed that after 5 min the residual alcohol was less than 250 ppm, decreasing from 30,000 ppm at 0 min to 200 ppm after 5 min and to 75.5 ppm after 10 min. The total volatiles of the FPC's were 7.8%, 5.3%, and 4.9%, respectively.

Steam desolventization of wet solids changed the color of the FPC's. A significant darkening, from a grayish tan to a grayish brown, occurred in those samples steamed for 5 and 10 min. A reflectance spectra of the 0-min and 10-min treatments is shown in Figure 1. Hunter L, a, and b values are presented in Table 3.

Desolventizing Dry Solids

Table 3 also shows the effects of steam desolventizing dry solids on protein solubility, emulsion stability, color, residual IPA, and total volatiles. The initial protein solubility, prior to treatment, was 28.2%. Although steaming the FPC for 0 min did not result in any great loss in protein solubility, the 5-min and 10-min steamed samples showed about a 57% loss in

TABLE 3.—Effect of steam desolventizing FPC wet solids and FPC dry solids on the salt soluble protein, emulsifying capacity, color, and volatile content.

Sample	Time	Salt soluble protein	Emulsifying capacity	Color			Residual isopropyl alcohol	Total volatiles
				L	a	b		
	min	*% of dry wt*	*% water separated*				*ppm*	*%*
Wet solids:								
Nondesolventized	--	32.29	--	--	--	--	--	--
	0	9.49	[1]20.0	62.02	+0.30	+11.72	30,000	7.76
	5	8.57	[1]24.3	52.94	+0.35	+11.76	200	5.29
	10	10.52	[1]20.7	50.83	+0.71	+11.22	75.5	4.91
Dry solids:								
Nondesolventized	--	28.23	0.0	--	--	--	55,000	11.44
	0	26.70	0.0	65.65	−0.60	+10.75	24,500	6.38
	5	12.71	[1] 5.0	62.12	−0.07	+12.15	1,000	5.35
	10	10.68	[1]15.0	61.71	−0.08	+12.50	367	4.91

[1] Separation into three phases: water, solids, emulsion.

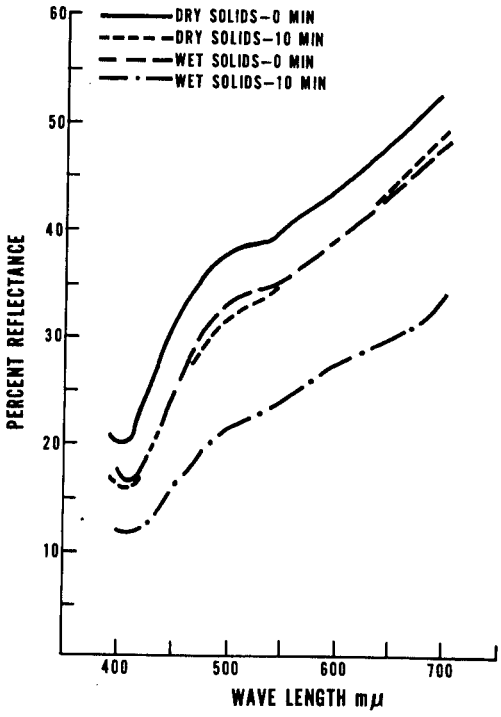

FIGURE 1.—Reflectance spectra of FPC's steam desolventized, as either dry solids or alcohol wet solids, at 2 to 3 psi for 0 or 10 min.

protein solubility as compared to the nonsteamed sample.

The emulsifying capacity and stability of the treated solids was affected in a manner similar to that for protein solubility. Both the nonsteamed and the 0-min treated samples of FPC's emulsified in oil and water systems. On the other hand, the solids steamed for 5 and 10 min showed a decrease in emulsion stability.

Steam desolventization of the dry solids reduced the residual IPA with each increment of exposure time. The initial residual content was 55,000 ppm, and after 10 min the level was found to be 367 ppm. The total volatiles of the treated solids ranged from 6.4% (0 min) to 4.9% (10 min).

The color of the FPC's after steaming showed only a slight darkening. The color changed from a grayish tan to a slight yellowish tan with respect to time of exposure. Hunter L, a, and b values are presented in Table 3. Figure 1 illustrates the reflectance spectra for the 0-min and 10-min FPC's and shows that the 10-min steamed dry solid sample was similar in its reflectance to the 0-min steamed wet solid sample; whereas the 0-min steamed dry solid was much lighter.

CONCLUSIONS

Two critical steps in the preparation of FPC by low temperature extraction with IPA are the drying and the desolventizing. Both stages involve heating: either dry or moist heat, or both. The results of this study showed that drying alcohol wet FPC solids at ambient conditions resulted in negligible loss in soluble protein and emulsifying capacity. Hot air drying of the wet solids, under vacuum, at temperatures ranging from 40° to 50°C to 110° to 120°C for 30 or 120 min resulted in a temperature dependent decrease in protein solubility. The dry FPC's, however, still retained emulsifying capacity. Under these drying conditions, the residual IPA was reduced to 2 to 3%. Higher drying temperatures of 140° to 150°C resulted in further loss of protein solubility and a complete loss in emulsifying capacity.

Removal of residual IPA, to a level of less than 250 ppm, by steam desolventization, was faster for wet solids than for dry solids. This procedure, however, brought about a 70% loss in protein solubility, a complete loss in emulsion stability, and a significant darkening of the product as compared to steam dry solids.

A similar loss in functionality, but at a slower rate and with less darkening of the FPC's, resulted from steaming dry solids.

Low temperature extraction coupled with low temperature drying produced FPC with greater functional properties than that produced by high temperature drying. To retain this functionality, methods other than steaming appear to be necessary.

ACKNOWLEDGMENT

The author wishes to extend his deepest appreciation to Thomas Brown for his valuable assistance in the course of this work.

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FISH LARVAE OF THE ESTUARIES AND COAST OF CENTRAL MAINE

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ABSTRACT

Seasonal sampling of fish larvae in the central Maine coast took 22 kinds of larvae; 17 were identified to species, 3 to family, and 2 were not identified. Larvae of a few highly abundant species were present in the winter and early spring. These hatched from demersal eggs and were concentrated in the upper estuaries. The remaining species were less abundant and were present during the spring and summer. Most of these larvae hatched from pelagic eggs and were not greatly concentrated in the upper estuaries. The larvae of only one commercially important species, *Clupea harengus harengus*, were found abundantly in the region.

There is little information on the species composition and abundance of larval fishes in the numerous estuaries and bays of the coast of Maine. During the past 10 years (1961-70) samples of larval herring have been taken in the central area of the Maine coast for a program of research on the prerecruit stage of the herring. In three of those years (1961, 1968, and 1970) other fish larvae also were identified. An examination of the first year's catch was reported by Graham and Boyar (1965). This paper reports on the 1968 and 1970 identifications and gives a more complete picture of the seasonal abundance and spatial distribution of the larvae; it also compares the results with surveys in other adjacent areas.

The area sampled is a system of drowned river valleys and bays typical of the Maine coast. It is bounded on the west by the Sheepscot estuary and on the east by the Damariscotta estuary, extends offshore approximately 4 miles to lat 43°45′N, and will be referred to in this report as the Boothbay region. The general ecology of the Sheepscot estuary was described by Stickney (1959), and the hydrography of the area was reported by Graham and Boyar (1965). The portion of the Sheepscot estuary sampled during this study is 14 miles long, has a drainage area of 148 square miles, varies from 20 to 60 m in depth, and is more typical of a long, narrow bay than an estuary. The portion of the Damariscotta estuary sampled is 11 miles long, has more freshwater dilution in its upper portion than the Sheepscot, and has a smaller drainage basin. The bay separating the two estuaries is a typical coastal indentation with relatively deep water, steep rocky shores, and very little freshwater dilution.

Other surveys of fish eggs and larvae from areas close to the coastal Gulf of Maine are pertinent to this study. Perlmutter (1939) and Wheatland (1956) identified the larvae from Long Island Sound, and Merriman and Sclar (1952) from Block Island Sound. Herman (1963) reported on the fish eggs and larvae of Narragansett Bay, R.I., and Pearcy and Richards (1962) on those of the Mystic River estuary, Conn. Marak and Colton (1961), Marak, Colton, and Foster (1962), and Marak, Colton, Foster, and Miller (1962) have reported for the offshore area of Georges Bank and the Gulf of Maine, and Fish and Johnson (1937) for the Gulf of Maine and Bay of Fundy.

METHODS

Eight stations were sampled twice a month from January through August 1968 and from November 1969 through October 1970 (Figure 1). Additional information was available from occasional sampling in 1971. The larvae were

[1] Northeast Fisheries Center, National Marine Fisheries Service, NOAA, West Boothbay Harbor, ME 04575.

Manuscript accepted June 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

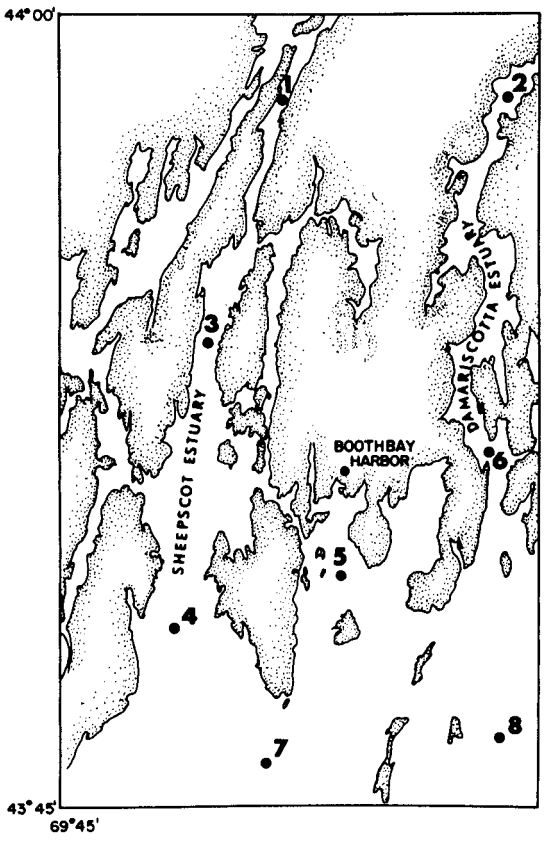

FIGURE 1.—Sampling stations in the Boothbay region, January through August 1968 and November 1969 through October 1970.

preserved in 5% Formalin[2] and identified in the laboratory. The stations were grouped according to general location within the sampling area and are termed upper estuarine stations (1, 2, and 3), lower estuarine stations (4, 5, and 6), and outer stations (7 and 8). The outer stations were approximately 4 miles from the headlands.

Larvae were collected with a Boothbay Depressor Trawl (Graham and Vaughan, 1966) using a 3-stepped oblique tow (10 min each level) from bottom to surface. The trawl was towed at 4 knots for 30 min. The amount of water strained was determined by using the opening of the net and the distance towed. The mesh opening of the trawl net (2 mm) was larger than that of the meter net (0.51 mm) used by Graham and Boyar (1965). Small larvae (<2 mm) probably escaped through the larger mesh, but the species composition of the larvae caught in both the Boothbay Depressor Trawl and meter net was similar.

Larval identification was based on known spawning time and on previously reported identifications. References used most often in identification were Colton and Marak (1969), Bigelow and Schroeder (1953), and Graham and Boyar (1965).

RESULTS

Twenty-two kinds of larvae were represented in the collections in the Boothbay region during January to August 1968 and November 1969 to October 1970 (Table 1); 17 kinds were identified to species, 3 to family, and 2 were not identified. All of the species were boreal with centers of abundance north of the mid-Atlantic coast, and many of the more abundant larvae do not occur south of New England. Most of the larvae, particularly the more abundant ones, hatch from demersal eggs.

SPECIES ABUNDANCE AND COMPOSITION

Larvae were most abundant during late winter to early spring (Figure 2). The dominant larvae at this time were *Pholis gunnellus, Liparis* sp., *Cryptacanthodes maculatus, Lumpenus lumpretaeformis,* and the Cottidae; they represented 91% of the total catch. In addition, *Anguilla rostrata* and a species of Gadidae (probably *Gadus morhua*) occurred in small numbers (0.1% and 0.01% of the total catch). The composition of the dominant kinds of larvae differed between years. The Cottidae was dominant in 1968 and *P. gunnellus* in 1970; *C. maculatus, L. lumpretaeformis,* and the *Liparis* sp. were more numerous in 1968 than in 1970.

Catches of larvae in the winter and early spring were large between February and April

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

TABLE 1.—Larval fish taken in the central Maine coast region January to August 1968 and November 1969 to October 1970.

Scientific name	Common name	Number of larvae		Egg deposition
		Jan.-Aug.	Nov.-Oct.	
Cottidae	Sculpins	6,222	4,053	Demersal
Pholis gunnellus (Linnaeus)	Rock gunnel	2,336	5,531	Demersal
Liparis sp.	Seasnail	1,610	106	Demersal
Anguilla rostrata (Lesueur)	American eel	19	11	Unknown
Cryptacanthodes maculatus Storer	Wrymouth	164	96	Unknown
Lumpenus lumpretaeformis (Walbaum)	Snakeblenny	328	225	Demersal
Gadidae	Codfishes	3	0	Pelagic
Aspidophoroides monopterygius (Bloch)	Alligatorfish	139	29	Unknown
Merluccius bilinearis (Mitchill)	Silver hake	0	4	Pelagic
Ammodytes americanus DeKay	American sand lance	0	2	Demersal
Sebastes marinus (Linnaeus)	Redfish	4	1	Ovoviviparous
Cyclopterus lumpus Linnaeus	Lumpfish	4	6	Demersal
Limanda ferruginea (Storer)	Yellowtail flounder	22	17	Pelagic
Osmerus mordax (Mitchill)	Rainbow smelt	12	0	Demersal
Syngnathus fuscus (Storer)	Northern pipefish	15	2	Oviparous
Scophthalmus aquosus (Mitchill)	Windowpane	23	8	Pelagic
Ulvaria subbifurcata (Storer)	Radiated shanny	127	82	Unknown
Enchelyopus cimbrius (Linnaeus)	Fourbeard rockling	21	3	Pelagic
Clupea harengus harengus Linnaeus	Atlantic herring	619	792	Demersal
Tautogolabrus adspersus (Walbaum)	Cunner	8	11	Pelagic
Species A		0	5	Unknown
Species B		117	22	Unknown

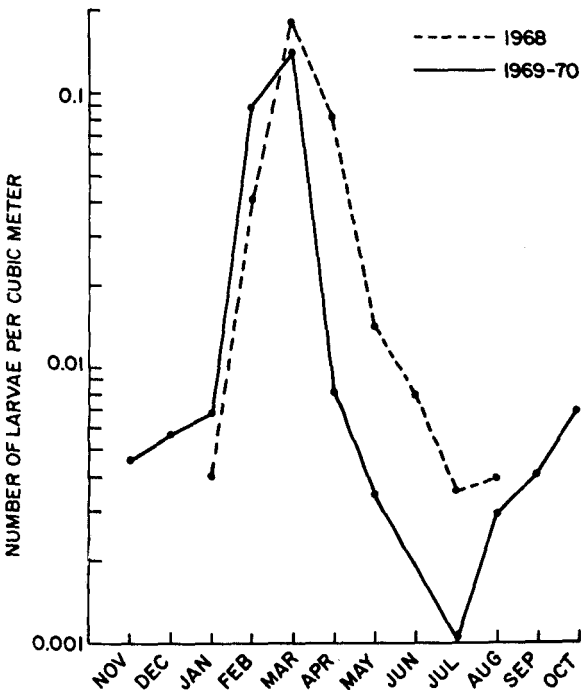

FIGURE 2.—Seasonal abundance of fish larvae in the Boothbay region, January through August 1968 and November 1969 through October 1970.

and largest during the first half of March. In both years the catches were similar. The average for the March peak was 0.18 per m³ in 1968 and 0.14 per m³ in 1970 and for the period between February and April, 0.08 per m³ in 1968 and 0.09 per m³ in 1970. The larvae were abundant longer in 1968 than in 1970; the large catches in 1968 extended into April and May.

In spring the numbers of larvae in the catch declined sharply with the end of the larval stage of the dominant species and continued gradually to decline to a low point in July and August. Most of the remaining larvae were taken in the spring and summer and, although fewer in numbers, more species were present. Species in this group were: *Aspidophoroides monopterygius, Merluccius bilinearis, Ammodytes americanus, Sebastes marinus, Cyclopterus lumpus, Limanda ferruginea, Osmerus mordax, Syngnathus fuscus, Scophthalmus aquosus, Ulvaria subbifurcata, Enchelyopus cimbrius, Tautogolabrus adspersus.* Of these, *U. subbifurcata* and *E. cimbrius* were obtained as larvae into the fall. *Clupea harengus harengus* hatched in September and October and was present in the area as larvae through May. The increased larval abundance in September and October was due to the hatching

of *Clupea harengus harengus* which was the only species abundant in the autumn.

The distribution of the larvae from offshore to the upper estuaries changed seasonally. Catches from the upper estuarine, lower estuarine, and outer stations (Figure 3) showed that the larvae in the winter and early spring were concentrated in the upper estuaries, while the larvae in the summer were more evenly distributed.

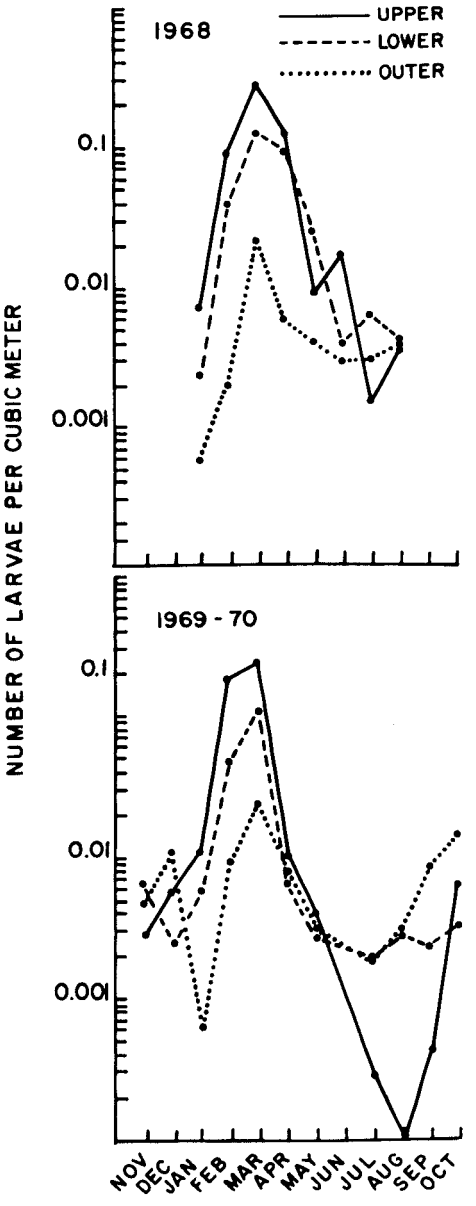

FIGURE 3.—The seasonal abundance of fish larvae in three areas of the Boothbay region; the upper estuary, the lower estuary, and outside the headlands.

The upper estuaries are probably important as nursery areas for the winter-early spring larvae. Most of this group were captured within the estuaries. From January to May the three upper stations contributed 68% of the catch in 1968 and 70% of the catch in 1970. Station 2 in the upper Damariscotta estuary produced the highest catches, accounting for 40% of all the larvae taken in 1968 and 65% in 1970. The distribution of the winter-early spring group of larvae was different within the estuaries between years. In 1968 the larvae were more evenly distributed among the upper stations than in 1970.

The seasonal abundance for each kind of larvae taken in the Boothbay region is shown in Figures 4 and 5. The more common kinds are discussed below.

Cottidae

Cottid larvae were present from January to July and their abundance reached a peak in March. Their distribution was upper estuarine and they were most abundant at station 2 (50% of all cottids in 1968, 74% in 1970). The total abundance of these larvae differed between years (6,222 in 1968 and 4,053 in 1970) because more cottids were taken at the other stations in 1968 (Figure 4A). Spawning probably occurred in the upper estuaries, inasmuch as cottids lay demersal eggs which do not drift, and yolk sac larvae were taken at the upper stations.

All cottid larvae were not identified to species, but Nuzrat Khan, Department of Biology, University of Ottawa, Ottawa, Canada (personal communication) recognized five species from 1,387 specimens of cottids that I sent to him. Of these, 689 were *Myoxocephalus scorpius;* 456, *Myoxocephalus octodecemspinosus;* 183, *Myoxocephalus aenaeus;* and 59, *Triglops* sp.

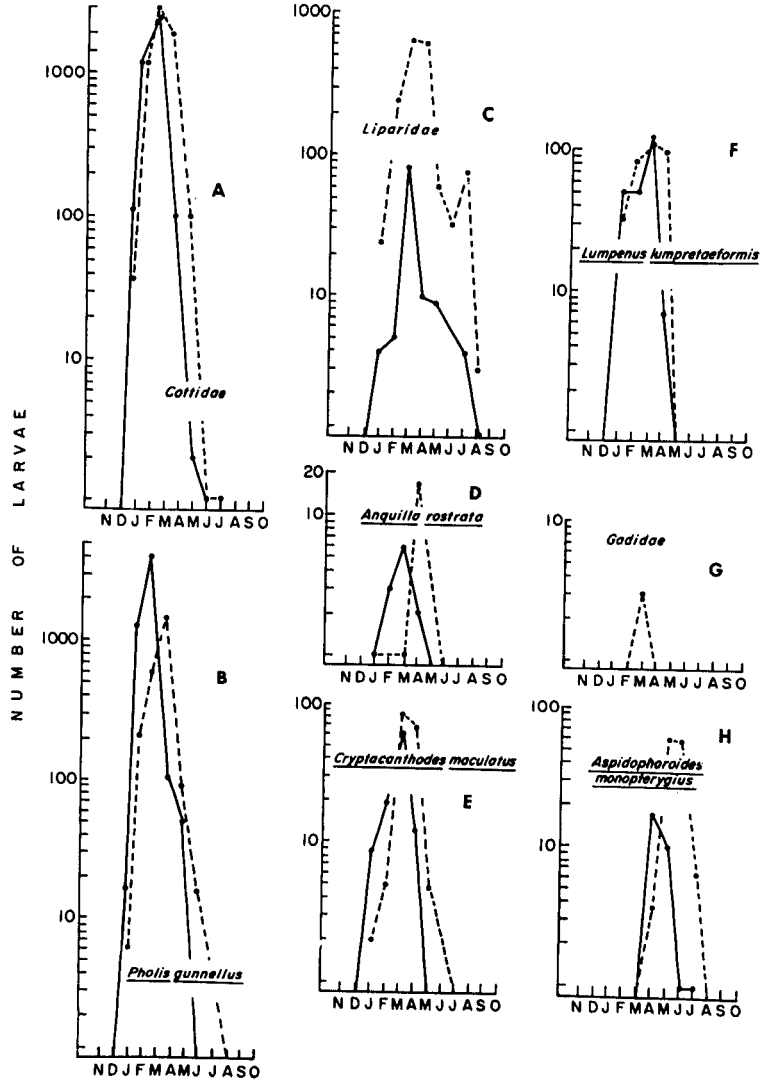

FIGURE 4.—Seasonal abundance of the following kinds of fish larvae in the Boothbay region, January through August 1968 and November 1969 through October 1970: A. Cottidae, B. *Pholis gunnellus*, C. Liparidae, D. *Anguilla rostrata*, E. *Cryptacanthodes maculatus*, F. *Lumpenus lumpretaeformis*, G. Gadidae, H. *Aspidophoroides monopterygius*.

Pholis gunnellus

The eggs of *P. gunnellus* are demersal, and yolk sac larvae were found in the upper estuaries during this study, suggesting that they were spawned there. The larvae appeared in the catches from January to July and reached peak abundance in February and March (Figure 4B). They represented 20% of the catch in 1968 and 50% of the catches in 1970. Their distribution was upper estuarine and, like cottids, they were most abundant at station 2 (28% of the catch in 1968 and 59% in 1970).

Liparis sp.

Liparid larvae were common in our catches in 1968 (14% of the catch) but less so in 1970 (1%) (Figure 4C). They probably spawn within the estuaries as they lay demersal eggs, and yolk sac larvae were found in the upper estuaries. The greatest number were taken in

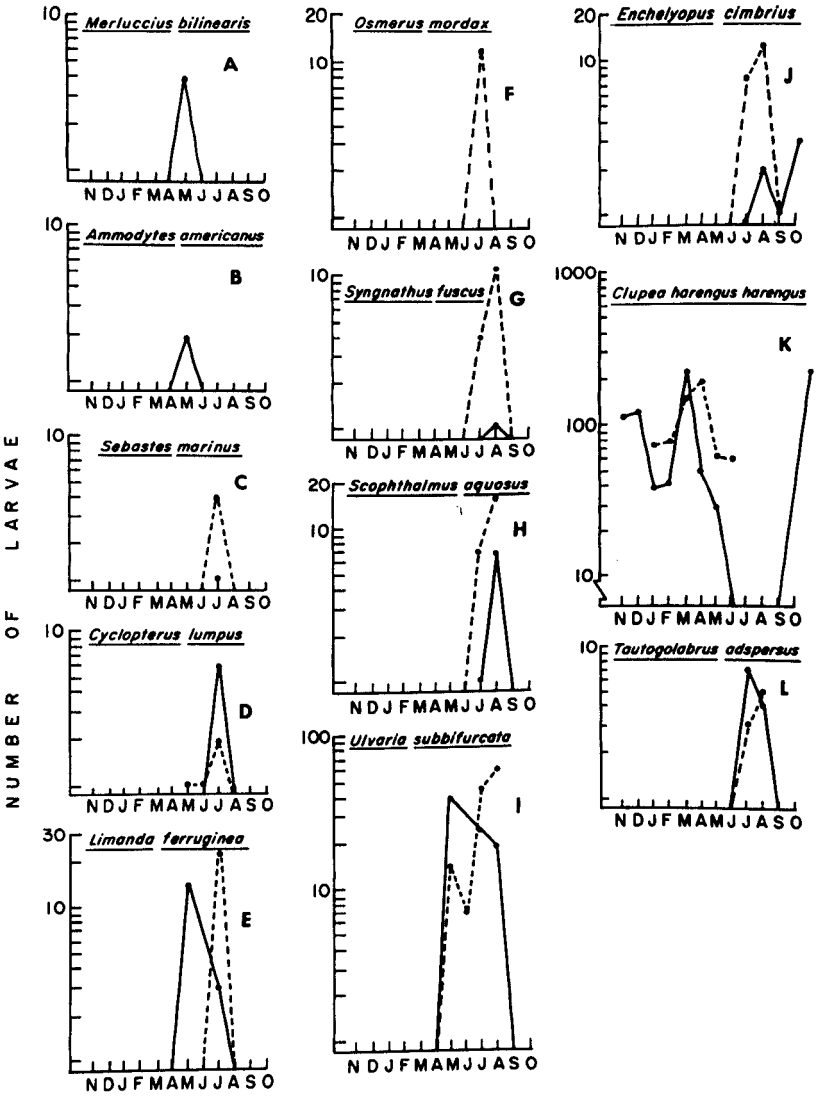

FIGURE 5.—Seasonal abundance of the following kinds of fish larvae in the Boothbay region, January through August 1968 and November 1969 through October 1970: A. *Merluccius bilinearis*, B. *Ammodytes americanus*, C. *Sebastes marinus*, D. *Cyclopterus lumpus*, E. *Limanda ferruginea*, F. *Osmerus mordax*, G. *Syngnathus fuscus*, H. *Scophthalmus aquosus*, I. *Ulvaria subbifurcata*, J. *Enchelyopus cimbrius*, K. *Clupea harengus harengus*, L. *Tautogolabrus adspersus*.

the upper estuaries, and the difference in abundance between years suggests that there was considerably less spawning in 1970 than 1968.

Lumpenus lumpretaeformis

L. lumpretaeformis probably spawns in the upper estuaries because yolk sac larvae were

found there and egg deposition, although not known, is probably demersal (it is for closely related forms). They were captured from January to April with a peak abundance in March (Figure 4F).

Aspidophoroides monopterygius

A. monopterygius larvae were abundant a little later than the winter-early spring group, ranging from April to July with a peak in April or May (Figure 4H). Their distribution was more lower estuarine than upper.

Ammodytes americanus and *Cyclopterus lumpus*

The larvae of *A. americanus* (Figure 5B) and *C. lumpus* (Figure 5D) were only rarely taken in this study but Graham and Boyar (1965) reported them abundant. However, these authors reexamined some of their specimens identified as *Cyclopterus lumpus* and *Ammodytes americanus* and found that most identified as *C. lumpus* were *Liparis* sp. and many identified as *A. americanus* were *Pholis gunnellus.*

Gadidae

Several kinds of gadids spawn in our sampling area. *Enchelyopus cimbrius* (Figure 5J) was one of the two dominant species from June until October in the lower estuaries and outer areas. A few larvae of *Merluccius bilinearis* (Figure 5A) were taken in May 1970. Three specimens of what was probably *Gadus morhua* (Figure 4G) were taken in March 1968. Subsequent sampling (1971) took a few more *G. morhua* in December as yolk sac larvae and also later stage larvae in February in the Sheepscot estuary.

Ulvaris subbifurcata

This was the other dominant species in the spring and summer (Figure 5I). It was present from April until September in the lower estuaries and outer areas.

Clupea harengus harengus

This is a pelagic species that lays demersal eggs and uses both the estuaries and bays as nursery areas during its larval stage from October to May (Figure 5K). It was the only commercially important species to do so and I would consider these areas important to the population density of the species.

Species A and B

At present we are attempting to identify these species. Species A is probably one of the Stichaeidae, possibly *Lumpenus maculatus.* Species B has been tentatively identified as *Hemitripterus americanus* but needs confirmation.

DISCUSSION

LARVAL NURSERY AREAS

Most of the fishes whose larvae were present in the Boothbay region may be placed in one of two groups: those that use the estuaries as primary spawning and nursery areas and those that do not.

The larvae found in the region during the winter and early spring (*Pholis gunnellus, Liparis* sp., *Cryptacanthodes maculatus* (Figure 4E), *Lumpenus lumpretaeformis,* and the Cottidae) belong to the first group. They were the most abundant species and their greatest concentration was in the upper estuaries. They are larvae of resident demersal fish that are not commercially important but are extremely abundant in the area. They use the bays and estuaries as nursery areas, depending to a large extent on these areas for their reproductive success. These species lay demersal eggs in the estuaries. Pearcy and Richards (1962) discussed the possibility that the larvae of demersal species in the Mystic River estuary maintained themselves there by concentrating in the counter currents near the bottom. The stepped oblique tow that was used in my study was not suitable for an analysis of the depth distribution of the larvae. The winter-early spring group of larvae,

however, were most abundant in the upper estuaries throughout their larval life, and therefore probably maintained themselves there by adapting to the circulation of water within the estuaries. These larvae disappeared from the catches very rapidly during April and May, which contributed to the rapidly declining spring catch. By this time they were approaching the juvenile stage and, being benthic fish, probably settled to the bottom and were not available to the sampling gear.

The remaining species (*Merluccius bilinearis, Sebastes marinus* (Figure 5C), *Cyclopterus lumpus, Limanda ferruginea* (Figure 5E), *Syngnathus fuscus, Scopthalmus aquosus* (Figure 5H), *Ulvaria subbifurcata, Enchelyopus cimbrius,* and *Tautogolabrus adspersus* (Figure 5L)) were present but not abundant in the spring and summer, suggesting that the estuaries were not their primary nursery areas. Possibly the numbers of spawning adults of these species were low in the bays and estuaries, or, as most of these species lay pelagic eggs, the eggs were dispersed before the larvae hatched.

Some species did not belong to either of the two above-mentioned groups: *Anguilla rostrata* (Figure 4D), a catadromous, and *Osmerus mordax* (Figure 5F), an anadromous species; *Aspidophoroides monopterygius,* which spawns later than the winter-early spring group, was not as common in the upper estuaries; *Ammodytes americanus*; and the Gadidae.

COMPARISON WITH OTHER AREAS OF THE NORTHWEST ATLANTIC

The results of surveys in other areas of the northwest Atlantic indicate the overall distribution of the three more abundant larvae of the Boothbay region. Cottid larvae occurred throughout the surveyed areas. *Myoxocephalus aenaeus* was dominant in the Mystic River estuary (Pearcy and Richards, 1962), Block Island Sound (Merriman and Sclar, 1952), and Long Island Sound (Wheatland, 1956); *M. octodecemspinosus* occurred in the offshore areas (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962); and *M. scorpius* occurred in the Gulf of Maine (Fish and Johnson, 1937) and appears from my survey to be dominant along the central Maine coast. The larvae of *Pholis gunnellus* appear to be more abundant in the estuaries than offshore. They were one of the most abundant species in the Mystic estuary (Pearcy and Richards, 1961) where they also concentrated in the upper estuaries. They were less abundant in the more open Narragansett Bay (Herman, 1963), rare offshore (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962), and absent from Long Island (Wheatland, 1956) or Block Island Sounds (Merriman and Sclar, 1952). Larvae of the Liparidae were taken in small numbers offshore (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962) and in the Gulf of Maine (Fish and Johnson, 1937) but not at all south of Cape Cod.

Pearcy and Richards (1962) found a dominant winter-early spring group of larvae in the Mystic estuary, but the more abundant species differed from those in the central Maine coast. The dominant species in the Mystic estuary were *Pseudopleuronectes americanus, Microgadus tomcod,* and *Myoxocephalus aenaeus.* In Narragansett Bay (Herman, 1963) the demersal winter-early spring group of larvae was less evident with only *Myoxocephalus* sp. dominant, and with many more pelagic forms. An abundance of pelagic forms might be expected in Narragansett Bay because the Bay is characteristically more like the open ocean than the smaller estuaries.

The spring and summer species of larvae were abundant enough in southern New England (Pearcy and Richards, 1962; Herman, 1963) to create a second summer peak in larval abundance that was absent in my survey of the Boothbay region. This was probably due to the absence of larvae of such species as *Stenotomus chrysops, Anchoa mitchilli, Cynoscion regalis,* and *Tautoga onitis* which have a more southern distribution and are only occasionally taken as adults along the Maine coast (Bigelow and Schroeder, 1953).

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EFFECTS OF TEMPERATURE AND SALINITY ON LARVAL DEVELOPMENT OF GRASS SHRIMP, *PALAEMONETES VULGARIS* (DECAPODA, CARIDEA)[1,2]

PAUL A. SANDIFER[3]

ABSTRACT

Larvae of *Palaemonetes vulgaris* were reared in the laboratory in a factorial experiment employing three temperatures (20°, 25°, and 30°C) and six salinities (5, 10, 15, 20, 25, and 30‰). Temperature and salinity exerted significant effects at the 1% level on survival of larvae through metamorphosis. The temperature-salinity interaction was also significant, but at the 5% level. Lowest survival occurred in 5‰ at all temperatures. In higher salinities, survival at 20° and 25°C was similar (>60%) but was significantly less at 30°C in most salinities. Temperature and salinity also influenced the rate of larval development. Development at 20°C required nearly twice the time as that at 25° and 30°C, but a retarding influence of salinity was slight and evident only at low salinities (5 and 10‰). Considerable variation in the number of larval instars was observed among animals which survived to the postlarval stage. Metamorphosis occurred as early as the fifth molt and as late as the twelfth. Salinity and temperature-salinity interaction had no detectable influence on the number of instars, but the effect of temperature was significant at the 1% level. Larvae reared at 25°C passed through fewer molts prior to metamorphosis than did those reared at 20° and 30°C. Comparing survival, rate of development and number of instars, optimal conditions for larval development occurred at a moderate temperature of about 25°C over a wide range of salinity (10 to 30‰).

The grass shrimp, *Palaemonetes vulgaris* (Say), ranges at least from Barnstable County, Mass., to Cameron County, Tex., (Williams, 1965) and is one of the most abundant estuarine decapods in this range. In the laboratory, Nagabhushanam (1961) found the species to be nearly euryhaline, tolerating salinities from 3 to 35‰. More recently, Bowler and Seidenberg (1971) found *P. vulgaris* to be less tolerant of low salinities (≤3‰) but more tolerant of high salinities (36 and 40‰) than its congener, *P. pugio*. In the York River, Va., these authors found that the percentage of the *Palaemonetes* population made up by *P. vulgaris* decreased markedly with decreasing salinity, and in North Carolina, Knowlton and Williams (1970) found *P. vulgaris* only in waters of 15 to 35‰ salinity.

Only Knowlton (1965, 1970) has studied the effects of temperature and salinity on *P. vulgaris* larvae, and his results were limited by the small number of experimental animals he used. The objectives of the present study were to determine the effects of temperature and salinity on survival and development of *P. vulgaris* larvae reared through metamorphosis in the laboratory.

MATERIALS AND METHODS

The experimental design was a 3 × 6 factorial using temperatures of 20°, 25°, and 30°C and salinities of 5, 10, 15, 20, 25, and 30‰. Test media were prepared by diluting seawater with

[1] Contribution No. 511 from the Virginia Institute of Marine Science, Gloucester Point, Va.

[2] This study was supported in part by the Sea Grant Program of the Virginia Institute of Marine Science, under contract GH67 from the National Oceanic and Atmospheric Administration, U.S. Department of Commerce. This paper is based on part of a dissertation to be presented to the Department of Marine Science, University of Virginia, in partial fulfillment of the requirements for the Doctor of Philosophy degree.

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Manuscript accepted May 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

distilled water, and temperature control baths were modified from Reed (1969). Each bath was equipped with a thermostat, two 125-w heaters, a maximum-minimum thermometer, and an air stone to circulate the water. A grate suspended in each bath supported the culture vessels. The baths were placed inside a cold room maintained at 11°C, where a 60-w bulb controlled by a timer provided 14 hr of light every 24 hr, approximately coincident with times of natural daylight. Although the temperature regimes are referred to above and throughout the paper as 20°, 25°, and 30°C, the observed temperatures (mean ± one standard deviation) were 20.3°C ± 0.7°C (range, 18.3° to 21.1°C), 25.4°C ± 1.0°C (range, 22.8° to 26.7°C), and 30.6°C ± 0.5°C (range, 29.4° to 31.7°C), respectively.

An ovigerous female was collected near Wachapreague, Va., on 12 June 1970. Salinity at the collection site was approximately 30‰. The shrimp was maintained in a glass bowl at 30‰ salinity and 25°C in the laboratory, and larvae were obtained on the day following collection. Active larvae were first placed in mass cultures at room temperature and fed newly hatched *Artemia* nauplii (California Brine Shrimp, Inc., Menlo Park, Calif.). Zoeae to be reared in 5, 10, and 15‰ salinity were acclimated in 15‰ for 4 hr, and those to be reared in higher salinities were maintained in 30‰ for 4 hr. Larvae were then transferred with a large-bore medicine dropper to test media in compartmented plastic boxes. Each box contained 18 compartments in rows of six, and one zoea in 50 ml of media was placed in every compartment. Three salinities were tested per box (i.e., each row of six compartments was a replicate of a particular temperature-salinity combination), and there were six boxes in each of the three water baths. Thus, there were three replicates (one in each of three boxes) of each temperature-salinity combination, and a total of 18 larvae was reared at each condition.

Larvae were transferred to clean boxes with fresh media and fed an abundance of newly hatched *Artemia* nauplii once daily. Molts, deaths, and maximum and minimum temperatures were recorded at this time. Mean temperatures and standard deviations were calculated from the maximum and minimum temperatures. The experiment was terminated after 40 days, when all survivors were in postlarval stages.

RESULTS

A detailed presentation of survival and developmental history of each larva reared in the present study is given in Appendix Table 1.

SURVIVAL

In general, survival was similar (>60%) at 20° and 25°C but was lower at 30°C in nearly all salinities. Survival in 5‰ salinity occurred only at 25°C, where 13 zoeae successfully completed the first molt, and two survived through metamorphosis; in contrast, at 20° and 30°C only two zoeae molted once, and none survived to molt again.

An analysis of variance on arcsin transformations (Steel and Torrie, 1960) of the percentage survival data showed differences in survival between temperatures and between salinities at the 1% level, and the temperature-salinity interaction was significant at the 5% level (Table 1). Student-Newman-Keuls' multiple range tests (Steel and Torrie, 1960) were used to explain the significant differences (Table 2). Perhaps the simplest way of looking at these differences in Table 2 is to compare survival in each salinity under each of the different temperatures, as is shown graphically in Figure 1. Thus, between 20° and 25°C there were significant differences in survival only in 5 and 30‰ salinity. Survival at 25°C, 5‰ was significantly greater than that at 20°C, 5‰, while at 20°C, 30‰ survival was significantly greater than at 25°C, 30‰. Comparing 20° and 30°C, survival at 20°C was significantly greater than that at 30°C in 10, 15, and 25‰. Finally, comparing 25° and 30°C, survival at 25°C was significantly greater than that at 30°C in 5, 10, 15, and 25‰. Highest overall percentage survival (88.9%) occurred at the combination 20°C, 20‰ (Table 2, Figure 1).

TABLE 1.—Analysis of variance for differences in survival of *Palaemonetes vulgaris* larvae through metamorphosis under different conditions of temperature and salinity.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*
Temperature	2	4,912.0345	2,456.0172	17.8613**
Salinity	5	21,212.5667	4,242.5133	30.8535**
Temperature × salinity	10	3,842.1588	384.2158	2.7941*
Error	36	4,950.1734	137.5048	
Total	53	34,916.9384		

** Significant at 1% level.
* Significant at 5% level.

TABLE 2.—Summary of Student-Newman-Keuls' multiple range tests to explain differences in survival of *Palaemonetes vulgaris* larvae at different temperature and salinity conditions.

Experimental conditions °C	Experimental conditions ‰	Mean (transformed % survival)	Means not overlapped by the same line are significantly different at the 1% level
30	5	0.0	
20	5	0.0	
25	5	16.1	
30	10	24.1	
30	15	31.5	
30	25	38.5	
25	30	52.0	
30	20	58.5	
30	30	58.5	
20	25	58.5	
25	10	62.2	
25	20	62.2	
20	30	65.9	
20	10	66.5	
25	25	67.0	
25	15	70.2	
20	15	70.2	
20	20	73.9	

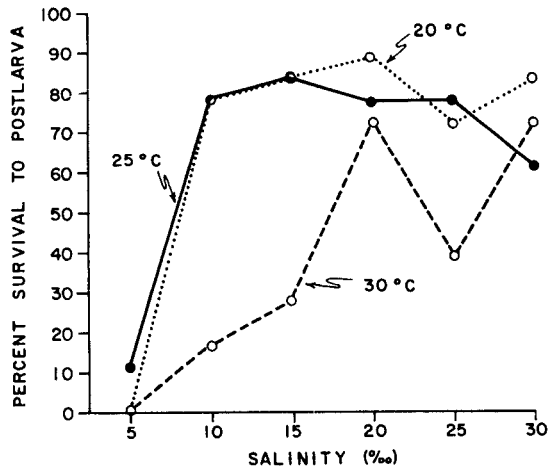

FIGURE 1.—Comparison of survival to postlarvae for *Palaemonetes vulgaris* zoeae reared at different temperatures and salinities.

RATE OF DEVELOPMENT

The effects of temperature and salinity (excluding 5‰) on the rate of larval development are shown in Figure 2. The effect of temperature was pronounced; development at 20°C was much slower than at 25° or 30°C. Mean duration of development (days) ± one standard deviation was 30.2 ± 3.8 (range, 23 to 39) at 20°C, 16.6 ± 2.7 (range, 14 to 25) at 25°C, and 15.7 ± 1.8 (range, 13 to 21) at 30°C. Salinity influenced the rate of development much less than did temperature. Survival in 5‰ salinity occurred only at 25°C, where the larvae in 5‰ generally required about 1 to 4 more days to pass a given stage than did larvae in higher salinities at the same temperature. Development in 10‰ also tended to be slightly slower than in higher salinities, regardless of the temperature (Figure 2). There was little apparent difference among developmental rates in 15 to 30‰. In general, a Q_{10} (20° and 30°C) of about 1.8 was typical of larval development.

Mean duration of instars (Table 3) was inversely related to temperature, reflecting developmental rate. Duration of successive instars tended to increase slightly at 20°C. The second instar was markedly short at 25° and 30°C, and the final instar was of longest duration at all temperatures. Overall mean instar duration (days) ± one standard deviation for animals which completed development was 3.6 ± 0.8 (range, 3 to 7) at 20°C, 2.2 ± 0.7 (range, 1 to 7) at 25°C, and 1.9 ± 0.6 (range, 1 to 4) at 30°C.

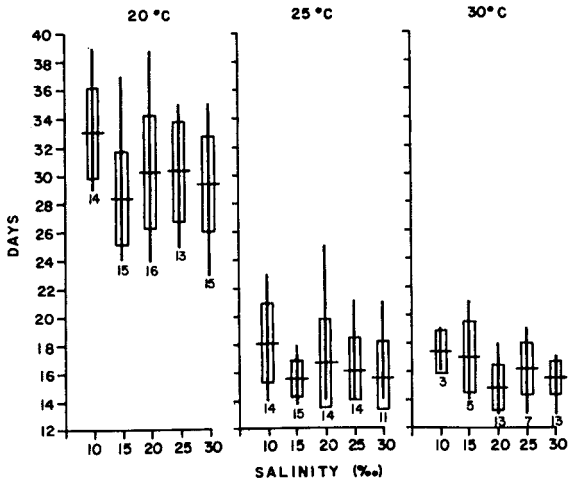

FIGURE 2.—Mean ± one standard deviation and range of days required for *Palaemonetes vulgaris* larvae to reach the postlarval stage at different temperatures and salinities (5‰ excluded) (numbers at the lower end of each range line indicate the number of animals which reached the postlarval stage at those conditions of temperature and salinity).

TABLE 3.—Mean duration (days) of *Palaemonetes vulgaris* larval instars at different temperatures. Final instar treated separately.

Instar	Temperature (°C)		
	20	25	30
	Days	*Days*	*Days*
I	3.0	2.0	2.0
II	3.1	1.4	1.0
III	3.1	2.0	1.2
IV	3.2	2.0	1.9
V	3.5	2.1	1.9
VI	3.8	2.1	2.0
VII	3.9	2.1	2.0
VIII	3.5	2.4	2.0
IX	3.7	[1]2.2	[1]1.8
X	[1]4	[1]2	--
XI	--	[1]2	--
Final	5.0	3.3	2.9

[1] Based on five or fewer larvae.

VARIATION IN NUMBER OF INSTARS

Most larvae metamorphosed at the 7th, 8th, or 9th molt, but there was much variation in number of instars. Metamorphosis occurred at the 5th through the 12th molts, and one zoea passed through 12 zoeal instars but never reached the postlarval stage.

The effects of temperature and salinity (excluding 5‰ because only two postlarvae were obtained there) on the number of larval stages are shown in Figures 3 and 4. Sample sizes were unequal, so an approximate method, the analysis of unweighted means (Snedecor, 1956) was employed to indicate significant effects (Table 4). The effect of salinity was not significant, although there appeared to be a slight tendency

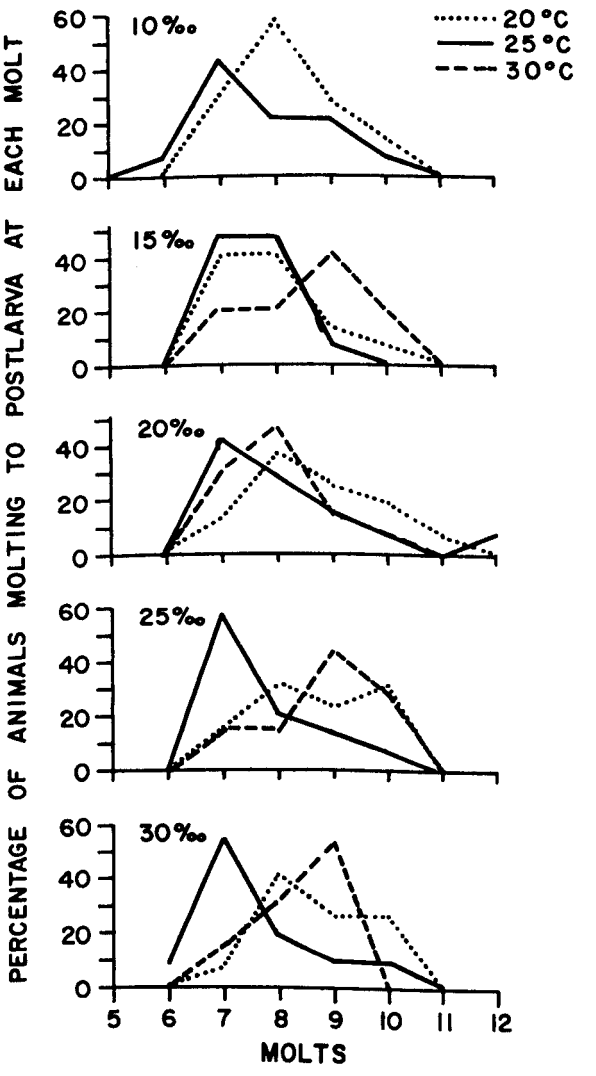

FIGURE 3.—Percentage of animals molting to postlarva at each molt under different conditions of temperature and salinity.

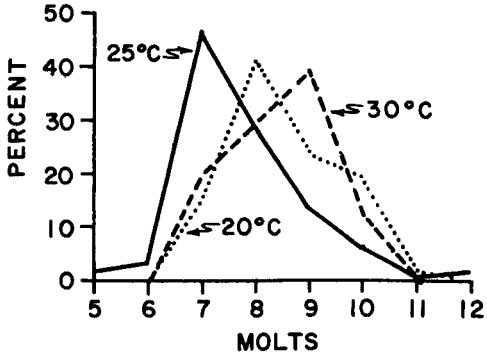

FIGURE 4.—Percentage of animals molting to postlarva at each molt under different temperatures.

for fewer instars in 15‰ than in other salinities. The temperature-salinity interaction also was not significant. However, the influence of temperature was significant at the 1% level, and mean numbers of instars ± one standard deviation were 8.5 ± 1.0 at 20°C, 7.8 ± 1.1 at 25°C, and 8.4 ± 1.0 at 30°C. A multiple mean test showed no difference between the mean numbers of larval instars passed at 20° and 30°C but indicated that animals reared at 25°C passed through significantly fewer instars in larval development.

DISCUSSION

Few previous studies have been concerned with the effects of temperature and salinity on *Palaemonetes* larvae. Sollaud (1919) reared larvae of *P. varians microgenitor* in the laboratory and found, as I did for *P. vulgaris*, that development was retarded at low temperatures and in low salinities and that more instars were passed at the lower than at the more moderate temperature tested. According to Broad and Hubschman (1962), development of larvae of *P. intermedius*, *P. pugio*, and *P. vulgaris* was unaffected by salinity above 20‰, but below 10‰ survival was poor. In the present study, survival in 5‰ was very poor, but in salinities of 10 to 30‰ at low and moderate temperatures (20° and 25°C), survival was high. More recently, Knowlton (1970) conducted a factorial experiment similar to mine, but he used only five larvae in each temperature-salinity combination. Knowlton (1970) found that at 20° and 25°C *P. vulgaris* larvae seemed to tolerate the entire range of salinity tested (15 to 35‰) equally well, with highest survival among larvae reared at 25°C. Lowest survival occurred among larvae reared at 30°C, where no larvae exposed to the low salinities (15 and 20‰) completed development. The results of the present study were fairly similar, except that some larvae survived through metamorphosis at 30°C in all salinities but 5‰. However, Knowlton's (1970) values for mean duration of larval life (37.3 ± 2.0 days at 20°C, 30.7 ± 2.0 days at 25°C, and 31.1 ± 4.3 days at 30°C) were considerably greater than corresponding values in the present study (30.2 ± 3.8 days, 16.6 ± 2.7 days, and 15.7 ± 1.8 days, respectively). Similarly, his values for mean instar duration were greater than values determined here.

The number of larval instars varied from 8 to 16 in Knowlton's (1970) study, while in the present study the observed range was 5 to 12. Knowlton (1965, 1970) also found that the number of larval instars increased with increasing

TABLE 4.—Summary of analysis of variance for differences in number of larval molts for *Palaemonetes vulgaris* larvae at different temperatures and salinities.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*
Total	14	4.0364		
Temperature	2	2.2770	1.1385	10.8017**
Salinity	4	0.5398	0.1349	1.2798 n.s.
Temperature × salinity	8	1.2196	0.1524	1.4459 n.s.
Error	[1]167		[1]0.1054	

** Significant at 1% level. n.s. Not significant.
[1] See Snedecor (1956) for computation of the error mean square in the method of unweighted means.

temperature. In contrast, larvae in my study passed through fewer instars at the moderate temperature (25°C) than at higher or lower temperatures, and at each temperature larvae required fewer molts to reach the postlarval stage in my study than in Knowlton's (1970). Similarly, Ewald (1969) found that *Tozeuma carolinense* larvae passed through fewer instars at 25°C than at 15° and 20°C. He also reported that there were marked differences in the numbers of instars among *T. carolinense* larvae from different populations. Perhaps a similar effect was partially responsible for differences between the numbers of *P. vulgaris* larval instars observed by Knowlton (1970) and by me.

The final zoeal instar was of greater duration than the other instars in both Knowlton's (1970) study and in mine, but the reason for the delay of this molt is not known. However, Hubschman (1963) reported that the X organ-sinus gland complex does not become functional as the primary molt regulator in *Palaemonetes* until after metamorphosis. He suggested that perhaps the rapid larval molting cycle was under the hormonal control of some type of larval molting gland, the existence of which remains speculative. The longer duration of the final zoeal instar thus may reflect transfer of control over molting from some unknown larval molt-regulating mechanism to the X organ-sinus gland complex, or breakdown of the larval regulatory mechanism prior to assumption of molt-regulating function by the X organ-sinus gland complex, or other internal reorganization prior to metamorphosis.

Because of the characteristic variability of temperature and salinity in estuaries, success of a particular decapod species may depend on the ability of the larvae to survive frequent exposure to suboptimal temperature-salinity conditions, to settle and/or metamorphose only under those conditions which are suitable for survival of the adult form, and to remain within, be carried into, or return to a given area to replenish the parental population. The number of larval instars may also be important, since ecdyses are critical periods in larval life, and highest mortality of cultured decapod larvae often occurs then (Ong, 1966; Knowlton, 1970; Roberts, 1971). Reduction of the number of premetamorphic molts thus may increase larval survival. So, considering survival, rate of development, and number of instars, it appears that optimal conditions for larval development of *P. vulgaris* occur at a moderate temperature of about 25°C in salinities of 10 to 30‰. Knowlton (1970) also concluded that a temperature of 25°C was optimal over the salinity range tested (15 to 35‰) in his experiment.

ACKNOWLEDGMENTS

I would like to thank my graduate committee (Drs. G. C. Grant, W. G. MacIntyre, W. C. Pinschmidt, Jr., and M. L. Wass, and especially Mr. W. A. Van Engel, Chairman) and my wife, Betty, for constant help and encouragement, and Drs. M. E. Chittenden and J. Loesch for advice regarding the design and analysis of the experiment and for critical review of the manuscript. I was the recipient of a National Defense Education Act Title IV Graduate Fellowship during the study.

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APPENDIX TABLE 1.--Comparison of survival and developmental rates of *Palaemonetes vulgaris* larvae reared at different temperatures and salinities.

Temperature (°C)	Salinity (°/oo)	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range
		Molt No. 1 Zoea I to zoea II				Molt No. 2 Zoea II to zoea III				Molt No. 3 Zoea III to zoea IV				Molt No. 4 Zoea IV to zoea V			
20	5	11.1	2	4.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	100.0	18	3.0	--	100.0	18	6.5	6-9	88.9	16	9.8	9-12	88.9	16	13.5	12-16
	15	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.1	9-10	100.0	18	12.3	12-17
	20	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
	25	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
	30	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
25	5	72.3	13	2.8	2-7	27.8	5	6.2	4-9	22.2	4	9.8	8-13	22.2	4	11.8	10-15
	10	100.0	18	2.0	--	100.0	18	3.8	3-4	100.0	18	5.8	4-6	100.0	18	7.8	7-8
	15	100.0	18	2.0	--	100.0	18	3.1	3-4	100.0	18	5.1	5-6	100.0	18	7.1	7-8
	20	100.0	18	2.0	--	100.0	18	3.2	3-5	100.0	18	5.2	5-7	100.0	18	7.2	7-9
	25	100.0	18	2.0	--	100.0	18	3.4	3-4	100.0	18	5.3	5-6	100.0	18	7.3	7-8
	30	100.0	18	2.0	--	100.0	18	3.3	3-4	100.0	18	5.3	5-6	88.9	16	7.3	7-9
30	5	11.1	2	2.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.9	4-5	94.5	17	6.9	6-7
	15	94.5	18	2.0	--	88.9	16	3.0	--	83.4	15	4.3	4-5	83.4	15	6.3	6-7
	20	100.0	18	2.0	--	100.0	18	3.0	--	94.5	17	4.1	4-5	94.5	17	6.1	6-7
	25	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.2	4-5	100.0	18	6.1	6-7
	30	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.2	4-5	94.5	17	6.0	--
		Molt No. 5 Zoea V to zoea VI				Zoea V to postlarva				Molt No. 6 Zoea VI to zoea VII				Zoea VI to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	88.9	16	17.4	16-20	0.0	0	--	--	83.4	15	21.4	20-25	0.0	0	--	--
	15	100.0	18	16.2	15-21	0.0	0	--	--	94.5	17	20.1	18-25	0.0	0	--	--
	20	100.0	18	15.4	15-19	0.0	0	--	--	94.5	17	19.1	18-23	0.0	0	--	--
	25	100.0	18	15.2	15-16	0.0	0	--	--	94.5	17	19.1	18-20	0.0	0	--	--
	30	100.0	18	15.1	15-16	0.0	0	--	--	100.0	18	18.7	18-19	0.0	0	--	--
25	5	16.7	3	12.7	12-13	5.6	1	22.0	--	16.7	3	14.7	14-15	0.0	0	--	--
	10	100.0	18	10.0	9-11	0.0	0	--	--	94.5	17	12.4	11-13	5.6	1	15.0	--
	15	100.0	18	9.2	9-10	0.0	0	--	--	100.0	18	11.2	11-12	0.0	0	--	--
	20	100.0	18	9.2	9-11	0.0	0	--	--	94.5	17	11.1	11-12	0.0	0	--	--
	25	94.5	17	9.4	9-10	0.0	0	--	--	94.5	17	11.5	11-13	0.0	0	--	--
	30	88.9	16	9.3	9-11	0.0	0	--	--	83.4	15	11.2	11-12	5.6	1	15.0	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	94.5	17	9.0	8-11	0.0	0	--	--	66.7	12	10.8	9-11	0.0	0	--	--
	15	66.7	12	8.3	8-9	0.0	0	--	--	55.6	10	10.6	10-11	0.0	0	--	--
	20	88.9	16	8.1	8-9	0.0	0	--	--	83.4	15	10.0	9-11	0.0	0	--	--
	25	100.0	18	7.9	7-9	0.0	0	--	--	94.5	17	9.9	9-11	0.0	0	--	--
	30	94.5	17	7.7	7-8	0.0	0	--	--	88.9	16	9.7	9-10	0.0	0	--	--
		Molt No. 7 Zoea VII to zoea VIII				Zoea VII to postlarva				Molt No. 8 Zoea VIII to zoea IX				Zoea VIII to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	83.4	15	25.4	24-29	0.0	0	--	--	38.9	7	29.0	28-30	44.5	8	30.9	29-35
	15	50.0	9	23.3	23-24	33.4	6	26.7	24-30	16.7	3	27.3	27-28	33.4	6	28.3	27-30
	20	83.4	15	22.8	22-24	11.1	2	26.0	24-28	44.5	8	26.4	25-27	33.4	6	27.5	27-28
	25	83.4	15	22.9	22-24	11.1	2	25.5	25-26	50.0	9	26.6	25-28	22.2	4	27.5	27-28
	30	94.5	17	22.1	21-23	5.6	1	23.0	--	55.6	10	25.3	24-27	33.4	6	27.2	26-28
25	5	5.6	1	18.0	--	0.0	0	--	--	0.0	0	--	--	5.6	1	21.0	--
	10	50.0	9	14.7	14-16	33.4	6	16.3	14-17	27.8	5	17.4	16-18	16.7	3	17.3	17-18
	15	50.0	9	13.3	13-14	38.9	7	14.6	14-15	5.6	1	15.0	--	38.9	7	17.0	16-18
	20	55.6	10	13.5	13-16	33.4	6	14.0	--	22.2	4	15.3	15-16	22.2	4	16.8	16-17
	25	50.0	9	13.8	13-16	44.5	8	14.8	14-16	33.4	6	16.2	15-18	16.7	3	16.0	--
	30	27.8	5	13.4	13-14	33.4	6	14.2	14-15	16.7	3	16.0	--	11.1	2	16.5	16-17
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	61.2	11	12.9	12-15	0.0	0	--	--	44.5	8	14.6	13-15	0.0	0	--	--
	15	33.4	6	12.7	12-14	5.6	1	15.0	--	22.2	4	14.5	14-16	5.6	1	16.0	--
	20	55.6	10	11.9	11-13	22.2	4	13.0	--	16.7	3	14.0	--	33.4	6	15.0	14-16
	25	66.7	12	11.8	11-13	5.6	1	13.0	--	38.9	7	13.6	13-14	5.6	1	15.0	--
	30	77.8	14	11.6	10-12	11.1	2	13.5	13-14	44.5	8	13.3	12-14	22.2	4	15.3	15-16

APPENDIX TABLE 1.--Comparison of survival and developmental rates of *Palaemonetes vulgaris* larvae reared at different temperatures and salinities.--Continued.

Temperature (°C)	Salinity (°/oo)	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range
		Molt No. 9								Molt No. 10							
		Zoea IX to zoea X				Zoea IX to postlarva				Zoea X to zoea XI				Zoea X to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	11.1	2	33.0	32-34	22.2	4	34.8	33-36	0.0	0	--	--	11.1	2	38.0	37-39
	15	5.6	1	32.0	--	11.1	2	32.0	--	0.0	0	--	--	5.6	1	37.0	--
	20	22.2	4	30.8	30-31	22.2	4	30.8	30-32	5.6	1	34.0	--	16.7	3	35.0	34-36
	25	27.8	5	29.6	28-31	16.7	3	32.3	31-33	5.6	1	35.0	--	22.2	4	34.0	32-35
	30	27.8	5	28.4	27-29	22.2	4	29.5	28-31	0.0	0	--	--	22.2	4	33.0	31-34
25	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	5.6	1	19.0	--	16.7	3	21.7	20-23	0.0	0	--	--	5.6	1	23.0	--
	15	0.0	0	--	--	5.6	1	18.0	--	0.0	0	--	--	0.0	0	--	--
	20	11.1	2	17.0	--	11.1	2	18.5	18-19	5.6	1	19.0	--	5.6	1	20.0	--
	25	16.7	3	18.7	17-20	11.1	2	19.5	18-21	5.6	1	23.0	--	5.6	1	20.0	--
	30	11.1	2	18.0	--	5.6	1	19.0	--	5.6	1	21.0	--	5.6	1	21.0	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	16.7	3	16.7	16-17	11.1	2	16.5	16-17	5.6	1	19.0	--	5.6	1	19.0	--
	15	11.1	2	17.0	16-18	11.1	2	17.0	--	0.0	0	--	--	5.6	1	21.0	--
	20	5.6	1	16.0	--	11.1	2	16.5	16-17	0.0	0	--	--	5.6	1	18.0	--
	25	11.1	2	15.5	15-16	16.7	3	16.3	16-17	0.0	0	--	--	11.1	2	18.0	17-19
	30	5.6	1	15.0	--	38.9	7	16.3	15-17	0.0	0	--	--	0.0	0	--	--
		Molt No. 11								Molt No. 12							
		Zoea XI to zoea XII				Zoea XI to postlarva				Zoea XII to zoea XIII				Zoea XII to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	0.0	0	--	--	5.6	1	39.0	--	0.0	0	--	--	0.0	0	--	--
	25	5.6	1	39.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
25	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	5.6	1	21.0	--	0.0	0	--	--	0.0	0	--	--	5.6	1	25.0	--
	25	5.6	1	26.0	--	0.0	0	--	--	5.6	1	28.0	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	25	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--

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ERYTHROCYTE DEGENERATION IN THE ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS* L.

STUART W. SHERBURNE[1]

ABSTRACT

Cytoplasmic inclusions, associated with erythrocytic degeneration, were found in the circulating blood of herring from Boothbay Harbor, Maine, and from Passamaquoddy Bay at Deer Island, N.B., Canada, in 1969. Except in one instance, when inclusions occurred in herring from water of 2°C, all herring from Boothbay Harbor having inclusions were taken from seawater temperatures of 13.8°C or above. A relationship appears to exist between inclusions in herring erythrocytes and stress factors, especially temperature extremes. At a temperature of 16°C, 96% of a sample of herring were affected with inclusions. Herring sampled at the highest temperature (16°C) were markedly different from all other samples in their blood morphology and had the highest incidence of inclusions. Inclusions were found in the Passamaquoddy Bay area in 2 of the 50 herring sampled from a seawater temperature of 9.8°C, the highest temperature sampled in that area.

Inclusions rarely occurred more than one to a red cell and varied in size from 1.3 to 3.9 μ. In herring containing a high incidence of inclusions, the larger inclusions were usually in the youngest red cells. Cells containing inclusions generally appeared rounded and swollen. Either an abnormally high percentage of up to 90% immature red cells or a low of 1 to 5% immature red cells generally characterized herring containing inclusions.

The blood of herring has been studied at the National Marine Fisheries Service Laboratory at Boothbay Harbor to find physiological indicators of environmental stress that may help us to determine causes of fluctuations in success of year classes. During this investigation I observed inclusion bodies in the cytoplasm of the red cells in many of the herring. In this report I describe these inclusion bodies, their incidence, and the abnormal blood cell morphology associated with these bodies.

Nonspecific cytoplasmic inclusions have been reported in *Fundulus* sp. (Gardner and Yevich, 1969) occurring in wet smears in May and July prior to, and at the beginning of the new breeding season, but not evident in fixed smears. The cytoplasm of erythrocytes from chinook salmon, *Oncorhynchus tshawytscha,* sockeye salmon, *Oncorhynchus nerka,* and adult rainbow trout, *Salmo gairdneri,* contained granular material following fixation procedures (Ridgway, 1956) that the author thought were of mitochondrial origin.

Laird and Bullock (1969) reported finding a distinctive inclusion body formed in the cytoplasm of infected cells associated with piscine erythrocytic necrosis which is responsible for massive red blood cell destruction in *Gadus morhua* from Passamaquoddy Bay. *Liparis atlanticus* from Kent Island, N.B., Canada, and *Myoxocephalus octodecemspinosus* from Portsmouth Harbor, N.H. were lightly infected.

MATERIALS AND METHODS

The 355 herring examined in this study from February through October 1969 consisted of 201 wild herring and 154 captive herring in 12 samples. The herring ranged in length from 12.5 to 30.4 cm and in weight from 10.6 to 214.5 g. The wild herring were taken from four fishermen's catches between central Maine and Canada. Three categories of herring are considered

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Manuscript accepted August 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

in this report: 1) long-term captive herring held 6 months before sampling began in February and terminated in June when the supply of test fish was exhausted, 2) short-term captives which consisted of herring held 2 weeks before being bled, and 3) wild herring that were taken when available. The captive herring were held in seawater which was pumped from the ocean through the tanks and which approximated the temperature of natural seawater. The water temperature was recorded at the site of capture in each instance.

A blood sample was taken from the heart of each herring and preserved in a modified Alsever's solution for serological studies; a microhematocrit was determined and a morphology slide made for each herring. The herring were measured for total length, weighed, sexed, marked, and frozen for reference. All herring were examined for gross parasitism.

The hematocrits and morphology slides were made of blood taken by direct heart puncture with a heparinized 75 mm × 1.3-1.5 mm outside diameter capillary tube. A small drop of blood from the tube was placed on a microscope slide, the tube sealed with plastic clay, and the smear made. The tubes were centrifuged in a microhematocrit centrifuge for 3½ min at 11,000 rpm and read in a microcapillary reader. Slides were air-dried and stained by either the Wright's or Wright-Giemsa staining method. Distilled water was used as a diluent for the Wright's and Giemsa stains. Cells were examined under oil immersion and photographed at 800 and 1250 powers. Hematocrits were measured as the volume percent of packed red cells to the total blood column. (The term "hematocrit" is used in this paper, although Widmark (1970) has suggested the term be replaced with "packed cell volume").

I classify herring erythrocytes according to the stage of development in the peripheral blood as erythroblasts, early polychromatics, middle polychromatics, late polychromatics or mature cells, depending upon their size and the amount of polychromasia present. These stages are described in Table 1. Reticulocytes cannot be identified readily without vital staining so are not included in Table 1. There are variations in individual herring in the size and shape between and within cell stages and the amount of polychromasia present is the best indicator as to the series to which the cell belongs.

RESULTS

The sample source, date of sampling, incidence of inclusion bodies, mean length, standard deviation and range in lengths, mean weight,

TABLE 1.—The developmental stages and the average size of erythrocytes in the peripheral blood of wild herring.

Stage	Description	Cell measurements[1] (microns)	
		Cytosome	Nucleus
Erythroblast	Round, slightly larger cell than the early polychromatic. Has a dark blue staining cytoplasm with lightly stained spaces. The round purple-red staining nucleus takes up most of the cell. Erythroblasts are scarce in normal samples.	7.8 × 7.3	5.9 × 6.2
Early polychromatic	The smallest immature red cell that is normally seen in any quantity. Has a light blue to gray staining cytoplasm and appears round. The nucleus takes up most of the cell.	7.8 × 7.1	4.6 × 3.3
Middle polychromatic	Round to slightly oval cell with a gray to light gray-orange staining cytoplasm. Cell is larger than the early polychromatic.	9.5 × 7.0	4.8 × 3.0
Late polychromatic	Slightly oval, has a larger cytoplasm and a smaller nucleus than the middle polychromatic. The cytoplasm appears light orange-yellow.	10.0 × 7.7	4.6 × 2.9
Mature erythrocyte	Oval, has a slightly larger cytoplasm and a slightly smaller nucleus than the late polychromatic. The cytoplasm appears orange-yellow to reddish. Late polychromatic and mature cells have essentially the same appearance with Wright's stain.	10.3 × 7.7	4.2 × 2.8

[1] Measurements based on 25 cells in each stage from a normal wild herring in March.

TABLE 2.—The occurrence of inclusion bodies in the cytoplasm of herring erythrocytes, 25 February-30 October 1969.

Sample source and category[1]	Date	Incidence in sample	Percent incidence	Water temp. (°C)	Mean length, SD, and range of sample (cm)	Mean weight, SD and range of sample (g)
Long-term captives	25 Feb.	0/25	0.0	1.3	15.3 ± 0.79(14.0-17.2)	20.2 ± 4.3(14.1- 29.0)
Wild, Sheepscot River, Boothbay Harbor	13 Mar.	1/35	2.9	2.0	16.4 ± 2.0 (13.5-19.0)	26.2 ± 9.7(14.0- 42.0)
Long-term captives	24 Mar.	0/25	0.0	3.3	16.0 ± 0.99(13.2-17.5)	20.7 ± 4.5(10.6- 29.4)
Long-term captives	21 Apr.	0/20	0.0	4.9	16.3 ± 0.99(14.3-17.7)	23.0 ± 5.0(14.9- 33.1)
Wild, Eastport, Maine	10 June	0/40	0.0	7.7	22.2 ± 3.0 (14.5-30.4)	80.3 ± 41.3(18.0-214.5)
Long-term captives	23 June	2/12	16.7	15.2	16.2 ± 1.4 (13.1-18.0)	22.8 ± 5.8(14.1- 34.7)
Wild, Spruce Point, Boothbay Harbor	8 July	5/76	6.6	13.8	15.5 ± 1.4 (12.5-18.5)	23.7 ± 6.6(12.8- 43.4)
Wild, Deer Island, N.B., Canada	16 July	2/50	4.0	9.8	21.0 ± 1.9 (13.9-25.2)	81.0 ± 21.1(13.6-133.0)
Short-term captives	22 July	24/25	96.0	16.0	16.0 ± 1.2 (14.4-18.0)	25.3 ± 5.7(17.6- 36.4)
Short-term captives	21 Aug.	3/25	12.0	14.0	16.1 ± 1.3 (13.2-18.6)	22.1 ± 6.2(11.7- 40.9)
Short-term captives	25 Aug.	0/10	0.0	15.5	17.7 ± 1.2 (15.3-20.0)	29.9 ± 7.4(18.5- 48.1)
Short term captives	30 Oct.	0/12	0.0	9.2	16.2 ± 1.1 (15.1-19.0)	20.6 ± 4.2(16.3- 27.6)

[1] Long-term captives—Boothbay Harbor herring held 6 months before being bled.
Short-term captives—herring from wild 8 July sample held 2 weeks before being bled.

and standard deviation and range in weights of all herring included in this study are given in Table 2.

DESCRIPTION OF INCLUSION BODIES

The inclusions are round, granular, intracytoplasmic and appear acidophilic with Wright's stain. The inclusions generally occur singly in the affected cells and vary in size with the largest inclusions usually in the youngest cells. A few red cells contained two inclusions. The bodies characteristically range in size from 2.3 to 3.3 μ in early polychromatics, 1.7 to 1.9 μ in middle polychromatics, and 1.3 to 1.6 μ in late polychromatics and mature erythrocytes. The inclusions vary from bright red to reddish-purple in contrast with the blue-gray cytoplasm of the young cells and the dull orange-yellow cytoplasm of the mature cells. Many inclusions have a dark-purple periphery with a light central zone; other inclusions are the same color throughout. Some of the larger inclusions appear to have at least four small, dense-staining particles within or along the periphery of the inclusion.

Inclusions were not found outside the red cells, nor were inclusions observed in any white cells of the 355 herring examined in this study.

MORPHOLOGY

Wild herring that did not contain inclusions ranged from 3 to 35% with an average of 20% immature erythrocytes, while captive herring without inclusions ranged from 2 to 25% with an average of 14% immature erythrocytes in their peripheral blood.

Two types of morphology usually characterized the blood of herring that contained inclusions: either upward to 90% immature red cells or a low of 1 to 5% immature red cells. The single herring with inclusions in March had the highest percentage of immature erythrocytes I had found in wild herring to that date. Eighty percent of the red cells were immature, with 12% of the immature and 90% of the mature cells affected with inclusions. Erythroblasts, rare in a normal blood sample, were abundant on this slide. The inclusions occurred singly in the cytoplasm and varied in size; the largest were in the youngest cells. The bodies ranged in size from 2.3 to 3.1 μ in early polychromatics, 1.7 to 1.9 μ in middle polychromatics, and 1.3 to 1.6 μ in late polychromatics and mature erythrocytes. The nucleus of the affected cells exhibited vacuolization and pyknosis. Abnormally large immature red cells (macrocytes) were evident with atypical cells present in all developmental stages (Figure 1). The remaining 34 herring in the sample had normal red cell morphology (Figure 2).

Inclusions first appeared in long-term captive herring in June in 2 out of 12 specimens. These two herring had the lowest hematocrits of the sample. The blood morphology of the two affected herring differed. One herring had 60%

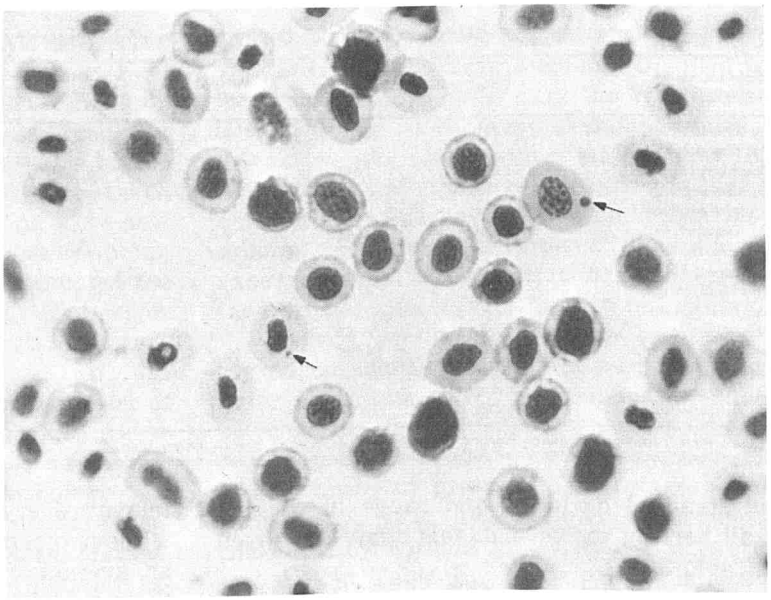

FIGURE 1.—13 March 1969. Photomicrograph of wild herring blood showing macrocytosis of the young cells. Early polychromatics are prevalent. Arrows point to an inclusion in a middle polychromatic and in a mature red cell.

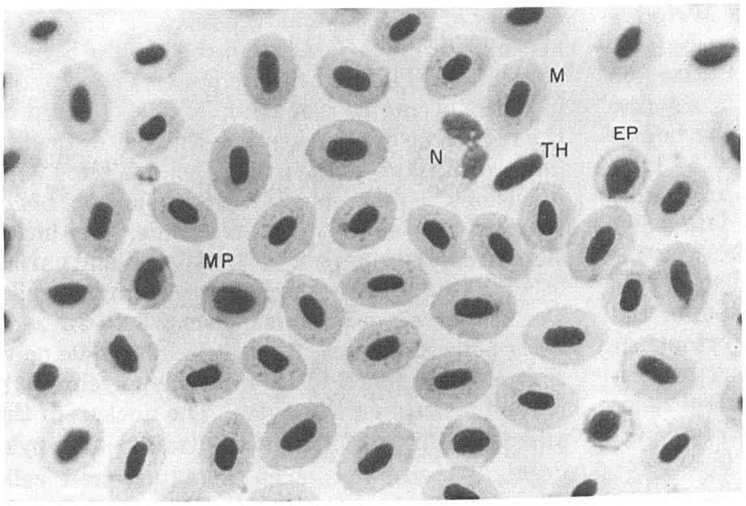

FIGURE 2.—13 March 1969. Photomicrograph of normal wild herring blood showing the absence of inclusions.

EP — early polychromatic erythrocyte
MP — middle polychromatic erythrocyte
M — mature erythrocyte
N — neutrophil
Th — thrombocyte

immature red cells with inclusions found in only 6% of the mature red cells; the other affected herring had 12% immature red cells with inclusions in 50% of the immature and 20% of the mature cells.

Nearly 7% (5/76) of the wild herring sampled on 8 July from Boothbay Harbor contained inclusions, and a few cells in several herring contained two inclusions. Four of the five affected herring contained over 70% immature red cells, the other 15%. Both abnormally large and small erythrocytes and many disintegrated cells were present. Anisopoikilocytosis (abnormal cell sizes and shapes) of all red cell developmental stages was evident. The nuclei of many affected erythrocytes contained two or

three large vacuoles. The affected mature cells were rounded instead of the usual oval (Figure 3); a typical rounded mature cell measured 10.1 × 9.4 μ for the cytosome, 3.7 × 3.4 μ for the nucleus, and 1.2 × 1.5 μ for the inclusion body. Vacuolization of the cytoplasm was evident in many red cells. Inclusions were present in some microcytic mature erythrocytes as small as 4 × 4 μ for the cytosome (less than one-half normal size). Inclusions in a few early polychromatics were larger than usual. One of the largest inclusions in a young cell was nearly as large as the cell nucleus—the cytosome measured 9.2 × 8.0 μ, the nucleus 4.7 × 3.7 μ, and the inclusion 3.9 × 3.6 μ (Figure 4). Otherwise inclusions in the wild herring of March and July were of the same size.

A relationship appears to exist in the occurrence of inclusions and abnormal red cell morphology with temperature extremes. The short-term captive herring sampled on 22 July at 16°C, the highest temperature at which samples were taken, were markedly different from all other samples in their morphology and incidence of inclusions. Ninety-six percent (24/25) of the herring had inclusions, and of those over half had inclusions in at least 90% of their red cells. A majority of the smears in this sample showed 5% or less intact immature red cells. Anucleated "balloon" cells were evident in all smears in this sample, some smears had up to 50% of these cells (Figure 5). The balloon cells appear pale red with Wright's stain, are similar in size, and range from 9.4 × 9.4 μ to 10.9 × 10.9 μ. Some of the cells appear to show diffusion of nuclear material into the cytoplasm. The smears with the greatest incidence of inclusions generally had the most balloon cells. The most heavily affected herring from the 8 July sample also showed these cells. In the smear free of inclusions a few balloon cells were seen, the intact cells appeared normal and 10% immature red cells were present (Figure 6). Such balloon cells are seen in apparently normal blood samples only occasionally and in very low frequency.

The short-term captive herring sampled on 21 August at 14°C showed a substantial decrease in inclusions with 12% of the sample affected, but many nonaffected fish had abnormal cells (Figure 7). Higher than normal seawater temperatures of up to 20.5°C (68.9°F) during August may account for the abnormal cells in herring without inclusions.

Inclusions were found in 2 of the 50 herring

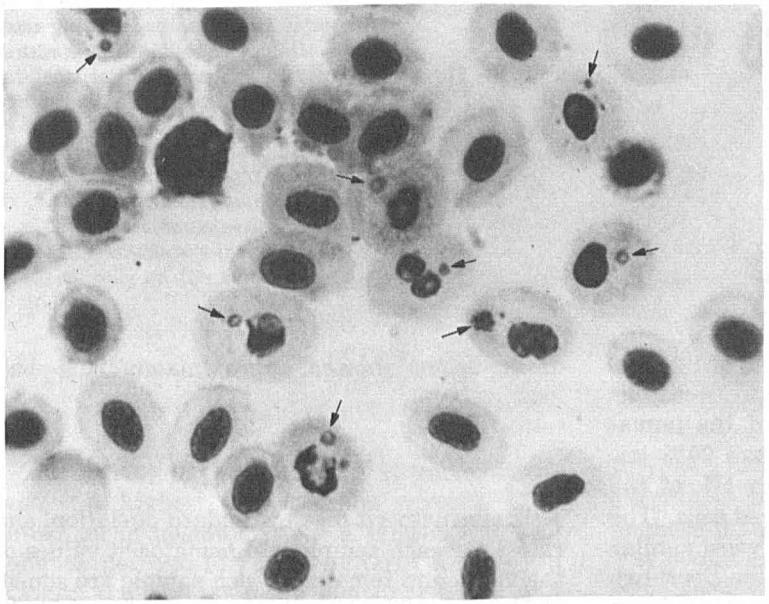

FIGURE 3.—8 July 1969. Photomicrograph of wild herring blood showing intracytoplasmic inclusions associated with nuclear degeneration and a ballooning of the red cells.

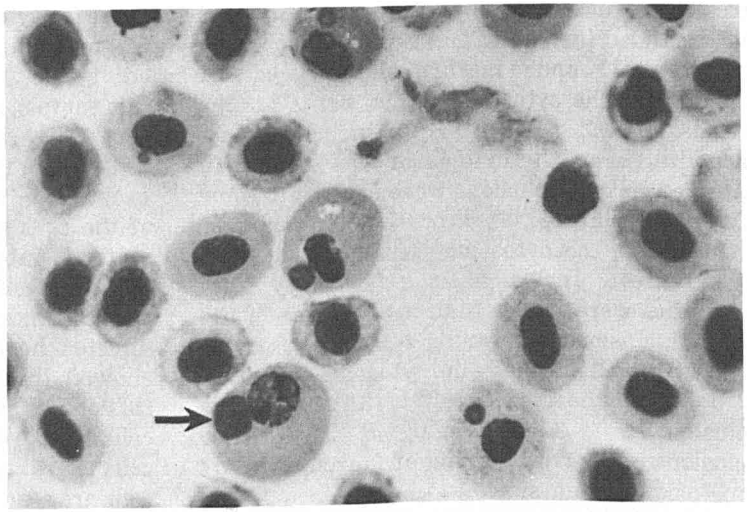

FIGURE 4.—8 July 1969. Photomicrograph of wild herring blood showing one of the largest inclusions seen in this study. The inclusion measures 3.9 × 3.6 μ, the cell nucleus 4.7 × 3.7 μ, and the cytosome 9.2 × 8.0 μ.

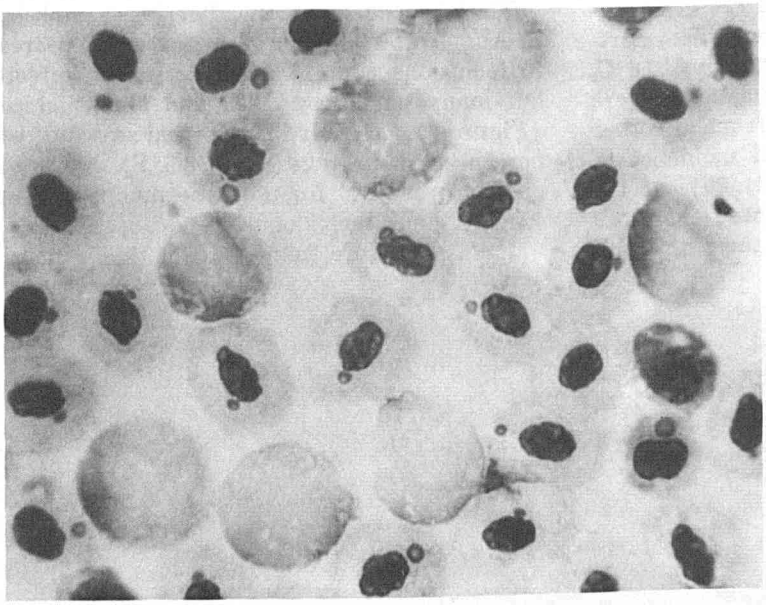

FIGURE 5.—22 July 1969. Photomicrograph of herring blood from a short-term captive, 2 weeks after placing wild fish from the 8 July sample in the tanks, showing nearly all of the red cells affected with inclusions, abnormal nuclei, and anucleated "balloon" cells.

sampled on 16 July from Deer Island, N.B., Canada. One herring had 25% immature red cells with inclusions in less than 1% of the immatures; the other affected herring had 90% immature red cells with inclusions in 1% of the immature and 90% of the mature red cells. The morphology and size of inclusions were similar to that of the 8 July samples from Boothbay Harbor. The smear with the greatest incidence of inclusions showed approximately 20% balloon cells.

HEMATOCRITS

The hematocrit mean, standard deviation, and range for each sample and hematocrit values of the males and females in each sample are shown in Table 3. The lowest hematocrit for an indi-

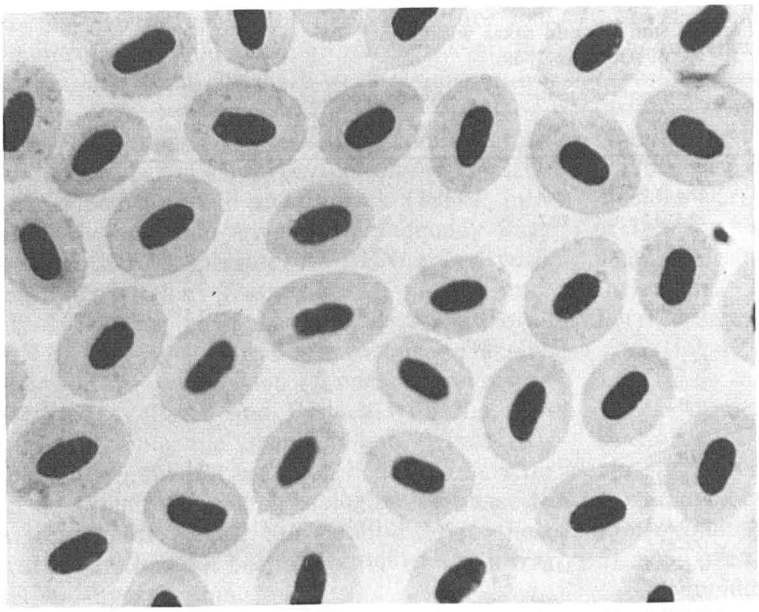

FIGURE 6.—22 July 1969. Photomicrograph of normal red cells from the only herring not affected with inclusions from a sample of 25 short-term captives.

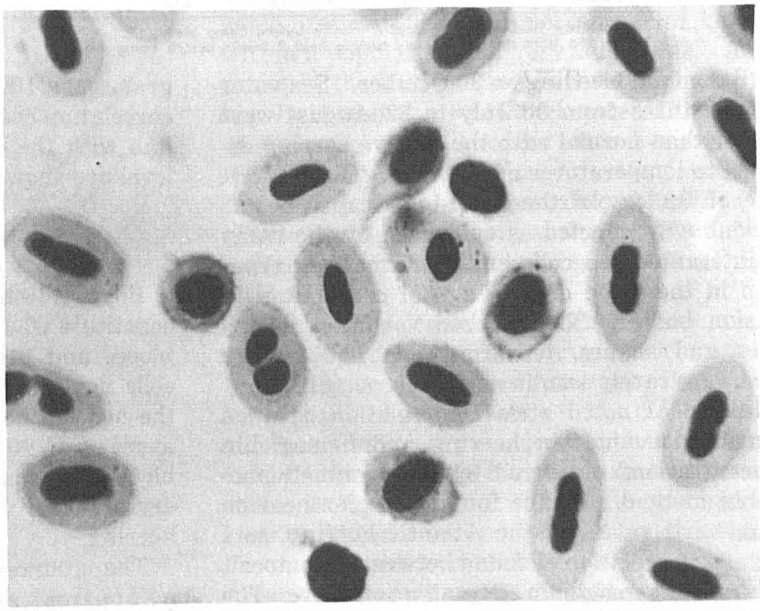

FIGURE 7.—21 August 1969. Photomicrograph of abnormal cells in short-term captive herring. Higher than normal natural seawater temperatures of up to 20.5°C (68.9°F) during August may account for the abnormal cells in herring not affected with inclusions. This herring had one of the lowest hematocrits of the sample (21 volumes percent); the scarcity of cells on the slide reflects this finding.

vidual herring in this study was 17 volumes percent; the highest, 54.5 volumes percent. The lowest mean hematocrit for a sample was 28.7 volumes percent for the long-term captives in March; the highest mean hematocrit was 41.4 volumes percent for a sample of wild herring in July. The *t*-test analysis revealed no significant differences in hematocrit values between sexes in these immature herring.

A consistent decrease is evident in the mean hematocrit values of the wild herring from the time they were placed in captivity on 8 July

TABLE 3.—Hematocrits of herring samples and sexes within each sample, 25 February-30 October 1969.

Date	Water temp. (°C)	Herring sampled (Number)	Hematocrits of samples		Mean hematocrits of:		Standard deviation
			Range (vol %)	Mean (vol %)	Males (vol %)	Females (vol %)	
Long-term captives[1]:							
25 Feb.	1.3	23	22.5-38.0	29.7			4.1
24 Mar.	3.3	25	22.5-36.0	28.7			3.6
21 Apr.	4.9	20	23.0-42.5	31.2			4.3
23 June	15.2	5	22.0-42.0		34.9		7.8
		7	22.5-43.5			36.3	7.9
		12	22.0-43.5	35.7			7.5
Wild, Spruce Point, Boothbay Harbor:							
8 July	13.8	27	27.0-54.5		42.2		6.0
		49	31.0-49.5			40.9	4.5
		76	27.0-54.5	41.4			5.0
Short-term captives[2]:							
22 July	16.0	13	25.0-47.0		40.5		6.1
		12	34.0-53.0			39.6	5.4
		25	25.0-53.0	40.1			5.7
21 Aug.	14.0	12	21.0-46.5		36.5		6.9
		13	17.0-52.5			35.4	8.9
		25	17.0-52.5	36.0			7.9
25 Aug.	15.5	4	23.0-31.5		28.6		3.8
		6	24.0-39.0			33.5	6.2
		10	23.0-39.0	31.6			5.7
30 Oct.	9.2	12	23.0-39.0	30.3			5.2

[1] Boothbay Harbor herring held 6 months before being bled.
[2] Herring from the wild 8 July sample held 2 weeks before being bled.

until the final bleeding on 30 October. Seawater temperatures from 30 July to 22 August were higher than normal with the captive herring exposed to temperatures of up to 20.5°C (68.9°F). The physiology of the short-term captives was undoubtedly affected as evidenced by the many disintegrated red cells and abnormal cell types seen in the blood of herring not containing inclusion bodies. The marked variation in cell sizes and shapes, teardrop cells and bizarre forms are rarely seen in normal herring blood.

In 1965 I noted a close correlation between hematocrit values in herring and hemoglobin concentrations measured by the cyanmethemoglobin method. I have found no references on hematocrit values of the Atlantic herring, so I include the relations I found between hematocrit values and hemoglobin concentrations here. The herring sampled in 1965 were long-term captive herring 12.7-25.4 cm in length. Hematocrits were taken as described in the present study. Blood for hemoglobin measurements was obtained from the heart and placed in a small test tube to which a drop of liquid heparin had been added. Hemoglobins were measured as grams per 100 ml. Regression analysis gave a correlation coefficient of 0.9333. The regression line with the confidence limits of Y at the 0.05 level are shown in Figure 8.

DISCUSSION

Boyar (1962) reported that mature red cells constitute 97-100% of all blood cells in herring blood, and the immature red cells plus white cells made up less than 3% of the total cells in the herring he examined. However, I found an average of 20% immature erythrocytes in the blood of normal wild herring and 14% immature erythrocytes in the blood of normal captive herring.

The occurrence of cytoplasmic inclusions had no apparent relationship to sex, length, weight, or hematocrits, nor did herring with inclusions show, on cursory examination, more than the usual parasites observed in samples without inclusions. The occurrence of inclusions is associated with other hematological abnormalities in the peripheral blood including upward to 90% immature red cells or a low of 1 to 5% immature

red cells in contrast to the 20% immature red cells normal for wild herring; microcytic erythrocytes less than one-half normal size; and varying degrees of anisocytosis and poikilocytosis. The affected red cells have some characteristics of piscine erythrocytic necrosis (PEN) as described by Laird and Bullock (1969), in a cod, *Gadus morhua*, from Passamaquoddy Bay. These authors associated the PEN in cod with viruslike particles. Walker (1971; pers. comm., July 1972) has confirmed the viral nature of PEN in cod by electron microscopy. He also confirmed the correlation of nuclear lesions as described by Laird and Bullock with the presence of cytoplasmic viroplasm and virions. Although I believe the inclusion bodies in herring can be explained as a physiological response to environmental stress, the possibility of their viral nature has not been ruled out and requires further investigation.

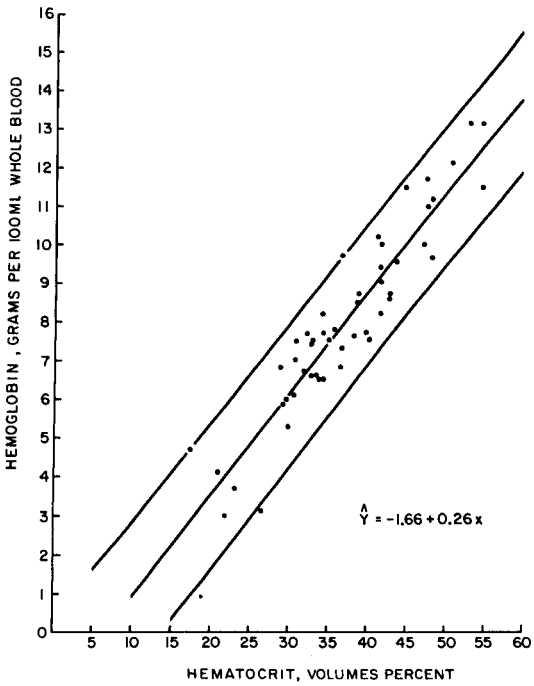

FIGURE 8.—Relation of hematocrit values to hemoglobin concentrations in captive herring during late winter, 1965.

A relationship appears to exist between inclusions in herring erythrocytes and stress factors, especially temperature extremes. Except in one instance when inclusions occurred in herring from water of 2°C, all herring from Boothbay Harbor (lat 43°50′N, long 69°40′W) having inclusions were taken from seawater temperatures of 13.8°C or above. At a temperature of 16°C, 96% of a sample of herring were affected with inclusions. Inclusions were found in 2 of 90 herring sampled from the Passamaquoddy Bay area (lat 45°00′N, long 67°00′W). These herring were taken from a seawater temperature of 9.8°C, the highest temperature sampled in that area. During the months of June and July water temperatures in the Passamaquoddy Bay area have, over a number of years, averaged approximately 4°C lower than in the Boothbay Harbor area (Colton and Stoddard, 1972).

The incidence of inclusions within a population can change rapidly, apparently with changing environmental conditions, and they are capable of affecting a high percentage of herring within a population in a very short time. As an example, the wild herring on 8 July from Boothbay Harbor had a 6.6% incidence of inclusions (5/76); however, 2 weeks after herring from this population were placed in the laboratory tanks, 96% of the herring sampled (24/25) were affected with inclusions, and over 90% of the red cells in individual herring contained these bodies.

These bodies, associated with erythrocytic degeneration characterized by necrotic nuclei, a ballooning degeneration of the red cells and the appearance of unusual cells in the blood, may be indicative of stress situations for immature herring in the wild. If the stress factors causing these inclusion bodies affect enough herring, they could conceivably have an adverse affect on the population structure endemic to certain areas. The erythrocytic degeneration found in herring may be due to a viral infection as described in other fishes by Laird and Bullock (1969) and confirmed by Walker (1971). The occurrence of such a viral infection in epidemic frequency would certainly be no less important to our understanding of fluctuations in abundance of herring populations.

ACKNOWLEDGMENTS

I wish to express my appreciation to George J. Ridgway and John E. Watson of the Northeast Fisheries Center, Boothbay Harbor Laboratory, National Marine Fisheries Service and to Roland Walker of the Rensselaer Polytechnic Institute who critically reviewed the manuscript and made suggestions to improve clarity of presentation. I thank Gareth W. Coffin of the Boothbay Harbor Laboratory for his excellent photomicrographic work.

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FOOD OF TUNAS AND DOLPHINS (PISCES: SCOMBRIDAE AND CORYPHAENIDAE) WITH EMPHASIS ON THE DISTRIBUTION AND BIOLOGY OF THEIR PREY *STOLEPHORUS BUCCANEERI* (ENGRAULIDAE)

THOMAS S. HIDA[1]

ABSTRACT

The results of examining the stomach contents of skipjack tuna (*Katsuwonus pelamis*), bigeye tuna (*Thunnus obesus*), yellowfin tuna (*Thunnus albacares*), kawakawa (*Euthynnus affinis*), common dolphin (*Coryphaena hippurus*), and the little dolphin (*Coryphaena equiselis*) caught by live bait pole-and-line fishing and trolling in the equatorial eastern Pacific and around the Samoa Islands are presented. Fishes, crustaceans, and molluscs were found to be important food items. The presence of the anchovy, *Stolephorus buccaneeri*, among the stomach contents was of particular interest, and information gained on their distribution, size frequency, fecundity, and food habits is presented.

This report is based mainly on observations and stomach sample collections that were made during *Charles H. Gilbert* cruise 116 to the equatorial eastern Pacific in October-November 1969 (Hida, 1970a) and cruise 117 to the Samoa Islands in February-April 1970 (Hida, 1970b). In this study, *Stolephorus buccaneeri* was first found in the stomach contents of bigeye and skipjack tunas caught in the equatorial eastern Pacific and again in the stomach contents of tunas caught around the Samoa Islands. Since there has been no food study made of tunas and dolphins from these areas and very few reports on the distribution and biology of *S. buccaneeri*, it is the intent of this paper to (1) describe the food items of the tunas and dolphins caught in these two geographically distant and environmentally diverse—oceanic versus insular—areas, (2) extend the known distributional range of *S. buccaneeri*, (3) report on biological information obtained from the anchovy specimens. *Charles H. Gilbert* is a U.S. Department of Commerce, NOAA research vessel assigned to the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service. Objectives of the cruises were to assess the distribution and abundance of surface swimming tunas, to tag and release skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) for migration and growth studies, and to collect blood samples of these tunas for subpopulation studies. Tunas and dolphins were caught by live bait pole-and-line fishing and by trolling. Threadfin shad, *Dorosoma petenense*, were transported from Honolulu in baitwells on both cruises and used as chum for the fishing operation. It was the exclusive baitfish used on cruise 116, while on cruise 117 supplementary baitfishes, mostly sardines, *Sardinella melanura* and *Herklotsichthys punctatus*, and a mackerel, *Rastrelliger kanagurta*, were caught in Pago Pago Harbor and used. Since anchovies were not used as live bait on either cruise, the occurrence of *S. buccaneeri* in the stomachs of the tunas examined indicates that this species is a natural food item in this area.

Many studies have been made on the food and feeding habits of tunas in the Pacific. Ronquillo (1953) examined the stomach contents of yellowfin tuna, skipjack tuna, kawakawa (*Euthynnus affinis*), and the common dolphin (*Coryphaena hippurus*) caught in Philippine seas.

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Manuscript accepted July 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

He found that juvenile fish, especially the acronurus larvae of Acanthuridae, were most important in their diet. Also of importance were members of the fish families Trichiuridae, Scombridae, Triacanthidae, Holocentridae, Balistidae, and Monacanthidae, and invertebrates such as squids, larval and juvenile stomatopods, larval crabs and shrimp. Hotta and Ogawa (1955) examined the stomach contents of skipjack tuna caught to the east and south of the main Japanese islands and reported that Scombridae, Engraulidae, Exocoetidae, and Holocentridae were major dietary items. Important invertebrates included squids, crab larvae, euphausiids, and shrimp. Alverson (1963) examined the stomach contents of skipjack and yellowfin tunas caught in the eastern tropical Pacific. He found euphausiids to be the main food items for skipjack tuna, followed by Gonostomatidae, Exocoetidae, and the "red crab," *Pleuroncodes planipes*; and for yellowfin tuna, the "red crab," the swimming crab (Portunidae), Thunnidae, Ostracidae, Exocoetidae, and Tetraodontidae. Waldron and King (1963) studied the stomach contents of skipjack tuna taken around the Hawaiian, Line, and Phoenix Islands and found that common dietary items were Gempylidae, Scombridae, Mullidae, Chaetodontidae, and Holocentridae. Larval and juvenile skipjack tuna, stomatopod larvae, shrimp, and crab megalops were also important. E. Nakamura (1965), upon examination of the stomach contents of skipjack tuna from the Marquesas and Tuamotu Islands, reported that scombrids, with skipjack tuna constituting a high percentage, were common food items. Serranidae, Lutjanidae, and Gempylidae were of importance as were stomatopods, crab megalops, and squids. It was concluded by Hotta and Ogawa (1955) that the tunas were nonselective in their feeding habits and ate whatever was available in the area.

Although these previous observations covered broad areas of the Pacific, no mention was made of any anchovy that may have been *S. buccaneeri* occurring in the stomach contents. An exception is a report by H. Nakamura (1936) on the food of yellowfin tuna caught in the Celebes Sea that mentioned an anchovy as one of the common food items. The area in which he found tunas containing the anchovy, the frequency of occurrence of the anchovy in tuna stomachs, and the numbers in which it occurred lead me to believe that it may have been *S. buccaneeri*.

METHODS

The stomachs of the troll and pole-and-line caught fish were removed after they were measured and sexed. Stomachs that appeared empty and those of most male tunas were examined in the field and their contents recorded. The rest were placed in muslin bags and preserved in 10% Formalin.[2] One of the objectives of the cruises was to collect 50 skipjack tuna and/or 50 yellowfin tuna blood samples from each school. Therefore, there were four occasions on which 50 stomach samples per school were collected.

In the laboratory, counts were made of the organisms in the stomachs whenever possible. Many of the partially digested fishes were identified by their vertebrae which were prepared by teasing away the muscles when necessary and staining with alizarin red. Skipjack tuna remains were identifiable by skeletons. Enough of the external characters of the anchovy usually remained for identification. Most of the other fishes were identifiable only to family. The stomach contents of the anchovy, which included many crustaceans, were identified by staining the organisms with methylene blue. Many of the copepods were identified to species but other invertebrates were identifiable only to major groups such as the Chaetognatha, Amphipoda, and shrimp.

STOMACH CONTENTS

EQUATORIAL EASTERN PACIFIC

The results of examining 268 skipjack tuna, 44 bigeye tuna (*Thunnus obesus*), 45 yellowfin tuna, 2 common dolphin, and 7 little dolphin (*Coryphaena equiselis*) caught on cruise 116 of the *Charles H. Gilbert* are presented in Table 1. The presence of *S. buccaneeri* in the stomach

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

TABLE 1.—Frequency occurrence of organisms in the stomachs of 268 skipjack tuna, 44 bigeye tuna, 45 yellowfin tuna, and 9 dolphin (2 common and 7 little) examined from cruise 116 of the *Charles H. Gilbert*.

Food items	Predators							
	Skipjack tuna		Bigeye tuna		Yellowfin tuna		Dolphin	
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*
Fishes:								
Alepisauridae	2	0.7	--	--	--	--	--	--
Bramidae	3	1.1	1	2.3	1	2.2	--	--
Chaetodontidae	--	--	1	2.3	--	--	--	--
Diodontidae	1	0.4	--	--	--	--	--	--
Engraulidae:								
Stolephorus buccaneeri	35	13.1	20	45.4	--	--	--	--
Exocoetidae	3	1.1	--	--	1	2.2	3	33.3
Gempylidae	4	1.5	4	9.1	4	8.9	--	--
Nomeidae	--	--	1	2.3	1	2.2	--	--
Scombridae:								
Auxis rochei	1	0.4	--	--	--	--	--	--
Katsuwonus pelamis	5	1.9	--	--	--	--	--	--
Sternoptychidae	--	--	1	2.3	--	--	--	--
Zeidae	--	--	1	2.3	--	--	--	--
Unidentified	9	3.4	1	2.3	7	15.6	2	22.2
Chum	100	37.3	20	45.4	22	48.9	--	--
Crustacea:								
Amphipoda	2	0.7	--	--	2	4.4	--	--
Euphausiacea	1	0.4	--	--	--	--	--	--
Shrimp	2	0.7	1	2.3	--	--	--	--
Mollusca:								
Argonauta	6	2.2	--	--	1	2.2	--	--
Heteropoda	1	0.4	--	--	3	6.7	--	--
Squids	22	8.2	6	13.6	8	17.8	2	22.2
Chaetognatha	1	0.4	--	--	--	--	--	--
Stomach empty	136	50.7	15	34.1	17	37.8	5	55.6

contents of 13.1% of the skipjack tuna and 45.4% of the bigeye tuna examined was of particular interest. Of the invertebrates, squids were most frequently found in the contents. Many of the stomachs examined were empty.

This study revealed that only a few varieties of organisms were eaten in the oceanic environment, which contrasted markedly with Ronquillo's (1953) work showing a great diversity of organisms eaten in an environment influenced by land. The fact that *S. buccaneeri* was found only in the stomachs of tunas from two schools that were close to each other suggests that it was not widespread in this area.

SAMOA ISLANDS

Table 2 shows the results of examining 205 skipjack tuna, 23 kawakawa, 24 yellowfin tuna, and 1 common dolphin which were caught on cruise 117 of the *Charles H. Gilbert*. *S. buccaneeri* occurred very frequently in the stomachs examined. Other fishes occurring frequently belonged to the families Acanthuridae and Holocentridae. Stomatopod larvae, of the invertebrates, occurred most frequently in the contents. Many of the stomachs examined were empty.

The variety of organisms eaten around the Samoa Islands was limited. However, a comparison of the studies shows a greater diversity ingested around Samoa than in the equatorial eastern Pacific, probably because of the proximity to the islands. The distribution of *S. buccaneeri* was found to be widespread in this area. Their frequency of occurrence in the stomachs suggested that they were an important forage for the tunas and dolphins here.

TABLE 2.—Frequency occurrence of organisms in the stomachs of 205 skipjack tuna, 23 kawakawa, 24 yellowfin tuna and 1 common dolphin, examined from cruise 117 of the *Charles H. Gilbert.*

Food items	Predators							
	Skipjack tuna		Bigeye tuna		Yellowfin tuna		Common dolphin	
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*
Fishes:								
Acanthuridae	45	22.0	1	4.3	4	16.7	--	--
Balistidae	13	6.3	2	8.7	1	4.2	--	--
Bramidae	--	--	--	--	1	4.2	--	--
Carangidae	3	1.5	--	--	--	--	--	--
Chaetodontidae	11	5.4	--	--	1	4.2	--	--
Dactylopteridae	1	0.5	--	--	--	--	--	--
Engraulidae:								
Stolephorus buccaneeri	38	18.5	4	17.4	6	25.0	1	100
Exocoetidae	5	2.4	--	--	--	--	--	--
Gempylidae	13	6.3	--	--	--	--	--	--
Holocentridae	61	29.8	2	8.7	2	8.3	--	--
Molidae	1	0.5	--	--	--	--	--	--
Monacanthidae	3	1.5	1	4.3	--	--	1	100
Mullidae	2	1.0	--	--	--	--	--	--
Ostraciidae	1	0.5	--	--	--	--	--	--
Pomacentridae	--	--	--	--	1	4.2	--	--
Scombridae:								
Katsuwonus pelamis	19	9.3	--	--	--	--	--	--
Unidentified	8	3.9	--	--	--	--	--	--
Siganidae	8	3.9	--	--	--	--	--	--
Synodontidae (?)	6	2.9	--	--	--	--	--	--
Tetraodontidae	2	1.0	--	--	--	--	--	--
Chum	66	32.2	--	--	--	--	--	--
Unidentified	36	17.6	2	8.7	2	8.3	1	100
Crustacea:								
Amphipoda:								
Phronima sp.	--	--	--	--	1	4.2	--	--
Crab megalops	2	1.0	2	8.7	--	--	--	--
Phyllosoma larvae	1	0.5	--	--	--	--	--	--
Shrimp	--	--	1	4.3	--	--	--	--
Stomatopod larvae	7	3.4	3	13.0	1	4.2	--	--
Mollusca:								
Squids	20	9.8	--	--	1	4.2	--	--
Stomach empty	64	31.0	14	60.8	10	41.7	--	--

NOTES ON *STOLEPHORUS BUCCANEERI*

DISTRIBUTION

Strasburg (1960) described *S. buccaneeri* from Hawaii and proposed the common name, roundhead. His holotype was a specimen taken in a nearshore bait seine haul close to Lehua Island. He also found a few specimens in the stomach contents of kawakawa caught about a mile offshore from Oahu. Matsui (1963) found this species in the bait samples he obtained around the island of Maui.

The abundance of *S. buccaneeri* in Hawaiian waters is not known. This is largely because the Hawaiian skipjack tuna fishermen use the anchovy, *Stolephorus purpureus*, as their principal baitfish. These two fish are almost identical and therefore difficult to distinguish from one another. Anchovies regurgitated on deck and found in the stomach contents of tunas are assumed to be their baitfish. At times, however, Hawaiian skipjack tuna fishermen have reported seeing skipjack tuna feeding on what they refer to as "offshore nehu" (liberal translation of the Japanese term used), which more than likely is *S. buccaneeri*. The distribution of *S. purpureus* is inshore while that of the *S. buccaneeri* seems to be generally offshore. It is therefore proposed that another common name of *S. buccaneeri* might be offshore nehu.

Besides Hawaii, Whitehead (1967) gave the distribution of the *S. buccaneeri* as the Red Sea,

Persian Gulf, Comoro Islands, east coast of Africa, Formosa, Hong Kong, Japan, the Philippines, Palau, southern India, and Singapore. He stated that they were very common in Hong Kong, Japan, and Hawaii.

Additional notes on the distribution of *S. buccaneeri* are given below; occurrences discussed are shown in Figure 1.

S. buccaneeri was first noticed on cruise 116 in the stomach contents of 4- to 12-kg bigeye tuna that were caught from a "boiling" school (see Scott, 1969) at lat 4°N and long 119°W. It was found again the next day in the stomach contents of skipjack tuna caught at lat 5°N on long 119°W, about 700 miles from Clipperton Island, the closest land. This occurrence is of interest because this species previously had been recorded only near land masses.

On cruise 117, *S. buccaneeri* was observed to be a common organism eaten by skipjack and yellowfin tunas, kawakawa, and dolphin caught around the Samoa Islands. Although it was very often eaten by tunas close to shore, it was neither seen nor caught while baiting in the inshore areas. Similarly, Robert E. K. D. Lee (pers. comm.) has found it eaten by yellowfin tuna and kawakawa caught near shore in the Fiji area but has not observed it during baiting operations in inshore waters.

In May of 1971 on cruise 53 of the *Townsend Cromwell*, *S. buccaneeri* juveniles were collected under a night light while the vessel was anchored in a depth of 25 m on Condor Reef in the Caroline Islands.

An estimated 20 kg of *S. buccaneeri* were caught in a close-to-surface haul made with a modified Cobb pelagic trawl (see Higgins, 1970 for a description of this trawl) 160 miles east of Agrihan Island in the Mariana Islands on cruise 55 of the *Cromwell* in November 1971. It was present in five other trawl hauls, in the stomach contents of a wahoo, *Acanthocybium solandri*, caught northwest of Ponape, and in several skipjack tuna caught by trolling north of Namorik during the same cruise.

John Naughton, National Marine Fisheries Service, Honolulu, informed me that several schools of yellowfin and skipjack tunas fished by the Hawaiian fishing vessel *Anela* around Majuro and Arno Atolls in April 1972 were feeding on schools of an anchovy resembling *S. buccaneeri*.

Wilson[3] cited that two Palauans trolling between Angaur and Peleliu Islands observed and sampled a school of kawakawa feeding on *S. buccaneeri*.

The occurrence of *S. buccaneeri* as discussed here in the equatorial eastern Pacific, Samoa Islands, Caroline Islands, Mariana Islands, Palau Islands, Marshall Islands, and Fiji in conjunction with previous records shows it to be a widespread Indo-Pacific (including eastern Pacific) species. Because it occurs in great abundance locally, such as at Fiji and the Samoa Islands, it is to be expected that details of its occurrence will be more likely noted.

SIZE

Most of the anchovies found in the stomach contents were in poor condition. The caudal fin and snout of many specimens were so badly digested that their standard lengths could only be estimated. The *S. buccaneeri* found in the bigeye tuna stomachs ranged from 30 to 57 mm in standard length (SL). Those found eaten by the skipjack tuna ranged from 20 to 58 mm. Those caught on cruise 117 of the *Charles H. Gilbert* near Samoa ranged from 23 to 78 mm. The samples from Condor Reef measured 15 to 30 mm while those from the trawl hauls caught close to the Mariana Islands ranged from 14 to 70 mm. The small postlarvae were semitransparent when alive and turned whitish when preserved in Formalin. They were identified by their exposed urohyal plate and posterior extent of their maxilla.

The presence of large numbers of postlarvae more than 100 miles from land, and adults as far as 700 miles from land, strongly suggests that this species is capable of completing its life cycle in an oceanic environment.

[3] Wilson, P. T. Observations of various tuna bait species and their habitats in the Palau Islands. Unpublished manuscript. Marine Resources Division, Trust Territory of the Pacific Islands, Saipan, Marianas 96950.

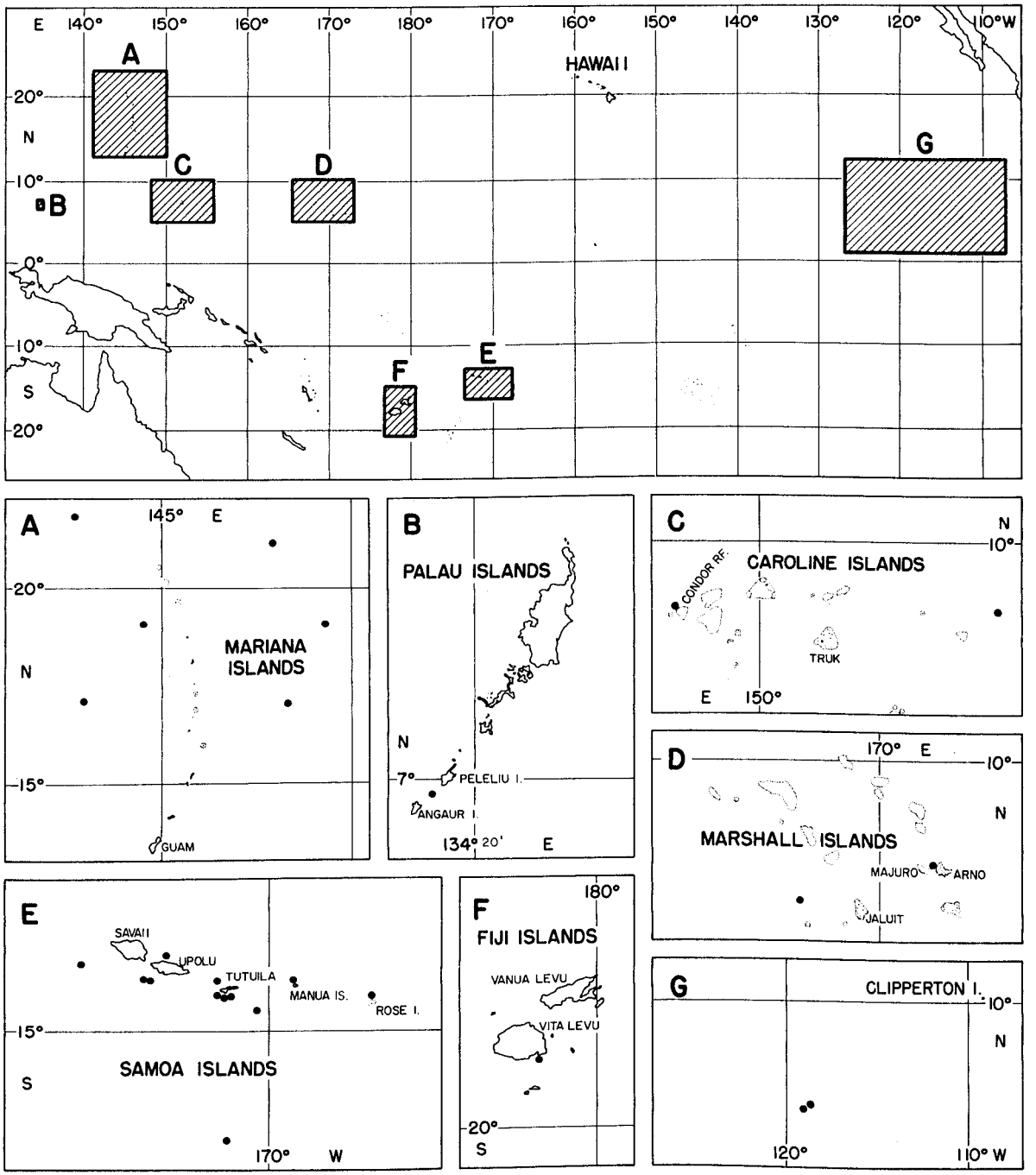

FIGURE 1.—The distribution of *Stolephorus buccaneeri* in the Pacific covered in this study.

FECUNDITY

Ova of 32 specimens of *S. buccaneeri* obtained from tuna stomach contents were measured: Specimens were 38-55 mm SL. From each subsample, diameters of 30 or more of the ova from the most advanced mode were taken. Their distribution ranged from 0.4 to 0.8 mm and peaked at 0.5 mm. The ova were opaque, granulated, and classified as maturing.

Since there are no previous estimates of fecundity, ova from the most advanced mode from two *S. buccaneeri* ovaries were counted. This method was based on the assumption that all of the ova in this mode constituted a single spawning. A 44-mm specimen contained 595 ova in her left ovary and 830 in her right, a total of 1,398. A 39-mm individual had 340 ova in her left ovary and 454 in her right, a total of 794.

FOOD STUDY

The examination of 58 stomach contents of *S. buccaneeri* recovered from tuna stomachs showed that crustaceans were important in their diet, as shown in Table 3. Only one stomach was found empty. The stomachs of *S. buccaneeri* in this study contained primarily calanoid copepods and other organisms. The copepods that were abundant in one or more anchovy stomachs from the equatorial eastern Pacific were *Candacia truncata* and *Euchaeta marina*. The cyclopoid copepod, *Oncaea venusta*, was common in one stomach. Copepods found in abundance in one or more anchovy stomachs taken from tunas caught from the Samoa Islands were *Candacia bispinosa* (?) *C. catula*, *C. truncata*, *Centropages gracilis*, *Euchaeta marina* and *Temora discaudata*. *C. truncata* and *E. marina* were the only two species that were abundant in both areas. Not unexpectedly, the close-to-shore samples from Samoa were represented by more species than those of the oceanic equatorial eastern Pacific. It should be noted, however, that there were many copepodites and badly digested specimens in the equatorial eastern Pacific samples, while those from the Samoa Islands were larger and in much better condition for identification purposes. Hiatt (1951) examined the stomach contents of the nehu, *S. purpureus*, caught from five major baiting areas in Hawaii and concluded that nehu were selective feeders in that they took the crustacean elements in the plankton. He found important food items to be copepods, ghost shrimp (*Lucifer*), barnacle nauplii, shrimp larvae, and crab larvae.

ACKNOWLEDGMENTS

I am indebted to Peter Whitehead of the British Museum (Natural History) for his identification and verification of *S. buccaneeri* samples. Thanks are also due to the crew members and scientific personnel of *Charles H. Gilbert* who were instrumental in collecting the samples.

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TABLE 3.—The stomach contents of *Stolephorus buccaneeri* found in tuna stomachs in the equatorial eastern Pacific and the Samoa Islands (A = abundant, C = common, P = present). [The numbers examined are in parentheses.]

Food items	Samoa Islands			Equatorial eastern Pacific	
	Skipjack tuna (10)	Yellowfin tuna (6)	Kawakawa (4)	Bigeye tuna (23)	Skipjack tuna (15)
Copepoda:					
Calanoids:					
Candacia bispinosa (?)	A	--	--	--	--
Candacia catula	A	P	--	--	--
Candacia simplex	P	--	--	--	--
Candacia truncata	A	--	--	--	A
Candacia sp.	--	--	P	--	--
Centropages gracilis	A	--	--	--	--
Centropages sp.	--	--	P	--	--
Eucalanus sp.	--	--	P	--	--
Euchaeta concinna	P	--	--	--	--
Euchaeta marina	A	--	--	A	--
Euchaeta sp.	--	--	P	P	P
Lucicutia flavicornis	P	--	--	--	--
Nannocalanus minor (?)	--	P	--	--	--
Pleuromamma xiphias	P	--	--	--	--
Scolecithricella ctenopus	P	--	--	--	--
Scolecithrix danae (?)	C	--	--	--	--
Temora discaudata	A	P	--	--	--
Temora sp.	--	--	P	--	--
Undinula darwini	P	--	--	--	--
Unidentified calanoids	P	P	P	C	A
Cyclopoids:					
Copilia mirabilis	P	--	--	--	--
Copilia sp.	--	--	P	--	--
Corycaeus limbatus (?)	--	P	--	--	--
Corycaeus spesiosus	P	--	--	P	--
Corycaeus vitreus (?)	P	--	--	--	--
Corycaeus sp.	P	P	--	P	P
Farranula concinna (?)	P	--	--	--	--
Farranula gibbula (?)	P	P	--	--	--
Farranula sp.	--	P	P	P	--
Microsetella rosea	P	P	--	--	--
Microsetella norvegica (?)	--	P	--	--	--
Oncaea conifera	--	--	--	P	--
Oncaea venusta	--	--	--	C	--
Oncaea sp.	P	P	--	P	P
Sapphirina gastrica (?)	P	--	--	--	--
Sapphirina sp.	P	--	P	P	--
Unidentified cyclopoids	--	P	P	A	C
Amphipoda	P	--	--	--	--
Mysidacea	--	--	--	P	--
Shrimp juvenile	C	P	P	P	P
Crab megalops	--	--	P	--	--
Chaetognatha	A	P	P	P	P
Gastropod larvae	P	P	--	--	--
Heteropoda:					
Atlanta inclinata	P	--	--	--	--
Atlanta sp.	P	--	--	--	--
Bivalve larvae	--	P	--	--	--
Ostracoda	P	P	--	--	--
Polychaeta	P	--	--	--	--
Pteropoda:					
Creseis virgula	--	--	--	--	P
Unidentified fish	P	--	P	--	--

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HARVEST AND REGROWTH OF TURTLE GRASS (*THALASSIA TESTUDINUM*) IN TAMPA BAY, FLORIDA[1]

JOHN L. TAYLOR,[2] CARL H. SALOMAN,[3] AND KENNETH W. PREST, JR.[3]

ABSTRACT

A comparison of leaf growth and new leaf production in plots of cut and uncut turtle grass, *Thalassia testudinum*, indicated that plants suffered no damage when harvested twice during a 6-month growing season in Boca Ciega Bay (Tampa Bay), Fla. In deeper or warmer waters where the growing season is protracted, three or more cuttings per year may prove practical.

One of the environmental catastrophes to occur in the past 30 years is the destruction of vast beds of turtle grass through dredge-fill operations, other types of coastal engineering, and pollution in its many forms (McNulty, 1961; Taylor and Saloman, 1968; McNulty, Lindall, and Sykes, in press). The most recent development that may affect turtle grass is the possibility of its harvest for use as a food supplement for livestock.

Interest in the nutrient content of turtle grass was first stimulated by Burkholder, Burkholder, and Rivero (1959), who showed that turtle grass leaves contain about 13% protein. Their analysis was substantiated by Bauersfeld et al. (1969), who further found that turtle grass in pellet form significantly increased the weight gain and feed utilization of experimental sheep over that of control animals when added to normal rations as a replacement for alfalfa at a level of about 10%. One of the many questions raised by the success of these feeding trials is whether or not beds of turtle grass can survive and regrow after harvest. This report presents results of a study in which leaves in an experimental plot of turtle grass were repeatedly cut, measured, and compared with those taken from a control area between August 1968 and November 1969.

In the Gulf of Mexico and Caribbean Sea, the dominant sea grass is turtle grass, *Thalassia testudinum* Koenig and Sims. Generally, it flourishes in estuaries and coastal waters from the level of low water to depths of 10 m or more depending on water clarity. Throughout its range in the central, western Atlantic, turtle grass meadows attain maximum development in muddy sands where average salinity is between 25 and 39‰ (Phillips, 1960; Hartog, 1970). Morphological features of turtle grass have been reported by Tomlinson and Vargo (1966) and Tomlinson (1969a, b), who showed that new grass beds are established from seeds, which mature during spring and summer months, or vegetatively by rhizome fragments that are broken off and relocated by storm action and currents. Kelly, Fuss, and Hall (1971) demonstrated that the normally slow and uncertain spread of turtle grass can be accelerated by transplanting and securing sprigs treated with naphthelene acetic acid. This procedure may prove useful in establishing and replacing turtle grass in unvegetated areas—especially through the northern part of its range where apparently there is little or no seed production (Phillips, 1960).

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Manuscript accepted June 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

Ecologists have shown that the turtle grass community exhibits great biological diversity and forms the basis of an extremely stable and productive ecosystem (Margelef, 1962; Odum, 1967). Its roots and rhizomes penetrate the bottom down to 25 cm or more in a matlike network that effectively binds and holds sediments and detritus against erosion, and provides a unique habitat for many benthic invertebrates (Bernatowicz, 1952; Voss and Voss, 1955; Ginsburg and Lowenstam, 1958; Phillips, 1960; Strawn, 1961; Thomas, Moore, and Work, 1961; O'Gower and Wacasey, 1967; Hartog, 1970). The broad, elongate leaves of turtle grass have a surface area of about 18 m^2 for each square meter of sediment they occupy, and usually represent a standing crop in excess of 1 metric ton (dry weight) per acre (Phillips, 1960; Gessner, 1971). Furthermore, leaves of turtle grass moderate water movements, offer attachment sites for various algae and sessile invertebrates, and serve as a feeding ground, shelter, and nesting area for many fishes and motile invertebrates (Humm, 1964; Stephens, 1966). The rich microbial biota that reduces and recycles much of the organic production from turtle grass beds has been recently described by Fenchel (1970).

PROCEDURE

Turtle grass leaves were harvested in August and October 1968 and in July and September 1969. The cutting was done within a 30 m^2 experimental plot in lower Boca Ciega Bay (Tampa Bay), Fla., where the standing crop of turtle grass on a dry, whole weight basis was 1,198 g/m^2 (Taylor and Saloman, 1968). The harvesting machine was designed and constructed by personnel at the Fisheries Service laboratory in College Park, Md., and consisted of an adjustable, motor-driven sickle bar mounted on a small, styrofoam barge. The cutting head was set about 10 cm above the bay bottom, and the barge was directed by hand as water depth was little more than 1 m at high tide.

Between harvests, weekly samples of at least 100 leaves were picked from plants dug by shovel within the experimental plot and from uncut plants that served as controls in the surrounding area. The point of leaf removal was at the leaf node. Leaf length was measured from both sample sets, and as an additional measurement of plant vigor, the number of new shoots per leaf cluster was also recorded from each set.

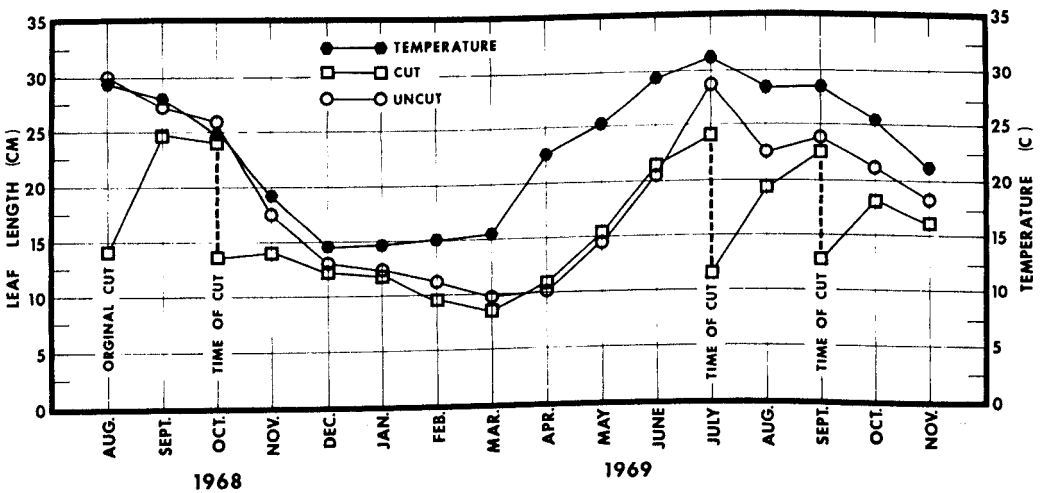

FIGURE 1.—Average monthly length of turtle grass leaves from cut and uncut plants, and related water temperatures in Boca Ciega Bay (Tampa Bay), Fla., between August 1968 and November 1969.

LEAF GROWTH AND REGROWTH AFTER HARVEST

Growth of turtle grass foliage and ultimate leaf length are largely controlled by water temperature and depth (Phillips, 1960; Strawn, 1961). In Tampa Bay, turtle grass normally exhibits a seasonal growth cycle in which leaves elongate rapidly from April to July and die back to short stubble between October and March. During the period of maximum leaf growth, blades develop at a rate of 5 cm per month or more and reach a total length of about 30 cm (Figure 1). Leaves harvested in the growing season had an equivalent or greater rate of regrowth and reached the height of uncut plants in about 2 months (Figure 1). Observed growth rates of both cut and uncut leaves were comparable to figures previously reported from southern Florida by Thomas et al. (1961) and Zieman (1968). Furthermore, harvesting had no apparent influence on production of new leaves. For each month, the average number of shoots produced by both cut and uncut plants was nearly the same (Figure 2).

Thus, from a comparison of leaf growth and new leaf production among cut and uncut plants, it seems likely that turtle grass in the Tampa Bay area can be harvested twice each year without adversely influencing plant vigor.

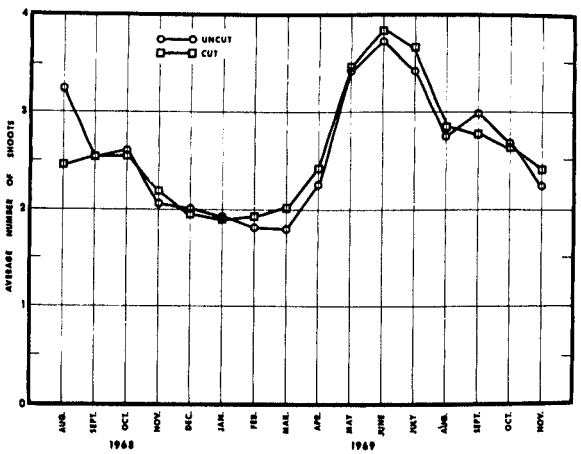

FIGURE 2.—Average monthly number of new shoots per leaf cluster for cut and uncut turtle grass plants sampled in Boca Ciega Bay (Tampa Bay), Fla., between August 1968 and November 1969.

DISCUSSION

Our findings show that turtle grass beds can sustain periodic cutting without apparent damage at intervals of about 2 months in the growing season. In deeper or warmer waters of the Gulf and Caribbean where turtle grass has a longer growing season, it may be practical to harvest leaves more than twice per year. Inherent, technical problems presented by offshore harvesting would probably be offset by the fact that turtle grass in deep water generally has longer leaves and greater biomass than plants growing in shallow areas (Burkholder et al., 1959; Phillips, 1960).

Offshore along the west coast of Florida estimates show that turtle grass grows over about 4 million acres of the sea floor, and in the Caribbean, turtle grass resources are even greater. Thus, the tonnage of turtle grass available for harvest is very large (Bauersfeld et al., 1969). However, from the standpoint of resource management, there are a number of questions that must be resolved before the harvest of turtle grass can be seriously considered by commercial enterprises. Principal queries include: (1) can turtle grass leaves regrow normally after more than two seasons of harvesting; (2) how are other plant and animal members of the turtle grass community influenced by harvesting operations; (3) what would be the consequences of removing vast amounts of primary production from the food webs in coastal waters; (4) would removal of foliage cause serious erosion of sediments in and around turtle grass beds; and (5) how would harvesting methods alter water clarity, and thereby influence populations of phytoplankton and pelagic fishes, and water recreation?

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THE INFLUENCE OF TEMPERATURE AND SALINITY ON THE TOXICITY OF CADMIUM TO THE FIDDLER CRAB, *UCA PUGILATOR*

JAMES O'HARA[1]

ABSTRACT

The concentrations of cadmium lethal to the fiddler crab, *Uca pugilator*, were determined for various environmental regimes of temperature and salinity. Mortality was greatest in high temperatures and low salinities when tested for 240 hr. Concentrations of cadmium were greatest in green gland followed by gill, hepatopancreas, and muscle.

The waste discharge of electroplating plants, lead and zinc mines, and chemical plants frequently contains toxic cadmium salts which contribute to the widespread environmental pollution (McKee and Wolf, 1963), and the importance of this pollutant has been stressed by its relationship with the crippling "itai-itai" disease of Japan (Kobayashi, 1971). The effects of cadmium on aquatic organisms have been investigated for numerous freshwater organisms (Doudoroff and Katz, 1953; Ball, 1967; Mount and Stephan, 1967), and while the cadmium is normally flushed down to the estuarine and marine environments, only Gardner and Yevich (1970), Jackim, Hamlin, and Sonis (1970), and recently Eisler (1971) have examined the effects of cadmium on estuarine forms. Eisler alone has reported the effects of normal variations in salinity and temperature on the toxic effect of cadmium on mummichogs.

The present report is part of a program to examine the effects of chronic exposure of cadmium to fiddler crab, *Uca pugilator*. This study examines the synergistic role of salinity and thermal stress on the acute toxicity of cadmium to the crabs.

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Manuscript accepted April 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

METHODS

Fifteen adult male ($\bar{x}$ = 2.2 g) and 10 adult female ($\bar{x}$ = 1.5 g) fiddler crabs were placed in 23 × 30 cm plastic boxes along with 250 ml of dilute filtered seawater. The containers were slightly tilted in the incubator so that the crabs could freely select total or partial immersion. No avoidance of the toxic solution was noted. Desired salinities were obtained by the addition of distilled water. The cadmium stock for all experiments was reagent grade $CdCl_2 \cdot 2\text{-}\frac{1}{2}\ H_2O$ made up to a stock solution of 1 mg Cd^{++} per ml water. Aliquots of this stock were added to each test chamber to bring the cadmium concentration to the desired levels of 1.0, 5.0, 10.0, 25.0, and 35.0 ppm Cd^{++}. All crabs were kept in constant temperature boxes on a 12-hr light-dark photoperiod for the 10-day duration of the experiment. The water was changed every third day to reduce the buildup of metabolic wastes and to keep the concentration of cadmium near the nominal level. Preliminary tests indicated no loss of cadmium from the test medium without organisms. Eisler (1971) showed less than 5% loss from similar concentrations of cadmium in dilute seawater. Dead organisms were removed every 24 hr during the tests.

To determine the synergistic effects of environmental stresses on the toxicity of cadmium, crabs were exposed to the different cadmium

concentrations in water of 10, 20, and 30‰ salinity maintained at 10°, 20°, or 30°C. Each experimental group had a control maintained in uncontaminated water, but subjected to the salinity and temperature stresses.

Cadmium concentrations in the tissues of crabs exposed to lethal concentrations were determined by use of radioactive cadmium (^{109}Cd) using the following procedure. Fifteen male and 15 female crabs were placed in 300 ml of filtered seawater of 20‰ salinity at 30°C. Each of three test chambers received 2.3 μc ^{109}Cd and an aliquot of stock soultion to bring the cadmium level to 5, 15, or 25 ppm Cd^{++}. These thermosaline regimes and cadmium concentrations were chosen because the acute toxicity tests show that they cause relatively high mortality rates. Four active animals (two males, two females) were sacrificed from each chamber at 0, 12, 24, 36, 48, and 60 hr. The animals were frozen until dissection of the tissues could be accomplished. Four tissues were digested and analyzed: hepatopancreas, gill, green gland, and thoracic muscle. Individual crabs were analyzed; since results from males and females showed no measurable difference, the results were pooled. Concentrations of ^{109}Cd were determined by liquid scintillation on a Packard Tricarb Model 3320 counter.[2] Since each 2.3 μc represented 1.5, 4.5, or 7.5 mg of cadmium in the test water, a simple ratio of counts per minute to microgram of cadmium was determined from spiked samples and used to calculate the amount of cadmium in the tissues. Concentrations of cadmium are expressed as parts per million wet weight of tissue.

RESULTS

ACUTE TOXICITY

In general, the higher temperatures and lower salinities produced the greatest cadmium toxicity. The susceptibility of fiddler crabs to cadmium was most pronounced in the thermosaline regime of 30°C and 10‰. The concentration fatal to 50% of the organisms in 240 hr (TLm-240 hr) was calculated to be 2.9 ppm Cd^{++} (American Public Health Association, 1971). At higher cadmium concentrations, the time required to kill 50% of the crabs was considerably reduced.

TABLE 1.—Cadmium concentrations (Cd^{++} in ppm) lethal to 50% of test organisms (TLm) at different salinities, times, and temperatures.

Salinity	Time	Temperature		
		10°C	20°C	30°C
‰	hr	ppm	ppm	ppm
10	48	--	--	11.0
	96	--	32.2	6.8
	144	51.0	21.3	4.0
	192	28.5	18.0	3.0
	240	15.7	11.8	2.9
20	48	--	--	28.0
	96	--	46.6	10.4
	144	--	23.0	5.2
	192	52.0	16.5	3.7
	240	42.0	9.5	3.5
30	48	--	--	33.3
	96	--	37.0	23.3
	144	--	29.6	7.6
	192	--	21.0	6.5
	240	47.0	17.9	5.7

Table 1 shows the influence of temperature, salinity, and cadmium concentration on the level of toxicant which kills 50% of the crabs in different time periods. The effect of temperature was extremely pronounced and TLm values were generally more influenced by temperature changes than by salinity levels within a thermal regime. The influence of salinity on the TLm-240 hr was most pronounced at 10°C and 10‰ and at higher cadmium concentrations in shorter times. The combined role of temperature and salinity on cadmium toxicity indicates that temperature is less influential at higher salinities.

TISSUE ACCUMULATION

Gills

In the first 12 hr of exposure, gill tissue accumulated cadmium in proportion to the exposure concentration (Figure 1). Thus, gill tissue from crabs exposed to 25 ppm Cd^{++} contained 110 ppm; gill tissue from those exposed

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

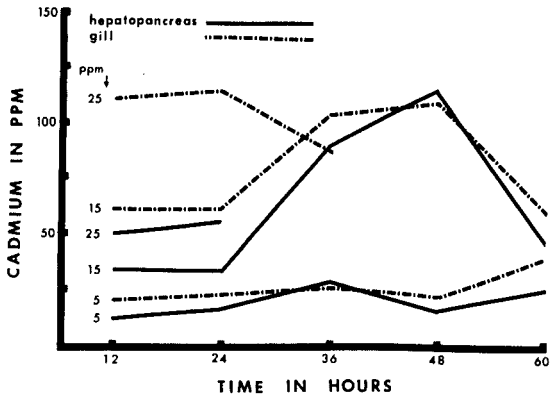

FIGURE 1.—Concentration of cadmium in gill and hepatopancreas of crabs in 5, 15 and 25 ppm Cd^{++} at 30°C, 20‰.

to 15 ppm Cd^{++} contained 59 ppm, while such tissue from those exposed to 5 ppm Cd^{++} contained 18 ppm. Each accumulation in gill tissue was about four times the concentration of cadmium in the surrounding water.

Gill tissues from crabs in 25 ppm Cd^{++} did not increase their cadmium concentration appreciably over 110 ppm in 24 hr and exhibited a decline in tissue concentration at 36 hr. The large mortality rate at 48 hr prevented reliable samples from being obtained. Gill tissue from crabs exposed to 15 ppm Cd^{++} showed an increase in cadmium content between 24 and 48 hr with a maximum accumulation of 109 ppm. The significance of the value around 110 ppm is unclear, but may represent a maximum tissue burden in terms of equilibrium with the external medium. The cadmium concentration in gill tissues from crabs sacrificed at 60 hr showed a marked reduction in cadmium content. Considering the large mortality of crabs in this concentration, the lower cadmium content in the tissues probably represents a reduced binding of the metal due to the destruction of tissue.

Crabs exposed to 5 ppm Cd^{++} continually concentrated cadmium in their gill tissue with a maximum of 39 ppm after 60 hr. No mortality occurred in this concentration, and only one animal died during this period in the acute toxicity tests. Significant mortality occurred only after 96 hr.

Hepatopancreas

The hepatopancreas from crabs in the different cadmium solutions concentrated cadmium about two times exposure level in 12 hr (25 ppm was concentrated to 50 ppm in tissue, 15 to 32 ppm in tissue, and 5 to 11 ppm in tissue). The hepatopancreas tissue in crabs exposed to the highest concentration was almost completely destroyed after 24 hr and precluded samples from these crabs (Figure 1). The hepatopancreas was changed from a firm glandular tissue to an amorphous and liquified condition. Crabs exposed to 15 ppm Cd^{++} showed an increase in cadmium levels to about 116 ppm in 48 hr, followed by a rapid decline. This decline might be associated with the destruction of the hepatopancreas tissue. Crabs exposed to water containing 5 ppm showed the same general increase in Cd^{++} concentration that was evident in gill tissue with a maximum of 24 ppm after 60 hr.

Green Gland

The bioaccumulation was highest in the green gland tissue (Figure 2) with maximum concentrations of 380 ppm in tissue from crabs exposed to 25 ppm, 171 ppm from crabs in 15 ppm, and 118 ppm from crabs in 5 ppm. These values are 12 to 20 times the exposure concentrations.

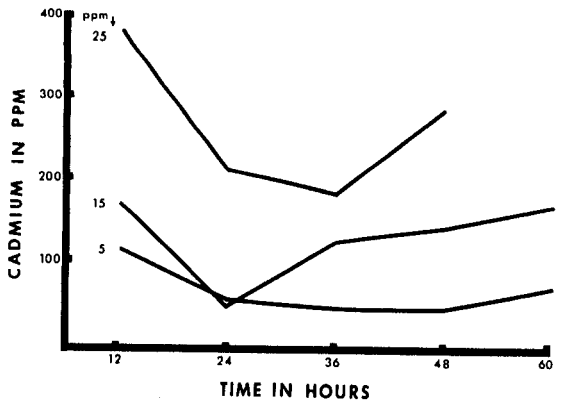

FIGURE 2.—Concentration of cadmium in green gland tissue of crabs in 5, 15 and 25 ppm Cd^{++} at 30°C, 20‰.

At all exposure levels the highest tissue accumulation occurred in the first 12 hr. At 24 hr, the concentrations in the green glands had shown a considerable decline and then increased steadily with values remaining over 10 times the exposure level. The 48-hr determination of 280 ppm is based on only two samples and needs verification.

Muscle

Muscle tissue remained almost constant over the entire time of the experiment, and tissue levels remained only slightly above the exposure levels with maximum concentrations of 29.3 ppm in crabs exposed to 25 ppm, 17.3 ppm from crabs in 15 ppm, and 8.9 ppm from crabs exposed to 5 ppm.

DISCUSSION

Cadmium toxicity is related to both temperature and salinity. The acute toxicity data for crabs maintained at different temperatures show a time delay in the onset of the lethal effect of cadmium. Whether this delay is due to differences in bioaccumulation rates or to differences in a temperature-dependent metabolic response to the metal remains to be examined. Fiddler crabs are often exposed to temperatures well in excess of 30°C, and higher temperatures would further accentuate the toxic effects of small amounts of cadmium.

There is a clear relationship of high susceptibility of fiddler crabs to cadmium in a low-salinity water. It has not been determined if this is due to interaction between the metal and the variety of salts in the seawater resulting in a nontoxic precipitate forming in proportion to the salinity (Bryan, 1971) or if the direction of the osmotic gradient in the higher salinities reduces the rate of entry of the metal.

The rapid accumulation of cadmium from the surrounding water results in considerable tissue destruction in the first 24 hr. High concentrations of cadmium were found in the gills and hepatopancreas of fiddler crabs. Similar results have been reported in crustacea exposed to zinc and mercury (Bryan, 1966; Vernberg and Vernberg, 1972) although high metal concentrations in the green glands were not reported for these metals. Gardner and Yevich (1970) reported gill tissue destruction in the mummichog beginning after 20 hr exposure to cadmium. The data presented here for Cd^{++} concentrations in fiddler crab gills indicate that 24 hr is the time when the cadmium content in crabs exposed to high Cd^{++} concentrations is reduced by tissue destruction. Yager and Harry (1966) showed a decrease in cadmium concentration in the liver of snails exposed to high concentrations of cadmium but attributed this decline to individual variation rather than to tissue destruction.

Mount and Stephan (1967) suggested that there is a threshold concentration of cadmium in the gill tissue of fishes and that death occurs when this concentration is exceeded. This threshold may be around 110 ppm for fiddler crabs.

The relationship between cadmium toxicity and temperature and salinity variation illustrates that physiological stresses, even within the usual ecological range experienced by the animals, lowers the tolerance of organisms to environmental pollutants.

ACKNOWLEDGMENTS

I wish to express thanks to Mrs. Barbara Caldwell and Mrs. Cary Clark for their technical help and to Dr. Winona B. Vernberg for her support and advice on the preparation of the manuscript. This study was supported by the Belle W. Baruch Coastal Research Institute, University of South Carolina.

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FISHES, MACROINVERTEBRATES, AND HYDROLOGICAL CONDITIONS OF UPLAND CANALS IN TAMPA BAY, FLORIDA[1]

WILLIAM N. LINDALL, JR., JOHN R. HALL, AND CARL H. SALOMAN[2]

ABSTRACT

Faced with statutory restraints that prohibit dredging and filling of estuarine bottoms, coastal developers have turned to alternate methods of providing water front property for homesites. One method, recently used in Tampa Bay, Fla., is the construction of access canals that lead from open water to upland acreage.

This paper presents biological and hydrological data from new upland canals together with some comparative data from older upland canals and bayfill canals. In all types of canals, as presently engineered, stratified, stagnant water causes low levels of dissolved oxygen in summer months, resulting in mortality or emigration among resident organisms. Means of alleviating the problems are discussed.

Among Florida's 322,000 ha of estuarine habitat less than 2 m deep, about 24,000 ha have been filled by coastal developers (Marshall, 1968). Public indignation over indiscriminant and unregulated exploitation of these areas has stimulated legislative action designed to conserve and protect natural resources in estuarine areas that remain (Linton and Cooper, 1971). Faced with statutory restraints, coastal developers have, in some instances, abandoned plans for further bay filling and now seek alternate ways to create premium homesites that will satisfy ever-increasing public demand for waterfront property. One way is the construction of access canals that lead from open water to upland acreage (Barada and Partington, 1972). This method was recently used in Tampa Bay in northeast St. Petersburg, Fla., to connect a housing development with the estuary.

Shortly after draglines removed earth plugs between the excavated canal system and the bay, property owners gave this Laboratory permission to monitor the canals so that ecological conditions in the manmade waterways could be documented. This report contains ecological data recorded at canal and control stations during the first 13 months after the waterway system was completed. Conditions within the upland canal are compared with those recorded in bayfill canals of Boca Ciega Bay, Fla., and older upland canals.

DESCRIPTION OF AREA

The study area, known as Tanglewood Estates, is located at the southern end of Old Tampa Bay on a tract of land that was originally drained by a small tidal inlet of approximately 0.5 ha (Figures 1 and 2). During development, the inlet was dammed and pumped dry. Canals were dug to a depth of approximately 4 m below mean low water and stabilized by concrete seawalls (Figure 3). Bay water was introduced into the ditches in June 1970 creating a canal system of approximately 1.6 ha. Average tidal range in the canal system is about 1 m.

PROCEDURES

Hydrological (five stations) and biological (four stations) samples were collected monthly

[1] Contribution No. 78, Gulf Coastal Fisheries Center, St. Petersburg Beach Laboratory, National Marine Fisheries Service.

[2] Gulf Coastal Fisheries Center, National Marine Fisheries Service, NOAA, 75 33d Avenue, St. Petersburg Beach, FL 33706.

Manuscript accepted July 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

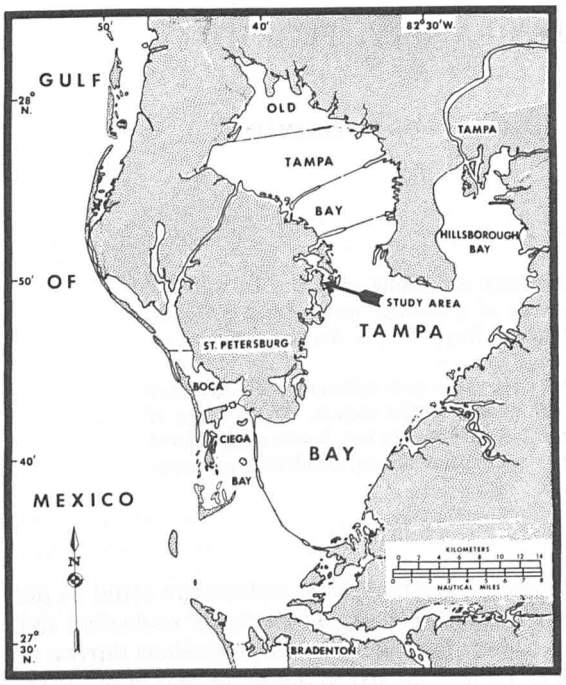
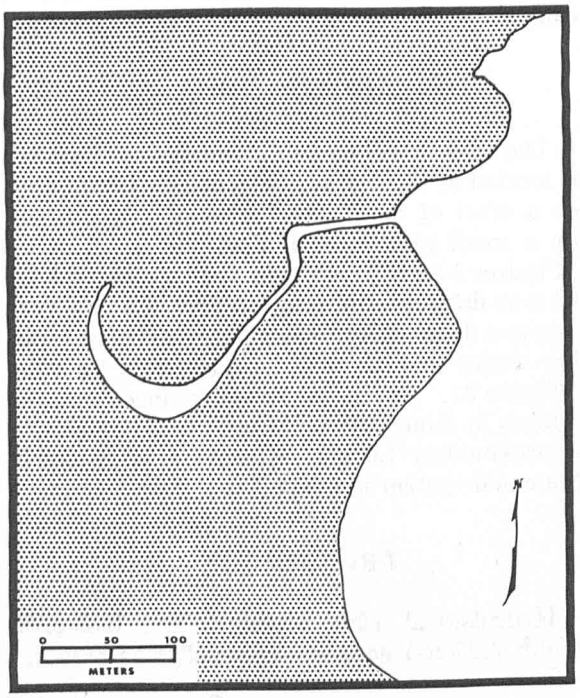


FIGURE 1.—Tampa Bay, Fla., showing location of study area.



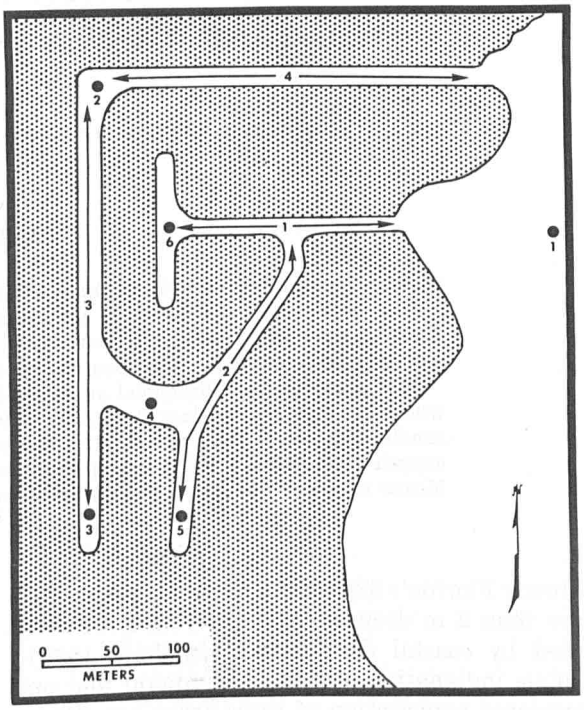


FIGURE 3.—Study area after alteration (hydrologic station ●; trawl station ⟷).

within the canals between 0830 and 1130 hr from August 1970 through August 1971. Also, a hydrological control station, Station 1, was established in the bayou adjacent to the development site to monitor ambient water conditions in a natural area (Figure 3). Hydrological factors were recorded from surface and bottom water and included water temperature, dissolved oxygen, and salinity. Temperature was recorded to the nearest tenth of a degree with a handheld mercury thermometer; dissolved oxygen was determined by a modified Winkler method (Strickland and Parsons, 1968); and salinity was determined with a Model 10401 TS Goldberg refractometer[3].

Fish and invertebrates were collected with a 4.8-m otter trawl composed of a 2.5-cm stretched

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

FIGURE 2.—Study area before alteration.

mesh body fitted with a 0.6-cm mesh inner liner in the cod end. No suitable control station for trawling was established in the adjacent bayou because of numerous snags and oyster beds. Specimens from the trawl were killed in a 10% Formalin-seawater solution and transferred to 50% isopropyl alcohol for preservation. All specimens were identified to species and enumerated.

RESULTS

TEMPERATURE

Only small differences were recorded between surface and bottom water temperature at canal stations or the control station in any sampling period (Table 1). With few exceptions, bottom temperatures were slightly lower than surface temperatures in all months except July and August 1971 when the situation was reversed. The greatest difference observed was at Station 4 in February when bottom temperature was 1.8°C lower than temperature at the surface.

SALINITY

Drought conditions prevailed throughout the Tampa Bay area during most of the study period, and, as a result, salinity rose almost steadily from 23.2‰ in August 1970 to greater than 30.0‰ by July 1971 (Table 1). During this period salinity at the control station was similar to that in the canals. Heavy rains in August 1971 reduced salinity values considerably. This was the only time during the study when stratification occurred at all stations. Bottom salinity at the control station was 9.0‰ higher than

TABLE 1.—Monthly hydrologic measurements of surface and bottom water, August 1970-August 1971.

Stn.	Depth	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Mean
							Temperature (°C)								
1	S	29.8	27.6	24.8	14.8	17.4	14.9	21.0	19.0	26.1	28.0	29.5	28.5	28.5	23.8
	B	--	27.5	24.7	14.7	16.7	14.7	20.8	19.0	26.4	27.8	29.5	29.0	29.4	23.4
2	S	29.5	27.4	24.8	14.8	17.2	15.2	20.8	19.2	25.8	27.8	29.0	29.0	28.4	23.8
	B	--	27.7	25.2	14.5	16.5	14.8	20.2	18.8	25.5	27.4	29.0	30.5	29.5	23.3
3	S	29.0	28.8	25.8	15.7	17.2	15.6	20.6	19.4	25.3	27.8	29.5	29.5	28.4	24.1
	B	--	28.5	24.7	15.5	17.0	15.6	19.7	18.4	25.1	27.2	29.4	30.1	30.0	23.4
4	S	29.5	28.7	25.5	15.2	17.3	16.1	20.6	18.7	25.5	28.0	29.4	29.1	28.5	24.0
	B	--	28.0	24.5	14.2	16.8	15.2	18.8	18.3	25.6	27.0	29.4	29.8	29.8	23.1
5	S	29.5	27.9	25.8	15.8	17.2	15.3	20.9	19.0	25.5	28.0	30.5	29.4	28.8	24.1
	B	--	27.8	24.9	15.3	17.0	15.2	20.7	19.1	25.5	27.0	30.0	30.3	29.8	23.6
6	S	29.5	28.1	25.2	15.5	17.7	16.0	21.0	19.5	25.9	28.2	30.0	29.1	28.8	24.2
	B	--	28.0	25.2	15.3	17.3	15.2	20.8	19.6	25.9	27.4	30.0	29.4	29.3	23.6
							Salinity (‰)								
1	S	24.72	25.67	25.67	27.61	29.00	29.06	26.72	29.78	30.06	29.94	31.39	30.17	13.28	27.16
	B	--	25.56	26.00	27.67	29.11	28.94	26.67	29.83	30.06	29.89	31.28	30.00	22.22	28.10
2	S	23.44	25.00	26.56	28.00	28.78	29.00	27.22	29.72	30.00	29.17	30.06	29.94	13.33	26.94
	B	--	25.28	26.56	27.94	28.72	29.06	27.94	29.67	29.89	29.33	30.72	30.22	27.89	28.60
3	S	23.22	25.11	26.11	27.94	29.00	29.06	27.39	29.44	29.89	29.17	30.61	29.61	13.61	26.94
	B	--	25.28	26.11	27.94	29.00	28.94	27.78	29.56	29.89	29.83	30.39	30.11	28.61	28.62
4	S	23.39	24.89	26.17	28.00	29.06	28.83	27.72	29.06	30.00	29.28	30.33	29.94	13.89	26.97
	B	--	24.56	26.44	27.89	29.06	29.06	27.67	30.06	30.11	29.72	30.83	29.00	28.00	28.62
5	S	23.39	25.11	26.39	28.06	28.94	29.00	27.61	29.44	29.89	29.61	30.72	29.28	13.89	27.03
	B	--	25.44	25.83	28.00	28.94	28.94	27.67	29.72	29.89	29.17	30.72	30.06	26.78	28.43
6	S	25.22	24.67	26.39	27.94	29.11	29.06	27.28	29.17	29.94	29.44	30.28	28.67	14.06	27.01
	B	--	24.56	26.28	27.94	28.89	28.83	27.50	29.83	29.89	29.83	30.44	29.00	25.72	28.23
							Dissolved oxygen (ml/liter)								
1	S	3.87	3.06	3.46	5.80	4.67	5.64	4.35	4.75	4.03	3.06	2.90	2.58	2.34	3.86
	B	--	3.62	3.38	5.64	4.83	5.23	4.35	4.67	4.11	2.98	3.06	2.66	2.18	3.89
2	S	4.19	3.87	4.43	5.72	4.43	5.07	4.67	4.91	3.22	4.27	3.14	2.18	3.63	4.13
	B	--	3.78	4.03	5.15	3.95	4.75	2.49	4.19	1.37	3.95	3.14	1.86	0.89	3.30
3	S	4.35	2.98	4.03	5.47	4.99	5.07	4.91	3.95	2.74	3.95	4.35	3.14	4.03	4.15
	B	--	2.66	2.42	5.40	4.51	4.35	1.13	3.10	1.62	2.98	3.46	0.00	0.82	2.70
4	S	4.35	2.26	4.27	5.64	4.75	5.31	4.67	3.78	2.66	4.59	3.62	3.30	4.67	4.14
	B	--	2.02	2.42	4.67	3.70	4.59	0.57	3.46	2.22	2.00	2.50	0.66	0.65	2.46
5	S	3.62	3.06	4.43	5.40	4.85	5.72	3.95	4.27	2.50	3.87	3.87	3.54	4.99	4.16
	B	--	2.90	4.35	5.23	4.75	4.59	2.66	3.14	2.34	2.98	3.81	0.08	0.57	3.12
6	S	4.19	2.90	4.51	5.64	5.15	5.23	4.75	4.67	3.30	3.22	3.71	2.98	4.43	4.12
	B	--	2.82	4.35	5.55	5.14	4.75	4.59	4.27	2.42	3.14	3.38	2.50	0.17	3.59

the surface. The stratification was even more evident at canal stations where the difference between surface and bottom values ranged between 11.6‰ (Station 6) and 15.0‰ (Station 3). In general, the most landward stations exhibited the greatest differences between surface and bottom salinities.

OXYGEN

Daytime concentrations of dissolved oxygen at the surface and bottom for each station are shown in Table 1. Only at the control station were surface and bottom values similar, varying linity at the control station was 9.0‰ higher than no more than 0.6 ml/liter at any one sampling time throughout the year. At this station the lowest observed concentration was 2.1 ml/liter (August 1971). Surface oxygen values within the canal system were comparable with those at the control station throughout the year. However, bottom oxygen dropped in the canals in February when less than 2.0 ml/liter was recorded at Stations 3 and 4. These values rose above 3.0 ml/liter in March, but in April and May dissolved oxygen near 2.0 ml/liter or less was recorded at several canal stations. In July less than 1.0 ml/liter was recorded at Stations 3, 4, and 5, and by August less than 1.0 ml/liter of oxygen was recorded at the bottom at all canal stations.

To determine the diel changes in oxygen concentration during the July sampling period, a 24-hr sampling program was conducted at each station. Results showed that surface and bottom values were similar only at the control station (Figure 4). Surface oxygen concentration in the canals corresponded with values recorded at the control station and never fell below 2.0 ml/liter. However, at all canal stations the bottom was nearly anoxic throughout the 24-hr sampling period.

FISHES AND MACROINVERTEBRATES

Thirty-six species and 10,497 individuals of vertebrates and invertebrates were collected within the canals during the year (Table 2). Of the 36 species, 32 were finfish (23 of sport or commercial value), 1 was the diamondback

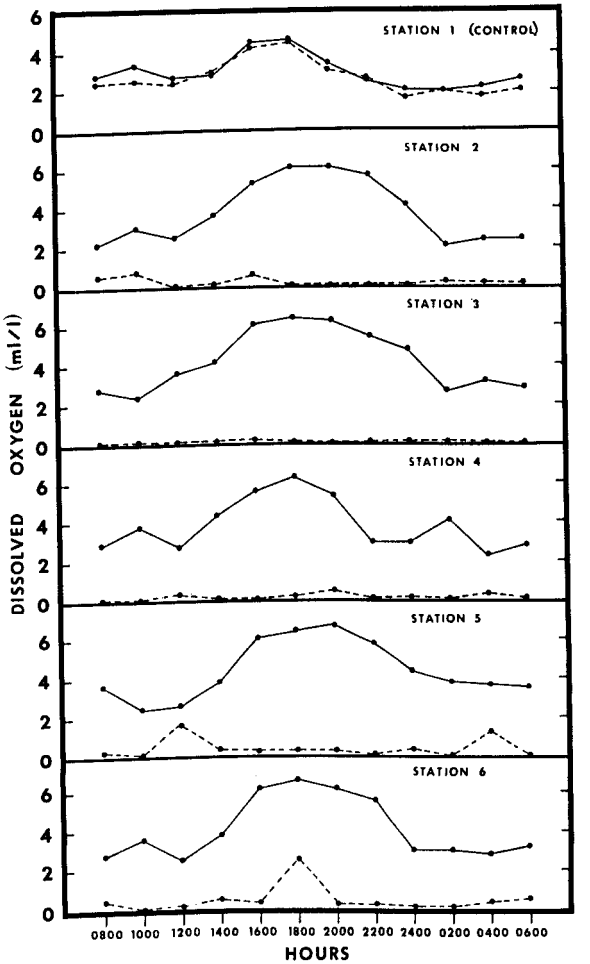


FIGURE 4.—Results of 24-hr oxygen survey in July 1971 (surface · ———— ·; bottom · -------- ·).

terrapin, *Malaclemys terrapin*, and 3 were commercially important invertebrates (blue crab, *Callinectes sapidus;* pink shrimp, *Penaeus duorarum;* and brief squid, *Lolliguncula brevis*).

The four species of fish caught in greatest abundance represented 92% of the total number of specimens. They were the bay anchovy (*Anchoa mitchilli*), spotfin mojarra (*Eucinostomus argenteus*), spot (*Leiostomus xanthurus*), and silver jenny (*Eucinostomus gula*). The bay anchovy alone made up nearly 72% of the total.

The brief squid was by far the most abundant invertebrate (84% of all invertebrates collected)

TABLE 2.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at all stations from August 1970 through August 1971. No individual collected in July and August 1971.

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
												Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:													
Anchoa mitchilli[1]	56	539	1,582	26	0	93	698	1,376	746	16	2,425	7,557	72.0
Eucinostomus argenteus[1,2]	0	120	135	241	220	153	16	25	6	0	5	921	8.8
Leiostomus xanthurus[1,2]	0	1	0	0	26	24	108	661	1	0	0	821	7.8
Eucinostomus gula[1,2]	0	0	18	82	164	99	1	8	0	0	0	372	3.5
Micropogon undulatus[1,2]	0	0	0	0	0	0	1	20	7	34	9	71	0.7
Cynoscion arenarius[1,2]	0	0	0	3	10	8	20	8	0	0	2	51	0.5
Menticirrhus americanus[1,2]	0	0	3	15	13	1	1	0	1	4	5	43	0.4
Pogonias cromis[1,2]	0	0	1	0	3	7	4	4	4	0	1	24	0.2
Archosargus probatocephalus[1,2]	0	0	0	2	10	4	2	1	1	2	1	23	0.2
Lagodon rhomboides[1,2]	0	0	1	4	6	3	0	6	1	0	0	21	0.2
Microgobius gulosus[2]	0	0	0	0	0	0	1	11	2	0	0	14	0.1
Cynoscion nebulosus[1,2]	0	3	4	4	0	0	1	0	0	0	2	14	0.1
Chaetodipterus faber[1]	0	0	4	0	1	2	0	1	1	0	4	13	0.1
Arius felis[1,2]	0	0	0	0	1	0	3	5	3	0	0	12	0.1
Malaclemys terrapin	0	0	0	2	0	0	0	1	5	4	0	12	0.1
Bairdiella chrysura[1,2]	0	0	1	0	2	5	1	0	0	0	1	10	0.1
Gobiosoma bosci[2]	0	0	0	0	0	0	0	7	1	1	0	9	0.1
Prionotus tribulus[2]	0	1	1	4	1	0	0	0	0	0	0	7	0.1
Orthopristis chrysoptera[1,2]	0	0	1	0	0	0	0	2	3	0	1	7	0.1
Sphoeroides nephelus[1]	0	0	0	3	1	1	0	0	0	0	0	5	0.1
Opisthonema oglinum[1]	0	0	0	0	0	0	0	0	0	0	4	4	0.0
Dasyatis sabina[2]	0	0	1	0	0	0	2	0	0	0	0	3	0.0
Mugil cephalus[1,2]	0	0	0	0	0	1	1	0	0	0	0	2	0.0
Chloroscombrus chrysurus[1]	0	0	0	0	0	0	0	0	0	2	0	2	0.0
Anchoa hepsetus[1]	0	0	0	0	0	0	0	0	0	0	2	2	0.0
Achirus lineatus[2]	0	0	0	0	0	0	0	0	0	0	2	2	0.0
Synodus foetens[1,2]	0	0	0	0	1	0	0	0	0	0	0	1	0.0
Opsanus beta[2]	0	0	0	0	0	0	0	1	0	0	0	1	0.0
Symphurus plagiusa[2]	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Sciaenops ocellata[1,2]	0	0	0	0	1	0	0	0	0	0	0	1	0.0
Paralichthys albigutta[1,2]	0	0	0	1	0	0	0	0	0	0	0	1	0.0
Chasmodes saburrae[2]	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Gymnura micrura[2]	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Invertebrates:													
Callinectes sapidus[1,2]	0	8	2	2	1	5	3	9	12	4	1	47	0.5
Penaeus duorarum[1,2]	0	4	2	7	2	4	5	1	0	0	1	26	0.3
Lolliguncula brevis[1]	0	45	55	93	43	4	15	6	29	87	20	395	3.8
Total species	1	8	15	15	18	19	18	19	16	9	17	36	
Total individuals	56	721	1,811	489	506	417	883	2,153	821	154	2,485	10,497	100.0

[1] Of commercial or sport value.
[2] Demersal or bottom feeder.

and made up nearly 4% of the total number of animals collected during the year.

The first trawl sample was made in August 1970, 2 months after bay water was introduced in the canal system. At that time the only species of fish found in the canals was the bay anchovy, and 98% of the specimens were taken at Station 4 (Figure 3; Tables 3, 4, 5, 6). By September, the blue crab, pink shrimp, brief squid, and four additional species of finfish were caught within the canal system. Station 4 contained seven species of vertebrates and invertebrates while Stations 2 and 3 contained five species each. No specimens were yet found at Station 1. In October, 5 months after water was introduced, fishes and invertebrates were found in all canals, and a total of 15 species were collected. Station 4, with 11 species, still contained the greatest faunal diversity. Stations 1, 2, and 3 contained 10, 5, and 4 species, respectively.

Through the winter, spring, and early summer months (November through June) an average of 16 species per month was collected throughout the area. The number of species and individuals at each station declined in April and May corresponding to reduction in dissolved oxygen, but in June the number of species and individuals increased again at all stations.

TABLE 3.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station I from August 1970 through August 1971. No individual collected in August and September 1970 and in July and August 1971.

Species	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
										Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:											
Anchoa mitchilli	118	16	0	1	77	31	0	9	412	664	58.9
Eucinostomus argenteus	49	1	6	51	13	9	5	0	4	138	12.3
Leiostomus xanthurus	0	0	2	3	41	50	0	0	0	96	8.5
Eucinostomus gula	10	3	41	39	0	0	0	0	0	93	8.3
Micropogon undulatus	0	0	0	0	0	1	0	21	0	22	2.0
Menticirrhus americanus	1	0	4	0	0	0	1	0	0	6	0.5
Archosargus probatocephalus	0	1	2	0	1	0	1	0	0	5	0.4
Malaclemys terrapin	0	2	0	0	0	1	0	2	0	5	0.4
Cynoscion arenarius	0	1	0	1	0	0	0	0	2	4	0.4
Lagodon rhomboides	0	0	0	2	0	1	1	0	0	4	0.4
Opisthonema oglinum	0	0	0	0	0	0	0	0	4	4	0.4
Microgobius gulosus	0	0	0	0	0	2	2	0	0	4	0.4
Chaetodipterus faber	1	0	0	0	0	0	1	0	1	3	0.3
Prionotus tribulus	1	2	0	0	0	0	0	0	0	3	0.3
Cynoscion nebulosus	0	2	0	0	0	0	0	0	0	2	0.2
Pogonias cromis	0	0	0	0	0	0	0	2	0	2	0.2
Orthopristis chrysoptera	1	0	0	0	0	0	0	0	1	2	0.2
Sphoeroides nephelus	0	2	0	0	0	0	0	0	0	2	0.2
Bairdiella chrysura	0	0	0	1	0	0	0	0	0	1	0.1
Chloroscombrus chrysurus	0	0	0	0	0	0	0	1	0	1	0.1
Gobiosoma bosci	0	0	0	0	0	1	0	0	0	1	0.1
Invertebrates:											
Lolliguncula brevis	5	3	6	1	4	0	0	16	5	40	3.6
Callinectes sapidus	1	0	0	2	3	1	7	3	1	18	1.6
Penaeus duorarum	2	1	0	1	2	0	0	0	0	6	0.5
Total species	10	10	6	9	8	9	8	7	8	24	
Total individuals	189	134	61	101	142	97	20	52	430	1,126	100.0

In the latter part of June, after our monthly sample, a severe outbreak of red tide occurred in a large part of Tampa Bay, including the study area. Massive fish kills were noted in the Bay through most of July (Karen Steidinger, Florida Department of Natural Resources Biological Laboratory, pers. comm.). Data are not available on the size of the kill, but an estimated 3,000 tons of various species were removed from beaches in the Bay area (Lloyd Dove, St. Petersburg Public Works Director, pers. comm.). No live specimens were collected in the study area during July or August. The absence of specimens during this period corresponded with low dissolved oxygen at the bottom.

DISCUSSION

At least 36 of the 265 species of finfish, shrimp, and crabs known to inhabit the Tampa Bay area (Springer and Woodburn, 1960; Dragovich and Kelly, 1964; Sykes and Finucane, 1966) utilized the study area throughout most of the year. It was not surprising to find bay anchovy as the dominant species as it is known to be dominant in bayfill canals of Boca Ciega Bay, Fla., (Taylor and Saloman, 1968) and in housing development canals in Texas (unpublished data[4]).

Although the majority of individual fishes taken in the study area was plankton feeders, most of the species (26) were demersal or bottom feeders based on knowledge of their life histories (Darnell, 1958; Springer and Woodburn, 1960; Odum, 1971). Taylor and Saloman (1968), using the same trawl size and procedures as in our study, reported that no demersal fishes were taken in bayfill canals of Boca Ciega Bay. However, examination of additional, unpublished data[5] from canals in Boca Ciega Bay showed that

[4] Unpublished data on file at Gulf Coastal Fisheries Center, National Marine Fisheries Service, NOAA, Fort Crockett, Building 302, Galveston, TX 77550.

[5] Unpublished data on file at Gulf Coastal Fisheries Center, National Marine Fisheries Service, NOAA, 75 33d Avenue, St. Petersburg, FL 33706.

TABLE 4.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station 2 from August 1970 through August 1971. No individual collected in August 1970 and in July and August 1971.

Species	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
											Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:												
Anchoa mitchilli	23	800	8	0	21	384	1,083	480	2	1,392	4,193	86.0
Leiostomus xanthurus	0	0	0	5	1	0	4	0	0	0	353	7.2
Eucinostomus argenteus	13	46	0	29	40	3	5	1	0	0	137	2.8
Eucinostomus gula	0	5	1	22	15	1	0	0	0	0	44	0.9
Micropogon undulatus	0	0	0	0	0	0	4	0	8	1	13	0.3
Lagodon rhomboides	0	0	0	5	1	0	4	0	0	0	10	0.2
Menticirrhus americanus	0	0	0	3	0	0	0	0	4	2	9	0.2
Cynoscion arenarius	0	0	0	1	0	3	3	0	0	0	7	0.1
Gobiosoma bosci	0	0	0	0	0	0	4	1	1	0	6	0.1
Bairdiella chrysura	0	0	0	0	4	0	0	0	0	1	5	0.1
Arius felis	0	0	0	0	0	0	3	1	0	0	4	0.1
Malaclemys terrapin	0	0	0	0	0	0	0	3	1	0	4	0.1
Cynoscion nebulosus	2	0	0	0	0	0	0	0	0	1	3	0.1
Sphoeroides nephelus	0	0	1	1	1	0	0	0	0	0	3	0.1
Microgobius gulosus	0	0	0	0	0	0	3	0	0	0	3	0.1
Archosargus probatocephalus	0	0	0	2	0	0	0	0	0	0	2	0.0
Chaetodipterus faber	0	0	0	0	0	0	0	0	0	2	2	0.0
Pogonias cromis	0	0	0	0	1	0	0	0	0	1	2	0.0
Anchoa hepsetus	0	0	0	0	0	0	0	0	0	0	2	0.0
Gymnura micrura	0	0	0	0	1	0	0	0	0	0	1	0.0
Prionotus tribulus	0	0	1	0	0	0	0	0	0	0	1	0.0
Synodus foetens	0	0	0	1	0	0	0	0	0	0	1	0.0
Chasmodes saburrae	0	0	0	0	1	0	0	0	0	0	1	0.0
Opsanus beta	0	0	0	0	0	0	1	0	0	0	1	0.0
Dasyatis sabina	0	1	0	0	0	0	0	0	0	0	1	0.0
Invertebrates:												
Lolliguncula brevis	2	15	0	2	0	0	2	18	13	4	56	1.2
Callinectes sapidus	4	0	2	1	0	0	1	2	0	0	10	0.2
Penaeus duorarum	0	0	3	1	0	0	0	0	0	1	5	0.1
Total species	5	5	6	12	10	5	12	8	6	10	28	
Total individuals	44	867	16	92	92	426	1,399	507	29	1,407	4,879	100.0

at least 13 of 21 species of fishes collected by trawl may be considered bottom feeders. Based on these data, it appears that new upland canals provide a better habitat for fishes than do much older bayfill canals in the sense that the former support greater abundance of species and individuals.

Undoubtedly, the lack of fish in the canals of Tanglewood Estates during the last 2 months of the study was due in part to effects of the red tide. Decomposition of the dead fish increased oxygen demand on the system during this period, but decline in dissolved oxygen in April and May and corresponding decline in the number of species and individuals indicated the system was deteriorating prior to the red tide outbreak. Our continued study will determine to what degree the system is stressed by low summer oxygen in the absence of red tide.

Others working in the Tampa Bay system have reported low bottom oxygen in areas of poor water circulation and soft sediment. Dragovich, Kelly, and Finucane (1966) recorded less than 2 ml/liter in June and August from a dredged location in central Boca Ciega Bay. In dredged and undredged areas of Hillsborough Bay, reduced oxygen near the bottom is common during the summer. There, the lack of dissolved oxygen has been attributed to sludge deposited from sewage, as well as high water temperature and poor water circulation (Saloman, Finucane, and Kelly, 1964; U.S. Federal Water Pollution Control Administration, Southeast Region, 1969). A similar condition is shared by older upland canals throughout south Florida (Barada and Partington, 1972) and certain housing development canals in Texas (see footnote 4). Oxygen depletion in all of these areas is the result of poor

TABLE 5.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station 3 from August 1970 through August 1971. No individual collected in July and August 1971.

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
												Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:													
Anchoa mitchilli	1	337	39	1	0	19	29	43	266	2	506	1,243	53.8
Eucinostomus argenteus	0	26	11	145	144	41	0	11	0	0	0	378	16.4
Leiostomus xanthurus	0	0	0	0	0	7	14	310	0	0	0	331	14.3
Eucinostomus gula	0	0	0	36	84	19	0	8	0	0	0	147	6.4
Cynoscion arenarius	0	0	0	2	9	6	0	5	0	0	0	22	1.0
Micropogon undulatus	0	0	0	0	0	0	0	5	5	3	4	17	0.7
Menticirrhus americanus	0	0	0	7	6	1	0	0	0	0	0	14	0.6
Pogonias cromis	0	0	0	0	1	2	4	3	1	0	0	11	0.5
Archosargus probatocephalus	0	0	0	0	2	2	1	1	0	0	0	6	0.3
Chaetodipterus faber	0	0	1	0	1	2	0	1	0	0	1	6	0.3
Arius felis	0	0	0	0	0	0	1	1	2	0	0	4	0.2
Cynoscion nebulosus	0	0	0	2	0	0	1	0	0	0	0	3	0.1
Microgobius gulosus	0	0	0	0	0	0	0	3	0	0	0	3	0.1
Lagodon rhomboides	0	0	0	1	0	0	0	1	0	0	0	2	0.1
Mugil cephalus	0	0	0	0	0	1	1	0	0	0	0	2	0.1
Achirus lineatus	0	0	0	0	0	0	0	0	0	0	2	2	0.1
Gobiosoma bosci	0	0	0	0	0	0	0	2	0	0	0	2	0.1
Malaclemys terrapin	0	0	0	0	0	0	0	0	2	0	0	2	0.1
Bairdiella chrysura	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Chloroscombrus chrysurus	0	0	0	0	0	0	0	0	0	1	0	1	0.0
Dasyatis sabina	0	0	0	0	0	0	1	0	0	0	0	1	0.0
Orthopristis chrysoptera	0	0	0	0	0	0	0	0	1	0	0	1	0.0
Prionotus tribulus	0	1	0	0	0	0	0	0	0	0	0	1	0.0
Symphurus plagiusa	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Invertebrates:													
Lolliguncula brevis	0	15	4	65	2	2	1	4	0	1	4	98	4.2
Callinectes sapidus	0	2	0	0	0	0	0	5	0	1	0	8	0.4
Penaeus duorarum	0	0	0	1	1	0	1	1	0	0	0	4	0.2
Total species	1	5	4	9	9	13	10	16	6	5	5	27	
Total individuals	1	381	55	260	250	104	54	404	277	8	517	2,311	100.0

circulation, accumulation of soft, organically rich sediments, and storm-water runoff from residential and agricultural areas.

Developers in the Tampa Bay area could reduce these problems in future projects through better design of canal systems. This would involve: (1) elimination of dead-end canals and (2) limiting depths to the euphotic zone approximately 1.5 m (5 ft) below mean low water. A flow-through system without deadends would insure better tidal exchange and circulation. Also, by limiting depths to approximately 1.5 m below mean low water, the canals probably would not serve as silt traps as readily as deeper canals, and stratification of the water column would be eliminated. In addition, light penetration would occur throughout the water column thereby allowing oxygen production through photosynthesis by benthic algae and diatoms.

Elimination of dead-end canals and limiting depths to the photic zone will not necessarily insure adequate flushing, however. A major factor that must be taken into account is water exchange through tidal action. Tidal range in most of Florida is very small, varying from 0.3 m to about 1.0 m, and will provide adequate water exchange in canals only short distances from the shoreline. Our data show serious oxygen depletion in the deep, dead-end canals only 150 m inland of the shoreline (Station 6). A safe distance for shallower, flow-through canals can best be determined by an environmental engineer knowledgeable of the tidal range and circulation patterns adjacent to the upland to be developed.

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TABLE 6.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station 4 from August 1970 through August 1971. No individual collected in July and August 1971.

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
												Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:													
Anchoa mitchilli	55	179	625	1	0	52	208	219	0	3	115	1,457	66.8
Eucinostomus argenteus	0	81	29	95	41	21	0	0	0	0	1	268	12.3
Eucinostomus gula	0	0	3	42	17	26	0	0	0	0	0	88	4.0
Leiostomus xanthurus	0	1	0	0	0	7	18	15	0	0	0	41	1.9
Micropogon undulatus	0	0	0	0	0	0	1	10	2	2	4	19	0.9
Cynoscion arenarius	0	0	0	0	0	1	17	0	0	0	0	18	0.8
Menticirrhus americanus	0	0	2	8	0	0	1	0	0	0	3	14	0.6
Archosargus probatocephalus	0	0	0	1	4	2	0	0	0	2	1	10	0.5
Pogonias cromis	0	0	1	0	2	4	0	1	1	0	0	8	0.4
Cynoscion nebulosus	0	1	4	0	0	0	0	0	0	0	1	6	0.3
Lagodon rhomboides	0	0	1	3	1	0	0	0	0	0	0	5	0.2
Arius felis	0	0	0	0	1	0	2	1	0	0	0	4	0.2
Microgobius gulosus	0	0	0	0	0	0	1	3	0	0	0	4	0.2
Orthopristis chrysoptera	0	0	0	0	0	0	0	2	2	0	0	4	0.2
Bairdiella chrysura	0	0	1	0	2	0	0	0	0	0	0	3	0.1
Chaetodipterus faber	0	0	2	0	0	0	0	0	0	0	0	2	0.1
Prionotus tribulus	0	0	0	1	1	0	0	0	0	0	0	2	0.1
Sciaenops ocellata	0	0	0	0	1	0	0	0	0	0	0	1	0.1
Paralichthys albigutta	0	0	0	1	0	0	0	0	0	0	0	1	0.1
Dasyatis sabina	0	0	0	0	0	0	1	0	0	0	0	1	0.1
Malaclemys terrapin	0	0	0	0	0	0	0	0	0	1	0	1	0.1
Invertebrates:													
Lolliguncula brevis	0	28	31	25	33	1	10	0	9	57	7	201	9.2
Callinectes sapidus	0	2	1	0	0	3	0	2	3	0	0	11	0.5
Penaeus duorarum	0	4	0	2	0	3	2	0	0	0	0	11	0.5
Total species	1	7	11	10	10	10	10	8	5	5	7	24	
Total individuals	55	296	700	179	103	120	263	251	17	64	132	2,180	100.0

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MATURITY, SEX RATIO, AND SIZE COMPOSITION OF THE NATURAL POPULATION OF AMERICAN LOBSTER, *HOMARUS AMERICANUS*, ALONG THE MAINE COAST[1]

JAY S. KROUSE[2]

ABSTRACT

From 1968 through 1970, American lobsters, *Homarus americanus*, were collected in coastal water near Boothbay Harbor, Maine. Length-frequency histograms graphically displayed the marked effects of high commercial exploitation on the natural lobster population. Sex ratios approximated a 1:1 relationship for sublegal lobsters (Maine minimum size is 81-mm carapace length). Length-weight relationship was determined for 454 lobsters. Shedding was observed to begin in spring and then peak in late summer.

On the basis of ovarian classification, presence of spermatophores in seminal receptacles, length-frequency distribution of berried females, and morphometric measurements, nearly all females above 100-mm carapace length were assumed to be mature, whereas only a few females between 81- to 90-mm carapace length were mature. Examination of male gonads suggested that male lobsters began maturing at relatively small sizes (50% mature at about 44-mm carapace length).

The American lobster, *Homarus americanus* Milne Edwards, is one of the most valuable and heavily exploited commercial species occurring along the Maine coast. Recognizing the urgent need for biological management of this inshore fishery, the Maine Department of Sea and Shore Fisheries initiated the Lobster Research Program in April 1966. The two primary phases of this program have encompassed: 1) probability sampling of the commercial lobster fishery along the entire Maine coast and 2) collection of prerecruit and legal-sized lobsters (minimum size in Maine is now 81-mm carapace length) near Boothbay Harbor, Maine (this phase began in March 1968). With data from these two independent sampling schemes, various population parameters have been calculated and then ultimately employed to estimate the minimum size limit for maximum sustainable yield (Thomas, 1971).[3]

The objectives of this paper, which are based upon data collections of the natural lobster population from Boothbay Harbor, are concerned with: 1) sex ratios; 2) incidence of molting; 3) length-weight relationship; 4) size composition of catch; and 5) the size at first sexual maturity for both sexes.

METHODS AND MATERIALS

Lobsters were collected in coastal waters near Boothbay Harbor, Maine, from April 1968 through December 1970. The following types of gear were used: (1) rectangular vinyl-coated lobster traps (1- × 2-inch and 1- × 1-inch mesh); (2) elliptical polyethylene lobster traps; (3) conventional wooden lobster traps; (4) a

[1] This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 3-14-R.

[2] Maine Department of Sea and Shore Fisheries, West Boothbay Harbor, ME 04575.

[3] Thomas, J. C. 1971. An analysis of the commercial lobster (*Homarus americanus*) fishery along the coast of Maine, August 1966 through December 1970. Unpublished manuscript, 73 p. Maine Department of Sea and Shore Fisheries, Completion Report.

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FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

shrimp try trawl with a cod end of 1-inch stretch mesh; and (5) a variable mesh monofilament gill net (four 25-ft sections of 1-, 2-, 3-, and 4-inch mesh). SCUBA divers were also employed on a few occasions to collect small male lobsters from which supplemental data were obtained for our maturity studies.

Of the aforementioned types of gear, considerably more fishing effort has been expended with wire traps. This disproportion of effort resulted from early fishing success experienced with wire traps and their relative suitability for hauling from a 17-ft Boston Whaler.[4] Subsequently, only 67 (2.6%) of 2,582 lobsters were captured with the other types of gear.

Carapace length (distance measured along midline from posterodorsal edge of carapace to posterior margin of eye socket) and total length (distance measured dorsally from tip of rostrum to tip of telson) were determined to the nearest millimeter for all lobsters sampled. Wet weights were recorded to the nearest 10 g.

MATURITY STUDY—GONAD EXAMINATION

Males

The vas deferens and/or testes of 204 male lobsters (carapace lengths ranged from 36 to 95 mm) were examined for the presence or absence of spermatophores (Figures 1 and 2). Males having spermatophores were considered mature. Because it was economically objectionable to sacrifice large numbers of lobsters, a method whereby the internal sex organs could be probed or extracted without any detrimental effects to the lobster was desirable. Initially, I attempted to withdraw sperm samples through a blunt hypodermic needle inserted into the vas deferens via its valvular orifice on the fifth pair of pereiopods. This technique produced inconsistent results and had to be abandoned. I then discovered that both the vas deferens and testis could be extracted with a forceps introduced through a small incision at the base of the fifth pair of walking legs. This procedure yielded reliable results and had no noticeable deleterious effects upon lobster survival throughout a postoperative period of several months.

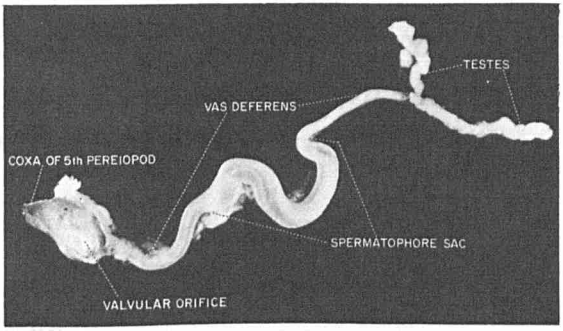

FIGURE 1.—Reproductive system dissected from a male lobster.

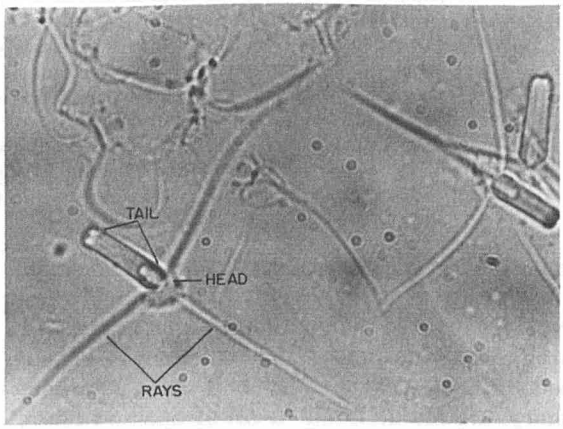

FIGURE 2.—Lobster sperm cells photographed under oil immersion at 970×.

Females

Ovaries were dissected from 158 female lobsters and then ovarian color and ova diameter (to nearest 0.1 mm) were recorded. Egg diameters were based on the average of a random sample of 10 eggs (distorted eggs were rejected) from each ovary. Using the criteria of ovarian color and ova diameter, ovaries were assigned to one of the following stages of development:

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

Stage of development	*Ovary color*	*Egg diameter (mm)*
immature	translucent white	⩽ 0.4
developing	yellow-orange	0.5-0.7
mature	dark green	⩾ 0.8

Two additional determinations were made for each female: 1) width of the second abdominal segment (distance between deepest part of pleura on ventral surface) and 2) examination of the seminal receptacle (structure where sperm is stored upon copulation until egg extrusion) for the presence of sperm. As a check on my technique for detecting spermatophores, I examined 31 berried lobsters from Canada and found sperm in all of them.

In conjunction with the annual berried female program, during which the State of Maine purchases from the pound owners lobsters that have become ovigerous while in captivity, carapace lengths were recorded for 1,150 berried females.[5] These data were obtained during the period 1966 through 1970.

RESULTS AND DISCUSSION

SEX RATIOS

Sex ratios were analyzed by assigning lobsters from catches during the period 1968 through 1970 to 5-mm carapace length size groups by sex. Midpoints of each size increment were then plotted against the number of lobsters in each of the respective size groups (Figure 3). Although differences did exist between the proportion of males to females within various size classes, these differences were not consistent from year to year, suggesting that they may have been artifacts of sampling. In 1969 and 1970 when the catches were relatively large (greater than 1,000 lobsters), the overall percentages of females were 48.1 and 50.3, respectively. While the sex ratio approached 1:1 in 1969 and 1970, in 1968, when the sample size was half that of the other two years, the proportion of females was 56.4%. This disparity may best be attributed to the smaller sample size in 1968.

[5] Maine law prohibits the possession or sale of egg-bearing female lobsters.

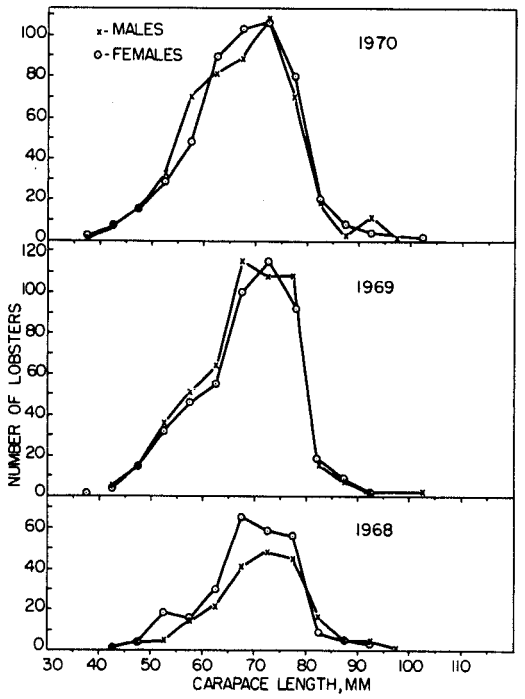

FIGURE 3.—Number of male and female lobsters grouped by 5-mm size classes from Boothbay Harbor, 1968 through 1970.

As the samples were predominantly composed of sublegal lobsters, our estimate of approximately a 1:1 sex ratio suggests that immature female and mature male lobsters have similar molting frequencies and increments of growth. In contrast to this, Herrick (1911), Templeman (1939), and Wilder (1953) have demonstrated that most sexually mature males molt annually and mature females every other year. In a tagging study conducted off Monhegan Island, Maine, Cooper (1970) found no significant differences in growth increments of male and female lobsters (average carapace length of 90 mm). Unlike the Maine findings, studies by Wilder (1963) in Egmont Bay, Prince Edward Island, and Squires (1970) and Ennis (1972) off Newfoundland revealed larger increments of growth for males than females for sizes above about 65-mm carapace length. Based on the maturity work of Templeman (1944), female lobsters from the aforementioned Canadian

study areas attain maturity at smaller sizes (50% mature between 70- to 80-mm carapace length) than Maine females as indicated by results of this present study; thus, I believe this explains why Canadian lobsters exhibited a differential growth rate between sexes, while Maine lobsters (our samples were markedly deficient of mature females) appeared to grow at the same rate regardless of sex.

MOLTING

Lobsters were classified as shedders (recently molted) when their carapace and/or chelipeds were soft to the touch (lacked normal rigidity). Because molting was observed to be concurrent for males and females, shedding data were combined for sexes (Table 1). While a few lobsters were observed to molt in spring, shedding did not reach a peak until September in 1968 and August in 1969 and 1970.

TABLE 1.—Percentage of soft-shelled lobsters in monthly samples from Boothbay Harbor, 1968 through 1970.

Month	1968	1969	1970
January	--[1]	0	--[1]
February	--[1]	--[1]	0
March	--[1]	0	0
April	0	0	4
May	0	0	1
June	0	3	4
July	2	6	19
August	1	10	24
September	16	1	18
October	10	0	17
November	1	--[1]	7
December	0	0	0

[1] No sample collected.

LENGTH-WEIGHT RELATIONSHIP

The regression of total wet weight on carapace length was calculated for 454 lobsters (206 males and 248 females) collected from April 1968 through March 1969. The equation used was $W = aL^b$, where W = wet weight in grams, L = carapace length in millimeters, and a and b are constants. The regression was fitted by the method of least squares using the logarithmic transformation $\log_{10}W = \log_{10}a + b \log_{10}L$.

Analysis of covariance on the regression coefficients as described by Steel and Torrie (1960) revealed no significant difference between sexes, so data from all lobsters were combined. The calculated regression equation was $\log W = -2.9052 + 2.9013 \log L$. This mathematical relationship is represented by the curve in Figure 4.

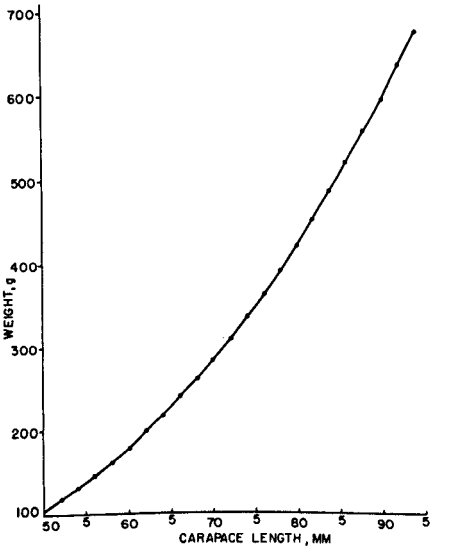

FIGURE 4.—Calculated length-weight relationship for 454 lobsters from Boothbay Harbor. The regression equation is $\log W = -2.9052 + 2.9013 \log L$.

SIZE COMPOSITION OF CATCH

I compiled length-frequency histograms of lobsters collected with wire traps in 1968, 1969, and 1970 (Figure 5). The effects of availability (term encompassing both vulnerability and accessibility) and the high rate of exploitation by the commercial fishery on our annual catches are manifested by the histograms.

The stepwise increase in numbers of lobsters with size up to approximately 70-mm carapace length led me to assume that this mode represented the size at which lobsters were fully vulnerable to our gear. Reduced vulnerability of lobsters smaller than 70-mm carapace length in our samples might best be attributed to the effects of gear selectivity and, possibly, the more seclusive behavior of small lobsters. In ecological studies of the lobster being conducted

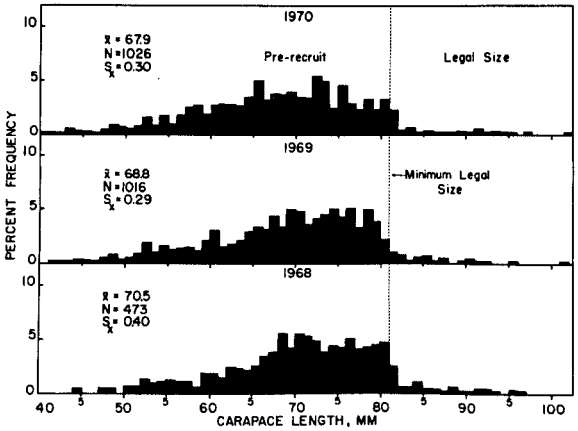

FIGURE 5.—Annual length-frequency distributions of lobsters sampled near Boothbay Harbor, 1968 through 1970.

in the Boothbay Harbor area, SCUBA divers have observed lobsters of less than 40-mm carapace length to be virtually inactive during nocturnal periods and apparently passing most of their early life within subterranean burrows (Richard A. Cooper, pers. comm.).

Sharp reductions in the number of lobsters above the minimum legal size (81-mm carapace length) reflected the influence of commercial exploitation. The legal-sized lobsters composed only 6 to 9% by number of the three annual catches.

For each annual length-frequency distribution, I attempted to select, on an objective basis, modes representative of assumed age or molt groups by analyzing the polymodal frequency distributions graphically with probability paper (Harding, 1949). Unfortunately, I discovered that I could not pick meaningful age or molt group modes due primarily to the limited size range (70- to 80-mm carapace length) over which our samples were considered to be representative of the natural lobster population. Since the increment of a lobster's growth was assumed to be about a 13 to 14% increase in carapace length (Wilder, 1953), it became apparent that our representative size range of 70- to 80-mm carapace length contained, at best, only one mode or possibly more if an age class experienced differential growth.

SIZE AT MATURITY

Males

In the Boothbay Harbor area, 50% of the male lobsters sampled were sexually mature at about 44-mm carapace length (Figure 6). The smallest mature male was 41-mm carapace length. Although sample size was limited for lobsters smaller than 45-mm carapace length, I do not believe that this significantly affected our conclusions.

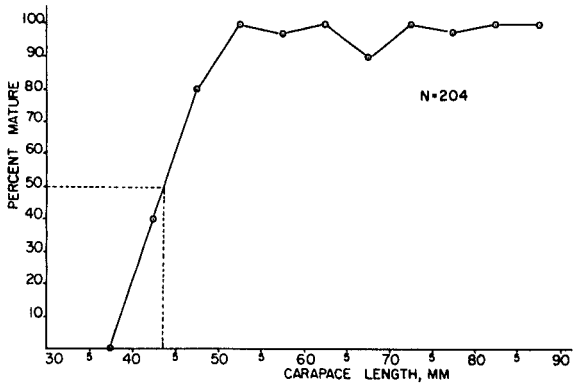

FIGURE 6.—Percentage frequency of mature male lobsters by 5-mm size classes.

In this study, maturity was solely based upon the criterion of presence or absence of sperm cells. Therefore, even though a lobster might appear to be physically mature (possessed sperm cells), this particular individual might be incapable of successfully copulating with a female. In mating experiments, Templeman (1934) observed that male lobsters were unable to mate with considerably larger females. In fact, the success of mating was greatest when the males were slightly larger than the females. As most females in the Boothbay Harbor area mature above the minimum legal size of 81-mm carapace length (discussed in following section), it appears that prerecruit males seldom contribute reproductively to the natural population.

Females

Size-frequency polygons of the three ovarian stages of development indicated that immature ovaries occurred in females from 51- to 89-mm carapace length; developing ovaries in females from 69- to 94-mm carapace length; and mature ovaries in females from 77- to 100-mm carapace length (Figure 7). Although the size ranges of the various ovarian stages overlapped considerably, the following trends are apparent: 1) immature ovaries predominated in females with carapace lengths less than 75 mm; 2) developing ovaries were most common at intermediate sizes (75- to 90-mm carapace length); and 3) mature ovaries gradually increased in frequency at sizes greater than 85-mm carapace length. Unfortunately, owing to difficulty in procuring legal-sized lobsters, the sample size of individuals between 85 and 100 mm in carapace length was limited to 47 lobsters; thus the task of determining size where approximately half the female lobsters became mature was confounded. However, the data indicated that a few females matured between 80- and 90-mm carapace length, but the onset of maturity for most females was at carapace lengths greater than 90 mm. This conclusion is further substantiated and expanded by the following facets of the maturity investigation.

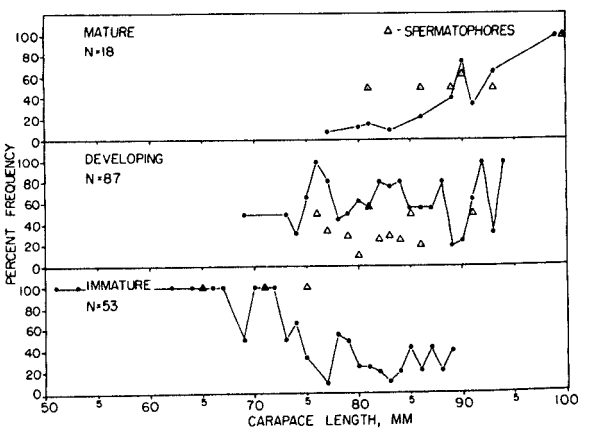

FIGURE 7.—Percentage frequency of the three ovarian stages of development and the occurrence of spermatophores (triangles) in the seminal receptacles.

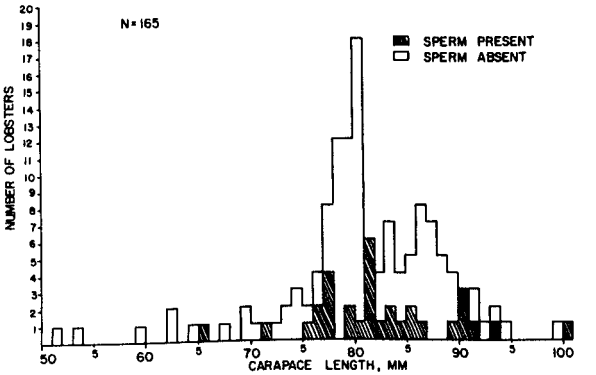

FIGURE 8.—Number of female lobsters with spermatophores in their seminal receptacles.

Spermatophores, the presence of which was another criterion for maturity, were detected more frequently in the seminal receptacles of mature females, particularly those females larger than 90 mm carapace length (Figures 7 and 8). Only 2 females with carapace lengths less than 75 mm had sperm cells, whereas 7 of 18 (39%) lobsters larger than 89-mm carapace length had spermatophores. From mating experiments, Templeman (1932, 1934) concluded that females had to be soft-shelled for mating to be accomplished successfully. Thus, females without spermatophores, even though their ovaries were classified as mature or well developed, would not be capable of spawning until they had undergone at least another molt and then, while soft-shelled, had copulated with a male. The absence of spermatophores in many females, which were observed to have developing or mature ovaries, suggested that these lobsters would not spawn until they advanced to the next molt class. Thus only 5 of 84 (6%) females from 80- to 90-mm carapace length were considered to be fully mature (possessed mature ovaries along with spermatophores), whereas the remaining 79 lobsters would not spawn until they attained carapace lengths of about 91 to 102 mm (assuming a 14% growth increment).

Templeman (1944) related the onset of sexual maturity of Canadian female lobsters with the relative increase in width of the second abdominal segment to total length. This morpho-

metric relationship was based on Templeman's (1935) observation that the female's abdomen markedly increases in width during maturation. I applied Templeman's method to my data on 482 females from inshore Boothbay Harbor (1968-71) and 31 berried Canadian lobsters (1970) as well as data on 217 females from inshore Boothbay Harbor collected in 1966 by Herbert C. Perkins of the National Marine Fisheries Service, West Boothbay Harbor, Maine. Carapace lengths were grouped by 5-mm size groups, and then abdominal widths of each size group were averaged. Ratios of abdominal width to carapace length were plotted against carapace length, and resulting curves were fitted by eye (Figure 9). Inflection points, which indicated size where maturity began, occurred at approximately 80-mm carapace length for both sets of Boothbay Harbor data. For the offshore population of American lobsters, Skud and Perkins (1969) reported an inflection point of 77 mm. Asymptotes, which denoted the size where all lobsters were assumed to be mature, appeared at about 115 mm for Perkins' Boothbay Harbor data, while an asymptote was not reached for my Boothbay Harbor data. I believe the asymptote at 115 mm was probably deceptively higher because of an insufficient number of lobsters sampled for sizes above 105 mm, which constituted less than 5% of the total sample. This conclusion was maintained both by Skud's and Perkins' (1969) data that demonstrated an asymptote at 100 mm and by the following section on length frequencies of ovigerous females from Maine. The relatively early maturity of Canadian females, particularly those inhabiting warm water of the southern part of the Gulf of St. Lawrence (Templeman, 1944), is demonstrated in Figure 9.

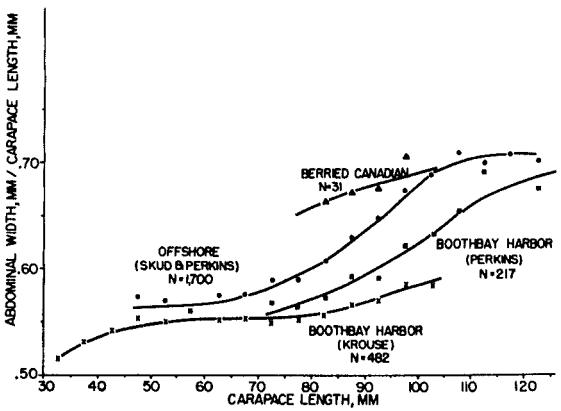

FIGURE 9.—Ratio of abdominal width to carapace length plotted against carapace length for Boothbay Harbor female data collected by Krouse and Perkins, berried Canadian female data, and Skud's and Perkins' study, 1969.

The length-frequency distribution of berried females taken along the Maine coast (Figure 10) disclosed that a few females began extruding eggs at 83-mm carapace length while the percentage of ovigerous females gradually increased to the first peak at 91 mm. The most pronounced mode occurred at about 105 mm, which was considered to be the size when nearly all females were mature. It should be mentioned that the modes at 91 and 105 mm corresponded with assumed age or molt class modes determined by Thomas (1971, see footnote 3) from commercial catch data.

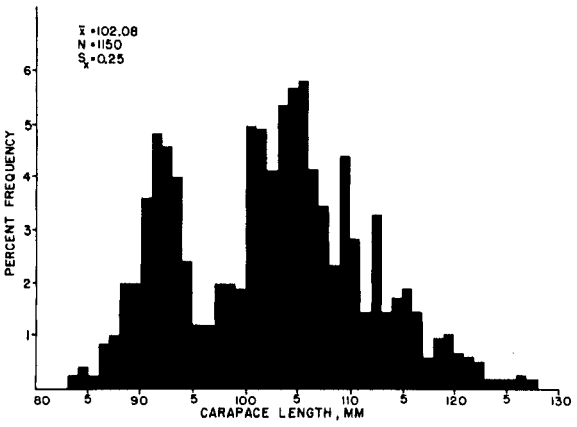

FIGURE 10.—Length-frequency distribution of native Maine berried females, 1966 through 1970.

The length-frequency distribution of berried females becomes particularly meaningful when compared with percent frequencies of female

lobsters from the commercial catch in the following size classes:

Carapace length	Percentage of total catch: Commercial	Percentage of total catch: Berried females
81-90 mm	80	11
91-100 mm	17	29
>100 mm	3	60

Because lobsters ranging in carapace length from 81 to 90 mm constituted approximately 80% of the commercial catch and only 11% of the berried female sample, it is apparent that only a very small percentage of females mature below 90-mm carapace length. Certainly the most marked disparity in size composition was for carapace lengths greater than 100 mm (3% commercial and 60% berried females). This would seem to validate the previous conclusion that most females above 100-mm carapace length are mature.

SUMMARY

This study which is concerned with the analyses of data collected from 1968 through 1970 on the natural population of American lobsters along the Maine coast has yielded the following information:

1. Sex ratio was 1:1, thus suggesting that differences in growth rate and molting frequency do not exist between mature males and immature females.
2. Molting was concurrent for males and females, with shedding reaching a peak in late summer.
3. The length-weight relationship for sexes combined was $\log W = -2.9052 + 2.9013 \log L$.
4. Length-frequency histograms revealed the high rate of exploitation by the commercial fishery and an increase in unavailability of lobsters progressively smaller than 70-mm carapace length.
5. Male lobsters begin maturing at relatively small sizes (50% mature at about 44-mm carapace length); however, because native Maine females rarely mature below the minimum legal size of 81-mm carapace length and males must approximate females' size to successfully mate, it is doubtful that prerecruit males contribute reproductively to the natural population.
6. Female maturity was assessed by the following methods: 1) classification of ovaries by color and ovum diameter to three stages of development; 2) examination of seminal receptacles for spermatophores; 3) morphometric relationship of abdominal width:carapace length ratio to carapace length; and 4) length-frequency distribution of native Maine berried females. From estimates by these four independent methods, I concluded that females seldom become sexually mature at a size less than 81-mm carapace length, and then only a small fraction of those females between 81 and 90 mm attain maturity, whereas, at carapace lengths greater than 100 mm, nearly all females are assumed to be mature. Bearing in mind the minimum legal size regulation of 81-mm carapace length, I demonstrated in this study that the majority of females are harvested commercially prior to their first opportunity to spawn. An obvious change in management suggested by the results of this study would be to increase the minimum size limit to insure successful spawning by a sizeable portion of the population. Based on results of this study and those from the commercial sampling phase of the Maine lobsters project, Thomas (1971, see footnote 3) deals specifically with minimum size limit increases as a means to achieve a maximum sustainable yield.

ACKNOWLEDGMENTS

I am indebted to James C. Thomas for his guidance and support throughout the course of this study and his review of the manuscript. Richard Hanley, Gerald Brackett, Robert Nunan, Stephen Ham, and Andrew Dolloff assisted with field collections and data compilations. Gareth Coffin of the Northeast Fisheries Center, National Marine Fisheries Service, West Boothbay Harbor, Maine, performed the photographic work.

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APPARENT GROWTH OF YELLOWFIN TUNA FROM THE EASTERN ATLANTIC OCEAN

J. C. LE GUEN[1,2] AND GARY T. SAKAGAWA[1,3]

ABSTRACT

Apparent growth of yellowfin tuna from the eastern Atlantic Ocean was estimated from modal progression of length-frequency distributions by two methods. One was to use fish of unknown age, which gave estimates of parameters of the von Bertalanffy growth function of $L_\infty = 194.8$ cm and $K = 0.035$, on a monthly basis. The other was to use fish of apparent known age, which resulted in $L_\infty = 175.2$ cm and $K = 0.044$. Although the parameter estimates were different, estimates of length at ages 1.5-4.5 years were quite similar with both approaches.

A comparison of growth estimates of yellowfin tuna was made. Estimates from analysis of length-frequency distributions appeared to be superior to those from analysis of scales because they were based on a larger range of fish sizes. However, observed lengths at ages 1.5-5 years were similar for both types of analysis and for yellowfin tuna from both the Atlantic and Pacific Oceans.

It is recommended that observed sizes at age rather than the estimated sizes at age from the von Bertalanffy function be used in estimating yield per recruitment of yellowfin tuna.

There have been several studies (e.g., Le Guen, Baudin-Laurencin, and Champagnat, 1969; Yang, Nose, and Hiyama, 1969) on growth of Atlantic yellowfin tuna (*Thunnus albacares*) but little agreement among them. The disagreement can be traced to at least three sources: first, the kinds of data, e.g., length-frequency distributions and scale readings have been different; second, the method of fitting the von Bertalanffy growth function has varied; and third, the range of fish sizes employed has been different. Because an accurate estimate of growth is important for estimating yield per recruitment by the Beverton and Holt approach (Schaefer and Beverton, 1963), one method that can provide information for rational management of the resource, a study was initiated to estimate growth from the best series of data available and, hopefully, to resolve the disagreement. In this report the results of that study on apparent growth of yellowfin tuna from modal progression of length-frequency distributions are presented and compared to growth estimates derived from published data and computed by standardized procedures.

PLAN OF ANALYSIS

Length frequency samples from commercial landings were employed in our study (Table 1). The fish were caught off Africa by baitboats and purse seiners and were sampled by French and Inter-American Tropical Tuna Commission (IATTC) scientists. (Scientists of the IATTC sampled the Atlantic tuna catch of U.S. vessels under a contract from the National Marine Fisheries Service.) The French scientists sampled the French catches, which were from three general regions—Abidjan, Ivory Coast; Dakar, Senegal; and Pointe-Noire, Congo—and the IATTC scientists sampled the American catches, which were from primarily the Gulf of Guinea. The IATTC samples were caught in both the Abidjan and Pointe-Noire regions, but because

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Manuscript accepted May 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

TABLE 1.—Sources of length data of Atlantic yellowfin tuna caught in the surface fishery off Africa.

Region	Year	Type of length measurement	Type of vessel sampled			Source
			Bait-boat	Small seiner[1]	Large seiner[2]	
Abidjan	1966	Predorsal		X		O.R.S.T.O.M., 1971
	1966-69	Predorsal	X	X		O.R.S.T.O.M., 1971
	1970	Predorsal	X	X	X	O.R.S.T.O.M., 1971
Dakar	1968	Fork	X			Champagnat and Lhomme, 1970
	1969	Predorsal	X	X		Champagnat and Lhomme, 1970
	1970	Predorsal	X	X	X	O.R.S.T.O.M., 1971
Gulf of Guinea	1968-70	Fork			X	Staff, Tuna Population Dynamics Project, 1971[3]
Pointe-Noire	1965-66	Predorsal	X	X		O.R.S.T.O.M., 1971
	1967-68	Predorsal	X	X		Le Guen et al., 1969
	1969	Predorsal	X	X		O.R.S.T.O.M., 1971
	1970	Predorsal	X	X		O.R.S.T.O.M., 1971
	1971	Predorsal	X	X		Unpublished data (Le Guen)

[1] Small purse seiner = less than 500 metric tons capacity.
[2] Large purse seiner = larger than 500 metric tons capacity.
[3] Staff, Tuna Population Dynamics Project. 1971. Size composition of the yellowfin and skipjack tuna purse seine fishery off the west coast of Africa 1968-1970. Unpublished manuscript, 28 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

they could not be separated as such, they were treated separately from the French data.

Two methods were employed in our analysis. One approach ("age unknown") was based on all samples from the four regions, for years 1965-70 and with age of size groups unknown. The second approach ("apparent age known") was slightly different. Only fish that were caught in an area from São Tomé to southern Angola, 1967-71, and with the apparent age of each size group known, were employed.

Growth was estimated with the von Bertalanffy growth function. This function is often expressed as,

$$L_t = L_\infty \, [1 - \exp - K \, (t - t_0)],$$

where L_t = length at age t, L_∞ = asymptotic length, K = growth rate, and t_0 = theoretical age when $L_t = 0$. It is fitted to growth data by various procedures (e.g., Walford, 1946; Abramson, 1963; Ricklefs, 1967; Gulland, 1969; Knight, 1969), most of them require data on size at known age. A least-squares procedure that does not contain this limitation was described by Fabens (1965). He fitted a von Bertalanffy function of the form

$$L_{t+\Delta} = L_t + (L_\infty - L_t) \, (1 - \exp - K)$$

to tag-return data, but his procedure is equally applicable to length observations of untagged fish made at t and again at a later date, $t + \Delta$, when the age of the fish is unknown. For tuna, Rothschild (1967) and Joseph and Calkins (1969) employed Fabens' procedure to estimate growth of skipjack tuna (*Katsuwonus pelamis*) from tagging data. We used the Fabens' procedure with monthly mean lengths for individual year classes to estimate growth of yellowfin tuna of unknown age. A computer program written by Tomlinson (Abramson, 1971) was employed to estimate L_∞ in centimeters and K, expressed on a monthly basis. For growth estimates based on apparent known age fish, we used a computer program written by Abramson (1963) and modified by Psaropulos (1966) of a least-squares procedure described by Tomlinson and Abramson (1961).

ANALYSIS WITH UNKNOWN AGE FISH

METHODS

Fish landed at Abidjan, Dakar, and Pointe-Noire (Figure 1) were measured for predorsal length (tip of snout to anterior base of the dorsal fin) by French scientists; fish were measured for fork length by IATTC scientists. In order to standardize the length measurements, we em-

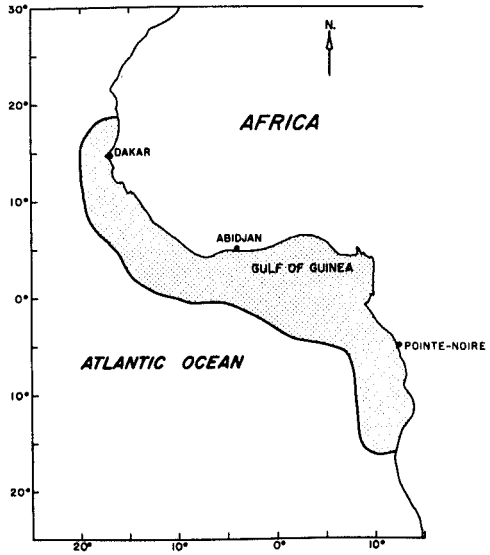

FIGURE 1.—Area off Africa where the surface fishery for yellowfin tuna operates.

ployed the relation, $\log L_f = 0.273 + 1.175 \log L_d$ to convert samples with predorsal length in centimeters (L_d) to fork length in centimeters (L_f). This relation is based on 508 observations and differs from $L_f = (3.624 + 0.212\ L_d)^2$, which was employed by Poinsard (1969). It has a slightly better correlation coefficient (r = 0.9943) than Poinsard's equation (r = 0.9940) (Lenarz, 1971).[4] Calculated fork lengths based on either equation are accurate only to 1-4 cm.

Monthly length-frequency distributions were tabulated by 4-cm-fork-length groups for samples from each region. Modes were identified and assumed to represent age classes within which lengths were normally distributed. Normal distributions were then fitted to the length frequencies of samples in which two or more modes were present, and the mean length of each age class was estimated (Table 2). A computer program for separating size classes in a mixture that was written and described by Hasselblad (1966) and modified by Tomlinson (1970)[5] was used to separate the age classes and estimate the mean lengths. For samples with only one prominent mode, the modal length, or midpoint of length interval of maximum frequency was considered the "mean length." Representative length-frequency distributions are shown in Figure 2.

Mean lengths for each sample are plotted in Figures 3-6. For each region a serial succession of increasing mean lengths with time was designated a year class, with only one recruited per year although two groups appear to be recruited

[4] Lenarz, W. H. 1971. Length-weight relations for five Atlantic scombrids. Unpublished manuscript, 9 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

[5] Tomlinson, P. K. 1970. Program for separating mixture of normal distributions. Unpublished manuscript, 2 p. California Department of Fish and Game, Operations Research Branch, Long Beach, CA 90802.

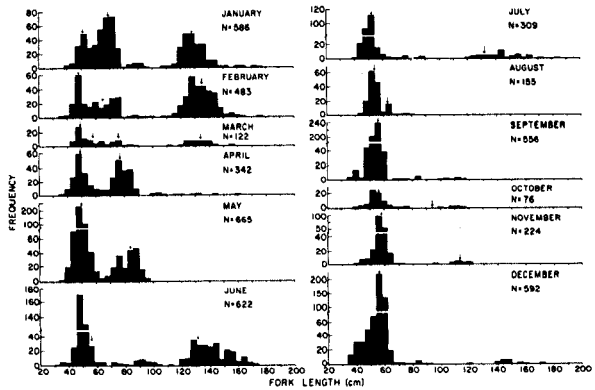

FIGURE 2.—Length-frequency distributions of samples from Pointe-Noire, 1970. Arrows indicate mean lengths of modal groups that were identified by curve fitting.

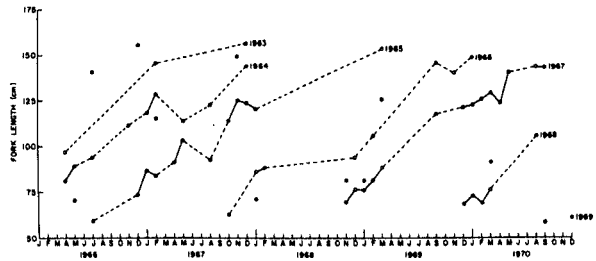

FIGURE 3.—Mean length of size groups of yellowfin tuna as a function of sampling date at Abidjan. Growth of the 1963-69 year classes are indicated

TABLE 2.—Mean lengths (cm) of modal groups identified in samples from Abidjan, Dakar, Gulf of Guinea, and Pointe-Noire. Values that were not used in the analysis of growth are shown in parentheses.

Region	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Abidjan	1966				80.7 97.2	(56.8) (70.8) 89.4		59.2 94.2 (140.9)				112.0	73.5 (155.2)
	1967	87.3 118.2	84.3 (115.4) 129.7 146.6		92.0	(48.5) 103.8 114.9			92.8 122.9	(56.0)	62.9 114.8	65.3 125.3 149.7	124.6 144.5 156.8
	1968	(71.7) 86.2 121.9	88.0									69.4 82.3	76.3 94.8
	1969	76.2 (82.3)	81.9 105.4	87.9 112.2 (125.5) 153.6						118.2 145.6		140.0	(50.1) 67.9 122.4
	1970	(54.8) 73.8 123.0 148.4	69.5 125.3	76.9 (92.1) 129.4	124.0	140.0			(55.6) 105.6 143.7	58.1 143.0		(48.0) (58.4)	(43.1) 60.6
Dakar	1968	(44.0)	(56.3) 117.9	(61.2) 122.3	(63.5) 120.7	72.0	(55.3) 70.1 (118.6)	76.0	(63.0) 81.2	(58.4) 88.4	62.3 89.6	66.9 100.1	64.0
	1969	(70.1) 79.4 102.3	75.3 102.6	75.5 105.0	79.9 113.9	(43.6) (57.4) 85.4 112.2	(49.0) (60.1) 93.7	(49.1) 90.9 107.8	(64.8) 95.7 108.2	(69.4) 102.5 118.5	62.4 (75.7) 123.8	53.2 (78.5) 124.5	(61.9) 74.0 119.9
	1970	64.8 124.8	(49.6) 71.8 (88.9) 126.0	(49.4) 73.5 (101.7) 124.3 145.1	(51.4) 72.5 (106.0) 126.4 147.2	(50.6) 76.2 132.4	(53.4) (70.5)	(55.3) (72.3)	(56.3) (74.3) 90.6 133.7	(39.7) (56.4) 92.4	(42.9) 59.2 (72.3) 100.8 145.2	(30.9) (45.0) 63.0 108.8 146.3	(46.4) (57.4) 69.9
Gulf of Guinea	1968								62.9 136.0 (160.2)	57.8 77.0 135.8	70.0 84.4		
	1969								56.8 112.7 124.7	(52.6) 120.3 132.6 151.3	(59.4) 121.5 153.4	156.0	
	1970						(54.8) 87.1 141.2	(55.5) 82.6 (106.8) 143.3 165.7	(56.0)	66.8 140.6	65.6 (103.9)		
Pointe-Noire	1965							(57.7) (78.1) 113.0	(57.4) (80.2) 116.4	59.1 104.0	60.3 (78.4) 121.1	60.0	
	1966									(64.0) 99.1 145.3		63.0 102.2	
	1967			(50.5) 86.9		(52.9) 90.6 113.8 155.9	(58.0) 88.8	(53.4) 102.1	(53.6) 104.0 113.0	(59.3) 105.1	(61.4) 108.4	112.0	(68.0)
	1968	(60.7) 122.7 (154.6)				(68.0)	(56.4) (73.4) 120.9	59.7 (71.1) (85.4) 134.0 140.0	62.2 (73.6) (90.9) 130.8 152.7	64.6 (75.3) (87.0) 143.8 (156.6)	65.9 (76.2) (91.9) 136.8	(75.0)	72.7 (89.5) (101.5)
	1969	76.0		86.3 (111.1)	49.6 94.3 (117.7) 148.4 164.8	100.0	(56.9) 104.2	(55.7) (112.9) 154.5	(45.8) (56.3) (117.5) 156.0	(57.7) 112.7	(57.4) 114.6	59.9 (127.7)	56.6 127.1
	1970	(51.5) 69.0 129.7	(48.5) 65.5 134.7	(48.8) (57.5) 75.6 134.1	(48.9) 76.8	(49.9) 82.8	(50.7) 131.8	(51.3) 132.2	(53.7) 62.2	(56.0)	(55.3) 93.5	(57.6) 113.5	(56.0)

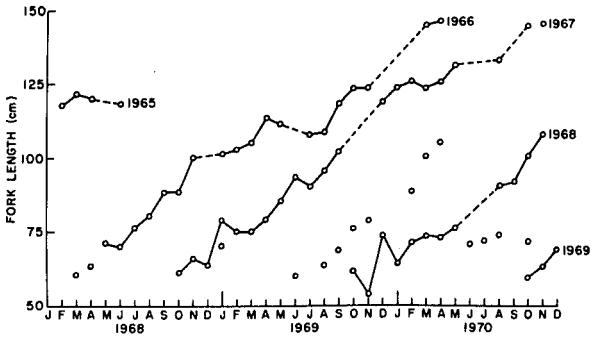

FIGURE 4.—Mean length of size groups of yellowfin tuna as a function of sampling date at Dakar. Growth of the 1965-69 year classes are indicated.

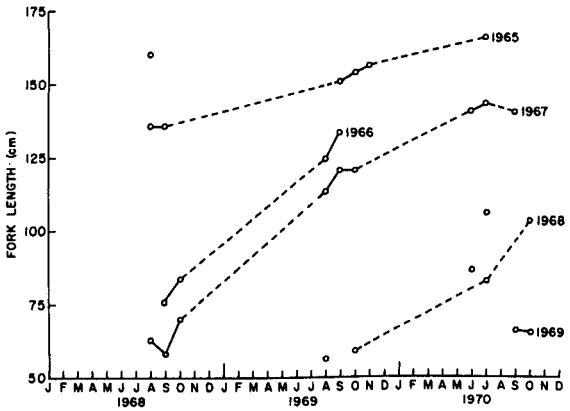

FIGURE 5.—Mean length of size groups of yellowfin tuna from the Gulf of Guinea. Growth of the 1965-69 year classes are indicated.

in some years. Recruitment is assumed to be completed in the second year of life (Le Guen et al., 1969).

RESULTS

Recruitment

Yellowfin tuna are recruited into the surface fishery when about 60 cm long. Recruitment is year-round but most pronounced during June to December. Two groups of yellowfin tuna appear to be recruited in some years. For example, in 1968 at Pointe-Noire (Figure 6) one group entered in January and another in August-September. The January group was of low relative abundance and persisted up to a length of about 90 cm, while the August-September group was of high relative abundance and discernible up to a length of about 140 cm. A similar phenomenon was described by Hennemuth (1961) and later verified by Davidoff (1963) for yellowfin tuna of the eastern Pacific Ocean. Hennemuth suggested that sampling bias, differential growth in a year class, and multiple spawning were some possible causes of the phenomenon. Variation in the seasonal distribution of fishing effort can be added as another possible cause.

Year Class Difference in Apparent Growth

Estimates of apparent growth for individual year classes for each region are shown in Table 3.

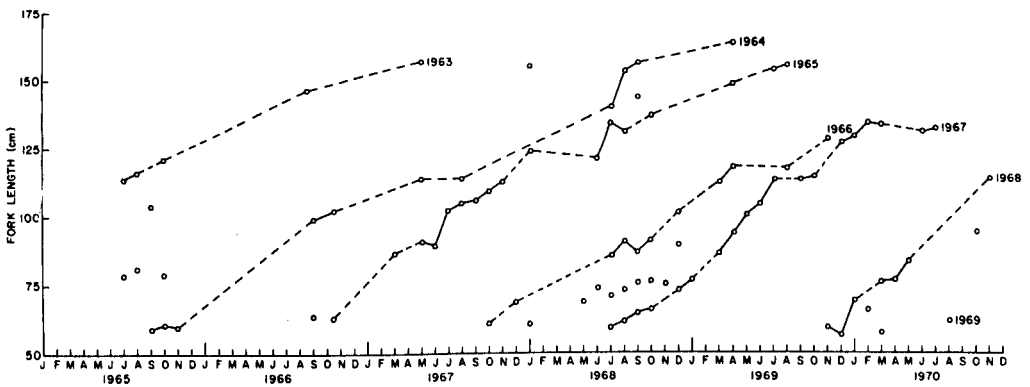

FIGURE 6.—Mean length of size groups of yellowfin tuna as a function of sampling date at Pointe-Noire. Growth of the 1963-69 year classes are indicated.

TABLE 3.—Estimates of parameters of the von Bertalanffy growth function for yellowfin tuna of unknown age from the eastern Atlantic Ocean.

Region	Year class	L_∞	K	No. of observations	Range of lengths (cm)
Abidjan	1963	Linear		2	97.2-156.6
	1964	138.6	0.137	9	80.7-149.7
	1965	275.2	0.016	11	59.2-153.6
	1966	Linear		9	62.9-148.4
	1967	155.1	0.086	13	69.4-143.7
	1968	Linear		4	67.9-105.6
	All years	185.0	0.043	48	59.2-156.6
Dakar	1965	Linear		2	117.9-122.3
	1966	Linear		18	70.1-147.2
	1967	201.5	0.038	20	62.3-146.3
	1968	557.2	0.008	11	53.2-108.8
	All years	307.9	0.017	51	53.2-147.2
Gulf of Guinea	1965	677.4	0.002	5	135.8-165.7
	1966	497.5	0.009	3	77.0-132.6
	1967	174.4	0.052	8	57.8-143.3
	1968	Linear		2	56.8- 87.1
	All years	185.0	0.041	18	56.8-165.7
Pointe-Noire	1963	168.3	0.067	5	104.0-155.9
	1964	273.9	0.017	10	59.1-164.8
	1965	162.9	0.059	16	63.0-156.0
	1966	191.9	0.024	11	61.4-127.7
	1967	160.2	0.051	17	59.7-134.7
	1968	177.8	0.033	8	56.6-113.5
	All years	210.1	0.027	67	56.6-164.8
All regions	1963	158.5	0.136	7	97.2-156.6
	1964	237.4	0.023	19	59.1-164.8
	1965	191.0	0.034	34	59.2-165.7
	1966	895.7	0.003	41	61.4-148.4
	1967	172.6	0.054	58	57.8-146.3
	1968	502.4	0.009	25	53.2-113.5
	All years	194.8	0.035	184	53.2-165.7

In some instances, the estimates of K and L_∞ are unexpectedly too high or too low, indicating that the estimates are inappropriate for the entire life span of the species. According to Knight (1968) and Le Guen (1971), a possible cause of variation in K and L_∞ is lack of size measurements for the entire life span of the species. This appears to be the case in some instances for our data. Length measurements for Dakar, for example, were from catches made predominantly by pole-and-line, or baitboats that generally catch small fish, a characteristic that is well documented (Pianet and Le Hir, 1971). Consequently, large fish were underrepresented in the samples, resulting in heavier weight on the lower size groups. Estimates of L_∞ were therefore unreasonably high, while those of K were unreasonably low. It should be noted that generally L_∞ and K are inversely correlated (Beverton and Holt, 1959).

For some year classes, apparent growth appears to be exceptionally faster than for others. Apparent growth of yellowfin tuna from Pointe-Noire can best illustrate this point (Figure 6). The 1965 and 1967 year classes grew at a faster rate than the 1964 or 1966 year class. The result was an apparent convergence of the growth curve for the 1964 year class with that for the 1965 year class, and the 1966 year class with the 1967 year class. In each case, there appears to be no relation between the time of recruitment and the rate of growth.

Regional Differences in Apparent Growth

For each region, the von Bertalanffy equation was fitted to data for all year classes combined. Apparent growth of yellowfin tuna from Abidjan, Gulf of Guinea, and Pointe-Noire was quite similar for sizes (ranged from about 60 to 160 cm long) observed in the samples (Figure 7). Apparent growth of Dakar fish, on the other hand, seemed exceptionally faster, which is at-

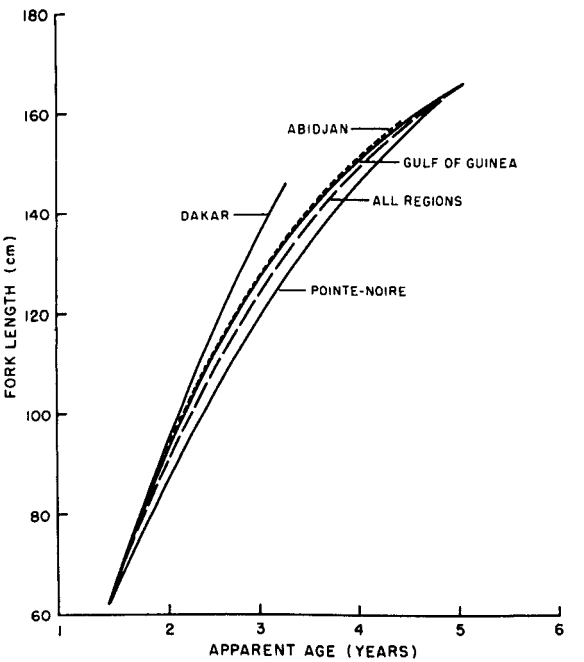

FIGURE 7.—Growth of yellowfin tuna from the eastern Atlantic Ocean.

tributed to lack of data on older fish as was discussed earlier. The range of mean length is 50 to 150 cm.

Estimated Length at Age

An estimate of $L_\infty = 194.8$ cm, and $K = 0.035$, on a monthly basis, was derived from data for all year classes and regions combined (Table 3). We believe these estimates are the "best," on the average, for yellowfin tuna of the eastern Atlantic Ocean, because they were based on data from a broad geographic area off Africa and a wide range of sizes. The estimated growth curve is quite similar to that for Abidjan, Gulf of Guinea, and Pointe-Noire (Figure 7). For individual year classes, however, estimates of L_∞ and K can be expected to deviate from the average, since there is an apparent difference in apparent growth among year classes (Table 3) and considerable scatter of observed mean lengths around the average curve (Figure 8).

Data on growth of tagged yellowfin tuna in the eastern Pacific and on the time of spawning in the Atlantic were used to estimate t_0 in months. The above best estimates of parameters of the von Bertalanffy equation were then used to estimate the length of yellowfin tuna at particular ages. A tacit assumption of this method of estimating length at age is that the von Bertalanffy function is a valid growth model for yellowfin tuna, and the date of birth is constant.

Schaefer, Chatwin, and Broadhead (1961) reported that yellowfin tuna of 40-49 cm long at tagging grew at a rate of 33 cm/year. They indicated that growth was probably adversely affected by tagging, implying that their estimate was too low.

Le Guen et al. (1969) reviewed the literature on time of spawning of yellowfin tuna in the Atlantic Ocean. They concluded that spawning occurred primarily at temperatures greater than 26°C and salinity of about 33.5‰. From seasonal distributions of temperature, salinity, and tuna larvae captured off Africa, they estimated that spawning peaked on about March 1 off Pointe-Noire and on about July 1 off Dakar.

From the above information together with the fact that recruitment into the surface fishery is generally from June to December, we estimated that yellowfin tuna were, on the average, 18 months old at recruitment, about 60 cm long, and $t_0 = 7.48$. Estimates of length at age were calculated with $L_\infty = 194.8$, $K = 0.035$, and $t_0 = 7.48$, employed in the von Bertalanffy function (Table 4). The estimates are graphed in Figure 8, together with monthly mean lengths of individual year classes of each region. There is considerable scatter of the data about the line and an indication that lengths at age 50 months and older are overestimated.

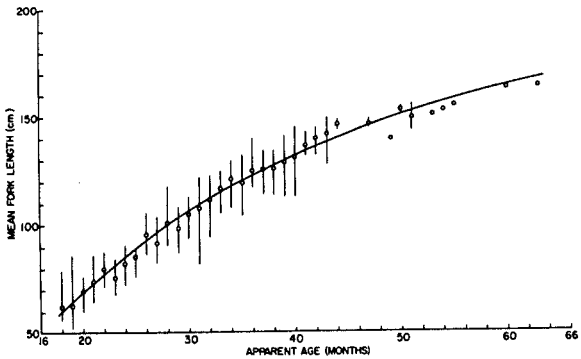

FIGURE 8.—Mean length of year classes of yellowfin tuna as a function of age. The curve is for all year classes and regions combined and is estimated by a von Bertalanffy growth function. Average of observed mean lengths (circles) and the range of mean lengths (vertical line) at various estimated ages are shown.

Estimated Weight at Age

Length can be converted to weight with a weight-length relation. Lenarz (see footnote 4) reported that the weight-length relation for yellowfin tuna from the eastern Atlantic is $W = 0.0000214\ L_f^{2.9736}$, where W = weight in kilograms and L_f = fork length in centimeters. This equation was employed to convert estimates of length at age to weight at age (Table 4).

ANALYSIS WITH APPARENT KNOWN AGE FISH

METHODS

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TABLE 4.—Observed and estimated size at various ages of yellowfin tuna from the Atlantic and Pacific Oceans. Length (cm) is shown for most ages, and weight (kg) in parentheses for a few ages. Estimated length is based on the von Bertalanffy growth function.

Age (years)	Source of data											
	Yang et al., 1969		Le Guen et al., 1969				Present study				Davidoff, 1963	
	Atlantic Ocean		Eastern Atlantic				Eastern Atlantic				Eastern Pacific	
			Pointe-Noire		All regions		São Tomé-Angola		All regions			
	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated
1.0	--	54.0	--	33.2	--	32.2	--	17.3 (0.1)	--	28.5 (0.4)	--	34.6
1.5	66.1	75.8	64.6	62.9	63.8	60.0	61.5	53.9 (3.0)	62.2	60.0 (4.2)	--	61.9
2.0	86.1	94.9	84.6	86.6	79.5	83.1	77.6	82.0(10.5)	82.3	85.5(11.9)	83.0	84.7
2.5	104.1	111.5	108.3	105.6	103.9	102.0	111.0	103.6(21.1)	105.0	106.2(22.7)	105.0	103.8
3.0	120.0	125.9	--	120.9	124.0	117.7	116.1	120.2(32.8)	125.0	123.0(35.1)	122.0	119.7
3.5	132.9	138.5	132.2	133.1	132.2	130.6	132.2	133.0(44.3)	140.6	136.6(48.0)	136.0	132.9
4.0	--	149.4	--	142.9	--	141.3	135.6	142.8(54.7)	--	147.6(60.5)	141.0	144.0
4.5	--	158.9	147.0	150.7	143.6	150.1	147.0	150.3(63.8)	153.4	156.6(72.0)	--	153.3
5.0	--	167.2	152.0	157.0	152.0	157.4	153.7	156.1(71.3)	164.8	163.8(82.4)	--	161.0

age fish were similar to those described by Le Guen et al. (1969) and are briefly described as follows. Predorsal length-frequency distributions were tabulated for monthly samples collected in 1967-71 off Pointe-Noire in an area from São Tomé to southern Angola. Modes were selected by comparison of successive maxima in the length-frequency distributions and mean predorsal length estimated for each size group by a method described by Gheno and Le Guen (1968). Mean dorsal lengths were then converted to fork lengths with the aid of Table 5, which was based on fish measured for both predorsal and fork lengths at Pointe-Noire. The data in Table 5 give a fork length-predorsal length relation of $\log L_f = 0.299 + 1.162 \log L_d$ that is not significantly different from the equation used earlier.

TABLE 5.—Predorsal length and fork length measurements of yellowfin tuna landed at Pointe-Noire, 1967-71.

Predorsal length (cm)	Mean fork length (cm)	Number of observations	Predorsal length (cm)	Mean fork length (cm)	Number of observations
12	39.0	11	31	109.5	46
13	40.9	21	32	111.3	33
14	45.0	18	33	116.1	27
15	47.3	37	34	118.8	19
16	50.0	36	35	122.9	26
17	53.9	33	36	132.3	24
18	57.2	58	37	134.7	35
19	59.8	83	38	138.4	25
20	63.1	66	39	143.7	28
21	66.3	43	40	145.7	29
22	71.0	20	41	149.7	29
23	74.6	23	42	152.3	14
24	76.0	18	43	158.8	5
25	81.1	16	44	164.0	5
26	84.2	16	45	166.3	10
27	89.0	9	46	172.0	6
28	92.8	21	47	175.4	8
29	99.1	28	48	177.8	7
30	104.9	27	49	179.8	2

An estimated age was assigned to each size group (Table 6) based on: (1) date of birth of yellowfin tuna caught off Point-Noire is on the average March 1 and (2) recruitment occurs in the second year of life (Le Guen et al,. 1969). Estimates of parameters of the von Bertalanffy function were then calculated with Psaropolos' (1966) computer program.

Length at age estimates were converted to weight at age with the weight-length relation of Lenarz (see footnote 4), which was mentioned earlier.

RESULTS

Estimates of parameters of the von Bertalanffy function were $L_\infty = 175.17$ cm (SE = 3.67), $K = 0.044$ per month (SE = 0.003), and $t_0 = 9.643$ months (SE = 0.815). These estimates are quite similar to those derived by Le Guen et al. (1969) for the Pointe-Noire region based on only data from 1967-68 (Table 7); but L_∞ is significantly lower and K significantly higher than our best estimates for yellowfin tuna from a larger area of the eastern Atlantic, even when the difference in range of lengths in the data is taken into account. On the other hand, length at age and weight at age estimates for ages 1-5 years are quite similar to those for the entire eastern Atlantic (Table 4). Thus, we conclude

TABLE 6.—Size classes (cm) of yellowfin tuna identified in samples from São Tomé to southern Angola. Year classes are separated by horizontal lines.

Age (months)	1967-68[1]	1969	1970	1971
18	64.5		58.5	
19			59.8	
20			61.4	
21	70.3			
22	85.0	75.3	68.6	58.5
23	85.1		71.0	63.1
24	84.6	82.6	74.6	68.6
25	89.0	90.9	81.1	72.8
26	90.6	104.9	82.6	74.6
27	91.0	107.2	92.8	76.0
28	95.5	107.2		86.6
29	102.6			
30	108.3	113.7		
31	107.7	116.1		
32	109.4	127.5		
33	114.5	127.5		
34	124.0			
35	120.0	111.3		
36		116.1		
37	122.0	118.8		
38	126.7			
39	123.5			
40	134.7			
41	136.8			
42	132.2			
43	139.0			
46			133.5	
47	138.6			
48			136.5	134.7
52	147.0		141.0	138.4
53	151.3		143.7	
54	147.0			
55	150.5			
60	152.0			155.5
61		149.7		156.0
64				158.8
65	163.4			160.0
66	161.9			
73		166.3		
74		168.1		
75		168.0		170.1
76				170.1
77				170.1

[1] Data from Le Guen et al. (1969).

that there is no appreciable difference in the estimate of apparent growth of yellowfin tuna from the region of the eastern Atlantic, illustrated in Figure 1 or from a smaller region within that part such as off Pointe-Noire.

COMPARISON OE GROWTH ESTIMATES

Studies on growth of yellowfin tuna have largely been based on two types of data: length-frequency distributions and scale readings. For comparative purposes we chose two studies that were based on scale readings—one each from the Pacific (Yabuta, Yukinawa, and Warashina, 1960) and Atlantic (Yang et al., 1969)—and three studies that were based on modal progression of length-frequency distributions—two from the Pacific (Davidoff, 1963; Moore, 1951) and one from the Atlantic (Le Guen et al., 1969)—for comparison with our best estimates for the eastern Atlantic. The procedure of estimating the parameters of the von Bertalanffy function was standardized with the use of the Fabens' (1965) procedure whenever appropriate data were available.

ESTIMATES FROM SCALE READINGS

Lengths at mark formation from interpretation of marks on scales were reported by Yabuta et al. (1960). They indicated that mark formation occurs twice a year, in March-April and in September-October, or 6 months apart in the western Pacific. An estimate of growth was calculated from their data with 6 months between marks (Table 7). Growth appears to be substantially slower in the western Pacific than in the eastern Atlantic (Figure 9). Either growth is indeed slower in the western Pacific or the interpretation of scale marks by Yabuta et al. is in error. The latter possibility is suggested by the absence in their data of fish greater than 119 cm long with a designated mark, although fish as large as 161 cm long were reportedly sampled. Moreover, only about 42% of their scales were readable. Other studies made in the western Pacific (see Shomura, 1966; Suzuki, 1971) suggest that growth was underestimated by Yabuta et al.

$L_\infty = 222.8$ cm and $K = 0.023$, on a monthly basis, were estimated by Yang et al. (1969). Their estimates were based on scale readings of 296 yellowfin tuna caught by the Atlantic longline fishery. Since Yang et al. used the Walford (1946) procedure to estimate growth, we recalculated growth with the Fabens' procedure using the data of Yang et al. and the assumption that the scale marks formed every 6 months. The results (Table 7) were not markedly different from the estimates by Yang et al. Compared to our best estimate of growth rate (K), on the other hand, their estimate is substantially

TABLE 7.—Estimates of parameters of the von Bertalanffy growth function for yellowfin tuna from the Atlantic and Pacific Oceans. Estimates are based on data reported in various studies, and were calculated by Fabens' (1965) procedure, except those of Le Guen et al. (1969).

Region	L_∞	K	Range of length (cm)	Source of data	Data
Atlantic Ocean	223.0	0.023	66-133	Yang et al., 1969	Scale readings; Table 6
Eastern Atlantic				Le Guen et al., 1969	Length frequencies; estimates reported by authors
Dakar	206.6	0.026	63-162		
Pointe-Noire	182.4	0.037	64-162		
All areas	191.7	0.032	63-162		
Eastern Atlantic				Present study	Length frequencies (Age unknown)
Abidjan	185.0	0.043	59-157		
Dakar	307.9	0.017	53-147		
Gulf of Guinea	185.0	0.041	57-166		
Pointe-Noire	210.1	0.027	57-165		
All areas	194.8	0.035	53-166		
Eastern Atlantic				Present study	Length frequencies (Age known)
São Tomé-Angola	175.2	0.044	58-170		
Central Pacific	191.9	0.036	47-168	Moore, 1951	Length frequencies; Table H
Eastern Pacific	200.3	0.030	69-148	Davidoff, 1963	Length frequencies; Table 6
Western Pacific				Yabuta et al., 1960	Scale readings; Table 5
Males	202.1	0.023	58-119		
Females	174.9	0.031	57-119		
All sexes[1]	188.4	0.027	57-119		

[1] Estimates were based on weighed average length for each scale mark reported by Yabuta et al. (1960). Sample size of each sex was used as the weighing factor.

smaller. Possibly this smaller K is caused by error in the interpretation of scale marks and the paucity of large fish in their data. The maximum number of marks observed by Yang et al. was five, with a corresponding mean length of 132.9 cm at time of fifth mark formation, but fish as large as 180 cm long were reportedly sampled. For our study, fish as large as mean length 166 cm were used in the calculations.

ESTIMATES FROM MODAL PROGRESSION

Davidoff (1963) examined modal progressions of length-frequency distributions of eastern Pacific yellowfin tuna caught by baitboats and purse seiners and calculated with the Walford procedure $L_\infty = 167$ cm and $K = 0.05$, on a monthly basis, which he noted were similar to earlier estimates reported by Hennemuth (1961). Davidoff's estimates were based on average modal length at each age of all year classes combined. Equal weight was therefore given to each datum point in his calculation.

Using the Fabens' procedure and data for each year class reported by Davidoff (his Table 6), we recalculated the growth estimates. The results, $L_\infty = 200.3$ and $K = 0.030$, are considerably larger for L_∞ and smaller for K than Davidoff's estimates but similar to our estimates for Atlantic yellowfin tuna (Table 7).

Hennemuth (1961) reported that fish 70 cm long in the eastern Pacific were about 20 months old. Entered into the von Bertalanffy equation, this gives a t_0 of 5.67 months with $L_\infty = 200.3$ and $K = 0.030$, and a means of estimating length at age for eastern Pacific yellowfin tuna. The results are shown in Table 4. They compared favorably with our estimates for Atlantic yellowfin tuna, although apparent growth in the eastern Atlantic is 0.9 to 2.8% faster than that in the eastern Pacific for ages 2 through 5 years.

Moore (1951) based his estimates of growth on length-frequency distributions of yellowfin tuna caught primarily by longline gear in the central Pacific. He used the Walford procedure and calculated $L_\infty = 190.0$ cm and $K = 0.037$ per month. Because of a limitation of Walford's

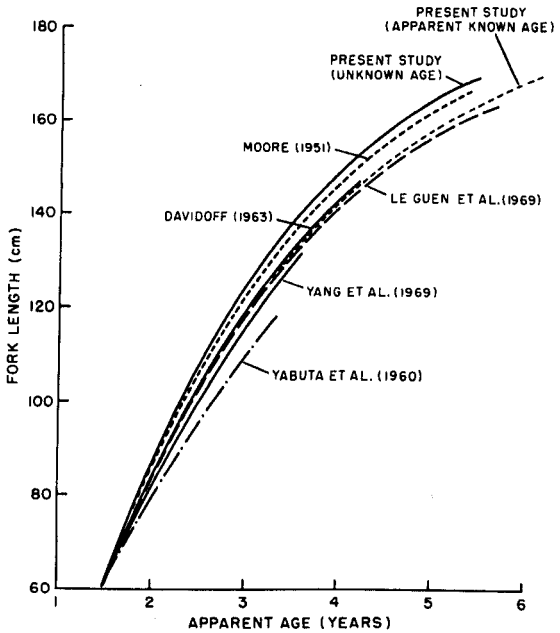

FIGURE 9.—Comparison of growth of yellowfin tuna from the Pacific and Atlantic Oceans. Curves were adjusted to a common base of age 1.5 years = 60 cm long and were estimated, except for that of Le Guen et al. (1969), from data reported in various studies.

method—requiring length measurements at equal time intervals—Moore was able to use only 16 out of his 25 observations. We recalculated L_∞ and K, using the Fabens' procedure and the 25 observations reported by Moore (his Table H). The estimates, $L_\infty = 191.9$ and $K = 0.036$, differ slightly from those of Moore and are very similar to our estimates for Atlantic yellowfin tuna.

Le Guen et al. (1969) estimated growth of yellowfin tuna from Dakar, Pointe-Noire, and both regions combined, based on modal progression of length-frequency samples (Table 7). Their samples were identical to some used in our study, but their estimate of growth for combined regions is slightly lower than ours; the difference in estimated lengths for ages 2 through 5 years is 2.8 to 4.3% less (Table 4). Part of the difference is in the method of analysis. The estimates by Le Guen et al. were based on mode selection from predorsal length distributions, and the lengths of size groups were not assumed to be normally distributed. Predorsal lengths were then converted to fork length; whereas in our best estimate predorsal length was converted to fork length by a log function before frequency distributions were analyzed, and the lengths of size groups were assumed to be normally distributed. Furthermore, Le Guen et al. assumed that the date of birth of fish of each year class of a region was the same and accordingly ages were assigned to size classes; such an assumption was not made for our estimate of K and L_∞; but for obtaining t_0 we assumed that yellowfin tuna of 60 cm long are 18 months old. Nevertheless, the difference is insignificant in view of the fact that there is considerable variability in observed mean lengths at age (Figure 7).

DISCUSSION

It is obvious from the results that estimates of growth of yellowfin tuna are quite variable and largely dependent on the method of analysis. Both the length-frequency and scale methods are based on various assumptions that are not always satisfied. For example, the assumption in the length-frequency method that size groups represent age groups, and the age groups are formed once a year, i.e., hatching within a short period, or season, is not completely satisfied for yellowfin tuna, since spawning occurs over several months (Matsumoto, 1966; Le Guen et al., 1969; Richards, 1969). Nevertheless, in many areas, as in the eastern Atlantic, there is generally a peak month of spawning (Le Guen et al., 1969) that can create a size group discernible in size-frequency distributions in later dates.

The scale method assumes that the scale marks are formed at regular intervals. So far, this assumption has not been satisfactorily verified for yellowfin tuna, although Yabuta et al. (1960) and Yang et al. (1969) have indicated that the marks formed every 6 months. Furthermore, because yellowfin tuna generally spawn over an extended season, the age at first annulus formation is not the same for all individuals of a year class. The back-calculated length at age I may therefore be questionable. It is surprising, however, that the observed lengths at age are remarkably similar for studies based on the scale and length-

frequency methods (Table 4). This suggests that the marks on scales of Atlantic yellowfin tuna are indeed layed down at regular intervals and that observed lengths at age rather than estimates of parameters of the von Bertalanffy function are more meaningful in comparison of growth of yellowfin tuna. For such a comparison, the average growth rate of Atlantic yellowfin tuna is 17 cm/6 months, based on the scale method, and 18 cm/6 months, based on the length-frequency method for ages 1.5-3.5 years.

The comparison of observed lengths at age also indicates that there is little difference between growth of Atlantic and Pacific yellowfin tuna (Table 4). Yang et al. (1969), on the other hand, suggested that growth is faster in the Atlantic than in the Pacific. We analyzed their data with analysis of covariance and found that their Walford curves for the Atlantic and Pacific yellowfin tuna were not significantly different from a common line ($F_{2,5} = 0.474$) nor from parallel lines ($F_{1,5} = 0.904$). Thus the suggestion by Yang et al. was not demonstrated by their data, but in fact, growth of yellowfin tuna appears to be similar in the two oceans.

Finally, since the parameters of the von Bertalanffy growth function are sensitive to the method of analysis and range of sizes used to estimate them, we recommend that the observed size at age rather than the estimated size at age from the von Bertalanffy growth function be used in estimating yield per recruitment. The Ricker (1958) model of yield per recruitment, for example, is appropriate for observed values.

ACKNOWLEDGMENT

We thank W. H. Bayliff, D. Kramer, and W. H. Lenarz for reading the manuscript and offering helpful suggestions.

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DESCRIPTIONS OF THE LARVAE OF FOUR NORTH PACIFIC PORCELLANIDAE (CRUSTACEA: ANOMURA)[1]

S. L. GONOR AND J. J. GONOR[2]

ABSTRACT

Complete descriptions are given of the zoea and megalopa stages of four porcelain crabs common in the rocky intertidal regions of the Pacific coast of North America. Both larvae reared in the laboratory and larvae taken from the plankton were available for the species *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles pubescens* Holmes, and *Pachycheles rudis* Stimpson. All four species have a short prezoea stage, two zoeae, and a planktonic megalopa stage. Extensive variation was found in setal numbers between left and right members of appendage pairs and between individuals in these larvae. Setal counts characteristics of species cannot be obtained from one or a few larvae, and ranges in the counts overlap considerably between species. The criteria of Lebour for grouping zoeal types in the Porcellanidae are applied to these four species and comparisons made between all available descriptions of porcellanid larvae. Intermolt growth of appendage buds occur in these four species, and it is concluded that this type of growth is the cause of most of the differences described previously as larval substages. Tabulations of species showing stage variation and intermolt growth are given.

All larval stages of four common Pacific coast rocky intertidal porcelain crabs have been reared in this laboratory. Material obtained from cultures and from the plankton was used for the descriptions given here of the larvae of each species. One of these species, *Pachycheles rudis*, has been described previously (Knight, 1966), and in this case the available material permitted this description to be expanded. Attention was also directed to variation in larval characteristics since adequate numbers of specimens were available for examination.

Gravid female porcelain crabs of the species *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles rudis* Stimpson, and *Pachycheles pubescens* Holmes were collected from rocky intertidal shores at Boiler Bay and Yaquina Head on the central Oregon coast. *P. rudis* was collected from the lower intertidal (—0.8 to —2.5 ft below mean lower low water) beneath *Phyllospadix* root mats on the seaward sides of large boulders. *Pachycheles pubescens* was collected from burrows and crevices in rock at the same tide level. The *Petrolisthes* species were gathered somewhat higher in the intertidal regions of the two sites beneath loosely bedded rocks and rubble. All four species occur in various other habitats as well (Haig, 1960) but were taken from these areas for convenience. Egg-carrying *Pachycheles rudis* were collected in May and June of 1968. In the same months of 1969, egg-bearing females of the other species were obtained for larval studies. Gravid females were also noted during other months of the year, in agreement with Knudsen's (1964) observations on the reproductive cycles of these species. The specific identity of the females used was confirmed by comparing them to the descriptions given by Haig (1690).

[1] Research supported in part by a traineeship from Grant Nos. 5T1-WP-111-02, -03, and -04, Federal Water Quality Administration, and by National Oceanic and Atmospheric Administration (maintained by the U.S. Department of Commerce) Institutional Sea Grant 2-35187.

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Manuscript accepted January 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

Female crabs were held individually in 1-liter beakers containing 600 ml of aerated, unfiltered seawater, standing in trays of running seawater ranging in temperature from 10.8° to 15.2°C. The water in the beakers was changed every 2 days. Larvae released by the females were removed from the beakers as soon as a hatch was discovered. Only actively swimming larvae of normal appearance were used.

Glassware for handling and culturing larvae was washed in fresh water, rinsed with distilled water, and steam autoclaved to minimize microbial contamination of the cultures. Seawater used for culturing was collected at high tide from the laboratory seawater system, passed through a sintered glass filter of pore size 40-60 mμ, and stored at 9°C in darkness. The salinity of this water ranged from 32.8 to 33.7‰.

Laboratory-hatched larvae of *Pachycheles rudis* and *Petrolisthes eriomerus* were cultured in flasks, while *P. cinctipes* larvae were reared in mass cultures only. Larvae from a single *Pachycheles pubescens* female were divided between flask and mass cultures. Light received by the larvae was not controlled. In all flask cultures larvae were maintained without aeration, initially with six to eight zoea I larvae per Erlenmeyer flask. The seawater volume allowance ranged from 25 ml per larva for early stages to 50 ml per larva for the larger later stages. Flasks were maintained at either 12°C or 15°C (± 0.01°C) in refrigerated baths of circulating water. All flask cultures were examined daily, mortality recorded, and newly molted larvae transferred to new cultures. Plankton tows were made intermittently from May through September of 1968 in Yaquina Bay and 1 mile outside the estuary along a rocky reef paralleling the shore. The catch was immediately resuspended in cold seawater and kept under refrigeration while being taken to the laboratory. Live porcellanid larvae obtained in these hauls were removed to fresh seawater, sorted by zoeal stage, and further separated into four groups on the basis of differences in the patterns of the primary red chromatophores. Larvae within each group were further divided and placed in flask cultures.

Mass cultures of laboratory-hatched *Petrolisthes cinctipes* larvae were maintained in 5-gal carboys filled with filtered seawater, with 150 or fewer larvae per carboy. Aerated mass cultures were immersed in baths of running seawater and experienced a temperature range of 10.8° to 15.2°C during the culture period and a maximum daily fluctuation of 2.5°C due to tidal influence. Larvae in mass culture were transferred to clean containers and fresh seawater every 14 days.

Zoea larvae were fed *Artemia salina* nauplii not more than 3 days old daily if required so that excess food was always present. The megalopa larvae required suspended algal material as food. Several monoalgal (*Tetraselmis* sp., *Isochrysis* sp.) and diatom (unidentified) cultures were tried singly and in combinations as a food source. Nutrient culture medium inoculated with raw seawater was also used as a source of food organisms. Small stones were introduced into the flasks to provide the megalopae with a surface for settling.

The larvae of the two *Petrolisthes* species and *Pachycheles rudis* were reared to the megalopa stage in cultures from embryos obtained from females held in the laboratory. Live larvae of these species taken from the plankton were reared to confirm stages obtained from the laboratory-hatched broods and to supplement laboratory-grown material for descriptive purposes. The larval history of *P. pubescens* was first described from larvae captured in the plankton and placed in laboratory cultures. Three gravid females of this species were collected later, and the identity of the planktonic larvae was confirmed by comparison with larvae released by one of the females and reared to the second zoeal stage.

Larvae in various stages of development were preserved for dissection primarily in 70% ethanol, but a few larval specimens were preserved in a mixture of 50% glycerine and 50% ethanol for chromatophore examinations. Both temporary and permanent slides were made of the dissected materials. Temporary mounts were made in glycerine, and permanent mounts were made in Zeiss hardening phase medium as well

as in Turtox CMC-9AB and CMC-10 media.[3] Drawings were made from both types of material with the aid of a Wild M-20 compound microscope and camera lucida attachment. Since the length of the rostral and posterior spines of zoeae is highly variable and dependent on a number of factors, only the carapace proper was measured to serve as an indication of zoeal size. This measurement was made from the point of junction of the posterior spines to the posterior margin of the orbital arch, using an ocular micrometer.

The term "seta" is used to indicate any firm-walled process, located on an appendage or other body surface, which is distinctly articulate at its base or attachment point (Figure 1). The figures are in part schematic and represent typical setal counts only. Setules are not represented in actual numbers and are often omitted entirely for clarity. Only one member of each setal pair present is figured for the exopodites of zoeal maxillipeds. Only the right member of each appendage pair is figured except for mandibles, which are sometimes drawn in pairs from the dorsal view.

Sexually mature females of the two genera considered in this study produce eggs of distinctly different types. *Pachycheles rudis* and *P. pubescens* females carry eggs which are 0.50 to 0.58 mm in size and brilliant yellow-orange when they are newly extruded. The eggs of *P. rudis*, as Knudsen (1964) and Knight (1966) observed, gradually change to a translucent amber color as the embryos develop and the yolk is absorbed. The color change with development is similar in *P. pubescens*. The age of the egg masses of the individual females collected in the field was unknown; however, the maximum length of time any female *P. rudis* carried eggs was 47 days, and two others carried eggs for 43 days before releasing larvae. This time may approach the length of time eggs are carried in this species. In both *Pachycheles* species, eggs hatched and all the larvae were released in a period of 10 to 20 hr. A hatch from a large female (carapace width 14.2-15.0 mm) may yield between 2,000 and 3,000 larvae but brood size varies (Knudsen, 1964).

In contrast, the eggs of *Petrolisthes cinctipes* and *P. eriomerus* are somewhat larger, 0.80 to 0.84 mm, and are deep scarlet to maroon in color, when newly extruded, similar to those of other species in the genus (Wear, 1965b; Greenwood, 1965). As Boolootian et al. (1959) also observed, the eggs gradually change to a translucent brownish red color as the embryos develop and the yolk is absorbed. Females of these two species were deliberately collected close to the hatching time; consequently, no information on the length of the brooding period was obtained. The time required for a female to complete a hatch is similar in these two *Petrolisthes* species but differs considerably from that observed for the *Pachycheles* species. Female *Petrolisthes* require 40 to 70 hr to release an entire group of larvae in the laboratory. Release of the larvae in these two species occurs in spurts with "resting" periods between each period of concentrated release.

The embryonic and larval histories of all four species observed in the laboratory have a number of characteristics in common. Fully developed embryos examined prior to eclosion possessed the full complement of primary red chromatophores found throughout the active larval life of these crabs. Although occasional minor variations were noted both in laboratory hatches and in larvae from the plankton, the occurrence and placement of the chromatophores is generally stable and is species specific, as various workers have noted in other species (Wear, 1964a, b, 1965a, b; Greenwood, 1965; Gore, 1968; Gurney, 1942). The primary chromatophores can thus be used to identify a larva to the species level at any stage of development.

In the hatching of all four species, females released larvae in the form of prezoeae. This has been observed in other porcellanid species, for example, by Lebour (1943), Greenwood (1965), Wear (1965b, 1966), and Gore (1968). The duration of this stage in the laboratory varies considerably and lasts from 10 min to about 1 hr in the species studied here. Prezoeae were never collected in the plankton.

[3] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

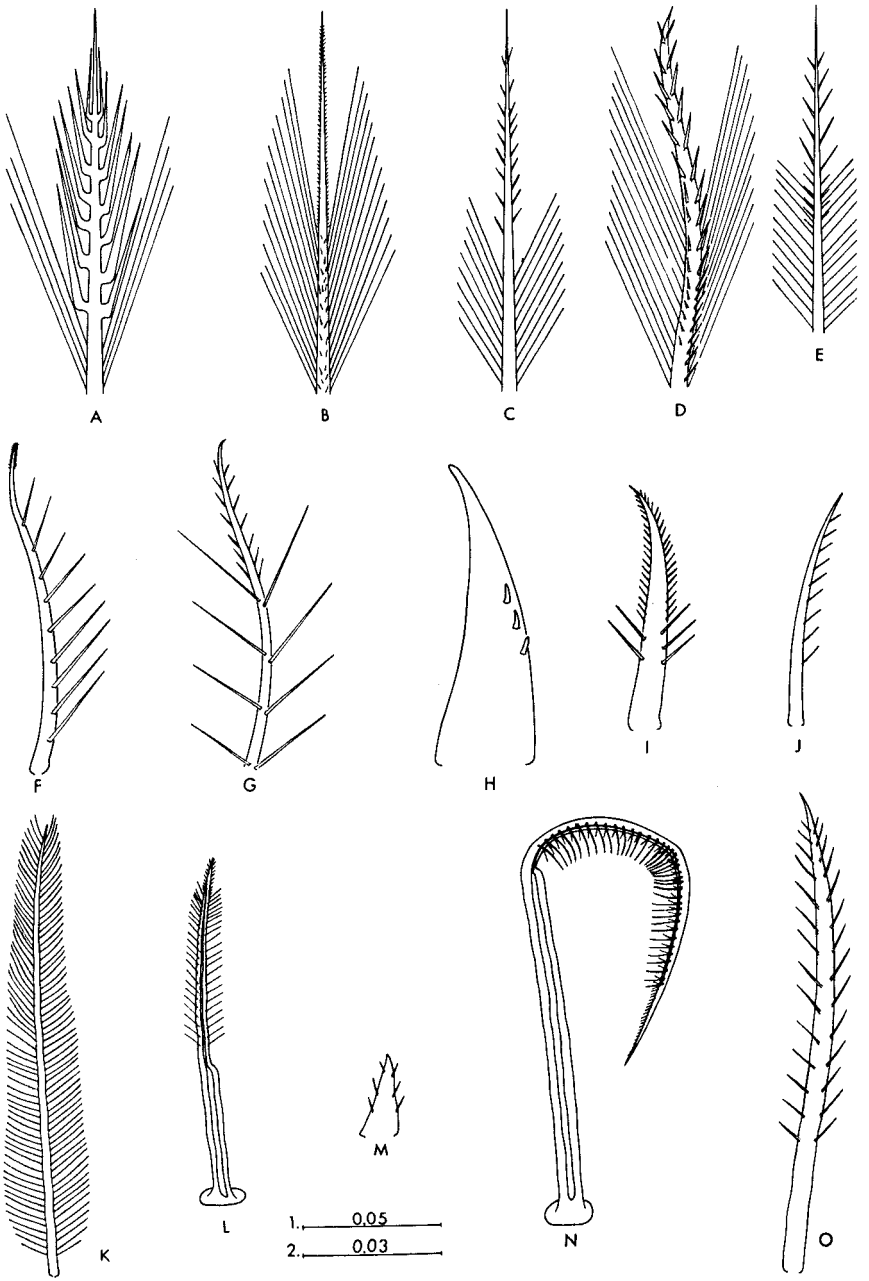

FIGURE 1.—Setal types in four porcellanid species studied: A-E (Scale 1), zoeal telson processes, distal portions: A - processes 3 and 4, *Pachycheles* spp.; B - processes 5, 6, and 7, *Pachycheles* spp.; C - median spine, Zoea II, *Pachycheles* spp.; D - processes 3 through 7, *Petrolisthes* spp.; E - median spine, Zoea II, *Petrolisthes* spp. F-K (Scale 2), zoeal maxillary setae, all four species. L, N (Scale 2), scythelike cleaning setae, straight and hooked, megalopa, pereiopod 5, all four species. M, O (Scale 2), "spikelike" and "brushlike" setae, megalopa, maxilliped III, all four species. Scales in millimeter.

After the larva has spent a period of time as a prezoea, the cuticle over the carapace is ruptured dorsally along the midline and the prezoea molts to the first true zoeal stage. The rostrum is the first portion of the body to be freed, followed by the functional mouth parts and natatory maxillipeds. The abdomen and telson are the last portions to be withdrawn from the cuticle. When the molt is completed, the natatory setae and setae of the telson, previously compacted and confined by the prezoeal cuticle, become fully extended and serve to keep the larva afloat and propel it through the water. The rostral spine, partially invaginated into the carapace in the prezoea, straightens out almost immediately following the molt. The posterior carapace spines which often, but not always, become tightly coiled immediately after the cuticle is shed may take several minutes to several hours to uncoil. The cuticle is shed virtually intact except for the original dorsal split. Often in later molts, the delicate elastic cuticle covering the pereiopod and pleopod buds is shriveled or damaged in the cast exoskeleton.

Larvae of all four species always pass through two true zoeal stages and one megalopal stage (terminology of Williamson, 1957) in the laboratory as do certain other porcellanids (Le Roux, 1961, 1966; Knight, 1966; Boschi, Scelzo, and Goldstein, 1967; Gore, 1968, 1970, 1971a, b, 1972). This was true of larvae hatched in the laboratory as well as those taken from the plankton.

In these four species, both zoeal stages demonstrate the remarkable property of intermolt growth in which certain of the larval appendages increase in size, apparently throughout the duration of a stage, while the larval cuticle remains intact. This phenomenon has been reported for various other porcellanid larvae (Le Roux, 1961, 1966; Kurata, 1964; Knight, 1966; Gore, 1968, 1970, 1971a, b, 1972) but has not yet been thoroughly investigated. Appendages may increase in size as much as threefold between molts as a result of this growth pattern.

The number of specimens of each stage dissected and examined is given in Table 1. The ranges given in the descriptions refer only to variations found within these specimens. Many other specimens were examined but not dissected.

LARVAL DEVELOPMENT OF *PETROLISTHES CINCTIPES* (RANDALL)

Larvae of *P. cinctipes* were reared using the mass culture method. The single megalopa thus obtained as well as one megalopa from the plankton were preserved and dissected for purposes of description.

PREZOEA
(Figure 2)

The prezoea of *P. cinctipes* is virtually spineless and hairless. The carapace has a generally rounded appearance because the rostral and posterior spines are curved downward and inward toward the center of the body. These spines are further compacted by being telescoped and invaginated into their respective portions of the carapace. The natatory setae are nonfunctional, withdrawn into the ends of the maxillipeds, and held in place by the prezoeal cuticle. The primary red chromatophores appear in the following locations: one on either side of the mouth; one distally on the basipodite of each second maxilliped; one distally in abdominal segment number two or between segments two and three; and one on either side of the body between the bases of maxillipeds one and two. The rostrum and posterior spines are tipped with red, and an additional red band appears on the rostrum proximal to the red tip and separated from it by a white or colorless band.

With the exception of the chromatophore numbers and arrangement, the prezoeal stages of the four species do not differ significantly. For this reason, a prezoea will be figured only

TABLE 1.—Number of porcelain crab larvae dissected and examined for this study.

Species	Zoea I	Zoea II	Megalopa
Petrolisthes cinctipes	11	4	2
Petrolisthes eriomerus	16	4	9
Pachycheles pubescens	9	6	9
Pachycheles rudis	12	12	7

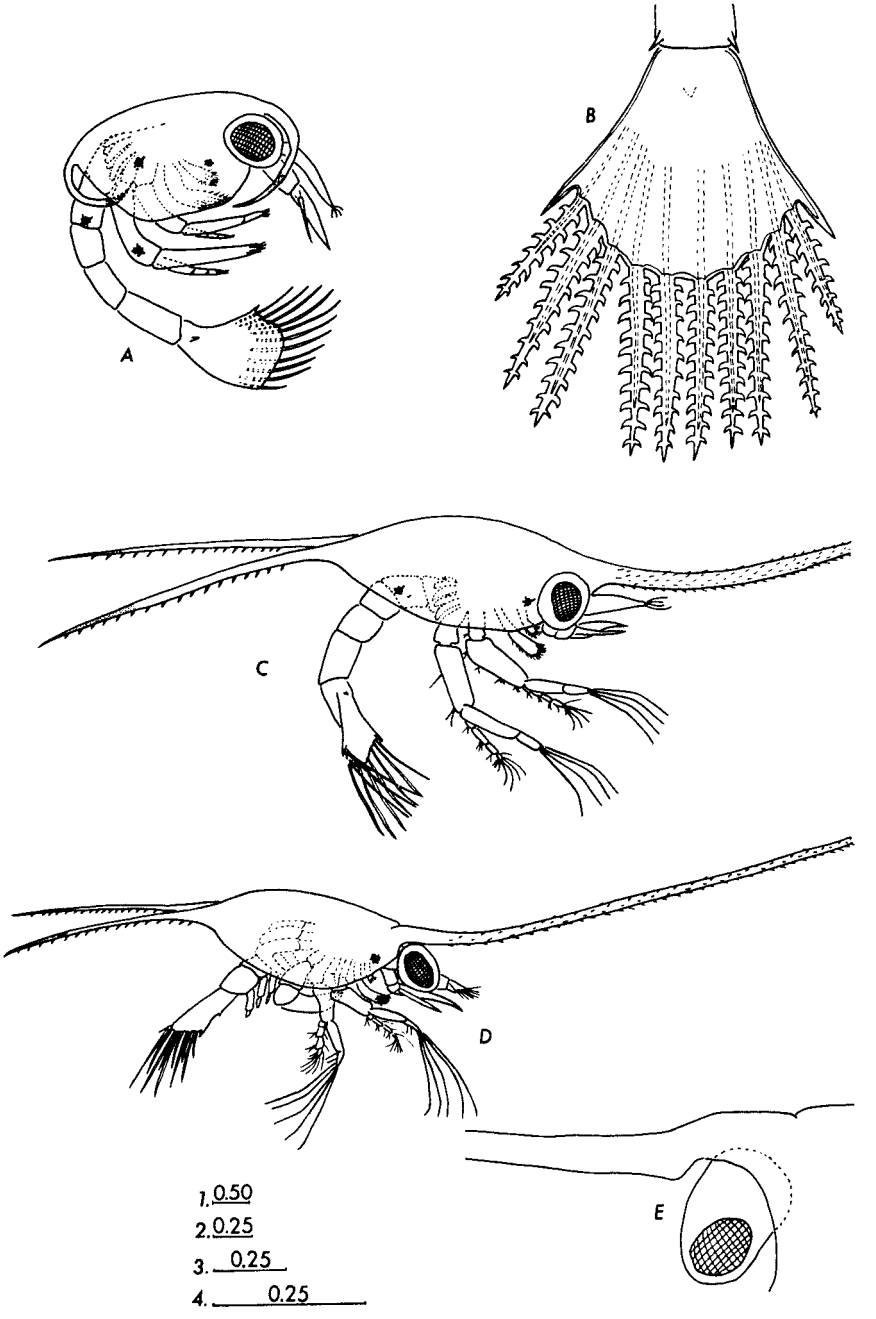

FIGURE 2.—Prezoea, Zoea I, Zoea II, entire: A - prezoea, *Petroli... inctipes* with primary chromatophores (Scale 3); B - prezoeal telson with modified cuticle, *Pachycheles pubescens* (Scale 4); C - *Petrolisthes eriomerus*, Zoea I with chromatophores (Scale 2); D - *Pachycheles pubescens*, Zoea II with chromatophores (Scale 1); E - *Petrolisthes* spp., Zoea II, ventral rostral bulge (Scale 3). Scales in millimeter.

once, and specific variations will be indicated in the text. Prezoeae were not dissected.

ZOEA I
(Figure 3)

Antennule unsegmented with five or six terminal processes including three aesthetascs and two or three setae.

Antenna biramous; endopodite fused with protopodite and bearing a terminal point and subterminal tubercle with a fine seta between; exopodite mobile, about 1½ times as long as endopodite, with three or four prominent distal spines and one long seta proximal to the spines.

Mandibles strongly sclerotized, heavily toothed, asymmetrical appendages.

Maxilla I with unsegmented endopodite bearing three or four terminal setae and a number of fine hairs along the anterior margin; basal endite with 9 or 10 stout spinous processes; coxal endite with 9 or 10 stout setae.

Maxilla II with unsegmented endopodite bearing eight or nine setae, grouped 3, 1-2, 3-4 proximal to distal, 3-2-4 being the most common grouping. Basal endite bilobed: distal lobe with 7 to 10 setae; proximal lobe with seven to nine setae. Coxal endite bilobed: distal lobe with four to six setae; proximal lobe with 8 to 11 setae. Scaphognathite with six or seven long plumose marginal setae, and one apical seta; numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with one or two distal setae. Basipodite with 9 to 11 setae most commonly grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with one to three distal setae, inner margin; segment 2 with two or three distal setae, inner margin; segment 3 with four to seven setae including two or three medial, one or two distal, inner margin, occasionally one long medial seta, outer margin; segment 4 with five to seven terminal setae and one proximal on outer margin. Exopodite two-segmented with four terminal natatory setae on distal segment. Additional groups of very fine hairs appear on endopodite segments 2, 3, and 4 and on segment 2 of exopodite as figured.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with three setae on inner margin grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with one or two distal setae, inner margin; segment 2 with one or two distal setae, inner margin; segment 3 with one medial and one or two distal setae, inner margin; segment 4 with three to five (usually five) terminal setae and one proximal seta, outer margin. Exopodite two-segmented with four terminal natatory setae on distal segment. Groups of very fine hairs appear on endopodite segments 2, 3, and 4 and on both segments of exopodite as figured.

Maxilliped III present as small bilobed bud which undergoes growth throughout stage.

Pereiopods present as five pairs of short limb buds, all without setae; none chelate; undergo growth during entire stage.

Abdominal somites numbering five; segments 3, 4, and 5 with serrated dorsal posterior margins; segments 4 and 5 each with a pair of strong ventrolateral spines on posterior margin.

Telson with seven symmetrically arranged pairs of processes, with central pair located on central prominence; outer margin to center line: one heavy, articulated lateral process with few spinules (not figured), one short fine seta, and five long plumose articulating setae; all long plumose setae armed distally with fixed curved spines (Figure 1D); fine hairs (not figured) on margin of telson between all major plumose setae and on central prominence; anal spine present.

Chromatophores as described in the prezoea; carapace 1.23 to 1.39 mm in length.

ZOEA II
(Figure 4)

Antennule biramous; exopodite with six or seven terminal processes including four aesthetascs and two or three setae, followed by five tiers of subterminal aesthetascs grouped 2, 3, 3, 4, 3 progressing proximally; three or four fine setae present on distal margin of protopodite.

Antenna biramous; endopodite same form as in zoea I; exopodite similar to zoea I, with three spines and one seta distally; exopodite and endopodite approximately equal in length.

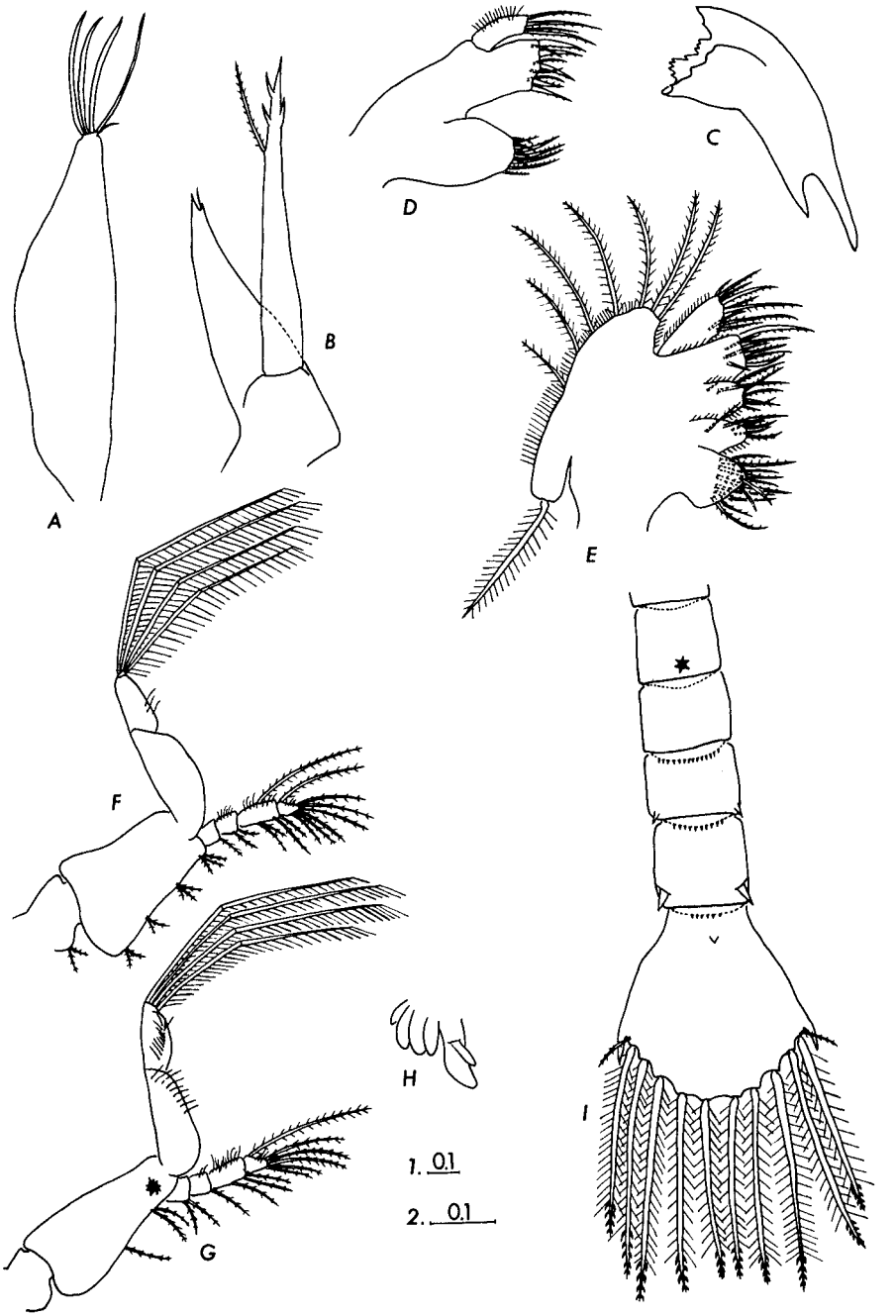

FIGURE 3.—*Petrolisthes cinctipes*, Zoea I: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II (A-E, Scale 2); F - maxilliped I; G - maxilliped II (F and G, Scale 1); H - maxilliped III and pereiopod buds (Scale 2); I - abdomen and telson, ventral (Scale 1). Scales in millimeter.

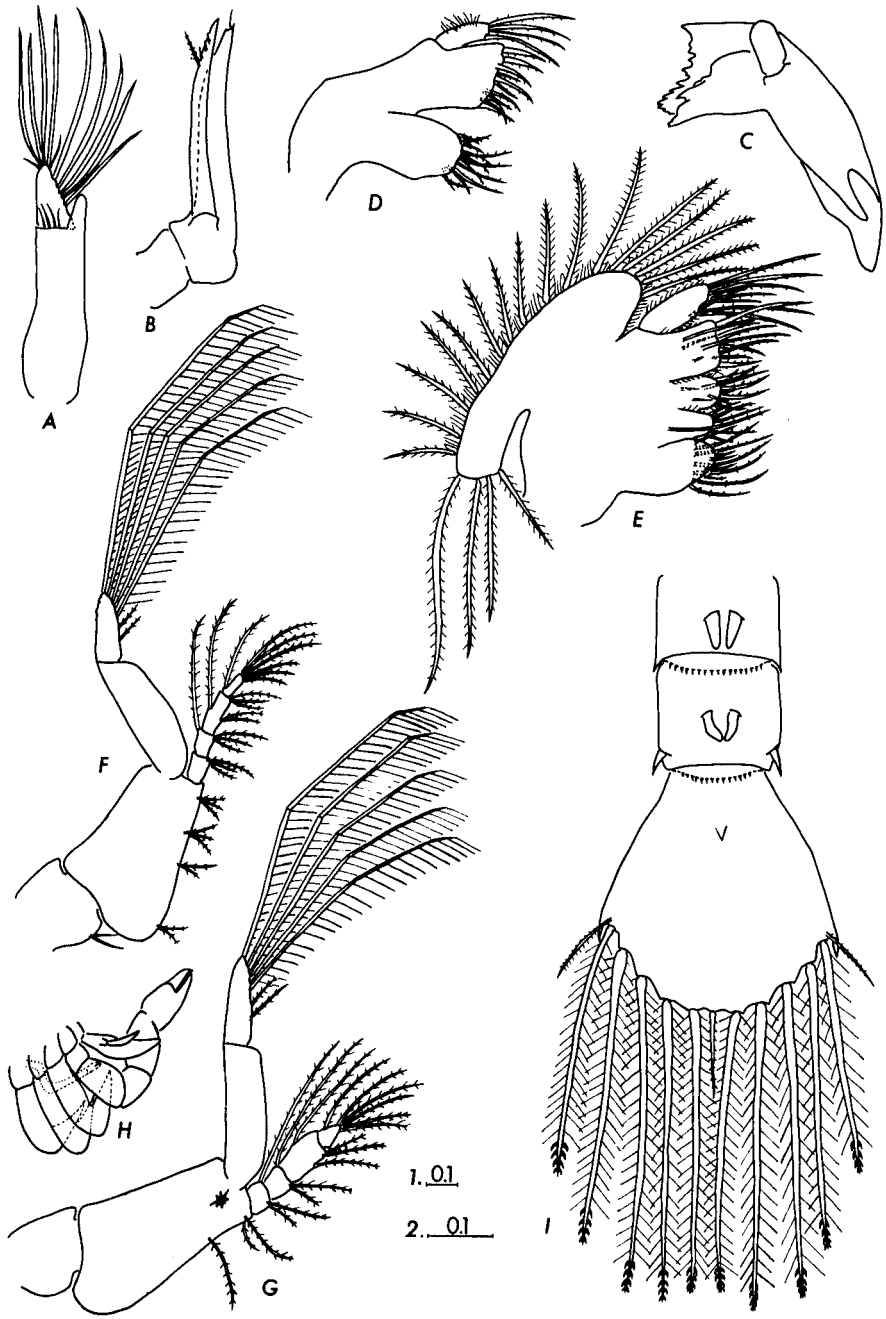

FIGURE 4.—*Petrolisthes cinctipes*, Zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II (A-E, Scale 2); F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopods; I - abdomen and telson (F-I, Scale 2). Scales in millimeter.

Mandibles larger than in zoea I and with prominent palp bud.

Maxilla I with unsegmented endopodite bearing four or five terminal setae and a number of fine hairs along anterior margin; basal endite with 10 or 11 setae; coxal endite with 11 to 13 setae.

Maxilla II with unsegmented endopodite bearing nine setae grouped 3, 2, 4 progressing distally. Basal endite bilobed; both distal and proximal lobes with 11 or 12 setae each. Coxal endite bilobed: distal lobe with seven setae; proximal lobe with 11 to 15 setae. Scaphognathite with 16 to 18 outer marginal setae, three apical setae and one on internal margin of posterior lobe (total 20 to 22 setae), all plumose. Fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with one or two distal setae. Basipodite with setae grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with three distal setae, inner margin; segment 2 with three distal setae, inner margin and one distal seta, outer margin; segment 3 with two medial and three distal setae, inner margin and one medial seta, outer margin; segment 4 with five or six terminal setae and one proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacks setae. Basipodite with three setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segments 1 and 2 each with two distal setae, inner margin and one distal, outer margin; segment 3 with one medial, two distal, inner margin and one medial seta, outer margin; segment 4 with four to six (usually five) terminal setae and one proximal seta on outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped III biramous, larger than in zoea I; endopodite curved anteriad; appendage grows and additional segments become defined during stage.

Pereiopods present as five pairs of limb buds, pairs one and five distinctly chelate; buds expand in size throughout stage and become distinctly segmented in a late zoea II.

Abdominal somites larger but otherwise similar to those in zoea I; pairs of pleopods, unequal in length, occur ventrally on segments 2, 3, 4, and 5; pleopods increase in length throughout stage.

Telson similar to form in zoea I but with single median seta (Figures 1E and 4I) added to central prominence and size increased; anal spine present.

Basic pattern of primary red chromatophores same as in prezoea and zoea I; however, new chromatophores appear in the late second stage zoea on the growing pereiopods and on body beneath carapace. Carapace 1.72 to 1.98 mm in length. Rostrum bears distinct ventral bulge just anterior to eyes (Figure 2E).

MEGALOPA
(Figures 5 and 6)

Antennule biramous with three-segmented peduncle. Dorsal ramus with six segments; segments 2, 3, and 4 each bear two tiers of aesthetascs and segment 5 bears one tier; numbers of aesthetascs per tier are approximately 3-4, 2-3, 3, 2, 2-3, 2, 2 progressing distally (specimens damaged); one long seta present on each of segments 3 and 4 associated with the distal aesthetasc tier. Ventral ramus with three distinct segments, the distal segment itself appearing indistinctly divided; setation as figured.

Antennal flagellum usually composed of 17 segments; peduncle three-segmented; hairs and bristles associated with the distal end of each segment along the length of the flagellum vary in number and pattern of distribution.

Mandible strongly sclerotized, partially cup-shaped appendage with bladelike leading edge which may be somewhat irregular but is not strongly toothed as in the zoea; three-segmented palp present with about six spinelike setae on terminal segment.

Maxilla I with probably two-segmented endopodite (specimens damaged) bearing one or more setae; basal endite with a total of 21 or 22 spines and setae arranged predominantly along the distal margin; coxal endite with approximately 26 processes, most of them slender setae in contrast to the spinelike processes of the basal

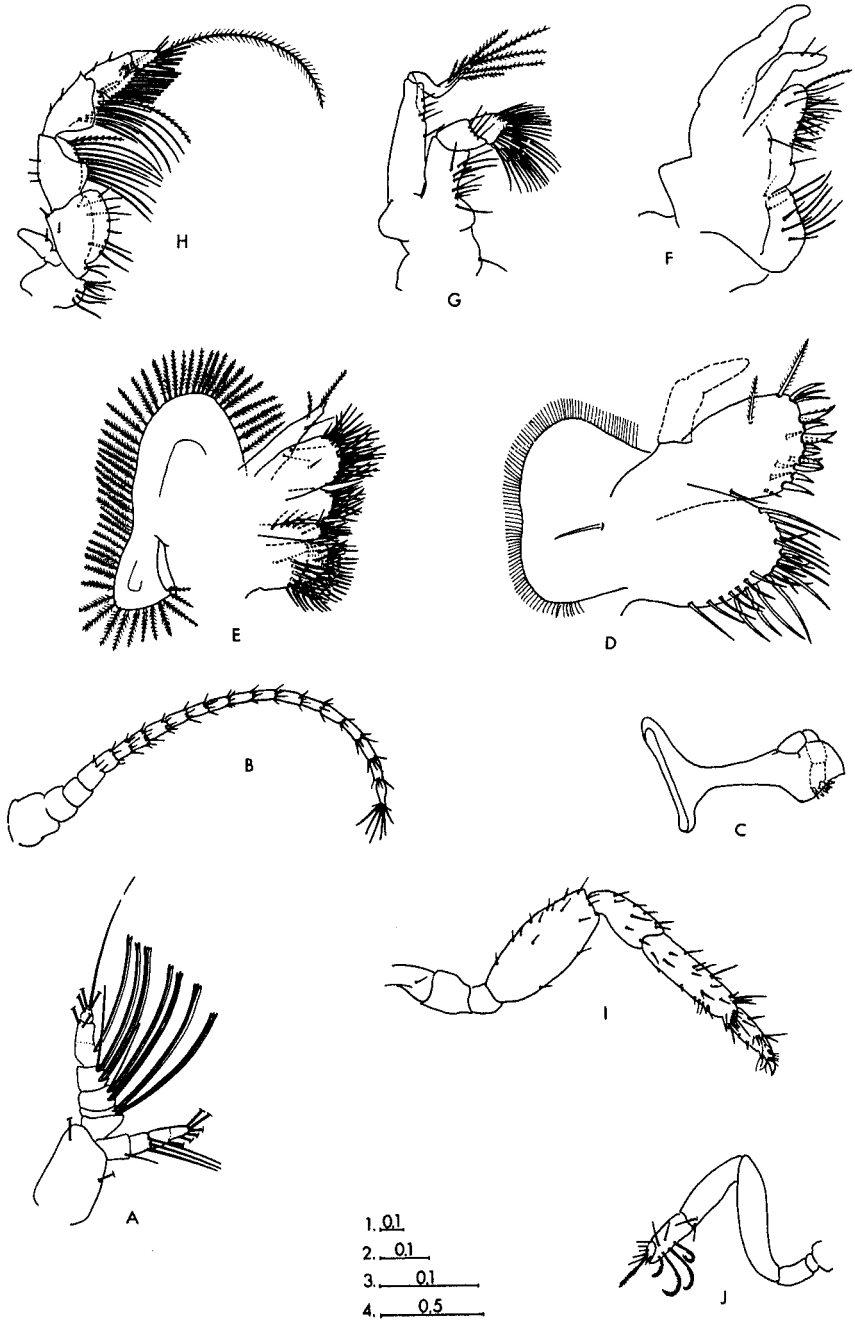

FIGURE 5.—*Petrolisthes cinctipes* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (B, G, H, J, Scale 1; A, C, E, F, Scale 2; D Scale 3; I, Scale 4). Scales in millimeter.

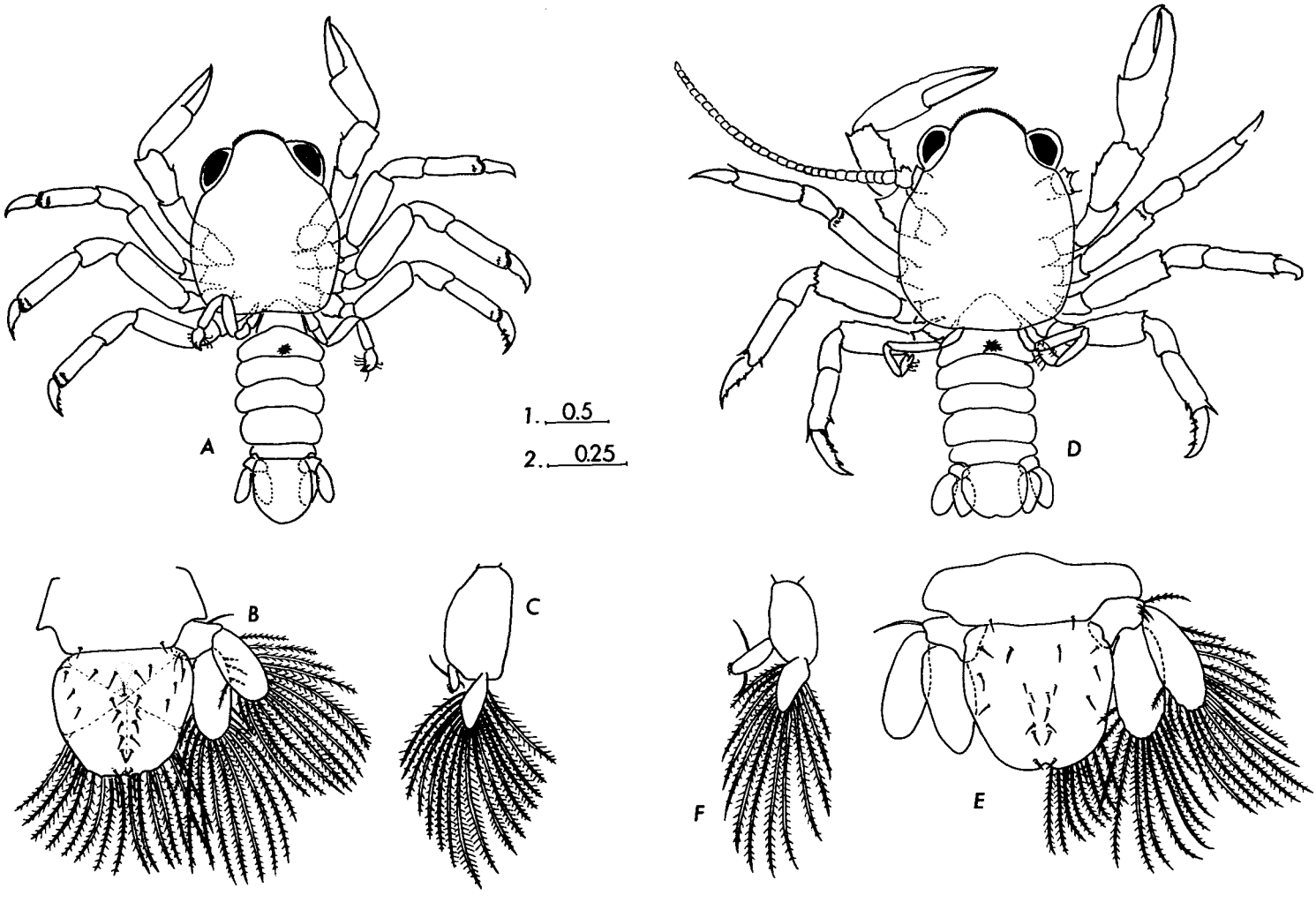

FIGURE 6.—*Petrolisthes cinctipes* and *P. eriomerus* megalopae: A - *P. cinctipes* megalopa, generalized, with chromatophore; B - *P. cinctipes* telson and uropods; C - *P. cinctipes* right third pleopod; D - *P. eriomerus* megalopa, generalized, with chromatophore; E - *P. eriomerus* telson and uropods; F - *P. eriomerus* right third pleopod (A, D, Scale 1; B, C, E and F, Scale 2). Scales in millimeter.

endite; a small fanlike exite also present, rimmed with very fine hairs.

Maxilla II with unsegmented endopodite bearing five setae. Basal endite bilobed: distal lobe with approximately 26 setae; proximal lobe with 13 to 15 setae. Coxal endite bilobed: distal lobe with nine marginal setae and six submarginal setae, dorsal surface; proximal lobe with about 20 marginal setae, 13 submarginals, dorsal surface, and 8 submarginal setae, ventral surface. Scaphognathite with approximately 50 marginal setae.

Maxilliped I biramous. Exopodite devoid of setae or hairs in specimens examined (two). Endopodite two-segmented in appearance, but indistinctly so; distal segment bears two short setae. Basal endite with 19 or 20 major marginal setae, 5 to 8 submarginal setae, dorsal surface. Coxal endite with about seven major marginal setae and six submarginal setae, three on dorsal surface and three on ventral surface.

Maxilliped II biramous. Exopodite consists of two distinct segments, the distal segment itself appearing indistinctly segmented; there are five to seven plumose setae on the distal segment and five setae on the internal margin of the first segment. Endopodite four-segmented, the distal two segments each bearing dense brushes of approximately 20 to 30 setae; segment 2 with four or five setae along distal margin; segment 1 with approximately 11 setae along the internal margin.

Maxilliped III biramous. Exopodite incompletely formed with two segments only; segment 2 with one small proximal seta. Endopodite specialized for filter feeding and consists of five segments; segment 2 with 10 to 12 major setae, dorsal internal margin; segment 3 with 9 or 10 major feeding setae, 3 or 4 short, stout brushlike setae, and 2 or 3 very short, spikelike setae all on the dorsal internal margin; segment 4 with nine major feeding setae along the internal ventral margin, six or seven minor feeding setae along dorsal internal margin; four or five major brush setae and two spikes, all along internal dorsal margin; segment 5 with six pairs of feeding setae and two minor brush setae terminally; other setation as pictured.

Pereiopods well developed and functional. Chelipeds slender and streamlined, generally dorsoventrally flattened with fine bristles over entire surface; outer margin of chelae produced in a series of spines; anterior margin of carpus with one major spine and a fine bristle associated with it. Pereiopods 2, 3, and 4 similar to each other in shape and setation as figured (Figure 5I). Pereiopod 5 chelate and armed with setae and bristles as shown; four to eight scythelike cleaning setae (Figure 1L, N) are also present.

Abdomen six-segmented; segments 2 through 5 each bearing one pair of pleopods. Pleopods biramous; exopodite with 16 plumose marginal setae; endopodite with two short setae and four hooks on margin. A single primary red chromatophore located on segment 2 or between 2 and 3. Segment 6 of the abdomen bears a pair of biramous uropods, the outer ramus usually having 14 and inner ramus with 15 marginal setae. Telson with 14 to 16 major plumose setae and 14 to 16 minor setae located between the major marginal setae. The dorsal surface of the telson bears a number of symmetrically placed pairs of fine hairs. In megalopae of advanced age, the beginning of the division of the telson into five plates can be seen beneath the cuticle. Upon molting to the first crab stage, the division of the telson is complete and distinct.

LARVAL DEVELOPMENT OF *PETROLISTHES ERIOMERUS* STIMPSON

Larvae of *P. eriomerus* were reared in unaerated Erlenmeyer flask cultures.

PREZOEA

The prezoea has essentially the same form as that described for *P. cinctipes* and differs only in one pair of primary chromatophores. *P. eriomerus* prezoeae lack the chromatophore on either side of the body between the bases of maxillipeds I and II which occurs in *P. cinctipes* larvae.

ZOEA I
(Figure 7)

Antennule unsegmented; five to six terminal processes including four aesthetascs and one or two setae.

Antenna biramous, with endopodite and protopodite fused; endopodite with terminal point, subterminal tubercle and fine seta between; exopodite approximately 1⅓ times as long as endopodite with one, two, or three prominent distal spines and one long seta proximal to spines.

Mandibles strongly sclerotized asymmetrical appendages, heavily armed with teeth and tubercles on leading edges.

Maxilla I with unsegmented endopodite bearing three to six terminal and subterminal setae and a number of fine hairs along anterior margin; basal endite with 9 or 10 setae; coxal endite with 8 to 10 setae.

Maxilla II with unsegmented endopodite which bears 7 to 10 setae, grouped 2-3, 2, 3-4 progressing distally. Basal endite bilobed: distal lobe with 8 to 10 setae; proximal lobe with 6 to 10 setae. Coxal endite bilobed: distal lobe with four to eight setae; proximal lobe with 7 to 11 setae. Scaphognathite with six to eight long plumose marginal setae and one strong apical seta. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with two or rarely three distal setae. Basipodite with 10 setae usually grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three distal setae, inner margin; segment 3 with usually two medial and three or rarely four distal setae, inner margin; segment 4 with five to seven terminal setae and one proximal seta, outer margin; segments 2 and 3 also bear groups of fine hairs as figured. Exopodite two-segmented, the distal segment bearing four terminal natatory setae.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with usually two but sometimes one distal seta and one medial seta, inner margin. Endopodite four-segmented: segment 1 with usually two but sometimes with one distal seta, inner margin; segment 2 usually with two but rarely one or three distal setae, inner margin; segment 3 with one medial seta or occasionally two setae, and usually two, but sometimes three distal setae, inner margin; segment 4 with three to five terminal setae and one proximal seta, outer margin; segments 2 and 3 also bear groups of fine hairs as figured. Exopodite two-segmented, the distal segment bearing four terminal natatory setae.

Maxilliped III a small bilobed bud which grows throughout stage.

Pereiopod buds simple, five pairs in number, growing throughout the duration of the stage.

Abdominal segments five in number; segments 3, 4, and 5 having serrations on dorsal posterior margins; segments 4 and 5 with strong ventrolateral spines on posterior margin.

Telson with seven symmetrically placed pairs of processes, with seventh pair on central prominence. Outer margin to center line: one heavy lateral spine fused with telson, one short fine seta, and five long plumose articulating setae, all armed distally with a series of short, curved fixed spines (Figure 1D); numerous fine hairs on telson margin (not figured) between all major plumose setae; anal spine present.

Chromatophore pattern as noted for the prezoea; extended rostrum with one terminal and one subterminal band of red color; posterior spines each with one terminal red band. Carapace 1.31 to 1.48 mm in length.

ZOEA II
(Figure 8)

Antennule biramous; exopodite with six or seven terminal processes including four aesthetascs and two or three setae followed by five tiers of subterminal aesthetascs grouped 3, 4, 3, 3, 2 proximal to distal.

Antenna biramous; endopodite same form as in zoea I; exopodite similar to that in zoea I with one to three spines, one seta distally; spines somewhat less prominent than in zoea I; exopodite approximately three-quarters length of endopodite.

Mandibles larger than in zoea I and with prominent palp bud.

FIGURE 7.—*Petrolisthes eriomerus* zoea I: A - antennule; B - antenna; C - mandibles; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and periopod buds; I - abdomen and telson (A-E, H, Scale 2; F, G, I, Scale 1). Scales in millimeter.

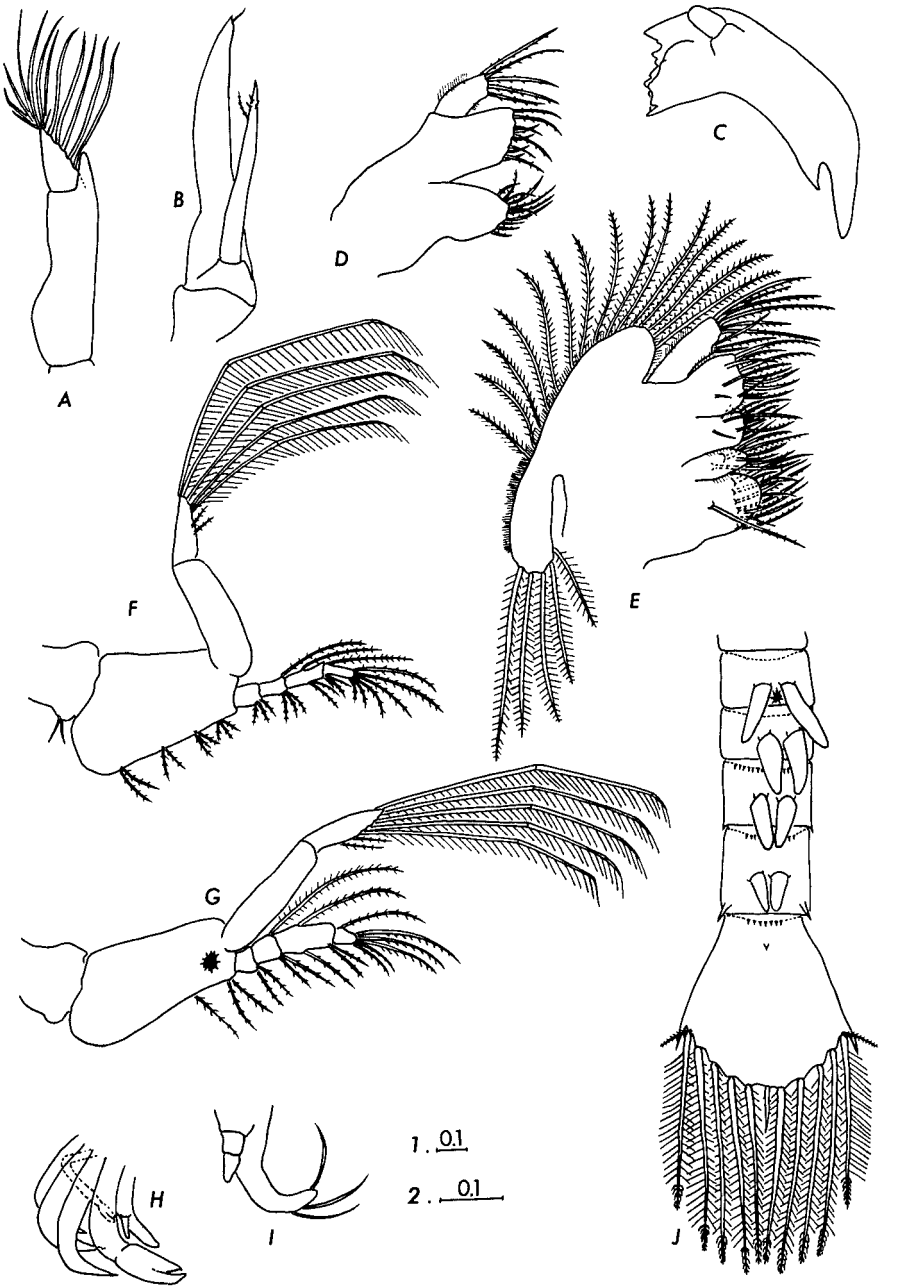

FIGURE 8.—*Petrolisthes eviomerus* zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopods; I - maxilliped III, late zoea II; J - abdomen and telson (A, B, F-H, J, Scale 1; C-E, I, Scale 2). Scales in millimeter.

Maxilla I with unsegmented endopodite bearing four to seven terminal and subterminal setae and a group of fine hairs along anterior margin; basal endite with 10 or 11 setae; coxal endite with 9 to 11 setae.

Maxilla II with unsegmented endopodite bearing nine setae grouped 3, 2, 4 progressing distally. Basal endite bilobed: distal lobe with 12 or 13 setae; proximal lobe with 11 or 12 setae. Coxal endite bilobed: distal lobe with five to seven setae; proximal lobe with 12 to 15 setae. Scaphognathite with 13 to 16 marginal, 3 apical, and 1 or 2 internal lateral setae (total 17 to 21); fine hairs present on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with two distal setae. Basipodite with setae usually grouped 2, 2, 3, 3 proximal to distal along inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three or four distal setae, inner margin and one distal seta, outer margin; segment 3 usually with two medial and three distal setae, inner margin and one medial, outer margin; segment 4 with four to seven terminal and one proximal seta, outer margin. Exopodite two-segmented, the distal segment bearing 14 natatory setae.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with three distal setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with two (occasionally one) distal setae, inner margin; segment 2 with two distal setae, inner margin and one distal setae, outer margin; segment 3 with one medial, two or rarely three distal, inner margin, and one medial seta, outer margin; segment 4 with five terminal setae and one proximal seta, outer margin. Exopodite with two segments, the distal segment bearing 14 natatory setae.

Maxilliped III biramous. Exopodite indistinctly divided with two segments; zero to three setae have been observed on endopodite. Endopodite with up to five segments apparent beneath cuticle, depending on the age of the zoea.

Pereiopod buds five pairs in number with first and fifth pairs distinctly chelate; buds increase in length throughout the stage.

Abdominal somites numbering five, similar to form in zoea I but larger and with paired pleopod buds of unequal length on segments 2 through 5; pleopods increase in length throughout the stage.

Telson similar to form in zoea I but larger and with one unpaired median seta on the central prominence (Figures 1E and 8J).

Pattern of primary chromatophores same as that in zoea I but new ones may be added on the growing pereiopods. Carapace 1.80 to 1.89 mm in length. Rostrum bears distinct ventral bulge just anterior to eyes.

MEGALOPA
(Figures 6 and 9)

Antennule biramous with three-segmented peduncle. Dorsal antennular ramus six-segmented; segments 2, 3, 4, and 5 with 2, 2, 2, 1 tiers of aesthetascs respectively; tiers, progressing distally, contain approximately 6-7, 6-7, 6-7, 3-4, 3, 2, 3 aesthetascs respectively; one long slender seta associated with the distal tier on each of segments 3 and 4. Ventral ramus with three segments; setation as figured.

Antenna long and slender with three-segmented peduncle; flagellum with 28 to 30 segments; most segments armed distally with variable numbers of short bristles and hairs as figured.

Mandible differs from toothed form in zoeal stages and is partially cup-shaped with slightly irregular bladelike leading edge; three-segmented palp has seven to ten spines on distal segment.

Maxilla I with indistinctly two-segmented endopodite bearing a single terminal seta on the distal segment and a single seta situated at base; basal endite with a total of about 25 stout spines and setae; coxal endite with a total of 32 stout setae. In addition, there is a single long seta proximally on the exopodite and a delicate exite edged with fine hairs associated with coxal portion of appendage.

Maxilla II with slender, indistinctly segmented endopodite bearing three terminal setae and one

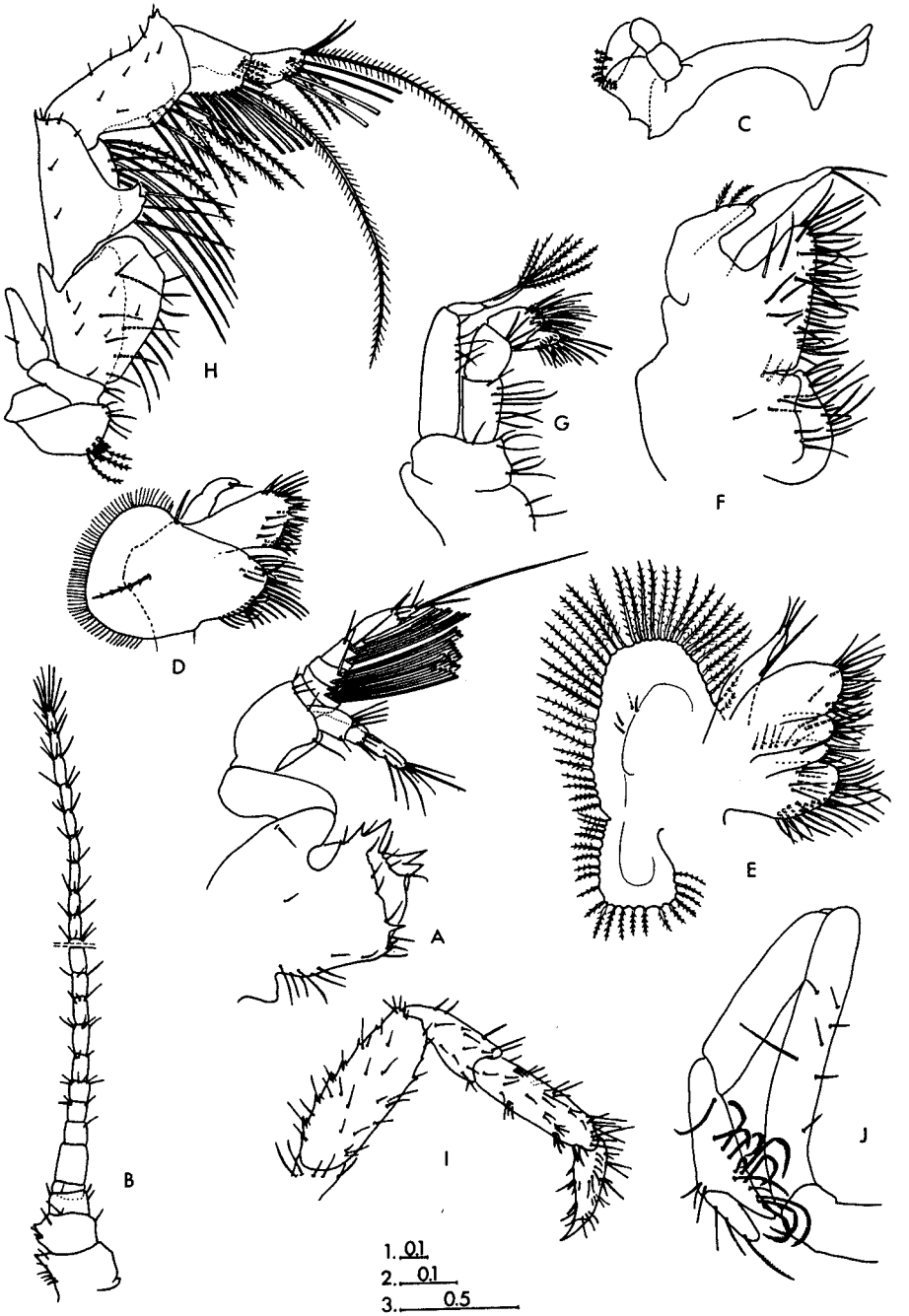

FIGURE 9.—*Petrolisthes eriomerus* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (B, G, H, Scale 1; A, C-F, J, Scale 2; I, Scale 3). Scales in millimeter.

lateral seta. Basal endite bilobed: distal lobe with 32 to 34 setae; proximal lobe with about 19 setae. Coxal endite bilobed: distal lobe with about 19 setae; proximal lobe with about 39 setae.

Maxilliped I with exopodite bearing three marginal setae; endopodite with two terminal setae in specimens dissected; basal portion of protopodite produced into triangular lobe bearing 35 to 42 setae; coxal lobe with numerous setae numbering 16 to 21 in specimens counted.

Maxilliped II with two-segmented exopodite usually bearing six setae on terminal segment and six internal marginal setae on proximal segment. Endopodite composed of four segments the distal two of which are armed with dense setal brushes each containing about 16 to 20 setae. Other setation as figured.

Maxilliped III with single-segmented exopodite bearing two very fine setae. Endopodite with five well-developed segments; segments 2 through 5 armed with filtering setae; segment 2 with 13 major setae along dorsal inner margin; segment 3 with three major ventral and four or five major dorsal internal marginal feeding setae, seven or eight minor submarginal brushlike setae dorsally and five ventral major submarginal brush setae; segment 4 with 10 major ventral marginal feeding setae, 9 minor dorsal marginal feeding setae, protuberance distally and dorsally on segment bearing a row of 5 major brush setae and a subordinate row of 4 spikelike setae and 1 fine seta; segment 5 with five major ventral and four or five dorsal (mixed major and minor) feeding setae, two slender terminal brush setae; three major brushes and two spikes on dorsal, submarginal bulge.

Pereiopods well developed and functional. Chelae slender, narrow, dorsoventrally flattened with two fixed spines present on internal margin of carpus. Walking legs all similar in form and setation as figured. Pereiopod 5 chelate with bristles and hooked setae for cleaning as figured.

Abdomen segments numbering 6, segments 2 through 5 with paired biramous pleopods; marginal setation of pleopod exopodites varies from 10 to 13, the higher numbers generally being found on the more proximal pleopods; each pleopod endopodite is armed with four small hooks and two setae. Segment 2 bears one chromatophore distally. A pair of biramous uropods articulate with segment 6; the outer ramus with 15 or 16 marginal setae, inner ramus with 10 or 11 marginal setae.

Telson with 15 or 16 major marginal plumose setae and usually four minor setae placed approximately symmetrically with respect to the center line of the telson between the major marginal setae; dorsal surface of telson bears about 10 pairs of fine setae in approximately symmetrical positions.

LARVAL DEVELOPMENT OF *PACHYCHELES PUBESCENS* HOLMES

Larvae taken from the plankton were reared in unaerated Erlenmeyer flask cultures and identified at a later date by comparison with laboratory hatched larvae.

PREZOEA

The general body form of *Pachycheles pubescens* is the same as that described for *Petrolisthes cinctipes* prezoeae; however, certain details of the prezoeal cuticle of the telson differ from *P. cinctipes*. The prezoeal cuticle of *Pachycheles pubescens* is produced into flat spines with toothed margins (Figure 2), an additional adaptation for swimming by abdominal flexion. Chromatophores occur as follows: one on either side of the mouth; one each on abdominal segments 1, 2, 3, and 5; and one on the telson.

ZOEA I
(Figure 10)

Antennule unsegmented with five or six terminal processes including three or four aesthetascs and one or two setae.

Antenna biramous with endopodite and protopodite fused; endopodite without subterminal tubercle or fine seta; exopodite 1¾ to 2 times as long as endopodite; usually three short stout, curved spines along internal lateral margin distally on exopodite, but spines occasionally number one or two and rarely four.

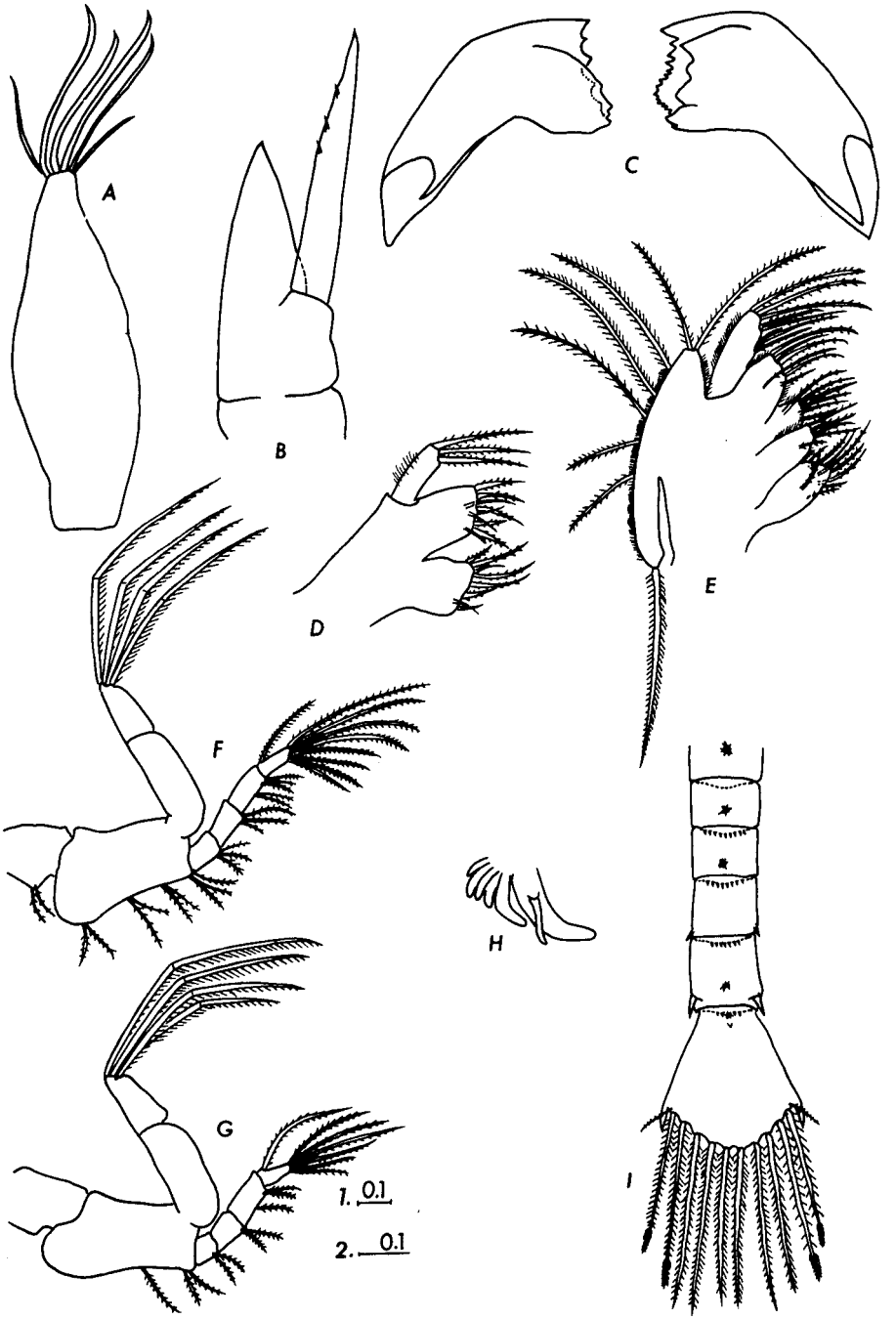

FIGURE 10.—*Pachycheles pubescens*, zoea I: A - antennule; B - antenna; C - mandibles; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopod buds; I - abdomen and telson (A-E, H, Scale 2; F, G, I, Scale 1). Scales in millimeter.

Mandibles strongly toothed, heavily sclerotized asymmetrical appendages.

Maxilla I with unsegmented endopodite bearing three to five terminal setae and a number of fine hairs along anterior margin; basal endite with eight or nine setae; coxal endite with seven to nine setae.

Maxilla II with unsegmented endopodite bearing eight or nine setae grouped 3, 2, 3-4 progressing distally. Basal endite bilobed: distal lobe with six to eight setae; proximal lobe with six to eight setae. Coxal endite bilobed: distal lobe with three to five setae; proximal lobe with six to nine setae. Scaphognathite with seven long plumose marginal setae and one apical seta on posterior lobe. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite usually with two distal setae. Basipodite usually with nine setae arranged 2, 2, 2, 3 proximal to distal along inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three distal setae, inner margin; segment 3 usually with one, sometimes two medial setae, and usually three, sometimes two or four distal setae, inner margin; segment 4 with seven to nine terminal setae and one long proximal seta, outer margin. Exopodite two-segmented with four natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with one medial, two distal setae, inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with two distal setae, inner margin; segment 3 with one medial and one or two distal setae, inner margin; segment 4 with five or six terminal and one proximal seta, outer margin. Exopodite two-segmented with four terminal natatory setae.

Maxilliped III present as small bilobed bud which increases in size during the stage.

Pereiopod buds numbering five pairs, simple; none chelate; buds increase in size throughout stage.

Abdominal somites five in number; segments 4 and 5 with prominent paired ventrolateral spines on posterior margin; segments 2 through 5 with serrated dorsal posterior margins.

Telson with seven symmetrically arranged pairs of processes with seventh pair on central prominence. Outer margin to center line: one heavy lateral spine fused with telson; one short, fine seta; five long plumose articulating setae, the outer two armed distally with fixed, curved spines (Figure 1A, B); fine hairs on margin of telson (not figured) between all major plumose setae and on central prominence.

Chromatophore pattern same as that described for prezoea. Rostrum commonly with three bands of red, one terminal and two subterminal, occasionally with only one subterminal band; both posterior spines tipped with red. Carapace 1.31 to 1.56 mm long.

ZOEA II
(Figure 11)

Antennule biramous; exopodite with six or seven terminal processes including three or four aesthetascs and two or three setae followed by five tiers of aesthetascs grouped 2, 3, 3, 4-5, 4-6 proceeding proximally. One long seta projects from distal portion of protopodite.

Antenna biramous; endopodite pointed terminally and armed subterminally with one fine seta and two small spines; exopodite unarmed and about two-thirds length of endopodite.

Mandibles increased in size; prominent palp bud present.

Maxilla I with unsegmented endopodite bearing three or four terminal setae and a group of fine hairs along anterior margin; basal endite with 9 or 10 heavy spinous setae; coxal endite with 8 to 11 heavy spinous setae.

Maxilla II with unsegmented endopodite bearing nine setae. Basal endite bilobed: distal and proximal lobes each with 9 to 11 setae. Coxal endite bilobed: distal lobe with four to seven setae; proximal lobe with 10 to 13 setae. Scaphognathite with 18 setae on outer margin and 3 strong apical setae on posterior lobe. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

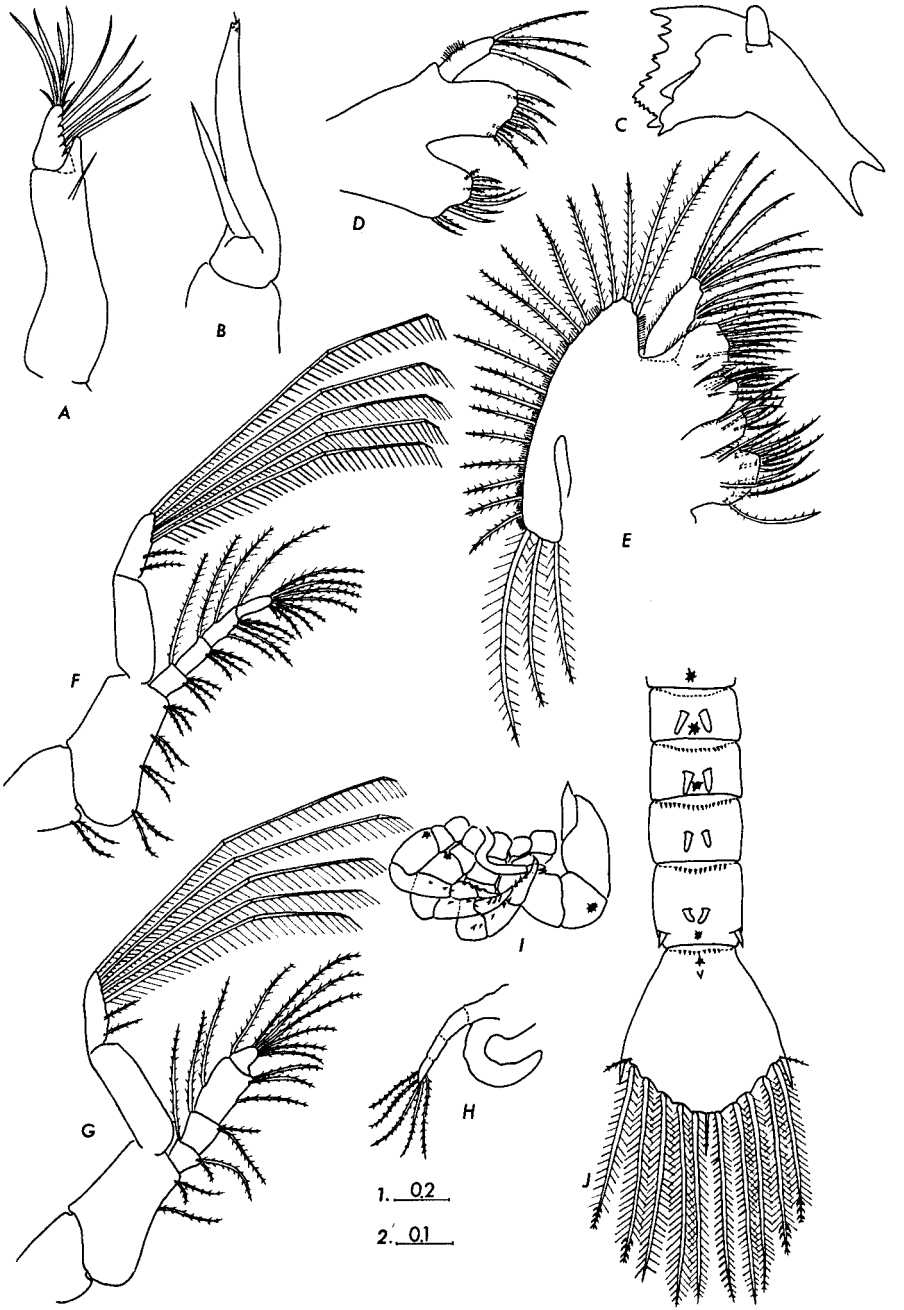

FIGURE 11.—*Pachycheles pubescens*, zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III, late zoea II; I - pereiopods; J - abdomen and telson, early zoea II (A, B, F-J, Scale 1; C-E, Scale 2). Scales in millimeter.

Maxilliped I biramous. Coxopodite usually with two distal setae. Basipodite usually with nine setae along inner margin grouped 2, 2, 2, 3 proximal to distal. Endopodite four-segmented: segments 1 and 2 each usually with three distal setae (segment 2 occasionally with four), inner margin and one distal seta, outer margin; segment 3 most commonly with one but occasionally two medial, two to four distal setae, inner margin and one medial seta, outer margin; segment 4 with 8 to 11 terminals and 1 proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite usually with three setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin and one distal seta, outer margin; segment 2 with one or two distal setae, inner margin and one distal seta, outer margin; segment 3 usually with one (occasionally none) medial, two distal setae, inner margin, and one medial seta, outer margin; segment 4 with five terminals and one proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped III a bilobed bud. Exopodite increases in size throughout stage; four to six setae present; one or two definite segments present beneath cuticle, depending on age of zoea. Endopodite entire or segmented with up to five segments beneath cuticle, depending on age; setae of megalopa stage visible beneath cuticle of advanced zoea.

Pereiopod buds enlarge during stage and become well developed; first and fifth pairs distinctly chelate. Spines and claws appear on pereiopods in advanced, premolt larva.

Abdominal somites larger than in zoea I but similar in form; segments 2, 3, 4, and 5 each bear a pair of pleopods of unequal length.

Telson increased in size; an unpaired median seta added on central prominence (Figures 1C and 11J); anal spine present.

Basic color pattern same as in zoea I; red chromatophores added to pereiopods and beneath carapace in zoeae of advanced age. Carapace 2.37 to 2.54 mm in length.

MEGALOPA
(Figures 12 and 13)

Antennule biramous, consisting of a three-segmented peduncle, a dorsal ramus with six segments, and a ventral ramus with three segments. Segments 2, 3, and 4 of dorsal ramus each bear two tiers of aesthetascs; segment 5 with only 1 aesthetasc tier. Numbers of aesthetascs per tier proximal to distal 7-8, 8, 6-7, 5, 4, 2, 3. One long seta associated with distal tier of aesthetascs on segments 2, 3, and 4. Other setation as figured.

Antennal flagellum composed of 29 to 30 segments in addition to the three-segmented peduncle; most segments bear variable numbers of fine bristles around the distal margin as figured.

Mandible highly sclerotized with three-segmented palp; terminal segment of palp with about 17 spines; grinding edge only slightly irregular with a generally bladelike form.

Maxilla I with a two-segmented endopodite bearing a single distal seta on terminal segment. Basal endite with 7 slender setae and 14 heavy spinelike setae along distal margin; also seven short, stout, spinelike setae submarginally on dorsal surface of segment. Coxal endite with four setae on dorsal surface and about 29 marginal and near submarginal setae; delicate fanlike coxal exite rimmed with hairs is present.

Maxilla II with unsegmented endopodite which bears five or six setae. Basal endite bilobed: distal lobe with 33 to 36 setae; proximal lobe with about 22 setae. Coxal endite bilobed: distal lobe with about 20 setae; proximal lobe with about 38 setae. Scaphognathite with about 68 marginal plumose setae and 5 short fine hairs on the surface of the fan.

Maxilliped I with exopodite bearing nine setae. Endopodite indistinctly two-segmented, bearing one seta on distal segment. Protopodite with about 52 setae. Coxal endite with about 23 setae.

Maxilliped II biramous; exopodite indistinctly two-segmented with eight or nine terminal setae; endopodite four-segmented, segments 3 and 4 having heavy terminal brushes of about 26 and 30 setae respectively; other setation as figured.

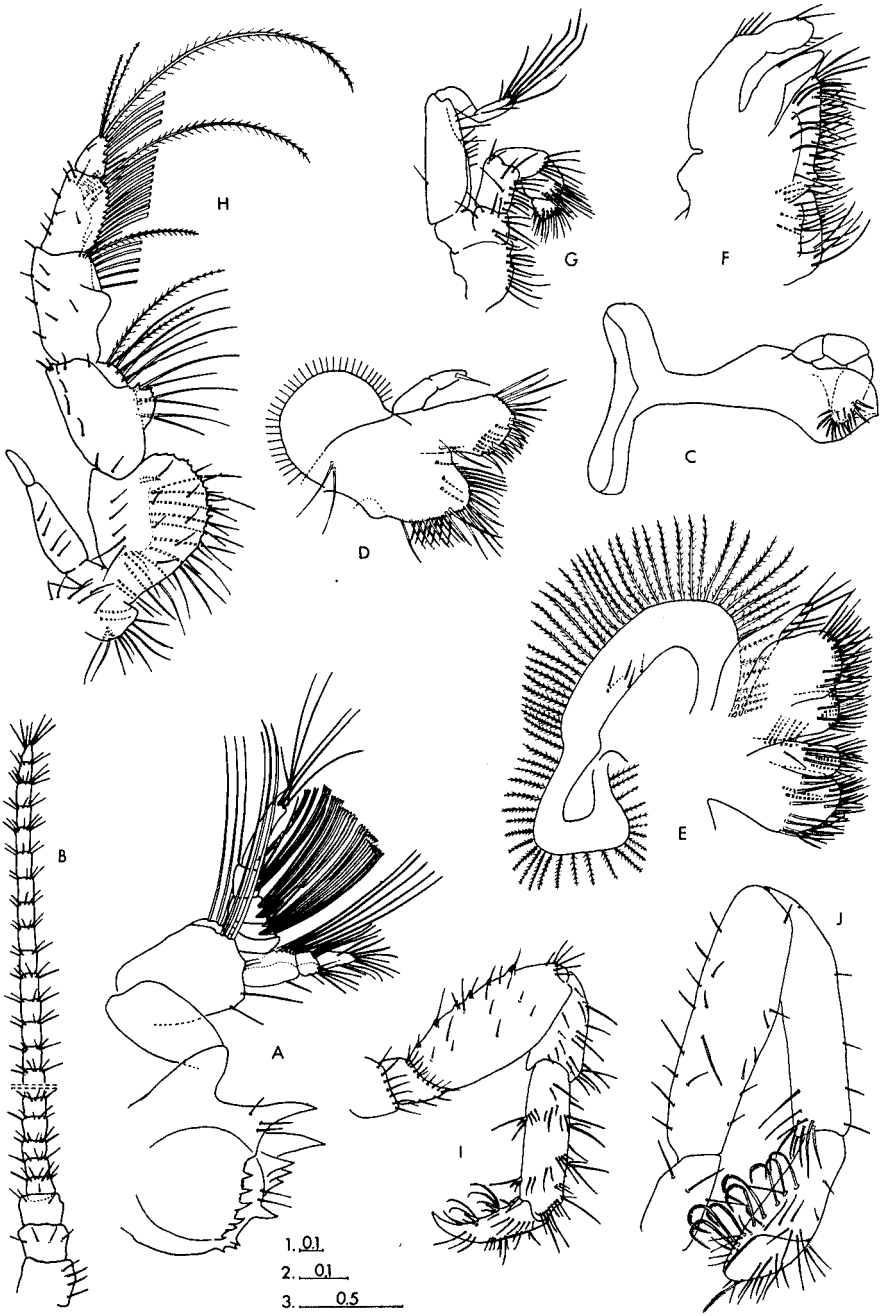

FIGURE 12.—*Pachycheles pubescens*, megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (A, C-F, J, Scale 2; B, G, H, Scale 1; I, Scale 3). Scales in millimeter.

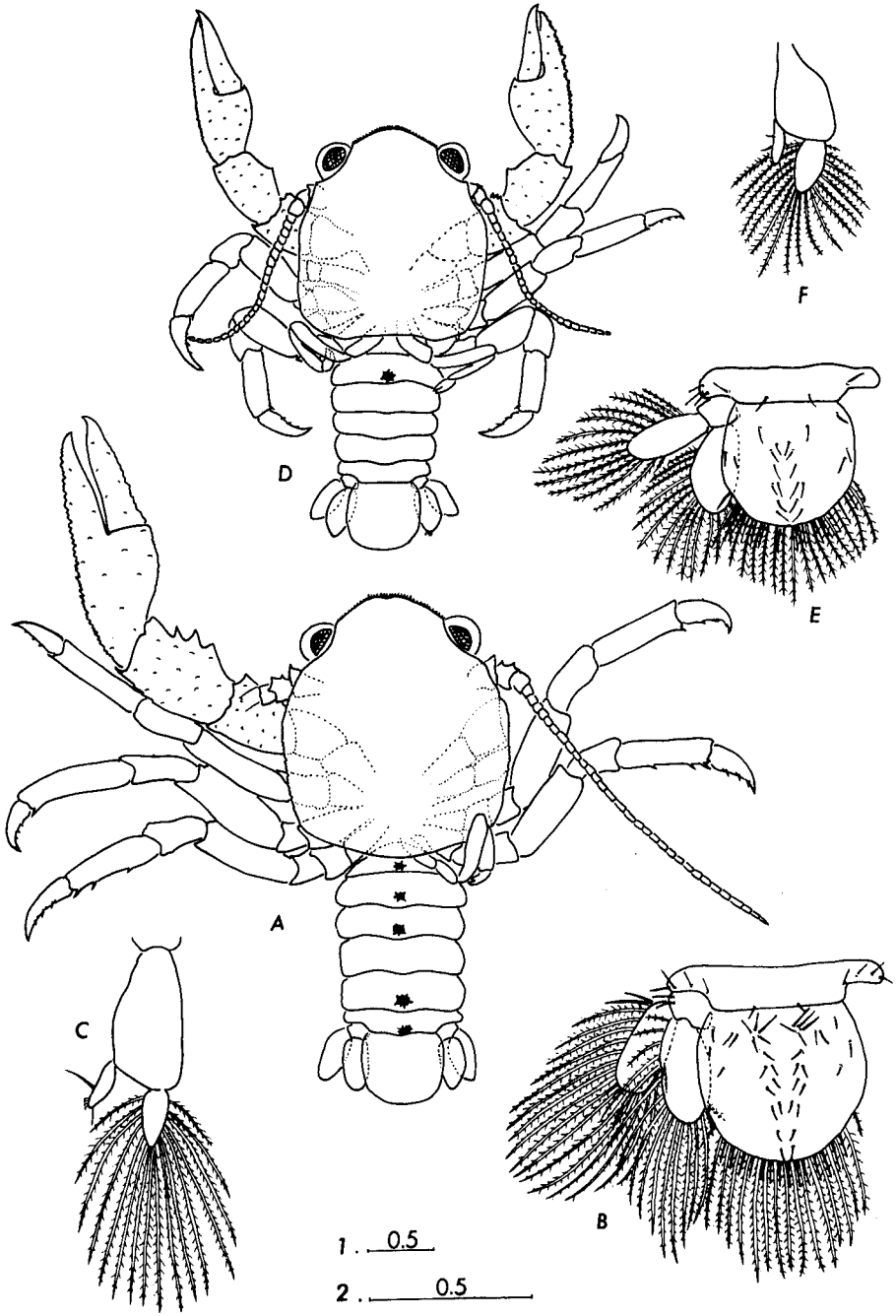

FIGURE 13.—*Pachycheles pubescens* (A-C) and *P. rudis* (D-F) megalopae, whole mounts: A - *P. pubescens* megalopa, whole mount; B - telson and uropods; C - right third pleopod; D - *P. rudis* megalopa, whole mount; E - telson and uropods; F - right third pleopod (A, D, Scale 1; B, C, E, F, Scale 2). Scales in millimeter.

Maxilliped III biramous; exopodite two-segmented, terminal segment being incomplete and lacking setae. Endopodite with five segments; segment 2 with 13 major marginal setae in double row (7, 6); segment 3 with five or six slender minor setae, outer margin, six major inner marginals, and nine brush setae, inner margin; segment 4 with five major and three spike-like brush setae, inner margin, 11 outer major marginals, and 7 inner minor auxiliaries; segment 5 with five pairs of major feeding setae, one or two pairs of minor terminal setae.

Pereiopods well developed and functional. Chelipeds large, swollen and bristly; two or three prominent fixed spines on the anterior margin of carpus. Three pairs of walking legs similar in form and setation as figured. Pereiopod 5 with 8 to 10 sickle-shaped setae and a number of other bristles.

Abdominal segments six in number, segments 2 through 5 with paired biramous pleopods bearing setae as follows: 16 marginal setae on exopodite; endopodite armed with four small hooks and two setae. Chromatophores appear posteriorly in segments 1, 2, 3, 5, and 6. Segment 6 bears a pair of biramous uropods, the outer rami each with about 19 plumose marginal setae and the inner with 17 or 18 such setae.

The telson has 15 or 16 major marginal setae. Minor marginal setae are present between almost all major setae. The dorsal surface of the telson is equipped with a number of very fine short hairs arranged in approximate symmetry as figured. Frontal margin of carapace as figured (Figure 13A).

LARVAL DEVELOPMENT OF *PACHYCHELES RUDIS* STIMPSON

In the laboratory, only a single *P. rudis* larva reared at 15°C and 33‰ salinity reached the megalopa stage. Laboratory-reared material was extensively supplemented with larvae from the plankton for purposes of examination.

Knight (1966) has dissected and accurately described the two true zoeal stages of *P. rudis*. She also adequately described the gross external morphology of the megalopa stage. Owing to high mortality in her cultures, she was forced to describe the larvae of this species on the basis of very few specimens. In this study, numbers of laboratory-hatched larvae surviving each stage in cultures were comparable to numbers obtained by Knight (1966), but the various stages were extremely abundant in the plankton. Knight's description of the species is expanded here using this more plentiful material.

PREZOEA

Body form is the same as that described for *Petrolisthes cinctipes* (Figure 2). Chromatophores occur as follows: one on either side of the mouth; one posteriorly in abdominal segment 2 or between segments 2 and 3. This is the least colorful of the species discussed here. Knight (1966) does not mention a prezoeal stage.

ZOEA I AND II

Table 2 indicates points in which the larvae studied here differ from those described by Knight (1966). Differences are minor but are included to establish a more accurate range of variability for this species.

MEGALOPA
(Figures 13 and 14)

Antennule biramous with three-segmented peduncle. Dorsal ramus with six segments, segments 2 through 5 bearing 2, 2, 2, and 1 tier of aesthetascs respectively. Aesthetascs are arranged 6, 6-7, 5-6, 3-4, 3-4, 2, 3 in tiers progressing distally. A single long plumose seta is associated with the distal tier on segments 2, 3, and 4. Ventral ramus distinctly three-segmented, the most distal segment being indistinctly divided. Other setation and spination as figured.

Antenna long, slender, with three-segmented peduncle; flagellum with 20 to 21 segments; variable numbers of fine hairs and bristles arranged distally on most segments as figured.

Mandible strongly sclerotized, partially cup-shaped appendage with three-segmented palp; distal segment of palp with about 13 terminal spines as figured.

TABLE 2.—Comparison of species descriptions of *Pachycheles rudis*.

Stage	Appendage	Knight (1966)	This study
Zoea I	Antennule	6 processes including 3 aesthetascs, 2 setae	6-7 processes including 4 aesthetascs, 1-2 setae
Zoea II	Antennule	7 processes, including 3 aesthetascs, 2 setae	6-7 processes including 4 aesthetascs, 2-3 setae
Zoea II	Maxilla I: Coxal endite	5 spines, 6 setae	10 setae
Zoea II	Maxilla II:		
	Basal endite, distal lobe	10-12 setae	11-12 setae
	Basal endite, proximal lobe	10 setae	10-11 setae
	Coxal endite, distal lobe	6 setae	6-7 setae
	Coxal endite, proximal lobe	10-12 setae	9-10 setae
Zoea II	Maxilliped I:		
	Basipodite	Setae grouped 2, 2, 3, 3	Setae grouped 2, 2, 2, 3
	Endopodite, segment 3	2 medial setae	1-2 medial setae
	Endopodite, segment 3	3 distal setae	3-4 distal setae[1]
	Endopodite, segment 4	7-8 terminal setae[1]	8-9 terminal setae[1]
Zoea II	Maxilliped II: Endopodite, segment 1	2 distal setae, inner margin	2-3 distal setae, inner margin
Zoea II	Maxilliped III: Exopodite	2 slender setae	2 slender setae, and 2-3 fine setae
All larval stages	Abdominal segment 2 or between 2 and 3	--	1 chromatophore
	Either side of mouth	--	1 chromatophore

[1] Most common occurrence in bold face.

Maxilla I with indistinctly two-segmented endopodite bearing two stout setae on distal segment. Basal endite with 8 long, slender and 16 stout, spinous setae on margin and 6 short setae on ventral surface. Coxal endite with about 26 marginal setae and 4 fine setae on ventral surface. Coxal exite present as delicate fleshy lobe rimmed with fine hairs. One proximal seta on appendage near articulation with gnathal skeleton.

Maxilla II with large numbers of setae. Endopodite unsegmented with five setae. Basal endite bilobed: distal lobe with about 35 setae; proximal lobe with 9 or 10 marginal and 4 submarginal setae. Coxal endite bilobed: distal lobe with 20 to 21 setae arranged as figured; proximal lobe with 30 to 35 setae arranged as figured. Scaphognathite with about 58 setae around the margin and 2 fine submarginal setae on the anterior lobe.

Maxilliped I with numerous setae. Exopodite fleshy with one seta on margin. Endopodite indistinctly two-segmented, bearing a single seta proximally. Protopodite produced into triangular lobe with about 35 to 45 marginal setae and 3 proximal setae as figured. Coxal lobe with a total of about 18 setae arranged as figured.

Maxilliped II biramous. Setation of coxopodite and basipodite variable, approximately as figured. Exopodite two-segmented with setae as figured, with eight or nine setae on terminal segment. Endopodite with four segments; segments 3 and 4 having distal brushes of short setae numbering about 24 to 28 and 16 to 20 respectively. Other setation as figured.

Maxilliped III biramous. Exopodite two-segmented but incompletely formed. Segments 2 through 5 of endopodite equipped with major feeding setae; segment 2 with 11 or 12 feeding setae of two lengths, dorsal margin; segment 3 with five or six feeding setae on ventral margin, seven feeding setae or dorsal margin, and seven brush setae of varying lengths; no spikelike setae on dorsal protuberance; segment 4 with 2 short setae, 5 major brushes and 4 spike setae on dorsal protuberance, 10 long feeding setae on ventral margin, and 9 scattered minor submarginal setae on ventral surface; segment 5 with 10 or 11 marginal setae and 2 or 3 short terminal setae. Other setation as figured.

Details of setation and form of the walking

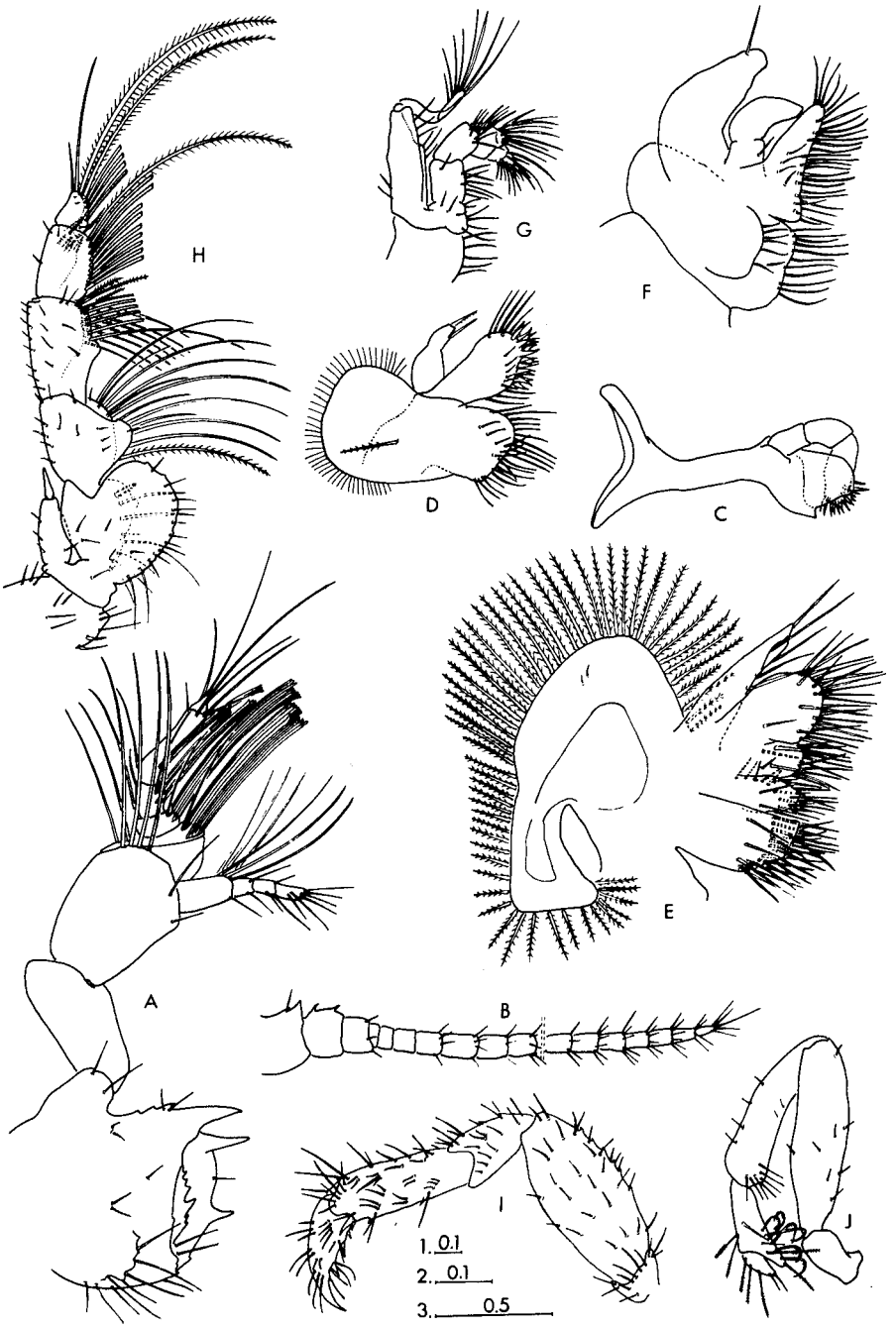

FIGURE 14.—*Pachycheles rudis* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (A, C-F, Scale 2; B, G, H, J, Scale 1; I, Scale 3). Scales in millimeter.

legs, the fifth pereiopods, the telson and sixth segment, and the frontal margin of the carapace are as figured.

DISCUSSION

The four species whose larvae are described here are the only porcellanids known (Haig, 1960) on the Pacific coast of North America north of Bodega Head, Calif., and we have found their larvae simultaneously in the plankton off the central Oregon coast. Both preserved and live zoea larvae of these four species can be readily assigned to genus on the basis of the number of long telson setae bearing conspicuous distal spines and the nature of these spines (Table 3). Once live or freshly killed zoeae are separated by genus using telson characters, individuals of the congeneric species can be separated to species on the basis of the distribution of the primary red chromatophores. Zoea larvae from preserved plankton samples cannot be identified to species easily once the chromatophores have faded. The only other nonvariable character found which distinguishes the species was maxillipedal setal counts, and it is possible that further study will indicate that these counts are also variable.

The two *Pachycheles* species differ in both zoeal stages by a single seta on the inner margin of segment two of the endopodite on maxilliped I (Table 4). In addition, second zoea larvae of these two species differ by a single seta on the outer margin of endopodite segment 1 on maxillipeds I and II (Table 4). Similar characters separate the larvae of the two *Petrolisthes* species. First zoeae differ by one seta on the inner margin of segment two of the endopodite of both maxillipeds I and II (Table 5). Second zoeae of these *Petrolisthes* differ by a single seta on the outer margin of the first segment of the endopodite on maxilliped II (Table 5). Megalopae of all four species can be readily differentiated on the basis of cheliped form and other finer characters (Figures 12-14).

Available knowledge of the larvae of *Pachycheles* species does not support Haig (1960) who, studying adult animals, suggested that *P. rudis* is most closely related to *P. stevensii*. A comprehensive comparison (Table 4) of the four most similar larvae of the *Pachycheles* species studied thus far does not definitely indicate such a relationship. On the basis of larval form and setal numbers, all four of the species are equally similar.

At this time too few porcellanid larvae have been described to use larval characters to draw firm conclusions about generic and specific relationships. There is however a need for means to identify as closely as possible porcellanid zoea larvae taken from the plankton in regions where larvae of all of the porcellanid species have not been reared. For all known porcellanid larvae of established specific identity, we have listed in Table 3 three morphological characteristics which appear to assign porcellanid zoeae to genera or generic groups. The following discussion evaluates the usefulness of these characteristics in grouping presently known larvae systematically. Planktonic larvae of uncertain adult origin are included and grouped with known larvae they most closely resemble, but are not discussed further. Two New Zealand porcellanids for which larvae have been described, *Petrolisthes novaezelandiae* and *P. elongatus*, have some unusual characteristics in both the larval and adult forms which distinguish them from all other porcellanids known. For this evaluation, they are conditionally placed with groups with which they share the larval characters listed in Table 3.

All presently known porcellanid zoeae can be placed in one of three groups on the basis of telson form. Lebour (1943) originally established two of these groups (A and B, Table 3) by distinguishing larvae of the genus *Porcellana* from larvae of the genus *Petrolisthes* as the genera were known at that time. Lebour's original *Petrolisthes* type telson group (B, Table 3) now includes all described species of the genera *Pachycheles* and *Megalobrachium* and all but one of the described *Petrolisthes* larvae, *P. novaezelandiae*. Wear (1964a) has suggested that the exceptional *P. novaezelandiae* be placed in the genus *Pisidia* on the basis of both larval and adult characters. Lebour's original *Porcellana* type telson group (A, Table 3) now includes all described larvae of the genera *Euceramus*, *Poly-*

TABLE 3.—Comparison of porcellanid larvae on the basis of distal armature of telson processes and telson form.[1]

Species	Position of armed telson processes		Type of armature on setae	Telson form	Author
	Zoea I	Zoea II			
Pachycheles rudis	3,4	3,4	All *Pachycheles* spp. have equal number of spines on inner and outer margins.	B	Knight, 1966
Pachycheles pubescens	3,4	3,4		B	This study
Pachycheles stevensii	3,4	3,4		B	Kurata, 1964
Pachycheles haigae	3,4	3,4		B	Boschi et al., 1967
Pachycheles natalensis	3-7	?	Spines most prominent on 5th process.	B	Sankolli, 1967
Megalobrachium poeyi	0	0		B	Gore, 1971
Petrolisthes cinctipes	3-7	3-7	Spines, equal number inner and outer margins (first 5 species listed).	B	This study
Petrolisthes eriomerus	3-7	3-7		B	This study
Petrolisthes armatus	3-7	3-7		B	Lebour, 1943, 1950 Gurney, 1938 Gore, 1970, 1972
Petrolisthes lamarckii	3-7	?	Spines most prominent on 5th process.	B	Sankolli, 1967
Petrolisthes boscii	3-7	3-7	Spines most prominent on 5th process.	B	Shenoy and Sankolli, 1967
Petrolisthes rufescens	?	?	Not mentioned.	B	Gohar and Al-Kholy, 1957
"*Porcellanella*" sp.	?	?	Not mentioned.	B	Menon, 1937
Petrolisthes elongatus	3-7	3-7	6 prominent spines, inner margin; less prominent spines, outer margin.	B	Wear, 1964b Greenwood, 1965
Petrocheles spinosus	4,5	4,5	6-8 spines, inner margin.	C	Wear, 1966
Petrolisthes novaezelandiae	3	3,4	5-6 spines, inner margin.	A	Wear, 1964a Greenwood, 1965
?*Petrolisthes* sp. I	?	?	Not mentioned.	A	Menon, 1937
?*Petrolisthes* sp. II	?	?	Not mentioned.	A	Menon, 1937
Porcellana platycheles	3	3	Long fine spines inner margin only (?)	A	Lebour, 1943
Porcellana ornata	3-7	?	"Hooks" minute, most prominent on 3rd process.	A	Sankolli, 1967
Porcellana sigsbeiana	3-7	3-7	Finely dentate	A	Gore, 1971b
Porcellana sayana (as *P. ocellata*)	3-7	?	According to figures, tips are similar, smooth, or finely serrated(?)		Brooks and Wilson, 1883
Pisidia longicornis	3	3	Well-defined spines, equal number inner and outer margins (first 3 species listed).	A	Lebour, 1943 Sars, 1889
Pisidia bluteli	3	3		A	Bourdillon-Casanova, 1956
Pisidia inaequalis	3	3		A	Gurney, 1938
Pisidia spinulifrons	3	?	Minute "hooks", more developed on outer than on inner margin.	A	Sankolli, 1967
Polyonyx gibbesi	0	0		A	Gore, 1968
Polyonyx quadriungulatus	3	3	More spines on outer than on inner margin.	A	Knight, 1966
Polyonyx hendersoni	3-7	?	Minute spines, most prominent on 3rd process.	A	Sankolli, 1967
Euceramus praelongus	3,4	3,4	Well-defined spines, equal number inner and outer margins.	A	Roberts, 1968

[1] A = Lebour's (1943) definition of *Porcellana* telson. Telson about 1½ times as wide as long with seventh pair of processes situated outside and below central prominence in stage I. In stage II, an eighth pair of processes is added on the central prominence.
B = Lebour's (1943) definition of *Petrolisthes* telson. Telson about as long as wide with seventh pair of processes situated on central prominence in stage I. In stage II, a single median spine (or setae) added.
C = Fits neither A nor B exactly.

onyx, *Porcellana*, and *Pisidia*. A third telson type (C, Table 3) has since been described and to date includes only the larvae of *Petrocheles spinosus* from New Zealand.

Among larvae possessing a similar telson form, further systematic separation following generic lines appears to be possible on the basis of the position of the long telson setae (processes 3 through 7) armed distally with conspicuous spines. This is particularly true of 13 larvae of known adult origin possessing the *Petrolisthes* type telson. Of these 13 species, only the larvae attributed to *Pachycheles natalensis* differ from other larvae of the same genus.

The known larvae possessing the *Porcellana* type telson are more difficult to group using telson seta armature alone. Only larvae of the single known species of *Euceramus* can be distinguished from other known larvae of this telson type on the basis of setal armature. In

TABLE 4.—Comparison of larvae of four *Pachycheles* species.
(All unlabeled figures are setal numbers; all serial listings are proximal to distal.)

Appendage	Zoea I				Zoea II			
	P. rudis Knight 1966 and this study	*P. pubescens* This study	*P. haigae* Boschi et al., 1967	*P. stevensii* Kurata 1964	*P. rudis*	*P. pubescens*	*P. haigae*	*P. stevensii*
Antennule	3-4 aesthetascs; 1-2 setae	3-4 aesthetascs; 1-2 setae	3 aesthetascs; 2-3 setae	?	biramous; aesthetasc tiers 4, 5, 3, 3, 2	biramous; aesthetasc tiers 4-6, 4-5, 3, 3, 2	biramous; aesthetascs 8-14, 3 terminals	
Antenna:								
Endopodite	1 fine seta	0	1 fine seta	1 fine seta	1 seta	1 seta, 2 small spines	1 seta	
Exopodite	3 spines	1-4 spines	4 spines	3 spines	(3) spines rudimentary or absent	0 spines	0 spines	
Mandible	no palp bud	no palp bud	no palp bud	no palp bud	pulp bed present	palp bud present	palp bud present	palp bud present
Maxilla I:								
Coxal endite	9	7-9	8	8	10-11	8-11	10	NOT
Basal endite	9	8-9	9	6	10	9-10	11	
Endopodite	4	3-5	4	4	4	3-4	4	
Maxilla II:								
Coxal endite, PL[1]	6-8	6-9	9	7	9-12	10-13	7-8	MENTIONED
Coxal endite, DL[1]	4	3-5	7	3	6-7	4-7	5-7	
Basal endite, PL	7	6-8	7	5	10-11	9-11	6-7	
Basal endite, DL	7-8	6-8	7	6	10-12	9-11	8-10	
Endopodite	9	8-9	7	9	9	9	8	OR
Scapognathite	6 + 1 apical	7 + 1 apical	8 + 1 apical	6 + 1 apical	20-22	21	21-24	
Maxilliped I:								
Coxopodite	2	2	none?	NOT	2	2	2	FIGURED
Basipodite	2, 2, 2, 3	2, 2, 2, 3	2, 2, 3, 3		2, 2, 2-3, 3	2, 2, 2, 3	2, 2, 2, 3	?, 2, 2, 3
Exopodite	4	4	4		14	14	14	14
Endopodite:								
Inner margin	3, 2, 5, 7-8	2-3, 3, 3-6, 7-9	2, 4, 7, 10	MENTIONED	3, 2, 5, 7-9	3, 3-4, 3-6, 8-11	2, 4, 7, 10	3, 3, 2, 10
Outer margin	0, 0, 0, 1	0, 0, 0, 1	0, 0, 0, 1		0, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1
Maxilliped II:								
Coxopodite	0	0	0		0	0	0	0
Basipodite	1, 2	1, 2	2	OR	1, 2	1, 2	1, 2	1, 2
Exopodite	4	4	4		14	14	14	14
Endopodite								
Inner margin	2, 2, 3, 5	2-3, 2, 3, 5-6	3, 3, 2, 7		2, 2, 3, 5	2-3, 1-2, 2-3, 5	3, 3, 2, 7	2, 2, 1, 6
Outer margin	0, 0, 0, 1	0, 0, 0, 1	0, 0, 0, 1	FIGURED	0, 1, 1, 1	1, 1, 1, 1	0, 1, 1, 1	1, 1, 1, 1
Maxilliped III	bilobed bud	bilobed bud			bilobed; 2 setae	bilobed; 4-6 setae	bilobed; 2 setae	bilobed; 2 setae
Pereiopods	5 pairs buds	5 pairs buds			5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate
Abdomen	5 segments, no pleopods	5 segments, no pleopods	5 segments, no pleopods	5 segments, no pleopods	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5
Primary chromatophores	Total 3	Total 7	Total 5?	?	Total 3	Total 7	Total 5(?)	?

[1] PL = proximal lobe.
DL = distal lobe.

TABLE 5.—Comparison of maxilliped setation in *Petrolisthes cinctipes* and *P. eriomerus*. (All serial listings are numbers of setae, arranged proximally to distally.)

Appendage	Zoea I		Zoea II	
	P. cinctipes	*P. eriomerus*	*P. cinctipes*	*P. eriomerus*
Maxilliped I:				
Coxopodite	1-2	2	1-2	2
Basipodite	2, 2, 3, 3	2, 2, 3, 3	2, 2, 3, 3	2, 2, 3, 3
Exopodite	4	4	14	14
Endopodite:				
Inner margin	1-3, 2-3, 4-7, 5-7	2-3, 3, 5-6, 5-7	3, 3, 5, 5-6	2-3, 3-4, 5, 4-7
Outer margin	0, 0, 0-1, 1	0, 0, 0, 1	0, 1, 1, 1	0, 1, 1, 1
Maxilliped II:				
Coxopodite	0	0	0	0
Basipodite	1, 2	1, 1-2	1, 2	1, 2
Exopodite	4	4	14	14
Endopodite:				
Inner margin	1-2, 1-2, 2-3, 3-5	1-2, 1-3, 3-4, 3-5	2, 2, 3, 4-6	1-2, 2, 3-4, 5
Outer margin	0, 0, 0, 1	0, 0, 0, 1	1, 1, 1, 1	0, 1, 1, 1

contrast, larvae belonging to species of the present genera *Porcellana, Pisidia,* and *Polyonx* exhibit several different patterns of armed telson setae, a fact which, when coupled with the confusion of adults of these genera in the past, suggests that systematic problems still exist among these groups. The only point worth noting at this time is that second zoeae of two of the three species currently bearing the genus name of *Pisidia* and the second zoea of *Petrolisthes novaezelandiae,* which Wear suggests is actually a *Pisidia,* all have similar setal armatures and possess three pairs of pleopod buds on the abdomen. All other porcellanid zoea II larvae known to species have four pairs of pleopod buds. In order to determine whether these two characters are of any value in distinguishing the larvae of the genus *Pisidia* from other larvae with the *Porcellana* type telson, the second zoea of *Pisidia spinulifrons* must be described, the identity of Menon's (1937) *"Petrolisthes"* species I and II, with three pleopod pairs, resolved and *Pisidia inaequalis,* with four pleopod pairs, reexamined as a member of the genus.

In the course of this study, a number of specimens of each stage were examined, and particular attention paid to morphological variation, especially in setal counts for the larval appendages, since larval variability has caused a great deal of confusion in the literature on porcellanid and other anomuran larvae. Morphological variations in setal numbers, spine lengths, etc. were found within individuals from the left to the right sides, between individuals of the same species, and between individuals of the different species studied. These findings emphasize the necessity of basing larval descriptions, especially setal counts, on examination of adequate numbers of larvae of each stage. Throughout the descriptions given here, only the range of setal numbers found is indicated. Because of the importance placed on setation formulae in descriptions of crustacean larvae, some of the setal count variations found and their implications will be analyzed in a separate paper.

Variability in the number of larval molts required to reach a specific point in development, apparently in response to varying environmental conditions, occurs in many Anomura (Table 6) and other decapod groups as well (e.g., Broad, 1957; Costlow, 1965). This type of variation has caused difficulties among larval systematists for some time and has in part given rise to the idea that either larvae produced under laboratory conditions are abnormal and should be discounted altogether or that such stages are extraneous and should be subgrouped under larval stages most commonly noted. This concept of substages or extra stages has served to confuse the developmental picture (Efford, 1970), particularly among the porcellanids, where another type of variability has been discovered which, unfortunately, has lent further support to the "substage" concept.

Intermolt growth in which certain appendages increase in size within a single larval stage without molt is a type of variability prevalent in porcellanids. All four species described here show

this type of growth. Lebour (1943, 1950) was probably the first author to notice specimens showing this phenomenon. Lebour observed some substage molting and concluded that each substage she found in plankton collections must necessarily have been separated from less advanced substages by a discrete molt. She subsequently proposed that *Pisidia longicornis* and *Porcellana platycheles* probably possessed a variable number of stages with two "essential" stages. She assumed that a molt always separated the "alternative" stages, or substages from each other. The variable molting sequence may indeed occur in these species under certain circumstances, as it does in other Anomura (Table 6), but it is probable that Ib and IIc substages in *Pisidia longicornis* and IIc in *Porcellana platycheles*, which were taken in plankton samples but never obtained by molt in the laboratory, were products of intermolt growth.

LeRoux (1961, 1966) subsequently reared the larvae of both species and reported only two "true" zoeal stages each of which underwent growth in certain appendage buds without molting. It is likely that these species have the potential for both intermolt growth and stage number variability and that Lebour found a combination of both while LeRoux did not. A similar case might also exist in the *Petrolisthes* larvae studied by Wear (1964a, b), although he reports definite ecdysis between each of his substages. Larvae of these species, like the *Pisidia* and *Porcellana* species mentioned above, may show both intermolt growth and variable stage numbers, depending on environmental circumstances, a possibility not considered for example, by Roberts (1968) and Gore (1970) in discussing substages.

Other authors have subsequently supported Lebour's original substage designation of growth forms even though no molting was observed (e.g., Boschi et al., 1967). This is a needless and confusing subdivision of an apparently continuous process and it obscures the nature of the flexibility of the animals. The term substage is now used in such a variety of ways that it should be abandoned altogether, as Gore (1970) has suggested, and attention directed to the possible occurrence of variation in both molting and development rates as observed by Costlow (1965) in the portunid *Callinectes sapidus*.

Intermolt growth to date has been recorded directly or indirectly in the larvae of 70% of the porcellanids studied for which two or more zoeal stages are known (Table 7). All these species have demonstrated abbreviated development (fewer number of molts necessary to attain juvenile adult form) compared to most other

TABLE 6.—Species of Anomura other than Porcellanidae for which stage number variability has been reported.[1]

Species of Anomura	Source
Pleuroncodes planipes	Boyd and Johnson, 1963
Emerita talpoida	Rees, 1959
Emerita analoga	Johnson and Lewis, 1942; Efford, 1970
Emerita rathbunae	Knight, 1967
Hippa cubensis	Hanson, 1969
Blepharipoda occidentalis	Knight, 1968; Johnson and Lewis, 1942
Calcinus tibicen	Provenzano, 1962a
Coenbita clypeatus	Provenzano, 1962b
Trizopagurus magnificus	Provenzano, 1967
Petrochirus diogenes	Provenzano, 1968
Birgus latro	Reese and Kinzie, 1968
Paralithodes camtschatica	Kurata, 1960

[1] Intermolt growth has not been reported in the larvae of any of the above species.

TABLE 7.—Species of Porcellanidae for which intermolt growth or stage number variability have been reported. Includes only species with both zoeae known.

Species	Intermolt growth[1]	Stage variability[1]	Author
Petrolisthes cinctipes	+	–	This study
Petrolisthes eriomerus	+	–	This study
Petrolisthes armatus	–	+	Gurney, 1938
	–	+	Lebour, 1943, 1950
	+	–	Gore, 1970, 1972
Petrolisthes elongatus	O	+	Wear, 1964b
Petrolisthes novaezelandiae	O	+	Wear, 1964a
Petrolisthes rufescens	O	–	Gohar and Al-Kholy, 1957
Petrolisthes sp. I	O	–	Menon, 1937
Petrolisthes sp. II	O	–	Menon, 1937
Porcellana sp.	O	–	Menon, 1937
Porcellana platycheles	+	–	Le Roux, 1961
	–	+	Lebour, 1943
Porcellana sigsbeiana	+	–	Gore, 1971b
Pisidia longicornis	+	–	Le Roux, 1966
	–	+	Lebour, 1943
Pisidia bluteli	O	–	Bourdillon-Casanova, 1956
Pisidia inaequalis	O	–	Gurney, 1938
Polyonyx gibbesi	+	–	Gore, 1968
Polyonyx quadriungulatus	+	–	Knight, 1966
Pachycheles pubescens	+	–	This study
Pachycheles rudis	+	–	Knight, 1966; this study
Pachycheles haigae	+	–	Boschi et al., 1967
Pachycheles stevensii	+	–	Kurata, 1964
Euceramus praelongus	+	–	Roberts, 1968
Petrocheles spinosus	–	–	Wear, 1965a
Megalobrachium poeyi	+	–	Gore, 1971a

[1] + = Occurrence reported.
– = Occurrence not reported.
O = Occurrence probable but not directly reported.

Anomura studied but not necessarily reduced time spent in the plankton. This suggests that intermolt growth might permit larvae of these species to develop to metamorphosis under a variety of conditions without passing through a large number of molts. This mechanism might thus be of survival value in reducing larval loss at molt by effectively decreasing the number of molts required under various conditions to reach the juvenile form.

As more larval histories are studied, it may be found that intermolt growth occurs in Anomura other than the Porcellanidae. If the function and value of intermolt growth has been correctly interpreted here, this form of variability might be expected among species with low numbers of larval molts required to attain the subadult. Only careful studies of more life histories can reveal the possible relationship of intermolt growth and variable stage numbers.

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FEEDING, CLEANING, AND SWIMMING BEHAVIOR IN LARVAL STAGES OF PORCELLANID CRABS (CRUSTACEA: ANOMURA)[1]

S. L. GONOR AND J. J. GONOR[2]

ABSTRACT

Pachycheles rudis, *Pachycheles pubescens*, *Petrolisthes eriomerus*, and *Petrolisthes cinctipes* have a swimming prezoeal stage of short duration. The prezoeal form is probably related to escapement of the larvae from the confined adult habitat.

Both zoeal stages are strong swimmers, moving both forward and backward by means of the maxillipedal exopodites, aided by the telson. Zoeae have a well-defined cleaning behavioral sequence for removal with the mouth parts of particles from the telson and the maxillipedal endopodites. The two zoeal stages are carnivorous and capture live prey upon contact but do not appear to locate prey visually. Prey are caught with the maxillipedal endopodites and held with the flexed abdomen and telson.

At the molt to megalopa, the larva becomes a filter-feeding herbivore like the adult. Other adultlike behavior of the megalopa includes use of the fifth legs for cleaning and attempts by older megalopae at swimming by clapping the abdomen. Megalopae filter feed only when suspended algal food is present; water movement enhances feeding but is insufficient alone to induce feeding. At first, using their abdominal pleopods, megalopae swim continuously, later swim intermittently, and finally settle permanently if a substrate suitable for clinging is available.

A large amount of information is available about the comparative larval morphology of most groups of decapod Crustacea. Further understanding of the adaptive significance of larval morphology and its changes during larval life requires comparable information, now largely lacking, about larval behavior and ecology. The present state of knowledge on the larvae of porcellanid crabs is typical in this respect, with a growing descriptive literature available but little known about other aspects of larval biology. A few observations on various features of porcellanid larval behavior have been given by Russell (1925), Spooner (1933), Foxon (1934), Gurney (1942), Lebour (1943), Greenwood (1965), and Knight (1966). None of these studies present a complete account of any behavior pattern throughout development. Information on food and feeding is incomplete and somewhat inconsistent. The detailed studies on feeding and respiration of adults by Nicol (1932) and Knudsen (1964) indicate that adult porcellanids are specialized filter feeders. The available information indicates that zoeae are carnivorous or possibly also detrital feeders. Since it is now known that decapod zoeae are typically strict carnivores capturing live prey, a change in diet and mode of feeding during the development of porcellanids would be expected, but has not been clearly described.

Large numbers of live larvae of all developmental stages and ages were available in laboratory cultures during a study of the larval development of four species of porcellanid crabs (Gonor and Gonor, 1973). Several aspects of the behavior of the larvae being cultured were studied closely throughout development. Special attention was given to the ontogeny of normal respiratory, feeding, cleaning, and locomotory behavior patterns from hatching through development to the first juvenile crab stage. These

[1] This research was supported in part by a traineeship from Grant Nos. 5T1-WP-111-02, -03, and -04, Federal Water Quality Administration and by National Oceanic and Atmospheric Administration (maintained by the U.S. Department of Commerce) Institutional Sea Grant 2-35187.

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Manuscript accepted February 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

observations are presented here to clarify some aspects of the ecology of both the larval and adult stages.

METHODS

The species used were *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles rudis* Stimpson, and *Pachycheles pubescens* Holmes. Adults of all of these species occur in the rocky intertidal or the shallow subtidal zone of the northeastern Pacific but their habitats differ (Haig, 1960). The *Petrolisthes* species occur in the upper intertidal beneath loosely bedded rocks and boulders, whereas the two *Pachycheles* species are crevice and burrow dwellers. *P. rudis* was collected from beneath root mats of the surf grass *Phyllospadix* in the lower intertidal zone and *P. pubescens* was collected from burrows and crevices in rocks. Both larvae captured alive in the plankton and larvae reared from eggs carried by females in the laboratory were available.

Gravid females were maintained in the laboratory at ambient sea temperatures until hatching occurred. Thereafter, larvae were cultured in filtered seawater kept at several constant temperatures and fed *Artemia* nauplii. Larvae captured in the plankton were similarly maintained in the laboratory. A detailed account of methods used in rearing and handling the larvae is given elsewhere (Gonor and Gonor, 1973).

RESULTS

In laboratory cultures, larvae of each of the four species showed similar basic patterns of locomotion, feeding, respiration, and cleaning, as well as changes in these patterns through time. Consequently, separate accounts for each species will not be given. Basic body and appendage form is sufficiently similar in the first and second zoeae for Figures 2 and 3, of second zoeal appendages, to be referred to in the text for both stages. The descriptions given below are summarized from observations repeated throughout the rearing study as each of the cultures was examined daily. Table 1 gives the number of larvae of each stage kept in culture for at least 2 days, and available for observations on behavior at some time during the 2-year period of the study.

PREZOEA

Females of all four species studied here release their larvae in the form of a prezoea (Figure 1).

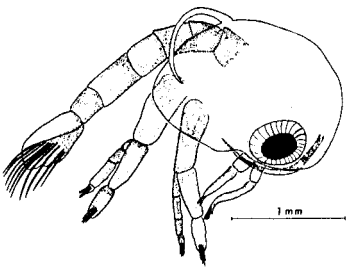

FIGURE 1.—Prezoea of *Pachycheles pubescens*, showing rounded form.

Gravid females were maintained in the laboratory for as long as 35 days, showing normal locomotion, feeding, and cleaning behavior before their eggs hatched. The following numbers of broods were hatched in the laboratory: *Pachycheles rudis*, 35; *P. pubescens*, 2; *Petrolisthes eriomerus*, 11; *P. cinctipes*, 10. In each case female behavior during hatching was of the normal type described elsewhere (Gonor and Gonor, 1973), and the larvae released were prezoeae which molted to viable first zoeae. The behavior patterns of the prezoea are simpler than those of later stages. Respiratory motions in the prezoea are effected by the fanlike scaphognathite of the second maxilla. The type of

TABLE 1.—Number and source of larvae of different stages available for behavioral observations.

Species	Zoea I	Zoea II	Megalopa
Petrolisthes cinctipes (reared)	727	19	1
Petrolisthes eriomerus (reared)	603	58	14
Pachycheles rudis (reared)	757	21	1
Pachycheles rudis (plankton)	76	58	28
Pachycheles pubescens (reared)	100	18	--
Pachycheles pubescens (plankton)	26	81	36
Total	2,289	255	80

cleaning behavior described below for the zoeal stages has not been observed in this stage. It probably is not present since the stage is short-lived and the major natatory and telson setae are confined beneath the larval cuticle.

Prezoeal locomotion consists of violent spasmodic flexions of the abdomen, and there is no feeding during this stage. The larva appears to be only slightly photopositive. The strong abdominal flexions finally split the cuticle longitudinally along the dorsal midline of the carapace just behind the point where the rostrum joins the carapace, and a first zoea emerges from the thin prezoeal cuticle.

ZOEAL STAGES

The behavior patterns of the first true zoea are considerably more complex than those of the prezoeal stage. Respiratory currents are still produced by the beating of the maxillae and are aided by swimming, as was also noted by Foxon (1934). Detrital particles often become entangled in the plumose setae of the maxillipeds and telson. Cleaning behavior is simple but well defined in this stage. The telson and the plumose setae along its posterior margin are cleaned by curving the abdomen under the thorax and dragging the telson posteriorly across the functional mouth parts, thus loosening and scraping off clinging debris. This scraping also serves to remove large pieces of detritus from the peripheral setae on the mouth parts and from the setae of the endopodites on both sets of maxillipeds. The endopodites are used in feeding and require frequent cleaning. Direct cleaning of the exopodites and natatory setae and of the carapace spines was never observed, however. The cleaning observed was indirect and probably accidental, since it consisted simply of freeing the body surface of entangled debris by larval motion and reversal of swimming direction.

The first zoea swims primarily by beating the maxillipedal exopodites (Figure 2) which have long natatory setae, but this may be augmented by motions of the telson. The maxilliped endopodites are held extended ventrally and do not function in swimming. The zoea are strong swimmers and due to the configuration of the carapace spines (Figure 3), swim predominantly backward and forward.

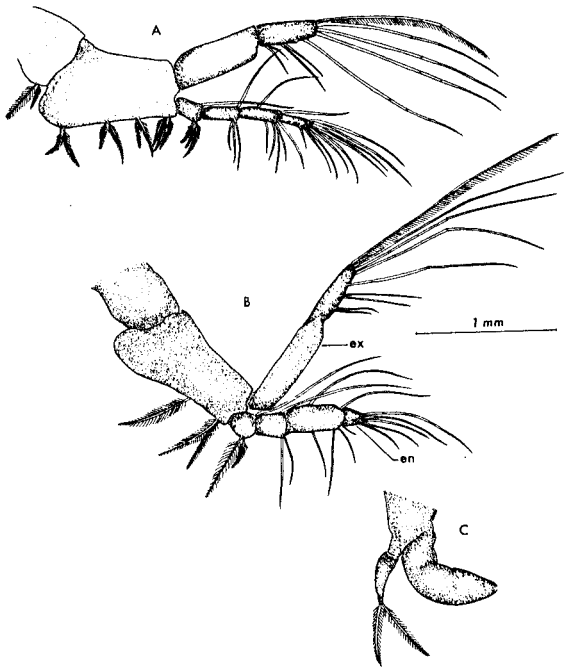

FIGURE 2.—Maxillipeds of Zoea II, *Pachycheles pubescens*, with setules omitted from most plumose setae. Ex - exopodite; en - endopodite; A - Maxilliped I; B - Maxilliped II; C - Maxilliped III.

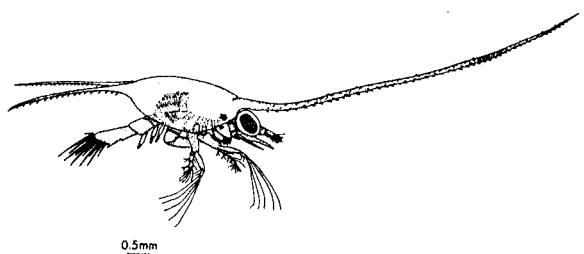

FIGURE 3.—Zoea II of *Pachycheles pubescens*, in forward swimming posture. Maxillipeds I and II rotated slightly for clarity.

Forward motion is accomplished by synchronously beating both sets of exopodites downward and posteriorly, with the telson extended posteriorly. Reversal of direction can be achieved very quickly by a forward snap of the telson and a

simultaneous change in the pitch of the maxillipeds so that the exopodites beat downward and anteriorly. This rapid adjustment sends the larva on its way backward with its posterior spines leading. Unlike some larvae of the Galatheidae (Foxon, 1934), which swim only backward with the telson leading, the zoeae of porcelain crabs swim almost equally well in either direction. Normally, zoeae swim forward, reversing direction on contact with an object.

Zoea larva are voracious predators and are cannibalistic if not well supplied with other types of food. However, true hunting behavior of the kind reported for certain other predatory zoeae (Knudsen, 1960) was not observed. In fact, when a potential food organism touches any portion of the rostrum or posterior spines, or the top or sides of the carapace, the zoea immediately moves away from the point of contact, apparently in an act of avoidance. If, however, the prey approaches the thoracic region of a zoea closely enough to touch the setae of the ventrally extended maxillipedal endopodites (Figures 2, 3) or the ventral surface of the first two segments of the abdomen, the zoea reacts immediately. The prey is clutched between the endopodites, and the telson is used to force it forward and upward within reach of the functional mouth parts. This sequence has been observed many times, with no indication that sight is involved in locating and capturing the prey. The zoea also demonstrates what appears to be sensitivity to water movements. If a prey organism passes near the thoracic or abdominal region of the zoea but does not touch the sensitive setae, the zoea, without the stimulus of direct contact, will go through all the motions normally associated with the capture of prey. In these cases, the prey is usually out of reach, and the attempts to capture the passing animal fail.

The second zoeal stage is only slightly more complex morphologically than the first stage, and behavior patterns remain essentially the same throughout both zoeal stages. Metamorphosis to the megalopa (Figure 4), however, brings about immediate and drastic changes in structures and habits of the larva. Basic behavior patterns which were stable in the zoeal stages undergo progressive changes throughout the megalopa stage, gradually becoming more adultlike in nature.

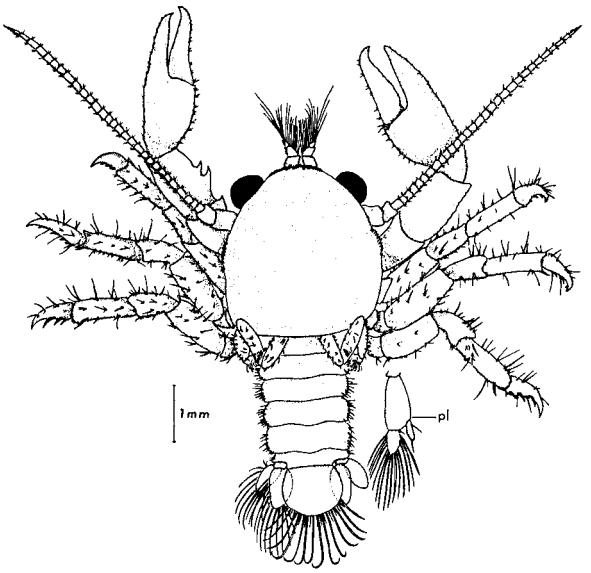

FIGURE 4.—Megalopa of *Pachycheles pubescens*, in forward pleopodal swimming posture, except antennae not extended posteriad. Pl, detail view of pleopod.

MEGALOPA

In the megalopa respiratory currents are produced primarily by fanning motions of the maxillary scaphognathites (Figure 5C) and are aided by the outward flicking of the setose exopodite of maxilliped II (Figure 5B). The outward flicking causes an exhalent current by "spooning out" the branchial cavity. The exopodite of maxilliped III is nonfunctional at this stage. In addition, a newly settled larva elevates its body above the substrate and concurrently vibrates its pleopods (Figure 4), thus increasing circulation of the surrounding water.

Cleaning behavior becomes highly complex in the megalopa. The fifth pereiopods (Figure 4), which are mobile, chelate, and armed with specialized hooked setae and dense clusters of short bristles, are carried folded along the sides of the carapace when not in use. These structures serve to clean all portions of the abdomen and telson, the three pairs of functional walking legs,

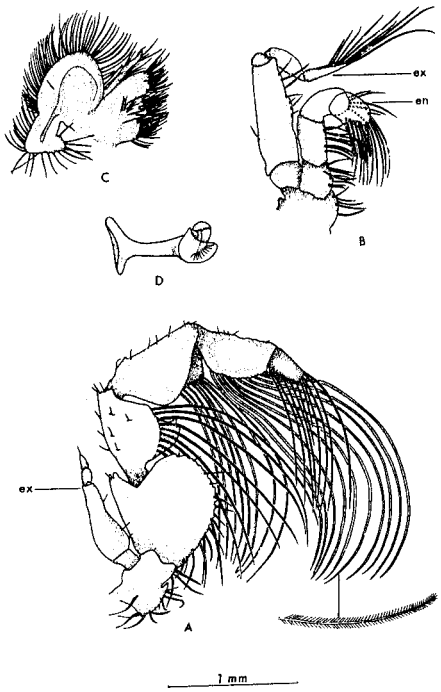

FIGURE 5.—Megalopa respiratory and feeding structures *Pachycheles pubescens*. Setules omitted from all plumose setae. Ex - Exopodite; en - endopodite; arrow - detail of a plumose seta. A - Maxilliped III; B - Maxilliped II; C - Maxilla II; D - mandible, anterior view, palp folded in place.

and the under side of the carapace in the branchial chamber. The foremost one-fourth of the carapace cannot be reached by these legs, and in dense algal suspensions, fine hairs on this portion of the megalopa may become entangled with algae and other detritus.

The chelipeds are freed of foreign matter by rubbing the dorsal surface of one on the ventral surface of the other in a simple lateral scraping motion. The antennules are cleaned singly or simultaneously in the following manner. An antennule is lowered to the level of a raised third maxilliped and inserted into a notch on the maxilliped formed by a long and a short group of dense setae. The setae and aesthetes of the antennule are then effectively combed free of particles as the maxilliped is drawn forward and down and the antennule passes between the setal brushes.

The grooming of the feeding mechanism is the most complex cleaning behavior. This behavior can be seen in actively feeding animals as well as in nonfeeding megalopae which have been placed in a dense suspension of algal cells. The long feeding setae of the third maxilliped (Figure 5A) are combed clean by the short dense setal brushes located on the two terminal segments of the second maxilliped (Figure 5B). The short setal brush is inserted at the bases of the feeding setae and rolled downward and inward toward the mouth following the long curve of the setae being combed. When the entire length of the filtering setae has been combed free of particles, the brushes of the second maxilliped are then combed out by the first maxilliped and inner mouth parts. Undesirable particles are rejected into the exhalent current and swept out by the flicking of the exopodite on maxilliped II.

The diet and feeding behavior of the megalopa are drastically different from those of the zoeal stages. Predatory habits are replaced immediately by filter-feeding habits when the molt is completed and the megalopal skeleton has become hard enough to permit motion. The megalopae of all four species rejected newly hatched *Artemia* nauplii as food and would feed only on suspended phytoplankton. Several monoalgal and diatom cultures (*Tetraselmis* sp., *Isochrysis* sp., and several unidentified diatoms) and nutrient culture medium inoculated with raw seawater were tried singly and in various combinations as food. In each case the megalopae fed on the suspended organisms in the cultures in the same manner.

The behavioral change from prey capture to suspension feeding is reflected in changes in mandibular and maxilliped form. The natatory second maxilliped and the functionless third maxilliped of the zoea become highly specialized parts of a complex feeding mechanism in the megalopa. The feeding pattern most commonly observed in the laboratory is composed of the following sequence of events.

The endopodite of the highly setose third maxilliped is extended and a "setal net" spread open. After a moment, the maxilliped is lowered and swung in toward the body, where the setae are

combed out by the process described earlier. The terminal brushes of the second maxilliped are subsequently cleaned by the first maxilliped and so on, until the particles initially trapped in the extended net finally reach the mandibles. Somewhere in this chain of events particles are sorted, and undesirable portions of the catch are ejected in the exhalent respiratory stream. Particles which are acceptable as food are ground up between the curved bladelike edges of the mandibles (Figure 5D) and passed into the mouth with the aid of the mandibular palp.

Most often the maxillipeds work rapidly and alternately, with one extended while the other is being combed. However, when a strong current of water runs steadily from a single direction, megalopae often extend only one maxilliped and leave it out for a time. When the setae have gathered a sufficient quantity of particles, the maxilliped is withdrawn and cleaned. At this point, the free maxilliped may be extended, or the same maxilliped may be extended again after it has been cleaned. The appearance of variable feeding behavior under varying conditions led to the question of the importance of water movement to megalopal feeding.

A 36-hr experiment was conducted in an effort to determine the effect of turbulence on feeding. Eighteen healthy megalopae, nine each of *Pachycheles rudis* and *P. pubescens*, were used. Each of the megalopae and a stone for it to cling to were placed in a flask of filtered seawater and starved for the first 13 hr of the experiment. A mixed algal suspension of *Isocrysis* sp. and *Tetraselmis* sp., previously found to be acceptable to megalopae as food, was supplied to the same 18 larvae for the remaining 24 hr of the experiment. At intervals of 2 hr, throughout the 36-hr period, the number of animals showing feeding motions was recorded before and after stirring the water. The flasks with the megalopae were held at 12°C in a water bath. The experiment was started at 0100 on one day and continued to 1300 the next before food was introduced, so that observations were made for both starved and fed conditions at night and during daylight hours.

Figure 6 summarizes the observations on the number of animals feeding under each condition, before and after stirring the water. When no food was present and the water was still, virtually no feeding activity was observed.

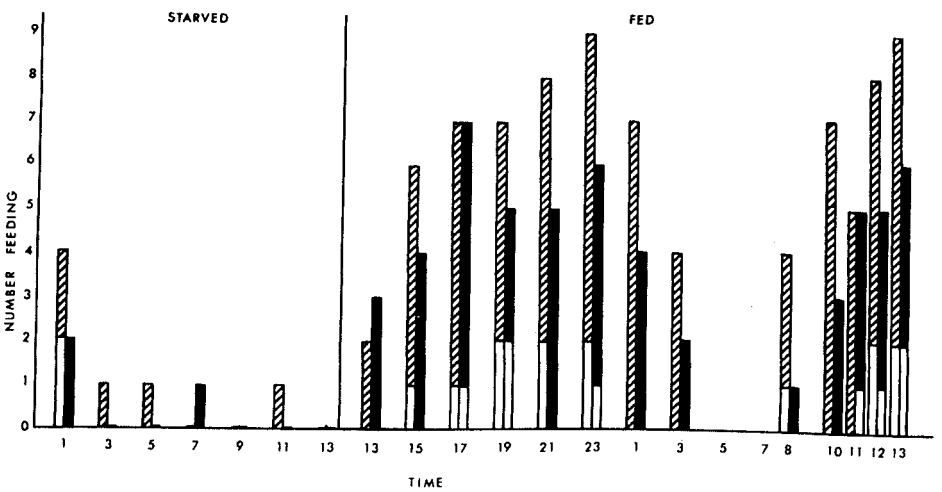

FIGURE 6.—Histogram showing effect of water movement on feeding behavior in megalopae of *Pachycheles pubescens* and *P. rudis* under starved and fed conditions. Left bars, *P. pubescens;* lower, open part of bar, number of larvae feeding in still water; cross-hatched part of bar, number feeding after agitation of water. Right bars, *P. rudis*; open part of bar, number of larvae feeding in still water; solid part of bar, number feeding after agitation of water.

Turbulence caused a few animals to undergo feeding behavior even when food was absent. When food was present, there usually was some feeding activity in still water. When the water was agitated and food was present, feeding behavior greatly increased. In the presence of food, water movement, although not essential for the initiation of feeding, favors both the initiation and maintenance of feeding activity, probably because turbulence suspends the particles so that they can readily be filtered. The results suggest that there is a periodicity to feeding activity, but the experiment was too brief to clearly demonstrate this. No effect of daylight or darkness on feeding behavior was observed.

Locomotory behavior gradually changed throughout the megalopa stage. The numbers of megalopae available for observation at different ages are indicated in Table 2, which gives the age of the megalopae in days since the molt from the second zoeal stage. Adultlike locomotory behavior slowly evolved as the megalopa grew older. Newly metamorphosed megalopae were strongly planktonic, swimming almost continuously by means of the pleopods, with the walking legs and chelipeds extended forward. After spending some time (1-4 days) as truly planktonic animals, the megalopae became more quiescent and began to demonstrate clinging tendencies. Small stones, to which the settling megalopae could cling, were introduced into the culture flasks at this point.

The megalopae which are just beginning to settle show no signs of recognizing a substrate suitable for settling. If a larva encounters a rock while swimming forward, it continues swimming motions, pushing against the obstacle with the extended chelipeds but not moving forward. However, if megalopae of this age are artificially introduced to a rough surface, walking legs first, by means of turbulence or by direct placement, they cling readily and will usually remain on that surface unless disturbed. As the megalopae increase in age, they appear to develop the ability to recognize a suitable substratum. Larvae of 2 weeks or older were seen to collide head on with a rock, stop swimming, and put the walking legs down. They then turned around and backed onto the piece of gravel.

TABLE 2.—Number and age in days of megalopae available for behavioral observations.

Species	Age in days							
	5	10	15	20	30	40	45	50
Pachycheles pubescens	34	32	27	23	18	9	4	
Pachycheles rudis	21	19	17	17	11	4	3	1
Petrolisthes eriomerus	14	8	7	1				
Petrolisthes cinctipes	1							
Total	70	59	51	41	29	13	7	1

In the laboratory, recently settled megalopae can be induced to leave an apparently suitable substrate if the water is stirred vigorously or if the larvae are touched. In addition, when a settling megalopa encounters a stone that is already occupied, it will remain there only if it can do so without contacting the other occupant. If the stone is too small to allow this, the settling megalopa will usually cling only momentarily and then resume swimming. In a few cases, however, the settling megalopa forced the original occupant to leave its stone and begin swimming.

A specialized form of behavior was observed in advanced megalopae of *Petrolisthes eriomerus*. After locating a stone, a swimming megalopa will settle on it and then elevate and lower both chelipeds simultaneously several times. If the megalopa then moves a short distance over the rock, the cheliped elevation sequence is often repeated. This activity was observed only in individuals that had just arrived on a substrate and was exhibited whether or not another megalopa was present on the rock.

An advanced behavior was observed in still older animals (30-33 days in *Pachycheles pubescens*). These megalopae could not be induced to use their pleopods when swimming, even when they were so disturbed that they would finally leave their rocks. Instead, a disturbed animal would bob up and down in the water, clumsily clapping the abdomen to the thorax. The presence of the four pairs of fully developed pleopods prevented effective swimming by this action. Adult porcelain crabs, whose pleopods are reduced in size and often in number, swim only by clapping the abdomen to the thorax. The

megalopae therefore show in this situation the behavior of adults.

Further development along the lines already established by the megalopa is shown by the succeeding juvenile stages. Respiratory currents become much stronger and well defined and are now aided by the tandem motion of the two sets of maxillipedal exopodites. Feeding movements are the same as those described here for the megalopa and for the adult by Nicol (1932). In adults, food preferences vary according to species. Knudsen (1964) reports that pelagic diatoms are the preferred food for *Petrolisthes eriomerus* but does not state the preferences of *Pachycheles rudis*. In the laboratory, adults of all species readily fed in unfiltered seawater, but only *Petrolisthes* females accept and ingest fragments of mantle and adductor muscle of *Mytilus*. The preferred adult locomotion is pereipodal walking, but swimming by abdominal clapping is also used, especially in *Petrolisthes*.

DISCUSSION

PREZOEA

Adults of both *Petrolisthes* species live where the larvae are released into turbulence caused by waves and currents. These conditions favor the presence of a short-lived, rounded initial larva with few body projections, that would more readily escape entangling algae and debris in the intertidal zone.

The habitats of the two *Pachycheles* species (Haig, 1960) more strongly favor a compact, rounded, initially spineless larval form. In many cases adults become so large that they are unable to pass out through the openings of the burrows or crevices they inhabit. Larvae are released within the adult burrow and must escape this confinement to survive. The prezoeal cuticle covering the telson in *P. pubescens* larvae is well modified for swimming. This was described by Gurney (1942) for other decapods and by Lebour (1943), Wear (1965), and Greenwood (1965) for other porcellanids.

These observations suggest that in the four species considered here, and probably in the family as a whole, the prezoea is a short-lived natural stage and is not a laboratory artifact as has often been suggested. Its existence as a transport stage is ecologically consistent with the natural habitat of the adults. Similar arguments have been put forth by Gore (1968) in defense of the interpretation of the prezoea as a natural stage in the commensal porcellanid *Polyonyx gibbesi*, which releases larvae from inside the tube of the polychaete *Chaetopterus*. Another observation supporting this argument is that, under laboratory conditions, true zoeae, with their long spines, respond very unfavorably to collisions, spine breakage, and collection of detrital material on the spines, all of which would be likely to occur in nature if full zoeae emerged from the eggs and were released into the adult environment. Photopositive swimming behavior would also prove useful to prezoeae released in burrows and crevices, and the larvae studied showed a photopositive response. This response was, however, weak under laboratory conditions.

ZOEA

With the passage of the larva through the prezoeal molt, the first true zoea emerges and becomes an actively swimming planktonic carnivore. Despite the good swimming ability and well-developed eyes of the zoea, no evidence of true hunting behavior was found. Instead, the larvae appear to rely entirely on chance encounters with prey, with capture behavior initiated by direct contact or by vibrations stimulating the maxillipedal endopodites and setae and the ventral surface of the abdomen. Similar stimulation of other parts of the body elicits an escape response by the zoea. Survival of these zoea in the plankton is probably highly dependent upon suitable prey density. The method of prey capture used by these larvae, involving the use of the telson to scoop up the prey and hold it from below, appears to be a feeding method used by zoea throughout the Decapoda. Knudsen (1960), for example, describes this method of feeding in xanthid Brachyura.

MEGALOPA

Many of the adult behavioral features described by Nicol (1932) appear in the megalopa

when the structures used first resemble those of the adult, but before the adult mode of life is adopted. Attempted swimming by abdominal clapping is an example of the development of an adult behavior pattern before the adult structure is completed. Megalopae of these four species clean the body with the fifth legs in the adult manner, a feature also observed for other porcellanid megalopae by Lebour (1943) and Knight (1966).

At the molt to megalopa there is an abrupt change from carnivorous to a filter-feeding, herbivorous habit. As Nicol (1932) first noted, adult Porcellanidae are specialized for filter feeding on suspended material. Adults of the two *Petrolisthes* species studied here will also sometimes accept pieces of mussel as food, but the two *Pachycheles* species will not. The observations on the megalopae of these species and those of Lebour on *Porcellana* species, indicate that the acquisition of morphological and behavioral adaptations to filter feeding in the Porcellanidae involve both the adult and megalopa stages. Although many other anomuran adults feed on particulate material by some mode of filter feeding, it is not known whether this also involves the late larval stages. No information could be found in the literature on feeding by their postzoeal stages. In hermit crabs, which are more generalized detrital-feeding Anomura, both zoea and postzoeal stages can be reared on *Artemia* nauplii, as found for example by Provenzano (1962).

Since population and species success depends upon the megalopae locating a suitable adult habitat, settling behavior is a critical part of later larval development. Settling behavior of barnacles, bryozoa, and some other forms has been studied; however, similar settling behavior in decapod Crustacea has not been studied, with the exception of shell selection by the glaucothoe stage of hermit crabs (Reese, 1962; Hazlett, 1971) and the coconut crab *Birgus latro* (Reese, 1968). For the megalopae studied here, the behavioral sequence of the true planktonic period, the settling and swimming period, and the period of final settlement seems to be highly specialized for substrate selection. Possession of this behavioral mechanism would permit, under natural conditions of turbulent water movement, older megalopae to select or reject substrates encountered by random contact. No information is available on how settled megalopae reach the final adult habitat after initial settlement, but postsettling megalopae and very young juveniles have been found clinging to the base of surf grass and under stones with adults.

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BIOLOGY OF THE PYGMY SEA BASS, *SERRANICULUS PUMILIO* (PISCES: SERRANIDAE)

ROBERT W. HASTINGS[1]

ABSTRACT

During the period from 1968 to 1971, numerous specimens of *Serraniculus pumilio*, were collected in shallow waters of the northern Gulf of Mexico. This paper presents biological data accumulated from these and other specimens in the fish collection of Florida State University and from scattered literature references regarding the species. The range of *S. pumilio* extends from North Carolina along the continental margin of the western Atlantic Ocean to Guyana, but it apparently does not occur in the West Indies. It has been collected at depths from 1 to 117 m, usually over sand or shell bottoms near coral or rock reefs or accumulations of mollusk shells. Individuals move about considerably, although they spend much time resting on the bottom. *S. pumilio* is a synchronous hermaphrodite, but pairs mate to exchange gametes and self-fertilization probably never occurs. Spawning occurs between March and August or September in the northern Gulf of Mexico. A length-frequency distribution of specimens collected in the northern Gulf is presented to show the growth rate of first year fish. Juveniles (15-20 mm SL) which appear inshore in September reach a size of 50-55 mm by the following June. Most fish move offshore to deeper water for the winter (January and February) and individuals larger than 55 mm apparently never appear inshore. Small crustaceans are the most important food items.

Since the pygmy sea bass, *Serraniculus pumilio*, was described in 1952 by Ginsburg, virtually nothing has been added to our knowledge of the species except for a few brief notes in general surveys of fishes. During a study of reef fishes in the northern Gulf of Mexico from 1968 to 1971, numerous specimens of *Serraniculus* were collected and notes were taken on their biology. The present paper is a synopsis of the information scattered in the literature and the new data accumulated during this study.

The generic allocation of the species used in this paper is tentative. Robins and Starck (1961) briefly discussed the characteristics of the genus *Serraniculus* but did not include the species in their review of the genus *Serranus*. Ginsburg (1952) noted that *Serraniculus* and *Dules* differ from *Serranus* in having six rather than seven branchiostegal rays, and that *Dules* differs from the other two genera in having the third dorsal spine greatly prolonged. After subsequent study Robins (personal communication) believes that *Serraniculus* is inseparable from *Dules*, but because *Dules* itself is so close to *Serranus*, he recommends no change until a morphological study of a wider range of serranid genera can be completed. According to Robins, *Serraniculus pumilio* and *Dules auriga* are distinct species.

METHODS

During the present study, 106 specimens of *Serraniculus pumilio* [15.8-54.1 mm standard length (SL)] were collected. Most of these (75) were collected at East Pass of Choctawhatchee Bay near Destin, Fla, where biweekly or monthly observations were made between June 1968 and December 1970. Others were collected from St. Andrew Bay near Panama City, from Apalachicola Bay, and from Alligator Harbor, Fla. A

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Manuscript accepted February 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

few were taken short distances offshore from these locations.

Numerous field observations were made while diving, and small groups of specimens (2-3) were maintained and casually observed for a few months in 20-gal aquaria.

Eighty-seven specimens were examined for gonad development. Most were examined superficially using a low-power (10-30×) dissecting microscope, and the stage of development of the ovarian portion of the gonad was estimated, following the definitions of Smith (1965) and Moe (1969). Sexual maturity (the presence of Stage 4 oocytes) was determined on the basis of ovarian tissue only, since very small individuals often contained some mature sperm, even though the ovarian tissue was immature. For 22 specimens the gonads were removed, embedded in paraffin, and sectioned. Most specimens had been originally preserved in 10% Formalin[2] and then transferred to 40% isopropyl alcohol. Gonads to be sectioned were removed from the fish, placed in Bouin's fluid for several days, dehydrated in ethyl alcohol, celloidin-methyl salicylate, and xylene, and then embedded in paraffin. Gonads were sectioned at 10 μ, mounted on microscope slides, and stained. Mallory-Heidenhain stain was used for most slides. This stain was easy to use and yielded good contrast between various tissues within the gonad.

Stomachs of 31 specimens were removed and their contents examined under a low-power dissecting microscope. Food items were identified to major group (usually class or order) and counted. The importance of each group was determined by calculating its frequency based upon the total number of food items counted and upon the number of fish containing each food type.

DISTRIBUTION

Briggs (1958) gave the range of *Serraniculus pumilio* as North Carolina to Florida, and the southwestern Gulf of Mexico in shore areas. Subsequent references (Bullis and Thompson, 1965; Cervigon, 1966) indicate that it occurs along the coast of the western Atlantic Ocean from North Carolina to Guyana. Most collections have come from the Atlantic coast of the southeastern United States and from the eastern Gulf of Mexico as a result of the numerous fisheries surveys in these areas (Reid, 1954; Springer and Bullis, 1956; Springer and Woodburn, 1960; Moe and Martin, 1965; Moe et al., 1966; Starck, 1968; Struhsaker, 1969). The species has also been collected in the western Gulf of Mexico off Texas (Ginsburg, 1952; Hildebrand, 1954) and in Campeche Bay off Mexico (Hildebrand, 1955). More recent collecting by the RV *Oregon* and RV *Pillsbury* off the coast of Colombia indicates that the species is also common in the Caribbean Sea (C. R. Robins, pers. comm.). Two specimens have been taken by the *Pillsbury* from off the coast of Honduras.

Serraniculus is unrecorded from the Bahamas (Böhlke and Chaplin, 1968) and apparently also absent from the other islands of the West Indies. Numerous species of fishes have similar continental distributions in the western Atlantic, while other species are restricted to the coral reef areas of the islands and portions of the Central and South American coast where the continental shelf is narrow. The factors which prevent the distribution of continental species in the islands are not completely understood, but probably include differing ecological conditions, as well as competition from closely related and better adapted island species (Robins, 1971). Physical barriers are undoubtedly not important since many of the species have pelagic larval stages, and some free-swimming species such as *Scomberomorus maculatus* are also absent from most of the West Indies. Ecological parameters which may be important are temperature, bottom type, salinity, and turbidity. Temperature may not be important for *Serraniculus pumilio* since it is distributed well into the tropics, but it is apparently more tolerant of low temperatures than are most of the coral reef fishes. *Serraniculus* may prefer continental sediments rather than coral reef debris, but accurate descriptions of substrates where it has been collected are unavailable. In general, the continental species, including *S. pumilio*, are more tolerant of vary-

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

ing conditions, but whether they require such changes is unknown. For species such as *S. pumilio*, which are territorial, competition by other species with similar habitat requirements may be important. Two potential competitors of *S. pumilio* are noted in the following section.

HABITAT

Serraniculus pumilio apparently occurs typically at moderate depths (10-70 m) over the continental shelf but may occasionally occur in shallow coastal waters less than 1 m deep. It has been recorded as deep as 117 m (Bullis and Thompson, 1965).

During this study, the species was often common in the shallow waters along the jetties at East Pass of Choctawhatchee Bay in depths of about 1-10 m but was usually absent during January and February. Inshore populations of *Serraniculus* apparently move offshore to deeper water during the winter. The lowest temperatures at which the species was recorded at East Pass were 13°-14°C. Shallowwater temperatures in the northern Gulf often drop below 10°C during the winter, while the temperature in water deeper than about 18 m usually remains above about 15°C. The minimum temperature extreme at which *S. pumilio* can survive may be about 13°C.

Like other small serranids, this species is most common over sand or shell bottoms near irregularities such as coral or rock outcrops. Springer and Woodburn (1960) noted that it was similar in this respect to *Centropristis ocyurus*, another species restricted to the continental shelf. *Serranus tigrinus* and *S. baldwini* (Robins and Starck, 1961) also occupy such habitats at about the same depth range as *Serraniculus pumilio*, but these two species are restricted primarily to coral reef areas of the West Indies where *Serraniculus* is not found.

A few specimens of *Serraniculus* have been collected in grass beds (mostly *Thalassia* and *Syringodium*) at the mouth of Alligator Harbor. However, in such areas, numerous bare patches of sand bottom are present, and there are accumulations of shell debris in places which provide suitable habitat for the species.

Apparently *Serraniculus pumilio* does not have a particularly restricted home range. The number of individuals observed on the East Pass jetties varied considerably, indicating that individuals were often moving into and out of the area. These observations were based upon adults or advanced juveniles; hence recruitment of populations on the jetties resulted from movement of adults, not from the immigration of recently spawned young. The pattern of movement of adults is not known, but more stable populations may occur on the numerous limestone reefs which lie short distances offshore in the area. Accumulations of mollusk shells occur over most of the sandy bottom in the area and small fishes such as *Serraniculus* could use such accumulations for shelter when moving over open bottoms. In this way *Serraniculus* could easily move the few miles from the offshore reefs to the jetties.

BEHAVIOR

Springer and Woodburn (1960) described *Serraniculus pumilio* as sedentary, but individuals apparently move about considerably. The fish rests on the bottom using its pelvic fins as props and moves about in short "hops" over the bottom. It appears to be territorial and protects its temporary abode (near a large shell, rock, or coral ledge) from intrusion by other fishes. The size of the area defended is not known, but when two or more individuals were placed in a 20-gal aquarium, one became dominant and forced the other fish to remain off the bottom, even when several rock piles were provided as hiding places.

During agonistic displays, *Serraniculus* spreads its dorsal and caudal fins and gill covers, and presents the lateral side of the body to the opponent (Figure 1). During these displays, the dark and light bands on the side of the body become more distinct and series of small, pale spots are clearly visible along the rays of the dorsal and caudal fins. These displays are followed by the fish beating the side of its opponent with its caudal fin and the posterior part of its body. When one individual proves subordinate, it retreats with its dorsal fin depressed and usu-

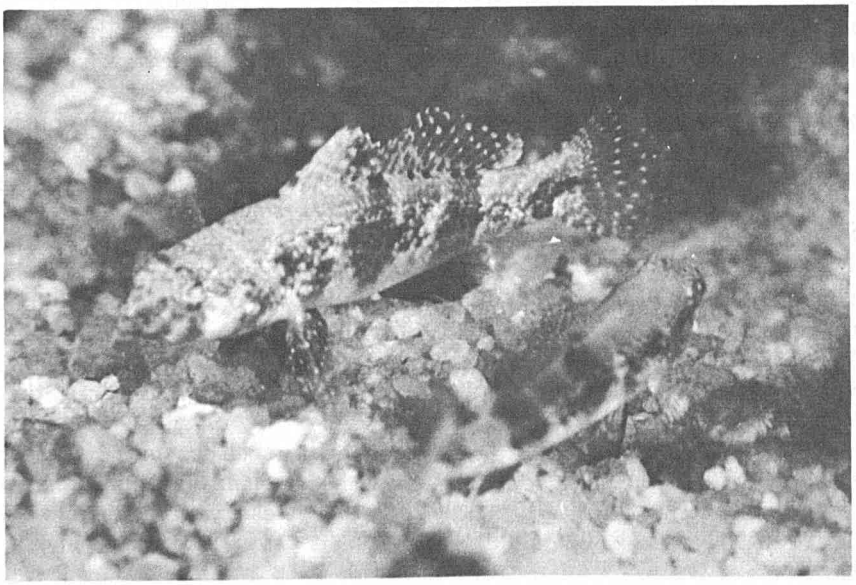

FIGURE 1.—Agonistic display of aquarium-held *Serraniculus pumilio*.

ally with the victor in pursuit. Quite similar agonistic behavior involving fin-spreading and tail-beating has been described in *Serranus scriba* (Kirchshofer, 1954). Subsequently, the subordinate individuals in an aquarium remained in precarious positions in the corners of the aquarium some distance above the bottom. When these fish left such positions, except during periods of feeding, they were soon attacked by the dominant individual and returned to their "sanctuaries" near the surface of the water.

Once, agonistic behavior was observed between two fish on the East Pass jetties, but in this case the retreating individual had its dorsal fin greatly expanded.

REPRODUCTION AND DEVELOPMENT

Microscopic examination of sectioned gonads (Figure 2) proves that *Serraniculus pumilio* is a synchronous hermaphrodite, as Ginsburg (1952) originally supposed. His statement that the testicular tissue is "interspersed with the masses of ripe roe" is misleading, however. The gonads of *Serraniculus* are identical to those of *Serranus* in that the testicular portion is well separated from the ovarian tissue and is restricted to narrow bands which lie along the ventral surface of each gonad (Reinboth, 1962; Smith, 1965).

The smallest and the largest specimens examined had both ovarian and testicular tissue in the gonad and many were seen with both mature eggs and sperm present. As with *Serranus*, internal self-fertilization is undoubtedly impossible since separate ducts are present to carry eggs and sperm. Clark (1959, 1965) found that under aquarium conditions, *Serranus subligarius* could fertilize its own eggs, but mates with another individual and exchanges gametes under normal conditions. Reinboth (1962) also induced self-fertilization in *Serranus scriba* but suggested that paired spawning normally occurs. The same is probably true for *Serraniculus*.

On 10 May 1968, several pairs of *Serraniculus pumilio* apparently involved in reproductive behavior were seen on the sand bottom at the base of the St. Andrew Bay jetties, on the Gulf side of the west jetty in water about 2 m deep. The water temperature was 23°C. Pairs would move slowly about in close proximity with one individual following behind the other. The trailing individual would repeatedly nudge the anal region of its mate. Clark (1959) noted such nudg-

ing behavior in spawning *Serranus*. Although no spawning clasps were observed, six specimens were collected, and subsequent examination revealed that all had large numbers of ovulated eggs within the lumen of their gonads. These specimens were 41.7-48.6 mm SL.

Based upon examination of gonads of preserved specimens, *Serraniculus pumilio* spawns between March and August or September. The number of small individuals collected during these months is limited, so the size at which maturity of the ovarian tissue is reached was not determined. There is some indication that it may be about 40 mm SL. Seven specimens (34.1-41.2 mm) collected in March were immature, while two (43.0 and 44.2 mm) were mature. One specimen (36.6 mm) collected in April had mostly immature gonads but had a few Stage 4 oocytes. Twelve specimens (40.6-49.5 mm) collected in May were mature, while two (40.5 and 40.8 mm) were mostly immature, with only a few Stage 4 oocytes. A few individuals as small as 23 mm SL contained mature sperm, even though the ovarian tissue was immature, but it is not known whether such individuals could successfully spawn as males. Reinboth (1962) noted a similar condition in *Serranus scriba* and *S. cabrilla*, in which the testicular portion of the gonads matured earlier in the annual reproductive cycle and also at a smaller size. He speculated that *S. scriba* in their first year of sexual maturity (120-140 mm body length) function only as males and that the ovarian tissue matures only in fish over 160 mm in length. He did not demonstrate actual spawning in such first-year males, however.

All 38 specimens (15.8-48.8 mm SL) collected in February, September, October, November, and December had immature gonads, although one specimen (42.7 mm) collected in October had a few mature oocytes in the posterior region of its gonad. All specimens larger than 43.0 mm collected from March through August had mature gonads. Specimens with ovulated eggs were collected in May, June, and July.

Nothing is known of the embryonic and larval development of *Serraniculus pumilio*. The eggs of *Serranus* are buoyant (Clark, 1959) and eggs and larvae of *Epinephelus* (family Serranidae) are pelagic (Moe, 1969), but it is not known if the same condition exists in *Serraniculus*. The smallest individual collected during this study (15.8 mm SL) has the general body shape and pigmentation of adults.

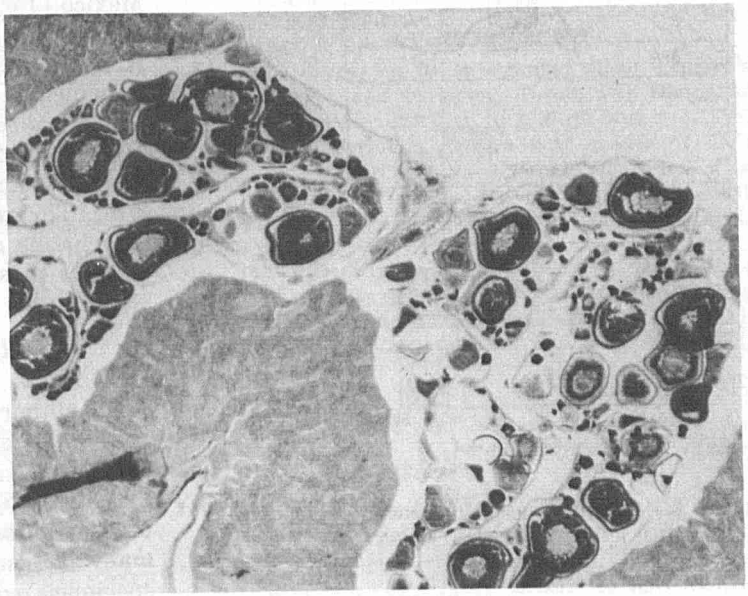

FIGURE 2.—Cross section through the basal (posterior) portion of the gonads of *Serraniculus pumilio* showing mature ovarian and testicular tissues.

GROWTH

A length-frequency distribution (Figure 3) of *S. pumilio* occurring in inshore waters indicates that all belong to the same year class and that no second year fish occur inshore. Small fish which were apparently spawned in the summer appear inshore in September, and some may remain throughout the winter. Most probably move to deeper water as the temperature drops and move inshore again in March. No adults were found after August. The largest specimen collected during this study (54.1 mm) is considerably smaller than the maximum size attained (80 mm SL—Ginsburg, 1952) so possibly the larger, second year fish remain offshore in deeper water.

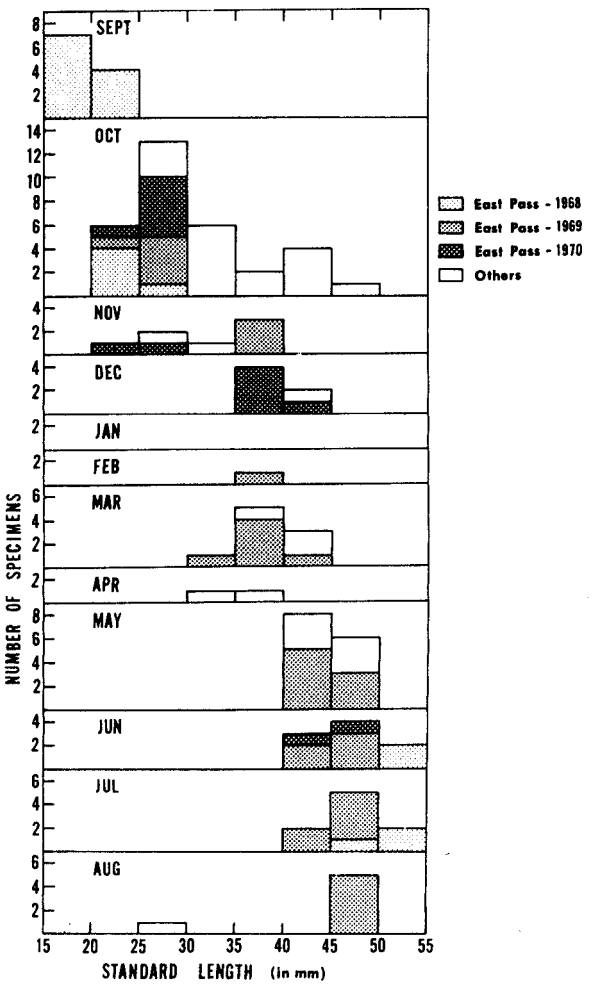

FIGURE 3.—Monthly length-frequency distributions of *Serraniculus pumilio* collected inshore at East Pass, Choctawhatchee Bay, Fla., and at other locations in the northern Gulf of Mexico.

FOOD HABITS AND PREDATION

Thirty-one specimens were examined for stomach contents, but two were empty. Results of stomach analyses are shown in Table 1. *S. pumilio* feeds predominantly upon crustaceans, which made up 91% of the total number of food items. Numerically, amphipods are the most common group, but shrimps and crabs comprise a larger volume of the stomach contents when present and may be the most important food items. *Serraniculus* appears to be an indiscriminate carnivore, feeding upon any small organism which it discovers, but showing preference for small crustaceans.

The extent of predation by other fishes on *S. pumilio* is not known. It seems strange that D. S. Jordan never found this species in his extensive studies of the stomach contents of snappers and groupers taken in the northern Gulf of Mexico (Jordan, 1884, 1886; Jordan and Gilbert, 1882, 1883; Jordan and Swain, 1885). Stephen A. Bortone (personal communication) found one specimen in the stomach of a *Lagodon rhomboides* collected in Apalachee Bay, 11 October 1969, about 2 miles south of the St. Marks lighthouse, Wakulla County, Fla., at a depth of about 3 m. The general cryptic coloration and sedentary habits of the pygmy sea bass may conceal it from most predators.

ACKNOWLEDGMENTS

The author was partially supported during this study by a grant from the Sport Fishing Institute. This grant also provided funds to purchase a boat for Florida State University which was used extensively during this study. I thank the many persons who assisted in the collection of specimens examined during this study, especially

TABLE 1.—Food habits of *Serraniculus pumilio* based on stomach analysis of 29 specimens (15.8-54.1 mm SL) collected in inshore waters of the northern Gulf of Mexico, 1968-71.

Food types	Number of items	Percent of total number	Number of fish containing each	Percent frequency of occurrence
Crustacea	262	91.0	28	96.5
Amphipods	110	38.2	17	58.6
Caprellid amphipods	12	4.2	6	20.7
Isopods	32	11.1	8	27.6
Copepods	20	6.9	7	24.1
Tanaidaceans	4	1.4	3	10.3
Cumaceans	1	0.3	1	3.4
Shrimps (adults)	18	6.2	10	34.5
Shrimp zoea (?)	23	8.0	7	24.1
Crabs (adults)	21	7.3	9	31.0
Crab megalops	14	4.9	2	6.9
Unidentified crustacean	7	2.4	5	17.2
Polychaetes	9	3.1	9	31.0
Unidentified wormlike organisms	13	4.5	1	3.4
Gastropods	1	0.3	1	3.4
Algae	(1 mass)	0.3	1	3.4
Fishes	2	0.7	2	6.9

Dr. Camm C. Swift and Stephen A. Bortone, both formerly of Florida State University. I also thank Dr. P. P. Graziadei of Florida State University who allowed me to use facilities in his histology laboratory in preparing microscope slides of sectioned gonads. I greatly appreciate the comments of Dr. C. Richard Robins of the Rosenstiel School of Marine and Atmospheric Science at the University of Miami (Florida) and his critical review of this manuscript. Special thanks are expressed to Dr. Ralph W. Yerger of Florida State University for his continued encouragement in my studies of marine fishes of the northern Gulf of Mexico and for reviewing and editing the original manuscript. I am indebted to my wife, Diana, for her encouragement and patience and for her assistance in typing.

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DESIGN AND EVALUATION OF A SAMPLER FOR MEASURING THE NEAR-BOTTOM VERTICAL DISTRIBUTION OF PINK SHRIMP, *PANDALUS JORDANI*

ALAN J. BEARDSLEY[1]

ABSTRACT

A shrimp sampler was constructed as one portion of a research effort dealing with the development of a fish-shrimp separator trawl. The sampler segregated shrimp caught in a series of 1-ft high vertical openings positioned between the seabed and a height of 13 ft above the seabed. Knowledge of the vertical distribution of shrimp was considered essential in the design of an efficient shrimp trawl. Results indicated that vertical distributions of shrimp vary, and the amount of light striking the seabed is suggested as the triggering stimulus. Auxiliary investigations conducted with the sampler dealt with evaluations of mesh size and tickler chain. Experiments indicated that mesh sizes smaller than 2 inches restrict the passage of shrimp. The weight of shrimp caught was nearly doubled when a tickler chain was used. The sampler may have application to both shrimp biologists and commercial fishermen.

Research was begun in our laboratory on trawls capable of separating pink shrimp, *Pandalus jordani*, from other marine organisms and debris while the net is being towed over the seabed (High, Ellis, and Lusz, 1969; Beardsley and High, 1970). Knowledge of the near-bottom vertical distribution of shrimp was considered essential to the design of an effective shrimp trawl since the vertical height of any bottom trawl should approximate the off-bottom distribution of the target species.

Subsequently a multipurpose shrimp sampler was designed to facilitate investigation of shrimp distributions above the seabed by 1-ft intervals. Auxiliary investigations conducted with the sampler included evaluating the effects of: (1) diel or circadian movements on the abundance of shrimp near the seabed; (2) light on shrimp vertical distribution; (3) mesh size on the retention of shrimp and other marine organisms; and (4) a tickler chain on shrimp catch rate and vertical distribution.

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Manuscript accepted July 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

METHODS AND MATERIALS

The shrimp sampler was designed for towing on the seabed either attached in the mouth of a conventional 57-ft Gulf shrimp trawl or directly to dandy lines without the net. All data presented in this paper resulted from tows without an attached net. This fishing configuration made the sampler easier to set and retrieve; it also eliminated the variability in shrimp catches caused by differences in fishing modes. Commercial trawling conditions were simulated using 5- × 7-ft otterboards, 15-fm dandy lines, and a towing speed of 2½ knots.

The shrimp vertical distribution sampler (Figure 1) consists of an aluminum frame partitioned into 18 openings each measuring 1 ft vertically by 2 ft horizontally. The sampler openings are positioned in six horizontal rows (1 ft high) and three vertical columns (2 ft wide), resulting in a triplicate series of vertical samples. A vertical extension was bolted with ⅜-inch bolts behind the sampler, permitting sampling as high as 12 to 13 ft above the seabed.

Individual collector bags of ¾-inch mesh[2] were lashed behind the sampler, thereby segregating and retaining the shrimp that entered the separate sampler openings. The dandy lines were attached to the sampler at the four center pad eyes and led freely through shackles at the four corner pad eyes. This method of attachment distributed the pull of the dandy lines across the face of the sampler in the event it hit a heavy object during a tow. Aluminum trawl floats (8-inch diameter) buoyed the sampler upright during setting and retrieving, whereas water pressure maintained this posture while towing.

During tickler chain (a device used to stimulate shrimp off of the seabed and into the trawl) evaluations, the chain was attached directly to the lower dandy lines with cable clamps and shackles. The length of chain was adjusted so it maintained a position 2½ ft in front of the bottom center of the sampler as determined by scuba diver observations.

Several mesh sizes[3] were evaluated using rectangular aluminum frames (separator panels) placed over the sampler openings (Figure 1). Aluminum teeth separated the panels on the front of the sampler. Although each frame had mesh of uniform size, the mesh size between frames varied between 1¼ and 3 inches. Comparisons of different mesh sizes were facilitated by placing the meshes to be compared on the lateral two columns of vertical openings on the sampler. Two-inch mesh webbing was placed over the center column of the sampler during mesh size comparisons so this column could act as a gross index of relative shrimp abundance on the fishing grounds. The tow direction was reversed after each tow, and the lateral two panels were exchanged on alternate tows to reduce any difference in catch efficiency by one side of the sampler or the other.

During fishing trials on shrimp beds off the Washington coast, adequate sample sizes (50-2,000 g of shrimp per collector bag) were obtained from tows of 10-min duration without separator panels and 15 min with separator panels.

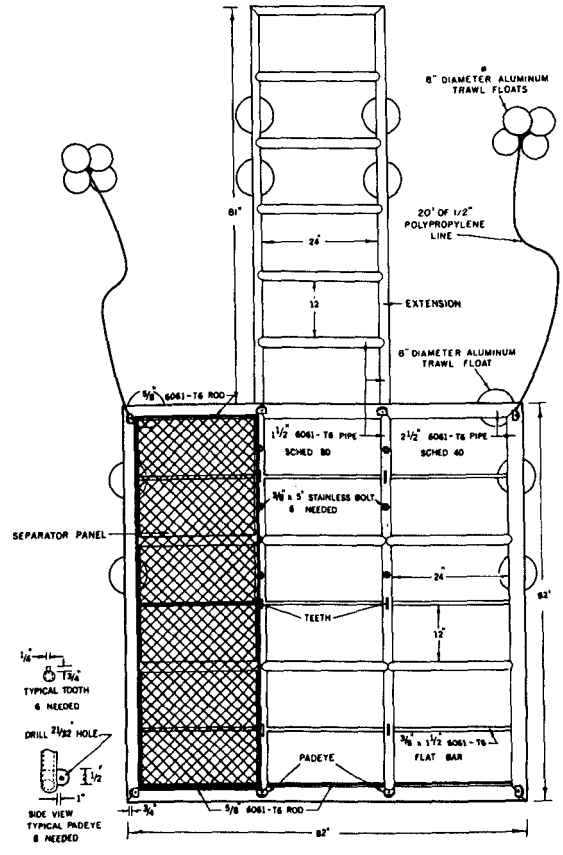

FIGURE 1.—Construction specifications for the shrimp sampler and extension.

The individual collector bags were emptied at the conclusion of each tow and the contents labeled and frozen. In the laboratory shrimp were thawed and the weight, the carapace length (base of eyestalk to the dorsal posterior margin of the carapace), and sex recorded.

PRELIMINARY EVALUATIONS OF THE SAMPLER

Scientist-divers first appraised the shrimp sampler in Puget Sound as it was being towed on bottom in 8 fm of water at 2½ knots. On each of eight tows the sampler was reported to

[2] All mesh sizes in this paper are stretched measure.

[3] The following mesh and thread sizes and materials were evaluated: 1¼-inch mesh, 9 thread, nylon and acetate; 1½-inch mesh, 15 thread, nylon; 1¾-inch mesh, 18 thread, nylon; 2-inch mesh, 12 thread, nylon; 2½-inch mesh, 21 thread, nylon; 3-inch mesh, 18 thread, nylon.

be upright, stable, less than 3 inches off the seabed, and perpendicular to the direction of tow.

Fishing trials were then conducted on populations of pink shrimp and spot shrimp, *Pandalus platyceros*, in 40-60 fm of water in Dabob Bay, Wash. Most shrimp were taken near the seabed (Figure 2), but substantial numbers of pink shrimp were taken as high as 5 to 6 ft off bottom, whereas no spot shrimp were found higher than 3 to 4 ft. This phenomenon was interpreted as a behavioral difference between the two species rather than a difference due to physical size as one might expect the larger spot shrimp to jump higher off the seabed.

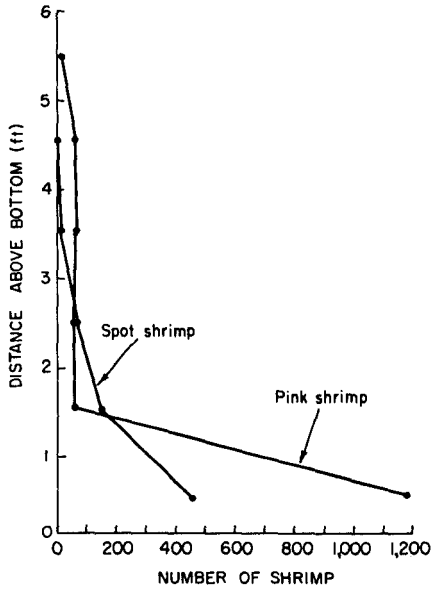

FIGURE 2.—Vertical distribution of pink and spot shrimp taken in four tows in Dabob Bay, Wash. Numbers of shrimp are totals for the 1-ft intervals.

Subsequent fishing trials with the shrimp sampler were conducted on pink shrimp beds of commercial importance off Grays Harbor, Wash. A total of nine tows were made without separator panels and nine with 2-inch mesh across the front of the sampler. Total weights and carapace lengths for shrimp in all sampler openings in each of the vertical columns for each fishing mode were pooled (54 samples). The means for these data are presented in Table 1.

These data were further analyzed using a three-way factorial analysis of variance with the three main effects being vertical columns and horizontal rows of the sampler and repetitive tows (Table 1). In tows without separator panels the weights of shrimp in vertical columns were significantly different ($F = 3.24$), but a comparison of starboard and port vertical columns revealed their difference was not significant ($F = 0.430$) at the 5% significance level. The average of starboard and port colmns for shrimp weight was significantly different from weights for the center column ($F = 6.06$). Analysis of the data for carapace length of shrimp without separator panels and for both shrimp weight and carapace length with 2-inch separator panels indicated no significant difference

TABLE 1.—Comparison of pink shrimp caught with and without 2-inch mesh separator panels on the front of the shrimp vertical distribution sampler. Means and F values were computed from 54 samples (i.e., six vertical openings over a nine-tow repetition).

Type of comparison	Degrees of freedom	Critical F value at 5% significance level	Without panels		With 2-inch panels	
			Weight	Length	Weight	Length
Mean[1]						
Starboard column			178.0	18.2	81.2	18.1
Middle column			156.0	17.9	83.3	17.8
Port column			172.0	18.3	86.6	19.9
F value						
All vertical columns	2,80	3.11	3.24	[2]1.20	[2]0.529	[2]0.699
Middle vs. ½(starboard + port)	1,80	3.96	6.06	[2]2.32	[2]0.017	[2]0.831
Starboard vs. port	1,80	3.96	[2]0.430	[2]0.074	[2]1.04	[2]0.56
Horizontal rows	5,80	2.33	10.4	6.28	4.65	3.78
Repetitive tows	8,80	2.05	52.0	5.81	15.0	4.71

[1] Weight in grams; length in millimeters.
[2] Not significantly different at 5% significance level.

between vertical columns. Since the differences in shrimp catches between port and starboard vertical columns were not significant during tows either with or without separator panels, later comparisons of the effect of mesh size on shrimp catches were made between the starboard and port vertical columns.

As might be expected, significant differences were evident for both horizontal rows on the sampler and repetitive tows. The differences in shrimp vertical distribution (horizontal rows) are discussed later in the paper. Differences in catch during repetitive tows were anticipated as shrimp samples were collected over several months on several shrimp beds.

DAYTIME VERTICAL DISTRIBUTION OF SHRIMP

In March 1969 a series of eight tows were made with the shrimp sampler in 71 fm off Destruction Island, Wash. Principal objectives were to determine if differences in number and size composition of shrimp would occur with increasing height off bottom. Four hauls were made without separator panels and four hauls with uniform 2-inch mesh across the front of the sampler. The greatest number of unmarketable (less than 15-mm carapace length) and marketable (15-mm carapace length or greater) shrimp were taken in sampler openings near the seabed. The ratio of marketable to unmarketable (pinhead) shrimp increased with distance off bottom (Figures 3 and 4). The relationship between distance off bottom and length-frequency of shrimp is shown in Figure 5 for the same series of tows. This figure indicates that shrimp were most abundant near the seabed and a high percentage were small.

Additional tows with the sampler under a variety of conditions (weather, time of day, season)

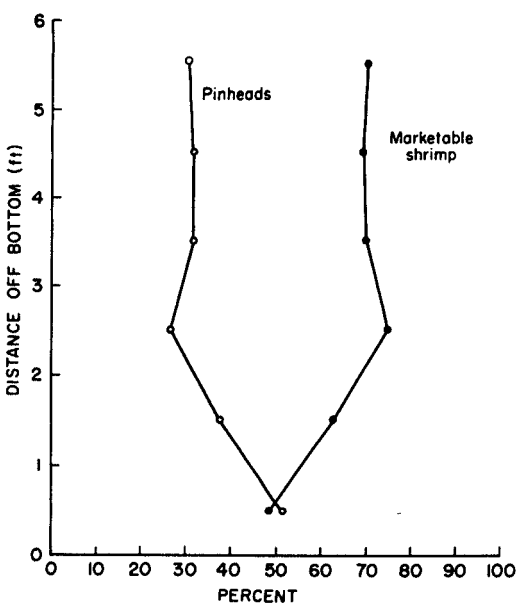

FIGURE 3.—Percentages of pinheads (shrimp less than 15-mm carapace length) and marketable shrimp in catches off Destruction Island, Wash., taken by the shrimp sampler without separator panels (four tows). The percentages indicate the percent composition at each 1-ft interval. Total weights for both pinhead and marketable shrimp increased near the seabed.

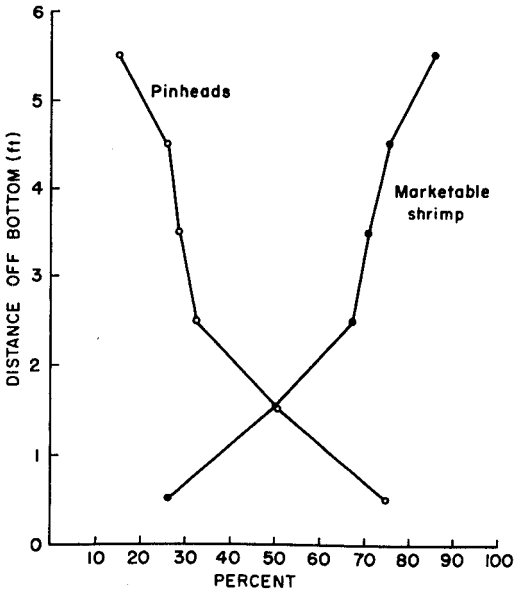

FIGURE 4.—Percentages of pinheads (shrimp less than 15-mm carapace length) and marketable shrimp in catches off Destruction Island, Wash., taken in four tows of the shrimp sampler with separator panels. The percentages indicate the percent composition at each 1-ft interval. Total weights for both pinhead and marketable shrimp increased near the seabed.

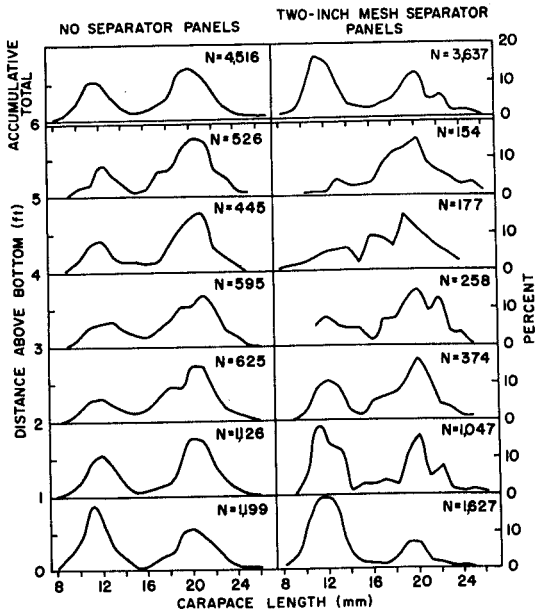

FIGURE 5.—Relation of length frequency of shrimp to distance off bottom for shrimp sampler tows off Destruction Island, Wash. Four tows were made with no separator panels and four with 2-inch separator panels. N is the total number of shrimp taken in the sampler openings with the cumulative totals for four tows shown at the top of the figure.

indicated the vertical distribution of shrimp is not static but subject to dynamic changes, often in a brief period of time. Representative midmorning tows for three different days are presented in Figure 6. Widely divergent shrimp distributions are evident in this figure. The most rapid alteration in shrimp distribution was observed between midmorning tows on 22 and 23 June (Figure 6). Over the same time period the weather changed from partly cloudy to complete overcast with rain. Commercial shrimp fishermen trawling on the same shrimp grounds reported a reduction in shrimp catches accompanying the change in cloud cover. As commercial shrimpers drag their trawls on bottom regardless of weather, it is conceivable that their nets were passing under large numbers of shrimp. During sunny weather with relatively clear water, shrimp were found concentrated near the seabed as on 9 August in Figure 6.

DIEL MOVEMENTS OF SHRIMP

Diel variations in shrimp distribution were investigated with the sampler during three day-night cycles using the shrimp sampler. All tows were 15 min in length and were made with 2-inch separator panels on the sampler. During any single diel cycle, all tows were made in the same direction and in the same location as indicated by the vessel's compass, depth sounder, and loran.

Vertical distributions for pink shrimp collected during three diel cycles are presented in Figure 7. Tows on 24 March were conducted under a cloudless sky with the greatest quantity of shrimp taken early in the day. Greatly reduced catches were taken at night. In general, shrimp appeared to be higher above the seabed during early morning and evening tows.

The weather preceeding 28 March was overcast with rain. Tows during 28 March (Figure 7) indicated shrimp were not plentiful near the

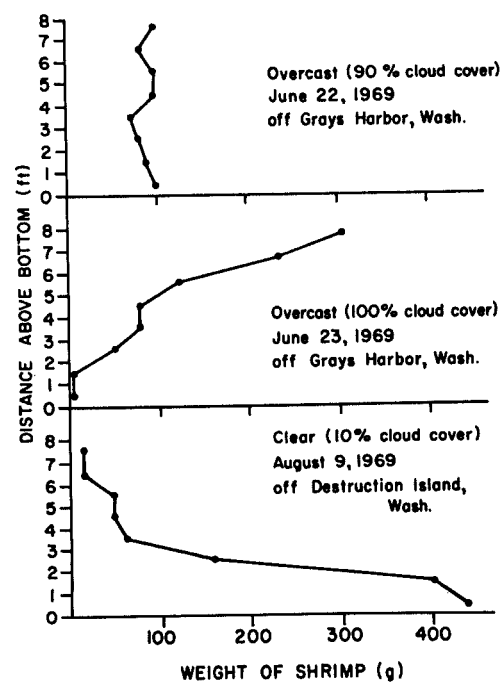

FIGURE 6.—Examples of three widely divergent shrimp vertical distribution patterns in the shrimp sampler on three different tows.

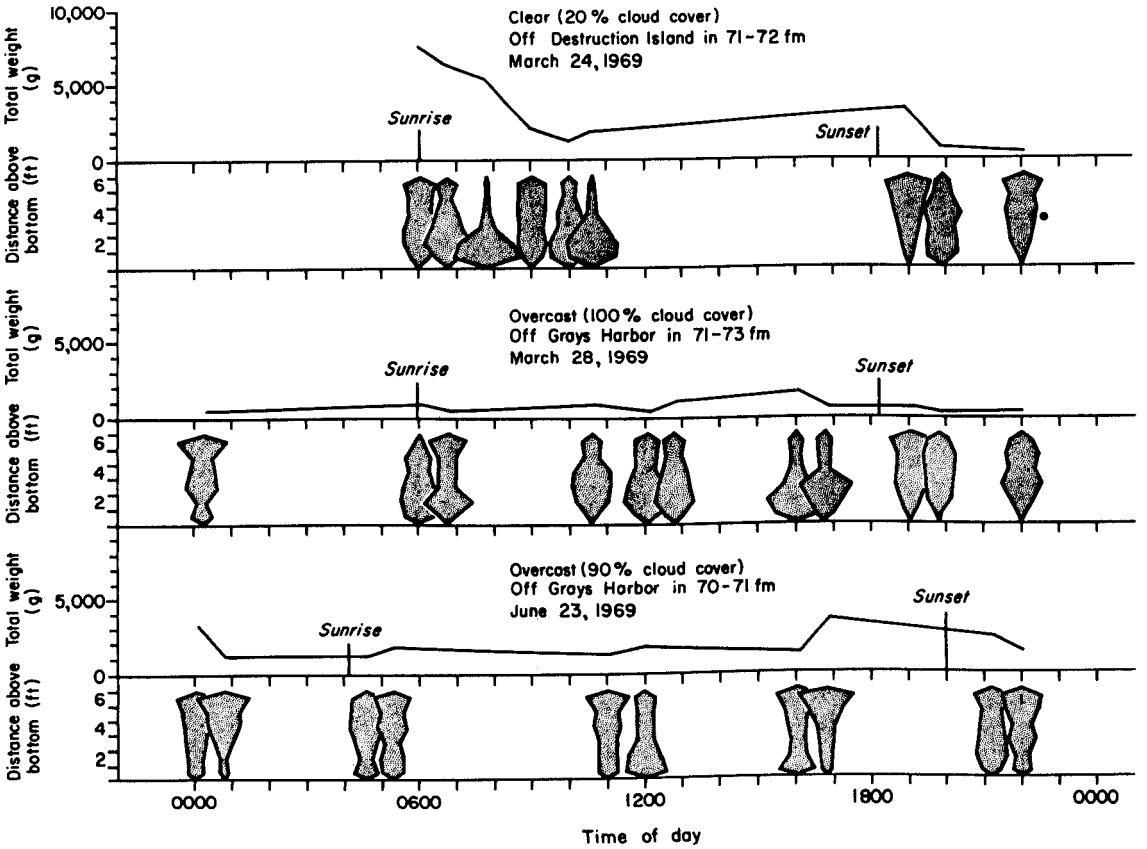

FIGURE 7.—Three different diel distributions of pink shrimp collected with the shrimp sampler. The varying width of each diagram represents the percentage proportion of the catch taken at various distances from the bottom of the sampler.

seabed. The greatest quantity of shrimp were taken during the day.

The tows on 23 June presented a valuable opportunity to observe the changes in shrimp vertical distribution accompanying a change in cloud cover. The 2 days preceeding 23 June were sunny. Tows with the shrimp sampler on these days indicated shrimp were concentrated near the seabed during daylight hours. Commercial fishermen working near the sample station were making good catches of shrimp.

On the evening of 23 June a zone of low barometric pressure moved into the area with resulting cloud cover and rain squalls on 23 June. Catches by commercial fishermen dropped to a fraction of those taken on previous days. The vertical distribution sampler indicated shrimp were well off bottom (Figure 7) with reduced shrimp abundance, compared with tows made on previous days. A most interesting situation occurred during tows made in twilight and after dark as the catch rates were much higher than in tows made in the preceeding daylight hours.

MESH SIZE EVALUATIONS

The effect of mesh size on the movement of shrimp was investigated by placing web of two different sizes on separator panels over the port and starboard vertical columns. A total of six different mesh sizes were evaluated in this manner. Two-inch mesh was placed over the center

TABLE 2.—Comparison of pink shrimp caught behind separator panels of differing mesh size. Means and F values were computed from 24 samples (i.e., six vertical openings over a four-tow repetition).

Item				F value		
				All vertical columns[1]	Middle vs. ½(starboard + port)[2]	Port vs. starboard[2]
Mesh size (inches)	1.0	2.0	1.5			
Mean weight of shrimp (g)	27.6	329.3	112.7	190.0	202.0	16.3
Mean length of shrimp (mm)	14.7	16.9	17.6	13.2	[3]2.03	24.3
Mesh size (inches)	1.75	2.0	2.0			
Mean weight of shrimp (g)	166.8	225.7	243.7	11.4	[3]1.98	20.9
Mean length of shrimp (mm)	19.1	19.1	19.2	[3]0.605	[3]0.330	[3]0.870
Mesh size (inches)	2.5	2.0	3.0			
Mean weight of shrimp (g)	231.3	222.0	260.7	9.67	[3]2.60	4.71
Mean length of shrimp (mm)	19.4	19.3	19.2	[3]0.948	[3]0.013	[3]1.88

[1] The F value at the 5% significance level is 3.32 with 2 and 30 degrees of freedom.
[2] The F value at the 5% significance level is 4.17 with 1 and 30 degrees of freedom.
[3] Not significantly different at 5% significance level.

vertical column as a control or index of the relative abundance of shrimp available.[4] The positions of the separator panels being evaluated (port and starboard) were switched after each set of two tows, and tow direction was altered 180° after each haul. This was done to reduce any sampling bias attributable to one side of the sampler or the other. Two different mesh sizes were compared over four consecutive tows.

The relationship between mesh size and the catch of shrimp as determined by tows with the shrimp sampler is shown in Table 2. The mean sample weight of shrimp catches increased directly with the mesh size, but the rate of increase diminished in mesh sizes above 2 inches. Differences between the total weight of catches taken with 2½-inch mesh and 3-inch mesh were significant ($F = 4.71$), but difference in the mean weights (231.3 and 260.7 g) for these mesh sizes was less than the differences between the means for 1-inch and 1½-inch mesh (27.6 and 112.7 g) and for 1¾-inch and 2-inch mesh (166.8 and 243.7 g). These differences are also suggested by the computed F values in Table 2. Figure 8 shows this relation between mesh size and catch from the data in Table 2. In this figure mean weight and carapace length (means) of shrimp catches for the six different mesh sizes have been converted into a percentage of the weight and length (means) taken by the center vertical column (control) with its standard 2-inch mesh separator panel.

In contrast, the mean carapace length of shrimp did not differ significantly with increasing mesh sizes above 1½ inches (Table 2 and Figure 8). This indicates that the larger shrimp are able to pass readily through the 1½-inch mesh if the meshes are open and held at right angles to the current. Meshes in the intermediate and cod end of conventional west coast shrimp trawls are 1½- to 1⅝-inch mesh. However, shrimp do not pass through these meshes in large quantities because the meshes are normally partially closed and nearly parallel with the current (High et al., 1969).

EFFECT OF TICKLER CHAIN ON SHRIMP CATCHES

Commercial shrimp fishermen in the northeastern Pacific commonly employ a contrivance called a "tickler chain" to excite shrimp off bottom in an effort to increase their catches. This chain is several feet shorter than the trawl footrope with the ends attached to the ends of the foot rope. In this configuration the tickler chain

[4] In the situation where small mesh sizes (i.e., 1¼ and 1½ inches) were being compared on the lateral vertical openings of the sampler, there is the possibility that shrimp catches in the center vertical opening (2-inch mesh) would be proportionally greater than when larger mesh sizes (i.e., 2½ and 3 inches) were being compared. The likelihood of shrimp avoiding the small mesh was considered remote on the basis of diver observations of fish pinned against the web in the separator panels and the presence of large numbers of gilled shrimp in small-mesh web on the separator panels at the conclusion of a tow.

TABLE 3.—Shrimp catches with and without a tickler chain attached to the shrimp vertical distribution sampler.

Location	Date	Time	Depth (fm)	Shrimp catch (g)	
				Without tickler chain	With tickler chain
Off Grays Harbor, Wash.	6-23-69	1150-1205	73	2,270	
		1256-1311	73		4,561
		1345-1400	73	3,208	
		1425-1440	73		8,198
		1515-1530	73	3,696	
		1610-1625	73		4,081
Off Destruction Island, Wash.	6-24-69	0915-0930	76	221	
		0958-1012	76		889
		1040-1055	76	4,064	
		1125-1140	76		1,276
	8-29-69	0655-0710	66	3,376	
		0820-0835	66		9,983
		0915-0930	66	3,451	
		1000-1015	66		8,900
	11-13-69	0903-0918	69	1,887	
		1000-1015	69		5,364
		1103-1118	69	1,942	
		1232-1247	69		3,906
		1327-1342	69	1,230	
		1415-1430	69		912
		1508-1523	69	1,569	
		1605-1620	69		3,574
			Total	26,914	51,644

precedes the footrope as the net is being towed on bottom. Even though the tickler chain is accepted and used by most shrimp fishermen under the assumption that it increases catches, very little is known about the effect of this chain on either the quantity of shrimp caught or the vertical distribution of shrimp as they enter the trawl.

Utilizing the unique features of the shrimp sampler, a brief examination of the effects of tickler chain on shrimp height distribution was undertaken. Unwanted fish and debris were eliminated from the shrimp catches by placing 2½-inch mesh webbing on separator panels over the entire face of the sampler. On alternate tows a length of ⅜-inch tickler chain was placed 2½ ft in front of the bottom of the sampler. All comparative tows were made in the same direction and over the same track line as determined by loran, compass, and depth sounder. Over a 4-month period 22 comparative hauls were made in this manner.

Table 3 shows the catch of shrimp by weight for these tows. Aggregate catches with the tickler chain were nearly twice as great as those without the chain. Summation of the total shrimp weights for each sampler height revealed that when the tickler chain was used, a greater proportion of shrimp were taken in the lower sampler openings in contrast to higher distribution without the chain (Table 4). The effects of a tickler chain on the size distribution of shrimp were also examined. The carapace lengths from shrimp in 200-g samples from each sampler opening were measured. These data indicate that at all distances off the bottom, there

TABLE 4.—Comparison of shrimp catches at various distances off the bottom in the shrimp vertical distribution sampler with (+) or without (—) the tickler chain. These data were computed from the 22 tows presented in Table 3.

Distance off bottom (ft)	Weight (g)			Percent of catch for each height interval	
	—	+	+/—	—	+
1	5,478	15,594	2.8	13.2	30.2
2	6,368	17,064	2.8	11.9	33.0
3	4,859	8,047	1.7	12.8	15.6
4	3,445	4,159	1.2	18.1	8.0
5	3,211	3,375	1.1	23.7	6.5
6	3,555	3,465	1.0	20.3	6.7
			Total	100.0	100.0

was no significant difference between sample means for shrimp carapace lengths in catches made with or without the tickler chain (Table 5).

TABLE 5.—Comparison of mean carapace length of shrimp (computed from 200-g samples) taken in the shrimp vertical distribution sampler with (+) or without (−) the tickler chain. These data were computed from the 22 tows presented in Table 3. The F value at the 10% significance level is 2.79 with 1 and 64 degrees of freedom.

Distance off bottom (ft)	Mean carapace length (mm)		F value
	−	+	
1	16.2	16.7	0.856
2	16.7	17.0	0.616
3	17.1	17.3	0.299
4	17.2	17.6	0.830
5	17.3	17.1	0.092
6	17.5	17.3	0.133

DISCUSSION

Confidence in the shrimp sampler as a research tool capable of indicating the height of shrimp near the seabed resulted from diver observations, trial tows in Dabob Bay, and statistical evaluations of catches made on offshore shrimp grounds. Neither daylight distributions of shrimp off the seabed nor abrupt changes in vertical distributions were expected. The parameters responsible for changes in distribution were not investigated, but other papers (Schaefers and Johnson, 1957; Schaefers and Powell 1958; Alverson, McNeely, and Johnson, 1960; Pearcy, 1970) indicate pink shrimp follow diel or circadian movements which may be triggered by changes in light levels. Similar differences in illumination during daylight hours may be the cause of more subtle alterations in shrimp distribution near the seabed. Tows with the shrimp sampler indicated shrimp were further from the bottom during daytime tows under overcast skies. Commercial fishermen using bottom trawls commonly report reductions in shrimp catches when they encounter turbid water and overcast weather, or both.

This evidence suggests changes in catch rates for pink shrimp are not due entirely to endogenous factors as their distribution appears to change in direct response to light intensity regardless of the time of day. Exogenous rhythmicity in crustaceans has been demonstrated previously by Skud (1968) where during a total eclipse of the sun over Maine in July 1963, crustaceans exhibited a variety of responses from no response to movements toward or away from the surface at totality. Data collected with the shrimp sampler suggest pink shrimp will move off bottom during the day (probably to feed) if the light intensity is reduced enough to present some protection from predators. These movements may also be directly associated with migrations of prey. One explanation for relatively dense concentrations of shrimp near the seabed at night during overcast weather is that these shrimp were able to come off the bottom during the day to feed and returned to the seabed when they became satiated.

The shrimp sampler indicated the highest proportion of small shrimp occur near the seabed. Commercial fishermen could avoid these shrimp by "flying" their nets 2 ft off bottom, but this strategy would also eliminate significant numbers of large shrimp from the catch. Separation and release of small shrimp once they enter the trawl is a difficult if not impossible task. Experiments with the shrimp sampler indicated that the mesh size necessary to segregate shrimp by size is extremely critical even in fully opened meshes at right angles to the current (Figure 8). The problem is compounded in a trawl where few meshes are fully opened and their orientation to the current varies. Moreover large numbers of shrimp are swept in mass into the trawl cod end and may never encounter trawl meshes. These factors reveal the futility of shrimp trawl mesh size restrictions when the design of the trawl is not considered.

Mesh size comparisons indicate that the optimum mesh size for separator panels in shrimp separator trawls should be 2 inches (Figure 8). Smaller mesh would reduce the catch of shrimp, and a larger mesh size would not appreciably increase the size or catch of shrimp captured but could introduce more contaminating organisms into the catch. These results compare favorably with fishing trials of shrimp separator trawls with different mesh sizes in the separator panel. Two-inch separator panels are now standard in this gear.

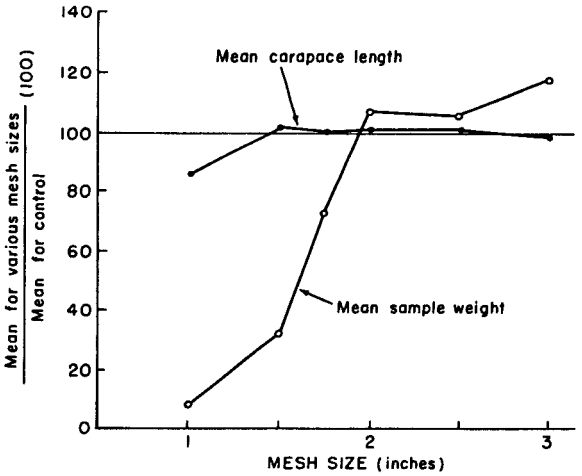

FIGURE 8.—Relationship between mesh size of separator panel and the means of shrimp length and total weight. The values for the mean carapace length and mean sample weight are compared with the shrimp catches (means) taken behind the 2-inch mesh separator panels (control).

The tickler chain caused a significant increase in the number of shrimp entering the lower portion of the shrimp sampler. This phenomenon suggests that the tickler chain either excites shrimp into the water column that normally would pass under the sampler or confuses shrimp so that they are unable to avoid the sampler. The fact that pink shrimp can be readily taken in a plankton sampler with an opening 15 cm in diameter indicates that avoidance may not be an important consideration. The major effect of the tickler chain is probably to move shrimp vertically where they are vulnerable to capture by the trawl.

The utility of the shrimp sampler in describing the vertical distribution of shrimp suggests that it would be a valuable tool for providing supportive evidence necessary for sound management decisions regarding shrimp resources. For example, in California, trawl surveys of the shrimp beds are used to estimate the quantity and quality of shrimp available and hence establish the quota size (Abramson, 1968). These analytical estimations of the standing stock of a shrimp bed are based on the assumption that catch per unit of effort is a function of stock density in the area being surveyed and that changes in catch per effort are directly proportional to changes in density (Ricker, 1958; Gulland, 1964). Equations relating population size to catch per effort for trawl gear (Alverson and Pereyra, 1969) require some knowledge of the vulnerability of shrimp within the influence of the trawl and the proportion of the total shrimp stock in the water column sampled by the trawl. Estimates for vulnerability of shrimp have traditionally been placed near 1 largely because of a lack of knowledge regarding the behavior of shrimp to trawls. With consideration of the size of the trawl opening and the erratic escape movements of shrimp, a vulnerability coefficient of 1 may be relatively accurate. However, use of the shrimp sampler has shown that the coefficient of catchability for a shrimp trawl which is towed a constant distance off bottom may vary dramatically from day to day. Often the catch coefficient would not approach 1 for a trawl having a 4-ft vertical opening. Thus the overall coefficient, which is a product of the vulnerability and catchability coefficient, may at times be considerably less than 1 if shrimp are being sampled with a conventional shrimp trawl. Moreover, the value for the overall coefficient would vary from day to day and reduce the accuracy of population size estimates. The tickler chain must also have an important effect on the vulnerability coefficient, but this relation has not been explored.

The greatest utility of the shrimp sampler in providing estimates of standing stock may be realized when the sampler is towed alternately with a standard trawl. This approach has been taken by scientists at the Auke Bay Fisheries Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, Alaska (James Olson, pers. comm.) where estimates were being made of the standing stock of shrimp in Kachemak Bay, Alaska. In this instance the sampler was used to determine the catchability coefficient of the standardized shrimp trawl used in the standing stock estimates.

The sampler has also been towed alternately with trawls in an experiment to measure the fishing power of four dissimilar shrimp trawls near Kodiak, Alaska (Lael L. Ronholt, North-

west Fisheries Center, National Marine Fisheries Service, NOAA, Kodiak, Alaska, pers. comm.) Biologists from the Fish Commission of Oregon (Jack G. Robinson, per. comm.) now insert a modified sampler, 2 ft wide by 9 ft tall, in the mouth of a conventional 41-ft Gulf shrimp trawl to achieve estimates of trawl efficiency.

ACKNOWLEDGMENTS

The enthusiastic support and advice of Richard M. McNeeley, Manager of the Conservation Engineering Program in the Division of Marine Fish and Shellfish, Northwest Fisheries Center, Seattle, Wash., are gratefully acknowledged. Donald D. Worlund, Division of Fisheries Data and Management Systems, Northwest Fisheries Center, Seattle, helped in the statistical evaluation. I also thank Robert P. Larsen, Skipper, and the crew of the NMFS research vessel *John N. Cobb* and Olaf Engel, Skipper of the chartered vessel *Baron*, for aid in the collection of shrimp samples.

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A REVIEW OF THE CHEMICAL AND NUTRITIVE PROPERTIES OF CONDENSED FISH SOLUBLES

JOSEPH SOARES, JR.,[1] DAVID MILLER,[2] SUSAN CUPPETT,[2] AND PAUL BAUERSFELD, JR.[2]

ABSTRACT

This paper attempts to review some of the pertinent data available on the chemical and nutritive properties of condensed fish solubles with special reference to condensed menhaden solubles. Information concerning other kinds of fish solubles from various published sources is tabulated for comparison. The results of three analytical and three biological studies of menhaden solubles are reported.

Data show that menhaden stickwater contains an average of 4.8% protein, 93.4% water, and about 1.25% lipid. The solids are concentrated about seven times by vacuum evaporation to yield condensed solubles. Data show that this product contains about 32% protein, 49% water, and 11% fat. Additional data are presented on the content of amino acids in fish solubles, which show that the indispensable amino acid tryptophan is relatively low and, on the content of essential inorganic elements which are shown to be present, generally in acceptable levels. Fish solubles are shown to be rich sources of choline, niacin, pantothenic acid, riboflavin, biotin, and vitamin B_{12}.

An experiment with broiler chicks showed that the average metabolizable energy content of 10 samples of condensed menhaden solubles from commercial plants located along the Atlantic and Gulf coasts was 2.03 kcal/g on an "as fed" basis. Average protein and fat digestibility was 89 and 57%, respectively.

Further studies with broiler chicks showed that significant unidentified growth factor responses could be obtained when 5% menhaden solubles was used in diets. A significant response was obtained even when the chicks were reared in a gnotobiotic environment. This indicates that the presence of bacteria is not necessary for solubles to produce a growth response in chicks.

This review attempts to discuss some of the more pertinent recent published and unpublished data available on the chemical and nutritive properties of condensed fish solubles. For many years stickwater was considered as a waste effluent and was not used in animal feeds or in other manufacturing processes. However, with the postwar surge in production of fish meal, this by-product began to be recognized for its nutritional value. In the presynthetic nutrient era, condensed fish solubles was recognized as an outstanding source of B vitamins and minerals for poultry and swine. Later, solubles was the principle source of the "animal protein factor" or vitamin B_{12}. Today we still consider condensed fish solubles to be valuable for these purposes, but now more emphasis is put on its unidentified growth factor content.

There are various sources and kinds of condensed fish solubles available in the United States. However, about 80% of the solubles used in this country are produced by the menhaden reduction industry located along the Atlantic and Gulf coasts. Since 1963, the quantity of solubles available for animal feedstuff supplementation in the United States has averaged about 90,000 tons annually.

However, because of the difficulty in handling, storing, and mixing the viscous condensed fish solubles, a considerable quantity of this product is dehydrated on a carrier to produce a free-flowing dry product. One such product is "full

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Manuscript accepted September 1972.

meal" containing 1 part condensed solubles to 3.5 parts of fish meal. This recombination of the two fish products is a logical approach as it is really equivalent to the original fish minus a major part of the original oil. Numerous other feedstuffs, such as soybean meal, alfalfa meal, or wheat middlings are also used to produce a free-flowing dry product consisting of one-half carrier and one-half dried condensed solubles.

PROCESS METHOD

Condensed fish solubles is one of two by-products produced by the wet reduction of whole fish to fish meal. Briefly, the production of condensed fish solubles by the "wet reduction" process involves cooking whole fish (e.g., menhaden) and subjecting the cooked fish to screw-type presses. The liquid fraction which passes through the screens of the presses is collected and separated by first passing through a vibrating screen to remove suspended material. The remaining liquor is either pumped into settling tanks for gravity separation or, more commonly, centrifuged to separate the oil and aqueous portion. Usually the centrifugation system consists of a three-phase centrifuge designed to separate oil, water, and suspended material. The aqueous portion in these centrifuges is collected in large storage tanks. During this storage process usually a quantity of sulfuric acid, or occasionally phosphoric acid, is added to the stickwater until a pH of 4.5 is reached (normal pH 6-7.0). The storage tanks are heated by steam coils to a temperature of approximately 150°F for 30 min to coagulate the proteins. The suspended and coagulated proteins are removed by centrifuges, and the free oil is removed by oil-separating centrifuges. The solid materials are dried on press cake and the liquid is called "stickwater." Table 1 shows the composition of several samples of stickwater produced in 1970. These samples contained an average of about 7% total solids and about 5% protein. The amino acid profile indicates that this protein is gelatinous in nature because of the relatively high glycine, proline, and alanine content.

Stickwater is then concentrated by means of vacuum evaporation, generally operated in units of three or more. Thus, the terms "triple effect" or "quadruple effect" are applied to the evaporation procedure. The evaporators may be horizontal or vertical, depending on the position of the steam tubes used for heat. Each evaporator consists of a series of tubes, usually vertical, holding the liquor and surrounded by steam. The tubes passing through the evaporator allow the vaporized water to escape at the top, and the partially evaporated product passes to the next unit at a lower position in the evaporator.

These evaporators are subjected to reduced pressure. The first unit is usually heated by low pressure exhaust steam from the boilers and is generally maintained at about 24 inches of mercury pressure (or under a slight vacuum). As the liquor reaches a predetermined concentration, it is drawn into the second unit. The vapors from the boiling liquor in the first unit are passed through the steam tubes of the second, and the liquor continues to boil by increasing the vacuum to about 28 inches of mercury.

In the third stage the process is either completed under a vacuum of about 30 inches of mercury or continued depending on the number of stages employed. When the liquor reaches approximately 50% solids, the process is finished and the solubles are stored. Thus, during the process the original material containing about 93% water is concentrated by a factor of at least seven. Other methods of condensing fish solubles have been and are used but not extensively enough to warrant further discussion here.

TABLE 1.—Chemical composition of Atlantic menhaden stickwater.[1]

Item	Amount	Item	Amount
	%		%
Protein (N × 6.25)	4.82	Valine	2.36
Moisture	93.43	Methionine	1.37
Ash	1.12	Isoleucine	1.59
Total fat	1.26	Leucine	3.34
Ether fat	0.83	Tyrosine	1.02
		Phenylalanine	2.12
	% nitrogen	Tryptophan	0.31
Ammonia	0.034	Taurine	3.55
		Asparctic acid	5.20
	% of protein	Serine	2.31
Lysine	4.45	Glutamic acid	8.22
Histidine	4.19	Proline	5.10
Arginine	1.89	Glycine	10.45
Threonine	2.06	Alanine	5.86

[1] Values are averages of data from three analyses.

TABLE 2.—Analytical data on condensed solubles.

Item	Menhaden solubles	Pacific sardine solubles	
	Lee (1956)	March (1962)	Lassen et al. (1951)
Dry solids, %	47.6 ± 3.5	50.3	50.0
Crude protein, % (N × 6.25)	33.5 ± 2.7	33.7	32.0
Ammonia, %	1.3 ± 1.1	--	--
Corrected protein,[1] %	27.2 ± 3.8	--	--
Fat, %	6.4 ± 3.2	4.3	7.0
Total ash, %	9.2 ± 2.0	9.2	12.0
Water-insoluble matter, %	4.5 ± 1.6	--	--
Water-insoluble ash, %	0.28 ± 0.21	--	--
pH	4.64 ± 0.54	4.5	--
Specific gravity	1.19 ± 0.03	1.2	--
Number of samples	32	?	?

[1] Corrected for ammonia-nitrogen 5.15.

COMPOSITION OF CONDENSED FISH SOLUBLES

Analytical data (Table 2) published by Lee (1956) showed that condensed fish solubles contained approximately 50% dry matter, which included protein (Kjeldahl nitrogen × 6.25), fat, minerals, and vitamins. According to the above author the major variable factors affecting composition were species and age of the fish, season and location of the catch, handling techniques, and type of plant equipment used during processing. Data describing other types of fish solubles produced in the United States are very scanty. However, Table 2 lists some average results for herring solubles reported by March (1962) and Lassen, Bacon, and Dunn (1951), and these appear very similar to the menhaden data.

Table 3 shows the proximate, total fat, and ammoniacal nitrogen composition of 24 condensed menhaden fish solubles samples collected during 10 months of the 1969 fishing season (Soares, Miller, and Ambrose, 1970). These samples were obtained from seven different fish meal plants located along the Middle Atlantic and Gulf coasts, and they represent regular commercial production. The methods for proximate analyses were all standard AOAC (Association of Official Analytical Chemists) methods except total fat, which is a chloroform-methanol extraction method of Bligh and Dyer that was modified by Smith, Ambrose, and Knobl (1964). Since the data from the Atlantic and Gulf samples did not differ significantly (although they are made from two different species of menhaden), it is presented together as an average. In general, these analyses indicate that the solids content is slightly more than 51%. The average concentration of protein (Kjeldahl N × 6.25) was 31.8% and that of ash was 7.8%. If these values are converted to a dry basis, they are very similar to those for menhaden fish meal reported by Kifer and Payne (1968) and Kifer, Payne, and Ambrose (1969). This is not to say that dried fish solubles is equivalent to fish meal in protein quality, but this only points out the relatively high protein content of this material even after allowing for nonprotein nitrogen (Table 3). The fat content, expressed on a dry basis is somewhat higher, however, than that found in fish meal. Ammoniacal nitrogen (which included volatile amines, etc.) makes up about 0.5% of the total nitrogen.

TABLE 3.—Proximate composition, total fat, and ammoniacal nitrogen content of menhaden fish solubles.[1]

Analyses	Average of 24 samples
	%
Protein (N × 6.25)	31.8 ± 2.52
Ash	7.8 ± 0.93
Ether fat	8.9 ± 2.13
Total fat	11.2 ± 2.09
Moisture	48.7 ± 2.18
Ammonia as % N	0.5 ± 0.23

[1] Soares, Miller, and Ambrose (1970).

PROTEIN

Biologically, the protein in solubles is considered inferior in quality because of its high content of gelatin, derived from fish collagen, which is low in the sulfur amino acids and almost completely devoid of tryptophan. Therefore, the essential amino acids content of the protein in condensed fish solubles is not adequate as a sole source of protein for the growth of chicks because tryptophan is deficient and the content of the other essential amino acids in condensed fish solubles is lower than that found in fish meal. Nevertheless, the protein may serve very well in a diet as a minor supplementary protein or in a diet otherwise adequate in amino acids since a 3% level of fish solubles contributes only 1% protein to the total diet.

AMINO ACIDS

Table 4 lists the amino acid composition of menhaden fish solubles published by Soares et al. (1970) and shows that solubles do contain some of the amino acids in reasonably high amount. All amino acids except available lysine, tryptophan, and cystine were analyzed by ion exchange column chromatography. Available lysine was determined by the method of Carpenter (1960). Tryptophan was determined by the method of Spies and Chambers (1948), and cystine was analyzed by a microbiological assay.

It is noteworthy that cystine averaged 1.05% of protein, which is slightly higher than the 0.9% of protein found in menhaden fish meal (Kifer and Payne, 1968). Glycine, an important amino acid in poultry rations since it is necessary for maximum growth of chicks, is the only other essential amino acid found in fish solubles at levels higher than in fish meal. As mentioned earlier, tryptophan is the first limiting amino acid based on chemical composition. Available lysine averaged about 83% of total lysine which is similar to the fish meal values that we have obtained. The taurine content is also shown, inasmuch as a recent report by Monson (1969) indicates that this amino acid may be one of the unknown growth factors. Table 4 also shows the amino acid composition of sardine and herring solubles. For the most part these data are similar to menhaden. However, some large differences exist in the histidine levels which are not explainable.

TABLE 4.—Amino acid content (% of protein) of various kinds of condensed fish solubles.

Amino acid	Menhaden solubles	Herring solubles[1]	Pacific herring solubles	Pacific sardine solubles
	Soares et al. (1970)	Laksesvela (1954)	Ewing (1963:291)	Lassen et al. (1951)
	% of protein			
Arginine	3.9 ± 0.65	5.2	4.5	4.3
Histidine	2.5 ± 0.80	0.7	6.0	5.8
Lysine	4.8 ± 0.56	4.3	4.3	4.9
Tyrosine	1.1 ± 0.20	0.7	--	--
Tryptophan	0.3 ± 0.07	0.1	0.4	0.4
Phenylalanine	2.1 ± 0.27	1.5	3.2	2.3
Methionine	1.6 ± 0.17	1.4	1.5	1.5
Cystine	1.1 ± 0.28	0.1	0.3	--
Threonine	2.1 ± 0.25	2.1	1.8	2.4
Leucine	3.7 ± 0.46	3.2	3.0	4.7
Isoleucine	1.9 ± 0.28	1.9	2.3	2.7
Valine	2.7 ± 0.35	2.5	3.4	3.0
Glutamic acid	8.1 ± 0.94	7.5	--	8.4
Glycine	8.7 ± 1.50	10.9	10.9	--
Proline	4.5 ± 0.60	--	--	6.7
Taurine	3.2 ± 0.50	?	--	--
Available lysine	4.0 ± 0.62	--	--	--
No. of samples	24	--	?	?

[1] Unknown origin.

MINERALS

The ash content of condensed solubles averages about 9% and occasionally is as high as 13% of total weight (Soares et al. 1970). The major inorganic elements (Table 5) are P, Na, and K.

TABLE 5.—Inorganic elements content of menhaden fish solubles.[1]

Inorganic elements	Average	Range	
		Low	High
	Percent	— — — *Percent*	— — —
K	1.57 ± 0.18	1.06	1.87
Na	1.14 ± 0.28	0.70	1.67
P	0.56 ± 0.14	0.20	0.80
Mg	0.11 ± 0.03	0.08	0.17
Ca	0.06 ± 0.02	0.03	0.11
	ppm	— — — — *ppm*	— — — —
Fe	573 ± 216.00	210.	1,000.0
Al	194.5 ± 224.00	16.0	640.0
Cu	44.3 ± 49.85	1.0	120.0
Zn	18.1 ± 7.93	4.0	31.5
Ba	5.25 ± 3.85	2.0	15.2
Mn	5.22 ± 3.37	2.0	14.2
Sr	3.73 ± 1.49	1.0	7.2
B	3.05 ± 1.64	1.0	6.4
Cr	2.86 ± 0.30	2.2	3.0
Se	2.4 ± 0.44	1.4	3.6

[1] Soares, Miller, and Ambrose (1970) and Soares and Miller (1970).

Chloride which is not included in Table 5 is also present in amounts about equal to Na. Others that are present in lower amounts include: Mg, Ca, Fe, Al, Zn, and Mn. The trace elements that are found at even lower levels include: Co, I, Ag, B, Ba, Cr, Li, Ni, Rb, Sr, Si, Se, and perhaps others not yet identified. Calcium and phosphorus analyses were determined by the method of Kingsley and Robnett (1958) as adapted for the Technicon. All other elements were determined by emission spectographic analysis.

These data show that the calcium and phosphorus levels are expectedly very low compared to fish meal since the major portion of these two elements are found in the bone which remains with the meal. Most of the other minerals in fish solubles also occur in lower concentrations than in fish meal. Selenium, however, tends to be found in concentrations that are equal to or greater than fish meal. Three minerals—aluminum, copper, and iron—were detected in quite variable concentrations. The average concentration of auminum in all solubles samples is somewhat lower than that reported by Kifer and Payne (1968) for fish meals from both the Atlantic and the Gulf coasts. The aluminum content of solubles from Atlantic coast plants was, however, considerably lower than that of menhaden fish meals, whereas the aluminum content of Gulf coast solubles was somewhat higher. Similar differences in aluminum content (unpublished data) were found in Gulf and Atlantic menhaden fish protein concentrate (FPC) made at the College Park Laboratory, starting with raw fish and using stainless steel equipment under aseptic conditions. Consequently, the higher aluminum content appears to occur in the Gulf species itself rather than as a contaminant after they are caught.

Selenium has become a focal point in trace mineral research since Schwarz and Foltz (1957) and Nesheim and Scott (1958) showed that it is essential for the prevention of dietary liver necrosis in rats and of encephalomalacia, exudative diathesis, and muscular dystrophy in chicks. Thompson and Scott (1968) have suggested that the range of 0.15 to 0.2 ppm is the desirable concentration for selenium in practical poultry diets. As little as 0.05 ppm selenium in the form of sodium selenite, however, has been found to prevent the physiological abnormalities mentioned above.

So far, the Food and Drug Administration has not permitted chemical compounds containing selenium to be added to the rations of livestock. For this reason, natural sources are currently the only available means of supplementing selenium in the diet. Fish meal has been shown to be a rich source of selenium by Kifer and Payne (1968) and Kifer et al. (1969).

A number of samples of fish solubles was obtained from commercial menhaden plants throughout the 1969 fishing season and analyzed for selenium. A total of 38 samples were analyzed—20 from fish meal plants along the Atlantic coast and 18 from plants along the Gulf coast.

Although neutron activation analysis was used to determine the selenium content of the fish meals reported in the above-mentioned papers, we found that this method did not give reliable results with fish solubles. Consequently, a wet

chemical method (Hoffman, Westerby, and Hidiroglou, 1968) was used.

Table 5 shows the average results from all analyses. The data showed that there were higher levels of selenium in the Gulf product than in the Atlantic coast product (2.59 ppm vs. 2.22 ppm) (Soares and Miller, 1970). However, the corresponding fish meals from these two areas (Kifer et al., 1969) did not contain significantly different concentrations of selenium. This observation indicated to us that selenium is present in greater concentrations in the water-soluble portion of fish rather than in the water-insoluble solids, and the higher levels of selenium found in Gulf menhaden fish solubles may reflect leaching from the relatively high selenium soils draining into the Mississippi River or other local environmental conditions. Further research, however, may reveal other explanations for these differences.

Regardless of whether or not Gulf menhaden solubles or Atlantic menhaden solubles are used in feeds, a level of 2-2.5% will supply the minimal level of 0.05 ppm selenium in the diet based on total chemical analysis.

Availability determinations of selenium in fish meal and solubles are now in progress. To date there is some indication that this selenium source is not as available as sodium selenite (Miller and Soares, 1972; Scott, pers. Comm. to Morris and Levander, 1970).

VITAMINS

The fat-soluble vitamins are present in small quantities in condensed fish solubles. In contrast, the contents of the various water-soluble vitamins are at least 50% greater in the condensed solubles than in fish meal. Fish solubles are considered very rich sources for vitamin B_{12}, choline, niacin, and one or more unknown factors.

Table 6 lists data from six reports on the vitamin content of condensed fish solubles. The data are somewhat spotty and are often labeled "condensed fish solubles" with little or no details on its origin. The data are particularly deficient in regards to the fat soluble vitamins, inositol, pyridoxine, and folic acid. However, there seems to be reasonable reliability in the values given for the remaining vitamins. In particular, each kilogram of solubles contains about 4,400 mg of choline, 270 mg of niacin, 38 mg of pantothenic acid, 11 mg of riboflavin, 0.5 μg of biotin, and 440 μg of vitamin B_{12}.

NUTRITIVE VALUE

METABOLIZABLE ENERGY AND NUTRIENT DIGESTIBILITY

Metabolizable energy (ME) is the energy derived from a feedstuff after subtracting from the gross energy value the amount of energy lost

TABLE 6.—Vitamin content of condensed fish solubles.

Vitamin	Source						Average
	1	2	3	4	5	6	
Choline, ppm	4,028.0	--	--	5,300.0	2,960.0	--	4,429.0
Niacin, ppm	169.0	307.0	325.0	230.0	308.0	--	268.0
Pantothenic acid, ppm	35.0	32.3	40.0	45.0	43.1	33.0	37.7
Folic acid, ppm	--	--	--	--	1.3	0.8	1.1
Inositol, ppm	--	--	--	--	352.0	--	352.0
Riboflavin, ppm	14.5	6.9	20.0	7.7	--	4.0	10.6
Pyriodoxine, ppm	--	8.3	--	--	--	34.0	21.2
Thiamine, ppm	5.5	2.9	4.0	--	--	5.0	4.4
Biotin, ppb	0.2	1.3	--	0.3	0.1	--	0.5
Vitamin B_{12}, ppb	--	640.0	--	400.0	550.0	180.0	443.0
Vitamin A, IU/g	--	360.5	--	--	--	5.8	183.0
Vitamin D, IU/g	--	55.0	--	--	--	--	55.0
Vitamin E, IU/g	--	--	--	6.0	--	--	6.0

[1] 1. National Research Council (1968).
2. Hideo, Murayama, and Yanase (1961).
3. Lassen, Bacon, and Dunn (1951).
4. Scott, Nesheim, and Young (1969:440).
5. Ewing (1963:291).
6. Murayama and Yanase (1960).

in the feces and urine. This parameter is universally accepted among poultry nutritionists as a valid estimate of dietary energy content and is very important in formulating least cost poultry rations.

Owing to the limited data available in the literature on the ME value of condensed fish solubles, Cuppett and Soares (in press) have conducted investigations concerning this property. Data were gathered on 10 of the menhaden solubles samples used in the analytical studies discussed earlier. The experimental design with a few modifications for convenience was similar to that used by Potter and Matterson (1960) for various common feed ingredients. In these experiments, eight 3-week-old White Rock broiler cockerels were placed in each battery pen. Each diet was fed to two groups of chicks for 5 days and excreta samples were collected for 3 days. Chromic oxide was incorporated in the diet at the 1% level as a marker. Fish solubles were fed at 0, 5, 10, and 15% levels. Analyses for proximate composition and gross energy were made on all diets and excreta samples.

The average ME value was 2.03 kcal/g which is somewhat higher than the calculated figures usually presented in feed analysis tables. These results are in good agreement with the data reported by Matterson et al. (1965) and Chu and Potter (1969) (Table 7). The ME value of all three reports averages 2.12 kcal/g (962 kcal/lb) with fat and protein digestibilities of 93.2 and 62.0%, respectively. It appears that much of the problem with lower calculated values reported in the various feedstuffs tables is due to underestimating the fat content of fish solubles.

TABLE 7.—Metabolizable energy and protein and fat digestibility evaluations of fish solubles in diets fed to young broilers and turkeys.

Source	Experimental animal	Metabolizamle energy	Fat digestibility	Nitrogen digestibility
		kcal/g	%	%
Matterson et al. (1965)	Chicken	2.094	--	--
Chu and Potter (1969)	Turkey	2.223	97.7	67.2
Cuppett and Soares (in press)	Chicken	2.030 ± 0.23	88.7 ± 2.48	56.2 ± 3.70
Average		2.12	93.2	62.0

UNIDENTIFIED GROWTH FACTOR(S)

The major contribution of condensed fish solubles is the unknown factor necessary for maximum growth of poultry and hatchability of eggs. Considerable evidence has been presented to demonstrate the existence of a stable unknown essential in condensed fish solubles. Combs, Arscott, and Jones (1954) indicated that the growth response obtained with arsanilic acid occurs only in the presence of the fish factors. The so-called fish factor is believed by Tamimine (1955) to be two components: one, organic in nature and the second, inorganic. Similar results were obtained by Steinke, Bird, and Strong (1963).

Combs et al. (1954) also reported a lack of chick growth response from fish solubles fed with penicillin. Similarly, Barnett and Bird (1956) found a lack of response with high levels of chloretetracycline. The conclusion is that the activity of the fish solubles occurs only in the presence of certain intestinal microorganisms. They also obtained no growth response when chicks were in new uncontaminated buildings. Actually, their bioassay method developed for evaluating the fish factor is dependent upon the ingestion of poultry excreta by the chicks on test. This would seem to confirm that beneficial bacteria flourish in the intestines of poultry only in the presence of the fish factor. Similar evidence exists for the essentiality of the fish factor for the hatchability of chicken and turkey eggs. However, there are some contradictory reports. The reason for the differences in the observations has not yet been elucidated.

TABLE 8.—Unidentified growth factor response from various sources of condensed fish solubles.

Reference	Animal	Fish solubles	Experimental period	Types of diet	Growth response
		%	*days of age*		*% of control*
Menge and Lillie (1960)	Chick	2	8-36	Conventional	105.0
Mason et al. (1961)	Chick	2	0-14	Conventional	122.0*
Mason et al. (1961)	Chick	2	0-28	Conventional	107.0*
Mason et al. (1961)	Chick	2	0-14	Purified	107.0
Mason et al. (1961)	Chick	4	0-28	Conventional	115.0*
Harrison and Coates (1964)	Chick	5	0-28	Conventional	113.0*
Harrison and Coates (1964)	Chick	5	0-28	All vegetables[1]	107.0*
Chu (1968)	Turkey	2-5	0-56	Conventional	106.0*
Harrison and Coates (1969)	Germ-free chick	5	0-28	Sterile conventional	104.0
Harrison and Coates (1969)	Conventional chick	5	0-28	Conventional	112.0*
Bhargava and Sunde (1969)	Chick	2	0-7	Purified	109.0*
Bhargava and Sunde (1969)	Chick	2	0-14	Purified	118.0*

[1] Only vegetable sources used.
* Statistically significant ($P<0.05$).

A compilation of recent reports (Table 8) in which the phenomena of unidentified growth factors in condensed solubles were studied brings out several interesting points. First, these data indicate that significant unidentified growth responses are still being observed even when every effort is made to supply all known nutrients in the experimental diets. Secondly, growth response seems to be maximal when the solubles content ranges from 2 to 5% of the diet and when these diets are fed to chicks for 14 to 21 days beginning with day-old birds. Growth responses tend to diminish as the birds become older. Furthermore, growth stimulations are consistently observed with battery-reared chicks fed conventional feeds or highly purified rations. Therefore, it is evident that stress, such as that found in field conditions, may not be necessary to obtain a significant growth response from feeding condensed fish solubles.

An interesting series of experiments conducted by Harrison and Coates (1964) showed that significant growth responses were obtained from chicks whose parents were maintained on conventional rations containing animal protein or all-vegetable rations. In fact, the average growth response was greater when the conventional diets were fed. In comparing the effects of feeding 5% solubles to conventional or germ-free chicks, a significant response was observed only with the conventional birds. This indicates that the presence of microbes does influence the magnitude of the growth response. However, these workers observed that the addition of a small amount of sterilized or fresh droppings to the diet caused a significant growth depression which could be counteracted by feeding fish solubles.

Miller and Soares (1972) have conducted some detailed experiments designed to study unidentified growth factors in fish solubles. They used virtually a complete chemically defined diet (Table 9) except for the sources of essential fatty acids, which were supplied as purified oils. The amino acid mixture was patterned after that of Dean and Scott (1965). The vitamins, minerals, and antioxidant were supplied in sucrose-based premixes (Miller and Soares 1972).

TABLE 9.—Basal composition for crystalline amino acid diet used to study unidentified growth factor responses in chicks.[1]

Ingredient	Amount
	g/kg
Sucrose	502.3
Crystalline amino acid[2]	225.3
Antioxidant premix[3]	2.0
Cellulose	80.0
Safflower oil	50.0
Menhaden oil	10.0
$CaCO_3$	5.0
$CaHPO_4$	26.9
Mineral mix[1]	28.5
Vitamin mix[1]	50.0
Choline Cl mix	20.0
	1,000.0

[1] Miller and Soares (1972).
[2] Dean and Scott (1965).
[3] Santoquin premixed one part with nine parts sucrose. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The diets in these experiments were balanced for energy, calcium, phosphorus, and total nitrogen. When fish solubles was added to the diets, the total nonessential amino acid content was balanced by adjusting the glutamic acid content, and the essential amino acid content was balanced by decreasing the amount of the respective crystalline amino acid in the diet. All additions of condensed fish solubles produced greater growth rates in chicks as compared to the controls.

One of the above experiments consisted of six treatments with four variables (Table 10) fed to day-old chicks (duplicate groups of 12) for 3 weeks. Diet 1 was our basic crystalline diet with no added protein whereas Diet 2 contained 5.0% fish solubles. A significant growth response was obtained by the addition of fish solubles. Diet 3 plus 0.5 ppm selenium (as sodium selenite) did not give any growth response over the control. Diet 4 containing 0.5 ppm selenium plus 0.82% proline (which Graber, Allen, and Scott (1970) suggest is an essential amino acid) gave a slight but nonsignificant response in growth. Similarly, Diet 5 with 0.5 ppm selenium, 0.82% proline, and 5% gelatin protein resulted in only a small growth response. Gelatin was incorporated in the diets because earlier experiments had shown that the presence of intact protein was beneficial to the overall growth response to crystalline amino acid diets. However, when gelatin and fish solubles (Diet 6) were incorporated in the diet, there again was a significant growth response that was similar to the response obtained with only fish solubles.

In a further experiment by Miller and Soares (1972) Diets 5 and 6 as listed in Table 10 were irradiated with 4.5 Mrad of gamma radiation by the method described by Soares et al. (1971) and were fed to conventional and gnotobiotic White Rock chicks. The results (Table 11) of an initial experiment indicate that condensed fish solubles is capable of exerting a growth response whether or not bacteria are present. It should be noted that both groups of chicks were housed under conditions making it possible for the ingestion of excreta which most likely occurred because of the type feeders used. Therefore, these data may not be in conflict with those of Harrison and Coates (1969) who observed that germ-free chicks consuming sterile diets intentionally contaminated with sterile fecal matter exhibited growth responses when fish solubles was included in the diet whereas similar chicks fed diets with no fecal contamination showed no response to fish solubles.

SUMMARY

This review shows that condensed fish solubles (particularly those made from menhaden) is quite rich in many essential nutrients needed for livestock production. This is especially true if the composition is expressed on a dry-matter basis, since half of the product consists of water. Most essential minerals and water-soluble vitamins are found in solubles in relatively high concentrations when compared with other common feedstuffs. Fish solubles is highly digestible and rich in energy (measured as metabolizable energy) and, if expressed on a dry-matter basis

TABLE 10.—Growth response and efficiency of feed conversion of chicks fed purified diets supplemented with selenium, proline, gelatin, and fish solubles.[1]

Item	Diet					
	1	2	3	4	5	6
Se, ppm	0	0	0.5	0.5	0.5	0.5
Proline, %	0	0	0	0.82	0.82	0.82
Gelatin, %	0	0	0	0	5.0	5.0
Menhaden fish solubles, %	0	5.0	0	0	0	5.0
Weight gain[2]	[3]233	[4]279	[3]236	[3]247	[3]242	[4]286
Feed efficiency	0.62	0.58	0.64	0.64	0.67	0.54

[1] Miller and Soares (1972).
[2] Average weight (g) of 18 day-old chicks.
[3], [4] Means bearing different superscripts are statistically different ($P<0.01$).

TABLE 11.—Growth response of chicks for purified diets containing selenium, proline, gelatin, and fish solubles.[1]

Environment	Menhaden solubles	Weight gain	Chicks
	%	g	Number
Diet 5			
Conventional	0	[2]69.6	16
Gnotobiotic	0	[2]69.5	6
Diet 6			
Conventional	5.0	[3]98.5	17
Gnotobiotic	5.0	[3]107.9	7

[1] Miller and Soares (1972).
[2], [3] Means bearing different superscripts are statistically different ($P<0.01$).

have a higher caloric density than fish meal. Currently the most important nutrient in condensed fish solubles is the unidentified growth factor because significant growth responses can be demonstrated with poultry and other species of livestock under field conditions as well as in the laboratory.

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HELMINTHS OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) FROM THE KVICHAK RIVER SYSTEM, BRISTOL BAY, ALASKA[1]

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ABSTRACT

A study of helminths infecting juvenile and adult sockeye salmon (*Oncorhynchus nerka*) leaving and entering the Kvichak River system, Bristol Bay, Alaska, was conducted in 1969. Ten helminths acquired in fresh water were found in smolts: *Diplostomulum* sp.; an unidentified trematode; *Diphyllobothrium* spp.; *Triaenophorus crassus* Forel, 1868; *Proteocephalus* sp.; *Eubothrium salvelini* (Schrank, 1790); *Neoechinorhynchus rutili* (Mueller, 1789); *Philonema oncorhynchi* Kuitunen-Ekbaum, 1933; *Rhabdochona* sp.; and *Contracaecum* sp. In addition to surviving larval stages of freshwater parasites, adults were infected by nine helminths acquired in the sea: *Gyrodactyloides strelkowi* Bykhovskaya and Polyanskaya, 1953; *Lecithaster gibbosus* (Rud., 1802); *Brachyphallus crenatus* (Rud., 1802); *Tubulovesicula lindbergi* (Layman, 1930); *Phyllobothrium caudatum* (Zschokke and Heitz, 1914); *Echinorhynchus gadi* Mueller, 1776; *Bolbosoma caenoforme* Heitz, 1920; *Anisakis* sp.; and *Contracaecum* sp. Infection incidences and intensities are tabulated where accurate data are available. Information on life histories is assembled from scattered sources, and some ecological aspects of helminths infecting Kvichak sockeye salmon are briefly discussed.

The Kvichak River system is the largest producer of sockeye salmon, *Oncorhynchus nerka* (Walbaum), among five river systems in Bristol Bay, western Alaska. Its drainage basin covers nearly 8,000 square miles and includes two large lakes, Iliamna Lake (90 miles long and up to 26 miles wide) and Lake Clark (50 miles long and up to 4 miles wide). Intensive studies on sockeye salmon from this system and the other four systems, the Wood River, Naknek River, Egegik River, and Ugashik River, have been underway since 1946 (Thompson, 1962). Recent research has been directed toward determining the biological basis for annual fluctuations in the number of seaward migrants and subsequent return of adults 2 and 3 years later, and providing a reliable estimate of the optimum escapement for each of these river systems (Burgner et al., 1969).

The survival rate for Kvichak River sockeye salmon is generally higher in the peak year of the abundance cycle than in other years since the total production from each year class comes in installments 4, 5, or 6 years later, depending on the total age of the adults when they return to spawn. The occurrence of mortality inversely related to density has been ascertained from observations, but its causes remain unidentified. Since the available records show that, generally, smolt production has been proportionate to adult escapement, it appears that losses occur primarily after the smolts leave the nursery areas, but the possibility remains that the predisposing conditions are found in fresh water. The adjustments that smolts make to environmental changes, their physiological condition, and their resistance to stress have been studied by those who seek the factors that underlie variations in survival rate among year classes in

[1] This study was supported by funds provided by the Washington Sea Grant Program, which is maintained by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce. Contribution No. 369, College of Fisheries, University of Washington.

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Manuscript accepted January 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

the sea. Parasitic infections are considered a possible factor; albeit their effects may be largely sublethal, nevertheless they might contribute to disproportionate survival rates.

A field study of the helminth fauna of sockeye salmon in the Kvichak system was commenced in 1968 and expanded in 1969. The immediate tasks were to (1) identify the parasites acquired in fresh water and those acquired in the sea, (2) determine the incidence and intensity of infections, and (3) review the available literature for information on life cycles. Earlier studies by Margolis (1963) concentrated on parasites of sockeye salmon in the North Pacific Ocean as biological indicators of continental origin; he noted that over 50 parasitic species of freshwater and marine origin are known to infect sockeye salmon occurring in the North Pacific Ocean and adjacent seas. Many of these parasites occur in other species of salmon that come from Eurasia and North America to feed and mature in these waters (Akhmerov, 1963; Mamaev, et al., 1959; Mamaev and Oshmarin, 1963; Zhukov, 1960).

MATERIALS AND METHODS

The Kvichak River system consists of Iliamna Lake and Lake Clark, their tributaries, and the Kvichak River, which leads to the sea (Figure 1). Smolts migrate seaward for a few weeks following ice breakup in late May, whereas adults return to spawning grounds in July. Samples were taken from four groups of fish in 1969 (Figure 1): 1) smolts, captured by fyke net at Igiugig, on the Kvichak River (Site I), between May 28 and June 6; 2) adults in Bristol Bay, collected by set nets at Pederson Point (Site II) during May; 3) adults in fresh water, taken by beach seine in the Newhalen River (Site III) during mid-July; and 4) spawners, collected by beach seine on spawning grounds at Finger Beach (Site IV), Woody Island (Site V), and Porcupine Island (Site VI) during August. No attempt was made to discriminate between smolts originating from Iliamna Lake and Lake Clark. Adults collected at Pederson Point in Bristol Bay were known from past tagging experiments to consist almost entirely of Kvichak sockeye.

The skin, gills, eyes, gastrointestinal tract, viscera, body cavity, and swim bladder of the fish were examined for helminths. Blood smears were prepared from each fish, gall bladder smears were made from adults, and brain tissue imprints were taken from smolts. Examinations were usually conducted on the day of capture. Thus, most helminths were recovered, tentatively identified, and counted while alive and before preservation in hot Formalin[5]-Acetic acid-Alcohol solution (standard solution). In some cases tissues were preserved in hot Bouin's solution (standard solution) for future dissection and examination for parasites. Representative specimens of cestodes and trematodes were stained in Delafield's hematoxylin and mounted for further study; nematodes were either stained

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

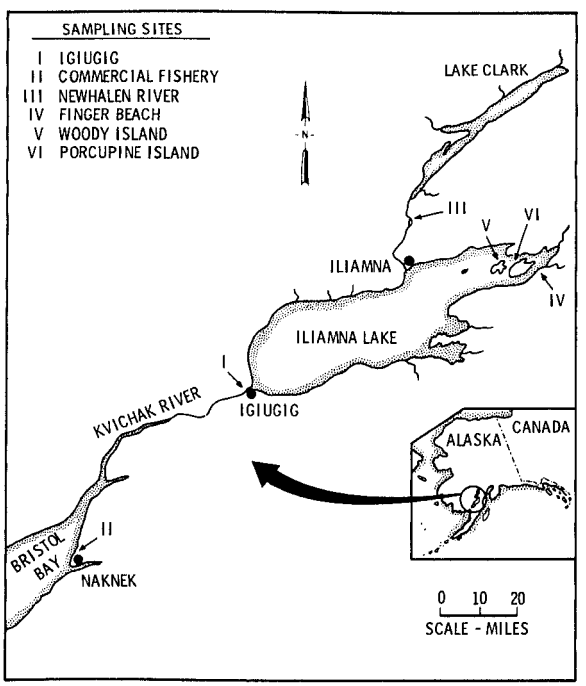

FIGURE 1.—Map of the Kvichak River system, showing sampling sites, with inset map showing its location in southwestern Alaska.

with methyl blue-lactic acid or cleared unstained in lactic acid, and examined unmounted. Blood and tissue smears were air dried, fixed in absolute methyl alcohol, and treated with Wright's blood stain.

In this report incidence and intensity are used to describe the percentage of infected hosts and the average number of parasites per infected fish, respectively. Incidences and intensities were determined with confidence for the relatively small smolts, but only the incidences were judged to be reliable for the adult fish because of difficulty in obtaining accurate counts of frequently abundant helminths.

To accurately determine the age of the host, scales from smolts and otoliths from adults were preserved and read for age, and the readings were checked against the recorded length of the fish. The smolts were from the 1966 and 1967 brood years and were designated as age 2 and age 1 according to the number of winters spent in fresh water. The adults were from the 1963, 1964, and 1965 brood years and had spent either two or three winters in the sea.

RESULTS AND DISCUSSION

Parasitological examinations were completed on 212 smolts, 88 adults from Bristol Bay, and 71 adults from fresh water. The identities and incidences of helminths in these fish are shown in Table 1 under appropriate area and age designations. No haematozoa, myxosporidians, microsporidians, leeches, or copepods were

TABLE 1.—Incidence of helminths in young and adult sockeye salmon from the Kvichak River system in 1969. (Incidence in parentheses as a percentage.)

Parasite[1]	Smolts[2]		Adults[2]						
	Kvichak River		Bristol Bay			Newhalen River		Spawning grounds	
	1.	2.	1.2	2.2	1.3 + 2.3	1.2	2.2	1.2	2.2 + 1.3
Number of fish sampled	60	152	32	46	10	33	2	26	10
Monogenea									
Gyrodactyloides strelkowi Bykhovskaya and Polyanskaya, 1953	0	0	1(3)	4(9)	1(10)	0	0	0	0
Digenea									
**Diplostomulum* sp. (spp?)	36(60)	102(67)	5(16)	7(15)	0	10(30)	2(100)	13(50)	2(20)
Lecithaster gibbosus (Rud., 1802)	0	0	29(91)	46(100)	10(100)	31(94)	1(50)	23(88)	7(70)
Brachyphallus crenatus (Rud, 1802)	0	0	3(9)	3(7)	0	3(10)	0	4(15)	1(10)
Tubulovesicula lindbergi (Layman, 1930)	0	0	0	0	0	2(6)	0	1(4)	0
Unidentified Digenea	0	2(1)	0	0	0	0	0	0	0
Cestoda									
**Diphyllobothrium* spp.	21(35)	100(66)	3(9)	6(13)	1(10)	0	0	0	0
**Triaenophorus crassus* Forel, 1868	0	4(3)	0	0	0	0	0	0	0
***Proteocephalus* sp. (spp?)	37(62)	72(47)	0	0	0	0	0	0	0
Eubothrium salvelini (Schrank, 1790)	1(2)	2(1)	0	0	0	0	0	0	0
***Phyllobothrium caudatum* (Zschokke and Heitz, 1914)	0	0	32(100)	46(100)	10(100)	33(100)	2(100)	26(100)	10(100)
Acanthocephala									
Neoechinorhynchus rutili (Mueller, 1780)	1(2)	20(13)	0	0	0	0	0	0	0
Echinorhynchus gadi (Mueller, 1776)	0	0	0	4(9)	2(20)	1(3)	0	0	0
***Bolbosoma caenoforme* Heitz, 1920	0	0	22(69)	34(74)	6(60)	4(12)	0	7(27)	1(10)
Nematoda[3]									
Philonema oncorhynchi Kuitunen-Ekbaum, 1933[4, 5]	60(100)	140(92)	23(72)	38(83)	7(70)	32(97)	2(100)	26(100)	9(90)
Rhabdochona sp.	0	8(5)	0	0	0	0	0	0	0
Anisakis sp. (spp.?)[5]	0	0	--	--	--	--	--	--	--
Contracaecum sp. (spp.?)[5]	1(2)	18(12)	--	--	--	--	--	--	--
*Other nematodes[6]	--	--	31(97)	45(98)	10(100)	33(100)	2(100)	20(77)	9(90)

[1] * = larvae (in fish intermediate host), ** = postlarvae (sexually undeveloped parasite).
[2] Age designation is based on Arabic numerals corresponding to the number of winters lived. Freshwater age precedes the dot, salt water age follows the dot; i.e., 2.2 = adult, 2 winters in fresh water, 2 winters in the sea.
[3] Examination of adult sockeye for nematodes was restricted to the digestive tract, viscera and body cavity.
[4] Incidence of P. *oncorhynchi* in smolts was based on larvae in the swim bladder; in adults, on encystation of mature worms among the viscera and on body cavity wall.
[5] Of nematodes preserved from Bristol Bay adult sockeye, the ratio (in total numbers) of *P. oncorhynchi* to *Anisakis* to *Contracaecum* was about 1:2:1.5.
[6] Primarily *Anisakis* and *Contracaecum* in Bristol Bay adult sockeye, primarily *Anisakis* in adults reaching fresh water.

detected. Some of the genera of helminths may be represented, in fact, by more than one species since specific identification of some immature forms was not possible. The parasites are considered under five taxonomic groups: Monogenea, Digenea, Cestoda, Acanthocephala, and Nematoda. Some data on the life cycle of each parasite, which are essential to an understanding of the cause-and-effect relationships for parasitic infections, are given where available.

MONOGENEA

No monogenetic trematodes of freshwater origin were found on the gills of smolts, although *Tetraonchus alaskensis* Price, 1937 has been reported from young sockeye salmon in the Wood River system (Margolis, 1963, tables). *Gyrodactyloides strelkowi* (Gyrodactylidae) parasitized the gills of five adults taken at Pederson Point. This viviparid is specifically a salmon parasite (Margolis, 1965) and is phylogenetically related to the genus *Gyrodactylus* which parasitizes primarily freshwater teleosts. Since *G. strelkowi* lives externally on its host and is adapted only to marine conditions, it is lost soon after the return of adult sockeye salmon to fresh water.

DIGENEA

Two species of dignetic trematodes were acquired by smolts in fresh water, and three species by maturing fish in the sea.

Metacercariae of the trematode genus *Diplostomulum* (Diplostomatidae) occurred in the eye lenses of over half of the smolts. The incidence of infection was slightly less in age 1 (60%) than in age 2 smolts (67%). Infection normally occurs via furcocercous cercariae that emerge from freshwater gastropods, penetrate the skin of various fish, and localize in their eyes as metacercariae. Studies on *Diplostomum spathaceum* (Rud., 1819), a widely distributed Palearctic species that matures in the intestine of gulls, indicate that infection of fish does not occur in brackish water, a result of the absence of required freshwater molluscan hosts (Cichowlas, 1961). The incidence of *Diplostomulum* in returning adults taken at Pederson Point was significantly lower (15-16%) than in departing smolts, but still less than in adults penetrating into the headwaters of the Kvichak; thus those fish that returned to spawn were again exposed to cercariae after re-entry.

Variable numbers of three hemiurid trematodes were found in the stomach and upper intestine of adult sockeye salmon from Bristol Bay: *Lecithaster gibbosus, Branchyphallus crenatus,* and *Tubulovesicula lindbergi* (Hemiuridae). All were acquired in the marine environs by ingestion of crustacean plankters that serve as second intermediate hosts and carry the stages maturing in sockeye salmon. The incidence of *L. gibbosus* in sockeye salmon at Pederson Point exceeded 90% and was only slightly less in adults collected from the spawning grounds. Margolis (1963) noted that the rate of infection by *L. gibbosus* in sockeye salmon was lower in offshore than in inshore areas and deduced that most parasites in maturing fish were acquired after they re-entered coastal waters. This conclusion was supported by data of Mamaev and Oshmarin (1963) for sockeye salmon taken along the Soviet eastern coast and of Boyce (1969) for those from British Columbia waters. The acquisition of the parasites in coastal areas is presumably related to the relatively high abundance of molluscan first intermediate hosts. Boyce (1969) found that marine snails of the genus *Thais* were the first intermediate host and the marine copepods *Centropages abdominalis* and *Pseudocalanus minutus* were the second intermediate hosts of *L. gibbosus* in coastal areas of British Columbia. *L. gibbosus* matures in 1 to 2 weeks and has a lifespan of about 2 to 9 months in pink salmon, whereas *Tubulovesicula lindbergi* matures in 2 to 4 months and lives at least 31 months in chum salmon (Margolis and Boyce, 1969). Thus most trematodes acquired in coastal waters and maintained in the digestive tract of sockeye salmon during their migration into the Kvichak system are likely to persist until their post-spawning death.

Branchyphallus and *Tubulovesicula* were of comparatively low incidence, and *Hemiurus levinseni* Odhner, 1905, a marine hemiurid known to infect adult salmon in the North Pacific, was

not found. The distribution of these parasites appears to be somewhat sporadic. Data tabulated by Margolis (1963) from Bristol Bay sockeye salmon in 1957 suggest that *B. crenatus* is more common (40% incidence) in Kvichak fish than our samples indicate, but concur on the relative scarcity of *T. lindbergi* and absence of *H. levinseni.*

CESTODA

The tapeworms belonged to five genera and, with the exception of *Eubothrium,* were either plerocercoid larvae, encysted among the viscera, or sexually immature, postlarval forms in the intestinal lumen. Presumably all infections were acquired by ingestion of cyclopid and/or diaptomid copepods containing infective procercoids.

Encysted plerocercoids belonging to the genus *Diphyllobothrium* (Diphyllobothriidae) were fairly common in the stomach walls of many smolts but also occurred, though less frequently, in the liver, spleen, and the intestinal wall. Since the incidence of infection was higher in smolts of age 2 (66%) than in those of age 1 (35%), it appears that the plerocercoids accumulate with continued sojourn of the fish in the lake environment. The incidence of *Diphyllobothrium* larvae in the viscera of adult sockeye salmon from Pederson Point, which had spent 2 or 3 years in the sea, was significantly lower (9-13%). Diphyllobothriasis is common in freshwater salmonids of the Northern Hemisphere (Becker and Brunson, 1967), but the identities and life cycles of many forms remain unclear. Vik (1964) reviewed the bionomics of *Diphyllobothrium,* and Stunkard (1965) and Meyer (1966) discussed taxonomic problems. Rausch (1954) described the plerocercoids of *D. ursi* Rausch, 1954, from juvenile and adult sockeye salmon and the adult cestodes from bears on Kodiak Island, Alaska. Rausch and Hilliard (1970) identified six species of *Diphyllobothrium* indigenous in Alaska and noted that several occur as plerocercoids in salmonids and other freshwater fishes. In all probability, the plerocercoids present in Kvichak sockeye salmon represent two or more species with different definitive hosts (birds or mammals) but with otherwise similar life cycles.

Larvae of *Triaenophorus crassus* (Triaenophoridae) were encysted in either the body cavity or muscle of only four smolts, all of which were age 2. None was detected in returning adults, although apparently the plerocercoids can survive in ocean-dwelling salmon for 4 or 5 years (Margolis, 1963). This cestode is specific for its definitive host, the northern pike (*Esox lucius*); however, the first intermediate host may be one of several species of freshwater copepods (Watson and Lawler, 1965), and the second is a planktivorous fish. Reviews of *T. crassus* and other species of *Triaenophorus* were made by Miller (1952), Lawler and Scott (1954), and Michajlow (1962). In the Kvichak system, the incidence of *T. crassus* in sockeye salmon smolts is apparently low, but it varies among other river systems bordering Bristol Bay (Margolis, 1963, 1967). The fact that Kvichak smolts are largely pelagic apparently accounts, in part, for the low incidence of infection by *T. crassus,* since copepods infected with procercoids will occur most abundantly in shallow, marshy inshore areas inhabited by pike. (Field observations by the second author in 1958 indicated that the incidence of *T. crassus* plerocercoids was higher in smolts from Lake Clark, which has a comparatively greater proportion of shoreline to water mass, than in those from Iliamna Lake.)

Tiny postlarvae of *Proteocephalus* sp. (Proteocephalidae) occurred in the intestinal lumen of about half of the Kvichak smolts, but the incidence of infection was lower in age 2 fish (47%) than in age 1 (62%). Presumably these cestodes had recently emerged after infected copepods were ingested and the smolts were fortuitous hosts in which further development was restricted. The larvae of *Proteocephalus* in age 2 smolts were no further advanced than those in age 1, and the incidence of infection was lower (47 versus 62%); thus it appears that these cestodes soon perish. No *Proteocephalus* occurred in returning adult sockeye. The favored definitive hosts of this parasite probably are resident fish in the Kvichak system.

Eubothrium sp. (Amphicotylidae), probably *E. salvelini* Schrank, 1790) on ecological

grounds, occurred as adults in the intestines of three smolts. This holarctic cestode appears to be rare in sockeye salmon in major Bristol Bay watersheds (Margolis, 1963, tables) but is sometimes common in salmonids from other areas. Infections of about 35% incidence occurred in sockeye smolts leaving Babine Lake, British Columbia, in 1952 and 1953 (Dombroski, 1955), and an incidence of 20-30% among these migrants has been recorded recently (Smith and Margolis, 1970). There is no teleost intermediate host for *Eubothrium,* and juvenile sockeye salmon become infected directly by ingestion of planktonic copepods carrying procercoids, such as *Cyclops strenuus* in Norway (Vik, 1963). *E. salvelini* apparently does not survive the sojourn of growing sockeye salmon at sea. Recent evidence suggests that cestodes of a related species, *Eubothrium crassum* (Bloch, 1779), found in returning Atlantic and Pacific salmon in rivers, are rarely the same worms carried to sea by smolts but are of marine origin, and that two biological races, one marine and one fresh water, exist (Kennedy, 1969).

Postlarval forms of *Phyllobothrium caudatum* (Tetraphyllidea) were found in the digestive tract of all fish taken at Pederson Point, the Newhalen River, and the spawning grounds (mean intensity, 16/fish). Little decrease was apparent in either incidence or intensity of infection in adults that reached fresh water despite their cessation of feeding. The unencysted postlarvae exist in a state of arrested development. They live in captive juvenile pink and chum salmon in seawater for at least 8 months with no change in form, but grow from 1 to 4 or 5 mm (Boyce, 1969). Moderate to heavy infections of phyllobothriids are acquired by nearly all species of salmon feeding in the North Pacific (Akhmerov, 1963; Margolis, 1963; Zhukov, 1960) and their numbers are apparently cumulative. The mature form and the definitive host of this cestode remain unknown, and some taxonomic confusion exists as to its specific identity. Williams (1968), who reviewed the Phyllobothriidae, concurred with Margolis (1963) in identifying the postlarvae from sockeye salmon in the North Pacific and adjacent seas as *P. caudatum.* The hosts of larval *Phyllobothrium* include marine cephalopods, elasmobranchs, teleosts, and mammals, but the mode of infection and subsequent behavior of the late procercoid and developing plerocercoid are not known (Williams, 1968).

ACANTHOCEPHALA

The incidence of *Neoechinorhynchus rutili* (Neoechinorhynchidae) among the smolts was low and tended to be greater among those of age 2 (13%) than those of age 1 (2%). None was found in returning adult sockeye. Tabulated data by Margolis (1963) indicate that this acanthocephalan does not survive the sockeye's ocean residence. *N. rutili* developed rapidly, and hence the parasites carried in the intestine of smolts were sexually mature. Margolis (1963) listed an incidence of 8% in Kvichak smolts examined in 1956.

N. rutili is an euryxenous parasite with wide dispersal in freshwater habitats of Eurasia and North America (Van Cleave and Lynch, 1950) and is the only species of the genus found in European freshwater fishes (Bullock, 1970). The only known intermediate host of *N. rutili* in North America is the ostracod *Cypria turneri* (Merritt and Pratt, 1964), whereas in Great Britain there are two known intermediate hosts, the ostracods *Cypria ophthalmica* and *Candona candida* (Walker, 1967). The ostracod *Cyclocypris laevis* and two species of *Sialis* (Insecta) are known to transmit the infective larvae to fish in Europe (Ginetsinskaya, 1958).

Echinorhynchus gadi (Echinorhynchidae) occurred in six adult sockeye salmon from Pederson Point. According to Margolis (1965), this acanthocephalan is widely distributed in northern seas; it is common in sockeye salmon taken off the Kamchatka Peninsula of the USSR but is generally rare in salmon captured in other areas, including the North American coast. *E. gadi,* like *N. rutili,* is an euryxenous parasite but differs in that it originates in the sea. It occurs in many families and genera of teleosts in the North Pacific and North Atlantic, particularly demersal fishes, but most commonly in the cods (Gadidae) (Linton, 1933; Margolis, 1965; Sindermann, 1966). The first intermediate hosts are marine amphipods, such as *Gammarus lo-*

custa, Amphithoe rubricata, and *Pontoporeia femorata* in European waters (Ginetsinskaya, 1958) and *Cyphocaris challengeri* off the coast of British Columbia (Ekbaum, 1938). Infections are gradually lost because of the relatively short lifespan of the mature parasite when anadromous salmon cease feeding (Ginetsinskaya, 1958).

Postlarval forms of *Bolbosoma* sp. (Polymorphidae), probably *B. caenoforme* on ecological grounds, were common in the intestine of adult sockeye salmon from Pederson Point (60-74% incidence), but the incidence decreased over a 3-month period as the fish penetrated into fresh water. The decrease in incidence was accompanied by a decrease in mean intensity from about 5 (range, 1-15) in fish taken from Bristol Bay to about 2 (1-6) in fish collected on the spawning grounds. Maturation of *B. caenoforme* appears to be inhibited in salmon, which are presumably accidental hosts. The definitive hosts are believed to be marine mammals. Nevertheless, there is a wide distribution and high incidence of this acanthocephalan in salmon feeding in waters of the North Pacific (Akhmerov, 1963; Mamaev et al., 1959; Margolis, 1963, table).

Four species of juvenile *Corynosoma* (Polymorphidae) were reported in sockeye salmon from the North Pacific and adjacent seas by Margolis (1958), but the incidence was less than 2%. One species, *C. villosum* Van Cleave, 1953, was reported in Ugashik River sockeye salmon in 1957 but not in other Bristol Bay adults (Margolis, 1963, table). No *Corynosoma* were found in Kvichak adult sockeye salmon during this study.

NEMATODA

Philonema oncorhynchi (Philometridae) was the common nematode parasitizing the smolts, but the incidence from our data was higher in age 1 (100%) than in age 2 (92%). Larval forms commonly occurred in the swim bladder, occasionally in the kidney, and rarely in other visceral organs. The larvae apparently leave the swim bladder or tissues during the sockeye salmon's sojourn at sea and enter the body cavity, where they mature in synchrony with maturation of the host (Margolis, 1970). In the adults taken at Pederson Point, the incidence of *P. oncorhynchi* exceeded 70%, and the mature worms were localized in the body cavity. Data tabulated by Margolis (1963) indicate that the incidence of this nematode in sockeye salmon returning to major Bristol Bay tributaries is generally high (92 - 100%) and that the intensity of the infections is relatively high (averaging 11-61 parasites/fish). There is little doubt that the very small nematodes reported in sockeye salmon smolts leaving Bristol Bay tributaries in 1956 (100% incidence) by Margolis (1963) were, as he assumed, larvae of *P. oncorhynchi.*

Recent data have elucidated the life cycle of this dracunculoid nematode, which infects salmonids in fresh water on both borders of the North Pacific Ocean. Gravid worms are presumably discharged along with eggs when the adult fish spawn, the worms burst to liberate thousands of larvae, and the larvae are ingested by a suitable copepod intermediate host, such as *Cyclops bicuspidatus* (Platzer and Adams, 1967). Invasive larvae are liberated from infected copepods in the stomach of sockeye smolts, penetrate the gut wall, and move through either the coelomic cavity or the mesentery and associated tissues to the swim bladder within 18 hr (Adams, 1969). Numbers of larvae carried by smolts moving seaward may reach the hundreds (Margolis, 1970), since the intensity of infection tends to increase during the freshwater life of the planktivorous smolts.

Two other nematodes were acquired by the smolts, *Rhabdochona* sp. and *Contracaecum* sp. *Rhabdochona* (Rhabdochonidae) occurred in the intestine of a few age 2 smolts (5%) but not in adult sockeye salmon taken at Pederson Point. Although little is known of the bionomics of various species of *Rhabdochona,* these nematodes are common in various North American freshwater fishes (Choquette, 1951). The incidence of *Contracaecum* was also low in age 1 (2%) and age 2 (12%) smolts, and about one immature nematode was found encysted in the viscera of each infected fish.

Contracaecum and *Anisakis* (Heterocheilidae) are cosmopolitan parasites of many marine fish-

es. Anadromous salmonids carry the parasites into fresh water. Nearly all adult sockeye salmon taken at Pederson Point harbored quantities of larval anisakids belonging to these two related genera. Accurate records of adults infected with either *Contracaecum* and/or *Anisakis* were not obtained, but the actual combined incidence was probably 100%, as tabulated for Bristol Bay sockeye salmon returning in 1957 by Margolis (1963). In our study, these helminths were listed simply as nematodes because of the difficulty of individually examining large numbers of parasites scattered throughout the viscera of the large fish. On the basis of preserved material from adult sockeye salmon taken at Pederson Point, the ratio of *P. oncorhynchi* to *Anisakis* to *Contracaecum* was about 1:2:1.5 by total numbers.

According to Margolis (1970), the typical life cycle of nematodes belonging to the superfamily Ascaridoidea (including all anisakids) occurring in fishes probably involves three hosts—a crustacean or other invertebrate as first intermediate host, a fish as second intermediate host, and a piscivorous fish, bird, or mammal as the definitive host—depending on the genus or species concerned. Whether the larval *Contracaecum* found in Kvichak smolts in this study are identical with those in returning adult sockeye salmon is problematical, but it is possible that stages liberated from spawning fish were acquired by some smolts.

INTENSITIES OF FRESHWATER HELMINTHS IN SMOLTS

Ten helminths with life cycles involving initial transfers in the freshwater environs were harbored by migrating Kvichak smolts (Table 1). One of the objectives of this study was a determination of the potential effects of these helminths, however subtle and indirect they may be. Some indication is provided by the intensity of infections in correlation with the site selected for latent or active development.

Ecologically speaking, the intensity of infection is roughly correlated with the incidence of infection because the more abundant the parasite, the greater will be the distribution of infections among all available hosts. Moreover, the higher the incidence and/or intensity of infection, the more favorable will be the sum of all synecological factors involved in sustaining a particular host-parasite association.

The intensities of the five common helminths acquired by smolts in Iliamna Lake and Lake Clark are given in Table 2. Accurate counts were not made of the ubiquitous *Philonema oncorhynchi* and data on the adventitious *Proteocephalus* sp. are omitted. Some additional data are included from smolts captured in previous years, preserved in Formalin, and subsequently examined. Of these helminths four occurred as immature or larval forms in the body cavity, tissues, or organs.

The acanthocephalan *Neoechinorhynchus rutili* inhabits only the intestine of smolts, where it rapidly matures. In this favored location the female releases the eggs, these are passed externally, and the worms eventually degenerate. Infection burdens were found to be low in this study, with usually one but sometimes two parasites per host. With such low intensities, fertilization of eggs in the intestine (which requires association of a male and a female) is exceptional and the parasite tends to be self-limiting. Consequently, the principal definitive hosts in the Kvichak system are probably resident fishes that sustain an infection foci. The data, though scanty, suggest that infection of smolts occurs primarily in Iliamna Lake since samples from Lake Clark and its tributary, the Newhalem River, harbored none. Data presented by Margolis (1963) for 25 Kvichak smolts in 1956 list an incidence of 8% and a mean intensity of one parasite per fish.

Diplostomulum sp., *Diphyllobothrium* spp., and *Triaenophorus crassus* persist in sockeye salmon as larvae throughout the life of their host. Completion of their life cycles requires that an infected fish be eaten by a predator or scavenger in which the parasite is able to mature and shed its eggs. *Philonema oncorhynchi* transforms from larvae to adult in sockeye and is liberated during the spawning act or upon the host's death.

Both the incidence and intensity of *Triaenophorus crassus* were low in Kvichak smolts in this

TABLE 2.—Incidence and intensity of some helminths from juvenile sockeye salmon in the Kvichak River system in 1961, 1966, 1968, and 1969. (Incidence is the percentage of the sample infected; mean intensity, from infected fish only, in parentheses.)

Parasite[1, 2]	Kvichak River			Iliamna Lake	Newhalen River	Lake Clark
	1966	1969		1968	1961	1968
	1.	1.	2.	2.	1.	2.
Number of fish sampled	50	60	152	50	50	50
**Diplostomulum* sp. (spp.?)	--	60(2.0)	67(2.5)	--	--	--
**Diphyllobothrium* spp.	24(1.3)	35(1.2)	66(1.8)	28(1.1)	26(2.0)	2(1.0)
**Triaenophorus crassus*	0	0	3(1.3)	0	20(1.5)	0
Neoechinorhynchus rutili	10(1.2)	2(1.0)	13(1.3)	2(1.0)	0	0
**Philonema oncorhynchi*	100	100	92	100	100	91

[1] * = larval parasites (in fish intermediate host).
[2] Examinations other than in 1969 were taken from fish preserved in 10% Formalin, which restricted accurate counts of *Diplostomulum* and *P. oncorhynchi*.

study (Table 2). Data from Kvichak smolts in 1964 and 1965 (Margolis, 1967) suggest that the incidence of *T. crassus* in Kvichak smolts is generally low, less than 3%, and that the usual intensity is but one or sometimes two plerocercoids per parasitized fish. *T. crassus* has been found regularly in samples from the Wood and Naknek Rivers but only occasionally in those from the Ugashik and Kvichak Rivers (Margolis, 1967).

Metacercariae of *Diplostomulum* occurred in the eye lenses of 60% of the Kvichak smolts in this study but the mean intensities were low, 2.0 to 2.5 parasites per fish. An incidence of 48% (25 fish examined) and an intensity of 2.0 in Kvichak smolts studied in 1956 were tabulated by Margolis (1963).

Margolis (1963) found that 15% of the Kvichak adults returning in 1957 were infected with *Diplostomulum* (mean intensity, 2) and our data (Table 1) closely agree. Thus the incidence but not the intensity of the infections is significantly lower in returning adults than in smolts. Whether this is due to the loss of metacercariae in the lenses of many ocean-dwelling fish, as suggested by Margolis and by Dogiel (1966), or perhaps to disproportionate loss of infected fish as our data hint is conjectural.

The incidence of *Diphyllobothrium* in age 2 Kvichak smolts was 66% from data obtained during this study, but intensities were usually low, with one or two plerocercoids per infected fish. Of the smolts examined from Bristol Bay tributaries in 1957 by Margolis (1963), Kvichak fish ranked second in level of incidence (52%), whereas those from the Egegik River were first with 88% incidence, and those from the Naknek were third with 20% incidence.

Data obtained in this study and provided by Margolis (1963) indicate that nearly all smolts leaving the major rivers of Bristol Bay are infected with larvae of *Philonema oncorhynchi*, but that the intensities vary widely, often exceeding 50 per fish.

It is beyond the scope of this paper to postulate on any effects that the parasites of Kvichak sockeye salmon may have upon the survival of their host. There is ample evidence in the literature that, given certain pre-disposing conditions, direct mortalities from mechanical damage, histopathological changes, and measurable effects upon size and growth rates of parasitized fish do occur. Any factor that results in environmental discrimination, such as the presence of internal and external parasites, would tend to lessen the chances of a fish for survival. The question of whether or not the various parasites occurring in Kvichak sockeye salmon, alone or in combination, cause losses of ecological significance remains to be explored.

POSTSCRIPT

David A. Pennell entered the College of Fisheries of the University of Washington as a graduate student in the fall of 1968. On August 1969, he was involved in a fatal airplane accident while collecting material in the field for his M.S. dissertation on the parasites of sockeye salmon in Bristol Bay, Alaska. This paper is published posthumously in honor of this promising and highly dedicated young man.

Dr. C. Dale Becker undertook to complete the manuscript from a preliminary analysis and report by Mrs. Nora R. Scofield. Supplemental data, collected earlier by Dr. Becker while with the Fisheries Research Institute, have been included in this paper. Assistance and advice were given by Drs. A. K. Sparks and O. A. Mathisen throughout the course of the study.

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AN ECOLOGICAL STUDY OF *GOBIOSOMA BOSCI* AND *G. GINSBURGI* (PISCES, GOBIIDAE) ON THE GEORGIA COAST[1]

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ABSTRACT

The ecology of two species of "scaleless" gobies, *Gobiosoma bosci* and *G. ginsburgi*, from estuarine and beach waters around Sapelo Island, Ga., is compared. Small patches of oysters, in addition to oyster reefs, are important nesting areas for both species. Numerous invertebrates and five other fishes are characteristic of the oyster patches. Habitats common to both species include reefs and patches of oysters, bottoms of estuarine rivers of moderate to high salinity, and burrows in an eroding clay deposit off Sapelo Beach. In contrast to *G. bosci*, *G. ginsburgi* ranges offshore, is thought to spawn in deep water, and is not found in fouling communities, marsh pools, and low salinities.

These gobies are sexually dimorphic in genital papilla, body size, and color. They nest in oyster shell. Males incubating and guarding their own eggs are cannibalistic on eggs of other individuals, apparently having the ability to distinguish their own nests or eggs from those of other individuals. Higher egg counts in nests than in ovaries prove that *G. bosci* is polygamous.

The spawning seasons of *G. bosci* and *G. ginsburgi* are apparently similar. The season of *G. bosci* is protracted to the south and correlates with water temperature.

Our study of the reproduction and ecology of the two species of "scaleless" gobies, the naked goby (*Gobiosoma bosci*) and seaboard goby (*G. ginsburgi*), was initiated when they were discovered incubating eggs in oyster shells at Sapelo Island, Ga. This provided the opportunity to compare certain aspects of the life history of these two secretive species and analyze their ecological relationship to oyster communities. There are some published ecological information on these two species (Dawson, 1966, 1969, and references therein) and some scattered reports on reproduction that are partially summarized by Breder and Rosen (1966).

Since most species of *Gobiosoma* are tropical (Böhlke and Robins, 1968), the genus probably originated in the tropics. However, the low spawning threshold of *G. bosci*, about 20°C (Nelson, 1928), suggests a temperate-water origin for this species. *G. bosci* ranges from Connecticut (Pearcy and Richards, 1962) and Long Island Sound to Campeche, Mexico (Dawson, 1969). *G. ginsburgi* ranges from the Wareham River and Woods Hole, Mass. (Ginsburg, 1933; Lux and Nichy, 1971), to Jekyll Island, Ga. (Dawson, 1966). *G. robustum* ranges from the Gulf of Mexico to the St. Johns River, Fla. (Tagatz, 1968), and has been found in Maryland (Schwartz, 1971). *G. longipala*, the Gulf cognate of *G. ginsburgi*, is considered a distinct species (Dawson, 1966). The similarity of these two species, however, leaves little doubt that they are derived from a common ancestor whose distribution was split by the emerged Florida plateau, which now functions as an ecological and/or physical barrier. In contrast, Atlantic and Gulf populations of *G. bosci* have not diverged recognizably.

G. bosci and *G. ginsburgi* are easily distinguished. *G. ginsburgi* has two ctenoid scales

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Manuscript accepted May 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

on each side of the caudal fin base and *G. bosci* is entirely scaleless. The best field characteristic for differentiating the two species is the color pattern on the sides of the body. In *G. bosci,* the sides are dark with eight or nine narrow, light bars that are of uniform width, and there are no dark spots along the lateral midline. During the breeding season the light bars of some males are obscured by increased pigmentation. In *G. ginsburgi,* the light bars broaden below the lateral midline, and there are dark spots or lines where the midline crosses the dark bars.

G. bosci and *G. ginsburgi* occur in large oyster reefs and small isolated patches of oysters that are partially exposed at low tide. The total area occupied by the small patches is relatively great since they border the maze of tidal creeks and occupy shallow mud flats in the lower reaches of the estuary where salinity is generally above 15‰. Two such sites were selected for detailed study. One is the mouth of Big Hole lagoon that separates Sapelo Island Beach from Cabretta Beach. The bottom is predominantly sand, but ebb tide currents have eroded deposits of hard clay that are derived from Pleistocene salt marshes. The gobies occupy the small reefs in sand and clay bottoms and often nest in isolated hinged shells that are stabilized in the clay. The second study site is a creek that runs under the boat house of the University of Georgia Marine Institute and that winds through the salt marsh. This is a typical salt marsh creek with a mud and shell bottom and mud banks that are bordered with cord grass (*Spartina alterniflora*). Small reefs along the bank and bottom are exposed when the approximately 2.1-m tide is low.

Some specimens were obtained by seining at Sapelo Island and other specimens by sampling with a bucket dredge and otter trawl in the estuary that ranges from the oligohaline Riceboro Creek to Sapelo and St. Catherines Sounds. The 30-ft (9.1 m) seine had ¼-inch (6.35-mm) mesh. The 20-ft (6 m) wide trawl had 1¼-inch (32-mm) mesh. A June collection is from Chatham County. Dip net collections were taken beneath floating docks at Halfmoon Landing and Carrs Neck Creek. Macroinvertebrates observed in reefs were collected by hand or dip net.

HABITATS

In the Sapelo Island region most collections of *G. bosci* and *G. ginsburgi* were made in patches of oyster shells or in isolated hinged shells. *G. bosci* occurs where shells are not available in Texas (Hoese, 1966) and in grassy areas in Chesapeake Bay (Hildebrand and Schroeder, 1928). Some *G. bosci* were collected in marsh pools, as they were by Kilby (1955), and some among fouling communities (including sea squirts, hydroids, barnacles, and small oysters) on pilings, and on the underside of floating docks in summer and winter, a habitat reported by Joseph and Yerger (1956).

Extensive trawling and dredging in a Georgia estuary for 3 years produced four collections of *G. bosci* at stations where water depth ranged from approximately 4.5 to 12.0 m. Two were from part of the lower estuary where shells are abundant on the bottom, and two were from the middle part of the estuary where the bottom has various amounts of sand, gravel, mud, and debris. A few were seined in sandy areas along Sapelo Beach where cover was scarce. On 4 March 1969, 9 *G. bosci* were found along with 114 *G. ginsburgi* and 7 *Hypsoblennius hentzi* in tubular burrows in an eroding clay outcrop on Sapelo Beach. Burrows such as these, apparently made by false angel wings (*Petricola pholadiformis*), may be overwintering sites for large portions of the goby populations. Gobies and other fishes become scarce on the reefs in fall and winter. Some *G. bosci* were found in mud and debris at the edge of oyster reefs at near-freezing water temperatures (Hoese).[4] At temperatures below 20°C many *G. bosci* were found in mud-bottom marsh pools, where they apparently burrow in the mud during the coldest part of the winter, as speculated by Hildebrand and Cable (1938). A mass migration of *G. bosci* to deeper waters of the sounds in the winter is unlikely, as they were trawled in shallows (generally less than 1.2 m) throughout the year (Dawson, 1966).

[4] Hoese, H. D. Studies on fishes associated with American oysters (*Crassostrea virginica*). Unpublished manuscript filed at University of Southwestern Louisiana.

We collected *G. bosci* at temperatures of 12.7° to 31.3°C. It is known to occur at temperatures of 1.5° (Hoese, see footnote 3) to 33.2°C (Gunter, 1945).

G. bosci is euryhaline and is common in low to moderate salinities. Dawson (1966) suggested that *G. bosci* apparently departs from the size-salinity relationship described by Gunter (1945) wherein the youngest individuals predominate in the low salinities. Our data generally support Gunter's observations as our three low-salinity (0-1.9‰) collections contained only 14- to 22-mm specimens. However, Dawson (1966) found most 9.5 to 11.0-mm *G. bosci* to occur at 14.8 to 24.7‰ salinities. *G. bosci* spawns in moderate to high-salinity waters and the 4- to 15-mm pelagic larvae move upriver by an unknown mechanism (Massmann, Norcross, and Joseph, 1963). Since the smallest specimens reported by Dawson (1966) apparently were recently spawned, his observation does not disprove the size-salinity hypothesis.

Habitats of *G. ginsburgi* and *G. bosci* overlap to some degree. *G. ginsburgi* was commonly found in oyster shells at Big Hole. It was rare in the marsh creek; here only a single 16-mm *G. ginsburgi* was collected, along with 44 *G. bosci*, on 12 February 1968. *G. ginsburgi* was more abundant than *G. bosci* in burrows in the eroding clay banks on the beach as noted above and in deepwater stations in the estuary. There were nine dredge and trawl collections of *G. ginsburgi* (13 specimens) in the estuary compared with four of *G. bosci* (4 specimens). In contrast to *G. bosci*, these collections of *G. ginsburgi* were all taken in shell areas. *G. ginsburgi* ranges offshore to a depth of 45 m (Dawson, 1966). Apparently it spawns in deep water, and its young do not migrate into low-salinity water. *G. ginsburgi* occurred in three dredge collections from 1.6 to 12.9 km (about 10 m depth) off the Georgia coast. *G. ginsburgi* was not found in shallow marsh pools, fouling communities, or in low salinities. We collected it at salinities of 24.9 to 34.1‰ in the estuary, and de Sylva, Kalber, and Shuster (1962) collected it at 22 to 30‰.

TABLE 1.—List of fishes and common macroinvertebrates that were associated with the subtidal patches of oyster shells in Georgia.

Polychaete worm	Shrimps
Nereis succinea	*Palaemonetes vulgaris*
	Palaemonetes pugio
Snails	Crabs
Urosalpinx cinerea	*Callinectes sapidus*
Terebra dislocata	*Menippe mercenaria*
Odostomia sp.	*Rhithropanopeus harrisi*
	Neopanope texana sayi
Bivalves	*Eurypanopeus depressus*
Petricola pholadiformis	*Panopeus herbstii*
Brachidontes exustus	*Pagurus longicarpus*
	Fishes
Isopods	*Gobiosoma bosci*
Sphaeroma quadridentatum	*Gobiosoma ginsburgi*
Cassidinidea lunifrons	*Gobiesox strumosus*
	Opsanus tau
Amphipods	*Hypsoblennius hentzi*
Gammarus sp.	*Chasmodes bosquianus*
Melita nitida	*Hypleurochilus geminatus*

ASSOCIATED SPECIES IN OYSTER PATCHES

Other fishes and conspicuous invertebrates were collected with the gobies for the purpose of characterizing the small oyster shell patches and to allow comparison with the larger, typical oyster reefs. The larger reefs are primarily intertidal in sounds and high-salinity rivers. The small reef patches are mostly subtidal and are subjected to a stronger ebb tide current and probably more erosion than the larger reefs in the mud flats.

Most of the invertebrates and all the fishes collected (Table 1) were reported for North Carolina oyster reefs by Wells (1961). The only records we add are the amphipod *Melita nitida* and the auger *Terebra dislocata*. Some species that we consider to be common in the subtidal reef patches were considered to occur in less than 20% of the collections in North Carolina (Wells, 1961). These include *Palaemonetes pugio, P. vulgaris, Callinectes sapidus, Menippe mercenaria, Rhithropanopeus harrisi, Pagurus longicarpus*, and *Cassidinidea lunifrons*.

The seven species of fishes (Table 1) are characteristic oyster reef species. They are intimately associated with the reefs. They remain within the interstices of the reef throughout the tidal cycle during the warmest months and all nest there to some degree. However, they become scarce or absent on the reefs in winter. Other fishes collected with oysters (Wells, 1961)

are temporary visitors, do not lay adhesive eggs in the shells, and are rarely found in the interstices of the reef.

The oyster association offers advantages to the gobies and other fishes. The reef provides nesting sites, food, and added protection from predators. A great diversity of reef invertebrates is available for food (Wells, 1961). *G. bosci* eat *Gammarus* and other crustaceans, annelids, small fish, ova (Hildebrand and Schroeder, 1928), and dying oysters (Hoese, 1964). They eat brine shrimp in aquariums and probably feed on other zooplankton in nature. *Gobiosoma* species may be significant predators in the food chain of an oyster community, but are probably unimportant as prey species unless their eggs are eaten. Hildebrand and Cable (1938) reported that eggs of *Chasmodes* attached in oyster shells were preyed on by the crab *Eurypanopeus depressus*. We found three *G. ginsburgi* in the stomach of *Urophycis floridanus*. *Gobiosoma* species are reported in the food of predaceous fishes, including several sciaenids (de Sylva et al., 1962; Darnell, 1958; Hoese, see footnote 3), but their secretive habits would protect them from predation when they occupy reefs.

SEXUAL DIMORPHISM

G. bosci and *G. ginsburgi* are sexually dimorphic in their color, body size, and genital papilla. Male *G. bosci* tend to be darker (Breder and Rosen, 1966), and males were observed to turn darker when they were actively defending their nests. Males reach a larger size than females and are generally larger (Tables 2 and 3) as in *G. robustum* (Springer and McErlean, 1961). For *G. bosci*, the largest male and female were 50 mm and 37 mm SL (standard length), respectively. Corresponding lengths of *G. ginsburgi* were 41 and 32 mm. Maximum recorded length of *G. bosci* is 58 mm (Schwartz, 1961). Male *G. ginsburgi* reach 53 mm total length (42 mm SL) (de Sylva et al., 1962).

The sexes are easily separable by the structure of the genital papilla (Ginsburg, 1933). The papilla of males is triangular and compressed, whereas the papilla of females is conical, fleshy, with a larger opening than in males, and with fingerlike projections around the tip. The papilla is poorly developed in juveniles, accounting for most of the unsexed specimens in Tables 2 and 3. The papilla is most developed during the breeding season in *G. robustum* (Springer and McErlean, 1961).

Ginsburg (1933) found a predominance of males in collections of *G. bosci*, *G. ginsburgi*, and *G. robustum* and considered this to be possibly due to gear selectivity for the larger gobies. With the exception of collections of guarded nests, there is a relatively even sex ratio in our collections of *G. bosci* and *G. ginsburgi*. For example, *G. bosci* was represented by 20 males

TABLE 2.—Monthly length frequencies of *Gobiosoma bosci* from the Georgia coast, April 1967-June 1970. M - male, F - female, U - sex unknown (including juveniles), I - incubation of eggs or larvae, G - gravid female. None were collected in September.

Length (mm)	Jan.	Feb.		Mar.		Apr.			May			June			July			Aug.		Oct.	Nov.		Dec.		Total
	F	M	F	M	F	MI	F	U	MI	FG	U	MI	F	U	MI	FG	U	M	U	M	M	F	M	U	
13-15			2											4			3		2					1	12
16-18		2	3											4			4		1						14
19-21		2	8											3							1				14
22-24		5	5		1							1			3			1				2			18
25-27	1	4	4	1	1					1					2										14
28-30	1	4	3					2	2	1		2	1			2			1	1			1		21
31-33		3			1					2		2	1		2	2		2					2		17
34-36		1	1	2		1			3			4			3	1					1				17
37-39		1		1			1		4		2	3			4	1					3				20
40-42		3		2					5		2	7			5										24
43-45						1			3			3			3										10
46-48				1		1						1													3
49-51									1																1
Total	2	25	26	7	3	3	1	2	18	4	4	23	2	11	22	6	7	3	4	1	5	2	3	1	185

TABLE 3.—Monthly length frequencies of *Gobiosoma ginsburgi*, from the Georgia coast, April 1967-June 1970. M - male, F - female, U - unidentifiable sex (including juveniles), I - incubation of eggs or larvae, G - gravid female.

Length (mm)	Jan.			Feb.	Mar.			Apr.		May			June	Aug.	Oct.	Nov.			Dec.	Total
	M	F	U	M	M	F	U	MI	U	MI	FG	U	MI	U	U	M	F	U	U	
8-10														1	1					2
11-13			2															1	1	4
14-16				1	2		1		1											5
17-19					9	8										1	1			19
20-22	1	1		1	5	10					1	1	1							21
23-25		1			8	10			1	2	1									23
26-28	1				9	17				5	1		1							34
29-31					6	8		5		2										21
32-34					4	1		1		3										9
35-37					11					1										12
38-40					4															4
41					1															1
Total	2	2	2	2	59	54	1	6	2	13	3	1	2	1	1	1	1	1	1	155

and 25 females in February collections from the tidal creek. March collections of *G. ginsburgi* from burrows in an eroding clay outcrop at Sapelo Beach included 59 males and 54 females. This even sex ratio also occurs in *G. robustum* (Springer and McErlean, 1961).

NESTING BEHAVIOR

G. bosci and *G. ginsburgi* apparently have evolved an instinctive ability to select nesting sites that will allow successful reproduction. They lay adhesive eggs inside dead, gaping, hinged oyster shells, which provide a clean stable substrate and protection from predators. The size of the aperture of the oyster shell, its submergence throughout the tidal cycle, and the amount of water circulation provided by tidal currents seem to be important criteria for selection of nesting sites in reef areas. Though nests were most commonly found in oyster shells, we collected one male *G. bosci* with eggs from a hinged quahog (*Mercenaria mercenaria*) shell. Nelson (1928) also reported *G. bosci* nesting in "clam" shells, and Breder (1942) found nests of the reproductively similar *G. robustum* in sponges and scallop shells.

We noted during our collection of nesting shells that all nests were below mean low tide, and none were found emerged during the extremely low spring tides. The gape of each nesting shell was just large enough to allow the goby to enter. This characteristic gape facilitated our recognition and collection of nests. Closing the shells before extracting them from the reef prevented escape of the parent gobies.

Nests seemed to be located where the tidal current restricted siltation and stagnation at low tide. Masses of developing eggs and larvae probably require a continuous flow of water to provide oxygen and remove metabolic waste products. In aquarium observations, male gobies provided additional circulation by fanning the egg masses with slow undulations of the caudal fin. They apparently display this behavior in nature because all egg masses examined were free of silt.

Male *G. bosci* and *G. ginsburgi* guard and aggressively defend the nest until the eggs hatch and larvae become free-swimming. In laboratory observations males even attacked inanimate objects such as pipettes which were inserted into the nest. In defensive display, the dorsal fin and pelvic disc were erected, the mouth was opened broadly, and the body color was darkened. The erected pelvic disc elevated the body and may function to make the goby appear larger.

Male *G. bosci* were observed to successfully defend their nests against other male *G. bosci* introduced in the vicinity of the nest. Attached eggs of *G. ginsburgi* placed with male *G. bosci* were promptly eaten, even when the males were guarding their own eggs. Furthermore, male *G. bosci* were cannibalistic when presented with unfamiliar unhatched eggs while guarding their own nests. Both species may be important predators on eggs of their own species and other species nesting in oyster reefs. Since we saw

no evidence that males ever eat their own eggs, they apparently are able to distinguish their own progeny or nest from those of other individuals. Male gobies do not fast while incubating eggs. In fact, they temporarily left their nests to feed on brine shrimp (*Artemia*) introduced into aquariums.

SPAWNING SEASON OF *GOBIOSOMA BOSCI*

The spawning season of many marine fishes becomes longer to the south along the U.S. Atlantic coast in relation to warmer waters. Naked gobies spawn in the warmer months and both ends of their spawning season become protracted to the south. In New York waters *G. bosci* probably spawns from June through August (Greeley, 1939; Perlmutter, 1939). Nests of *G. bosci* were found in late May and June in New Jersey (Nelson, 1928). Small *G. bosci* (4-7 mm) occur from June through October in Delaware (de Sylva et al., 1962). Spawning apparently occurs from May through October in Virginia (Massmann et al., 1963; Schwartz, 1961; Hildebrand and Schroeder, 1928). On the Carolina coast spawning is from June to October (Kuntz, 1916; Breder and Rosen, 1966) and possibly beginning in late April or early May (Hildebrand and Cable, 1938). We found *G. bosci* nesting in oyster patches only during the peak of its spawning season in Georgia, from April 24 through July (Table 2). Its spawning season commences in early April in Mississippi and extends to October in Mississippi (Dawson, 1966) and Tampa Bay (Springer and Woodburn, 1960).

The spawning season of *G. bosci* probably ranges from a 3-month period, June-August, in New York to a 6- or 7-month period on the Gulf coast. Mean monthly water temperatures can be used as a rough indication of the relationship of temperature and spawning season; however, these may be somewhat extreme for the months at the beginning and ending of the breeding season. Temperature data are from U.S. Coast and Geodetic Survey (1961) stations at Montauk, Long Island, N.Y.; Breakwater Harbor, Del.; Gloucester, Va.; Southport, N.C.; and Eugene Island, La. Mean temperatures at the beginning and ending of spawning were 16° and 21°C in New York, 20° and 17°C in Delaware, 20° and 19°C in Virginia, 18° (April) or 23° (May) and 26°C in North Carolina, and 20° and 23°C on the central Gulf coast. Spawning commenced at 20°C in New Jersey (Nelson, 1928). Pending more thorough studies of spawning seasons, it can be concluded that spawning of *G. bosci* commences in the spring when water temperatures are 16° to 20°C and terminates in the fall or late summer.

The peak of spawning activity is in the warmest months, May through August, from New York to the Gulf coast. Therefore, this peak is related to temperature seasonally, but it does not change geographically in relation to temperature as Dahlberg (1970) demonstrated for the Atlantic menhaden, although summer maximums (mean monthly temperatures) range from 21°C in New York to 30°C in Louisiana. Higher summer maximums of 30° to 31°C in Tampa Bay apparently suppressed the spawning of a congener, *G. robustum* (Springer and McErlean, 1961).

SPAWNING SEASON OF *GOBIOSOMA GINSBURGI*

Available data indicate that the spawning season of *G. ginsburgi* is very similar to that of *G. bosci*. *G. ginsburgi* probably spawned from July to October in Delaware as 2 to 6-mm larvae were found in these months (de Sylva et al., 1962). One *G. ginsburgi* was ripe in May in Virginia (Hildebrand and Schroeder, 1928). In oyster patches males were incubating nests on April 24 when the shallowwater temperature was 26°C in May and June. An 8-mm specimen dredged in Sapelo Sound on August 28 was probably spawned in August. If spawning continued into the fall as in Delaware, it may be restricted to deep waters since no nests were found after June. The stomach of a *Urophycis floridanus* contained three female *G. ginsburgi* (22-30 mm) that were gravid and appeared to be ready to spawn. The *U. floridanus* was trawled on 1 May 1969 in water depth over 7.6 m in the North Newport River, Liberty

County, Georgia. An abundance of shell on bottom probably would provide a suitable spawning site.

EGG SIZE AND FECUNDITY

To analyze fecundity, eggs were counted in nests and ovaries. Eggs from ovaries of three *G. bosci* and one *G. ginsburgi* were counted and measured (Table 4). Thirty-five to 50 randomly selected eggs from both ovaries were measured with a filar micrometer eyepiece adapted to a 20× dissecting scope. Random egg diameter measurements were made as in Springer and McErlean (1961).

TABLE 4.—Sizes and numbers of eggs from ovaries of *Gobiosoma bosci* and *G. ginsburgi* in Georgia. Two size classes were found in *G. ginsburgi*.

Standard length	Date caught	Diameter of eggs		Number of eggs
		Average	Range	
mm		*mm*	*mm*	
G. bosci				
27	19 May 1970	0.195	0.112 - 0.247	701
28	19 May 1970	0.170	0.112 - 0.242	966
35	11 July 1967	0.599	0.526 - 0.720	1,382
G. ginsburgi				
25	1 May 1969	0.154	0.112 - 0.211	
		0.602	0.549 - 0.684	434

In one ripe *G. ginsburgi*, ova of two size classes were equally distributed throughout the ovary. Large ova were 0.55 to 0.68 mm, and small ova were 0.11 to 0.21 in diameter. In *G. robustum* the size range was somewhat greater and ripe ova were 0.476 to 0.782 mm (Springer and McErlean, 1961). The immature eggs may be spawned the following year or not at all. Springer and McErlean concluded that it is possible that sufficient time remains in the fall for the small egg class to be spawned; however, they also observed that the late spawners (mostly in fall) were entirely or mostly of a different year class than the early spawners (mostly in spring). In the fall, females matured at small sizes, 14.6 mm in *G. robustum* and 12.9 in *G. longipala* (Dawson, 1966). In three gravid *G. bosci* we found none of the small size class of eggs in the ovaries.

Springer and McErlean (1961) reported up to 402 eggs in a single ovary and approximately the same number in left and right ovaries of *G. robustum*. Our counts are based on both ovaries. Four nests of *G. ginsburgi* contained 354, 400, 790, and 1,884 eggs. Distinctly different stages of development were apparent in the largest nest. One female *G. ginsburgi* (25 mm) had 435 ripe eggs plus a similar number of immature ova. Fourteen *G. bosci* nests contained 332 to 2,000 eggs and three others had 3,933, 8,000, and over 9,000 eggs. The fact that three gravid females contained only 701 to 1,382 eggs points to a polygamous nature of the males. Further evidence of polygamy is the difference in developmental stages of adjacent egg masses in nests of *G. bosci* and *G. ginsburgi*. This polygamous behavior occurs in a closely related group, *Gobius*, and in an oyster associate, the oyster toadfish, *Opsanus tau* (Breder and Rosen, 1966). However, Runyan (1961) concluded that variation of developmental stages within *Gobiesox* egg clusters probably resulted from deposition on successive days, and she found no evidence for polygamy.

Fishes characteristic of oyster reefs have evolved parallel patterns of reproductive behavior. Adhesive eggs are incubated and guarded by the males. There are various degrees of reliance on oyster shells for nests. The extent of polygamy is not known. Low fecundity is characteristic of fishes that exhibit parental care. We found that egg counts in oyster shells were 319, 1,001, and 2,302 for *Gobiesox* and 1,058, 1,502, and 3,856 for *Chasmodes*. Runyan (1961) found 1,600 eggs in an average-sized female *Gobiesox* and 300 to 2,500 eggs in shells.

ACKNOWLEDGMENTS

Thanks are extended to Dr. V. G. Springer, U.S. National Museum, Dr. W. S. Woolcott, University of Richmond, and Dr. H. D. Hoese, University of Southwestern Louisiana, for many valuable comments on this manuscript. We thank Richard W. Heard, Jr., for providing the dredge collections.

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CALORIC MEASUREMENTS OF SOME ESTUARINE ORGANISMS[1]

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ABSTRACT

The caloric content per gram dry weight, per gram ash-free dry weight, and per gram live weight was determined for 51 species of organisms, representing the Ctenophora, Mollusca, Annelida, Arthropoda, Echinodermata, and Chordata, collected from the shallow estuarine system near Beaufort, N.C. Least squares regression analysis showed a highly significant correlation between caloric content per gram dry weight and the percentage organic matter. Decalcification of molluscan tissues did not significantly lower caloric values. We observed significant differences for caloric values of species grouped by phylum, and an evolutionary trend toward increasing energy content per gram live weight. We also observed a frequency distribution of energy which was skewed toward lower values.

Existing publications on the caloric content of organisms (Golley, 1961; Slobodkin and Richman, 1961; Paine, 1964; Cummins, 1967; Brawn, Peer, and Bentley, 1968; Cummins and Wuycheck, 1970) list few species which spend all of or part of their life histories in estuaries. In 1968 we began a survey of the caloric content of estuarine organisms. With knowledge of the caloric content of these species-populations our data on biomass in the shallow system of estuaries near Beaufort, N.C., could be converted to standing crop energy to facilitate the analysis of energy flow in this system. The means for these populations are presented as calories per gram dry weight, per gram ash-free dry weight, and per gram live weight to permit investigators who do not have access to a calorimeter to estimate energy units for their estuarine biomass data.

[1] This research was supported through a cooperative agreement between National Marine Fisheries Service and U.S. Atomic Energy Commission.

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Manuscript accepted January 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

METHODS

Organisms were collected in the Newport River estuary and surrounding estuaries near Beaufort. Detailed descriptions of the hydrography of this shallow estuarine system are presented by Williams (1966), Williams and Murdoch (1966), and Thayer (1969). The Newport River has a mean depth of 1.2 m, and the water column generally lacks vertical stratification. Salinity and temperature range from 13 to 35‰ and 7° to 32°C. The sediments of this estuary are primarily of shell and sand near the ocean with finer sands, clays, and silts predominating toward the mouth of the river.

Organisms were processed promptly after collection. All organisms, except ctenophores, were rinsed with distilled water, blotted, and weighed. Ctenophores were rinsed with distilled water and weighed intact without blotting. Gut contents of all organisms were included in the analyses, and this may have accounted, especially in the case of ctenophores, for some of the variability in caloric measurements. Meats were removed from the larger molluscs by shucking and from the smaller molluscs by decalcification with 20% HCl. Decalcification normally required 2-4 min,

after which the meat and shell matrix were removed, rinsed with distilled water, blotted, and dried. The majority of organisms and molluscs meats were dried in a lyophilizer and ground to pass through a 40-mesh sieve. Samples collected during 1968 were dried at 60°C in an oven; no attempt was made to compare the results of caloric measurements on freeze-dried and oven-dried samples.

Caloric determinations were made with a Phillipson type oxygen microbomb calorimeter (Gentry Wiegert Instruments).[4] Three to eight pellet replicates, weighing from 5 to 25 mg dry weight each, were run for each sample. After each combustion a nitric acid determination and correction was made (Parr Instrument Co., 1960). In addition, sulfur content of each sample was determined (American Public Health Association, 1965) and a sulfur correction was made on each replicate. Subsamples of each material were ashed in a muffle furnace at 500°C for 36 hr. Caloric content on a dry weight and an ash-free dry weight basis were calculated according to the Parr Manual (Parr Instrument Co., 1960) and Phillipson (1964).

RESULTS AND DISCUSSION

We combusted 425 pellets of 93 samples representing 51 species-populations collected from the estuarine system near Beaufort. The values we obtained for ash content, percent dry weight, and caloric content based on dry weight, ash-free dry weight, and live weight are presented in Appendix Table 1. Some general conclusions have emerged from calorimetric studies, with which our data agree, but specific values and relations for an estuarine system have not been presented before.

We observed a statistically significant relation between energy content per gram dry weight and the percent of organic matter in the sample ($r = 0.857$; $d.f. = 91$) (Figure 1). The least squares regression equation was

$$Y = 0.0604X - 0.420,$$

where Y is kilocalorie per gram dry weight and X is the percent organic matter (ash-free dry weight) in the sample. This equation is similar to those obtained by chemical composition techniques (Ostaypenya and Sergeev, 1963) for marine and freshwater organisms:

$$Y = 0.0616X - 0.286$$

and for marine crustaceans and molluscs:

$$Y = 0.0617X - 0.531.$$

The similarity of the three regression equations suggests a general relation between the caloric content and the percent dry matter of all aquatic organisms. We are continuing to collect and analyze samples, however, to determine whether there are seasonal differences.

The linear regression suggests that if there are changes in chemical composition of the organic matter, primarily differences in the percent lipid material, they are obscured in this relation by relatively large amounts of inorganic substances in the dry tissues of the organisms. We therefore analyzed the correlation between energy content per gram organic matter and the percent organic matter in the samples. Where applicable, corrections for endothermy (Paine, 1964, 1966) were applied. The resulting correlation, although significant, was low ($r = 0.333$; $d.f. = 91$) indicating great scatter about the regression line. The least squares regression equation was:

$$K = 0.0183X + 3.991,$$

where K is kilocalorie per gram organic matter and X is the percent organic matter. The slope of this line is significantly greater than zero, indicating that the organic matter of the species tested did not have a constant proportion of lipid, protein, and carbohydrate materials. These chemical differences were not obvious from the regression analysis of energy per gram dry weight because they were masked by inorganic substances.

It is possible that acid digestion of molluscs may have altered their caloric content. Paine

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

(1966) stated that acid digestion would reduce the ash content and the endothermal effect but that the influence of this treatment on the caloric content of the treated samples is not known. Richards and Richards (1965) found small amounts of organic carbon were lost from *Nassarius trivitattus* during decalcification, and this would cause some loss of energy from the samples. Since the majority of gastropods and some of the pelecypods analyzed were decalcified prior to analysis (Appendix Table 1), we analyzed the effect of decalcification on the caloric content of eight sets of mollusc tissues, including three sets of *Modiolus demissus* from Virginia, North Carolina, and Georgia (Table 1).

To determine the maximum effect of decalcification larger organisms were decalcified for a longer period of time than in the routine analysis. Twelve organisms of each set were shucked and one-half of each group was placed in 20% HCl for 15 min (3-8 times longer than for routine analysis of small molluscs). All samples were then dried in a lyophilyzer, and the ash content of the dried material was measured after combustion for 36 hr in a muffle furnace at 500°C. Although decalcification generally tended to reduce the caloric values, in two cases, *Modiolus demissus* (from Virginia) and *Tagelus plebeius*, differences between untreated and decalcified tissue caloric values were significantly different at the 5% level (Table 1). These data suggest that although the shorter decalcification time employed in routine analysis may have lowered the caloric content of the molluscs through protein hydrolysis and extraction of carbon, the decrease probably was insignificant and would not have appreciably affected the regression equation.

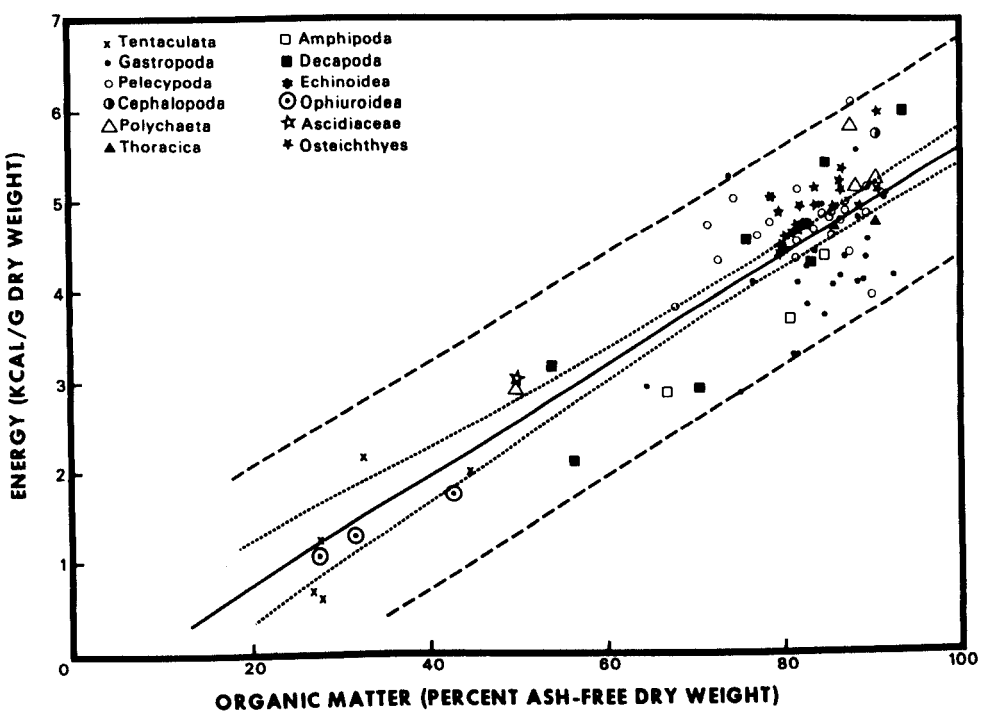

FIGURE 1.—Relation between the caloric and organic content of estuarine organisms. Solid line is the linear regression line; dashed line represents the 95% confidence limits for the prediction equation; dotted line represents the 95% confidence limits for the regression line.

TABLE 1.—Summary of changes in ash and caloric content of decalcified and nontreated tissues of some estuarine molluscs. In each case, six organisms were combined and six caloric measurements made for each combined sample. HCl treatments were for 15 min.

Organism	Collection area	Treatment	Ash %	kcal/g ash-free dry weight	± Standard deviation
Brachidontes recurvus	Florida	None	11.8	5.232	0.056
		HCl	2.5	5.034	0.081
Chione cancellata	North Carolina	None	10.5	5.817	0.096
		HCl	3.7	5.754	0.081
Mercenaria mercenaria	North Carolina	None	18.3	5.235	0.185
		HCl	11.1	5.282	0.045
Modiolus demissus	Virginia	None	11.9	5.036*	0.010
		HCl	3.6	4.783*	0.085
Modiolus demissus	North Carolina	None	15.7	5.118	0.046
		HCl	6.3	4.998	0.087
Modiolus demissus	Georgia	None	5.4	5.102	0.051
		HCl	4.8	5.053	0.095
Mytilus edulis	Virginia	None	13.5	5.006	0.046
		HCl	3.3	5.068	0.045
Tagelus plebeius	North Carolina	None	16.5	5.471*	0.104
		HCl	12.6	4.751*	0.166

*Significantly different at the 0.05 level.

Significant differences in energy content between phyla were observed on the basis of ash-free dry weights and live weights. The phyla show an orderly phylogenetic progression of energy content only on the basis of live weight (Table 2). This is partially the result of decreasing water content of more structurally advanced phyla; we observed significant differences among phylum means for water content which followed a similar trend. Not all phylum means were significantly different, however. The significant overall phylum effect can be attributed to ctenophores' having a significantly lower energy content than the annelids, arthropods, and chordates, but there are no significant differences among the foregoing three phyla nor among the ctenophores, echinoderms, and molluscs (Table 2). Also, within the phylum Mollusca and the class Crustacea the more advanced or more specialized groups (Cephalopoda and Decapoda) had significantly higher caloric contents per gram live weight than the less advanced groups. Although the values we obtained in this study may have resulted from a fortuitous selection of organisms, we feel that the species analyzed are representative of their phyla and that the relation between caloric content, percent dry weight, and percent organic matter, and the phylogenetic position reflects an evolutionary trend for increased caloric content per gram live weight as a result of increased proportion of living tissue with increasing phylogenetic position.

TABLE 2.—Analysis of variance of energy content, in kilocalorie per gram live weight, for all species examined, and listed in Appendix Table 1, and the mean kilocalorie per gram live weight for each taxon.

Source of variation	Degrees of freedom	Mean square	*F* ratio
Among phyla	5	2.494	34.01**
Within phyla	87	0.073	
Total	92	2.567	

Phylum	Mean kcal/g live weight
Ctenophora	0.049
Mollusca	0.373
Echinodermata	0.393
Annelida	0.850
Arthropoda	1.027
Chordata	1.156

**Significant at the 0.01 level.

The differences in caloric content may have arisen from variation in the growth or reproductive stage, or the energy content of the food source. The ctenophores and gastropods showed differences of as much as 1 kcal/g between sampling periods (Appendix Table 1, columns C and D). The variation in the gastropods may have

been the result of increased lipid content prior to spring spawning. We feel that the large variation observed for the ctenophores was partially the result of high energy food in the gut contents. February and March are periods of high zooplankton abundance in the Newport River estuary, and ctenophores may exert heavy predation pressure on zooplankton (Hyman, 1940; Herman, Mihursky, and McErlean, 1968). Consequently, high energy zooplankton (Comita and Schindler, 1963) in the gut may have caused the high caloric values obtained during this period.

The Osteichthyes showed trends in their caloric content which were associated with life history stages and feeding habits. Adult fishes did not show the temporal variation in caloric values which was observed for many of the other taxonomic groups (Appendix Table 1). Postlarval and juvenile stages generally had higher caloric (per unit dry weight and per unit ash-free dry weight) and lower ash contents than their adult stage. The higher caloric content per unit dry weight is of course partly due to the lower ash content. The higher caloric content per unit ash-free dry weight is probably the result of consumption of high energy food such as zooplankton (Comita and Schindler, 1963) by postlarval and juvenile fishes. Adult *Brevoortia tyrannus*, a planktonic feeder, tended to have have higher (but not significant) caloric values (mean 6.018 kcal/g ash-free dry weight) than adult carnivore-omnivore feeding types (mean 5.748 kcal/g ash-free dry weight). The higher values obtained for menhaden are not surprising since up to 28.7% of the wet weight of these fishes may be fats (Perkins and Dahlberg, 1971).

On the basis of limited data Slobodkin and Richman (1961) argued that the frequency distribution of energy (per gram ash-free dry weight) in a "haphazard collection of species" is skewed right, i.e., the modal frequency is at the lower end of the energy range. They explain this distribution by stating that ". . . there has always been selection for maximum number of reproducing progeny, but only sporadic selection for high energy content/gm." Even if there always has been selection for maximum number of reproducing progeny, the analysis of energy content relative to spawning time will affect the results. The argument also ignores the evolution of other life history strategies resulting in fewer offspring with higher survival rates (Mac Arthur and Wilson, 1967; Gadgil and Bossert, 1970) where there may be long-term storage of energy in individual organisms. Cummins and Wuycheck (1970) presented a frequency distribution similar to that of Slobodkin and Richman (1961) and stated that the distribution resulted from the predominance of plant values in their data. We suggest, with Paine (1964), that it may have been premature for Slobodkin and Richman to recognize a particular type of distribution. By combining the results of 15 species of invertebrates with Slobodkin and Richman's data on 17 species, Paine observed a more symmetrical distribution.

If, as indicated by our samples, there is an evolutionary trend toward increased energy content, the predominance of structurally more advanced species in our sample would result in a frequency distribution skewed left as shown in Figure 2. The predominance of advanced species in our samples is consistent with available check lists for the Beaufort area (Duke University Marine Laboratory, 1953; Turner and

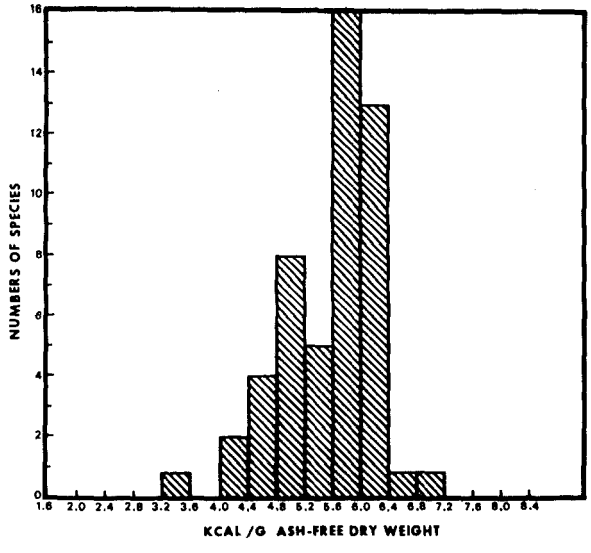

FIGURE 2.—Frequency distribution of energy in a system of shallow estuaries. The values are means for the 51 species presented in Appendix Table 1.

Johnson).[5] The mean of the distribution is 5.57 kcal/g ash-free dry weight, the median is 5.74 and the mode is 5.80. We are continuing to obtain caloric data on these and other species throughout the year to determine whether the frequency distribution of energy in organisms from the Newport River estuary is continually skewed left (Figure 2) or because of seasonal variations follows some other pattern, such as the normal distribution suggested by Paine (1964).

ACKNOWLEDGMENTS

We wish to thank the numerous individuals at the Atlantic Estuarine Fisheries Center for their assistance in the collection of organisms and for their advice during the preparation of this manuscript. Dr. Kenneth W. Cummins and Dr. David G. Frey were helpful in the initial review of the manuscript.

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APPENDIX TABLE 1.—Summary of data collected during caloric analysis of estuarine organisms.

Classification	Collection date	Combustions	(Col. A) Ash	(Col. B) Dry/ live wt	(Col. C)	(Col. D) Energy content	(Col. E)
		Number	%	%	*kcal/g dry wt*	*kcal/g ash-free dry wt*	*kcal/g live wt*
Ctenophora							
Class Tentaculata							
Mixed ctenophores	12-10-69	4	73.2	2.3	[1]0.652 ± 0.419	2.428 ± 1.563	0.014
Mixed ctenophores	1-10-70	6	72.5	2.7	0.579 ± 0.188	1.934 ± 0.546	0.016
Mixed ctenophores	1-22-70	4	72.7	2.8	1.210 ± 0.102	4.439 ± 0.373	0.082
Mixed ctenophores	2-5-70	4	55.5	3.9	2.000 ± 0.103	4.490 ± 0.224	0.079
Mixed ctenophores	3-17-70	4	67.6	2.4	2.178 ± 0.344	6.725 ± 1.062	0.054
Mean			68.3	2.8	1.324	4.003	0.049
Mollusca							
Class Gastropoda[2]							
Bittium varium	11-20-69	6	15.3	10.2	3.696 ± 0.111	4.357 ± 0.119	0.377
B. varium	12-17-69	5	16.4	9.1	4.414 ± 0.199	5.279 ± 0.236	0.402
B. varium	2-11-69	4	23.5	12.2	4.087 ± 0.129	5.334 ± 0.177	0.499
Mitrella lunata	11-20-69	5	18.3	14.8	3.274 ± 0.105	4.005 ± 0.127	0.485
M. lunata	1-14-70	5	7.7	16.1	4.139 ± 0.156	4.483 ± 0.169	0.666
M. lunata	2-11-70	4	10.6	12.5	4.533 ± 0.248	5.060 ± 0.286	0.567
Nassarius obsoletus	11-7-69	4	10.9	9.7	4.096 ± 0.098	4.595 ± 0.111	0.397
N. vibex	8-21-69	4	14.3	6.2	4.027 ± 0.123	4.698 ± 0.145	0.250
N. vibex	11-20-69	3	23.9	6.3	2.855 ± 0.110	3.752 ± 0.144	0.180
N. vibex	2-11-70	3	11.4	5.5	4.805 ± 0.091	5.425 ± 0.098	0.264
N. vibex	3-19-70	4	11.8	4.6	5.575 ± 0.123	6.319 ± 0.139	0.258
Anachis avara	10-29-69	3	18.9	7.3	3.288 ± 0.042	4.108 ± 0.147	0.240
A. avara	12-17-69	4	17.2	7.5	3.816 ± 0.175	4.583 ± 0.214	0.286
A. avara	1-14-70	4	13.8	6.5	4.158 ± 0.153	4.816 ± 0.200	0.270
A. avara	2-11-70	4	17.7	7.8	4.208 ± 0.222	5.099 ± 0.275	0.328
Crepidula convexa	12-17-69	3	35.7	8.8	2.908 ± 4.263	4.553 ± 0.410	0.256
C. fornicata	12-17-69	5	18.4	7.3	4.066 ± 0.132	4.981 ± 0.161	0.297
C. fornicata	4-15-70	4	15.4	6.0	4.957 ± 0.213	5.858 ± 0.252	0.272
C. fornicata (eggs)	4-15-70	4	36.5	7.8	5.248 ± 0.142	8.269 ± 0.223	0.408
Pyramidella fusca	1-14-70	3	11.7	8.6	4.081 ± 0.382	4.621 ± 0.432	0.351
P. fusca	2-11-70	4	26.1	4.0	5.287 ± 0.249	7.158 ± 0.339	0.211
Retusa canaliculata	1-14-70	3	10.7	7.8	4.357 ± 0.281	4.880 ± 0.314	0.340
R. canaliculata	2-11-70	4	8.8	6.2	5.014 ± 0.128	5.491 ± 0.147	0.311
R. canaliculata	3-19-70	4	8.8	5.9	5.072 ± 0.041	5.514 ± 0.044	0.314
Urosalpinx cinerea	2-11-70	3	13.0	4.6	4.369 ± 0.057	5.623 ± 0.060	0.201
Mean			16.7	[8]8.1	4.253	5.154	0.337
Class Pelecypoda							
Pecten irradians	1-14-70	4	12.1	6.0	6.106 ± 0.050	6.949 ± 0.052	0.366
Mercenaria mercenaria	1-2-69	7	25.4	3.1	5.040 ± 0.279	6.757 ± 0.374	0.156
M. mercenaria	12-17-69	5	13.4	3.8	4.793 ± 0.229	5.535 ± 0.264	0.182
Chione cancellata	1-2-69	5	14.4	4.4	4.886 ± 0.150	5.668 ± 0.216	0.215
C. cancellata	12-17-69	3	16.4	4.5	4.699 ± 0.141	5.623 ± 0.169	0.211
C. cancellata	2-11-70	4	18.8	7.7	4.369 ± 0.176	5.381 ± 0.221	0.336
C. cancellata[2]	3-19-70	3	10.5	[8]3.3	5.152 ± 0.072	5.754 ± 0.081	0.170
Tagelus divisus	4-25-69	6	12.2	12.3	4.414 ± 0.442	5.027 ± 0.504	0.543
Modiolus demissus	1-10-69	6	13.0	12.0	5.014 ± 0.342	5.765 ± 0.393	0.601
Crassostrea virginica	12-30-68	6	21.9	3.7	4.756 ± 0.235	6.090 ± 0.301	0.176
C. virginica	4-3-69	6	22.9	3.2	4.605 ± 0.308	5.973 ± 0.400	0.147
Anomia simplex	1-14-70	2	13.0	5.8	4.922	5.660	0.285
Teredo navalis	12-24-69	3	14.4	24.4	4.826 ± 0.079	5.639 ± 0.093	1.178
T. navalis	1-14-70	4	14.8	22.7	4.859 ± 0.165	5.703 ± 0.192	1.069
Macoma balthica[2]	1-14-70	3	10.0	[8]9.9	3.955 ± 0.146	4.391 ± 0.168	0.392
M. balthica[2]	2-11-70	4	18.2	[8]9.0	4.558 ± 0.119	5.776 ± 0.151	0.410
M. tenta[2]	2-11-70	4	27.2	[8]9.2	4.320 ± 0.020	5.935 ± 0.039	0.397
M. tenta[2]	3-19-70	4	28.3	[8]8.2	4.738 ± 0.085	6.611 ± 0.119	0.389
Pinna serrata	3-19-70	4	18.9	8.9	5.129 ± 0.200	6.322 ± 0.247	0.456
Anadara transversa	2-11-70	4	14.9	4.2	4.612 ± 0.134	5.425 ± 0.157	0.194
A. transversa	3-19-70	4	10.3	3.5	4.884 ± 0.088	5.462 ± 0.098	0.171
Mean			16.7	8.1	4.792	5.783	0.383
Class Cephalopoda							
Loligo brevis	12-31-68	5	9.4	18.3	5.743 ± 0.359	6.342 ± 0.398	1.051

See footnote at end of table.

APPENDIX TABLE 1.—Summary of data collected during caloric analysis of estuarine organisms.—Continued.

Classification	Collection date	Combustions	(Col. A) Ash	(Col. B) Dry/ live wt	(Col. C)	(Col. D) Energy content	(Col. E)
		Number	%	%	*kcal/g dry wt*	*kcal/g ash-free dry wt*	*kcal/g live wt*
Annelida							
Class Polychaeta							
Amphitrite ornata	1- 2-69	7	50.7	25.4	2.912 ± 0.311	5.906 ± 0.616	0.303
Diopatra cuprea	4-28-69	6	11.9	25.4	5.176 ± 0.433	5.878 ± 0.492	1.315
Nereis pelagica	11-20-69	3	12.2	16.6	5.854 ± 0.128	6.671 ± 0.144	0.972
N. pelagica	2-11-70	3	9.5	15.4	5.252 ± 0.184	5.827 ± 0.204	0.808
Mean			21.1	20.7	4.798	6.070	0.849
Arthropoda							
Order Thoracica[2]							
Balanus balanoides	12-24-69	6	14.1	10.2	4.715 ± 0.235	5.326 ± 0.275	0.481
B. balanoides	1-14-70	5	9.6	10.4	4.777 ± 0.242	5.273 ± 0.278	0.497
Mean			11.8	[3]10.3	4.746	5.299	0.489
Order Amphipoda							
Carinogammarus mucronatus	10-29-69	4	19.4	26.7	3.694 ± 0.322	4.582 ± 0.400	0.986
C. mucronatus	2-11-70	4	15.5	24.7	4.397 ± 0.054	5.202 ± 0.057	1.086
Amphithoe longimana	11-20-69	4	33.3	31.4	2.909 ± 0.188	4.358 ± 0.281	0.913
A. longimana	1-14-70	6	32.3	31.6	3.820 ± 0.209	5.647 ± 0.309	1.207
Mean			25.1	[4]28.6	3.705	4.947	1.048
Order Decapoda							
Paleomonetes pugio	12-31-68	6	15.3	27.4	5.416 ± 0.424	6.393 ± 0.501	1.484
Callinectes sapidus—adult	1-22-69	6	46.4	32.6	3.202 ± 0.375	5.974 ± 0.693	1.044
C. sapidus—immature	11-20-69	5	29.9	27.2	2.945 ± 0.251	4.204 ± 0.358	0.801
Pinnotheres ostreum	4- 8-69	6	6.5	18.5	6.034 ± 0.277	6.357 ± 0.303	1.116
Peneus setiferus	11- 4-69	6	17.7	23.3	4.735 ± 0.163	5.751 ± 0.197	1.103
Callianassa stimpsoni	11-20-69	6	17.1	26.3	4.249 ± 0.113	5.128 ± 0.135	1.117
Upogebia affinis	3-27-69	6	24.4	26.7	4.597 ± 0.376	6.080 ± 0.488	1.227
Libinia dubia	1-14-70	5	44.0	61.9	2.123 ± 0.200	3.215 ± 0.302	1.314
Mean			25.2	[4]30.5	4.163	5.388	1.151
Echinodermata							
Class Echinoidea							
Arbacia punctulata—meat	1-20-69	6	21.6	1.0	5.031 ± 0.467	6.416 ± 0.597	0.050
Class Ophiuroidea							
Ophioderma brevispina	11-20-69	1	72.5	52.3	1.043	3.797	0.551
O. brevispina	1-14-70	4	57.3	32.5	1.763 ± 0.255	4.601 ± 0.667	0.573
O. brevispina	3-19-70	4	68.7	30.7	1.289 ± 0.155	4.438 ± 0.532	0.397
Mean			66.2	38.5	1.365	4.279	0.507
Chordata							
Class Ascidiacea							
Mogula manhattensis	1- 3-69	6	50.3	7.3	3.002 ± 0.332	6.039 ± 0.668	0.219
Class Osteichthyes							
Lagodon rhomboides—adult	12-17-68	7	18.3	26.7	4.665 ± 0.126	5.709 ± 0.153	1.245
L. rhomboides—adult	11-25-69	7	20.6	24.5	4.399 ± 0.308	5.543 ± 0.388	1.078
L. rhomboides—post larval	1-14-70	4	9.2	11.2	6.001 ± 0.420	6.418 ± 0.422	0.672
Brevoortia tyrannus—adult	1-14-70	5	13.7	30.9	5.376 ± 0.210	6.112 ± 0.238	1.661
B. tyrannus—adult	1-22-70	5	13.9	30.2	5.202 ± 0.094	5.925 ± 0.107	1.571
B. tyrannus—post larval	4-22-69	6	9.2	18.5	5.128 ± 0.365	5.694 ± 0.454	0.949
Fundulus heteroclitus—adult	12-24-68	5	19.8	28.5	4.589 ± 0.109	5.722 ± 0.135	1.308
F. majalis—adult	12-17-69	5	20.7	30.2	4.880 ± 0.102	6.155 ± 0.132	1.474
Paralichthys dentatus—adult	8-21-69	7	16.3	23.3	4.927 ± 0.295	5.427 ± 0.345	1.148
P. dentatus—immature	1-14-70	4	11.3	20.7	4.953 ± 0.130	5.588 ± 0.144	1.025
Leiostomus xanthurus—adult	11-25-69	5	16.5	23.9	5.139 ± 0.126	6.152 ± 0.150	1.228
L. xanthurus—adult	5-28-69	5	18.0	22.1	4.948 ± 0.192	6.035 ± 0.234	1.094
Micropogon undulatus—adult	5-28-69	6	19.3	23.7	4.638 ± 0.184	5.744 ± 0.226	1.099
Mugil cephalus—adult	2-27-69	4	20.2	28.3	4.487 ± 0.196	5.393 ± 0.237	1.270
M. cephalus—post larval	1-22-70	2	13.7	24.8	5.142	5.959	1.275
Gobiosoma bosci—adult	10-29-69	4	19.4	32.1	4.758 ± 0.207	5.900 ± 0.256	1.527
Symphurus plagiusa—adult	11- 6-69	6	20.5	22.6	4.492 ± 0.120	5.650 ± 0.138	1.015
S. plagiusa—post larval	11- 6-69	6	14.5	22.5	4.904 ± 0.143	5.735 ± 0.171	1.103
Mean			16.4	24.7	4.924	5.826	1.208

[1] Mean ± 1 standard deviation.
[2] Decalcified with 20% HCl.
[3] Dry weight from dry weight of meat plus protein matrix of shell.
[4] Includes carapace.

NOTES

ATLANTIC THREAD HERRING (*OPISTHONEMA OGLINUM*) - MOVEMENTS AND POPULATION SIZE INFERRED FROM TAG RETURNS

Atlantic thread herring, *Opisthonema oglinum* (Lesueur), occur from Massachusetts southward along the Atlantic coast of the United States, throughout the Gulf of Mexico, and into the Caribbean (Berry and Barrett, 1963; Reintjes and June, 1961). In the South Atlantic area this species is occasionally caught by purse seine vessels fishing for menhaden, *Brevoortia tyrannus*. In the period 1968 through 1970 the catch of thread herring in the South Atlantic averaged 2,000 metric tons. Thread herring have been considered a potential supplement to the declining menhaden catch on the Atlantic coast, although very little is known about population size, distribution, or movement of this species.

The primary objective of this study was to determine if the thread herring population is large enough and is distributed widely enough to provide an alternate resource for the Atlantic menhaden fishery. In September 1968, we tagged 1,582 thread herring about 1 mile off the North Carolina coast: 299 approximately 2 miles west of Beaufort Inlet and 1,283 approximately 5 miles east of Bogue Inlet (Figure 1).

Tags were recovered on magnets at menhaden processing plants during the manufacture of fish meal. Magnets had been installed earlier at all of the plants for recovery of steel tags placed in menhaden. Primary magnets are located in the plant conveyor system between the fish scrap driers and the scrap storage shed. Almost all tags pass over these magnets the same day fish are processed. Secondary magnets were located at other positions in the conveyor system and may not recover tags until months after the fish are landed when the scrap is ground into meal or is shipped from the plant.

Test tags were placed in dead fish entering the plant to determine recovery efficiences. Each week 100 tags were put into fish at each plant, and recoveries throughout the season from these tests were averaged to determine the plants' recovery efficiency.

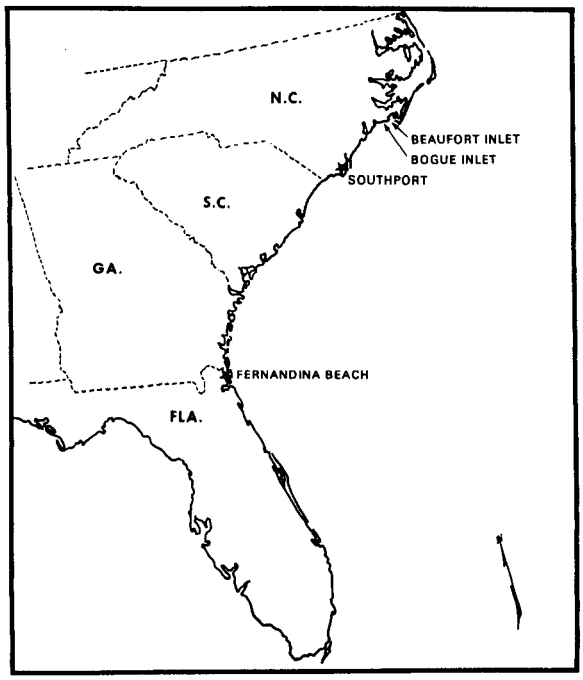

FIGURE 1.—South Atlantic coast of the United States showing areas of tag release and recovery.

Recovery Efficiencies

Average recovery efficiencies were calculated for each recovery area by recovery year. The following formula was used to determine recovery efficiency for each test:

$$\text{Recovery efficiency} = \frac{\text{Number of test tags recovered}}{\text{Number of test tags released}}$$

Methods and Materials

The tags and methods currently being used to tag menhaden were applied to thread herring.

A manually operated gun with a magazine holding 100 tags (14 mm × 3 mm × 0.5 mm) was used to insert the tags. Individually numbered tags enabled us to determine species, date, and location tagged, and date and location recovered. The gun was designed so that approximately 5 mm of the tag protruded from its barrel. The incision for inserting the tag was made by pushing the tag through the body wall. By holding the end of the barrel against the fish and depressing the plunger, a tag was inserted approximately 5 mm through the body wall into the body cavity (Figure 2). Tests were not performed to determine tagging mortality. However, experiments on menhaden indicate a tagging mortality—tag shed rate of 10-20% for fish over 110 mm having this tag.[1]

Thread herring were tagged aboard menhaden carrier vessels. Fish were dipped from the purse seine, placed in live boxes (2 ft × 2 ft × 4 ft) supplied with running seawater, tagged, and immediately released overboard. Each box held 200-500 thread herring (average 150 mm fork length) for as long as 45 min. Fish did not exhibit overexcitement or die when held in these numbers. Water temperature was 23°C. Average recovery efficiencies and the range of efficiencies are shown for each recovery area by year in Table 1. All recovery efficiencies were calculated from recoveries on primary magnets except the Fernandina Beach, Fla., area in 1968. Only one tag was recovered there on a secondary magnet. Using the average recovery efficiencies, we estimated the total number of tagged fish recaptured from our field tagging (Table 2).

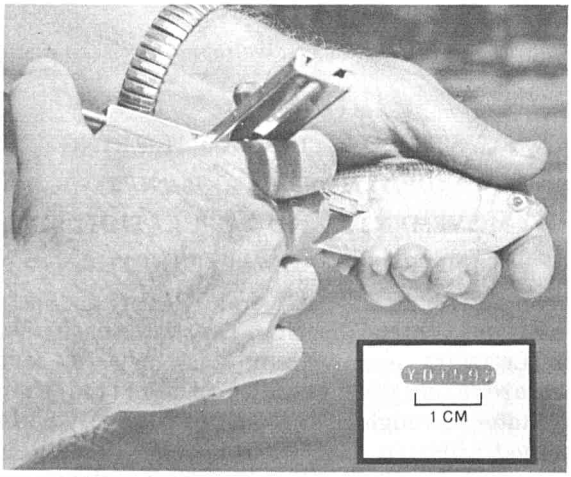

FIGURE 2.—Close-up of thread herring being tagged. Inset: Stainless steel tag.

Movements

Directions of the movements of fish were determined from recaptures of tagged thread herring (Figure 3). In the South Atlantic the menhaden fishing fleets operate near the processing plants, and catches are landed on the same day they are caught. A daily inspection of magnets enabled us to determine the area and date of tag recapture.

In 1968 an estimated 92 tagged fish were recaptured. Twelve of these tagged fish were recaptured near Southport, N.C., about 75 miles south of the release site within 25 days after release. Two months after release, the fish had migrated about 370 miles south to Fernandina

[1] Kroger, R. L., and R. L. Dryfoos. Preliminary tagging and tag-recovery experiments with Atlantic menhaden, *Brevoortia tyrannus*. Manuscript in preparation. National Marine Fisheries Service, Atlantic Estuarine Fisheries Center, Beaufort, NC 28516.

TABLE 1.—Tag recovery efficiencies by year and location where tagged thread herring were recovered, 1968-70.

Recovery year	Recovery location: Chesapeake Bay, Va.		Beaufort, N.C.		Southport, N.C.		Fernandina Beach, Fla.	
	Average	Range	Average	Range	Average	Range	Average	Range
	Percent recovery							
1968	No recoveries		52	47-65	67	60-78	33	28-62
1969	67	25-81	49	36-72	77	46-98	22	5-67
1970	No recoveries		No recoveries		70	46-92	No recoveries	

TABLE 2.—Actual and estimated numbers of tagged thread herring recaptured, 1968-70, from 1,582 releases near Beaufort, N.C., September 1968.

Recovery date	Recovery location							
	Chesapeake Bay, Va.		Beaufort, N.C.		Southport, N.C.		Fernandina Beach, Fla.	
	Actual	Estimated	Actual	Estimated	Actual	Estimated	Actual	Estimated
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
1968								
September			39	75				
October			1	2	8	12		
December							1	3
1969								
May					1	1		
July	1	2						
September			7	14	8	11		
October					7	9		
November							2	9
December			1	2				
1970								
October					3	4		

Beach, as indicated by the estimated recapture of three fish there. The Florida recaptures were made prior to November 15, the last day thread herring were caught. The tags were recovered in December on a secondary magnet.

In the spring of 1969 no thread herring were landed. The single recovery in Southport was most likely a holdover from the previous season. There was no offshore spring fishery near Beaufort; thus no possibility of recoveries there.

The recaptures in Chesapeake Bay, Va., came from fish that could have been caught off the northern coast of North Carolina and transported to the Bay as some Chesapeake Bay vessels fished off the North Carolina coast during that period. The plant did not report any thread herring landings, so the thread herring probably were mixed with menhaden.

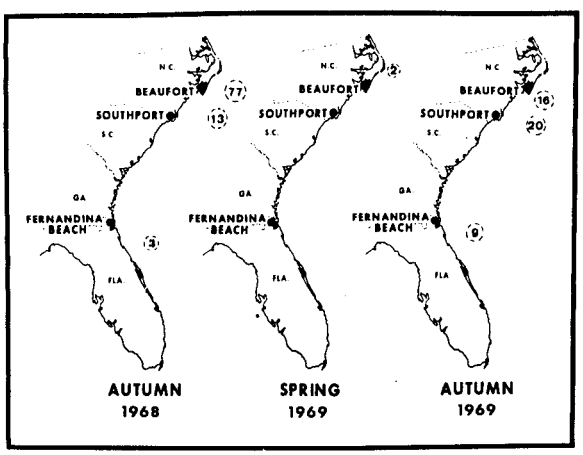

FIGURE 3.—Southerly movements of Atlantic thread herring along South Atlantic coast of the United States, 1968-70.

In the autumn of 1969 tagged thread herring were recaptured sequentially along the South Atlantic coast from Beaufort to Fernandina Beach, again indicating a southerly fall migration. An estimated 16 were recaptured in September at Beaufort, 20 in September and October at Southport, and 9 in December at Fernandina Beach. The December recoveries at Beaufort are the result of tags probably lodged in the conveyor system because thread herring were landed only in September.

In 1970 thread herring were landed only during the autumn. Four fish were estimated recaptured at Southport in October. There was no fishing at Fernandina Beach in late October and November when thread herring are usually caught in that area.

Results from this experiment indicate that thread herring migrate south in the autumn along the South Atlantic coast (Figure 3). Southerly migration rates were estimated from elapsed time and distance between areas. In 1968, about 10 days after release, several tagged fish were recaptured near Cape Fear, N.C., 75 miles south of the tagging site. An additional recapture was made about 370 miles south off

Florida within 53 days after release. The average distance traveled each day from Beaufort to Cape Fear and from Beaufort to Florida was 7.0 miles. In 1969 elapsed time between first recaptures at Beaufort and Florida was 56 days, resulting in an average distance traveled of 6.6 miles per day. From Southport to Florida, the elapsed time was 48 days or 6.1 miles per day. From these recoveries, we estimate that thread herring migrate south in fall at a rate of 6 to 7 miles per day.

Population Size

An estimate of the size of the thread herring population moving south from Beaufort to Southport, in September 1968, can be made using the number tagged (less those recaptured before leaving the Beaufort area), the estimated number recaptured at Southport, and the catch at Southport (Table 3). An estimate of population size from our tagging data requires the assumption that the entire population moves as a group. That assumption is supported by the fact that tagged fish were recaptured with almost all thread herring catches.

For this estimate we are given (Ricker, 1958):

C = Number of thread herring landed at Southport.

M = Effective number of tagged fish at large.

R = Estimated number of tagged fish recaptured at Southport.

$\hat{N}$ = Estimated population size.

then,

$$\hat{N} = \frac{M\,(C+1)}{R+1}$$

or

$$\hat{N} = \frac{(1{,}505)\ (6{,}535{,}583)}{14}$$

$$= 702.6 \text{ million fish} \pm 355.6 \text{ million (95\% confidence interval)}$$

This estimate, made so soon after tagging, could be misleading. No adjustment is possible for the degree of mixing of tagged with untagged fish in the population. Fishing at Southport may have been concentrated on the tagged portion of the population. No adjustment was made for tag loss from shedding and mortality. These effects would produce an underestimate of the stock size. On the other hand, this calculation might overestimate population size because we were unable to determine rate of recruitment.

TABLE 3.—Thread herring landings and estimated number of tags recovered by area from 1968-70.

Area	1968	1969	1970
Chesapeake Bay, Va.			
Number of fish landed	0	[1]0	0
Number tags recovered	0	2	0
Beaufort, N.C.			
Number of fish landed	14,385,394	15,737,303	8,259,404
(metric tons)	(849.4)	(898.6)	(453.4)
Number tags recovered	77	16	0
Southport, N.C.			
Number of fish landed	6,535,582	19,548,161	34,383,824
(metric tons)	(385.9)	(1,116.2)	(1,887.5)
Number tags recovered	13	20	4
Fernandina Beach, Fla.			
Number of fish landed	5,275,548	2,367,776	[2]0
(metric tons)	(311.5)	(135.2)	
Number tags recovered	3	9	0

[1] None of the landings were reported as thread herring.
[2] Fishing terminated early in October before thread herring normally are caught in area.

The one tag recovery from Florida was not used to estimate population size. A single recovery and a low magnet efficiency provide an imprecise estimate of recaptures.

Another estimate can be made using the recoveries and landings from September through November 1969. In this case, sufficient time elapsed for mixing of tagged fish in the population, but tag loss or recruitment were not taken into account. In this estimate:

$$\hat{N} = \frac{(1{,}487)\ (37{,}653{,}241)}{46}$$

$$= 1{,}217.2 \text{ million fish} \pm 355.1 \text{ million (95\% confidence interval)}$$

We feel these estimates, although very gross, are indicative of the population size for the purpose of this study. The catch of thread herring in 1968 was approximately 1,547 metric tons and in 1969 was 2,150 metric tons (Table 2), while in 1968 and 1969 the average catch of men-

haden in the South Atlantic summer fishery alone was 34,435 metric tons.

Estimates of the thread herring population size expressed in metric tons equal approximately 45,000 ± 23,000 in 1968 and 71,000 ± 21,000 in 1969. The 95% confidence intervals suggest that true population size might vary from 22,000 to 92,000 metric tons. Thus, the thread herring resource appears capable of supporting a larger fishery at this time since not more than 10% of the population was harvested in 1968 or 1969, but it does not appear to have the capacity to offer an alternate resource for the Atlantic menhaden fishery. Thread herring distribution is generally limited to the South Atlantic area, whereas Atlantic menhaden are distributed along most of the Atlantic coast of the United States. A 50% harvest rate, at most, would amount to little more than the present menhaden landings in the South Atlantic summer fishery.

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MERISTIC CHARACTERS OF SOME MARINE FISHES OF THE WESTERN ATLANTIC OCEAN[1]

This report presents data on meristic characters from radiographs of 642 species of marine fishes representing 113 families, collected from Cape Hatteras, N.C., to northern Brazil, including the Gulf of Mexico and the Caribbean Sea. Most of the specimens were collected on cruises of the National Marine Fisheries Service. The chartered vessel *Silver Bay* and the NMFS research vessel *Oregon* made these cruises from the Exploratory Fishing and Gear Research Base, Pascagoula, Miss., and the Exploratory Fishing and Gear Research Station, St. Simons Island, Ga. Additional material was obtained from shrimp trawling and beach seining in coastal Georgia. Papers by Hollister (1936, 1937a, b, 1940, 1941), Clothier (1950), Hubbs and Lagler (1958), and Lagler, Bardach, and Miller (1962) were helpful in determining vertebral and other skeletal characters. The phylogenetic arrangement and spelling of families, genera, and species were made, when applicable, in accordance with the American Fisheries Society's *List of Common and Scientific Names of Fishes* (Bailey, 1970).

Methods and Procedures

We x-rayed at least four specimens of most species; for some species fewer than four were available. Specimens ranged from 12 to 580 mm standard length (SL). Specimens smaller than about 60 mm SL were x-rayed with a soft-ray machine and larger specimens with a hard-ray machine.

Counts of precaudal and caudal vertebrae, dorsal and anal spines, and soft rays, and primary and secondary caudal rays were made with the aid of a dissecting microscope or an x-ray illuminator. These meristic counts for all species were made independently by each of us;

[1] Contribution No. 99, National Marine Fisheries Service, Southeast Fisheries Center, Brunswick Laboratory, Brunswick, GA 31520.

we exchanged radiographs and checked each other's work; then at a later date and following the same procedures, we reread the radiographs.

The counts (Table 1) very likely do not represent the complete range for any species because too few specimens have been examined. Counts from specimens with obvious deformities or any recognizable abnormality or aberration are not included. When more than one separate dorsal or anal fin is present, and composed of soft rays only (e.g., Gadidae and Moridae), the count for the anterior fin is followed by a comma and the count for the posterior fin. Dashes are used to separate counts, or to replace counts to indicate that we were unable to make an accurate count from the radiograph.

In the dorsal fin in *Macrozoarces americanus* (Zoarcidae), two groups of soft rays are separated by spines. Finlets in Carangidae, Gempylidae, Scomberesocidae, and Scombridae are separated from fin-ray counts by a plus (+) sign. A plus sign is also used to show a divided anal fin in Sternoptichidae.

Cyclopterus lumpus and *Enchelyopus cimbrius* normally occur north of the study area, but their meristics were available and are included in this paper for comparative purposes. Some species which are anadromous have been included, e.g., *Alosa sapidissima,* even though the adults have been taken only in fresh or brackish waters. Other species, e.g., *Agonostomus monticola,* are reported in the literature as occurring in fresh water only but are included here because at times they have been found in the ocean (Anderson, 1957).

Definitions

In the following definitions we have tried to provide a general scheme for distinguishing the meristic characters of 642 different species although all specimens of all 642 species do not agree with our guidelines.

Total vertebrae: All vertebrae, includes the anteriormost centrum, and the urostyle which we count as the terminal centrum.
Precaudal vertebrae: Vertebrae with no hemal arches or hemal spines.
Caudal vertebrae: Vertebrae with hemal spines; typically the first hemal spine is associated with one or more anterior proximal radial elements of the anal fin. Our definition of precaudal and caudal vertebrae will not work for all species because in certain groups, e.g., Clupeidae, transitional centra may be present. If transitional centra are known to occur, the total number of vertebrae is a more meaningful character than a precaudal and caudal vertebral separation.
Spines: All true spines are median unpaired structures, without segmentation; they are usually stout and rigid with sharp tips and are never branched.
Rays (Soft rays): Are usually, though not always, branched and flexible, and are paired and segmented. Dorsal and anal fin-ray counts include all rays observed. If the terminal ray is bifid and articulated with a single pterygiophore, it is counted as one ray. Dorsal or anal fin spines are tabulated as a group; a spine in the second fin (if a spine is present) is counted with the spines of the anterior fin.

We distinguished caudal primary (principal) soft rays as those which articulate with the hypural bones. Typically the primary rays include all of the branched rays plus one dorsal and one ventral unbranched ray. In some species the primary caudal rays may all be branched. Some species have primary rays only. Primary rays often overlap onto the epural bones or hemal spine of the penultimate vertebra, and our personal judgment, based upon our interpretation of the literature, was used to determine if the ray was primary or secondary (procurrent). In a few species no distinction between primary and secondary rays could be made from the radiograph, and the total number of caudal soft-rays is listed.

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TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE Total	VERTEBRAE Precaudal	VERTEBRAE Caudal	DORSAL FIN Spines	DORSAL FIN Rays	ANAL FIN Spines	ANAL FIN Rays	CAUDAL FIN Total	CAUDAL FIN Dorsal secondary rays	CAUDAL FIN Dorsal primary rays	CAUDAL FIN Ventral primary rays	CAUDAL FIN Ventral secondary rays
	mm	No.	Number											
ACANTHURIDAE														
Acanthurus bahianus	48	1	22	9	13	9	27	3	22	28	6	8	8	6
Acanthurus chirurgus	27-110	5	22	9	13	9	23-24	3	21-23	26	5	8	8	5
Acanthurus coeruleus	26- 81	4	22	9	13	9	26-28	3	25	26-27	5	8	8	5-6
ALBULIDAE														
Albula nemoptera	310	1	77	46	31	0	22	0	9	35	9	10	9	7
Albula vulpes	130-170	3	69	42	27	0	18-19	0	8- 9	33	8	10	9	6
ALEPISAURIDAE														
Alepisaurus ferox	105-145	2	50-51	-	-	0	-	0	-	35-38	-	-	-	-
ANOPLOGASTERIDAE														
Anoplogaster cornuta	55- 82	2	25-27	12	13-15	0	16-18	0	9	-	6	-	9	6-7
ANTENNARIIDAE														
Antennarius multiocellatus	41- 60	2	18	10	8	3	12	0	6- 7	9	0	4	5	0
Antennarius ocellatus	57	1	19	10	9	3	13	0	8	9	0	4	5	0
Antennarius radiosus	66- 98	4	19	10	9	3	13	0	8	9	0	4	5	0
Antennarius sanguineus	33	1	19	10	9	3	13	0	7	9	0	4	5	0
Histrio histrio	70- 84	4	18	10	8	3	12	0	7	9	0	4	5	0
Lophiocharon tenebrosus	66	1	18	10	8	4	12	0	7	9	0	4	5	0
Phrynelox scaber	57- 86	3	18	10	8	3	12	0	7	9	0	4	5	0
ARGENTINIDAE														
Glossanodon pygmaeus	62- 82	4	45	23	22	0	10-11	0	10	38-40	9-11	10	9	9-10
Microstoma microstoma	195	1	47	31	16	0	12	0	8	40	11	10	9	10
ARIIDAE														
Arius felis	94-145	4	50-52	22	28-30	2	7	0	18-19	53-55	19-20	7	8	19-20
Bagre marinus	152-164	2	53-54	22	31-32	2	7	0	26-28	58-59	22-23	7	8	21
ASTRONESTHIDAE														
Astronesthes similis	42- 85	4	53-55	37	16-18	0	11-12	0	19-20	32-35	8- 9		9	5- 7
ATELEOPIDAE														
Ijimaia antillarum	220-325	4	127-129	29-31	97-100	0	9	0	82-89	-	-	-	-	-
ATHERINIDAE														
Allanetta harringtonensis	58- 64	4	43-44	22-23	21	7-8	10	1	11	33-36	8- 9	9	8	8-10
Membras martinica	54- 92	3	43	19	24	5	7-8	1	18-19	32-35	7- 8	9	8	8-10
Menidia beryllina	30- 37	4	41-42	18	23-24	5	6-8	1	17-18	-	-	9	8	-
Menidia menidia	28- 57	4	39-41	16-17	23-24	5	7-8	1	21-25	35-38	9-11	9	8	9-10
AULOPIDAE														
Aulopus nanus	133-195	2	48	33	15	0	15	0	11-12	34-35	8- 9	10	9	7
AULOSTOMIDAE														
Aulostomus maculatus	90-225	2	57	21	36	10	28	0	29	20	3	7	7	3
BALISTIDAE														
Alutera heudeloti	89-174	3	20	7	13	2	36-39	0	40-42	12	0	6	6	0
Alutera monoceros	121	1	23	7	16	2	47	0	50	12	0	6	6	0
Alutera schoepfi	95-165	4	23	7	16	2	33-35	0	35-37	12	0	6	6	0
Alutera scriptus	52-118	4	21	7	14	2	44-47	0	47-49	12	0	6	6	0
Balistes capriscus	155-174	3	18	7	11	3	27-28	0	24-25	12	0	6	6	0
Balistes vetula	105-180	3	18	7	11	3	29-30	0	27-28	12	0	6	6	0
Cantherhines pullus	51- 92	4	19	7	12	2	34-36	0	30-32	12	0	6	6	0
Canthidermis maculatus	49- 85	4	18	7	11	3	24	0	21-22	12	0	6	6	0
Canthidermis sufflamen	59- 90	4	18	7	11	3	26-28	0	23-25	12	0	6	6	0
Monacanthus ciliatus	66- 68	4	19	6	13	2	30-32	0	31-32	12	0	6	6	0
Monacanthus hispidus	72-123	6	19	7	12	2	32-34	0	32-34	12	0	6	6	0
Monacanthus setifer	77-111	9	19	7	12	2	27-30	0	27-31	12	0	6	6	0
Xanthichthys ringens	40- 65	4	18	7	11	2	29	0	24-25	12	0	6	6	0
BATHYCLUPEIDAE														
Bathyclupea schroederi	109-125	4	31	10	21	1	9	1	38	33-35	8- 9	9	8	8- 9
BATHYPTEROIDAE														
Bathypterois bigelowi	105-113	4	49-51	24-25	25-26	0	12-13	0	8-10	27-29	45	10	9	4- 5
BATRACHOIDIDAE														
Opsanus beta	115-158	3	32	10	22	3	24-25	0	21-22	18	2	7	7	2
Opsanus pardus	111-184	2	34	11	23	3	26	0	22	18	2	7	7	2
Opsanus tau	121-160	3	34-35	11	23-24	3	27	0	22-23	18	2	7	7	2
Porichthys porosissimus	82-147	5	44-45	12	32-33	2	36-37	0	33-34	15	2	6	7	0
Thalassophryne maculosa	35- 59	2	26	8	18	2	18	0	16-17	16	2	6	7	1
BELONIDAE														
Ablennes hians	70-350	4	93-95	60-62	33	0	23-25	0	26	25-28	5- 7	7	8	5- 6
Platybelone argalus	171-295	4	71	44-45	26-27	0	13	0	17-19	22-25	2- 5	7	8	5
Strongylura marina	175-188	4	73-74	47-48	25-26	0	15-16	0	18-19	24-25	4- 5	7	8	5
Strongylura notata	186-287	4	58-59	36-37	21-22	0	13-14	0	14-15	25-26	5	7	8	5- 6
Tylosaurus acus	124-193	4	91	60-62	29-31	0	23-24	0	20-21	28-29	6- 7	7	8	7
Tylosaurus crocodilus	108-235	4	82	54-55	27-28	0	21-22	0	20-21	28-30	6- 7	7	8	7- 8
BERYCIDAE														
Beryx decadactylus	180	1	24	10	14	4	14	4	29	28	5	10	9	4
BLENNIIDAE														
Chasmodes bosquianus	52- 70	4	34-35	10	24-25	11	18-19	2	18-19	19	3	7	6	3
Chasmodes saburrae	41- 60	4	33-34	10	23-24	11	17-18	2	17-18	17-19	2- 3	7	6	2- 3
Entomacrodus nigricans	40- 62	4	34	11	23	13	14-15	2	16	26-27	7	7	6	6- 7
Hypleurochilus geminatus	33- 43	4	32-33	10	22-23	12	14-15	2	16-17	21-23	4- 5	7	6	4- 5
Hypsoblennius hentzi	66- 86	4	32-34	10	22-24	12	15	2	16-17	23-24	5- 6	7	6	5
Hypsoblennius ionthas	85	1	33	10	23	12	15	2	17	23	5	7	6	5
Ophioblennius atlanticus	59- 65	5	33	10	23	12	20	2	21	27-29	7- 8	7	6	7- 8

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRATE Total	VERTEBRATE Precaudal	VERTEBRATE Caudal	DORSAL FIN Spines	DORSAL FIN Rays	ANAL FIN Spines	ANAL FIN Rays	CAUDAL FIN Total	CAUDAL FIN Dorsal secondary rays	CAUDAL FIN Dorsal primary rays	CAUDAL FIN Ventral primary rays	CAUDAL FIN Ventral secondary rays
	mm	No.	Number											
BOTHIDAE														
Ancylopsetta antillarum	111-200	4	36	10	26	0	62-69	0	51-54	18	1	9	8	0
Ancylopsetta cycloidea	107-153	4	34-35	10	24-25	0	65	0	49-51	18	1	9	8	0
Ancylopsetta dilecta	126-154	4	36	10	26	0	72-75	0	54-58	18	1	9	8	0
Ancylopsetta kumperae	110-220	4	36	10	26	0	76-79	0	60-63	18	1	9	8	0
Ancylopsetta microctenus	94-218	4	35	10	25	0	62-71	0	51-55	18	1	9	8	0
Ancylopsetta quadrocellata	69-195	4	37	11	26	0	68-73	0	54-57	18	1	9	8	0
Bothus lunatus	54-232	7	40	10	30	0	91-98	0	72-75	17	0	9	8	0
Bothus maculiferus	132-217	3	39-40	10	29-30	0	91-98	0	72-76	17	0	9	6	0
Bothus ocellatus	70-134	4	35-37	10	25-27	0	79-85	0	61-64	17	0	9	8	0
Chascanopsetta prorigera	133	1	55	16	39	0	115	0	86	17	0	9	8	0
Citharichthys amblybregmatus	105	1	35	10	25	0	81	0	67	17	0	9	8	0
Citharichthys arctifrons	101-110	4	36-37	10	26-27	0	76-84	0	63-67	17	0	9	8	0
Citharichthys cornutus	68-77	4	35-36	9-10	25-26	0	79-82	0	63-65	17	0	9	8	0
Citharichthys dinoceros	80-98	4	37	10	27	0	91-94	0	71-73	17	0	9	8	0
Citharichthys gymnorhinus	47	1	34	10	24	0	74	0	59	17	0	9	8	0
Citharichthys macrops	100-147	4	34-35	10	24-25	0	79-84	0	62-63	17	0	9	8	0
Citharichthys spilopterus	87-129	5	34-35	10	24-25	0	75-80	0	57-61	17	0	9	8	0
Cyclopsetta chittendeni	162-169	4	36-37	10	26-27	0	85-87	0	65-68	17	0	9	8	0
Cyclopsetta fimbriata	152-177	4	36-37	10	26-27	0	82-84	0	62-65	17	0	9	8	0
Engyophrys senta	69-82	4	37-38	10	27-28	0	74-80	0	60-64	17	0	9	8	0
Etropus crossotus	109-120	4	35-36	10	25-26	0	79-82	0	63-66	17	0	9	8	0
Etropus microstomus	83-100	4	34-35	10	24-25	0	76-79	0	56-61	17	0	9	8	0
Etropus rimosus	80-95	4	34-35	10	24-25	0	77-79	0	57-63	17	0	9	8	0
Gastropsetta frontalis	112-186	4	37-38	10	27-28	0	61-64	0	46-51	17-18	0-1	9	8	0
Hippoglossina oblonga	156-211	4	41-42	11	30-31	0	76-82	0	61-67	18-19	1	9	8	0-1
Microlene antillarum	110-129	4	45-46	10-11	35-36	0	105-108	0	80-88	17	0	9	8	0
Microlene atrimana	80-118	2	52-53	11	41-42	0	117-121	0	98-103	[illegible]	0	9	8	0
Microlene megalepis	78-90	5	43-44	10	33-34	0	91-93	0	72-74	17	0	9	8	0
Microlene sessilicauda	91-130	4	46-47	10-11	36	0	93-104	0	76-83	17	0	9	8	0
Paralichthys albigutta	105-221	4	37	10	27	0	75-80	0	58-61	18	1	9	8	0
Paralichthys dentatus	137-173	4	41-42	11	30-31	0	87-90	0	66-70	18	1	9	8	0
Paralichthys lethostigma	95-213	4	37	10	27	0	82-90	0	64-71	18	1	9	8	0
Paralichthys squamilentus	161-195	3	38	10	28	0	76-85	0	60-64	18	1	9	8	0
Scophthalmus aquosus	111-120	4	34-36	11	23-25	0	64-71	0	50-54	17	0	9	8	0
Syacium gunteri	92-114	4	34-35	10	24-25	0	74-81	0	60-63	17	0	9	8	0
Syacium micrurum	97-154	4	34-35	10	24-25	0	85-87	0	67-70	17	0	9	8	0
Syacium papillosum	157-228	4	35-36	10	25-26	0	85-91	0	67-72	17	0	9	8	0
Trichopsetta caribbaea	84-156	23	41-43	10-11	31-33	0	95-102	0	75-81	17	0	9	8	0
Trichopsetta melasma	72-207	16	41-43	10-11	31-33	0	98-104	0	80-85	17	0	9	8	0
Trichopsetta orbiculus	97-117	2	40	10	30	0	91-92	0	70-73	17	0	9	8	0
Trichopsetta ventralis	75-143	18	40-41	10	30-31	0	89-95	0	69-75	17	0	9	8	0
BRANCHIOSTEGIDAE														
Malacanthus plumieri	222	1	24	10	14	6	53	1	51	39	12	8	7	12
BROMACEROTIDAE														
Bregmaceros atlanticus	42-48	4	47-49	13	34-36	0	44-46	0	46-47	31-32	-	-	-	-
CALLIONYMIDAE														
Callionymus agassizi	102-132	4	21	7	14	4	8	0	7	15	3	5	5	2
Draconetta acanthopoma	88	1	23	8	15	3	14	0	13	16	3	6	6	1
Draconetta oregona	70-103	3	23	8	15	3	14	0	13	16	3	6	6	1
CAPROIDAE														
Antigonia capros	44-87	4	22	10	12	8	33-35	3	30-32	19	4	6	6	3
Antigonia combatia	85-115	4	22	10	12	9	28-29	3	26-27	18-19	3-4	6	6	3
CARANGIDAE														
Alectis crinitus	71-91	4	24	10	14	7-8	19	3	16	35-36	9-10	9	8	9
Caranx bartholomaei	113-140	4	24	10	14	9	25-27	3	22-23	33-34	8-9	9	8	8
Caranx crysos	191-212	4	25	10	15	9	23	3	19-20	33-34	8-9	9	8	8
Caranx hippos	99-104	4	24	10	14	9	19-20	3	16-17	34	9	9	8	6
Caranx latus	51-160	4	24	10	14	9	20-21	3	17	33-34	8-9	9	8	8
Caranx ruber	82-137	4	24	10	14	9	27-28	3	24-26	32-35	8-9	9	8	7-9
Chloroscombrus chrysurus	88-125	4	24	10	14	9	26-27	3	26-27	32-35	8-9	9	8	7-9
Decapterus macarellus	180-195	4	24	10	14	9	32-33+1	3	25-26+1	35-36	9	9	8	9-10
Decapterus punctatus	125-155	4	25	10	15	9	31-33+1	3	26-28+1	35	9	9	8	9
Elagatis bipinnulata	60-90	4	24	10	14	7	25-26+1	2	18+1	34-39	7-11	9	8	10-11
Hemicaranx amblyrhynchus	41-54	2	26	10	16	9	28-29	3	24-25	34-35	9	9	8	8-9
Naucrates ductor	245	1	25	10	15	5	26	3	16	36	11	9	8	10
Oligoplites saurus	140-182	3	26	10	16	6-7	20	3	19-20	32-35	9-10	9	8	6-8
Selar crumenophthalmus	147-166	4	24	10	14	9	24-26	3	21-23	31-33	7-8	9	8	7-8
Selene vomer	94-142	4	24	10	14	9	21-22	3	17-18	32-33	8-9	9	8	7
Seriola dumerili	147-205	4	24	10	14	8	28-32	3	20-21	36-41	9-13	9	8	10-11
Seriola rivoliana	47-235	6	24	10	14	8	29-31	3	29-31	36-42	11-13	9	8	8-12
Seriola zonata	187-245	4	24	11	13	9	35-37	3	20	34-40	8-12	9	8	9-11
Trachinotus carolinus	125-182	4	24	10	14	7	24-25	3	21-22	32-33	8	9	8	7-8
Trachinotus cayennensis	327	1	24	10	14	6	26	3	27	32	8	9	8	7
Trachinotus falcatus	39-68	4	24	10	14	7	19-20	3	16-18	30-31	7	9	8	7
Trachinotus goodei	17-60	4	24	10	14	7	19	3	17-18	31-32	7-8	9	8	7
Trachurus lathami	120-150	4	24	10	14	9	29-31	3	27-28	35-37	9-10	9	8	9-10
Vomer setapinnis	117-160	4	24	10	14	9	21-22	3	16-18	32-34	8-9	9	8	7-8
CARAPIDAE														
Carapus bermudensis	126-165	3	118-122	16	102-106	0	-	0	-	0	0	0	0	0
CENTRISCIDAE														
Macrorhamphosus scolopax	68-115	4	24	8	15	7	10-11	0	18-19	27-28	9-10	4	5	9-10
CENTROPOMIDAE														
Centropomus ensiferus	122-280	3	24	10	14	9	9-10	3	6	36-38	10-11	9	8	9-10
Centropomus undecimalis	56-168	5	24	10	14	9	10	3	6	37-40	11-12	9	8	9-11
CHAETODONTIDAE														
Chaetodon aya	56-90	4	24	10	14	12-14	17-19	3	14-15	24-25	4-5	9	8	3-4
Chaetodon capistratus	49-67	3	24	10	14	12-13	18-20	3	16-17	23	3	9	8	3
Chaetodon ocellatus	99-130	4	24	10	14	12-13	18-20	3	16-17	23	3	9	8	3
Chaetodon sedentarius	82-99	4	24	10	14	13-14	21-23	3	17-19	22	3	9	8	3
Chaetodon striatus	28-92	4	24	10	14	12	20-21	3	16-17	23-24	3-4	9	8	3
Holacanthus bermudensis	98-140	4	24	10	14	14	18-19	3	18-19	25	4	9	8	4
Holacanthus ciliaris	62-183	3	24	10	14	14	20	3	20	25	4	9	8	4
Holacanthus tricolor	113-173	4	24	10	14	13-14	17-19	3	18-19	25	4	9	8	4
Pomacanthus arcuatus	77-128	4	24	10	14	10	28-29	3	22-23	24-25	4	9	8	3-4
Pomacanthus aureus	236-250	2	24	10	14	9	30-31	3	23-24	23-25	3-4	9	8	3-4
Prognathodes aculeatus	52	1	24	10	14	13	19	3	16	24	4	9	8	3
CHAULIODONTIDAE														
Chauliodus sloanei	145-185	4	50-52	-	-	0	5-6	0	11-12	-	7	10	9	-

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
CHAUNACIDAE														
Chaunax pictus	61-123	4	19-20	12	7-8	1	11-12	0	7	9	0	4	5	0
CHEILODIPTERIDAE														
Apogon aurolineatus	40	1	24	10	14	7	9	2	8	29	6	9	8	6
Apogon binotatus	30-60	3	24	10	14	8	8-9	2	7-8	31-32	7-8	9	8	7
Cheilodipterus affinis	39-54	3	24	10	15	7	9	2	7-9	32-34	7	9	8	5-7
Epigonus occidentalis	103-136	4	25	10	15	8	10	2	9	38-39	10-12	9	8	10-11
Epigonus pandionis	99-112	4	25	10	15	8	9-10	2	9	35-37	9-11	9	8	7-10
Phaeoptyx conklini	34-46	3	24	10	14	8	9	1-2	8	27-31	5-7	9	8	5-7
Phaeoptyx pigmentaria	44	1	24	10	14	7	9	2	8	30	7	9	8	6
Phaeoptyx pseudomaculatus	78-87	4	24	10	14	8	9	2	8	30-32	7-8	9	8	6-7
Phaeoptyx quadrisquamatus	42	1	24	10	14	8	9	2	8	31	7	9	8	7
Synagrops bella	118-160	4	25	10	15	10	9	2	7	35-36	10	9	8	8-9
Synagrops pseudomicrolepis	83-89	4	25	10	15	10	10	2	9	41-42	12-13	9	8	12-13
Synagrops spinosa	80-115	4	25	10	15	10	8-9	2	7	35	9	9	8	9
CHLOROPHTHALMIDAE														
Chlorophthalmus agassizi	107-127	7	46-48	18	28-30	0	10-12	0	8	43-46	13-14	10	9	11-13
Parasudis truculenta	135-140	4	39	17	22	0	10	0	8-9	40-42	11-13	10	9	11-13
CLINIDAE														
Labrisomus guppyi	30-57	3	35	11	24	19	10-11	2	18-19	29	8	7	6	8
Labrisomus nuchipinnis	90-110	4	34	11	23	18	12	2	18-19	28-30	8-9	7	6	7-8
Starksia y-lineata	12-14	2	31	10	21	19	7	2	14-15	-	-	-	-	-
CLUPEIDAE														
Alosa aestivalis	137-215	6	47-51	14-16	33-35	0	17-18	0	16-20	32-34	7-8	10	9	6-7
Alosa mediocris	118	1	54	17	37	0	19	0	22	35	9	10	9	7
Alosa sapidissima	103-121	5	56-57	18-19	37-38	0	16-19	0	19-21	33-34	7-8	10	9	7
Brevoortia gunteri	190	1	44	14	30	0	20	0	21	36	9	10	9	8
Brevoortia patronus	24-170	5	45-46	16	29-30	0	20-21	0	21-23	34-36	8-9	10	9	7-8
Brevoortia smithi	72-82	5	45-46	14-15	30-31	0	19-20	0	21-24	33-35	8	10	9	6-8
Brevoortia tyrannus	140-233	3	48	18-19	29-30	0	20-22	0	21-24	32-35	7-9	10	9	6-7
Clupea harengus	190-247	4	55-57	23-25	32-33	0	17-19	0	17-18	37-41	10-13	10	9	8-9
Dorosoma cepedianum	137-215	4	48-50	11-13	35-39	0	13-15	0	32-36	35-37	9-11	10	9	7
Dorosoma petenense	37-62	7	43-44	11-13	30-32	0	14-16	0	22-24	34-35	9	10	9	6-7
Etrumeus sadina	107-125	5	48-50	15-17	32-34	0	18-21	0	11-12	31-32	6-7	10	9	6
Harengula pensacolae	64-77	4	40-42	12-14	27-29	0	16-18	0	17-18	33-35	8-9	10	9	6-7
Jenkinsia lamprotaenia	27-47	8	38-42	19-21	19-21	0	10-12	0	13-15	23-24	3-4	9	8	3
Opisthonema oglinum	57-192	9	45-49	12-13	32-36	0	20-22	0	20-24	34-35	9	10	9	6-7
Sardinella anchovia	23-29	6	45-47	16	29-31	0	16-19	0	16-17	34	8	10	9	7
CORYPHAENIDAE														
Coryphaena equiselis	77-100	4	33	14	19	0	51-54	0	24-27	40-41	11-12	9	8	12
Coryphaena hippurus	91-130	4	31	13-14	17-18	0	58-60	0	27-28	39-43	11-13	9	8	10-13
CORYPHAENOIDIDAE														
Coelorhynchus carminatus	170-205	2	75-78	12	63-66	0	-	0	-	-	-	-	-	-
Nezumia bairdii	350	1	-	14	-	2	10	0	110	-	-	-	-	-
CYCLOPTERIDAE														
Cyclopterus lumpus	387	1	29	11	18	6	10	0	11	15	3	5	5	2
CYNOGLOSSIDAE														
Symphurus civitatus	108-132	4	47-49	9	38-40	0	90-91	0	73-75	12	0	6	6	0
Symphurus diomedianus	128-181	4	48-49	9	39-40	0	90-92	0	74-76	10-11	0	5	5-6	0
Symphurus marginatus	100-112	4	52-53	9	43-44	0	95-98	0	81-84	12	0	6	6	0
Symphurus minor	45-50	2	43	9	34	0	75-76	0	60	10-11	0	5	5-6	0
Symphurus piger	91-106	4	47-48	9	38-39	0	84-87	0	68-72	12	0	6	6	0
Symphurus plagiusa	121-135	4	46-48	9	37-39	0	86-89	0	70-72	10	0	5	5	0
Symphurus plagiusa	147-194	4	50-42	9	41-43	0	94-98	0	78-83	11-12	0	6	5-6	0
Symphurus pusillus	91-118	3	53-54	9	44-45	0	95-99	0	83-85	12	0	6	6	0
Symphurus urospilus	96	1	44	9	35	0	85	0	69	11	0	5	6	0
CYPRINODONTIDAE														
Cyprinodon variegatus	34-54	4	26-27	12	14-15	0	12-13	0	11-12	28-29	-	-	-	-
Floridichthys carpio	48	1	23	9	14	0	11	0	9	31	-	-	-	-
Fundulus grandis	65-111	4	33-35	15-16	18-20	0	11-12	0	11	38-42	-	-	-	-
Fundulus heteroclitus	62-72	4	33-34	14	19-20	0	11-12	0	10-11	36-40	-	-	-	-
Fundulus lucius	17-32	10	31-33	12-13	18-20	0	8-9	0	10-11	33-34	-	-	-	-
Fundulus majalis	30-85	4	34-35	15	19-20	0	13-14	0	10-12	37-40	-	-	-	-
Fundulus similis	44-81	5	35-36	15	20-21	0	12-13	0	11-12	36-40	-	-	-	-
DACTYLOPTERIDAE														
Dactylopterus volitans	110-162	4	22	8	14	-	8	0	6	15	3	5	5	2
DIODONTIDAE														
Chilomycterus schoepfi	60-115	5	18-20	-	-	0	10-12	0	9-11	9	0	4	5	0
Diodon holacanthus	97-125	4	-	-	-	0	12-14	0	12-15	9	0	4	5	0
Diodon hystrix	37-168	3	-	-	-	0	15	0	16	9	0	4	5	0
DIRETMIDAE														
Diretmus argenteus	82-95	4	29-30	13	16-17	0	25-26	0	20-21	29	5	10	9	5
ECHENEIDAE														
Echeneis naucrates	210-268	3	30	14	16	0	34-37	0	32-35	37-40	10-11	9	8	10-12
Echeneis neucratoides	103-137	2	30	14	16	0	37	0	33	40	13	9	8	10
Phtheirichthys lineatus	50-81	2	38-39	18	20-21	0	35	0	35	39	11	9	8	11
Remora remora	74-158	6	27	12	15	0	24-26	0	22-24	39-43	11-13	9	8	11-13
ELEOTRIDAE														
Dormitator maculatus	76-77	2	27	12	15	8	8	1	10	32-33	9	8	7	8-9
ELOPIDAE														
Elops saurus	180-233	4	78-80	55-56	24	0	26-28	0	18-19	36-37	9-11	10	9	7-8
Megalops atlanticus	75-115	3	55-56	33-34	22	0	16	0	24-25	32-33	7	10	9	6-7
EMMELICHTHYIDAE														
Emmelichthyops atlanticus	77	1	26	11	15	11	11	3	9	40	12	9	8	11

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
ENGRAULIDAE														
Anchoa cubana	48-67	3	40-44	21-24	19-21	0	14-15	0	22	32-34	7	10	9	6-8
Anchoa hepsetus	65-75	4	42-43	21-22	20-21	0	16	0	20-22	33-36	7-9	10	9	7-8
Anchoa lyolepis	51-82	3	41-43	21-22	20-21	0	14-15	0	21-22	32-35	7-8	10	9	6-8
Anchoa mitchilli	57-67	4	40-41	19	21-22	0	14-15	0	26-27	35-36	9	10	9	7-8
Anchoa spinifer	117-133	4	42-43	17	25-26	0	15-16	0	38-39	37-39	10-11	10	9	8-9
Anchoa tricolor	95	1	43	22	21	0	15	0	21	30	6	10	9	5
Anchoviella lepidentostole	63-70	4	40	19	21	0	14-15	0	22-24	31-36	6-9	10	9	6-8
Anchoviella perfasciata	28-35	4	43-44	-	-	0	14	0	-	-	-	10	9	-
Cetengraulis edentulus	117	1	41	20	21	0	16	0	25	35	8	10	9	8
Lycengraulis grossidens	140-145	2	43	20	23	0	15	0	27	35	8	10	9	8
EPHIPPIDAE														
Chaetodipterus faber	48-103	4	24	10	14	9	21-23	3	17-18	27-29	5-6	9	8	5-6
EXOCOETIDAE														
Cypselurus comatus	41-182	4	42	26-27	15-16	0	12	0	7-9	26-28	5-6	7	8	6-7
Cypselurus cyanopterus	49-100	4	44-45	30-31	14	0	12-13	0	9-10	27-29	5-6	7	8	7-8
Cypselurus exsiliens	45-186	2	44-45	30	14-15	0	15	0	10	27-28	5-6	7	8	7
Cypselurus furcatus	58-105	3	45-46	29-31	14-16	0	13-14	0	10	29-33	6-9	7	8	8-9
Cypselurus heterurus	197-228	4	46-47	31	15-16	0	13-14	0	9-10	26-29	5-6	7	8	6-8
Fuleptorhamphus velox	190	1	72	46	26	0	22	0	23	23	4	7	8	4
Exocoetus obtusirostris	157-177	3	44-45	26-27	18	0	14	0	14	26-28	5-6	7	8	6-7
Hemiramphus balao	57-70	4	54-56	38-39	16-17	0	13-14	0	11-13	24-27	5-6	7	8	4-6
Hemiramphus brasiliensis	50-90	4	52-53	35-37	16-18	0	13-15	0	12-13	24-25	5	7	8	4-5
Hirundichthys affinis	121-210	3	45-47	29	16-18	0	10-11	0	11-12	30	6	7	8	9
Hirundichthys rondeleti	212	1	45	29	16	0	12	0	12	28	6	7	8	7
Hyporhamphus unifasciatus	137-173	4	51-52	33-34	17-18	0	14-15	0	16	23-24	4-5	7	8	4
Oxyporhamphus micropterus	100-134	4	50	18-19	31-32	0	14-15	0	15-16	23	4	7	8	4
Parexocoetus brachypterus	97-115	4	39	23	16	0	12	0	13-14	23	4	7	8	4
Prognichthys gibbifrons	30-73	4	43-45	27-29	15-16	0	9-12	0	8-9	26-27	4-5	7	8	7
FISTULARIDAE														
Fistularia petimba	240-420	3	82-83	-	-	0	16	-	15	-	-	-	-	6
Fistularia tabacaria	245-470	2	84-85	-	-	0	15	0	14-15	26	6	7	7	6
GADIDAE														
Enchelyopus cimbrius	137-230	4	51-52	16	35-36	0	45-48	0	37-43	30-34	-	-	-	-
Melanogrammus aeglefinus	285	2	53-55	20-21	33-34	0	15,22,22-24	0	24,26,22-23	57-58	-	-	-	-
Merluccius albidus	165-185	4	51-52	25	26-27	0	12,13,36-37	0	37-38	39-42	-	-	-	-
Merluccius bilinearis	245-300	4	54	27-28	26-27	0	12,13,39-41	0	38-41	34-36	-	-	-	-
Phycis chesteri	198-265	4	47-49	15	32-34	0	10,55-60	0	48-54	28-31	-	-	-	-
Urophycis chuss	80-105	4	48	15	33	0	9-10,53-58	0	45-54	30	-	-	-	-
Urophycis cirratus	317-337	3	51	16	35	0	10,62-64	0	54-55	32	-	-	-	-
Urophycis earlli	282	1	46	15	31	0	10,59	0	53	30	-	-	-	-
Urophycis regius	82-177	4	45-46	13-14	31-33	0	8-9,47-51	0	45-50	30-32	-	-	-	-
Urophycis tenius	84-115	4	56-57	14-15	42	0	6,57-59	0	53-57	-	-	-	-	-
GEMPYLIDAE														
Gempylus serpens	210	1	53	34	19	32	12+8	3	-	29	4	9	8	8
Lepidocybium flavobrunneum	373	1	32	17	15	9	19+5	3	12+4	37	10	9	8	10
Neoepinnula orientalis	115-167	4	32	16	16	17	18	3	18	35-37	9-10	9	8	9-10
Nesiarchus nasutus	215-245	3	36	22	14	22-23	22-23	3	18-19	33-34	7-8	9	8	9
Ruvettus pretiosus	270-310	3	32	16	16	13-15	18-19+2	2	17-18+2	34-37	9-10	9	8	8-10
GERREIDAE														
Diapterus olisthostomus	160-163	2	24	10	14	9	10	3	8	38	11	9	8	10
Diapterus rhombeus	80-105	4	24	10	14	9	10	2	9	37-38	10-11	9	8	10
Eucinostomus argenteus	123-145	4	24	10	14	9	10	3	7	37-38	10-11	9	8	10
Eucinostomus gula	107-143	4	24	10	14	9	10	3	7	37-38	10-11	9	8	10
Eucinostomus lefroyi	128	1	24	10	14	9	10	2	8	36	10	9	8	9
Gerres cinereus	180	1	24	10	14	9	10	3	7	33	8	9	8	8
GOBIESOCIDAE														
Gobiesox strumosus	36-49	4	25-26	14	11-12	0	11	0	10	-	-	-	-	-
GOBIIDAE														
Gobionellus boleosoma	35	1	26	10	16	6	11	0	12	32	9	8	7	8
Gobionellus shufeldti	51	1	26	10	16	6	12	0	13	30	8	8	7	7
Gobiosoma bosci	29-50	4	27	11	16	7	12-13	0	11	30-32	8-9	8	7	8-7
Gobiosoma ginsburgi	28	1	27	11	16	7	12	0	11	32	9	8	7	8
Gobiosoma robustum	25-31	4	27	11	16	7	11-12	0	10-12	31-32	8-9	8	7	7-9
Microgobius gulosus	31-45	4	27	11	16	7-8	16-17	0	17-18	30	8	8	7	7
GONOSTOMATIDAE														
Argyripnus atlanticus	60-73	4	46-47	16	30-31	0	10-11	0	-	-	-	10	9	-
Bonapartia pedaliota	51-70	2	37-38	17	20-21	0	19	0	29	-	-	10	9	-
Gonostoma bathyphilum	127	2	38-39	17	21-22	0	13	0	24	-	-	-	-	-
Gonostoma elongatum	135-215	4	41	17	24	0	13-14	0	29-31	38-41	10-12	10	9	9-10
Maurolicus muelleri	43	4	32-33	12	20-21	0	-	0	-	-	-	-	-	-
Polymetme corythaeola	122-165	4	45	18	27	0	11-12	0	28-34	-	-	10	9	-
Triplophos hemingi	172-183	2	59	19	40	0	10-11	0	57	-	-	-	-	-
GRAMMICOLEPIDAE														
Grammicolepis brachiusculus	78-90	4	36-37	10	26-27	6	27-29	2	27-29	17	1	7	8	1
Xenolepidichthys dalgleishi	70-75	4	37-38	10	27-28	5	29	2	28-29	17	1	7	8	1
GRAMMISTIDAE														
Rypticus bistrispinus	61-70	4	25	10	15	2	25-26	0	15-16	24-26	4-5	9	8	3-4
Rypticus maculatus	82-152	4	24	10	14	2	24-25	0	15-16	25-26	4-5	9	8	4
Rypticus saponaceus	50-175	4	24	10	14	3	24-25	0	17	24-25	3-4	9	8	4
HOLOCENTRIDAE														
Corniger spinosus	103-124	4	27	11	16	12-13	13-14	4	11	28-29	5	10	9	4-5
Holocentrus ascensionis	141-200	4	27	11	16	11	15	4	10	30	6	10	9	5
Holocentrus bullisi	74-108	4	27	11	16	11	11-12	4	7-8	30	6	10	9	5
Holocentrus coruscus	105	1	27	11	16	11	11	4	7	30	6	10	9	5
Holocentrus rufus	48-153	2	27	11	16	11	14-15	4	9-10	29-30	6	10	9	4-5
Holocentrus vexillarius	61-65	4	27	11	16	11	13	4	9	30-31	6	10	9	5-6
Myripristis jacobus	68-115	4	26	11	15	11	13-15	4	12-13	27-28	5	10	9	3-4
Ostichthys trachypomus	74-105	4	26	11	15	12	12-13	4	11	28	5	10	9	4
ISTIOPHORIDAE														
Tetrapturus albidus	62-80	4	23-24	12	11-12	43-47	6-7	16-18	6-8	35-38	10	9	8	8-11
KYPHOSIDAE														
Kyphosus incisor	34-50	4	26	10	16	10-11	13-14	3	13	34	9	9	8	8
Kyphosus sectatrix	33-53	4	26	10	16	11	12	3	11	33	8	9	8	8

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
LABRIDAE														
Bodianus pulchellus	187-215	3	28	11	17	12	10	3	11-12	32-33	9-10	7	7	9
Clepticus parrai	38	1	28	11	17	12	10	3	12	37	12	7	7	11
Decadon puellaris	115-152	4	28	11	17	11	10	3	10	34-35	10-11	7	7	10-11
Halichoeres bathyphilus	120-137	2	25	10	15	9	11	3	12	26	6	7	7	6
Halichoeres bivittatus	123-140	4	25	10	15	9	11	3	12	26-27	6-7	7	7	6
Halichoeres maculipinna	57-83	2	25	10	15	9	11	3	11	26-27	6-7	7	7	6
Halichoeres radiatus	307	1	25	10	15	9	11	3	12	26	6	7	7	6
Hemipteronotus martinicensis	98	1	25	9	16	9	11	3	12	26	6	7	7	6
Hemipteronotus novacula	118-152	4	25	9	16	8-9	12-13	4	12	21-23	4-5	7	7	3-4
Lachnolaimus maximus	112-122	4	30	13	17	14	11	3	10-11	26-28	6-7	7	7	6-7
Tautoga onitis	363	1	35	17	18	17	11	3	8	28	7	8	7	6
Thalassoma bifasciatum	87	1	25	10	15	8	13	3	11	25	6	7	7	5
Thalassoma nitidum	41-55	5	25	10	15	8	12-13	3	10-11	24-26	5-6	7	7	5-6
LOBOTIDAE														
Lobotes surinamensis	19-40	4	24	11	13	12	15-16	3	11	23-25	3-5	9	8	3
LOPHIIDAE														
Lophius americanus	86-98	2	25-26	14	11-12	-	-	0	9-10	-	-	-	-	-
LUTJANIDAE														
Apsilus dentatus	202	1	24	10	14	10	9	3	8	42	13	9	8	12
Ocyurus chrysurus	95-160	3	24	10	14	10	11	3	8	39-41	12-13	9	8	10-11
Lutjanus analis	165-197	4	24	10	14	10	14	3	9	35-36	9-10	9	8	8-9
Lutjanus apodus	32-99	4	24	10	14	10	14	3	8	33-33	7-8	9	8	7-8
Lutjanus aya	94-172	7	24	10	14	10	14	3	9	35-37	9-10	9	8	8-10
Lutjanus buccanella	92-147	4	24	10	14	10	14	3	7-8	36-37	10	9	8	9-10
Lutjanus griseus	112-150	4	24	10	14	10	14	3	8	31-33	8	9	8	6-8
Lutjanus jocu	81-170	4	24	10	14	10	14	3	8	33-34	8-9	9	8	8
Lutjanus mahogoni	86-150	4	24	10	14	10	11-12	3	8	34-36	9-10	9	8	8-9
Lutjanus synagris	100-115	4	24	10	14	10	12	3	8	32-35	8-9	9	8	7-9
Lutjanus vivanus	95-143	3	24	10	14	10	14	3	8	37-38	10-11	9	8	10
Ocyurus chrysurus	157-173	4	24	10	14	10	13	3	8-9	34-35	9	9	8	8-9
Pristipomoides aquilonaris	88-178	4	24	10	14	10	11	3	7-8	39-41	11-12	9	8	10-12
Pristipomoides freemani	135-155	4	24	10	14	10	11	3	8	39-40	12	9	8	10-11
Pristipomoides macrophthalmus	55-173	7	24	10	14	10	11	3	8	41-43	11-13	9	8	12-13
Rhomboplites aurorubens	123-144	4	24	10	14	12	11	3	8	36-38	10-11	9	8	9-10
Symphysanodon typus	111-123	4	25	10	15	9	10	3	7	40-42	12-13	9	8	11-12
MALACOSTEIDAE														
Malacosteus niger	90	1	47	-	-	0	18	0	21	-	-	-	-	-
MICRODESMIDAE														
Microdesmus carri	31-34	2	67-68	37	30-31	0	-	0	-	23	5	7	6	5
MORIDAE														
Brosmiculus imberbis	135-165	4	50-51	17	33-34	0	10,53-56	0	56-62	34-37	-	-	-	-
Laemonema barbatulum	90-185	2	59	17	42	0	5-6,59	0	67	28	-	-	-	-
Physiculus fulvus	115-122	4	48-49	14	34-35	0	10-11,50-58	0	60-64	23-24	-	-	-	-
MUGILIDAE														
Agonostomus monticola	28-30	3	25	12	13	5	8	2	10	32-34	9-10	7	7	9-10
Mugil cephalus	105-155	4	24	12	12	5	8	3	8	28-30	7-8	7	7	7-8
Mugil curema	84-105	4	24	12	12	5	8	3	9	28-29	7-8	7	7	7-8
Mugil incilis	35	2	24	12	12	5	8	3	9	29-30	8	7	7	7-8
Mugil trichodon	58-105	4	24	12	12	5	7-8	3	8-9	28-29	7	7	7	7-8
MULLIDAE														
Mulloidichthys martinicus	90-134	4	24	10	14	9	8	2	6	31	8	8	7	8
Mullus auratus	97-126	3	24	10	14	9	8	2	6	33	9	8	7	9
Pseudupeneus maculatus	113-155	4	24	10	14	9	8	2	6	34-35	10	8	7	9-10
Upeneus parvus	100-134	4	24	10	14	8	8	2	6	31	8	8	7	8
MYCTOPHIDAE														
Centrobranchus nigroocellatus	24-27	4	36	16	20	0	9-11	0	16-18	30-31	6	10	9	5-6
Diaphus anteorbitalis	117-162	4	35	16	19	0	15	0	15	31-32	6-7	10	9	6
Diaphus dumerilii	51-80	4	35-36	16	19-20	0	13-14	0	14-15	30-31	6	10	9	5-6
Diaphus lampropsa	68-97	5	34	16	18	0	15	0	14	31-32	6-7	10	9	6
Diaphus rafinesquei	68-81	5	34	16	18	0	12-13	0	14	31-32	6-7	10	9	6-7
Diaphus termophilus	48-51	4	35	16	19	0	13-14	0	14-15	32-33	7	10	9	6-7
Gonichthys cocco	20-47	4	39-40	15	24-25	0	11	0	21-23	31-32	6	10	9	6-7
Hygophum macrochir	33	1	35	16	19	0	12	0	20	34	8	10	9	7
Lepidophanes guentheri	44	1	37	16	21	0	14	0	14	34	8	10	9	7
Lepidophanes suprolateralis	100	1	34	16	18	0	12	0	14	32	7	10	9	6
Myctophum affine	62-76	3	35-37	15	20-22	0	13	0	18-20	34-36	8-9	10	9	7-8
Myctophum asperum	26-68	4	37	15	22	0	12-13	0	17-18	35-37	8-9	10	9	8-9
Myctophum nitidulum	55-68	4	38	15	23	0	13	0	19-20	35-37	8-9	10	9	8-9
Myctophum obtusirostris	42-61	2	35	15	20	0	13	0	18	34-35	8	10	9	7-8
Notoscopelus elongatus	25	1	38	17	21	0	21	0	-	44	12	10	9	13
Symbolophorus rufinum	51-52	2	37	15	22	0	14-15	0	20-21	36-37	9	10	9	8-9
NEOSCOPELIDAE														
Neoscopelus macrolepidotus	117-136	4	31-32	14	17-18	0	13	0	12-13	34	8	10	9	7
OGCOCEPHALIDAE														
Dibranchus atlanticus	75-142	3	18	5	13	-	-	-	-	-	-	-	-	-
Halieutichthys aculeatus	65-87	4	17	5	12	-	-	-	-	-	-	-	-	-
Ogcocephalus nasutus	110-127	4	19	-	-	-	-	-	-	-	-	-	-	-
Ogcocephalus parvus	55-95	4	18	-	-	-	-	-	-	-	-	-	-	-
Ogcocephalus vespertilio	100-130	4	17-18	-	-	-	-	-	-	-	-	-	-	-
OPHIDIIDAE														
Lepophidium brevibarbe	165-260	4	72	15	57	0	127-129	0	106-111	-	0	-	-	0
Lepophidium cervinum	190-240	4	72-74	15	57-59	0	132-134	0	112-117	9	0	4	5	0
Lepophidium jeannae	210-275	4	74-75	14	59-61	0	135-139	0	114-116	9	0	4	5	0
Lepophidium kallion	155-165	2	71-72	14	52-58	0	130-135	0	108-115	9	0	4	5	0
Lepophidium marmoratum	150-180	2	71-72	14-15	57	0	128	0	108	9	0	4	5	0
Lepophidium profundorum	200-220	4	72	14	57	0	126-132	0	106-108	9	0	4	5	0
Ophidion beani	210-230	4	66-67	16	50-51	0	115-125	0	96-100	9	0	4	5	0
Ophidion grayi	190-265	4	64-65	16	48-49	0	133-144	0	98-105	9	0	4	5	0
Ophidion holbrooki	125-260	4	66-67	16	50-51	0	120-136	0	98-111	9	0	4	5	0
Ophidion welshi	175-210	4	66-67	16	50-51	0	138-146	0	114-121	9	0	4	5	0
Otophidium omostigmum	60-122	3	57-59	14	43-45	0	102-105	0	82-85	9	0	4	5	0
Rissola marginata	145-180	4	68-69	15	53-54	0	147-158	0	118-124	9	0	4	5	0

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
SCIAENIDAE														
Bairdiella chrysura	46-142	12	25	11	14	12	19-22	2	8-10	31-34	8-9	9	8	5-8
Bairdiella ronchus	135-153	2	25	11	14	11	23-24	2	8	34	9	9	8	8
Cynoscion arenarius	150-177	3	25	13	12	11	25-27	2	10-12	28-33	6-8	9	8	5-8
Cynoscion jamaicensis	180-215	4	25	13	12	11	24-26	2	9	30-32	7-8	9	8	6-7
Cynoscion leiarchus	112-178	3	25	13	12	11	23-23	2	11	31-32	7-8	9	8	7
Cynoscion nebulosus	31-220	8	25	13	12	11-12	24-27	2	10-11	29-33	6-9	9	8	5-7
Cynoscion nothus	121-130	4	27	14	13	11	28-30	2	9	30-32	7-8	9	8	6-8
Cynoscion regalis	28-165	10	25	13	12	11	24-28	2	10-12	29-33	7-9	9	8	5-7
Cynoscion virescens	90-175	5	25	14	11	11	27-30	2	7-8	28-31	6-7	9	8	5-7
Equetus acuminatus	90-104	6	25	10	15	10-11	36-40	2	6-8	30-32	7-8	9	8	6-7
Equetus lanceolatus	100-122	4	25	10	15	13-14	46-50	2	6	27-28	6-7	9	8	4-5
Equetus punctatus	77-197	5	25	10	15	13	44-49	2	7-8	29-31	7	9	8	5-7
Equetus umbrosus	148-165	4	25	10	15	9-11	36-39	2	7	31-32	7-8	9	8	7
Isopisthus parvipinnis	112-173	4	25	10	15	7	20	2	19-20	30-35	7-9	9	8	6-9
Larimus breviceps	152-173	4	25	10	15	11	24-28	2	6-7	29-30	6-7	9	8	6
Larimus fasciatus	27-130	10	25	10	15	11-12	25-27	2	6	28-31	6-7	9	8	4-7
Leiostomus xanthurus	27-182	15	25	10	15	11-12	29-32	2	12-13	29-33	6-8	9	8	6-8
Macrodon ancylodon	221-230	3	26	14	12	10-11	29-30	2	9-10	30	6-7	9	8	6-7
Menticirrhus americanus	171-195	4	25	10	15	11	24-26	2	7-8	32-33	8-9	9	8	7
Menticirrhus littoralis	72-143	4	25	10	15	11	24-25	2	7	30-31	7-8	9	8	6
Menticirrhus martinicensis	210-233	2	25	10	15	11	23	2	7	31-32	8	9	8	6-7
Menticirrhus saxatilis	75-213	4	25	10	15	11	23-25	2	7-8	29-31	6-8	9	8	6
Micropogon furnieri	140-235	5	25	10	15	11	26-28	2	7-8	34-36	9-10	9	8	7-9
Micropogon undulatus	101-200	5	25	10	15	11	28-29	2	8	33-34	8-9	9	8	8
Nebris macrops	148-177	4	25	11	14	9	30-34	2	10	31-33	8	9	8	6-8
Odontoscion dentex	145-180	4	25	12	13	12	21-23	2	9	35-37	9-11	9	8	9
Ophioscion costaricensis	118	1	25	10	15	11	21	2	9	35	9	9	8	9
Paralonchurus brasiliensis	112-153	4	29	11	18	11	29-30	2	8	28-30	6	9	8	5-7
Paralonchurus peterei	105-155	4	25	10	15	11	31-33	2	7	27-28	5	9	8	5-6
Pogonias cromis	28-163	6	24	10	14	11	21-23	2	6	32-33	8-9	9	8	7
Sciaenops ocellata	20-26	5	25	10	15	11	23-25	2	7-8	32-36	8-10	9	8	7-9
Stellifer lanceolatus	38-108	7	25	10	15	12-13	21-24	2	7-9	30-35	7-9	9	8	6-9
Stellifer rastrifer	137-168	4	25	10	15	12-13	21-23	2	8-9	33-36	9-10	9	8	7-9
Stellifer stellifer	47	1	24	9	15	12	20	2	8	34	9	9	8	7
Umbrina gracilicirrhus	87-174	4	25	10	15	11	22-23	2	7-8	30-33	7-8	9	8	6-
SCOMBERESOCIDAE														
Scomberesox saurus	51-58	5	66-67	40	26-27	0	10-11+5	0	13+6	21-25	3-4	7	8	3-6
SCOMBRIDAE														
Auxis thazard	52-115	5	39	20	19	11-12	11-12+8	-	14+7-8	41	13	9	8	11
Euthynnus alletteratus	38	1	39	19	20	17	12+7	-	13+7	-	-	9	8	-
Euthynnus pelamis	370	1	41	22	19	16	14+9	2	13+7	-	-	9	8	-
Sarda sarda	330	1	50	25	25	22	14+9	3	11+7	-	-	9	8	-
Scomber japonicus	170-180	4	30-31	14	16-17	10-11	12+4-5	2	11+4-5	35-38	8-11	9	8	10
Scomber scombrus	68	1	31	14	17	11	11+5	2	11+5	-	-	9	8	-
Scomberomorus cavalla	120-150	5	42-43	17	25-26	16	14-16+8-11	4	13-15+8-9	43-44	13-14	9	8	13
Scomberomorus maculatus	155-220	4	52-53	21	31-32	18-19	18-19+8-9	4	14-16+7-8	41	12	9	8	12
Thunnus albacares	580	1	39	18	21	13	12+-	-	12+-	-	-	9	8	-
Thunnus atlanticus	500	1	39	19	20	14	14+8	1	12+7	-	-	9	8	-
Thunnus thynnus	75	1	39	18	21	17	12+8	2	12+7	45	15	9	8	13
SCORPAENIDAE														
Helicolenus dactylopterus	186-210	4	25	10	15	12	12	3	5	34-36	10-12	7	7	9-10
Neomerinthe beanorum	75-91	4	24	9	15	12	9	3	5	26-29	7-8	7	7	5-7
Neomerinthe pollux	222	1	24	9	15	12	10	3	5	27	7	7	7	6
Pontinus castor	63-69	3	24	9	15	12	10-11	3	5	25-27	6-7	7	7	5-6
Pontinus longispinis	108-135	4	24	9	15	12	9	3	5	27-28	7	7	7	6-7
Pontinus macrolepis	54-76	4	24	9	15	12	9	3	5	27-29	7-8	7	7	6-7
Pontinus rathbuni	83-105	3	24	9	15	12	9	3	5	27	7	7	7	6
Scorpaena agassizi	86-127	4	24	9	15	12	9	3	5	25-26	6	7	7	5-6
Scorpaena bergi	71-133	3	24	9	15	12	9	3	5	27-29	7-8	7	7	6-7
Scorpaena brasiliensis	92-187	4	24	9	15	12	8-10	3	5	26-28	6-7	7	7	6-7
Scorpaena calcarata	107-135	4	24	9	15	12	9	3	5	25-27	6-7	7	7	5-6
Scorpaena dispar	96-126	4	24	9	15	12	9	3	5	26-27	6-7	7	7	6
Scorpaena inermis	73-158	3	24	9	15	12	8-9	3	5	26	6-7	7	7	5-6
Scorpaena isthmensis	91-122	4	24-25	9	15-16	12	9	3	5	27-29	7-8	7	7	6-7
Scorpaena petricola	24	1	24	9	15	12	9	3	5	26	7	7	7	5
Scorpaena plumieri	165-197	2	24	9	15	12	9	3	5-6	24-25	5-6	7	7	5
Setarches guentheri	85-110	4	24	10	14	12	9	3	5	29	8	7	7	7
Trachyscorpia cristulata	147-204	3	25	9	16	12	9	3	5	30	8	7	7	8

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
OPISTHOGNATHIDAE														
Lonchopisthus higmani	54-84	4	28	10	18	11	18	3	16-17	23	3-4	8	8	3-4
Opisthognathus macrognathus	116-131	2	30	10	20	11	17	3	17	23	4	8	8	3
Opisthognathus maxillosus	75-105	3	28	10	18	11	15	3	14-15	24-25	5	8	8	3-4
OSTRACIIDAE														
Lactophrys polygonia	26-120	4	13	8	5	0	10	0	-	-	0	5	5	0
Lactophrys quadricornis	42-148	5	14	8	6	0	10	0	-	-	0	5	5	0
PEMPHERIDAE														
Pemphris schomburgki	82	1	25	10	15	5	8	3	32	29	7	9	8	5
PERCOPHIDIDAE														
Bembrops anatirostris	130-216	4	28	9	19	6	14-15	0	17-19	34-36	10-11	8	7	9-10
Bembrops gobioides	163-192	4	30	9	21	6	16-17	0	17-18	34-36	10-11	8	7	9-10
Bembrops macrosma	145-160	4	28	9	16	6	14	0	17-18	36-37	11-12	8	7	10
Chriomystax squamentum	72-74	2	28	9	19	6	15	0	18	40-41	13	8	7	12-13
PLEURONECTIDAE														
Glyptocephalus cynoglossus	220-230	2	57-58	11-12	45-47	0	108-117	0	91-101	22-23	0-1	11	11	0
Foscilopsetta albomarginata	104-107	4	40-41	10	30-31	0	61-64	0	53-54	20	1	9	8	2
Foscilopsetta beani	90-104	4	41-42	10	31-32	0	63-66	0	53-56	20	1	9	8	2
POECILIIDAE														
Gambusia affinis	23-26	4	32-33	14	18-19	0	7-8	0	11	23-28	-	-	-	-
Heterandria formosa	16-20	4	31	14	17	0	7-8	0	9	24	-	-	-	-
Poecilia latipinna	20-24	4	29-30	13-14	15-17	0	13-14	0	8	30-32	-	-	-	-
POLYMIXIIDAE														
Polymixia lowei	108-127	4	28	12	16	5	29-30	4	15	29	6	9	9	5
Polymixia nobilis	130-195	3	28	12	16	5	35-36	4	16-17	29	6	9	9	5
POLYNEMIDAE														
Polydactylus octonemis	63-66	4	24	10	14	9	11-12	3	13	41-43	12-13	9	8	12-13
Polydactylus virginicus	22-24	3	24	10	14	8-9	10-12	3	12-13	-	-	9	8	-
POMACENTRIDAE														
Abudefduf analogus	115	1	26	11	15	13	12	2	10	26	6	8	7	5
Abudefduf saxatilis	55-126	3	26	11	15	13	13	2	12	26-27	6	8	7	5-6
Chromis enchrysusus	75-82	4	26	11	15	13	12	2	12	25	5	8	7	5
Chromis insolatus	55-60	4	26	11	15	13	12	2	11	24-25	5	8	7	4-5
Pomacentrus fuscus	55-62	4	26	11	15	12	15-16	2	13-14	25	5	8	7	5
Pomacentrus leucostictus	40-51	4	26	11	15	12-13	15	2	13	25	5	8	7	5
Pomacentrus planifrons	38	1	26	11	15	12	15	2	13	25	5	8	7	5
POMADASYIDAE														
Anisotremus surinamensis	119-165	2	26	10	16	11-12	17-18	3	9	42-43	13	9	8	12-13
Anisotremus virginicus	86-178	3	26-27	10	16-17	12	16-17	3	10-11	38-39	10-11	9	8	10-11
Conodon nobilis	135-155	4	26	10	16	12	13	3	7	39-40	11-12	9	8	11
Genyatremus luteus	142-190	4	26	10	16	13	11-13	3	11	35-37	10	9	8	8-10
Haemulon album	161-238	2	26	10	16	12	16-17	3	7-8	39-40	12-13	9	8	9-11
Haemulon aurolineatum	93-133	4	26	10	16	13-14	14-15	3	9	36-41	11-12	9	8	10-11
Haemulon chrysargyreum	128	1	26	10	16	12	14	3	9	41	13	9	8	11
Haemulon flavolineatum	95-135	3	26	10	16	12	14	3	8	33-36	9-10	9	8	6-9
Haemulon melanurum	97-115	4	26	10	16	12	15-16	3	8	37-40	10-12	9	8	10-11
Haemulon plumieri	77-227	4	26	10	16	12	15-16	3	9	37-39	9-12	9	8	10-11
Haemulon steindachneri	137-160	4	26	10	16	12	16	3	9	39-41	11-12	9	8	11-12
Haemulon striatum	88-102	4	26-27	10	16-17	13	13-15	3	8-9	39-42	12-13	9	8	10-12
Orthopristis chalceus	117-163	4	26	10	16	12-13	15	3	10-11	41	12-13	9	8	11-12
Orthopristis chrysopterus	95-103	4	26	10	16	12-13	15-16	3	13	40-42	12-13	9	8	11-12
Orthopristis ruber	152-185	4	26	10	16	12	15	3	10	38-40	12	9	8	9-11
Pomadasys corvinaeformis	125-170	4	26	10	16	12	15-16	3	7	38-39	11-12	9	8	10-12
POMATOMIDAE														
Pomatomus saltatrix	142-210	4	26	11	15	9	24-25	3	26-28	35-36	9-10	9	8	9-10
PRIACANTHIDAE														
Cookeolus boops	159	1	23	10	13	10	12	3	12	25	5	8	8	4
Priacanthus arenatus	137-188	4	23	10	13	10	14	3	14-15	26-28	5-6	8	8	5-6
Priacanthus cruentatus	135	1	23	10	13	10	13	3	14	24	4	8	8	4
Pristigenys alta	89-135	4	23	10	13	10	11	3	10	24	4	8	8	4
RACHYCENTRIDAE														
Rachycentron canadum	455	1	25	11	14	10	29	2	24	41	16	9	8	8
SCARIDAE														
Cryptotomus roseus	57-67	3	25	10	15	9	10	3	9	25-27	7	7	6	5-6
Nicholsina usta	117-148	3	25	10	15	9	10	3	9	26-28	7-8	7	6	6-7
Scarus croicensis	69-210	3	25	10	15	9	10	3	9	25-27	6-7	7	6	6-7
Sparisoma chrysopterum	67-95	3	25	10	15	9	10	3	9	28	8	7	6	7
Sparisoma radians	81-121	4	25	10	15	9	10	3	9	25-27	6-7	7	6	6-7
Sparisoma rubripinne	74-92	2	25	10	15	9	10	3	8-9	26-26	7-8	7	6	6-7
Sparisoma viride	192	1	25	10	15	9	10	3	9	28	8	7	6	7

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
SERRANIDAE														
Anthiasicus leptus	191-295	4	26	10	16	10	14	3	8	40-43	13-14	8	7	12-14
Centropristis ocyurus	125-155	4	24	10	14	10	11	3	7	34-35	9-10	9	8	8
Centropristis philadelphica	101-167	4	24	10	14	10	11	3	7	34-35	9-10	9	8	7-9
Centropristis striata	97-180	4	24	10	14	10	11	3	7	34-35	9-10	9	8	8
Cephalopholis fulva	78-235	4	24	10	14	9	15	3	8-9	35-36	9-10	9	8	9
Chorioritirtius eukrines	82	1	24	10	14	8	12	3	8	33	8	9	8	8
Dermatolepis inermis	373	1	24	10	14	11	19	3	9	31	7	9	8	7
Diplectrum bivittatum	105-113	4	24	10	14	10	12	3	7	39-40	12	9	8	10-11
Diplectrum formosum	133-175	4	24	10	14	9-10	12	3	7	38-40	11-12	9	8	10-11
Diplectrum radiale	92-155	4	24	10	14	10	12	3	7	37	11-12	9	8	8-9
Epinephelus drummondhayi	275-285	2	24	10	14	11	16	3	9	37-40	10-12	9	8	10-11
Epinephelus flavolimbatus	165-205	4	24	10	14	11	14	3	9	33-35	8-9	9	8	8-9
Epinephelus guttatus	177-205	2	24	10	14	11	16	3	8	35-37	9-10	9	8	9-10
Epinephelus mystacinus	148	1	24	10	14	11	14	3	9	34	9	9	8	8
Epinephelus nigritis	170	1	24	10	14	10	14	3	9	33	8	9	8	8
Epinephelus niveatus	74-146	4	24	10	14	11	13-14	3	9	33-34	8-9	9	8	7-8
Epinephelus striatus	100-202	2	24	10	14	11	17	3	8	36	10	9	8	9
Hemianthias vivanus	52-102	6	26	10	16	9-10	13-14	3	8	39-41	12-13	8	7	11-13
Mycteroperca bonaci	120	1	24	10	14	11	17	3	12	38	11	9	8	10
Mycteroperca falcata	240	1	24	10	14	11	17	3	11	38	11	9	8	10
Mycteroperca interstitialis	127	1	24	10	14	11	16	3	11	37	10	9	8	10
Mycteroperca microlepis	122-205	3	24	10	14	11	16-17	3	10-12	37	10-11	9	8	9-10
Mycteroperca phenax	49-66	3	24	10	14	11	16-17	3	11	37-38	10-11	9	8	9-10
Mycteroperca venenosa	393	1	24	10	14	11	16	3	11	37	10	9	8	10
Ocyanthias martinicensis	74-104	4	26	10	16	10	15	3	7	33	9	8	7	9
Paranthias furcifer	65-94	2	24	10	14	9	18-19	3	9	40	12	9	8	11
Petrometopon cruentatum	103-125	3	24	10	14	9	14	3	8	33-34	8-9	9	8	8
Pikea cubensis	66-107	4	24	10	14	8	13	3	7-8	34-35	9	9	8	8-9
Pronotogrammus aureorubens	125-195	4	26	10	16	10	15	3	8	33-34	9-10	8	7	9
Schultzea beta	52-57	4	24	10	14	10	11-12	3	7	36-38	10-11	9	8	9-10
Serraniculus pumilio	29-44	3	24	10	14	9-10	11	3	7	34-35	9-10	9	8	7-8
Serranus annularis	45-66	4	24	10	14	10	12	3	7	32-33	8	9	8	7-8
Serranus atrobranchus	75-87	4	24	10	14	10	11-12	3	7	35-36	10	9	8	8-9
Serranus chionaraia	33-47	4	24	10	14	10	11-12	3	7	32	8	9	8	7
Serranus maytapi	59-72	4	24	10	14	10	11-12	3	6-7	37-38	10-11	9	8	10
Serranus notospilus	99-125	4	24	10	14	10	12	3	7	38-39	11-12	9	8	10-11
Serranus phoebe	112-140	4	24	10	14	10	12	3	7	36-38	10-11	9	8	9-10
Serranus subligarius	60-76	4	24	10	14	10	13-14	3	7	31-32	7-8	9	8	7
Serranus tabacarius	48-117	4	24	10	14	10	12	3	7	34-36	9-10	9	8	8-9
Serranus tortugarum	49-63	3	24	10	14	10	12	3	7	33-34	8-9	9	8	8
SOLEIDAE														
Achirus inscriptus	70-93	5	27-28	9	18-19	0	54-58	0	40-44	15-16	0	7-8	8	0
Achirus lineatus	94-118	3	28	9	19	0	53-58	0	40-43	16	0	8	8	0
Gymnachirus melas	52-117	8	35-36	9	26-27	0	60-70	0	44-51	16	0	8	8	0
Trinectes maculatus	60-92	4	28-29	9	19-20	0	51-55	0	41-42	16	0	8	8	0
SPARIDAE														
Archosargus probatocephalus	69-112	4	24	10	14	12	10-12	3	9-10	32-33	8-9	9	8	7
Archosargus rhomboidalis	168-195	3	24	10	14	13	10-11	3	10	32-33	8	9	8	7-8
Diplodus holbrooki	137-157	4	24-25	10-11	14	12-13	14-15	3	13-14	33-34	8-9	9	8	8
Lagodon rhomboides	72-76	4	24	10	14	12	11	3	11	34-38	10-11	9	8	7-10
Pagrus sedecim	129-162	4	24	10	14	12	10	3	8	35-37	9-10	9	8	9-10
Stenotomus caprinus	109-148	4	24	10	14	12	12	3	11-12	33-34	9	9	8	7-8
Stenotomus chrysops	107-144	4	24	10	14	12	12	3	11	34-37	9-10	9	8	8-10
SPHYRAENIDAE														
Sphyraena borealis	122-206	2	24	12	12	6	9	2	9	35	9	9	8	9
Sphyraena guachancho	168-220	4	24	12	12	6	9	2	8	36	10	9	8	9
Sphyraena picudilla	254	1	24	12	12	6	9	2	9	35	9	9	8	9
STEPHANOBERYCIDAE														
Stephanoberyx monae	70	2	30-31	10	20-21	0	12-13	0	11-12	39-41	10-11	10	9	10-11
STERNOPTYCHIDAE														
Argyropelecus aculeatus	50-57	4	35-36	11	24-25	0	9	0	7+7	32-36	8-11	10	9	5-6
Argyropelecus affinis	51-57	4	38-39	11	27-28	0	7-9	0	7+5	-	9-10	10	9	-
Argyropelecus gigas	52	1	39	11	28	0	9	0	7+5	-	9	10	9	-
Argyropelecus hemigymnus	19-21	2	38	11	27	0	-	0	-	-	-	-	-	-
Polyipnus asteroides	50-67	4	33	10	23	0	14-15	0	15-17	35-36	9-11	10	9	6-7
Polyipnus laternatus	27-40	4	33-34	10	23-24	0	14-15	0	15-16	36	10	10	9	7
Sternoptyx diaphana	32-47	5	29-30	11	18-19	0	9-11	0	14	33-35	7-8	10	9	7-8
STROMATEIDAE														
Cubiceps melanus	128-164	4	30-31	15-16	15	12	15-16	3	14-15	35-37	9-10	9	8	9-10
Cubiceps nigriargenteus	100-115	4	31	15	16	12	15	3	15	35-37	9-10	9	8	9-10
Nomeus gronovii	88-138	4	41-42	16	25-26	12-13	27-28	2	26-27	34-35	8-9	9	8	9
Peprilus alepidodus	61-77	4	30	13	17	3	44-46	3	41-43	28	6	9	8	5
Peprilus paru	178	1	30	13	17	3	43	3	40	29	6	9	8	6
Poronotus triacanthus	115-120	4	32	12	20	3	43-47	3	39-44	31-44	7-9	9	8	7-8
Psenes cyanophrys	67-123	4	31	14	17	11	25-26	3	26-27	33-34	8-9	9	8	8
Psenes pacificus	75-112	3	31	14	17	10-11	25-28	3	24-25	32-34	8-9	9	8	7-8
Psenes regulus	83-193	4	31	14	17	12-13	14-15	3	14-15	36-41	10-12	9	8	9-12
Tetragonurus atlanticus	160	1	45	23	22	15	9	2	9	36	11	8	7	10
STYLEPHORIDAE														
Stylephorus chordatus	215	1	53	-	-	-	-	-	-	-	-	-	-	-
SYNGNATHIDAE														
Hippocampus erectus	105-180	4	49-51	13	36-38	0	19-20	0	-	0	0	0	0	0
Micrognathus crinigerus	65	1	56	17	39	0	-	0	-	-	-	-	-	-
Syngnathus dunckeri	47-52	4	50-53	18	32-35	0	-	0	-	10	-	-	-	-
Syngnathus elucens	40	2	49-50	18	31-32	0	-	0	-	10	-	-	-	-
Syngnathus floridae	115-122	3	51-52	18	33-34	0	-	0	-	-	-	-	-	-
Syngnathus fuscus	108-295	4	55-60	19-21	36-39	0	35	0	-	10	-	-	-	-
Syngnathus louisianae	175-240	4	51-52	19-20	32	0	-	0	-	10	-	-	-	-
Syngnathus mackayi	185-240	4	50-53	20	30-33	0	27-28	0	-	10	-	-	-	-
Syngnathus pelagicus	72-102	4	49-52	18-19	31-33	0	28-29	0	-	10	-	-	-	-
Syngnathus scovelli	87-95	4	49-51	17-18	31-33	0	29-32	0	-	-	-	-	-	-
Syngnathus springeri	55-263	7	61-62	24-25	37-38	0	-	0	-	10	-	-	-	-

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
SYNODONTIDAE														
Saurida brasiliensis	50-112	5	46-50	-	-	0	11	0	11	37-40	9-11	10	9	9-10
Saurida caribbaea	80-108	5	52-58	-	-	0	11-12	0	11-12	40-42	11-12	10	9	10-11
Saurida normani	53-330	6	49-52	-	-	0	11-12	0	10-11	41-45	11-13	10	9	11-13
Saurida suspicio	32-72	5	49-52	-	-	0	10-11	0	10-11	38-40	10-11	10	9	9-10
Synodus foetens	89-345	5	56-61	-	-	0	11-12	0	12	41-43	11-12	10	9	11-12
Synodus intermedius	62-190	5	47-50	-	-	0	12-13	0	11-12	40-42	11-12	10	9	10-11
Synodus poeyi	60-165	8	44-46	-	-	0	10-11	0	10	39-44	10-13	10	9	10-12
Synodus saurus	32-213	6	55-58	-	-	0	12-13	0	9-11	46-49	14-16	10	9	13-14
Synodus synodus	35-142	6	54-57	-	-	0	12-13	0	8-9	43-49	12-16	10	9	12-14
Trachinocephalus myops	84-207	5	54-57	-	-	0	11-13	0	14-15	45	13	10	9	13
TETRAODONTIDAE														
Canthigaster rostrata	58	1	17	8	9	0	9	0	8	11	0	5	6	0
Lagocephalus laevigatus	74-152	4	19	8	11	0	14-15	0	12-13	11	0	5	6	0
Sphoeroides cutaneus	107-113	3	18	8	10	0	9	0	8	11	0	5	6	0
Sphoeroides dorsalis	118-187	4	17	8	9	0	8	0	7	11	0	5	6	0
Sphoeroides maculatus	99-178	3	19	8	11	0	8	0	7	11	0	5	6	0
Sphoeroides nephelus	50-142	5	19-20	8	11-12	0	8	0	7	11	0	5	6	0
Sphoeroides spengleri	106-125	4	17-18	8	9-10	0	8	0	7	11	0	5	6	0
Sphoeroides testudineus	72-129	4	18	8	10	0	8	0	7	11	0	5	6	0
TRACHICHTHYIDAE														
Hoplostethus mediterraneus	75-88	4	26	11	15	6	13	3	9	33-34	7-8	10	9	7
TRIACANTHODIDAE														
Hollardia hollardia	71-90	4	20	8	12	6	16-17	0	15	12	0	6	6	0
Parahollardia schmidti	51-60	4	20	8	12	6	15	0	13	12	0	6	6	0
TRICHIURIDAE														
Benthodesmus simonyi	590	1	157	-	-	-	-	2	-	-	-	-	-	-
Benthodesmus tenuis	430-465	4	127-132	-	-	-	121-132	2	71-81	-	-	-	-	-
Trichiurus lepturus	310-380	4	169-173	39-40	130-134	3	132-138	2	89-107	-	-	-	-	-
TRIGLIDAE														
Bellator brachychir	55-63	4	26	10	16	11	10-11	0	11	31-33	9-10	7	6	8-10
Bellator egretta	94-108	4	26	10	16	11	11	0	11	30-32	9-10	7	6	8-9
Bellator militaris	61-92	5	25-26	10	15-16	11	11	0	9-10	27-30	7-9	7	6	7-8
Bellator ritteiroi	30-59	8	26	10	16	11	11	0	9-11	27-28	7-8	7	6	7
Prionotus alatus	81-130	4	26	10	16	10	12-13	0	11	30-31	9-10	7	6	8
Prionotus beani	72-133	4	26	10	16	10	12	0	11	28-31	9	7	6	6-9
Prionotus carolinus	172-168	4	26	10	16	10	13	0	12	31-33	9-10	7	6	9-10
Prionotus evolans	113-157	4	26	10	16	10	12	0	11	32-35	10-11	7	6	9-11
Prionotus ophryas	98-137	4	26-27	10	16-17	10	12-13	0	10-11	25-27	6-7	7	6	6-8
Prionotus paralatus	89-118	4	26	10	16	9-10	12	0	11	31-32	9-10	7	6	9
Prionotus pectoralis	157-225	4	26-27	10	16-17	10	12-13	0	11-12	31-34	9-11	7	6	9-11
Prionotus punctatus	97-153	4	26	10	16	10	11-12	0	11	32-35	10-11	7	6	9-11
Prionotus roseus	113-145	4	26	10	16	10	12-13	0	11	29-30	8-9	7	6	8
Prionotus rubio	157-173	4	26	10	16	10	12	0	10-11	31-32	9-10	7	6	9
Prionotus scitulus	79-172	4	26	10	16	10	13	0	12	30-33	10-11	7	6	7-10
Prionotus stearnsi	98-113	4	26	10	16	9-10	12	0	10-11	33-34	10-11	7	6	10
Prionotus tribulus	90-193	4	26	10	16	10	12	0	11	30-33	9-10	7	6	8-10
Peristedion antillarum	92-120	4	31	9	22	6	16	0	-	28	8	6	6	8
Peristedion brevirostre	92-98	2	32	9	23	-	-	0	-	25	7	6	6	6
Peristedion ecuadorensis	127-142	4	33-35	9	24-26	-	-	0	-	25-27	7-8	6	6	6-7
Peristedion gracile	110-130	4	34-35	9	25-26	8	14	0	21-23	27-28	8	6	6	7-8
Peristedion greyae	87-105	3	34-35	9	25-26	8	18-20	0	18-21	28	8	6	6	8
Peristedion imberbe	107-135	4	34-35	9	25-26	8	18	0	-	26-28	7-8	6	6	7-8
Peristedion longispatha	122-135	4	32-33	9	23-24	-	-	0	-	26	7	6	6	7
Peristedion miniatum	118-148	4	33	9	24	-	-	0	-	26-28	7-8	6	6	7-8
Peristedion schmitti	73-94	4	31-33	9	22-24	-	-	0	-	26	7	6	6	7
Peristedion truncatum	115-133	3	33-34	9	24-25	-	-	0	19	26	7	6	6	7
Peristedion unicuspis	136-153	2	33	9	24	8	19-20	0	20	25-26	6-7	6	6	7
URANOSCOPIDAE														
Astroscopus guttatus	230	1	25	11	14	5	13	0	13	22	5	7	6	4
Astroscopus y-grecum	80-110	4	25	11	14	5	13-14	0	13-14	25-26	6-7	7	6	6-7
Gnathagnus egregius	83-125	4	28	11	17	0	12-14	0	16-17	28-29	8-9	7	6	7-8
Kathetosoma albigutta	85-117	3	25	10	15	0	14-15	0	12-13	22	5	7	6	4
Kathetosoma cubana	62-118	5	26	11	15	0	14-15	0	13-14	23	5	7	6	5
XIPHIIDAE														
Xiphias gladius	53-170	4	26	14	12	-	52	-	-	31-32	7-9	9	8	7
ZEIDAE														
Cyttopsis roseus	85-115	4	31	10	21	7	28-29	2	28-29	20-21	3-4	6	7	4
Parazen pacificus	105-118	4	34	12	22	8-9	26-29	1	31-33	27-28	8-9	5	6	8
Zenopsis ocellata	68-75	4	35	12	23	8-9	24-26	3	22-25	15	1	6	7	1
ZENIONTIDAE														
Zenion hololepis	60-72	4	27	11	16	5-6	26-28	1-2	22-23	18	3	6	7	2
ZOARCIDAE														
Macrozoarces americanus	340-390	4	137-138	25-27	111-112	18-21	90-94+28-31	0	113-115	-	-	-	-	-

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FREQUENCY AND DURATION OF FLOW REVERSAL IN THE LOWER COLUMBIA RIVER, APRIL 1968-MARCH 1970

The hydraulic head generated by some heights of tide can result in changes in direction of current in the lower Columbia River when volume discharges fall below a critical value. In connection with this phenomenon, Clark and Snyder (1969) conducted a study to determine the timing and extent of reversal of flow during an extreme condition of low discharge of water from the river. They determined that flow reversals could increase the accumulation of discharged effluents per given volume of river water by as much as 3.5 times over the accumulation at mean flow rates. Their report showed the need for a continuing record of direction of current in the lower Columbia River to determine the importance of flow reversal at different discharge rates. To help satisfy this need, a floating laboratory (Snyder, Blahm, and McConnell, 1971) was established on the lower Columbia River at river kilometer 117.5 (river mile 73) near Prescott, Oreg., where speed and direction of current were recorded. This report describes the flow-reversal phenomenon at river kilometer 117.5 from data collected between April 1968 and March 1970.

Procedure

The velocity of the river current was measured with a Savonius meter[1] suspended from the laboratory to determine the frequency and duration of flow reversal in the lower Columbia River. With the exception of 21 days, the flow was monitored continuously for a 2-year period. Flow data obtained at Prescott were related to the daily discharge of the river and to the time and height of ocean tides near the river's mouth at Astoria, Oreg.

Daily average flow for the period 1 April 1968 to 30 June 1969, was "gauged flow" furnished by the U.S. Geological Survey office in Portland, Oreg.; daily average flow for the period 1 July 1969 to 31 March 1970, was from information furnished by U.S. Geological Survey offices in Portland, Oreg., and Tacoma, Wash. Time and height of oceanic tides were for Astoria, Oreg.; these data were obtained from tide charts of the NOAA (National Oceanic and Atmospheric Administration) National Ocean Survey.

Our observations of direction and speed of current were used to determine the duration and frequency of flow reversals. Only those flow reversals of 60-min duration or longer were considered to constitute true reversals. Duration of flow reversal was defined as the time interval between positive downstream flows wherein the

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

downstream flow stops, then moves upstream and stops, and then moves downstream again.

Data Analysis

River discharge and height of tide are independent variables in the analysis of flow reversal in the lower Columbia River. The average monthly flow at Prescott is characterized by high bimodal peaks that occur annually in the winter and spring. The higher high tides typically occur during the same period.

River Flow

The flow of the Columbia fluctuated greatly during our study. It averaged 6,768 cubic meters per second (m^3sec^{-1}) or 239,000 cubic feet per second (cfs) and ranged from 2,209 to 14,442 m^3sec^{-1} (78,000 to 510,000 cfs). High flow occurred during June 1968 and May 1969; these high discharges were associated with water from melting snow in areas east of the Cascade Mountains. High river flow in January (Figure 1) was associated with precipitation in areas west of the Cascades. Low flows occurred during September in both years. Average monthly flows exceeded 8,495 m^3sec^{-1} (300,000 cfs) for only 5 months of the 24-month period; this fact is important in that it was only when the flow was below this level that reversal became significant at Prescott.

Tidal Height

High tides ranged from 1.5 to 3.1 m (4.9 to 10.1 ft). Tides of 2.0 to 2.6 m (6.6 to 8.5 ft) occurred most frequently. Tidal influence produces differences in water elevations in the Columbia River that can be measured upstream as far as Bonneville Dam (river km 225.3, river mile 140).

Characteristics of Flow Reversal

During the 2 years of the study, 646 flow reversals of 60 min or longer (Table 1) were observed and related to high tides. Reversals occurred most frequently in August, September, and October—normally the period of lowest discharge—and least frequently in May and June—the period of highest river discharge. Tidal heights at Astoria which produced flow reversals ranged from 1.5 to 3.0 m (4.9 to 9.9 ft).

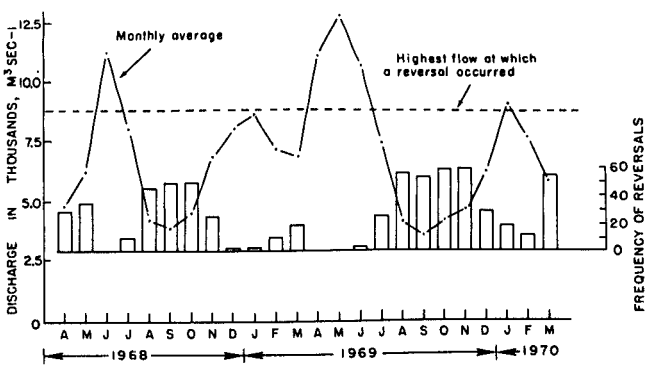

FIGURE 1.—Average monthly Columbia River discharge, at Prescott, Oreg., April 1968-March 1970. Frequency of flow reversals lasting more than 60 min and highest discharge at which a reversal occurred are also indicated.

TABLE 1.—Frequency of flow reversals (≥ 60 min) measured in the lower Columbia River at Prescott, Oreg., April 1968-March 1970.

Period	Number of flow reversals (by month)												Total
	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	
1968-69	29	35	0	10	46	49	50	26	3	3	10	19	280
1969-70	0	0	2	25	56	54	57	58	29	19	12	54	366
Total	29	35	2	35	102	103	107	84	32	22	22	73	646

Twenty-one flow reversals of 5 hr or longer were recorded. Few reversals of 60 min or longer were recorded during river discharge above 8,495 m^3sec^{-1} (300,000 cfs), regardless of the height of the tide. This relation is illustrated in Figure 1, where average monthly discharge is compared to the frequency of flow reversal.

The lowest high tide at which reversal was recorded (90 min) was 1.5 m (4.9 ft), at 3,936 m^3sec^{-1} (139,000 cfs). The highest high tide at which a reversal was recorded (155 min) was 3.0 m (9.9 ft) at 6,173 m^3sec^{-1} (218,000 cfs). Two 3-m (10-ft) tides occurred during the study period at 7,759 and 7,985 m^3sec^{-1} (274,000 and 282,000 cfs) without producing a reversal of 60 min or longer. The longest period of reversal was 5¾ hr at a tide height of 2.7 m (8.9 ft) and 5,550 m^3sec^{-1} (196,000 cfs) which occurred 8 March 1970.

A regression analysis was made for each tide level to estimate the critical discharge below which a flow reversal of 60 min or greater could be expected. Discharges that allowed flow reversals at 1.5-, 1.8-, 2.1-, 2.4-, and 2.7-m (5-, 6-, 7-, 8-, and 9-ft) tides were 4,530; 5,720; 5,861; 6,852; and 8,636 m^3sec^{-1} (160,000; 202,000; 207,000; 242,000; and 305,000 cfs; Figure 2). The rate of discharge from the river and tidal height appear to be independent variables while flow reversal is the dependent variable in the analysis.

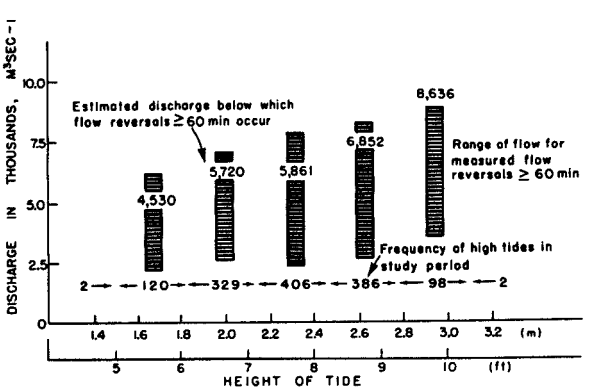

FIGURE 2.—Graphs showing range of flow of the Columbia River for various tidal heights at Astoria, Oreg. The number within each bar is the estimated discharge below which flow reversals of 60 min or longer occur at Prescott, Oreg., for a given tidal height. The number below each bar gives the frequency of occurrence of the tide height for the study period.

Discussion

During the time interval examined, reversal of direction of current (≥ 60 min) at Prescott occurred every month except June 1968 and April and May 1969. It is important to discover that the reversals in flow are frequent as previous work in this area only indicated that they could occur at very low river discharges. Because of the frequent occurrence of flow reversals in the region of the lower Columbia River near Prescott, the regulation of waste discharges in this area should receive special attention as these reversals in flow tend to produce pockets of high concentration of wastes in the river system when the waste discharges are constant in time (Clark and Snyder, 1969).

Acknowledgment

We gratefully acknowledge the helpful suggestions of A. C. Duxbury, Department of Oceanography, University of Washington, in preparing the manuscript.

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LONG-TERM OLFACTORY "MEMORY" IN COHO SALMON, *ONCORHYNCHUS KISUTCH*[1]

Many experiments have correlated the importance of olfaction and the precise homing of sexually mature salmon. As juveniles, the fish are presumably imprinted on the natural odors of their natal-area water (Hasler, 1966). The odors apparently serve as cues to guide the adult's return. Thus, some type of "odor memory" must persist from the time of the downstream journey of the smolt to the return of the sexually mature adult. For introduced Lake Michigan coho salmon, *Oncorhynchus kisutch*, this is either ½ year (precocious males) or 1½ years.

The existence of long-term olfactory memory persisting over this time period has only been inferred. Idler et al. (1961) and Fagerlund et al. (1963) found that already homed salmon made unconditioned behavioral responses to home water. Hara, Ueda, and Gorbman (1965), Ueda, Hara, and Gorbman (1967), and Oshima, Hahn, and Gorbman (1969a) found specific EEG (electroencephalographic) responses to home-stream water. Hara (1970) in his review of this EEG technique states: "This electric response [from the olfactory bulbs] is specific in the sense that it cannot be evoked by water from spawning sites of other groups of breeding salmon." The EEG and behavioral studies strongly suggest long-term memory of the juvenile's stream experience. However, since these workers used homed adults that had recently experienced home water, the data are evidence only of an odor memory lasting from the time of removal from the home stream to the time of testing.

We tested coho salmon that were exposed to a synthetic odoriferous substance for 1 month during smoltification and then removed from any conceivable influence of this substance for 10 months. Ten months later these fish and controls were examined for olfactory bulbar EEG responses (after Hara et al., 1965) to the imprinting substance.

Materials and Methods

On 7 April 1970, approximately 2,500 hatchery-raised coho salmon smolts (1½ years old) were put into each of two contiguous 25-m sections of a raceway at a Wisconsin State fish hatchery at Crystal Springs. We marked the fish to eventually distinguish the upper section control subjects from the lower section experimentals. A small drop (⅓ m) prevented water in the lower section from reentering the upper section. Immediately below the drop a dilute concentration of morpholine was introduced by infusion pump at a rate to maintain a steady-rate concentration of 10^{-5} ppm. This value is one order of magnitude above an avoidance threshold of unconditioned coho salmon fingerlings (Wisby, 1952). On 5 May 1970, 1 month after initiation of the morpholine treatment, all but 50 fish from each raceway section were trucked to Lake Michigan and released as part of another experiment. The 100 remaining fish were moved to a hatchery near Madison, Wis., and held together in a single outside raceway for 10 months prior to EEG tests.

Our testing procedure was generally similar to that used by Hara et al. (1965) to examine olfactory bulb responses to home-stream water. The subject was paralyzed with gallamine triethiodide (2 mg/kg), restrained, and the gills perfused with tap water. One of the olfactory bulbs was exposed, and an electrode (Transidyne General, model 415[2]) was placed on the surface near the rear margin. The responses evoked by perfusion of the ipsilateral naris were amplified (Bioelectric Instruments, model DS2c) and recorded on a two-channel oscillograph (Hewlett Packard, model 7712B) for later analysis. This oscillograph was equipped with an integrating preamplifier for efficient quantification of bulbar activity. Therefore, all responses reported later

[1] This work was completed under financial support from the National Science Foundation (Grant No. GB 7616X) to Prof. Hasler and the University of Wisconsin Sea Grant Program which is a part of the National Sea Grant Program maintained by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce.

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

are expressed as the sum of the positive areas under the response wave form.

Beginning on 25 February 1971, one fish was examined per day with 1% and 0.01% morpholine stimuli. Fourteen fish were used. Each test was started at approximately 1000 hr. Every subject was tested with the morpholine concentrations and the responses compared with responses to 0.06 N NaCl. Stimuli were randomly ordered and presented for 10 sec followed by 75 sec of tap water rinse. The stimulus series was then repeated seven times.

Results

Fish that had been exposed to 10^{-5} ppm of morpholine as smolting juveniles evidenced significantly higher bulbar EEG activity over controls when tested with 1% and 0.01% concentrations of morpholine (Table 1). Responses to 1% morpholine gave a Mann-Whitney value of $U = 5$ (Siegel, 1956) with probability of 0.006 that the control group and the experimental group were drawn from the same treatment population. Responses to the 0.01% level were less markedly, but still significantly, different ($U = 11$, $P = 0.049$).

Discussion

Exposure to low concentrations of morpholine produced a sensitization which lasted at least 10 months. But, we did not attempt to determine whether this observed sensitization was exclusively to morpholine or to other stimulatory products. Casual observation of our data did not reveal the experimental subjects to be more responsive to NaCl than the controls; but this comparison was difficult to make in our experimental design because of the changing relationship between response amplitudes and background activity levels. (Hence, the necessity of continual comparison of morpholine response with NaCl response, our reference.) Even if overall olfactory responsiveness is increased as a result of pretreatment, sensitization to morpholine is still proportionally greater (experimental vs. control) 10 months later. We hypothesize that exposure to morpholine imprinted the fish during one of the critical periods in the life of the coho salmon, a period when the fish is undergoing physiological changes in preparation for entering a marine environment.

Independent evidence indicates the existence of a critical period. The Wisconsin Department of Natural Resources allows approximately 1 month of imprinting during the period of smoltification before releasing the fish into the river system. Imprinting for less time or at different stages of the life cycle seems to result in more straying (Peck, 1970).

Morpholine was chosen as the imprinting substance since the responses of fingerling coho salmon to it have been investigated (Wisby, 1952). Consequently, the concentration could be chosen with knowledge of the performance parameters of the coho salmon. It was necessary to be above threshold but not so high as to cause enthusiastic avoidance or sublethal damage. Because of the vagaries of the flow measurements

TABLE 1.—Morpholine-elicited EEG responses of morpholine-imprinted coho salmon compared with those of controls. E designated subjects were imprinted with morpholine at a concentration of 10^{-5} ppm; C designated were controls. Median EEG responses of each fish to 1% morpholine and 0.01% morpholine stimuli are ranked (ties carry averaged ranks) and Mann-Whitney U values and probability values are shown for each treatment level.

1%														
Group	C	C	C	C	C	C	E	E	E	E	E	C	E	E
Median[1]	63.5	100	140	220.5	230	250	255	266.5	287	333	351.5	600	915	917
Rank	1	2	3	4	5	6	7	8	9	10	11	12	13	14
						$U = 5$	$P = 0.006$							
0.01%														
Group	C	C	E	C	C	C	E	E	C	E	E	C	E	E
Median[1]	0	0	0	0	0	25.6	38.5	41.5	45	45	50	50	67	77.5
Rank	3	3	3	3	3	6	7	8	9.5	9.5	11.5	11.5	13	14
						$U = 11$	$P = 0.049$							

[1] Median response = $\left(\frac{\text{response morpholine}}{\text{response 0.06 N NaCl}} \times 100\right)$ for eight trials.

in the raceway, one order of magnitude above threshold was chosen. Nevertheless, Wisby (1952) reported some avoidance at this concentration. We did not, however, observe any avoidance where the substance was metered into the raceway. It should be noted that concentrations at the delivery tube could be as high as 100 ppm before mixing took place. But, since the substance was delivered immediately below the falls caused by the separating dam, mixing was assumed to be rapid and complete.

Although fish were treated with very low concentrations of the morpholine, EEG responses were not evident until 100 ppm was reached in responsive fish. But, other workers have also found a relative lack of sensitivity with electrophysiological methods. Home-stream responses disappeared with dilution of home-stream water to 5% (Oshima, Hahn, and Gorbman, 1969b), and Sutterlin and Sutterlin (1971), recording from the olfactory epithelium of Atlantic salmon, *Salmo salar,* found no response to morpholine at 0.9 ppm. Yet Wisby (1952) got clear behavioral manifestations of perception at concentrations of 10^{-6} ppm.

Acknowledgments

Special thanks go to Ronald Poff and Jerry Kryka of the Department of Natural Resources, Wisconsin for providing fish and hatchery space.

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HYPORHAMPHUS AUSTRALIS X *HY. MELANOCHIR*, A HYBRID HALFBEAK (HEMIRAMPHIDAE) FROM AUSTRALIA

The purpose of this note is to report the first known occurrence of hybridization in the family Hemiramphidae. According to Schwartz (1972) it is also the first known hybrid within the order Synentognathi (or suborder Exocoetoidei according to some recent classifications).

Three species of sea garfishes (halfbeaks) of the genus *Hyporhamphus* occur in Australia-New Zealand waters (Collette[1]): *Hy. ihi* Phillipps, the New Zealand garfish or piper; *Hy. australis* (Steindachner), the eastern sea garfish; and *Hy. melanochir* (Valenciennes), the southern sea garfish. The three species are very closely related but differ in numbers of gill rakers, vertebrae, dorsal and anal fin rays, relative length of the upper and lower jaw, and placement of the pelvic fins. They are almost completely allopatric but the ranges of *Hy. australis* and *Hy. melanochir* overlap at Eden in southern New South Wales near the Victoria border.

During a year's study at the Australian Mu-

[1] Collette, B. B. The garfishes (Hemiramphidae) of Australia and New Zealand. Unpublished manuscript.

TABLE 1.—Numbers of fin rays, gill rakers, and vertebrae in *Hyporhamphus australis*, *Hy. melanochir*, and a hybrid between the two species.

	Dorsal rays						Anal rays					
	15	16	17	18	*N*	$\bar{x}$	17	18	19	20	*N*	$\bar{x}$
Hy. australis												
New South Wales	29	68	10		107	15.82	12	63	24	2	101	18.16
Eden, N.S.W.		2			2	16		2			2	18
Hybrid-Eden			1		1	17			1		1	19
Hy. melanochir												
Eden			1		1	17			1		1	19
Victoria	1	28	33	2	64	16.56		19	37	8	64	18.83

	First arch gill rakers														
	27	28	29	30	31	32	33	34	35	36	37	38	39	*N*	$\bar{x}$
Hy. australis															
New South Wales					3	6	9	16	23	28	10	6	2	103	35.10
Eden, N.S.W.									1	--	1			2	36
Hybrid-Eden						1								1	32
Hy. melanochir															
Eden			1											1	29
Victoria	1	2	11	15	14	11	6							60	30.60

	Second arch gill rakers														
	21	22	23	24	25	26	27	28	29	30	31	32	33	*N*	$\bar{x}$
Hy. australis															
New South Wales			1	--	7	6	10	16	16	19	17	6	2	100	28.91
Eden, N.S.W.								1	--	--	--	1		2	30
Hybrid-Eden								1						1	28
Hy. melanochir															
Eden		1												1	22
Victoria	1	5	10	17	20	4	2							59	24.19

	Total vertebrae								
	55	56	57	58	59	60	61	*N*	$\bar{x}$
Hy. australis									
New South Wales		7	33	10				50	57.06
Eden, N.S.W.			1	1				2	57.5
Hybrid-Eden					1			1	59
Hy. melanochir									
Eden						1		1	60
Victoria				6	3	2		11	58.64

seum in 1969-70, I visited the Sydney fish market almost every week to obtain fishes. Origin of specimens from throughout New South Wales was determined by identifying the fishery cooperative which offered each box of fish for auction.

On 8 April 1970, I selected, more or less at random, four sea garfishes from several boxes of large specimens from Eden, New South Wales. (These specimens, all females, have been catalogued into the U.S. National Museum collections: USNM 207518-292 mm standard length; 207519-269 mm; 207520-280 mm; and 207521-264 mm). The smallest of the four specimens (USNM 207521) was separated from the other three on the basis of its low gill-raker counts (29 on the first arch, 22 on the second). This count is characteristic of the Victorian population of *Hy. melanochir* (Table 1). Two of the other three specimens (USNM 207518-9) had gill-raker counts typical for *Hy. australis*. The fourth specimen (USNM 207521) had gill-raker counts intermediate between *Hy. melanochir* and *Hy. australis*.

The small specimen of *Hy. melanochir* had 17 dorsal and 19 anal rays in agreement with the modes for the Victorian population (Table 1). The pair of *Hy. australis* had 16 dorsal and 18 anal rays in agreement with the modes for that species. The fourth specimen, like the *Hy. melanochir*, had counts of 17 dorsal and 19 anal rays.

Intermediacy in gill-raker count suggested that the fourth specimen might be a hybrid between *Hy. australis* and *Hy. melanochir;* hence, pigment comparisons were made prior to preservation. There was more yellow on the anterior edge of the anal fin in the small *Hy. melanochir* than in the two *Hy. australis*. The fourth specimen was intermediate. Pigmentation in the pectoral fin was most prominent in the *Hy. melanochir* and the fourth specimen where the melanophores formed a spot distally in the fin. The pigment was distributed all over the fin in the two *Hy. australis*. Scattered small melanophores gave a mottled appearance to the lateral line along the body in the *Hy. melanochir*. This pigment was absent in both *Hy. australis*. A trace of pigment was present in the fourth specimen.

The three larger specimens had a more prominent ridge in the middle of the upper jaw than did the small *Hy. melanochir*. The upper jaw of the *Hy. melanochir* was distinctly shorter than its width (width/length ratio 1.33), in agreement with 35 Victorian specimens of the species (0.92-1.49, mean 1.16). The two *Hy. australis* had the upper jaw about as long as wide (ratios 0.99 and 0.96) as do 32 other *Hy. australis* (0.86-1.29, mean 1.00). The fourth specimen was intermediate (ratio 1.23) between Eden specimens of the two species but within the usual range of *Hy. melanochir* (Figure 1).

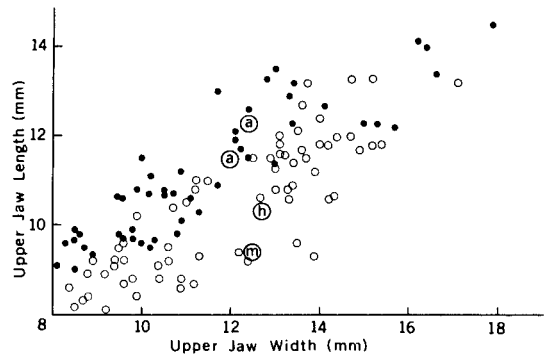

FIGURE 1.—Relationship of upper jaw length to upper jaw width in two species of Australian halfbeaks. Open circles indicate *Hyporhamphus melanochir*; dots *Hy. australis*. Four specimens from Eden, New South Wales indicated by letters: a for *Hy. australis*; m for *Hy. melanochir*; and h for *Hy. australis* × *melanochir*.

Otoliths were extracted from all four specimens while fresh and were examined shortly thereafter by otolith specialist John E. Fitch, who was told only that the four sets of otoliths had come from some Australian halfbeaks. He concluded that two sets (the *Hy. australis*) were of one species, one set (the small *Hy. melanochir*) was of a second species, and the fourth set was intermediate. *Hy. australis* has a much longer (relative to height) sagitta than *Hy. melanochir* (Figure 2). Length divided by height averages (left and right sagittae measured) 1.91 and 1.93 for the two *Hy. australis*, 1.43 for the *Hy. melanochir*, and 1.72 for the fourth specimen. *Hy. australis* has a more pointed rostrum than *Hy. melanochir*, and has a vertical groove near the rostrum on the external side that is

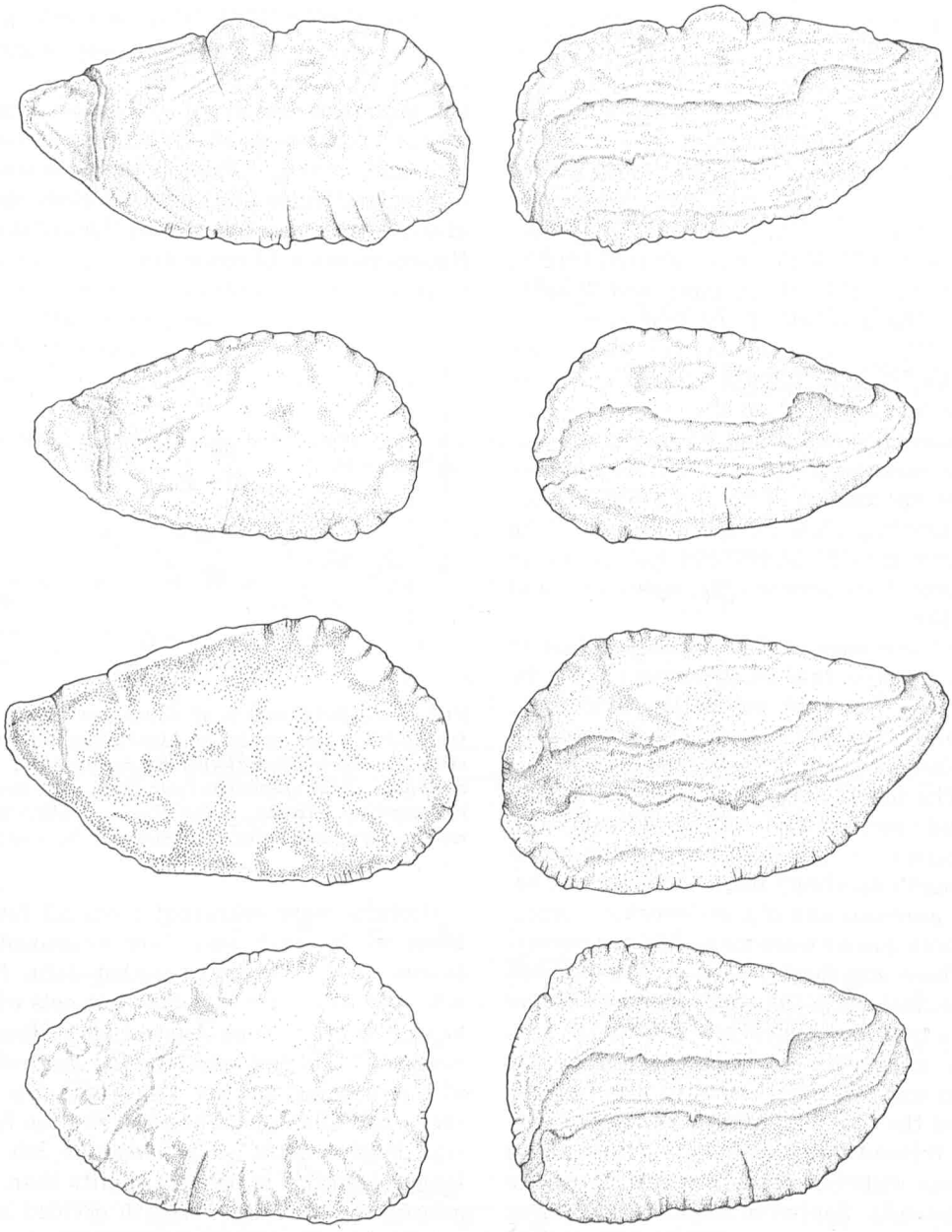

FIGURE 2.—Otoliths (sagittae) of two species of halfbeaks from Eden, New South Wales, Australia. Outer surface on left, inner surface, with sulcus, on right. Top to bottom: *Hyporhamphus australis*, 292 mm SL (standard length); *Hy. australis*, 269 mm SL; *Hy. australis* × *melanochir*, 280 mm SL; and *Hy. melanochir* 264 mm SL.

absent in *Hy. melanochir*. The fourth specimen is intermediate with a faint rostral groove.

Vertebral counts also indicate hybridization. The small *Hy. melanochir* had 60 vertebrae, at the high end of the range for nine Victorian specimens (Table 1). The two *Hy. australis* had 57 and 58 vertebrae, comparing well with 50 New South Wales specimens. The fourth specimen was intermediate with 59 vertebrae.

Based on its intermediacy in gill-raker and vertebral counts, pigmentation, upper jaw length, and otolith structure, I conclude that the fourth specimen is a hybrid between *Hy. australis* and *Hy. melanochir*. The two species are essentially allopatric and show character displacement as their ranges approach, that is, the Victoria population of *Hy. melanochir* differs more from the neighboring New South Wales population of *Hy. australis* than do populations of *Hy. melanochir* from further west, in South Australia and Western Australia (Collette, see footnote 1).

I thank Daniel M. Cohen and Robert H. Gibbs, Jr., for reviewing the manuscript, John E. Fitch for examining the otoliths, Frank J. Schwartz for checking his manuscript on fish hybrids, R. Budd for permitting access to the Sydney fish market, and Keiko Moore for preparing the illustrations.

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CONTRIBUTION ON THE SPAWNING OF *AUXIS* SP. (PISCES, SCOMBRIDAE) IN THE ATLANTIC OCEAN

The frigate mackerel (*Auxis* sp.) are apparently among the most abundant scombrids in the tropical Atlantic Ocean. They form a substantial part of the diet of skipjack tuna, *Katsuwonus pelamis*; yellowfin tuna, *Thunnus albacares* (Dragovich, 1970a); and bluefin tuna, *T. thynnus* (Dragovich, 1970b); and, therefore, it is important to understand their life history and their role in the trophodynamics of tropical ocean ecosystems. We report on the examination of ovaries from 76 frigate mackerel collected from the eastern and western tropical Atlantic, and off Cape Hatteras, N.C. (Figure 1).

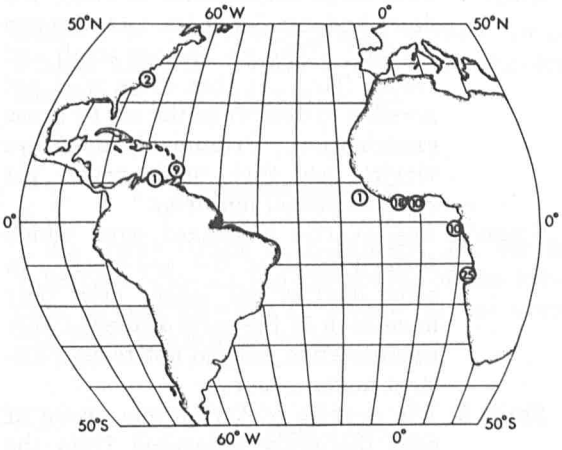

FIGURE 1.—Location and number of *Auxis* sp. captured (in circle) from which ovaries were examined.

The genus *Auxis* may be composed of two species, *A. thazard* (Lacépède) and *A. rochei* (Risso). We were not able to assign the specimens in our study to either species because the published diagnostic characters were not reliable for species identification. More taxonomic work is needed on the genus (William J. Richards, Southeast Fisheries Center, Miami Laboratory,

[1] Contribution No. 222, Southeast Fisheries Center, Miami Laboratory, National Marine Fisheries Service.

National Marine Fisheries Service, pers. comm.).

The ovaries were removed from specimens that had been fixed in 10% Formalin[2] and stored in 40% isopropanol. A wedge-shaped sample was taken from each ovary and about 200 eggs, 0.25 mm (one micrometer unit) in diameter or greater, were measured, following the method described by Clark (1925). The eggs were selected along an edge of the sample corresponding to the radius of the ovary. We determined that eggs below 0.25 mm formed most of the egg-stock present in all mature females throughout the year. In some ovaries, eggs about 0.25 mm in diameter appeared to be in the early stages of yolk accumulation because they were more opaque than the stock eggs. Each ovary was classified according to the following stages:

Stage 1. This stage corresponds to stage 1-S described by Schaefer and Orange (1956): "The gonads are small and ribbon-like. At this stage it is not possible to determine the sex by gross examination. Presumably these are virgin fish that have never yet reached sexual maturity."

Stage 2. The ovaries contained eggs which formed most of the egg-stock. In some ovaries the larger eggs may have been in the early stages of yolk accumulation but did not form a distinct modal group.

Stage 3. The ovaries contained one group of eggs distinctly separated from the egg-stock. Modal diameters of this group were from 0.375 to 0.675 mm.

Stage 4. The ovaries contained two groups of eggs distinctly separated from the egg-stock. Modal diameters of the group formed by the larger eggs were from 0.875 to 0.975 mm.

Selected egg diameter frequency distributions from stages 2, 3, and 4 are shown in Figure 2.

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

Our evidence indicates that *Auxis* from the tropical Atlantic mature at about 290 mm fork length (Table 1). Fish with ovaries in stages 2, 3, or 4 were considered mature; fish which contained stage 1 ovaries were considered immature. The smallest mature fish (stage 3) from the eastern Atlantic was 270 mm and the largest

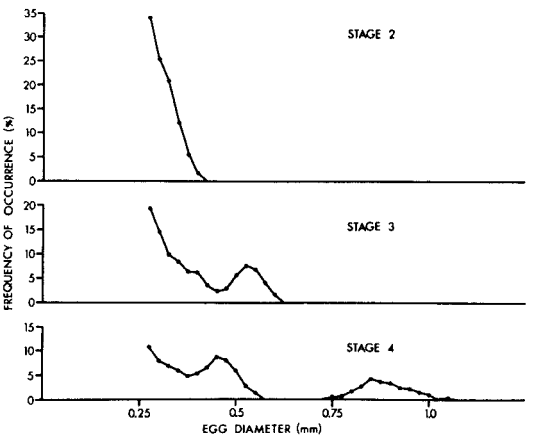

FIGURE 2.—Percent egg diameter frequency distribution from selected ovaries in stages 2, 3, and 4 (smoothed by a moving average of 3).

TABLE 1.—Number of mature and immature *Auxis* examined from the eastern and western tropical Atlantic by 10-mm length intervals.

Length interval (mm)	Eastern Atlantic		Western Atlantic	
	Immature	Mature	Immature	Mature
210-219	1	--	--	--
240-249	2	--	--	--
250-259	1	--	--	--
260-269	2	--	--	--
270-279	1	2	2	--
280-289	1	12	--	--
290-299	--	6	--	--
300-309	--	2	2	1
310-319	--	1	--	2
320-329	--	1	--	--
330-339	--	1	--	--
340-349	--	2	--	2
350-359	--	1	--	--
360-369	--	6	--	--
370-379	--	2	--	--
380-389	--	1	--	--
390-399	--	3	--	--
400-409	--	2	--	--
410-419	--	2	--	--
420-429	--	1	--	1
430-439	--	2	--	--
440-449	--	3	--	--
450-459	--	3	--	--
460-469	--	3	--	--

immature fish was 285 mm. From the western Atlantic, the smallest mature fish (stage 3) was 309 mm and the largest immature fish was 307 mm. There is an indication from the specimens we examined that the eastern Atlantic *Auxis* mature at a slightly smaller size than the western Atlantic *Auxis*. It is possible, however, that this is an artifact resulting from our sample size. Table 1 also indicates the length distribution of specimens used in our study. The two specimens captured off Cape Hatteras were 458 and 459 mm and both had stage 3 ovaries. These are not included in Table 1.

Ovaries in stages 3 and 4 were taken as evidence that spawning was imminent. *Auxis* with ovaries in a spawning condition were captured from the eastern Atlantic in February, March, April, June, September, and October, and from the western Atlantic in March and April. The two specimens from off Cape Hatteras were captured in July and August, and both contained ovaries in spawning condition. The number of *Auxis* examined in each stage of ovary development by month and area of capture is shown in Table 2.

TABLE 2.—Number of *Auxis* examined in each stage of ovary development by month and area of capture.

Area	Stage	Feb.	Mar.	Apr.	June	July	Aug.	Sept.	Oct.
Eastern Atlantic	1	--	--	--	--	--	--	--	8
	2	--	4	2	--	--	--	--	10
	3	1	12	7	2	--	--	10	2
	4	--	--	--	--	--	--	--	6
Western Atlantic	1	--	--	4	--	--	--	--	--
	2	--	--	1	--	--	--	--	--
	3	--	2	3	--	--	--	--	--
Cape Hatteras, N.C.	3	--	--	--	--	1	1	--	--

The number of eggs released per spawning is estimated for five specimens that contained stage 4 ovaries. These were captured off the Ivory Coast on 15 October 1967 at lat 4°31′N, long 5°18′W. The method used to determine the number of eggs released per spawning was to estimate the number in the most mature modal group, assuming that these eggs would be released at next spawning (Simmons, 1969).

The results show that *Auxis* from 360 to 455 mm fork length release from 56,000 to 148,000 eggs (Table 3). Rao (1964) determined

TABLE 3.—Estimated number of eggs in the most advanced mode for *Auxis* of different lengths.

Fork length (mm)	Eggs in the most advanced mode
360	95,000
361	58,000
396	56,000
440	148,000
455	103,000

that a 442-mm frigate mackerel captured off the southwest coast of India would have released 280,000 eggs at next spawning. A large variation should be expected due to the small sample size. The equation describing our regression line calculated by the method of least squares is

$$Y = -127.262 + 0.542X,$$

where Y is the number of eggs in the most advanced mode in thousands and X is the fork length of the fish in millimeters.

Acknowledgments

We thank Grant L. Beardsley, Jr., for his valuable advice during the course of the investigation and Edward D. Houde for his useful criticism of this manuscript.

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GPO 986-440

A UNITED STATES DEPARTMENT OF COMMERCE PUBLICATION

NOAA FSYB-A 71-2

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U. S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Seattle, Wash.
APRIL 1973

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Seattle, Washington

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402 - Subscription price: $8.00 per year ($2.00 additional for foreign mailing). Cost per single issue - $2.25.

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SCIENTIFIC ADVICE ON CATCH LEVELS

J. A. GULLAND AND L. K. BOEREMA[1]

ABSTRACT

The sustainable yield, or maximum sustainable yield, has been used to provide, on an objective scientific basis, target figures for the catches to be taken from a heavily exploited stock that is under regulation. The simple concept of sustainable yield does not, however, provide a completely adequate guide when the biological system is complex. Certain other quantities—the replacement yield, the sustainable yield from a stock in equilibrium, the maintainable yield, and the catch for desired harvesting rate—are defined which correspond more closely to the biological reality.

One or other of these will provide a better guide for management, depending on the nature of the divergence from the simple model. In whale populations the major divergence is the lag between changes in adult stock and changes in recruitment; replacement yield or maintainable yield are the most useful. In many fish stocks, fluctuations in year-class strength are more important: catch for desired harvesting rate may be better.

Various fishing research organizations are concerned with the setting of annual catch quotas or other measures for the management of the resources which are their responsibility. Agreement on the level of these quotas is more easily reached if they are determined by objective scientific criteria. Apart from the continuing difficulty in making precise assessments concerning any wild animals, this guidance is difficult to provide without some agreed basis on how the "correct" catch should be calculated.

At present there is not a single theoretical model for determining this catch that combines all the desirable features of (a) being readily understandable (at least in general outline) to the decision makers, (b) describing and predicting in a realistic manner, and to an acceptable degree of precision the events in every fish stock to which it may need to be applied, and (c) capable of being applied to a specific fishery without great demands in data and analysis. The models associated with Schaefer (1954) on the one hand and with Ricker (1958) and Beverton and Holt (1957) (in the simple form when no account is taken of fishery-induced changes in recruitment) on the other fail, for many important fisheries, to satisfy the second criterion. The density-dependent form of the Ricker-Beverton Holt approach is more satisfactory in this regard, but makes heavy demands on data and analysis. Despite these difficulties, and in the absence of a single uniformly acceptable model, some objective guidance can be given on the magnitude of the catches that can be taken from heavily exploited stocks, and such guidance is being used by many regional commissions [e.g., IWC (International Whaling Commission), Inter-American Tropical Tuna Commission, ICNAF (International Commission for the Northwest Atlantic Fisheries)] in framing regulations. This paper explores some of the bases of such guidance, in the hope of facilitating the future preparation of advice on desirable catch levels.

SUSTAINABLE YIELD

The concept of a sustainable yield as often applied in practice, and more particularly the idea of the maximum sustainable yield, is based on a simplified model of a natural animal population in which the population is treated as a single unit, ignoring the fact that there are individuals of different ages, etc.; it also ignores all disturbing influences on the population, other than removals by man. If such a population has been reduced below the limiting carrying

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Manuscript accepted October 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

capacity of its environment, it will tend to increase. In the simplified case the rate of increase will depend solely on the abundance of the population (or the abundance of the exploitable part of the population).

On the basis of this simple model, it is clear that if the annual removals by man (catch) are equal to the annual natural increase, the size of the population will remain unaltered, and such a catch can be sustained indefinitely. For such a situation the sustainable yield can be defined as being equal to the net rate of natural increase and represents the yield which can be maintained indefinitely while also maintaining the stock size at the same level.

The rate of increase, as a proportion of the population, generally decreases as the population increases. The absolute value of this natural increase, and hence the sustainable yield, is small for very small populations and is also small for large populations as they approach the limiting value. It will be greatest for some intermediate level of population which is the population abundance giving the maximum sustainable yield (MSY) (see Figure 1).

If the population is less than the level giving the MSY, no catch greater than the sustainable yield can be maintained for more than a short time. The population will be reduced each year by an amount approximately equal to the difference between the catch and the sustainable yield. The sustainable yield will in turn be reduced, leading to an ever faster reduction, which, if the amount caught is maintained by fishing harder and harder, will in a fairly short time lead to the "commercial extinction" of the stock.

On the other hand, if the population is above the MSY level, catches greater than the sustainable yield corresponding to that population level, can be maintained indefinitely, provided that they are not greater than the MSY. This is because, as these catches reduce the population toward the MSY level, the sustainable yield will increase. When the population is reduced to the level at which the sustainable yield is equal to the catch, then the catch can be maintained indefinitely without further change. The maintainable yield may then be defined as the largest catch that can be maintained from the population, at whatever level of stock size, over an indefinite period. It will be identical to the sustainable yield for populations below the level giving the MSY, and it will be equal to the MSY for population at or above this level. In the latter case harvesting the maintainable yield will involve for a short transitional period a change in population abundance as it is thinned out to the MSY level.

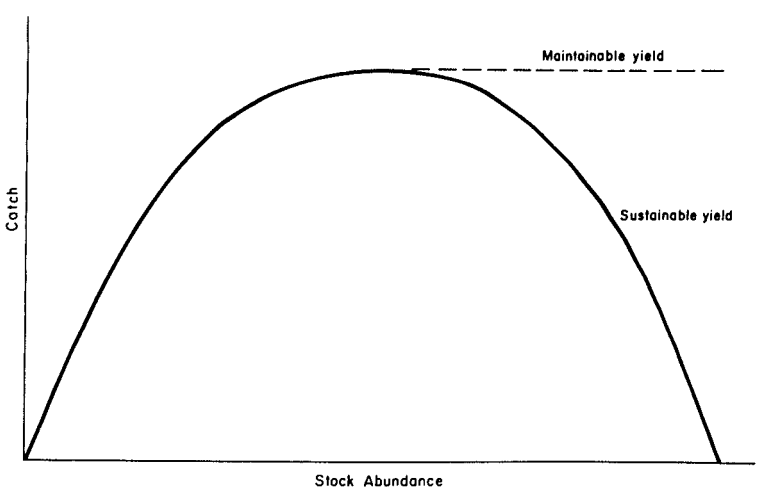

FIGURE 1.—Sustainable yield and maintainable yield as function of stock abundance.

The simplified description above does not in fact fit precisely the actual situation in the sea. Two main divergences may be mentioned: 1) the fact that the net rate of natural increase will depend on past events as well as on the current abundance and 2) there are many sources of variation, other than exploitation, in the abundance of populations. The most important of these for many fish species of commercial importance is natural fluctuations, especially in recruitment, caused by variations in environmental conditioning. Other causes of variation, e.g., changes in the availability or distribution of fish, will have significant effects on the success or otherwise of the fishery in a particular season, but will not be discussed here. The first of these is particularly significant for whales, and the second for some fish populations, especially in temperate and subarctic waters.

LAG EFFECTS

For whales, the net rate of natural increase in the exploitable part of the population is usually expressed in numbers and is the difference between the number of animals dying from natural (nonfishery) causes, which will be some fairly constant proportion of the number in the current stock, and the numbers of recruits entering the exploitable stock, which will be closely proportional to the numbers of mature animals alive some years previously, at least at small to moderate population sizes. As the population approaches its equilibrium, unexploited level, the recruits will be less, or the mortality more, or both, than expected from a purely proportional relationship with population abundance. If the abundance of the stock is changing, the concept of a sustainable yield becomes complicated. If, for example, the stock has recently been reduced, then the recruits during the year will have come from a parent population that is greater than the current mature stock. The number of recruits may then be appreciably greater than the number of natural deaths, so that quite a large catch could be taken and still leave the population at the end of the year the same size that it was in the beginning. However, such a catch could not be sustained indefinitely, since the number of recruits in later years will decrease. For such a stock a number of different terms may need to be defined.

The replacement yield for a given year is the catch which, if taken, will leave the abundance of the exploitable part of the population at the end of the year the same as at the beginning. This is specific to a particular year and includes no concept of continuity. Even if the replacement yield is taken in one year, it is unlikely that the replacement yield in the following year will be the same, unless this population has remained at around the same abundance for some time (not less than the time span between birth and recruitment).

The simple definition of the sustainable yield refers to an equilibrium situation and cannot strictly be used in a situation of changing stock size. When the population has been changing it may be convenient to define the (equivalent) sustainable yield as the sustainable yield from a population of the same abundance (or with the same abundance of the exploited phase), which has remained at this level of abundance for a long time. It is the value that would be obtained from reading off the yield corresponding to the abundance in a figure such as Figure 1. Hence if the catch taken is set equal to this sustainable yield, the population abundance will not, in general, remain unaltered.

It is evident that if the stock (or its exploitable phase) has recently been decreasing, and, as in the case of whales, the recruits are roughly proportional to the abundance of an earlier and larger parent stock, the replacement yield is greater than the sustainable yield of the present stock size. If, on the other hand, the stock has recently been increasing, the replacement yield is equal to the difference between the recruitment from a smaller parent stock and the natural mortality of the greater present stock and may therefore be lower than the sustainable yield of either the parent stock size or the present stock size.

In a situation in which the stock is above the level of maximum sustainable yield, the maintainable yield, as defined above, which is equal to the maximum sustainable yield, is not affected by recent changes in stock size. If the

stock is changing and is below the level of MSY, however, the maintainable yield is equal neither to the replacement yield nor to the sustainable yield corresponding to the abundance of either parent or present stock, but will be at a level between the sustainable yields of these two stock sizes. Maintenance of the catch at the level of maintainable yield will ultimately lead to an equilibrium situation with a stock size in between the original "parent" and "present" stock sizes.

It should be noted that if the stocks are below MSY level and have recently been decreasing, the maintainable yield is lower than the replacement yield, whereas if the stocks have recently been increasing, the maintainable yield is the higher of the two. Any catch lower than the maintainable yield, if kept at the same level for a sufficient period of time, will ultimately lead to a rebuilding of the stocks, even though in the short term it may cause some decrease.

If the population is below the MSY level, setting the catch equal to the estimated sustainable yield will, as has been frequently pointed out, lead to an unstable situation. If the estimate used is only just too high the stock will start to decline, the gap between the catch and the actual sustainable yield will widen at an accelerating rate, and the stock will decline ever more rapidly until the catch is adjusted. As pointed out by Y. Fukuda (pers. comm.) this can occur, if there are natural fluctuations, even if the catch taken is exactly equal to the sustainable yield under average conditions. Suppose, for example, there is a poor year for reproduction, leading to reduced recruitment. Then the catch, if unchanged, will reduce the stock, and this reduced stock will have a smaller sustainable yield, even under average conditions. A fixed catch will then continue to deplete the stock at an accelerating rate. Similarly, a favorable if transient fluctuation and a fixed catch will result in a continuous increase in population to above the MSY level.

The significance of the differences among the various terms can perhaps best be illustrated with some hypothetical examples of different actions which might have been taken after the serious decline in the fin whale stocks in the late 1950's and early 1960's. For simplicity, it has been assumed that the stocks have been declining by 10,000 whales per year from a level of 120,000 in 1960 to 70,000 in 1965, figures which are roughly similar to the decline as estimated by the Scientific Committee of the IWC. Recruitment rate has been taken for the purpose of this example at 8%, recruitment age at 5 years, and natural mortality rate at 4%, which values were assumed to remain constant within the range of stock sizes of the examples (see Table 1).

TABLE 1.—Trends in population and catch of Antarctic fin whales, if, after 1965, catches were set equal to the replacement yield, or to the sustainable yield. (Thousands of animals.)

	Catch = replacement yield				Catch = sustainable yield			
Year	Stock	N[1]	R[2]	Catch	Stock	N[1]	R[2]	Catch
1960	120				120			
1961	110				110			
1962	100				100			
1963	90				90			
1964	80				80			
1965	70	2.80	9.60	6.80	70	2.80	9.60	2.80
1966	70	2.80	8.80	6.00	74.0	2.96	8.80	2.96
1967	70	2.80	8.00	5.20	76.88	3.08	8.00	3.08
1968	70	2.80	7.20	4.40	78.72	3.15	7.20	3.15
1969	70	2.80	6.40	3.60	79.62	3.18	6.40	3.18
1970	70	2.80	5.60	2.80	79.66	3.19	5.60	3.19
1971	70	2.80	5.60	2.80	78.88	3.16	5.92	3.16
1972	70	2.80	5.60	2.80	78.48	3.14	6.18	3.14

[1] N = numbers dying from natural causes = 4% of current stock.
[2] R = numbers of recruits = 8% of adult stock 5 years earlier.

If from 1965 onward, catch quotas had been introduced equal to the replacement yield, the stock would have been maintained at the level of 70,000 whales, and the quota would have been 6,800 whales in 1965, declining by 800 per year to 2,800 whales in 1970, after which the number would have remained at this level.

If, on the other hand, the sustainable yield had been taken every year the catch quota would have been 2,800 in 1965, slowly rising to 3,190 in 1970, then declining to 3,130 in 1973 and stabilizing at about 3,140 thereafter, at which time the stock size would practically have stabilized at 78,560 whales.

The highest constant annual yield which could have been taken from 1965 onward—the maintainable yield—would have been about 3,125 whales, which would have led to a stock size of about 78,200 whales by the mid-1970's (Figure 2a).

For the purpose of demonstrating the effect of increasing stock size, the effects of different catch quotas have been calculated for the situation in which the stock has risen from 70,000 to 80,000 whales over a 5-year period (say, from 1965 to 1970) by 2,000 whales per year. Catch quota equal to the replacement yield, which would maintain the stocks at 80,000 whales, would have been 2,400 whales in 1970, increasing by 160 whales per year to 3,200 whales in 1975, after which the figure would remain constant.

If the sustainable yield had been taken, the catch quota in 1970 would have been 3,200 whales, decreasing to 3,120 in 1974 and thereafter stabilizing at around 3,130, and a stock size of around 78,310 whales.

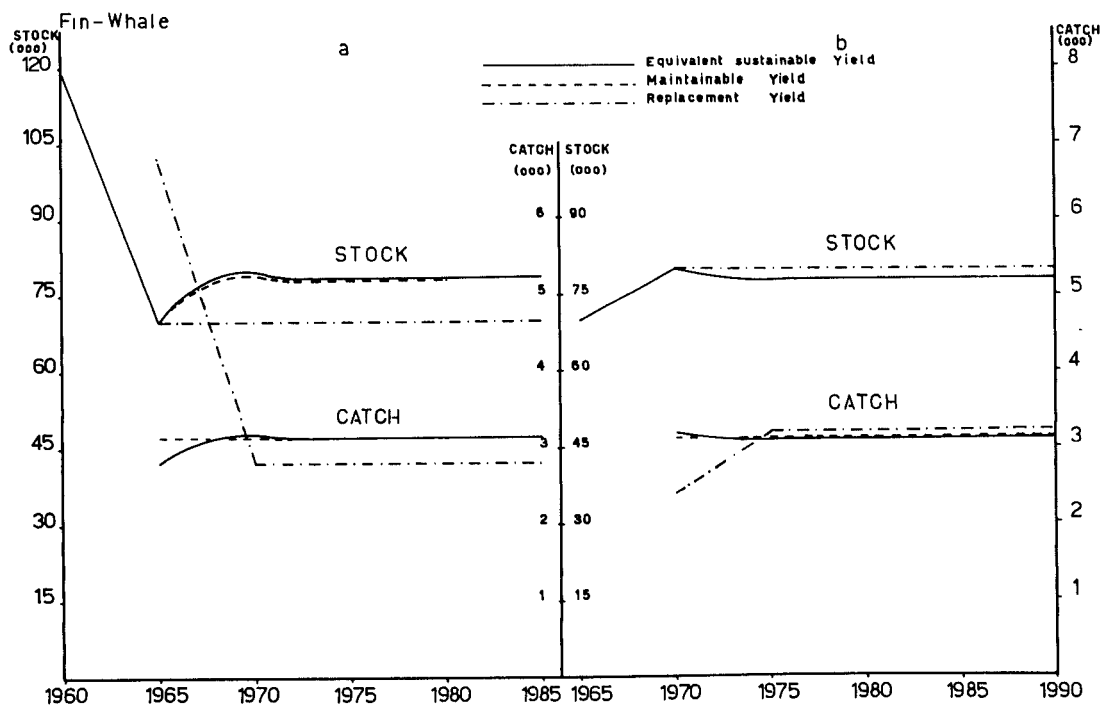

FIGURE 2.—Examples of catch level and stock size resulting from regulating catches of fin whales at the level of equivalent sustainable yield, maintainable yield, and replacement yield respectively, in the case that the regulations were introduced a) after a constant decline in the stock (in the example assumed to have taken place from 1960 till 1965) and b) after a constant increase in the stock size (in the example assumed to have taken place from 1965 till 1970). Parameters used in these models are specified in the text.

The maintainable yield would in this case have been 3,134 whales, leading to a stock size of about 78,360 whales in the later 1970's (Figure 2b).

These examples demonstrate some general features. Firstly, they show that catch regulations based on replacement yield, equivalent sustainable yield or maintainable yield will all lead to an equilibrium situation in which the stock size and permitted catch reach a stable level. In the case in which the stock has recently been changing, regulation based on replacement yield will maintain the stock at the level at which it was at the start of this regulation, but catches regulated at the level of sustainable yield or of maintainable yield will lead to a different stock level. If the stock had recently been declining, the long-range stock level and yield would then be rather higher than that based on taking the replacement yield, and if the stocks had recently been decreasing, the long-range equilibrium would be reached at a somewhat lower stock size. Although there are some differences in catch level between regulations based on sustainable yield and on maintainable yield in the first years after introduction, the long-term effects of these two criteria for regulation are very similar.

It would thus seem that replacement yield, which maintains the stock at the same level, but requires changing quotas in the first years, and maintainable yield, which is the highest catch that can be maintained indefinitely from the stock size available, but will lead to a change in stock size in the first years, will provide the best guide for whaling management decisions in situations in which stock sizes have recently been changing.

Any scientific advice on these matters should be clearly defined. Part of recent confusion about frequently changing estimates of permissible yield by the Scientific Committee of the IWC has been due to insufficient definition of the terminology as outlined above.

Finally, it may be noted, from the arguments given above, that the rate of increase of population depleted well below its level of MSY, but completely protected thereafter, is less than the net recruitment rate in an equilibrium situation. For example, for recruitment rate 8%, recruitment age 5 years, and natural mortality rate 4%, the net recruitment rate in equilibrium situation is 4%, but the rate of increase in recovering, unfished, population in any year would be about 3% of the stock size in that year, or about 3.5% of the size of the parent stock (the stock size 5 years earlier).

NATURAL FLUCTUATIONS

For fish, on the other hand, the lag effects on the average are less disruptive to the simple model than natural fluctuations, among which changes in year-class strength are the most striking. Where differences in year classes are very large, it is likely that when a strong year class enters the fishery the stock will increase whatever catch is taken (within practicable limits); when a succession of strong year classes is replaced by a run of poor ones, the stock may decrease even if fishing is cut back virtually to nothing. In this situation it is difficult to talk about a sustainable or maintainable yield.

However, it is precisely in the situation of a declining stock, when strong year classes are being replaced by weak ones, that concern about the management of the stock is likely to be greatest, and when scientists are often asked for advice (e.g., regarding herring in subarea 5 of ICNAF). Sometimes the advice is requested in general terms, allowing the scientists to describe the situation in detail, but leaving the decision as to the control measures (such as the level of catch quotas) to administrators. At other times the administrators cannot decide easily among themselves on the amount of catch that should be taken and ask the scientists for an explicit figure of the "correct" or "desirable" catch. This requires some objective basis for determining this, analogous to the sustainable or replacement yield for whales.

The simplest case is that in which the abundance of recruits (strength of the year class) is independent of the abundance of the parent stock. All that management can do is make the best use of whatever recruitment happened to occur, that is, to maintain fishing at whatever level is considered the optimum position on the yield-per-recruit curve. In the simplest situation the curve of yield per recruit

as a function of fishing effort will have a clear maximum, for which the corresponding fishing mortality can be reasonably easily determined. This fishing mortality might then be considered as being one possible value of the optimum fishing mortality. However, in practice the yield curve will be quite flat in the neighborhood of the maximum. This may make determination of the position of the maximum difficult and will certainly mean that obtaining the absolute maximum (e.g., moving from the effort giving 99% of the catch to that giving 100%) will require a disproportionate increase in effort and hence in costs (Gulland, 1968a). Given particular values of the price of fish and costs of exerting unit fishing mortality, a mortality which will maximize the net economic yield can be calculated, and might be considered the optimum for the given economic situation. Different economic conditions will result in somewhat different optima, but for most conditions the optimum will lie within a fairly narrow range. It is, therefore, possible to define a target of the desirable fishing mortality in the middle of this range which will receive general acceptance, or at least, especially for a heavily fished stock, a minimum target at the upper end of this range. Whatever the precise objectives and economic conditions of any individual country participating in a fishery, the reduction of the amount of fishing to this target level should be desirable.

A more objective method of calculating a limiting value to desirable fishing mortality may be derived from considering the marginal yield, i.e., the increase in total yield achieved by adding one extra unit of effort (Gulland, 1968b). The marginal yield will be equal to the slope of the tangent to the curve of catch against fishing effort. It will always be less than the catch per unit effort, which is the slope of the line joining the point in the curve to the origin. The economic optimum, i.e., the greatest net economic return, occurs when the value of the marginal yield is equal to the marginal costs of a unit of effort. At the point giving the maximum physical yield the marginal yield will be zero. Clearly from any practical viewpoint, it would be undesirable to increase the amount of fishing beyond the level at which the value of the marginal yield is small compared with the costs of the extra unit of effort required to produce that yield. The question then arises as to what might be considered as small. An arbitrary figure, which has in fact been used in connection with the herring on Georges Bank (ICNAF, 1972) is a marginal yield equal to one-tenth of the original catch per unit effort in the very lightly exploited fishery. This is illustrated in Figure 3. The two straight lines through the origin show catches per unit effort

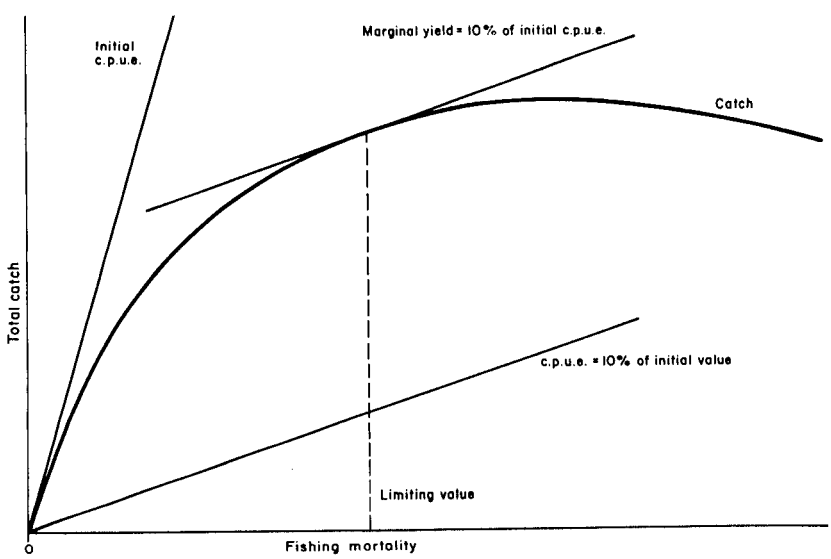

FIGURE 3.—Determination of an economic optimum position at which the marginal yield is 10% of the initial catch per unit effort.

in the nearly unexploited fishery—the tangent to the catch curve at the origin—and a catch per unit effort of 10% of this value. The limiting point beyond which any increase in fishing would certainly not be worthwhile—assuming a marginal yield of 10% of the initial catch per unit effort is not worthwhile—is where the tangent to curve is parallel to this 10% line. The selection of 10% is arbitrary but once the 10% figure is accepted the corresponding catch can be calculated objectively. Thus it can be used to provide a Commission or other management body objective guidance based on scientific grounds.

Unless there are marked density-dependent changes in mortality or growth this target will be achieved by exerting some fixed rate of fishing mortality. It may be noted that the optimum fishing mortality, exerted at a constant rate during the whole of its life, above the age at first capture, is the same for any strength of year class, but slightly larger catches would in principle be obtained by fishing less hard when the fish are young, and harder when they are old, i.e., concentrating catches more at the age when the total biomass of the year class is at its maximum. The fishing mortality in a particular year which leads to the greatest catch over a period will be the mean of the best mortality for each year class present, weighted according to their strengths. If the year classes are equal, this will be equal to the optimum constant rate for a single year class during its entire life. If there is a big variation in year-class strength there would be some theoretical advantage, other things being equal, in fishing slightly harder when the strongest year class present is middle-aged (since they will not grow much more but will suffer losses by natural mortality), and less hard when the strong year classes have just recruited. However, the theoretical increases in yield are not likely to be great, and it is simpler to keep, as the objective, the same constant fishing mortality independent of year-class change. From an economic standpoint the optimum level of fishing mortality will increase slightly when strong year classes are present, because then it becomes more worthwhile to squeeze out an extra 1 or 2% of the maximum yield. For those few fisheries for which the investigators are fortunate enough to have immediately available a measure of total effort which provides a measure of fishing mortality consistent from year to year, the optimum level of fishing can be defined at once in terms of total fishing effort, without the need for year to year adjustments.

Usually difficulties of standardization in a multinational or multigear fishery, or changes in the effectiveness of a nominal unit of effort, will mean that the amount of fishing in each year will have to be controlled in terms of total catch. The scientists can, in principle, given adequate information, calculate what the magnitude of this catch should be, taking into account the strength of the year classes already present in the fishery, and those that will be recruited during the year in question. This catch might be defined as the catch for optimum harvesting rate.

Often a precise optimum level of fishing mortality cannot be defined or cannot be agreed upon. It is still possible to estimate the catches in each year which would be required to attain any prescribed value of fishing mortality. These mortalities may be those which occurred at some previous time when it was believed that the fishery was in better condition (in some general, unspecified sense) than the present, or some convenient figure which the scientists believe approximates to the optimum condition. In this way the scientists, without preempting the administrators' duty to decide on the objective of management, can provide some figures derived in a reasonably objective way, on which it may be possible for agreement to be reached. An example of such calculations are those made by the Assessments Sub-Committee of ICNAF for the cod stock at West Greenland. This stock undergoes moderately strong year-class fluctuations, and estimates have been made of the catches required to attain fishing mortalities of 0.8 and 0.6, as set out in Table 2 (from ICNAF, 1970).

It may be noted that for virtually all patterns of mortality, there is a drop in predicted catch from 1969 to 1970 and again from 1970 to 1971, due to the entry of weak year classes into the fishery.

TABLE 2.—Catches (thousands of tons) of cod from the West Greenland stock in 1970 and 1971 corresponding to different values of fishing mortality (in parentheses).

1968	1969	1970	1971
382 (0.8)	225 (0.6)	178 (0.6)	159(0.6) 203(0.8)
		224 (0.8)	143(0.6) 182(0.8)

For most fish stocks there is a reasonable likelihood that changes in the abundance of the adult stock brought about by fishing will have some effect on the average level of recruitment, though the extent of such effects may not be known. When they are known, they can be incorporated into the calculations to obtain the catch rates corresponding to different objectives.

The management of salmon stocks generally corresponds to this situation. The relation between spawning stock (escapement) and subsequent recruitment is usually claimed to be known and has a maximum at some intermediate level of spawning stock. The catches are adjusted to obtain some desired level of escapement. This might be the level giving—under average conditions—the maximum recruitment, though a more nearly optimum strategy would be to take a rather larger catch, such that the immediate gain in increased catch would be more than the expected loss (with or without any discounting). In such a situation it is possible to define, purely on biological grounds, a catch for maximum recruitment; and also, using both biological and economic considerations, a catch for optimum spawning (or optimum escapement).[2]

The nature of the Pacific salmon fisheries—the movement of the prespawning fish through the fishing area during a short season and the spawning and subsequent death of all those not caught—makes relatively easy the visualization of the catches as defined here, since they are equal to the number of fish arriving at the fishing grounds, less the escapement required for maximum recruitment, or the optimum escapement respectively. However, the same definition could apply to any fishery, though in practice it can be applied only in those few fisheries for which the stock/recruit relationship is well known. It may be noted that these definitions lead to very great fluctuations in the catch that should be taken. Very large catches may be taken from good runs, but the allowable catch would fall to a very low level, or even zero, when the run is poor, and little, if at all, above the required escapement. The proportion of the stock (run) that is harvested decreases rapidly with decreasing run and falls to zero as soon as the size of the run drops to or below the target escapement.

Unfortunately, for most fisheries there is little firm information on the relation between adult stock and average recruitment. An obvious example of the resultant difficulties in defining objectively any specific catch quota is occurring for both the herring and haddock on Georges Bank (subarea 5 of ICNAF). For the haddock there has been an unprecedented run of poor year classes (those of 1964 to 1970 inclusive) which, combined with exceptionally heavy fishing in 1966 and 1967, has reduced the stock to a very low level. Though the more recent of the weak year classes (since about 1968) were associated with a low parent abundance, the earlier ones came from moderate to large stocks —in fact stocks of about the same abundance as those giving the very large year classes of 1962 and 1963. Thus although it is highly probable that the decline in adult stock is among the causes of the run of poor year classes, it is certainly not the only cause.

The ICNAF scientists have, therefore, pointed out that the sensible policy is to take action to

[2] This outline of the scientific rationale of salmon management ignores the great practical difficulties of management of any specific salmon fishery—the mixture at sea of fish from several different stocks, the difficulty of obtaining accurate measures of the incoming run before the start of the very short season, etc. These are outside the scope of the present note.

build up the spawning stock, since this will almost certainly increase the probability of future year classes being of average strength or better. However, there is no guarantee that, even if in the extreme case the catches are cut to zero, there will be any increase in recruitment compared with what would have occurred with unrestricted fishing.

This means that, since there is no good knowledge of the stock/recruit relation, there is no catch uniquely definable on scientific grounds as the best catch, though the optimum policy, for a stock at a low level, must lie between catching nothing (for the most rapid rebuilding of the adult stocks) and fishing at the rate which makes the best use of those fish which have, in fact, been recruited.

A catch that can be objectively defined, which will often lie in this range and which may also be a reasonable catch to take for the benefit of the fishery, is the replacement catch. This can be defined, in exactly the same way as before, as that catch which will ensure that the stock at the end of the year is the same as that at the beginning of the year. The stock in question could be the spawning stock, or the total fishable stock, and its magnitude could be expressed either as weight or numbers. (The use of numbers makes calculations easier and clearer.)

For example, recent reports of ICNAF's Assessment Sub-Committee have set out the changes in the numbers in the Georges Bank haddock stock, separating additions through recruitment, and removals by fishing and natural mortality. Thus during 1970 there were 16 million recruits, and some 3 million fish died through nonfishing causes, i.e., a net natural increase of 13 million fish, which was about twice the catch in numbers (ca. 5.3 million). However, because the deaths (through both fishing and natural cases) were mainly of large fish (average age in U.S. landings were 6.6 years of 2.4 kg weight), the deaths (in weight) were much larger than the weight of recruits, though this was almost balanced by the growth of the survivors. Thus the catch of 12,000 tons was about equal to the net natural additions, i.e., the catch was equal to the replacement catch, in weight, though less than the replacement catch in numbers.

The replacement catch varies very greatly. Thus between 1968 and 1969 when the natural deaths in the Georges Bank were 5 million fish and the recruits only 1 million, the stock, in numbers, could be maintained only by introducing 4 million fish onto the grounds, i.e., a replacement catch of minus 4 million fish. Conversely, when a very strong year class is recruited to the fishery, the replacement catch would be large and require a fishing effort well in excess of that giving the optimum mortality. The variation in the replacement catch, defined in terms of weight, will be less severe. Even so, it is clear that the replacement catch cannot be used blindly as the determinant for the catch to be taken in any particular season. It will, however, provide some sort of guide as to whether the proposed action will improve things (proposed catch is less than the replacement catch), or allow them to get worse. Unfortunately it is not a perfect guide. For example the average condition of the stock, over a period, will be maintained only if, when a strong year class is entering the fishery, the opportunity is taken to build up the stock to balance the occasions when poor year classes occur, i.e., less than the replacement catch should be taken when strong year classes are being recruited. Also, the practical application depends on obtaining good and early estimates of the strength of the incoming recruitment.

Regulations, such as catch quotas, based on a catch defined in terms of a particular harvesting rate would seem to form a better guide. Though the optimum mortality cannot be determined unless the form of the stock/recruit relation is known, an optimum rate (for any given economic or social policy) can be calculated on the assumption of constant recruitment. If the recruitment is affected by the abundance of the adult stock and the stock is at a low level, the optimum rate must be somewhat less. Therefore an upper bound can be set on the desirable level of catch. Further, various assumptions can be made concerning the form of the stock/recruit curve, and the corresponding relation between fishing mortality and total yield calculated. The scientific advice could then be presented in four columns: the first would list the possible objectives; the

second would give assumptions that could be made about the recruitment; the third and fourth columns would then give the fishing mortality necessary to achieve the objective and the corresponding catch in the forthcoming season. For example, for a purely hypothetical stock the information could be given as follows:

Objective and recruitment	*Optimum F*	*Catch* (tons)
Maximum physical yield:		
Constant	1.2	110,000
Moderately density-dependent	0.9	84,000
Strongly density-dependent	0.6	59,000
Maximum economic yield:[1]		
Constant	0.8	76,000
Moderately density-dependent	0.7	68,000
Strongly density-dependent	0.5	50,000

[1] For a certain set of assumptions on costs and prices.

While this still leaves a wide choice open—a range of over twofold, the more extreme values might be ignored so that the real choice may not be large, and the information provides a useful basis for determining management action.

REBUILDING DEPLETED STOCKS

A special problem arises when advising on the management of badly depleted stocks, especially one (e.g., of whales) in which recruitment is closely dependent on the abundance of the adult stock.

For such a stock calculations can be made of the replacement yield, or equivalent sustainable yield, but this should not imply that these are the proper objectives. Rather action should be taken to rebuild the stock. This is done most rapidly by cutting the catches to zero for a period. The optimum strategy between this (making the greatest present sacrifice for the maximum long-term benefit) and merely maintaining the situation (making no present sacrifice) will be determined by a number of factors, mainly economic. This will include the relative values placed on present and future catches, alternative employment for the excess men and equipment in the present fisheries, etc. For example, it would be much easier to stop for a period the offshore herring fishery on Georges Bank, since the vessels concerned can switch to other fisheries, than to do the same for Antarctic whales.

The general policy to be followed by the management body—to aim for the maximum physical yield from a given stock, or some lesser physical yield but with greater economic benefits, to rebuild a depleted stock quickly or merely prevent its further decline—must be determined by that body taking all factors into account and cannot be decided purely on biological grounds. What can be determined by objective scientific calculations is the actual procedure to be followed—specifically the catch to be taken in each season—to implement the chosen policy. This note has been concerned purely with a discussion of this second step.

ACKNOWLEDGMENTS

Our thanks are due to D. G. Chapman, Y. Fukuda, R. Hennemuth, T. D. Iles, J. Joseph, and B. Rothschild for helpful comments on early drafts of this paper.

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COMPARATIVE STUDY OF ADAPTATIONS FOR CONTINUOUS SWIMMING AND HYDROSTATIC EQUILIBRIUM OF SCOMBROID AND XIPHOID FISHES

JOHN J. MAGNUSON[1, 2]

ABSTRACT

Scombroid fishes swim continuously with pectoral fins extended as lifting hydrofoils to counter their weight in water. Their gas bladder is often reduced or absent. Typical speeds were observed from seven species and compared with the speeds expected from them to maintain hydrostatic equilibrium. The expected speeds were computed from a model I developed using data on the lifting area of extended pectoral fins and the weight of the fish in water.

Lifting areas of the pectoral fins were determined from photographs of dead fishes. Mass-length relations were determined and converted to weight in water from data on water density and fish density.

Typical observed speeds varied among species from 0.33 to 2.19 lengths/sec. Scombroids of the same fork length differed greatly in mass, density, and pectoral fin areas. Swimming speed required for maintaining hydrostatic equilibrium should be greater for fishes with greater mass, higher density, and smaller pectorals. Expected speeds were computed. They were highly correlated with observed speeds, $r = +0.89$. Thus, the model accurately predicted typical swimming speeds of scombroids, which suggests that variations in mass, density, and the lifting area of the pectoral fins, through the mechanism of maintaining hydrostatic equilibrium, can account for about 80% of the variation in typical swimming speeds. Expected speeds (centimeters per second) generated from the model either increased with fork length or reached a maximum and declined for larger fish. The latter pattern occurred if gas bladders were relatively larger in older fish or even absent in younger fish.

Scombroids with faster typical speeds have larger dark muscles and higher concentrations of blood hemoglobin than those with slower speeds. Differences in body shape were not closely related to differences in typical speeds.

Larger fishes should have more difficulty maintaining a speed which is sufficient for hydrostatic equilibrium without a gas bladder or large pectoral fins. The occurrence of gas bladders and long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes. Both were more common among larger species. Each species with a maximum mass $\geqslant 70$ kg had a gas bladder while only 26% of those species $\leqslant 6$ kg had a gas bladder. Further analyses suggested that a gas bladder and large pectorals may be increasingly more important for large species if they are to swim at energetically prudent speeds.

Scombroid fishes are negatively buoyant, pelagic, oceanic fishes. The scombroids include the mackerels, tunas, and bonitos. They swim continuously with pectoral fins extended. This behavior produces lift that balances their weight in water. Some attain large size. Xiphoids are the largest teleosts and powerful swimmers that share the pelagic environment with the scombroids.

General considerations of buoyancy mechanisms of negatively buoyant fishes are discussed by Aleev (1963) and Alexander (1967, 1968).

In regard to scombroids, Magnuson and Prescott (1966) observed that continuous swimming was apparently not entirely determined by a need for gill ventilation, as Pacific bonito,

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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

Sarda chiliensis, swam with their mouth closed as much as 40% of the time. Presumably the fish could have conserved energy by swimming more slowly with the mouth open more often. Minimum speed was also not regulated for food search (Magnuson, 1969); kawakawa, *Euthynnus affinis*, swam at the same speed day and night even though they were exclusively diurnal feeders. When deprived of food for several days, they swam slower and slower in absence of food stimuli. If typical speed had been regulated by feeding motivation, the fish would have been expected to swim faster—become more active—as motivation to feed increased.

Typical swimming speeds of *E. affinis* were well explained by the minimum speed required to produce sufficient lift on the pectoral fins to keep from sinking. Magnuson (1970) presented a model to predict minimum speed required of *E. affinis* to maintain hydrostatic equilibrium. Minimum speeds were estimated from the animal's weight in water and the lifting area, primarily of the pectoral fins.

Differences between the morphology and typical speeds of yellowfin tuna, *Thunnus albacares*, and *E. affinis* (Magnuson, 1966a) suggested that the variations in area of pectoral fins and volume of gas bladder might also be explained as various solutions for countering negative buoyancy. Many other specializations of scombroids related to swimming speed and activity may be adaptations to the speeds required for hydrostatic equilibrium rather than maximum, burst speeds (Magnuson, 1970).

In regard to xiphoids, a recent review on their functional morphology by Ovchinnikov (1970) did not consider the gas bladder or buoyancy mechanisms in discussions on the function of pectoral fins.

Purposes of the present paper are to (1) test whether the model mentioned above generally predicts typical swimming speeds of scombroid fishes, (2) consider the adaptive radiation in the morphology especially of the gas bladder and pectoral fins which together with swimming speed contribute to the mechanism by which scombroids maintain hydrostatic equilibrium, and (3) consider problems associated with large body size and maintenance of hydrostatic equilibrium among scombroid and xiphoid fishes.

SWIMMING SPEEDS

Typical swimming speeds were observed for five scombroid fishes in 7.2-m diameter swimming pools at Kewalo Basin, Honolulu, Hawaii, from underwater photographs of wahoo, *Acanthocybium solandri*, swimming at sea, and from previously published records on *Sa. chiliensis* (Magnuson and Prescott, 1966). Observed swimming speeds were determined or available for seven species of six different genera.

Methods for obtaining swimming speeds were described by Magnuson (1969). Fishes were observed for short periods at 1- to 4-hr intervals (0000-2400) during their first month in captivity. Observations were made for two consecutive 24-hr periods during which the fish were fed and not fed (Figure 1). On fed days they were fed to satiation with thawed smelt or shrimp once or twice usually at 0900 and 1600 hr. Data collected during the "day not fed" and the "night after not fed" were used for the estimates of the minimum typical swimming speed to compare with body morphology. These estimates were based on 19-212 min (median 68 min) of recorded speeds for each species. With the exception of 36-cm long bigeye tuna, *Thunnus obesus*, where only 1 fish was observed, measurements from 6 to 40 fish (median 12 fish) made up each estimate. Water temperatures were 23°-26°C and salinity 33‰.

Typical speeds of *Ac. solandri* were from 17 cinema sequences averaging 2.59 sec each. The films were taken from underwater viewing ports in the RV *Charles H. Gilbert* and an observation raft described in Nakamura (1972).

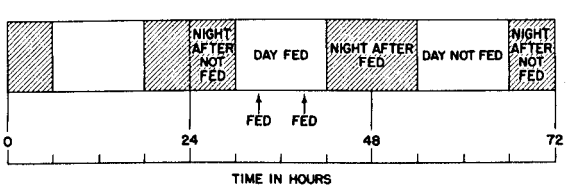

FIGURE 1.—Observation schedule for measurements of typical swimming speeds presented in Figure 2.

The observations that scombroid fishes swim continuously (Figure 2) would appear to be generalizable but the speeds, expressed either as body lengths per second (*l*/sec) or centimeters per second (cm/sec), differ considerably from one species to another or within species depending upon the size. Typical speeds ranged from 0.33 *l*/sec for *Ac. solandri* to 2.19 *l*/sec for the bullet mackerel, *Auxis rochei*. All species other than *Ac. solandri*, namely the skipjack tuna, *Katsuwonus pelamis*, *Sa. chiliensis*, *E. affinis*, *T. obesus*, *T. albacares*, and *Au. rochei*, had typical speeds greater than 1 *l*/sec. None of the species ever stopped swimming. The slowest speeds observed ranged from 0.12 *l*/sec for *Ac. solandri* to 1.97 *l*/sec for *E. affinis*. The typical speed of *T. obesus*, 36 cm FL (fork length), was 1.31 *l*/sec but the larger 55-cm *T. obesus* swam only 1.08 *l*/sec. Three length groups of the *K. pelamis* were also observed and their speeds differed among sizes.

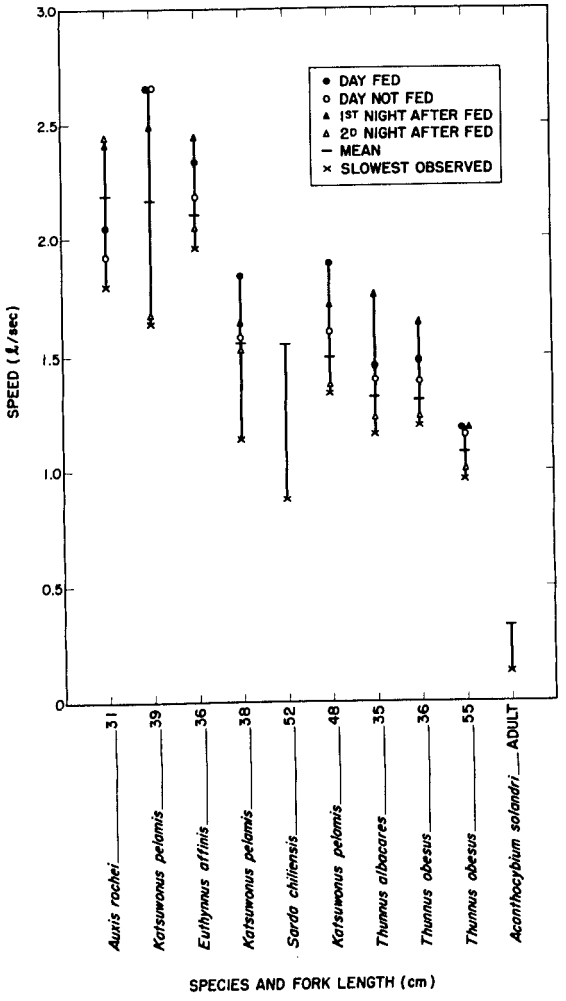

FIGURE 2.—Typical swimming speeds of seven scombroids.

SPEEDS REQUIRED FOR HYDROSTATIC EQUILIBRIUM

Variations in the typical swimming speeds among scombroids would result from differences in both the weight of the fish in water and the lifting area of the pectoral fins. Weight in water depends on mass and density of the fish. All specimens of chub mackerel, *Scomber japonicus*, and *Sarda chiliensis* used for morphometric and mass measurements were collected near Los Angeles, Calif. Specimens of all other species were collected in the central Pacific almost always near the Hawaiian Islands.

Variations in Weight

Not all scombroids have the same mass-length relationship (Figure 3). *K. pelamis* was heaviest and *Ac. solandri* lightest at a given length. For example, at a length of 75 cm, *Ac. solandri* has a mass less than 2 kg and *K. pelamis* greater than 9 kg. Other species were intermediate.

When submerged in water the fish displaces water which also has mass. If the gas bladder is large enough, the volume of water that a fish displaces may have the same mass as the fish. The weight of the fish in water, or conversely the lift required to keep the fish from sinking, is equal to the excess mass of the fish times the acceleration of gravity (Alexander, 1967; Magnuson, 1970). The excess mass of the fish is the difference between the mass of the fish and the mass of the water it displaces. It can be computed by multiplying the mass of the fish by $(1 - \frac{D_e}{D_f})$ where D_e is the density of the environment or seawater and D_f is the density of the fish. The

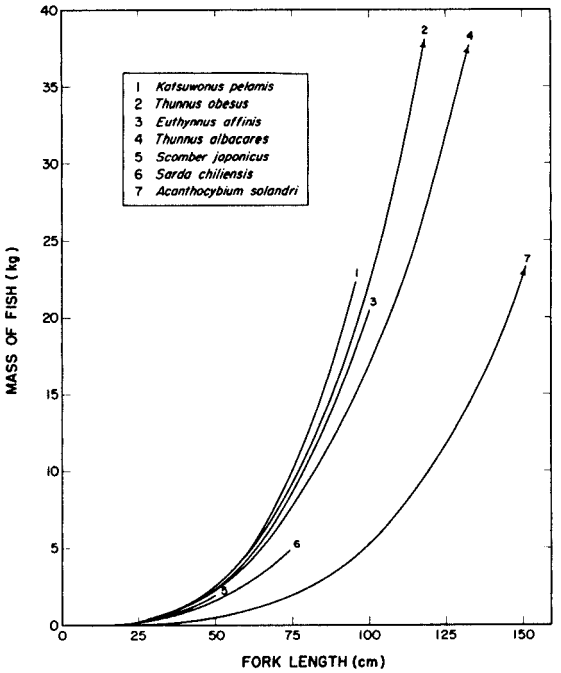

FIGURE 3.—Comparison of mass against length relationships among seven scombroid species. Information on regression equations in Table 4.

acceleration of gravity, g, is equal to approximately 980 cm/sec^2.

The influence of a gas bladder can be clearly seen by contrasting data for *K. pelamis* with *T. albacares*. Gas bladder volumes were determined with an x-ray method of Chang and Magnuson (1968) on fish immediately after they were killed. *K. pelamis* has no gas bladder but *T. albacares* has a gas bladder which grows allometrically, becoming progressively larger as the fish increases in mass (Figure 4a). *T. albacares*, 2 kg or less, has no gas in the bladder, but the gas bladder then grows rapidly until the fish is at least 8 kg. These differences in gas bladders of *K. pelamis* and *T. albacares* influence the density of the two species (Figure 4b). The density of *K. pelamis* remains approximately the same over the entire size range. However, once the gas bladder begins to grow in *T. albacares* the density of the fish becomes less, decreasing from approximately 1.09 g/ml for 2-kg fish to 1.05 g/ml for 10-kg fish. These differences in density have a corresponding influence on the lift required to keep the fish from sinking (Figure 4c). The lift required for *K. pelamis* increases in almost direct proportion to the increase of mass. But the lift required to keep *T. albacares* from sinking increases more slowly as the density of the fish becomes less. In fact, the lift required to keep *T. albacares* from sinking appears to approach asymptotically a maximum near 200 × 10^3 dynes.

Variations in the densities of various species and sizes can be examined in Table 1, where the mean densities of various species are given and the multipliers are computed to convert the mass of the fish to the lift required to keep them from sinking. All species with markedly lower densities, such as *Sc. japonicus*, *T. albacares*, *T. obesus*, and *Ac. solandri*, have gas bladders at some point in their life history. The more dense species, *Sa. chiliensis*, *Au. rochei*, *E. affinis*, and *K. pelamis*, have no gas bladder.

Lift to prevent the fish from sinking is 10 to 20 times greater for larger *K. pelamis*

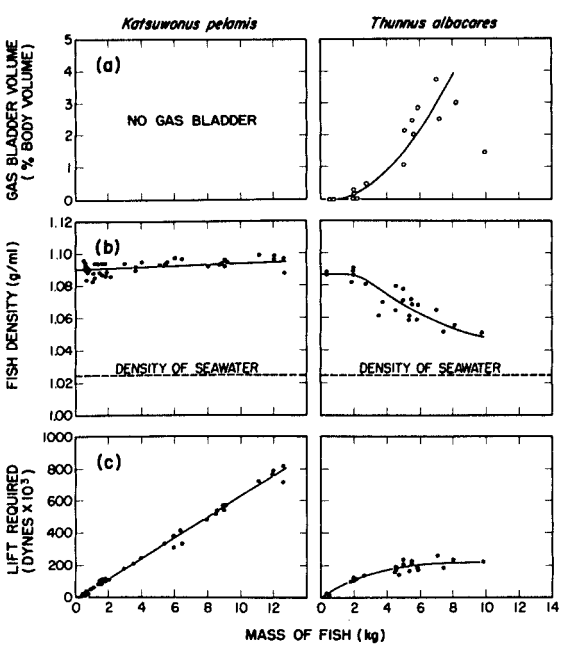

FIGURE 4.—Comparisons between *Katsuwonus pelamis* and *Thunnus albacares* of the relations between fish mass and (a) gas bladder volume, (b) fish density, and (c) lift required for hydrostatic equilibrium.

TABLE 1.—Densities (D_f) of eight scombroid species by size group and the multipliers to convert mass of fish (M_f in grams) to the lift (L in dynes) required for hydrostatic equilibrium. Multipliers[1] computed for seawater with densities of 1) 1.022 g/ml and 2) 1.025 g/ml. Measurements by methods described by Magnuson (1970).

Mass	*Scomber japonicus*	*Acanthocybium solandri*	*Sarda chiliensis*	*Auxis rochei*	*Euthynnus affinis*	*Katsuwonus pelamis*	*Thunnus albacares*	*Thunnus obesus*
0.00-1.99 kg:								
Number of fish	18		3	12	36	47	3	1
D_f (g/ml):								
Mean	1.054		1.075	1.086	1.087	1.090	1.086	1.066
SD	0.011		0.004	0.002	0.004	0.003	0.003	
Range	1.024		1.069	1.082	1.074	1.083	1.082	
	1.069		1.080	1.089	1.093	1.096	1.088	
Multiplier (1)	28.0		48.4	57.8	58.6	61.2	57.8	40.5
(2)	28.0		45.7	55.1	56.0	58.5	55.1	37.7
2.00-3.99 kg:								
Number of fish			10		23	4	4	17
D_f (g/ml):								
Mean			1.080		1.088	1.090	1.087	1.047
SD			0.006		0.009	0.003	0.004	0.010
Range			1.067		1.082	1.086	1.081	1.026
			1.086		1.094	1.094	1.090	1.064
Multiplier (1)			52.7		59.5	61.2	58.6	23.4
(2)			50.0		56.8	58.5	56.0	20.7
4.00-5.99 kg:								
Number of fish					3	4	12	
D_f (g/ml):								
Mean					1.091	1.094	1.068	
SD					0.004	0.001	0.007	
Range					1.086	1.093	1.059	
					1.095	1.095	1.080	
Multiplier (1)					62.3	64.6	42.2	
(2)					59.3	61.8	40.0	
6.00-7.99 kg:								
Number of fish						2	2	
D_f (g/ml):								
Mean						1.097	1.058	
SD						0.000	0.006	
Range						1.097	1.052	
						1.097	1.065	
Multiplier (1)						67.0	33.4	
(2)						64.4	30.6	
8.00-9.99 kg:								
Number of fish						6	2	
D_f (g/ml):								
Mean						1.094	1.054	
SD						0.001	0.002	
Range						1.093	1.051	
						1.096	1.056	
Multiplier (1)						64.6	29.8	
(2)						61.8	27.1	
≥ 10.00 kg:								
Number of fish		7				5		
D_f (g/ml):								
Mean		1.028				1.096		
SD		0.007				0.004		
Range		< 1.022				1.088		
		1.042				1.099		
Multiplier (1)		5.78				66.3		
(2)		2.94				63.5		
All sizes (without gas bladders only):								
Number of fish			13	12	62	68		
D_f (g/ml):								
Mean			1.078	1.086	1.087	1.091		
SD			0.006	0.002	0.004	0.004		
Range			1.067	1.082	1.074	1.083		
			1.086	1.089	1.095	1.099		
Multiplier (1)			51.0	57.8	58.6	62.0		
(2)			48.2	55.1	56.0	59.3		

[1] $[(1 - \frac{D_e}{D_f})980]$ where D_e is the density of environment.

(no gas bladder) than for *Ac. solandri*, which has a large gas bladder. These differences would also significantly influence the speed required to maintain hydrostatic equilibrium, and on this basis species without gas bladders are expected typically to swim faster than those with gas bladders.

Variations in the Lifting Area of Pectoral Fins

The lift produced by a hydrofoil is directly proportional to its lifting area, thus those species with a larger lifting surface should be capable of swimming at a slower speed, all other things being equal. The primary lifting surfaces of *E. affinis* are the pectoral fins (Magnuson, 1970), although other surfaces such as the caudal keel may counter some of the weight. The lifting area of the pectoral fins is the area of the extended pectoral fins as viewed from above plus the area of the body between the fins. It was determined for the various species from photographs of dead fish as described by Magnuson (1970).

Pectoral fins of scombroids are analogous to variable sweepback wings; they can be fully extended, swept back, or laid against the body (Magnuson, 1970). Species such as *E. affinis* and *K. pelamis* swam with the fins swept back about 40°, but the two species with the largest pectoral fins, *T. albacares* and *T. obesus*, swam with the fins swept back about 60° (Table 2). Sweepback angles measured from dead fish used for morphometric measurements were not as great as those from fish swimming in tanks. Measurements from dead fish were 7° and 14° for *E. affinis* and *K. pelamis* and 29° and 36° for *T. albacares* and *T. obesus*. Thus, some bias occurs in the estimation of the lifting area for swimming fish from the dead fish. This bias is probably slight because, although the actual area of the pectoral fin decreases rapidly as the fins are swept back, the total lifting area does not (Magnuson, 1970). Measurements of sweepback from other dead fishes used for morphometric measurements averaged 10° for *Sc. japonicus*, 24° for *Ac. solandri*, 16° for *Sa. chiliensis*, and 10° for *Au. rochei*.

Differences in pectoral fin lifting areas among scombroids are illustrated in diagrammatic dorsal views of seven species at the same length (Figure 5). Lifting areas differ markedly among species and among sizes for the same species (Figure 6). *T. obesus* has, among the species here, the largest lifting

TABLE 2.—Average sweepback of pectoral fins for swimming captive fishes. *n* equaled the number of fish. Λ was averaged for left and right fins.

Species	Day fed			Day not fed[1]			Fed and not fed combined		
	Λ (degrees)		*n*	Λ (degrees)		*n*	Λ (degrees)		*n*
	Mean	SD		Mean	SD		Mean	SD	
Euthynnus affinis	34	8.5	15	32	12	15	43	10	30
Katsuwonus pelamis	43	15	101	43	13	53	43	14	154
Thunnus albacares	61	3.1	11	55	3.7	3	60	4.0	14
Thunnus obesus	61	5.0	64	56	7.5	45	59	6.7	109

[1] Two days after fed for *E. affinis* and *T. albacares*; 1 day after fed for *K. pelamis* and *T. obesus*.

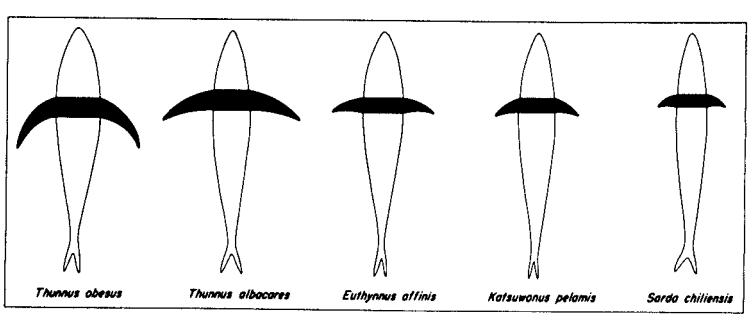

FIGURE 5.—Diagrammatic dorsal views of five scombroid species to dramatize the variation in the lifting areas of the pectoral fins for various species. Drawn from photographs of dead fish ca. 50 cm in fork length.

area at a given length, and *Ac. solandri* has the smallest. For example, at a fork length of 125 cm, *T. obesus* has a lifting area greater than 500 cm², whereas *Ac. solandri* has a lifting area near 150 cm² (Figure 6). These differences should have a marked effect on the minimum speed required to maintain hydrostatic equilibrium. Those with larger pectorals such as *T. albacares* and *T. obesus* should have a slower minimum speed than those with smaller pectorals.

Predicted Swimming Speed

The model used by Magnuson (1970) to predict the minimum speed required for hydrostatic equilibrium was

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

All terms used here and elsewhere in this paper are listed below:

l = fork length (cm)
L_t = total weight of fish in water (dynes)
L_f = all lift produced by the total lifting area of the pectoral fins (dynes)
L_k = lift produced by keel (dynes)
A_{f_e} = area of pectoral fins
A_{f_t} = total lifting area of pectorals (cm²)
A_k = lifting area of keel (cm²)
C_{L_f} = coefficient of lift for the pectoral fins based on all lift produced by pectorals and on total lifting area of pectorals
C_{L_k} = coefficient of lift for the keel
V_{100} = speed of fish with pectorals continuously extended (cm/sec)
Λ = sweepback angle of pectoral fins (degrees)
D_e = ρ = density of water = 1.022 g/ml in Kewalo tanks, 1.025 g/ml at sea
D_f = density of fish (g/ml)
M_f = fish mass.

To test predictive value of this model for a number of species, computed speeds were compared with observed speeds. Typical swimming speeds were computed twice: first, assuming the keel provided significant lift, and second, assuming all the lift was provided by pectoral fins. Results from these computations and the data used to make them are presented in Table 3. Regressions in Table 4 were used to determine the mass of the fish and the area of the lifting surfaces for calculations of minimum hydrostatic speeds. The mass of the fish was converted to required lift by using the conversion factors from Table 1. Lift coefficients were from Table 7 of Magnuson (1970)—those determined for *E. affinis* on the basis of total lifting area of the pectorals.

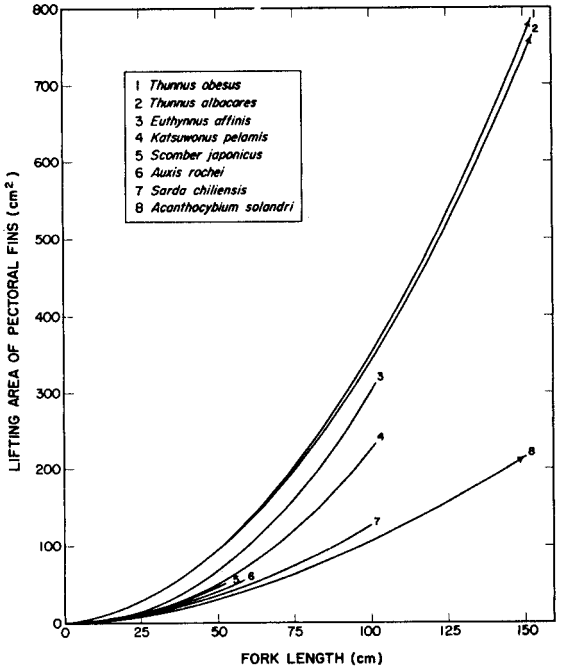

FIGURE 6.—Comparison of lifting area of pectoral fins against length relationships among eight scombroid species. Information on regression equation in Table 4.

Several comments should be made about the use of the lift coefficients from *E. affinis* for all species considered in the present text. The lift coefficient calculated on the basis of the total lifting area of pectorals represents lift on the pectorals, interference lift on the body owing to the pectorals, and the interference lift on the pectorals owing to the presence of the body. At best the coefficient is only a convenient but arbitrary standard frequently used in aerodynamic literature.

TABLE 3.—Computed speeds required for hydrostatic equilibrium and the morphometric data used to make the computations along with the typical swimming speeds observed for scombroids. Lift coefficients from Magnuson (1970). Masses, areas, and required lift from equations in Table 4 and fork length of captive fishes.

Species	l (cm)	(a) M_f (g)	(b) Multiplier to convert M_f to L_f	(a × b) L_f (dynes × 10^3)	A_k (cm^2)	(c) A_{f_t} (cm^2)	Surface loading of pectorals ($L_f \div A_{f_t}$) (dynes/cm^2)	Computed hydrostatic speeds (V_{100})[1] Without keel[2] (cm/sec)	Without keel[2] (l/sec)	With keel[3] (cm/sec)	With keel[3] (l/sec)	Observed speed of fishes (cm/sec)	Observed speed of fishes (l/sec)
Auxis rochei	31	498	57.8	28.8	[4]3.3	17.7	1,630	56	1.8	57	1.8	68	2.2
Katsuwonus pelamis	39	1,090	61.2	66.7	5.51	27.4	2,430	69	1.8	70	1.8	84	2.2
Euthynnus affinis	36	832	58.6	48.8	5.41	31.6	1,540	55	1.5	56	1.6	76	2.1
Katsuwonus pelamis	38	996	61.2	61.0	5.20	25.9	2,360	68	1.8	69	1.8	59	1.6
Sarda chiliensis	57	2,320	52.7	122.	11.8	45.9	2,660	72	1.3	71	1.2	88	1.5
Katsuwonus pelamis	48	2,180	61.2	133.	8.79	43.7	3,040	77	1.6	78	1.6	72	1.5
Thunnus albacares	35	858	57.8	49.6	6.11	47.0	1,060	45	1.3	47	1.4	46	1.3
Thunnus obesus	36	854	40.5	34.6	5.87	52.1	664	36	1.0	38	1.0	47	1.3
Thunnus obesus	55	3,290	23.4	77.0	15.8	116.	664	36	0.66	38	0.68	60	1.1
Acanthocybium solandri	125	[5]12,400	[6]5.78	71.7	51.6	163.	440	29	0.23	28	0.22	[7]41	0.33

[1] With equation 1. [2] $C_{L_k} = 0, C_{L_f} = 1$. [3] $C_{L_k} = 0.9, C_{L_f} = 0.8$.
[4] Estimated by comparing data with *K. pelamis* and then taking from *K. pelamis* regression.
[5] Estimated from length-weight relation given by Iversen and Yoshida (1957).
[6] From Table 1, $D_e = 1.022$ g/ml.
[7] Speed (cm/sec) = speed (l/sec) × length (cm) = 0.33 × 125 = 41.

Lift coefficients vary with sweepback, angle of attack, aspect ratio, the ratio of fin span to body width, and taper ratio (Lawrence and Flax, 1954). The differences in these parameters among species or within species were not evaluated, but comparisons made below between observed and calculated speeds suggest that the assumption about a constant lift coefficient based on total lifting area was not too bad. The coefficients used here should be more accurate for scombroids with short pectorals because *E. affinis* has short pectorals. The span of the pectorals, tip to tip, for *E. affinis* is about 2.4 times the body width.

Correlation coefficients (Table 5) were computed to discover how closely the observed swimming speeds were associated with fork lengths of the fish, the mass of the fish, the required lift to keep the fish from sinking, the lifting area of pectoral fins, the surface loading of pectoral fins, and the predicted swimming speed. Relations between observed speed and fork length, mass of fish, required lift, and lifting area of the pectoral fins were all nonsignificant statistically. But when required lift and the lifting area were considered jointly as surface loading of the pectorals, the correlation was significant ($P < 0.005$). Surface loading is the weight carried per unit area of lifting surface. Predicted speeds were also highly correlated with observed speeds (Table 5, Figure 7). The highest correlation, +0.89, between observed and predicted speeds in body lengths per second suggested that the hydrostatic equilibrium requirement of continuous swimming accounts for approximately 80% of the variation in observed swimming speeds. The model predicts typical swimming speeds of scombroids well and suggests that the variations in mass, density, and the lifting area of the pectoral fins can account for almost all variations in observed swimming speeds among scombroids.

Observed speeds averaged 9.8 cm/sec or 0.2 l/sec faster than computed speeds. The computation of V_{100} assumed that the pectorals were continuously extended but this was not always the case. Thus, the fact that observed speeds were greater than V_{100} is not surprising. *E. affinis*, for example, had the pec-

TABLE 4.—Regression equations ($\log y = \log a + b \log l$) with relevant data and 95% confidence intervals used to compute fish mass (M_f), area of pectoral fins (A_{f_e}), lifting area of pectoral fins (A_{f_t}), and keel area (A_k) for nine species of scombroid fishes. Measurements made by methods described in Magnuson (1970).

y	Species	n	Range in l (cm)	$\log l$	$\log y$	$\log a$	a	b	S_b	SE est.	Confidence limit on b	Confid. limit on $\overline{\log y}$ / $\overline{\log l}$
M_f	*Sc. japonicus*	20	26.9- 41.4	1.5434	2.7630	−2.4353	0.00367	3.37	0.1458	0.0345	±0.31	±0.0725
	Ac. solandri	—	—	—	—	—	—	—	—	—	—	—
	Sa. chiliensis	13	45.3- 65.1	1.7524	3.3647	-1.4100	0.0389	2.72	0.1770	0.0284	±0.39	±0.0625
	Au. rochei	11	33.9- 40.4	1.5546	2.9038	-2.3143	0.00485	3.36	0.4557	0.0290		
	E. affinis	63	31.6- 67.8	1.6251	3.1383	-1.9666	0.0108	3.14	0.0388	0.0632	±0.08	±0.1265
	K. pelamis	68	24.1- 82.9	1.6395	3.1977	-2.3098	0.00490	3.36	0.0180	0.0212	±0.04	±0.0424
	T. albacares	52	28.4-106.9	1.7859	3.6236	-1.4828	0.0329	2.86	0.0420	0.0325	±0.08	±0.0653
	T. obesus	26	36.3-150.5	1.8421	3.8440	-2.0173	0.00961	3.18	0.0868	0.1606	±0.18	±0.3315
A_{f_e}	*Sc. japonicus*	25	26.9- 40.1	1.5407	1.0005	-2.1543	0.00701	2.05	0.1864	0.0426	±0.39	±0.0881
	Ac. solandri	7	122.8-148.8	2.1112	1.9565	-2.1931	0.00641	1.97	0.7864	0.0551	±2.02	±0.1417
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.3020	-2.2358	0.00581	2.02	0.4993	0.0800	±1.10	±0.1761
	Au. rochei	11	31.9- 40.4	1.5499	1.0380	-2.0348	0.00923	1.98	0.7455	0.0586	±1.69	±0.1326
	E. affinis	37	33.7- 64.3	1.6440	1.3759	-2.3010	0.00500	2.24	0.0940	0.0475	±0.19	±0.0964
	K. pelamis	33	24.3- 82.9	1.7271	1.3722	-2.3840	0.00413	2.17	0.0562	0.0477	±0.11	±0.0974
	T. albacares	32	28.4-148.8	1.7920	1.9453	-1.2351	0.0582	1.78	0.0631	0.0602	±0.13	±0.1229
	T. obesus	25	46.1-150.5	1.8496	2.0613	-1.0477	0.0896	1.68	0.0445	0.0828	±0.09	±0.1713
A_{f_t}	*Sc. japonicus*	25	26.9- 40.1	1.5407	1.3394	-1.7012	0.0199	1.97	0.2520	0.0576	±0.65	±0.1481
	Ac. solandri	7	122.8-148.8	2.1112	2.2192	-1.5031	0.0314	1.76	0.5700	0.0399	±1.25	±0.0878
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.6472	-1.4634	0.0344	1.78	0.3892	0.0613	±0.86	±0.1350
	Au. rochei	10	31.9- 40.4	1.5505	1.3546	-1.2418	0.0573	1.67	0.7115	0.0557	±1.64	±0.1284
	E. affinis	37	33.7- 64.3	1.6440	1.6920	-2.0182	0.00959	2.26	0.0855	0.0432	±0.17	±0.0877
	K. pelamis	33	24.3- 82.9	1.7271	1.7402	-2.1255	0.00749	2.24	0.0545	0.0462	±0.11	±0.0943
	T. albacares	32	28.4-136.0	1.7920	2.1402	-1.2154	0.0609	1.87	0.0478	0.0456	±0.10	±0.0931
	T. obesus	25	46.1-150.5	1.8496	2.2599	-1.2090	0.0618	1.88	0.0391	0.0366	±0.08	±0.0757
A_k	*Sc. japonicus*	—	—	—	—	—	—	—	—	—	—	—
	Ac. solandri	—	—	—	—	—	—	—	—	—	—	—
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.0761	-1.2104	0.0616	1.30	0.4784	0.0766	±1.05	±0.1687
	Au. rochei	—	—	—	—	—	—	—	—	—	—	—
	E. affinis	41	33.7- 67.8	1.6479	0.9548	-3.0017	0.000996	2.40	0.1501	0.2477	±0.30	±0.5011
	K. pelamis	34	24.3- 82.9	1.7128	1.0154	-2.8386	0.00145	2.25	0.0761	0.1308	±0.16	±0.2667
	T. albacares	36	34.0-136.0	1.8005	1.3687	-2.7033	0.00198	2.26	0.0986	0.1786	±0.20	±0.3624
	T. obesus	25	46.1-150.5	1.8496	1.4489	-2.8729	0.00134	2.34	0.1284	0.2387	±0.27	±0.4940

TABLE 5.—Correlations between observed speeds of scombroids and the fork length, mass, required lift for hydrostatic equilibrium, surface loading, and computed speeds with and without the keel included in the calculation.

Correlates		r_{xy}	$P(n = 10)$
y	x		
V_{obs} (cm/sec)	Fork length (l) (cm)	-0.37	N.S.
V_{obs} (cm/sec)	Mass of fish (M_f) (g)	+0.44	N.S.
V_{obs} (cm/sec)	Required lift (L_t) (dynes)	+0.44	N.S.
V_{obs} (cm/sec)	Lifting area of pectorals (A_{f_t}) (cm^2)	-0.54	N.S.
V_{obs} (cm/sec)	Surface loading of pectorals (dynes/cm^2)	+0.77	<0.005
V_{obs} (cm/sec)	V_{100} without keel (cm/sec)	+0.79	<0.005
V_{obs} (cm/sec)	V_{100} with keel (cm/sec)	+0.78	<0.005
V_{obs} (l/sec)	V_{100} without keel (l/sec)	+0.89	<0.0005

torals extended only about 75% of the time at typical speeds. The percent of extension of the pectorals varied greatly from species to species. The species with the longest pectorals, *T. obesus* and *T. albacares*, almost never appressed their pectoral fins while swimming at typical speeds.

Typical speeds of each species over its length range (Figure 8) were computed from equation 1 using values for M_f, A_{f_t} from Table 4, and values of D_e from Table 1, ρ was set at 1.025 g/ml. Since the inclusion of lift from the keel had little effect on computed speeds (Table 3), the computations were made on the basis that all lift came from the pectorals.

The three species with the fastest predicted swimming speeds—*K. pelamis*, *Sa. chiliensis*, and *E. affinis*—have no gas bladder (Figure 8), while species with the lowest predicted speeds—*T. albacares*, *T. obesus*, *Sa. japonicus*, and *Ac. solandri*—have gas bladders. *Ac. solandri*, the species with the lowest predicted speed, has the largest gas bladder and the lowest density.

Among the three species without gas bladders, *K. pelamis* is the heaviest for its length and has the fastest minimum speed. The predicted speeds of *Sa. chiliensis* and *E. affinis* are quite similar, even though *E. affinis* is considerably heavier at a given length than

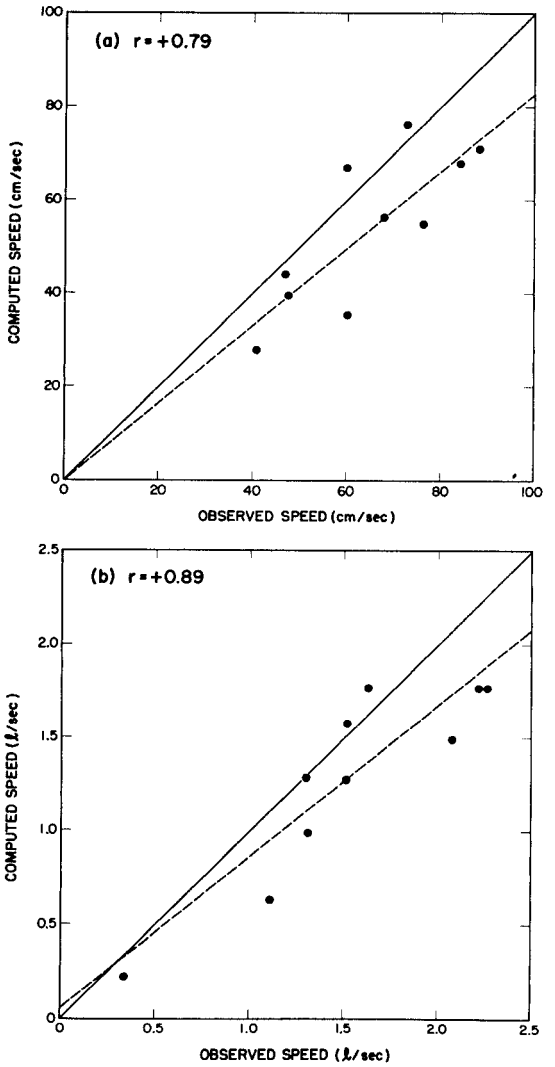

FIGURE 7.—Correlation between observed swimming speeds of scombroids and the computed minimum speed for hydrostatic equilibrium (a) in cm/sec, and (b) in body lengths/sec. Data from Table 3. Solid line shows expectation for perfect agreement and dashed line is the linear regression of expected speed on observed speed. Correlation coefficients, r, are given on graph.

Sa. chiliensis (Figure 3). This difference results from the difference in the lifting area of pectoral fins (Figure 6). *E. affinis* has lifting areas twice the size of *Sa. chiliensis* at a given length. Interestingly, the minimum speeds predicted for *K. pelamis* were almost identical to the speeds predicted by Shuleikin

(1966) as most efficient for migration by aquatic organisms.

Among the species with gas bladders, *T. albacares* and *T. obesus* have the largest pectorals, but *Ac. solandri* with small pectorals swims the slowest. The difference appears to be primarily from differences in gas bladder volume and resulting density. The large gas bladder and low density of *Ac. solandri* more than compensate for small pectoral fins.

At larger sizes all species swim slower in body lengths per second (Figure 8b), but owing to the allometric growth of the gas bladder, both large *T. albacares* and *T. obesus* can swim at slower speeds even in absolute units (centimeters per second). Their weights in water increase more slowly than their lifting areas after the fish attain approximately 50 cm FL.

A word of warning about Figure 8 is that the predicted speeds are extrapolated outside of the range for which morphometric and body density data were available. In addition, the density data for *Ac. solandri* was based only on animals 125 cm long. Likewise, the density data on *T. obesus* was limited.

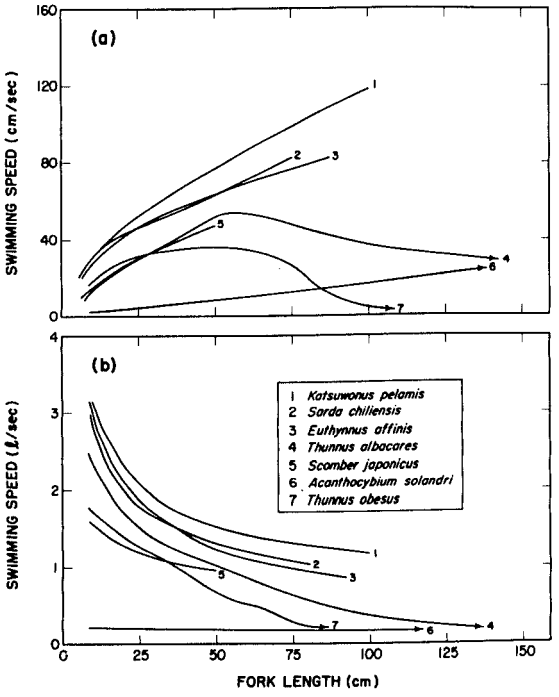

FIGURE 8.—Estimated minimum swimming speeds of seven scombroid fishes for maintaining hydrostatic equilibrium in (a) cm/sec and (b) body lengths/sec. Estimates from equation 1 and data in Table 4. See text for explanation.

OTHER FEATURES ASSOCIATED WITH BASAL SPEED

Scombroid fishes have many adaptations for efficient continued movement through the water. They have a high hemoglobin level (Klawe, Barrett, and Klawe, 1963), a large dark muscle (Kishinouye, 1923) for continuous locomotion (Rayner and Keenan, 1967), and a streamlined shape (Walters, 1962; Aleev, 1963; Alexander, 1967). The following analyses were to determine whether these adaptations were strongly associated with the basal or typical swimming speed. If differences in these characteristics varied closely with differences in typical speed, then I would argue that these adaptations were primarily selected for continuous slow swimming rather than maximum, burst speeds. Data on the burst or maximum speeds of these species are limited but do not indicate a strong association with typical speed. The burst speeds of 6-21 *l*/sec for *T. albacares* and 12-19 *l*/sec for *Ac. solandri* measured by Walters and Fierstine (1964) with a piscatometer at sea were approximately the same even though typical speed observed for *Ac. solandri* was less than one-fourth those of *T. albacares* (Table 3). Maximum speeds of four species measured photographically at sea or in shoreside tanks differ from species to species but not in relation to the typical speeds (Table 6).

TABLE 6.—Comparison of typical and maximum speeds observed from four scombroids.

Species	Speed (*l*/sec) Typical (Table 3)	Maximum	Source for maximum speeds
Thunnus albacares	1.3	10	Yuen (1966)
Sarda chiliensis	1.5	6.5	Magnuson and Prescott (1966)
Katsuwonus pelamis	1.5 1.6 2.2	14.4	Yuen (1966)
Euthynnus affinis	2.1	12.5	Walters (1966)

Dark muscle size was determined from dissections of fresh material—the difference in the coloration of the dark muscle and the rest of the muscle block was sufficiently visible that the entire dark muscle could be removed and weighed. Its size was expressed as a percentage of fish mass. Body shape was determined from dorsal and lateral photographs of fresh dead fish. The maximum body height (H) and maximum body width (W) as a percent of fork length were averaged to represent the maximum thickness ($\frac{H + W}{2}$) of the body. The position of maximum thickness along the length of the fish was expressed as percent of fork length. It was determined by averaging the measurements from both dorsal and lateral views. Usually the position of maximum height for a species was 1 to 3% (of fork length) more posterior than the position of maximum width.

Data on dark muscle, blood hemoglobin, maximum body thickness, and the longitudinal position of maximum body thickness are presented for seven scombroid species in order of decreasing typical swimming speeds in Table 7. The size of the dark muscle (Table 7) ranged from 1.8% of the body mass for *Ac. solandri*, 125 cm long, to 10.3% of body mass for *Au. rochei*, 31 cm long. Within single species, the relative size of the dark muscle is smaller for larger animals. For example, *T. obesus* approximately 55 cm long have a dark muscle 7.7% of the body mass, whereas those 125 cm long have a red muscle of 4% of the body mass. I observed the same trend but with different magnitudes for other species for which a wide range of lengths were examined. Blood hemoglobin ranged from 10.4 g/100 ml of blood for *Ac. solandri* to 19.2 g/100 ml for *Au. rochei* (Table 7). This range includes values comparable to mammals—man for example has ca. 15 g/100 ml.

Typical speeds were positively correlated (Figure 9) with dark muscle size ($r = +0.86$, $n = 9$, $P < 0.005$) and with blood hemoglobin ($r = +0.83$, $n = 9$, $P < 0.005$). Approximately 70% of the variation in both dark muscle size and hemoglobin concentration are associated with variation in typical speeds. The size of the dark muscle and the concentration of hemo-

TABLE 7.—Relative size of dark muscle, blood hemoglobin concentration, and body morphology of various scombroids for comparison with the typical swimming speeds. Dark muscle and body morphology from present study. Fish ordered by decreasing swimming speeds (*l*/sec).

			Dark muscle			Hemoglobin		Body morphology					
Species	Fork[1] length (cm)	Observed speed (*l*/sec)	(% M_f)	95% confidence interval on mean	n	(g/100 ml)	Source	Fork[2] length (cm)	n	H Maximum body height (% *l*)	W Maximum body width (% *l*)	$(H + W) \div 2$ Maximum thickness (% *l*)	Distance from snout to position of maximum thickness (% *l*)
Au. rochei	31	2.19	10.3	±0.4	7	19.2	Barrett and Williams (1965)	32- 37	10	24.3	17.4	20.8	40.2
K. pelamis	39	2.17	8.4	±0.2	15	16.7	Barrett and Connor (1962)	37- 43	9	25.4	17.8	21.6	43.0
E. affinis	36	2.11	8.1	±0.5	22	—	—	37- 43	7	27.2	18.0	22.6	40.4
K. pelamis	38	1.55	8.4	±0.2	15	16.7	Barrett and Connor (1962)	37- 43	9	25.4	17.8	21.6	43.0
Sa. chiliensis	57	1.54	6.2	±0.4	4	12.9	Barrett and Williams (1965)	45- 65	12	21.8	15.1	18.4	39.5
K. pelamis	48	1.49	7.5	±0.3	18	16.7	Barrett and Connor (1962)	44- 57	12	26.3	18.6	22.4	42.0
T. albacares	35	1.31	7.4	—	2	14.3	Barrett and Connor (1962)	28- 45	6	27.8	16.8	22.3	41.2
T. obesus	36	1.31	—	—	—	15.6	Barrett and Williams (1965)	46- 48	3	28.6	17.9	23.2	35.5
T. obesus	55	1.08	7.7	±0.6	13	15.6	Barrett and Williams (1965)	50- 60	13	28.7	18.5	23.6	37.5
Ac. solandri	125	0.33	1.8	±0.5	6	10.4	Barrett and Williams (1965)	123-130	6	14.6	10.4	12.5	37.3

[1] Lengths of fish observed for swimming speed. Dark muscle data for fish of approximately same lengths.
[2] Lengths for body morphology.

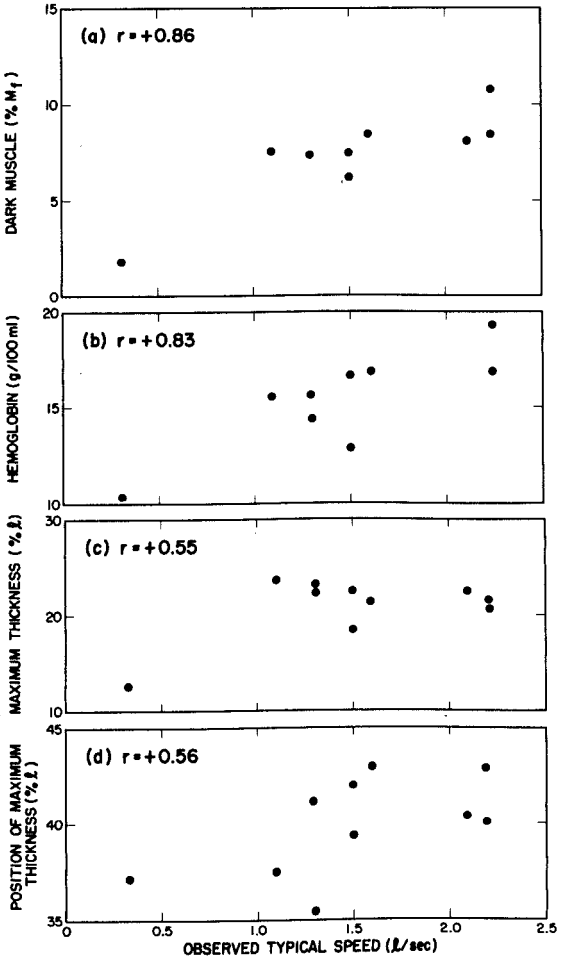

FIGURE 9.—Relation between observed swimming speeds and (a) the relative size of the dark muscle and (b) the concentration of blood hemoglobin, (c) maximum thickness of body, and (d) the position of maximum thickness along the length of the fish. Data from Table 7. Correlation coefficients, r, are given on graph.

globin are also highly correlated ($r = +0.82$, $n = 8$, $P < 0.005$). As expected, the dark muscle used for continuous slow speed is larger for species with faster typical swimming speeds. However, concentrations of blood hemoglobin also appear to be keyed to typical speeds and routine metabolism. Differences in need to transport oxygen sufficient for burst speeds apparently influenced hemoglobin levels little. Perhaps this is so because an oxygen debt can be temporarily incurred for burst activity.

Typical speeds in body lengths per second (Figure 9c, d) were also correlated with maximum thickness of the body ($r = +0.55$, $n = 10$, $P < 0.05$) and with the position of maximum thickness ($r = +0.56$, $n = 10$, $P < 0.05$). If speed is given in centimeters per second, the correlation +0.21 and +0.49 with maximum thickness and the position of maximum thickness are not statistically significant at $P < 0.05$.

Maximum thickness of the body ranged from 12.5 to 23.6% of fork length but only *Ac. solandri* had a value less than 18% (Table 7). Only 30% of the variability in thickness is associated with typical speeds. Thus, these variations do not appear to be closely related to differences in typical speeds (Figure 9c) with the exception that the species with the lowest typical speed, *Ac. solandri*, also had a low thickness ratio that would not be expected to minimize drag. Minimum drag should result from thickness ratios near 22% (Alexander, 1967). Differences among *Auxis*, *Katsuwonus*, *Sarda*, and *Thunnus* vary over a narrow range near 22% in a manner not related to typical swimming speeds.

Scombroids with faster typical speeds tend to have the thickest part of their body more posteriad (Figure 9d). Only 30% of this variation is associated with basal speed, but the trend is sensible in that the more laminar flow profiles should occur in the faster fishes.

In conclusion, all four characteristics, size of dark muscle, hemoglobin concentration, body thickness, and the position of the thickest part of the body are statistically related in a sensible manner to the variations in slow typical speeds of scombroids. The relations are poorer for the two characteristics involved in reducing drag, apparently because these features are more important at burst speeds than at typical speeds.

PROBLEMS ASSOCIATED WITH LARGE SIZE

Among the scombroid and xiphoid fishes, there is a great diversity in maximum body size, areas of pectoral fins, and the presence or size of the gas bladder. Data on these

TABLE 8.—Published data for scombroid and xiphoid fishes on maximum mass, the presence or absence of a gas bladder, and the relative length of pectoral fins. Species are ordered from smallest to largest known mass. Where only the length was known, mass was estimated from Figure 3 from a similarly shaped species.

Species	Maximum size			Gas bladder		Pectoral fins	
	Mass	Fork length	Source[1]	Present	Source[1]	Short (<20% FL) Long (≥20% FL)	Source[1]
	kg	*cm*					
Rastrelliger faughni	—	(20)	24	Yes	24	Short	24
Rastrelliger brachyosoma	—	(22)	19	Yes	24	Short	19
Rastrelliger kanagurta	—	(28)	19	Yes	24	Short	19
Cybiosarda elegans	1	—	6	No	10	Short	9
Scomberomorus multiradiatus	—	—	—	—	—	Short	10
Scomber japonicus	—	(35)	3	Yes	24	Short	9
Scomber australasicus	—	(45)	1	Yes	24	Short	24
Scomberomorus queenslandicus	2	(75)	6	—	—	Short	10
Scomberomorus sierra	2	(59)	7	—	—	Short	10
Scomberomorus koreanus	—	(60)	10	—	—	Short	10
Scomberomorus sinensis	—	(65)	10	—	—	Short	10
Scomberomorus guttatus	—	(82)	6	No	9	Short	9
Auxis rochei	—	(60)	6	No	9	Short	8
Scomberomorus concolor	—	(68)	10	No	9	Short	9
Sarda orientalis	3	—	20	No	13	Short	13
Scomber scombrus	3	—	3	No	24	Short	9
Auxis thazard	4	—	15	No	9	Short	41
Scomberomorus tritor	4	(98)	31	No	9	Short	9
Scomberomorus maculatus	5	—	2	No	9	Short	9
Euthynnus lineatus	5	—	5	No	12	Short	12
Sarda sarda	5	—	4	No	21	Short	9
Scomberomorus semifasciatus	—	(100)	25	No	9	Short	25
Scomberomorus niphonius	—	(101)	25	No	9	Short	25
Sarda chiliensis	—	(72)	16	No	12	Short	9
Scomberomorus lineolatus	6	—	18	No	40	Short	40
Grammatorcynus bicarinatus	11	—	36	Yes	36	Short	36
Orcynopsis unicolor	13	—	32	No	32	Short	9
Allothunnus fallai	14	—	6	No	35	Short	6
Thunnus atlanticus	16	—	17	Yes	11	Long	11
Scomberomorus regalis	16	—	3	No	9	Short	9
Euthynnus affinis	—	(100)	6	No	21	Both	41
Katsuwonus pelamis	22	—	6	No	39	Short	14
Euthynnus alleteratus	—	(122)	23	No	12	Short	12
Thunnus tonggol	27	—	6	No (rudimentary)	11	Both	11
Scomberomorus cavalla	37	—	4	No	10	Short	25
Thunnus maccoyii	—	(145)	11	Yes	11	Long	11
Thunnus alalunga	44	—	6	Yes	11	Long	11
Gasterochisma melampus	—	(165)	6	Yes	9	Short	22
Scomberomorus commerson	59	—	29	No	10	Short	25
Acanthocybium solandri	63	—	6	Yes	9	Short	9
Gymnosarda unicolor	80	—	21	Yes	21	Both	37
Tetrapterus pfluegeri	90	—	33	Yes	28	Both	33
Tetrapterus angustirostris	90	—	33	Yes	28	Short	34
Tetrapterus belone	90	—	33	Yes	33	Short	33
Istiophorus albicans	90	—	33	Yes	28	Short	33
Tetrapterus albidus	90	—	33	Yes	28	Both	33
Thunnus albacares	135	—	6	Yes	11	Long	11
Istiophorus platypterus	150	—	30	Yes	28	Short	27
Tetrapterus audax	180	—	33	Yes	28	Both	34
Thunnus obesus	198	—	6	Yes	11	Long	11
Xiphias gladius	536	—	27	Yes	26	Short	27
Makaira mazara (Jordan and Snyder)	—	(430)	27	—	—	Both	27
Makaira indica	700	—	30	Yes	28	Long	27
Thunnus thynnus	730	—	38	Yes	11	Both	11
Makaira nigricans	900	—	33	Yes	28	Both	34

[1] Abe and Takashima (1959).
[2] Beardsley and Richards (1970).
[3] Bigelow and Schroeder (1953).
[4] Breder (1948).
[5] Calkins and Klawe (1963).
[6] Collette and Gibbs (1963).
[7] Collette, Talbot, and Rosenblatt (1963).
[8] Fitch and Roedel (1963).
[9] Fraser-Brunner (1950).
[10] Gibbs and Collette (pers. comm.).
[11] Gibbs and Collette (1966).
[12] Godsil (1954).
[13] Godsil (1955).
[14] Godsil and Byers (1944).
[15] Gosline and Brock (1960).
[16] Hildebrand (1946).
[17] Idyll and de Sylva (1963).
[18] Jones and Silas (1962a).
[19] Jones and Silas (1962b).
[20] Kikawa (1963).
[21] Kishinouye (1923).
[22] Lahille (1905).
[23] Marchal (1963).
[24] Matsui (1967).
[25] Munro (1943).
[26] Nakamura et al. (1951).
[27] Nakamura, Iwai, and Matsubara (1968).
[28] Norman and Fraser (1948).
[29] Ogilby (1954).
[30] Osipov, Kizevetter and Zhuravlev (1964).
[31] Postel (1955).
[32] Postel (1956).
[33] Robins and de Sylva (1963).
[34] Royce (1957).
[35] Serventy (1948).
[36] Silas (1963a).
[37] Silas (1963b).
[38] Tiews (1963).
[39] Waldron (1963).
[40] Williams (1960).
[41] Williams (1963).

characters were surveyed from the literature and are presented in Table 8. To determine whether the hydrostatic requirements of swimming have had some influence on or interact with the maximum size, the occurrence of gas bladders and the occurrence of long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes (Table 9). The distinction between short and long fins was arbitrarily set at a pectoral length of 20% or more of body length at any point in the life history.

Larger species apparently require a gas bladder but smaller species do not. All of the 14 species ≥ 70 kg had gas bladders but only 26% of 19 species ≤ 6 kg had gas bladders (Table 9). Medium size fish, 7-69 kg, were intermediate. The largest species without a gas bladder was *Scomberomorus commerson* at 59 kg (Table 8). Apparently the presence of a gas bladder is obligatory for those species greater than 60 kg. The gas bladder overcomes some weight in water, reduces minimum required speeds, and results in a design that could reduce energy expenditures for the larger species.

The larger fishes also tend to have relatively longer pectoral fins. Of the 15 species ≥ 70 kg, 67% have long pectorals at some stage in their life history but none of the 25 species ≤ 6 kg ever have long pectorals (Table 9). Medium size fish, 7-69 kg, were intermediate.

The two adaptations that make slower speeds possible, large pectorals and a gas bladder, have some tendency to occur together. Of 24 species without a gas bladder, 92% (22 species) have short pectoral fins and of 25 species with a gas bladder only 48% (12 species) have short pectoral fins (Table 8). Apparently small species require neither large pectorals nor a gas bladder to have a required swimming speed slow enough to maintain. For these species, in most cases, the advantages of not having a gas bladder or the drag associated with large pectoral fins have overweighed the advantage of a slow required speed in the course of evolutionary history. Apparently large species have achieved speeds slow enough for a consistent overall design by the joint effects of pectorals and the presence of a gas bladder. For these species if the gas bladder were large enough, large pectorals were not necessary; but if the gas bladder were not large enough, selection occurred for large pectorals.

Thus large species have a gas bladder and may or may not have long pectoral fins, while small species may or may not have a gas bladder and in neither case have long pectorals. In addition, large xiphoids with the large gas bladder may be able to use the pectoral for functions other than lift production. For example, the reduction of pelvic fins among xiphoids means that the pectorals must also produce any downward forces often ascribed to the pelvics.

The joint influences of maximum mass, body density, and lifting areas on minimum possible speeds give some perspective to the problem of large size (Figure 10). Surfaces of minimum swimming speeds were calculated for hypothetical 1-, 10-, and 100-kg scombroids with a lift coefficient of 1.0 for the pectoral fins. The keel was assumed to produce no lift. As expected, the smaller the gas bladder, that is, the greater (D_f - D_e), the faster the fish must swim to maintain hydrostatic equilibrium. Also, the smaller the pectoral fins (A_{f_l}), the faster the fish must swim.

For small scombroids of 1 kg, changes in the density have little influence on required speed. And once the pectoral fins reach at least 50 cm², further increases in area have little influence on required speed. A 1-kg scombroid would be about 40 cm long. Fish this long

TABLE 9.—Occurrence of a gas bladder and the occurrence of long pectoral fins among scombroid and xiphoid fishes with different maximum masses. (A summary of Table 8.)

Item	Maximum mass (kg)						
	≤6		7-69		70-900		Total
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*
Gas bladder:							
Present	5	26	6	40	14	100	25
Absent	14	74	9	60	0	0	23
Total	19	100	15	100	14	100	48
Pectoral fins:							
Long	0	0	5	33	10	67	15
Short	25	100	10	67	5	33	40
Total	25	100	15	100	15	100	55

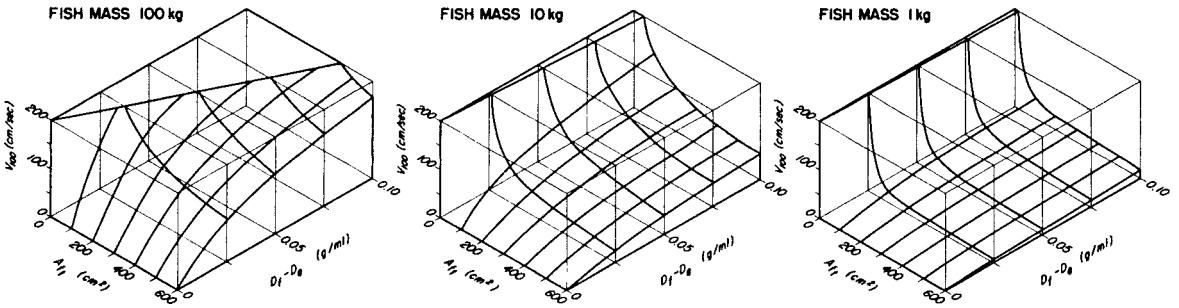

FIGURE 10.—Surfaces of minimum speeds required for hydrostatic equilibrium computed with different values of A_{f_t} and $(D_f - D_e)$ for hypothetical scombroids with a mass of 1, 10, or 100 kg. Speeds were computed from equation 1 with $\bar{C}_{L_f}$ set at 1.0 and D_e or ρ set at 1.025 g/ml.

should be able to maintain speeds near 100 cm/sec according to data from nonscombroids summarized in Figure 18 of Magnuson (1970). If there were some disadvantage to having a gas bladder, the loss of the bladder would not impose impossible levels of activity. Thus, the absence of a gas bladder and the occurrence of small pectorals among some small scombroids are consistent with the expectations of Figure 10 for 1-kg fish.

If hypothetical 10-kg and then 100-kg scombroids are considered (Figure 10), the presence of a gas bladder can be seen to be increasingly important to retain low levels of swimming activity. Required speed decreases rapidly with increasing pectoral size up to about 100 cm² for 10-kg fish and up to 200 cm² for 100-kg fish compared to 50 cm² for 1-kg fish. For a 100-kg fish and $(D_f - D_e) = 0.025$, as lifting areas increase from 200 to 700 cm², required speed declines to about 100 cm/sec. This constitutes a significant reduction in speed and helps explain why 100-kg *Thunnus* have pectoral lifting areas as great as 700 cm². Large scombroids could reduce energy expenditures with larger than expected pectoral fins.

Computed minimum speeds were slower than 40 cm/sec for a 100-kg *Thunnus* (Figure 8). If its pectoral fins were as small as those of *K. pelamis*, it would have to swim at least 90 cm/sec; and if it also had no gas bladder, its minimum speed would have to be 160 cm/sec.

Adaptations that serve to make low activity possible for large scombroids and xiphoids may reduce required speed well below the endurance speed or even below the most physiologically efficient speed for a species to migrate. No data on maximum endurance speeds are available for fish this large, but endurance speeds of sockeye salmon, *Oncorhynchus nerka*, in centimeters per second, increases as length increases (Brett, 1965). The relationship, speed $= 19\ l^{0.5}$, was determined from *O. nerka*, 8 to 54 cm FL, over periods only as long as 1 hr. Another data set (Hunter, 1971) for the jack mackerel, *Trachurus symmetricus*, is similar but based on shorter fish, 9-18 cm long, for longer periods, 6 hr. The relation was speed $= 22\ l^{0.6}$. Extrapolation of these relationships from a salmonid, 50 cm long, or a carangid, 18 cm long, to scombroids, about 80 and 180 cm long, seems a bit unrealistic, but if done indicates that the required speeds, even for a large hypothetical fish with short pectoral and no gas bladder, are considerably below the extrapolated endurance speeds. And a 100-cm *T. albacares* with its gas bladder and large pectorals swims at speeds less than one-sixth the extrapolated endurance speeds of a salmonid and less than one-fourth the speeds predicted by Shuleikin (1966) as most efficient for migration. Shuleikin's theoretical model was based on the speed at which the fish expended the least energy to overcome internal friction of muscles and external friction from movement through water.

Perhaps for the large fish the capability for low speed, makes possible speeds which are energetically prudent in an ecological sense.

Unfortunately the energy balances for these species are not known, especially in regard to energy expended for energy encountered as prey and in regard to energy conserved by low activity during times of day that feeding does not occur. However, in my view the most consistent explanation for the adaptations that reduce required speeds among larger scombroids and the xiphoids is that the speeds must be energetically prudent; and the larger the fish, the less likely this would be possible without a gas bladder and large lifting hydrofoils. Alternatively, but less likely in my opinion, perhaps Brett's and Hunter's estimates of endurance speeds and Shuleikin's estimate of the most efficient speed for migration are overestimates of the physiological capabilities of large scombroids and xiphoids for sustained swimming.

Larger scombroids are then not able to avail themselves of whatever advantages have been achieved by some smaller species and individuals of scombroids by the loss of a gas bladder. Problems of large size among scombroids become either the possibility of an energetically imprudent basal speed requirement to maintain hydrostatic equilibrium or a loss (Magnuson, 1966b; Aleev, 1969), owing to a large gas bladder, in vertical mobility especially near the sea surface. I have observed *K. pelamis*, a species without a gas bladder, swim vertically upward at burst speeds in the top 10 m of the sea. Large scombroids and xiphoids would be expected to live either (1) deep in the water column where rapid vertical excursions have little effect on gas expansion or (2) immediately below the surface and making no rapid upward excursions. The pressure change experienced in an ascent from 10 m to the surface results in a 100% increase in the volume of an unrestricted gas bladder but an ascent from 100 to 90 m results in an increase in volume of only 10%. Alternatively, (3) to retain rapid vertical mobility, those with gas bladders and living near the surface would require remarkably strong-walled gas bladders that could maintain the gas at greater than ambient pressures. A casual review of the natural history of large scombroids and xiphoids suggests that all three alternatives are evidenced in one form or the other. The most unlikely species would be one with a large, thin-walled gas bladder that also cruised at 10 m below the surface and chased its prey or escaped predation vertically toward the sea surface.

ACKNOWLEDGMENTS

My special thanks go to Randolph K. C. Chang at the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA for his help in collecting and processing of data throughout the course of this study. I also thank the many employees of the above Laboratory and at the Laboratory of Limnology for their help during many phases of the research and John H. Prescott and Jerry Goldsmith of Marineland of the Pacific, Palos Verdes, Calif., for help in obtaining morphometric data on *Sarda* and *Scomber*. I appreciate the helpful review of the manuscript by Barry S. Muir, Fisheries Research Board of Canada at Halifax, and Robert H. Gibbs, Jr., Smithsonian Institution. Support for the study came almost entirely from the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA (formerly the Bureau of Commercial Fisheries Biological Laboratory).

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ASYMMETRY ANALYSIS IN FISHES: A POSSIBLE STATISTICAL INDICATOR OF ENVIRONMENTAL STRESS

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ABSTRACT

One of the more difficult tasks in evaluating the possible deleterious effects of multiple toxicants on natural communities is in defining subtle sublethal effects before the onset of chronic morbidity. We reason that before detectable changes in either species diversity or species abundance occur subtle changes must take place in a number of important processes, ranging from molecular to behavioral changes. Unfortunately, changes in these parameters have proven most difficult to detect with current methodology. We, therefore, have been examining the possible use of fluctuating asymmetry as a possible measure of environmental stress.

Fluctuating asymmetry is simply the random deviation from perfect symmetry of any bilateral anatomical character. It is, therefore, a nonspecific measure of developmental perturbation.

Using asymmetry analysis on three species of marine teleost—barred sand bass, *Paralabrax nebulifer*; grunion, *Leuresthes tenuis*; and barred surfperch, *Amphistichus argenteus*—from southern California and Baja California, we have been able to define two possible asymmetry trends, historical and geographic. Asymmetry values are shown to increase as we approach highly populated areas (southern California) both from the north and south and also with time within southern California. Such increases in asymmetry correlate well with the known distribution of various toxicants from this same area.

Biological indices are urgently needed for efficiently assessing the effects of man-induced environmental stresses on the marine environment, a task widely acknowledged as both important and difficult (National Scientific Committee on Oceanography of the NAS-NRC Ocean Affairs Board, 1971). Several general approaches are now being used with mixed results: 1) the documentation of die-offs or sterility, such as results from anoxia, thermal shock, pesticides, industrial wastes, oil spills, etc., 2) the detection and description of anomalies ascribable to microorganisms associated with sewage, 3) the quantification of changes in species diversity and community organization, sometimes attributable to thermal, domestic, or industrial effluents, and 4) population changes in certain indicator species which are themselves either resistant or sensitive to specific pollutants (Wilber, 1969). Many of the above methods have been criticized for their insensitivity, lack of standardization, and for being useful only after the occurrence of significant biotic changes. The method we propose may be a useful and sensitive alternative under certain conditions.

Our approach is morphological and is based on fluctuating asymmetry, the random signed differences between the right and left sides of a bilateral character (Van Valen, 1962). The extent to which deviations from perfect symmetry occur is thought to be an estimate of the regulatory capacity of the developmental system in a particular environment. Our working hypothesis is that asymmetry will be increased under certain kinds of environmental stress due to the failure of homeostatic regulatory mechanisms. Such developmental effects might occur before the concentration of toxicants in waters or food reach levels high enough to cause widespread morbidity. It would be slightly easier to use variation per se, such as estimated by the standard deviation or coefficient of variation of a unilateral char-

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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

acter, to measure such perturbations, but such variation is complex and probably of little use in measuring developmental homeostasis or stability of individuals within a population (Thoday, 1958; Soulé and Cuzin-Roudy, in press). The recent discovery that morphological variation may be highly correlated with mean heterozygosity based on electrophoretic analysis (Soulé and Yang, in press) reemphasizes this point.

Adams and Niswander (1967) suggested that, "It is possible that an overwhelming environmental stress (i.e., teratogen) could [cause] . . . increased asymmetry." We, therefore, decided to examine fluctuating asymmetry as a possible measure of environmental stress. Previous studies of asymmetry have not emphasized the environmental component (for references see Mather, 1953; Thoday, 1958; Reeve, 1960; Sakai and Shimamoto, 1965). The use of paired structures to analyze bilateral developmental differences in fish was first suggested by Hubbs and Hubbs (1945).

MATERIALS AND METHODS

To field test this hypothesis we chose three species of marine teleost fish—barred sand bass, *Paralabrax nebulifer*; grunion, *Leuresthes tenuis*; and barred surfperch, *Amphistichus argenteus*. These species belong to different families and differ greatly in their life histories. They are also abundant throughout the area of study, they are easily captured, and large collections were available from museums for comparative space and time series analyses.

Barred sand bass are generalized carnivores (Quast, 1968) and probably approach the longevity of kelp bass (*P. clathratus*), which can survive at least 32 years in the wild (Young, 1963). Barred sand bass are also of significant importance to the sport fishing industry in southern California (Pinkas, Oliphant, and Haugen, 1968) and are apparently nonmigratory (Young, 1969). Adults (those fish older than 1 year) live offshore in rock-sand ecotonal areas, except during the spawning season when they migrate short distances to sandy areas to spawn (Turner, Ebert, and Given, 1969). From examination of adults, barred sand bass appear to be secondarily gonochoristic, as are kelp bass (Smith and Young, 1966), and are undoubtedly broadcast spawners.

Grunion are small atherinids that mature in about a year, are thought to be nonmigratory, live only 2 or 3 years, and are found in inshore waters (Walker, 1952). They spawn on sandy beaches during the high tides from late February or March through August or September (Walker, 1952). Grunion lack teeth and it is, therefore, assumed that they feed on small organisms (Frey, 1971).

Finally, barred surfperch are found almost exclusively in the surf zone and feed predominantly on sand crabs, *Emerita analoga*, which constitute roughly 90% of their diet (Carlisle, Schott, and Abramson, 1960). From tagging studies, barred surfperch appear to be nonmigratory (Carlisle et al., 1960). In contrast to barred sand bass and grunion, surfperch are viviparous (Eigenmann, 1894), with an apparent maximum life span of 6 years for males and 9 years for females (Carlisle et al., 1960).

All reference to length in this paper refers to the standard length in millimeters, defined as extending from the anterior notch between the premaxillaries to the end of the hypural plate. Variability is expressed as one standard error (SE) or one standard deviation (S) on either side of the mean.

Character Analysis

Seven characteristics were used for asymmetry analysis:

1. Number of pectoral fin rays: A count of the total number of pectoral fin rays, including the uppermost unbranched ray.
2. Total gill rakers: A total count of rakers and all raker rudiments that could be seen under a dissecting microscope. "Secondary" rakers, which frequently occur in barred sand bass with badly deformed rakers (Valentine and Bridges, 1969), were excluded from the count.
3. Scales above the lateral line: A count started approximately two scale rows in front of the first dorsal fin spine and extending ventral-posteriorly along a natural scale row to the pored lateral line scales.
4. Scales below the lateral line: A count

begun between the first anal fin spine and the vent, extending dorso-anteriorly along a natural scale row to the pored lateral line scales.

5. Pored lateral line scales: A count begun with the first anterior pored lateral line scale, usually located under or adjacent to the opercular series, and extending posteriorly to the end of the hypural plate. When the hypural plate is reached, a straight pin is inserted in the last pored scale counted and pushed through the caudal peduncle. When the scales are counted on the other side of the fish, the pin designates the point at which counting should cease.

6. Length of the dentaries: Measured from the symphysis to a small notch at the posterior edge of the dentary.

7. Length of the posterior lateral projection of the epiotic: Measured from the medial notch defining the projection to the tip of the projection.

Where practical, all characters were counted under a binocular microscope. For specimens too large to fit under a microscope, a magnifying glass was used.

Statistical Analysis

The procedure for meristic (countable and discrete) characters follows. For each individual in a sample, the count taken from the left side is subtracted from the corresponding count on the right to obtain the signed difference. Next, the standard deviation of the signed differences (S_{r-l}) is calculated for each sample. Then, the mean of the character ($\bar{x}_{r+l}$) is calculated for each sample by adding the absolute scores for both sides and dividing by the sample size. Finally, the squared coefficient of asymmetry variation (CV_a^2) for each population is defined as follows:

$$CV_a^2 = \left(\frac{S_{r-l} \times 100}{\bar{x}_{r+l}}\right)^2$$

F tests are employed to test for significant differences in asymmetry. We follow Lewontin (1966) in using the squared coefficient of variation as an analogue to the variance.

To obviate scaling problems associated with growth in morphometric characters (nondiscrete, measurable), each measurement (item) is divided by a suitable "general size" measurement (e.g., we utilize the length of the cranium as the standardizing measurement when studying bilateral bones in the cranial region). Each morphometric measurement is so treated before obtaining the signed difference. The variance of the resulting differences is then treated as if it were a CV_a^2 value.

After the above analyses had been performed on a series of barred sand bass from southern (N = 74) and Baja California (N = 101), we decided to restrict further asymmetry analyses to total gill raker and pectoral fin ray counts since asymmetry in all of the other characters showed a significant association with asymmetry in these (Table 1). Furthermore, pectoral fin rays and gill rakers are the easiest characters to quantify and appear to be the most accurate counts that can be taken on barred sand bass. For both grunion and barred surfperch only the pectoral fin ray and total gill raker counts were used for asymmetry analysis.

Locality Designations

We consider Point Fermin, the first major point north of the Los Angeles-Long Beach Harbors, to be our pivotal locality. Point Fermin is situated approximately equidistant between Point Conception and the California-Mexico border, the northern and southern boundaries for southern California. The distances between Point Fermin and the other localities mentioned in this paper are indicated in Table 2.

RESULTS

Barred Sand Bass

In our original analyses of barred sand bass asymmetry data, we used all characters previously listed. Results from these analyses are presented in Table 1. For all characters, both meristic and morphometric, asymmetry values for southern California barred sand bass are significantly higher than for Baja California or Mexican barred sand bass.

Of interest is the relation between asymmetry and length. Mexican barred sand bass were

TABLE 1.—Comparison of CV_a^2 values and character means ($\bar{x}_{r+l}$) of barred sand bass from southern California and Baja California.

Character	CV_a^2 values: Southern California	N	CV_a^2 values: Baja California	N	F ratios	F ratio probabilities	Character means: Southern California	Character means: Baja California	t test probabilities
Dentaries / cranium[1]	[2]0.8056	66	[3]0.4868	66	1.621	<0.05	0.984	1.001	<0.01
LEP / cranium[1]	[2]10.3121	66	[4]5.4020	60	1.908	<0.01	0.546	0.484	<<0.001
Scales above lateral line	[5]8.5488	101	[6]3.8534	74	2.219	<0.001	37.485	37.595	<0.9
Scales below lateral line	[5]6.9209	101	[6]1.6268	74	4.254	<<0.001	74.465	75.189	<0.2
Pored lateral line scales	[5]2.2300	101	[6]0.5427	74	4.107	<<0.001	141.901	139.000	<0.001
Pectoral fin rays	[7]1.9604	295	[8]0.4101	210	4.780	<<0.001	35.068	35.448	<0.001
Total gill rakers	[7]8.3009	295	[8]1.9648	210	4.225	<<0.001	53.139	53.648	<0.1

[1] Variances for dentaries / cranium and lateral epiotic projections (LEP) / cranium × 10^4.
[2] Mean standard length 288.4 ± 6.1 mm (SE).
[3] Mean standard length 293.7 ± 6.5 mm (SE).
[4] Mean standard length 292.9 ± 6.8 mm (SE).
[5] Mean standard length 287.0 ± 4.9 mm (SE).
[6] Mean standard length 293.6 ± 6.5 mm (SE).
[7] Mean standard length 193.6 ± 3.2 mm (SE).
[8] Mean standard length 193.3 ± 4.4 mm (SE).

TABLE 2.—Locality designation and approximate straight-line distance to Point Fermin.

Locality	Miles to Point Fermin
San Simeon	210
Santa Rosa Island[1]	100
Carpinteria	85
Point Fermin	0
Belmont Shore	9
San Clemente	53
San Diego	101
California-Mexico border	116
Bahia San Quintin (Mexico)	270
Bahia Sebastian Vizcaino (Mexico)	435
Turtle Bay (Mexico)	475
Southern Baja California (Mexico)	550-750

[1] Santa Rosa Island is 26 miles to sea from the nearest point of land, which is itself 100 miles from Point Fermin.

grouped into size classes (Table 3). From these data it would appear that in small individuals (< 100 mm) pectoral fin ray asymmetry may decrease as size increases, while gill raker asymmetry may decrease. For gill rakers the trend is probably an effect of incomplete development, character means are always lowest in smaller size classes (Tables 3, 4, 5).

Southern California barred sand bass were likewise grouped into size classes (Table 4). Comparing the data in these two tables (3 and 4) will illustrate three notable differences. First, small southern California fish (0.0-49.9 mm) have higher asymmetry levels than do their Mexican counterparts. Second, pectoral fin ray asymmetry increases with size in southern California barred sand bass, instead of decreasing and plateauing, as in Mexican barred sand bass. Third, the largest southern California fish have asymmetry levels four to five times higher than do Mexican fish. (In southern California barred sand bass the association of asymmetry in both characters with standard length is highly significant, $P < 0.01$, using Kendall's coefficient of concordance; Snedecor, 1956.)

Further analyses of these data suggest that these geographic differences in asymmetry are the consequence of both ontogenetic and historical processes that have been occurring in the southern California population. The possible ontogenetic change is an increase in asymmetry with size (age). The possible historical process is a secular increase in asymmetry. Both hypotheses are sufficient to account for the observed trends. Unfortunately, data are lacking to resolve this problem by straightforward regression analyses. Nevertheless, the following analyses suggest that both processes are operating.

First, the ontogenetic theory is examined by following cohorts (cohort, in this case, being defined as specimens spawned in the same year, regardless of the size or age of the fish at the time of capture). Our only collections containing enough specimens to perform such an analysis are those hatched in 1957, 1958, and 1959

TABLE 3.—CV_a^2 values and character means ($\bar{x}_{r+l}$) by size class of barred sand bass from Baja California.

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 49.9	31	44.5 ± 0.8	1.0708	0.7428	35.290	51.613
50- 99.9	32	66.8 ± 2.5	0.7532	1.4556	35.656	53.094
100-149.9	33	115.7 ± 2.1	0.6724	2.3264	35.606	54.364
150-249.9	19	196.9 ± 7.4	0.4220	1.4668	35.316	54.316
250-299.9	36	279.8 ± 2.1	0.4592	2.6348	35.278	54.083
300 and up	59	329.5 ± 3.5	0.4088	2.3332	35.475	54.136

TABLE 4.—CV_a^2 values and character means ($\bar{x}_{r+l}$) by size class of barred sand bass from southern California.

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 49.9	19	39.1 ± 1.4	1.3553	5.8338	34.789	50.842
50- 99.9	27	70.6 ± 2.8	0.9405	8.2111	34.852	52.556
100-149.9	80	130.1 ± 1.4	1.8461	6.0791	35.150	52.888
150-199.9	39	162.9 ± 1.6	2.1140	10.7590	35.077	54.846
200-249.9	28	228.5 ± 2.8	1.8782	11.5168	35.321	52.893
250-299.9	70	278.6 ± 1.6	2.8201	7.3304	35.014	53.186
300 and up	32	365.1 ± 7.7	2.3502	11.0300	35.094	53.656

TABLE 5.—CV_a^2 values and character means ($\bar{x}_{r+l}$) for southern California barred sand bass probably hatched in 1957, 1958, and 1959.

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 99.9	21	49.1 ± 3.6	1.2116	4.4860	34.905	50.950
100-199.9	21	146.5 ± 3.8	1.1729	5.5034	35.476	54.952
200-299.9	14	278.9 ± 5.0	1.8465	9.3107	34.928	53.000
300 and up	21	357.7 ± 7.7	1.9322	13.0783	35.048	53.429

(Table 5). These three cohorts were pooled to increase sample size. From Table 5 it is evident that both pectoral fin ray and gill raker asymmetry increased as these particular cohorts aged. The specimens do not exist to perform a similar analysis on Mexican barred sand bass, although we might infer from Table 3 that significant asymmetry changes cease when fish exceed 100 mm.

An historical trend of increasing asymmetry is also indicated. In Figure 1 the appropriate specimens are grouped by their probable dates of hatch. There is evidence for plateauing of this trend since fish hatched after 1966 appear to be no more asymmetric than those hatched in the late fifties. A sampling problem may exist because the collections differ in the average size of specimens examined. This could partially account for the apparent plateauing. To examine this, fish of similar size and age were analyzed (Table 6). The plateau is still apparent, so it is probably real.

To summarize the barred sand bass data, there is evidence for two asymmetry trends in southern California—an increase with size (age) and the other with time. An attempt to partition the asymmetry contributions of these two probable sources by using multiple regression produce inconclusive results due, we think, to the inadequate nature of the samples.

TABLE 6.—CV_a^2 values by year of hatch in the 100.0-199.9 mm size class of barred sand bass from southern California.

Date of hatch[1]	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers
1956 and before	23	127.3 ± 3.1	0.6692	2.4805
1957, 1958, 1959	21	146.5 ± 3.8	1.1791	5.5033
1963, 1964, 1965	51	149.3 ± 2.4	2.7476	10.8313
1966 and later	20	133.4 ± 4.7	2.5353	7.7993

[1] The 1960, 1961, and 1962 year of hatch class of fish were not included in this analysis since $N = 4$.

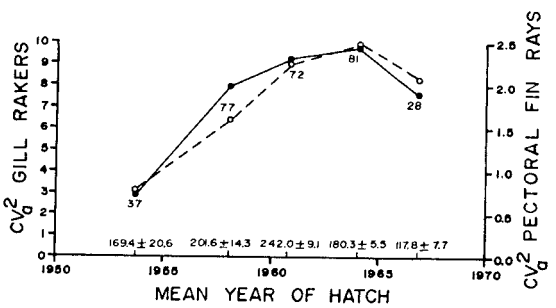

FIGURE 1.—CV_a^2 values for southern California barred sand bass grouped by probable year of hatch. Closed circles, gill rakers; open circles, pectoral fin rays. Numbers on upper abscissa indicate mean length of specimens in samples ± SE. To increase sample sizes fish from several consecutive years of hatch were pooled as follows: up to and including 1956; 1957 through 1959; 1960 through 1962; 1963 through 1965; 1966 and later.

Figure 2 graphically demonstrates how asymmetry values vary with increasing size, both in our Mexican fish and in fish from our southern California cohorts analysis.

Grunion

Only two bilateral meristic counts were made on grunion, the number of pectoral fin rays and total gill rakers. Most grunion were probably not over 2 years old and, hence, were not grouped into classes based on dates of hatch but rather only by dates of collection (Table 7). Our Turtle Bay sample is not large enough to determine asymmetry trends with body size.

The Turtle Bay collection has the lowest CV_a^2 values. Contemporary San Quintin and San Diego collections have statistically increasing CV_a^2 values with time. We employed Kendalls' coefficient of concordance (Snedecor, 1956) on the data in Table 7 to test for asymmetry trends with date of capture for both characters in grunion from Belmont Shore. The results are significant, $0.05 < P < 0.01$, indicating a significant association between year of collection and asymmetry for both characters.

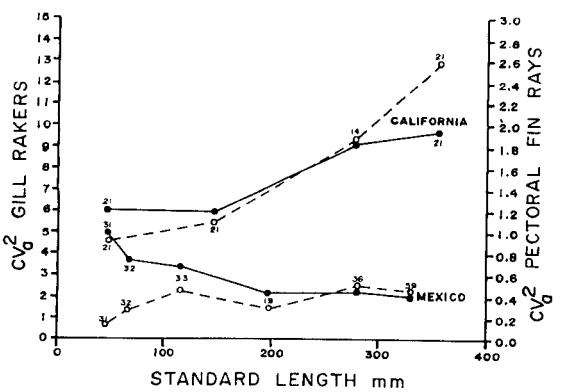

FIGURE 2.—CV_a^2 values for Mexican and California barred sand bass, by standard length. Mexican fish grouped by 50-mm size classes, all years of hatch combined. California fish grouped by 100-mm size classes, only fish hatched in the period 1957-59 included. Dots, gill rakers; open circles, pectoral fin rays. Numbers by data points indicate sample sizes.

Barred Surfperch

For this species, as for grunion, only pectoral fin rays and gill rakers were used in our analyses. From the data presented in Table 8 it can be seen that the barred surfperch data

TABLE 7.—CV_a^2 values and character means ($\bar{x}_{r+l}$) of grunion by locality.

Locality	Date	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
Turtle Bay	1948	49	109.5 ± 1.2	0.7340	0.8344	29.082	68.020
San Quintin	1970	57	126.8 ± 1.5	0.8376	1.5192	28.947	67.057
San Diego	1970	60	137.7 ± 1.6	1.0484	1.3832	28.383	68.000
Belmont Shore	1950-51	51	107.7 ± 1.2	.7364	2.6328	28.451	65.588
Belmont Shore	1963	30	77.8 ± 1.6	1.6376	2.9272	28.533	65.000
Belmont Shore	1966	22	81.9 ± 0.9	3.0388	2.8396	27.864	62.045
Belmont Shore	1968-69	27	97.3 ± 2.8	3.4248	4.2464	27.963	64.444

TABLE 8.—CV_a^2 values and character means ($\bar{x}_{r+l}$) of barred surfperch by locality.

Locality	Date	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
Bahia Sebastian Vizcaino	1952	61	126.1 ± 7.4	0.8028	0.7896	54.597	40.097
Bahia San Quintin	1970-71	44	196.5 ± 6.6	0.7484	1.6328	54.727	39.909
Belmont Shore	1958	73	108.1 ± 3.4	1.2204	2.3268	55.301	38.534
Belmont Shore	1969-70	44	98.2 ± 2.5	2.1660	4.6272	55.364	39.341
Carpinteria	1970	15	164.9 ± 0.5	0.5892	3.6308	53.933	38.667
Santa Rosa Island	1954	56	92.5 ± 7.4	1.5252	1.0700	52.339	38.125
San Simeon	1949	30	112.0 ± 5.4	.4736	1.1476	53.067	38.633

closely approximate the previously presented asymmetry trends for both barred sand bass and grunion. The two oldest collections, Bahia Sebastian Vizcaino and San Simeon, uniformly have low CV_a^2 values. The other relatively old collection, Santa Rosa Island, has moderately high pectoral fin ray asymmetry. The majority of specimens in this collection (37 of 56) are small, ranging between 46 and 77 mm. Barred surfperch, at parturition, are between 42 and 53 mm (Carlisle et al., 1960). A possible explanation for the higher Santa Rosa value is that these small individuals have not yet been exposed to prolonged stabilizing selection. The only other young barred surfperch available for comparison are 18 from Bahia Sebastian Vizcaino (50.1-77.5 mm). Of these 18 specimens, 5 are asymmetric for pectoral fin rays. For our Santa Rosa Island specimens 11 of 37 are asymmetric. Differences are not statistically significant.

To examine the association of asymmetry and size we grouped our three oldest collections (Bahia Sebastian Vizcaino, Santa Rosa Island, San Simeon) and analyzed these collections by size class. Table 9 shows the results of this analysis. Neither gill raker nor pectoral fin ray asymmetry appear to increase with size (age). In Table 8, Figure 3, gill raker data points from Bahia Sebastian Vizcaino, Santa Rosa Island, and San Simeon are connected (solid line) because we feel that these three populations probably represent what might be termed "unperturbed" populations. All three collections are old, all were taken at least 100 miles from Los Angeles and all are probably little exploited by other than natural predators.

Also in Figure 3, all relatively recent collections (San Quintin, 1970-71, Belmont Shore, 1969-70, and Carpinteria, 1970) are connected by a dashed line. The extremely elevated CV_a^2 value for the Belmont Shore collection of 1969-70 should be noted, as well as the high value at Carpinteria.

DISCUSSION

In the discussion of these results we find it necessary to distinguish between two levels of causation. The first is the origin of the asym-

TABLE 9.—CV_a^2 values and character means ($\bar{x}_{r+l}$) by size class of barred surfperch.[1]

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 74.9	52	58.6 ± 1.1	1.5348	0.8844	52.923	38.904
75-124.9	36	87.4 ± 1.2	0.6924	1.0908	53.639	39.278
125-174.9	34	144.8 ± 2.0	0.6400	1.0008	53.294	38.794
175 and up	26	201.8 ± 3.5	0.9012	0.8728	54.346	39.385

[1] Includes specimens from Bahia Sebastian Vizcaino, San Simeon, and Santa Rosa Island.

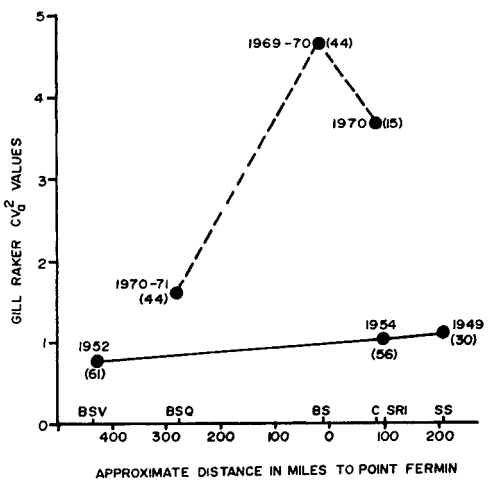

FIGURE 3.—Geographic and historic CV_a^2 trends in barred surfperch. Connected points are more or less "contemporary" samples. Letter codes are as follows: BSV, Bahia Sebastian Vizcaino; BSQ, Bahia San Quintin; BS, Belmont Shore; C, Carpinteria; SRI, Santa Rosa Island; SS, San Simeon. Dates of collection and sample sizes (N) for each collection are as indicated.

metry differences, and the second is the maintenance of these differences. We consider two possible origins: genetic and environmental. The parallel dichotomy with regard to maintenance is that the observed patterns are maintained by natural selection differentials in time and space, or the patterns are maintained by a geographically stable pattern in the distribution of the relevant environmental factor(s). (Other combinations of causative categories exist, but are rejected for lack of evidence and are ignored here.)

The hypotheses explaining our results are grouped into three categories: (A) hypotheses assuming a genetic origin, (B) hypotheses assuming an environmental origin stemming from natural causes, and (C) hypotheses assuming an environmental origin stemming from various pollutants.

Arguments for Category A Hypotheses

All genetic explanations assume the relaxation of stabilizing selection, thus allowing the accumulation of "abnormal" genotypes in the population resulting in an increase in the asymmetry variance of bilateral characters.

Various changes that could bring about such a decrease in the intensity of stabilizing selection in the populations studied are thought to have occurred in the recent past. These changes are of four types: (1) increased cropping of adults by fishermen, (2) a fish population explosion, (3) a decrease in the predator-prey ratio, and (4) an increase in the carrying capacity of the environment. A rapid increase in a population (type 2) depends on a high juvenile recruitment rate. In this respect, the effect of a population explosion is similar to that of increased fishing pressure on adults (type 1), although the former change is usually more transient than fishing pressure changes.

Fishing pressure and the number of fish being caught in southern California are increasing (Frey, 1971). Given that the adult populations of the three species in question have remained stable (there is no evidence to the contrary), then at some stage the removal of adults must be compensated for by increased survival of recruits. One possible consequence of this is an increase in the probability of survival

of abnormal or extreme juveniles. The geographical concordance of asymmetry in these fish and human population density in the area studied is certainly suggestive. Furthermore, asymmetry has apparently been increasing in southern California over the past two decades, as has the number of anglers.

There is evidence that a population explosion of southern California barred sand bass occurred some time during the time period 1957-59. Before this time barred sand bass constituted a minor fraction of the "bass" catch in southern California marine waters ("bass" refers to barred sand bass, kelp bass, and spotted sand bass, *P. maculatofasciatus*), whereas in 1964 they constituted over 50% of the bass catch from private sport fishing vessels (Pinkas et al., 1968). The rapid proliferation of one or two year classes of fish has been known to produce, at least temporarily, phenotypically aberrant cohorts (Whitney, 1961). Similar patterns may be postulated for asymmetry.

A decrease in the predator-prey ratio should have similar effects. One factor maintaining low variability and possibly low asymmetry variances is the elimination of phenotypically and, presumably, genetically deviant individuals via centripetal or stabilizing selection. With less predation there might be higher survival of deviants. Elimination of piscivorous predators may have resulted from increased fishing pressure and reduction in marine piscivorous birds and mammals.

Domestic sewage outfalls in closed bodies of water are known to stimulate productivity (MacKenthun, 1965, for a review). Similar stimulatory effects on marine phytoplankton are to be expected. Increasing primary productivity should lead to higher overall productivity and an increase in the carrying capacity of the environment, particularly near outfalls. An increasing carrying capacity should result in continual growth in the size of the populations of marine organisms associated with outfalls. Increases in asymmetry can easily be correlated with the increasing volume of sewage effluents in southern California. The apparent increase in size of barred sand bass populations can also be so correlated. The higher concentrations of fish near outfalls (reported by fishermen) as opposed to adjacent areas would also be cited. These larger populations of fish may be a direct result of the increased availability of food in areas near outfalls.

Evidence Against Category A Hypotheses

Increased cropping of adult fishes through angler success leading to an increase in asymmetry is a difficult hypothesis to test with the species we have chosen to study. Virtually no data exist on the numbers of grunion and barred surfperch taken yearly. Fisheries statistics for the three basses are pooled by the California Department of Fish and Game, making separation by species most difficult. Most of the bass catch is, however, composed of kelp and barred sand bass. Separating the bass catch into kelp and barred sand bass is difficult.

Prior to 1957 barred sand bass composed a very minor portion of the bass catch (Frey, 1971). From 1947 to 1959 the bass fishery experienced a general decline, reaching a 23-year low of 428,656 bass caught in 1959. Beginning somewhere around the early 1960's barred sand bass began constituting an increasing portion of the bass catch and by 1964, barred sand bass made up roughly half of the bass catch from private fishing vessels (Pinkas et al., 1968). It would, therefore, seem logical that the increase in the bass catch resulted as much from an increase in barred sand bass as from kelp bass. We have seen no information that the proportion of barred sand bass in the bass catch is declining. The total bass catch has been above 1 million for the past 7 years, averaging 1.2 ± 0.109 million individuals from 1963 to 1969. It would, therefore, appear that the barred sand bass population has stabilized.

Recall from Figure 1 that CV_a^2 values in barred sand bass have been increasing from at least 1954 through 1964. During this same period the bass catch passed through a declining phase and then a rapid increase in catch. If fishing pressure were to account partially for these data, we would expect to see relatively stable levels until sometime around 1960, when levels should begin to climb due, on one hand,

to the population explosion of barred sand bass and, on the other, to increased angler success. No such trends are to be found in our data. As previously mentioned, catch data for grunion and barred surfperch are lacking so that it is impossible to examine these species for the possible effects of fishing pressure.

The effects of a population explosion on asymmetry variance should be temporary and will cease when the population stabilizes. The highest asymmetry values should reflect periods of exceptionally high juvenile recruitment.

Our data on probable year of hatch and cohorts analyses show that asymmetry values of barred sand bass are lower in 1957-59 than in later periods. Recall that this is the time when a population explosion of barred sand bass is supposed to have begun. If the asymmetry is genetic and/or congenital, then the low asymmetry of these fish is inconsistent with the above prediction. For our data to support such an hypothesis it would have to be shown that the population of barred sand bass and, for that matter, grunion and barred surfperch, have been continually increasing. Our data do not support this premise. No data exist for either barred surfperch or grunion which can be used as a basis on which to test this premise.

The question of shifting predator-prey ratios is most difficult to analyze. There undoubtedly exist changes in such ratios not only from year to year, but also seasonally. Whether such changes can result in significant shifts in asymmetry variances is unknown. The fact that all three species occupy different habitats, all appear to be undergoing similar asymmetry changes, and all are probably preyed upon by different predators would seem to argue against such a simple cause and effect explanation.

Fish density around outfalls may be high, but this has never been shown to be an effect of the local productivity gradient. A logical alternative is that outfalls, being constructed over sand or muddy bottoms, provide an artificial habitat. Studies by the California Department of Fish and Game (Turner et al., 1969) have shown that artificial reefs in predominantly sandy areas of low relief rapidly attract large assemblages of fish. Barred sand bass were the most frequently observed species and were reported inhabiting artificial reefs within hours after construction terminated.

That larger populations of some species (e.g., barred sand bass) are apparently residing in southern California now than in the past may be ascribed to fluctuations in normal environmental conditions. Furthermore, of the three species studied, only barred sand bass and possibly grunion are likely to be found around sewer outfalls. Barred surfperch are predominantly inshore and seldom venture past the surfzone. They are, therefore, unlikely to be affected as much as are the other two species, unless an increase in primary productivity is widespread. Yet data on asymmetry for all three species are similar.

Arguments for Category B Hypotheses

Naturally occurring, clinally varying abiotic factors would also seem to be a logical source of induced meristic variation since asymmetry increases from Mexico northward. Experimentally, Schmidt (1919, 1920) with brown trout, *Salmo trutta*, and the blenny, *Zoarces viviparus*; Lindsey (1954, 1958) with the paradise fish, *Macropodus opercularis*; Blaxter (1957) with the herring, *Clupea harengus*; Tåning (1952) with the sea trout, *Salmo trutta trutta*; and others have clearly demonstrated that temperature plays a very important role in determining the ultimate meristic counts in a wide range of fishes. Barlow (1961) stated that a good correlation exists between cooler environmental temperatures and higher meristic scores. Other environmental factors such as light intensity (McHugh, 1954, with the grunion), light duration (Lindsey, 1958, with the kokanee, *Oncorhynchus nerka*), oxygen and carbon dioxide tensions (Tåning, 1944, 1952, with the sea trout), and salinity (Heuts, 1947, with the stickleback, *Gasterosteus aculeatus*) have been examined with similar results. About the only factors studied that have not been shown to significantly alter meristic counts are pH and phosphate and nitrate concentrations (Tåning, 1952).

Arguments Against Category B Hypotheses

If asymmetry were to correlate well with mean annual water temperature, we would expect that it should continue to increase with latitude. Our data for barred surfperch are inconsistent with this hypothesis, as are those of Hubbs and Hubbs (1945), who have conducted the only large-scale study of asymmetry encompassing a large latitudinal transect. Hubbs and Hubbs (using a statistic differing from that used here) studied the asymmetry of pectoral fin rays in the Pacific staghorn sculpin, *Leptocottus armatus*, from Sitkalidak Island, Alaska, to Mission Bay, in southern California. Of the 12 populations examined, the highest asymmetry values were from their southern most samples, Anaheim and Mission Bays in southern California (Table 10). The Tau coefficient (Snedecor, 1956), applied to these data, indicate a significant negative asymmetry correlation, $P < 0.05$, with increasing latitude.

Finally, not only are asymmetry values increasing clinally, they also appear to be increasing temporally. We know of no environmental variable showing these continuous trends. Most variables show cyclic fluctuations, whereas our asymmetry values apparently do not.

Arguments for Category C Hypotheses

This hypothesis assumes only that as environmental stress increases so should asymmetry. At this point in time we must leave unspecified what type of stress may produce increases in asymmetry, although preliminary experiments with grunion would seem to indicate that p,ṕ-DDT may have this effect (Valentine and Soulé, 1972).[4] As a first approximation, we might assume that specific ubiquitous pollutants known to interfere with various metabolic processes might logically be suspect. Two such groups of agents are known to occur in the southern California environment (marine, terresterial, and atmospheric), chlorinated hydrocarbons (Risebrough et al., 1967; Schmidt, Risebrough, and Gress, 1971; Duke and Wilson, 1971; Burnett, 1971; Munson, 1972) and heavy metals (Tatsumoto and Patterson, 1963; Brooks, Presley, and Kaplan, 1967; Schroeder, 1971; Galloway, 1972). The distribution of pollutants in southern California waters is similar to the distribution of asymmetry values (Burnett, 1971; Galloway, 1972). This hypothesis would attribute the increases in asymmetry in the species studied to the presence of pollutants and possibly to duration of exposure.

[4] Valentine, D. W., and M. Soulé. 1972. Asymmetry: The effect of p, p′-DDT on the development of fins in the grunion (*Leuresthes tenuis*). Unpublished manuscript.

TABLE 10.—Pectoral fin ray asymmetry in the Pacific staghorn sculpin, *Leptocottus armatus*.[1]

Locality	N	$\bar{x}_{r+l}$	[2]$\frac{100(l+r)}{N}$
Alaska			
Sitkalidak Island	174	38.89	16.67
Admirality Island	104	38.49	22.12
Washington			
Puget Sound	245	38.06	20.41
Grays Harbor	103	37.82	15.53
Oregon			
Nestucca Bay	136	37.94	17.65
California			
Humboldt Bay	221	37.91	19.91
San Francisco Bay Region	223	—	21.97
Elkhorn Slough	145	—	22.75
Morro Bay	218	36.63	20.18
Santa Barbara	397	36.77	20.65
Anaheim Bay	109	37.01	29.36
Mission Bay	119	—	24.37

[1] Data recalculated from Hubbs and Hubbs (1945, Tables VII and VIII).

[2] Hubbs and Hubbs used this statistic to express "the amount of overall asymmetry . . . as a percentage figure in which l and r represent counts that are higher . . . on the left and right sides, respectively, and N is the total number of specimens, symmetrical plus asymmetrical, in the sample."

Arguments Against Category C Hypotheses

The only contraindicative evidence thus far is that if these asymmetries were the result of toxicants, we might expect to find behavioral and reproductive effects. None has as yet been observed, although our preliminary observations on the low viability of first spawned grunion eggs is suspicious (Valentine and Soulé, see footnote 4).

CONCLUSIONS

Several of the explanations presented assume a genetic origin of the asymmetries and involve altered demographic parameters: improved conditions leading to population growth; de-

creased predation resulting in decreased selection; increased fishing pressure. The potential interactions among these processes are manifold. Some are virtually mutually exclusive. For instance a population explosion of predators (including barred sand bass) is inconsistent with a model based on decreased predation. Some models have a superficial complementarity. For instance, a general increase in marine productivity, though resulting in population growth, would not necessarily alter selection against divergent phenotypes. Predator-prey ratios, for instance, might be expected to remain relatively constant.

Most theories that would appear to explain these data are based on a genetic hypothesis. It is not easy to sustain these hypotheses in view of the apparent age-dependency of the asymmetry. Skeletal abnormalities in these same fish (Valentine, in press) show similar temporal and spatial patterns. We tentatively conclude that the environmental stress hypothesis gives the best fit to the data. It is very possible that this approach may be limited in application to the detection of stress induced by agents affecting calcium metabolism, transport, or deposition. Recent experiments, conducted in our laboratory, with the fruit fly, *Drosophila melanogaster*, re-emphasizes this point. We attempted to increase the asymmetry of sternopleural chaeta by raising fruit flies from eggs to adults in culture medium treated with various toxicants (methylmercury chloride, cupric sulfate, tetraethyl lead, and p,p′-DDT). Toxicant concentrations ranged from 1 ppb (part per billion) to lethality and egg concentrations from 1 to 200 per vial. Results, in all instances, were negative.

Asymmetry analysis, if it proves fruitful for measuring environmental stress, has some important benefits. We think such an assay would:

1. permit continuous monitoring of the health of biological communities via periodic checks of specific sensitive organisms;
2. permit the detection of long-term trends (decades) by comparing preserved material with contemporary materials;
3. permit economies to be made in the monitoring of communities and;
4. increase the lead time between the detection of significant biological changes and community morbidity.

SUMMARY

The data presented show two trends, an increase in bilateral asymmetry with time and a consistent spatial pattern. Data for grunion and barred surfperch taken at one locality, Belmont Shore, near Los Angeles, over two decades clearly show increasing temporal asymmetry values. Data from barred sand bass and the other two species show increasing geographic trends from deep Baja California (an area virtually uninhabited) to southern California. Additionally, barred surfperch asymmetry values decrease north of Los Angeles, so that asymmetry is apparently not responding strictly to a latitudinal trend. Several hypotheses were examined, and it is tentatively concluded that environmental toxicant stress is the likeliest explanation.

We believe asymmetry analysis may be developed into a useful tool for examining the sublethal effects of multiple toxicants on natural or laboratory populations. Such analyses are relatively easy to perform and, thus, offer significant advantages over other commonly used assays.

ACKNOWLEDGMENTS

We would like to thank Allen Mearns, Irwin Haydock, Stuart Brody, Edward Fager, and John Isaacs for offering constructive comments throughout the duration of this research. Their suggestions were not always incorporated into our research effort, so they are blameless for any errors. We should also like to thank Ralph Miller, Jr., of H & M Landing in San Diego, for allowing D. W. Valentine to collect specimens from his ships while operating in Mexican waters. Without the support of H & M Landing and its personnel, it would have been impossible for us to obtain many of our Mexican samples.

Work contained herein was supported by grants from the Marine Life Research Group (Scripps Institution of Oceanography, No. 1273) and a contract from the Southern California

Coastal Water Research Project (No. 02304). The second author is supported by NSF grants GB 8525 and GB 27358.

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DISTRIBUTION OF SAND LANCE, *AMMODYTES* SP., LARVAE ON THE CONTINENTAL SHELF FROM CAPE COD TO CAPE HATTERAS FROM RV *DOLPHIN* SURVEYS IN 1966

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ABSTRACT

Postlarvae of one species of sand lance, which rasembled *Ammodytes marinus* exactly, were collected along the east coast of the United States between Martha's Vineyard, Mass., and Cape Hatteras, N.C. (lat 41° to 35°N), in January-February, April, May, and December 1966. They were more abundant in tows taken at night than in tows taken during the day. Recently hatched specimens (4-8 mm) were more abundant in shallow water. Diurnal migrations are probably related to feeding in all larger size groups.

The greatest abundance of sand lance larvae occurred in winter off the mouths of the principal estuaries (southern New England, Delaware and Chesapeake Bays). Dispersing rapidly offshore, they were taken all the way to the edge of the continental shelf. As they grew, abundance appeared to be directly related to that of plankton organisms, which in turn were somewhat affected by the presence of estuaries along the coast. By mid-May, larvae were not available to us in this region, probably moving to coastal beaches, up into the estuaries, or onto the bottom.

Sand lances, *Ammodytes* sp., are found in great abundance on offshore banks, along the coast, and in estuaries from Greenland to Virginia (Richards, Perlmutter, and McAneny, 1963; Scott, 1968). They are important as a food item for both commercial and sport fish, yet the biology of the sand lances of North America is not well known. Postlarval sand lances commonly occur along the southern New England coast from early December until April (Wheatland, 1956; Richards, 1959, 1965; Pearcy and Richards, 1962; Herman, 1963; Richards et al., 1963; Williams, Richards, and Farnworth, 1964). In New Jersey (Croker, 1965), Delaware Bay (de Sylva, Kalber, and Shuster, 1962), and in the region of Chesapeake Bay (Norcross, Massman, and Joseph, 1961), postlarvae occur from January through April.

In 1966, postlarvae were abundant in collections from four cruises (January-February, April, May, and December) made over 12 transects between the coast and the edge of the continental shelf from Martha's Vineyard to Cape Hatteras. These collections were made by personnel at the Sandy Hook Marine Laboratory, Highlands, N.J., as part of a program to determine the extent to which migratory fishes are associated with estuaries during their early life histories.

METHODS AND MATERIALS

Details of the design of the RV *Dolphin* surveys, collecting methods, station positions, and physical data are included in Clark et al. (1969). From December 1965 through December 1966, a series of 92 stations on 14 transects, from Martha's Vineyard to Cape Lookout, N.C., were sampled every 6 weeks with two Gulf V plankton nets towed simultaneously for 30 min (Figure 1, Table 1). Where water depth permitted, oblique tows were made at two levels:

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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

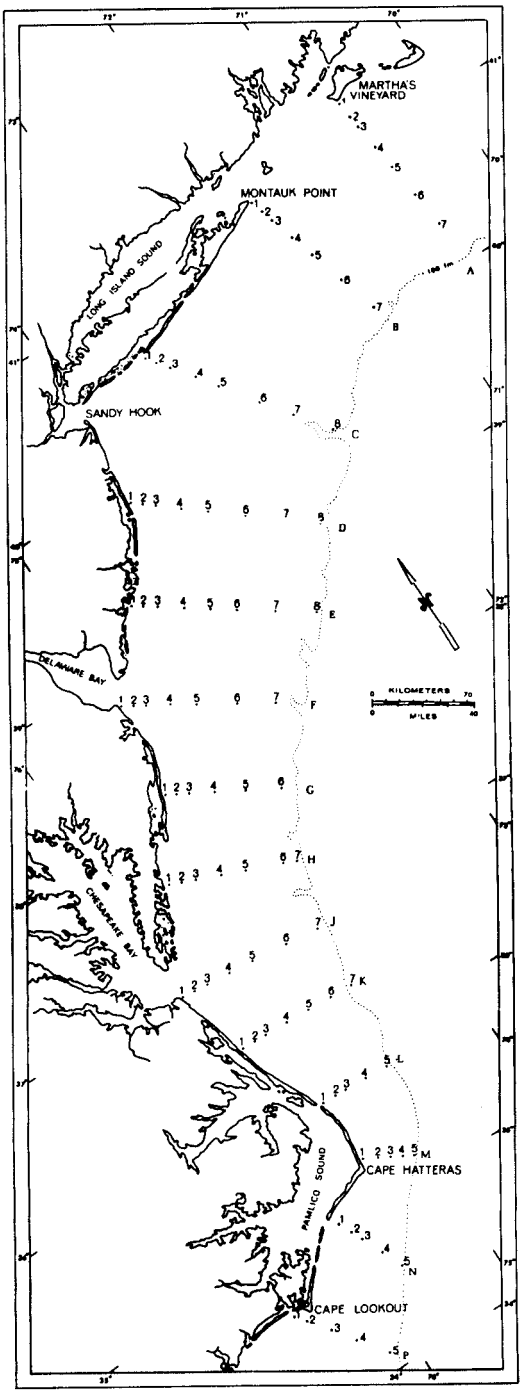

FIGURE 1.—RV *Dolphin* survey, 1965-66. Locations of transects and collecting stations.

TABLE 1.—RV *Dolphin* survey, 1965-66. Transect locations.

Transect	State	Locality
A	Massachusetts	Martha's Vineyard
B	New York	Eastern Long Island
C		Western Long Island
D	New Jersey	Barnegat Inlet
E		Great Egg Inlet
F	Delaware	Cape Henlopen
G	Maryland	Assateague Island
H	Virginia	Eastern Shore
J		Cape Henry
K	North Carolina	Currituck Beach
L		Oregon Inlet
M		Cape Hatteras
N		Ocracoke Inlet
P		Beaufort Inlet

shallow (0 to 15 m) and deep (18 to 33 m). Collections were made during a 24-hr workday on all cruises, so the number of tows by night and by day varied on each transect from cruise to cruise. Cruises were designed to give information on the time and place of occurrence of many species of fish larvae over an extensive geographic area, and sampling was inadequate to estimate mortality or recruitment. For purposes of comparison, numbers of larvae are expressed as the number taken per tow. Zero catches were not included in these computations but are indicated in appropriate figures. A midwater trawl of 6.4-mm cod end mesh used for collecting juvenile fishes did not catch sand lances. This net was not used extensively during the first four cruises in areas where sand lance juveniles would have been expected. Plankton samples were preserved in 5% Formalin,[3] and all fish eggs and larvae were sorted under a microscope. Sand lances were identified, counted, and measured (total length) with an ocular micrometer. No demersal eggs or sand lance larvae with large yolk sacs were collected.

To determine the number of *Ammodytes* species represented in these collections, we checked pigmentation carefully on all specimens. Meristic characters counted were dorsal and anal fin rays and vertebrae. Skeletons of specimens, within the length range of 34 to 60 mm, were prepared by the enzyme presoak method of Ossian (1970). Following 7 to 14

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

days of soaking in "Biz," the vertebrae of a few specimens could be counted.

RESULTS

Appearance and Meristic Character Counts

According to pigmentation and general appearance, all sand lance larvae in these collections are similar to those described by Richards (1965) and listed as *Ammodytes marinus* by Macer (1967). In this group, Macer included *A. hexapterus* and *A. dubius* of the eastern coast of North America which Richards et al. (1963) previously separated.

The number of larvae examined varied among three cruises; some larvae could not be used because of net damage, and others were too small to have developed fin rays or the total complement of vertebrae. The mean, range, and standard deviation of the meristic counts are listed in Table 2 for specimens from each cruise regardless of locality. Although a slight increase in meristic counts was noticeable as the season progressed, it was not significant.

TABLE 2.—Meristic character counts of larval sand lances from three cruises of the RV *Dolphin*, 1966.

Cruises	Anal fin rays	Dorsal fin rays	Vertebrae
January-February:			
Mean	28.38	57.75	—
Standard deviation	1.10	1.73	—
Range	27-30	56-60	—
Number	16	4	0
April:			
Mean	28.95	59.21	67.43
Standard deviation	1.13	1.76	1.83
Range	27-32	55-63	65-71
Number	86	52	30
May:			
Mean	29.47	58.27	69.40
Standard deviation	1.13	1.00	0.87
Range	27-30	55-60	68-70
Number	19	11	5

There was no evidence from pigment patterns, meristic counts, or seasonal abundance of these larvae that we had more than one species of sand lance between December and May south of Cape Cod, Mass. As Reay (1970) pointed out, the specific definitions of *Ammodytes* in the northwest Atlantic are tenuous, so it is presumptuous to be definite in naming species. Variations in appearance and meristic character counts of these postlarvae appeared to be primarily due to the stage of development. Rate of development fluctuates during the different months because of changes in the physical characteristics of the water at the time of hatching and early growth. As shown previously by Richards (1965), individuals in colder water take longer to develop dorsal and anal fin rays and a full set of vertebrae. Specimens collected in spring were more fully developed than those of an equal length taken in winter.

Numbers of Postlarvae in Night and Day Collections

The time of day during which a particular station was occupied varied between cruises; therefore, the diel time factor must be considered before discussing geographical and seasonal distribution of the sand lance larvae.

The greater catch rate of night tows compared to day tows is apparent from Table 3, in which all night collections are separated from all day collections (including dawn and dusk) regardless of location. In general, there was a higher percentage of positive tows at night than during the day. Roughly 34% of the night tows contained larvae, while only 23% of the day tows were positive. When all tows are considered, larvae were more consistently taken at night throughout all the cruises. The mean number of larvae at night dropped from 16/tow in winter to 5.1 and 5.6/tow in April and May, respectively. During the following spawning season, in December, the mean number of larvae per tow at night was just less than 1. A daylight mean of 5.3 larvae/tow in winter dropped to 1.9/tow in April and 0.1/tow in May. None were taken during the day on the cruise of the following December. Thus, a seasonal change in availability was evident in both day and night tows and was due primarily to dispersion, net avoidance, and mortality. Further analysis of the diurnal distribution of the larvae is not warranted by these

TABLE 3.—The number of sand lance larvae taken at night and during the day from four 1966 RV *Dolphin* cruises.

Item	Night					Day[1]				
	Total	Jan.-Feb.	Apr.	May	Dec.	Total	Jan.-Feb.	Apr.	May	Dec.
Tows										
Total	289	77	71	61	80	250	49	70	83	48
Successful	98	43	40	12	3	57	24	27	6	0
Larvae caught	1,684	1,235	362	34	53	402	258	136	8	0
Larvae per tow (all)	5.8	16.0	5.1	5.6	0.7	1.6	5.3	1.9	0.1	0
Ratio night to day (all tows included)	3.6	3.0	2.7	56.0						

[1] Includes tows taken at dawn and dusk.

data. More precise sampling is necessary before conclusions can be drawn concerning diurnal distribution at different depths.

Geographic Distribution

In general, sand lance larvae were most abundant off southern New England and the region off Delaware Bay (Figure 2). They were less common along the northern New Jersey shore and along the Maryland coast to Chesapeake Bay. South of Chesapeake Bay, they decreased steadily in numbers and were not in samples south of Cape Hatteras. Larval distributions for each cruise are shown in Figures 3, 4, 5, and 6 for shallow and deep tows. Physical data for each cruise are related to larval distribution here.

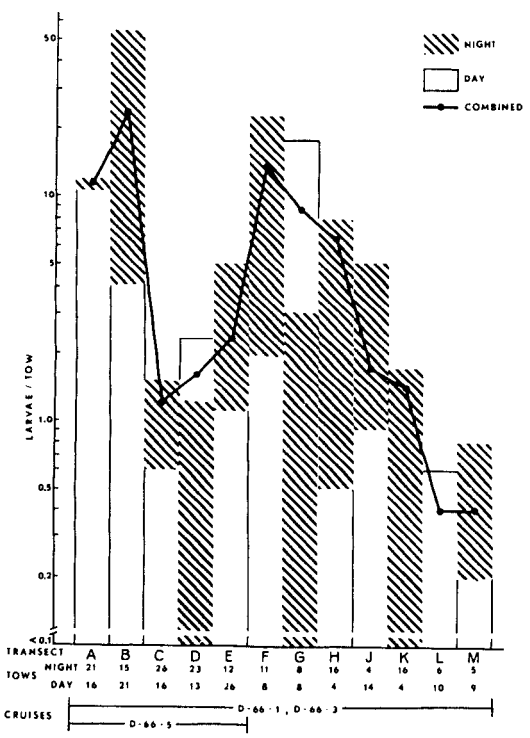

FIGURE 2.—Numbers of sand lance larvae per tow taken in day and night tows by transect.

During the cruise in early December 1965, no larvae occurred in any of the collections. However, during the first week of December 1966, larvae were abundant inshore near Martha's Vineyard and eastern Long Island, N.Y. (Figure 3). They were not found elsewhere in samples from 2 weeks earlier. The catches of larvae in December occurred in water from 8° to 10°C, similar to nearshore temperatures from New Jersey north and offshore of southern New England. Salinity in the area of larval occurrence was 32 to 33‰ over much of the sampling region. Plankton was sparse in the area of capture (<55 to 100 ml/tow).

During the cruise in January-February, larvae occurred in patches throughout the entire area (Figure 4). In shallow tows, none were taken within 15 miles of Long Island (a situation which has occurred before—Richards et al., 1963), off Great Egg Inlet, N.J., at the mouth of Chesapeake Bay, nor off the Oregon Inlet, N.C. Larvae were most abundant 40 miles off Montauk Point, N.Y., eastward to Martha's Vineyard. A second area of abundance occurred within 15 miles of the Maryland coast in the water mass moving southward out of Delaware Bay and extended north 40 miles off the New

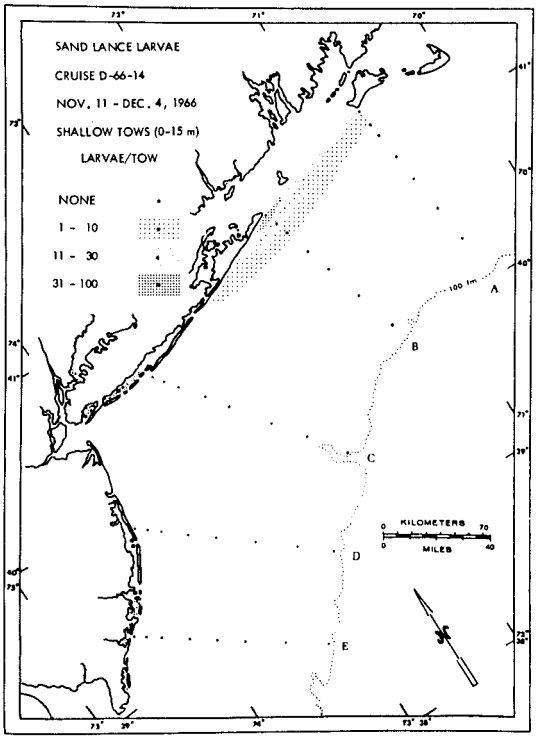

FIGURE 3.—Distribution and abundance of sand lance larvae in the December cruise in shallow tows.

Jersey coast in the latitude of Barnegat Inlet, N.J. Off the mouth of Chesapeake Bay, the greatest numbers occurred during the winter. Norcross et al. (1961) reported a similar seasonal peak in capture rate off Chesapeake Bay during 1960. Data from the deep tows were similar, with the greatest abundance off Montauk Point extending southward offshore. Another group occurred off Delaware Bay, extending in a band to North Carolina (Figure 4). Temperatures in the areas of capture in winter varied from 0° to 6°C and salinities varied from 31 to 33‰. Plankton volumes were less than 100 ml/tow from deep offshore water, but approached 200 ml/tow near the mouths of some estuaries.

During April, sand lances were more widely dispersed and occurred closer to shore from Martha's Vineyard to Assateague Island, Md., than in winter (Figure 5). Similar numbers were taken south to Cape Henry, Va., but further offshore. None occurred farther south, except from a small patch near the surface off Cape Hatteras. As before, larvae were most abundant throughout the water column off the southern New England coast. Only offshore of Maryland were larvae in comparable numbers. Within these same areas, the plankton volumes had increased since winter, providing a good source of food for larvae longer than 5 mm (Covill, 1959). Temperatures had warmed slightly from winter, but most larvae were still taken in water of less than 7°C. The few near Chesapeake Bay and Cape Hatteras were taken in warmer water up to 13°C. Bottom temperature was about 1°C lower than at the surface. Larvae were distributed throughout the salinity range of 31 to 33‰ found in most of the sampled area but were absent in the less saline water off Delaware and Chesapeake Bays. Plankton volumes were similar to those offshore in winter, but those between 10 and 40 miles offshore along Long Island and southern New England showed a slight increase.

By May, larvae occurred only in the northern half of the sampled region, and none were found south of Delaware Bay (Figure 6). In shallow tows, larvae were distributed in two groups—one group within 15 miles of the coast and the other group 5 to 40 miles offshore. Larvae occurred in deep tows only in two areas—inshore off Martha's Vineyard and offshore off western Long Island. Surface temperatures were all above 7°C, and the 10°C isotherm was nearshore off New Jersey and offshore of Maryland. Bottom temperatures were about 3°C cooler than those at the surface. Thus, larvae occurred in waters between 6° and 10°C. Apparently, temperatures south of New Jersey, where larvae were taken earlier in the year, were too warm in May.

Most of the inshore tows from Massachusetts to Delaware were taken at night, which might account for the apparent inshore abundance but not the discontinuous distribution, since intervening stations with no larvae were also sampled at night. Water mass characteristics and plankton distribution may have been important factors in separating these groups. Larval distribution is difficult to relate to salinity distribution. In the past,

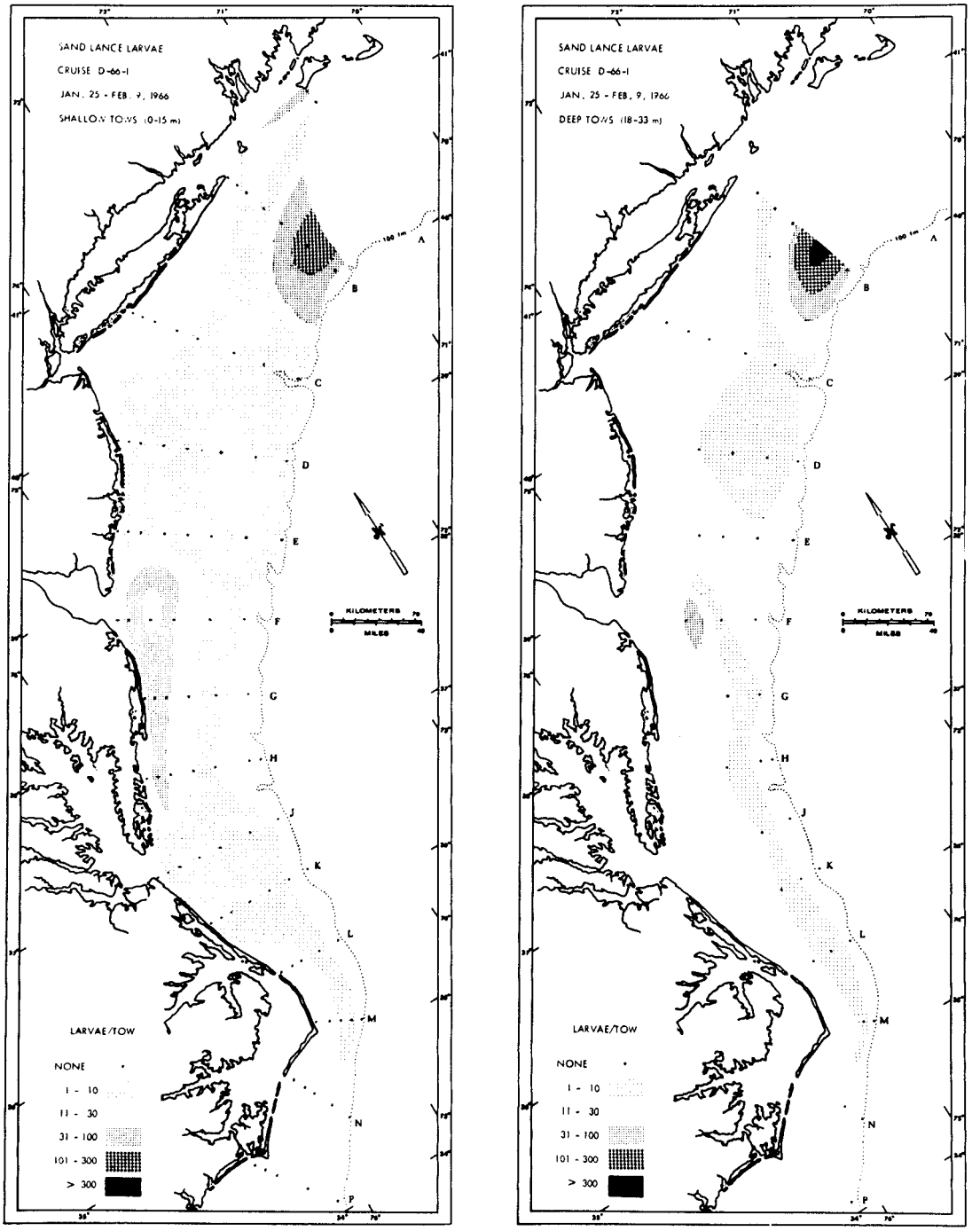

FIGURE 4.—Distribution and abundance of sand lance larvae in the January-February cruise in shallow (left) and deep (right) tows.

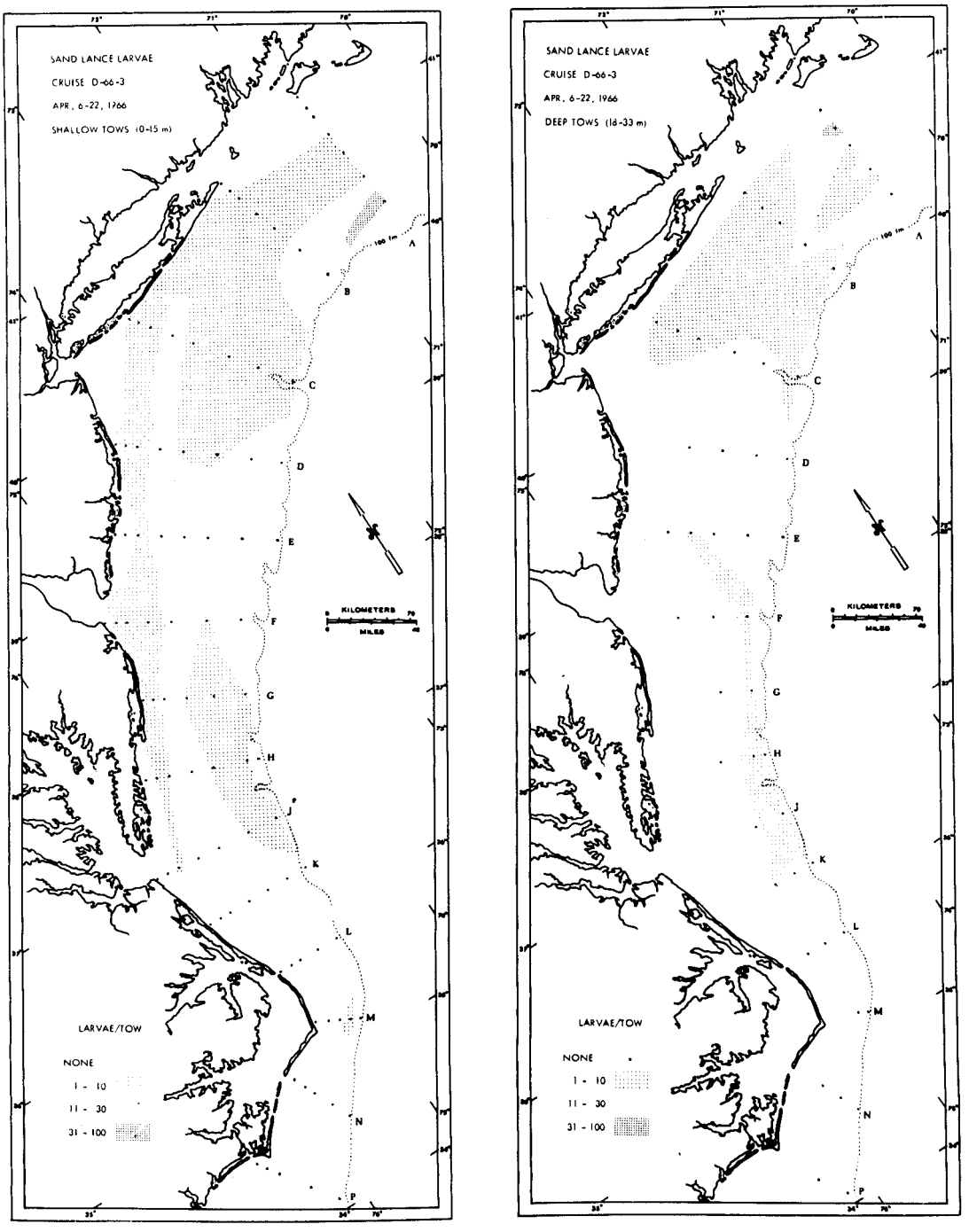

FIGURE 5.—Distribution and abundance of sand lance larvae in the April cruise in shallow (left) and deep (right) tows.

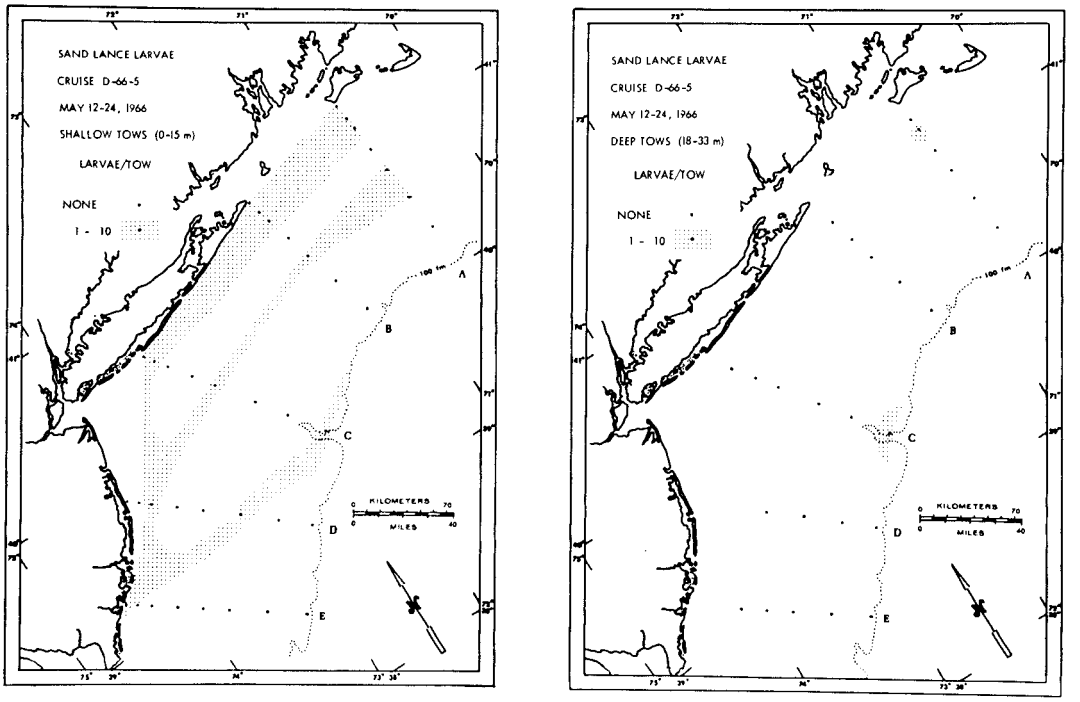

FIGURE 6.—Distribution and abundance of sand lance larvae in the May cruise in shallow (left) and deep (right) tows.

Norcross et al. (1961) found no sand lance larvae off Chesapeake Bay in salinities lower than 30‰, yet Wheatland (1956) found them in Long Island Sound in salinities as low as 24.2‰. Croker (1965) found them in Sandy Hook Bay below 28.6‰, and studies from Delaware Bay indicated larvae occurred in water of 4.3‰ to less than 1.8‰ salinity (Norcross et al., 1961). Plankton distribution was similar to that of the larvae; inshore and offshore volumes of 100 to 200 ml/tow were separated by a low volume strip of 55 to 100 ml/tow. Thus, food was available for both inshore and offshore groups off Long Island and New Jersey. Although plankton abundance was as great off Chesapeake Bay, we found no sand lances in this area.

Distribution and Movements of Larvae of Different Sizes

Figure 7 shows the length frequencies of sand lance larvae for each cruise, and Figures 8, 9, and 10 depict the distributions of five size groups (between 4 and 60 mm). Table 4 gives the depth distribution of these size groups by night and by day. Larvae were seldom taken in deep water tows only, but in many instances they occurred only in tows above 15 m. All larvae collected in December were 4 to 8 mm long.

The total length range generally increased during the spring (Figure 7), and as larvae grew they dispersed away from the coast and decreased in apparent abundance (Figures 8 to 10; Table 4). The greatest number of those of small size occurred inshore at the northern end of the range of these cruises in late fall off Martha's Vineyard and eastern Long Island. Some also appeared in early winter near Delaware Bay. However, lack of many early winter collections, selectivity of the 0.5-mm mesh of the Gulf V sampler, and the hatch from demersal rather than pelagic eggs lowered the chance of sampling the smallest size group in proportion to their abundance. The greatest

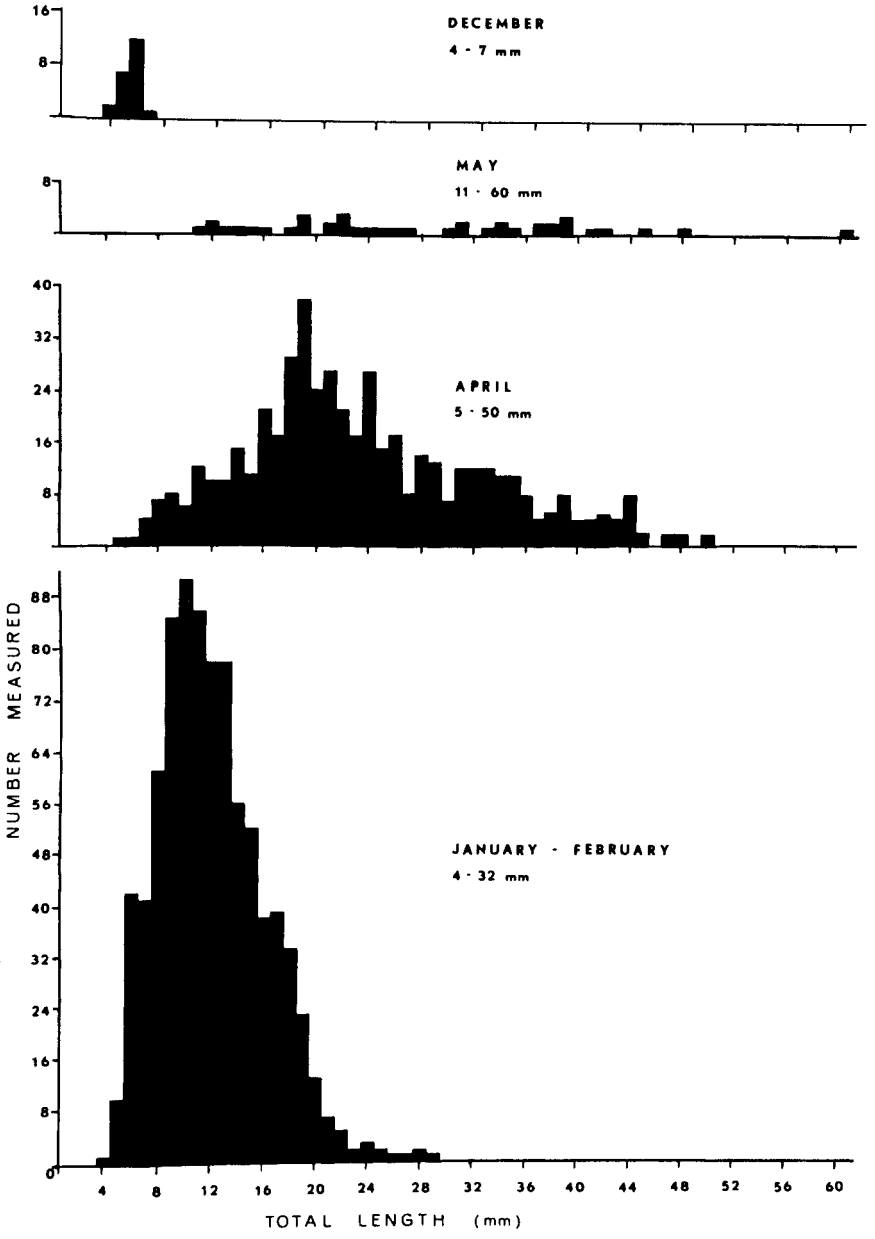

FIGURE 7.—Length frequencies of sand lance larvae from four RV *Dolphin* cruises from January to May and December 1966.

TABLE 4.—Total number of sand lance larvae per positive tow, and the numbers of larvae per tow within five size groups, in shallow and deep tows during the night and during the day, from four 1966 RV *Dolphin* cruises.

	Night							Day					
	Shallow				Deep			Shallow			Deep		
Item	Jan.-Feb.	Apr.	May	Dec.[1]	Jan.-Feb.	Apr.	May	Jan.-Feb.	Apr.	May	Jan.-Feb.	Apr.	May
Number of positive tows	32	27	11	3	11	13	1	18	20	5	6	7	1
Number of larvae:													
Total	697	258	33	53	538	104	1	232	110	7	26	26	1
Per positive tow	21.8	9.6	3.3	17.7	48.9	8.0	1.0	12.9	5.5	1.4	4.3	3.7	1.0
Measured	461	250	33	22	228	103	1	224	109	7	26	26	1
Per tow by size groups:													
4- 7 mm	2.5	—	—	17.7	1.1	0.2	—	3.5	0.2	—	0.2	—	—
8-16	16.4	1.3	0.6	—	40.3	1.6	—	7.2	1.7	—	3.2	1.3	—
17-30	2.9	5.0	1.2	—	7.5	5.3	1.0	2.2	3.0	0.4	1.0	2.1	—
31-50	—	3.2	1.0	—	—	1.0	—	—	0.7	1.0	—	0.3	1.0
>50	—	—	0.2	—	—	—	—	—	—	—	—	—	—

[1] Only category with catches in December.

number of specimens of large size, i.e., above 30 mm, occurred from New Jersey south.

The greatest number of recently hatched larvae—those from 4 to 8 mm—were taken inshore in late fall and early winter off southern New England and in early winter along the Maryland and Virginia coasts (Figure 8). Additional small specimens taken in April off Montauk Point indicate a long spawning season (Figure 9). In winter, they were caught mostly during the day and in shallow water, yet some occurred offshore in deep water south of Montauk Point in winter and off Barnegat Inlet in spring. The absence of this group in May (Figure 10) suggests spawning probably ceased by late March or early April, as previously noted by Norcross et al. (1961) and Wheatland (1956). Distribution of this size group did not seem to be correlated with the distribution of zooplankton organisms. Larvae of this size are still dependent on phytoplankton for food (Covill, 1959).

The size group containing specimens from 8 to 17 mm was most abundant in winter (Figures 7 and 8) and well dispersed along the coast between Montauk Point and south of Chesapeake Bay. By April, larvae in this size group occurred primarily from Martha's Vineyard to Barnegat Inlet. They were still available in that region in May. Larvae of 8 to 17 mm were most abundant at night in deep tows. During the day, they occurred primarily in surface collections, probably because they were feeding there (Table 4). Their horizontal distribution coincided somewhat with that of greatest plankton volumes along the coast during the winter and April cruises. Covill (1959) indicated that sand lances are primarily zooplankton feeders by about 9 mm.

Larvae longer than 17 mm were much less common in midwinter than those of the smaller size groups (Figures 7 and 8). They were primarily offshore off the New Jersey-Delaware Bay area and Chesapeake Bay south to Cape Hatteras, indicating that spawning had begun as early as late November or early December, as previously indicated by Norcross et al. (1961) and Williams et al. (1964). By April, those between 17 and 31 mm were the most abundant group of larvae, being found well offshore off southern New England and inshore off Delaware Bay (Figure 9). None were taken nearshore off Chesapeake Bay; the larvae there were all much larger. In May, a few specimens were taken 10 to 15 miles off southern New England and Long Island (Figure 10).

During winter, there were no specimens larger than 31 mm (Figures 7 and 8). In April, large specimens were common. Off Long Island and New Jersey, they occurred in small

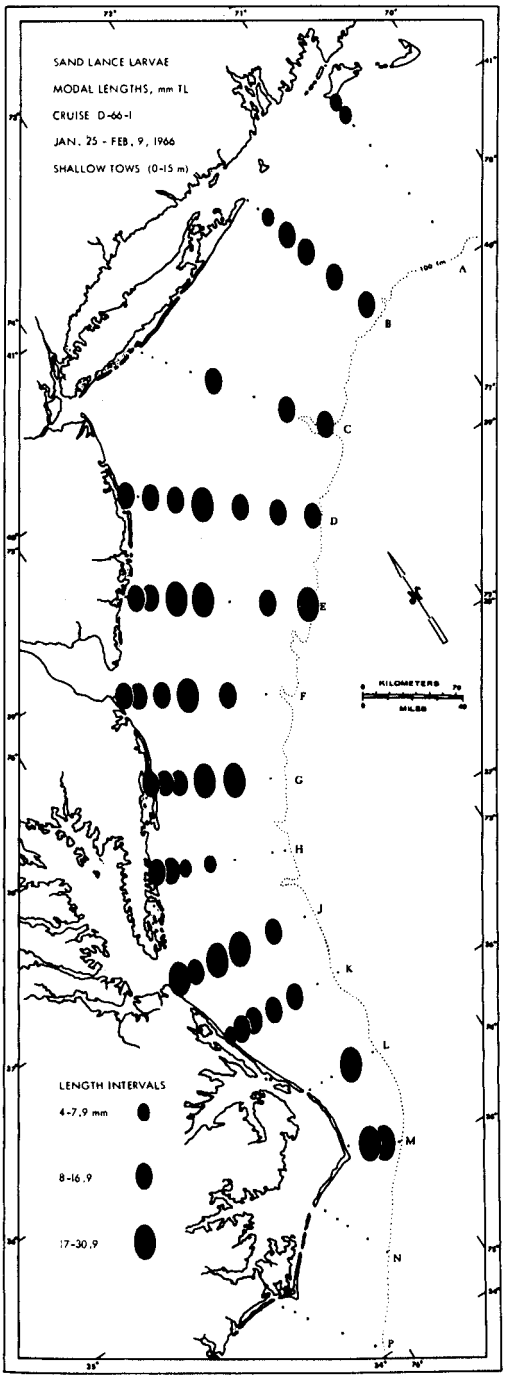

FIGURE 8.—Distribution of sand lance larvae in three length groups from the January-February cruise.

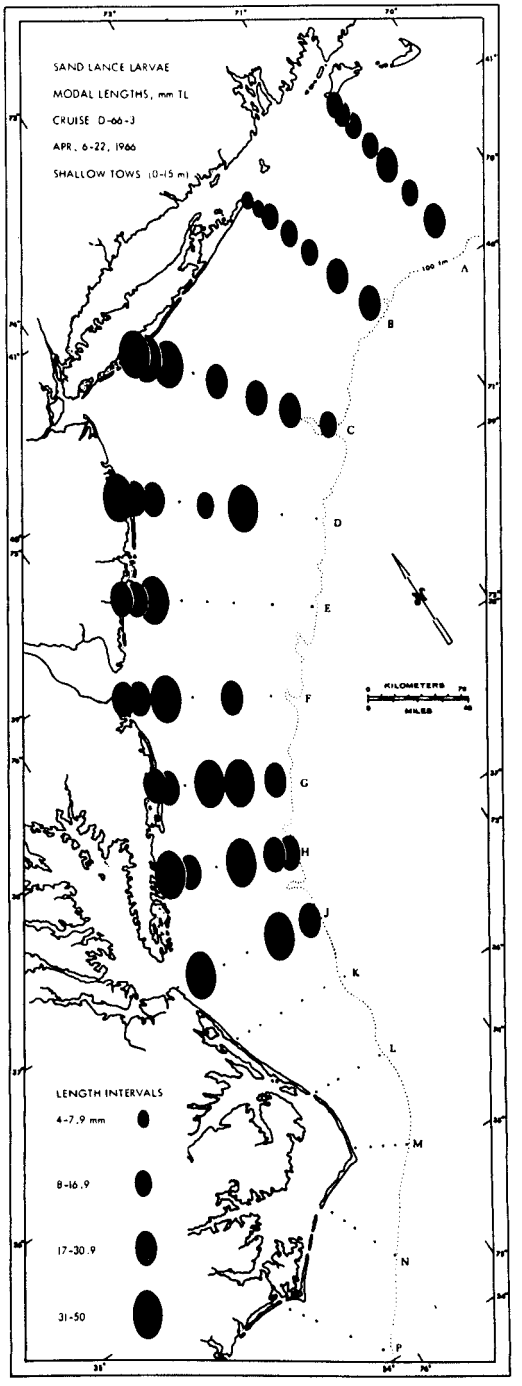

FIGURE 9.—Distribution of sand lance larvae in four length groups from the April cruise.

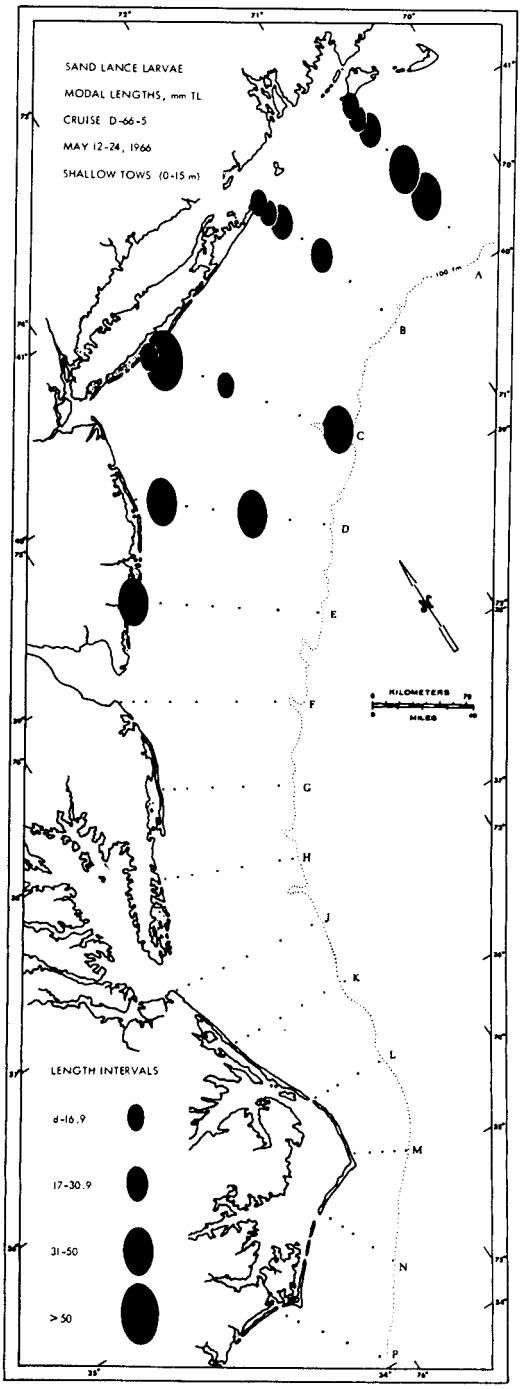

FIGURE 10.—Distribution of sand lance larvae in four length groups from the May cruise.

patches inshore; further south (Figure 9), they extended 20 to 40 miles offshore. During May, specimens larger than 31 mm made up half of those collected (Figure 10). Off southern New England and New York, they were offshore, while along the New Jersey coast they were found close to shore. Their distribution, particularly off Long Island, correlated with that of greatest plankton volumes (Clark et al., 1969). Few larvae larger than 30 mm were collected in deepwater tows either at night or in the daytime. In shallow tows in April and May, the lesser abundance of large larvae by day than at night probably resulted from net avoidance (Table 4).

CONCLUSIONS

Sand lances between lat 35° and 41°N had a long spawning season—from late November to late March. Because larvae became dispersed throughout a large area over a protracted period, the precise location and depth of major spawning areas along the coastal zone were difficult to determine. Nevertheless, it appeared that spawning location was greatly influenced by coastal topography in this region. The greatest numbers of recently hatched individuals occurred in late fall and early winter inshore off southern New England, and Delaware and Chesapeake Bays. In former years within these estuarine regions, spawning occurred in Long Island Sound (Wheatland, 1956; Richards, 1959), Narragansett Bay (Herman, 1963), and Delaware Bay (de Sylva et al., 1962), but apparently neither in Block Island Sound (Merriman and Sclar, 1952) nor inside Chesapeake Bay (Norcross et al., 1961). Judging by our collection of recently hatched individuals in some offshore areas, spawning must occur both offshore and inshore.

Evidence indicated that complicated movements occurred during development of larval sand lances. Hatched from demersal eggs (Williams et al., 1964), eventually larvae were dispersed throughout the water column, where they drifted generally offshore and slightly south. Within this general drift, they tended to move toward the surface during the day for feeding purposes and back into deeper water at night. Their availability to the Gulf V sampler

apparently decreased after they reached 25 mm. During May, larvae and juveniles disappeared from the water column. General migration back to the coast or to the bottom on offshore banks was indicated.

The long spawning season, causing hatching to take place from late November through mid-April, was evidenced by the patchy distribution of small specimens and the multimodal character of length frequencies. Interspersion of groups prevented accurate analysis of growth during the hatching season.

All larvae, regardless of hatching date, had similar melanophore patterns and meristic counts, and resembled postlarval *Ammodytes* previously found from Greenland to Virginia and postlarval *A. marinus* from northern European waters. Differences in meristic character counts probably resulted from temperature effects on development time required to attain adult characteristics.

Data described in this paper show two overlapping areas of larval abundance, indicating that the southern New England sand lances may be separate from those found off Delaware Bay. In addition, earlier evidence suggests that inshore and offshore groups exist (Richards et al., 1963; Scott, 1968). Unfortunately, data from these cruises are not sufficient to determine the definite existence of separate inshore and offshore populations south of Cape Cod. However, it appears that the distribution of all sand lances may be related to estuaries.

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APPENDIX TABLE - R.V. DOLPHIN 1965-66 ICHTHYOPLANKTON SURVEY. DATA ASSOCIATED WITH GULF V CATCHES OF SAND LANCE LARVAE.

CRUISE STAT. C66 1	TOW DEPTH (M)	********* LARVAE ********** NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE	DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (C) *** RANGE	MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE	MEAN
A 1	0- 6	50	50	8.9	5.5 20.8	26 1	1627	DUSK	16	1.1	1.1	1.1	1.1	1.1	NONE	-	32.3 32.3 32.3
A 2	0-15	27	27	10.6	6.3 23.2	26 1	1729	NIGHT	33	0.8	0.9	0.9	0.8	0.9	NONE	-	32.4 32.4 32.4
B 3	0-15	21	21	9.2	5.8 14.5	26 1	0429	NIGHT	48	3.2	3.2	3.2	3.2	3.2	NONE	-	32.3 32.3 32.3
B 4	0-15	1	1	11.8	11.8 11.8	26 1	0254	NIGHT	60	4.1	4.1	4.1	4.1	4.1	NONE	-	32.3 32.3 32.3
B 4	18-33	13	13	10.3	5.5 14.6	26 1	0254	NIGHT	60	4.1	4.1	4.1	4.1	4.1	NONE	-	31.9 32.3 32.2
B 5	0-15	37	36	11.5	7.3 16.3	26 1	0115	NIGHT	73	4.8	4.8	4.8	4.8	4.8	NONE	-	32.3 32.5 32.4
B 5	18-33	25	23	11.5	6.9 15.2	26 1	0115	NIGHT	73	4.8	4.8	4.8	4.8	4.8	NONE	-	32.3 32.4 32.4
B 6	0-15	237	57	10.4	6.5 17.5	25 1	2347	NIGHT	80	4.9	4.9	4.9	4.9	4.9	NONE	-	32.3 32.3 32.3
B 6	18-33	344	73	11.0	7.0 20.6	25 1	2347	NIGHT	80	4.9	4.9	4.9	4.9	4.9	NONE	-	32.3 32.4 32.3
B 7	0-15	68	51	12.1	9.6 16.4	25 1	2144	NIGHT	89	4.8	4.8	4.8	4.8	4.8	NONE	-	32.3 32.4 32.4
B 7	18-33	52	52	11.1	8.5 14.6	25 1	2144	NIGHT	89	4.8	4.8	4.8	4.8	4.8	NONE	-	32.4 32.5 32.4
C 5	0-15	2	2	13.5	13.0 14.0	3 2	2208	NIGHT	48	3.8	3.8	3.8	3.8	3.8	NONE	-	32.4 32.6 32.5
C 7	0-15	4	4	14.4	12.3 17.4	4 2	0220	NIGHT	67	4.7	5.0	4.8	4.7	7.1	WEAK	47-56	32.6 32.7 32.6
C 7	18-33	6	6	12.5	10.0 17.0	4 2	0220	NIGHT	67	5.0	5.0	5.0	4.7	7.1	WEAK	47-56	32.6 32.8 32.7
C 8	0-15	4	4	13.8	12.9 15.3	4 2	0408	NIGHT	110	5.8	5.8	5.8	5.8	7.8	WEAK	83-88	33.1 33.3 33.2
D 1	0- 6	4	3	13.2	11.0 15.6	4 2	1729	NIGHT	16	0.8	0.9	0.9	0.8	0.9	NONE	-	31.8 31.9 31.9
D 3	0-15	1	1	13.0	13.0 13.0	4 2	1910	NIGHT	25	1.9	1.9	1.9	1.9	1.9	NONE	-	32.7 32.8 32.7
D 4	0-15	1	1	12.2	12.2 12.2	4 2	2028	NIGHT	27	2.4	2.4	2.4	2.4	2.4	NONE	-	32.8 33.0 32.9
D 5	0-15	1	1	21.2	21.2 21.2	4 2	2220	NIGHT	37	2.9	2.9	2.9	2.9	2.9	NONE	-	32.9 33.1 32.9
D 5	18-24	1	0	20.0	20.0 20.0	4 2	2220	NIGHT	37	2.9	2.9	2.9	2.9	2.9	NONE	-	33.3 33.5 33.5
D 6	0-15	19	19	14.4	12.0 17.8	4 2	1210	DAY	50	3.2	3.2	3.2	3.2	3.1	NONE	-	32.6 32.7 32.6
D 6	18-33	2	2	14.6	13.0 16.3	4 2	1210	DAY	50	3.1	3.1	3.1	3.2	3.1	NONE	-	32.7 33.1 32.9
D 7	0-15	2	2	13.1	12.2 14.0	4 2	1016	DAY	70	4.8	4.8	4.8	4.8	7.1	WEAK	47-55	32.9 33.3 33.0
D 7	18-33	5	5	14.5	13.4 17.4	4 2	1016	DAY	70	4.8	4.9	4.8	4.8	7.1	WEAK	47-55	33.1 33.3 33.1
D 8	0-15	2	2	16.6	15.5 17.8	4 2	0827	DAY	110	4.8	5.0	4.9	4.8	7.2	WEAK	91-99	33.0 33.2 33.1
E 2	0- 6	2	2	15.3	13.4 17.2	5 2	0415	NIGHT	17	-1.4	-1.3	-1.3	-1.4	-1.2	NONE	-	31.6 31.7 31.7
E 3	0- 6	9	9	14.5	7.3 17.5	5 2	0508	NIGHT	20	-0.5	-0.5	-0.5	-0.5	-0.5	NONE	-	31.0 33.2 32.3
E 4	0-15	1	1	18.0	18.0 18.0	5 2	0635	DAWN	30	1.3	1.3	1.3	1.3	1.3	NONE	-	32.5 33.3 32.9
E 5	0-15	1	1	24.0	24.0 24.0	5 2	0804	DAY	37	2.9	2.9	2.9	2.9	2.9	NONE	-	32.6 33.3 32.8
E 7	0-15	22	22	13.5	5.9 22.0	5 2	1126	DAY	66	4.8	4.9	4.8	4.8	6.4	NONE	-	33.6 34.0 33.9
E 9	0-15	1	1	17.1	17.1 17.1	5 2	1326	DAY	121	5.6	5.6	5.6	5.6	5.6	NONE	-	33.6 33.6 33.6
F 2	0- 6	7	7	13.7	10.8 16.4	6 2	0520	NIGHT	22	-1.6	-1.6	-1.6	-1.6	-1.3	NONE	-	30.7 31.8 31.2
F 3	0-15	90	59	13.5	10.3 20.5	6 2	0359	NIGHT	24	-1.4	-0.6	-1.2	-1.4	0.5	NONE	-	31.1 32.4 31.6
F 4	0-15	25	24	14.9	10.3 20.4	6 2	0242	NIGHT	26	0.7	0.9	0.8	0.8	0.8	NONE	-	32.6 33.2 32.7
F 5	0-15	32	30	16.4	12.5 19.6	6 2	0108	NIGHT	34	1.5	1.8	1.7	1.6	1.5	NONE	-	32.6 33.2 33.0
F 5	18-24	84	47	16.9	12.6 21.8	6 2	0108	NIGHT	34	1.5	1.5	1.5	1.6	1.5	NONE	-	33.2 33.4 33.3
F 6	0-15	3	3	14.9	12.5 16.4	5 2	2246	NIGHT	52	5.1	5.1	5.1	5.1	5.1	NONE	-	33.3 34.3 33.7
F 6	18-33	1	1	17.2	17.2 17.2	5 2	2246	NIGHT	52	5.1	5.1	5.1	5.1	5.1	NONE	-	33.8 34.1 34.0
G 1	0- 6	28	28	9.6	4.9 21.4	6 2	0946	DAY	13	-0.1	-0.1	-0.1	-0.1	-0.1	NONE	-	32.5 32.5 32.5
G 2	0- 6	60	50	11.9	6.9 22.7	6 2	1046	DAY	16	0.8	0.8	0.8	0.8	0.8	NONE	-	33.3 33.3 33.3
G 3	0-15	33	33	12.9	5.4 19.1	6 2	1147	DAY	21	1.1	1.2	1.2	1.1	1.1	NONE	-	33.3 33.5 33.4
G 4	0-15	14	13	15.7	12.2 18.9	6 2	0103	NIGHT	27	2.6	2.7	2.6	2.6	2.8	NONE	-	32.7 33.3 33.0
G 5	0-15	1	1	17.9	17.9 17.9	6 2	1428	DAY	52	3.6	3.7	3.6	3.6	4.3	NONE	-	33.0 33.2 33.1
G 5	18-33	12	12	11.8	9.6 18.0	6 2	1428	DAY	52	3.9	4.1	4.0	3.6	4.3	NONE	-	33.4 33.9 33.7
G 6	18-33	1	1	16.9	16.9 16.9	6 2	1611	DAY	86	5.3	5.5	5.4	5.5	5.3	NONE	-	34.2 34.5 34.3
H 1	0- 3	15	15	10.9	5.6 18.6	7 2	0253	NIGHT	11	-0.2	1.4	-0.2	-0.2	0.2	NONE	-	31.5 31.7 31.6
H 2	0- 6	47	45	10.1	6.0 17.7	7 2	0200	NIGHT	16	0.5	0.7	0.6	0.5	0.7	NONE	-	31.6 32.0 31.8
H 3	0- 6	13	13	14.3	6.8 22.2	7 2	0059	NIGHT	22	1.5	1.6	1.6	1.5	1.6	NONE	-	32.2 32.4 32.3
H 4	0-15	11	11	14.7	5.0 25.5	6 2	2332	NIGHT	27	2.8	2.8	2.8	2.8	2.8	NONE	-	32.7 33.0 32.9
H 5	18-24	3	3	16.9	15.5 18.6	6 2	2206	NIGHT	35	4.7	4.7	4.7	4.5	4.7	NONE	-	33.5 33.5 33.5
J 2	0- 6	1	1	20.2	20.2 20.2	7 2	0812	DAY	12	0.6	0.6	0.6	0.6	0.6	NONE	-	30.0 30.4 30.2
J 3	0- 6	3	3	11.1	7.8 13.6	7 2	0906	DAY	12	1.1	1.2	1.2	1.1	1.2	NONE	-	31.5 31.7 31.6
J 4	0-15	1	1	19.0	19.0 19.0	7 2	1030	DAY	20	2.4	2.6	2.4	2.6	2.4	NONE	-	32.3 32.7 32.6
J 5	0-15	2	2	21.9	20.8 23.1	7 2	1143	DAY	26	3.5	3.6	3.5	3.6	3.5	NONE	-	32.9 33.0 33.0
J 6	0-15	3	3	17.2	14.1 19.0	7 2	1321	DAY	35	5.1	5.4	5.1	5.4	5.3	NONE	-	33.4 33.6 33.5
J 6	18-24	2	2	12.1	5.8 18.4	7 2	1321	DAY	35	5.1	5.3	5.2	5.4	5.3	NONE	-	33.6 33.7 33.6
K 1	0- 6	1	1	6.6	6.6 6.6	8 2	0138	NIGHT	15	1.5	1.6	1.5	1.6	1.5	NONE	-	30.9 31.2 31.1
K 2	0-15	4	4	15.0	11.6 17.8	8 2	0038	NIGHT	25	1.5	1.9	1.6	1.8	2.1	NONE	-	31.2 32.1 31.6
K 3	0-15	3	3	19.7	16.7 24.0	7 2	2332	NIGHT	22	3.4	3.8	3.5	3.8	3.4	NONE	-	32.6 32.6 32.6
K 4	0-15	4	4	22.0	14.0 27.8	7 2	2220	NIGHT	31	4.1	4.1	4.1	4.1	4.1	NONE	-	32.6 32.8 32.7
K 5	0-15	6	6	19.7	16.8 21.9	7 2	2101	NIGHT	34	5.1	5.1	5.1	5.1	5.2	NONE	-	33.3 33.3 33.3
K 5	18-24	8	8	18.8	13.5 29.9	7 2	2101	NIGHT	34	5.1	5.1	5.1	5.1	5.2	NONE	-	33.3 33.3 33.3
L 4	0-15	2	2	25.0	17.6 32.5	8 2	1050	DAY	48	5.0	5.1	5.1	5.1	4.8	NONE	-	32.8 32.9 32.9
L 4	18-33	4	4	22.9	14.6 28.1	8 2	1050	DAY	48	4.8	4.9	4.8	5.1	4.8	NONE	-	33.0 33.0 33.0
M 3	0- 6	1	1	22.1	22.1 22.1	8 2	1822	NIGHT	20	3.9	3.9	3.9	3.9	4.0	NONE	-	32.3 32.3 32.3
M 4	0-15	2	2	22.0	20.0 24.0	8 2	1915	NIGHT	42	5.3	5.4	5.3	5.4	5.3	NONE	-	32.2 33.2 32.7
M 4	18-33	1	1	18.7	18.7 18.7	8 2	1915	NIGHT	42	5.3	5.3	5.3	5.4	5.3	NONE	-	33.0 33.1 33.1

APPENDIX TABLE -- CONTINUED

CRUISE STAT. C66 3	TOW DEPTH (M)	********* LARVAE ********** NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE	DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (C) *** RANGE	MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE	MEAN
A 1	C- 6	13	13	15.3	8.2 29.7	6 4	1757	DUSK	22	3.6	3.6	3.6	3.6	3.7	NONE	-	31.6 31.7 31.6
A 2	0-15	18	15	23.8	8.9 47.4	6 4	1911	NIGHT	36	3.3	3.5	3.5	3.5	3.0	NONE	-	31.7 32.1 32.0
A 3	0-15	26	26	17.5	8.4 39.7	6 4	2110	NIGHT	47	3.4	3.5	3.5	3.5	3.0	NONE	-	32.0 32.3 32.1
A 3	18-33	20	19	15.0	5.6 28.7	6 4	2110	NIGHT	47	3.0	3.4	3.1	3.5	3.0	NONE	-	29.1 32.3 30.1
A 4	0-15	10	10	19.4	5.3 29.8	6 4	2238	NIGHT	51	3.4	3.7	3.6	3.6	2.8	NONE	-	31.9 32.5 32.2
A 4	18-33	35	35	21.5	10.9 34.4	6 4	2238	NIGHT	51	2.8	3.3	3.0	3.6	2.8	NONE	-	29.4 32.4 30.5
A 5	0-15	1	1	18.5	18.5 18.5	7 4	0029	NIGHT	62	3.6	3.7	3.7	3.7	2.7	NONE	-	32.0 33.4 33.0
A 5	18-33	2	2	17.5	13.5 21.6	7 4	0029	NIGHT	62	3.0	3.5	3.5	3.7	2.7	NONE	-	33.2 33.6 33.4
A 6	0-15	5	5	22.3	15.5 35.5	7 4	0208	NIGHT	73	3.4	3.7	3.6	3.7	2.7	NONE	-	32.4 33.2 32.7
A 7	0-15	73	70	20.6	13.4 31.3	7 4	0355	NIGHT	111	3.4	3.6	3.5	3.6	3.5	NONE	-	33.1 33.5 33.3
A 7	18-33	23	23	21.6	16.9 40.1	7 4	0355	NIGHT	111	2.9	3.3	3.2	3.6	3.5	NONE	-	33.5 33.8 33.6
B 1	C- 6	11	10	13.5	6.8 26.0	7 4	1650	DAY	24	4.7	4.7	4.7	4.7	4.7	NONE	-	30.3 30.9 30.6
B 2	0-15	10	10	13.5	7.6 22.9	7 4	1556	DAY	39	6.2	6.6	6.4	6.4	6.1	NONE	-	31.7 32.2 32.1
B 3	C-15	4	4	14.2	12.8 15.7	7 4	1455	DAY	52	4.8	5.0	4.9	5.0	4.7	NONE	-	31.4 32.1 32.0
B 3	18-33	1	1	19.6	19.6 19.6	7 4	1455	DAY	52	4.7	4.7	4.7	5.0	4.7	NONE	-	29.6 30.9 30.2
B 4	C-15	6	6	19.6	14.2 23.5	7 4	1324	DAY	62	5.3	5.5	5.4	5.5	4.8	NONE	-	32.8 33.5 33.2
B 4	18-33	3	3	21.2	18.1 25.9	7 4	1324	DAY	62	5.0	5.2	5.2	5.5	4.8	NONE	-	33.7 34.1 33.9
B 5	C-15	9	9	15.5	11.9 18.1	7 4	1156	DAY	77	4.2	4.5	4.5	4.9	3.9	NONE	-	31.0 32.5 31.6
B 5	18-33	3	3	23.6	16.7 36.5	7 4	1156	DAY	77	3.7	4.1	3.9	4.9	3.9	NONE	-	30.4 32.7 31.9
B 6	0-15	11	11	18.4	13.6 22.5	7 4	1005	DAY	87	4.4	4.7	4.6	4.7	2.8	NONE	-	32.2 33.2 32.8
B 6	18-33	12	12	15.5	10.5 20.5	7 4	1005	DAY	87	4.1	4.3	4.3	4.7	2.8	NONE	-	33.2 33.3 33.2
B 7	0-15	19	19	22.4	13.9 34.1	7 4	0801	DAY	95	3.5	3.9	3.8	3.9	3.3	NONE	-	32.4 33.4 33.1
B 7	18-33	4	4	16.3	14.4 19.6	7 4	0801	DAY	95	3.4	3.5	3.5	3.9	3.3	NONE	-	33.4 33.6 33.5
C 1	C-15	1	1	39.0	39.0 39.0	8 4	0005	NIGHT	21	4.5	5.0	4.9	5.0	3.5	NONE	-	31.7 32.4 32.2
C 2	0-15	6	6	37.8	31.5 42.8	8 4	0058	NIGHT	28	4.0	5.2	5.0	5.2	4.0	NONE	-	31.6 32.5 32.1
C 3	0-15	2	2	33.8	33.1 34.6	8 4	0156	NIGHT	33	4.2	4.9	4.8	4.9	3.9	NONE	-	30.6 31.4 30.9
C 3	18-24	4	4	31.6	29.8 34.0	8 4	0156	NIGHT	33	3.9	4.1	4.0	4.9	3.9	NONE	-	31.5 31.7 31.6
C 4	18-33	1	1	35.0	35.0 35.0	8 4	0316	NIGHT	44	4.4	4.4	4.4	5.0	4.4	NONE	-	33.4 33.9 33.7
C 5	0-15	2	2	25.5	22.5 28.5	8 4	0445	NIGHT	50	5.2	5.3	5.3	5.2	5.1	NONE	-	33.6 33.8 33.7
C 5	18-33	2	2	19.8	17.7 21.9	8 4	0445	NIGHT	50	5.0	5.1	5.1	5.2	5.1	NONE	-	33.8 34.3 34.0
C 6	C-15	1	1	19.2	19.2 19.2	8 4	0644	DAY	58	5.7	5.9	5.8	5.9	5.3	NONE	-	32.9 33.8 33.3
C 7	0-15	1	1	23.7	23.7 23.7	8 4	0851	DAY	69	5.4	5.5	5.5	5.5	5.2	NONE	-	33.5 33.7 33.6
C 8	0-15	2	2	17.9	16.3 19.6	8 4	1048	DAY	273	4.6	5.2	5.1	5.2	5.7	NONE	-	32.8 33.5 33.3
C 8	18-33	2	2	25.3	22.3 28.4	8 4	1048	DAY	273	4.4	4.5	4.5	5.2	5.7	NONE	-	33.6 34.0 33.8
D 1	C- 6	4	4	34.3	31.1 41.3	9 4	0213	NIGHT	18	5.9	6.0	5.9	6.0	5.5	NONE	-	30.8 31.6 31.2
D 2	0- 6	6	6	30.9	24.9 38.6	9 4	0125	NIGHT	19	6.0	6.1	6.1	6.1	5.3	NONE	-	31.5 32.0 31.8
D 3	C-15	4	4	31.3	28.6 34.1	9 4	0035	NIGHT	21	6.1	6.1	6.1	6.1	5.6	NONE	-	31.4 32.7 32.1
D 5	0-15	2	2	16.5	9.8 23.3	8 4	2127	NIGHT	40	5.4	6.0	5.7	6.0	5.2	NONE	-	32.0 33.1 32.6
D 6	0-15	1	1	44.1	44.1 44.1	8 4	1930	NIGHT	57	5.6	6.2	6.1	6.2	5.2	NONE	-	33.0 33.9 33.5
E 1	0- 6	20	20	36.7	21.3 45.5	13 4	0056	NIGHT	14	6.7	6.7	6.7	6.7	6.7	NONE	-	30.7 30.9 30.8
E 2	0- 6	26	26	37.5	22.2 48.2	13 4	0228	NIGHT	19	6.4	6.4	6.4	6.4	6.6	NONE	-	30.8 31.0 30.9
E 3	C-15	3	3	41.6	31.8 50.0	22 4	1912	NIGHT	22	7.4	7.6	7.5	7.5	7.4	NONE	-	31.3 31.4 31.3
E 5	18-24	1	1	24.4	24.4 24.4	22 4	1640	DAY	37	6.3	6.4	6.3	7.2	6.3	NONE	-	31.6 31.8 31.7
F 2	0- 6	4	4	29.1	25.8 31.0	14 4	1146	DAY	20	6.5	6.9	6.7	6.9	6.3	NONE	-	30.0 30.3 30.1
F 3	0-15	5	5	24.7	20.9 32.9	14 4	1243	DAY	27	6.3	6.5	6.4	6.5	6.3	NONE	-	31.1 31.4 31.2
F 4	C-15	5	5	37.3	33.7 44.0	14 4	1404	DAY	24	6.2	6.3	6.2	6.3	6.1	NONE	-	31.3 31.7 31.5
F 6	0-15	1	1	18.2	18.2 18.2	14 4	1719	DAY	52	6.2	6.3	6.3	6.3	6.2	NONE	-	32.2 32.3 32.3
F 7	18-33	2	2	31.3	27.8 34.8	14 4	1910	NIGHT	70	4.9	5.2	5.0	5.0	5.4	NONE	-	32.5 32.6 32.6
G 1	C- 6	3	3	33.8	28.5 37.8	15 4	0655	DAY	15	6.9	6.9	6.9	6.9	6.9	NONE	-	29.9 30.1 30.0
G 2	0- 6	4	4	24.4	21.1 31.6	15 4	0454	NIGHT	16	6.7	6.7	6.7	6.7	6.3	NONE	-	30.6 30.8 30.7
G 4	0-15	1	1	43.8	43.8 43.8	15 4	0204	NIGHT	38	6.0	6.1	6.1	6.0	6.1	NONE	-	32.2 32.4 32.3
G 5	0-15	1	1	44.3	44.3 44.3	15 4	0045	NIGHT	57	6.5	6.5	6.5	6.5	6.5	NONE	-	32.4 32.8 32.7
G 6	0-15	1	1	26.0	26.0 26.0	14 4	2245	NIGHT	94	5.0	5.0	5.0	5.0	5.6	NONE	-	32.0 32.3 32.1
G 6	18-33	1	1	32.6	32.6 32.6	14 4	2245	NIGHT	94	5.0	5.1	5.0	5.0	5.6	NONE	-	32.5 32.8 32.7
H 2	0-15	1	1	32.0	32.0 32.0	15 4	1452	DAY	21	8.5	8.6	8.5	8.6	8.5	NONE	-	31.4 31.9 31.7
H 3	C-15	1	1	30.4	30.4 30.4	15 4	1548	DAY	25	7.8	8.2	7.9	8.2	7.0	NONE	-	32.3 32.8 32.6
H 5	C-15	1	1	40.2	40.2 40.2	15 4	1911	NIGHT	37	6.6	6.9	6.7	6.9	6.6	NONE	-	32.3 32.4 32.4
H 6	0-15	7	7	26.1	21.4 37.5	15 4	2210	NIGHT	80	6.2	6.8	6.5	6.8	6.2	NONE	-	32.4 32.7 32.5
H 6	18-33	3	3	33.1	26.9 37.3	15 4	2210	NIGHT	80	6.2	6.2	6.2	6.8	6.2	NONE	-	32.4 32.5 32.5
H 7	0-15	23	21	29.6	22.2 41.3	15 4	2320	NIGHT	129	5.0	5.6	5.4	5.6	5.2	NONE	-	32.1 32.4 32.2
H 7	18-33	2	2	29.0	26.0 32.1	15 4	2320	NIGHT	129	5.0	5.4	5.3	5.6	5.2	NONE	-	32.4 32.6 32.5
J 3	C- 6	1	1	35.5	35.5 35.5	16 4	0825	DAY	19	8.9	8.9	8.9	8.9	8.5	NONE	-	31.8 31.8 31.8
J 6	0-15	4	4	35.6	33.2 39.5	16 4	0406	NIGHT	58	7.0	7.4	7.3	7.4	6.9	NONE	-	32.0 32.6 32.3
J 7	C-15	6	6	28.7	25.9 31.1	16 4	0212	NIGHT	92	6.7	6.8	6.7	6.8	6.4	NONE	-	32.3 32.5 32.4
J 7	18-33	8	8	28.3	24.2 35.8	16 4	0212	NIGHT	92	6.4	6.6	6.5	6.8	6.4	NONE	-	32.5 32.7 32.6
K 5	18-24	1	1	39.6	39.6 39.6	19 4	1553	NIGHT	37	7.7	7.9	7.8	8.8	7.7	NONE	-	32.7 32.8 32.8
M 4	C-15	2	2	30.6	17.1 44.2	20 4	1245	DAY	62	12.4	15.2	13.7	12.4	18.6	STRONG	13-20	30.7 32.2 31.6

APPENDIX TABLE -- CONTINUED

CRUISE STAT.	TOW DEPTH (M)	********* LARVAE ********** NUMBER TOTAL	MEAS.	LENGTHS (MM TL) MEAN	RANGE		DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (C) *** RANGE		MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE		MEAN
D66 5																				
A 1	0- 6	6	6	25.5	11.9	41.6	12 5	2002	NIGHT	19	7.8	7.8	7.8	7.8	7.8	NONE	-	32.5	32.6	32.6
A 2	0-15	1	1	15.2	15.2	15.2	12 5	2109	NIGHT	33	7.3	7.4	7.3	7.4	7.2	NONE	-	32.4	32.6	32.5
A 3	0-15	1	1	21.4	21.4	21.4	13 5	0008	NIGHT	37	7.2	7.2	7.2	7.2	6.6	NONE	-	31.9	32.4	32.3
A 3	18-33	1	1	24.7	24.7	24.7	13 5	0008	NIGHT	37	6.6	7.2	6.8	7.2	6.6	NONE	-	32.2	32.4	32.3
A 5	0-15	1	1	37.8	37.8	37.8	13 5	0325	NIGHT	62	6.3	6.3	6.3	6.3	4.6	STRONG	35-36	32.2	32.6	32.5
A 6	0-15	1	1	39.2	39.2	39.2	13 5	0534	DAY	76	6.5	6.5	6.5	6.5	4.3	WEAK	35-42	32.2	33.3	32.9
B 1	0- 9	7	7	35.7	16.7	60.5	13 5	2133	NIGHT	22	7.7	8.3	8.0	8.3	7.2	NONE	-	30.2	31.2	30.6
B 2	0-15	6	6	19.1	12.7	27.9	13 5	2038	NIGHT	34	7.1	7.7	7.5	7.7	5.0	NONE	-	31.3	31.9	31.7
B 3	0-15	3	3	19.8	18.7	21.2	13 5	1936	NIGHT	52	7.5	7.5	7.5	7.5	4.9	WEAK	17-23	31.7	32.0	31.8
B 5	0-15	1	1	30.0	30.0	30.0	13 5	1641	DAY	72	6.6	7.6	7.4	7.6	4.1	WEAK	12-15	32.6	33.3	32.9
C 1	0-15	4	4	24.3	14.7	38.7	14 5	2124	NIGHT	21	8.0	8.8	8.7	8.8	8.0	WEAK	12-14	30.9	31.8	31.3
C 2	0-15	1	1	57.8	57.8	57.8	14 5	2030	NIGHT	30	8.3	8.7	8.6	8.7	7.4	WEAK	17-20	31.1	31.7	31.5
C 5	0-15	1	1	35.2	35.2	35.2	14 5	1675	DAY	51	7.6	7.8	7.7	7.8	6.4	NONE	-	32.6	32.7	32.7
C 8	0-15	2	2	36.1	33.3	39.0	14 5	0615	DAY	400	6.8	7.3	7.1	7.3	8.3	NONE	-	33.2	33.3	33.2
C 8	18-33	1	1	23.8	23.8	23.8	14 5	0615	DAY	400	6.3	7.0	6.7	7.3	8.3	NONE	-	33.4	33.8	33.5
C 3	0-15	1	1	41.8	41.8	41.8	16 5	2058	NIGHT	26	8.7	9.2	9.0	9.2	7.7	WEAK	20-23	31.5	31.7	31.7
D 6	0-15	2	2	32.5	31.0	34.0	17 5	0155	NIGHT	54	8.0	8.1	8.0	8.1	6.8	NONE	-	30.3	30.9	30.6
E 1	0- 6	2	2	40.4	31.9	48.9	18 5	0414	DAWN	15	11.8	11.8	11.8	11.8	11.8	NONE	-	29.1	29.3	29.3
D6614	(M)			(MM TL)			1966 D M	(EST)		(M)							(M)			
A 1	0- 3	11	11	5.7	5.1	6.2	4 12	1956	NIGHT	17	7.4	7.5	7.5	7.5	8.5	NONE	-	32.9	32.9	32.9
B 1	0- 6	41	41	5.2	4.4	6.9	3 12	1937	NIGHT	20	8.3	8.4	8.4	8.3	8.5	NONE	-	31.8	31.9	31.9
B 3	0-15	1	1	5.1	5.1	5.1	3 12	2210	NIGHT	48	10.0	10.0	10.0	10.0	10.0	NONE	-	33.0	33.0	33.0

FOOD AND GROWTH PARAMETERS OF JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN CENTRAL COLUMBIA RIVER[1]

C. DALE BECKER[2]

ABSTRACT

Juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Hanford area of the free-flowing central Columbia River, Wash., consume almost entirely adult and larval stages of aquatic insects. Their diet is dominated by midges (Diptera: Chironomidae). By numbers, adult midges provided 64 and 58% of the diet and larval midges 17 and 18% of the diet, in 1968 and 1969, respectively. The families Hydropsychidae (Trichoptera or caddisflies), Notonectidae (Hemiptera or true bugs), and Hypogastruridae (Collembola or springtails) are of minor numerical importance with a combined utilization of 7% in 1968 and 15% in 1969.

Distinctive features of food and feeding activity of juvenile chinook salmon at Hanford are fourfold: 1) the fish utilize relatively few insect groups, predominantly Chironomidae; 2) they depend largely upon autochthonous river organisms; 3) they select prey drifting, floating, or swimming in the water; and 4) they are apparently habitat opportunists to a large extent. Analyses were made of variations in diet and numbers of insects consumed between six sampling stations distributed along a 38-km section of the river. Data are provided on feeding intensity, fish lengths, length-weight relationships, and coefficients of condition. Seasonal changes in river temperature and discharge, as well as variations in regulated flow levels, are environmental features influencing feeding, growth, and emigration of fish in the Hanford environs.

Food habits of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), have been reported from various habitats including the Sacramento River, Calif. (Rutter, 1904); lower Sacramento-San Joaquin system, Calif. (Sasaki, 1966); lower Chehalis River and upper Grays Harbor system, Wash. (Herrmann, 1970); middle Willamette River, Oreg. (Breuser, 1954); and tributaries of the central Columbia River, Wash. (Chapman and Quistorff, 1938). Initial observations on feeding bionomics of juvenile chinook salmon in the central Columbia River were conducted in 1968 (Becker, 1970a). The study was expanded in 1969. The objectives of this report are to present data based on the more extensive 1969 investigation and to discuss theoretically the influence of environmental features.

The mainstem Columbia River above Bonneville Dam has been altered during recent decades into a nearly consecutive series of artificial impoundments arising from hydroelectric development. Only one section of the main channel now survives in its natural, free-flowing condition. This section extends from Richland, Wash., some 93 km upriver to Priest Rapids Dam, where it forms the northern and northeastern boundaries of the Atomic Energy Commission's Hanford Reservation (Figure 1).

Most spawning grounds for salmonids throughout the mainstem Columbia River have now been inundated by the reservoir complex (Fulton, 1968). Maintenance of salmonid resources is due largely to providing access over otherwise impassable dams, propagating young fish in hatcheries and spawning channels,

[1] This study was supported by Contract AT(45-1)-1830 with the United States Atomic Energy Commission.
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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

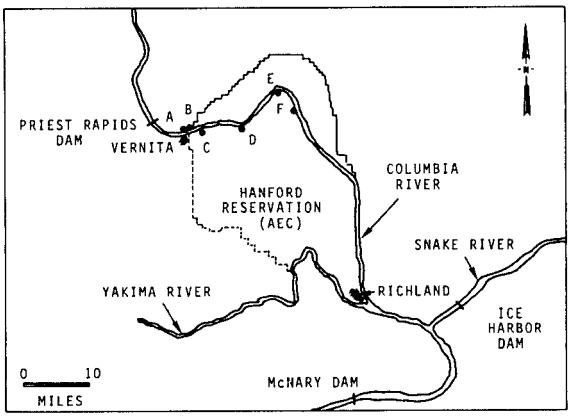

FIGURE 1.—The Hanford environs of the free-flowing Columbia River between Richland, Wash., and Priest Rapids Dam.

and protecting spawning and rearing areas in available tributaries. The free-flowing Hanford section, however, still supports a sizable spawning population of fall chinook salmon that has produced an increase from about 300 redds in 1960 to about 4,500 redds in 1969 (Watson, 1970). The annual contribution of seaward migrants from the Hanford population to the combined natural production of the Columbia and Snake Rivers is not known. But the Hanford population has clearly acquired considerable importance in sustaining natural salmonid runs within the Columbia River Basin.

ENVIRONMENTAL CONDITIONS

River temperatures and discharges are two factors potentially influencing the availability of food organisms, feeding activity, and growth of juvenile chinook salmon in the central Columbia River. The ecological aspects of these two factors are evaluated in the Discussion of this report.

The annual cycles of temperature and discharge (Figure 2) are essentially similar from year to year. Temperatures are lowest in January and February when eggs of fall chinook salmon are buried in the gravel, rise during the spring as fry emerge, and peak during August and September. From the standpoint of known thermal requirements (Brett, 1952), temperatures are well below the thermal preferendum of juvenile chinook salmon (12°-14°C) in March and April, enter the preferred range in May and June—when conditions are presumably optimum for feeding and growth, and extend into the upper zone of thermal tolerance during July and August.

Temperatures at Priest Rapids Dam (above Hanford) were somewhat lower than those

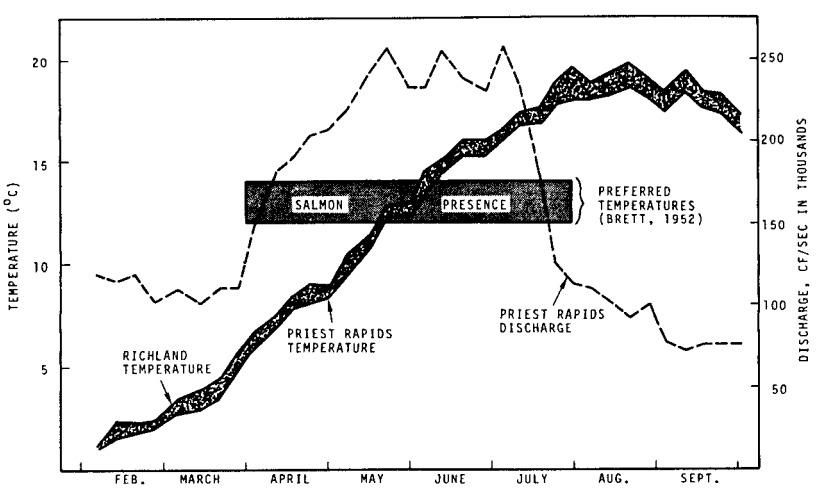

FIGURE 2.—Temperature and flow conditions in the central Columbia River during the spring and summer of 1969, in relation to the presence and preferred temperatures of juvenile fall chinook salmon.

at Richland (below Hanford) in 1969 largely because of thermal discharges from operating plutonium-production reactors on the Hanford reservation.[3] Solar radiation also contributes heat to the free-flowing river above Richland during the summer (Moore, 1968). Maximum daily temperatures recorded in 1969 at Priest Rapids Dam and Richland were 19.7° and 20.6°C, respectively. These peaks were well below the apparent upper incipient lethal level of 25.1°C for juvenile chinook salmon, experimentally determined (Brett, 1952).

The annual volume of river flow in the central Columbia River ranges from about 40,000 to over 300,000 cfs (1,133-8,500 m³/sec). Flows are low during the fall and winter, but increase and peak during April, May, and June due to the seasonal runoff of the spring freshet. In 1969, flows increased about 6 weeks earlier than normal because of operational releases at Grand Coulee Dam on the upper Columbia River. High flows were sustained for about 3 mo, then decreased sharply in July, and minimum summer flows occurred in late August and September.

The discharge data illustrated in Figure 2 are based on weekly means and fail to reveal the extent of either weekly or daily fluctuations in river levels that occur from flow regulation at Priest Rapids Dam. Flows are generally reduced on weekends and increased during the week in response to consumer demands for hydroelectric power (Figure 3). Similar but less extreme variations are induced daily. Water in excess of reservoir capacity is discharged over spillways at Priest Rapids Dam during the spring spate. Weekly fluctuations in river volumes are more variable at other seasons because greater need exists to conserve reservoir water supplies for hydroelectric production. At these times, such as in March and August 1969, flow regulation on weekends may result in changes of water level in the Hanford area of up to 2 m in 24 hr.

[3] Four reactors were discharging heated water in 1968 and the spring of 1969. The effluents issued as point discharges from subsurface locations in midriver at depths exceeding 6 m, and the mixing zones extended downstream in narrow bands prior to dispersal. Juvenile salmonids feeding in inshore areas below the reactors were not directly exposed to thermal increments.

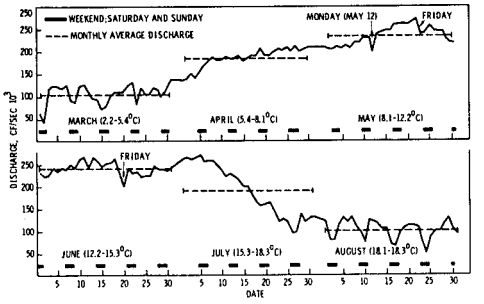

FIGURE 3.—Weekly and daily fluctuations in flow volumes in the central Columbia River due to regulation at Priest Rapids Dam, above Hanford, March-August 1969.

Juvenile fall chinook salmon occur in the Hanford area of the Columbia River from late March to mid-July (Figure 2) (Mains and Smith, 1964; Becker, 1970b). During this span the eggs hatch, fry leave the gravel of the riverbed, and juvenile fish occupy inshore feeding areas for indeterminate periods of feeding and growth before departing seaward. Most juveniles lingering at Hanford emigrate by the end of July. The short residence span is a historical characteristic of juvenile fall chinook salmon originating in the central Columbia River. However, the timing of the seaward migration of juvenile salmonids passing through the upper and lower Columbia River system is now delayed by the reservoir complex (Park, 1969; Raymond, 1969).

METHODS

Juvenile chinook salmon of the 0-age group, produced by adults spawning during the fall of 1968, were collected by seines at stations along the river banks from 4 March to 29 July 1969. The sampling span corresponded to the annual presence of fish following emergence from the gravel and preceding seaward migration. Stomach analyses of 769 fish were made from samples collected at roughly weekly intervals, when available. All samples were collected between 0900 and 1500 hr, and preserved in 10% buffered Formalin[4] immediately

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

after capture to stop digestive action. The fish were later measured (fork length, FL) and eviscerated. All measurements were taken after 7 days of preservation to obtain consistency, since Formalin causes some initial shrinkage. Organisms in the stomachs were identified individually to the lowest practical category under a dissecting microscope with the aid of appropriate taxonomic texts, classified according to their developmental stage, and enumerated. Insects represented by chitinous head capsules, particularly larval Chironomidae, were counted as complete organisms whereas fragmented body parts were excluded.

The 1968 study quantified only the food organisms consumed. Methods in 1969 were modified to provide data on fish length-weight relationships and dry weight (biomass) of the stomach contents. Fish were individually blotted with absorbent paper to remove excess fluid prior to weighing. After identification and enumeration of food organisms, the entire stomach content of each fish was placed in a miniature watch glass, air dried at least 24 hr in a controlled atmosphere, and weighed.

Collecting stations were distributed along a 38-km section of the Columbia River extending downstream from the Highway 240 bridge at Vernita, Wash. Six primary stations, shown in Figure 1 (A, B, C, D, E, F), and four supplementary stations were used. Samples from all 10 stations were combined in summations of food organisms utilized (see Tables 1 and 2), but only data from the six primary stations were used for subsequent statistical treatment.

RESULTS

Food Organisms Utilized

Throughout their sojourn at Hanford, over 95% of the diet of juvenile chinook salmon consisted of insects. The prey included adult, subadult, and larval stages of semiaquatics, various developmental stages of aquatics, and winged adults of terrestrials (Table 1). Comparison of the 1968 and 1969 data in Table 1 reveals that the organisms consumed were essentially similar in two successive years.

The Chironomidae (midges) were the dominant insect group utilized. Emerging subadults and adults were captured in abundance, 64% in 1968 and 58% in 1969. Midge larvae were taken less extensively, 17% in 1968 and 18% in 1969. Few midge pupae and no pupal exuviae were noted.

The order Diptera provided 83% and 78% of all insects utilized in 1968 and 1969, respectively. Other insect groups were of less importance in terms of numbers, but not necessarily in volume (or nutritional value) since sizes of different species vary considerably. The relatively large Trichoptera (caddisflies), consisting primarily of *Hydropsyche cockerelli* (Hydropsychidae), were numerically the second most important order. Like the midges, most caddisflies eaten were recently emerged adults associated with the water-air interface. Other groups of secondary importance were the families Notonectidae (Hemiptera or true bugs), primarily small *Notonecta* nymphs, and the Hypogastruridae (Collembola or springtails).

Few Ephemeroptera (mayflies), often important dietary items of salmonids in other streams, and no Plecoptera (stoneflies) were detected in the stomach contents. Unpublished data from limited bottom samples, sporadic drift samples, inspection of stones, and trapping of adult insects by light attraction at night indicate that populations of mayflies and particularly stoneflies are low in the central Columbia River. Zooplankton, originating primarily from the Priest Rapids reservoir and present in the river drift, were utilized in small quantities by only a few fish.

Seasonal Changes in Diet

Some change occurs in the diet of juvenile chinook salmon from March to July (Table 2). The Chironomidae accounted for the greatest proportion of food organisms each month on a numerical basis, with the most larval and adult midges being consumed in March and April. Hemiptera and Collembola, both consisting of small forms, received maximum utilization in April, May, and June when rising river volumes inundated shoreline areas. Adult Trichoptera were consumed primarily in June

TABLE 1.—Organisms consumed by juvenile chinook salmon (0-age group) in the central Columbia River. (435 fish examined in 1968 and 769 fish in 1969.)

Food organism	1968[1] Number	1968[1] %	1969 Number	1969 %
Diptera:				
Adults:				
Chironomidae[2]	5,973	63.5	11,062	58.2
Dolichopodidae	31	0.3	6	[3]0.0
Empididae	13	0.1	4	0.0
Simuliidae	4	0.0	52	0.3
Culicidae	0	—	6	0.0
Ephydridae	1	0.0	3	0.0
Heleidae	0	—	1	0.0
Stratiomyidae	0	—	1	0.0
Dixidae	0	—	1	0.0
Unidentified	82	0.9	193	1.0
Larvae:				
Chironomidae	1,596	17.0	3,450	18.1
Dolichopodidae	18	0.2	4	0.0
Empididae	0	—	1	0.0
Simuliidae	55	0.6	54	0.3
Ephydridae	1	0.0	1	0.0
Heleidae	3	0.0	0	—
Muscidae	3	0.0	0	—
Unidentified	7	0.1	9	0.0
Pupae:				
Chironomidae	7	0.1	18	0.1
Tipulidae	5	0.1	0	—
Heleidae	0	—	2	0.0
Unidentified	5	0.1	4	0.0
Total Diptera	7,804	83.0	14,872	78.3
Hemiptera:				
Notonectidae	248	2.6	918	4.8
Mesoveliidae	34	0.4	2	0.0
Macroveliidae	1	0.0	0	—
Corixidae	1	0.0	1	0.0
Saldidae	4	0.0	8	0.0
Hebridae	1	0.0	0	—
Unidentified	11	0.1	27	0.1
Total Hemiptera	300	3.2	956	5.0
Coleoptera:				
Adults:				
Unidentified	4	0.0	23	0.1
Larvae:				
Dytiscidae	26	0.3	13	0.1
Noteridae	1	0.0	0	—
Hydrophilidae	1	0.0	1	0.0
Elmidae	0	—	1	0.0
Ptilodactylidae	1	0.0	0	—
Unidentified	1	0.0	16	0.1
Total Coleoptera	34	0.4	54	0.3
Lepidoptera:				
Unidentified adults[4]	3	0.0	187	1.0
Unidentified larvae[4]	0	—	21	0.1
Total Lepidoptera	3	0.0	208	1.1
Trichoptera:				
Adults:				
Hydropsychidae	277	2.9	948	5.0
Psychomyiidae	0	—	3	0.0
Calamoceratidae	0	—	6	0.0
Hydroptilidae	0	—	12	0.1
Unidentified	93	1.0	44	0.2
Larvae:				
Hydropsychidae	18	0.2	93	0.5
Psychomiidae	13	0.1	5	0.0
Phryganeidae	1	0.0	0	—
Rhyacophilidae	0	—	2	0.0
Unidentified	13	0.1	27	0.1
Total Trichoptera	415	4.4	1,140	6.0
Ephemeroptera:				
Subimagos:				
Unidentified	8	0.1	0	—
Nymphs:				
Baetidae	1	0.0	24	0.1
Unidentified	0	—	4	0.0
Total Ephemeroptera	9	0.1	28	0.1
Hymenoptera:				
Unidentified adults	26	0.3	27	0.1
Homoptera:				
Adults:				
Aphididae	49	0.5	245	1.3
Aleyrodidae	1	0.0	0	—
Unidentified	40	0.5	28	0.1
Total Homoptera	90	1.0	273	1.4
Collembola:				
Hypogastruridae	115	1.2	974	5.1
Other insects:				
Thysanoptera	35	0.4	11	0.1
Megaloptera	1	0.0	1	0.0
Unidentified adults	0	—	98	0.5
Unidentified larvae	0	—	11	0.1
Unidentified	165	1.7	51	0.3
Total other insects	201	2.1	172	0.9
Total insects	8,997	95.7	18,704	98.4
Other food items:				
Fish larvae	0	—	18	0.1
Acari	276	2.9	169	0.9
Zooplankton	[5] 30	0.3	[5] 15	0.1
Algae	[6] 1	0.0	0	—
Arachnida	93	1.0	97	0.5
Plant seeds	5	0.1	1	0.0
Total other food items	405	4.3	300	1.6

[1] 1968 data from Becker (1970a).
[2] Primarily emerging subadults.
[3] Less than 0.05%.
[4] Primarily *Parargyractic* sp. (Pyralidae).
[5] Number of fish containing small quantities of Cladocera, Ostracoda, Copepoda, or Amphipoda.
[6] A quantity of *Anacystis*.

TABLE 2.—Monthly changes in diet of juvenile chinook salmon in 1969, all sampling stations combined.

Food organism	Consumption per month (%)				
	March	April	May	June	July
Diptera[1]	99.5	88.8	70.2	77.2	84.8
Chironomidae, adults	67.1	62.4	50.4	52.4	77.2
Chironomidae, larvae	31.8	24.6	17.4	22.8	6.3
Hemiptera[1]	—	3.2	13.2	2.6	T[2]
Coleoptera	T	T	T	T	T
Lepidoptera	—	T	T	3.3	T
Trichoptera[1]	—	T	T	10.2	13.0
Ephemeroptera	—	T	—	T	T
Homoptera	—		T	3.4	T
Hymenoptera	—	T	T	T	T
Collembola[1]	T	5.6	13.8	1.4	—
Unknowns	—	—	T	T	—
All other insects	—	T	T	1.3	T
Total insects	99.5	97.6	97.2	99.4	97.8

[1] Major insect groups utilized.
[2] "T" = "Trace," less than 1% by number in stomach contents.

and July, in association with summer emergence of the univoltine caddisfly populations. A minor group, the semiaquatic Pyralidae (Lepidoptera or moths and butterflies), were taken most heavily in June.

Some correlation of diet (Table 2) with fish size (Figure 4) was evident. Chinook salmon fry were relatively small (35-40 mm FL) and had incompletely absorbed yolk sacs when they emerged from the gravel and began feeding in March and April. Food organisms selected by fry were predominantly small forms, primarily midges but some *Notonecta* nymphs and Collembola were included. Adult Trichoptera in June and July were selected primarily by large fish (>50 mm FL) capable of capturing and swallowing these larger insects.

Use of Drift Organisms

The developmental stages of insects ingested by juvenile chinook salmon reveal that most were floating, drifting, or swimming in the water when captured. This was apparently the situation for the selection of most Chironomidae, Hydropsychidae, *Notonecta* nymphs, and Hypogastruridae, the four main insect forms utilized. Relatively few insect stages normally adhering to epibenthic substrates or living within gravel interstices were represented in the stomach contents.

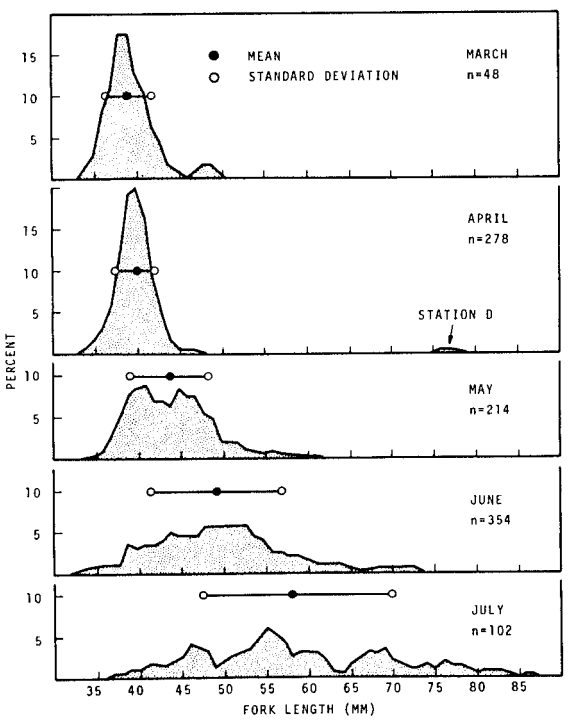

FIGURE 4.—Monthly length-frequency distributions of all juvenile chinook salmon collected at Hanford in 1969. (Data smoothed by a moving mean of three's.)

Although autochthonous insects predominated, some allochthonous terrestrial forms were ingested. The orders Homoptera, Hy-

menoptera, and Thysanoptera are almost entirely of terrestrial origin, and other true terrestrials occur among the adult Diptera, Coleoptera, and Lepidoptera, other than the Pyralidae (Table 1). The terrestrials were probably seized while drifting, either submerged or on the surface film. Since the river drift of allochthonous insects contributed less than 4% of the total food organisms by number, they were of relatively low value to the diet of juvenile chinook salmon in this study.

Variability in Diet

On a proportional basis, some differences in food occurred between the six primary stations and some intersite influences were evident (Table 3). Adult midges were highly utilized at Station D (70.1%), a shallow, semi-enclosed backwater area with somewhat warmer temperatures than other stations, but not larval midges (6.1%). *Notonecta* nymphs were captured primarily at Stations A (7.3%) and E (7.4%), both with extensive areas of marginal vegetation. Adult *Hydropsyche* were taken primarily at Stations B (9.2%) and C (7.2%), both with rubble substrates and partially exposed to flow of the main channel. Larval caddisflies were captured primarily at Station C (9.0%). Collembola were taken most extensively at Stations A (16.5%) and D (6.0%) where extensive mud-water interfaces existed. Proportional variations between stations were probably influenced by numerous intersite features including type of substrate, exposure to current flow, changes in seasonal and regulated water levels, and possibly feeding preferences of individual fish.

Although juvenile chinook salmon at all primary stations appeared to consume the same general types of food, Table 3 indicates some differences on the basis of relative proportions. To explore these differences more fully, the percentages of major food organisms in seven categories (adult and larval Chironomidae, Hemiptera, adult and larval Hydropsychidae, Collembola, and "all other insects") consumed within and between stations were retabulated on a monthly basis. Additionally, the samples were arbitrarily separated into "upper" (A, B, C) and "lower" (D, E, F) stations because of the distance separating them. Analysis by percent similarities (Whittaker and Fairbanks, 1958) was then applied with the formula:

TABLE 3.—Proportions of main insect groups utilized by juvenile chinook salmon at six primary stations, combined 1969 data.

Food organism	Relative proportion (%) at station:						
	A	B	C	D	E	F	Total
All Diptera	67.4	78.2	75.7	79.5	77.5	84.9	76.4
Chironomidae, adults	38.1	44.3	49.8	70.1	60.0	60.6	54.5
Chironomidae, larvae	26.6	31.1	24.3	6.1	15.9	21.9	19.6
Hemiptera (Notonectidae)	7.3	4.6	2.6	4.2	7.4	1.1	5.0
All Trichoptera	6.3	9.6	16.6	6.6	6.0	3.3	6.8
Hydropsychidae, adults	5.9	9.2	7.2	6.1	4.8	2.5	5.7
Hydropsychidae, larvae	0.0	0.1	9.0	0.2	0.2	0.0	0.6
Collembola (Hypogastruridae)	16.5	2.2	0.0	6.0	2.7	1.2	6.5
All adults[1]	73.0	67.3	64.4	91.5	82.7	76.1	78.4
All larvae[2]	27.0	32.7	35.6	8.5	17.3	23.9	21.6

[1] Includes all winged forms, aquatic insects as well as terrestrials, plus Hemiptera and Collembola.
[2] Includes larvae, pupae, nymphs, and other stages normally associated with benthic substrates.

$$PS_c = 100 - 0.5 \Sigma [a-b] = \Sigma \min (a, b);$$

where PS_c = percent similarity of community samples at different stations, and a and b are, for a given species (or group), the percentages of samples A and B which that species (or group) represents. This method, as adapted for food organisms, permits comparison of diets within stations being studied. It quantitatively measures the relative similarity in terms of species numerical composition, in this case, occurrence in the stomach contents of juvenile chinook.

Percent similarities for all possible monthly combinations of samples were compiled and entered in a diamond matrix (Figure 5). Values of combined samples for all upper and lower stations ranged from a low 58.5 in May, 68.8 in April, 70.4 in June, to 75.5 in July (dark areas).

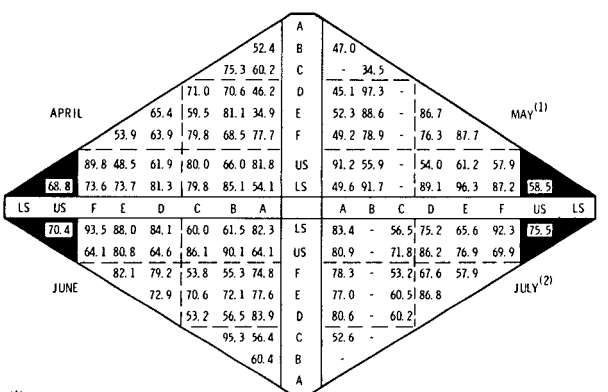

FIGURE 5.—Diamond matrix comparison of percent similarities (PS_c) between and within upper (A, B, C) and lower (D, E, F) stations based on major food organisms consumed, April-July 1969.

Monthly computed figures within and between individual stations ranged above and below these values. No consistent pattern was evident. An upper station (A, B, or C) sometimes showed a high similarity value when compared with a lower station (D, E, or F) and sometimes a low value. For example, values for Station A versus F were high in April (77.7), June (74.8), and July (78.3) but low in May (49.2). The calculations were consistent with the conclusion that, despite the general similarity in diet (PS_c above 50% in most cases), proportional variations between stations occurred randomly in response to site habitat features and the feeding activity of individual fish.

Variability in Feeding Intensity

Mean numbers of insects in the stomach contents revealed an increasing trend from March to July (Figure 6). This increase corresponded with the span when fish size and water temperature were simultaneously increasing. During March and April, when fish

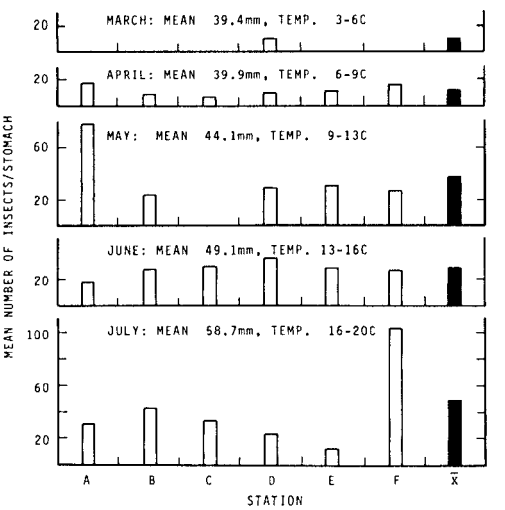

FIGURE 6.—Number of insects in stomach contents of juvenile chinook salmon at six primary stations, in relation to mean fish lengths and water temperature.

were small and temperatures were low (3°-9°C), mean numbers of insects contained were minimum, about 10 per fish. Mean numbers increased to 38 in May and decreased to 28 in June. A peak of 47 was reached in July when the fish were large and temperatures ranged from 16° to 20°C. The May samples were influenced by high utilization of Hypogastruridae at Station A on 20 May, and the July samples by adult midges at Station F on 29 July, the last time fish were available. If these samples were excluded, mean numbers of insects contained in May and July did not

differ greatly from those in June. Yet a slight increase throughout the season was evident.

High variations within and between samples, related to feeding of individual fish, preclude meaningful comparison between stations on the basis of number of insects per stomach. Number of insects contained under field situations is, at best, a rough index to nutrition and subsequent growth. There are several reasons. First, insects vary widely in size from minute midges to large caddisflies; large number of small insects in a stomach is not necessarily equivalent to a few large insects in terms of energy supplied. Second, the relative nutritional value may vary between like amounts of different kinds of food organisms. Third, stomach contents reveal only feeding at the approximate time a sample was taken and not the preceding meals responsible for growth. Fourth, digestion rates, metabolism, and energy consumption that result in growth are highly temperature dependent, particularly over the March to July range of 2° to 20°C that occurs in the central Columbia River. Fifth, changes in water levels influence current patterns, availability of food supply and, more or less, expenditure of energy required for a fish to obtain a "full meal."

Total stomach biomass provides better information on daily rations from natural river ecosystems. Feeding intensity on the basis of the relationship between fish size and stomach biomass was calculated as:

$$FI = \frac{w}{W} \times 100;$$

where FI = feeding intensity, w = dry weight of stomach contents in grams, and W = weight of juvenile chinook salmon in grams (Olmsted and Kilambi, 1971).

Amounts of food in the stomachs of individual fish varied widely. To minimize random sample variations, feeding intensities were tabulated on the basis of combined samples for each collection date at all primary stations (Table 4). The few fish taken in March were available only at Station D, where water temperatures were somewhat higher than in the main channel due to intragravel seepage of warm water from the shoreline. These fish revealed a relatively high feeding intensity compared to fish at all primary stations in April.

FI values from grouped samples generally increased as the season progressed and the river water warmed. The highest feeding intensity in June and early July reflects primarily an increase in the size of food organisms consumed, particularly by inclusion of adult Trichoptera (Table 2).

TABLE 4.—Feeding intensity (*FI*) of juvenile chinook salmon in the central Columbia River, 1969. (Samples combined by collection date.)

Date	Number of fish	Mean fish: Length (mm)	Mean fish: Weight (g)	Feeding intensity (*FI*)
March 4	19	38.7	0.59	0.32
11	10	38.9	0.60	0.83
April 8	75	39.7	0.62	0.32
15	58	39.8	0.62	0.19
24	57	40.0	0.66	0.14
29	56	40.7	0.70	0.14
May 13	50	41.6	0.82	0.37
20	50	45.1	1.15	0.48
27	50	46.4	1.24	0.17
June 3	50	47.2	1.38	0.70
10	38	48.7	1.69	0.57
16	57	53.6	2.30	0.66
24	40	54.1	2.15	0.45
July 2	30	54.6	2.27	0.60
7	10	49.8	1.64	0.50
15	20	59.7	2.97	0.68
21	10	68.1	4.25	0.38
29	10	78.1	6.36	0.40

Variability in Fish Lengths

The expanding standard deviation in Figure 4 indicates an increasing size range from month to month. Lengths of juvenile chinook were relatively uniform at each station during April and early May when recruitment to shoreline zones was initiated and temperatures were low. Variations in mean fish lengths within and between stations appeared with further growth in late May, as temperatures increased, and these variations became extreme in June and July. Statistical comparison of sample mean lengths throughout the season, by Duncan's Multiple Range Test, revealed significant differences that supported this observation.

Considerable turnover of fish presumably took place along the shore during the period of high river discharge and thereafter. The inference is

that groups of fish at each station were composed largely of transitory groups. Interstation turnover probably resulted from irregular movements of fish along the shoreline and seaward migration, in response to such factors as physiological stimuli, high river discharge, rising water temperature, and daily and weekly fluctuations in regulated water levels.

The combined mean lengths of fish collected at upper and lower stations provide a clearer picture of growth in relation to season (Figure 7). The slight curvilinear relationship reveals an increase in growth rates under warming temperature regimes in June and July.

Length-Weight Relationship

Although lengths of juvenile chinook salmon varied randomly between and within samples, the length-weight relationship for fish of equal size is a relatively consistent parameter. Furthermore, the relationship is characteristic of a given habitat and may indicate the adequacy of all synecological conditions leading to fish growth and development in that environment.

Preliminary statistical comparison of length-weight relationships by a nonlinear least-squares-fitted power function revealed no significant differences between stations. Consequently, the length-weight relationship of juvenile chinook salmon at Hanford was calculated by the standard regression equation Log Y = Log A + b Log X. The regression was slightly curvilinear throughout the 40 to 80 mm size range (Figure 8). The computed values transform the equation to Log $\hat{Y}$ = -12.52 + 3.31 Log X.

Coefficients of Condition

In fisheries biology, the coefficient of condition is used primarily as an aid in determining the general physical status of fish stocks in different environments. The standard equation is:

$$K = \frac{W(10^5)}{L^3};$$

where K is the coefficient of condition, W is the weight of the fish in grams, L is the length of the fish in mm, and the factor 10^5 brings the value of K near unity.

Calculations were made on the basis of juvenile chinook salmon in 10-mm size groups from all primary stations combined (Table 5). K was lowest (1.08) for the 36-45 mm size group, i.e., the smallest fish emerging from the gravel in early spring and beginning to feed at low river temperatures. K values increased to the range of 1.3 to 1.4 for the larger size groups. Indices of FI for the

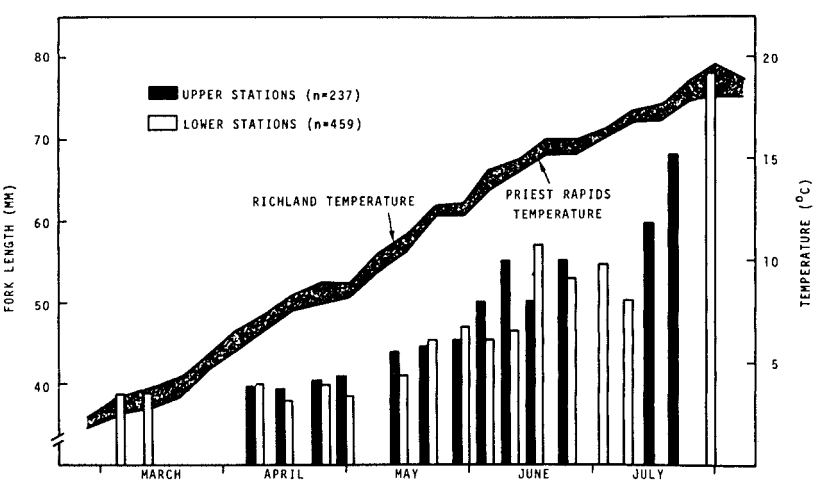

FIGURE 7.—Growth of juvenile chinook salmon at upper and lower stations, March-July 1969, in relation to Columbia River temperatures.

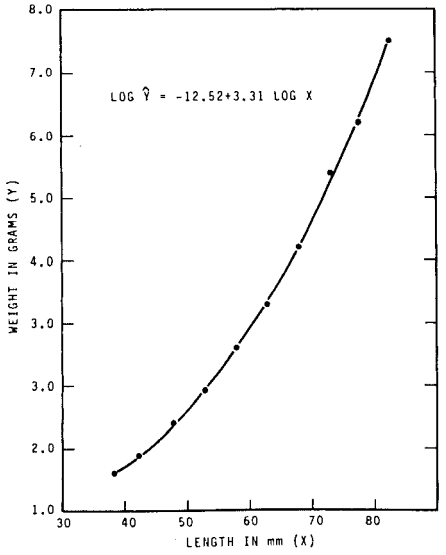

FIGURE 8.—Length-weight relationship of juvenile chinook salmon in the central Columbia River, March-July 1969.

various size groups, included in Table 5, show that the ratio of stomach food biomass to fish weight generally increases as the fish become larger. The *FI* value was low for the eight fish in the largest size group (76-85 mm) collected in late July.

DISCUSSION

Food Organisms

Distinctive features of feeding activity for juvenile chinook salmon in the central Columbia River appear to be fourfold: first, the fish utilize relatively few insect groups, predominantly Chironomidae; second, they depend largely upon autochthonous river organisms; third, they select prey drifting, floating, or swimming in the water; and fourth, they are apparently habitat opportunists to a large extent. These features are not necessarily unique among young salmonids in lotic environments. Here, in the free-flowing Columbia River, they demonstrate a close relationship with existing stream conditions.

Chironomids are of variable importance to the diet of juvenile chinook salmon in other streams. An early study conducted in the Sacramento River indicated that young chinook salmon consumed midges only to a limited extent, although floating and drifting insects did form the greatest portion of their diet (Rutter, 1904). Young chinook salmon in tributaries of the central Columbia River above Hanford in 1938 utilized few, if any, midges, although the fish fed almost exclusively on insects and the order Diptera was of greatest numerical importance (Chapman and Quistorff, 1938); these fish were relatively large, up to 152 mm, and were probably young spring chinook salmon. The food of juvenile chinook salmon in the middle Willamette River in 1958 was 39% Diptera, primarily midges, and 40% Ephemeroptera (Breuser, 1954). Emigrating chinook salmon in the lower Sacramento-San Joaquin system consumed primarily insects (90%) in 1964 but only 16% were midges (Sasaki, 1966). Adult and immature midges were a major dietary item of juvenile chinook salmon in the lower Chehalis River, along with other Diptera, Trichoptera, Plecoptera, and Ephemeroptera, in 1965 (Herrmann, 1970).

Published records reveal that insects dominate the food of other species of juvenile

TABLE 5.—Mean length, mean weight, coefficient of condition (*K*) and feeding intensity (*FI*) for 10-mm size groups of juvenile chinook salmon in the central Columbia River, March-June 1969.

Size group[1] (mm)	Number of fish	Length (mm)	Weight (g)	*K*	*FI*
36-45	411	40.5	0.72	1.08	0.33
46-55	177	50.1	1.63	1.30	0.51
56-65	57	59.1	2.76	1.34	0.55
66-75	27	70.1	4.68	1.40	0.63
76-85	8	79.0	6.53	1.33	0.25

[1] The few fish under 36 and over 85 mm in fork length were omitted.

salmonids in river habitats. However, the precise species of prey will differ between and even within various lotic systems because the existence and production of insect taxa is influenced by diverse edaphic factors.

Visual stimulation is important to the feeding of young salmonids (Chapman, 1966). Juvenile chinook salmon at Hanford exhibit considerable selection of living food organisms since nonliving material, such as insect exuviae and plant seeds, rarely occurred in their stomachs. Apparently this selection was due, in large part, to prey movement that evoked the feeding response. A preference for suspended organisms was also indicated, since benthic stages of aquatic insects were relatively unutilized by Hanford fish.

Determination of preference for a particular food organism depends on the ratios of ingredients making up the food complex and their occurrence in the stomach of fish (Allen, 1942; Ivlev, 1961). Although I obtained some invertebrate drift samples in the central Columbia River, which demonstrated an abundance of chironomid larvae, the data were inadequate for accurate determination of ratios over the entire season. Feeding apparently corresponded roughly to food organisms occurring free in the water, but not necessarily in proportion to the food actually available.

Chinook salmon fry consumed small midges most extensively whereas fingerlings tended to include larger insects in their diet. The relationship of increasing fish size to increasing food size in young salmonids has been recognized (Lindström, 1955; Hartman, 1958). Food utilized by small salmonids are subject to limitations imposed by the size of the fish whereas food utilized by larger fish can be very diverse (Mundie, 1969). However, diversity is clearly limited to what is available in a given ecosystem.

Ecological Aspects

The central Columbia River remains a large flowing river with a relatively vast water mass, rapid current velocities, and minimum shoreline habitat in relation to discharge volume. Living in stream environments requires considerable expenditure of energy that must be balanced by food consumption. Growth occurs only when energy provided by food exceeds energy expended in feeding and other activities. Energy can be conserved by juvenile salmonids in three ways: (1) leaving stream conditions to enter a lake or sea; (2) living in the stream below the main impact of the current; or (3) living predominantly in slack water, in pools, and in marginal back eddys (Mundie, 1969).

Examples of habitat selection associated with energy conservation can be noted. Young chinook salmon and steelhead trout, *Salmo gairdneri*, in Idaho streams inhabit velocities and depths in relation to body size, shifting to faster and deeper water as growth occurs (Chapman and Bjornn, 1969; Everest and Chapman, 1972). Similarly, chinook salmon fry in the Big Qualicum River, British Columbia, occupy marginal areas while the larger fish move into habitats of progressively higher velocity (Lister and Genoe, 1970). Since my samples were obtained entirely from shoreline areas that could be effectively seined, they reflect feeding in those habitats. A possible shift of larger fish to deep water would remain undetected.

Because metabolic rates of cold-blooded animals such as fish increase as temperatures rise, more food must be consumed for growth of juvenile chinook salmon to be maintained as the season advances and the water warms. My data show that feeding intensity, on the basis of both number of insects and total stomach biomass, tended to increase from March to July.

Although chironomids are small and individually low in nutritional value, they are utilized throughout the season by juvenile chinook at Hanford and their abundance compensates for a lack of size. The adult caddisflies appearing in June and July are large and provide greater nutritional value per individual at a time when temperatures are high and more energy is required for fish growth. By dry weight, 1 adult *Hydropsyche cockerelli* is equal to 35 adult midges. Although the calories available per gram of dry weight for chironomids (5,424) and hydropsychids (5,386) are nearly equal (Cummins and Wuycheck, 1971), considerably less energy is required to capture 1 prey organism than 35.

Invertebrate drift is important to the feeding of stream fish, and particularly so at Hanford. The significance of the drift phenomenon is that of increasing the availability of food and supplementing possible site limitations on insect production; moreover, under conditions of high discharge, the quantity of drift organisms passing downriver per unit of time is higher than under low flow conditions (Waters, 1969). If this is true for the central Columbia River, the annual spring spate increases the availability of food organisms to juvenile chinook salmon during their period of maximum abundance.

Changes in river water levels, both seasonal and regulated, appear to have unique significance at Hanford by exerting an influence on populations of aquatic insects and juvenile chinook salmon in inshore areas. The influence is apparent in at least four theoretical ways.

First, the annual increase in river discharge in April and May (Figure 2) inundates barren shoreline areas that are exposed to air during the preceding winter. Recolonization of flooded inshore areas by aquatic insects depends upon larvae in the drift, which may occur rapidly, or upon the deposition of eggs by adults. There are no available data on recolonization rates of recently inundated areas at Hanford. But detached insect larvae usually spend only a short time in the drift and re-attach as soon as possible (Elliott, 1967).

Second, weekly and daily variations in water level resulting from flow regulation at Priest Rapids Dam (Figure 3), which periodically floods and exposes vast stretches of shoreline areas, restricts insect recolonization and incorporates marginal dwellers into the river drift. On this basis, it is not surprising that the diet of juvenile chinook salmon includes food organisms that normally live along the shoreline such as *Notonecta* nymphs, adult springtails, and terrestrial Arachnida (spiders).

Third, station occupation by juvenile chinook salmon appears to be temporally limited. Young salmonids commonly occupy relatively small home areas (ecological niches) for a period of feeding and growth prior to seaward migration (Chapman, 1966; Edmondson, Everest, and Chapman, 1968; Chapman and Bjornn, 1969). Analysis of data from fish collected at the primary stations reveals considerable variation in sizes from week to week after mid-May. At least part of this variation must result from weekly changes in regulated water level at Priest Rapids Dam (up to 2 m in 24 hr on weekends) that implements population turnover.

Fourth, the eminent decline in river discharge volume from the annual spring spate (> 300,000 cfs) to the summer period of low flow($\simeq$40,000 cfs) suggests that the falling water level is one factor involved in prompting seaward juvenile chinook salmon still lingering at Hanford. At any rate, the seasonal increase and then decrease in river flows accompanied by rising temperatures (Figure 2) are the main environmental factors correlated with seaward migration. These phenomena, which have occurred annually throughout recorded history, may well have played an evolutionary role in the development of the spring migration characteristic for young fall chinook salmon produced in the Columbia River ecosystem.

ACKNOWLEDGMENTS

Numerous individuals provided assistance in various capacities. L. R. Heaton, E. F. Prentice, E. W. Lusty, O. L. Jackson, T. M. Clement, and E. G. Tangen aided in field collections. R. T. Jaske, Manager of Water Resources Systems, Battelle Northwest Laboratories, provided temperature and discharge data for the central Columbia River. C. E. Cushing and K. R. Price reviewed this manuscript.

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SOME ASPECTS OF THE ECOLOGY OF LANTERNFISHES (MYCTOPHIDAE) IN THE PACIFIC OCEAN NEAR HAWAII

THOMAS A. CLARKE[1]

ABSTRACT

Most species of myctophids collected near Hawaii showed ontogenetic differences in vertical distribution and migration. Newly transformed juveniles of several species did not regularly migrate. Within both day and night depth ranges, the smaller fish tended to occur shallower than the adults. Few differences were related to sex or reproductive condition. Large fractions of populations of three species appeared not to migrate at certain seasons. Seasonal changes in size composition of populations and ripeness of mature females indicated that most abundant species spawn principally in the spring and summer and live about 1 year. The size-depth patterns of congeners and closely related species were quite different, while similar-sized individuals of dissimilar species tended to co-occur at the same depths.

Comparison of day and night estimates of abundance and size composition indicated that there was little differential avoidance by most species. There were differences between catches by a 10-ft Isaacs-Kidd trawl and a modified Cobb pelagic trawl related to both species and size with neither trawl showing a distinct advantage for all species. Comparison of catches at full and new moon indicated that at full moon most species occurred about 50 m deeper and avoided the Isaacs-Kidd trawl better than at new moon.

The average standing crop of myctophids was about 0.32 g(wet weight)/m^2, and the yearly turnover rate was estimated at roughly twice the standing crop. Myctophids and other vertically migrating micronekton appear to be very important in the trophic structure of the tropical open ocean and probably account for most of the consumption of zooplankton.

Myctophids or lanternfishes are one of the dominant families of mesopelagic fishes and are generally thought to be important in the open ocean ecosystem because of their frequent occurrence and apparently great abundances. The bulk of early work was concerned primarily with taxonomy and distribution. Most recent work has concentrated on one aspect of their ecology, diurnal vertical migration. Myctophids have been shown in a number of cases, e.g., Paxton (1967), Badcock (1970), to undertake substantial migrations from depths of several hundred meters during the day to the upper 100-200 m at night, but few studies have done more than describe the vertical distribution patterns and suggest possible relationships of these to gradients in temperature or light with depth or with the position of sonic scattering layers. There are numerous gaps in our knowledge of other aspects of the ecology of this ubiquitous group of fishes. Moreover, previous work has not been equitably distributed in a geographic sense; most has been carried out at higher latitudes.

Among others, Badcock (1970) has indicated that there are size-specific differences in migration patterns of some species of myctophids, but ontogenetic changes in depth distribution have not been studied quantitatively. Similarly, Nafpaktitis (1968) has indicated that in some species of the genus *Diaphus* the mature females do not migrate. It is not known whether either of these patterns is typical or widespread within the family. Extensive life history data have been presented for some abundant northern species, *Benthosoma glaciale* (Halliday, 1970), *Stenobranchus leucopsaurus* (Smoker and Pearcy, 1970), and *Myctophum affine* (Odate, 1966), but the life histories of most species, particularly tropical ones, remain unknown.

This paper presents and discusses data on myctophids collected in several series of mid-

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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

water trawl samples taken in the Central Pacific Ocean near Hawaii. The majority of the samples were collected during four series which attempted to cover the upper 1,000 m day and night at 3-mo intervals over a period of 1 year. The aims of the sampling were to determine the vertical migration patterns of the species present and to examine changes in abundance, size composition, and reproductive state with depth and season. In addition, changes in vertical distribution and avoidance with changing phases of the moon were investigated, and the catching ability of a 10-ft Isaacs-Kidd mid-water trawl was compared with that of a much larger anchovy trawl. The results allow detailed description of many aspects of the life history and ecology of myctophids. It is possible from these data to consider interspecific relationships with respect to time and space and to estimate the importance of myctophids and other micronekton in the tropical, open ocean ecosystem.

MATERIALS AND METHODS

A total of 221 mid-water trawl samples were taken for this study. Fifty-four were taken with a 6-ft Isaacs-Kidd (IK) mid-water trawl, 157 with a 10-ft IK trawl, and 10 with a modified Cobb pelagic trawl (CT). All trawls were fished without opening-closing devices. Thirty-seven IK tows were taken during September and November 1969 to provide preliminary data. The remaining tows consisted of four general types: a series of 31 6-ft IK tows taken in July 1970 to check various aspects of sampling, four series of 26-35 10-ft IK tows each taken at 3-mo intervals from September 1970 to June 1971, 17 10-ft IK tows taken in September and October 1971 to determine effects of moon phase on sampling, and 10 CT tows taken in conjunction with the 10-ft IK tows during February-March 1971.

All tows except those of November 1969 were taken west of the island of Oahu, Hawaii, roughly along a line between lat. 21°20′N; long. 158°20′W and lat. 21°35′N; long. 158°35′W. The depth of water for all tows was 1,800 m (1,000 fm) or more. BT casts to 300 m made during the study indicated that seasonal temperature changes in the study area were nearly the same as for a nearby station (lat. 22°10′N; long. 158°W) studied more thoroughly by Gordon (1971). Presumably the depth profiles of other physical-chemical factors given by Gordon (1970, 1971) are also representative of the study area. The November 1969 tows were taken near Gordon's station.

The IK trawls were of standard dimensions and were lined with 6.35 mm (¼ inch) knotless nylon mesh anteriorly and 4.75 mm (3/16 inch) knotless nylon mesh posteriorly. The 10-ft IK terminated with a 1.0-m diameter plankton net of 333 μ nitex; the 6-ft, with a 0.5-m diameter net. The CT, described in detail by Higgins (1970), had 19-mm stretch mesh in the main body and a cod end lined with 6.35-mm mesh. Diver observations of the CT have indicated that the mouth opening under tow is about 12 m wide by 8 m high (Higgins, 1970).

IK trawls were fished from the University of Hawaii RV *Teritu*. Unless otherwise noted, the procedure was the same for all tows. The trawl was shot with the ship moving about 1.75 m/sec (ca. 3.5 knots), and the cable was paid out so that just enough tension was maintained to keep the net from fouling. For deeper (over 300 m) tows, the ship was slowed to ca. 1.0 m/sec for a few minutes after the cable was paid out to allow the trawl to sink farther. These procedures were designed to minimize forward motion while the trawl descended to towing depth. The trawl was towed at depth for 2-3 hr at a speed of about 1.75 m/sec. For retrieval, the ship was slowed to ca. 1.0 m/sec, again to minimize forward motion while the trawl was above sampling depth. Cable was retrieved as fast as possible; the average rate varied between 30 and 60 m/min. The rate was considerably faster than 60 m/min when there was more than 1,000 m of wire out. The CT was fished in a similar manner from the National Marine Fisheries Service (NMFS) RV *Townsend Cromwell*.

Depth of tow was determined by time-depth recorders (Benthos, Inc.)[2] attached to the trawl. For depths of less than 300 m the trawl reached

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

towing depth within a few minutes after cable was paid out and usually stayed within 5 m of this depth during the entire tow. For deeper tows, the trawl frequently took some time to descend to maximum depth and often moved up and/or down gradually during the tow. In all cases, however, a single, most frequently fished depth was assigned to each tow.

For some IK tows an acoustic telemeter (Benthos, Inc.) was used to determine depth while underway and to reach desired depth, but in most cases the amount of cable required to reach a given depth had to be estimated beforehand. This method required some practice, and, needless to say, depth coverage was more even for the later cruises.

Towing speed for the IK was, in some cases, measured by a TSK flowmeter attached to the trawl and rigged to signal, through the telemeter, every 500 revolutions. In all cases, position of the ship was determined by visual or radar fixes at ½- to 1-hr intervals during the tow and speed calculated from these data. The towing speed for the IK varied between 1.54 and 1.98 m/sec with most tows about 1.75 m/sec. The CT was towed at about 1.5 m/sec.

Assuming 100% filtering efficiency and a speed of 1.75 m/sec, the 10-ft IK sampled about 9.4×10^4 m^3 per 2-hr tow. At 1.5 m/sec, the CT sampled just over 10^6 m^3 per 2-hr tow or about 11 times the IK tows. Only fish over 10-mm long were considered sampled quantitatively by the IK since smaller individuals could pass through the meshes. Larger fish, up to 25-30 mm long, appeared to escape through the CT meshes.

The July 1970 (5-10 July 1970) series of tows with the 6-ft IK were designed primarily to determine whether significant changes in vertical distribution occurred in the upper layers during the course of night and to obtain an estimate of sample variability. At depths of 50 m and 100 m, five 2-hr tows were taken from dusk to dawn on a single night, and one replicate tow was made during the following night. Dusk, dawn, and night tows were taken at other depths in the upper 400 m. In addition, day tows were taken between 500 and 1,125 m.

The four quarterly series of 10-ft IK tows were designed to sample for seasonal changes and were intended to be replicate surveys of the upper 1,000 m both day and night. Since preliminary day tows caught no nonlarval myctophids above 300 m, no attempt was made to cover the upper layers during the day. The dates of the cruises were 14-17 and 20-24 September 1970; 8-10 and 13-17 December 1970; 26 February-3 March and 19 March 1971; and 8-11 and 15-19 June 1971. The series will subsequently be called September 1970, December 1970, March 1971, and June 1971. Depths sampled for these series and the July 1970 series are given in Figure 1.

In addition to some gaps in depth coverage during September 1970, the shallow night tows were made at both full and new moon. Subsequent analyses showed that the depth distribution and avoidance for many species changed considerably with moon phase, and as a consequence, some populations were sampled

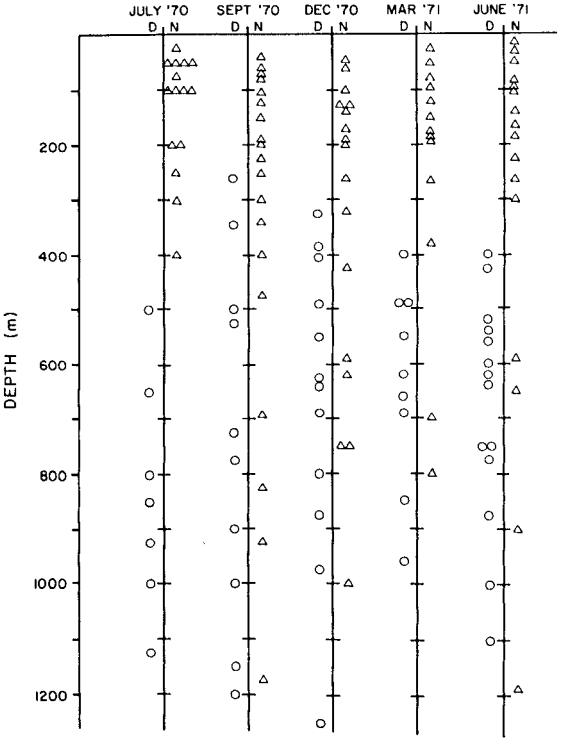

FIGURE 1.—Depths of Isaacs-Kidd trawl samples taken during July 1970, September 1970, December 1970, March 1971, and June 1971. Day samples are designated by circles, night samples by triangles.

twice and others not at all during the September 1970 series. This also occurred to a lesser extent during the December 1970 series. All night tows above 200 m were made during new moon for the March 1971 and June 1971 series. The March 1971 series was incomplete due to a storm, and the 400-700 m zone was not sampled at night. Such limitations are taken into account in interpreting the data.

The CT tows were taken in conjunction with the March 1971 IK series. Eight night tows were taken at 25-m intervals between 25 and 200 m during the same three nights that IK tows were taken at or near these depths. The IK-CT pairs were unfortunately not all taken simultaneously. All tows but one were 2 hr at depth; the 25-m CT tow was only 15 min long, but catches of some species were sufficient for useful analyses. Two day tows at 300 and 400 m were also taken with the CT during this period.

To determine effects of moon phase on vertical distribution and avoidance at night, 10-ft IK tows of 1½ hr each were made at depths of 15, 45, 65, 80, 100, 125, 145, and 165 m on 17-19 September 1971 (new moon) and at 20, 50, 75, 100, 130, 170, and 190 m on 4-6 October 1971 (full moon). This series, designated September 1971, also provided useful data on other aspects.

During December 1970 and June 1971, three and four, respectively, short oblique tows were made to depths of 250-300 m at night in order to roughly estimate the catch due to ascent and descent through the upper layers. The cable was paid out as described above, but the ship was slowed and the trawl retrieved immediately. A longer oblique tow was made in June 1971 to 330 m at night. Fifty meters of cable was paid out every 15 min in an attempt to sample all depths equally.

The dusk and dawn tows taken during July 1970 indicated that myctophids had completed their upward migration by 2000 hr and had begun to descend by 0400-0500 hr. All subsequent night tows were taken between these times. Differences between tows taken in sequence at 50 and 100 m through the night were not markedly greater than differences between tows taken at the same hour on two successive nights. There was no trend among the species which indicated that anything analogous to a "mid-night dispersal" occurred. Therefore, all night tows were considered together regardless of what period of the night they were taken. No comparable study was made to check on possible changes in depth distribution during the day. It was assumed that no changes took place during the day between 0800 and 1600 hr.

Specimens were preserved in Formalin. Standard length was measured to the nearest mm for all collected by IK. For some CT collections of over 1,000 individuals per species, a subsample of several hundred was measured. Wet weights of blotted specimens were determined to the nearest mg for small individuals and to the nearest 10 mg for larger fish or whole samples.

Insufficient replicate samples were taken to reliably specify the variance associated with the estimate of abundance from a single tow. There was considerable variability in the catches of the two series of four tows each taken at 50 and 100 m in July 1970. (Appendix Table 1.) In particular, one tow in the 100 m series caught much higher numbers of several species. This variability, probably related to patchiness in the organisms sampled and differences in avoidance due to differences in ship's speed, cloud cover (light), etc., limits interpretation of some of the data. Where I have drawn conclusions without statements of statistical significance, I have attempted to be conservative. Features not consistently evident from a series of tows should be regarded as tentative.

The significance of differences between two samples in size composition was determined using the Kolmogorov-Smirnov test (Tate and Clelland, 1957). Two samples were considered significantly different if the probability (one-tailed) associated with the maximum difference between the cumulative size-frequency curves was less than 0.05. The overall significance of the differences is somewhat altered because multiple tests were often made with the same data. In most cases, the trends observed were obvious and consistent, and it is doubtful that large errors resulted from the procedure.

There were relatively few significant differences in size composition between replicates at the same depth. For 10 sets of data for eight

species caught in abundance in the replicates at 50 and 100 m during July 1970, there were no significant differences between size-frequency curves in seven and only one sample in each of the other three sets differed significantly from one or more of the other replicates.

Not all individuals were sexed and no detailed gonad studies were done. Size at maturity was taken as the minimum size at which females were found with obviously ripened ova. A variable number of each species were examined. For abundant species, sex was determined for about 50 juveniles, and sex ratio of mature fish and ripeness of mature females were determined for samples from several depths and seasons. If significant or nearly significant differences between samples were noted, a larger series was examined to determine trends. It was assumed that the percentage of females among mature fish and the percentage of ripe out of total mature females were distributed as a binomial and that the differences in percentages were considered significant if the 95% confidence limits did not cross zero.

For species collected in low numbers, the data from each series were simply pooled to estimate overall size composition and relative abundances. For abundant species, total numbers and overall size composition for the entire water column were computed by a rectangular integration of the depth-abundance curves. Numbers collected were adjusted to a 2-hr towing time. It was assumed that abundance and size composition from the depth sampled were the same for the layer between the midpoints between that depth and the next shallower and next deeper depth sampled; i.e., abundance estimated from a sample at depth z_i was assumed constant throughout $(z_{i-1} + z_i)/2$ to $(z_i + z_{i+1})/2$ where z_{i-1} was the next shallower depth sampled and z_{i+1} the next deeper. The number of individuals of each size in each sample was weighted accordingly.

Differences in the numbers and size composition of these calculated totals could not be compared statistically since no estimate of the variances of the data were available, but where depth coverage was adequate, calculated totals and size-frequency curves were used to roughly compare whole series for day and night, seasonal, full and new moon, and IK and CT differences. The calculated size-frequency curves for December 1970 and June 1971 could be compared with those of the oblique tows when sufficient specimens of a given species were taken in the latter. Unless there were obvious deficiencies in depth coverage, etc., the calculated curves agreed closely with those from the oblique tows.

RESULTS

A total of 47 species of myctophids were collected. The number collected, size range, size at maturity for females, and day and night depth ranges are given in Table 1. Unless noted under individual species headings (below), the individuals caught did not deviate from species descriptions in Wisner (1971, manuscr.[3]), Nafpaktitis (1968), or Nafpaktitis and Nafpaktitis (1969).[4] The percentage of ripe females among total mature females examined for each of the four quarterly cruises is given for several abundant species in Table 2.

The depth ranges given in Table 1 are the best estimates based on all available data. Because the trawl was open during descent and ascent, some individuals were caught in tows made below the levels where they occurred. For abundant species, catches below the depth ranges given were low and consistently close to those of short oblique tows (see Appendix Table 2). A few cases where substantial numbers were caught near the day depth at night are discussed below under the species headings. For rarer species, where the chances of being caught in a tow at their actual depth were not much greater than the chances of being caught in transit by deeper tows, catches due to contamination could not be readily distinguished and the lower depth limits in Table 1 may be erroneous. In most cases, the values given are conservative.

[3] Wisner, R. L. Unpubl. manuscr. Annotated and illustrated key to the identification of fishes of the family Myctophidae of the eastern Pacific Ocean, eastward of 160° West Longitude.

[4] Specimens of most species will be deposited at the U.S. National Museum, Los Angeles County Museum, Scripps Institution of Oceanography, and the Bernice P. Bishop Museum in Honolulu.

TABLE 1.—List of myctophid species collected, the number collected, size range, size at maturity, night and day depth ranges, and seasons when juveniles were present or present in markedly higher abundances. Under "Number collected" the figures given are the totals from the four quarterly series of samples; where few or none were caught in these series, the total number caught in all other samples is given in parentheses. Figures in parentheses under "Size range" are for dipnetted specimens.

Species	Number collected	Size range (mm)	Size at maturity (mm)	Night depth (m)	Day depth (m)	Juveniles
Protomyctophum beckeri	0 (3)	34-38	—	400 ?	400 ?	—
Benthosema suborbitale	1,157	9-38	25	15-75	490-620	June (Mar.)
Benthosema fibulatum	14 (30)	10-72	—	15-165	500-550	—
Diogenichthys atlanticus	27	12-22	17	15-100	400-600	—
Hygophum proximum	696	12-51	38	25-150	500-700	June, July
Hygophum reinhardti	413	12-48	33	50-175	550-900	all ?
Myctophum nitidulum	18 (34)	13-54 (65)	57	0-15?	600-800	—
Myctophum obtusirostrum	15 (59)	12-63 (77)	58	0-15?	500-700	—
Myctophum spinosum	5 (32)	34-93 (115)	110 ?	0-15?	600 ?	—
Myctophum selenoides	14 (24)	9-67	62	25-150	300-500	Mar., June
Symbolophorus evermanni	186	15-86	70	0-125	600-900	—
Loweina laurae	2 (3)	22-43	—	250 ?	690 ?	—
Loweina terminata	1	22	—	—	825	—
Centrobranchus choerocephalus	22	12-37	29	0-150	490-650	—
Centrobranchus andreae	4 (6)	14-47	—	100-165	640-650	—
Lobianchia gemellari	177	9-59	41	25-360	410-560	June, July, Sept.
Lobianchia urolampa	1 (1)	25-26	—	100 ?	—	—
Diaphus bertelseni	6 (79)	17-38	—	100-150	300 ?	—
Diaphus "glandulifer"	37	12-73	55	95-225	425-600	—
Diaphus schmidti	823	9-47	31	15-80	490-625	June, July, Sept.
Diaphus fragilis	56	10-83	61	15-120	520-600	Sept.
Diaphus rolfbolini	104	9-76	65	50-200	490-690	June, July, Sept.
Diaphus elucens	132	7-65	48	15-100	490-600	Sept.
Diaphus adenomus	7	71-126	—	—	495-550	—
Diaphus chrysorhynchus	7 (27)	11-84	—	75-125	550	—
Diaphus metopoclampus	1	49	—	185	—	—
Diaphus theta	0 (1)	23	—	145	—	—
Diaphus sp. A	253	9-36	25	25-85	490-525	July, Sept.
Diaphus sp. B	165	9-64	42	30-190	490-560	June
Diaphus anderseni	261	10-29	20	95-260	300-560?	June, July, Sept., Dec.
Diaphus brachycephalus	100	9-61	28	30-200	300-600?	June, July, Sept.
Notolychnus valdiviae	1,267	9-25	20	80-150	525-640	Sept. (Mar., June)
Lampadena luminosa	77	15-77	—	75-250	525-725	June, July, Sept.
Lampadena urophaos	44	17-115	100 ?	95-140	620-775	—
Lampadena anomala	1 (2)	30-49	—	300-400	800	—
Taaningichthys bathyphilus	55	20-72	51	590-930	620-800	—
Taaningichthys minimum	71	20-64	53	150-475	640-775	Mar.
Taaningichthys paurolychnus	2	20-22	—	1,175	1,000	—
Lampanyctus niger	1,946	12-135	60	100-310	640-900	Dec. (Sept.)
Lampanyctus nobilis	384	15-114	98	40-140	590-1,200	all ?
Lampanyctus steinbecki	2,362	14-56	43	80-275	625-1,000	July, Sept.
Lampanyctus tenuiformis	14	28-136	125	250-300	640-775	—
Triphoturus nigrescens	2,120	9-38	30	25-75	540-775	June, July
Bolinichthys longipes	1,458	11-56	37	50-150	525-725	June, July, Sept.
Bolinichthus supralateralis	85	12-90	88 ?	95-225	490-690	Sept., Dec.
Ceratoscopelus warmingi	3,911	11-79	45	15-140	620-1,000	Mar., June, July
Notoscopelus caudispinosus	6 (17)	20-125	111 ?	75-125	590-680	—

Eight species—*Protomyctophum beckeri*, *Loweina laurae*, *L. terminata*, *Centrobranchus andreae*, *Diaphus metopoclampus*, *D. theta*, *Lampadena anomala*, and *Taaningichthys paurolychnus*—were taken so rarely that little other than their capture in the area can be noted. For 39 species, the individual accounts below include where possible the following aspects: deviations from depth ranges given in Table 1; changes in size composition and sex ratio with depth; differential avoidance between day and night, IK and CT, and full and new moon; and changes in size composition, abundance, and reproductive state with season.

TABLE 2.—Proportion of females with developed ova among total mature females (figures in parentheses) examined for 10 species from September 1970 and 1971, December 1970, March 1971, and June 1971 samples. Significant differences between values are noted in text.

Species	September		December		March		June	
Benthosema suborbitale	0.39	(18)	0.98	(62)	1.00	(38)	—	(0)
Hygophum proximum	.78	(37)	.72	(7)	0.91	(22)	0.86	(22)
Diaphus schmidti	.375	(8)	—	(0)	.88	(59)	1.00	(11)
Diaphus sp. A	.96	(46)	1.00	(8)	.89	(9)	1.00	(14)
Notolychnus valdiviae	.70	(54)	.71	(69)	.91	(11)	.89	(38)
Lampanyctus niger	.35	(51)	.76	(95)	.88	(69)	.53	(47)
Lampanyctus steinbecki	.64	(42)	.44	(22)	.81	(103)	.78	(122)
Triphoturus nigrescens	.54	(13)	.39	(142)	1.00	(41)	.94	(36)
Bolinichthys longipes	.67	(12)	.12	(17)	.81	(70)	.88	(17)
Ceratoscopelus warmingi	.60	(102)	.62	(124)	.52	(48)	.70	(27)

Differences in sex ratio with size and season are of somewhat dubious significance and will be treated in the discussion.

Benthosema suborbitale

Small (10-12 mm) *B. suborbitale* tended to remain at depth both day and night. On all three cruises where night samples were taken near the day depth, low but probably significant numbers of small fish were taken. In June 1971, the number caught at about 550 m was nearly equal to that caught at 25 m at night and at the same depth during the day. In all cases except the June 1971 series the size-frequency curves of the deep night catches differed significantly from those of most other tows, the differences being due to much greater proportions of 10- to 12-mm fish in the deep night tows. There was no evidence that larger fish did not migrate regularly.

The depth ranges for this species were rather narrow relative to the sample spacing, and populations at a given time were usually made up of one size class. There were, however, significant differences between the size-frequency curve at 25 m and those at 50 and 80 m in March 1971. The difference was due to the absence of fish <25 mm at 50 and 80 m rather than a decrease of larger fish at 25 m. Other night series also showed a trend for smaller fish to occur higher in the water column.

There was no indication of differential day-night avoidance. The calculated size-frequency curves for day and night samples from each series agreed quite well with each other, except for June 1971. The total calculated numbers agreed well in June 1971, but for the other series, the day totals were 1.5 – 2× higher than the night totals. This difference was probably a result of the weighting factors assigned to the day tows being too large, i.e., the depth range was probably narrower than the relatively wide-spaced samples indicated.

The IK appears to sample *B. suborbitale* as well or better than the CT. The calculated total for the CT series was 7× that for the IK; factors for individual pairs varied between 4.2 and 8.8×. There were no significant differences between size-frequency curves of IK-CT pairs at the same depths, and the calculated curves for the two series agreed well. The fact that the CT size-frequency curves did not differ from those of the IK suggests that the lower CT estimates of abundance were not due to escapement through the meshes. If the latter had been substantial, the smaller fish would have escaped more frequently, and size composition of the catches would have differed from those of the IK.

At new moon, *B. suborbitale* occurred mostly above 50 m at night; at full moon the population was centered at about 75 m with practically none above 50 m (Figure 2). The size-frequency curves of both the individual samples and those calculated from the new and full moon series agreed closely. The numbers at peak depths were similar, and the calculated total for new moon was only 1.25× that for full moon. Thus the change in depth distribution apparent in the full moon samples was mainly if not totally due to a depression of the night depth by about 50 m.

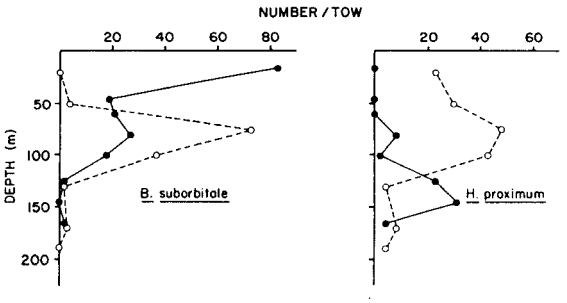

FIGURE 2.—Number of individuals of *Benthosema suborbitale* (left) and *Hygophum proximum* (right) caught per tow at several depths in the upper layers at night during new moon (solid circles and lines) and full moon (open circles, dashed lines) during September 1971.

Size composition and abundance showed a definite seasonal pattern. In June 1971, about 70% were 10-15 mm; there were a few adults and practically no intermediate sizes. The calculated size-frequency curves (Figure 3) shifted to the right from June to March indicating changes in size-composition due to growth. Though calculated day totals were higher than night totals for all but the June 1971 series, the rank order was the same for both, abundances being highest in December, lowest in June, and intermediate and nearly equal in September and March.

It appears that *B. suborbitale* spawns principally in the spring and summer. A few young (10-15 mm) are present by March and many by June. A substantial portion are 20-25 mm long

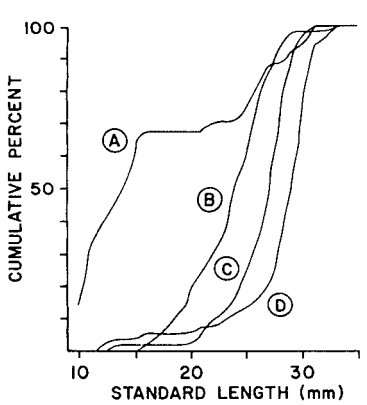

FIGURE 3.—Cumulative size-frequency curves for *Benthosema suborbitale* at four seasons. Size composition was calculated (see text) from samples taken throughout the water column in June 1971 (A), September 1970 (B), December 1970 (C), and March 1971 (D).

by September, but apparently not all have reached the minimum size caught by the trawl until later. Most fish are mature by December when maximum abundance occurs. There is apparently little growth in size between December and March and a decrease in total numbers. By June, most of the adults are gone and the next generation has begun to reach trawlable size. The percentages of mature females with ripe ova (Table 2) correlate with these trends; they were significantly higher in December and March, before the periods when juveniles appeared.

Benthosema fibulatum

B. fibulatum is apparently epibenthic or restricted to nearshore areas. In Hawaii, large individuals (45-95 mm) are regularly taken in bottom trawls at depths of 100-190 m at night (P. J. Struhsaker, pers. comm.), and large catches have been made by NMFS in CT tows at 25-100 m over areas where the bottom depth is about 600 m. Only eight of the individuals taken during this study were of the size taken by inshore trawls, 40-72 mm. The rest were 15-27 mm and mostly taken in the upper 100 m at night.

Diogenichthys atlanticus

D. atlanticus, although quite abundant in the Equatorial Pacific (Hartmann, 1971), was captured rarely in Hawaiian waters. About 80% of the individuals collected were adults, but the presence of 11- to 15-mm fish several times of the year suggests some spawning may occur in this area.

Hygophum proximum

In June 1971, nine small *H. proximum* (12-14 mm) were caught at about 650 m at night. As low as this catch was, it was higher than any shallow night catch and unlikely due to contamination. Similar numbers of this size were caught near this depth during the day and none in the shallow night tows, suggesting that the smallest *H. proximum* caught by the trawl do not regularly migrate. Individuals of this

size were, however, taken in shallow night tows during July 1970 and March 1971.

H. proximum appeared to avoid the IK at night more during new moon (see below) and was sampled best by the CT and by the full moon IK series. Both of these series indicated similar depth distribution but different trends in size composition with depth (Figure 4). In the CT series the curves for 75, 100, and 125 m were all similar and differed significantly from those at 25 and 50 m. Over 50% of the deeper catches were less than 30 mm, most about 20 mm. In the 25- and 50-m catches, which also differed significantly from each other, only 30% and 10% individuals were under 30 mm. Comparison of curves from IK catches at new moon during December and March 1971 also showed significant differences, with only the larger fish occurring above 50-60 m and smaller ones predominating deeper.

In the September 1971 series, the size-frequency curves for full moon tows at 25 and 50 m differed significantly from each other and

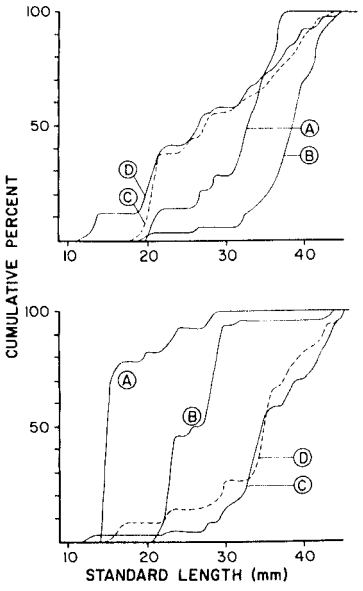

FIGURE 4.—Cumulative size-frequency curves for *Hygophum proximum* collected at different depths in the upper layers at night. Top: Cobb trawl samples taken at new moon during March 1971; depths of tows and number of individuals were: 25 m, 14 (A); 50 m, 150 (B); 75 m, 276 (C); and 100 m, 83 (D). Bottom: Isaacs-Kidd samples taken at full moon in September 1971 at 20 m, 23 (A); 50 m, 30 (B); 75 m, 48 (C); and 100 m, 43 (D).

from the curves at 75 and 100 m. The catch was almost all <15 mm at 25 m, 20-30 mm at 50 m, and over 30 mm for the deeper tows. In full moon tows during September 1970 at 80 and 100 m, the size-frequency curves differed significantly and indicated that most fish at 80 m were <30 mm and most at 100 m were >30 mm.

In the daytime during September 1970, size-frequency curves for *H. proximum* differed significantly, with a greater proportion of juveniles in shallower water. In March 1971 and June 1971, similar nonsignificant trends were present. All data indicated that individuals over 40 mm rarely occurred above 600 m.

At new moon during September 1971, high catches were made at 125 and 150 m with a few at 80 m (Figure 2). At full moon, catches were high between 20 and 100 m with practically none deeper. The calculated total for full moon was 3× that for new moon, and the calculated size-frequency curves indicated that new moon tows had missed most of the larger fish. These data, combined with the changes in size composition with depth, indicate that the smaller fish occur about 75-100 m deeper at new moon and the adults about 25-50 m shallower at new moon. The latter, however, appear to avoid the IK much more at new moon. Consequently, *H. proximum* was not sampled well by most IK night series.

The CT data also indicate that avoidance of the IK by larger fish was substantial. The calculated total for the CT series was 14.5× that for the March 1971 IK night series, and calculated size-frequency curves indicated much lower proportions of larger fish in the IK catches. The greatest difference was at 75 m where the IK caught only 5 as opposed to the CT's 276. Comparison of individual size-frequency curves indicated that some fish under 20 mm probably passed through the CT's meshes. Thus avoidance of the IK by larger fish is even greater than indicated by comparison of the calculated totals.

The calculated totals were much larger for the day series in March 1971 and June 1971, but day and night totals were close for September 1970 when the night tows in *H. proximum*'s depth range were taken during full moon. (Few were caught in December 1970 during day or

night.) Both of the September 1970 estimates were close to that for full moon in September 1971. Thus there appears to be less avoidance of the IK during the day than at night during new moon.

For March 1971, the calculated total from the CT series was only about 3.7× that of the day IK series, and the calculated size-frequency curves for the two series agreed closely. Thus the IK appears to sample *H. proximum* by day better than the CT at night. Since day tows and full moon night tows with the IK appear to sample this species about equally well, the IK may give better estimates of abundance and size composition than the CT at full moon. Kuba (1970) found that the IK sampled *H. proximum* better than the CT in night tows in equatorial waters. Most of his tows where this species was caught were taken near full moon.

The calculated day totals indicated that *H. proximum* was distinctly more abundant in September and March than in December or June. The calculated size-frequency curves for March 1971 and September of both years were similar and indicated that most fish were mature or nearly so. None less than 15 mm were caught in September or December, but a few 10-15 mm were caught in March 1971. Fish 12-14 mm long were present in fair numbers during the June 1971 series and abundant in July 1970. This suggests that *H. proximum* spawns principally in spring or early summer. The percentages of mature females with developed ova were highest in March and June but did not differ significantly from the other values.

Hygophum reinhardti

H. reinhardti was less abundant and occurred slightly deeper than its congener, *H. proximum*, but the data indicated that similar sampling problems existed. So few *H. reinhardti* were caught in the March 1971 IK series that it was impossible to make quantitative comparisons with the CT data, but it appeared the IK missed substantial numbers at 75-100 m and sampled about as well as the CT in deeper water. Though catches were low during both September 1971 series, the full moon series caught overall higher numbers and indicated a shallower night depth than the new moon series. In all four regular series, catches of day tows were generally higher than those of night tows.

Size-frequency curves from the CT series indicated no trends in size composition with depth. The curves for IK tows in September 1970 at 150 and 195 m differed significantly with few fish >20 mm at 195 m and few <20 mm at 150 m. Three-day tows in September 1970 showed no individuals over 20 mm at 520 m and most over 20 mm at 775 and 900 m. There were no obvious seasonal changes in abundance. Juveniles (<15 mm) and females with developed ova were present at all seasons.

Myctophum spp.

Three species of *Myctophum*—*M. nitidulum*, *M. obtusirostrum*,[5] and *M. spinosum*—apparently occur at or near the surface at night. They were regularly dipnetted at the surface at night, but few were caught in the trawls, even in preliminary tows at 10-m depth. Individuals considerably larger than the trawl-caught specimens were frequently taken by dip net. These species are relatively solid-bodied and are probably strong swimmers. They probably avoid the trawl easily in the process of avoiding the ship itself.

The few day catches of these species were mostly from 500 to 800 m but may well have been due to contamination. These species are distinctly countershaded, and in life the upper color is quite blue, suggesting that they occur at shallow, well-lighted depths during the day where they can avoid the trawl. Nevertheless, the rarity of even small individuals in the trawl catches indicates that none of the three were abundant.

Myctophum selenoides

At night, small (<30 mm) *M. selenoides* were taken mostly between 50 and 100 m. The larger fish were below 100 m and mostly around 150 m. Only three were taken during the day, one by

[5] *Myctophum obtusirostrum* is the correct name for the species called *M. branchygnathum* by Nafpaktitis and Nafpaktitis (1969) and others (B. G. Nafpaktitis, pers. comm.).

CT at 300 m and two by IK at 500 m. The low numbers of juveniles as well as adults in the trawl catches suggest that rarity of *M. selenoides* was not due to avoidance. Small fish (8-13 mm) were caught only in March and June 1971, indicating that this species spawns locally—probably in the spring.

Symbolophorus evermanni

The larger individuals of *S. evermanni* are undersampled by the IK. Kuba (1970) showed this in Equatorial Pacific waters. During March 1971 CT catches were 28-35/tow as compared with 1-2/tow for the IK at similar depths. The CT tows indicated that *S. evermanni* was most abundant at 50-100 m at night and showed no differences in size frequency with depth. On one occasion, November 1969, several large individuals were dipnetted at the surface.

Day tows with the IK caught no individuals above 500 m and most between 600 and 800 m. A few substantial catches, 6-8/tow, came from 800 to 900 m. There was some indication that fish <20 mm do not regularly migrate; particularly in September 1970, most of the shallow catches were larger fish, and most small individuals were taken in night tows around 800 m.

Centrobranchus choerocephalus

Most catches of *C. choerocephalus* were at 550-650 m during the day. The night depth appeared to be between 100 and 200 m for both IK and CT samples, but on one occasion, September 1969, seven individuals were dipnetted at the surface.

Lobianchia gemellari

L. gemellari was never taken in large numbers. At night, all individuals caught above 100 m were <25 mm, and those over 40 mm were caught only below 150 m. The CT series, which caught fair numbers, also showed this trend with significant differences in size-frequency curves. Substantial catches of larger fish were made as deep as 300 m at night, but there were no differences in sex ratio or percentage of ripe females between deep and shallow catches of adults.

There was no evidence that this species avoided the IK better than the CT nor that there was a day and night difference in avoidance of the IK. Also the depth distributions and abundances in full and new moon were not grossly different.

The pooled IK data indicated that juveniles, <25 mm, were most abundant in the summer (July 1970, June 1971) and least so in December 1970. Curiously, there were few juveniles present in September 1970 but many in September 1971. Adults were most abundant in March 1971 when few juveniles were present.

Lobianchia urolampa

Only two juvenile *L. urolampa* were taken in this study. This species is apparently nearshore or epibenthic. Adults (48-99 mm) have been taken in bottom trawls at depths between 124 and 190 m at night (P. J. Struhsaker, pers. comm.).

Diaphus bertelseni

The identity of this form with the Atlantic *D. bertelseni* is not certain since only one large individual was taken. The species was caught on only two occasions. Many were taken in the March 1971 series including 70 in one CT tow at 125 m at night. One each was taken at 300 and 400 m with the CT during the day suggesting that this species has a shallow day depth. All March 1971 specimens were between 17 and 31 mm—most between 17 and 25 mm. The only other individual taken was a 38-mm specimen from 100 m at night during the July 1970 series.

Diaphus "glandulifer"

The form designated here as *D.* "glandulifer" appears to be an undescribed species (R. L. Wisner, pers. comm.). Gill raker counts were mostly $8+1+15-16$, lower than those for *D. glandulifer* from the Western Pacific (Wisner, see footnote 3). Accessory luminescent tissue occurred regularly in specimens over 30 mm

at POL, VLO, SAO-3, Pol, and Prc-4. In 8 out of 20 specimens over 50 mm, there was accessory tissue at PO-4, VO3, or both.

Only small (<20 mm) *D.* "glandulifer" were caught above 150 m, the larger individuals being around 200 m and deeper at night. This species was rare at all seasons, and most specimens were either in a 27-39 mm group or over 45 mm. Catches of a few less than 20 mm suggest that this species may occasionally spawn in the area.

Diaphus schmidti

There was no indication that any sizes of *D. schmidti* sampled by the trawl did not regularly migrate to the upper layers at night. There were significant differences in size-frequency curves from different depths at night. The number and percentage of juveniles (<25 mm) were greatest around 25 m. The number of larger fish was greatest at 50 m, but the percentages of small and large fish were roughly equal. At 75-80 m most or all the individuals were larger. Only the day samples from March 1971 were spaced closely enough to suggest that there were similar size-frequency changes within the day depth range.

Because *D. schmidti* occurred over a relatively narrow depth range during the day and was frequently caught in only one tow per series, it was impossible for some series to assign realistic weighting factors for calculation of total numbers. However, the calculated night size-frequency curves agreed closely with those of the day samples.

The calculated size-frequency curves for CT and IK in March 1971 agreed quite closely, but the calculated total for the CT was 15× that of the IK. The difference in totals was due to relatively much greater catches by the CT at 75 and 100 m. The CT caught only 1.7 and 6.3× the IK at 25 and 50 m, but caught 65 and 45× more at 75 and 100 m, respectively. The pairs of individual size-frequency curves at 25 and 50 m differed significantly and indicated that the IK caught more larger fish, while the curves at 75 and 100 m from the CT did not differ from those of the IK at 80 m. Since both large fish and juveniles occurred shallower and only large fish deeper, it appears that the CT undersampled larger fish in shallow zones and the IK undersampled them in deeper zones.

The full moon samples indicated that peak depth was around 75 m and caught none at 20-50 m where new moon tows indicated maximum abundance. The calculated total for full moon was about three-fourths that of new moon, and the calculated size-frequency curves indicated a somewhat larger proportion of juveniles during full moon. Thus *D. schmidti* occurs deeper at full moon, and larger individuals may avoid the net more frequently.

D. schmidti apparently spawns in late spring and summer and matures in about 1 year. In June 1971, the population consisted mostly of either juveniles or adults with few individuals between 20 and 30 mm. Both juveniles and 20- to 30-mm individuals were present in September 1970 and 1971. In December 1970, almost all were 20-30 mm, and in March 1971, almost all were over 30 mm. Percentages of ripe females were significantly higher in the March and June 1971 series than in the September 1971 series. Practically none were mature in December 1970.

Diaphus fragilis

D. fragilis was caught most frequently at night at 25-50 m (new moon) and 100-125 m (full moon). The CT catches were low and did not indicate that this species was avoiding the IK in appreciable numbers. *D. fragilis* was distinctly more abundant in September 1970 and 1971 and least so in December 1970 and March 1971. It is one of the dominant species of myctophids in Pacific equatorial waters (Hartmann, 1971) but its presence in low numbers near Hawaii cannot be ascribed entirely to immigration. Fair numbers of small (<20 mm) individuals were caught in September, suggesting that some spawning occurs in the summer.

Diaphus rolfbolini

Pooled size-depth data indicated that *D. rolfbolini* <20 mm occurred principally above 100 m, those 20-45 mm around 100 m, and

those over 45 mm below 125 m. *D. rolfbolini* was caught in roughly similar numbers at all seasons; however, trends in size composition were evident from the pooled data. In July 1970, September 1970 and 1971, and June 1971, 50% or more of the catches were <20 mm. In December 1970, almost all were between 20 and 40 mm, and in March 1971, both CT and IK catches were mostly between 45 and 55 mm. Individuals over 55 mm were present in low but consistent numbers all year round and may be more than 1 year old.

Diaphus elucens

D. elucens showed definite changes in size composition with depth at night. Size-frequency curves from the CT series in March 1971 differed significantly. There were two size groups present at that time, 32-47 mm and 49-63 mm. The smaller size group made up 80%, 73%, and 20% of the catches in tows at 50, 75, and 100 m, respectively. The number of smaller fish was roughly equal in the two shallower tows and those of larger fish comparable in the two deeper ones. In September 1971, full moon, 98 individuals 7-11 mm long were caught at 20 m, and 12 of 13-17 mm at 50 m. Few of these sizes were taken in deeper water where some larger individuals were caught. No trends could be recognized in the daytime samples.

The pooled IK data indicated that *D. elucens* spawns in late summer and reaches maturity in about 1 year. In June 1971 and July 1970, most individuals were over 40 mm. In September 1970 there were two distinct size classes, 10-13 mm and over 46 mm with practically none in between. In September 1971, new moon, there was a broad group 10-29 mm and a few over 50 mm. In the full moon series, there was a distinct group at 7-11 mm, a smaller group at 12-18 mm, and practically none larger. In December 1970, 70% were 23-41 mm, and in March 1971, the two size groups mentioned above were present in both IK and CT data.

Diaphus sp. A and B

D. sp. A and B are superficially similar to each other and resemble most closely *D. mollis* from the Atlantic, but both appear to be distinct species. All but the smallest specimens can be readily distinguished. Species A has a rounded opercular margin, and the eyes of Formalin-preserved specimens are distinctly green. In species B, the upper opercular margin is distinctly angular or hooked, and the eyes are yellow-white. The counts for fully developed gill rakers were usually 4+1+10 for species A and 5+1+10−12 for species B. Species B matures at and reaches a much larger size than species A.

Species A was taken in abundance (>10/tow) only 13 times, and size-frequency curves could be compared only for samples from the July 1970 and March 1971 CT series. These both indicated significant differences with the smaller fish occurring in shallower water. The one daytime comparison possible, in September 1970, showed no difference between tows at 500 and 575 m. There was no evidence that any sizes did not migrate regularly.

There were no obvious differences in abundance and size frequency between day and night tows. Two CT tows in March 1971 caught species A similar in size composition to the two positive IK tows, but the CT catches were highest at 50 m and substantial at 75 m whereas the IK indicated a peak at 25 m and only a few at 50 m. At new moon, the depth of highest catch was at 45 m and at full moon was at 75 m. The catch at new moon was about 5× that at full moon, indicating greater avoidance as well as depression during full moon.

Abundance was distinctly higher during July 1970 and September 1970 and 1971 with the largest proportion of small fish at these times. Abundance was distinctly lowest in June 1971 and almost all were adults. These data suggest that species A spawns in the summer and reaches maturity in about 1 year. However, the condition of the ovaries did not indicate a restricted spawning season; 89-100% of the mature females were ripe at all seasons (Table 2).

Only the juveniles (<15 mm) of species B occurred above 100 m. Abundance was highest in June 1971 and most of the catch was juveniles

at that time. Juveniles were also present in July 1970 and September 1971.

Diaphus anderseni

At night, adults of *D. anderseni* occurred mostly around 200 m whereas the juveniles (<13 mm) were found only around 100 m. *D. anderseni* had one of the shallowest day depths (Table 1) and most limited migrations of all the species considered, the adults covering only about 100-200 m each night. In all series but March 1971, catches were mostly small juveniles and adults, but in March 1971 both CT and IK tows indicated the population was composed entirely of intermediate-sized fish. Apparently this species spawns over the greater part of the year.

Diaphus brachycephalus

Numbers of *D. brachycephalus* were quite low except in September 1970 when large numbers of juveniles (<20 mm and most <15 mm) were collected around 50 m at night. The larger individuals caught at 150-200 m were mostly females. Five of the 10 larger males (over 40 mm) taken at night were caught below 300 m, suggesting that the larger males migrate little or not at all. Presence of 9- to 12-mm fish in June, July, and September and their absence in December and March indicated that *D. brachycephalus* spawns in the summer. The June and September samples included both very small and adult fish; the March samples were mostly intermediate sizes (15-30 mm) suggesting that this species reaches adult size within 1 year.

Diaphus adenomus and *D. chrysorhynchus*

D. adenomus and *D. chrysorhynchus* are both apparently epibenthic and associated with shallow water. *D. chrysorhynchus* (54-98 mm) is frequently taken in bottom trawls at 75-190 m at night and *D. adenomus* (41-153 mm) at 180-185 m at night. Both are taken down to 500-600 m during the day (P. J. Struhsaker, pers. comm.). Individuals of the sizes taken near the bottom were rarely caught in mid-water. The *D. adenomus* were all taken during the day by IK. Thirteen of the *D. chrysorhynchus* collected were larger fish (56-84 mm). These were taken sporadically at all seasons, eight of them in the upper layers at night. The remaining 21 specimens were all 11-17 mm and all taken in the upper layers at night during the September 1971 series, 11 of them in one tow at 80 m. This suggests that this species spawns in late summer and that the young are pelagic. Unless substantial numbers of adults of these species are able to avoid both CT and IK, it appears that the larger fish caught pelagically were wanderers.

Notolychnus valdiviae

Significant differences in size-frequency curves from several series indicated that smaller *N. valdiviae* occurred higher in the water column. In both September 1970 and 1971 series, the catch at night at 80-100 m was almost totally <15 mm and at 115-145 m mostly over 20 mm. In other series, single pairs differed significantly, but trends were not as obvious because most of the fish were of one size class. Two day tows in September 1970 at 525 and 725 m also differed significantly with 60% of the fish <20 mm in the shallow tow and over 90% >20 mm in the deep tow.

In September and December 1970, night catches of *N. valdiviae* near the day depth were larger than that expected from contamination. Substantial catches were also made in the upper layers during these series. In September 1970, roughly 70% of the population remained at depth. There were relatively more larger fish in the nonmigrating fraction (Figure 5). In December 1970, roughly 50% did not migrate, but there was little difference in size composition between shallow and deep catches. There were no significant differences in either sex ratio of mature fish or ripeness of mature females between the shallow and deep night catches. There was no indication that any sizeable fraction of the population did not migrate in either March or June 1971.

The calculated totals for day and night agreed fairly closely and indicated no differential avoidance. Likewise, the calculated size-

frequency curves were quite similar. The agreement of numbers and curves was closest for June 1971. This indicates that since the night data were all from shallow tows, most, if not all, of the population migrated at that time. There was little point in comparing CT-IK data since most fish were apparently small enough to pass through the coarser CT meshes.

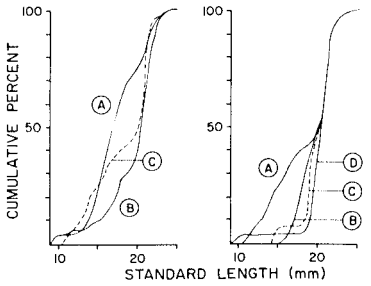

FIGURE 5.—Cumulative size-frequency curves calculated for *Notolychnus valdiviae* (left) from samples taken during September 1970 in the upper layers at night (A), near the day depth at night (B), and during the day (C); and (right) from samples taken throughout the water column in September 1970 (A), December 1970 (B), March 1971 (C), and June 1971 (D).

The new moon series in September 1971 indicated the population was mostly between 75 and 145 m while at full moon it was between 130 and 190 m. The calculated size-frequency curves agreed closely, but the new moon series calculated total was about 3× that of full moon. This suggests that *N. valdiviae* occurs about 50 m deeper and avoids the net better during full moon. The latter seems questionable since even adults are quite small and unlikely to avoid the trawl. Although full moon tows below 200 m in other series made no substantial catches, it is possible that some of the population was below the deepest depth sampled during the September 1971 full moon series.

Both day and night calculated totals indicated that *N. valdiviae* was distinctly most abundant in September and least so in March; the values for December were slightly higher than those for June. Both September series indicated large proportions and numbers of smaller (<15 mm) fish. A few small fish were present in March and June, but in December none were <17 mm (Figure 5). The percentages of mature females with developed ova for March and June were significantly higher than those for September and December.

Lampadena luminosa

No individuals of *L. luminosa* over 32 mm were caught above 100 m at night, but a few, 16-24 mm, were taken shallower. The rest of the catches, of both large and small fish, were mostly between 150 and 250 m. Five fish, 16-18 mm, were taken during the day at 525-550 m, but most day catches of all sizes were between 650 and 750 m. In June 1971 and July 1970, the catch was almost exclusively <25 mm fish; in September these small fish still predominated but there were also several 25- to 40-mm individuals caught. Only one specimen was caught in December 1970, and in March 1971, 80% of the catch was over 35 mm. None of the individuals captured were mature, suggesting that the adults are larger than the maximum size collected and likely take more than 1 year to mature.

Lampadena urophaos

L. urophaos was caught rather sporadically; only one each was caught at night in September and December 1970, and none during the day in December 1970 or June 1971. All sizes appeared to be present throughout the ranges given. One fish 18 mm long was caught in December and several <30 mm were taken in March, June, and July. Otherwise, most of the fish were 35-65 mm with a few individuals over 90 mm. One ripe female, 98 mm, was collected in March.

Taaningichthys bathyphilus

T. bathyphilus was taken regularly between 600 and 1,000 m and occasionally deeper both day and night. Highest catches were between 700 and 800 m. It was the only myctophid which definitely did not migrate. Size composition of the catches was roughly similar at all seasons with most individuals 30-60 mm long.

Taaningichthys minimus

Other reports, e.g., Davy (1972), have stated that *T. minimus* does not migrate, but all night catches in this study were well above the day depth range. Individuals 20-30 mm long were caught between 150 and 250 m at night and larger fish between 200 and 400 m. None were taken in night tows below 475 m. Of 32 fish caught in March 1971, 27 were 20-24 mm and only 1 was over 50 mm. In other seasons, all were over 30 mm, and most over 50 mm, suggesting that *T. minimus* spawns principally in late winter or early spring. Too few mature females were taken to correlate gonad ripeness with the changes in size composition.

Lampanyctus niger

Most *L. niger* less than 25 mm long were taken at depth both day and night, indicating that the majority of the smaller fish do not regularly migrate. In December 1970, no individuals under 50 mm were caught in the upper layers, and large catches with about 50% larger than 50 mm were taken near the day depth at night (Figures 6 and 7). The mature individuals taken in deep night samples did not differ from those of shallower samples in sex ratio or percentage of ripe females. Smaller peaks at depth during the night were present during other series, but catches of fish over 25 mm could not be discriminated from contamination.

In the upper layers at night, the size-frequency curves from catches above 150-165 m were usually significantly different from those in deeper tows (Figure 7). Few individuals over 50 mm were caught above 165 m, and below 200 m, 50-100% of the catches were over 50 mm. Similar stratification by size was evident in some day series and suggested, nonsignificantly, that individuals less than 50 mm rarely occurred deeper than 750 m.

The calculated totals for day and night agreed well for all but the June 1971 series (day was 1.6× night). The calculated size-frequency curves differed greatly for the September 1970 and June 1971 series. The difference for September 1970 may well have been due to missing

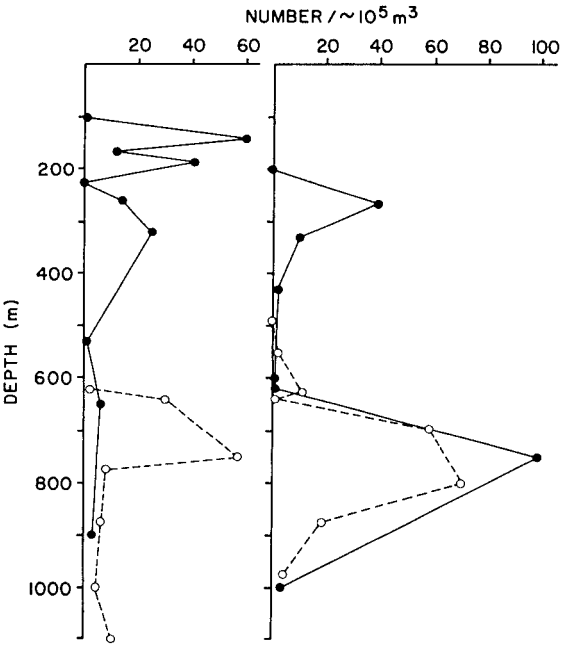

FIGURE 6.—Depth-abundance profiles for *Lampanyctus niger* from samples taken by Isaacs-Kidd trawl during June 1971 (left) and December 1970 (right). Night samples are designated by solid circles connected by solid lines; day samples by open circles and dashed lines. Numbers collected were adjusted to a 2-hr towing time with volume filtered of ca. 10^5 m^3.

juveniles at depth at night. The discrepancies for June 1971 were principally due to an exceptionally large catch of 30- to 36-mm fish at 140 m at night.

L. niger, especially the larger individuals, apparently avoided the CT more than the IK. The ratio of CT to IK catches was low (1.2-5.8) for all depth pairs except at 100 m where the CT caught 18 to only 1 in the IK. The calculated total for the CT was only 2.3× that for the IK tows above 200 m. The individual size-frequency curves were significantly different in three of four pairs but not consistent in direction. The calculated size-frequency curves indicated that the CT caught lower percentages of 50- to 70-mm individuals.

During the new moon series, *L. niger* was caught at 145 and 165 m—the deepest samples, but at full moon none were caught. It is not known whether all of the population occurred below 190 m, the deepest depth sampled at full moon, or whether there was increased avoidance.

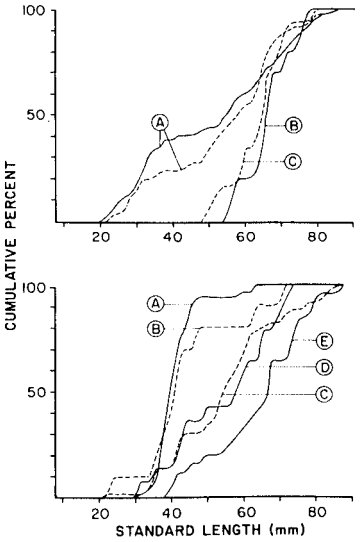

FIGURE 7.—Cumulative size-frequency curves for samples of *Lampanyctus niger* collected at different depths at night. Top: December 1970—two samples from 750 m of 119 and 174 individuals (A); 320 m, 10 (B); and 250 m, 39 (C). Bottom: June 1971—140 m, 60 individuals (A); 165 m, 12 (B); 185 m, 41 (C); 260 m, 14 (D); and 300 m, 25 (E).

The calculated totals indicated for both day and night series that *L. niger* was most abundant during December 1970; the figures for other series were all similar and about one-half of those from December 1970. Except for slightly higher percentages of smaller (<40 mm) fish in December and September 1970, there were no distinct differences in the calculated size frequencies. The percentages of mature females with developed ova for both December 1970 and March 1971 were significantly higher than those for June 1971 and September 1970. Together these data indicate that *L. niger* spawns principally in the early part of the year and that most of the juveniles are recruited to the trawlable population by December.

NOTE (Added in press)

The name *Lampanyctus niger*, used above, included both individuals with weakly developed pectoral fins and those without pectoral fins. Recently, M. A. Barnett informed me that, in specimens collected north of Hawaii, there are differences in other features which correlate with the presence or absence of pectoral fins. All of our specimens have been reexamined and, regrettably, there appear to be at least two forms present. The taxonomic status of these forms cannot be evaluated. A world-wide revision of species of the *Lampanyctus niger-ater-achirus* complex will be necessary to fully elucidate the problem (cf. Nafpaktitis and Nafpaktitis, 1969). Consequently, the text above was left unaltered, and the following supplementary data is offered here. The latter must be regarded as tentative since it was impossible to identify all specimens with certainty due to damage during collection.

Roughly one-half the specimens have no pectorals. These, designated as Form A, also differ from the others in that the PVO_2 photophore is well separated from PVO_1 and above the level of PO_4. The SAO_3 is usually posterior to AOa_1, and AOa + AOp is 5-6 (rarely 4) + 6-7 (rarely 8) = 12-13 (rarely 11). Form A appears to reach maturity at about 57-58 mm and reaches a maximum size of 74 mm.

In the remaining specimens, the pectoral fin was variously developed but always present. The PVO_2 was closer to PVO_1 and at or below the level of PO_4. SAO_3 was usually anterior to or above AOa_1. The majority of these had AO counts of 5(4) + 6(7) = 11. These, Form B, reached maturity at about 70 mm, and the maximum size was 84 mm. Among the specimens with pectorals, the eleven largest individuals (85-125 mm) and about two percent of the smaller ones had higher AO counts—5-6 + 6-7 (rarely 8) = 12-13 (14). None of these larger fish were mature, suggesting the presence of a third form, Form C.

Thus there appear to be two very similar forms that were common and roughly equal in abundance and a larger, much rarer form. The depth distributions, migrations, size-depth patterns, and seasonal changes of Forms A and B are quite similar and essentially as described above under *Lampanyctus niger*. The co-occurrence in abundance of two such similar forms contrasts with the patterns of most other closely related species. Further investigation of not only the taxonomic status, but also the geographic distribution of these forms will be necessary to determine if, as with the *Hygophum*

spp., Hawaii is near the edge of their ranges. Little can be said about Form C; it appears to have a depth distribution and migration pattern similar to those of the other two.

Lampanyctus nobilis

L. nobilis apparently does not begin migrating until about 25-30 mm long. A few small fish were taken in shallow tows at night, but most were taken at 625 and 750 m at night during September and December 1970. The absence of small individuals in deep night tows during March and June 1971 was probably due to widely spaced sampling since substantial numbers of small ones were caught in day tows then. There was no evidence that other sizes did not migrate regularly.

There were few instances where enough *L. nobilis* were taken to make comparisons of size composition and depth, but several pairs of size-frequency curves showed significant differences. Individuals <30 mm were mostly above 75-80 m at night, and most fish below 100 m were >40 mm. All night catches of exceptionally large individuals (16 of >95 mm) were below 100 m. During the day, catches above 750-800 m were almost all <25-30 mm, and the only substantial catches of fish >40 mm were at 1,150 and 1,200 m in September 1970. The only mature individual caught during the day, 100 mm long, came from a tow at 1,250 m. It is possible that the lower end of the day depth range was not adequately sampled.

L. nobilis avoids the IK in substantial numbers. In March 1971, the CT tows indicated a depth range similar to that of the IK series (Figure 8), except that a large catch was made at 175 m, below a catch of almost none at 150 m. The size-frequency curve from the 175 m CT tow looked like a composite of the shallower tows. This catch was likely due to excessive contamination and was disregarded. The calculated total for CT was 18× that for the IK principally due to catches at 100 and 125 m which were 21.4× and 24.8× the IK catches at these depths. The size-frequency curves for individual pairs differed significantly and like the calculated total curve indicated that the IK missed individuals over 40-45 mm. Thus

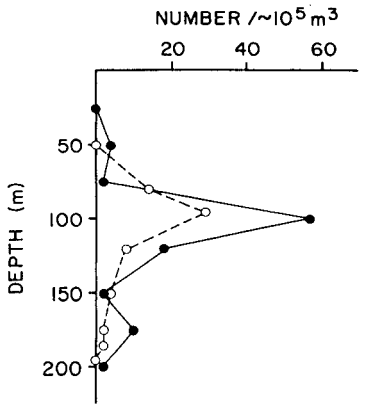

FIGURE 8.—Estimates of abundance of *Lampanyctus nobilis* at different depths at night during March 1971 from samples with the Cobb trawl (CT) (solid circles and lines) and Isaacs-Kidd trawl (IK) (open circles, dashed lines). CT catches were adjusted to the same volume filtered by 2-hr tows with the IK, ca. 10^5 m^3.

L. nobilis was probably about twice as abundant as the IK tows indicated.

At new moon in September 1971, *L. nobilis* occurred between 60 and 125 m with peak abundances at 75 and 100 m. At full moon, the only individual caught was from 190 m. Tows below 200 m taken during full moon in other series made no substantial catches. Thus the difference between the new and full moon series was probably due to greatly increased avoidance at full moon.

There were no gross seasonal differences in abundance or size composition apparent from the IK data except that *L. nobilis* may have been slightly less abundant in June 1971. Small (<25 mm) fish were present in comparable numbers in September 1970, December 1970, and June 1971 (the proper depth zone was not adequately sampled in March 1971 day or night).

With the exception of a 78-mm individual, all ripe females were over 97 mm and were rarely caught—once in September, once in March, and twice in June. The presence of juveniles indicated that spawning regularly occurs in the area, and the presence of immature sizes in fair abundance suggests that adults should be more abundant than catches of either IK or CT indicated. It seems likely that these larger fish avoided both trawls in substantial numbers.

Lampanyctus steinbecki

All postlarval *L. steinbecki* appeared to migrate regularly. Within the night and day depth ranges, the size-frequency curves were usually displaced to the right with increasing depth (Figure 9). The differences were significant only in September and December when several size classes were present in abundance. In these cases the differences were due to changes in absolute numbers of both small and large individuals, the shallower samples being composed almost entirely of juveniles and the deeper ones of adults only. Consistent, significant differences in size-frequency curves of day samples indicated that adults (>40 mm) occurred mostly below 850-900 m and few smaller fishes occurred at these depths.

The percentages of females among mature fish tended to decrease with depth in the March 1971 night samples. The values for samples from 95, 120, 135, 175, and 265 m were 82, 63, 64, 55, and 44%, respectively. The only significant differences were between the highest value and the two lowest ones. There were some significant differences among the June 1971 night samples, but no trend with depth was evident.

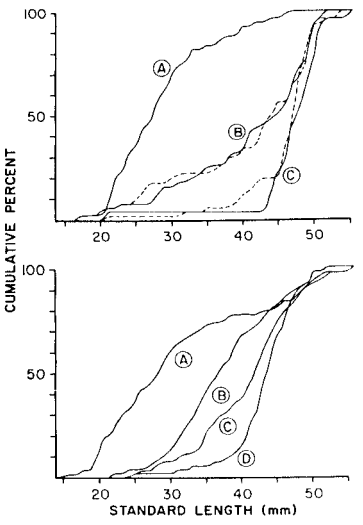

FIGURE 9.—Top: Cumulative size-frequency curves for samples of *Lampanyctus steinbecki* collected at night during new moon, September 1971, at depths of 80 m, 58 individuals (A); 100 m, 59 (B, solid line); 125 m, 46 (B, dashed line); 145 m, 49 (C, dashed line); and 165 m, 28 (C, solid line). Bottom: Cumulative size-frequency curves for *L. steinbecki* calculated from samples taken throughout the water column in September 1970 (A); December 1970 (B); March 1971 (C); and June 1971 (D).

The calculated totals were higher for the day series in all cases. The day totals were relatively highest for the September and December 1970 series (2× and 1.6× night totals, respectively) and were probably in part a result of poor timing of the night samples with respect to moon phase. For March and June 1971 the day totals were about 1.5× higher than night. Except for December 1970 the calculated size-frequency curves for day and night series were quite similar. Thus all sizes appear to avoid the IK better at night.

The individual CT tows caught from 0.7 to 4.5× their paired IK tows, and there was no obvious trend in differences of the size-frequency curves. The calculated curve for the CT was displaced slightly to the right of both night and day IK curves for March 1971, but the calculated CT total was only 3.4× the night IK total. Apparently *L. steinbecki* avoids the CT more than the IK.

During new moon in September 1971 the peak depths were at 80 and 100 m, and at full moon none were caught above 120 m. The catches at 170 and 190 m at full moon both exceeded the peak catches at new moon. The water column totals were nearly equal, but the full moon calculated curve and the individual curves were displaced far to the left of new moon curves indicating substantially greater numbers of 20- to 40-mm individuals. The new moon tows seemed to miss substantial numbers of juveniles; and if large numbers of larger fish occur below 190 m at full moon (there was some evidence for this from full moon tows in other series), it is possible that full moon tows may also sample the larger fish better. The increase in night depth with full moon, about 100 m for the juveniles, was about twice that observed for other species.

Both day and night calculated totals indicated that *L. steinbecki* was least abundant in March 1971 and present in comparable numbers during the rest of the seasons. The calculated size-frequency curves (Figure 9) indicated that 80% of the individuals were immature in September

1970, with 50% under 30 mm. In December 1970, most fish were still immature, but the peak size group was 30-40 mm. In March and June 1971, about 65 and 90% of the fish, respectively, were mature. The percentages of ripe females among mature females were highest in March and June 1971 and were significantly lower than all others in December 1970. Thus *L. steinbecki* appears to spawn principally in the spring and summer and to reach trawlable size by September. Most fish appear to live about 1 year.

Lampanyctus tenuiformis

L. tenuiformis differs from *L. steinbecki* principally in size at maturity and relative positions of a few photophores. Counts of fin rays, etc., for the two species were either identical or overlapping. Individuals over about 40 mm could be distinguished by the relative development of the gonads, but it is possible that some smaller, damaged *L. tenuiformis* were erroneously identified as *L. steinbecki*. Owing to the former's rarity, as evidenced by the few larger individuals, any error is almost certainly negligible.

Only four *L. tenuiformis* were taken at night, and the larger two of these (120 and 138 mm) were taken in tows near the day depths. Thus the night depth range given in Table 2 is quite uncertain. *L. tenuiformis* appears to spawn near Hawaii; four females (123-138 mm) with ripened ova and two small juveniles (28 and 32 mm) were collected.

Triphoturus nigrescens

T. nigrescens <15 mm were caught only in a night tow at 650 m in June 1971, suggesting that small juveniles do not migrate. In December 1970, high catches of larger fish were made during the night both in the upper layers and at the day depths. Calculated totals indicated roughly 60% of the population did not migrate. Calculated size-frequency curves for shallow night, deep night, and day samples all were quite similar and also agreed closely with the curve from fish taken in three short night oblique tows from 0 to 300 m. Differences in sex ratio and percentage of mature females with developed ova between the deep and shallow samples were small and nonsignificant.

Large numbers of more than one size class were caught only in July and September 1970. There were significant differences between size-frequency curves indicating that fish <20 mm occurred mostly above 50 m at night and above 650 m during the day. Adults occurred mostly below 50 m at night and below 650-700 m during the day.

Owing to low numbers in June 1971 and poor timing of shallow night tows in September 1970, day and night comparisons could be made only for December 1970 and March 1971. The day calculated totals were larger in both series, 1.3× for December 1970 and 3.8× for March 1971. The larger discrepancy in March 1971 may have been due to missing nonmigrating fish at night. The calculated size-frequency curves for day and night agreed closely.

The CT tows in March 1971 caught only 2.5-4× the IK tows; the calculated total for the CT was 2.6× that for the IK night series. The calculated size-frequency curve for the CT was nearly identical to both the day and night IK curves, and most fish were over 30 mm. Apparently *T. nigrescens* is better able to avoid the CT, but it is possible that some fish of even the larger sizes could have escaped through the coarser CT meshes.

T. nigrescens appears to have a 1-year generation cycle with spawning principally in spring and summer. Abundance was distinctly highest in December and extremely low in June and September 1971 with substantial and roughly equal numbers present in September 1970 and March 1971. *T. nigrescens* was also abundant in July 1970 with most of the population either adults or <20 mm. In September 1970, 65% of the population was 20-28 mm with few adults, and in December, 85% were over 25 mm. In March 1971, 85% were over 30 mm and none <24 mm. In June 1971, the catches were made up almost entirely of adults or fish <15 mm. The conditions of the ovaries were correlated with the changes in size frequency. The percentages of mature females with developed ova (Table 2) were low

in September and December 1970 and were significantly higher in March and June 1971.

The decline in abundance observed for *T. nigrescens* in June and September 1971 was the most dramatic change observed among all the species during the study period. The difference between the series in July and September 1970 and those of June and September 1971 suggest that either spawning success or larval survival was markedly lower in 1971. The only obvious factor correlated with this change was a significant increase in the percentage of females among mature fish in June 1971. Whether there was a causal relationship between the two changes cannot be determined from the data.

Bolinichthys longipes

Apparently almost all *B. longipes* of the sizes sampled regularly migrate. The only indication of nonmigration was a catch of seven small (12-14 mm) individuals at 650 m during the night in June 1971; individuals of these sizes were caught frequently during the day tows but rarely at night in the upper layers suggesting that some small individuals do not migrate. Within each series there were relatively few significant differences between size-frequency curves of the separate tows. These indicated that the smaller fish tended to be found shallower at night. Differences between day tows clearly indicated (Figure 10) that few fish less than 20 mm occurred deeper than 625 m and few larger than 30 mm occurred above this depth.

In the March 1971 night samples, the percentages of females among mature fish decreased with depth. The values were 73% at 80 m, 59% at 95 m, 32% at 120 m, and 46% at 135 m. The first two values were significantly different from the latter two. Insufficient mature fish were caught to compare values at different depths in other series.

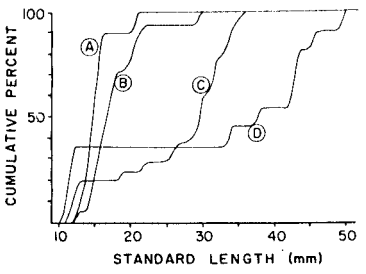

FIGURE 10.—Cumulative size-frequency curves for samples of *Bolinichthys longipes* collected during the day during June 1971 at depths of 560 m, 11 individuals (A); 600 m, 18 (B); 620 m, 21 (C); and 640 m, 11 (D).

The calculated totals agreed well for the day and night series, but calculated size-frequency curves differed for almost all pairs. Depth coverage was best for the March and June 1971 series, and the calculated curves were closest for the March 1971 series. The curves for the June 1971 series differed mostly because of a greater frequency and number of small individuals in the day. The numbers caught were quite low for all tows of this series, and inclusion of seven small individuals from a deep night tow (see above) in the calculations brought both the calculated totals and curves into very close agreement for the June 1971 series.

The CT tows indicated that peak depth was at 75-100 m and caught fair numbers of *B. longipes* at 25-50 m where the IK caught few or none. The IK peak depth was at 100 m and substantial numbers were caught at 125 and 135 m where CT catches were relatively low. The ratios of CT to IK numbers were 9.4 and 5.6 at 75 m and 100 m, respectively, but only 1.1 at 125 m. The calculated CT total was 5× that for the IK. The IK and CT size-frequency curves were similar at 75 m but differed significantly at 100 and 125 m due to larger percentages of fish over 35 mm in the CT catches. The calculated CT curve was displaced to the right also due to higher percentages of fish over 35 mm. Thus it appears that the CT sampled *B. longipes* as well or better than the IK above 100 m, but in the deeper zones the IK gave higher estimates of abundance in spite of missing some larger fish.

At new moon, *B. longipes* was abundant between 60 and 125 m and peaked at 80-100 m. At full moon, practically none were caught above 130 m and the peak was at 170-190 m. Full moon tows in other series indicated that few occurred deeper. The new moon catch at 60 m and the full moon catches at 130 and 170 m were similar in size composition; almost all fish were <20 mm. The 190-m curve at full

moon resembled those from 125 m and 145 m at new moon. The calculated total for full moon was 1.4× that for new moon and the calculated size-frequency curves differed considerably. Both differences were due to larger catches of 17- to 23-mm fish at full moon. Both these data and the CT-IK comparisons indicate that the IK missed some smaller fish in the upper layers at new moon. If these differences are real, they could in part account for the apparent lower numbers and percents of juveniles estimated in night series (see above).

There were substantial numbers of juveniles (<20 mm) in the June, July, and September series with few in December 1970 and practically none in March 1971. The percentages of mature females with developed ova (Table 2) were highest in March and June 1971 and significantly lower in December 1970. These suggest that spawning occurs principally in spring and summer and that the juveniles have reached trawlable size within a few months.

Bolinichthys supralateralis

No *B. supralateralis* over 53 mm long were taken above the day depth range. Out of 15 such individuals, only 3 were caught during deep night tows. These could well have been contaminants and do not clearly confirm that the larger individuals do not migrate. However, out of 50 smaller fish caught at night, 10 were caught in tows within the day depth range suggesting that all sizes may not regularly migrate. In the upper layers at night, fish less than 20 mm occurred between 100 and 200 m, but only two between 20 and 30 mm and none over 30 mm were caught above 200 m. All sizes appeared to occur throughout the day depth range.

The pooled IK size-frequency data indicated that *B. supralateralis* spawns principally in late summer and fall and that it may take at least 2 years to reach maturity. There were distinct, well-separated size classes in all but the March 1971 series where only 11 fish were caught. Small fish, 12-20 mm long, were most abundant and made up the majority of the catch in September and December 1970. It appeared that this group was represented by 24- to 35-mm individuals in June 1971. A second year class was suggested by size classes present only in the December 1970 and June 1971 series (41-53 mm and 47-59 mm, respectively). A few fish larger than 60 mm were caught in all series and may represent a third year class. The only female with developed ova was 88 mm long, almost the largest specimen taken. It is likely that such large individuals avoid the trawl in addition to being rather rare.

Ceratoscopelus warmingi

The smallest *C. warmingi* regularly collected in the trawl do not appear to regularly migrate. At night, individuals 15-19 mm long were caught both between 20 and 100 m and at 600-700 m. In June 1971, when these sizes were most abundant, about two-thirds of the juveniles remained at depth. There was no indication that larger fish did not regularly migrate.

Within both day and night depth ranges the size-frequency curves differed significantly. Except during June 1971, at night few fish over 40 mm were caught above 50 m and few smaller individuals were caught below 75 m. In the June 1971 series, however, large numbers of 15- to 19-mm fish were caught down to 140 m, throughout most of the night range. During the day, few individuals over 20 mm occurred at 600-700 m, and larger individuals occurred principally below 750-800 m.

At night the percentage of females among mature *C. warmingi* tended to decrease with depth. In March 1971, when large numbers of mature fish were caught at several depths, 89% of the mature fish from 25 to 30 m were females. At 50 and 80 m the value was 64%, significantly lower. The value at 95 and 100 m was 33%, and at 120 m was 31%. Both were significantly lower than the values from shallower tows. Similar, but nonsignificant, trends were present in the September and December 1970 series. The only day series where sufficient numbers of mature fish were collected at several depths was in December 1970; there were no trends or significant differences in percentages of females.

Comparison of day and night series was possible only for the June 1971 series due to poor timing of the night samples with respect to moon phase in September and December 1970 and inadequate coverage in March 1971. Both the calculated totals and size-frequency curves for June 1971 agreed quite closely. Since about 85% of the fish in this series were <20 mm, any differences for larger fish would be difficult to detect, but the other series showed no obvious indications of differential day-night avoidance.

The CT caught only 4 × as many *C. warmingi* as the IK at 25 m, but outfished the IK by factors of 12-14 × between 50 and 100 m. The calculated CT total was 7.4 × the IK total; when only fish over 25 mm were included, the factor was 8.3. The size-frequency curves were similar at 25 m but differed significantly for the deeper tows, the CT catching larger proportions of larger individuals. The calculated curves differed similarly, even when only fish over 25 mm were included. Apparently, some of the smaller fish passed through the CT meshes, thus accounting for the differences at 25 m where these fish were more abundant, but the CT appeared to sample the larger fishes, particularly those over 35 mm, better than the IK.

At new moon in September 1971, the depth of peak abundance was at 45 m, and the majority of the population was between 15 and 100 m. During full moon, the peak depth was at 130 m, and the population was mostly between 100 and 170 m. The calculated total for new moon was about twice that for full moon, and the new moon tows caught slightly larger proportions of fish over 35 mm.

The calculated totals indicated that *C. warmingi* was present in comparable numbers in December 1970, March 1971, and June 1971 and much less abundant in September 1970, but the calculated size-frequency curves differed greatly (Figure 11). In June 1971, the population was about 90% juveniles (14-17 mm), and in December 1970, about 60% were over 40 mm with few under 20 mm. In March 1971, 70% of the juveniles were 20-40 mm, and in September 1970, most were either under 25 mm or over 45 mm. Changes in the numbers of juveniles accounted for most of the changes in abundance,

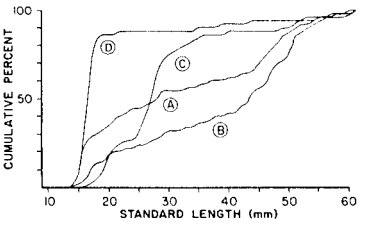

FIGURE 11.—Cumulative size-frequency curves of *Ceratoscopelus warmingi* calculated from samples taken throughout the water column in September 1970 (A); December 1970 (B); March 1971 (C); and June 1971 (D).

but adults were definitely most abundant in December 1970 and almost absent in June 1971.

The large numbers of immature fish in March 1971 (particularly, a peak at 25-30 mm) suggest that some recruitment had taken place between December and March. The size composition of the population in June 1971 indicated a springtime spawning also. The percentage of ripe females was highest in June 1971, but none of the differences between series were significant. It appears that *C. warmingi* spawns over a long season, but principally during the first half of the year, and that there are either peaks within this season or marked fluctuations in larval and juvenile mortality.

Notoscopelus caudispinosus

N. caudispinosus was captured very rarely, but several fish, 20-25 mm, caught in March and June 1971 suggest that it may spawn in this area or nearby. It is possible that the larger individuals avoid both the CT and IK and are more abundant than the collections indicate.

DISCUSSION

Rare species

The majority of the species collected were rather rare. Only 19 species were present in moderate to high abundance and showed strong evidence of spawning in the area. A few of the rarer species appear to have primary centers of abundance elsewhere. The single *Diaphus theta* collected was certainly an expatriate from North Pacific transitional waters (Paxton, 1967), and four species are restricted to nearshore waters

(*Benthosema fibulatum*, *Diaphus adenomus*, *D. chrysorhynchus*, and *Lampadena urolampa*). *Diogenichthys atlanticus* and *Diaphus fragilis* are more abundant in Equatorial Pacific waters (Hartmann, 1971). The principal range of *Lampanyctus tenuiformis* is not clearly known.

Nineteen of the rarer species—*Protomyctophum beckeri*, *Myctophum* spp., *Loweina* spp., *Centrobranchus* spp., *Diaphus bertelseni*, *D. metopoclampus*, *D. "glandulifer," Lampadena luminosa*, *L. anomala*, *Taaningichthys* spp., *Bolinichthys supralateralis*, and *Notoscopelus caudispinosus*—appear to be typical of central or equatorial-central waters but are nowhere commonly collected (Bekker, 1966; Nafpaktitis, 1968; Nafpaktitis and Nafpaktitis, 1969; Gibbs et al., 1971; Wisner, 1971; Davey, 1972). Five of these species—*Myctophum selenoides*, *Diaphus* "glandulifer," *Lampadena luminosa*, *Taaningichthys minimus*, and *Bolinichthys supralateralis*—appear to spawn in the study area. *Lampadena urophaos*, although designated as a transitional water mass species by Paxton (1967), would appear to belong with the above group. It appears to spawn in this area, and a rough comparison of the present study's and Paxton's catch per effort indicates that it is more abundant near Hawaii.

Avoidance

Although it was not possible to set confidence limits for the calculated totals and size-frequency curves, in most species the differences between day and night totals were not large enough to suggest that there was substantially greater avoidance at either time. The exceptions, *Lampanyctus steinbecki* and the *Hygophum* spp., were sampled better during the day than at new moon at night. They also apparently avoid the IK better at new moon than at full and may be sampled equally well by night tows at full moon and day tows.

These results contrast with those of Pearcy and Laurs (1966) off Oregon. They noted substantial differences in day-night avoidance among mesopelagic fishes. The differences were in the opposite direction of the few noted in this study; most of their species avoided the net better during the day. Pearcy and Laurs used a 6-ft IK, and perhaps the larger trawl used in the present study sampled fishes relatively better during the day.

The IK-CT comparisons show that, as Harrisson (1967) and others have suggested, no single net will adequately sample all species. The IK gave higher estimates of overall abundance than the CT for many species analyzed, but greatly underestimated the abundance of two species, *Symbolophorus evermanni* and *Lampanyctus nobilis*. The CT sampled the *Hygophum* species better at night during new moon, but the IK probably samples them as well or better during the day or during full moon at night. Even allowing for escapement of small fishes through the CT meshes, the CT caught higher proportions of larger fishes of some species, e.g., *Ceratoscopelus warmingi* and *Lampanyctus steinbecki*. Neither net effectively sampled the mature sizes of *Lampanyctus nobilis*, *Lampadena luminosa*, and *Bolinichthys supralateralis*.

There was evidence for some species that one trawl sampled better at some depths only. The IK appeared to sample *Hygophum reinhardti* and *Bolinichthys longipes* as well or better than the CT at the deeper end of their night depth ranges, but the CT sampled as well or better at the shallower end. For *Diaphus schmidti* and *Diaphus* species A, the CT appeared to underestimate abundance at the shallower end of the depth range and caught relatively more fish at the deeper end. Obviously, more data are needed since one or two very high or low catches could have produced these results.

Harrisson (1967) using only roughly comparable pairs of samples, suggested that a larger otter-type trawl towed at 1 m/sec caught more larger fish than an IK towed at 1.5 m/sec. Aron and Collard (1969), however, have shown that towing speed had an important effect on an IK's estimates of abundance and size composition for one of the more abundant species collected in their study. Kuba (1970) found that in the Equatorial Pacific, the IK at 2 m/sec sampled most species' abundance and size composition as well or better than the CT at 1.5 m/sec. It would appear that the higher speed used for the IK tows in this study gave

a greater overall advantage than the increased "stealth" of the larger CT.

The full-new moon series indicated that most species occurred deeper at full moon and that several avoided the trawl better at full moon. The *Hygophum* species appeared to do just the opposite. The changes suggest that it is best overall to sample the upper 200 m at new moon only. A mixed sampling program can result in some populations being sampled twice and the depth range and abundance overestimated, or most of the population being missed and abundance underestimated.

Most species appeared to occur 50-75 m deeper at full moon. Data presented by Clarke (1970), however, indicate that in clearest ocean water, the depths of isolumes at full moon are about 200 m greater than at new moon. This suggests that the fishes occurred at higher light levels at full moon and may explain the increased avoidance noted then. The data of Blaxter and Currie (1967) indicate that this is possible. They observed that the depth of a sonic scattering layer was depressed by artificial light but to a light level about 10 times brighter than that at which the layer normally occurred.

Intraspecific Variations in Migration

Most myctophid larvae appear to occur in the upper layers (Ahlstrom, 1959). Whether they descend just prior to or just after metamorphosis is not known, but at least some species do not begin to undertake regular, extensive diurnal migrations immediately after metamorphosis. The data indicate that the recently metamorphosed juveniles of *Benthosema suborbitale*, *Lampanyctus niger*, *L. nobilis*, and *Ceratoscopelus warmingi*, and possibly *Hygophum proximum*, *Symbolophorus evermanni*, and *Bolinichthys longipes*, do not regularly migrate. More thorough sampling of the deeper layers at night with opening-closing devices may show this to be a general feature of myctophids.

Nafpaktitis (1968) has suggested that gravid females of some myctophids do not migrate. No evidence of this was found. The larger males of *Diaphus brachycephalus* and the larger individuals of *Bolinichthys supralateralis* appeared to remain at depth both day and night, but in both cases data were too few to be certain. In the latter species, there was no clear relation to maturity or reproductive condition. Most of the "nonmigrating" *B. supralateralis* were immature.

Large fractions of the populations of three species, *Notolychnus valdiviae*, *Lampanyctus niger*, and *Triphoturus nigrescens*, appeared to remain at the day depth during the night on some occasions. It is unlikely that the deep night catches were due to contamination, i.e., encountering aggregations in the upper layers on the way up or down. The numbers caught at depth during the December 1970 series were in all cases considerably larger than those caught in short oblique tows made during the same series. Also it seems unlikely that patches would be encountered only by tows made to the same depths where the species were found during the day. Finally, the day and night calculated totals and size frequencies agreed well for all three species in December. If the deep night catches had been contaminants, the night totals would have been much larger than those for the day.

There were no obvious differences between the migrating and nonmigrating fractions of the populations. The nonmigrating fraction of *Lampanyctus niger* tended to be smaller and that of *Notolychnus valdiviae*, larger in September 1970, but there was considerable overlap between both fractions of the populations in both cases. For *Triphoturus nigrescens* and *N. valdiviae* in December 1970, both fractions of the populations were nearly identical in size composition. Thus the difference in behavior was not entirely a function of size. There was no case where shallow and deep night samples differed in sex ratio or percentage of ripe females. The number of specimens involved was rather large in all cases, so it is doubtful that more data would produce clearer trends or any explanation related to the parameters measured here.

Most species showed significant differences in size composition with depth. *Symbolophorus evermanni* was the only species present in abundance for which all sizes appeared to occur throughout the depth range. In the great

majority of species, the juveniles tended to occur shallower than adults. The trend was more obvious in the night samples due to closer sample spacing, but probably holds for the daytime depth distribution in most cases. *Hygophum proximum* and *H. reinhardti* were anomalous in that at night during new moon the adults tended to occur shallower than the juveniles.

The changes in size composition with depth may be an artifact caused by larger fish avoiding the trawl better at lesser better-lighted depths. However, many small species such as *Benthosema suborbitale*, *Diaphus schmidti*, *Triphoturus nigrescens*, and *Notolychnus valdiviae* are unlikely to avoid the trawl even as adults, and the trends with depth were as evident with these species as with the larger species. Also the same trends were evident from CT data for species which the CT appeared to sample larger individuals relatively better. Furthermore, avoidance by larger fish would only partly explain the changes noted for many species, i.e., the smaller fish were absolutely less abundant with depth.

The ecological significance of the trends in size with depth is not clear. The juveniles are removed to some extent from predation by adults, but this is of doubtful significance since other predators are probably more important. Possibly the smaller fish are less visible to predators than are the adults in the better-lighted shallow layers. In those species where adults occur farther below the juveniles in the day than at night, it may be related simply to the juveniles being unable to make longer migrations. This pattern could be related to distribution of food. It is quite likely that juveniles require greater concentrations and smaller average particle size of food than adults, and optimal conditions for juveniles may occur shallower than for adults.

Sex Ratios

Sex ratios of mature and juvenile fish of several species are compared in Table 3. The difference is significant for only one species, *Diaphus schmidti*, and in that case, the ratios did not differ significantly when data for mature fish from a single sample with a very large proportion of females was not included. For most species there was a tendency for higher proportions of females among immatures, but the figures are suspect in the sense that the data were not properly weighted to account for possible trends with depth or season. Legand and Rivaton (1970) have noted opposite trends in sex ratio with size for three species of myctophids. (However, their criteria for separating "larger" from "smaller" fish is not entirely unbiased and the proportions given for one species, *Benthosema simile*, do not differ significantly.)

TABLE 3.—Proportions of females among juveniles and mature fish for nine species of myctophids. Number of specimens examined is given in parentheses.

Species	Juveniles		Adults	
Benthosema suborbitale	0.48	(54)	0.51	(230)
Hygophum proximum	.58	(67)	.46	(192)
Diaphus schmidti	.43	(56)	.62	(127)
Notolychnus valdiviae	.50	(70)	.45	(402)
Lampanyctus niger	.65	(55)	.57	(456)
Lampanyctus steinbecki	.65	(48)	.51	(535)
Triphoturus nigrescens	.59	(49)	.48	(452)
Bolinichthys longipes	.58	(66)	.48	(239)
Ceratoscopelus warmingi	.59	(96)	.58	(456)

Given that there may be trends in sex ratio with size, recognition of trends with depth or season was made difficult because there were only a few series where sufficient numbers of similar-sized fish were captured at several depths or several seasons. Thus, significant trends in sex ratio with depth were observed for mature fish of only a few species. Quite possibly, more data would show that these trends are the rule rather than the exception. When data were pooled for all mature fish examined from each series (Table 4), some significant differences in sex ratio were observed. In most cases one series showed significantly higher or lower percentage of females than the rest with no suggestion of seasonal trends. Again, however, differences in depth composition of the samples or size composition of the fishes pooled for a series may have either obscured trends or have been responsible for the few significant differences observed.

Seasonal Trends

In considering seasonal trends, it was assumed

TABLE 4.—Proportion of females among total mature fish at different seasons for 10 species of myctophids. Total number examined is given in parentheses.

Species	September		December		March		June	
Benthosema suborbitale	0.51	(35)	0.59	(105)	0.42	(90)	—	
Hygophum proximum	.56	(66)	.32	(22)	.34	(64)	0.55	(40)
Diaphus schmidti	.36	(22)	—		.71	(100)	.52	(21)
Diaphus sp. A	.57	(81)	—		.32	(28)	.52	(27)
Notolychnus valdiviae	.48	(133)	.49	(141)	.23	(48)	.48	(80)
Lampanyctus niger	.58	(86)	.52	(183)	.58	(119)	.69	(68)
Lampanyctus steinbecki	.42	(99)	.55	(40)	.63	(163)	.52	(233)
Triphoturus nigrescens	.52	(25)	.45	(314)	.48	(85)	.80	(45)
Bolinichthys longipes	.41	(29)	.43	(40)	.50	(139)	.55	(31)
Ceratoscopelus warmingi	.73	(15)	.59	(29)	.32	(41)	.46	(26)

that the same or equivalent populations were sampled on each cruise. Possible changes due to horizontal advective transport were ignored. Advection rates, especially for organisms which spend one-half of their time below the surface layers, and horizontal gradients in the parameters measured—abundance, size composition, etc.—are probably low. It seems unlikely that populations which had been subjected to greatly different environmental conditions were advected into the study during the periods between cruises.

The most likely possibility of change due to advection would be related to seasonal north-south shifts of water masses. Near Hawaii in the upper layers, water transitional between North Pacific Central and North Pacific Equatorial displaces North Pacific Central water during the summer. This shift is known to affect the abundance of skipjack tuna (Seckel, 1969).

The absence of marked changes in species composition and relative abundance of the myctophid fauna suggest that north-south shifts of water masses did not, during the study period, markedly affect populations. Two examples illustrate this particularly well. *Diaphus schmidti*, a species of myctophid which apparently does not occur much further south than Hawaii, was consistently taken here in abundance, while a very similar congener, *D. garmanni*, which is very abundant from at least lat. 12°30′N and further south (Hartmann, 1971), was never taken. Two species, *Diogenichthys atlanticus* and *Diaphus fragilis*, which are very abundant in equatorial waters (Hartmann, 1971), were taken consistently but never in great numbers near Hawaii.

Most species that showed seasonal changes in size composition appeared to reach maturity in about 1 year. The larger species—*Lampadena* spp., *Lampanyctus nobilis*, *Bolinichthys supralateralis*, and *Notoscopelus caudispinosus*—probably take longer. In many species the adults nearly or completely disappeared at about the same time that juveniles became most abundant suggesting that few individuals live longer than 1 year.

The ages at maturity and life spans of colder water species of myctophids, e.g., *Benthosema glaciale* (Halliday, 1970), *Stenobranchus leucopsaurus* (Smoker and Pearcy, 1970), are considerably greater than those suggested here for tropical species. Murphy (1968) has presented data on epipelagic clupeoid fishes which show a marked decrease in age at maturity, the number of reproductions, and life span related to year-to-year variability in spawning success. He suggests that the latter is directly related to year-to-year variability in the physical environment. It is not unreasonable that the same trend exists for a mesopelagic family that occurs in both variable high-latitude waters and in the more stable tropical open ocean.

Most species appear to spawn predominately in the spring or summer. Primary production measurements taken by S. A. Cattell near Hawaii during 1969-70 indicate that primary production and productivity index are much higher during March-June than the period from October to January. Zooplankton production probably lags behind the peaks in primary production only slightly. Assuming that this seasonal pattern recurred during the present study, the period of principal spawning for most myctophid species appears to be timed

with respect to the seasonal peak in production of food.

In many of the abundant species, the seasonal changes in abundance and size composition were quite pronounced. When these were combined with size-dependent differences in migration habits, the depth-abundance profile also changed with season. Consequently, samples from only one period may give a misleading picture of vertical distribution and abundance. This would be particularly true in the tropics where, as opposed to longer-lived species at higher latitudes, several different size classes are not often present in abundance at all seasons.

Interspecific Relations

Many species of myctophids, including some congeners that are very similar morphologically, occur together in the water column yet must be ecologically segregated. From this study it is possible to examine several relevant factors: depth distribution, size range, and size changes with depth and season. Owing to better data for some of these aspects for the nighttime, only night distributions will be considered. There are, however, some data (Backus et al., 1968 Barham, 1970) that suggest that myctophids are rather inactive during the day and that interspecific patterns at night are probably more meaningful ecologically.

In Figure 12, depth-size patterns are diagrammed for 16 of the 19 most abundant species. For each species, a straight line is drawn connecting the size-depth coordinate for smallest size-shallowest depth with that for largest size-deepest depth. *Symbolophorus evermanni*, which showed no trend, and the *Hygophus* species, which will be discussed separately, have been omitted. Extremes of depth of capture and size range have been ignored; consequently, the ranges shown in Figure 12 are, in some cases, narrower than those given in Table 1. The straight lines are of course only a rough approximation to the actual patterns of size and depth; it is realized that more data would probably result in polygons for each species.

The species can roughly be separated into three groups. The first group includes eight species whose young occur principally at about 25 m and the adults between 75 and 125 m, depending on size. In the second group of three species, the pattern is similar except that the young occur principally at 80-100 m and the adults down to 150-250 m, again depending on size. The third group includes four species with sharper gradients in size with depth where juveniles occur around 50 m and larger fish are mostly between 150 and 200 m. Two of the rarer species, *Myctophum selenoides* and *Lampadena luminosa*, appear to have patterns like those of the third group. *Diaphus anderseni* has a depth-size pattern different from any of those illustrated, but two rarer species, *Taaningichthys minimus* and *Bolinichthys supralateralis*, appear to have similar patterns.

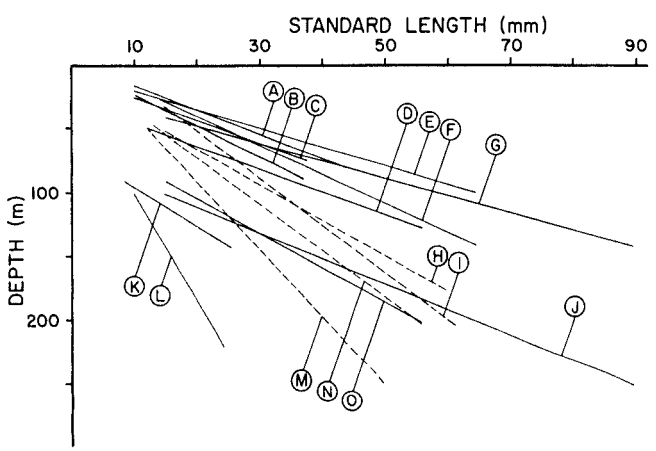

FIGURE 12.—Depth-size profiles (see text) in the upper 250 m at night for 16 species of myctophids: *Diaphus schmidti* (A), *Diaphus* sp. A (B), *Benthosema suborbitale* and *Triphoturus nigrescens* (C), *Bolinichthys longipes* (D), *Diaphus elucens* (E), *Ceratoscopelus warmingi* (F), *Lampanyctus nobilis* (G), *Diaphus rolfbolini* (H), *Diaphus* sp. B (I), *Lampanyctus niger* (J), *Notolychnus valdiviae* (K), *Diaphus anderseni* (L), *Lobianchia gemellari* (M), *Diaphus brachycephalus* (N), and *Lampanyctus steinbecki* (O).

Within the first two groups, similar sizes of the species tend to occur at similar depths. The depth-size patterns of four species in the first group—*Benthosema suborbitale*, *Diaphus schmidti*, *D.* sp. A, and *Triphoturus nigrescens*—are nearly identical. Within the third group, the juveniles co-occur with similar-sized individuals of the first group and the adults with larger fish of the second group.

Judging from the seasons of peak juvenile abundance (Table 1) most species in group one have similar reproductive cycles; large numbers of juveniles were present in the June or July samples. Juveniles were present in substantial numbers also in September for *Diaphus schmidti*, *D.* sp. A, and *Bolinichthys longipes*. *D. elucens* showed a peak in September only. *Benthosema suborbitale* and *Ceratoscopelus warmingi* showed large numbers of juveniles also in March. In group two, *Notolychnus valdiviae* and the smallest *Lampanyctus steinbecki* co-occur in summer and fall. *L. niger*, in spite of its apparent later season of maximum recruitment, is recruited at a larger size and co-occurs with similar sized *L. steinbecki* over much of the year. Thus there is a good deal of overlap in time as well as depth and size range for these species.

In general, congeners and closely related species, except *Hygophum* spp., have different size-depth patterns at night. Within each of the above groups, there are few congeners, and the co-occurring congeners are rather dissimilar. The four species of group one whose patterns are closest are of three genera, and the two congeners, *Diaphus schmidti* and *D.* sp. A, are quite different morphologically. Similarly, in group two, the *Lampanyctus* spp. belong to different groups within the genus.

Taaningichthys minimus and *T. bathyphilus* differ in that only *T. minimus* migrates. *Bolinichthys longipes* and *B. supralateralis* differ not only in morphology, size, and depth distribution but also in overall abundance. The two most similar *Lampanyctus* species, *L. steinbecki* and *L. nobilis*, which were present in abundance, have different night depth ranges and different sizes at maturity. Among the *Diaphus* species, closely related or similar species-pairs are distinctly separated even though most species appear to have similar reproductive cycles with peak juvenile abundance in June or September and nearly the same day depths. *D. rolfbolini* and *D. elucens* have different depth distributions at night. *D.* sp. A and *D.* sp. B differ in depth distribution and also in size at maturity. The species-pair of *D. anderseni* and *D. brachycephalus* differs similarly.

The depth-size patterns of the different species suggest that closely related species differ in their responses to physical factors and that genera or groups within genera have different biological requirements. Strong gradients in temperature, salinity, and light exist in the upper 250 m, particularly for temperature and salinity between 100 and 250 m. These are the most obvious factors to explain the differences in patterns of closely related species. Within each group, however, similar-sized individuals of dissimilar species co-occur under identical physical conditions. For them to co-exist, it would seem that they must be specialized with respect to biological factors.

A likely hypothesis is that the species within a group have different food preferences. Morphological differences between species within the groups include many features probably related to finding or capturing food; relative size of the eye and gape and the number, spacing, and structure of gill rakers. Closely related species of different groups are often rather similar in these respects.

The behavior of the *Hygophum* species appeared to be different from that of the other myctophids. The change in size-depth pattern between new and full moon was unique. The juveniles of *H. proximum* co-occurred with those of species of the second group at new moon and occurred shallower than those of the first group at full moon. The changes in avoidance with moon phase were also unique and suggest that the *Hygophum* species responded to something besides the visual stimulus of the trawl.

The *Hygophum* species were the only two congeners that occurred together in even roughly comparable numbers [see Note (Added in press) under *Lampanyctus niger*]. The two species are quite similar morphologically. *H.*

reinhardti is more slender and has higher numbers of AO photophores, gill rakers, and fin rays. There was, however, a great deal of overlap in these features, and except for adult males separation of the two species was the most difficult of all species collected. (Indeed, comparison of Hawaiian specimens with *H. proximum* from equatorial waters, where *H. reinhardti* does not occur, indicated that the specimens from Hawaii were more like *H. reinhardti* in body proportions than those from the equator.)

The seeming overlap between these two species may be anomalous in that the study area is at the edge of the principal ranges of both. According to Bekker (1965), *H. proximum* occurs principally below lat. 20°N and *H. reinhardti* above lat. 20°N in the central part of the Pacific. Over most of their ranges these two species do not appear to occur together in abundance, and Hawaii appears to lie in the transition zone between one species and the other.

Importance in the Ecosystem

The estimated total numbers of individuals per 10^3 m^2 for nine abundant species is given in Table 5 for each of the quarterly series and the CT series in March 1971. These numbers are the calculated totals from the best series (day or night) from each quarter. Using the same weighting factors, the biomass per 10^3 m^2 for each species was calculated and is given in Table 6.

TABLE 5.—Estimated number (individuals/10^3 m^2) for nine species of myctophids at different seasons. Numbers are totals calculated (see text) from samples taken throughout the water column by Isaacs-Kidd trawl (IK) during September 1970, December 1970, March 1971, and June 1971 and by Cobb trawl (CT) during March 1971.

Species	Number/10^3 m^2				
	Sept.	Dec.	March		June
			IK	CT	
Benthosema suborbitale	23	40	26	20	14
Hygophum proximum	26	6	49	14	14
Diaphus schmidti	21	14	19	30	25
Notolychnus valdiviae	104	68	12	—	23
Lampanyctus niger	57	163	62	9	55
Lampanyctus steinbecki	82	75	43	16	81
Triphoturus nigrescens	45	248	96	7	23
Bolinichthys longipes	58	23	44	24	13
Ceratoscopelus warmingi	55	176	196	153	155
Total	471	813	547	273	403

TABLE 6.—Estimated biomass (wet weight in g/10^3 m^2) for nine species of myctophids at different seasons. Figures were calculated by the same method as those in Table 5.

Species	g/10^3 m^2				
	Sept.	Dec.	March		June
			IK	CT	
Benthosema suborbitale	4	11	10	7	1
Hygophum proximum	19	2	29	11	2
Diaphus schmidti	4	3	10	17	4
Notolychnus valdiviae	6	5	1	—	2
Lampanyctus niger	59	244	102	18	37
Lampanyctus steinbecki	34	34	43	11	61
Triphoturus nigrescens	5	41	19	1	3
Bolinichthys longipes	13	5	30	20	8
Ceratoscopelus warmingi	56	221	103	130	40
Total	200	566	347	215	158

The figures are probably low for several reasons. Neither IK nor CT filtered with 100% efficiency; Pearcy and Laurs (1966) estimated that filtering efficiency was 85% for a 6-ft IK with coarser mesh than used here. There is a negative bias due to avoidance. Substantial avoidance of either the IK or CT was demonstrated for many species, and some likely avoided both. This probably affected the biomass estimates more since the larger fish are more likely to avoid the net. (The CT figures for *Lampanyctus niger* are deceptively low since substantial numbers were caught by IK below the deepest depth sampled by the CT.) For March 1971, the estimated total number is about 7% higher and that for biomass about 20% higher if CT estimates for *Hygophum reinhardti* and *Lampanyctus nobilis* are included and the higher of the two estimates (IK or CT) is used for the other species. It was not possible to estimate reliably numbers and biomass for the less abundant species. They amounted to about 10% of the total numbers caught by the four quarterly series and would probably increase the estimates of total numbers and biomass by a similar factor.

The low totals in June reflect the fact that for most species few adults were present and the juveniles of the next generation were not fully recruited to the population. Other differences were largely due to changes in one or two important species. The peak in total numbers in December was due principally to

high values for *Triphoturus nigrescens* and *Lampanyctus niger*, and the peak in total biomass then was caused mainly by the larger numbers of *L. niger*, a large species, and the fact that *Ceratoscopelus warmingi* had the highest percentage of adults at this time. Overall, *C. warmingi* and *L. niger* were clearly the dominant species with respect to both numbers and biomass.

The average number of myctophids per m^2 was about 0.55 and the average biomass was about 0.32 g/m^2. These figures are lower than those given by Pearcy and Laurs (1966) for total mesopelagic fishes in the upper 1,000 m off Oregon—1.5 individuals and 3.6 g/m^2 for the night tows. The total number of the three dominant myctophids off Oregon was about $0.78/m^2$. Analyses of other fishes collected off Hawaii is not yet complete, but inclusion of other groups, particularly the hatchetfishes, *Cyclothone*, and larger stomiatoids would likely raise the average number and possibly the average biomass to values comparable to those of Pearcy and Laurs.

Preliminary analyses of the biomass of other groups of micronekton indicate that most of the biomass in the upper 250 m at night is in the form of vertically migrating groups which are not present during the day and that the myctophids dominate the fauna as a whole. The only other important group of vertically migrating fishes were the gonostomatids whose biomass, principally from *Gonostoma* spp., was about one-fourth that of the myctophids. The myctophid biomass was one to two times that of the caridean shrimps and about one to four times that of the larger euphausiids, *Thysanopoda* spp.

The biomass of epipelagic fishes and larval fishes over 10 mm was about one-sixth that of the myctophids. The figure for epipelagic fishes may be low due to higher concentrations very near the surface, where the sampling was inadequate, and possibly greater avoidance. In general, however, the data agree with Ahlstrom's (1969) conclusions, based on abundances of larval fishes, that vertically migrating, mesopelagic groups—principally myctophids and gonostomatids—dominate the open ocean fish fauna.

Conservatively, the average biomass of micronekton is at least three times that of the myctophids or about 1.0 g/m^2. Most myctophids appear to have a 1-year life cycle, and in many species, the population is nearly totally replaced by each new generation. The difference between the highest and lowest estimates of myctophid biomass is greater than the average value. Yearly production is then probably higher than the average standing crop. It is not unreasonable to assume that the dynamics of other groups of micronekton are similar and that micronekton production is about twice the average standing crop.

If, following Ryther (1969), it is assumed that ecological efficiency in the open ocean is about 10% for each trophic level and the organisms are about 10% carbon, then a production of 0.2 g C/m^2 by the micronekton would require production of 2 g $C/m^2/yr$ by the trophic level below. The yearly primary production in this area is about 50 g $C/m^2/yr$ (S. A. Cattell, pers. comm.) with about 5 g $C/m^2/yr$ available to the third trophic level and 0.5 g $C/m^2/yr$ to the fourth. For the rather conservative estimate of micronekton production to result, ecological efficiencies must be higher than 10% or the food chain in the open ocean must be shorter than generally assumed by Ryther (1969) and others, i.e., the micronekton must be consuming a large fraction of production by herbivores.

A final point concerns the fate of micronekton production; about 2 $g/m^2/yr$ must be consumed by higher carnivores. Studies of the feeding habits of such predators as tuna; dolphin, *Coryphaena*; and lancet fish, *Alepisaurus* (Gibbs and Collette, 1959; King and Iversen, 1962; Haedrich and Nielsen, 1966; Fourmanoir, 1971) indicate that these predators consume few vertically migrating forms such as myctophids or gonostomatids. Tuna and dolphin appear to eat mostly epipelagic forms. Unless the standing crop of epipelagic micronekton has been greatly underestimated here or its turnover rate is greater than that of vertically migrating forms, the "typical" predators of the open ocean are consuming only a fraction of the production by micronekton. In order to identify the principal energy pathways in the open

ocean, more work is needed on the food habits of poorly studied pelagic predators such as sharks, porpoises, gempylids, and squids. Further attempts, such as those of Forster (1971), to collect potential mesopelagic predators are also needed.

ACKNOWLEDGMENTS

I am grateful to all the people who struggled with the trawls day and night during the work at sea. Among the many who assisted are A. R. Hartmann, D. M. Kuba, T. Okamura, J. P. Vansant, and D. A. Ziemann. I also thank Captain Red Scholtz and the crew of the venerable RV *Teritu*.

The comparative series between IK and CT was made possible by the cooperation and assistance of the Southeast Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA. B. E. Higgins was in charge of the RV *Townsend Cromwell* operations.

Numerous others assisted in sorting the samples; special thanks are due to Barbara Baldwin and Kay Koons. Patricia Wagner assisted in all phases of the work. I am particularly grateful for her conscientious and careful efforts. I also thank John Caperon for use of his computer facilities. B. G. Nafpaktitis and R. L. Wisner assisted in identification of specimens, and the latter kindly made available a very useful unpublished manuscript. R. E. Young critically reviewed the manuscript and made helpful suggestions.

This research was supported by NSF Grant GB-23931 and funds from the University of Hawaii, Hawaii Institute of Marine Biology.

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APPENDIX TABLE 1.—Catches of myctophids in two series of four night tows each taken at 50 m and 100 m during July 1970. Only species with an average catch of 10/tow or more are considered separately. All tows were 2 hr at depth. The first three tows of each series were taken successively on the same night; the fourth was taken on the night immediately preceding (50 m) or following (100 m) the other three.

Species	Catch/tow			
	1	2	3	4
50-m series:				
Benthosema suborbitale	38	57	22	30
Diaphus schmidti	18	21	23	29
Diaphus sp. A	14	22	8	20
Triphoturus nigrescens	32	46	22	40
Bolinichthys longipes	24	49	40	38
Ceratoscopelus warmingi	237	226	120	214
Total myctophids in 50-m series	399	437	267	446
100-m series:				
Hygophum proximum	8	9	11	25
Notolychnus valdiviae	1	2	3	46
Lampanyctus steinbecki	7	30	47	73
Lampanyctus nobilis	0	12	20	64
Bolinichthys longipes	45	51	38	141
Ceratoscopelus warmingi	37	25	31	32
Total myctophids in 100-m series	127	164	184	447

APPENDIX TABLE 2.—Catches of several species of myctophids in short oblique tows and ranges of catches from horizontal tows. Given for each series are the range of catches considered positive in estimating lower limits of depth ranges (+'s) and the range considered negative and due to contamination (–'s). For the December 1970 and June 1971 series, the catches of short oblique tows are also given. Each of the four December tows made two cycles simulating descent and ascent of the trawl during horizontal tows, each of the three June tows made one descent and ascent.

Species	September 1970		December 1970		Oblique			March 1971		June 1971		Oblique			
	+	–	+	–	1	2	3	+	–	+	–	1	2	3	4
Benthosema suborbitale	14-68	0-9	10-114	0-4	1	3	1	12-84	0-5	6-24	0-4	0	0	0	0
Hygophum proximum	9-88	0-7	6-14	0-3	0	0	0	6-45	0-2	5-21	0-4	0	0	0	0
Diaphus schmidti	14-74	0-7	23-41	0-6	2	2	1	7-51	0-5	7-101	0-3	0	0	1	1
Diaphus sp. A	9-36	0-4	21	0-2	0	0	0	10-29	0-5	6-7	0-2	1	0	0	0
Notolychnus valdiviae	11-130	0-6	10-116	0-8	0	4	1	17-19	0-10	11-84	0-10	3	6	2	4
Lampanyctus niger	11-180	0-7	10-174	0-7	0	12	14	23-69	0-8	12-93	0-10	3	2	6	4
Lampanyctus steinbecki	18-311	2-13	15-77	0-12	7	9	6	12-58	0-5	9-90	0-6	6	0	0	0
Triphoturus nigrescens	11-108	0-7	27-288	0-13	11	32	17	15-116	0-8	5-34	0-4	1	0	0	0
Bolinichthys longipes	19-148	0-8	13-61	0-6	2	1	1	19-93	0-4	7-25	0-6	0	0	1	1
Ceratoscopelus warmingi	14-126	0-10	14-265	0-10	2	2	4	16-248	0-8	11-145	0-5	3	6	2	4

CELL TYPES, DIFFERENTIAL CELL COUNTS, AND BLOOD CELL MEASUREMENTS OF A PORTUGUESE SHARK, *CENTROSCYMNUS COELOLEPIS*, CAPTURED AT 700 FATHOMS

STUART W. SHERBURNE[1]

ABSTRACT

A Portuguese shark, *Centroscymnus coelolepis*, 620 mm (24.4 inches) in total length captured in a lobster trap 700 fm deep at Hudson Canyon in February 1971 had a mean erythrocyte size of 33.4 × 23.6 μ, which is larger than any previously recorded for the class Chondrichthyes. Both neutrophils and heterophils were found in the blood, whereas earlier reports describe only one or the other from the same elasmobranch.

Most sharks are shallowwater forms, with relatively few representatives from the deeper parts of the ocean. Bigelow and Schroeder (1948:494-499) reported that the Portuguese shark is strictly a deepwater shark, found chiefly in depths greater than 200 fm; it has been recorded down to 1,487 fm. The smallest recorded specimen is about 9 inches long, and the largest, about 44 inches. Off the North American coast it occurs mostly in temperatures of 5° to 6°C; off Portugal, between 4° and 11°C; and in the Mediterranean, at 12° to 13°C.

Few detailed studies have been made of either the blood or the blood-forming organs in elasmobranchs, probably because of difficulty in obtaining the necessary material (Saunders, 1966a). In this report I describe the cell types, differential cell counts, and measurements of both the erythrocytes and leukocytes in the blood of a Portuguese shark, *Centroscymnus coelolepis*. I report on this specimen because of its unusually large cell sizes in all cell categories. Cell measurements revealed erythrocytes larger than those in all but a few of the vertebrates, and the cells appear to be the largest reported for the class Chondrichthyes.

A search of the literature reveals no previous blood work has been reported on this species.

MATERIALS AND METHODS

The Portuguese shark examined for this report was a female, 620 mm (24.4 inches) in total length, and was captured in a lobster trap 700 fm deep at Hudson Canyon on 21 February 1971.

Smears were made with blood obtained by direct heart puncture of the live shark. A small incision was made over the heart area through which a heparinized capillary tube 75 × 1.1-1.2 mm was inserted into the heart and allowed to fill three-quarters full. A small drop of blood from the tube was placed on a microscope slide, the tube sealed with plastic clay and the smear made. Three capillary tubes were used to make four blood smears and the microhematocrit determination. The sealed tubes were centrifuged for 3 min at 11,000 rpm. Both a microcapillary reader and a millimeter rule were used in measuring the packed red cell volume, buffy coat, and plasma volumes.

The slides were air-dried and stained with Wright's and with Wright's and Giemsa's stains, and the staining times were varied.

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Manuscript accepted August 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

The best stain was obtained with 1½ min in Wright's followed by 20 min in Giemsa's stain; that slide was used in this study.

Cells were examined under oil immersion at 800 and 1200 power. Cells were measured at 800 power. Cell classification followed that of Saunders (1966a) for elasmobranch blood cells.

RESULTS AND DISCUSSION

This deepwater Portuguese shark had larger blood cell sizes, a lower hematocrit, and a different white cell differential count than those reported for other sharks.

Cell Differentials

Six classifications of cells were present: mature erythrocytes, immature erythrocytes, lymphocytes, heterophils, neutrophils, and thrombocytes. I found no monocytes, eosinophils, or basophils in the material I studied.

Mitotic division occurs in the circulating blood, for mitosis, in all stages, was present in a few cells in the blood smear (Figures 1, 2).

An erythrocyte differential count of a random sample of 100 red cells revealed that mature erythrocytes constituted 92% of the total, immatures 7%, and erythroblasts 1%.

The percentage of mature red cells agrees closely with Saunders' (1966a, b) findings for other elasmobranchs, but the white cell differential of this shark differed substantially from those of other elasmobranchs reported by Saunders. This shark had 73% lymphocytes, 22% thrombocytes, and 5% heterophils; whereas in 13 species of elasmobranchs Saunders found a maximum of 32% lymphocytes and 20-85% thrombocytes, and in 9 species, 3-54% heterophils. The large difference in lymphocyte frequency may be an individual characteristic of this specimen, for Saunders found a substantial difference between the white cell differentials of two adult specimens of sandbar shark, *Carcharhinus milberti*. Saunders also reported that either heterophils or neutrophils, but not both, are found in any given species of elasmobranch; however, I found a few neutrophils in addition to heterophils on close examination of the blood in this shark. Several were located at the end of the smear where a differential would not normally be made because of mechanical distortion of the cells; others were discovered in the area where a differential might be made, though the neutrophils could be easily overlooked because of their scarcity.

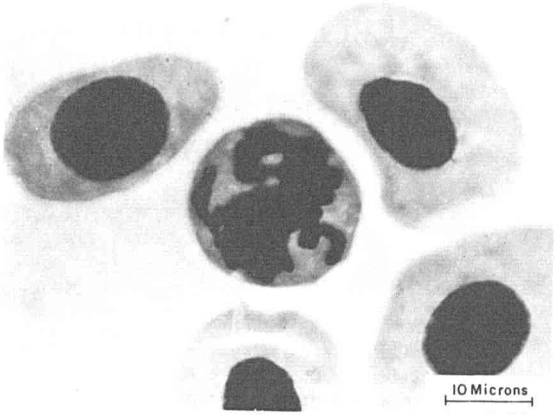

FIGURE 1.—Mitosis-Prophase.

FIGURE 2.—Mitosis-Anaphase.

Table 1 lists the measurements of all cells described in this report.

Mature Erythrocytes

The mean size of the Portuguese shark mature erythrocytes (Figure 3) is the largest

TABLE 1.—Blood cell measurements in microns of a Portuguese shark, the mean ± standard deviation and range in parentheses.

Cell type	Number of cells measured	Cytosome		Nucleus	
		Length	Width	Length	Width
Mature erythrocyte	200	33.4 ± 2.5 (26.5 – 40.6)	23.6 ± 1.8 (18.7 – 28.1)	13.4 ± 0.7 (12.2 – 15.4)	10.2 ± 0.6 (9.1 – 11.7)
Immature erythrocyte	10	25.8 ± 2.2 (21.8 – 27.9)	16.4 ± 2.2 (14.0 – 20.1)	15.0 ± 0.7 (14.0 – 16.1)	12.8 ± 1.0 (10.9 – 14.0)
Erythroblast	1	28.1	17.5	18.7	15.9
Heterophil	10	23.8 ± 1.5 (22.3 – 25.0)	22.6 ± 1.3 (21.8 – 25.0)	10.8 ± 1.2 (9.4 – 12.5)	15.2 ± 1.5 (12.8 – 17.2)
Lymphocyte	10	17.8 ± 2.2 (15.6 – 20.3)	16.8 ± 1.2 (14.0 – 18.7)	16.2 ± 2.0 (14.0 – 19.5)	14.7 ± 1.1 (12.5 – 16.4)
Thrombocyte	20	23.4 ± 2.7 (18.7 – 28.0)	13.2 ± 1.6 (10.9 – 17.2)	16.6 ± 1.1 (14.5 – 18.7)	9.4 ± 1.0 (7.8 – 11.1)
Neutrophil	5	23.6 ± 1.2 (21.8 – 25.0)	23.2 ± 0.9 (21.8 – 24.2)	11.2 ± 1.3 (9.4 – 12.5)	18.9 ± 2.7 (15.6 – 21.7)

reported for the Chondrichthyes, including the rays, which characteristically possess larger cells than sharks. A comparison of some of the largest recorded erythrocyte dimensions for the Chondrichthyes (Altman and Dittmer, 1961) with the Portuguese shark is listed below.

Species	*Erythrocyte dimensions (Dry films)*
Portuguese shark, *Centroscymnus coelolepis*	33.4 × 23.6 μ
Electric ray, *Torpedo nobiliana*	29.8 × 23.1 μ
Little skate, *Raja erinacea*	24.3 × 13.9 μ
Spiny dogfish, *Squalus acanthias*	22.7 × 15.2 μ
Hammerhead shark, *Sphyrna zygaena*	15.2 × 11.2 μ

Immature Erythrocytes

One thousand erythrocytes were counted on the slide and 8.6% of the cells were immature. A few erythroblasts were seen, and measurements of a typical one are listed in Table 1. Immature erythrocytes are easily distinguished from the mature cells by their larger nucleus and smaller cytosome (Figure 3).

Heterophils

Heterophils stained clearly to show purplish nuclear material and eosinophilic rods. The heterophils are quite round and similar in size (Figure 4).

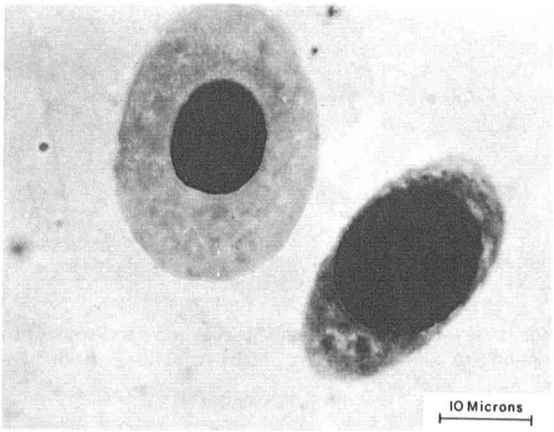

FIGURE 3.—Mature erythrocyte on the left, immature erythrocyte on the right.

Lymphocytes

Lymphocytes stained well with the purplish nucleus taking up most of the cell space. The cytoplasm stains a medium to deep blue and often shows blebs extending from the cell wall (Figure 5).

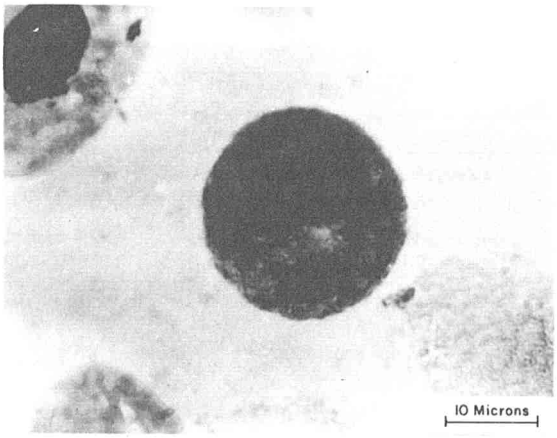

FIGURE 4.—Heterophil showing rod-shaped granules.

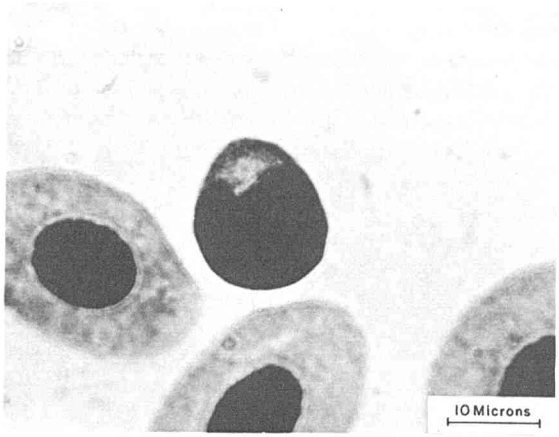

FIGURE 5.—Lymphocyte and three erythrocytes. This lymphocyte does not have blebs extending from the cell wall.

Thrombocytes

Thrombocytes, which are characteristically some of the smallest cells found in the peripheral circulation, were as large in this shark as many mature erythrocytes in other vertebrate species. The stained nucleus is ovoid with pink to red dotted cytoplasm. Since there is quite a range in the length of some of these cells due to fingerlike cytoplasmic projections, I measured 20 ovoid thrombocytes (Figure 6).

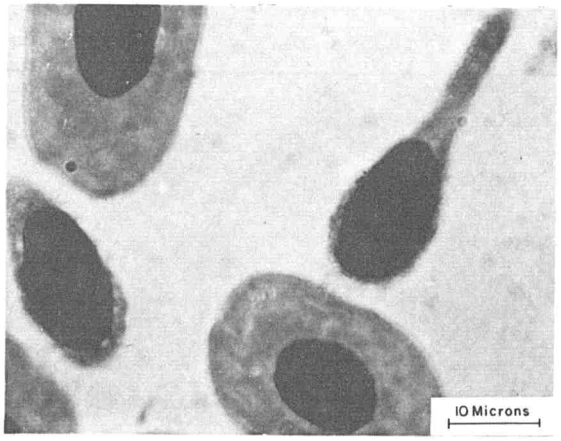

FIGURE 6.—Two thrombocytes, one with a fingerlike cytoplasmic projection.

Neutrophils

Neutrophils were scarce and were discovered only when the whole slide was studied in detail. They are within the same size range as the heterophils but are distinguished by the absence of eosinophilic rod-shaped granules and the colorless cytoplasm (Figures 7, 8).

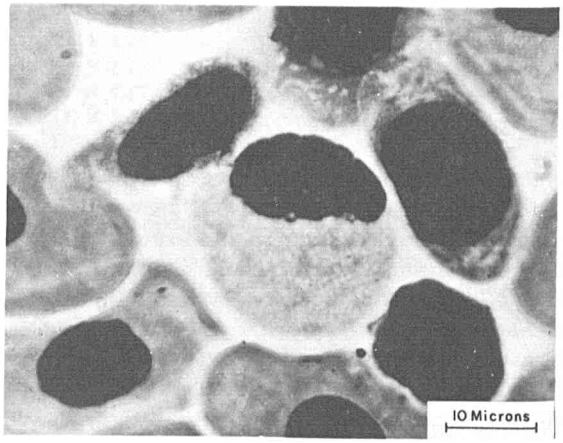

FIGURE 7.—Center: A neutrophil located at the end of the smear where other cells have been mechanically distorted. Clockwise: Immature erythrocyte, lymphocyte, mature erythrocyte, and thrombocyte.

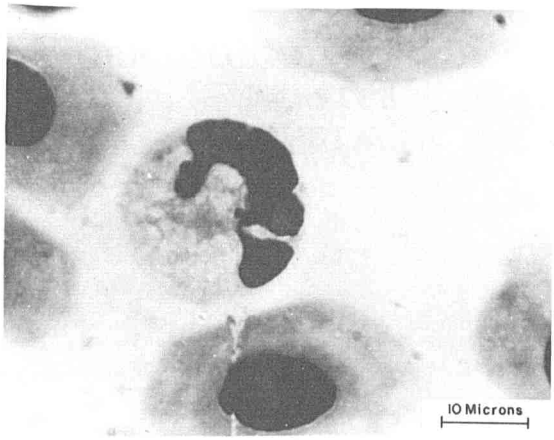

FIGURE 8.—Neutrophil showing a segmented nucleus.

Hematocrit

The packed cell volume of this deepwater shark was less than that reported for other sharks. In a 62 mm whole blood column, 52 mm was clear plasma, 2 mm buffy coat, and 8 mm packed erythrocytes. This was a 13% hematocrit compared with 17-32% from 11 wild dogfish (Burger, 1967) and 23.1% for the hammerhead shark (Altman and Dittmer, 1961).

The blood of the Portuguese shark examined showed no evidence of abnormality. There was no hemolysis in the plasma, and though the absolute cell sizes were larger than previously reported for other sharks, the staining and morphological characteristics of each cell category were typical of shark cells.

ACKNOWLEDGMENT

I wish to thank Gareth W. Coffin of the Northeast Fisheries Center, Boothbay Harbor Laboratory, National Marine Fisheries Service for the photomicrographic work.

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MORPHOLOGICAL STUDY OF DIAGNOSTIC CHARACTERS IN WESTERN ATLANTIC *HEPOMADUS* (CRUSTACEA, DECAPODA, PENAEIDAE)

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The collections made during the expeditions of the *Oregon*, *Oregon II*, and the RV *John Elliott Pillsbury* almost tripled the number of specimens of *Hepomadus* previously recorded from the western Atlantic. The taxonomic status of the material has been assessed through a study of the external morphology and an investigation of variations of morphological, morphometric, and meristic characters. It is demonstrated that intermediates are present between extremes of variations and, consequently, all specimens are assigned to a single species, *Hepomadus tener* Smith.

The gap in our knowledge of the genus *Hepomadus* results from the great paucity of collections taken beyond the continental shelf of America. Although recent material caught in the course of the expeditions of the *Oregon*, *Oregon II*, and the RV *John Elliott Pillsbury*, in addition to five specimens taken by the *Albatross* in 1885 and 1886 which have not been reported, have almost tripled the number of specimens previously recorded from the western Atlantic (18), the total number of known specimens is only 51.

The purpose of this paper is to demonstrate that all specimens of *Hepomadus* that have been taken in the western Atlantic (including the Sargasso Sea, the Gulf of Mexico, and the Caribbean) belong to a single species, *Hepomadus tener* Smith, 1884. My study has drawn from the works of earlier investigators, and I have corroborated their observations on the great variation in many morphological and a few morphometric and meristic characters within this species. Additional material from a greater number and more widely distributed localities, however, have led me to conclude that features which have been suggested as probably useful in differentiating species of *Hepomadus* in the region are not valid. Similarly, all other characters analyzed here for the first time show a wide range of variation, with intermediate stages present between the extremes. One meristic and two morphological characters, however, have been found reliable for separating *H. tener* and *H. glacialis* Bate, 1881, which is known only from the western Pacific.

PRESENTATION OF DATA

The c.l. (carapace length—linear distance between orbital margin and midposterior margin of carapace) and r.l. (rostral length—linear distance from apex to orbital margin) are measured to the nearest 0.5 mm. The ratios presented in the tables are given to the nearest 0.05. Certain ratios are not given for every specimen because the rostrum is damaged in many of them, and, in some, the spine on the third pleonic somite is broken. The ocean depths have been recorded to the nearest meter. Finally, the scales accompanying the illustrations are in millimeters.

The following abbreviations are used for repositories of specimens: TAMU-Department of Oceanography, Texas A&M University; UMML-Institute of Marine Sciences, University of Miami; USNM-National Museum of Natural History, Smithsonian Institution; and YPM-Peabody Museum of Natural History, Yale University.

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Manuscript accepted September 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

HEPOMADUS TENER SMITH, 1884

Figures 1-10

Hepomadus tener Smith, 1884: 409, pl. 9 fig. 7-8. Holotype: ♂ USNM 5464. Type-locality: off mouth of Chesapeake Bay, 5,394m, 2 October 1883, *Albatross* stn 2099 (lat 37°12′20″N, long 69°30′W).-Smith, 1887:689, pl. 19, fig. 3-3a.-Bouvier, 1908: 57, pl. 1, fig. 5, pl. 13, fig. 1-12.-Burkenroad, 1936:86.-Ramadan, 1938:55.-Roberts and Pequegnat, 1970:43, fig. 3-2D.-Pequegnat and Roberts, 1971:9.

Hepomadus tener?.-Wood-Mason and Alcock, 1891:189.

Aristaeus (Hepomadus) tener?.-Alcock, 1901:42.

Hepomadus glacialis.-A. Milne Edwards and Bouvier, 1909:194, fig. 13-19, pl. 1, fig. 3. [Not *Hepomadus glacialis* Bate, 1881.]

Material

United States

New Jersey: 1 ♀, USNM, off Atlantic City, 2,601 m, 11 August 1885, *Albatross* stn 2563.

Delaware: 1 ♂, USNM, off mouth of Delaware Bay, 3,206 m, 18 September 1886, *Albatross* stn 2715. 1 ♀, USNM, off mouth of Delaware Bay, 2,983 m, 18 September 1886, *Albatross* stn 2716.

Virginia: 1 ♂, holotype, USNM 5464. 1 ♀, USNM, off mouth of Chesapeake Bay, 3,740 m, 10 September 1884, *Albatross* stn 2226. 1 ♂ 1 ♀, YPM, and 1 ♀, USNM, off Back Bay, 2,266 m, 24 October 1886, *Albatross* stn 2727.

North Carolina: 1 ♀, YPM, off Roanoke Island, 1,542 m, 11 November 1883, *Albatross* stn 2115.

Florida: 1 ♀, USNM, S of Santa Rosa Island, 1,463 m, 2 September 1970, *Oregon II* stn 11206.

Alabama: 1 ♂ 1 ♀, USNM, off Mobile Bay, 2,683 m, 2 March 1885, *Albatross* stn 2379. 2 ♀ USNM, off Mobile Bay, 1,555-1,829 m, 28 July 1962, *Oregon* stn 3664. 2 ♂ 1 ♀, USNM, off Mobile Bay, 1,646 m, 28 January 1970, *Oregon II* stn 10897.

Louisiana: 1 ♀, USNM, off Grand Terre Islands, 2,652 m, 28 July 1959, *Oregon* stn 2574.

Texas: 1 ♂, TAMU, off Padre Island, 1,399 m, August 1969, *Alaminos* stn 68-A-11-7.

Mexico

Tamaulipas: 1 ♂, TAMU, of Boca San Rafael, 3,384-3,493 m, November 1968, *Alaminos* stn 68-A-13-10. 1 ♂, TAMU, off Boca San Rafael, 3,658 m, March 1968, *Alaminos* stn 68-A-3-3B. 1 ♂ 1 ♀, TAMU, off Tampico, 1,774 m, August 1969, *Alaminos* stn 69-A-11-87.

Veracruz: 1 ♂, USNM, NE of Cabo Rojo, 896 m, 3 June 1970, *Oregon II* stn 10955. 3 ♂, USNM, SE of Cabo Rojo, 1,280 m, 3 June 1970, *Oregon II* stn 10957. 1 ♀, USNM, SE of Cabo Rojo, 1,097 m, 3 June 1970, *Oregon II* stn 10956.

Yucatan: 1 ♂, TAMU, NW of Progreso, 3,841 m, March 1968, *Alaminos* stn 68-A-3-5B.

Bahamas

1 ♂, YPM, Turks Island Passage, 1,646-1,728 m, 12 April 1927 *Pawnee* stn 54.

Haiti

1 ♂ 1 ♀, USNM, Gulf of Gonave, 3,109-3,493 m, 1 July 1970, *Pillsbury* stn 1180.

Tobago

1 ♂, USNM, NW of Charlotteville, 920-1,244 m, 2 July 1969, *Pillsbury* stn 847. 2 ♀, USNM, NE of Man of War Bay, 1,817-1,847 m, 1 July 1969, *Pillsbury* stn 844.

Western Caribbean

2 ♀, USNM, NW of Cayos Hobbies, 933 m, 24 October 1970, *Oregon II* stn 11217.

Panama

1 ♀, USNM, off Punta Manzanillo, 1,639 m, 25 March 1884, *Albatross* stn 2144.

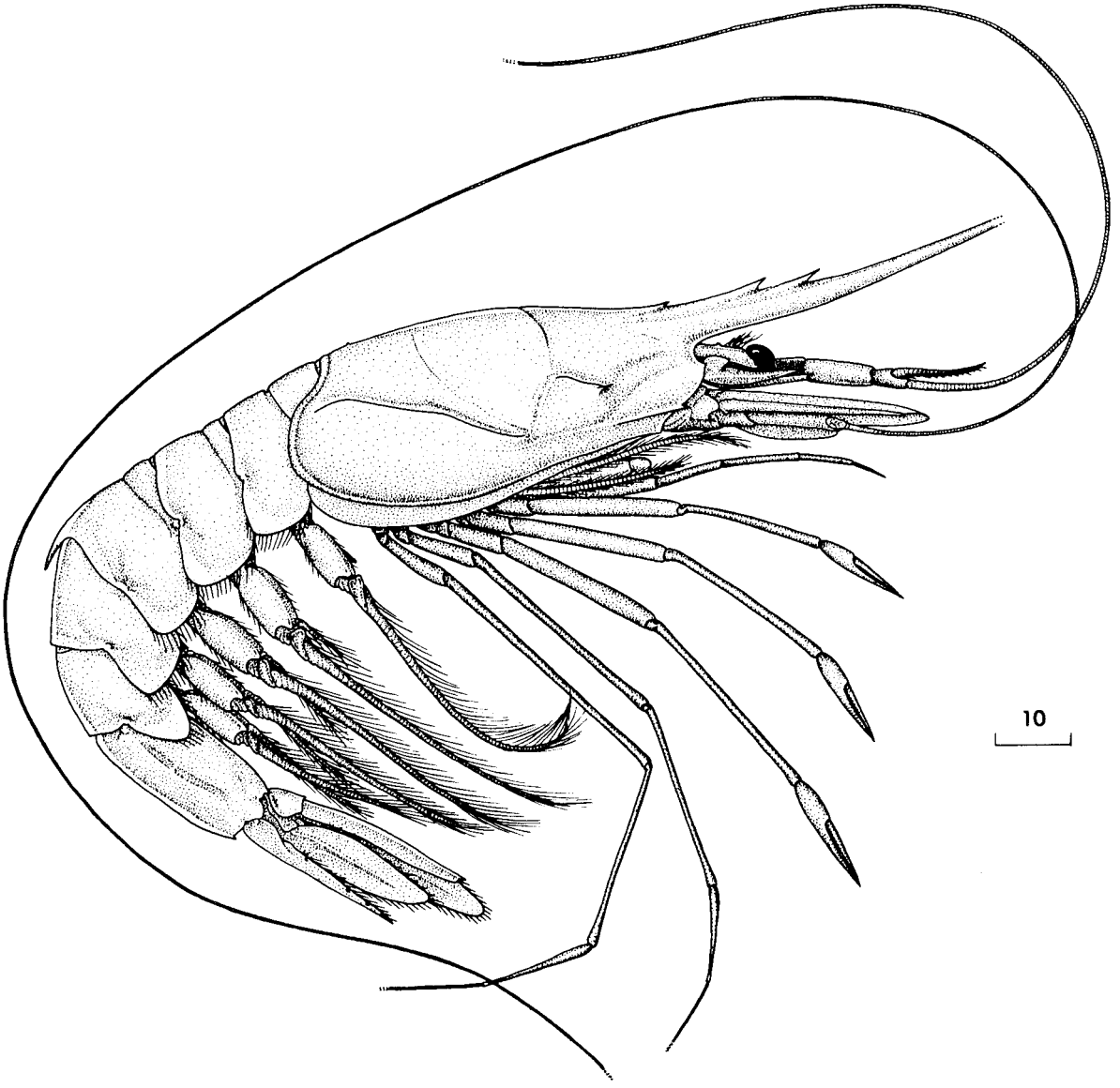

FIGURE 1.—*Hepomadus tener* Smith. Lateral view, ♀ 51 mm c.l., off Mobile Bay, Ala.

Colombia

1 ♂ 1 ♀, UMML, off Islas de San Bernardo, 1,271 m, 4 November 1970, *Oregon II* stn 11240. 3 ♂, USNM, off Isla de Barú, 1,097 m, 5 November 1970, *Oregon II* stn 11242. 1 ♀, USNM, off Puerto Colombia, 1,097 m, 8 November 1970, *Oregon II* stn 11245. 1 ♂ 1 ♀, TAMU, N of Cabo de la Aguja, 4,152 m, 24 July 1970, *Alaminos* stn 70-A-10-48. 1 ♀, USNM, NW of Península de la Guajira, 1,500 m, 27 July 1966, *Pillsbury* stn 454.

Description

Body slender and lacking setae (Figure 1). Dorsum of carapace almost straight or very slightly convex, convexity extending beyond postcervical sulcus (Figure 3A). Rostrum styliform, straight to slightly upturned in young (Figure 2), pronouncedly inclined dorsad in large individuals of both sexes; in young females and, apparently, in all males length of rostrum not exceeding 0.70 that of carapace, in larger females rostral length increasing with increasing size of shrimp to as much as 1.25 length of carapace, and surpassing antennular peduncle by about 0.3 of its own length. Rostral teeth 3, first tooth located slightly posterior to orbital margin, and rather far from second tooth; second and third teeth separated by interval varying from 0.3 to 0.6 of distance between first and second tooth. Postrostral carina (inconspicuous in young individuals) long, extending to about 0.8 length of carapace, and followed by rather minute dorsal tubercle, located near posterior margin; adrostral carina extending from orbital margin to near tip of rostrum, stronger and sharp basally. Orbital spine absent; antennal spine short, acute; branchiostegal spine produced and sharp; hepatic spine prominent. Cervical sulcus well marked, extending to middorsum of carapace, ending there at about 0.45 length of carapace from orbital margin; postcervical sulcus faint, concave except for almost straight, short, dorsal portion, ending at middorsum of carapace at 0.3 of carapace length from posterior margin; hepatic sulcus almost horizontal; orbito-antennal sulcus short and linear; branchio-cardiac sulcus well marked, its length slightly more than half that of carapace, extending from near posterior margin of carapace to posterior end of hepatic sulcus.

Antennular peduncle length about 0.55 that of carapace; stylocerite produced distally into very slender, sharp spine, barely reaching base, or extending to midlength, of acute distolateral spine; first segment bearing minute ventromesial spine in young, occasionally spine persisting in animals of 24 mm c.l.; dorsal flagellum extremely long, about 4.5 times length of carapace, or 1.1 times total length of shrimp.

Scaphocerite 2.0 to 2.1 times as long as broad, and surpassing antennular peduncle by 0.1 to 0.2 of its own length; lateral rib produced distally into sharp spine overreached by lamella; antennal flagella incomplete in all specimens examined.

Labrum (Figure 4A, B) consisting of two

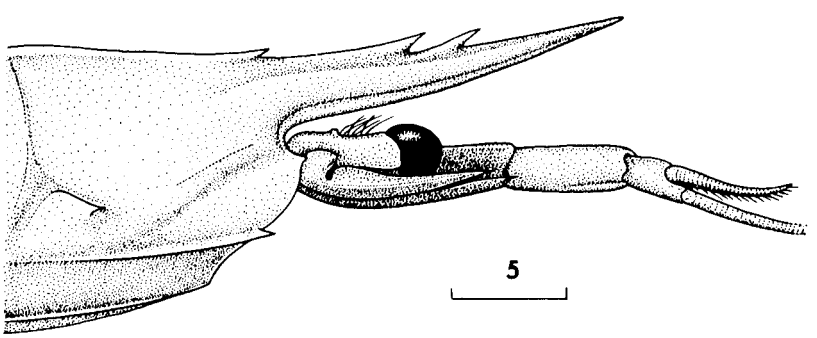

FIGURE 2.—*Hepomadus tener*. Anterior region, ♂ 28 mm c.l., mouth of Delaware Bay, Del.

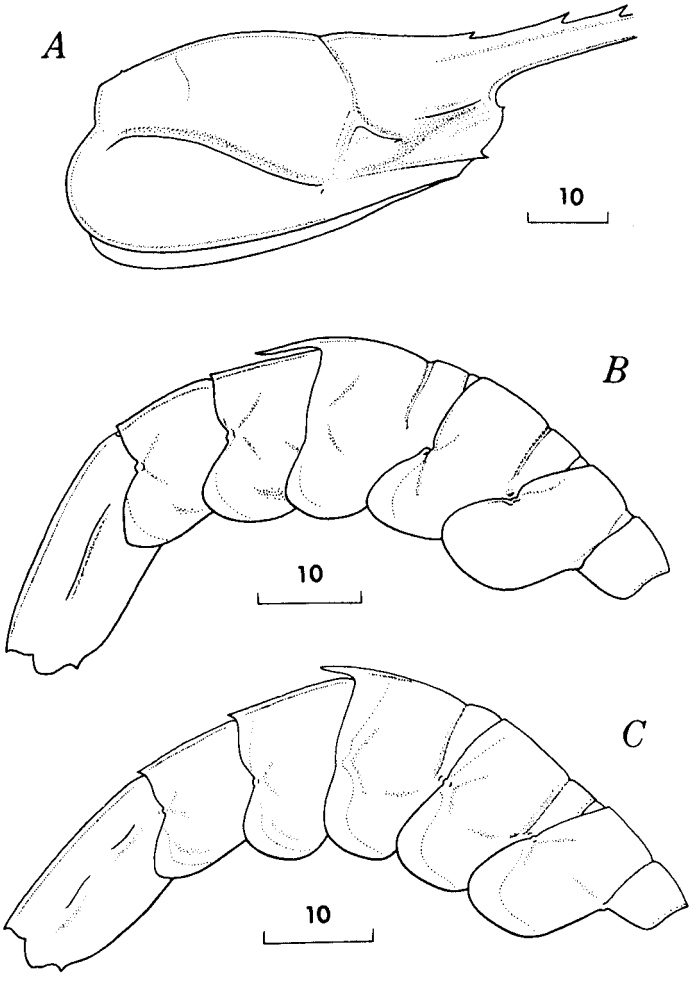

FIGURE 3.—*Hepomadus tener*. A. Lateral view of carapace, ♀ 52 mm c.l., off Back Bay, Va. B. Lateral view of abdomen, ♀ 51 mm c.l., off Atlantic City, N.J. C. Lateral view of abdomen, ♂ 35.5 mm c.l., SE of Cabo Rojo, Veracruz.

lightly sclerotized lobes: 1) anterodorsal lobe, subtriangular in outline, often bearing longitudinal, ventromedian carina, and ending anteriorly in vertical, apical ridge; lateral walls of lobe tapering from apical ridge posteriorly, and ending in caudally divergent, cornified, epistomal bars; and 2) posteroventral lobe, subtrapezoidal, delimited by lateral ribs projecting anteriorly as paired, small convexities on margin of lobe; posterior portions of ribs turning mesially but not meeting in midline.

Mandibular palp with proximal lobe of second segment ranging from blunt to acute. Second maxilla with endite of basis, "maxillary palp," bearing 2 to 4 strong and 1 to 4 weak setae [occasionally none according to A. Milne Edwards and Bouvier (1909) on a specimen identified as "*H. glacialis*"] on upper side of distolateral portion; and 2 to 5 strong and 1 to 4 weak setae, or none, on the lower side; in addition, 1 to 6 long, plumose, distal setae often present on upper side (Figure 5B, C). Number of setae on endite of right and left maxilla often different in same individual of this species as in holotype of *H. glacialis* (Figure 5D, E, left second maxilla). Exopod of first maxilliped with proximomesial border bearing 4 to 7 long, rigid setae.

Third maxilliped reaching base to distal end of third antennular segment, its dactyl with mesial side broadening abruptly at distal end

of proximal fourth forming excavation bearing strong setae on its proximal side, and tapering distally; first pereopod extending as far as, or very slightly beyond, third maxilliped; second pereopod reaching midlength of third antennular segment or surpassing it by tip of dactyl; third pereopod reaching distal end of antennular peduncle or exceeding it by almost 0.5 length of dactyl; fourth pereopod surpassing antennular peduncle by length of dactyl and 0.2 to 0.5 that of propodus; fifth pereopod overreaching antennular peduncle by length of dactyl and 0.5 or entire length of propodus—last two pairs of pereopods, especially their dactyls, slender. Ischium of third maxilliped bearing minute distomesial spine; merus of first and second pereopods with ventral distomesial spine movable, and rather stout. In females, coxae of last three pairs of pereopods produced mesially into plates covered with long setae and bearing anteriorly prominent, blunt tooth. In males, coxae of fifth pair of pereopods with large, obtuse to strongly acute tooth on anteromesial margin.

Abdomen with middorsal carina extending from about midlength of third somite through sixth, carina rounded on third, sharp from fourth posteriorly; posterodorsal margin of third somite bearing broad-based, prominent spine, its length 0.3 of, to equivalent to, distance between transverse sulcus and posterior margin of somite; posterodorsal margin of fourth and fifth somites varying from straight (Figure 1) to armed with well-developed, small spine (Figure 3B, C); sixth somite bearing small spine at posterior end of dorsal carina, paired posteroventral teeth, and two pairs of prominent lateral cicatrices; latter occasionally almost fused into one. Telson with four pairs of lateral minute, movable spines, posteriormost pair flanking very small terminal portion; median sulcus short, disappearing well anterior to terminal portion, mesial ramus of uropod longer than telson, and lateral ramus considerably overreaching mesial.

Petasma (Figure 6A, B) with median lobe tapering distolaterally from distal extremity of row of cincinuli (hooklike structures along mesial margin of median lobes of petasma that serve to interlock its two halves), and with elongate, subelliptical, sclerotized lapel on inner surface, extending along distomesial margin; lateral lobe very broad proximally, narrower and rounded distally; ventral costa with distal 0.4-0.5 of its length free from adjacent portion of ventrolateral lobule, and strongly curved

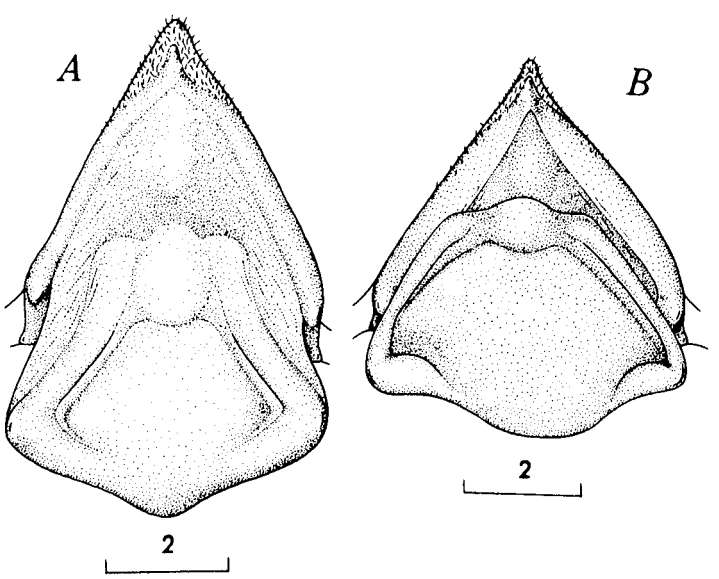

FIGURE 4.—*Hepomadus tener*. Ventral views of labra: A. ♀ 43.5 mm c.l., S of Santa Rosa Island, Fla. B. ♀ 44 mm c.l., off Back Bay, Va.

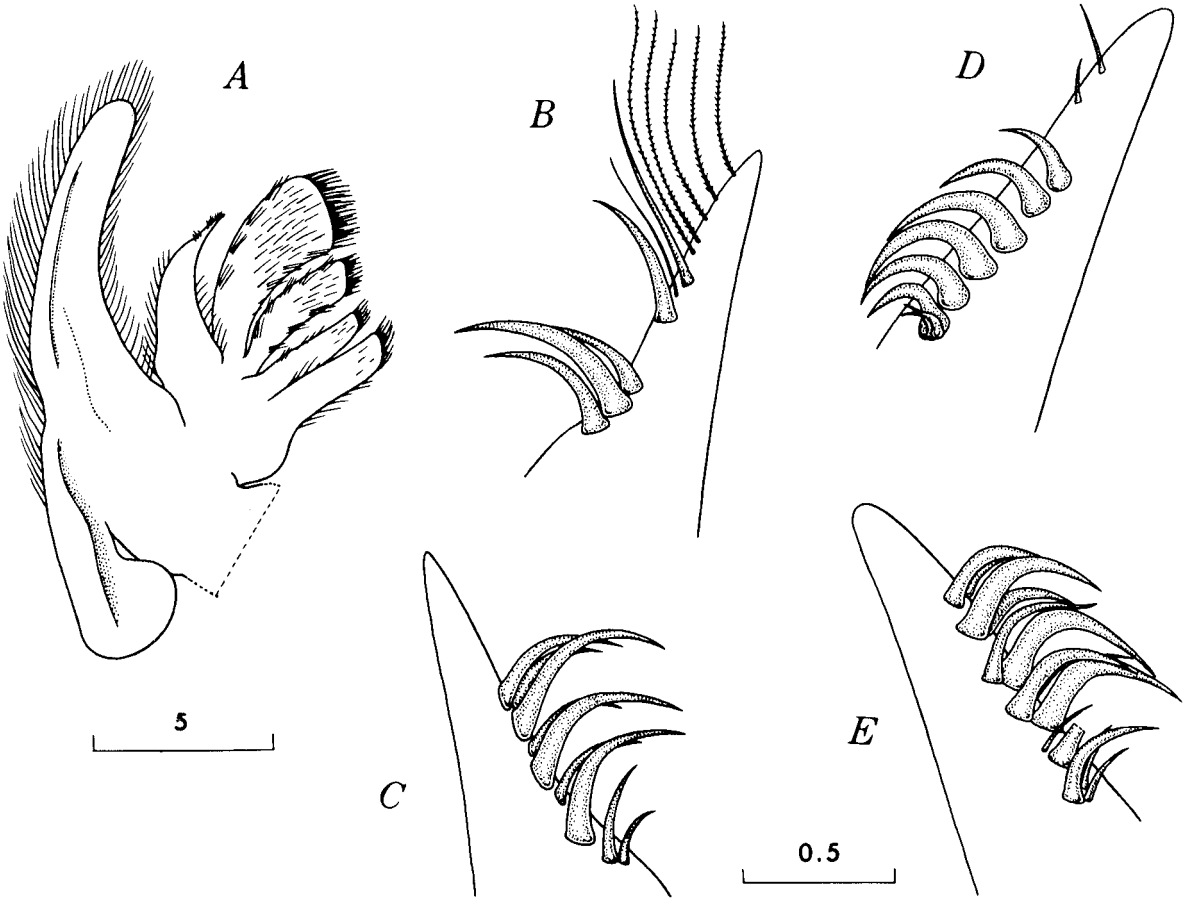

FIGURE 5.—*Hepomadus tener*. A. Dorsal view of left second maxilla, ♀ 51 mm c.l., off Atlantic City, N.J. B. Distalmost part of upper side of left endite, same specimen. C. Lower side of same endite. *Hepomadus glacialis* Bate, holotype, ♀ 65 mm c.l., near Yokohama, Japan. D. Distalmost part of upper side of endite of left second maxilla. E. Lower side of same endite.

laterally forming short, sinuous projection; articular sclerite produced proximomesially into strong, subrectangular spur situated immediately distal to large, platelike, mesially directed projection of basis of pleopod.

Appendix masculina (Figure 7A, B) broad, subfoliaceous, bearing long marginal setae on distal portion and secondary row along short rib, latter delimiting dorsal extremity of ventrally inclined distomesial portion of appendix. Appendix interna narrow, elongate, gently tapering distally to rounded extremity, and extending almost as far as, or somewhat beyond, appendix masculina.

Sternite XIII in males bearing lanceolate, median plate; sternites VIII through XII with high median ridge produced anteriorly into acute spine in males as well as in females.

Thelycum (Figure 8) with median plate on sternite XIII very elongate, reaching between midlength and anterior margin of sternite XII, roughly lanceolate, with gently undulate, or irregular, lateral margins, and rather abruptly tapering anteriorly forming usually obtuse, occasionally acute, triangular projection; sternite XIV weakly convex ventrally, convexity often embraced posteriorly by semicircular groove.

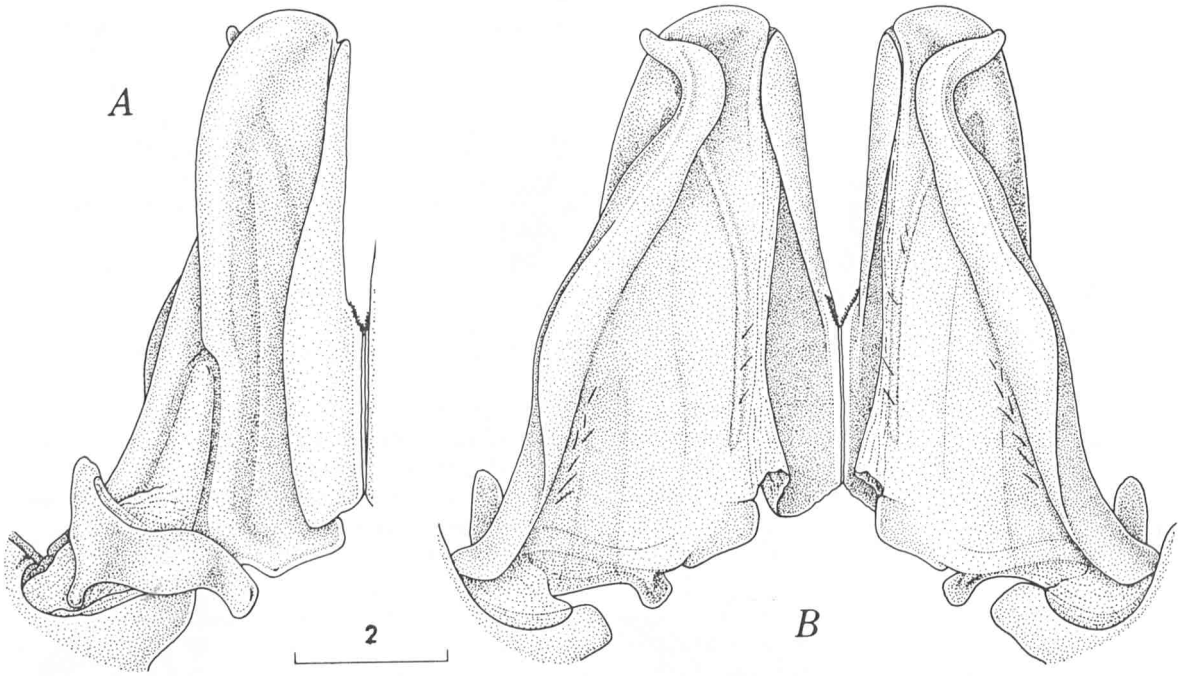

FIGURE 6.—*Hepomadus tener*. Petasma: A. Dorsal view of left half, ♂ 35.5 mm c.l., SE of Cabo Rojo, Veracruz. B. Ventral view of same petasma.

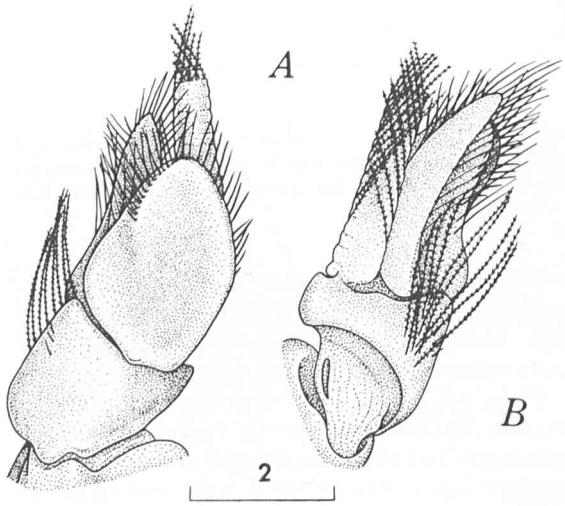

FIGURE 7.—*Hepomadus tener*. Appendices masculina and interna: A. Dorsal view of right appendix masculina and proximal part of endopod, ♂ 35.5 mm c.l., SE of Cabo Rojo, Veracruz. B. Ventral view, inclined slightly mesad, of appendices interna and masculina of same specimen.

Distribution

Off the Atlantic coast of the United States, from New Jersey southward, through the Sargasso Sea, to the Gulf of Mexico and Caribbean Sea, *H. tener* has been found at depths from 765 m (Roberts and Pequegnat, 1970) to about 5,400 m. This is the first time this species has been reported from the Caribbean, where it is widely distributed.

There are only two records of *H. tener* from localities outside the western Atlantic. Wood-Mason and Alcock (1891) questionably identified a much damaged female from the Bay of Bengal in 2,396 m. Later, Alcock (1901) apparently referring to the same specimen stated that the depth was 2305 m, and indicated that the epipod of the somite XIII consists of a tiny filament. This identification needs confirmation because the epipod is small, subrectangular and lamelliform in the western Atlantic material, as Burkenroad (1936) observed.

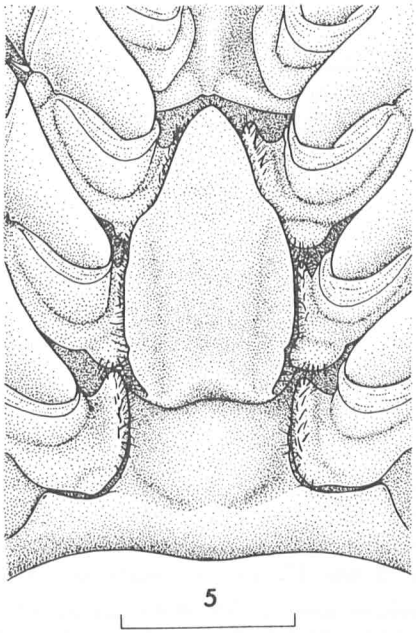

FIGURE 8.—*Hepomadus tener*. Thelycum, ♀ 47 mm c.l., off Back Bay, Va.

The other record is that of a female reported by Ramadan (1938) from off Zanzibar [Tanzania], in 2,930 m; this record leaves no doubt as to the presence of *H. tener* in the western Indian Ocean.

DISCUSSION

Previous authors (Smith, 1886; Bouvier, 1908; Burkenroad, 1936; Roberts and Pequegnat, 1970) who have reported *H. tener* from the western Atlantic have cited a number of differences between their material and specimens that had been described earlier. In addition to these western Atlantic records of this species, Milne Edwards and Bouvier (1909) identified a male from SW of Dry Tortugas Islands as *H. glacialis* on the basis of several features, including the presence of a well-defined spine on the midposterior margin of the fourth and fifth pleonic terga but, at the same time, pointed out other characters that distinguish their specimen from the type of *H. glacialis*.

Burkenroad (1936) presented a detailed discussion of the differences in various characters (e.g., shape of the proximal projection, "inner lobe," of the second segment of the mandibular palp, relative lengths of the stylocerite and the scaphocerite, development of the postrostral carina, length of the spine at the midposterior margin of the third pleonic tergum) among known specimens of *H. tener*, and interpreted the differences as individual variations or those due to differential growth rates. He also noted that the small male assigned to *H. glacialis* by Milne Edwards and Bouvier differs from *H. tener* (according to their description), in possessing a larger rostrum, a smaller interval between the last two rostral teeth, a shorter spine on the third pleonic tergum, an obtuse posteroventral tooth on each side of the sixth pleonic somite, and in lacking setae on the upper side of the endite of the basis of the second maxilla. He concluded that if such differences exist, the small male belongs to a species other than *H. tener*. Furthermore, Burkenroad stated that his specimens had no trace of a spine at the midposterior margin of the fourth and fifth pleonic terga, and that the presence of those spines in the male reported by Milne Edwards and Bouvier is the strongest reason for identifying the latter as *H. glacialis*. Later, Ramadan (1938) after examining the type of *H. glacialis*, cited three features by which Milne Edwards' and Bouvier's specimen differs from the type, and suggested that it probably represents an undescribed species.

The study of collections at my disposal as well as data presented in previous descriptions of other material indicate that all known western Atlantic *Hepomadus* are different from *H. glacialis*. During the course of the investigation it also has become evident that a considerable degree of variation exists among specimens from the region. In each of the characters considered, however, there is a broad range of variation, which seems to indicate that all the specimens belong to a single species, *Hepomadus tener*.

The principal differences between *H. glacialis*, the holotype of which has been made available to me, and *H. tener* are given in Table 1.

To analyze the various characters considered by previous authors to be of possible diagnostic

TABLE 1.—Characteristics distinguishing *Hepomadus glacialis* (holotype) from *H. tener*.

Feature	*H. glacialis* (holotype)	*H. tener*
Dorsum of carapace	Strongly arched to postcervical sulcus	Almost straight or very slightly arched, convexity extending beyond postcervical sulcus
Postrostral carina	Interrupted, disappearing on cardiac region, becoming distinct again and extending almost to posterior margin of carapace	Uninterrupted, extending posteriorly about 0.8 length of carapace
Setae on endite of basis of second maxilla		
Upper side	5 and 6 strong, 10 and 4 weak (right and left endite, respectively)	0; 2-4 strong, 1-4 weak
Lower side	5 and 9 strong, 3 and 5 weak	0; 2-5 strong, 1-4 weak

value in differentiating two species of western Atlantic *Hepomadus*, I have divided the material into three somewhat arbitrary groups based on the shape of the midposterior margin of the fourth and fifth pleonic terga: Group 1, straight; Group 2, slightly produced into a short, sometimes barely perceptible, projection; and Group 3, produced into a conspicuous spine. Intermediate stages (Group 2) between the two extremes (Groups 1 and 3) have not been discussed previously, although Bouvier (1908), in his description of a male *H. tener* from the Sargasso Sea, indicated that the dorsal carina of the fourth and fifth pleonic terga is produced into a small projection.

As stated above, Burkenroad indicated that in the specimen reported by Milne Edwards and Bouvier, which fits into Group 3, the interval between the last two rostral teeth is smaller than in the specimens with straight margins (Group 1) he had studied. I have found that this tooth interval varies considerably, from 0.30 to almost 0.60 of the distance between the first and the second tooth, and that the variations are not correlated with the shape of the posterior margin of the pleonic terga (Figure 9). It is true that according to the figure of Milne Edwards and Bouvier, in their Group 3 male (17 mm c.l.), the interval is 0.30, whereas in the Group 2 male described by Bouvier, the interval is 0.55 [according to his Figure 2, on plate 13], and in the female with 47 mm c.l., from off Virginia, belonging to Group 1, which Burkenroad had studied, the interval is 0.50. However, in the male holotype of *H. tener* (17.5 mm c.l., Group 1), which Burkenroad had not seen, the interval is 0.30, as in the 17 mm c.l. male of Group 3. Furthermore, among the material I have examined, two females of Group 3 of about same size (36 mm c.l. and 37 mm c.l.) possess a tooth interval of 0.40 and 0.60. Finally, in a small female of 14.5 mm c.l. and in another of 47 mm c.l., both belonging to Group 2, the tooth interval is about the same, 0.35 and 0.40, respectively. The data presented herein demonstrate that there are no significant differences in the tooth interval between the three groups.

The available information is too meager—particularly on animals of Group 1—to determine whether or not a clear correlation exists between the relative length of the rostrum and the shape of the midposterior margin of the fourth and fifth pleonic terga. Nevertheless, the ratio of the length of the rostrum to the length of the carapace in the specimens examined by me are presented in Table 2.

The relative length of the posteromedian spine on the third pleonic tergum varies greatly, from 0.3 of, to equivalent to, the distance between the transverse groove and the posterior margin of the tergum (adjacent to base of spine). The correlation of this ratio with increase in size of the animals seems obscure, and the correlation of the relative length of the spine with the shape of the midposterior margin of the fourth and fifth pleonic terga does not appear to indicate the presence of more than

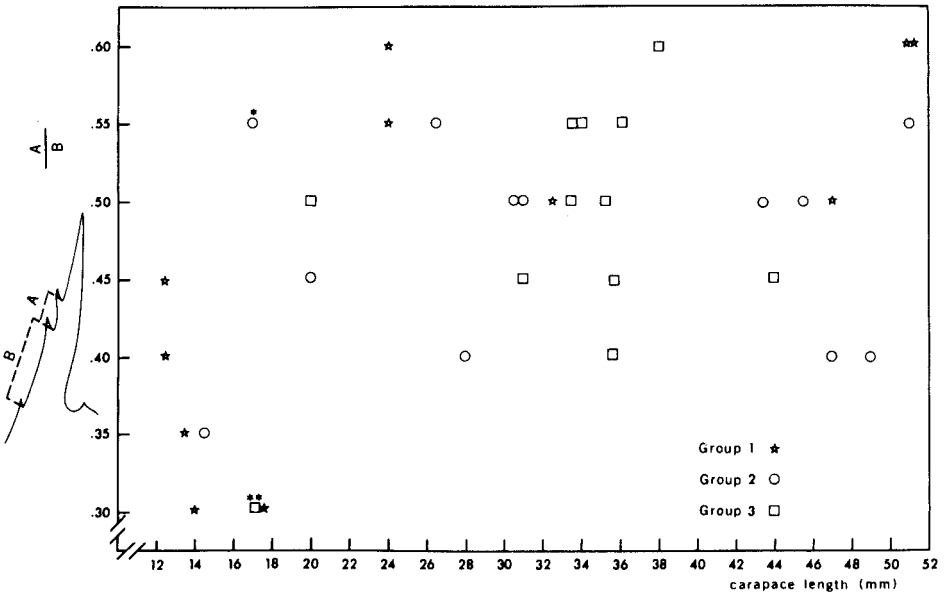

FIGURE 9.—Ratio of interval between last two rostral teeth (A) to interval between first two teeth (B) plotted against carapace length in the three groups (see text) of *Hepomadus tener*.

* Bouvier, 1908, pl. 13, fig. 2.
** A. Milne Edwards and Bouvier, 1909, pl. 1, fig. 3.

TABLE 2.—Ratio of rostrum length to carapace length at various carapace lengths (c.l.) in the three groups (see text) of *Hepomadus tener*.

c.l.	Group 1	Group 2	Group 3
12.5	♀ 0.45	—	—
	♀ 0.55	—	—
14	♂ 0.55	—	—
14.5	—	♀ 0.60	—
17.5	♂ 0.45	—	—
20	—	—	♂ 0.65
24	♂ 0.70	—	—
28	—	♂ 0.50	—
30.5	—	♀ 0.60	—
31	—	—	♂ 0.55
33.5	—	—	♀ 1.00
34	—	—	♂ 0.60
35.5	—	—	♂ 0.60
36	—	—	♀ 1.10
37	—	—	♀ 1.10
43.5	—	♀ 0.90	—
44	—	—	♀ 0.90
45.5	—	♂ 0.70	—
51	—	♀ 1.25	—

one species. In the specimens of Group 1, the ratio varies from 0.55 to 0.90 (Figure 10), in those of Group 2, from 0.30 to 1.0, and finally, in specimens of Group 3 the ratio varies from 0.30 to 0.45, except for a single individual in which the ratio is 0.55. It thus seems as if the specimens of Group 1 possess a longer spine on the third pleonic tergum than those of Group 3, but in specimens of Group 2 that spine may be as long as, or even longer, than in the specimens of Group 1, or as short as in those of Group 3.

The setation of the endite of the basis of the second maxilla varies within the same limits in the three groups, i.e., 0, or 2 to 4 strong and 1 to 4 weak setae on the upper side; and 0, or 2 to 5 strong and 1 to 4 weak setae on the lower side. Inasmuch as setae are found in many combinations and are lacking on the lower side in a few of the specimens examined by me, it seems highly probable that the absence of setae from the upper side of the endite in the specimen reported by Milne Edwards and Bouvier (1909) may very well fall within the range of individual variation within the species. I have not seen this specimen which is neither in the collection nor is it registered in the card catalog of the Museum of Comparative Zoology (Herbert W. Levi, pers. comm.).

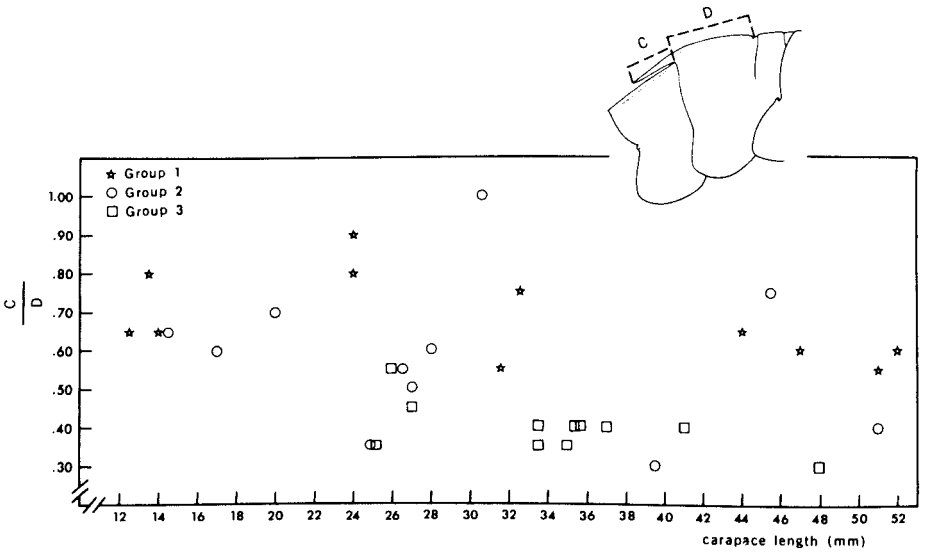

FIGURE 10.—Ratio of length of spine (C) on third pleonic tergum to distance between transverse groove and posterior margin of tergum (D) plotted against carapace length in the three groups (see text) of *Hepomadus tener*.

The differences which earlier authors have pointed out in the labrum, "epistome," among *Hepomadus*, seem to be due to changes in the relative position of its two lobes in preserved specimens. The posteroventral lobe may be only slightly raised and continuous with the anterodorsal lobe, or the posteroventral lobe may be thrust over the anterodorsal so that the two lobes become distinctly delimited.

Another character that has been cited as supposedly useful in differentiating species of *Hepomadus* in the western Atlantic is the shape of the posteroventral teeth of the sixth pleonic somite; however, it is variable, ranging from broadly triangular to subspiniform, in all three groups.

In addition to the features which have been studied by previous workers and discussed above, I have found that the length of the third pair of maxillipeds and five pairs of pereopods shows individual variation, but no consistent differences occur between the three groups; furthermore, the appendix interna may fall short or overreach the appendix masculina within each group, and also the two cicatrices on the sixth abdominal somite not only may be widely separated or almost fused within each group, but also both extremes are found in specimens of a single lot (e.g., 1 ♂ 1 ♀ taken off Alabama, at *Albatross* stn 2379).

The three groups of *H. tener* are not geographically isolated, but Groups 1 and 2 have been found off the east coast of the United States, the former ranging southward to the Bahamas and the latter to the Sargasso Sea. All three groups live in the Gulf of Mexico and the Caribbean Sea.

ACKNOWLEDGMENTS

I am indebted to Willard D. Hartman (YPM), Willis E. Pequegnat (TAMU), and Gilbert L. Voss (UMML) for making material available; also to Anthony L. Rice of the British Museum (Natural History) for placing at my disposal the holotype of *Hepomadus glacialis* Bate. Grateful acknowledgment is extended to Horton H. Hobbs, Jr., of the Smithsonian Institution (SI); Bruce B. Collette of the Systematics Laboratory, National Marine Fisheries Service, NOAA (NMFS), for invaluable suggestions made during the preparation of this work; and Thomas E. Bowman (SI) and

Austin B. Williams (NMFS) for their critical review of the manuscript. I wish to thank María M. Diéguez for preparing the drawings.

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HELMINTH PARASITES OF PORPOISES OF THE GENUS *STENELLA* IN THE EASTERN TROPICAL PACIFIC, WITH DESCRIPTIONS OF TWO NEW SPECIES: *MASTIGONEMA STENELLAE* GEN. ET SP. N. (NEMATODA: SPIRUROIDEA) AND *ZALOPHOTREMA PACIFICUM* SP. N. (TREMATODA: DIGENEA)

MURRAY D. DAILEY[1] AND WILLIAM F. PERRIN[2]

ABSTRACT

Parasite frequencies in 72 spotted porpoise, *Stenella graffmani* (Lönnberg, 1934), and 19 spinner porpoise, *S.* cf. *S. longirostris* (Gray, 1828), are reported and analyzed with respect to age of host. In addition to the new nematode *Mastigonema stenellae* gen. et sp. n. from the fore stomach of *S. graffmani* and the new fluke *Zalophotrema pacificum* sp. n. from the pancreatic duct of *S. graffmani* and *S.* cf. *S. longirostris*, parasites reported include *Anisakis simplex, Halocercus delphini, Crassicauda* sp., *Campula rochebruni, Tetrabothrium forsteri, Strobilocephalus triangularis, Phyllobothrium delphini*, and *Monorygma grimaldii*. Irreversible lesions in the ventral region of the skull due to infection of the air sinuses by a *Crassicauda*-like nematode were more frequent in skulls of calves of *S. graffmani* than in skulls of subadults and adults (129 specimens total), indicating that the parasite, or a condition correlated with its occurrence, is a significant factor in natural mortality of the spotted porpoise in the eastern tropical Pacific.

Porpoises of the genus *Stenella* are of great importance to the U.S. tropical tuna fishery (Perrin, 1969, 1970a). Yellowfin tuna associate with porpoise schools in the eastern Pacific, and the fishermen make use of this association in locating and capturing the tuna. Despite this economic importance, little is known of the ecology of the porpoises. Parasites have been previously reported from *Stenella longirostris, S. roseiventris, S. coeruleoalba, S. attenuata*, and *S. graffmani* (Dailey and Brownell, 1972). These reports have usually been from a small sample and did not include numbers of parasites per animal or percentage of sample infected. This report deals with two members of the genus in the eastern tropical Pacific: the spotted porpoise and the spinner porpoise. The taxonomy of the genus is currently in a chaotic state. Spinner porpoises from the eastern Pacific have been referred by recent authors to *Stenella microps* (Gray, 1846) and to *S. longirostris* (Gray, 1828)—Perrin and Hunter (1972). The spotted porpoise *S. graffmani* (Lönnberg, 1934) was described from Acapulco, but Rice and Scheffer (1968) recently referred all spotted porpoises to *S. dubia* (G. Cuvier, 1812), a decision that does not reflect a concensus of current opinion (Perrin, 1970b; Mitchell, 1970; Caldwell et al., 1971). We here refer the spotted porpoise examined to *S. graffmani* and the spinner porpoise tentatively to *S. longirostris*. The "eastern" and "whitebelly" spinner porpoises (Perrin, 1972) are considered to be geographical variants within one species and are not treated separately. This usage is provisional pending the results of current taxonomic investigations.

MATERIALS AND METHODS

We examined 72 specimens of *S. graffmani* and 19 of *S.* cf. *S. longirostris* (11 eastern and 8 whitebelly). These were collected during the course of investigations of morphology and reproduction. We collected parasites as we prepared skeletons of the animals for use

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Manuscript accepted September 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

as museum specimens. Capture data and museum numbers are presented in Appendix Tables 1 and 2. Also, we examined 67 skulls of spotted porpoise and 29 of spinner porpoise from museum collections, for bone damage caused by nematode infection. The museum specimens were from the eastern tropical Pacific and are listed below. Abbreviations used are: AMNH, American Museum of Natural History, New York; LACM, Los Angeles County Museum; SDMNH, San Diego Museum of Natural History; USNM, United States National Museum, Washington, D.C.

S. graffmani: AMNH130216, LACM27412, 27413, 27419, 27420, 27421, 27422, 27425, 27426, 27427, 27428, 27429, 27431, 27434, 31362, 31431; SDMNH20637, 21199; USNM-261427, 261428, 261429, 261430, 261431, 261432, 261433, 261434, 395264, 395265, 395266, 395267, 395268, 395615, 395616, 395617, 395618, 395926, 395927, 395928, 395929, 395935, 395936, 395937, 395938, 396027, 396029, 396034, 396037. The following LACM specimens, identified by field numbers, had no museum numbers when examined: GDF42, GDF57, MI563, RLB404, RLB500, WAW42, WAW51, WAW55. The following specimens, identified by field numbers are in the research collection at the Southwest Fisheries Center (SWFC below), La Jolla, Calif: CV160, JSL88, JSL89, JSL90, JSL95, RICE65-1, RICE66-3, WFP7, WPSG-01, WPSG02, WPSG03.

S. cf. *S. longirostris:* LACM27414, 27423, 27424, 27428, 27430, 27432, 27433; SDMNH-21200, 21427; USNM395269, 395270, 395271, 395272, 395273, 395274, 395275, 395930, 395931, 395932, 395933, 395934, 396030, 396032, 396035; LACM field numbers GDF56, RLB238, RLB405, WAW43, WAW50, WAW-52, WAW53, WAW54, WAW58, WAW60; SWFC field numbers CV240, CV241, CV245, RICE65-149, RICE67-102.

While rough-cleaning the porpoise carcasses for skeletal preparation, we examined the blubber, mesenteries, peritoneum, musculature, blowhole region, maxillary sinuses, mammary glands, and viscera (esophagus, stomachs, heart, lungs, liver, spleen, kidneys, gonads, intestine) for larval and adult parasites. We searched 3-m lengths of the intestine at the duodenal end, mid-length, and posterior end. Counts of cysts in the blubber should be considered as relative indices; we did not examine all the blubber carefully. We filled out a data form for each carcass indicating precisely which areas had been checked for parasites. All worms and cysts were fixed in Lavdowsky's (Formalin[3]-Acetic acid-Alcohol) or Bouin's fluid and stored in 70% ethanol. Cestode, trematode, and acanthocephalan whole mounts were stained with celestine blue B or Semichon's carmine. Specimens were sectioned singly or in situ at 6, 8, and 10 μ and stained with Mayer's hematoxylin and eosin Y or Mallory's trichrome. All material except nematode whole mounts were dehydrated in ethanol, cleared in xylene, and mounted in Piccolyte. Nematodes were cleared and mounted in glycerine. Drawings were made with the aid of a drawing tube. Measurements are given in millimeters unless otherwise stated. Average measurements are given with ranges in parentheses.

THE PARASITES

Counts of parasites collected are tabulated in Appendix Tables 1 and 2.

Nematoda

Anisakis simplex (Rudolphi, 1809, det. Krabbe, 1878)

This nematode was the most frequent parasite collected during this study. The taxonomic criteria used in identification of these specimens were those presented by Davey (1971) in his revision of the genus *Anisakis*. *A. simplex* was found in the stomachs of both host species and represents a new host report for both *S. graffmani* and *S. longirostris*. Anisakids have been previously reported from other species of *Stenella* (Delyamure, 1955; Kagei et al., 1967; Zam, Caldwell, and Caldwell, 1971; Dailey and Brownell, 1972).

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

Halocercus delphini Baylis and Daubney, 1925

This parasite has been reported previously from the genus *Stenella* by Zam et al. (1971). They found three of 17 *S. plagiodon* (Cope, 1866) taken off the Florida coast infected with *H. delphini*. This report represents a new host record from *S. graffmani* and *S. longirostris*. Infections occurred in bunches with the anterior ends of the parasites embedded in capsules found outside of the bronchial walls (Figure 1). The body of each parasite lies in the bronchiole oriented in an anterior direction, never towards the apex of the lobe, similar to the orientation described for *Skrjabinalius cryptocephalus* (see Delyamure, 1955).

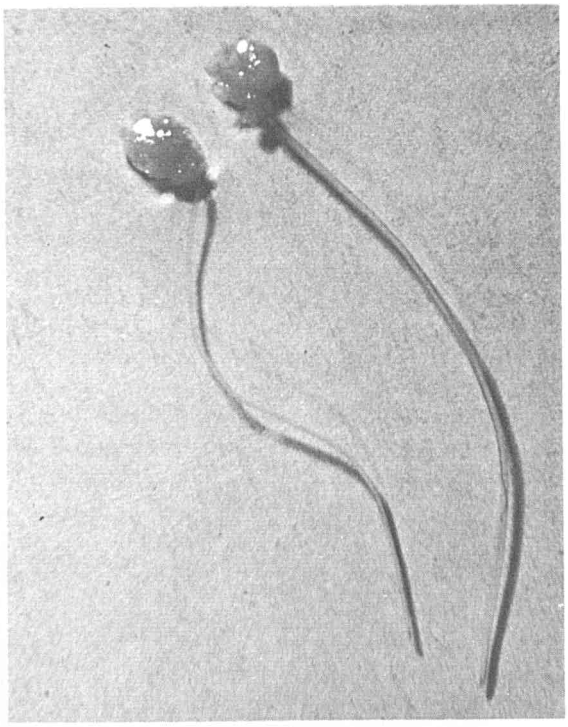


FIGURE 1.—*Halocercus delphini* with anterior end embedded in capsule. (X7)

Mastigonema stenellae gen. et sp. n. (Nematoda: Spiruridae)

This nematode is described from three female specimens taken from the forestomachs of two *S. graffmani* (both recovered prior to present study) and one *S. longirostris*.

Mastigonema gen. n. (Ascaropsinae)

Mouth with two unlobed lips. Cervical cuticle not inflated or flanged. Buccal capsule cylindrical, with few connecting, annular, thickenings. Esophagus long, not divided into anterior and posterior portions; valve of typical spiruroid form. Females prodelphic, ovaries postesophageal. Vulva in middle third of body. Cuticle transversely striated. Oviparous. Parasites of Cetacea.

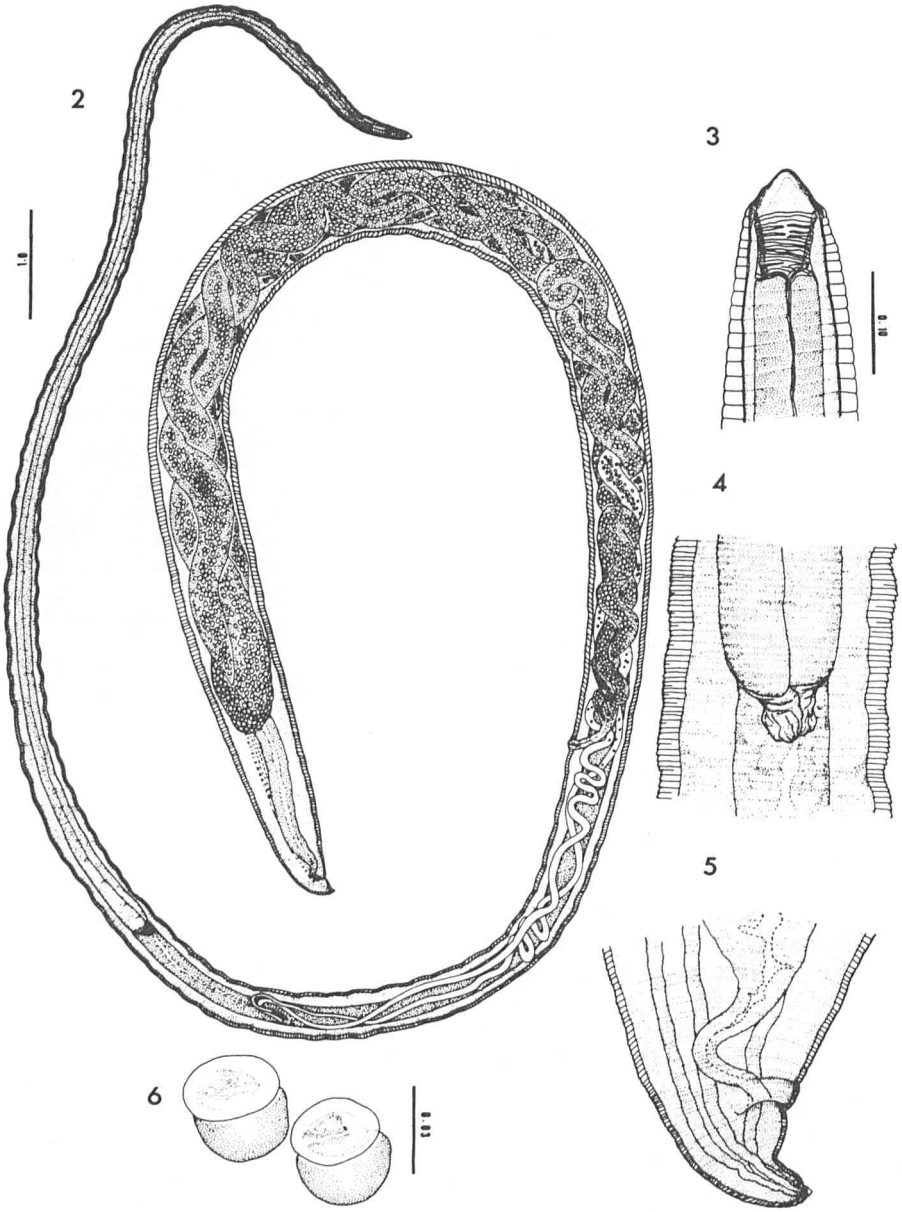
Mastigonema stenellae sp. n. (Figures 2-6)

With characters of the genus: body whip-shaped, with thin anterior and enlarged posterior portions. Stoma triangular; two large lips. Buccal capsule reinforced with connecting rings, cervical papillae present, eggs with enlarged cap.

Female: 25.5 (23.5-28.5) long by 1.2 in maximum width, 7.0 from posterior end. Buccal capsule 0.054 long, tapering from 0.045 wide at anterior to 0.032 at esophageal junction. Nerve ring 0.281 from anterior end, surrounding esophagus. Esophagus 8.5-11.7 long, widening at approximately 2.59 from anterior end. Ovaries directed anteriorly then reflexing sharply. Vulva muscular, 16.64 from anterior, vagina vera 0.13 long by 0.086 wide, vagina uterina 0.81 long by 0.11 wide. Eggs 0.034 long by 0.032 wide, with swollen cap slightly larger than bottom portion. Anal lip large, anus 0.22 from posterior tip. Tail conical with large mucron.

Hosts: *Stenella graffmani*, *S. longirostris*.
Location: Forestomach.
Locality: Eastern tropical Pacific Ocean; holotype from *S. longirostris* collected at approximately lat 8°N, long 107°W.
Type specimens: USNM Helminth Collection holotype female No. 72159, paratype No. 72160.

Remarks: A search of the literature indicates this is the first report of a spirurid



FIGURES 2-6.—*Mastigonema stenellae* sp. n.: 2. Entire worm. 3. Cephalic region, showing annular thickenings. 4. Esophageal-intestinal valve. 5. Caudal region. 6. Eggs, showing enlarged caps.

nematode parasitizing a marine mammal. The general body shape of this nematode is similar to that seen in *Vasorhabdochona cablei* Martin and Zam, 1967, *Trichospirura leptostoma* Smith and Chitwood, 1967, and *Freitasia teixeirai* Baruš and Coy, 1965. However, the structure of lips and buccal capsule place it in the subfamily Ascaropsinae rather than with the rhabdochonids. Of the genera in this subfamily it most closely resembles the genus *Pereirai* Cuocolo, 1943. It differs from *Pereirai* in the following characteristics; lips are unlobed, cuticular flange is lacking, buccal capsule has few annular thickenings, esophagus not divided into anterior and posterior portions, and vulva in posterior half of body.

Crassicaudidae Skrjabin et Andrews, 1934

Crassicauda sp. A single infection of this tissue nematode was found in the 78 animals examined (1.3%). The worms were in the abdominal muscle adjacent to the mammary gland of *S. longirostris*. A large abdominal cyst was also found in the same area. Sections revealed large numbers of *Crassicauda* sp. eggs as well as portions of the female worm (Figure 7). Entire worms were not recovered so specific identification was not possible. However, egg

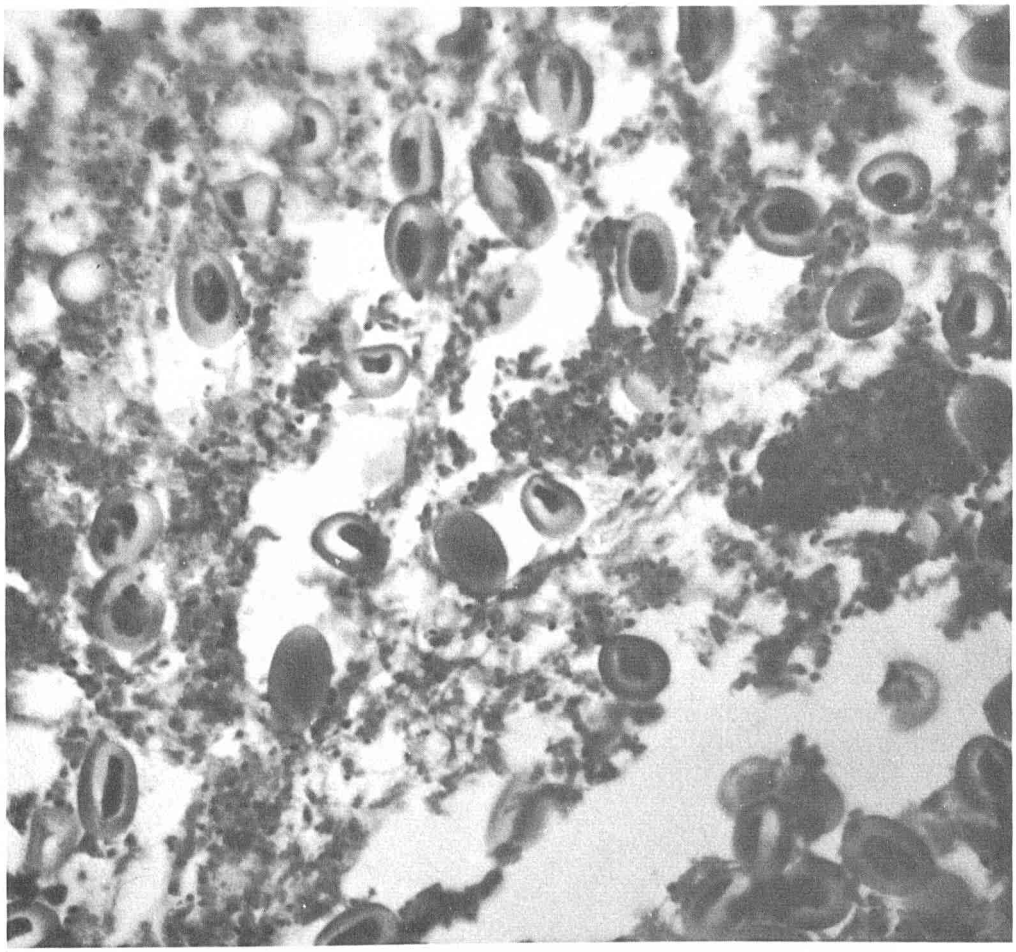


FIGURE 7.—Section through abdominal cyst with *Crassicauda* eggs. (X150)

measurements resemble those given for *C. grampicola* by Johnston and Mawson (1941) from Risso's porpoise, *Grampus griseus* (Cuvier, 1812), taken at New South Wales, Australia.

Another single specimen with *Crassicauda* affinities was recovered by James G. Mead, University of Chicago, Department of Anatomy, while dissecting the head of a *S. graffmani*. The worm was taken from the pterygoid air sinus. The pterygoid bone was eroded in the region in which the specimen was found. We assume that extensive bone damage found by us in other specimens we examined (Figure 8) was also caused by infestations of this nematode, although, judging from the published literature, the possibility cannot be dismissed that more than one species is involved. Reysenbach de Haan (1957) reported *Stenurus globicephalae* Baylis and Daubney, 1952, in the sinuses and cava tympani of the pilot whale, *Globicephala melaena* (Traill, 1809). Norris and Prescott (1961) collected "large quantities of a nematode (*Stenurus* sp.)" from the lateral air sinus of a dall porpoise, *Phocoenoides dalli* (True, 1885). Tomilin and Smyshlyayev (1968) reported that a "nematode *Stenurus minor* attacks the hearing organs of the Black Sea porpoise *Phocaena* and by clogging the cavity around the earbone may kill its host or severely complicate its existence." Brodie (1971) reported *Crassicauda* sp. as a middle ear parasite of the white whale, *Delphinapterus leucas* Pallas, 1776, in Cumberland Sound, Baffin Island. Yamada (1956) examined skulls of approximately 80 false killer whales, *Pseudorca crassidens*, from a stranded group of approximately 150 and found "basket-like" lesions in the pterygoid region of 40 skulls. He ascribed the damage to parasitic infection, "most probably by nematodes," and stated that such damage is a common occurrence in *Grampus* and *Globicephala* in Japanese waters.

Trematoda

The trematodes recovered during this study are represented by two genera known from marine mammals and three specimens of one genus that has been found in teleost hosts.

Zalophotrema pacificum sp. n.
(Figures 9 and 10)

Description: Based on measurements from 26 specimens. With characteristics of the genus. Body elongate. Dorsoventrally flattened, 10 mm (8.3-12.6) long by 1.7 mm (1.4-2.0) wide. Cuticle spinose. Oral sucker 535 μ (398-592) long by 575 μ (439-673) wide; opening slightly subterminal. Pharynx pyriform, 494 μ (398-541) long by 314 μ (255-367) wide. Intestinal cecum bifurcates immediately caudad to pharynx with each lateral branch dividing into short anterior and long posterior portions. Both anterior and posterior cecal branches contain numerous diverticula; anterior branch terminating lateral to posterior edge of oral sucker, posterior branch terminating near posterior end of body. Excretory pore terminal. Acetabulum 600 μ (520-710) in diameter, located approximately mid-body. Cirrus unarmed. Testes large, lobed, in tandem and extending posterior to equatorial third of body. Ovary pretesticular, lobed, 333 μ (235-418) long by 477 μ (310-765) wide. Mehlis's gland posterior and dorsal to ovary. Uterus coiled, preovarian. Genital pore just preacetabular. Vitellaria follicular, occupying entire anterior half of body from level of genital pore to shoulder region of ceca, extending posterior from genital pore in lateral bands to posterior end of body. Eggs, oblong, operculate, round in cross-section, mean measurements of 20 eggs, 61 μ long by 42 μ wide.

Hosts: *Stenella longirostris*, *Stenella graffmani*.

Location: Pancreatic duct.

Locality: Eastern tropical Pacific Ocean; holotype from *S. graffmani* collected at lat 12°5′N, long 93°18′W.

Type specimen: USNM Helm. Coll. No. 72158.

Remarks: Currently there are three species in the genus *Zalophotrema* (Stunkard and Alvey, 1929): *Z. hepaticum* Stunkard and Alvey, 1929, described from the bile ducts of a California sea lion, *Zalophus californianus* (Lesson, 1828), at the New York Aquarium; *Z. curilensis* Gubanov, 1952, from the bile ducts of

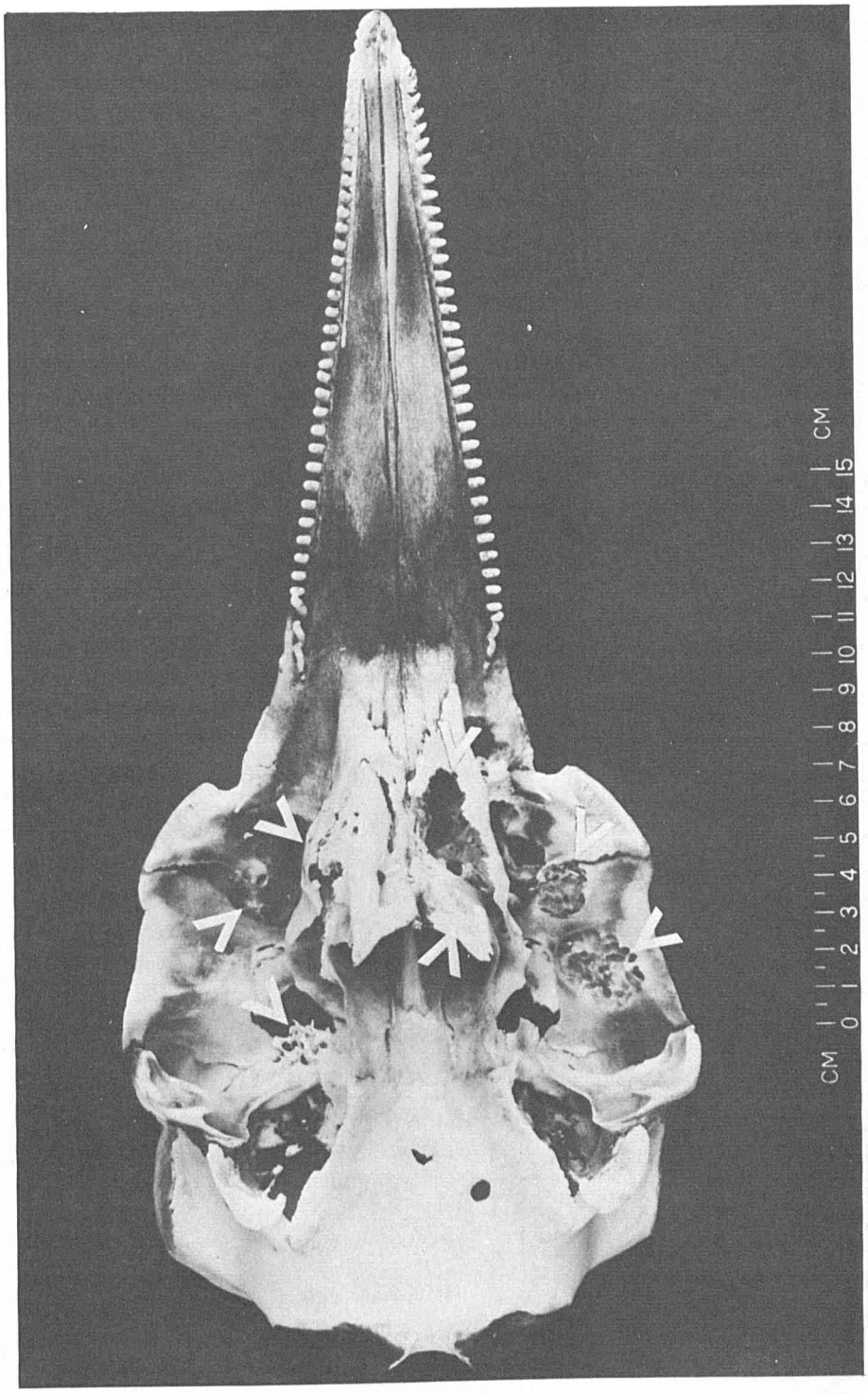
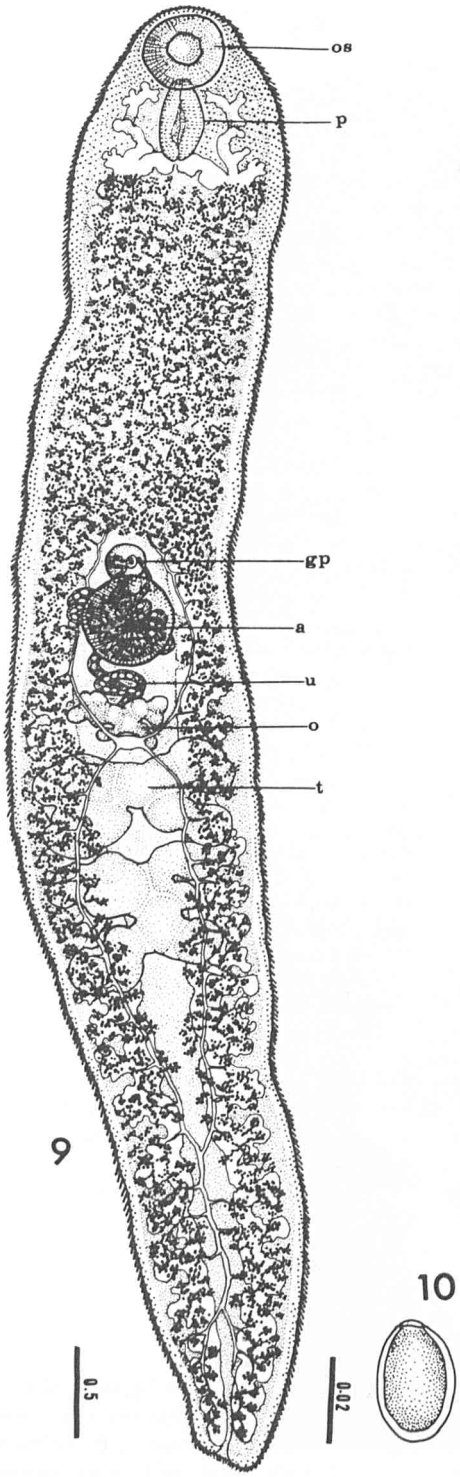


FIGURE 8.—Ventral view of skull of spotted porpoise, *Stenella graffmani*, showing bone lesions (arrows).



a sperm whale, *Physeter catodon* L; and *Z. lubimowi* Petrov and Chertkova, 1963, from the liver of a southern sea lion, *Otaria byronia* (Blainville, 1820) at the Moscow Zoo. *Zalophotrema pacificum* sp. n. can be easily separated from the three previously described species. *Z. lubimowi* differs from all other species in the genus in that it does not have confluent vitellarian fields anteriorly. *Z. curilensis* differs from *Z. pacificum* by larger body size (18-22.5 mm long by 5-7 mm wide) as well as the acetabulum being larger than the oral sucker. *Z. pacificum* sp. n. is most similar to *Z. hepaticum* in general body shape but differs in the following characteristics: body width (*Z. hepaticum* 3.0-3.6 mm wide), sucker ratio (in *Z. hepaticum* oral sucker almost twice as large as acetabulum while in *Z. pacificum* sp. n. suckers are approximately same size), ratio of distance between suckers to body length (*Z. hepaticum* 1:13, *Z. pacificum* sp. n. 1:2.5), distribution (percentage) of preacetabular vitellaria (*Z. hepaticum* nearly twice as large as those of Z. pacificum sp. n.), and egg size (75 μ long by 50 μ wide in *Z. hepaticum*).

Campula rochebruni (Poirier, 1886) Bittner et Sprehn, 1928

This parasite was recovered from the stomachs and hepatopancreatic ducts of three (two *S. graffmani* and one *S. longirostris*) of 78 (3.9%) animals examined. This is a new host record for this parasite and represents the first report from the genus *Stenella*. *C. rochebruni* was originally described from *Delphinus delphis* L. in European waters.

Incidental Trematodes

Three specimens of the genus *Hirudinella*

FIGURES 9-10.—*Zalophotrema pacificum* sp. n. 9. Entire worm, ventral view; 10. egg. Abbreviations used: a - acetabulum; gp - genital pore; o - ovary; os - oral sucker; p - pharynx; t - testis; u - uterus.

Garsin, 1730, were recovered from the forestomachs of three hosts (two *S. longirostris* and one *S. graffmani*). Members of this genus are commonly parasites of teleost fishes and were probably ingested with a meal of fish and not established parasites of these hosts.

Cestoda

Tetrabothrium forsteri (Krefft, 1871) Fuhrmann, 1904

This cestode was recovered from the intestine of over 50% of the examined hosts and occurred in both *S. graffmani* and *S. longirostris*. This is the first report of this parasite from either of these hosts. *T. forsteri* (Krefft, 1871) was first described by Krefft (1871) under the name of *Taenia forsteri* from *Delphinus delphis* L. (= *D. forsteri*) caught off the coast of New Zealand and later transferred to the genus *Tetrabothrium* by Fuhrmann (1904). A complete review of the literature on this species is given by Delyamure (1955).

Strobilocephalus triangularis (Diesing, 1850) Baer, 1932

This tetrabothriid has a complex taxonomic history that is covered by Delyamure (1955). The parasite apparently anchors its scolex in the colon wall when small and grows inside a fibrotic capsule formed by the host (Figures 11 and 12). This is the first report of this parasite from the genus *Stenella*. It has been reported from the Pacific Ocean by Baer (1955), who described material taken from an unidentified dolphin captured in the waters of the Marshall Islands. There are numerous reports of the parasite from Atlantic Ocean hosts (*Hyperoodon ampullatus*) (Forster, 1770) (= *H. rostratus*), *Mesoplodon bidens* (Sowerby, 1804), *Lagenorhynchus acutus* (Gray, 1828), *Steno bredanensis* Lesson, 1828 (= *S. frontatus*), *Delphinus* sp. (Delyamure, 1955).

Phyllobothrium delphini (Bosc, 1802) and *Monorygma grimaldii* (Moniez, 1881) Baylis, 1919

These larval cestodes were recovered from

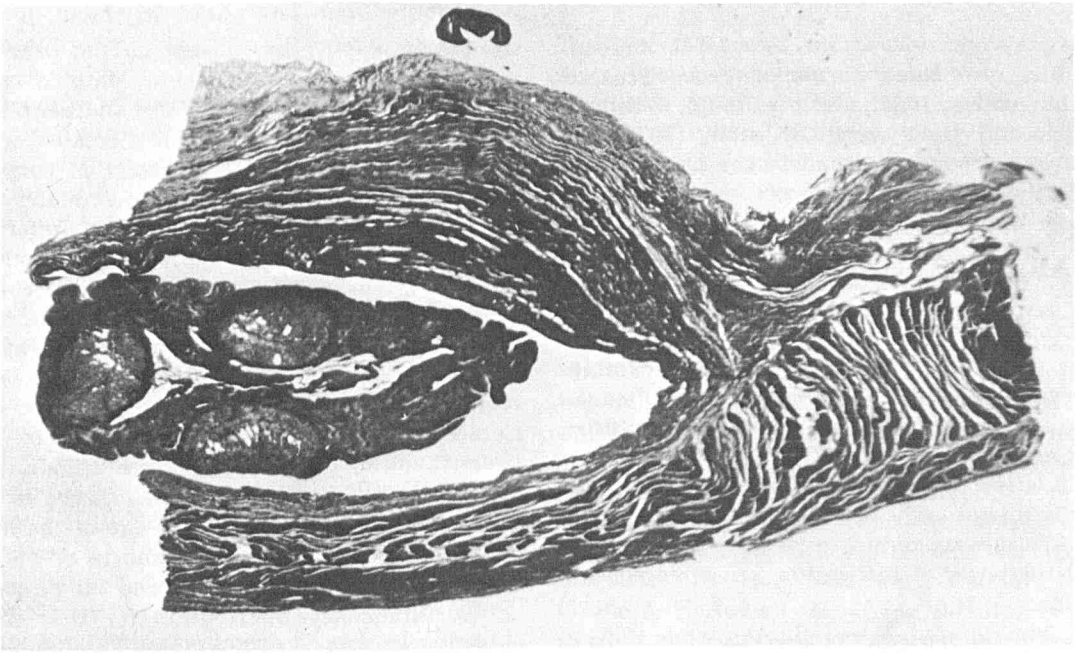


FIGURE 11.—Section through the capsule and scolex of *Strobilocephalus triangularis* from the rectum of *S. graffmani*. (X10.5)

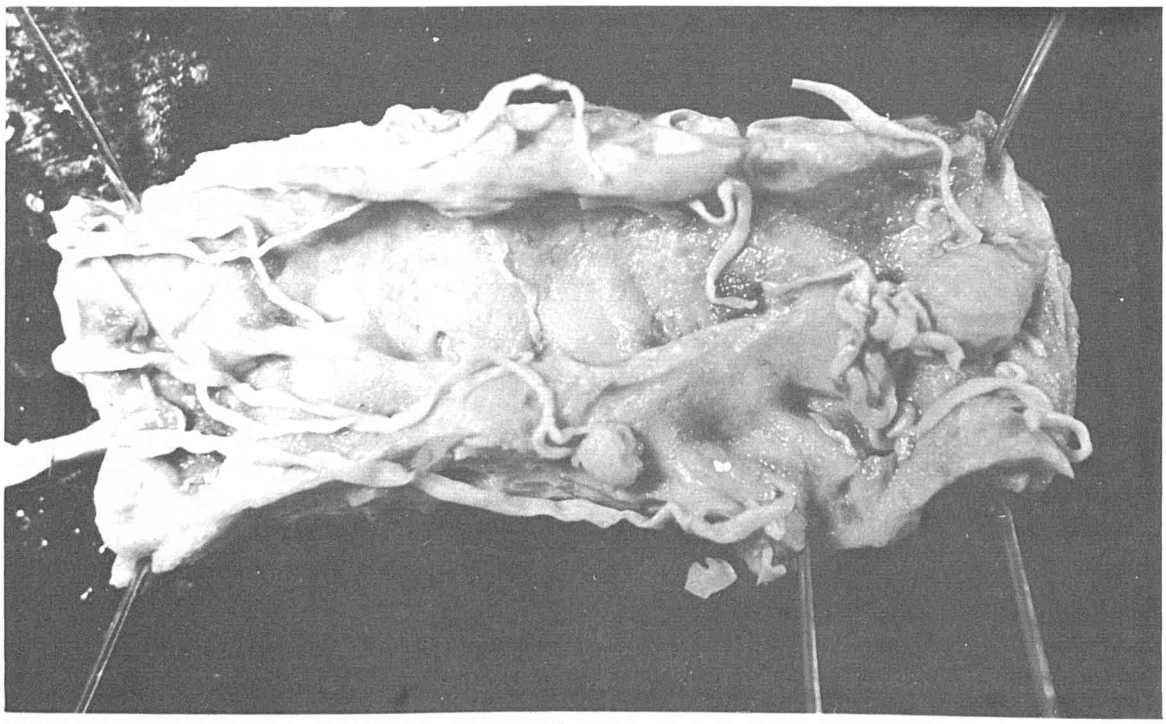


FIGURE 12.—*Strobilocephalus triangularis* attached in rectum of *Stenella graffmani*. (X1)

a large proportion of the animals examined. The history of these worms has been discussed by Delyamure (1955), Dollfus (1964), Williams (1968), and Dailey and Brownell (1972). *P. delphini* was always found in the blubber and *M. grimaldii* in the mesenteries.

PARASITE LOAD RELATIVE TO AGE OF HOST

The availability of data for a large sample of porpoise specimens, especially of *S. graffmani*, dissected in relatively uniform manner provides an unique opportunity to examine infection relative to age of the host for certain of the more frequently encountered parasite species. We discuss only the parasite species for which patterns of infestation are apparent in the data.

Spotted Porpoise, *Stenella graffmani*

The sample of *S. graffmani* examined may be divided into four age classes on the basis of total length, the developmental pattern categories defined by Perrin (1970b) and degree of sexual maturity (Figure 13). Females were classified as adult by the presence of corpora of ovulation in the ovaries and males by presence of spermatogenesis in the seminiferous tubules, as determined by histological examination. Sixty-one of the 72 specimens were collected during a 1-month period, and the first three modes probably represent discrete reproductive cohorts. Analysis below of parasitism relative to age is in terms of the four age classes, except as noted in the case of the *Crassicauda*-like nematode in the air sinuses.

The percent infection for *Anisakis* in *S. graffmani* shows increase with age of the host (Figure 14), but very large numbers of worms were found only in subadults, and the parasite number frequency distribution for that class is obviously skewed to the right. The inference to be drawn is that either some reduction in number of worms occurs in a heavily infected porpoise as it matures, due to the life cycle

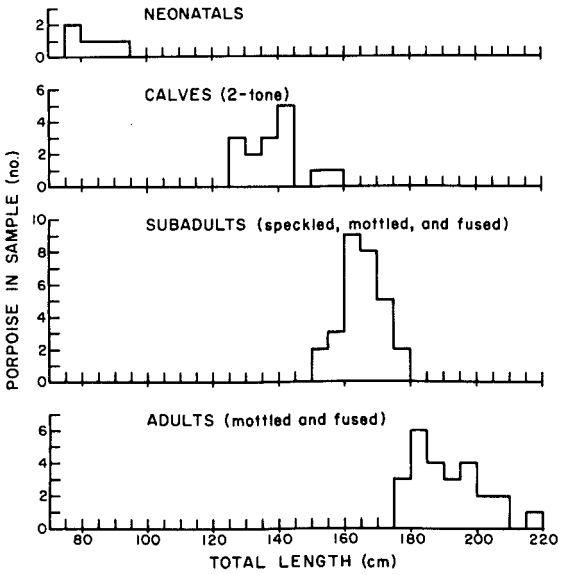


FIGURE 13.—Frequency distributions of total length, by age class, of spotted porpoise, *Stenella graffmani*, included in sample examined for parasites.

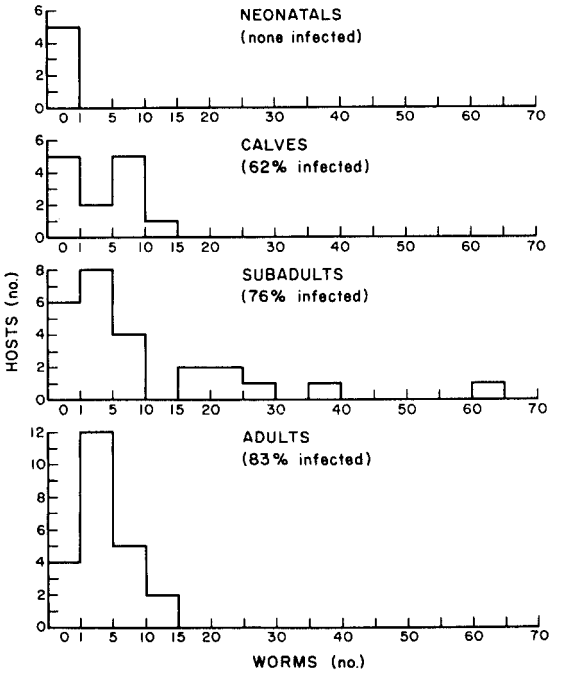


FIGURE 14.—Frequency distributions of levels of infection by *Anisakis* in four age classes of *Stenella graffmani*.

of the parasite and/or to possibly differential feeding habits of young and mature porpoise, or heavily infected individuals die before attaining maturity.

The case of the *Crassicauda*-like parasite in the air sinuses of *S. graffmani* certainly provides the most dramatic instance of infection varying with age. As stated above, the sinuses were not searched during dissection of most of the porpoise specimens, and only one specimen of the *Crassicauda*-type was recovered. Direct evidence, however, is provided of heavy infection by the areas of bone erosion on the lower surfaces of the skull (as illustrated in Figure 8). Given this circumstance, we expanded the series of porpoise specimens examined to include skeletal specimens in various museum collections. In all, 129 skulls of spotted porpoise from the eastern tropical Pacific were examined (see Materials and Methods). Since correlated data on size, reproductive condition, and color pattern were not available for most of the museum specimens examined, it was necessary to use other criteria of age for those specimens. The fetal and neonatal skulls examined were all from specimens we dissected. Those of the remaining skulls that were museum specimens were relegated to the three categories of calves, subadults, and adults by criteria of cranial features, using the sample of skulls from specimens we dissected to correlate these features with total length, sexual maturity, and color pattern. Museum skulls were assigned to the calf class when in condylobasal length, telescoping of facial elements, and closure of occipital sutures, they had not reached the adult condition. Skulls exhibiting adult length, telescoping, and occipital closure were divided into adults and subadults by the criterion of presence or absence of distal fusion of the premaxillary and maxillary bones of the rostrum. Rough correlation of the onset of fusion with attainment of sexual maturity was found among the skulls from specimens for which external data were also available (Table 1. Errors in classifying subadult skulls as adult and vice versa are approximately equal. Results of examination of the 129 skulls for bone damage (Table 2) demonstrate clearly that the rate of infection is very much higher in

TABLE 1.—Incidence of distal fusion of pmx (premaxillary) and mx (maxillary) bones in specimens of *Stenella graffmani*.

Age class[1]	Examined	Pmx and mx fused	Error in classification
Subadults	31	6	19.4%
Adult	21	18	14.3%

[1] As determined by criterion of total length, color pattern, and sexual maturity.

TABLE 2.—Lesions of the ventral side of the skull in *Stenella graffmani*, presumably due to infection by a *Crassicauda*-like nematode.

Age class	Range of condylobasal length	Examined	Lesions present
	(mm)		
Nearterm fetuses and neonatals	209-236	10	0
Calves	302-359	18	8 (44.4%)
Subadults	356-446	45	5 (11.1%)
Adults	360-466	56	4 (7.1%)
Total		129	17 (13.2%)

calves than in subadults or adults. What is more, the most severely damaged skulls were those of calves. Such extensive damage is certainly irreversible, in that if repaired, traces would still be apparent in the form of bone callouses, depressions, or altered shape of bone elements. No such traces were found in any of the adult skulls examined, although we searched for them carefully. We conclude, therefore, that heavy damage is indicative of a probably morbid condition and that parasitism or a correlated condition is a significant factor in natural mortality of the spotted porpoise in the eastern tropical Pacific.

The patterns of infection relative to age by cysts of the cestodes *Monorygma* and *Phyllobothrium* (Figure 15) closely resemble each other, with little or no occurrence before subadulthood and 100% occurrence and greatest numbers in adults. As these are larval forms, the cysts presumably would have to be ingested by predators of the porpoise in order for the life cycles of the parasites to progress. Killer whales, *Orcinus orca*, have been observed by Perrin to prey on spotted porpoise, and sharks of several species have been observed to feed on dead and injured spotted porpoise during tuna fishing operations (Leatherwood, Perrin, Garvie, and La Grange, manuscript).[4] Killer whales and/or sharks are therefore possible candidates for terminal hosts of these two cestodes, although adult Tetraphyllidea have only been found in elasmobranchs. However, a life cycle involving a warm blooded intermediate host serving a cold blooded definitive host has not been previously demonstrated.

The two nonlarval cestodes, *Tetrabothrium forsteri* (Figure 16) and *Strobilocephalus triangularis* (Table 3), exhibit different patterns of occurrence, more like those of the nematodes, occurring with greatest numbers and frequencies in calves in the case of *T. forsteri* and in calves and subadults in the case of *S. triangularis*. This was especially striking for *S. triangularis*. In the two calves and two subadults with extremely heavy infections, the last meter of the intestine was all but blocked and swollen to three or four times its normal diameter. No adult examined was found to be infected with *S. triangularis*.

Spinner Porpoise, *Stenella* cf. *S. longirostris*

The smaller sample of spinner porpoise was divided into three age classes on the basis of length and sexual maturity, with subadults again defined as immature animals of adult size. Despite the small number of data for the spinner (Appendix Table 2), some differences are apparent between the patterns of infection for this species and for *S. graffmani*. For *Anisakis*, the specimen with the greatest number of worms (CV285) was a large adult female, which contrasts with the finding for *S. graffmani*, in which heaviest infections occurred in subadults. Bone erosion suggesting severe infection of the ventral air sinuses by a nematode was encountered in only 1 skull (of a subadult) of 53 examined. The parasite specimen was not recovered, precluding identification, but the damage was similar to that caused by the *Crassicauda*-like nematode in *S. graffmani*.

[4] Leatherwood, J. S., W. F. Perrin, R. L. Garvie, and J. C. La Grange. Observations of sharks attacking porpoise (*Stenella* spp.). (Unpubl. manuscr.)

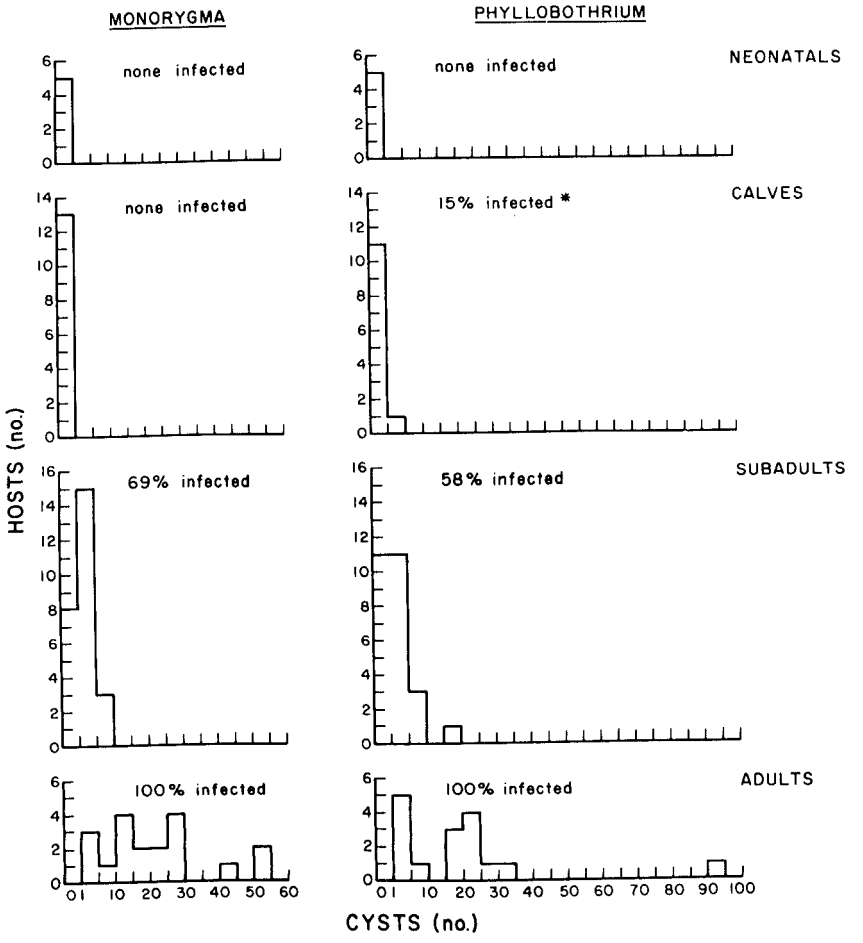


FIGURE 15.—Frequency distributions of levels of infection by cysts of *Monorygma grimaldii* and *Phylobothrium delphini* in four age classes of *Stenella graffmani*.

Infection by cestode cysts showed the same pattern as in *S. graffmani*, except that one adult specimen was found to be free of *Phyllobothrium* cysts. Also, as in *S. graffmani*, calves were most heavily infected with *T. forsteri*, and *Strobilocephalus triangularis* was encountered only in an immature specimen, a calf.

ACKNOWLEDGMENTS

The authors would like to express their appreciation to Gerald Schmidt, University of Northern Colorado; John Schacher, University of California, Los Angeles; Mary Pritchard, University of Nebraska; May Belle Chitwood, University of California, Davis; Kenneth S. Norris, University of California, Los Angeles; and Leo Margolis, Fisheries Research Board of Canada, Nanaimo, for their help and advice during the study. We would also like to give special thanks to Barry L. Hill, Lorraine G. Peterson, and Kenneth S. Raymond, for their valuable technical contributions. Randolph Jose, Ralston-Purina Corporation; Craig J. Orange, Inter-American Tropical Tuna Commission; and the captains and crews of the tuna vessels *Carol Virginia*, *Pacific Queen*, *Conquest*, *Marietta*, and *Queen Mary* helped us obtain porpoise for dissection. Richard G. Van Gelder, American Museum of Natural History; Donald R. Patten,

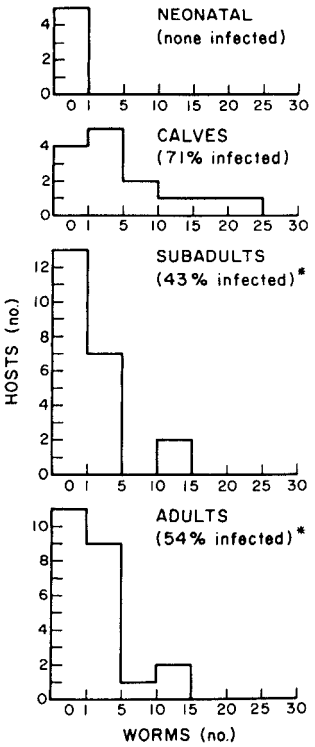


FIGURE 16.—Frequency distributions of levels of infection by *Tetrabothrium forsteri* in four age classes of *Stenella graffmani*.

TABLE 3.—*Strobilocephalus triangularis* in *Stenella graffmani*.

Age class	Examined	Infected
Neontals	5	0
Calves	14	3 (21.4%)
Subadults	26	3 (11.5%)
Adults	23	0
Total	68	6 (8.8%)

Los Angeles County Museum; Joseph R. Jehl, Jr., San Diego Museum of Natural History; and Charles O. Handley, Jr., U.S. National Museum, kindly made materials in their charge available for study.

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APPENDIX TABLE 1.—Parasites in *Stenella graffmani*.

Host						Parasites noted										
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Terrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllobothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balanae*
CV259	USNM395276	6	1,676	M	3	0	—	0	0	0	2	0	0	0	0	0
CV260	USNM395277	6	1,750	F	4	1	—	0	0	0	0	0	1	3	0	0
CV261	USNM395278	2	1,657	F	3	1	—	0	0	0	0	0	0	2	1	0
CV262	USNM395279	2	1,646	F	3	20	—	0	0	0	1	1	0	0	0	0
CV263	USNM395328	6	1,759	M	3	35	—	0	0	0	0	0	0	5	0	0
CV264	USNM395329	6	1,716	M	3	0	—	0	0	0	2	0	18	7	0	0
CV265	USNM395330	2	1,954	M	4	1	—	0	0	0	4	0	20	26	0	2
CV266	USNM395331	2	1,681	M	3	1	—	0	0	0	0	+	0	2	0	0
CV267	USNM395332	2	1,787	M	4	2		0	0	0	0	0	18	23	0	0
CV268	USNM395333	2	1,900	F	4	4	—	0	0	0	2	0	—	27	0	0
CV269	USNM395334	2	1,837	F	4	2	—	0	0	0	0	0	—	14	0	0
CV270	USNM395336	2	1,815	F	4	0	—	0	0	0	1	0	5	52	0	1
CV271	USNM395337	2	1,821	F	4	8	—	0	0	0	0	0	—	13	0	0
CV272	USNM395338	2	1,850	F	4	0	—	0	0	0	2	0	25	45	0	1
CV273	USNM395339	2	1,630	M	3	61	—	0	0	0	0	0	0	1	0	1
CV274	USNM395385	6	1,782	M	3	0	—	0	0	0	+	0	0	5	0	0
CV275	USNM395386	6	1,570	M	3	2	—	0	0	0	1	0	8	3	0	0
CV276	USNM395387	6	1,578	M	3	16	—	0	0	0	0	0	0	1	0	0
CV277	USNM395388	2	1,816	F	4	8	—	0	0	0	0	0	5	2	0	1
CV278	USNM395389	6	1,632	M	3	18	—	0	0	0	0	0	2	0	0	0
CV279	USNM395390	6	2,183	M	4	8	—	0	0	0	5	0	27	50	2	0
CV280	USNM395391	6	2,032	M	4	14		0	0	0	5	0	32	14	0	0

APPENDIX TABLE 1.—Parasites in *Stenella graffmani*.—*Continued*.

Host						Parasites noted										
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Tetrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllobothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balanae*
CV281	USNM395392	6	1,739	F	3	27	—	0	0	0	+	0	1	1	0	0
CV282	USNM395393	6	1,740	F	3	2	—	0	0	0	2	0	6	4	0	0
CV283	USNM395394	6	2,021	M	4	5	—	0	0	0	13	0	90	28	0	0
CV284	USNM395395	2	1,927	F	4	0	—	0	0	0	0	0	—	—	0	1
CV286	USNM395397	2	1,647	M	3	0	—	0	0	100+	0	0	3	2	2	0
CV287	USNM395417	2	1,732	M	3	0	—	0	0	0	0	0	4	7	0	0
CV289	USNM395594	2	1,767	M	4	0	0	0	0	0	2	0	3	4	0	0
CV290	USNM395595	2	1,627	F	3	0	0	0	0	0	6	0	0	1	0	0
CV291	USNM395596	6	1,927	F	4	1	—	0	0	0	0	0	24	9	0	0
CV292	USNM395597	2	1,895	M	4	5	0	0	34	5	15	0	—	—	0	0
CV293	USNM395598	6	1,996	M	4	2	—	0	0	0	0	0	5	12	0	0
CV295	USNM395527	6	1,390	M	2	9	0	0	0	0	19	0	0	0	1	2
CV296	USNM395528	2	1,298	M	2	0	0	0	0	0	0	+	0	0	0	0
CV297	USNM395529	6	1,429	F	2	2	0	0	0	0	1	0	0	0	0	2
CV298	USNM395530	2	1,540	M	3	4	0	0	0	0	5	+	0	0	0	0
CV300	USNM395532	6	1,438	M	2	11	0	0	0	0	20+	0	0	0	2	2
CV303	USNM395535	6	1,433	M	2	0	0	0	0	0	4	0	0	0	0	0
CV304	USNM395458	2	862	M	1	0	0	0	0	0	0	0	0	0	0	0
CV305	USNM395459	2	780	F	1	0	0	0	0	0	0	0	0	0	0	0
CV306	USNM395460	6	913	M	1	0	0	0	0	0	0	0	0	0	0	0
CV307	USNM395461	2	803	F	1	0	0	0	0	0	0	0	0	0	0	0
CV308	USNM395466	6	793	F	1	0	0	0	0	0	0	0	0	0	0	0
CV309	USNM395463	6	1,878	F	4	9	0	0	0	0	9	0	21	26	0	0
CV310	USNM395464	2	1,801	M	4	3	0	0	0	0	1	0	21	17	0	0
CV311	USNM395465	6	1,995	M	4	4	0	0	0	0	3	0	18	23	0	0
CV312	USNM395462	2	1,640	F	3	7	0	0	0	0	0	0	1	0	0	0
CV313	USNM395467	2	1,601	M	3	8	0	0	0	0	5	0	0	2	0	0
CV314	USNM395468	2	1,842	F	4	1	0	0	0	0	0	0	+	+	0	0
CV315	USNM395603	2	1,621	M	3	7	+	0	0	0	12	0	3	5	0	0
CV316	USNM395604	2	1,679	M	3	12	0	0	0	0	0	0	1	4	0	0
CV317	USNM395605	2	1,375	M	2	7	0	0	0	0	5	0	0	0	0	2
CV318	USNM395606	2	1,444	F	2	8	0	0	0	0	0	0	0	0	0	0
CV319	USNM395607	6	1,681	F	3	2	0	0	0	0	1	0	5	0	0	0
CV320	USNM395608	2	1,670	M	3	20	+	0	0	0	13	0	7	0	0	0
CV321	USNM395609	2	1,525	M	3	1	0	0	0	0	0	0	1	0	0	0
CV322	USNM395610	6	1,423	F	2	9	0	0	0	0	6	0	0	0	0	0
CV323	USNM395611	2	1,617	M	3	5	0	0	0	0	0	0	4	2	0	0
CV324	USNM395612	6	1,356	F	2	0	0	0	0	0	13	0	+	0	0	0
CV325	USNM395613	6	1,348	M	2	4	+	0	0	0	8	0	1	0	2	2
PQ01	USNM395407	lat ~8°N, long 107°W	1,978	M	4	3	—	0	0	0	0	0	5	18	0	0
PQ02	USNM395408	lat ~8°N, long 107°W	1,590	M	2	7	—	0	0	0	0	+	0	0	0	0
[4]PQ04	USNM395410	lat ~8°N, long 107°W	1,677	F	3	3	—	0	0	0	0	0	2	8	1	0
WFP10	CAS15662	lat ~14°N, long 100°W	1,865	F	4	11	—	0	0	0	0	0	—	—	0	0
WFP11	UCMP86284	lat ~14°N, long 99-108°W	1,304	M	2	—	+	—	—	—	—	+	—	—	—	—
WFP12	MVZ140640	lat ~14°N, long 100°W	1,671	M	3	—		—	—	—	—	0	—	—	—	—
WFP13	UCMP23071	lat ~10°N, long 100°W	1,572	M	3	—	0	—	—	—	—	—	—	—	—	—
WFP19	CAS15663	lat ~10°N, long 100°W	1,536	M	3	—	0	—	—	—	—	—	—	—	—	—
WFP20	MVZ140643	lat ~10°N, long 100°W	1,708	F	3	—	0	—	—	—	—	—	—	—	—	—
WFP3	LACM37549	lat 14°30′N, long 99°10′W	1,252	F	2	0	0	0	0	0	2	0	0	0	0	2
WFP4	LACM37550	lat 14°30′N, long 99°10′W	1,260	M	2	0	0	0	0	0	0	0	0	0	0	0

[1] CAS = California Academy of Sciences, San Francisco
LACM = Los Angeles County Museum
MVZ = Museum of Vertebrate Zoology, University of California, Berkeley
USNM = United States National Museum, Washington, D.C.

[2] Locality for collection number 2: lat 12°51′N, long 93° 18′W
Locality for collection number 6: lat 7°11′N, long 90°32′W

[3] 1 = near term fetus or neonatal
2 = calf
3 = subadult
4 = adult

[4] This specimen also infected with *Crassicauda*.

APPENDIX TABLE 2.—Parasites in *Stenella* cf. *S. longirostris*.

Host						Parasites noted										
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Tetrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllbothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balanae*
CV285	USNM395396	2	1,769	F	4	56	—	0	50+	50+	3	0	27	13	2	0
CV288	USNM395593	6	1,726	F	4	2	—	0	—	—	—	—	+	+	—	—
CV294	USNM395526	6	1,494	F	2	1	+	0	0	0	10	0	8	0	1	0
CV299	USNM395531	2	1,189	M	2	4	0	0	0	0	5	0	0	0	0	4
CV301	USNM395533	2	1,396	F	2	0	0	0	0	0	0	0	0	0	2	0
CV302	USNM395534	2	1,184	M	2	9	0	0	0	0	20+	0	0	0	0	1
PQ03	USNM395409	lat ~8°N, long 107°W	1,571	F	3	8	0	0	0	0	8	0	8	2	2	6
PQ05	USNM395411	lat ~8°N, long 107°W	1,680	F	4	5	—	0	0	0	0	0	13	13	0	0
PQ06	USNM395412	lat ~8°N, long 107°W	1,729	F	4	9	—	1	0	0	0	0	0	4	1	0
PQ07	USNM395413	lat ~8°N, long 107°W	1,761	F	4	9	—	0	0	0	0	0	8	6	1	0
PQ08	USNM395414	lat ~8°N, long 107°W	1,734	M	4	1	—	0	0	0	2	0	7	17	0	0
PQ09	USNM395599	lat ~8°N, long 109°45′W	1,727	M	4	1	0	0	0	0	0	0	21	8	1	2
PQ10	USNM395600	lat ~8°N, long 107°W	1,086	F	2	7	—	0	0	0	0	0	0	0	0	1
PQ11	USNM395601	lat 8°N, long 109°45′W	1,054	F	2	0	—	0	0	0	6	+	0	0	0	1
WFP14	CAS15664	lat ~14°N, long 99-108°W	1,618	F	4	—	+	—	—	—	—	—	—	—	—	—
WFP15	CAS15665	lat ~14°N, long 100°W	1,637	M	4	—	+	—	—	—	—	—	—	—	—	—
WFP21	MVZ140641	lat ~14°N, long 100°W	1,651	M	3	—	+	—	—	—	—	—	—	—	—	—
WFP22	CAS15668	lat ~10°N, long 100°W	1,750	M	4	—	—	—	—	—	—	—	—	—	—	—
WFP6	LACM37551	lat 10°40′N, long 108°40′W	896	F	2	0	0	0	0	0	0	0	0	0	0	0

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LACM = Los Angeles County Museum
MVZ = Museum of Vertebrate Zoology, University of California, Berkeley
USNM = United States National Museum, Washington, D.C.

[2] Locality for collection number 2: lat 12°51′N, long 93°18′W
Locality for collection number 6: lat 7°11′N, long 90°32′W

[3] 1 = near term fetus or neonatal
2 = calf
3 = subadult
4 = adult

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VERTICAL DISTRIBUTION PATTERNS OF GOLDEYE, *HIODON ALOSOIDES*, IN FORT PECK RESERVOIR, MONTANA

JAMES L. COOPER[1]

ABSTRACT

In November 1967 and continuing into December 1969, the goldeye, *Hiodon alosoides* (Rafinesque), in Fort Peck Reservoir, Mont., exhibited seasonal vertical distribution patterns, which seemed to be related to the surface-water temperature. When surface-water temperatures were above 8.9°C (summer and early fall), the goldeye congregated near the surface. During the late fall, ice-covered period, and spring when surface temperatures varied between 8.9° and 1.1°C, the goldeye usually congregated between the 8- and 32-ft level. However, it is the opinion of the author that the goldeye were following the food source and were not responding to temperature per se.

The goldeye, *Hiodon alosoides* (Rafinesque), is one of two shadlike freshwater fishes belonging to the Family Hiodontidae. Distribution of goldeye is limited in the United States and Canada (found mostly in the prairie States and Provinces). The goldeye is generally described as being found in shallow, turbid lakes and large river systems (Battle and Sprules, 1960; Kennedy and Sprules, 1967) and in the shallow waters of large lakes (Kennedy and Sprules, 1967). However, Bajkov (1930) observed that goldeye were found on the surface over deep water in Lake Winnipeg, Manitoba, and Borges (1950) netted goldeye in the deep water of the Lake of the Ozarks, Mo., in September.

Fort Peck Reservoir is basically a deep, clear body of water in contrast to the lakes generally described as being inhabited by goldeye. However, goldeye were netted during 1966 in quantity on the surface in clear water. Good numbers of goldeye continued to be netted in clear water during 1967-70 (unpublished data available in annual report form of Montana Fish and Game Department).

Mature goldeye often exceed 15 inches in total length in nutrient-rich bodies of water; the Montana record is 18.7 inches total length (Brown, 1971) and was taken from Nelson Reservoir, a fertile lake about 70 miles from Fort Peck Reservoir. In Fort Peck Reservoir, the goldeye rarely exceeded 15 inches in total length and most were less than 14 inches total length; they seldom lived longer than 8 years; most spawned in June; and they withstood water temperatures as low as 1.1°C (unpublished data).

The coho salmon, *Oncorhynchus kisutch*, which was first introduced in 1969, was the only species to compete with goldeye for food in pelagic areas of the reservoir. In shallow-water areas, the goldeye contributed to the diets of sauger, *Stizostedium canadense*; walleye, *S. vitreum vitreum*; and northern pike, *Esox lucius* (personal observations).

The goldeye is one of the most important commercial fish taken from the reservoir. The goldeye are trucked to Winnipeg, Manitoba, which has the only substantial commercial market (up to 1 million lb of drawn fish are utilized annually). However, it has only been since 1967 that the market for goldeye from Fort Peck Reservoir has been significant. Declining populations of goldeye in Canadian waters, probably due to overharvesting by commercial fishermen, were responsible for the interest in Fort Peck Reservoir's goldeye (goldeye harvest from Fort Peck Reservoir varied from 53,318 to 199,279 lb round weight during 1967-71). See Battle and Sprules (1960), Grosslein and Smith (1959), and Kennedy and Sprules

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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

(1967) for a past history of the commercial fishery in Canada and the United States.

To better understand the problems associated with harvesting goldeye from the clear waters of Fort Peck Reservoir, the availability of goldeye to gill net fishermen at different times of the day and year was investigated. Emphasis was placed on selective fishing; i.e., floating gill nets, 8 ft deep, were set in open-water areas away from shallow bays and shorelines to avoid game fish. The results of selective netting revealed that goldeye were present in commercial quantity away from shallow, turbid areas and that the catch consisted of almost 100% goldeye (unpublished data).

However, during the winter, spring, and late fall, the goldeye were not gilled in the floating gill nets. Preliminary netting with 8-ft-deep, sinking gill nets (nets were set obliquely and horizontally at different depths) indicated that the goldeye were present during the fall and spring periods, but usually at the 20- to 30-ft level. To better determine some of the parameters associated with the vertical distribution of goldeye, the following study was begun in November 1967.

DESCRIPTION OF FORT PECK RESERVOIR AREA AND SAMPLING SITE

Fort Peck Reservoir is located in sparsely populated northeastern Montana. At maximum pool the reservoir has a surface area of 245,000 acres, a maximum depth of 225 ft near the dam, and an irregular shoreline over 1,500 miles long. Only the Missouri River and Musselshell River continuously flow into the reservoir. There are detailed descriptions of the area (U.S. Fish and Wildlife Service, 1952).

The water of the reservoir is clear except for the shallow ends of large bays and upper ends of the two main arms (Missouri Arm formed by the Missouri River and the Big Dry Arm formed by the intermittent Big Dry Creek). Surface-water temperatures varied from freezing in winter (the Reservoir is completely ice-covered for almost 4 mo) to the low 20°C in summer.

There was little indication of thermal stratification. During the ice-cover period, the water temperature in the sampling area was 1.1°C from the surface to at least a depth of 50 ft. Also, water tapped from approximately 140 to 160 ft below the surface for the turbines at the dam was 1.1°C during most of the above period (records kept by U.S. Corps of Engineers at Fort Peck). The continued withdrawal of water for power production (10,000 cfs) probably discouraged formation of a winter inverse stratification. The almost ever present prairie winds and withdrawal of water for power production probably discouraged the formation of a true summer thermocline. During the warm months of July and August, the temperature from the surface to depth of 50 ft varied only a few degrees Celsius in the sampling area. Phenicie (1950) found little evidence of a thermocline, and he recorded a high temperature of 8.3°C at a depth of 180 ft. Temperature data kept by the U.S. Army Corps of Engineers during July and August were usually in the 9°-13°C range for water taken from the 140- to 160-ft level.

The area sampled was open water located from ½ to 1 mile off a point of land near the west end of Fort Peck Dam. The water was clear, and depths ranged from 50 ft to over 100 ft. Netting efforts in other parts of the lower reservoir area by the Montana State Fish and Game Department and commercial fishermen indicated that the sampling site was representative of open, clear-water areas of the lower reservoir.

MATERIALS AND METHOD

To determine the vertical distribution of the goldeye, a floating nylon gill net was used. The net measured 100 ft long and 40 ft deep. The webbing, of No. 139 nylon twine, was 1½-inch mesh, square measure. The net was divided into five horizontal sections, each 8 ft deep. The depth of 40 ft was chosen since numerous (approximate number not known) test-netting efforts during spring, summer, and fall of 1966-69 gilled few goldeye below the 40-ft depth (oblique, horizontal, and bottom sets were utilized). Most of the Montana State Fish and Game Department and commercial

fishery goldeye nets have No. 139 nylon twine. This 1½-inch mesh was selected because it gilled more goldeye than 1-inch, 1¼-inch, 1¾-inch, or 2-inch mesh (unpublished data). Eight-foot sections represented the width of gill nets used for goldeye on the Reservoir.

Usually the net was set for overnight and then lifted. It was observed that daylight sets rarely caught many goldeye in clear water. The exact time of setting and lifting the net usually had little influence on the catch as long as the net was set well before dusk and lifted after sunrise. Because so few goldeye were caught in overnight sets during the ice-cover period in 1968, the net was set for several days before lifting during the 1969 ice-cover period.

RESULTS

The vertical distribution pattern can be followed in Table 1.

During the summer and early fall, the goldeye exhibited maximum stratification within 8 ft of the surface, and they were easily captured by floating gill nets. The summer and early fall pattern began in 1968 and 1969 once the surface temperature reached 7.2°C and remained above 13.3°C.

The late fall pattern in 1967, 1968, and 1969 eventually exhibited the reverse of the summer pattern; i.e., the greatest concentration in the top 40 ft was between the 32- and 40-ft level. However, the goldeye did not move quickly from the surface to deeper depths. There was a transitional period during which the goldeye were scattered throughout all depths sampled (0-40 ft). The late fall pattern began as the surface temperature approached 6.1°C in 1967 and 8.9°C in 1968 and 1969.

During the ice-cover period, the goldeye appeared to concentrate between the 8- and 32-ft level; however, few goldeye were taken per night set. In 1968, the catch per night set was 22 goldeye; in 1969, the equivalent catch per night set was 3.5 goldeye. In contrast, the ice-free period usually had catches of 60 or more goldeye per night set. The water temperature was 1.1°C both winters.

The goldeye vertical distribution pattern in the spring was not as predictable as in other periods. The goldeye were caught at all depths, near the surface, or near the 40-ft depth. No clear relationship between the distribution pattern and temperature was evident. Apparently quick shifts in wind direction affected surface temperatures more in spring than in summer and fall. Since the warm surface-water column in summer and fall penetrated to deeper levels than the spring warm surface column, maybe upward convection currents more easily displaced surface water in the spring.

DISCUSSION

The following discussion concerns mostly the open-water area; i.e., little reference is made to the goldeye that may habitually seek shallow, turbid conditions such as would be found in small bays and near river mouths.

It is evident that the goldeye in the sampling area do exhibit consistent seasonal vertical distribution patterns and that the patterns can usually be predicted from the surface-water temperature. The cause of the patterns is not clear, but it is suspected that the goldeye is following the food source, which in Fort Peck Reservoir consists of zooplankton, terrestrial insects, aquatic insects, and small fishes. It is believed from observations (regurgitation of stomach contents when goldeye were forced through the mesh), daytime versus night-time sets, and cursory stomach examinations that the goldeye do most of their feeding at night during the summer and early fall when zooplankton and terrestrial and emergent aquatic insects are available on or near the surface. Work by Bajkov (1930) and Grosslein and Smith (1959) support the above contention as does work by Sprules (1947).

It is not known whether the goldeye move to deeper water during the day. Surface sets over clear, deep water during the day have caught few goldeye although sets in turbid, shallow areas often produce substantial catches. Possibly the fish gilled in the shallow, turbid water could not see the net.

Obviously, terrestrial insects do not contribute significantly to the diet during the

TABLE 1.—Vertical distribution pattern of goldeye in an open-water area of Fort Peck Reservoir, from November 1967 into December 1969.

[Number of goldeye per night per 8-ft deep section of 100-ft net.]

Pattern	Date	Temperature (°C)[1]	Depth (ft) 0-8	8-16	16-24	24-32	32-40
1967							
Summer-early fall	20 Nov.	8.9	48	28	7	1	0
	24 Nov.	7.8	66	56	22	4	2
Late fall	5 Dec.	6.1	18	46	51	40	52
	16 Dec.	4.4	1	6	26	25	44
1968							
Winter ice-cover	17 Jan.	1.1	0	9	14	6	3
	9 Feb.	1.1	4	14	8	2	0
	15 Feb.	1.1	2	0	1	0	0
	16 Feb.	1.1	2	3	0	1	0
	23 Feb.	1.1	0	13	1	0	0
	1 Mar.	1.1	0	4	7	0	0
Spring	11 Apr.	2.8	1	7	9	6	2
	19 Apr.	3.2	14	31	47	41	25
	23 Apr.	3.2	2	6	5	4	0
	24 Apr.	7.2	6	17	16	11	7
	25 Apr.	3.9	20	11	3	1	3
	1 May	5.0	86	82	86	57	40
	12 May	6.1	11	10	15	6	15
Summer-early fall	20 May	7.2	21	14	13	10	16
	24 May	8.3	12	4	2	5	3
	6 June	12.2	41	39	38	20	20
	13 June	13.3	41	8	5	6	6
	26 June	15.6	75	35	18	18	18
	17 July	19.4	37	8	11	3	3
	25 July	18.7	38	7	5	2	2
	6 Aug.	20.0	51	18	3	5	5
	27 Aug.	17.8	61	19	15	13	22
	4 Sept.	17.2	26	10	17	14	6
	10 Oct.	14.4	34	26	16	7	10
	23 Oct.	12.8	86	79	19	10	10
	12 Nov.	10.6	37	35	9	13	6
Late fall	22 Nov.	8.9	15	21	26	11	9
	3 Dec.	7.2	5	20	20	29	8
	10 Dec.	6.1	0	12	18	14	18
	18 Dec.	5.0	0	9	21	50	57
1969							
Winter ice-cover	15 Jan.	1.1	0	6	15	20	9
	6 Feb.	1.1	0	0	1	0	0
	6-10 Mar.	1.1	0	1	2	0	0
	10-13 Mar.	1.1	1	5	1	2	0
	13-18 Mar.	1.1	2	2	7	1	0
	18-25 Mar.	1.1	1	2	6	2	0
	25 Mar.-3 Apr.	1.1	1	9	1	3	0
	3-7 Apr.	1.1	2	5	4	5	0
Spring	22-24 Apr.	2.8	12	14	28	17	19
	1 May	3.3	0	1	3	4	3
	8 May	3.9	24	9	6	14	15
	14 May	8.3	63	9	8	6	8
	21 May	7.2	3	8	5	5	11
	29 May	6.7	18	26	22	8	8
	6 June	14.4	77	11	7	10	9
	13 June	7.8	19	26	6	5	3

TABLE 1.—Vertical distribution pattern of goldeye in an open-water area of Fort Peck Reservoir, from November 1967 into December 1969.—Continued.

[Number of goldeye per night per 8-ft deep section of 100-ft net.]

Pattern	Date	Temperature (°C)[1]	Depth (ft) 0-8	8-16	16-24	24-32	32-40
1969 — Continued							
Summer-early fall	20 June	13.3	52	24	26	12	5
	11 July	16.7	110	77	39	21	21
	16 July	[2]	27	6	8	10	5
	23 July	17.2	46	14	5	2	1
	27 Aug.	21.1	46	21	25	6	4
	18 Sept.	[2]	60	45	40	16	12
	9 Oct.	15.0	55	35	19	1	4
	22 Oct.	[2]	25	23	17	9	7
	30 Oct.	10.6	21	11	5	1	2
	5 Nov.	11.1	19	15	3	8	5
	15 Nov.	9.4	23	11	4	2	2
Late fall	19 Nov.	8.9	10	20	11	8	6
	21 Nov.	8.3	6	21	20	9	1
	26 Nov.	7.8	8	9	3	2	7
	9 Dec.	5.6	0	1	16	21	35

[1] Taken at surface.
[2] Temperature not known.

late fall, winter, and early spring. Cursory examination of stomachs and observation of regurgitated materials during the above periods showed that goldeye preyed almost exclusively on cladocerans.

To better understand if goldeye in fact follow the food source during the late fall, winter, and early spring, the seasonal vertical distribution patterns of cladocerans would have to be known. Although no studies have been conducted to establish distribution patterns of Fort Peck Reservoir zooplankton, work by other investigators indicated that many zooplankters exhibit seasonal vertical migratory patterns. Accordingly, the season migrations are not necessarily hydrographic (McLaren, 1963), but it has been suggested by some authors that winter hibernation of zooplankton may just be an interruption of diurnal rhythm; i.e., once the body of water cools to a given temperature, diurnal movement is no longer advantageous and ceases. Possibly, the goldeye is browsing on zooplankton which have ceased to exhibit diurnal movement patterns similar to their summer pattern, thus accounting for the late fall, winter, and spring distribution patterns exhibited by the goldeye.

ACKNOWLEDGMENTS

This study was partially financed through the Bureau of Commercial Fisheries Research and Development Act, Public Law 88-309. Thanks are due Montana State Fish and Game Department personnel, Robert G. Needham and Danial M. Welsh for their assistance in collecting the goldeye and related data, and William Alvord for his many suggestions concerning the manuscript.

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A MERISTIC AND MORPHOMETRIC COMPARISON OF THE HAKES, *UROPHYCIS CHUSS* AND *U. TENUIS* (PISCES, GADIDAE)[1, 2]

J. A. MUSICK[3]

ABSTRACT

Urophycis chuss and *U. tenuis* are shown to be statistically different for several meristic and morphometric characters. The ranges of the number of lateral line scales are distinct, *U. chuss* having 95 to 117 and *U. tenuis* having 119 to 148. The numbers of gill rakers on the epibranchial of the first gill arch are distinct, *U. chuss* having three and *U. tenuis* having two. The number of abdominal vertebrae and the regression of head length on standard length can be used to distinguish between the two species, with certain reservations. Two characters previously used in the literature to distinguish between the two species are not valid. These are: the relation of upper jaw length to the distance from the snout to the posterior margin of the orbit, and the relation of the distance from the origin of the pelvic fin to the anus to the length of the pelvic fin. Samples of *U. tenuis* from off New England and Nova Scotia appear to be morphometrically different from those from the Gulf of St. Lawrence.

The genus *Urophycis* Gill (1963) includes at least seven species of gadid fishes endemic to the western Atlantic Ocean (Svetovidov, 1948:105). The most abundant of these in the area north and east of Delaware Bay are *U. chuss* (Walbaum, 1792) and *U. tenuis* (Mitchill, 1814) which are difficult to distinguish (Figures 1 and 2). These two species have been repeatedly confused since *U. tenuis* was first described by Mitchill (1814), who recognized the meristic differences between them but apparently did not always recognize the species by sight, because he gave the maximum weight for *Gadus longipes* (= *U. chuss*) as 18 lb. *U. chuss* rarely, if ever, exceeds 6 lb, whereas *U. tenuis* may reach 40 lb or more, and often exceeds 18 lb (Musick, 1969). Among the long list of confused and misnamed accounts in the literature, the outstanding ones are Rafinesque-Schmaltz (1818), Storer (1839), Kaup (1858), Cornish (1907, 1912), and Vladykov and McKenzie (1934) who placed *U. tenuis* within the synonymy of *U. chuss*, after a "study of the literature."

Both *U. tenuis* and *U. chuss* are taken commercially throughout their ranges. The International Commission for the Northwest Atlantic Fisheries (ICNAF) has the responsibility of reporting the annual catch statistics for all major species, including *U. chuss* and *U. tenuis*, taken in the ICNAF area. Musick (1967)[4] pointed out that the statistics for *Urophycis* frequently were in error because of misidentification. Recently, Leim and Scott (1966:217) were compelled to discuss the biology, distribution, and commercial value of *U. chuss* and *U. tenuis* together because of the confused treatment of species in earlier Canadian literature.

The purpose of this paper is to test the validity of certain characters previously used in the literature to distinguish between *U. chuss* and *U. tenuis* and to examine additional characters of potential diagnostic value. Seven

[1] Virginia Institute of Marine Science Contribution No. 518.

[2] Based on part of a doctoral dissertation presented to Harvard University.

[3] Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[4] Musick, J. A. 1967. Designation of the hakes, *Urophycis chuss* and *U. tenuis* in I.C.N.A.F. statistics. Int. Comm. Northwest Atl. Fish., Res. Doc. 67-76, No. 1872, 5 p. (Unpubl.)

Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

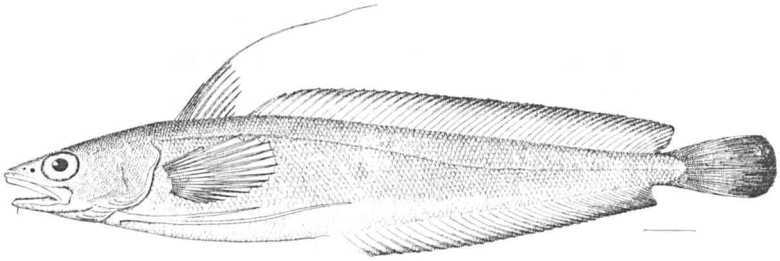

FIGURE 1.—*Urophycis chuss*, drawing from USNM 28707, courtesy of the Smithsonian Institution.

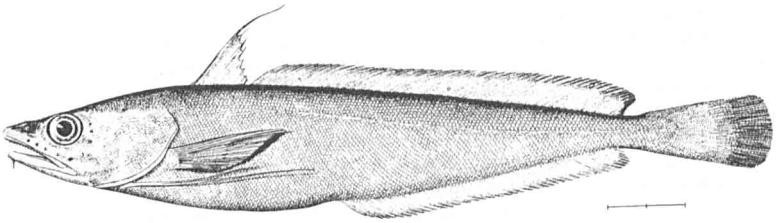

FIGURE 2.—*Urophycis tenuis*, drawing from USNM 21029, courtesy of the Smithsonian Institution.

meristic and 10 morphometric characters were examined on 136 *U. chuss* and 170 *U. tenuis*. Six meristic and four morphometric characters were chosen for statistical analysis.

METHODS

All samples were taken between the Gulf of St. Lawrence and the Virginia coast (Figure 3 and Appendix Table). Preliminary studies suggested that *Urophycis* of the *chuss-tenuis* complex from the study area could be readily placed into two morphs by body shape and scale size, thicker-bodied, small-scaled individuals being similar to published descriptions of *U. tenuis* and slim-bodied, larger-scaled specimens resembling descriptions of *U. chuss*. Thus specimens were tentatively identified. *U. tenuis* was present in the entire sampling area, whereas with the exception of a few Nova Scotian shelf specimens *U. chuss* was found in the Gulf of Maine and south and west of there. Samples of *U. tenuis* were available, by chance, from three geographic areas: the Gulf of Maine and southern New England waters (N.E.), the eastern coast of Nova Scotia from the vicinity of Halifax to the north and east (N.S.), and the Northumberland Straits in the Gulf of St. Lawrence adjacent to Prince Edward Island (P.E.I.). This geographic segregation of samples was maintained for statistical analyses because *U. tenuis* was predominant in Canadian waters where the species of *Urophycis* have been regarded with confusion for many years, especially in the Gulf of St. Lawrence. The data from all specimens of *U. chuss* were treated as one statistical sample.

Length in the rest of this paper refers to standard length unless designated otherwise. Specimens 50 mm long or less were cleared and stained following a method modified from Hollister (1934) to count the number of fin rays, gill rakers, and vertebrae. Fin rays on larger specimens were counted with the aid of a fine needle and occasionally by x-ray examination. All radiographs were taken on Picker "Pictronix 200"[5] x-ray equipment, using Gevaert D7 Structurix Industrial x-ray Safety Film (Unipac), and developed by the procedure outlined by Bartlett and Haedrich (1966). Vertebral numbers on specimens longer than 50 mm were determined from radiographs and, in two instances, by dissection. Lateral line scale rows were counted from a point directly above the upper corner of the opercular opening to the base of the midcaudal ray.

All measurements taken from specimens

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

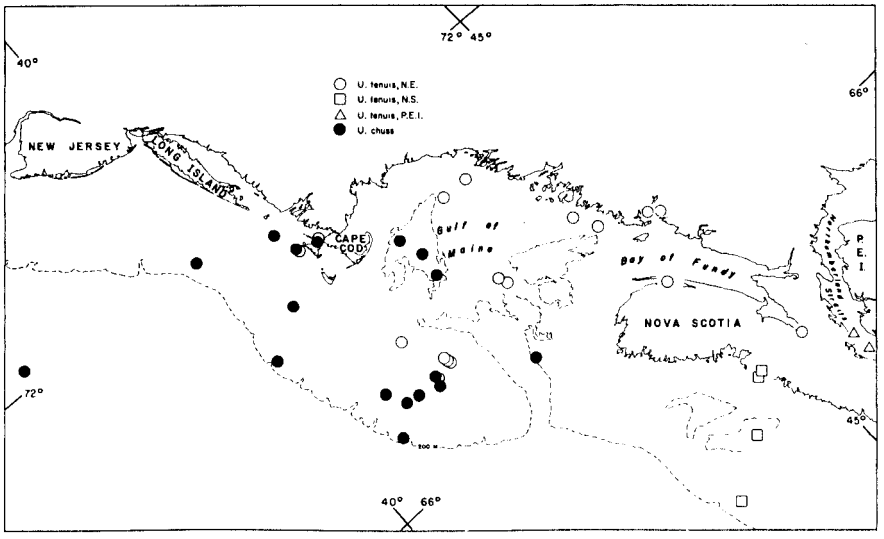

FIGURE 3.—Localities where *Urophycis* were collected for a study of meristics and morphometrics. *U. chuss* was compared with samples of *U. tenuis* from New England (N.E.), Nova Scotia (N.S.), and the Gulf of St. Lawrence (P.E.I.).

smaller than about 600 cm were made with fine-pointed dividers. Larger specimens were measured with calipers consisting of a meter stick and sliding brass "jaws." When possible, measurements were made on the left side of the specimens.

The number of fin rays in the second dorsal fin and in the anal fin, the number of abdominal vertebrae, and the total number of vertebrae were each subjected to an analysis of variance. (Snedecor, 1956:246). Abdominal vertebrae are those anterior to the caudal vertebrae. An analysis of variance of the number of lateral line scales was performed only among the three samples of *U. tenuis* because the ranges of variation of *U. chuss* and *U. tenuis* do not overlap. The gill rakers were counted on the epibranchial of the first gill arch. The raker found at the joint between the epibranchial and ceratobranchial was not included in the count.

The meristic data have been summarized in Figures 4 to 8, and the method of graphing follows that of Hubbs and Hubbs (1953). For each sample the range of variation is shown by a heavy horizontal line, the mean ($\bar{x}$) by a small narrow triangle. The blackened part of each bar comprises two standard errors of the mean ($2s_{\bar{x}}$) on either side of $\bar{x}$. One-half of each black bar, plus the white bar at either end, outline one standard deviation (s) on either side of $\bar{x}$; s indicates dispersion; $2s_{\bar{x}}$, reliability of $\bar{x}$.

Tests of significance were performed at the 1% level, and if no difference was found, at the 5% level. Statistical significance is designated as follows: NS = not significant; * = significant at the 5% level; ** = significant at the 1% level. If significance was found, Duncan's Multiple Range Test was conducted at the 1% and 5% probability levels (Duncan, 1955, 1957). The results of Duncan's test include within the same parentheses those samples which are not significantly different.

The effect of allometric variation on character validity in *Urophycis* has not been considered in the past. In the present study, an attempt was made to measure specimens of all sizes. All values were transformed to logarithms to reduce the correlation between the variance and the mean (Mottley, 1941), and regressions were computed for each character for each of the four samples. Every sample was tested against each of the others by an analysis of covariance (Steel and Torrie, 1960). Variances were tested for homogeneity. Hetero-

geneous variances in most instances could be attributed to disparities between the ranges of the independent variables of the regressions. Elimination of high or low independent values from one or both regressions usually resulted in homogeneity. When the variances were heterogeneous and the ranges of independent variables were about the same in both regressions, heterogeneity was attributed to intrinsic properties within the samples and they were considered significantly different. If the variances of the regressions were homogeneous, the analysis of covariance was continued and the slopes were tested. The adjusted means were tested if the slopes were not significantly different at the 1% level.

Analyses of covariance were performed between males and females in each sample before interarea comparisons were attempted. No sexual dimorphism was found.

Bigelow and Schroeder (1953:222) contended that the position of the rear of the upper jaw, relative to the position of the eye, was a dependable character for separating *U. chuss* from *U. tenuis*. This character may not be reliable because the position of the rear edge of the maxillary depends on the extent to which the mouth of the fish is open. A more accurate method of quantifying the character was used in this study. The distance from the snout to the posterior margin of the maxillary (upper jaw length) was compared to the distance from the snout to the posterior margin of the orbit. A second morphometric character used by many authors to distinguish between *U. chuss* and *U. tenuis* is the length of the ventral fin relative to the position of the anus. However, Bigelow and Schroeder (1953), Goode and Bean (1895), and others have pointed out that this character may not be dependable. An analysis was made of the regression of ventral fin length on the distance from the origin of the ventral fin to the anus.

Subjective observations suggest that *U. tenuis* has a larger head and forebody than *U. chuss*. Therefore, regression analyses were made of the preanal length and head length on standard length. Hubbs and Lagler (1958:25) advocate measuring head length from the tip of the snout to the "most distant point of the opercular membrane," which may vary, depending on whether the fish's operculum is expanded or closed tightly against the head. Head length is defined here as the distance from the tip of the snout to the upper, inner angle of the opercular opening. Preanal length is defined here as the distance from the tip of the snout to the anus.

RESULTS

Meristic Analysis

Number of Rays in Second Dorsal and Anal Fins and of Abdominal Vertebrae (Figures 4-6)

The statistical analyses for these three characters yielded the same results for all comparisons. The analysis of variance showed heterogeneity at the 1% level, and the Duncan's test separated all samples of *U. tenuis* from *U. chuss*. There were no significant differences among the samples of *U. tenuis*.

Total Number of Vertebrae (Figure 7)

Heterogeneity of variance was shown at the 1% level. Duncan's test showed significant differences between *U. chuss* and both *U. tenuis* N.E. and *U. tenuis* P.E.I. However, there were no significant differences between *U. chuss* and *U. tenuis* N.S., nor among the samples of *U. tenuis*.

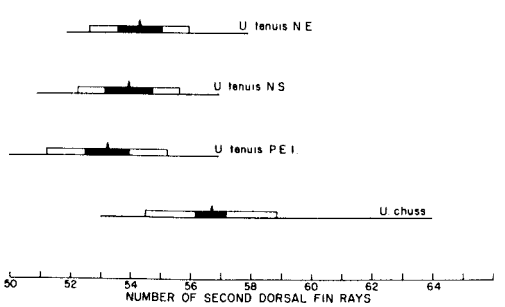

FIGURE 4.—Comparison of the number of rays in the second dorsal fin among three samples of *Urophycis tenuis* and one of *U. chuss*. Range—horizontal line. Mean ($\bar{x}$)—small narrow triangle. Two standard errors of the mean on either side of $\bar{x}$—blackened part of each bar. One standard deviation on either side of $\bar{x}$—one-half of each black bar, plus the white bar at either end.

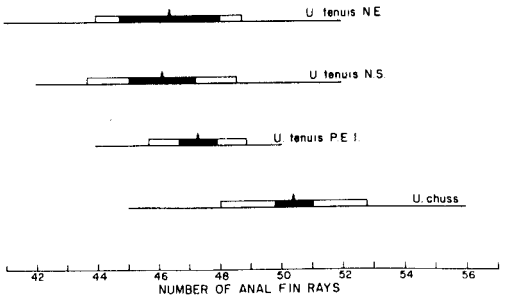

FIGURE 5.—Comparison of the number of rays in the anal fin among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

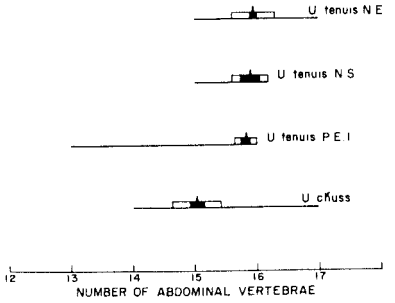

FIGURE 6.—Comparison of the number of abdominal vertebrae among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

Number of Lateral Line Scales (Figure 8)

The ranges of variation of the two species did not overlap. There were no significant differences among the samples of *U. tenuis*.

Number of Gill Rakers on the Epibranchial

The gill rakers of 56 *U. chuss* and 111 *U. tenuis* were counted. All *U. chuss* had three gill rakers on the epibranchial, and all *U. tenuis* had two.

Morphometric Analysis

Regression of Distance from Snout to Posterior Margin of Orbit on Upper Jaw Length (Figure 9, Table 1)

All regressions were linear. *U. tenuis* N.S.

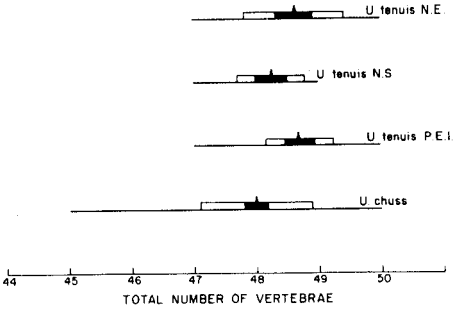

FIGURE 7.—Comparison of the number of vertebrae among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

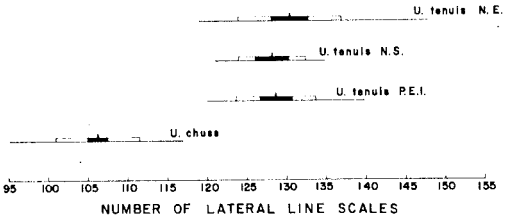

FIGURE 8.—Comparison of the number of lateral line scales among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

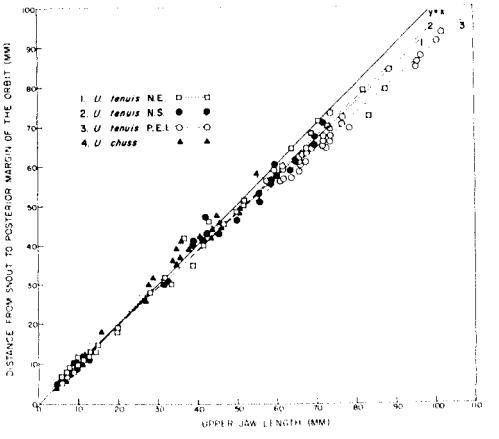

FIGURE 9.—Regression of the distance from the snout to the posterior margin of the orbit on upper jaw length from three samples of *Urophycis tenuis* and one of *U. chuss*.

TABLE 1.—Summary of all morphometric comparisons of *Urophycis tenuis* and *U. chuss*.

	U. tenuis[1]		*U. chuss*
	N.S.	P.E.I.	
U. tenuis:			
N.E.:[2]			
a.	NS	*	**
b.	*	—	**
c.	NS	**	**
d.	NS	*	**
N.S.:			
a.		NS	*
b.		—	**
c.		NS	**
d.		**	**
P.E.I.:			
a.			NS
b.			—
c.			**
d.			*

[1] N.S. = eastern coast of Nova Scotia from vicinity of Halifax to north and east.
P.E.I. = Northumberland Straits in Gulf of St. Lawrence adjacent to Prince Edward Island.
NS = not significant.
* = significant at 5% level.
** = significant at 1% level.
[2] N.E. = Gulf of Maine and southern New England waters.
Regression of:
a. distance from snout to posterior margin of orbit on upper jaw length.
b. length of pelvic fin on distance from origin of pelvic fin to anus.
c. head length on standard length.
d. preanal length on standard length.

was not significantly different from *U. tenuis* N.E. or P.E.I. Regression coefficients for the latter two samples were significantly different at the 5% level. The adjusted mean for *U. chuss* was significantly different from that of *U. tenuis* N.E. at the 1% level and from that of *U. tenuis* N.S. at the 5% level. No significant differences were found between *U. chuss* and *U. tenuis* P.E.I.

The contention of Bigelow and Schroeder (1953:223), that this character "can be relied on, even for very small fish," is not borne out. If true, all values of *U. tenuis* would be on or to the right of the line $y = x$, and those for *U. chuss* would be to the left of the line (Figure 9).

Regression of Length of Pelvic Fin on Distance from Origin of the Pelvic Fin to Anus (Figure 10, Table 1)

This relationship was linear for *U. chuss*, but the values for *U. tenuis* seemed to be curvilinear. The slope of the regression changed when the independent variable reached 150 to 160 mm. Most values for *U. tenuis* P.E.I. were

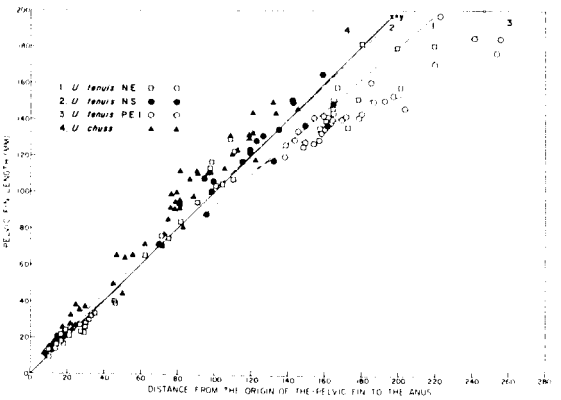

FIGURE 10.—Regression of pelvic fin length on the distance from the origin of the pelvic fin to the anus from three samples of *Urophycis tenuis* and one of *U. chuss*.

distributed above the change in slope and could not be compared to the other samples. An analysis of covariance was performed among the linear portions of the three remaining sample regressions. *U. tenuis* N.E. and *U. tenuis* N.S. were significantly different from *U. chuss* at the 1% level and from one another at the 5% level. The doubts of earlier workers concerning the validity of this character are borne out. If valid, all values for *U. chuss* would be on or to the left of the line $y = x$, and those for *U. tenuis* would be to the right of the line (Figure 10). Although most values for *U. chuss* do show this relationship, a few are to the right of the line, and many values for smaller specimens of *U. tenuis* are to the left.

Regression of Head Length on Standard Length (Figure 11, Table 1)

Regressions for all samples were linear. *U. tenuis* N.S. was not significantly different from *U. tenuis* N.E. or *U. tenuis* P.E.I. The adjusted means of the latter two were different at the 1% level. *U. chuss* was significantly different at the 1% level from all samples of *U. tenuis*. This character may be useful in distinguishing between *U. chuss* and *U. tenuis* longer than about 150 mm, particularly when used in addition to the gill raker and scale characters discussed above.

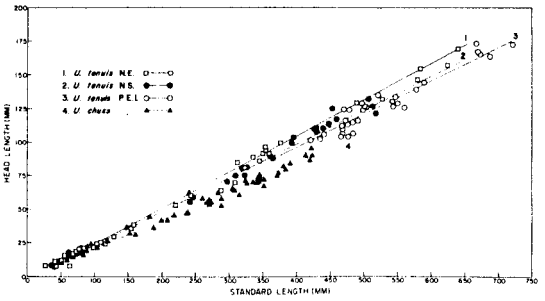

FIGURE 11.—Regression of head length on standard length from three samples of *Urophycis tenuis* and one of *U. chuss*.

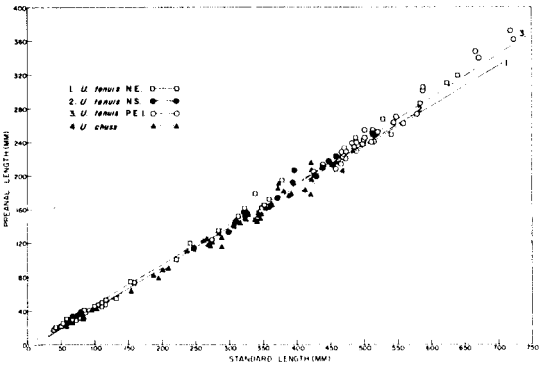

FIGURE 12.—Regression of preanal length on standard length from three samples of *Urophycis tenuis* and one of *U. chuss*.

Regression of Preanal Length on Standard Length (Figure 12, Table 1)

All regressions were linear. *U. tenuis* P.E.I. was significantly different from *U. tenuis* N.E. at the 5% level and from *U. tenuis* N.S. at the 1% level. There was no significant difference between the latter two samples. *U. chuss* was significantly different from *U. tenuis* N.E. and *U. tenuis* N.S. at the 1% level and from *U. tenuis* P.E.I. at the 5% level. Although *U. chuss* is statistically different from all samples of *U. tenuis*, there is much overlap between them and the character is not useful in species identification.

DISCUSSION

There were significant differences between *U. chuss* and all samples of *U. tenuis* for all meristic characters except the total number of vertebrae. The ranges of the numbers of lateral line scales of the two species did not overlap, and this character can be used with confidence to distinguish between them.

U. chuss invariably had three gill rakers on the epibranchial of the first gill arch, *U. tenuis* had but two. The difference is diagnostic. Mujib (1967) was in error when he reported that the epibranchial of *U. chuss* was devoid of gill rakers.

The numbers of abdominal vertebrae for each of the species showed little variability, most *U. tenuis* having 16 and most *U. chuss* having 15. This character may be valuable in identifying collections of postlarval and juvenile hakes in which the scales have not yet formed and when the mean number of abdominal vertebrae may be computed for an entire sample (Robert Marak, pers. comm.) but should not be relied upon for identification of single specimens.

None of the meristic characters showed statistically significant differences among the samples of *U. tenuis*. Such differences may exist but could have been masked by the grouping of several year classes in each sample (Appendix).

Morphometric analyses (Table 1) show that *U. tenuis* N.E. and *U. tenuis* N.S. are quite similar. *U. tenuis* P.E.I. differs from both of the latter and, of the three, is the most similar to *U. chuss*. This pattern suggests character displacement in *U. tenuis* off New England where it is sympatric with *U. chuss*. However, final judgment on the existence of character displacement should be withheld until small specimens of *U. tenuis* from the Gulf of St. Lawrence are available for examination. Morphometric differences between *U. tenuis* in the Gulf of St. Lawrence and those from Nova Scotian and New England waters may have a strong biological basis. The Gulf of St. Lawrence group gathers in large spawning aggregations during June in the Northumberland Strait (Stephen Nepszy, pers. comm.), whereas the Nova Scotia-New England group probably spawns in the fall (Musick, 1969). Thus, the two groups may be reproductively isolated.

ACKNOWLEDGMENTS

I wish to thank R. L. Edwards and M. D. Grosslein of the Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, Mass., for providing me with the opportunity to participate in cruises aboard RV *Albatross IV* and for research facilities, computer services, and much valuable advice and direction. Thanks are also due to G. W. Mead, formerly of the Museum of Comparative Zoology, Harvard University, for constructive criticism on ichthyological matters and for pursuing with patience the tedious task of editing early drafts of the dissertation from which this paper has been extracted. Part of my research was supported by National Science Foundation grants G-19727 and GB-3167 to the Harvard Committee on Evolutionary Biology (Principal Investigator, Reed C. Rollins).

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APPENDIX

All specimens examined are listed in the Appendix Table. Because of the relatively large size attained by both species, it was often impossible to preserve large samples of study material in Formalin, and many fresh or frozen specimens were examined and discarded. Fresh material was collected aboard the RV *Albatross IV*, RV *Cameron*, and the trawler *Cap'n Bill III*. Also, many fresh and frozen specimens were examined from commercial catches of hake landed at Souris, Prince Edward Island.

APPENDIX TABLE—Specimens of *Urophycis chuss* and *U. tenuis* examined.

Specimen designation or catalog number	Number of specimens	Standard length (mm)	Date	Position or location: Lat. N	Long. W	Name of vessel	Cruise number	Station number
			Urophycis chuss					
Frozen	23	237-376	27 May 1964	40°03′	69°36′	*Cap'n Bill III*		
Frozen	29	130-413	9 July 1964	3 miles S of Gay Head, Mass.		*Cap'n Bill III*		
Frozen	8	255-306	3 Aug. 1964	40°37′	67°06′	*Albatross IV*	64-10	65
Frozen	7	210-426	27 July 1964	41°09′	71°17′	*Albatross IV*	64-10	2
Frozen	11	180-470	5 Aug. 1964	41°27′	68°23′	*Albatross IV*	64-10	75
Frozen	4	371-478	16 Aug. 1964	43°08′	69°49′	*Albatross IV*	64-10	125
Frozen	2	298-519	10 Aug. 1964	Wilkinson's Basin, Gulf of Maine		*Albatross IV*	64-10	
Frozen	9	300-482	6 Aug. 1964	42°19′	69°45′	*Albatross IV*	64-10	86
Frozen	2	372-378	20 Aug. 1964	42°37′	66°34′	*Albatross IV*	64-10	162
Cleared and stained	14	19-31	15 Nov. 1960	37°27′	72°16′			
Cleared and stained	22	21-48	20 Aug. 1961	40°41′	70°06′	*Eugenie VIII*	8	
MCZ[1] 45420	1	119	27 Nov. 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45421	4	59-105	22 Dec. 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45422	1	154	4 Aug. 1964	41°29′	67°29′	*Albatross IV*	64-10	71
MCZ 45423	1	385	25 Feb. 1966	43°59′	62°49′	*Cameron*		
Cleared and stained	1	104	20 July 1966	40°59′	67°33′	*Albatross IV*	66-9	152
Cleared and stained	3	83-87	19 July 1966	40°48′	67°57′	*Albatross IV*	66-9	119
MCZ 45426	2	33-37	9 July 1965	42°23′	68°40′	*Albatross IV*	65-6	7
MCZ 45427	1	67	1 Nov. 1964	41°10′	67°31′	*Albatross IV*	64-13	72
MCZ 45428	1	54	28 Oct. 1964	50°07′	71°47′	*Albatross IV*	64-13	28
			Urophycis tenuis					
New England:								
Frozen	1	269	9 July 1964	3 miles S of Gay Head, Mass.		*Cap'n Bill III*		
Frozen	2	278, 325	5 Aug. 1964	41°27′	68°23′	*Albatross IV*	64-10	75
Frozen	3	490-542	16 Aug. 1964	43°08′	69°49′	*Albatross IV*	64-10	125
Frozen	3	490-1,030	19 Aug. 1964	44°13′	67°54′	*Albatross IV*	64-10	150
Frozen	1	562	19 Aug. 1964	44°24′	67°33′	*Albatross IV*	64-10	151
Frozen	3	580-625	17 Aug. 1964	42°59′	68°01′	*Albatross IV*	64-10	136
MCZ 45412	12	81-273	5 Aug. 1964	41°45′	67°37′	*Albatross IV*	64-10	72
MCZ 45413	2	44-116	4 Aug. 1964	41°29′	67°29′	*Albatross IV*	64-10	71
Cleared and stained	3	51-65	21 July 1965	41°45′	67°37′	*Albatross IV*	65-10	
MCZ 45414	4	221-360	14 July 1965	43°31′	69°49′	*Albatross IV*	65-10	60
Cleared and stained	1	62	11 July 1965	41°45′	67°38′	*Albatross IV*	65-10	27
Cleared and stained	1	53	21 July 1965	41°45′	67°39′	*Albatross IV*	65-10	
MCZ 45187	1	1,119	12 July 1965	43°00′	67°55′	*Delaware*	65-6	42
MCZ 45414	2	54-58	25 May 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45415	3	38-85	4 June 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45416	1	78	7 July 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45417	1	55	14 June 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45418	1	154	24 July 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45419	2	50, 68	17 May 1962	Great Harbor, Woods Hole, Mass.				
ROM[2] 4289	1	50	17 June 1927	St. Andrews, N.B.				
ROM 23088	1	59	25 July 1923	Shubenacadie River, N.S.				
ROM 9828	10	70-125	17 June 1936	Head of St. Mary's Bay, N.S.				
ROM 4291	1	51	29 June 1927	Birch Cove, N.B.				
ROM 12224	2	67, 72	9 July 1928	Passamaquoddy Bay, N.B.				
ROM 6600	1	85	5 Aug. 1915	St. Andrews, N.B.				

APPENDIX TABLE—Specimens of *Urophycis chuss* and *U. tenuis* examined.—*Continued.*

Specimen designation or catalog number	Number of specimens	Standard length (mm)	Date	Position or location		Name of vessel	Cruise number	Station number
				Lat. N	Long. W			
			Urophycis tenuis—Continued					
Nova Scotian shelf:								
MCZ 45429	21	242-537	25 Feb. 1966	43°59′	62°49′	*Cameron*		
ROM 7070	4	38-50	16 June 1938	43°11′	62°08′			
ROM 7071	4	60-65	4 July 1938	Northeast Cove, Bedford Basin, Halifax, N.S.				
ROM 11495	4	71-80	16 June 1934	Halifax Harbor off Dartmouth, N.S.				
ROM 7072	2	65, 68	5 July 1938	Stevens Island, Bedford Basin, Halifax, N.S.				
Gulf of St. Lawrence:								
Fresh	38	422-725	July 1966	4 miles NW of Arisaig Point, Northumberland Strait by a Danish seiner				
Frozen	34	395-571	Aug. 1964	Northumberland Strait, from filleting house, Souris, P.E.I.				

[1] MCZ = Museum of Comparative Zoology at Harvard University, Cambridge, Mass.
[2] ROM = Royal Ontario Museum, Toronto, Ontario, Canada.

ALBACORE OCEANOGRAPHY OFF OREGON — 1970

WILLIAM G. PEARCY[1]

ABSTRACT

During July 1970, albacore boats trolling surface jigs (jig boats) had record catches in an area off the mouth of the Columbia River. The jig fishery declined suddenly in late July and was poor throughout the remainder of the summer. No obvious oceanographic changes were correlated with these drastic changes in fishing success. Favorable water temperatures extended through August, traditionally the month of highest albacore landings in Oregon.

Bait boats, which chum with live bait, had good fishing off Oregon from mid-August to October, indicating that the poor success of jig boats during this time was caused by the behavior of albacore relative to surface-trolled fishing gear. It is postulated that albacore descended into subsurface water in response to a change in availability of their preferred prey, the saury; here they were less accessible to jig boats than bait boats. Saury were common in the stomachs of albacore during periods of good jig fishing and were usually the dominant food where high albacore catches were made by our research vessel.

The first albacore catches of the season were probably from an area of warm temperature and low salinity representing Columbia River plume water. The subsequent migration to the north appeared to be along the oceanic edge of the plume. In general, high catches by boats were not within the core of the plume but in 15.5°C water, especially in areas where a horizontal thermal gradient was apparent.

During the summer season albacore (*Thunnus alalunga*) usually migrate into waters off the Oregon coast where upwelling and Columbia River water form a complex ecotone between coastal and oceanic waters (Owen, 1968; Pearcy and Mueller, 1970; Pearcy, 1971). The albacore fishery here fluctuates greatly among years as a result of variations of abundance and availability of albacore and fishing effort (Johnson, 1962).

Marked fluctuations of catches may also occur within a single summer and the 1970 albacore season off Oregon is a spectacular example of within-season changes in fishing success. The fishery got off to an early start in mid-July and jig boats reported exceptionally high catches (up to 1,400 fish/boat day) during late July. Record landings of over 4,000 tons were recorded for July. During late July and early August, however, the jig fishery virtually disappeared. Boats fishing in the region of the Columbia River, where high catches of 800-1,300 fish per boat day were reported on 30 July, averaged only 50 fish on 31 July.[2] Although jig fishing continued to be poor during the rest of the summer off Oregon, bait boats enjoyed good fishing into October.

The purpose of this paper is to describe ocean conditions and albacore catches in Oregon waters during the summer of 1970 in hopes of better understanding the small-scale spatial distribution of albacore tuna and the dramatic changes in their availability that occurred in 1970.

SOURCES AND TREATMENT OF DATA

Catch data for the 1970 albacore season off Oregon were derived from fish boat logs sent directly to us from fishermen or obtained through other agencies from fishermen. Thirty-three jig boats and two bait boats submitted usable records to us from our original dis-

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[2] Laurs, R.M. 1970. U.S. Bur. Commer. Fish., Albacore Bull. No. 70-3 and 70-4, La Jolla, Calif.

Manuscript accepted October 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

tribution of 421 special logs to fishermen in Oregon, Washington, and California prior to the 1969 albacore season. These logs were unique in that they were designed to obtain several entries per day from fishermen so that variations of catch rate over small spatial areas could be examined. In addition, the Fish Commission of Oregon obtained 116 jig boat and 8 bait boat logs, California Department of Fish and Game made available 45 jig boat and 8 bait boat logs, and the Inter-American Tropical Tuna Commission provided 2 jig boat and 11 bait boat logs.

The catches of each type of boat were averaged for each day regardless of fishing location off Oregon. Catches of jig boats were also assigned to 10′ latitude × 10′ longitude blocks based on their reported loran positions. Generally catches could be assigned to a specific block. If a boat cruised over a large area and catches could not be assigned to specific blocks, the data were not plotted. No adjustment was made for the effect of boat size or number of lines on catches. It should be pointed out that our catch data do not necessarily represent average catches made by the fleet in an area because they are from only part of the fleet.

Sea-surface temperature was measured on remote sensing overflights using a Barnes PRT-5 infrared radiometer[3] at an altitude of 150 m or 500 ft (Pearcy and Mueller, 1970). A total of 15 flights were made from 22 July to 15 September on HU-16 aircraft either from the U.S. Air Force 304th Aerospace Rescue and Recovery Squadron, Portland, Oreg., or from the U.S. Coast Guard Station, Port Angeles, Wash.

On two RV *Cayuse* cruises, temperature was measured with bathythermographs, and temperature and salinity with a Salinity-Temperature-Depth system. Stations were usually 10 miles apart. On the 27 July-2 August cruise, water transparency was determined with a submarine photometer, and 6-ft Isaacs-Kidd midwater trawl collections were taken at 5 knots to a depth of about 100 m along the cruise track at night. Volume of water filtered was estimated from flowmeters mounted in the mouth of the trawl.

Albacore were caught from the *Cayuse* by fishing between hydro stations using standard trolling methods with a maximum of eight lines. Time and location of catches during daylight hours were recorded. All fish collected were measured in fork length; stomachs removed and preserved immediately with Formalin for subsequent examination of their contents.

CATCHES AND EFFORT

Statistics on catches and effort of jig and bait boats reporting to us are summarized in Figure 1. The 1970 Oregon jig season got off to an early and intense start. The first albacore of the season were reported on 15 July, the day that fishermen and processors reached a price agreement. Thereafter, three peaks of excellent fishing success occurred for jig boats: on 17, 22, and 28 July. Catches on these days averaged between 300 and 400 fish per boat day. The catch rate then declined drastically to about 55 fish per day between 28 and 31 July and never fully recovered during the remainder of the season, although success improved from 17-20 August.

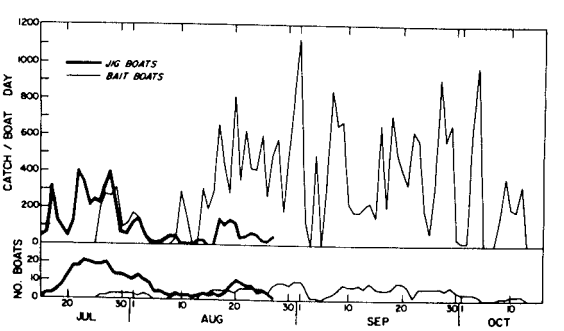

FIGURE 1.—Average number of albacore caught per day by jig boats and bait boats that submitted log sheets (above) and the number of reporting boats (below), 15 July-20 October 1970.

The number of jig boats reporting catches increased rapidly after the season began and then declined steadily from 27 July to mid-August (Figure 1). According to Laurs (see footnote 2), as jig fishing deteriorated off

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

Oregon, it improved off southern California to its best level in about 3 years. For this reason the west coast jig fleet largely emigrated to California waters in August after the early collapse of the Oregon fishery.

Similar trends in the catches by both bait and jig boats existed between mid-July and early August. Peaks in catches occurred on 26-29 July and 1-2 August, followed by a common decline to very low catches on 4 August (Figure 1).

In contrast to these trends early in the season, bait boats often had excellent fishing after July, while jig fishing was poor or nonexistent. Average daily catches of bait boats remained below 320 fish per day until mid-August, followed by catches that often exceeded 500 fish per boat day from mid-August to early October. The large daily fluctuations in the catches are due in part to the small number of boats reporting.

Statistics for landings of albacore in 1970, provided by Hreha (unpublished data, Fish Commission of Oregon), are shown in Table 1. Jig boat landings were largest in July, the month of highest catches as shown in Figure 1, and progressively declined during subsequent months. According to Hreha (unpublished) about one-half of the albacore landed in August were caught in July by jig boats, and about one-half the total catch of both jig and bait boats for the 1970 season was actually caught in July. This seasonal distribution of Oregon landings in 1970 is unusual compared with other years. August is commonly the month when most albacore are landed in Oregon. Since 1961, August ranked first during 7 years and September ranked first during 2 years. July, the best month in 1970, had not ranked first in landing during the preceding 20 years (Ayers and Meehan, 1963; Meehan and Hreha, 1969).

TABLE 1.—Oregon albacore landings (metric tons and number) (Hreha, pers. comm.)

Month	Jig boat landings		Bait boat landings	
	Tons	*Number*	*Tons*	*Number*
July	3,342	450	0	0
August	2,760	869	492	13
September	569	89	2,038	55
October	306	59	130	6
Total	[1]7,218	[1]1,515	2,660	74

[1] Totals for jig boats include minor landings for November and December.

Table 1 also reveals the importance of the large jig fleet in the Oregon albacore fishing. Total landings by jig boats exceeded those by bait boats despite the deterioration of the fishing after July and despite the larger tonnage per landing (Table 1) or average catch per day (Figure 1) by the larger, but less numerous, bait boats.

MOVEMENT OF THE FLEET

Figure 2 shows the approximate location of albacore jig boats that reported catches during the summer of 1970. Generally boats were highly aggregated on a geographic basis—

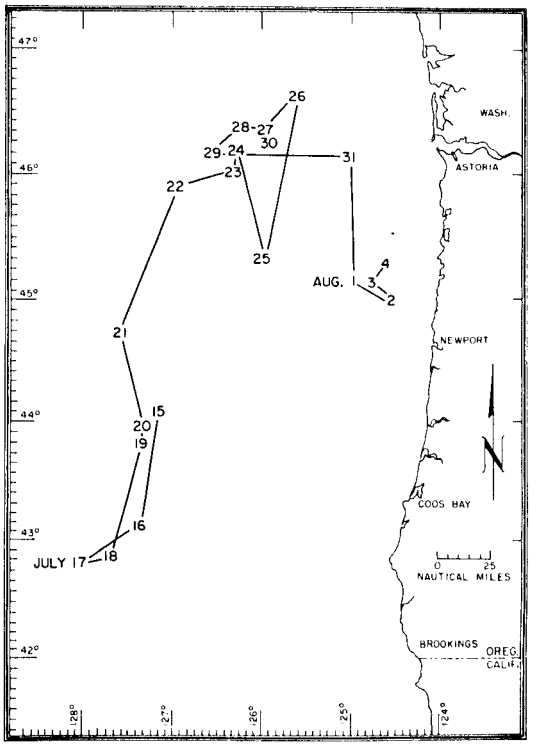

FIGURE 2.—Approximate geographic center of the albacore jig fleet from 15 July to 4 August 1970.

this plot thus estimates the central location of the fleet.

The first albacore of the 1970 season off Oregon were caught between Newport and Coos Bay on 15 July, and the subsequent early fishery during 15-21 July was localized about 140 miles off the central and southern Oregon coast. Boats shifted rapidly northward during 20-22 July and then were localized about 100 miles off the Columbia River during 22-29 July. (An exception was 25 July, when most boats moved south about 50-60 miles.) Between 29 and 31 July, during the major decline of the fishery, boats moved inshore to within 60 miles of the mouth of the Columbia River. This was followed by a shift to the south in early August and then an additional inshore movement to within 30 miles off the central coast. After 4 August the number of jig boats reporting catches was less than 11 and positions are not noted in Figure 2.

Thus the jig fishery off Oregon moved northward during July and became localized in the region off the Columbia River, where most of the fish were caught during the 1970 season. During the rapid decline of catches, jig boats moved inshore and to the south. Fishermen say that such an inshore movement of albacore may occur late in the season (September-October) when fish apparently form dense schools closer to shore and are often difficult to catch on trolled jigs. The bait boat fishery for albacore usually peaks late in the season, after jig catches decline (R. M. Laurs, pers. comm.). Thus both the inshore movement of the jig fishery and the good bait fishery occurred anomalously early in 1970.

OCEANOGRAPHIC CONDITIONS

In hopes of learning more about oceanographic conditions off Oregon and how changes in catches are related to upwelling and the Columbia River plume, we conducted weekly aircraft flights to obtain data on sea-surface temperature using infrared radiometers and fielded several cruises to determine ocean conditions both before the albacore season and later in the area of the albacore fleet. This section summarizes ocean features found during the 1970 albacore season. North-south and east-west components of winds are given in Figure 3 to aid in interpretation of wind-driven ocean circulation.

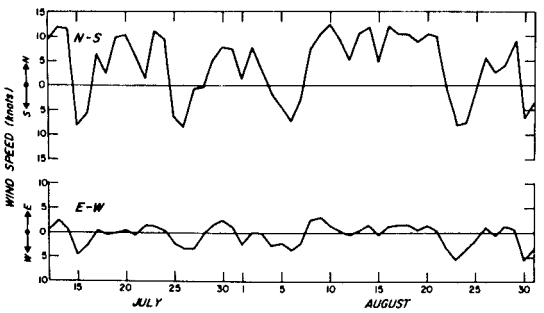

FIGURE 3.—Components of average daily wind velocities recorded at Newport, Oreg.

Cruise—7-10 July

Results of this preseason albacore cruise, off northern and central Oregon (Figure 4), illustrate the influence of both upwelling and

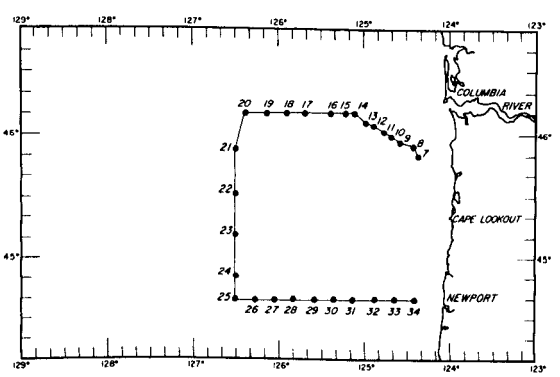

FIGURE 4.—Location of STD (Salinity-Temperature-Depth probe) stations during the preseason albacore cruise, 7-10 July 1970. (*Cayuse* 7007A).

Columbia River plume on the ocean environment. Isolines of salinity and temperature in the east-west sections (off the Columbia River and Newport, Figure 5a, b, e, f) slope upwards towards shore and are indicative of upwelling, the replacement of near-surface waters with deeper, saline, low-temperature water. The low-salinity waters of the Columbia River plume are evident in all sections. Plume

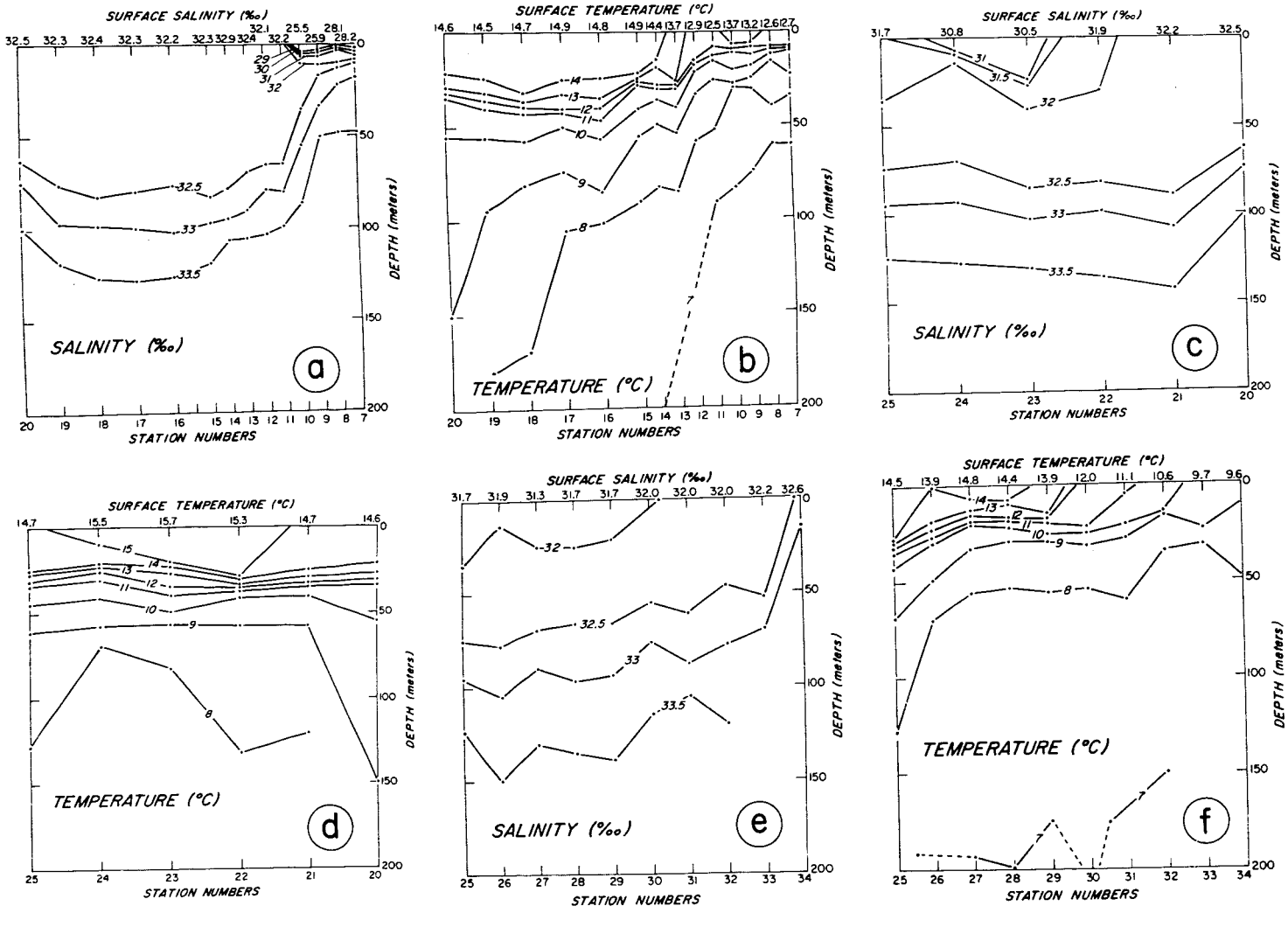

FIGURE 5.—Salinity sections: a) Stations 7-20, west of the Columbia River; c) Stations 20-25, along the north-south station line; e) Stations 25-34, along the Newport Station line. Temperature sections: b) Stations 7-20, d) Stations 20-25, f) Stations 25-34.

waters with salinities less than 32.2‰ (Owen, 1968) were found within 30 miles of shore near the mouth of the Columbia River (Stations 7-10, Figure 5a), as a lens of low-salinity water located along the north-south section 110 miles offshore (between Stations 22 and 25, Figure 5c), and greater than 50 miles offshore along the Newport transect (Stations 25-30, Figure 5e). The warmest water encountered on the cruise was along the north-south section, 110 miles offshore, where water 15°C and warmer was localized in a lens to a maximum depth of 20 m and surface temperatures as warm as 15.7°C were recorded (Figure 5d). This water, which was warmer than average in July, coincided with the low-salinity lens from the Columbia River plume. The correlation between low salinity and warm temperature early in the summer has been previously observed by Owen (1968) who described a causal basis. The strong pycnocline produced by the low-salinity water constrains mixing, and near-surface waters are heated by insolation more rapidly than surrounding waters. This relationship between salinity and temperature depends on heating rates and varies with season. Evans (1972) found that highest temperatures in the plume occurred inshore of the salinity minimum and that heat content was not a good indicator of the plume even though the temperature pattern is.

Infrared SST—15 July (Figure 6)

Our first sea-surface temperature (SST) flight was made by coincidence on the day that albacore catches were first reported off Oregon. Fish were caught about 120-160 miles off Heceta Head (Figures 2 and 6) where the fishing vessel *Spirit* reported surface temperatures of 16°C. This warm water was probably associated with a lens of low-salinity Columbia River plume water, similar to the situation found earlier in July on the cruise (Figure 5). As a result, the early location of the fishery and its subsequent movement to the north (Figure 2) may have been along plume waters, which are often the warmest waters available off Oregon during the early summer (Owen, 1968).

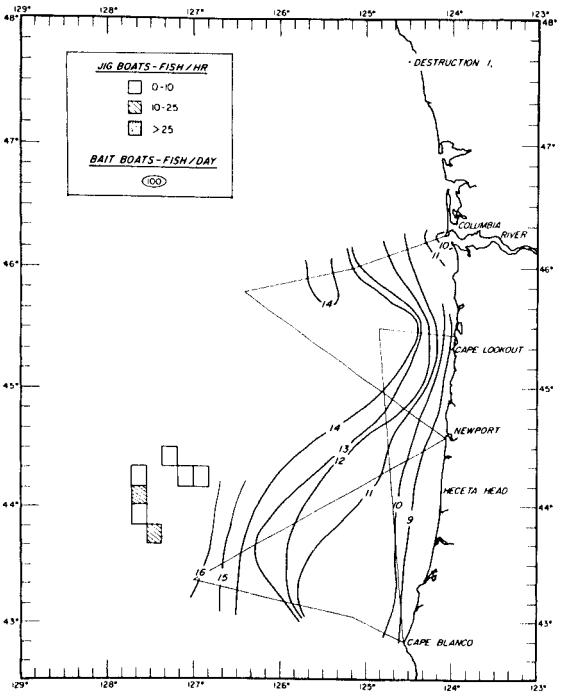

FIGURE 6.—Sea-surface temperatures (degrees Celsius) recorded by infrared radiometry on 15 July 1970. The flight track of the aircraft is shown by the narrow lines. Catch rates of albacore are indicated for jig boats by shading of 10′ blocks. In other figures, dashed lines denote isotherms based on temperatures recorded by fish boats. Daily catches of bait boats are shown by encircled numbers.

Coastal upwelling was obvious on this flight as a long band of cold (8°-9°C) water along most of the coast (Figure 6). Although average winds on 15 July were not from the direction to induce upwelling, winds on the preceding days were northerlies (Figure 3) and hence conducive to coastal upwelling. Mixture of these upwelled cold waters with the warmer Columbia River water probably masked the inshore portion of the Columbia River plume which often contrasts with upwelled water as a tongue of warm water emanating from river mouth in early summer (Budinger, Coachman, and Barnes, 1964; Owen, 1968; Pearcy and Mueller, 1970).

Infrared SST—22 July (Figure 7)

This was the day of the first large peak in average jig boat catches. (Figure 1). Most of the catches were made northwest of the SST flight and were arranged in a northeast-southwest pattern, possibly along the seaward boundary of the Columbia River plume. Highest catch rates (25-55 fish/hr) in this area were reported by fishermen trolling along the 15.5°C isotherm. High catches were also made along the 15.5°C isotherm 55 miles off Cape Lookout and along the 15°C isotherm 70 miles off the southern Washington coast.

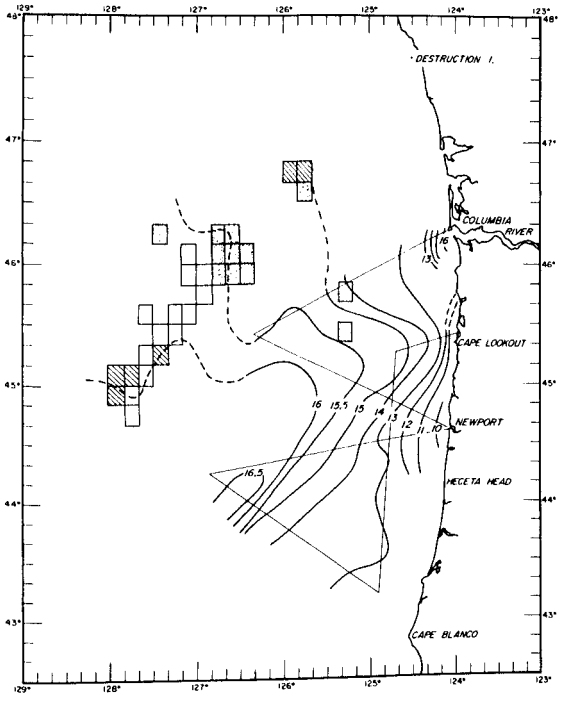

FIGURE 7.—Sea-surface temperature and albacore catch rates, 22 July 1970. Dashed lines are isotherms based on temperatures reported by fishing boats. See Figure 6 for explanation of catch notation.

The surface temperatures show an inshore-offshore gradient produced by upwelling and plume waters. Temperatures were generally warmer than on 15 July (Figure 6), however, suggesting less intense upwelling or more heating of surface waters on 22 July than on 15 July. The plume is apparent as a tongue of warm water (maximum 16.8°C) extending towards the mouth of the Columbia River.

Infrared SST—29 July (Figure 8)

This SST pattern for the day after the second big peak in jig catches (Figure 1) reflects obvious changes compared to previous patterns. Temperatures are much warmer—over 13°-14°C nearshore and over 18°C within 25 miles of the coast. These high temperatures are explained by the absence of northerly winds to induce upwelling during 26-28 July (Figure 3) and by the rapid heating of surface waters during this period of reduced wind-induced mixing, especially in the low-salinity plume that has been shifted close inshore.

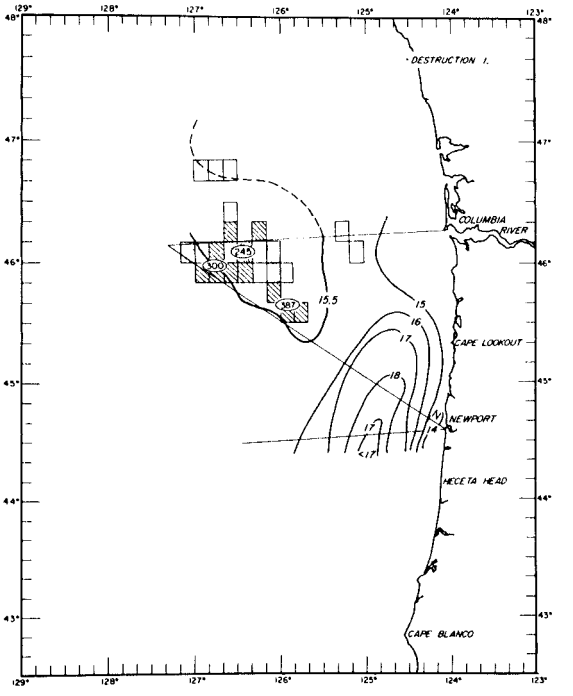

FIGURE 8.—Sea-surface temperatures and albacore catch rates, 29 July 1970. Dashed line is an isotherm based on temperatures reported by fishing boats. See Figure 6 for explanation of catch notation.

Fishing activity was localized almost entirely in a tongue of 15.5°C, blue-green water off the Columbia River (Pearcy, 1971). All the high catch rates during this day were reported

along the southern edge of this tongue. Note that three bait boats were also fishing this same region. They reported scores of 245-387 fish per day, not much higher than the jig boats which averaged 215 per day on 29 July, and below the 400 fish averaged by jig boats on 28 July.

Infrared SST—30 July (Figure 9)

The results of this SST flight show how rapidly the surface conditions can change in an area in 1 day. As a result of the onset of northerly winds (see Figure 3), renewed upwelling is now apparent along the coast between Cape Lookout and Newport. Surface temperatures near Newport were less than 10°C compared with 14°C on 29 July. Moreover, offshore temperatures were cooler on the 30th than the 29th, and no 18°C water was found on 30 July. The cooler surface water probably resulted from mixing due to increased wind stress. Note also the two separate areas of 16°C water along the southern flight lines.

Most of the fishing activity this day was again located off the Columbia River. Catches continued to decline, however, from an average of 215 fish per boat on the 29th to only 65 fish per boat on the 30th. Best success on this day (up to 17 fish/hr) was in the vicinity of 15.5°C, blue water off the Columbia River.

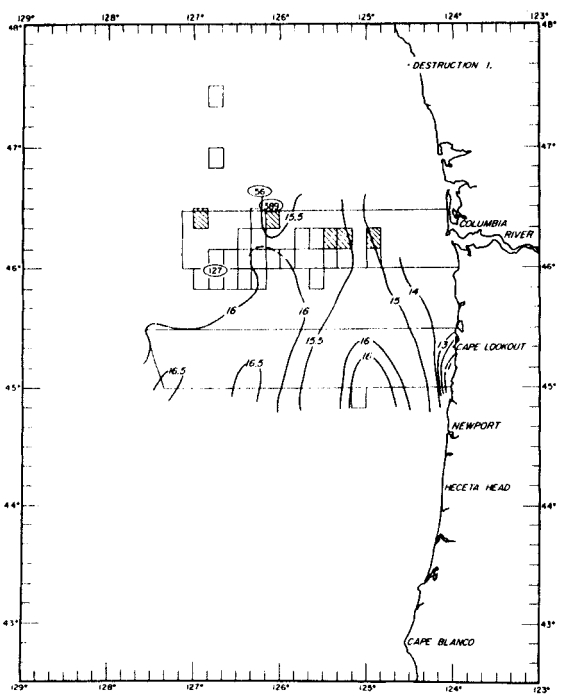

FIGURE 9.—Sea-surface temperatures and albacore catch rates, 30 July 1970. See Figure 6 for explanation of catch notation.

Infrared SST—31 July (Figure 10)

Fishing success continued its decline on 31 July with no jig boats reporting catches over 10 per hr and daily catches averaging a meager 55 albacore. Two bait boats also reported low catches, 75 and 68 fish per day.

Winds were again northerly (Figure 3) and infrared coverage by the aircraft was interrupted inshore because of the fog along the coast produced by cold, upwelled water. A pool of cool (15°C), green water was found 65 miles offshore about the same distance offshore that the band of cooler water was located on 30 July (Figure 9).

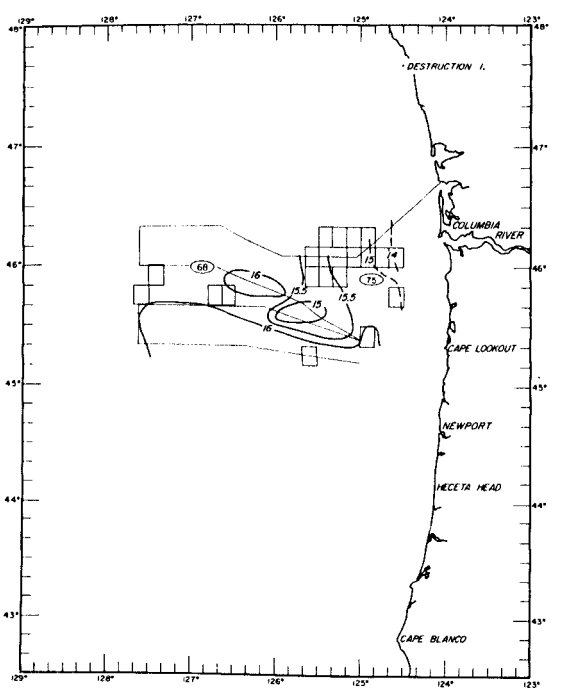

FIGURE 10.—Sea-surface temperatures and albacore catch rates, 31 July 1970. See Figure 6 for explanation of catch notation.

Infrared SST—5 August (Figure 11)

By this time the average catch of jig boats was less than 50 per day and only eight boats were reporting. The continued decline of the jig fishery did not appear to be associated with drastic changes of sea-surface temperature conditions, however. Water of 15°-16°C, was widespread offshore and south of the Columbia River.

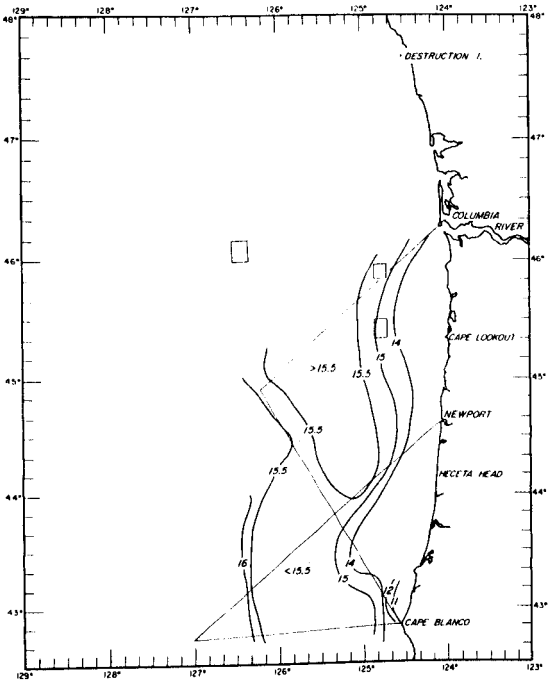

FIGURE 11.—Sea-surface temperatures and albacore catch rates, 5 August 1970. See Figure 6 for explanation of catch notation.

Coastal upwelling was not pronounced and cold water was absent inshore at Newport and the Columbia River. This situation is explained by south-westerly winds during the last 3 days (Figure 3). Plume waters were not obvious as a warmwater tongue off Oregon because of the general heating of offshore waters this late in the summer and possibly because of the lack of northerly winds that push the plume to the south along the Oregon coast.

Infrared SST—19 August (Figure 12)

During the period of 17-19 August jig catches increased to over 100 fish per day. These improved catches resulted in an increase in reported effort (10 boats on 20 August). Again sea-surface temperatures were similar to days in July when good catches were made by jig boats.

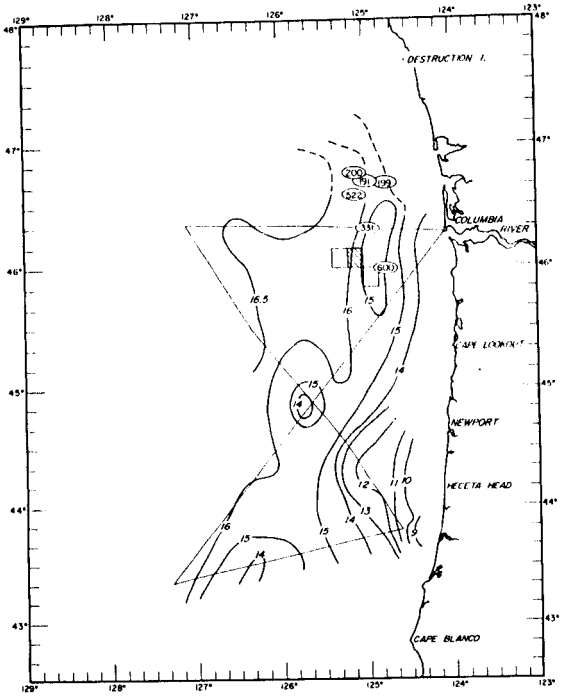

FIGURE 12.—Sea-surface temperatures and albacore catch rates, 19 August 1970. See Figure 6 for explanation of catch notation.

The six bait boats, reporting 191 to 600 fish per day, were located 30-40 miles from shore, near the mouth of the Columbia River in 15°-16.5°C water. This is the same general area where the jig boats were fishing.

Infrared SST—16 September (Figure 13)

Although no jig boats reported catches after late August, bait boats had good fishing throughout September and early October (Figure 1).

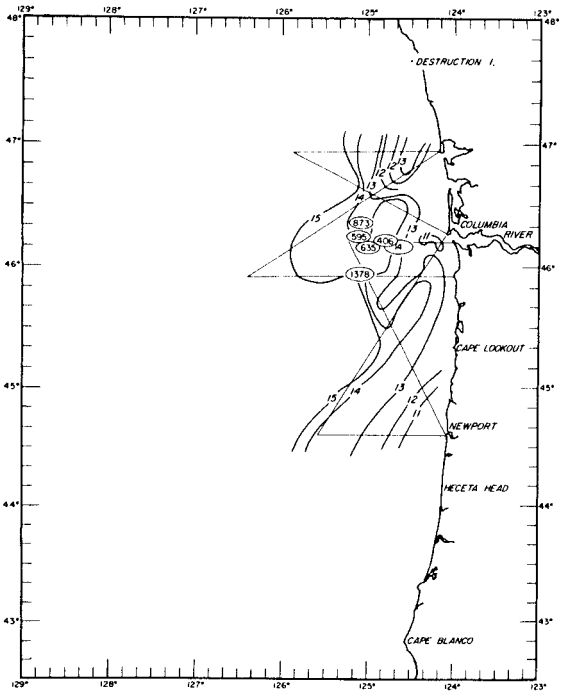

FIGURE 13.—Sea-surface temperatures and albacore catches, 16 September 1970. Numbers encircled indicate the daily catch of individual bait boats.

On 16 September bait boats were again concentrated near the mouth of the Columbia River where a finger of 14°C water extended toward shore. Judging from our data, this distribution of bait boats near the Columbia River was a common pattern, indicating favorable conditions for concentration of albacore in this area.

Cruise—27 July-2 August

A cruise was conducted in the general area of the early albacore fishery to compare oceanographic conditions in areas of high and low catch rates and to obtain albacore for a study of their food habits. The ship operated in the region of the jig fishery during the major decline in fishing success, 27 July to 2 August (Figure 1).

Oceanographic Conditions

Sea-surface temperatures measured during

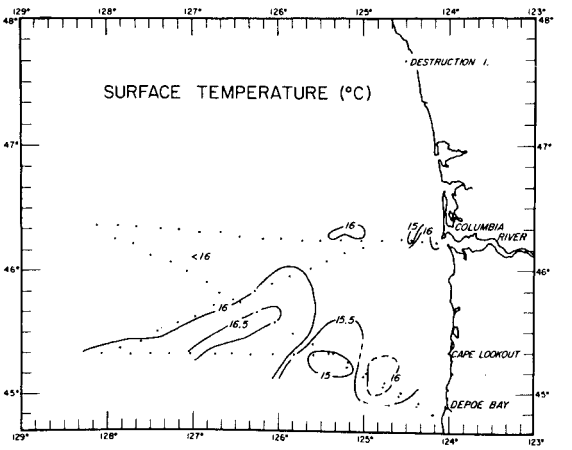

FIGURE 14.—Sea-surface temperatures recorded on the 27 July-2 August cruise. Dots indicate stations. (*Cayuse* 7007D)

the week of the cruise show two regions of warm (16°C or greater) water separated by a tongue of cooler 15°-15.5°C water (Figure 14). This pattern corroborates that found on 30 July by infrared radiometry from an aircraft (Figure 9), when 16°C water was also located in two areas off the northern coast. The temperature section along the outbound cruise track extending offshore in a northwesterly direction (Depoe Bay stations) shows these two areas of warm (16°C) surface water (Figure 15). The slope of the isotherms towards the coast is indicative of upwelling, but nearshore surface temperatures were above 13°C, implying little upwelling during this period of weak winds (Figure 3). The thermocline was located between 20 and 50 m, generally deepening farther offshore.

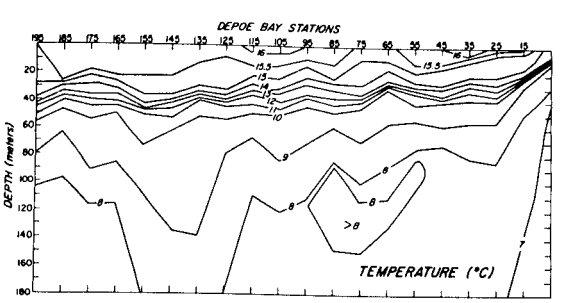

FIGURE 15.—Temperature section along the stations extending northwest of Depoe Bay on the outbound leg, 27-29 July.

The temperature section from the inbound track off Cape Lookout and Depoe Bay (Figure 16), made during the end of the cruise when

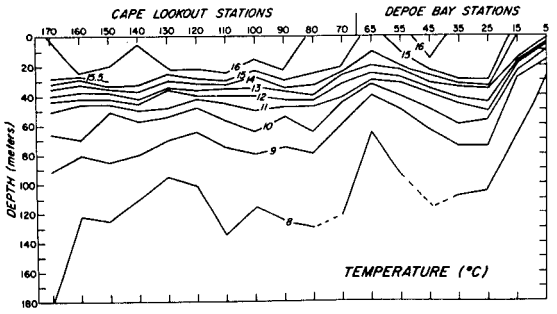

FIGURE 16.—Temperature section along the east-west stations offshore of Cape Lookout and Depoe Bay stations, inbound leg, 1 and 2 August. The Depoe Bay stations are the same ones shown in Figure 15 but 6 days later.

winds were blowing from the north, shows more evidence for upwelling than the earlier outbound track. The 15°C isotherm intersected the surface farther offshore and isotherms slope more steeply nearshore. However, surface temperatures are again not suggestive of strong upwelling. Inshore along the Depoe Bay Stations, the 16° and 15°C isotherms were deeper on the inbound than outbound legs, indicating a deepening of the mixed layer depth during the intervening time, but neither mixed layer depths beyond 75 miles off the coast or the depth of the 15°C isotherm increased noticeably with time. Surface water of 16°C was still located in two areas, which is consistent with the outbound leg, and facilitated the areal plot of surface temperature from all data.

Two extensions of low-salinity water (<32‰) are seen emanating from the Columbia River, one to the south and one to the southwest of the river mouth (Figure 17). These lobes of low salinity correspond with the regions of warmest temperature seen in Figure 14 and support the premise that warm water is often associated with low salinity. This correlation is not apparent close to the river mouth, however, because of admixture of plume with cool upwelled water and insufficient time for warming of the low-salinity lens.

Light extinction coefficients, calculated from photometer casts during daytime were lowest

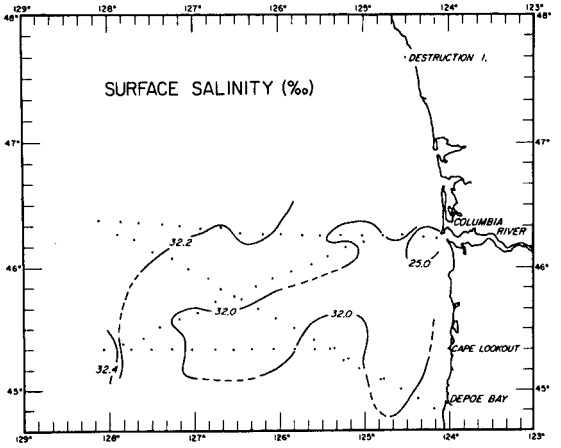

FIGURE 17.—Surface salinity measured during the cruise, 27 July-2 August 1970. Dots indicate stations.

offshore, increased in the region of the plume, and were highest along the coast (Figure 18). This agrees with Pak, Beardsley, and Park (1970) who found higher concentrations of light scattering particles in the low-salinity, warm plume waters than offshore.

Albacore Catches

The catch rates of albacore by the *Cayuse* during the cruise are shown between daylight stations in Figure 19. Highest catches were

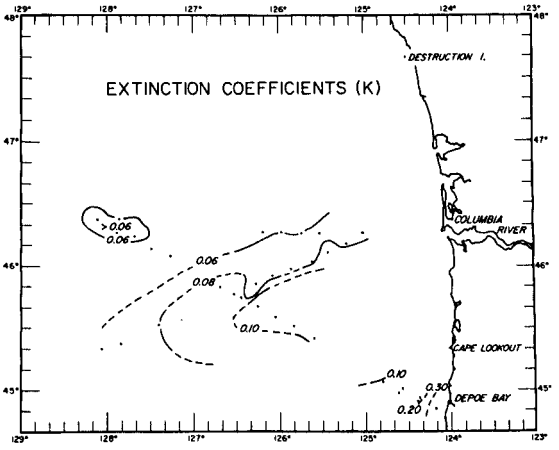

FIGURE 18.—Extinction coefficients of downwelling irradiance, $k = (\ln I_0 - \ln I_d)/d$, where I_0 is surface intensity and I_d is the intensity at depth d. Dots indicate stations where photometer casts were made.

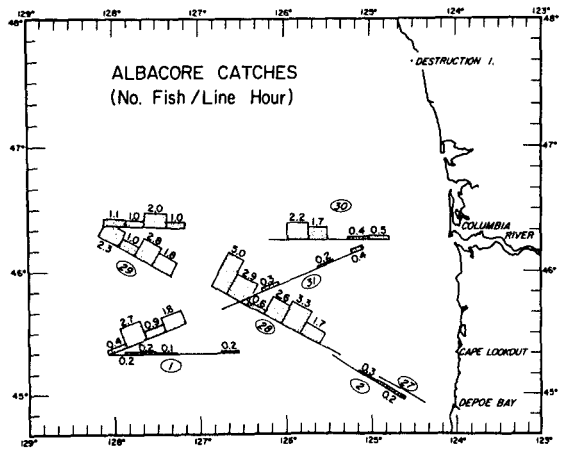

FIGURE 19.—Catch rates of albacore (fish landed per line hour) while the *Cayuse* steamed during daylight hours. Numbers above histograms indicate catch per line hour. Numbers encircled below a group of histograms denote the calendar day during the cruise (27-2 August).

made on the first half of the cruise, which corresponds to the trend of catches by commercial boats in the area (Figure 1). Fish ranged from 57 to 80 cm fork length. Catches were made along much of the cruise track and were not confined to one local area. Within individual days, however, highest catches often occurred along the offshore edge of the plume. For example, on 28 July peak catches of 3.3 and 2.9-5.0 fish/line hr were made in the vicinity of 32.0‰ and 16°C surface water (Figures 14 and 17). These were areas along the edge of the plume where the horizontal temperature and salinity gradients were more intense than in other areas (Depoe Bay Stations 85-95 and 115-135 (Figure 15)). Lowest catches on 28 July of 0.6 fish/line hr were made within the core of the plume at Stations 105-115 where salinity was 31.5‰ or lower and temperatures were above 16°C. Catches also declined along the northernmost cruise track as the ship entered a finger of 16°C and 32‰ water on 30 July.

On 31 July, after the major drop in average catches by the fleet, largest catches (2.7 fish/line hr) were not in the general area of previous high catches on 28 July but farther offshore, 160 miles off Cape Lookout. In this area the 16°C isotherm sloped to the surface (Figure 16), again indicating a horizontal thermal gradient.

A few fish were caught on 1 and 2 August, in nearshore waters, 25-50 miles off Depoe Bay. No fish were caught in the same area 6 days earlier. During the intervening time, the mixed layer depth deepened and transparency increased at the stations where fish were caught. At the station 25 miles offshore, for example, the extinction coefficient was 0.17 on 27 July compared with 0.11 on 2 August; the depth of the 15°C isotherm descended from 5 to 30 m. Thus nearshore catches late in the cruise may be correlated with increased water clarity and increased depth of favorable water temperatures.

Albacore Food Habits

The proportion of fishes, crustaceans, and squids found in the stomachs of albacore caught from the *Cayuse* is illustrated in Figure 20. In general, albacore caught within 130 miles of shore had been feeding largely on fishes, whereas squids and sometimes euphausiids were more important constituents of stomach contents farther offshore. An "S" within the pie diagrams denotes where saury, *Cololabis saira*, was the predominant food (>50% of the wet weight biomass).

On 28 July when large catches were made by the *Cayuse* and the commercial fleet, albacore were observed jumping at the surface in pursuit of saury. On this day sauries constituted nearly all the stomach contents of albacore, many of which had full stomachs. Saury predominated only twice in stomachs of albacore examined from offshore (beyond long 127°W), on 29 July and 1 August, but composed most of the stomach contents of albacore examined off the Columbia River on 30 July. Thus saury was the main forage of albacore along the outside edge of the Columbia River plume, but usually not beyond the plume during 28-30 July. After 30 July, saury was a less important food item, and ragfish, *Icosteus aenigmaticus*, and rockfish, *Sebastes*, were more common than they were earlier. In addition, sergestid shrimp constituted all the stomach contents of two albacore caught near

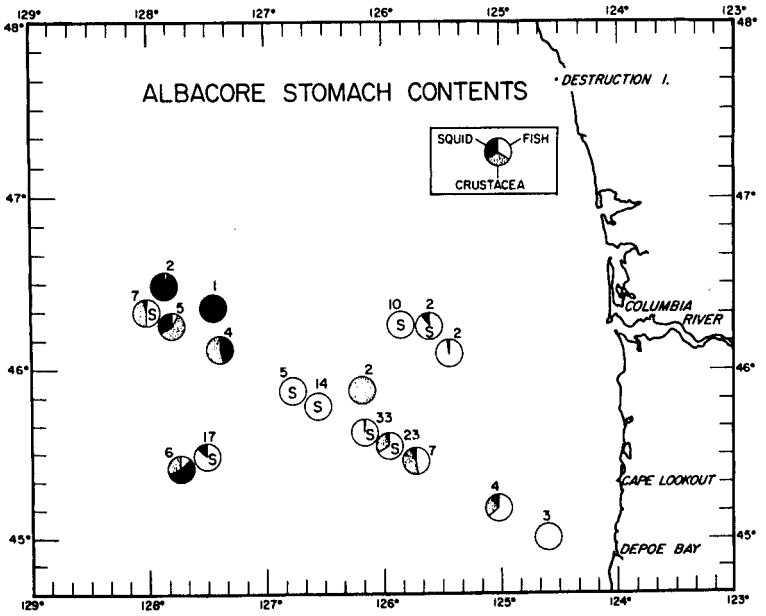

FIGURE 20.—The proportion of squids, fishes, and crustaceans (on a weight basis) in the stomach contents of albacore caught by the *Cayuse*, 27 July-2 August 1970. Numbers indicate the number of stomachs examined. "S" denotes where saury made up over 50% of the biomass of stomach contents.

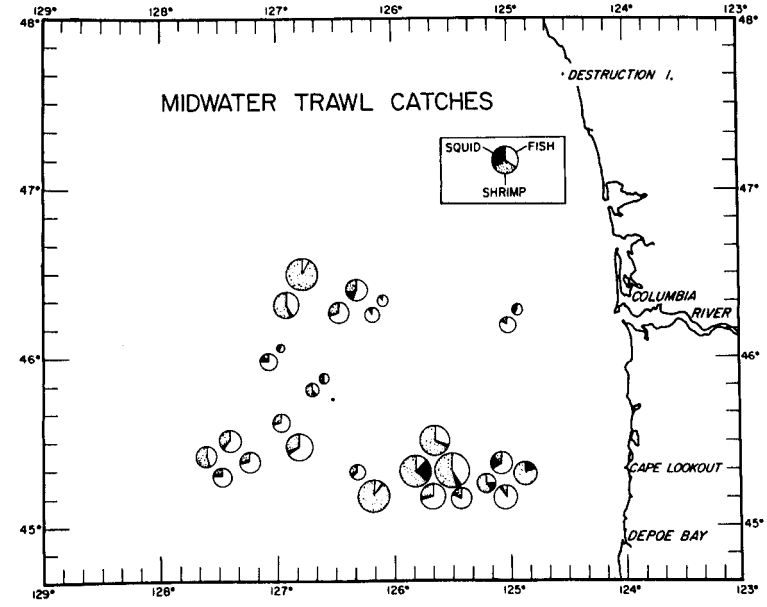

FIGURE 21.—The proportion of squids, fishes, and shrimps (on a weight basis) in 6-ft Isaacs-Kidd midwater trawl tows to 100-m depth at night, 27 July-2 August 1970. The total biomass of these groups combined for each tow is proportional to the logarithm of the diameter of the circles.

the area where saury had been eaten several days before.

Highest albacore catch rates also occurred where albacore were feeding on saury. All catch rates were ranked from highest to lowest for locations where food data was available (see Figures 19 and 20). The sum of the ranks was then compared for areas where saury predominated (>50% of the stomach biomass) and where saury did not predominate stomach contents. Catch rates were significantly higher in areas where sauries predominated stomach contents than in areas where saury were not predominant. (Mann-Whitney U Test, $P<0.01$, n_1 9, n_2 9). The decreased albacore catch rate after 28 July

is thus associated with a decreased availability of saury in near-surface waters where jig fishing for albacore is most effective.

The biomass of fishes, shrimps and squids per 1,000 m^3 of water filtered in nighttime midwater trawl tows is shown in Figure 21. Note that the diameter of the circles is proportional to the logarithm of total biomass of the tows. The highest catches were usually composed of the shrimp *Sergestes similis* in plume waters. Fishes often predominated catches, but when they did, the total biomass was generally intermediate or low. Squids were usually present but composed a relatively small portion of the biomass.

A comparison of midwater trawl catches and tuna stomach contents reveals some obvious differences. Saury was rarely if ever caught in trawls but was common as forage especially during the first part of the cruise. Squids sometimes predominated in albacore caught offshore but were unimportant components in the trawl collections, though no trawl was towed in the offshore region where squids were common in stomachs on 30 July. Few midwater trawl and albacore catch stations coincided exactly. Nevertheless the correlation between albacore catches and midwater trawl catches sometimes appeared negative. For example, lowest biomass of micronekton (Figure 21) and euphausiids (not shown) occurred in the region of high albacore catch rates (5.0 and 2.9 in Figure 19). Perhaps such a negative relationship was caused by the grazing of albacore or their carnivorous prey.

DISCUSSION

Our present state of knowledge about the behavior of albacore and the influence of the ocean environment is inadequate to explain the drastic fluctuations of catches by jig boats that occurred off Oregon in 1970. The large concentration of albacore located by the jig fleet in July 1970 off the Columbia River was very vulnerable to surface jigs and record catches were made. In contrast, boats that trolled through this same area, and Oregon waters that had been productive in past years, often reported "no fish days" in August.

Oceanographic changes that correlate with these catch variations were not obvious. Winds were variable during the entire summer with the prevailing northwesterlies being interrupted occasionally by weak frontal systems and concomittant southerly winds (Figure 3). The first large peak in catches per day was during a period of strong northerlies; the second peak, during calm sea conditions. Sea-surface temperatures remained within the "preferred" thermal range, 14.4°-16.1°C (Alverson, 1961), over much of the region during August, usually the best month for albacore fishing. Mixed layer depths also did not change appreciably and 15°C water was usually found to 20-40 m offshore of coastal waters.

The fact that bait boats had good fishing after the demise of the jig fishery suggests that albacore were present off Oregon but not susceptible to capture by jig fishing from August through mid-October. This can be explained by changes in the vertical distribution and behavior of albacore. Surface-towed jigs are most effective on fish feeding near the surface, whereas bait boats, by chumming an area, are better able to attract fish from subsurface schools.

Because albacore was feeding mainly on surface schools of saury during the second peak in jig boat success and because a significant positive relationship existed between albacore catches and feeding on saury, it is postulated that the collapse of the jig fishery was related to a change in the availability of the saury, the major prey of the albacore during the preceding period in 1970, and usually the most important food of albacore off Oregon in other years (Pearcy, unpubl. data). Saury could have been grazed down, emigrated out of the area, or descended into deeper water. Any of these could have induced the large concentration of albacore to migrate into deeper water where better feeding conditions existed and where they would be relatively inaccessible to surface trolled jigs.

During late August we repeated a cruise in the same region as the 27 July-2 August cruise, off northern Oregon and the mouth of the Columbia River. Nineteen albacore were caught on jigs. Anchovy larvae, small rock-

fishes, and *Sergestes* were the most common organisms in their stomachs. Only one saury was identified. Examination of the feeding habits of bait-caught albacore during the late summer would be of particular interest. Absence of saury from these fish would suggest that saury was not available to albacore for the remainder of the season in this region off Oregon, and albacore fed on alternate food organisms from subsurface waters. These changes in the behavior of albacore show similarities with the schooling and foraging behavior of bluefin tuna, *Thunnus thynnus*, schools off Baja California noted by Scott and Flittner (1972). They found that the occurrence of jumping and boiling schools on the surface was related to foraging on baitfish, whereas subsurface schools, which produced the largest purse seine catches per set, fed more on red crab, *Pleuroncodes planipes*.

A major conclusion of this paper is in accord with the hypothesis that the geographic range of tuna is established by temperature but food supply is largely responsible for distributions within this range (Blackburn, 1964; 1969 Nakamura, 1969). If this hypothesis is correct, it follows that accurate predictions of albacore concentrations in time and space must consider abundance and availability of forage organisms. Moreover, the depth distribution of the preferred albacore food will have pronounced influence on the relative successes of jig and bait fisheries, as the 1970 season off Oregon demonstrated.

ACKNOWLEDGMENTS

I thank D. F. Keene for helping to analyze the data; L. H. Hreha, W. L. Craig, and R. M. Laurs for supplying catch data; G. A. Flittner, R. W. Owen, D. A. Panshin, and R. M. Laurs for their comments on the manuscript; the U.S. Air Force 304 ARRS Squadron in Portland, Oreg. and the U.S. Coast Guard Station in Port Angeles, Wash. for providing remote sensing flights; and the skippers of fishing boats for keeping albacore logs. This research was supported by the U.S. Naval Oceanographic Office (Spacecraft Oceanography, Contract N6 22306-70-C-0414), the former Bureau of Commercial Fisheries (Contract No. 14-17-0002-333) and the National Oceanic and Atmospheric Agency Institutional Sea Grant (2-35187).

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AGE AND GROWTH OF THE WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, ON GEORGES BANK

FRED E. LUX[1]

ABSTRACT

Lengths calculated at each scale annulus from 510 winter flounder, *Pseudopleuronectes americanus*, collected on Georges Bank during 1963-66 provided a measure of growth up to 12 years of age. Growth was more rapid on Georges Bank than on inshore areas. Females grew faster than males after age 2. Fish from eastern Georges Bank grew slightly faster than those from western Georges Bank. Bertalanffy growth equations were computed for each sex.

The winter flounder, *Pseudopleuronectes americanus* (Walbaum), found in Atlantic coastal waters from Newfoundland to Cape Hatteras, is a common fish in the New England and middle Atlantic catch. Landings by commercial fishermen, mostly with otter trawls, averaged 12,000 metric tons annually in the period 1966-70. In addition, there is a large sport fishery since the species occurs in shallow coastal waters easily accessible to saltwater anglers. The estimated angler catch in 1965 was 13,000 tons (Deuel and Clark, 1968).

Most of the catch is made in the New England area where the species is found on both inshore and offshore grounds. There appear to be a number of distinct groups in this area, judging from movement of tagged fish and variation in numbers of fin rays (Perlmutter, 1947; Bigelow and Schroeder, 1953; Lux, Peterson, and Hutton, 1970). One of these groups is on Georges Bank where the fish are larger and have more fin rays than on inshore areas. There is almost no movement of winter flounder between Georges Bank and inshore grounds. The growth material presented here is for winter flounder from Georges Bank.

On the basis of size, color, and fin ray number, Kendall (1912) determined that the winter flounder from Georges Bank comprised a separate species, which he named *P. dignabilis*. Bigelow and Schroeder (1953), however, considered the differences as no more than racial, a view which presently prevails.

Studies of winter flounder growth on inshore areas, summarized by Berry, Saila, and Horton (1965), Poole (1966), and Kennedy and Steele (1971) indicated that age determination from hard body parts is difficult and that growth rate varied with area. Females grew faster than males, at least after the first few years.

There is no previous study on growth of winter flounder on Georges Bank although it has long been known that winter flounder there grow much larger than on inshore grounds (Bigelow and Schroeder, 1953).

MATERIALS AND METHODS

The fish for the study were obtained from research vessel and commercial catches in 1963-66. The research vessel samples were from National Marine Fisheries Service *Albatross IV* groundfish surveys (Grosslein, 1969). Since the otter trawl used had a ½-inch mesh liner in the cod end, both large and small fish were obtained. Six additional samples were collected from catches of commercial otter trawlers, and these contained only fish greater than 36 cm in total length.

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Manuscript accepted October 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

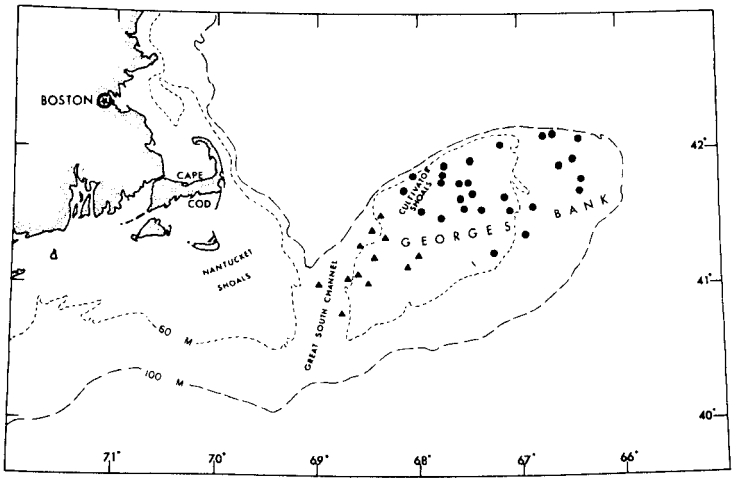

FIGURE 1.—Locations on Georges Bank where winter flounder were collected for age and growth studies. (Dots: eastern Georges Bank; triangles: western Georges Bank.)

Locations where samples were taken for the study cover most of the northern half of Georges Bank (Figure 1). Otter trawl catches from the *Albatross IV* groundfish surveys suggest that there are two somewhat separate areas of winter flounder abundance on Georges Bank. The area of greatest abundance extends from Cultivator Shoal eastward to about long 67°W. This is the area where most of the Georges Bank commercial catch is taken. The other area is southwest of Cultivator Shoal and extends westward from there to about long 69°W. The two areas are roughly shown by plotting catches of winter flounder from eight groundfish surveys on Georges Bank (Figure 2). Although sampling was relatively uniform over the entire Bank to a depth of 200 m (see figures in Grosslein, 1969), catches of five or more winter flounder per otter trawl station were made only in the above-defined areas. Growth was computed separately for fish from these two areas (Figure 2).

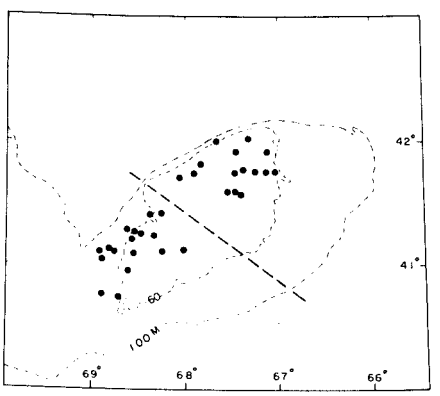

FIGURE 2.—Georges Bank stations (30-min otter trawl hauls) where five or more winter flounder were caught during fall groundfish surveys in 1963-70. (Dashed line indicates the boundary between east and west Georges Bank for the growth study.)

Scales were used for age determination since these appeared easier to interpret than otoliths and had the advantage of greater ease for calculation of lengths at earlier ages. The scales were removed from the eyed side of fish along the lateral line in the area just anterior to the caudal peduncle. Total length in millimeters and sex were recorded for each scale sample. Except where noted, lengths given herein are total lengths.

Impressions of the scales were made in transparent cellulose acetate strips. These were viewed with a microprojector using 40× magnification, and year marks (annuli) were identified and counted. Criteria for distinguishing annuli were the same as those used for New England yellowtail flounder, *Limanda ferruginea*, (Lux and Nichy, 1969) which, like the winter flounder, have ctenoid scales. With the exception of the first year, spring and summer growth was characterized by widely spaced circuli (rapid length accretion) and fall and winter growth, by closely spaced circuli (slow length accretion). The outer edge of the zone of closely spaced circuli was con-

sidered to be the annulus. Slight checks in growth consisting of only a few closely spaced circuli were considered to be false annuli and were ignored in assigning age. In the first year all circuli are closely spaced. The annulus here was taken to be the outermost of these circuli.

Ages were assigned to each fish by the author and, independently, by an assistant. For some scales reliable growth calculation appeared impossible because of regeneration, erosion, resorption, or checks. These, making up about 15% of the total sample, were omitted from the calculations. As might be expected, the proportion of rejected scales was much higher for large fish (Table 1).

TABLE 1.—Length-frequency distribution of winter flounder collected on Georges Bank in 1963-66 and proportions included in the growth calculations, by 5-cm intervals.

Length interval (cm)	Total number of fish	Included in calculations	
		Number	Percent
11-15	4	4	100.0
16-20	11	11	100.0
21-25	18	18	100.0
26-30	27	26	96.3
31-35	28	28	100.0
36-40	80	73	91.2
41-45	108	101	93.5
46-50	158	133	84.2
51-55	94	69	73.4
56-60	55	38	69.1
61-65	15	8	53.3
66-70	4	1	25.0
Total	602	510	84.7

Age was determined, to the extent possible, for the rejected scales and length at age of these fish was compared with that of fish included in the growth calculations to determine if bias was introduced by the rejection of part of the sample (Figure 3). While the samples were rather small in the older ages, there appeared to be no difference in growth of the two groups of fish.

Totals of 412 fish from eastern Georges Bank and 98 from western Georges Bank were included in the calculations. All of the commercial samples, consisting of 225 fish, were from eastern Georges Bank.

Length at each annulus was calculated from measurements of anterior scale radii. The relationship of body length to scale length approximated a straight line, except for curvi-

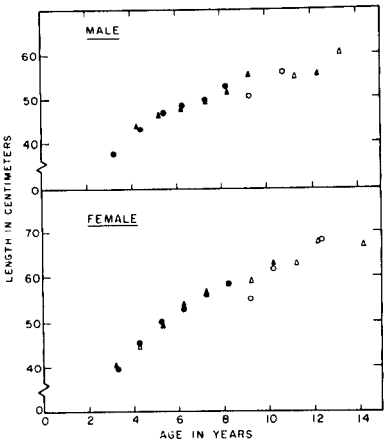

FIGURE 3.—Mean lengths at capture by age group for fish from commercial samples included in growth calculations (circles) and those rejected (triangles). (Open symbols represent fewer than three fish.)

linearity among the smallest fish (Figure 4). Direct proportion growth calculations therefore were made using the equation

$$l_n = C + \frac{S_n}{S}(l - C)$$

where l_n is the fish length at the time of formation of the nth annulus, C is the fish length at scale formation, S_n is the anterior scale radius to the nth annulus, S is the anterior scale radius at capture, and l is the

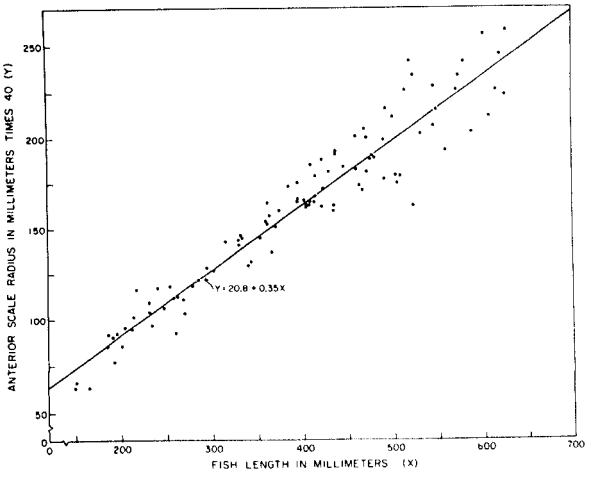

FIGURE 4.—Body-scale relationship of Georges Bank winter flounder based on measurements of 101 fish.

fish length at capture (Fraser, 1916). Two scales were measured for each fish. A nomograph was used to facilitate computations (Carlander and Smith, 1944).

For the value of C an estimated fish length at scale formation of 20 mm was used. This was based on examination of winter flounder 17 to 25 mm long collected in Massachusetts coastal waters in early June 1962 (Lux and Nichy, 1971). I have assumed that scale formation occurs at about the same length on Georges Bank where I have collected no fish of the above sizes.

Evidence, indicating that marks identified as annuli on the scales of winter flounder from Georges Bank were actual year marks, was obtained from several sources. The main lines of this evidence are summarized below.

1. There is a correlation between age and size in that increase in number of annuli is accompanied by an increase in fish size (Figure 5).
2. Lengths at various annuli calculated from scales correspond with empirical lengths at the same ages determined from reading scales (Figure 5).
3. There is agreement on length at age of fish from the same age-groups collected in different years (Table 2) and agreement on calculated growth among different year classes (Tables 3 and 4).
4. Distinguishing permanent marks consisting of unpigmented spots on the eyed side of the fish occurred in successive years in an estimated 4 to 13% of winter flounder from the 1959 year class on eastern Georges Bank (Lux, in press). This white spotting appears to occur in far less than 1% of the fish of a year class normally. White-spotted fish of the 1959 year class were collected in 1964, 1965, and 1966. Those from 1964 had 5 annuli on their scales; those from 1965, 6 annuli, and those from 1966, 7 annuli, showing that 1 annulus was added each year. The mean lengths of spotted fish from this year class showed regular increases over these 3 years (Table 5). Growth rate was unaffected by white spotting.

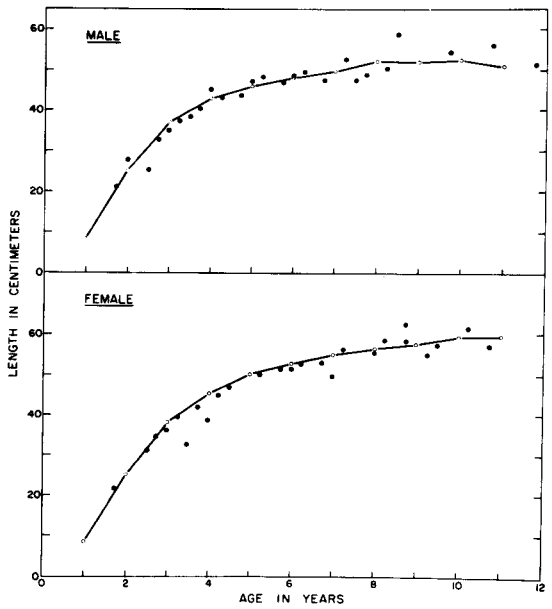

FIGURE 5.—Mean length at age from scale age determinations (dots) compared with mean calculated length at each annulus (open circles) for male and female winter flounder from eastern Georges Bank.

TABLE 2.—Number (n) of fish in each sample and mean length in centimeters (cm) at capture by age group for male and female winter flounder from eastern Georges Bank in 1963-66.

Age group	Year caught	Male		Female	
		n	cm	n	cm
II	1965	12	29.4	8	32.7
	1966	8	30.1	5	35.8
III	1964	2	38.2	4	39.4
	1965	5	38.4	3	32.7
	1966	27	39.3	38	39.2
IV	1963	—	—	1	47.8
	1964	18	43.8	18	45.0
	1965	—	—	2	46.6
	1966	11	43.4	10	42.9
V	1964	20	47.1	7	50.8
	1965	—	—	—	—
	1966	14	46.6	9	50.5
VI	1964	10	48.3	7	50.6
	1965	12	49.3	11	54.1
	1966	18	47.8	10	52.1
VII	1963	1	51.4	—	—
	1964	5	49.8	—	—
	1965	1	44.1	2	55.8
	1966	24	49.6	28	55.0
VIII	1964	6	54.3	1	61.0
	1965	1	58.9	—	—
	1966	4	51.0	7	56.6

TABLE 3.—Number (n) of fish in each sample and calculated mean length in centimeters (cm) at each annulus, for each year class and for all year classes combined, for male and female winter flounder collected on eastern Georges Bank in 1963-66.

Year class	Number of annuli																							
	1		2		3		4		5		6		7		8		9		10		11		12	
	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm
Males																								
1955	2	6.2	2	19.2	2	33.6	2	40.8	2	44.6	2	46.6	2	47.8	2	49.0	2	50.0	1	50.4	1	50.8	—	—
1956	4	11.4	8	24.4	8	38.5	8	45.1	8	49.2	8	51.2	8	52.5	7	54.0	1	54.3	1	55.1	—	—	—	—
1957	5	8.6	8	23.8	8	38.1	8	43.8	8	47.4	8	49.7	8	51.0	3	54.2	2	53.4	—	—	—	—	—	—
1958	9	7.5	15	22.6	15	36.4	15	42.5	15	45.8	15	47.8	5	48.4	4	50.7	—	—	—	—	—	—	—	—
1959	46	9.8	56	28.0	56	39.0	56	43.9	56	46.5	36	48.4	24	49.2	—	—	—	—	—	—	—	—	—	—
1960	27	8.2	36	25.8	36	37.6	36	43.2	18	45.8	18	47.5	—	—	—	—	—	—	—	—	—	—	—	—
1961	11	7.8	16	23.4	16	36.1	14	42.6	14	45.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1962	12	8.3	16	24.9	16	36.3	11	41.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1963	34	7.1	39	24.7	39	35.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1964	8	8.6	8	25.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1965[1]	26	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	184	8.2	204	25.5	196	37.3	150	43.3	121	46.4	87	48.4	47	49.9	16	52.6	5	52.2	2	52.7	1	50.8	—	—
Females																								
1954	1	6.2	2	23.9	2	40.0	2	49.2	2	54.4	2	57.6	2	59.9	2	61.6	2	62.7	2	63.6	1	66.8	1	67.4
1955	1	8.2	3	28.1	3	40.6	3	46.6	3	50.4	3	52.1	3	53.7	3	54.7	3	55.7	2	55.4	2	56.0	—	—
1956	1	10.5	2	22.7	2	39.6	2	46.3	2	51.4	2	54.0	2	56.3	2	57.8	1	56.6	—	—	—	—	—	—
1957	3	9.1	3	25.6	3	39.9	3	46.3	3	50.2	3	52.8	3	54.6	3	55.9	3	56.9	—	—	—	—	—	—
1958	10	6.9	16	22.0	16	37.6	16	44.6	16	48.9	16	51.6	9	54.8	7	56.2	—	—	—	—	—	—	—	—
1959	43	10.8	47	29.5	47	40.8	47	47.2	46	50.8	39	53.4	28	55.0	—	—	—	—	—	—	—	—	—	—
1960	21	8.2	28	24.0	28	37.6	28	44.7	10	49.0	10	51.6	—	—	—	—	—	—	—	—	—	—	—	—
1961	10	7.2	15	23.6	15	37.8	11	44.6	9	48.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1962	7	6.4	13	19.3	13	32.2	10	40.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1963	38	7.9	46	24.7	38	36.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1964	2	8.7	5	24.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1965[1]	26	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	163	8.4	180	25.1	167	38.0	122	45.4	91	50.1	75	52.8	47	55.1	17	56.7	9	57.7	4	59.5	3	59.6	1	67.4

[1] Includes males and females.

RESULTS

The computed lengths at each annulus for male and female winter flounder from eastern and western Georges Bank in 1963-66 (Tables 3 and 4, Figure 5) show that females grow faster than males after the second year. This pattern of growth is similar to that of New England yellowtail flounder in which sexual maturity usually occurs at age 3 (Lux and Nichy, 1969). Limited evidence from the present study indicates that Georges Bank winter flounder also begin to attain maturity at age 3.

The fish from western Georges Bank appeared to grow a little less rapidly, at least in early years, than those from the eastern part of the Bank, and their growth is therefore presented separately (Tables 3 and 4, Figure 6). However, the sample from western Georges Bank is too small to precisely define growth there. Growth in length for both of the grounds is rapid until age 5 or 6. Then it tends to decrease sharply, especially for males (Figure 6).

Growth by year class on eastern Georges Bank (Table 3) suggested that fish from the 1959 year class grew slightly faster than those from other years. The data at hand, however, are inadequate for a conclusive examination of this question.

Following the first 2 years, the growth of fish on Georges Bank is faster than that of fish on inshore areas (Figure 6). Although the growth of this species on the inshore grounds apparently varies widely from place to place

TABLE 4.—Number (n) of fish in each sample and calculated mean length in centimeters (cm) at each annulus for each year class and for all year classes combined, for male and female winter flounder collected on western Georges Bank in 1963-66.

Year class	Number of annuli																							
	1		2		3		4		5		6		7		8		9		10		11	
	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm
Males																								
1958	3	6.3	6	17.9	6	31.2	6	39.0	6	44.3	2	49.0	2	50.8	—	—	—	—	—	—	—	—	—	—
1959	3	5.9	3	17.0	3	29.9	3	36.9	3	40.6	3	43.4	1	43.5	—	—	—	—	—	—	—	—	—	—
1960	12	6.4	14	21.1	14	34.4	5	38.8	5	42.2	4	45.4	—	—	—	—	—	—	—	—	—	—	—	—
1961	6	6.6	6	20.8	4	28.5	4	36.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1962	4	7.1	4	19.2	4	35.1	2	44.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1963	18	7.2	18	23.1	7	35.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1965[1]	1	9.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	47	6.8	51	21.0	38	33.2	20	38.6	14	42.8	9	45.5	3	48.4	—	—	—	—	—	—	—	—	—	—
Females																								
1954	1	8.6	1	25.2	1	38.8	1	46.4	1	50.5	1	54.2	1	56.6	1	58.8	1	60.4	1	61.6	1	62.4		
1955	1	8.2	1	17.2	1	27.6	1	37.2	1	45.4	1	50.0	1	54.0	1	56.4	1	58.0	1	59.0	—	—		
1956	3	7.3	3	21.9	3	35.5	3	44.5	3	49.7	3	53.4	3	55.9	2	58.4	2	60.0	1	61.0	—	—		
1957	2	6.2	2	17.6	2	29.0	2	38.8	2	44.6	2	48.2	2	50.9	2	52.6	—	—	—	—	—	—		
1958	1	6.7	1	20.0	1	30.2	1	37.4	1	40.9	—	—	—	—	—	—	—	—	—	—	—	—		
1959	5	7.7	5	24.1	5	37.1	5	44.1	5	49.8	5	52.6	1	55.6	—	—	—	—	—	—	—	—		
1960	12	7.3	14	21.8	14	33.5	14	39.8	14	44.5	1	53.6	—	—	—	—	—	—	—	—	—	—		
1961	9	7.4	9	19.7	7	29.6	7	37.1	1	42.4	—	—	—	—	—	—	—	—	—	—	—	—		
1962	2	6.8	2	20.3	2	36.2	2	42.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
1963	4	7.1	5	23.5	4	37.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
1964	1	14.0	1	26.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
1965[1]	1	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
Total	42	7.5	44	21.6	40	33.6	36	40.4	28	46.1	13	52.1	8	54.5	6	56.2	4	59.6	3	60.5	1	62.4		

[1] Sex unknown.

TABLE 5.—Length-frequency distributions of white-spotted winter flounder of the 1959 year class obtained from commercial catches in 1964-66 from eastern Georges Bank.

Length (cm)	May-June 1964		April 1965		April 1966	
	Male	Female	Male	Female	Male	Female
46	3	1	1	—	—	—
47	3	—	3	—	4	—
48	2	—	—	—	2	—
49	4	—	3	—	—	—
50	1	1	3	—	5	—
51	1	—	1	1	1	—
52	—	3	—	—	2	3
53	—	2	1	3	—	—
54	—	—	1	4	—	4
55	—	—	—	1	—	3
56	—	—	—	2	1	4
57	—	—	—	1	—	3
58	—	—	—	1	—	2
59	—	—	—	—	—	3
60	—	—	—	—	—	1
Total	14	7	13	13	15	23
Mean	48.0	51.1	49.4	54.5	49.7	55.9

(Berry et al., 1965; Poole, 1966; Kennedy and Steele, 1971), it does not approach the rate on Georges Bank at any inshore location where it has been described. Growth of females was greater than males after the first few years in all areas, except off Newfoundland where there appeared to be no difference in the age range covered (Figure 6).

Calculated growth to the first annulus was about 7 or 8 cm for both sexes on Georges Bank (Tables 3 and 4). Although no 0-group fish were obtained from Georges Bank for length comparison, this size agrees closely with the lengths of 0-group winter flounder from inshore Massachusetts waters (Lux and Nichy, 1971). There the 0-group fish by late fall averaged 8.7 cm long in 1961 and 7.3 cm in 1962. There was no apparent growth difference with sex in these inshore fish, for in late October 1962 the males were 7.3 cm long (n =

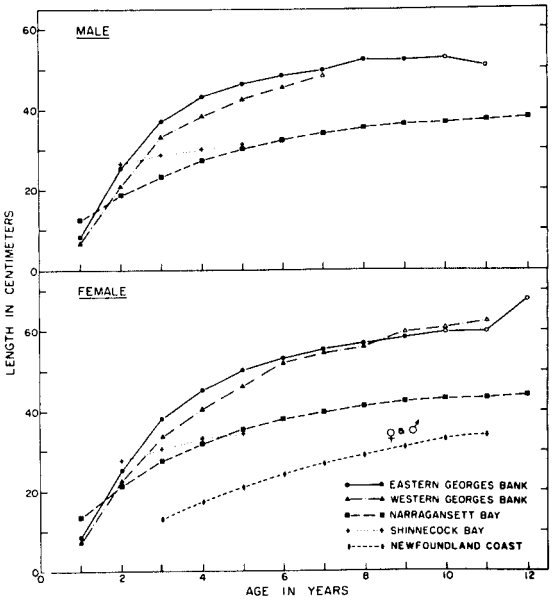

FIGURE 6.—Mean calculated lengths at each annulus for male and female winter flounder from Georges Bank compared with growth data for fish from Narragansett Bay, R.I. (Berry et al., 1965), Shinnecock Bay, N.Y. (Poole, 1966), and Conception Bay, Newfoundland (Kennedy and Steele, 1971). (Open symbols for Georges Bank represent fewer than five fish.)

10) and females, 7.2 cm (n = 18). Length in late fall of the first year in Connecticut waters in 1958 and 1959 was similar to the above, being about 7.0 cm standard length (Pearcy, 1962), which is about 8.7 cm total length. Lengths calculated at the first annulus on otoliths of winter flounder in Rhode Island waters by Berry et al. (1965) were somewhat greater, being 12.5 cm for males and 13.5 cm for females.

Bertalanffy growth equations of the form

$$l_t = l_\infty [1 - \exp(-K(t - t_0))]$$

in which l_t is length at age t, l_∞ is the theoretical maximum length, K is the rate of change in length increment, and t_0 is the age at which growth in length theoretically begins, were fitted by the method of Ricker (1958), to the mean lengths at each age for males and females from eastern Georges Bank (Table 3). The resulting equations

$$l_t = 550 [1 - \exp(-0.37(t + 0.05))] \quad \text{(male)}$$
$$l_t = 630 [1 - \exp(-0.31(t - 0.05))] \quad \text{(female)}$$

express the growth rates for fish of age 3 and beyond (Figure 7).

Estimates of l_∞ given here are principally for use in developing a mathematical expression of growth rather than to accurately portray maximum attained length. The l_∞ of 55.0 cm for males, for example, is somewhat shorter than the maximum observed length of 57.0 cm. Likewise, the l_∞ of 63.0 cm for females is considerably shorter than the 70.0 cm maximum observed.

Inclusion of more large and old fish in the samples might have altered the form of the computed growth curves slightly. Until more accurate equations are derived, however, those given above will provide reasonable accuracy for yield per recruit calculations for both eastern and western Georges Bank.

ACKNOWLEDGMENT

Robert N. Hersey, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, made independent age determinations of the fish included in this study and performed most of the growth calculations. His assistance is gratefully acknowledged.

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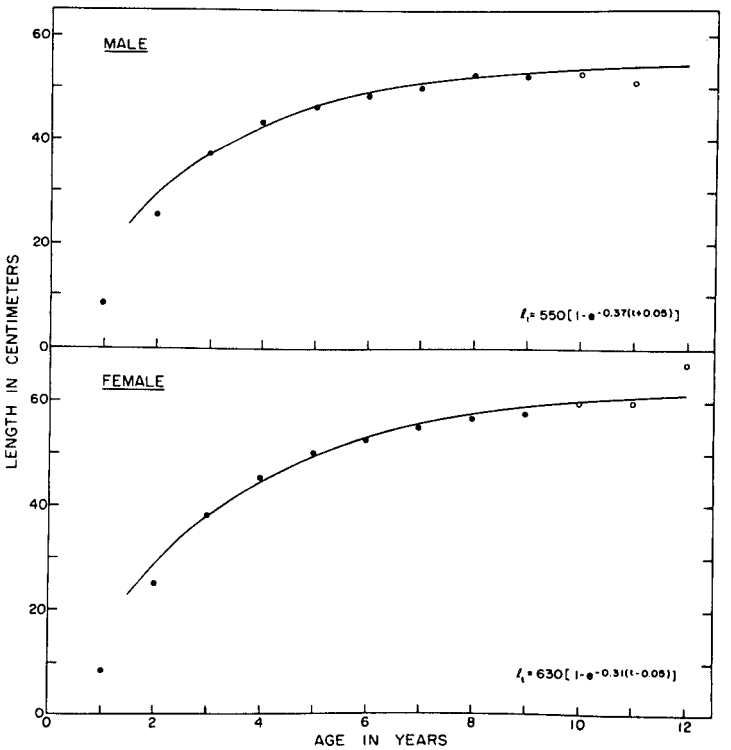

FIGURE 7.—Mean calculated lengths at each annulus for male and female winter flounder from eastern Georges Bank and the fitted Bertalanffy growth curves. (Open circles represent fewer than five fish.)

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PROBLEM OF BIAS IN MODELS TO APPROXIMATE OCEAN MORTALITY, MATURITY, AND ABUNDANCE SCHEDULES OF SALMON FROM KNOWN SMOLTS AND RETURNS

ROBERT H. LANDER[1]

ABSTRACT

The problem of methodological bias in estimating ocean mortality or survival, maturity, and abundance of multireturn species of Pacific salmon (*Oncorhynchus* spp.) is examined heuristically with a data base for which no unbiased estimators exist. The case of hatchery coho salmon (*O. kisutch*) is emphasized to treat the problem in its simplest form (two returns). Models previously reported by Ricker, Fredin, and Cleaver are considered in the context of their application in biomass computations and the particular problem of bias in approximating average and interval-specific mortality coefficients during ocean life. A new scheme is introduced as the limit-mean model, and the assumptions in all four models are contrasted. Numerical examples for a hypothetical cohort demonstrate a wide range of bias in estimates of different parameters from the same model and also in estimates of the same parameter from different models applied in different situations. For the hypothetical data, overall performance is best for the limit-mean model with the offshore catch known; this model also provides estimates of natural and fishing mortality rates offshore during the last year at sea. For coho and chinook salmon, (*O. tshawytscha*) caught off western North America, it is recommended that 1) maturity be directly sampled to help provide nominally unbiased estimates for certain of the parameters and 2) research be intensified on determining offshore catch by origin independently of marking smolts.

Three oceanic fisheries have motivated research on the geographic origins, distribution patterns, and changes in biomass during the marine life of salmon. One is the Japanese mothership fishery, since 1952 by drift gill nets west of long 175°W in the North Pacific Ocean—mainly for pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon (Fukuhara, 1953). Another is the offshore troll and sport fishery from California to Alaska for chinook (*O. tshawytscha*) and coho (*O. kitsutch*) salmon (Godfrey, 1965; Mason, 1965). Third is the drift net fishery for Atlantic salmon (*Salmo salar*), since 1964 off southeast Greenland and northern Norway (Horsted, 1971).

The results of biomass computations based on growth and natural mortality estimates must be combined with catches (real or assumed) by natal origin in order to assess the impact of offshore vis-a-vis inshore fishing (Taguchi, 1961a, 1961b; Doi, 1962; Ricker, 1962, 1964; Parker, 1963; Fredin, 1964; Hirschhorn, 1966; Cleaver, 1969; Henry, 1971, 1972). Investigators have recognized the scarcity of existing field data, the high cost of direct marking/recovery at sea, and the technical difficulties of obtaining unbiased data and constructing realistic models to approximate the time distribution of mortality (Ricker, 1962; Parker, 1960, 1962, 1963, 1968; Fredin, 1964; Lander et al., 1967; Cleaver, 1969).

Biased estimates can distort the interpretation of actual time changes in biomass of a cohort and impede the application of rational conservation measures. On the other hand, reasonably accurate approximations to interval-specific mortality can be useful not only in biomass computations: they may help also to predict returns from the sea and thereby to improve management of inshore salmon fisheries (e.g., Gilbert, 1963).

In this report I review three published models for approximating ocean mortality schedules

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Manuscript accepted October 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

as applied in biomass computations, examine the particular problem of bias in mortality estimates, and introduce another model to extend the indirect approach developed by Parker (1962), Ricker (1962), Fredin (1964), and Cleaver (1969). Bias in estimated maturity and abundance schedules is examined also.

METHODS AND LIMITATIONS

The indirect approach is applicable to species in which maturing adults from the seaward migrants in a given year (or smolt class) return to their natal area in 2 or more years: single-return pink salmon are excluded. The following minimum data are required for multireturn species: 1) origin-specific number of seaward migrants or smolts in a given year, 2) number of survivors returning from the ocean each year until the smolt class is extinct, and 3) intervals between times of seaward migration and of each return or spawning escapement. An offshore fishery may or may not exist; origin-specific catch data for the inshore fishery or an offshore fishery may or may not be available. No unique solution exists for the mortality, maturity, and abundance schedules from the foregoing data base: different combinations of mortality and maturity schedules can generate the same set of observed data.

I consider only the bias due to the absence of unique solutions in estimating models. Data on the numbers of smolts and returning adults may be biased additionally in practice; in fact, the very existence of basic data is unfortunately the exception in wild stocks (e.g., Gilbert, 1963). Data as observed in practice are assumed here to be accurate in order to emphasize the methodological problem.

The number of mortality, maturity, and abundance parameters increases formidably with the number of returns and with the possible regimes of offshore-inshore exploitation. The case of only two returns, typical of hatchery and most wild stocks of coho salmon south of British Columbia (Shapovalov and Taft, 1954; Godfrey, 1965; Drucker, 1972), is emphasized throughout.

Finally, the study is heuristic. Explicit equations for bias are available for only two of the four models as treated here. The equation for one of the two is tedious to write for just one parameter—say the monthly coefficient of total mortality between times of outmigration and of the last return—and descriptive equations for bias are very cumbersome when estimates for all mortality, maturity, and abundance parameters are considered. Relations among all parameters are evident from initial description of the actual situation, however, and are utilized for some numerical comparisons from a set of hypothetical data. These numerical comparisons of bias are selective also with respect to the two general cases considered: 1) catch data unknown and 2) catch data known from marking (or otherwise identifying) smolts and from sampling the catch for recoveries. I try to avoid unfair comparisons between models, to compare them where justified, and to demonstrate how small bias in one parameter estimate may translate to large bias in another estimate from the same model.

ACTUAL SITUATION

Pertinent events of the life history (Shapovalov and Taft, 1954; Godfrey, 1965; Johnson, 1970; Drucker, 1972), observational data, and parameters are related below for coho salmon in the southern part of their freshwater range in North America.

Spawning occurs during November-January and typically the surviving fry are free-swimming during the next February-April. The cohort stays in fresh water until downstream migration of survivors begins about a year later at time $t = t_0$; the actual time of entry to the ocean, some weeks later, depends on physiological condition, stream flow and temperature, and distance from spawning areas. Our mortality schedule starts at time $t = t_0$ and includes downstream mortality of smolts unless their number is known when they enter the sea.

The first return from the sea is in the year of outmigration (6-9 mo later) and occurs at time $t = t_1$, usually during October-December or about 2 years after eggs are spawned. This first return is all or nearly all males or "jacks."

Few jacks are recorded from offshore fisheries but some are taken in freshwater fisheries. Time $t = t_1$ ends our first mortality interval and starts the second.

The immature age-2 fish remaining at sea (males plus females) are reduced in numbers by natural mortality alone for about 6-8 more mo until their recruitment to offshore fishing at time $t = t_r$. For about 5 mo thereafter, offshore then inshore fishing operate along with natural mortality. About a year after the jacks return, age-3 adults appear in the final escapement at time $t = T$ to render the smolt class extinct for our purposes. Thus t_1 and t_r divide the effective life span, $T - t_0$, into three subintervals.

Basic notation follows:

N_0 = number of smolts at time $t = t_0$
E_1 = number of jacks in first return or spawning escapement at time $t = t_1$
N_1 = number of age-2 immatures at sea at time $t = t_1$
N_r = number of recruits to offshore fishing at time $t = t_r$
C = number of fish caught offshore
E_2 = number of adults in second (last) return or spawning escapement at time $t = T$
m = fraction of the cohort which matures as jacks near time $t = t_1$
s_1, s_2 = survival fractions during $t_1 - t_0$ and $t - t_1$, respectively
Z_1, Z_2 = monthly coefficients of natural plus fishing mortality during $t_1 - t_0$ and $T - t_1$, respectively
M_2 = monthly coefficient of natural mortality during $T - t_1$
F = monthly coefficient of fishing mortality in offshore waters during $T - t_r$
Z_T^* = monthly coefficient of total mortality during $T - t_0$
u = exploitation rate in offshore fisheries
e = base of natural logarithms.

The following relations summarize the actual situation:

$$E_1 = N_0 s_1 m = m N_0 e^{-Z_1(t_1 - t_0)}. \quad (1)$$

$$N_1 = N_0 s_1 (1 - m) = (1 - m) N_0 e^{-Z_1(t_1 - t_0)}. \quad (2)$$

$$N_r = N_1 e^{-M_2(t_r - t_1)}. \quad (3)$$

$$C = u N_r = [F/(F + M_2)] \times [1 - e^{-(F + M_2)(T - t_r)}] N_r. \quad (4)$$

$$\begin{aligned} E_2 &= N_r e^{-(F + M_2)(T - t_r)} \\ &= N_1 e^{-M_2(T - t_1) - F(T - t_r)} \\ &= N_1 s_2 = N_1 e^{-Z_2(T - t_1)} \\ &= N_0 s_1 s_2 (1 - m) = N_0 s_1 s_2 - E_1 s_2 \\ &= (1 - m) N_0 e^{-Z_T^*(T - t_0)}. \end{aligned} \quad (5)$$

We have also the general definitions of the mortality coefficients:

$$\begin{aligned} Z_T^* &= (-\ln s_1 s_2)/(t - t_0) \\ &= [Z_1(t_1 - t_0) + Z_2(T - t_1)]/(T - t_0). \end{aligned} \quad (6)$$

$$\begin{aligned} Z_2 &= (-\ln s_2)/(T - t_1) \\ &= [M_2(T - t_1) + F(t - t_r)]/(T - t_1). \end{aligned} \quad (7)$$

$$Z_1 = (-\ln s_1)/(t_1 - t_0). \quad (8)$$

If the smolts are not marked (or otherwise identified) to estimate C and the inshore catch by origin, then the escapement data (E_i) come from hatchery counts or natural spawning areas. If only the inshore catch is identified by origin, a value of E_i is the sum of inshore catch plus "escapement" from inshore fishing to the spawning area in a given year (usually called the "return" or "run" by salmon biologists); it occurs somewhat earlier in time and of course exceeds the value of E_i without inshore catch data available. Thus with inshore catch data available, $Z_1 = M_1$ (the offshore catch of jacks being absent or negligible), Z_2 includes only offshore mortality, and $Z_2 = M_2$ if no offshore fishery exists ($F = C = 0$). The indirect approach was developed mainly from data without offshore fishing mortality but with inshore catches known. If an offshore fishery exists (as on the coho salmon emphasized

here), both C and the inshore catch may be identified by origin (e.g., Worlund, Wahle, and Zimmer, 1969; Johnson, 1970). The possibilities of 1) C known but inshore catch unknown with respect to origin or 2) offshore fishing present but inshore fishing absent are too remote for consideration here. Our two general cases—C known and unknown—are therefore defined and the inshore catch is implicit in E_i. Figure 1 contrasts the extinction of a smolt class with and without offshore fishing.

It is evident from Equations 1-5 that the s_i and m are confounded, and no unique solution exists. This fact and the existence of offshore salmon fisheries led to development of the indirect approach.

ESTIMATING MODELS

Three existing models are reviewed in terms of biomass computations, bias in estimated mortality schedules is considered, and a new estimating scheme is introduced.

Ricker's (1962) Model

This model is based on convincing if indirect evidence (not direct measurements) that most natural mortality during the ocean life of sockeye salmon occurs well before the fish are large enough to be recruited to an offshore fishery. In the context of Equations 6-8 with $F = C = 0$:

$$[M_1(t_1 - t_0) + M_2(t_r - t_1)]/(t_r - t_0) = M_r^* > M_2. \quad (9)$$

In Equation 9, M_r^* is the average monthly rate of natural mortality during $t_r - t_0$, t_0 being the date when (say) half the smolt class enters the sea in 1 year and t_r the date of potential recruitment offshore the next year (say). Parker (1968) demonstrated from direct marking/recovery of pink salmon that natural mortality is highest during the first few weeks of ocean life. To my knowledge, salmon biologists all agree that $M_1 > M_2$.

In the absence of direct measurements, Ricker's model assumes $m = 0$ and $s_2 = 1.0$ on the E_1 jacks (Equations 1 and 5); it treats $E_1 + E_2 = \Sigma E_i$ as a single escapement at time $t = T$, with the following result from Equation 5:

$$\hat{Z}_T^* = \hat{Z}_i = \hat{M}_i = M_{rL}^* = M_{2U} = -\ln(\Sigma E_i/N_0)/(T - t_0). \quad (10)$$

In Equation 10 the caret symbol (^) denotes, an estimate, and the subscripts L and U denote lower and upper limits, respectively.

Because $M_{2U} < \hat{G}$ (the estimated growth coefficient) after $t = t_r$ for most age and maturity groups of commercial size in offshore waters, Ricker (1962) concluded that offshore fishing is biologically wasteful. Those biomass computations assume 100% availability to an offshore fishery, however, and overestimate minimum losses. Ricker (1964) later mentions the availability in connection with the growth-mortality balance in pink and chum salmon and computes weight losses from offshore fishing as a fraction of maximum possible yield (inshore fishing only) for any fixed spawning escapement required for reproduction. Biomass calculations of Parker (1963) and Fredin (1964) also assume full availability. Although the evidence indicates offshore fishing reduces total yield (see also Cleaver, 1969; Henry, 1971, 1972), I emphasize that schedules of growth, mortality, and availability must be combined in order to assess the impact of existing or potential offshore fisheries: management restrictions, fleet size, and bad weather always prevent continuous, complete availability of a stock offshore.

Ricker's model (Equation 10) was applied only to situations where $F = C = 0$. The direction if not the magnitude of bias in the mortality schedule is known from evidence already cited, i.e., $\hat{M}_1 < M_1$ and $\hat{M}_2 > M_2$. When an offshore fishery exists ($F > 0$ in Equation 4) and $Z_1 = M_1$ as noted for coho salmon, Equation 10 may be used as the estimator, $\hat{Z}_T^* = \hat{Z}_1 = \hat{Z}_2$, and the bias defined in terms of known data and the unknown maturity parameter, m. Absolute bias (B) is defined as:

$$B = \text{estimate minus parameter value.} \quad (11)$$

Applying Equations 10 and 11 and the actual values of Z_i from Equations 1 and 5 when C is unknown:

$$B_{(\hat{z}_T^*)} = [T - t_0]^{-1}[-\ln(\Sigma E_i/N_0) + \ln(E_2/N_0) - \ln(1-m)]. \quad (12)$$

$$B_{(\hat{z}_1)} = [T - t_0]^{-1}[-\ln(\Sigma E_i/N_0)] + [t_1 - t_0]^{-1}[\ln(E_1/N_0 - \ln m]. \quad (13)$$

$$B_{(\hat{z}_2)} = [T - t_0]^{-1}[-\ln(E_i/N_0)] + [T - t_1][\ln(E_1/N_0) - \ln(E_2/N_0) - \ln m + \ln(1-m)]. \quad (14)$$

Fredin's (1964) Model

Ricker's model accounts for the magnitude but not for the actual timing of preultimate returns (again, for the magnitude of E_1 in Equations 1-5 here). Fredin (1964) accounts both for magnitude and actual timing. His Model 1 is based on Equation 11 of Parker (1962), who separates relatively high natural mortality on small juveniles plus returning adults—both in inshore waters—from relatively low natural mortality in offshore waters. Parker's results actually derive, however, from his Equations 13 and 14 and utilize data from paired groups of marked smolts. I consider only the information available from a single group of smolts (marked or unmarked).

Thus Model 1 of Fredin (1964) assumes with Ricker (1962) that $Z_T^* = Z_1 = Z_2$; more strictly, the assumption is again that $M_T^* = M_1 = M_2$ because Fredin deals also with data not influenced by offshore fishing. Substituting the assumption in Equation 5 gives an estimator in the relation:

$$E_2/N_0 = e^{-\hat{Z}_T^*(T - t_0)} - (E_1/N_0)e^{-\hat{Z}_T^*(T - t_1)}. \quad (15)$$

Equation 15 is solved by trial and error unless one applies more advanced mathematical properties. Equation 15 differs from Equation 10, so values of $\hat{Z}_T^*$ from the same data obviously will differ. We anticipate less bias in $\hat{Z}_T^*$ from Equation 15 because it accounts for the actual timing of the E_1 jacks. With no explicit definition for $\hat{Z}_T^*$ in Equation 15, however, relations for bias (e.g., Equations 12-14) cannot be written and Equation 15 is later evaluated numerically.

Finally, Fredin's Models 2-4 employ various assumptions to accord with the reality, $Z_1 > Z_2$ (or $M_1 > M_2$). Although no "estimators" in the sense of Equation 15 are available from his Models 2-4 in the indirect approach, it is interesting that calculated maturity schedules were relatively insensitive to the different time distributions of mortality Fredin assumed between his Models 1-4.

Cleaver's (1969) Model

This model was developed specifically to utilize inshore and offshore catch data as known from a landmark study which evaluated the bioeconomic contribution of 1961-64 brood chinook salmon from Columbia River hatcheries (Worlund et al., 1969). Its basic assumption in the context of Equations 1-5 is that $M_2 = 0$ during $T - t_1$. The result is one-sided limits for certain parameters:

$$E_2/(C + E_2) = s_{2U} = e^{-Z_{2L}(t - t_1)}. \quad (16)$$

$$N_{1L} = E_2/s_{2U} = C + E_2. \quad (17)$$

$$m_U = E_1/(E_1 + N_{1L}). \quad (18)$$

As actually applied (Cleaver, 1969; Henry, 1971), the model used data on four escapements to the river (E_i) at ages 2-5 from a given smolt class and data on offshore catches (C_i) of immature plus currently maturing fish at ages 3-5 (unfortunately, marked recoveries in the offshore catch were not sampled for maturity—the catch being taken by small vessels and landed dressed with heads on). Values of E_i and C_i led to rejection of the hypothesis that Z_i was constant for ages 3-5 in offshore waters (certain resulting values of $m_i > 1.0$ implying more mature fish than were present in the total marked populations). Rejection of constant Z_i was deduced (by values of C_i and E_i) to be mainly from variation in F_i. Recalling the basic assumption ($M_i = 0$ during the last year or $M_2 = 0$ here), the authors then examined

the effects on M_i, F_i, and N_i of constant, nontrivial values of natural mortality, M_c, on all recruited age groups ($M_2 > 0$ during $T - t_r$ in our notation). The effect of offshore fishing on hatchery stocks in terms of age-specific escapements to the river was computed (with $F = 0$) for different values of M_c.

The model yields no point estimators and therefore no equations for bias, but is important here for several reasons. First, it utilizes known offshore catch data for the first time in the indirect approach. Second, it emphasizes the need for direct sampling of the offshore catch for maturity by origin (i.e., after marking smolts): the resulting $\hat{m}$ would give nominally unbiased estimates of all parameters but F and M_2 in Equations 1-8. Third, the calculated maturity schedules changed little with changes in M_c after recruitment to offshore fishing (Cleaver, 1969; Henry, 1971); this agreement with Fredin's (1964) result, based on varying the time distribution of natural mortality during all of ocean life for sockeye salmon, evidently is quite general for the 3-4 returns these three authors treated. Finally, reliance of the Cleaver model on one-sided limits (Equations 15-17) led directly to development of the last model.

Limit-Mean Model

Given the foregoing development of the indirect approach, it is natural to consider 1) devising two-sided limits on (say) Z_i or s_i initially and 2) taking for each parameter a value intermediate between these limits as a nontrivial estimator with unknown bias. The opposite and usual procedure in population problems is to derive nominally unbiased estimators and their variances (thus confidence limits) from statistical theory (e.g., the change-in-ratio estimators reported definitively by Paulik and Robson, 1969).

Offshore Catch Unknown

In this case C may be considered "unknown" because either 1) no offshore fishery exists ($Z_i = M_i$) on the target population and we deal actually with the M_i as Ricker (1962) and Fredin (1964) did, or 2) an offshore fishery exists (Z_2 includes $F > 0$ as in our coho salmon) but techniques to evaluate $C > 0$ are not applied. The survival product, $s_1 s_2$, is the target parameter. Limits on the s_i are devised initially with the help of Assumption 1 ($s_{1U} = s_{2L} = s$) and Assumption 2 ($s_{2U} < 1.0$).

Assumption 1 is based on the evidence cited earlier which demonstrates almost incontrovertibly that $M_1 > M_2$. Now $t_1 - t_0$ (Equation 1) is shorter for coho salmon emphasized here—6-9 mo at the outside—than the $T - t_1 \simeq 12$ mo of ocean life remaining in the stocks south of British Columbia (Shapovalov and Taft, 1954; Godfrey, 1965; Drucker, 1972). It is most unlikely that $s_1 > s_2$, however, even when the intensive offshore fishery during $T - t_r \simeq$ 4-5 mo is considered. Assumption 1 gives from Equation 5 the quadratic:

$$s^2 - (E_1/N_0)s - E_2/N_0 = 0 = s_{1U} s_{2L} = (s_1 s_2)_L . \quad (19)$$

Only one root is possible and the solution of Equation 19 is:

$$s = s_{1U} = s_{2L} = 0.5 \left\{E_1/N_0 + [(E_1/N_0)^2 + 4E_2/N_0]^{1/2}\right\} . \quad (20)$$

A reasonable value for Assumption 2 ($s_{2U} < 1.0$) depends on the stock and species. Murphy's (1952) often cited point estimates for coho salmon during their last year of ocean life serve as a guide for later numerical illustration. His estimates are 16-51% for 12 successive smolt classes (1938-49); only three estimates exceed 50%, of which two are 51%. Today's more intensive offshore fishery probably reduces s_2 below that in 1947 to which his estimated maximum, $\hat{s}_2 = 57\%$, applied. [In the next section I use $s_{2U} = 50\%$ but assign no value here. Other estimates and limits warrant mention: 68% by Parker (1962) as a point value grossly averaged for various smolt classes, stocks, and species; 51-80% as point estimates for sockeye salmon by Fredin (1965) and Mathews (1968); and 39-73% as upper limits by Cleaver (1969) for chinook salmon of ages 3-5 taken along with coho salmon

offshore.] Applying Assumption 2 in Equation 5:

$$(E_2 + E_1 s_{2U})/N_0 = s_{1L} s_{2U} = (s_1 s_2)_U . \quad (21)$$

The geometric mean of limits in Equations 19 and 21 is then taken arbitrarily to be the estimator:

$$[(s_1 s_2)_L (s_1 s_2)_U]^{1/2}$$
$$= [\{0.25E_1/N_0 + [0.25(E_1/N_0)^2 + E_2/N_0]^{1/2}\}$$
$$\times (E_2 + E_1 s_{2U})/N_0]^{1/2}$$
$$= \widehat{s_1 s_2} = e^{-\hat{Z}_T^*(T - t_0)}. \quad (22)$$

From Equations 1-3, 5, and 22 we finally have:

$$\hat{s}_2 = (\widehat{s_1 s_2} - E_2/N_0)/(E_1/N_0)$$
$$= e^{-\hat{Z}_2(T - t_1)}. \quad (23)$$

$$\hat{s}_1 = \widehat{s_1 s_2}/\hat{s}_2 = e^{-\hat{Z}_1(t_1 - t_0)}. \quad (24)$$

$$\hat{N}_1 = E_2/\hat{s}_2 . \quad (25)$$

$$\hat{m} = [1 - E_2/E_1 \hat{s}_2]^{-1} = E_1/(E_1 + \hat{N}_1). \quad (26)$$

$$\hat{N}_r = \hat{N}_1 e^{-\hat{Z}_2(t_r - t_1)}. \quad (27)$$

The form of the middle member of Equation 26 (from the ratio of Equation 5 to Equation 1) is included for its practical import: if an offshore catch is identified by origin from any technique whatsoever, then subsampling it for maturity gives an independent estimate ($\hat{m}$) from which s_2 then can be estimated without data on the number of smolts. As noted in connection with Cleaver's model, an independent maturity estimate also gives nominally unbiased estimators for the system when N_0 is known (excluding, again, the subdivision of $\hat{Z}_2$ into $\hat{F}$ and $\hat{M}_2$ as evident from Equation 7 when $t_r \neq t_1$). Even though all estimates contain unknown bias, with no offshore fishery the values of $\hat{Z}_2$ ($=\hat{M}_{2U}$) from Equation 23 and of $\hat{N}_r$ from Equation 27 might prove useful in biomass computations.

Offshore Catch Known

It is not necessary to assume as in the Cleaver model that $M_2 = 0$ during all of $T - t_1$. Assumption 3 is: $M_2 = 0$ during $T - t_r$ when offshore fishing occurs. This gives:

$$N_{rL} = C + E_2 . \quad (28)$$

Solving Equation 20 (as in the case of C known) and inserting the result in Equation 2:

$$N_{1U} = N_0 s_{1U} + E_1 . \quad (29)$$

Assumption 4 is: $F = 0$ during $T - t_r$. By Assumptions 3 and 4 we would observe $C + E_2$ instead of just E_2 at time $t = T$ (similarly, Ricker's model utilizes $E_1 + E_2$ at time $t = T$). Because $C + E_2$ and N_{1U} are both too high, the coefficient, X, relating these artificial population sizes may be defined and used as below:

$$X = -\ln[(C + E_2)/N_{1U}]/(T - t_1). \quad (30)$$

$$N_{rU} = N_{1U} e^{-X(t_r - t_1)}. \quad (31)$$

The geometric mean of limits in Equations 28 and 31 is taken arbitrarily as the estimator:

$$(N_{rL} N_{rU})^{1/2} = \hat{N}_r. \quad (32)$$

We then have from Equations 4 and 5, 7, and 32:

$$C/\hat{N}_r = \hat{u}. \quad (33)$$

$$-\ln(E_2/\hat{N}_r)/(t - t_r) = \widehat{F + M_2} . \quad (34)$$

$$(\hat{u})(\widehat{F + M_2})/[1 - e^{-(\widehat{F + M_2})(T - t_r)}] = \hat{F}. \quad (35)$$

$$(\widehat{F + M_2}) - \hat{F} = \hat{M}_2 . \quad (36)$$

$$[\hat{M}_2(T - t_1) + \hat{F}(T - t_r)]/(T - t_1) = \hat{Z}_2. \quad (37)$$

Given $\hat{Z}_2$ from Equation 37, remaining estimates for the case of C known may be calculated in

the following sequence from relations given previously:

Estimate	*Relation*
$\hat{s}_2$	Equation 7
$\hat{N}_1$	Equation 5
$\hat{m}$	Equation 26
$\hat{s}_1$	Equation 1
$\hat{Z}_1 (= \hat{M}_1)$	Equation 8
$(\widehat{s_1 s_2})$, $\hat{Z}_T^*$	Equation 6
$\hat{M}_T^*$	Equations 9 and 36

Bias

Equations for bias in $\hat{Z}_T^*$ and in other estimates can be written for the cases of C unknown and known. The equations are much longer than for the Ricker model (e.g., Equations 12-14), however, because estimators from the limit-mean model involve so many substitutions. The equations are therefore not written out but the next section gives numerical examples of bias.

NUMERICAL EXAMPLES OF BIAS

Cleaver's model gives no unique estimators as noted earlier, and it is evident that bias from the Ricker and Fredin models cannot be compared fairly with bias from the limit-mean model when offshore fishing is absent. Thus Equations 10 (Ricker model) and 15 (Fredin model) utilize the information that $M_1 \geqslant M_T > M_2$ (Ricker, 1962; Parker, 1968), hence $\hat{M}_T = M_{2U}$ as mentioned with Equation 10. For the limit-mean model without offshore fishing, however, it is interesting to see how relative bias differs among the estimates of mortality or survival, maturity, and abundance.

With offshore fishing present and $C > 0$ unknown, we expect $\hat{Z}_2 - Z_2$ or $\hat{Z}_T^* - Z_T^*$ to be less from the Ricker and Fredin models than $\hat{M}_2 - M_2$ or $\hat{M}_T - M_T$ without offshore fishing. For comparisons with bias from the limit-mean model, I use $\hat{Z}_T^* = \hat{Z}_2$ and the resulting $\hat{s}_2$ as the initial estimate for the Ricker model; $\hat{Z}_T^*$ and $\widehat{s_1 s_2}$, for the Fredin model. With $C > 0$ known I illustrate bias for the limit-mean model only—again to avoid possibly unfair comparisons with the Ricker and Fredin models.

Data published by Johnson (1970) guided selection of certain hypothetical values for input parameters: the resulting values of Ei/N_0 are intermediate between those he reported for small and large smolts (1964 brood), and in that respect may be typical of coho salmon reared at hatcheries on the lower Columbia River. The value of F assigned here is close to that calculated recently by K.A. Henry of the Northwest Fisheries Center, National Marine Fisheries Service, NOAA, and myself for the 1965-66 brood coho salmon reared at a group of Columbia River hatcheries. All time intervals are accurate to within 1.0 mo and probably to within 0.5 mo as actually

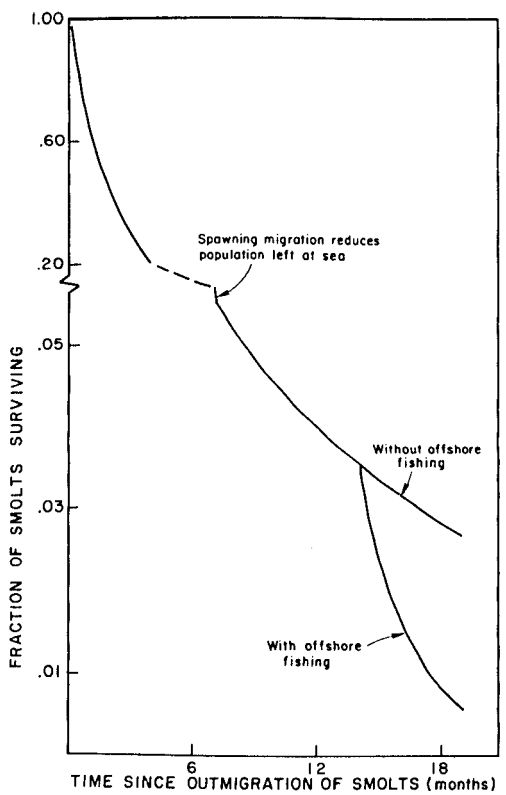

FIGURE 1.—Extinction of a hypothetical smolt class of coho salmon with and without offshore fishing during the last year at sea. Natural mortality is $M_1 = 0.40$/mo during the first $t_1 - t_0 = 7$ mo and 10% of the population matures as jacks; $M_2 = 0.06$/mo during the last $T - t_1 = 12$ mo with or without offshore fishing; and an offshore fishing rate of $F = 0.30$/mo during the last $T - t_r = 5$ mo gives a final population (E_2/N_0, including the inshore catch in both cases) about 22% of that with $F = 0$.

recorded for most coho salmon reared artificially in that watershed. I assume the intervals are known to within 1.0 mo even if $C > 0$ is unknown. Incidentally, all input values are the same as used for Figure 1 to illustrate the extinction of a smolt class with and without offshore fishing.

Table 1 summarizes the hypothetical input values, data, models, assumptions, and estimating schemes as applied to calculate the estimates and values of bias in Table 2. The latter incorporates a few measures to simplify presentation and facilitate comparisons within and between models. Parameter values are repeated from Table 1 and all values are rounded to four places after carrying six in

TABLE 1.—Parameter values, data, models, assumptions, and estimating equations as numbered in text and applied in Table 2 to a hypothetical smolt class of coho salmon.

Parameter value used as input and defined from Equations 1-9		Data	Models, assumptions, and equations
M_1 = 0.40/mo	$t_r - t_0$ = 14 mo	E_1/N_0 = 0.006081	1. With no offshore fishing ($F = C = 0$), apply limit-mean model by assuming $s_{1U} = s_{2L} = s$ (Equation 20) and s_{2U} = 0.50 (Equation 21). Solve Equations 22-27.
M_2 = 0.06/mo	$T - t_1$ = 12 mo	C/N_0 = 0 (for $F = 0$)	
F = 0, 0.30/mo	$T - t_0$ = 19 mo	C/N_0 = 0.025013 (for $F = 0.30$)	2. With offshore fishing but $C > 0$ unknown, assume $m = 0$ and $s_2 = 1.0$ on E_1/N_0, hence $\hat{Z}_i = \hat{Z}_T^*$ for Ricker model (Equation 10): use $\hat{Z}_T^* = \hat{Z}_2$, solve Equation 7 for $\hat{s}_2$, then Equation 5 for $\hat{s}_1 s_2 = E_2/N_0 + (E_1/N_0)\hat{s}_2$, and Equations 24-27. For Fredin model, assume $\hat{Z}_i = \hat{Z}_T^*$ and solve Equations 15 and 22-27. For limit-mean model, proceed as in Item 1 above, noting E_2/N_0 is now smaller.
Z_2 = 0.185000/mo (for $F = 0.30$/mo)	s_1 = 0.060810	E_2/N_0 = 0.022640 (for $F = 0$)	
M_r^* = 0.230000/mo	s_2 = 0.486752 (for $F = 0$)	E_2/N_0 = 0.005944 (for $F = 0.30$)	
M_T^* = 0.185263/mo	s_2 = 0.108609 (for $F = 0.30$)	Time intervals as at left	
Z_T^* = 0.264211/mo (for $F = 0.30$/mo)	$s_1 s_2$ = 0.029599 (for $F = 0$)		3. With offshore fishing and $C > 0$ known, apply limit-mean model by assuming $s_{1U} = s_{2L} = s$ (Equation 20), $M_2 = 0$ during $T - t_r$ (Equation 28) and $F = 0$ during $T - t_r$. Solve Equations 20 and 28-37, then Equations 7, 5, 26, 1, and 6.
m = 0.10	$s_1 s_2$ = 0.006605 (for $F = 0.30$)		
$t_1 - t_0$ = 7 mo	u = 0 (for $F = 0$)		4. Although $\hat{M}_2$, $\hat{F}$ and $\hat{u}$ are solved only as in Item 3 above, solutions for various mortality coefficients are available from Equations 6-9 by applying survival estimates and $F \geq 0$ as appropriate in Items 1-2 (see section on Actual Situation in text).
$t_r - t_1$ = 7 mo	u = 0.695584 (for $F = 0.30$)		
$T - t_r$ = 5 mo	N_1/N_0 = 0.054729		
	N_r/N_0 = 0.035960		

TABLE 2.—Values of parameters, selected estimates, and relative bias in estimates (read each set down in that order), from models as summarized in Table 1. Values are rounded to four places after carrying six in calculations; a dash (—) indicates no estimate.

Offshore fishing	Offshore catch	Model	$s_1 s_2$	s_1	s_2	m	N_1/N_0	N_r/N_0	F	M_2	u
Absent	0	Limit-mean	0.0296	0.0608	0.4868	0.1000	0.0547	0.0360	0.0000	0.0600	0.0000
			0.0286	0.0910	0.3143	0.0668	0.0432	0.0432	—	—	—
			-0.0354	0.4962	-0.3544	-0.3317	0.6060	0.2000	—	—	—
Present	>0, unknown	Ricker	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0063	0.1031	0.0613	0.0590	0.0970	0.0195	—	—	—
			-0.0436	0.6947	-0.4356	-0.4100	0.7719	-0.4588	—	—	—
		Fredin	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0062	0.1536	0.0403	0.0396	0.0475	0.0232	—	—	—
			-0.0629	1.5261	-0.6290	-0.6041	-0.1315	-0.3553	—	—	—
		Limit-mean	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0076	0.0279	0.2726	0.2181	0.0218	0.0102	—	—	—
			0.1510	-0.5414	1.5099	1.1806	-0.6016	-0.7159	—	—	—
Present	>0, known	Limit-mean	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0065	0.0758	0.0852	0.0802	0.0697	0.0383	0.2884	0.0850	0.6526
			-0.0215	0.2468	-0.2152	-0.1979	0.2742	0.0659	-0.0384	0.4165	-0.0617

calculations. Bias is expressed as the ratio, (estimate-parameter value)/parameter value. Values for F, M_2, and u are given for the limit-mean model with $C > 0$ known but values for mortality and bias are not given for the other examples. Values of E_i/N_0 include the inshore catch as if smolts are marked. It should be noted for the last two items that 1) bias in estimated mortality coefficients not shown in Table 1 can be calculated readily from the survival estimates, Equations 6-9, and parameter values in Table 1; and 2) whenever the E_i/N_0 are from spawning areas only, $C > 0$ *and* the inshore catch are unknown but the calculations proceed exactly as in Tables 1 and 2 with lower values of E_i/N_0 which include the effects of inshore fishing (see section on Actual Situation).

Table 2 shows striking contrasts in bias between estimates of different parameters from a given model. The limit-mean model with no offshore fishing, for instance, underestimates the target parameter, s_1s_2, by only 4% but overestimates N_1/N_0 by 61% and N_j/N_0 by 20%. Also in that example, $\hat{s}_2 \simeq 49\%$ is close to the assumed upper limit, $\hat{s}_{2U} = 50\%$ (Table 1); s_2 is 35% too low and $\hat{M}_2 \simeq 0.0965$/mo (calculation from Equation 7 with $F = 0$ not shown) exceeds $M_2 = 0.0600$/mo. Thus $\hat{M}_2 = M_{2U}$ and $(\hat{N}_j/N_0) = (N_j/N_0)_U$ in the example.

With $C > 0$ and unknown, the Ricker model as used here gives smaller bias in estimates of s_1s_2, s_1 and m; the Fredin model as used here, of N_1/N_0 and N_j/N_0; and the limit-mean model, of m. For these and all examples, bias in estimates of s_1s_2, s_2 and m is in the same direction; of the s_i and of s_1 and m, in opposite directions: this result is completely general and is dictated by the fixed relations between these parameters and data (N_0 and E_i) in Equations 1 and 5. Again evident is the wide range of bias values for different parameter estimates within a model: -4% to 77% for the Ricker model, -6% to 153% for the Fredin model, and -72% to 151% for the limit-mean model.

With $C > 0$ known, N_j/N_0 (instead of s_1s_2) is the target parameter (Table 1) and the estimate is 6% too large. In addition to providing the only point estimates shown for F, M_2 and u, the limit-mean model performs better in these examples for the six other parameters than when offshore fishing is absent or when $C > 0$ is unknown. Bias in all six estimates is in the same direction as without offshore fishing and opposite in direction to bias from the limit-mean model with $C > 0$ unknown. Finally, the addition of offshore catch data given the smallest range of bias values for estimates of all six parameters: -22% to 27%.

SUMMARY AND CONCLUSIONS

1. The indirect approach for approximating interval-specific mortality parameters is applicable to multireturn species of salmon when data are available on at least a) the origin-specific number of smolts, b) the origin-specific numbers of adults returning from the sea each year until the smolt class is extinct, and c) the time intervals between seaward migration of smolts and each return. An offshore fishery may or may not exist and the origin-specific catches inshore or offshore may be known (as from marking/recovery experiments) or unknown.

2. Nominally unbiased estimators of mortality (or survival), maturity, and abundance do not exist in this situation because different combinations of mortality and maturity schedules can generate the same set of observable data. In connection with biomass computations, Parker (1962), Ricker (1962), Fredin (1964), and Cleaver (1969) developed models for approximating interval-specific mortality. The latter three models are reviewed in connection with the problem of bias and a new model is introduced. Observable data are assumed to be accurate in order to focus attention on bias from the models themselves. To sharpen the focus, the problem is reduced to the case of two returns and the pertinent portion of the life history of coho salmon south of British Columbia is emphasized.

3. Equations 1-9 and Figure 1 summarize the actual situation and include the situation with no offshore fishing ($F = C = 0$) to help relate the case of two returns to models developed mainly with data from more returns and, except for Cleaver's model, with natural but

not fishing mortality operating in offshore waters.

4. Mortality estimates from the Ricker (1962) and Fredin (1964) models (Equations 10 and 15, respectively) both utilize for biomass computations the independent evidence that natural mortality coefficients are highest in small, "prerecruit" stages of ocean life and lowest in later stages when fish are large enough to be exploited in offshore as distinct from inshore waters; both models give an average rate of natural mortality which is an upper limit for "prerecruits" and a lower limit for "postrecruits" (quotation marks above indicate these models were developed and applied to hypothetical as distinct from actual offshore fisheries). Ricker's model treats preultimate returns or spawning escapements as if none of those fish mature and all survive until the end of ocean life as observed with the last actual return. Equations 12-14 express absolute bias in mortality estimates from the Ricker model in terms of the unknown maturity parameter and observable data without offshore fishing or with an offshore catch unknown. Fredin's model accounts for actual timing of all returns and therefore approximates more closely than Ricker's model the actual mortality coefficients for any set of data taken when no fishery operates offshore. Fredin's model is solved by trial and error so explicit bias equations cannot be written. When offshore fishing occurs but the origin-specific offshore catch is unknown, it is reasonable to expect from both models less (unknown) bias in mortality coefficients than without offshore fishing; i.e., to use calculated values along with the fixed relations in Equations 1 and 5 as estimates of actual mortality rather than as limits for natural mortality.

5. Biomass computations of Ricker (1962), Parker (1963), and Fredin (1964) overestimate minimum losses in yield. Although the evidence indicates growth typically exceeds mortality in potential and actual postrecruits, the implicit assumption of full availability is in error: management restrictions, fleet size, and bad weather always prevent continuous, complete availability of a stock in offshore waters.

6. Cleaver's (1969) model is the first actually to utilize known offshore catches (but see Equation 7 of Ricker, 1964). Its basic assumption is that natural mortality is absent during the last year of ocean life; the assumption leads to certain one-sided limits, e.g., to the minimum population about a year before the last return (Equations 16-18). The model does not give unique estimators or bias equations but is the basis for the limit-mean model.

7. The limit-mean model with offshore fishing absent or offshore catch unknown assumes a) the survival between times of outmigration and of the first return does not exceed survival between times of the first and second returns (Equations 19-20) and b) the latter survival is less than 1.0 (Equation 21). The result is lower and upper limits on the product of these two survival fractions. The geometric mean of limits is taken arbitrarily as an estimator of the product (Equation 22), then the fixed relations among parameters and observable data (Equations 1-5) give estimates of the survival, maturity, and abundance schedules (Equations 23-27). With an offshore catch known by origin, the first assumption above (Equation 20) gives an upper limit for the number of immatures at sea near the time of the first return (Equations 2 and 29). The additional assumptions of no fishing or natural mortality after recruitment offshore gives lower and upper limits for the number recruited (Equations 28 and 31). The geometric mean is taken arbitrarily as an estimator (Equation 32) to give estimates of the exploitation rate, fishing, and natural mortality coefficients (Equations 33-37). Other estimates for survival, mortality, maturity, and abundance are then available. The limit-mean model involves many substitutions and the cumbersome bias equations are not given.

8. Numerical examples of relative bias for a hypothetical smolt class of coho salmon are explained and presented in Tables 1 and 2. Values are chosen for close agreement with data and estimates for coho salmon actually reared at Columbia River hatcheries. The four examples in Table 2 show a wide range of bias in estimates of different parameters from the same model, and also for the same parameter as estimated from different models in

different situations. Overall performance is best with these hypothetical values for the limit-mean model with offshore catch known, and this model also provides estimates of fishing and natural mortality rates offshore.

9. Direct sampling for maturity in offshore catches, when known by origin, would give nominally unbiased estimators for all parameters but those mentioned last in Item 8 above, and further would permit estimation of survival or mortality during about the last year at sea *without* data on the number of smolts. Although Atlantic salmon caught off Greenland are nearly all immature (Horsted, 1971), it may be recommended for coho and chinook salmon caught off western North America that a) maturity be monitored systematically by time and area and b) research be intensified on determining catch by origin independently of marking smolts (e.g., separating hatchery fish from wild fish by scale patterns).

ACKNOWLEDGMENTS

For their comments on earlier drafts of the manuscript I thank J. A. Gulland of the Food and Agriculture Organization of the United Nations, D. G. Chapman of the University of Washington, and K. A. Henry, G. Hirschhorn, and D. D. Worlund of the National Marine Fisheries Service. I am grateful to the editorial referees whose suggestions led to the present version.

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THE DISTRIBUTION OF SUMMER FLOUNDER, *PARALICHTHYS DENTATUS*, EGGS AND LARVAE ON THE CONTINENTAL SHELF BETWEEN CAPE COD AND CAPE LOOKOUT, 1965-66

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ABSTRACT

Eggs and larvae of summer flounder, *Paralichthys dentatus*, were collected with Gulf V plankton nets between Cape Cod, Mass., and Cape Lookout, N.C., during a 1-year survey of continental shelf waters. The most productive spawning grounds were located off New York and New Jersey. Spawning began in northern parts of the survey area, progressed southward with the season, and ended off Cape Lookout. We collected eggs north of Chesapeake Bay from September to December and south of the Bay from November to February, and larvae north of Chesapeake Bay from September to February and south of the Bay from November to May. Most spawning occurred at temperatures between 12° and 19°C, but the pelagic eggs were caught at mean temperatures from 9.1° to 22.9°C, and the larvae from 0° to 23.1°C.

Fishery scientists generally agree that the shallow, protected waters of bays, rivers, and sounds along our eastern seaboard provide essential habitat for many marine fishes. The occurrence of juvenile fishes in estuaries has led biologists to conclude that a major role of the estuarine zone is its function as a sanctuary or nursery ground for young fishes, many of which are spawned at sea. In 1965, the Sandy Hook Laboratory at Highlands, N.J., began a study to elucidate the degree of estuarine dependence of young fishes by studying their distributions from egg through juvenile stages. Impetus for the study resulted from the accelerated degradation of the estuarine zone and a concurrent decline in some of our most valuable coastal fishery yields.

We began our program with a 1-year survey of the continental shelf between Cape Cod, Mass., and Cape Lookout, N.C., to determine the duration of spawning, define the areas of spawning, and trace the dispersal of pelagic eggs and larvae of all marine sport fishes that we caught. This report describes the offshore distribution of eggs and larvae of the summer flounder, *Paralichthys dentatus*, a highly prized catch for both sport and commercial fishermen.

The life history of summer flounder is understood only in broad outline. The geographic range of the species encompasses estuarine and continental shelf waters from Maine to Florida (Gutherz, 1967). Within this range, the species' population structure remains to be determined. Migratory habits of summer flounder in the Middle Atlantic Bight have been outlined from seasonal changes in the location of commercial and sport catches. From the returns of tagged fish, Poole (1962) and Murawski (1970) added support to the general concept that yearly movements of summer flounder are not extensive. The adults migrate shoreward in spring from wintering grounds near the edge of the continental shelf. They summer in shallow coastal waters and adjacent estuaries and, in the fall, again move offshore. Both Poole and Murawski noted the strong tendency of adult fish to return in subsequent years to the area where they had been tagged. Shortly after the adults begin their fall migration, they begin to spawn, presumably on or near the bottom. Eggs and early larval stages have been found only at sea, and young-of-the-year juveniles only in or near the mouths of estuaries.

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Manuscript accepted October 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

Because young-of-the-year have not been captured at sea, biologists have presumed they cannot survive there and, at an early stage of development, must seek an estuarine habitat. This presumption has been challenged, but not systematically tested.

THE CRUISE SCHEDULE

Eight cruises were completed from December 1965 through December 1966. During each cruise, we planned to sample at 92 stations situated along 14 transects. Transects originated as nearshore as water depths would allow the RV *Dolphin* to enter, and extended seaward to depths near or beyond the 183-m depth contour (Figure 1).

The sequence for sampling transects varied, depending primarily on weather (Table 1). On our first cruise in December, inclement weather forced us to omit the two northernmost transects. We sampled at four additional stations

TABLE 1.—Cruise schedule, sequence of sampling transects, and number of stations occupied during RV *Dolphin* ichthyoplankton survey, 1965-66. Sampling interruptions in excess of 48 hr are shown, whether or not the sampling sequence was affected.

Cruise	Sampling dates	Transect or station sampling sequence	Number of stations
D-65-4	3-15 Dec. 1965	C to P	80
D-66-1	25-26 Jan. 1966	B, A-1 and -2	86
	2- 9 Feb. 1966	C to P	
D-66-3	6- 9 Apr. 1966	A to D	92
	13-16 Apr. 1966	E-1 and -2, F to J-7 to -3	
	19-21 Apr. 1966	J-1 and -2 to P	
	22 Apr. 1966	E-8 to -3	
D-66-5	12-25 May 1966	A to P	92
D-66-7	17-20 June 1966	A to D	92
	22-25 June 1966	L to P	
	25-29 June 1966	K to E	
D-66-10	5-10 Aug. 1966	A to F	92
	21-26 Aug. 1966	G to P	
D-66-11	13-14 Sept. 1966	A and B (except B-3)	30
	17-18 Sept. 1966	B-3, C and D	
D-66-12	28 Sept.-6 Oct. 1966	M, N, L to F, E-1 to -3, D-1 to -3	92
	11-15 Oct. 1966	E-4 to -8, F-8 to -4, C to A	
	20 Oct. 1966	P	
D-66-14	9-14 Nov. 1966	E to J (except F-7, E-8)	92
	15-19 Nov. 1966	P to K, F-7, E-8	
	1- 4 Dec. 1966	D to A	

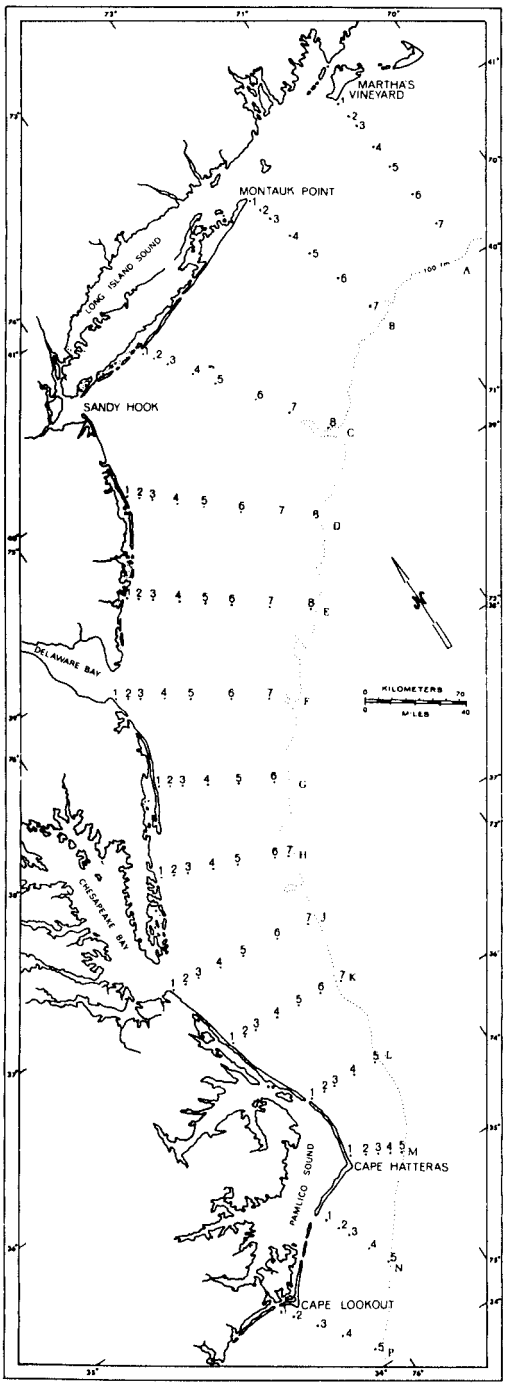

FIGURE 1.—Transects and collecting stations of plankton survey conducted from December 1965 through December 1966.

(designated transect X) off the outer banks of North Carolina. On our second cruise, inclement weather forced us to omit four stations on the northernmost transect, and an outflow of ice from Delaware Bay prevented sampling at the inboard station off Cape Henlopen. We occupied all stations during cruises in April, May, June, and August. In September, adverse weather resulted in a 2-day interruption shortly after we began sampling, and gear problems required a second unscheduled port call soon thereafter. Because of these delays, we rescheduled the cruise after completing only the four northern transects. Although bad weather also interrupted the final two cruises, we occupied all stations.

SAMPLING METHODS

We used Gulf V high speed nets (Arnold, 1959) to collect plankton. These had 0.33-mm Monel[2] wire netting with 12 meshes/cm and a mesh aperture of 0.52 mm.

To assure reaching below the thermocline, or that part of the water column encompassing most pelagic eggs and larvae, we sampled to a maximum depth of 33 m, using two Gulf V nets. One net, hereafter referred to as net no. 1, fished at 3-m depth intervals from surface to 15 m; the other, net no. 2, fished at 3-m depth intervals from 18 to 33 m. We sampled at each depth interval for 5 min. Tows lasted 30 min. In depths less than 33 m, we altered the sampling pattern of net no. 2 by decreasing the number of sampling depth intervals and increasing the towing time at each interval to 10 or to 15 min. Sampling depths for net no. 1 were similarly adjusted in depths less than 15 m (Figure 2). The RV *Dolphin* usually traversed 4.6 km/tow, traveling at a constant engine speed. We preserved plankton samples in 5% buffered Formalin.

Catch per standard tow was used as a measure of relative abundance for eggs and larvae. A standard tow consisted of one or both nets fishing for 5 min at each of the six depth intervals within its vertical sampling range (see Figure 2). The catches were adjusted to equalize sampling effort at all depth levels when either net was limited to sampling at less than six intervals. For example, when only three intervals were sampled during the 30-min tow, the catch was halved. When two intervals were fished, it was reduced by two-thirds. The adjusted catch of net no. 2 was added to that of net no. 1 at stations where both nets fished simultaneously. All catches of eggs and larvae discussed herein are adjusted.

We recorded vertical temperature and salinity data at each station (Clark et al., 1969). Surface temperature was measured with a stem thermometer, subsurface temperature with a mechanical bathythermograph, and salinity with an induction salinometer. Salinity data were recorded at 5-m depth intervals to a maximum depth of 40 m.

Fish eggs and larvae were separated from the plankton collections by microscopically examining aliquots of a sample placed in a gridded Petri dish. Methods employed to check sorting accuracy and measured plankton volumes are described by Clark et al. (1969).

Larvae on which the caudal rays had not formed were measured from the tip of the snout to the tip of the notochord. More developed specimens were measured from the tip of the snout to the base of the median caudal rays. Specimens larger than 9 mm were considered postlarvae because they were laterally flattened. Marginal fin ray counts fell within the adult range and migration of the right eye was underway on specimens over 10 mm.

THE SEASONAL DISTRIBUTION OF EGGS

We sampled during parts of two different spawning seasons, for our survey started too late in 1965 and ended too early in 1966 to determine the beginning of the one season or the end of the other. In spite of the possibility of year-to-year variations in the onset and duration of spawning, data for the 2 years were combined and treated as a single complete season.

Although the summer flounder's spawning

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

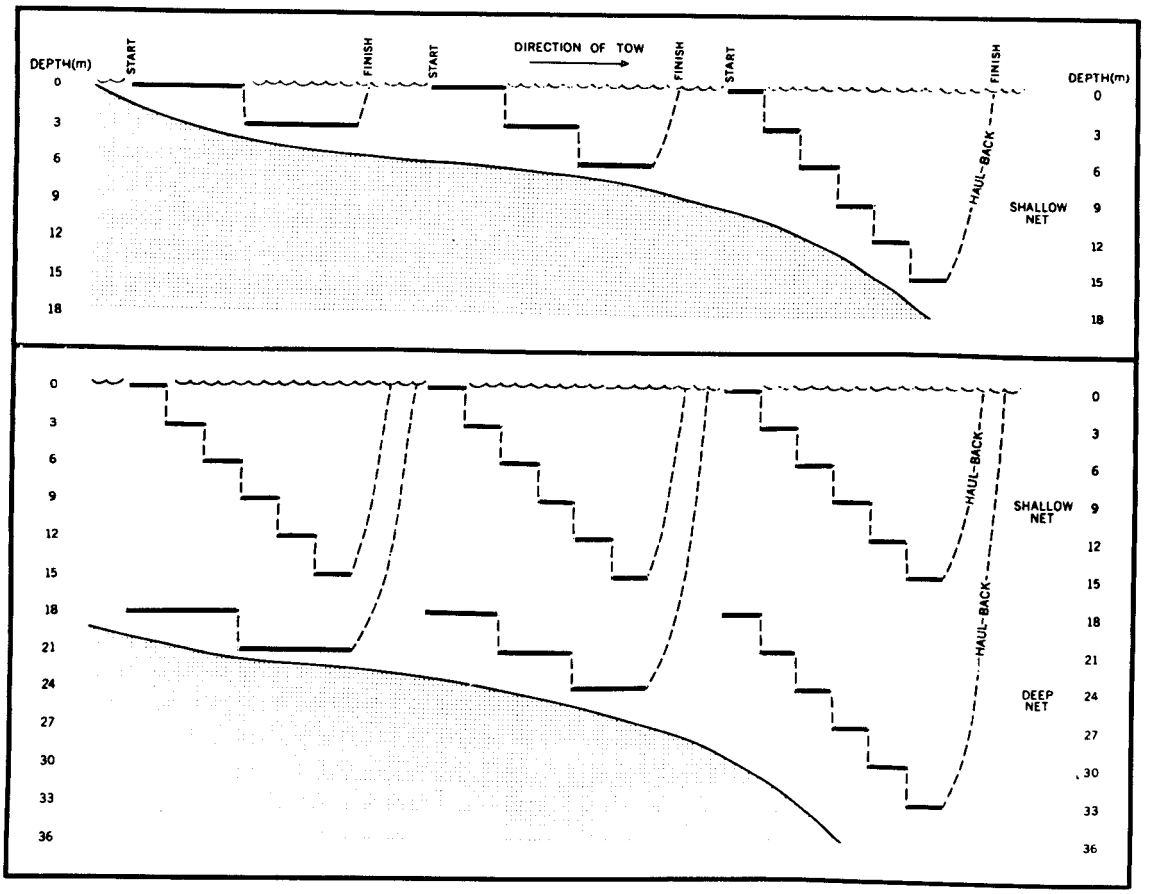

FIGURE 2.—Vertical sampling profiles for 30-min tows with Gulf V nets. The number of sampling depths in the step-oblique pattern was determined by depth of water. Sampling profiles on the right side of the figure were considered standard tows.

season usually peaks in the fall along the Middle Atlantic Bight, data are lacking on the duration of the season. Herman (1963) reported the earliest seasonal occurrence of young from larvae captured in Narragansett Bay, R.I., in July 1957. He concluded that spawning had commenced during the summer. Gravid females taken as late as mid-April off Nantucket Island led Bigelow and Schroeder (1953:267-270) to conclude that spawning occurred through spring. During our survey, it appears that some spawning may have lingered into early spring in waters off North Carolina, but not as far north as New England. Nor can I find other data to substantiate that spawning normally begins as early as July or ends as late as April off southern New England.

After studying gonads from fishes landed by the winter trawl fishery, Eldridge (1962) concluded that most spawning off the Virginia Capes occurred in November. Eldridge's findings agree closely with those of Murawski (1965), who observed a sharp rise in maturation of gonads in fish caught off New Jersey during the first half of October and running ripe females from late September through early November. Our results generally agree with these authors. In 1966, spawning evidently began in the northern part of the Middle Atlantic Bight in early September, progressed southward with the season, and ended in February off Cape Lookout. The season reached its peak in October north of Chesapeake Bay and in November south of the Bay.

We first caught eggs in mid-September. Most of these were 9 to 19 km off western Long Island where depths were 22 to 31 m (Figure 3). Because this September cruise was cancelled after sampling only the four northernmost transects, the data do not show the full distribution of eggs within the area we normally surveyed. Results of the following cruise, however, suggest that spawning in the first half of September was limited to the area between southern New England and New Jersey.

All eggs caught in October were at stations north of Chesapeake Bay, most of them off New Jersey and Delaware. Stations 22 to 61 km offshore over depths of 20 to 48 m accounted for 96% of the catch. No eggs were caught south of Chesapeake Bay (Figure 4).

In November, the area of spawning had moved southward, for concentrations of eggs were now 65 km east of Assateague Island, Md., and 9 to 19 km off the outer banks of North Carolina. Ten days elapsed from the time we started sampling off Atlantic City until we were able to sample the four northern transects. During that period, spawning apparently ended off New York and southern New England, for we caught only one egg in that sector (Figure 5). Considering the substantial number of larvae taken on the four northern transects, it seems probable that the distribution of eggs at the outset of the cruise in November extended further north than shown in Figure 5, perhaps as far as Martha's Vineyard or beyond.

By December (1965), spawning within most of the survey area had ended, for we found eggs only at stations in the southern portion (Figure 6). The following cruise in late January and early February proved even less productive. We caught four eggs at the most southerly station off Cape Lookout. Eggs were absent from samples taken on cruises in April, May, June, and August.

VERTICAL DISTRIBUTION OF EGGS

Our sampling program was not designed to study the vertical distribution of eggs and larvae. The patterns of distribution, however, suggest that summer flounder eggs drift largely within the shallow depths sampled by net no. 1. At stations where both nets fished, net no. 1 caught 75% of the eggs and net no. 2 probably caught some of the remaining 25% in the upper levels during setting and retrieval. This tendency of summer flounder eggs to float near the surface was observed during a rearing experiment set up to obtain early larval stages. All artificially fertilized eggs floated in water collected from just beneath the surface, or in the least dense part of the water column, at the site where gravid adults presumably would have spawned soon thereafter. By floating near or at the surface, the eggs were available to our nets for only a part of the 30-min tow. A short incubation period, 72 to 75 hr after fertilization at an average water temperature of 17.5°C (Smith and Fahay, 1970), may also affect the availability of eggs by limiting their dispersion away from the spawning site. Thus, the buoyancy of eggs and their relatively short incubation period probably account for our nets catching fewer eggs than larvae.

THE SEASONAL DISTRIBUTION OF LARVAE

Judging from the changes in the number of eggs in our samples, summer flounder spawned north of Chesapeake Bay from September to December and south of the Bay from November to February. As expected, larvae were taken at the same time as the eggs, and also over a longer period. We caught larvae in the northern half of the survey area from September to February, and in the southern half from November to May.

Larvae as well as eggs of the 1966 brood appeared first in our collections of mid-September, when we sampled only the four northernmost transects (Figure 3). The small number and size of larvae collected then, the more widespread distribution of eggs than larvae, and the absence of both in June and August all indicate that spawning had recently started, probably during the first week of September. The October cruise produced the largest catch of summer flounder larvae of the survey. All larvae were caught north of Chesa-

peake Bay, some as far as 111 km offshore, but most from 22 to 83 km offshore over depths of 31 to 57 m. Although the distribution of larvae was continuous, distinct concentrations occurred off Martha's Vineyard, off Long Island and northern New Jersey, and off Delaware Bay (Figure 4). By November, the distribution of larvae had spread throughout the survey area, apparently with a center of concentration 56 km off New Jersey, where water depths ranged from 22 to 53 m (Figure 5).

In December (1965), we found concentrations of larvae off New Jersey and North Carolina. The area of greatest abundance was 37 to 83 km off the New Jersey coast, at about the same location where we found larvae most abundant during the November (1966) cruise (Figure 6). By the end of January, the number of larvae and the area of their distribution had diminished, most of them being south of Cape Hatteras (Figure 7). In April, we found larvae only in the southern extreme of the survey area (Figure 8). In May, we caught seven larvae which probably represented remnants of late spawning off the outer banks of North Carolina, since we found no more during the next two cruises.

The seasonal progression of spawning from north to south, evident from the distribution of eggs and larvae, was further substantiated by the progressively smaller larvae that were caught as we sampled southward on late fall and winter cruises. In September, the newly spawned larvae were confined to a small area off western Long Island and northern New Jersey. By October, larvae were distributed over almost the entire northern half of the survey area. In November, when they were spread throughout the survey area, those south of Delaware Bay were smaller than those north of the Bay. In December (1965), larvae generally were largest north of Delaware Bay, and progressively smaller at more southerly stations, the smallest occurring south of Cape Hatteras. Those south of Cape Hatteras in February were small and newly hatched, while most of those to the north had started to metamorphose. By April, when larvae were found only south of Cape Hatteras, most had started to metamorphose (Appendix Table 1).

THE RELATION OF SPAWNING TO WATER TEMPERATURES

Spawning occurred principally within a temperature range of 7°C during the year of our survey. Over the whole season, we caught 77% of the eggs where bottom temperatures were between 12° and 19°C. This percentage would probably be higher if some dispersion by coastal circulation were taken into account. Miller (1952)[3] found surface water drifting from 6 to 37 km/day within the survey area. A minimal drift of 9 km daily would be sufficient to place the origin of 98% of the eggs we caught in bottom waters between 12° and 19°C. There was no evidence that salinity had any effect on the distribution of eggs or larvae.

At the beginning of the season, in September, the summer thermocline remained intact. Water temperatures at the surface and bottom differed by as much as 14.6°C. The greatest concentration of eggs was located off Long Island, shoreward of the cold mass of bottom water that persists during the summer months from New York to as far south as Chesapeake Bay (Bigelow, 1933). Where eggs were most abundant at the surface, bottom temperatures were between 18° and 19°C (Figure 9). The few eggs caught seaward of the cold bottom water might have been spawned by a group of fish that either had migrated from northerly waters around the outer edge of the cold bottom water or by a group that remained in deep water throughout the year. By October, the thermocline was less pronounced than in September, and most of the eggs occurred over bottom temperatures between 13° and 17°C (Figure 9). As in September, the seaward distribution of eggs appeared restricted by the cold mass of bottom water which remained intact off Long Island and New Jersey. It seems certain, therefore, that the inshore edge of the cold water delimited the seaward extent of the fall migration of spawning fish.

[3] Miller, A. R. 1952. A pattern of surface coastal circulation inferred from surface salinity-temperature data and drift bottle recoveries. Woods Hole Oceanogr. Inst. Ref. No. 52-58, 14 p. (Unpubl. manuscr.)

By so doing, the mass of cold water may play a major role in the success or failure of spawning off the Middle Atlantic States, depending on the time when it becomes mixed with surrounding water by late summer and fall storms.

By November, water was mixed and temperatures uniform from surface to bottom, except at those stations on the seaward end of transects. Eggs occurred in greatest numbers off northern Virginia, over 11.7°C bottom water, and off the outer banks of North Carolina, where the bottom temperature was 15.0°C. The northern limit of the principal area of distribution was along the transect off Great Egg Inlet, N.J., where we started the cruise. At that time, bottom temperatures exceeded 12°C (Figure 10). By the time we began sampling the four northernmost transects (see Table 1), bottom temperatures had fallen below 12°C and spawning had practically ended in the northern part of the survey area. It continued in the southern part, where in December (1965) we caught eggs over bottom temperatures of 12° to 19°C (Figure 10). By late January, bottom temperatures were less than 12°C at all but five stations, and we caught eggs only at the most southerly one, where the bottom temperature was 17.8°C.

Presuming that spawing occurs on the bottom, it is limited to a narrow temperature range. The eggs, however, which subsequently rise, are evidently more temperature tolerant than their spawning parents, for we found them at water temperatures as cold as 9.1°C and as warm as 22.9°C, though mostly from 13.0° to 17.9°C. Judging from the hatching time for artificially fertilized eggs, reported by Smith and Fahay (1970), those taken offshore in 9.1°C water required about 142 hr to hatch; those taken at 22.9°C, only 56 hr. Most of the eggs collected during the survey would have hatched 74 to 94 hr after fertilization. Although larvae occurred over a still wider mean temperature range than eggs (0° to 23.1°C), they were most abundant at mean temperatures of 9.0° to 17.9°C (Appendix Table 2). Other workers also have captured young summer flounder over a wide range of both temperature and salinity. Williams and Deubler (1968) caught postlarvae in Pamlico Sound water ranging in temperature from 2° to 22°C and in salinity 0.02 to 35.0‰. Tagatz and Dudley (1961) caught young of 11 to 180 mm in length at temperatures between 9.4° and 31.2°C and salinities between 8.7 and 37.0‰, and Deubler and White (1962) kept post larvae for 33 days in water with a salinity of 40‰.

GEOGRAPHICAL SPAWNING AREAS AND SPAWNING POPULATIONS

Although summer flounder occur occasionally as far north as Maine and as far south as Florida, fishing records indicate that they are most abundant from Cape Cod to Cape Lookout. Thus, it is doubtful that much spawning occurred north or east of our northernmost transect. The most important spawning grounds within the survey area were off New York and New Jersey. We caught the greatest numbers of eggs within 46 km of shore. Larvae were most abundant 22 to 83 km offshore. In some instances, we caught the young stages at our most seaward stations, but, considering the known offshore range of adults, it is unlikely that significant numbers of eggs or larvae occurred beyond our outermost stations. The numbers of eggs and larvae were relatively low off Virginia, increased off the outer banks of North Carolina, and declined off Cape Lookout (Appendix Table 3). Cape Lookout, however, should not be considered the southern limit of spawning, for we caught larvae as far south as Daytona Beach, Fla., in January 1968. Plankton collections south of Cape Lookout in 1953, 1954, and 1967[4] contained summer flounder larvae (Figure 11). More sampling is needed to assess the importance of spawning grounds south of Cape Lookout.

Although research on summer flounder has been sporadic and limited in geographic scope, there is mounting evidence that separate spawning populations exist. The occurrence of distinct areas of egg and larvae abundance at different times of the spawning season; the tag returns of Poole (1962) and Murawski (1970), indicating a general inshore-offshore

[4] Unpublished data on file at Middle Atlantic Coastal Fisheries Center, National Marine Fisheries Service, Highlands, N.J. 07732.

movement and a strong tendency of fish to return in subsequent summers to the same area; the short time between departure from the inshore summering grounds and the onset of spawning, which would limit prespawning movement; and, finally, the differences in gill raker and anal ray counts between summer flounder collected at Chesapeake Bay and at Beaufort, N.C. (Ginsburg, 1952) strongly suggest the likelihood of different populations. Judging from our survey in 1965-66, one segment of the species appeared to spawn principally north of Delaware Bay, a second from Virginia to Cape Hatteras, and a third south of Cape Hatteras. The biological evidence is supported by commercial landings. The catch from ports between Maryland and Massachusetts declined by 66% from 1960 through 1967. During the same period, Virginia landings fluctuated but a decline was not evident. In North Carolina, landings increased. If effort remained relatively constant along the coast, it is unlikely that such trends would have occurred if the various coastal fisheries depended on one population.

LARVAL MOVEMENTS

The net transport of water along the Middle Atlantic Bight is generally southerly to southwesterly in the fall (Bumpus and Lauzier, 1965; Norcross and Stanley, 1967). Although pelagic eggs and early larval stages drift in sea currents, it appears that the summer flounder larvae we collected had not drifted far from the spawning areas. Larvae of all stages of development caught off New York and New Jersey, and off North Carolina, were taken in the general vicinity of the eggs (Figures 12 to 16). Although there is no evidence to relate the movement of young summer flounder to known current patterns, early juvenile stages have been captured only in estuaries, suggesting that the young fish are estuarine dependent. Their tolerance to wide ranging temperatures and salinities further suggests that they are physiologically adapted to utilize the estuarine zone for nursery grounds. Judging from our collections and the size of specimens collected at inlets along the coast, the shoreward migration begins after the young fish metamorphose and become capable swimmers.

Most of the postlarvae in our collections were caught at night. Of the 114 specimens larger than 9 mm, 91 (80%) were taken after dark. Additional sampling with modified collecting gear should confirm whether the significantly greater nighttime catch resulted from net avoidance during the day or from diel movements of the metamorphosing young fish. Arnold (1969) noted that metamorphosing postlarvae of the European plaice, *Pleuronectes platessa*, may go quickly to the bottom when not actively swimming. Pearcy (1962) made a similar observation on winter flounder, *Pseudopleuronectes americanus*, considering both the small and large larvae to be partially benthic animals. If postlarval summer flounder behave similarly to the above postlarval flatfishes, then perhaps day-night differences in the catch may reflect periods of low and high activity rather than net avoidance. In this case, the postlarvae would be largely unavailable to our nets when not swimming, which they might do mostly at night. If, on the other hand, the difference between day and night catches reflects net avoidance, towing speeds in excess of 9.3 km/hr are required to adequately sample postlarval summer flounder when using nets with a mouth opening comparable to a Gulf V.

ACKNOWLEDGMENTS

I thank L. A. Walford for his many helpful suggestions during the course of the survey, and for critically reviewing the manuscript; and Elmer J. Gutherz, National Marine Fisheries Service, Pascagoula, Miss., for providing the additional data on larval summer flounder catches south of Cape Lookout.

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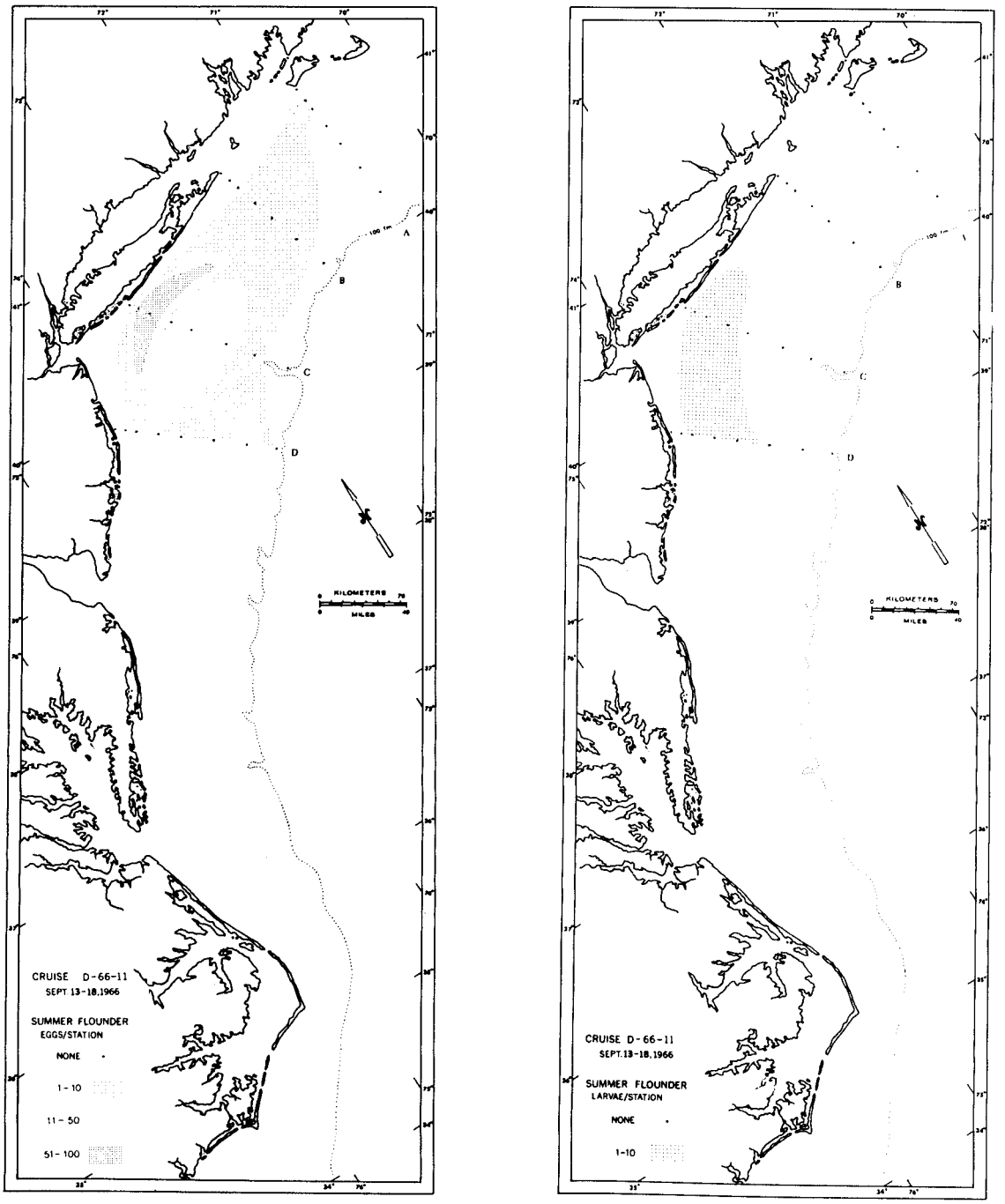

FIGURE 3.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-66-11.

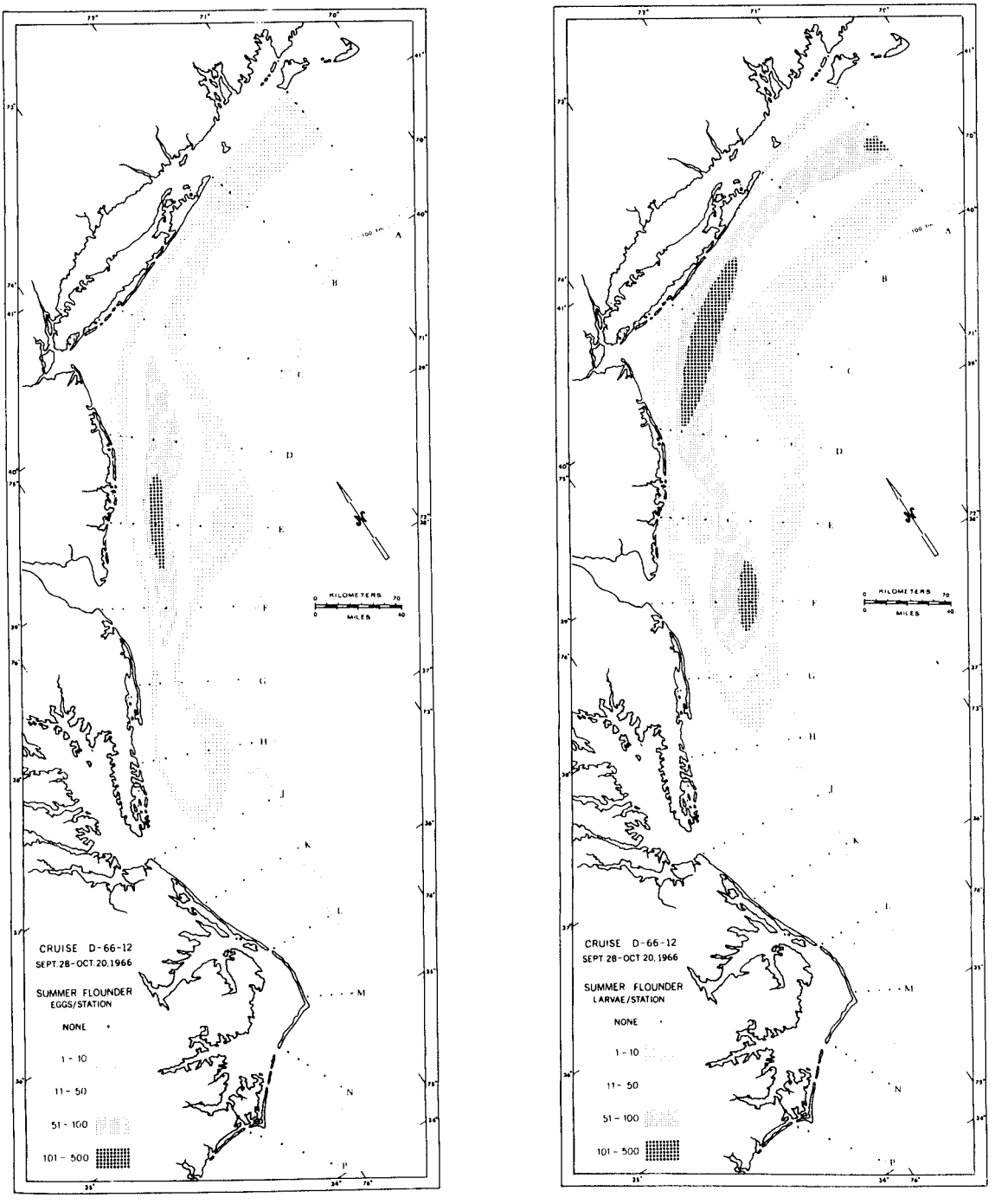

FIGURE 4.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-66-12.

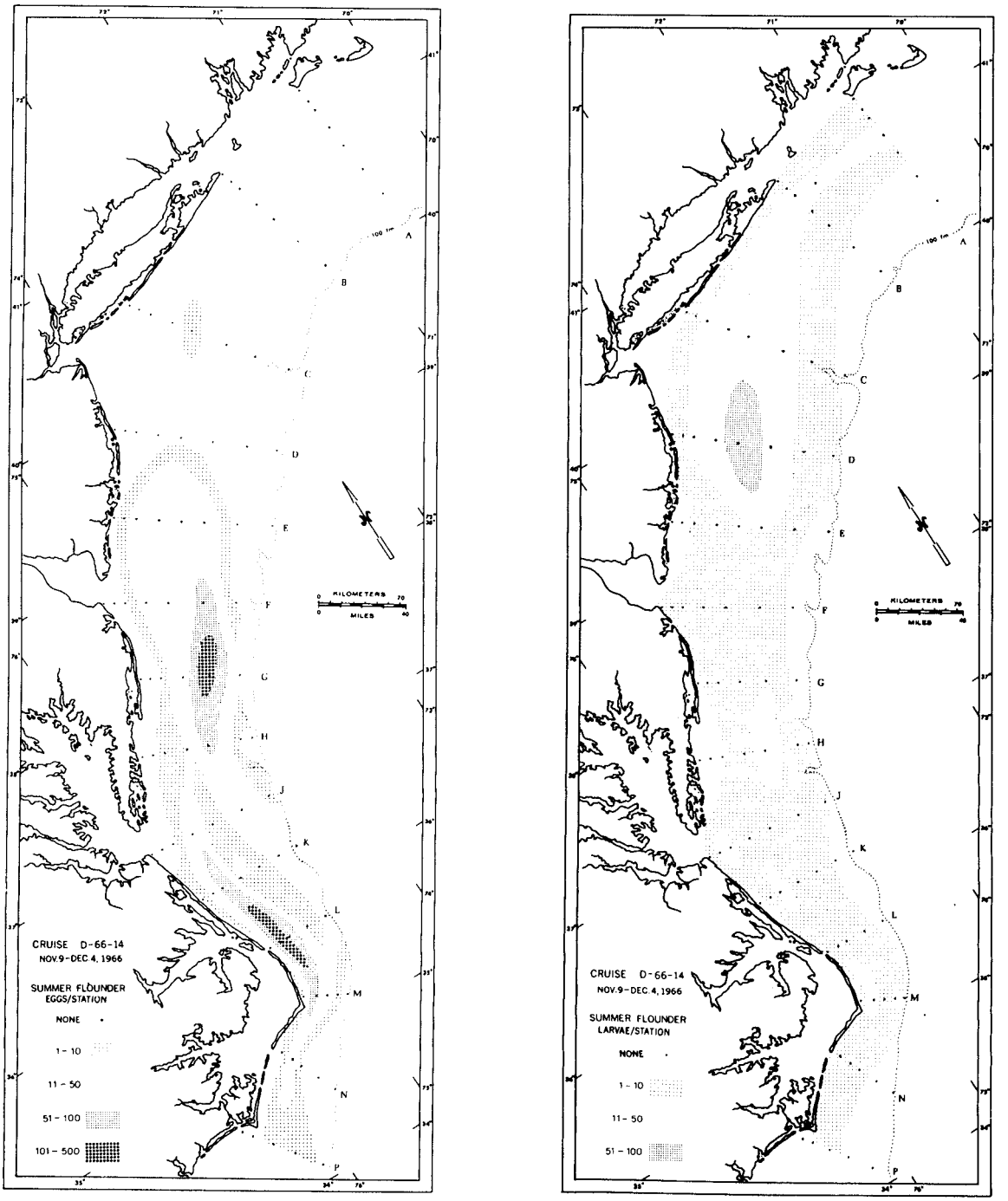

FIGURE 5.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-66-14.

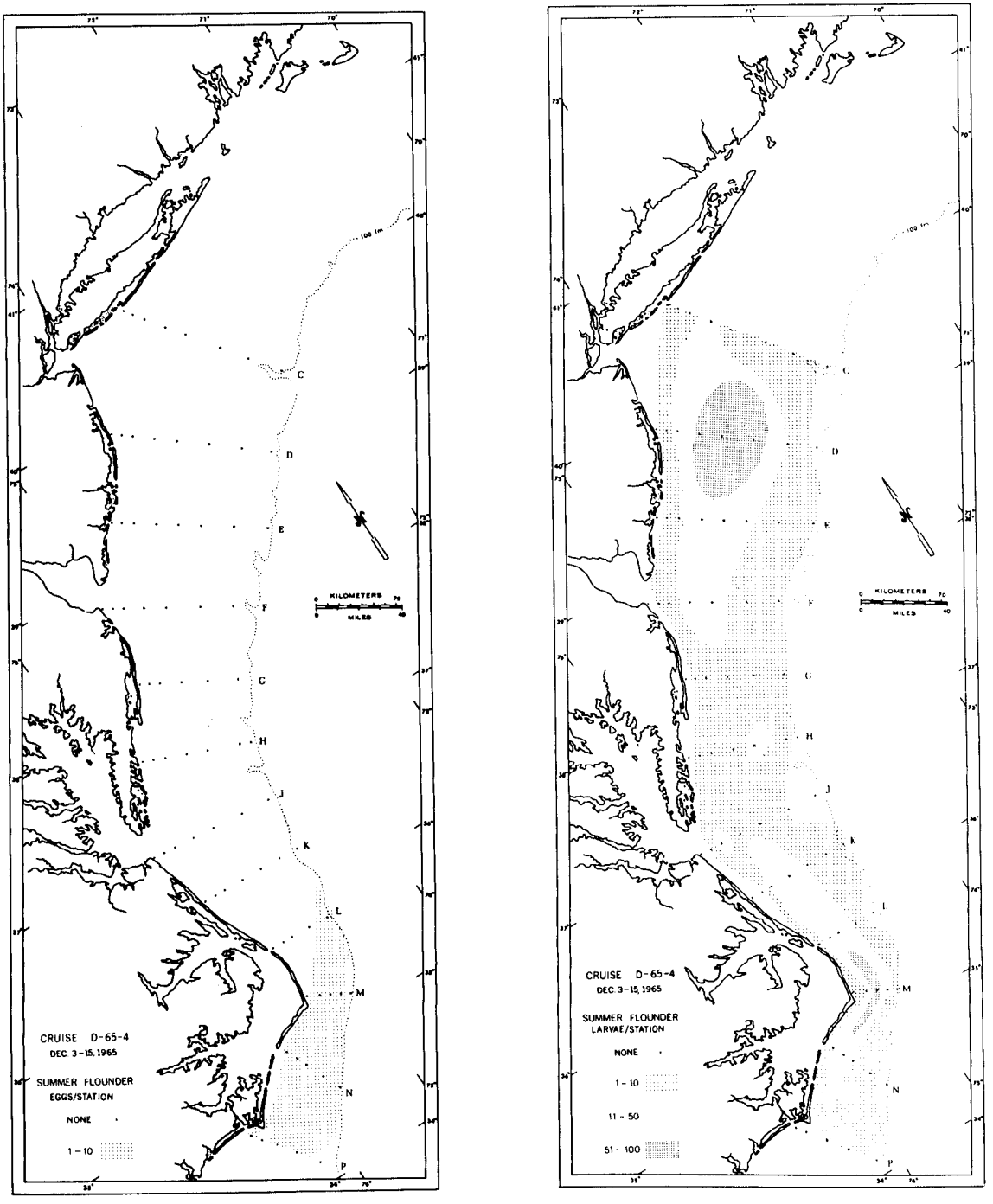

FIGURE 6.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-65-4.

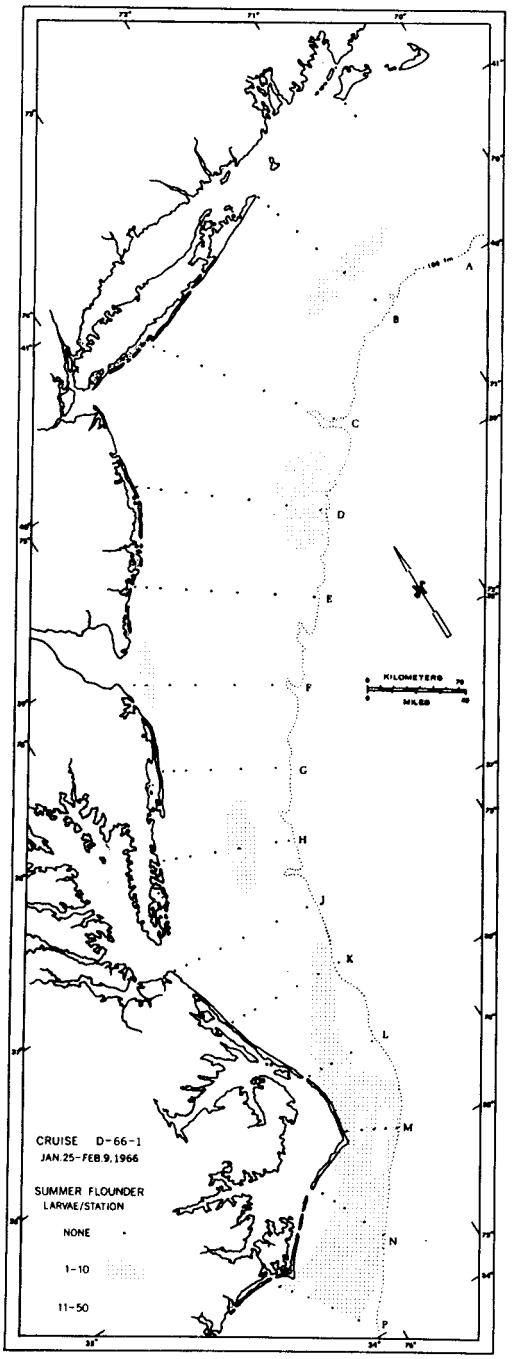

FIGURE 7.—Distribution and relative abundance (adjusted) of summer flounder larvae from Cruise D-66-1.

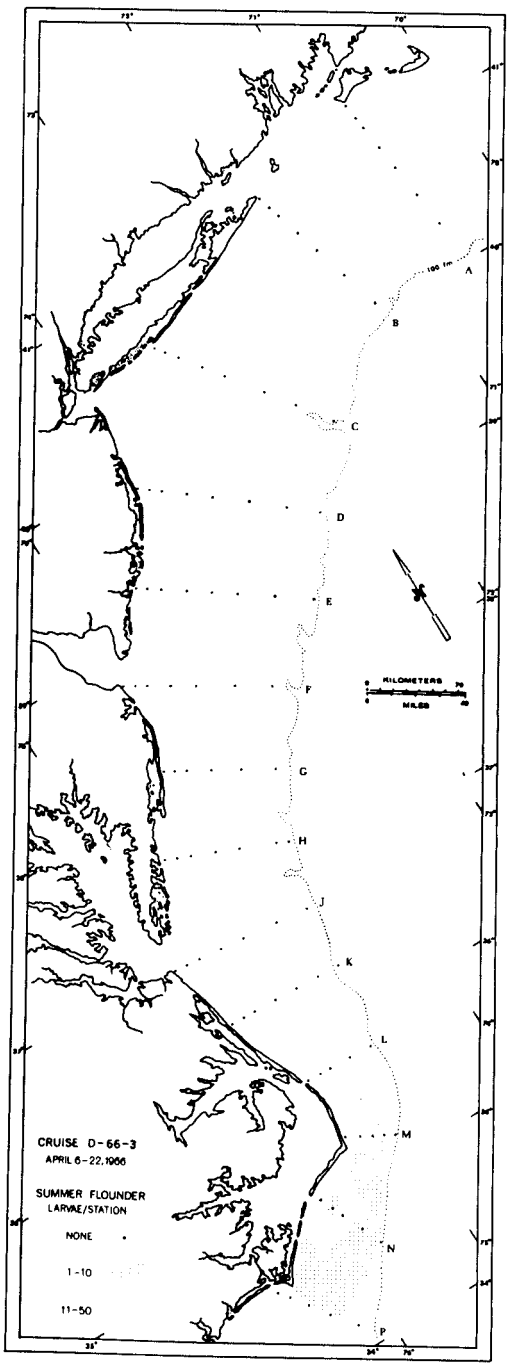

FIGURE 8.—Distribution and relative abundance (adjusted) of summer flounder larvae from Cruise D-66-3.

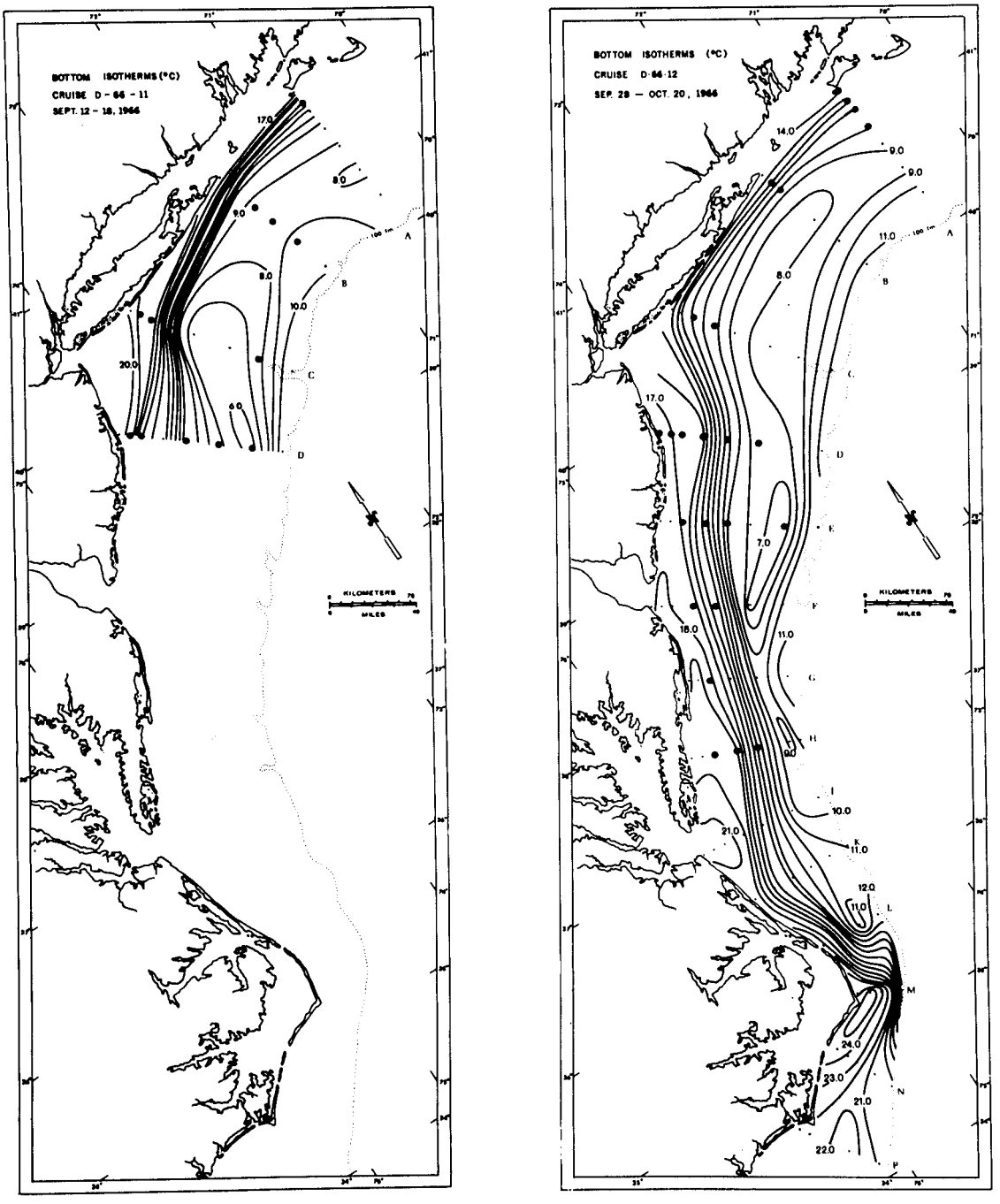

FIGURE 9.—The occurrence of pelagic eggs of summer flounder and associated bottom temperatures from Cruise D-66-11 (left) and Cruise D-66-12 (right). Eggs occurred at station positions shown by a large dot.

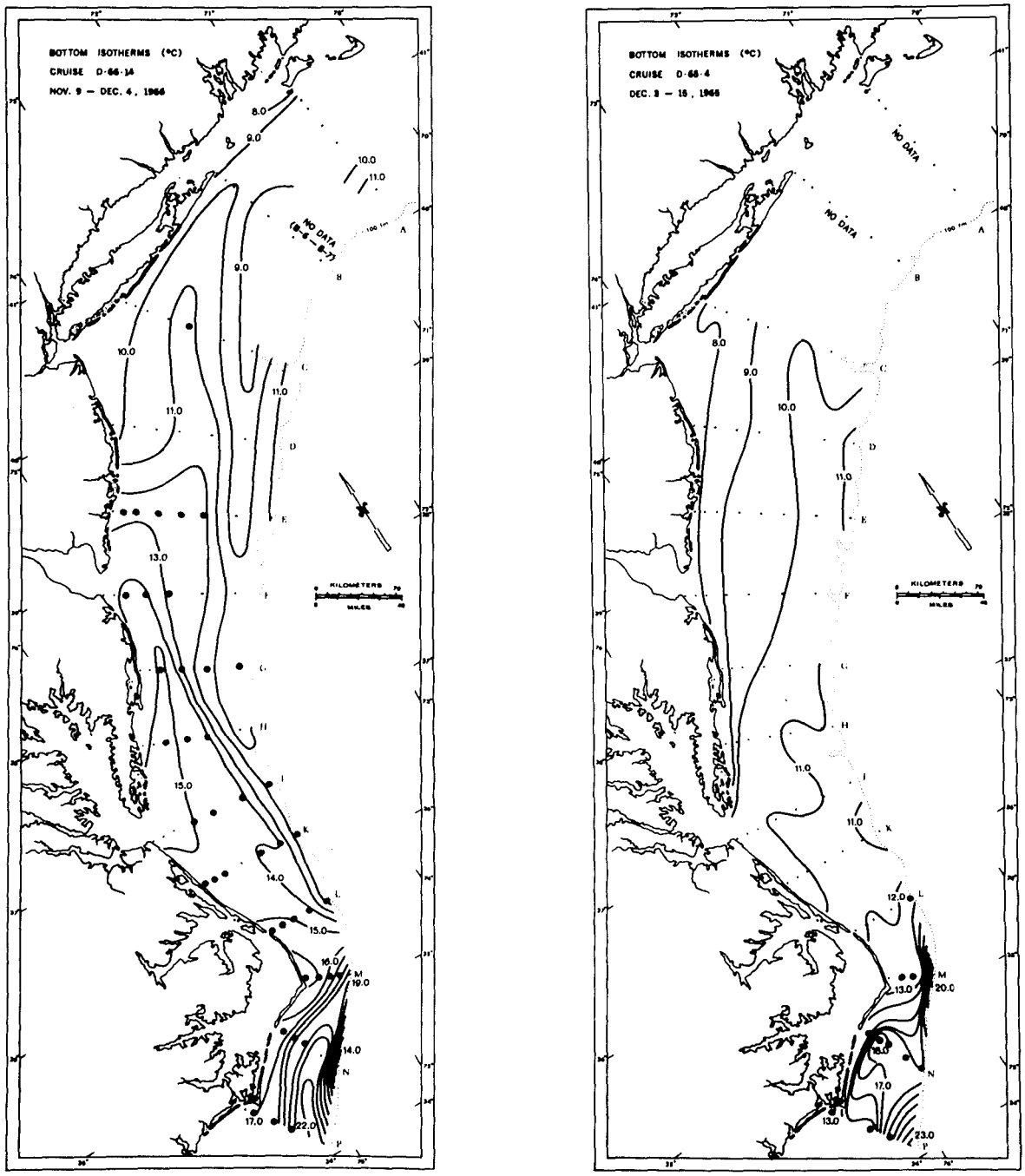

FIGURE 10.—The occurrence of pelagic eggs of summer flounder and associated bottom temperatures from Cruise D-66-14 (left) and Cruise D-65-4 (right). Eggs occurred at station positions shown by a large dot.

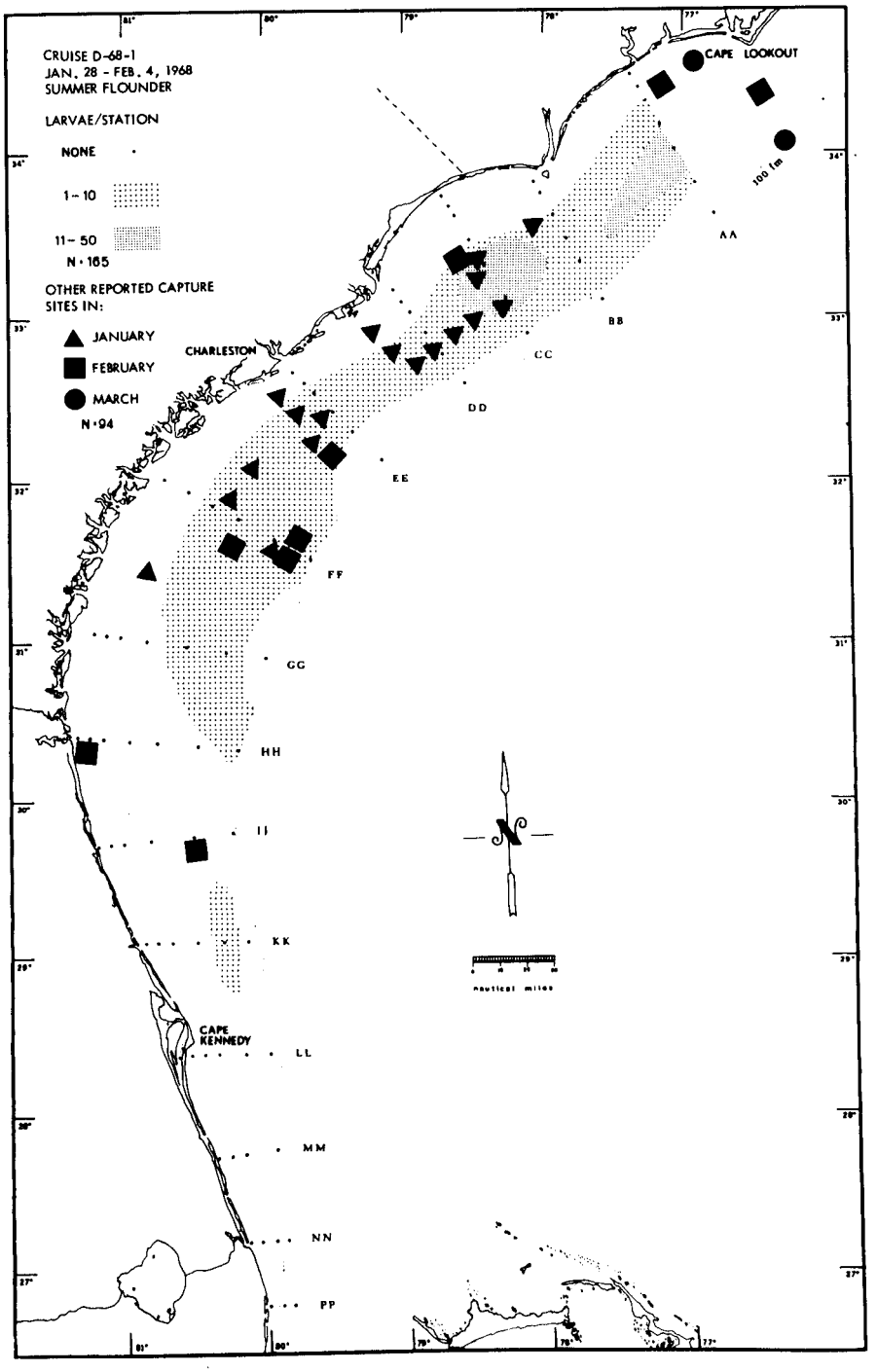

FIGURE 11.—Distribution and relative abundance of summer flounder larvae captured by RV *Dolphin* between New River, N.C., and Palm Beach, Fla., in 1968, and other reported capture sites of summer flounder larvae.

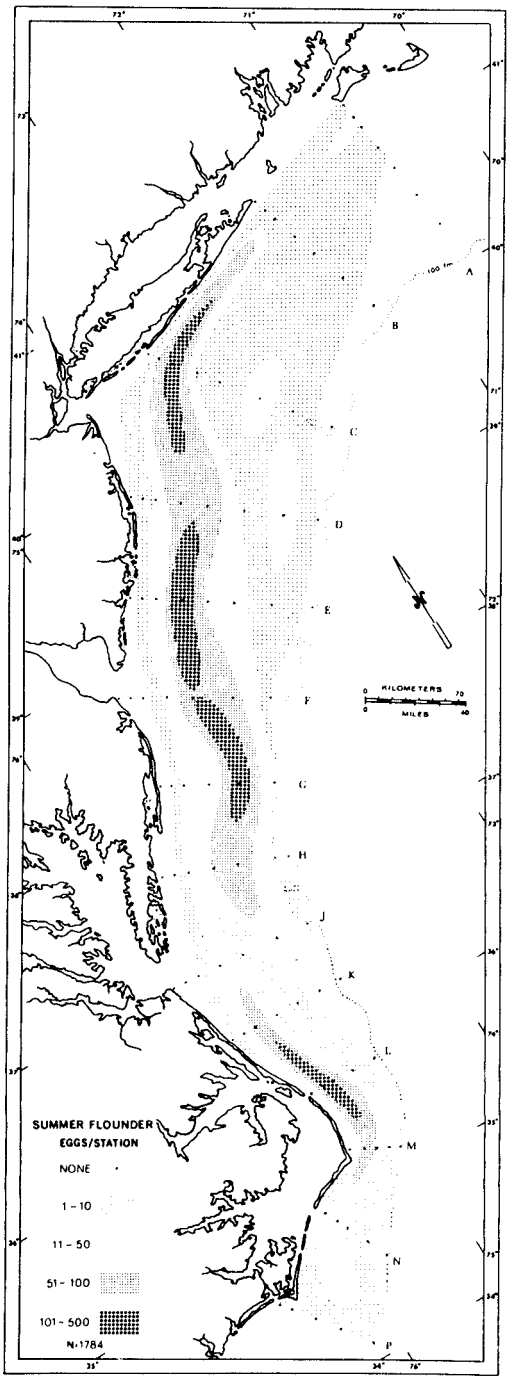

FIGURE 12.—Distribution and relative abundance (adjusted) of summer flounder eggs from 1965-66 plankton survey.

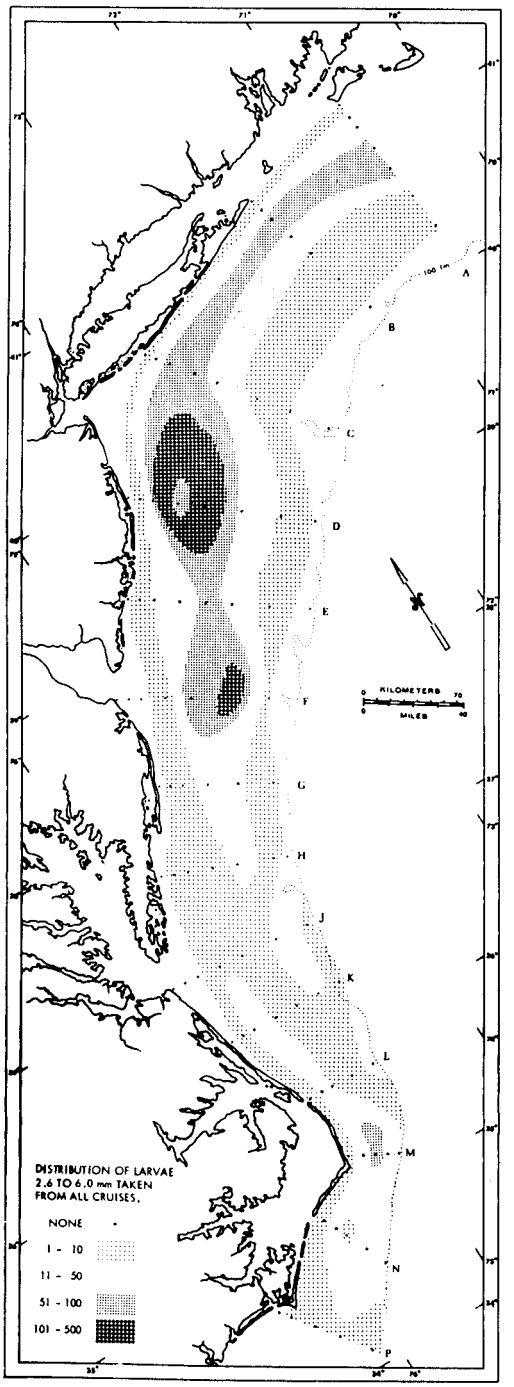

FIGURE 13.—Distribution and relative abundance (adjusted) of summer flounder larvae 2.6 to 6.0 mm from 1965-66 plankton survey.

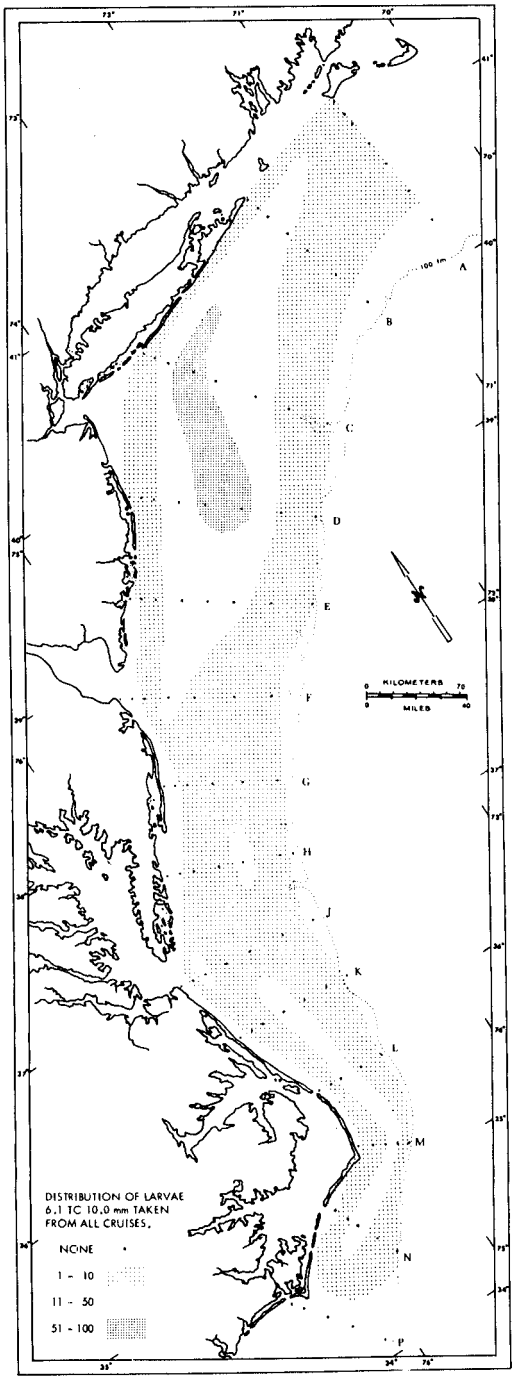

FIGURE 14.—Distribution and relative abundance (adjusted) of summer flounder larvae 6.1 to 10.0 mm from 1965-66 plankton survey.

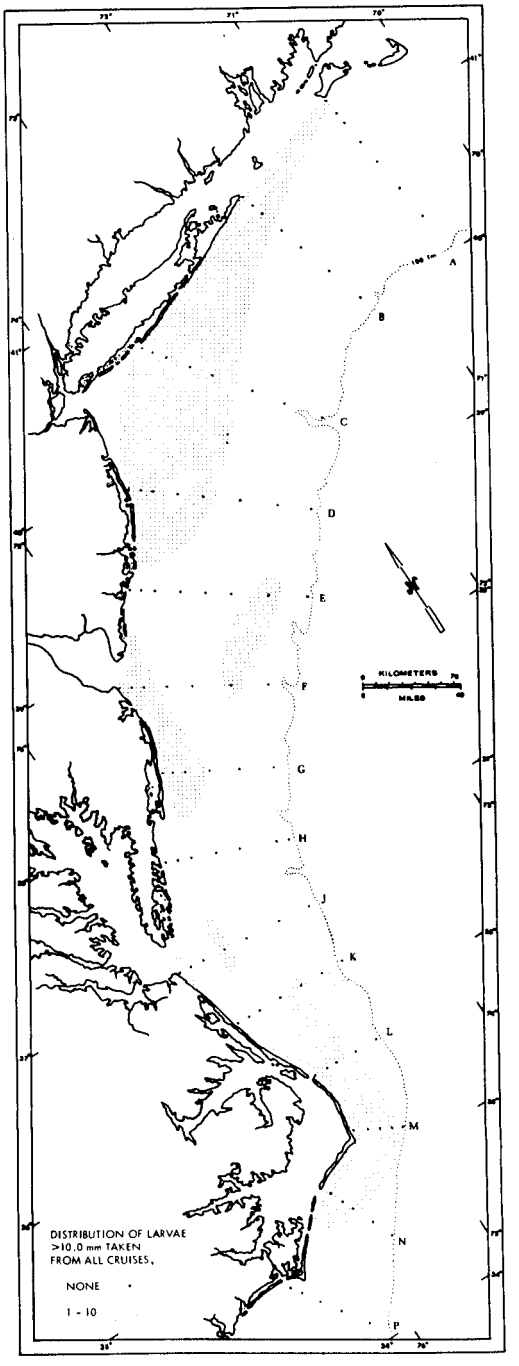

FIGURE 15.—Distribution and relative abundance (adjusted) of summer flounder larvae greater than 10.0 mm long from 1965-66 plankton survey.

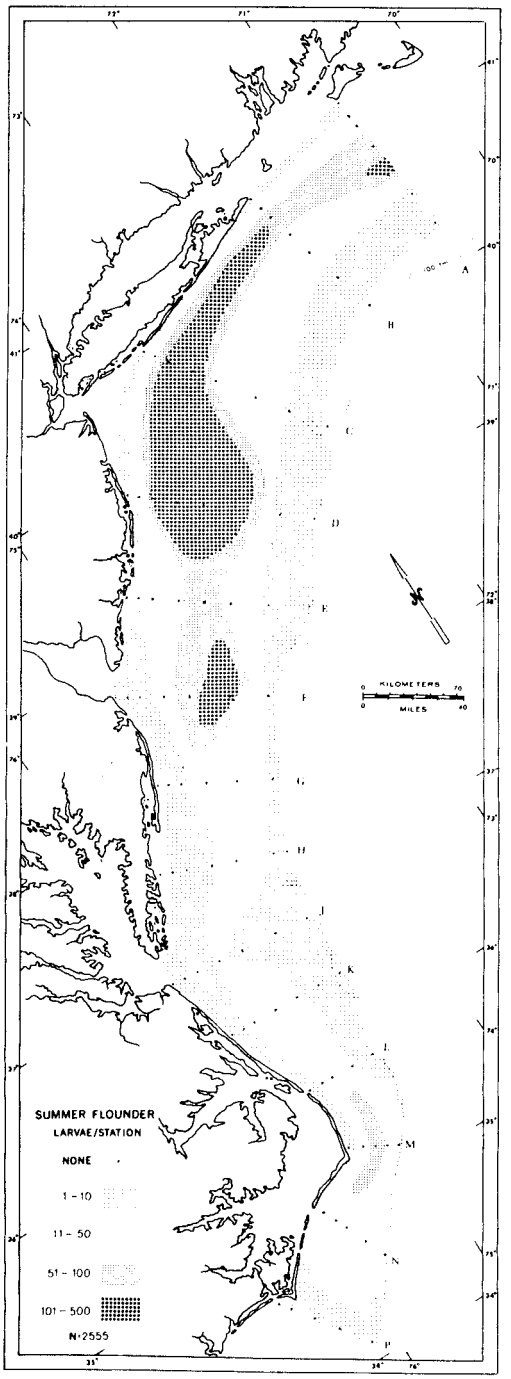

FIGURE 16.—Distribution and relative abundance (adjusted) of summer flounder larvae from 1965-66 plankton survey.

APPENDIX TABLE 1.—The length-frequency distribution of summer flounder larvae (to nearest 0.5 mm) taken on cruises from late summer to spring. Numbers are adjusted to standardize sampling effort of the two nets. Section I extended from Cape Cod to Cape Henlopen (Transects A to F); II from Cape Henlopen to Cape Hatteras (Transects G to M); and III from Cape Hatteras to Cape Lookout (Transects N and P). The survey began with the December 1965 cruise and ended with the November-December 1966 cruise.

Standard length (mm)	Cruise D-66-11 Sept. 1966				Cruise D-66-12 Oct. 1966				Cruise D-66-14 Nov.-Dec. 1966				Cruise D-65-4 Dec. 1965			
	Section				Section				Section				Section			
	I	II	III	Total	I	II	III	Total	I	II	III	Total	I	II	III	Total
2.6- 3.0	1			1	36			36	1	6	1	8		6	5	11
3.1- 3.5	5			5	148	3		151	12	17	3	32	5	30	18	53
3.6- 4.0	4			4	271	8		279	25	11	2	38	12	54	21	87
4.1- 4.5	3			3	182	10		192	42	9	1	52	19	47	13	79
4.6- 5.0	1			1	126	2		128	54	19	1	74	26	30	11	67
5.1- 5.5	1			1	112	1		113	46	9	1	56	48	23	6	77
5.6- 6.0					87			87	34	4		38	64	16	5	85
6.1- 6.5					69	1		70	20	10		30	60	30	1	91
6.6- 7.0					54			54	14	8	1	23	52	22	3	77
7.1- 7.5					18	1		19	17	8		25	34	26	2	62
7.6- 8.0					15			15	13	1		14	17	13	2	32
8.1- 8.5					7			7	17	1		18	18	11		29
8.6- 9.0					2			2	12			12	10	11		21
9.1- 9.5									9	1		10	6	7		13
9.6-10.0									2			2	2	6	1	9
10.1-10.5					1			1	7	1		8	4	3		7
10.6-11.0									6	5		11		5		5
11.1-11.5									3	2		5	2	2		4
11.6-12.0									1			1		1		1
12.1-12.5									1			1		2		2
12.6-13.0									1			1				
13.1-13.5													1	1		2
Total	15			15	1,128	26		1,154	337	112	10	459	380	346	88	814

Standard length (mm)	Cruise D-66-1 Jan.-Feb. 1966				Cruise D-66-3 Apr. 1966				Cruise D-66-5 May 1966				All cruises			
	Section				Section				Section				Section			
	I	II	III	Total	I	II	III	Total	I	II	III	Total	I	II	III	Total
2.6- 3.0													38	12	6	56
3.1- 3.5			4	4									170	50	25	245
3.6- 4.0			7	7			3	3					312	73	33	418
4.1- 4.5			5	5									246	66	19	331
4.6- 5.0			5	5			1	1					207	51	18	276
5.1- 5.5	1		3	4			1	1					208	33	11	252
5.6- 6.0							2	2					185	20	7	212
6.1- 6.5		1	2	3						1		1	149	43	3	195
6.6- 7.0			1	1			3	3					120	30	8	158
7.1- 7.5	1			1									70	35	2	107
7.6- 8.0		1		1			4	4					45	15	6	66
8.1- 8.5		2		2		1	6	7					42	15	6	63
8.6- 9.0	1	6	1	8		1	5	6		1		1	25	19	6	50
9.1- 9.5	1	4	1	6			5	5		2		2	16	14	6	36
9.6-10.0		1	1	2			2	2					4	7	4	15
10.1-10.5		3		3			3	3					12	7	3	22
10.6-11.0		1		1			1	1					6	11	1	18
11.1-11.5		1		1			1	1		2		2	5	7	1	13
11.6-12.0													1	1		2
12.1-12.5										1		1	1	3		4
12.6-13.0		1		1									1	1		2
13.1-13.5													1	1		2
Total	4	21	30	55		2	37	39		7		7	1,864	514	165	2,543

APPENDIX TABLE 2.—The relation of adjusted catch size of summer flounder eggs and larvae to mean temperature of water sampled by net no. 1 or no. 2. Only successful tows are included.

Mean temperature	Size of catch: 1-10 Eggs	1-10 Larvae	11-50 Eggs	11-50 Larvae	51-100 Eggs	51-100 Larvae	101-500 Eggs	101-500 Larvae	Total Eggs	Total Larvae
°C	Number of tows									
Less than 2.0		1								1
3.0- 3.9		4								4
4.0- 4.9		4								4
5.0- 5.9		1		1						2
7.0- 7.9		5								5
8.0- 8.9		11		4						15
9.0- 9.9	1	26		9		1			1	36
10.0-10.9		29		8						37
11.0-11.9	2	14		4		1			2	19
12.0-12.9	8	17	1	5		1			9	23
13.0-13.9	8	18	7	3	1				16	21
14.0-14.9	6	27	10	10	2	4	2		20	41
15.0-15.9	7	14	5	1	1	1			13	16
16.0-16.9	3	5	4	5					7	10
17.0-17.9	5	10	2	2	1	1	1	1	9	14
18.0-18.9	2	7	2	2					4	9
19.0-19.9	1	5			2				3	5
20.0-20.9	9	4	1	2					10	6
21.0-21.9	2	2							2	2
22.0-22.9	1	2							1	2
23.0-23.9		2								2
Total	55	208	32	56	7	9	3	1	97	274

APPENDIX TABLE 3.—The adjusted catch of summer flounder eggs and larvae, showing effort and relative densities by section and by transect. Section I extended from Cape Cod to Cape Henlopen; II from Cape Henlopen to Cape Hatteras; and III from Cape Hatteras to Cape Lookout. All stations sampled within a section where eggs or larvae occurred are included in density estimates, whether or not eggs or larvae were caught.

Section	Transect	Location	Eggs: Number of Standard tow	Eggs: Number of Eggs	Eggs: Catch per standard tow	Larvae: Number of Standard tow	Larvae: Number of Larvae	Larvae: Catch per standard tow
I	A	Martha's Vineyard, Mass.	21	21	1.0	23	224	9.7
	B	Eastern Long Island, N.Y.	21	17	0.8	28	186	6.8
	C	Western Long Island, N.Y.	24	179	7.5	40	388	9.7
	D	Barnegat Inlet, N.J.	24	187	7.8	40	637	15.9
	E	Great Egg Inlet, N.J.	16	241	15.1	32	210	6.6
	F	Cape Henlopen, Del.	14	167	11.9	27	253	9.4
Total			120	812	6.8	190	1,898	10.0
II	G	Assateague Island, Md.	18	192	10.7	30	72	2.4
	H	Eastern Shore, Va.	21	142	6.8	35	54	1.5
	J	Cape Henry, Va.	21	54	2.6	35	21	0.6
	K	Currituck Beach, N.C.	21	151	7.2	35	77	2.2
	X	Currituck Beach[1] to Oregon Inlet	4	0	0.0	4	54	13.5
	L	Oregon Inlet, N.C.	15	243	16.2	25	67	2.7
	M	Cape Hatteras, N.C.	15	126	8.4	25	151	6.0
Total			115	908	7.9	189	496	2.6
III	N	Ocracoke Inlet, N.C.	15	44	2.9	20	141	7.1
	P	Beaufort Inlet, N.C.	15	20	1.3	20	20	1.0
Total			30	64	2.1	40	161	4.0
Grand total			265	1,784	6.7	419	2,555	6.1

[1] Sampled only during December (1965) cruise.

EFFECTS OF TRANSPORTATION ON SURVIVAL AND HOMING OF SNAKE RIVER CHINOOK SALMON AND STEELHEAD TROUT

WESLEY J. EBEL, DONN L. PARK, AND RICHARD C. JOHNSEN[1]

ABSTRACT

The homing ability of adult fish that were captured during their seaward migration as juveniles and then transported downstream (from Ice Harbor Dam to Bonneville Dam) was not diminished. Data from returning adults indicated survival of adult fish that had been transported downstream as juveniles was higher than that of fish not transported. The percentage of increased survival ranged from 50 to 300% depending on the river environment during the time of transport. Information on the timing of the seaward migration and the extent of mixing of seaward runs of spring and summer chinook salmon, *Oncorhynchus tshawytscha*, was also obtained.

Losses to juvenile and adult Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, populations migrating in the Columbia and Snake Rivers have increased drastically in the last decade because of the effects of recently completed dams. The reservoirs formed by these dams have inundated some important spawning and rearing areas, have created new passage problems for both adult and juvenile migrants, and, in most cases, have significantly changed the aquatic environment to the detriment of salmonid fishes.

Gas bubble disease caused by high concentrations of dissolved nitrogen gas, resulting from the spilling of water at dams, has been pinpointed by the National Marine Fisheries Service (NMFS) (Ebel, 1969; Beiningen and Ebel, 1970; Ebel, 1971) as a major cause of salmon and steelhead trout mortalities. Nitrogen gas in the atmosphere is forced into solution as the water plunges into deep spill basins; the dissolved gas remains in solution in impounded sections of the river resulting in several hundred kilometers of water supersaturated with nitrogen gas through which fish must migrate. Another significant source of mortality can be due to passage of fish through turbines, particularly when indirect mortalities due to predation on fish emerging from turbines are included. These mortalities will persist even if nitrogen levels are reduced. Recent estimates (Raymond, 1970)[2] of losses to juvenile populations migrating downstream in the Snake and Columbia Rivers—that reflect losses from all sources, including nitrogen supersaturation—indicate that chinook salmon, *O. tshawytscha*, and steelhead trout from the upper Snake River drainage may be reduced to critically low numbers unless action is taken to reduce these losses.

NMFS has been conducting transportation experiments since 1965 to find ways of reducing these losses. Since 1968 we have been concentrating on an experiment where migrating juvenile salmon and trout—mostly spring and summer chinook salmon—are collected at Ice Harbor Dam and transported to two locations downstream. The experiment was designed to determine the effect of transportation on survival and homing.

Past information (Ellis and Noble, 1960; unpublished hatchery records of Washington,

[1] Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2] Raymond, H. L. 1970. A summary of the 1969 and 1970 outmigration of juvenile chinook salmon and steelhead trout from the Snake River, Progress Report. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Biol. Lab., Seattle, Wash. Unpubl. manuscr.

Manuscript accepted September 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

Oregon, and California) concerning the effect of transportation of hatchery stocks of juvenile chinook salmon, coho salmon, *O. kisutch*, and steelhead trout on homing indicates that the homing mechanism is disrupted by the transportation process. In these experiments, the majority of the adults returned to the location of release and not to the hatchery of origin.

We recognized this in pursuing our experiments but felt confident that different results would be obtained because we were dealing with juvenile fish, captured during their seaward migration, that had an entirely different life experience before being collected and transported. The wild stocks among our captured fish had lived for a year or more in their parent stream, were actively smolting at the time of capture, and had traversed several hundred kilometers of stream before they were transported. Captured hatchery stocks also were actively smolting at the time of capture and had traversed many kilometers before being collected. Transport experiments done by others have been conducted with hatchery stocks taken directly with no stream experience from hatchery ponds. Previous experiments (Groves, Collins, and Trefethen, 1968; Hasler and Wisby, 1951; and others) on mechanisms used by fish for homing suggest that the experience during the time that the juvenile salmon migrates seaward is important in enabling the fish to receive olfactory and visual cues necessary for homing as an adult. Since we were eliminating only a portion of the fish's migration route by transporting, we hypothesized that a fish would be successful in seeking its home stream and that survival to the spawning grounds as well as to the fishery would be increased.

The adult returns from releases of juvenile chinook salmon in 1968 and 1969 and of juvenile steelhead trout in 1969 and 1970 were obtained in 1970 and 1971. This report describes the results of the experiment based on information compiled to date. Adult returns from chinook salmon releases in 1969 and steelhead trout releases in 1970 were insufficient because 2- and 3-ocean returns are needed from data that will be obtained in 1971 and 1972 and, therefore, are not included in this report. A supplementary report will be made as additional information is received in future years.

METHODS

General Experimental Design

Three groups (one control and two transported) of migrating chinook salmon (spring- and summer-run populations) and steelhead trout were collected from gatewells at Ice Harbor Dam. Gatewell dip net hauls were mixed, then the test and control groups were selected randomly from the pooled dip net hauls. These were marked by removal of the adipose fin and with a thermal brand and a magnetized wire tag. The control, or non-transported, group was released about 15 km above Ice Harbor Dam. The transported groups were released 5 km downstream from John Day Dam on the Oregon side of the Columbia River and 1 km downstream from Bonneville on the Washington side of the river (Figure 1). A separate brand was assigned to each group and was changed weekly. A distinguishing color-coded wire tag was also assigned to the control and to the experimental groups. In 1968 one color-code was used on both transported groups. In 1969 and 1970 separate codes were assigned to each transported group.

All groups were hauled in a tank truck of 18,900-liter (5,000-gal) capacity that has been

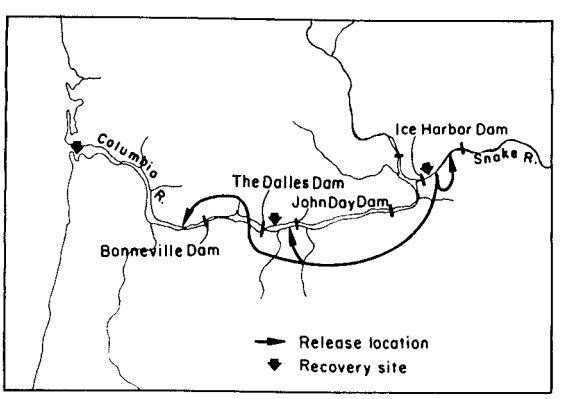

FIGURE 1.—Columbia and Snake Rivers, showing release and recovery sites of migrating chinook salmon and steelhead trout.

described by Ebel (1970). All releases were made at dusk. Records were kept of mortality during marking and at time of release.

This general procedure has been repeated during three downstream migrations—from 1968 through 1970. Each year our goal was to mark at least 50,000 fish per group but, because of low collection efficiency at the gatewells in 1969-70, this goal was reached only in 1968. In 1969 and 1970, steelhead trout were also included in the experiment.

Collection, Marking, and Hauling Procedures

In 1968-69 fish were obtained for the experiment by dipnetting them from gatewells (Bentley and Raymond, 1969). An orifice bypass system (Park and Farr, 1972) was completed in 1970 by the U.S. Army Corps of Engineers; we used this system as a source of fish in the spring of 1970. In 1969 and 1970, fish collected in the above manner were hauled by tank truck to a holding facility where they were held for about 24 hr before marking in denitrified water which had been pumped from the Snake River. Minor gas bubble disease subsided during the holding period, and presumably our holding procedure relieved some of the stress from this disease caused by the newly constructed dams upstream. In 1968, the disease was not a problem, and the fish were held and marked on the intake deck of the dam.

Fingerlings were brought into a marking building where they were anesthetized, examined for marks, and sorted by species. Marked fish were returned to the river; each of the remaining unmarked fish was cold-branded with liquid nitrogen (Mighell, 1969), the adipose fin was excised, and a magnetized wire tag was inserted in the snout (Jefferts, Bergman, and Fiscus, 1963). Before being placed into the transport truck, each fish went through a magnetic field (to magnetize the tag) and a detection coil; an improperly tagged fish was automatically rejected and returned to the marker for retagging. Steelhead trout and chinook salmon were kept in separate compartments in the truck whenever both species were hauled simultaneously. Load densities were governed by the size of a day's catch which never exceeded 10,000 fish. Thus loads were less than 60 g of fish per liter (½ lb. per gal) of water, which allowed a large margin of safety without loss of fish.

Water chemistry measurements were taken at the time of release for every load transported in 1968; in 1969 and 1970 only occasional water chemistry checks were made. Concentrations of ammonia, nitrogen, dissolved oxygen, carbon dioxide, pH, and total alkalinity were recorded.

Evaluation of Downstream Survival of Juveniles

Comparisons of the downstream survival of juvenile chinook salmon and steelhead trout released in the pool above Ice Harbor Dam and at John Day Dam were based on the proportions of these groups recovered from the gatewells by dipnetting at The Dalles Dam. Additional sampling with beach seines and purse seines was attempted in the Columbia River estuary. Samples from the estuary were to be used to evaluate survival to the sea.

Evaluation of Returning Adults

The effect of transportation on the survival and homing of adult fish was evaluated by comparing recoveries of transported and nontransported groups at various sites in the river system. These included returns to the sport, commercial, and Indian fisheries in the lower Columbia River; to Ice Harbor Dam on the lower Snake River; to Rapid River Hatchery (Idaho); and to the spawning grounds.

At Ice Harbor Dam about 80% of the run of adult fish ascends the south ladder enroute to the spawning grounds. We installed in this ladder a tag detector and adult separator device that intercepted tagged salmon and trout (Durkin, Ebel, and Smith, 1969) and diverted them into a holding pen (Figure 2). The tagged fish from our study were readily identified by the missing adipose fin. These were anesthetized and further examined for brands. If the brand was recognizable, the origin of the fish

could be determined without having to extract the magnetic tag from the snout. Fish with recognizable brands were then dart-tagged and released so that further information might be obtained upon recapture upstream or to identify the fish in case it fell back over the dam and ascended the ladder a second time. If a fish was known to be tagged but the brand was indistinguishable, it was tagged with a serially numbered dart and hauled to the Rapid River Hatchery where the fish was allowed to mature for spawn taking. The tag was then extracted after spawning, and the test or control group was determined from the color code.

The Columbia River gill net fishery below Bonneville Dam, the Indian fishery above the dam, and the sport fishery (primarily below the dam) were sampled throughout the spring chinook salmon run to provide information concerning the returns of our marked fish to the lower river. Closure of the summer fishery on chinook salmon prevented sampling of this segment of the run in the lower river. Steelhead trout were sampled in the sport and commercial fisheries of the lower river, but first year returns of fish from those marked in 1969 were insignificant.

Surveys of spawning grounds were conducted with the cooperation of the Washington Department of Fisheries, Fish Commission of Oregon, and the Idaho Fish and Game Department. Most of the surveys were in the Snake River drainage of Idaho, but hatcheries and spring and summer chinook spawning grounds in the upper Columbia River were also checked for strays.

RESULTS

Effect of Transport Mortality and Tag Loss on Analysis

Two factors that have bearing on the assessment of effects of transportation are transport mortality and tag loss.

Transport mortality is actually a combination mortality resulting from stresses of handling, marking, and hauling. During this study, mortality prior to hauling was less than 2% of the total number of fish collected. Of those marked and transported, however, about 5% died. This mortality was subtracted from the tallies of release group data in this report. Attempts were made to determine a delayed mortality after transport. These tests failed because holding conditions were unfavorable

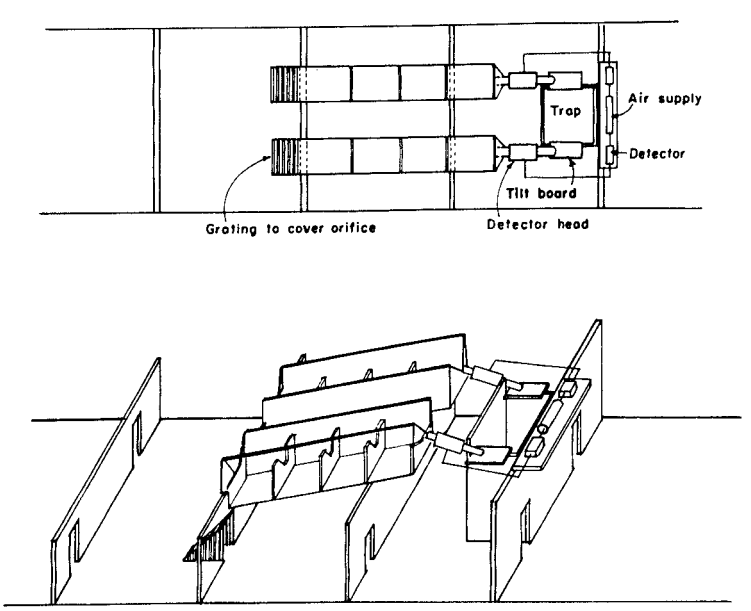

FIGURE 2.—Diagrammatic sketch of tag detector and separator device used for adult salmon and trout in south ladder of Ice Harbor Dam. Note trip board deflects tagged fish into trap.

and most fish probably died from factors other than stress from hauling.

One test, conducted with steelhead trout on 27-28 May, gives insight into the effect of transportation on smolts. Two groups of about 3,500 smolts each were released at the control group release site. Group I was treated similarly to that of our normal control group; i.e., the fish were hauled for about 1 hr before being released in the impoundment upstream from Ice Harbor Dam. Group II was treated in a like manner but was hauled for 7 hr before being released at the same site as group I. (This was approximately 2 hr longer than our typical hauls to date, but if transport tests in the future are made from points upstream, it is conceivable that 7 hr would be a minimum trip.) Upon examination of returns at Ice Harbor Dam, significantly ($\chi^2 = 4.300$; d.f. = 1) fewer fish returned from the long-haul group. More tests are required to establish an accurate posttransport mortality percentage.

Tag loss does not affect our information relating to effect of transportation on downstream survival. All data were adjusted for marking, handling, and transport mortality. Loss of tags is important when considering the results from returning adult fish. Insofar as affecting results of this study, apparent "tag loss" can occur in three ways: 1) Faulty machine operation—the smolt may never have been tagged; 2) the tag may be rejected at some time after being properly inserted in the snout; and 3) the fish can be tagged but the tag is not adequately magnetized. All have the same result—the returning fish cannot be detected. In 1968 our best information on initial tag loss was obtained from sampling at The Dalles Dam and from releases below Bonneville Dam. Although tag loss differed between release groups, overall weighted average tag loss on chinook salmon was 9.2%. Numbers of chinook salmon (transported and control) mentioned in this report have been adjusted on this basis. Tagging procedures were refined in 1969-70 so that tag loss is now less than 1% for both chinook salmon and steelhead trout.

Effect of Transportation on Downstream Survival of Juveniles

The best information concerning the effect of transportation on downstream survival of juveniles was obtained from catches in the gatewells of The Dalles Dam. The numbers of transported and nontransported (control) chinook salmon and steelhead trout that were marked and released are shown in Table 1. Recoveries at The Dalles Dam included only those fish transported to John Day Dam and the control releases above Ice Harbor Dam. Survival of the transported groups released at Bonneville Dam was estimated by recoveries in the estuary. Marked chinook salmon obtained from beach seine catches in the estuary were too limited (40 in 1968; none in 1969 and 1970) to reveal significant information. Table 2 compares recaptures of control and transported fish in 1968 that were released before and after heavy spilling began at The

TABLE 1.—Number of transported and nontransported (control) juvenile chinook salmon and steelhead trout that were marked and released, 1968-70 (figures adjusted for tag loss).

Release site and (in parentheses) experimental group of fish	1968	1969		1970	
	Chinook	Chinook	Steelhead	Chinook	Steelhead
Ice Harbor Dam (control)	80,335	24,217	25,313	8,624	18,347
John Day Dam (transported)	40,895	14,782	20,430	10,159	20,935
Bonneville Dam (transported)	42,420	13,529	—	10,173	31,282
Total	163,650	52,528	45,743	28,956	70,564

TABLE 2.—Releases and recaptures of transported and nontransported juvenile chinook salmon (transported fish were released below John Day Dam and nontransported fish were released above Ice Harbor Dam) that were recaptured at The Dalles Dam from releases before and after spilling began, 1968 (figures not adjusted for tag loss).

	Nontransported (control) fish					Transported fish				
Dates of release	Number released	Number recaptured	Dates of recapture	Percentage recapture	Recovery efficiency[1]	Number released	Number recaptured	Dates of recapture	Percentage recapture	Percentage increase in survival[2]
Before spill:										
4/2-4/5	425	13	4/22-5/8	—	—	0	0	—	0	—
	—	3	5/9-5/29	—	—	—	—	—	—	—
	—	16	—	3.76	5.74	—	—	—	—	—
4/8-4/12	4,128	175	4/22-5/22	—	—	1,352	67	4/16-5/16	—	—
	—	4	5/29-6/4	—	—	—	—	—	—	—
	—	179	—	4.34	4.56	—	—	—	4.96	—
4/15-4/19	7,843	1	4/26	—	—	7,305	416	4/22-5/25	—	—
	—	253	5/1-5/25	—	—	—	3	5/26-6/6	—	—
	—	17	5/26-6/14	—	—	—	0	—	—	—
	—	271	—	3.46	4.56	—	419	—	5.74	—
4/22-4/26	17,499	436	5/6-6/7	2.49	3.87	4,517	184	4/25-5/27	4.07	—
Totals	29,895	902	—	—	—	13,174	670	—	—	—
Cumulative average	—	—	—	3.02	5.09	—	—	—	5.09	69
After spill:										
4/28-5/4	15,711	241	5/9-5/30	—	—	9,222	347	5/1-5/25	—	—
	—	12	5/31-6/13	—	—	—	10	5/26-6/11	—	—
	—	253	—	1.61	3.88	—	357		3.87	—
5/5-5/11	21,964	190	5/16-6/11	0.86	3.88	8,730	340	5/8-6/12	3.89	—
5/12-5/17	11,371	48	5/22-6/12	0.42	2.64	6,446	212	5/16-6/14	3.29	—
5/18-5/22	5,200	—	—	—	—	2,791	27	5/22-5/30	—	—
	—	—	—	—	—	—	5	5/31-6/10	—	—
	—	7	5/27-6/6	0.13	1.15	—	32	—	1.15	—
5/23-6/7	2,290	0	—	0.00	0.00	3,601	4	6/5-6/12	0.11	—
Total	56,536	498	—	—	—	30,790	945	—	—	—
Cumulative average	—	—	—	—	0.88	—	—	—	3.07	249
Grand total	86,431	1,400	—	—	—	43,964	1,615	—	—	—
Cumulative average	—	—	—	1.62	3.67	—	—	—	3.67	127

[1] Recovery efficiency based on average percentage recapture of transported fish at The Dalles Dam for the recovery period shown. One hundred percent survival assumed between release site below John Day Dam and The Dalles Dam.
[2] Percentage increase in survival of transported groups equal to [(recovery efficiency) (100)/(% recapture of control)] - 100.

Dalles Dam. Recovery rates of survivors to The Dalles Dam varies tremendously depending on flow condition. Because the controls released at Ice Harbor Dam often took several days to reach The Dalles Dam, the recapture rate varied and was spread out over a longer period than the test groups. The recapture rate computed for the controls was therefore based on average recapture rate measured throughout the recovery period of the controls. As the table indicates, this rate was based on average percentage recovery rate of the test groups released during that period. It should be stressed that spilling also occurs at upstream dams once steady spilling begins at The Dalles. Before heavy spilling, the data indicate that survival of fish transported to John Day Dam was increased about 69% ; the ratio of recapture of transport/control fish was 1.7:1. After heavy spilling, survival was increased by about 250% or 3.5:1.

In 1969 (Table 3), heavy spilling occurred

throughout the recapture period at The Dalles Dam. The overall average recovery of chinook salmon indicates that transportation increased survival by about 90%, or a ratio of about 1.9:1. Recapture data from steelhead trout indicated a 245% increased with a ratio of about 3.5:1. No downstream survival data were obtained in 1970.

Returns of Adult Spring and Summer Chinook Salmon to Ice Harbor Dam

Table 4 lists the number of adult salmon successfully detected, separated, and identified at the automatic separator in the south ladder at Ice Harbor Dam. It should be stressed that the observed return represents only a fraction of the total return of marked fish to Ice Harbor Dam. The observed tally is low for the following reasons: 1) Approximately 20% of the run at Ice Harbor passes up the right bank (North) fishway which did not have a tag detection device; 2) the tag detection system in the left bank (South) fishway was less than 100% efficient; 3) the system was operated less than full time during salmon runs; and 4) some tag losses had occurred between tagging and recovery.

The combined adult returns of spring and summer chinook salmon at Ice Harbor Dam to 31 July 1971 from juveniles marked in 1968 (Table 4) indicate that survival from releases at Bonneville Dam were significantly (χ^2 = 33.184; d.f. = 1) greater (2.0:1) than those from control releases at Ice Harbor. When these returns at Ice Harbor are divided into spring and summer seasonal races and

TABLE 3.—Releases and recaptures of transported and nontransported juvenile chinook salmon and steelhead trout transported fish were released below John Day Dam and nontransported fish were released above Ice Harbor Dam) that were recaptured at The Dalles Dam, 1969 (figures not adjusted for tag loss).

	Nontransported (control) fish					Transported fish				
Species and dates of release	Number released	Number recaptured	Dates of recapture	Percentage recapture	Recovery efficiency[1]	Number released	Number recaptured	Dates of recapture	Percentage recapture	Percentage increase in survival[2]
Chinook salmon:										
4/11-4/19	5,297	43	4/22-5/7	0.81	1.88	5,159	35	4/17-4/29	0.68	—
4/20-4/27	6,977	68	4/28-5/15	0.97	2.19	2,301	24	4/23-4/29	1.04	—
4/28-5/4	2,844	15	5/8-5/14	0.53	1.35	4,538	105	4/29-5/12	2.31	—
5/5-5/11	4,312	17	5/13-5/23	0.39	0.94	666	9	5/8-5/16	1.35	—
5/12-5/18	3,553	15	5/19-5/27	0.42	1.07	521	3	5/15-5/19	0.58	—
5/19-5/25	1,947	12	5/23-6/2	0.62	1.07	1,497	16	5/21-6/2	1.07	—
5/26-6/1	561	1	6/4	0.18	.80	878	7	6/3-6/5	0.80	—
Total	25,491	171	—	—	—	15,560	199	—	—	—
Cumulative average	—	—	—	0.67	1.28	—	—	—	1.28	91
Steelhead trout:										
4/11-4/19	1,184	8	4/23-5/2	0.68	—	0	0	—	—	—
4/20-4/27	3,812	11	4/28-5/8	0.29	1.59	0	0	—	—	—
4/28-5/4	2,379	14	5/8-5/21	0.59	1.36	4,207	67	5/2-5/16	1.59	—
5/5-5/11	6,036	27	5/9-5/23	0.45	1.46	4,635	63	5/7-5/20	1.36	—
5/12-5/18	7,497	25	5/16-6/2	0.33	1.24	6,785	106	5/15-5/27	1.56	—
5/19-5/25	4,421	14	5/23-6/9	0.32	0.74	3,441	32	5/21-6/4	0.93	—
5/26-6/1	1,316	1	6/4	0.08	—	2,437	14	5/28-6/4	0.57	—
Total	26,645	100	—	—	—	21,505	282	—	—	—
Cumulative average	—	—	—	0.38	1.31	—	—	—	1.31	245

[1] Recovery efficiency based on average percentage recapture of transported fish at The Dalles Dam for the recovery period shown. One hundred percent survival assumed between release site below John Day Dam and The Dalles Dam.
[2] Percentage increase in survival of transported groups equal to [(recovery efficiency) (100)/(% recapture of control)] - 100.

TABLE 4.—Percentage of transported and nontransported (control) juvenile chinook salmon (released in 1968) that were recaptured as adults at Ice Harbor Dam, 1 April through 30 September 1970 and 1971.

Release site and (in parentheses) experimental group of fish	Number of juveniles released[1]	Number recaptured as adults	Percentage return as adults	
			Observed	Estimated[2]
Ice Harbor Dam (control)	80,335	117	0.14	4.3
John Day Dam (transported)	40,895	64	0.16	4.7
Bonneville Dam (transported)	42,420	128	0.30	9.0
Total	163,650	309	0.19 Ave.	5.6

[1] Adjusted for initial tag loss.
[2] Based on a comparison of the known recovery of fish with magnetized wire tags at Ice Harbor Dam and the subsequent recovery of these and other marked fish at a hatchery upstream from Ice Harbor. Returning fish identified at the dam were marked with dart tags and released to continue their migration upstream. Numbers of dart-tagged fish arriving at Rapid River Hatchery were compared with the recovery of other wire-tagged fish not previously detected and identified at Ice Harbor Dam.

compared (Table 5), benefits from transportation are defined by time. Returns of spring chinook salmon are in a ratio of 1.8:1 (transport/control) and summer chinook salmon in a ratio of 2.8:1.

TABLE 5.—A comparison between transported and nontransported groups of chinook salmon based on numbers of transported and nontransported juvenile fish (released at Bonneville and John Day Dams) that were recaptured as adults at Ice Harbor Dam in 1970 and 1971.

Release site (of juveniles) and seasonal race of salmon[1]	No. of salmon recaptured[2] as adults at Ice Harbor Dam		Transport/control ratio of fish
	Transported	Nontransported (control)	
Below Bonneville Dam:			
Spring chinook salmon	161	88	1.8:1
Summer chinook salmon	82	29	2.8:1
Below John Day Dam:			
Spring chinook salmon	92	88	1.05:1
Summer chinook salmon	36	29	1.24:1

[1] Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn. We classified adult salmon captured at Ice Harbor Dam prior to 2 June as spring chinook and those taken from 2 June through 31 July as summer chinook.
[2] Numbers recaptured adjusted in relation to numbers released (Table 1).

Combined adult returns from the John Day release were only slightly more than returns from the controls. Although the poorer returns from releases at John Day are unexplained at this time, it is possible that the stress on the fish from having to pass two dams (The Dalles and Bonneville) plus the stress of being hauled may have eliminated any benefit from transport prior to spilling. If returns from this release are again separated into seasonal races, however, the ratio of transport to control of the summer chinook salmon is about 1.3:1.

A comparison of adult returns to Ice Harbor Dam from the Bonneville releases with estimates of juvenile survival at The Dalles Dam indicates a correspondence. Prior to heavy spilling when the majority of the spring chinook salmon migrated, the recovery ratio of juveniles released before spilling began was 1.7:1 (transport/controls); adult return ratio at Ice Harbor was 1.8:1 for spring chinook salmon. After heavy spilling when the majority of the summer chinook salmon migrated, the recovery ratio of juveniles released then was 3.5:1; adult return ratio of summer chinook salmon was 2.8:1.

Logically, the adult return ratios indicated from those transported to Bonneville Dam should show more benefit from transport than the juvenile ratios showed at The Dalles Dam because the controls still had to pass two dams, The Dalles and Bonneville, before reaching the ocean. This is not the case; only the spring chinook salmon show a greater ratio; the summer chinook salmon transport/control return ratios for juvenile migrants were higher than the adult ratios established at Ice Harbor Dam.

Returns of Adult Steelhead Trout to Ice Harbor Dam

The first adults returning from control releases and those transported to John Day in 1969 appeared at Ice Harbor Dam in the fall of 1970; in the following year, a second group of older fish returned. We detected 143 steelhead trout with coded wire tags and identified them in the trap at Ice Harbor Dam in 1970 and 1971. Of these, 46 were from the control

release, 97 from the transported release—a ratio of 2.1:1 of transport/control. This return ratio is higher than that shown for the returns of summer chinook salmon transported and released at John Day. Although the juvenile fish migrated downstream in different years (1968 for chinook salmon; 1969 for steelhead trout), environmental conditions were similar. During both years, heavy spilling prevailed at the time of release and concentrations of dissolved nitrogen gas were very high.

If gas bubble disease caused by supersaturation of nitrogen was the main factor determining survival of these groups, susceptibility of the salmon and trout to lethal levels of nitrogen gas in the river must have been similar or the ratios of returning adults would not have been similar. This, of course, is merely a hypothesis; several other factors which cause change in survival could also have been responsible for the similarity of the ratios.

This return ratio also indicates that the ability of steelhead trout to return or "home" to Ice Harbor Dam was not appreciably affected by transporting the seaward migrants around a portion of their downstream route.

Recovery of Marked Chinook Salmon in Commercial and Sport Fisheries

Returns to the commercial and sport fisheries in the lower Columbia River (Table 6) are based on the spring fishery and indicate a definite benefit from transportation. The return ratio of transported fish (John Day-Bonneville releases combined) to control fish was 1.4:1. The marked increase in the transport/control ratio for summer-run adults taken at Ice Harbor Dam is not reflected in the commercial fishery because of the closure on summer-run chinook salmon.

It was not possible to distinguish between returns to the fishery from releases at Bonneville and John Day because of the loss of the identifying brands. Brands which would have enabled identification by release site were obliterated by gill-net abrasion. Transported and control groups could be distinguished by magnetic tags, but only two codes were used—one for the controls and one for the transported fish. However, if the percentage of adult returns obtained at Ice Harbor—where brands of fish returning from releases at Bonneville and John Day were visible—is applied to the total transport returns obtained in the commercial fishery, the ratio of transport/control becomes 1.7:1 for fish transported to Bonneville Dam.

TABLE 6.—A comparison between transported and nontransported groups of chinook salmon based on numbers of transported and nontransported juvenile fish that were recaptured as adults by commercial and sport fisheries in the lower Columbia River, 23 February through 11 August 1970 and 1971.

Location of fisheries	No. of salmon recaptured as adults	
	Transported	Nontransported (control)
Upstream from Bonneville Dam (Indian fishery)	37	16
Downstream from Bonneville Dam	95	78
Total	132	94

Returns of Adults to Spawning Grounds

Spring and Summer Chinook Salmon

Spawning ground surveys (Figure 3) and examination of tagged adult fish at Rapid River Hatchery near Riggins, Idaho, provided further information concerning the ratios of transport/control spring and summer chinook salmon at their "home" destination. During the study, 65 tagged fish were recovered from Rapid River Hatchery; an additional 29 were from sport fishermen and spawning ground surveys. Of these fish, 52 were from the transported groups and 42 from the control group. By adjusting for the ratio of John Day to Bonneville returns, we estimated that 36 of the 52 transported fish were from the group released at Bonneville Dam. The ratio, then, of transport/control fish for the group released at Bonneville becomes 1.7:1 when computed on the basis of the number of juveniles released per group. This is nearly identical to

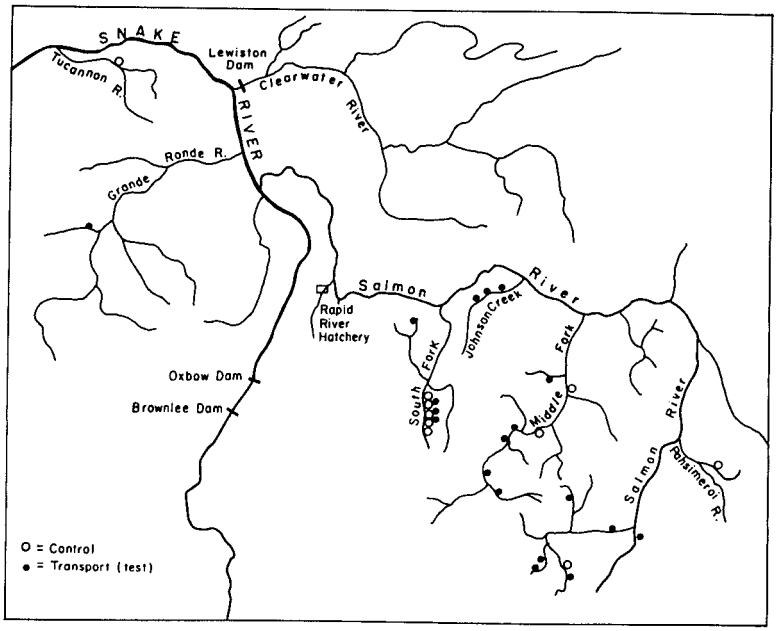

FIGURE 3.—Location of tagged adult chinook salmon returns from spawning ground surveys and returns of tags from sport fishermen in the Snake River drainage.

the ratio at Ice Harbor Dam for the Bonneville release, indicating no straying or loss of homing between Ice Harbor Dam and the spawning grounds.

The chinook salmon spawning grounds of the Okanogan and Methow Rivers and the hatcheries on the Columbia River above and below the mouth of the Snake River were checked for returning tagged adults, but no tagged fish were found. Thus, if straying to these areas did occur, it was too small to detect.

Steelhead Trout

Information on the return of adult steelhead trout to their spawning ground is based solely on recoveries of dart tags by sport fishermen. To date (January 1972) only nine tags have been recovered—two from the control group and seven from the transported group.

Timing of Seaward Migration of Juvenile Fish in Relation to Adult Returns

Spring and Summer Chinook Salmon

During marking of juveniles in 1968, a distinctive brand was used each week for the transport and control groups. These identifying brands provided a means of comparing the timing of the downstream migration of the juvenile fish with the timing of the upstream (spawning) migration of the adult fish. Only a small number (57) of adult returns could be used for this comparison because the brand on the adult fish had to be absolutely legible to determine the time of downstream migration. Returns from the control group could not be used because poor environmental conditions caused by supersaturation of dissolved nitrogen gas apparently wiped out whole groups of juvenile fish that were released during the highest nitrogen concentration. For example, over 37,000 fish were marked for the control group and released between 5 May and 27 May; only 1 adult fish was recovered from those marked during that period.

Adult returns of juveniles marked and transported between 12 April and 13 May indicate that the juvenile population at that time is mixed, with juvenile summer and spring chinook salmon evenly dispersed. Of 37 adult returns from groups marked and transported during this period, 20 were spring chinook and 17 were summer chinook salmon.

Adult returns (14 of 20) from those marked and transported after 13 May indicated that about 70% of the juveniles migrating seaward after that date were summer chinook salmon. All returns (11) from those marked after 19 May were summer chinook salmon—again indicating that the latest juvenile outmigrants are from summer chinook salmon populations.

This, in part, explains why the benefit from transport (2.8:1 ratio of transport/control fish) was so much higher for summer chinook salmon than for spring chinook salmon. After heavy spilling at dams, from early May on, a higher proportion of the juvenile population consisted of summer chinook salmon. The obvious implication is that the control groups released from this time on were largely wiped out by gas bubble disease, caused by high concentrations of nitrogen gas from the heavy spillway discharges.

Steelhead Trout

Juvenile steelhead trout were transported from 28 April to 1 June 1969, each group being marked with a distinctive weekly brand; 90% of those that returned as adults in 1970 arrived at Ice Harbor between 24 September and 14 October. There was no particular relation between time of seaward migration and time of return. Adult returns from juveniles marked between 28 April and 1 June were equally distributed throughout the return period, 24 September-14 October.

We examined scales to determine whether the adults were predominantly 1- or 2-year freshwater smolts at the time of their downstream migration. All adults had lived 2 years or more in fresh water. Only 19 scale samples, however, had legible freshwater annuli. The size of these fish was of interest. After spending only 1 year in the ocean, they averaged 61 cm and 2.6 kg. No significant difference was found between size of control fish and transported fish.

Retention of Cold Brand and Magnetic Tag

We were particularly interested in determining the percentage of brand retention on adult fish that had been cold branded as juveniles during the course of this study. Both cold (Mighell, 1969) and hot (Groves and Novotny, 1965) brands have been used successfully as short-term marks on chinook salmon and steelhead trout; up to the time of this study, however, no information was available concerning the retention of the brand to adulthood by chinook salmon and steelhead trout.

Clifford Long (National Marine Fisheries Service, Pasco, Wash., pers. comm.) determined that the brand was retained by 70% of the jack coho salmon marked for his studies; the Fish Commission of Oregon had similar results with coho salmon they had branded (Groves and Jones, 1969). Although we attempted to duplicate the techniques used by the above authors, the salmon and trout that we branded did not retain brands as well as the retention reported for coho salmon. Forty percent of our brands were not detectable on the spring and summer chinook salmon when they returned as adults (Table 7). The brand was legible (Figure 4) on 38% but only partially legible on 22%. Of the steelhead trout brands, 64% were legible, 24% illegible, and 12% partially legible. The size and physiological condition of the fish at the time of marking may have affected brand retention. The chinook salmon and steelhead trout we marked were smolting. Size range of the chinook salmon was 80-140 mm and of the steelhead trout, 160-250 mm.

Average overall tag loss for all groups was determined by comparing returns to Rapid River Hatchery of: 1) adults with adipose fin clips and wire nose tags with 2) adults with adipose fin clips only.

Approximately 27% of the juvenile chinook

TABLE 7.—Quality of marks ("cold" brands) on adult chinook salmon and steelhead trout that had been branded as juveniles during their downstream migration.

Species	Total no. of fish examined	Fish with legible marks		Fish with partially legible marks		Fish without readily identifiable marks	
		No.	%	No.	%	No.	%
Chinook	212	80	38	46	22	86	40
Steelhead	115	74	64	13	12	28	24

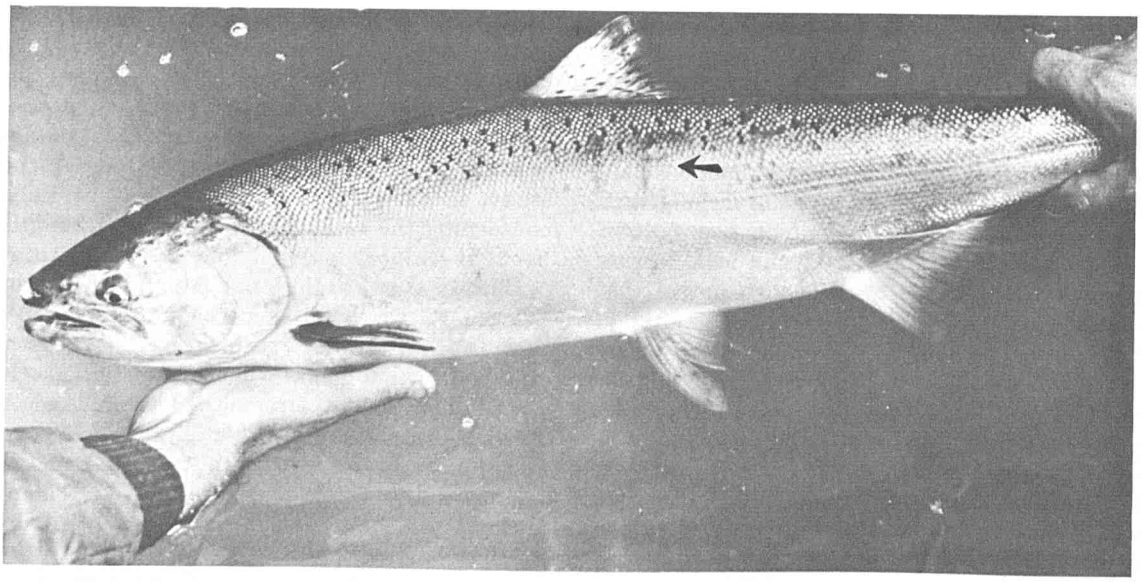

FIGURE 4.—Spring chinook salmon with legible brand (arrow) captured at Ice Harbor Dam, spring 1970.

salmon we tagged lost their tags between the time they were released as juveniles and returned as adults. The weighted average initial tag loss of all groups measured after release of juveniles in the river was 9.2%. This was computed by checking recaptured juveniles with brands and clips at The Dalles Dam and by checking samples of fish released below Bonneville Dam. Obviously an additional 18% tag loss occurred sometime after the 9.2% figure was established. This is much higher than the loss (0.31%) determined by Bergman et al. (1968). There are several possible explanations for this high loss: 1) The population we marked had a much wider size range than the hatchery stock Bergman et al. used, and this could have resulted in poor placement of the tag in those fish that were either too large or small for the tagging machine; 2) our fish taggers were inexperienced in operation of the machine; or 3) the Snake River has a high incidence of pathogens which could cause infection of the tag wound, resulting in rejection of the tag at a later date.

A combination of the above factors probably accounts for the high tag loss in our initial experiments. We believe that continued training and experience of the tagging personnel will result in a major reduction of tag loss in the future. For example, initial tag loss in 1969 was reduced to 5% and in 1970, to less than 1%. Although the loss was high in 1968, it could be compensated for mathematically. The basic information we needed from the data was not affected.

DISCUSSION

All comparisons between the returns of transported and control groups of spring chinook salmon indicate that survival was definitely increased by transporting juvenile fish to a release site downstream from Bonneville Dam. The ratios varied from 1.7:1 in the commercial fishery to 1.8:1 at Ice Harbor Dam. Comparison between the control and transported groups of summer chinook salmon can be made only at Ice Harbor Dam. No returns were obtainable in the sport and commercial fishery because direct fisheries on these fish have been restricted in recent years due to decline in the size of run; only nine returns were obtained on the spawning grounds. The return ratio (2.8:1) at Ice Harbor Dam, however, clearly indicates a definite increase in survival of transported summer chinook salmon.

These ratios also provide information on the effect of transportation on homing and

straying. A steadily decreasing ratio of transport/control numbers from the commercial fishery below Bonneville to the spawning grounds would indicate a loss of homing ability, straying, or differential mortality between groups. The ratios established for the test group released at Bonneville were 1.7:1, 1.8:1, and 1.7:1 for the commercial fishery, Ice Harbor Dam, and the spawning grounds, respectively. This indicates that no loss of the transport group occurred between Astoria (Oreg.), Ice Harbor Dam, and the spawning grounds. The same relation between ratios exists if the returns from releases at John Day and Bonneville Dam are combined; i.e., no loss of the transport groups occurred between Astoria and Ice Harbor Dam. If the homing ability of some fish was lost, any loss of fish due to straying was compensated for by an increase in survival and return of transported fish to both the fishery and spawning grounds.

Certain assumptions have been made to determine, and then compare, ratios and percentage returns of fish from transported and control groups. These are:

1. No differential mortality occurred between control and transported fish as they moved upstream from the mouth of the river to the spawning grounds; i.e., adult return ratios of the numbers of transport/control fish in the commercial and sport fishery in the lower river can be directly compared with the observed ratios at Ice Harbor Dam and the spawning grounds to provide an indicator of the effect of transportation on homing or straying.

2. The adult return ratio of John Day/Bonneville transported fish remained constant after these fish entered the Columbia River. We must assume this when the ratio is used to determine the actual number of fish of the John Day and Bonneville groups in returns to the commercial fishery and to spawning grounds (where the brands were not visible) and when it is then necessary to rely on the single tag code to calculate return data for the two transported groups.

3. Native and hatchery stocks in our control and transported groups were recovered at the same rate by the detector and separator at Ice Harbor Dam. This assumption is necessary inasmuch as the estimated percentage return of all adults to Ice Harbor (Table 4) was based solely on the ratio of observed recoveries of a hatchery stock (Rapid River stock) at Ice Harbor and those subsequently recovered at the hatchery. Recoveries of native fish on the spawning grounds from fish identified at Ice Harbor were insufficient for use in this application.

4. Rate of maturity and timing of migration is the same for transport and controls. Since ocean and river fishing rates are not the same on fish maturing early and returning early as they are on fish maturing late and returning late, this assumption is required.

The most significant result of this study is that the ability of the chinook salmon and steelhead trout to return to Ice Harbor Dam was not destroyed or even seriously affected by transporting seaward migrants around a major part of their downstream route. Overall returns from transported groups, except those from the early releases at John Day Dam, were significantly greater than those from the control group. These results are radically different from any achieved to date in other experiments (Ellis and Noble, 1960; unpublished hatchery records of Washington, Oregon, and California) where hatchery stocks exclusively had been transported. We are therefore convinced that our original hypothesis is acceptable—namely, that a fish's experience from the period beginning with smolting to the time the fish is collected for transport is critical. Our understanding of the mechanisms of homing is still limited, however, and much more must be learned to fully understand what the critical factors are in determining what is needed to provide anadromous salmon and trout with homing cues. Experiments to pinpoint the critical requirements for imprinting are needed. If these factors can be determined, it might be possible to provide the necessary experience in a hatchery prior to transport which would enable transport of fish directly from the rearing areas to locations downstream and thus eliminate much of the usual downstream mortality and still achieve satisfactory

returns to the hatchery concomitant with greater returns to the fishery.

The information we have to date is sufficient to consider the feasibility of a major collection and transportation system on the Snake and Columbia Rivers. An evaluation of a prototype system was initiated at Little Goose Dam on the Snake River in the spring of 1971. The results of that study, we believe, should lead to a determination of whether collection and transportation of juvenile salmon and trout is, indeed, feasible and can provide substantial protection for runs from upriver areas.

CONCLUSION

1. The homing of adult fish that were captured during their seaward migration as juveniles and then transported (from upstream of Ice Harbor Dam to below Bonneville Dam) downstream was not reduced by the transportation operation. A comparison of the transport/control ratios of returning adults in the lower river with those at Ice Harbor Dam and the spawning grounds indicated that no loss to the transport groups occurred between the estuary, Ice Harbor Dam, and the spawning ground. Straying of either the transported or control groups was not indicated in surveys of hatcheries and spawning grounds.

2. Data from adult returns indicated that transportation of naturally migrating juvenile spring- and summer-run chinook salmon and of steelhead trout from upstream of Ice Harbor Dam to below Bonneville Dam definitely increased returns (50-300%) to the fishery and to Ice Harbor Dam, depending on the river environment during the time of transport.

3. Transportation of juvenile spring chinook salmon to the release site below John Day Dam did not increase their survival (as evidenced by adult returns) during the period before the dams began heavy spilling but did increase survival about 15% after heavy spilling began.

4. The juvenile population of chinook salmon migrating seaward past Ice Harbor Dam from 12 April to 13 May in 1968 was of mixed seasonal races—with juvenile summer and spring chinook salmon mixed and evenly dispersed throughout the period. After 13 May, about 70% of the juvenile chinook salmon were summer-run fish.

5. Quality of brands on adult fish that had been marked as juveniles (using tools that were chilled with liquid nitrogen) varied between species—38% of the marks on spring and summer chinook salmon were legible compared with 64% on steelhead trout.

6. Relative effects of transport over controls is demonstrated, but effects of handling on both groups has not been evaluated. Thus, the survival of transported fish needs to be compared with survival of undisturbed migrants and is currently being studied.

ACKNOWLEDGMENTS

The authors wish to thank the fishery biologists from the Fish Commission of Oregon, the Washington Department of Fisheries, and the Idaho Fish and Game Departments, who assisted in recovering tags from adults in the commercial and sport fisheries and the spawning grounds. We also wish to thank Paul Winborg, Project Engineer, U.S. Army Corps of Engineers, at Ice Harbor Dam for his patient cooperation during this continuing experiment.

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DIGESTIVE SYSTEM AND FEEDING HABITS OF THE CUNNER, *TAUTOGOLABRUS ADSPERSUS*, A STOMACHLESS FISH[1,2]

LABBISH NING CHAO[3]

ABSTRACT

The cunner, *Tautogolabrus adspersus*, completely lacks a morphologically or physiologically distinct stomach. The alimentary tract consists of the pharynx followed by a short esophagus with an esophageal-intestinal valve at the junction of esophagus and intestine. The intestine has three limbs and an S-loop. The intestinal bulb where the bile duct enters is present at the anterior end of the first limb. The border between the posterior end of S-loop and the rectum is marked by the intestinal-rectal valve. Histological and histochemical observations indicate that the rodlet cells, wandering cells, longitudinal muscle layers, and the rectal valve differ in minor ways from those of other stomachless fishes. Different forms of rodlet cells are found in the bile duct. An alkaline condition (pH values between 7.0 and 8.5) prevails throughout the alimentary tract. Alkaline phosphatase reaction was demonstrated only when food was present in the gut. Cunner are carnivorous, and the feeding habits change with growth. Juveniles feed mainly on planktonic crustacea and adults on sessile animals (mussels and barnacles). The time between ingestion and defecation of mussels (Mytilidae) by cunner is 10 to 14 hr. Intact mussels can pass through the alimentary tract of the fish undamaged and alive.

The most abundant labrid of the New England region, the cunner, *Tautogolabrus adspersus* (Walbaum), lacks a stomach. The absence of a stomach is here defined as the lack of an expansion of the alimentary tract between the end of the esophagus and the entrance of the bile duct into the intestine (Figure 1). The mucosa of this region lacks gastric epithelium and gastric glands. The alimentary tract is alkaline and lacks peptic digestion. Lack of a stomach appears to be a phylogenetic characteristic of the family rather than an adaptive one associated with feeding in this particular species.

The absence of a morphological stomach in teleostean fishes has been recorded in various species of several families, i.e., Atherinidae, Blenniidae, Callionymidae, Cobitidae, Cyprinidae, Cyprinodontidae, Gobiesocidae, Gobiidae, Labridae, Mugilidae, Poeciliidae, Scaridae, and Syngnathidae. These families have different feeding habits as noted by Ishida (1936), Barrington (1942), Suyehiro (1942), and Al-Hussaini (1947b) and are not closely related phylogenetically. Al-Hussaini (1949a) also recorded different feeding habits among three stomachless species of the family Cyprinidae: *Cyprinus carpio*, *Rutilus rutilus*, and *Gobio gobio*; they are herbivorous, omnivorous, and carnivorous, respectively. Physiological lack of stomach has been noted in various fishes: *Fundulus heteroclitus* by Babkin and Bowie

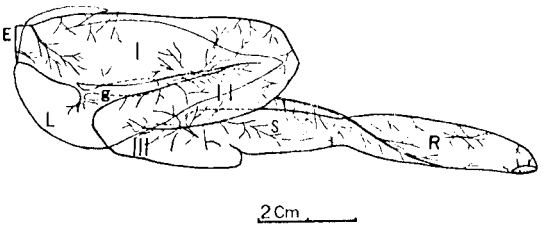

FIGURE 1.—Lateral view of the alimentary tract of a 280-mm SL cunner. E, esophagus; g, gallbladder; I, II, III, sections of intestine; S, S-loop of intestine; L, liver; R, rectum.

[1] Contribution No. 19, Marine Science Institute, Northeastern University, Nahant, MA 01908.

[2] A portion of a thesis submitted to the Department of Biology, Northeastern University, Boston, Mass., in partial fulfillment of the requirements for the degree of Master of Science in Biology, January 1972.

[3] Virginia Institute of Marine Science, Gloucester Point, VA 23062. (VIMS Contribution No. 539.)

Manuscript accepted September 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

(1928); Cyprinidae by Szarski (1956); *Spheroides niphobles* by Ishida (1936); Scaridae and Labridae by Gohar and Latif (1959). Both morphological and physiological characters of the stomachless fishes appear to be characteristic of the Labridae.

The morpholoy and histology of the entire alimentary tract in the cunner were described from the protrusible lip to the anal papillae. A histochemical study was made on the gut, i.e., the postpharyngeal portion of the alimentary tract. Also, feeding habits and habitat, gut contents, and the movement and digestion of food were investigated.

MATERIALS AND METHODS

The fish were collected at East Point, Nahant, Mass., from May to September 1970 and 1971. Larger specimens, over 100 mm SL (standard length), were taken by hook and line fishing along the shore, and smaller ones in plankton hauls, by bottom dredging, hand netting, and rotenone poisoning in tide pools. Some specimens were maintained in constant running seawater aquaria and fed with mussels (Mytilidae).

Histological and histochemical studies were made after starvation (7-10 days) and after feeding. Specimens less than 40 mm SL were killed in 10% Formalin,[4] larger ones by severing the spinal cord and by intracoelomic injection of Dilantin (sodium diphenylhydantoin, USP) anesthetic (0.1 ml/10 g body weight). Tissues were fixed with absolute acetone, Baker's Formalin, Bouin's (also with seawater), Helly's, Hollande-Bouin's or Zenker's fixatives in order to demonstrate specific cell types. After fixation, dehydration was done in two ways: the standard method of ethyl alcohol or from water to Cellosolve (2-ethoxyethanol). Infiltration and embedding were carried out using Steedman polyester wax (1960); serial sections were cut at 1 to 8 μ. A variety of routine histological and histochemical stains were used, including hematoxylins (Ehrlich's, Galigher's, Heidenhain's Iron Alum, Groat's) counterstained with eosin or fast green, Giemsa (Mallory, 1944, in Humason, 1967), Gomori's trichrome (1950, in Humason 1967), Heidenhain's azan (1938, in Humason, 1967), Masson's trichrome mixture (Gurr, 1956, in Humason, 1967). Histochemical methods included: alcian blue (Steedman, 1950; modified by Mowry, 1956, 1963, in Humason, 1967), periodic acid Shiff's technique (McManns and Mowry, 1960, in Humason, 1967), toluidine blue (Lillie, 1929, in Humason, 1967). Acid and alkaline phosphatase tests were done by Gomori's modification according to Pearse (1960).

To determine the natural food and feeding habits, gut contents were examined immediately after capture, or specimens were frozen for subsequent examination. Also the feeding habitat was observed by SCUBA diving. Food movement and digestion rates were observed in specimens from 150 to 200 mm SL which were fed whole, small mussels less than 20 mm (shell length), or the visceral mass of larger mussels. Cunners were either fed daily or were starved for 7 days prior to experimentation. Fish were allowed to feed voluntarily on a cluster of mussels during the ½- to 1-hr periods. Uneaten mussels and broken shells were removed after the feeding period. Carmine, Chinese ink, or ultramarine blue were injected into the visceral mass as indicators. Fishes were killed by severing the spinal cord at the base of the skull, at 1-hr intervals from 0 to 36 hr after feeding. Autopsy was done immediately after sacrificing the fish in order to locate the position of the food. All pH values of the gut lumen were determined from narrow range pH papers.

Ten adults (180-240 mm SL) and 6 juveniles (30-34 mm SL) were used for histological and histochemical studies, and 68 specimens (30-300 mm SL) for analyses of gut contents.

RESULT

Morphology and Histology of the Alimentary Tract

As reported by previous authors for other labrids (Barrington, 1942; Suyehiro, 1942; Al-Hussaini, 1947b; Gohar and Latif, 1959,

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

1961), the alimentary tract of the cunner consists of neither a morphologically nor a physiologically differentiated stomach. The alimentary tract can be divided into several regions; the preesophageal cavities, esophagus and esophageal-intestinal valve, intestine, rectal valve and rectum, and associated organs.

Preesophageal Cavities

This region has three parts: the mouth, buccal cavity, and pharyngeal cavity (Figure 2).

MORPHOLOGY.—Cunners have large caninelike or incisorlike teeth on the premaxillary and dentary bones. The protrusible premaxillary bears three or four rows of conical teeth directed posteriorly, as are the two or three rows of dentary teeth. The most anterior rows of both premaxillary and dentary teeth are two to four times larger than the other rows. Also, the anterior most teeth are larger than the following ones on the same row. Teeth from 15 specimens (130-230 mm SL) numbered 32-66 on the premaxillary and 21-44 on the dentary. The number of teeth increases with the size of the fish. Developing teeth were found at the edges of the older teeth on all tooth bearing bones. Longitudinal ridges of mucous membrane extended from the vomer to the pharynx on the roof of the buccal cavity. The buccal valve is located posterior to the buccal cavity (Figure 2). There are no teeth on the vomer and palatine bones. A large tongue covers the entire floor of the anterior pharyngeal cavity and forms a sublingual cavity. The pharyngeal cavity is bounded laterally by gill arches. A yellowish brown mucous layer, patchlike and thicker than that in the buccal cavity, covers the entire roof and posterior part of the floor. Strong mucous secreting activities occur in this area. Both the upper and lower pharyngeal teeth are surrounded partially by this mucus. The pharyngeal teeth (upper 41-59, lower 28-56) are multitubercular and molariform. A pair of upper pharyngeal bones attach to the epibranchial bones and a triangular lower pharyngeal plate is attached to the basibranchial bones.

HISTOLOGY.—The mouth is lined with a stratified epithelium of the transitional type without a cuticular surface. The mucosa is thrown into ridges which start at the inner side of the protrusible lips (Figure 3) and extend to the esophagus. Taste buds lie on the crest of the ridges, and basophilic mucous secreting cells occur at the sides and bases, but the large acidophilic mucous cells present in the skin are absent here (Figure 3). Polyhedral cells and low-columnar cells constitute the rest of the layer. The mucosal layer and

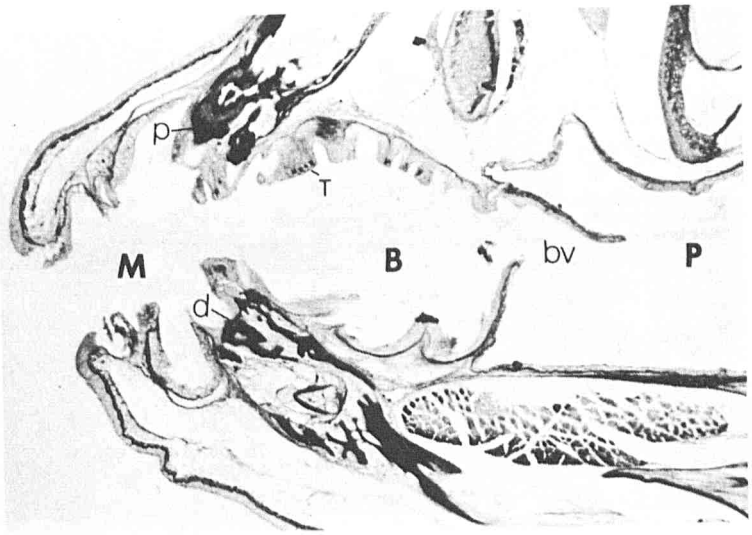

FIGURE 2.—Mouth (M), buccal cavity (B), and pharyngeal cavity (P) of a 40-mm SL juvenile cunner (× 40; power of observation). bv, buccal valve; d, dentary teeth; p, premaxillary teeth; T, taste bud.

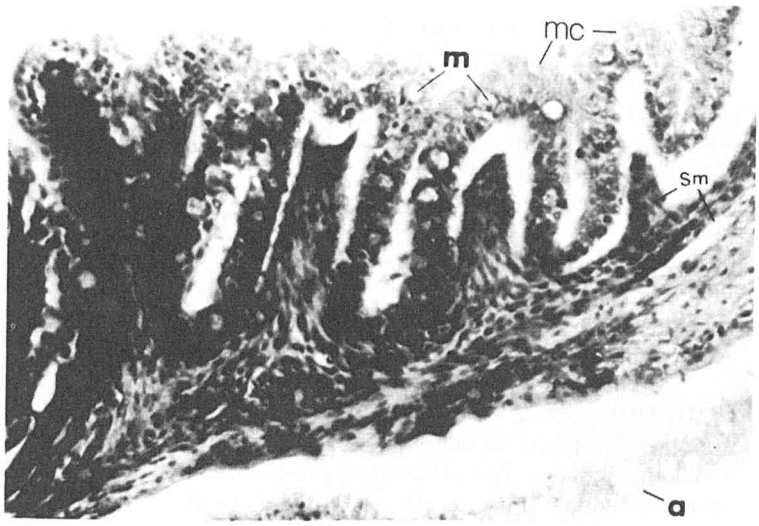

FIGURE 3.—Distribution of mucous secreting cells at sides and base of the mucosal ridges of protrusible lip in cunner (× 250, x.s.). a, acidophilic mucous secreting cell; m, basophilic mucous secreting cell; mc, mucosal layer; Sm, submucosa.

the ridges are deepest in the region of the teeth where the mucosa may be over 10 cells thick. Elsewhere, the mucosa is four to six cells thick, except for the sublingual area and the lateral side of the buccal cavity where a thickness of only one or two cells may prevail. The lateral mucosa of the pharyngeal cavity (the internal epithelium of the opercle) is one cell thick and is entirely constructed of mucous secreting cells attached to the opercle by a thin layer of connective tissue (Figure 4). The ridges or mucosal folds are more prominent on the midlines of the roof and floor of the pre-pharyngeal regions. There are no ridges on the surface of the sublingual cavity. The submucosa is a layer of fibrous connective tissue under the mucosa. It is continuous throughout this region, and the thickness is closely correlated with the depth of the mucosal folds.

Taste buds occur from the inside of the lips to the pharyngeal teeth (Figures 3 and 5) and occasionally are found on the gill arches. No taste buds were observed on the external side of lips, anterior sublingual cavity, or the lateral wall of the pharyngeal region. The aggregation of taste buds is closely related to the papillae

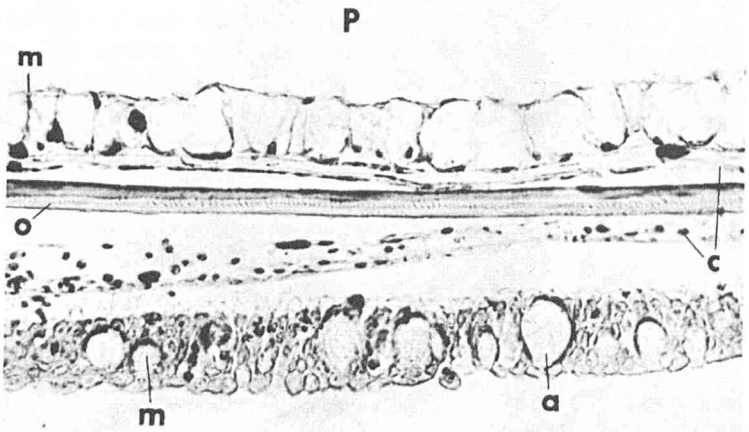

FIGURE 4.—Lateral mucosa of the pharygeal cavity (P) entirely covered with mucous secreting cells in cunner (× 250, x.s.). a, acidophilic mucous secreting cells; c, connective tissue; m, basophilic mucous secreting cell; o, opercle.

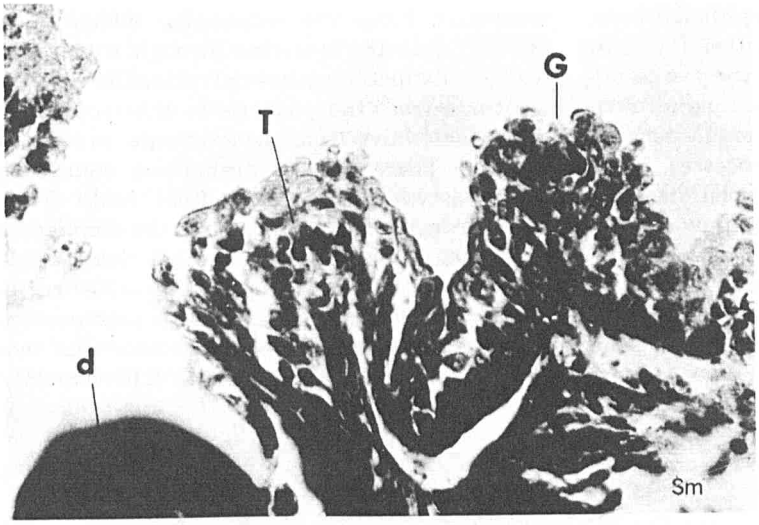

FIGURE 5.—Taste buds (T) on the mucosa of protrusible lip of cunner (× 400). d, dentary tooth; G, gustatory pore; Sm, submucosa.

folds, i.e., to the middle lines of this region and to the teeth. The taste bud is an ovoid structure of epithelial cells (Figure 5). A gustatory pore is present at the tip of each taste bud. A thickening of the submucosal layer contains the nerve fiber and forms the base of the taste bud.

Basophilic mucous secreting cells continue from the external lips and appear throughout this region. Mucous cells increase in numbers posteriorly. The lateral surface of the pharyngeal cavity and the ridges among the teeth are covered by mucous secreting cells. Beneath the basal membrane of the mucous layer, the submucosa is formed of a thick layer of collagen fibers toward the posterior part of the pharyngeal cavity. The areolar connective tissue of the tunica propria and submucosa are similar in this region. Lymphocytes and granulocytes are apparent in the submucosa of the ridges among the pharyngeal teeth. Circular muscles which connect to the head bones are external to the areolar connective tissue.

The epithelium and submucosa of the tongue are similar to that of the pharyngeal cavity but are much more compact (Figure 6). Posteriorly,

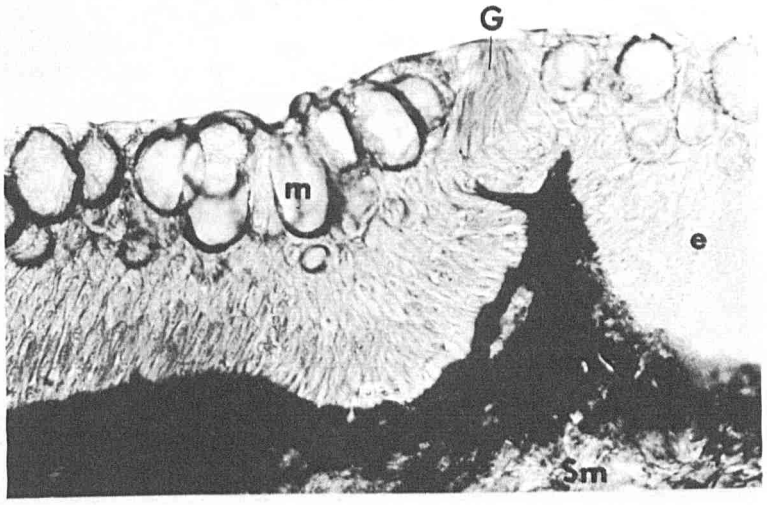

FIGURE 6.—Mucosa (e) and submucosa (Sm) of the tongue of cunner with hairlet sensory organ (× 400). e, epithelium (mucosa); G, gustatory pore of hairlet sensory organ; m, basophilic mucous secreting cells.

the submucosa below the dorsal epithelial layer is thicker than beneath the ventral layer. A flaplike structure directed posteriorly was observed on the ventral side of the tongue. Sensory organs, consisting of numerous sensory cells provided with hairletlike processes, occur on the tongue (Figure 6) and open into the pharynx through a gustatory pore.

Esophagus and Esophageal-Intestinal Valve

Posterior to the pharyngeal teeth, the pharynx constricts markedly to form a short muscular tube, the esophagus, which opens directly into the intestine through a muscular valve. Distinct longitudinal ridges (Figure 7) continue from the pharynx to the esophageal-intestinal valve and then diverge in the intestine. There are no transverse connecting cores between the longitudinal folds. These folds branch shortly anterior to the esophageal-intestinal valve (Figure 8). The mucous cells in the epithelium disappear in this region (transitional zone). This is more prominent in small specimens (less than 40 mm SL) than in larger specimens (200 and 210 mm SL).

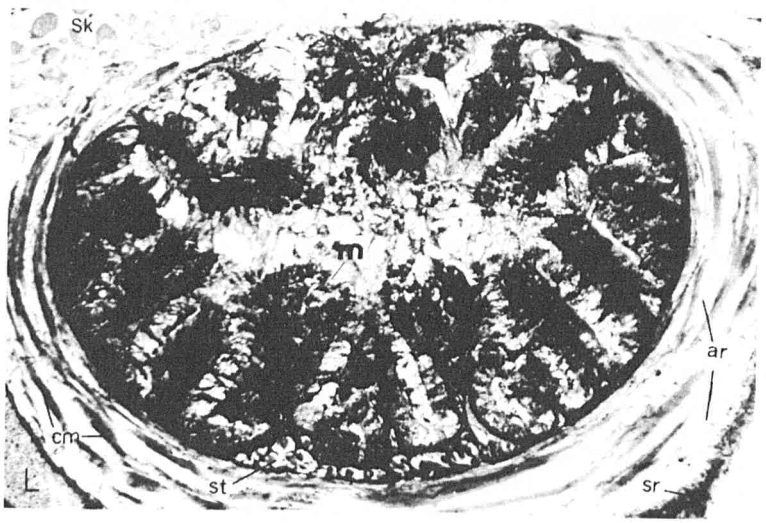

FIGURE 7.—Longitudinal ridges of the anterior esophagus of a 40-mm SL juvenile cunner (× 40, x.s.). ar, areolar connective tissue; cm, circular muscle layer; L, liver; m, mucous; Sk, skeletal muscle; sr, serosa; st, striated muscle.

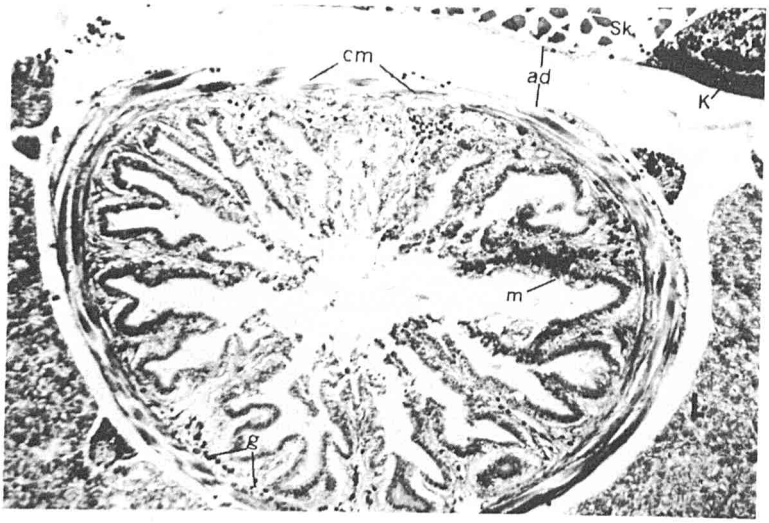

FIGURE 8.—Transitional zone anterior to the esophageal-intestinal valve in the esophagus of a 40-mm SL cunner (× 40, x.s.). ad, adventitia; cm, circular muscle layer; g, granulocyte; K, kidney; L, liver; m, mucous secreting cell; Sk, skeletal muscle.

MUCOSA.—The epithelium of the anterior esophagus is a modified transitional type (Figure 9) with large mucous cells extending to various depths from the surface. While the esophagus proceeds posteriorly, the stratified epithelium gradually becomes simple columnar in the transitional zone between the esophagus and intestine. The flattened nucleus of each mucous cell is pressed against the base by the large vacuole. The mucous secreting cells do not narrow appreciably where they open into the lumen. They can occupy nearly the entire surface and thickness of the epithelium, and they decrease in numbers from anterior to posterior. Also, smaller mucous cells with large vacuoles filled with mucous were found among the basal cells in the anterior half of the esophagus (Figure 9). The columnar epithelium appears gradually while the mucous cells decrease toward the transitional zone. The large oval nuclei of columnar cells are located at the basal level under the level of the mucous cells in the transitional zone. The basal cell layer appears to maintain a uniform thickness throughout the esophagus. These cells are small with relatively large nuclei. Occasionally, taste bud like structures were found at the tip of major folds in the most anterior part of the esophagus. No cilia are present on the epithelium of the esophagus. The mucosal layer of the esophageal-intestinal valve is similar to that of the transitional zone, except for an increased number of mucous secreting cells, especially, in the distal portion of the valve (Figure 10).

SUBMUCOSA.—The submucosal layer is an areolar connective tissue between the epithelium and the muscularis. The stratum compactum (Figure 9) is a layer of compacted fibrous connective tissue attached to the basal membrane of the epithelium. The rest of the areolar connective tissue is highly vascularized. Longitudinal bundles of striated muscles extend from the pharynx to the base of the esophageal-intestinal valve in the connective tissue. Also, in the anterior half of the esophagus, these longitudinal muscles are dispersed irregularly up to half of the depth of the folds in the submucosa (Figures 7, 9). Collagen fibers constitute the framework of the submucosal layer. The vascular system is scattered in this framework, and leucocytes, lymphocytes, fibrocytes, and granular cells are present. The granulocytes first appear in the posterior half of the esophagus (Figure 8). The submucosa becomes much thicker on both sides of the esophageal-intestinal valve. Increasing numbers of granulocytes appear in the submucosa of the intestinal side of the valve.

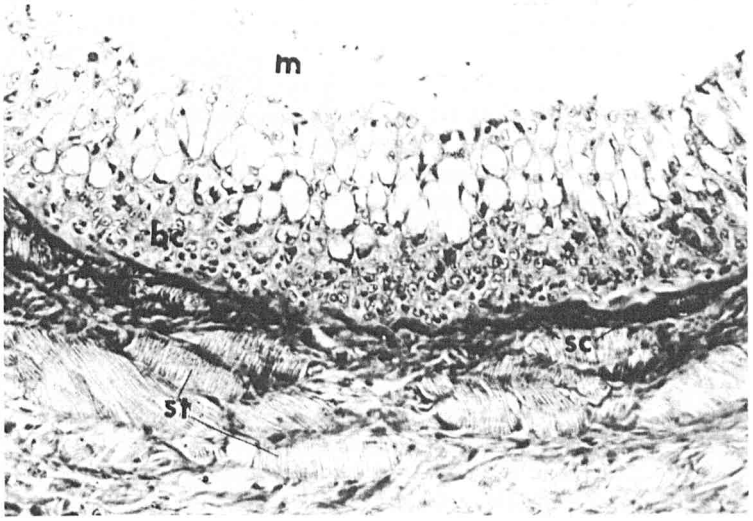

FIGURE 9.—Mucosa and submucosa of the anterior esophagus of a 200-mm SL cunner (× 400, x.s.). m, mucous secreting cell; sc, stratum compactum; st, striated muscle.

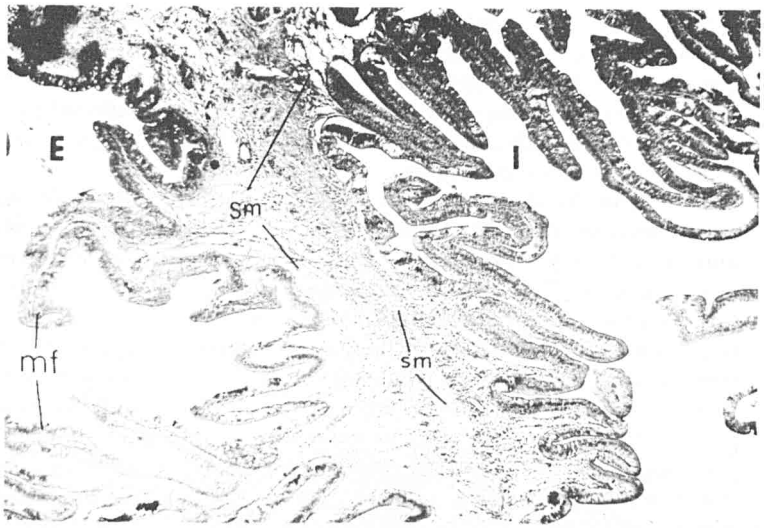

FIGURE 10.—The esophageal-intestinal valve of a 240-mm SL cunner (× 40). E, esophagus; I, intestine; mf, mucosal fold; sm, smooth muscle; Sm, submucosa.

MUSCULARIS AND SEROSA.—A very thick circular layer of striated muscles continues from the pharynx forming the external muscular layer of the esophagus (Figures 7, 8). It is invaded by elements of the vascular system accompanied by connective tissue; thus it is a loose rather than a compact layer. This muscularis appears to decrease in thickness posteriorly toward the esophageal-intestinal valve, where it forms a triangular, sphincterlike structure along the base of the valve fold. The basal muscularis of the valve is formed of smooth and striated muscles and retains significant connective tissue components. Leucocytes, fibroblasts, and a few granular cells also occur in this connective tissue. The distal portion of the valve contains a single undivided smooth muscle layer (Figure 10). This ring is continuous with the circular muscle layer of intestine.

The anterior esophagus is attached to the associated skeletal muscles by a layer of adventitious tissue. After passing through the transverse septum, the esophagus separates from the visceral wall ventrally. The dorsal wall of the midesophagus is attached to the kidney and skeletal muscles by a thin layer of adventitia (Figures 7, 8). The ventral side is covered by the peritoneal lining (serosa) and is separated from the circular muscularis by a varying thickness of areolar connective tissue (Figure 7). Posteriorly, the serosa increases in thickness in the vicinity of the esophageal-intestinal valve.

Intestine

The intestine starts posterior to the esophageal-intestinal valve and extends to the rectal valve. The intestine can be divided into four sections (Figure 1). The first section (I) begins dorsally and proceeds posteriorly and slightly to the left. It turns ventrally and extends anteriorly to the right as section II. The second loop curves abruptly posterior at about the level of the intestinal bulb. The third section (III) proceeds posteroventrally to an S-shaped loop which is connected by a short, straight portion of the intestine to the rectum. Intestinal veins from sections I, II, III, and the S-loop are associated with the anterior mesenteric vein and the posterior mesenteric vein from the rectum (Figure 1). The intestine has a consistent histological organization throughout its length with minor cytological variations. The mucosa is more complex in the intestine than in the esophagus and has zigzag folds as well as secondary and tertiary folds. The intestinal bulb is a dilation of the anterior portion of the intestine where the latter joins the esophagus. The mucosal folds of the intestinal bulb are deeper than in other portions of the intestine. There are four distinguishable layers

in the intestinal wall: mucosa, submucosa, muscularis, and serosa (Figure 11).

MUCOSA.—The epithelium of the mucosa consists mainly of columnar absorptive cells and goblet cells. The columnar absorptive cells of the cunner are similar to those of the stomachless cyprinids described by Al-Hussaini (1949a). The epithelium can be divided into the same four regions: the free border, the subborder, the supranuclear, and the infranuclear zones (Figures 12, 13, 14). The free border of the mucosa is sharply defined throughout the intestine. The striated border (or subborder) in the active digestive epithelium (Figure 14) is slightly thicker than in the inactive (Figure 13) epithelium. It stains intensively with periodic acid-Schiff (PAS) (Figure 15) and shows very prominent digestive effects in the active epithelium (Figure 14). In the resting cell of starved fish, the cytoplasm can be divided into a subcuticular zone and a layer of fine granules (Figures 12, 13). The subcuticular zone in starved fish is a compara-

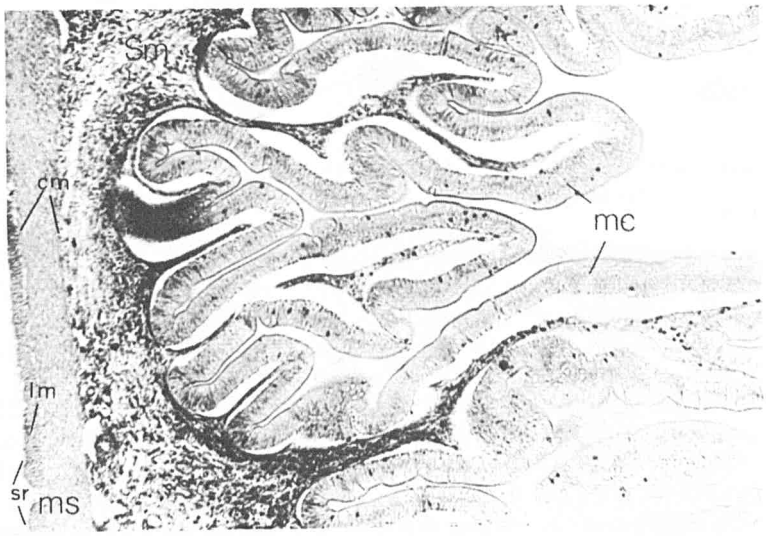

FIGURE 11.—Mucosal folds of the posterior section I of the intestine of a 240-mm SL cunner (× 100, x.s.). cm, circular muscle layer; lm, longitudinal muscle layer; mc, mucosa; ms, muscularis; Sm, submucosa; sr, serosa.

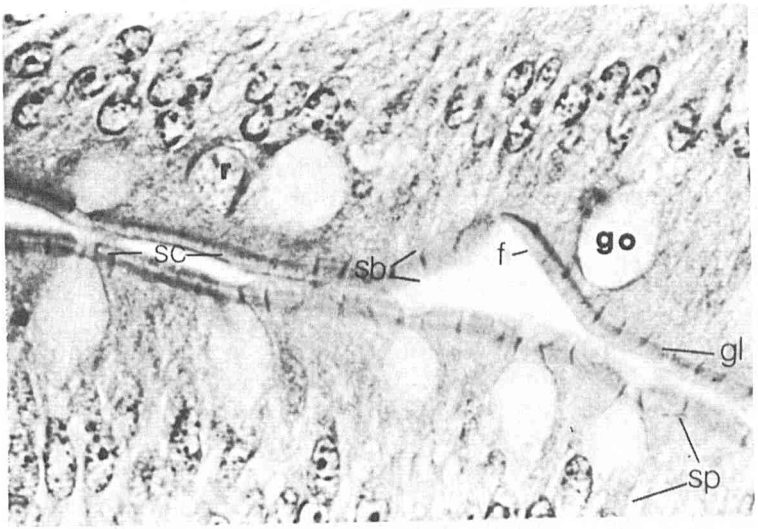

FIGURE 12.—Free border (f) of the columnar epithelium of the intestine (I) of cunner (× 1,000). gl, granular layer; go, goblet cell; r, rodlet cell; sb, subborder; sc, subcuticular zone; sp, supranuclear zone.

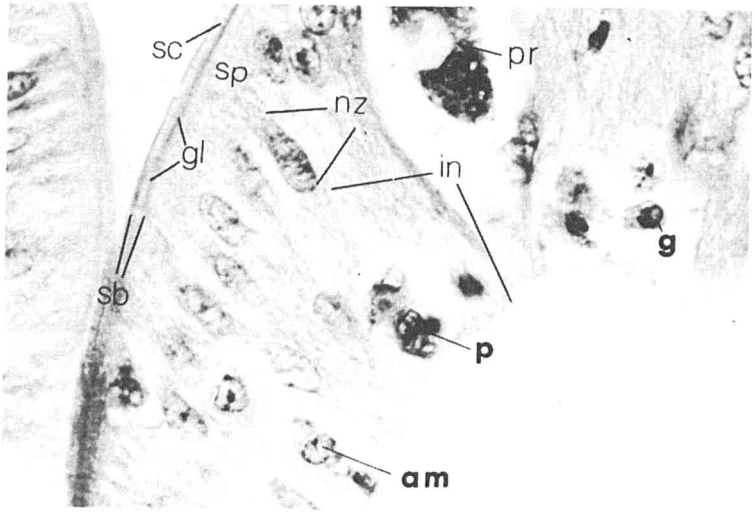

FIGURE 13.—The mucosal epithelium of the intestine (II) of cunner (× 1,000). am, ameobocyte; g, granulocyte; gl, granular layer; in, infranuclear zone; nz, nuclear zone; p, polymorpho-leucocyte; pr, parasite; sb, subborder; sc, subcuticular zone; sp, supranuclear zone.

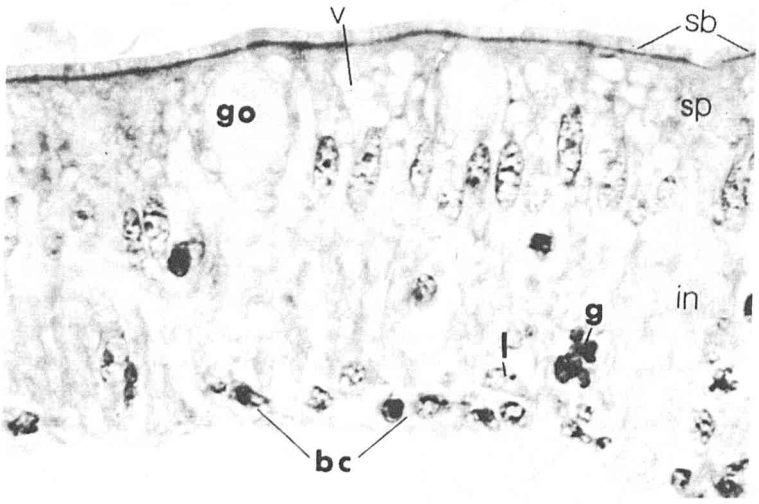

FIGURE 14.—The active absorption epithelium of the posterior intestine (III) of cunner (× 1,000). bc, basal cells; g, granulocyte; go, goblet cell; in, infranuclear zone; l, lymphocytelike cell; sb, striated border (subborder); sp, supranuclear zone; v, vacuole.

tively clear region and has a higher affinity for eosin Y than the other regions. Cell membranes are indistinguishable or indistinct resulting in a homogeneous appearance. The granular layer (Figures 12, 13) continues to the supranuclear zone and is more basophilic than other parts of the nonnuclear zones. In well-fed specimens, the resting cells have the same appearance as in the starved ones. Numerous unstained vacuoles are present in the subborder and the supranuclear zone of the active cells of the absorptive epithelium (Figure 14). In many cases, vacuoles also appeared in the infranuclear zone. The granular cytoplasm of the active cells forms a strong basophilic network around the vacuoles.

The nuclei of absorptive cells are ellipsoidal with abundant basophilic granulation and a large centrally located nucleolus. The nuclei are located at the middle or the basal third of the columnar epithelium at the intestinal bulb and then gradually move to the upper third of the epithelium posteriorly. As a result, the depth of the supranuclear zone decreases slightly posteriorly. The nuclei of the developing absorptive cells, the goblet cells, and other non-

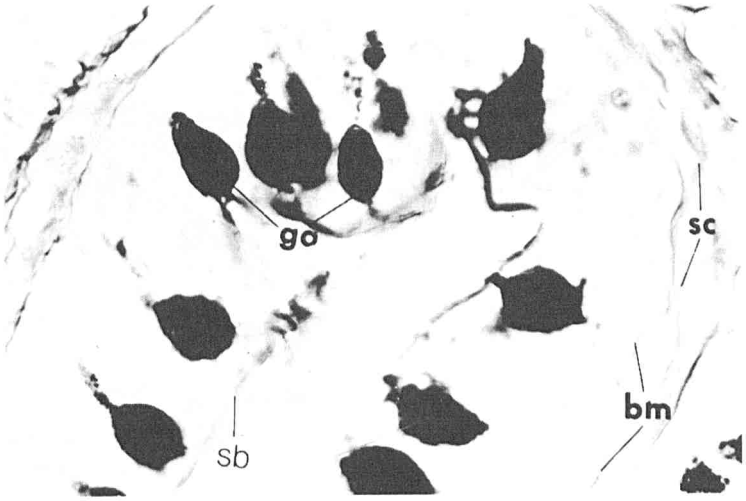

FIGURE 15.—PAS demonstration of goblet cells (go) in the intestinal epithelium (II) of cunner (× 1,000). bm, basement membrane; sb, subborder; sc, stratum compactum.

absorptive cells are found always in the infranuclear zone. The mucous secreting cells in the intestine (Figures 12, 14, 15) differ morphologically from the mucous cells in the preesophagus (Figures 3, 4, 6, 9). They are elongate with a thin neck extending to the surface and a rodlike root extending straight down to the infranuclear region (Figures 12, 15). The ovoid nucleus of the mucous cell sits at the bottom of this root. Only the mucous secreting cells near the esophageal-intestinal valve of the intestinal bulb are the same shape as the mucous secreting cells of the esophagus. Mucous cells also appear to develop in the infranuclear region and grow or extend gradually to the lumen.

A very distinct type of cell, the rodlet cell, a term introduced by Bullock (1963) for these cells in salmonids, was also found in the mucosa of the cunner (Figure 12). They are distributed throughout the intestine but are more abundant in sections II and III. They are most abundant in the bile duct (Figure 16) and inner epithelium of the gallbladder (Figure 17). The elongate, oval, rodlet cells are usually located in the supranuclear region of the mucosa and

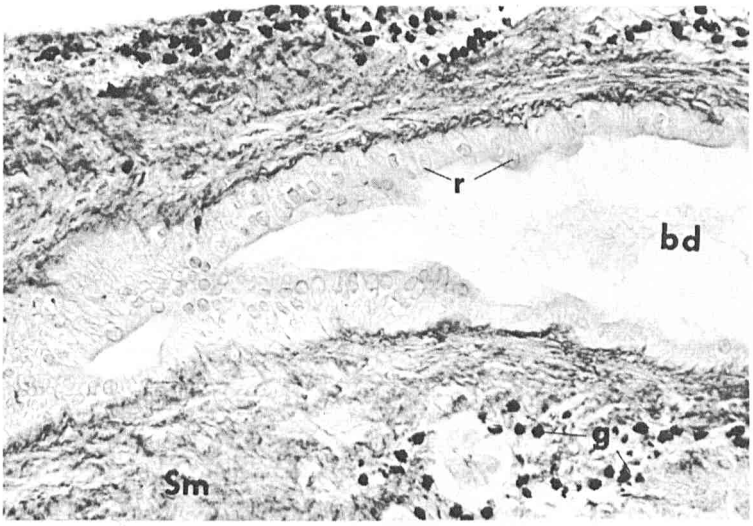

FIGURE 16.—The bile duct (bd) of cunner with abundant rodlet cells (r) (× 400). g, granulocytes; Sm, submucosa.

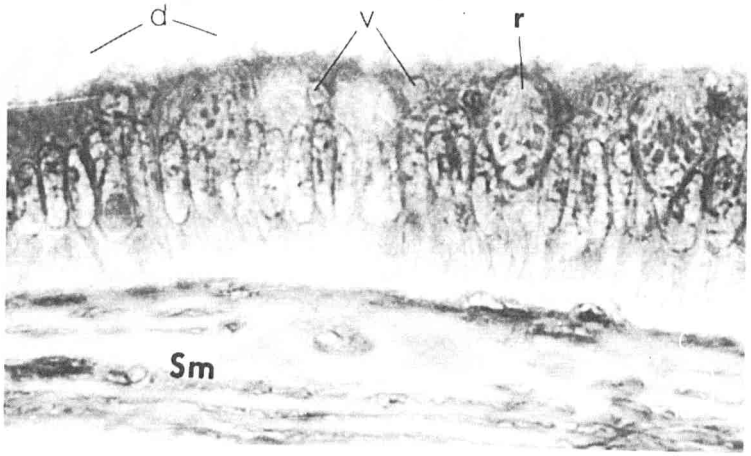

FIGURE 17.—Epithelium in the gallbladder of cunner showing rodlet cells (r), vacuoles (v), and digitiform processes (d) (× 1,000). n, nucleus of rodlet cell; Sm, submucosa.

are in direct contact with the lumen. The cytoplasm of the rodlet cells (Figure 17) consists of many granules with a threadlike structure extending from each granule to the distal end of the cell. These granules are acidophilic and stained deeply with PAS technique. A large nucleus is near the base of the cell. Various developmental stages of the rodlet cells can be observed in some of the bile duct preparations.

SUBMUCOSA.—The submucosa, which forms the core of the mucosal folds of the intestine, is a single homogeneous layer of fibrous connective tissue between the epithelium and muscularis (Figure 11). The stratum compactum, a thin layer of dense connective tissue, can be identified just beneath the mucosa (Figure 15). The collagenous fibers in the submucosa are more dense at the posterior portions of the intestine and rectum. Several cell types are scattered in the collagenous tissue. The most abundant cells are fibroblast of different stages. The young fibroblast has an ovid nucleus and basophilic astral cytoplasm (Figure 18). The fibrocytes (mature fibroblasts) are most easily seen in the submucosa of the top of the folds. It is very difficult to see any cytoplasm in these fusiform cells. The nuclei of fibrocyte is elongate or oval in shape with a

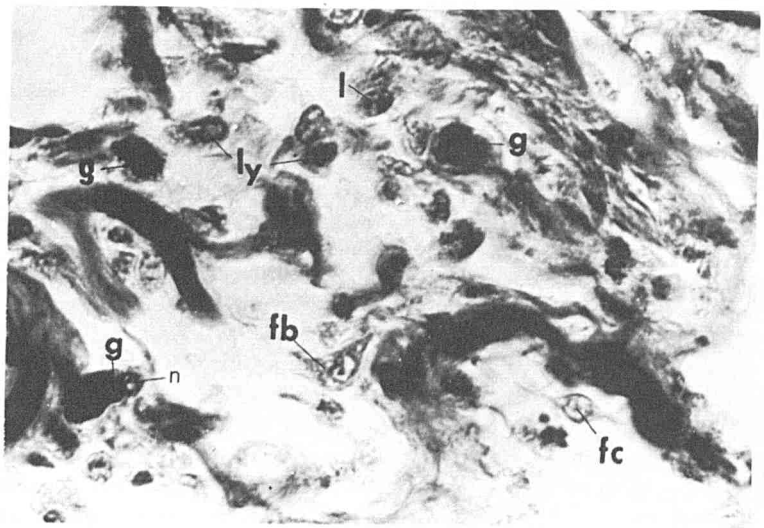

FIGURE 18.—The submucosa of the intestine of cunner (× 1,000). fb, fibroblast; fc, fibrocyte; g, granulocyte; l, lymphocytelike cell; ly, lymphocyte; n, nucleus of granulocyte.

very dense eccentric nucleolus (Figure 18). Granular wandering cells occur in the mucosa, submucosa, and muscularis (Figures 13, 14, 18), and are most abundant in the submucosa at the base of the mucosal folds. In the mucosa they are found in both the supranuclear and infranuclear zones. These cells are packed with basophilic granules. The nuclei are always pushed to the cell margin by the large granules (Figure 18). Some of the granulocytes present in the mucosa have very large compact inclusion bodies (Figures 14, 18). The polymorphonuclear leucocytes represent one type of wandering cell (Figure 13). Its nucleus has two or three lobes, and there are very fine neutrophilic granules in the cytoplasm. These leucocytes were encountered only in the infranuclear zone and the submucosal layer of the fold. A lymphocytelike type of cell was encountered also in the infranuclear zone or the base of the epithelium. This type of cell has two nucleoli in the clublike nucleus and very little cytoplasm (Figures 14, 18). They also were encountered in the submucosa occasionally. The typical lymphocytes with large nuclei and thin basophilic cytoplasm were found in the submucosa (Figure 18). At least one type of amoebocyte (Figure 13) was found in the mucosa and submucosa. This type of amoebocyte has a round nucleus with karyosomes applied to the nuclear membrane and rays extending from the nucleolus which is often eccentric. Numerous spherical granules and vacuoles occur in the cytoplasm. There are no significant differences in the distribution or types of wandering cells in the submucosa throughout the intestine.

MUSCULARIS AND SEROSA.—The typical vertebrate muscularis of inner circular and outer longitudinal smooth muscle prevails in the intestine of the cunner (Figure 11). A very thin layer of smooth, longitudinal muscle fibers (no more than two cells thick) can often be seen inside the circular muscle layer. These fibers appear at random in the first three sections of the intestine and become more prominent (two to four cells thick) from the S-loop to the rectal valve. A nerve plexus usually can be found between the muscle layers. The serosa is of a more uniform thickness than that in the esophagus and abuts directly on the extended muscularis.

Rectal Valve and Rectum

A muscular flap valve is present at the juncture of the intestine and rectum. The rectal valve is formed by a folding of the circular muscle layer and is not a sphincter valve of thickened muscularis. The two layers of the fold are separated by connective tissue (Figure 19). This layer of connective tissue contains granular cells which are more abundant in the submucosa of the rectal side of the valve. The

FIGURE 19.—Intestinal-rectal value of a 210-mm SL cunner (× 40, l.s.). cm, circular muscle; I, intestine; lm, longitudinal muscle; R, rectum; Sm, submucosa; sr, serosa.

nerve plexus, blood vessels, and longitudinal muscles merge in the connective tissue at the base of the rectal valve. Some bundles of the circular layer remain associated with the longitudinal layer at the base.

The rectum proceeds posteroventrally to the anus. In the anterior part of the rectum, the absorptive cells of the mucosa show more vacuoles in the supranuclear zone in well-fed specimens. The submucosal layer has more granulocytes than the intestine. The vascular system is also more prominent. The longitudinal muscle layer just inside the circular layer is distinct posterior to the rectal valve. Posteriorly in the rectum, the number of mucous cells decreases gradually and then increases around the anus. The epithelium of the rectum continues to the anal papillae (Figure 20). Granulocytes are the most abundant cell type in both the internal folds and external papillae of the anus. The circular muscle layer at the end of the rectum forms a sphincterlike structure. The longitudinal muscles and the nerve plexus radiate into the connective tissue around the anus. The serosa is replaced by an adventitia composed of an extensive development of fibrous connective tissue.

Associated Organs

GALLBLADDER—The gallbladder is half embedded into the liver and opens anteriorly into the intestinal bulb via the common bile duct. The bile is usually dark green and has pH values between 7.5 and 8.5. The fullness of the gallbladder was usually inversely correlated to the fullness of the intestine. It is a highly elastic structure which becomes more elongate when full. The columnar epithelial cells of the mucosa have fingerlike projections extending toward the lumen (Figure 17); however, there are no mucosal folds. A small vacuolelike structure present in each columnar epithelial cell of the gallbladder at the supranuclear zone is stained intensively in fast green, analine blue, and PAS preparations. Rodlet cells are present and are more concentrated in the bile duct than in the bladder itself (Figures 16, 17). The submucosa is a rather thin layer of very dense collagenous tissue in which a few granulocytes, fibrocytes, lymphocytes, and capillaries are present. Smooth muscle cells occur beneath the serosa, but their arrangement (spiral, random, etc.) could not be ascertained. The mucosa and submucosa of the bile duct are similar to those of the intestine; but mucous secreting cells are completely absent. The rodlet cells in the bile duct increase abruptly in number near its entrance into the intestine.

PANCREAS.—The pancreas is diffuse, forming small nodules, and consists of numerous small lobules scattered with fat and vascular

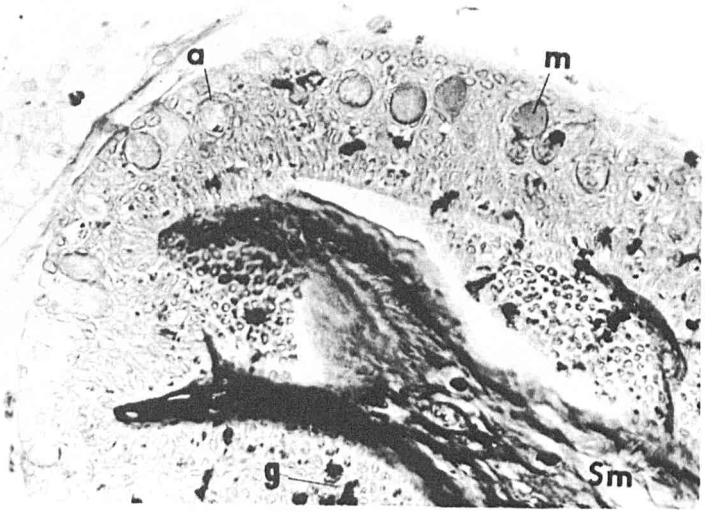

FIGURE 20.—External surface of the anal papillae of a 210-mm SL cunner (× 400). a, acidophilic mucous secreting cell; g, granulocyte; m, basophilic mucous secreting cell; Sm, submucosa.

tissue in the mesentery (omentum). It is also dispersed into the liver in the vicinity of the bile duct. Granulocytes are very abundant around the pancreas and the hepatopancreatic complex. The pancreatic duct joins the bile duct near the entrance of the latter into the intestine. The mesenteric membranes are more prominent during late summer when fatty tissue accumulates after the active feeding season.

LIVER.—The liver is divided into three lobes. The central lobe, the largest one, is triangular in shape and the tip continues to the loop of sections I and II of the intestine (Figure 1). In large specimens this lobe elongates posteriorly and covers the spleen ventrally. Two smaller lobes extend lateral-dorsally to cover most parts of the esophagus and the intestine bulb.

Histochemistry

The PAS technique intensely stains the free border and subborder of the intestinal epithelium as well as the basal membrane and goblet cells (Figure 15). The goblet cells and the granules in the granulocytes and amoebocytes give the strongest PAS reaction. Alcian blue and toluidine blue methods stained only the mucoid contents of the goblet cells, indicating the presence of acid mucopolysaccharide and mucin. None of the methods showed any secretory activity by the rodlet cells. There were no distinct differences in these reactions in the different portions of the intestine.

Throughout the alimentary tract the pH value ranged between 7.0 and 8.5. Acidic conditions were not found in either fed or starved specimens. Also, acid phosphatase tests were negative in all cases. Alkaline phosphatase can be demonstrated at the border of the epithelium throughout the gut except anterior to the esophageal-intestinal valve (Figure 21). No positive reaction for alkaline phosphatase was found in the epithelium of the gallbladder, bile duct, or pancreatic duct. Alkaline phosphatase activity was intense in the intestinal bulb and rectal valve, and it was most obvious on the distal surface of the intestinal folds in the presence of food particles.

Food and Feeding Habits

Cunners at East Point are abundant inshore during the summer and may feed intertidally during high tide. Cunner were observed swimming in the kelp beds and using the kelps *Agarum*, *Alaria*, *Laminaria*, etc. as shelter. Juveniles (less than 100 mm SL) moved intertidally or into tide pools where they use brown algae *Ascophyllum* and *Fucus* as shelter. The intestinal contents of 68 specimens (Table 1) show that the cunner is primarily carnivorous

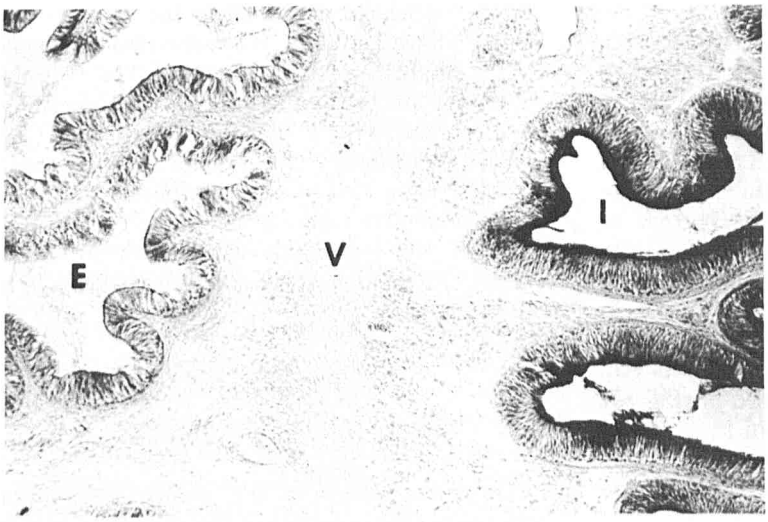

FIGURE 21.—Alkaline phosphatase test of the esophageal-intestinal valve (V) of a well-fed 180-mm SL cunner (× 100, l.s.). E, esophagus; I, intestine.

TABLE 1.—Gut content of 68 cunners, *Tautogolabrus adspersus*, from Nahant, Mass.

Standard length (mm)	30-50		100-225		230-300	
Age group (years old)	0+ -1+		1+ -4+		4+ -6+	
Specimens with food	8		27		10	
Occurrences	No.	%	No.	%	No.	%
Mussels (*Mytilus, Modiolus*)			27	100.0	5	50
Bivalve larvae			5	18.5		
Gastropod (*Littorina, Thias*, etc.)			9	33.3	1	10
Barnacles (*Balanus*)			11	40.7	5	50
Sea urchin (*Strongylocentrotus*)			7	25.9	3	30
Crustaceans (amphipod, copepod, isopod, etc.)	8	100.0	3	11.1	1	10
Decapod (crabs)			1	3.7	3	30
Tunicate (*Amaroucium*)			2	7.4	2	20
Polychaete			1	3.7		
Seaweeds with epiphytic animals (Bryozoa, Hydrozoa, etc.)	1	12.5	9	33.1	3	30
Intestinal parasites						
Acanthocephala			3	11.1	3	30
Nematode					1	10

during the active feeding season (May to September). The foods were mainly mussels *Mytilus edulis* and *Modiolus modiolus*, barnacle *Balanus balanoides*, tunicate *Amaroucium* sp., and small specimens of the green sea urchin, *Strongylocentrotus drobachiensis*. Entire gut contents may consist entirely of one species mentioned above or, usually, of a mixture of these foods. Also some seaweeds, such as *Chondrus*, *Laminaria*, *Polysiphonia*, and *Porphyra*, were often associated with the animal foods. Occasionally, crabs, amphipods, and microcrustaceans (copepods, etc.) were found. In juvenile specimens (less than 40 mm SL), amphipods and microcrustaceans were the main food. The food was well triturated in most cases although entire mussels (less than 20 mm shell length) and, in one specimen, a crab leg longer than the first portion (I) of the intestine (Figure 1) was observed. In aquaria, cunners found their food by sight. They may pick up a whole mussel from the bottom or catch falling ones as they are introduced into the tank. Also, they removed small mussels one by one or as batches from clusters. Occasionally, the food, as well as mussel shell fragments, was spat out and reswallowed. Feeding activities greatly decreased during the winter when water temperature in the aquaria dropped below 4°-6°C. This was especially noticeable in the large individuals caught during the previous summer.

Movement and Digestion of Food Materials within the Gut

The gut in unfed cunner had little or no fluid in the lumen. The intestine and rectum were rather constricted with thick walls. During feeding, small mussels were picked up with the jaw teeth and triturated by the pharyngeal teeth before entering the esophagus. The crushed mussels were pushed back into the eophagus and intestine due to continuous food ingestion during the feeding period. Feeding continued until the food was packed up to the sigmoid loop (Figure 1) and occasionally even to the rectal valve or rectum. The intestinal lumen distends and the wall in turn becomes thinner when the gut is full. The shells of one feeding period always moved as a unit separate from the next feeding period. A period of 10-14 hr was required for mussel shells from a single feeding period (½-1 hr) to pass through the alimentary tract. The compact mass of shells moving along the intestine sometimes straightened the S-loop. Food storage in this stomachless fish was achieved mainly by the intestine anterior to the S-loop. The loop between sections I and II formed a saclike reservoir (Figure 1). Ingested foods remained in section III longer than in the other loops suggesting that this section may be responsible for more digestion and absorption than the other sections. Fluid developed in the lumen during and for a short while after the presence of shells. The amount of bile secretion depended on the quantity of food ingested. The volumes could not be estimated in the present study. In most fish with a full gut which were dissected immediately after capture, the gallbladders were shrunken or contained brownish fluid. The entire range of pH value found in all parts of the gut, both empty and full, was 7.0-8.5, thus suggesting alkaline digestion in the cunner gut.

DISCUSSION

Digestive System

The morphology of the mouth and buccal and pharyngeal cavities of the cunner is similar

to the labrids described by Al-Hussaini (1947b). The buccal valve (Figure 2) is similar to that of *Julis aygula* reported by Gohar and Latif (1961), except for the obvious thickening of the mucous layer of the anterior surface in juvenile cunners. The rather short relative length of the gut of the cunner, i.e., the postpharyngeal portion of the alimentary tract, is about 0.8-1.0 of standard length. The extensive vascularization of the serosa and adventitia of the rectum and the strong alkaline phosphatase activity of the rectal mucosa indicate that this region is very active in absorption and/or secretion. The S-loop of the intestine may be unique because it was not described for other labrids by Suyehiro (1942) and Gohar and Latif (1959, 1961) nor in some other stomachless fishes reported by Babkin and Bowie (1928) and Al-Hussaini (1949a). Bullock (1967) recorded a similar flexure in the posterior portion of the intestine of *Gambusia affinis*. The S-loop was somewhat straightened by large amounts of food in the lumen. Alkaline phosphatase tests show weak positive reaction in the S-loop. The significance of the loop may be mechanical rather than physiological. There are no successive constrictions of the intestine in cunner as observed by Gohar and Latif (1961) in *Pseudoscarus harid* and credited by those authors to *Julis aygula*.

Epidermal mucous secreting cells in the epithelium of the alimentary tract of cunner are mostly concentrated in the postpharyngeal cavity and the esophagus and on the anal papillae. These cells have no stalklike elongation at the bottom of the globule nor a narrow necklike structure before the open end (Figures 3, 4, 6, 9, 20) as do those of the intestine and rectum (Figures 12, 14, 15). No precise histochemical differentiation of these mucous cells was obtained. These different types of mucous cells have been reported by Al-Hussaini (1947a), Gohar and Latif (1961), Mohsin (1962), Bullock (1967), Western (1969), and Bucke (1971) in various fishes. Al-Hussaini (1949b) and Bullock (1963), following the terminology of Baker (1942), described the free border of the absorptive columnar cells in the intestine as divided into a superficial layer, a canal layer (or microvilli region), and a granular layer. These were also distinct in the cunner gut.

The rodlet cells are similar to those discussed by Bullock (1963) in the intestine of salmonid fishes and the pear-shaped cell of Al-Hussaini (1949b) recorded in *Gobio gobio*. These cells appeared throughout the gut except in the anterior intestinal bulb and the posterior rectum as in *Gambusia affinis* (Bullock, 1967). They are also found in the bile duct, gallbladder, and collecting duct of the kidney of the cunner. Bullock (1963) also described the appearance of rodlet cells in the kidney of *Catostomus* species. Al-Hussaini (1964) described the mitosis of the pear-shaped cell in *Cyprinus carpio*. He stated that experimental evidence indicated the pear-shaped cell may originate from goblet cells in *C. carpio* and *Gobio gobio* and from wandering blood or connective tissue cells in *Rutilus rutilus*. No comparable evidence of the division nor origin of the rodlet cells was found in this study. Bishop and Odense (1966) proposed that the pear-shaped cell may be a possible enzyme source in the intestine of the cod, *Gadus morhua*. But the negative phosphatase reactions of the rodlet cells in the cunner agree with Bullock's 1963 findings for salmonids. Different cytological or developmental stages of rodlet cells were observed in the mucosa of the bile duct, gallbladder, and intestine. The rodlet cells and their empty capsules, which have no distinct nuclei, were partially or entirely free from the mucosa of the bile duct. Occasionally, ejection of granules from the rodlet cells was seen. Rodlet cells have not been described in labrids prior to the present account. The question remains as to whether they are normal cells or coccidian parasites (Plehn, 1906).

The submucosal layer of the cunner gut is composed of a rather homogeneous fibrous connective tissue. There is neither muscularis mucosa nor lamina propria. The stratum compactum in various fishes has been discussed by Al-Hussaini (1947a), Burnstock (1959), Gohar and Latif (1961), Mohsin (1962), Bullock (1963), and Bucke (1971). In cunner it is a thin layer of regularly arranged fibers immediately beneath the mucosa. In oblique sections, fibrils can be seen passing from the

stratum compactum into the basement membrane.

Granulocytes in the submocosa of cunner can migrate to both the mucosa and the muscularis. According to Bolton (1933), basophilic granule cells occur in vast number in connective tissue throughout the gut of salmonid fishes. He suggested that they were histogenous cells developed from mesenchymal cells. Al-Hussaini (1949b) mentioned that two types of granulocytes also occurred in the intestine of a variety of fishes; some stained blue with Giemsa stain (*Trigla hirundo* and *Salmo trutta*), and others stained red with Giemsa (*Scarus sordidus, Rutilus rutilus, Gobio gobio, Atherina forskali, Cyprinus carpio, Crenilabrus melops,* and *Mulloides auriflamma*). Bullock (1963, 1967) stated that the granulocytes had varying results in staining reaction according to the different pH value of the stain, which was also true in this study. Large granulocytes, densely packed with granules which appear purplish with Giemsa stain, were abundant in the mucosa of cunner (Figure 14); smaller granulocytes were present which have smaller red staining granules in Giemsa (Figure 18). In addition, a type of granulocyte was observed in which the granules were condensed against the nucleus (Figure 13). Bullock (1963) found cells intermediate between granulocytes and globule leucocytes in salmonids but not in *Gambusia affinis* (Bullock, 1967). This intermediate type cell was found in various levels of the epithelium and submucosa of cunner intestine. No precise cytochemical demonstration of the possible relationships between granulocytes and leucocytes was obtained in this study. The wandering nature of the granulocytes did not seem to correspond in any way with the food contents in the intestine of the cunner. Aggregations of granulocytes occurred in the submucosa of the bile duct, rectal valve, and anal papillae of the cunner (Figures 16, 19, 20). Granulocytes similar to those in the intestine were also very abundant in the pancreas and kidney. The function of granulocytes may differ from species to species (Al-Hussaini, 1949b). The fine granules of the granulocytes were stained with PAS in many specimens of cunner. No evidence that granulocytes help in the absorption and transportation of digested foods was found in cunner as reported for other teleosts (Al-Hussaini, 1949b; Mohsin, 1962). Special aggregations of other types of wandering cells such as: polymorphonuclear leucocytes, lymphocytes, and amoebocytes were not found. The presence of amoebocytes (Figure 13) with large vacuoles and a large nucleus as observed in this study does not appear to have been previously recorded.

The muscularis of the esophageal-intestinal valve (Figure 10) and rectal valve (Figure 19) are formed of circular muscles. Gohar and Latif (1959, 1961) mentioned only one layer of muscle fibers in both the esophageal-intestinal valve and the rectal valve of the labrid *Julis aygula*. This is true in the esophageal-intestinal valve of the cunner, but in the rectal valve of the cunner, the circular muscle layer is folded and the two folds are separated by fibrous connective tissue. Al-Hussaini (1947a, 1947b) indicated two separate muscle layers in the ileo-rectal valve of the stomachless *Atherina forskali*, and Western (1969) described the same arrangement in *Cottus gobio*. It would appear that a more careful analysis of the intestinal-rectal (ileo-rectal) valve is required.

The differentiation of duodenum and ileum reported to occur in stomachless labrids (Gohar and Latif, 1961) was not found in the intestine of the cunner. Histological differentiation of the intestine was not mentioned by Curry (1939), Al-Hussaini (1947b), Khanna (1961), nor Bullock (1967) in other stomachless fishes. Thickening of the circular muscle layer at the anterior end of the rectum in cunner was similar to that in other species of stomachless fishes (Dawes, 1929; Al-Hussaini, 1947a, 1947b; Khanna, 1961; Gohar and Latif, 1961; Mohsin, 1962; Bullock, 1967). However, the additional thin layer of longitudinal muscle fibers present inside the muscularis in the rectum of the cunner was not reported by these investigators.

Al-Hussaini (1949b) reported that alkaline phosphatase was most abundant in the free border of the absorptive cell of three species of stomachless minnows—*Cyprinus carpio, Gobio gobio,* and *Rutilus rutilus*. Similar results were found along the free border of the

intestinal epithelium of the cunner in cells which are in direct contact with the food. An extremely strong alkaline phosphatase reaction was found in the intestinal bulb and anterior half of the rectum in the cunner. This reaction seems to be restricted to the free border of the epithelial layer of the intestine and rectum. Evidence of active rectal digestion also has been reported by Babkin and Bowie (1928), Ishida (1936), Al-Hussaini (1949b), Bullock (1967), and Western (1971) in other stomachless fishes.

The close association of the pancreas and bile duct in cunner observed in this study agrees with the observations of Gohar and Latif (1959) for another labrid, *Julis aygula*. Vacuoles (which stained intensively with fast green or with aniline blue) were observed in the supranuclear zone of the columnar epithelium of the gallbladder (Figure 17). No reference to this situation was found in the literature, and no data were acquired in this study to determine the function of these vacuoles.

Feeding Habits

Cunners are most active in daytime both in aquaria and in the field. Their activity decreased sharply during the night, the fish lying against objects on the bottom or hiding in crevices. Torpid behavior was observed during the day when the water temperature in the aquarium fell below 4°C. Bigelow and Shroeder (1953) and Green and Farwell (1971) also noticed that cunners become torpid during winter.

Cunner reach their greatest inshore abundance in summer (July- August). They were absent from the summer habitat from early November to late April. Observations made by SCUBA diving indicate that the offshore movements began as the water temperature dropped below 11°C (September 1971). A slight migration of cunner during the winter was postulated by Johansen (1925) and also reported by Bigelow and Schroeder (1953) and Green and Farwell (1971). Local fishermen reported the species to be present in deeper (more isothermal) waters in the winter. Juveniles tended to move into shallow water in early spring as reported by Johansen (1925). Some juveniles were collected during this season in brackish water at the Jackson Laboratory of the University of New Hampshire on Great Bay, N.H. This is in accordance with the statements of Johansen (1925) but is contrary to those of Bigelow and Schroeder (1953).

Cunners fed on both sessile (*Mytilus edulis* and *Modiolus modiolus*) and moving animals (*Fundulus heteroclitus*, *Gammarus oceanicus*, *Nephtys bucera*, *Nereis virens*, and *Cerabratulus lacteus*) in the laboratory and also acted as scavengers. Gut content analyses (Table 1) indicate that cunner are carnivorous rather than omnivorous in contrast to statements by Johansen (1925) and Bigelow and Schroeder (1953). There was no evidence that cunner actively consume algae in the aquarium even when starved. Algae found in the gut of cunner are always small and undigested and are frequently associated with digested epiphytic animals (bryozoans, hydrozoans, and larval molluscs). A change of prey was noted between juvenile and adult cunner (Table 1). Juveniles feed mainly on motile crustaceans in the water column, adults on sessile or sedentary animals. A few large, offshore specimens showed a further change in feeding habits.

In this study almost every adult specimen had mussel shells in the gut. Mussels *Mytilus edulis* and *Modiolus modiolus* cover the rock faces in the feeding habitat from which the cunner were taken. Most of the mussels eaten by cunner were less than 2 years old. Many other labrids are also mollusk feeders (Suyehiro, 1942; Al-Hussaini 1947b; Gohar and Latif, 1959). Randall (1967) recorded the food habits of 11 species of western Atlantic wrasses —all of which, except for the plankton feeding *Clepticus parrai*—tended to feed on hard-shelled invertebrates such as mollusks, crustaceans, and echinoderms. No algae were mentioned by these authors except that 5 out of 50 specimens of *Halichoeres poecilopterus* had seaweeds (*Ulva*, etc.) present (Suyehiro, 1942).

Feeding habits of cunner are related to their jaws, teeth, pharyngeal mill, and also the length of the intestine as reported for other stomachless fishes (Suyehiro, 1942; Al-Hussaini,

1949a; Gohar and Latif, 1961; Mohsin, 1962; Weatherley, 1963). The protrusible jaws of the cunner have sharp caninelike teeth which are adapted to catching, picking, and scraping animal foods. The strong muscles (hypobranchial and branchiomeric muscles) associated with the mouth can keep the jaws closed tightly, and quick movements of the body could help in detaching sessile organisms from the rocks. The molariform pharyngeal teeth of the cunner serve as a mill to grind up the hard shells of the ingested foods. The probability that well-developed pharyngeal teeth have taken over the mechanical function of the stomach among the stomachless fishes had been suggested previously by Barrington (1942, 1957), Suyehiro (1942), Al-Hussaini (1947b), and Gohar and Latif (1961).

Ingested foods passed rapidly through the buccal cavity and pharynx in the cunner as in most bony fishes. In the present study, the movement of mussels through the intestine of cunners fed in the laboratory, required 10 to 14 hr. Intact and alive mussels were found in all parts of the gut of freshly killed specimens both in the field and aquarium. Some of these mussels (less than 16 mm shell length) still were able to resettle. Field observations indicated that the largest individual mussels (over 100 mm shell length) were scattered on the surface of bare rocks 5 to 10 m below the tidal zone. However, the major population of the mussels formed patches or clusters in the intertidal zone. Perhaps cunner play a role in the vertical distribution of mussels.

No specific area of food storage was found in the cunner; the gut of fish which had been fed all they desired was completely packed with food, and it appeared that the entire intestine can serve as a storage organ while digestion is being completed. The intestinal bulb of stomachless fishes may substitute as a storage organ (Babkin and Bowie, 1928; Barrington, 1942; Al-Hussaini, 1947a; Khanna, 1961; Mohsin, 1962; Bullock, 1967).

Alkaline conditions (pH 7.0-8.5) prevailed throughout the gut in all specimens of cunners examined. In starved controls, there was little variation in pH value observed among regions of the intestine. However, in feeding fishes, the pH varied in a random fashion from region to region and showed no significant gradient. Phosphatase tests show a positive reaction for alkaline phosphatase, but negative for acid phosphatase. Intercellular digestion per se in the cunner is exclusively alkaline. Among other stomachless fishes, alkaline digestion was observed throughout the gut by Babkin and Bowie (1928), Ishida (1936), Barrington (1942, 1957), Al-Hussaini (1947a), Gohar and Latif (1959, 1961), and Bullock (1967).

Szarski (1956) discussed the advantages of alkaline digestion in stomachless freshwater fishes. He referred to the high biological value in retention of essential ions, which could also apply to the present species. Cunners feed mainly on shelled animals and the incidence of tooth damage is high. As is evident from having developing teeth along the edge of the old ones on the premaxillary, dentary, and pharyngeal bones. The apparent continuous regeneration and growth of teeth needs large amounts of calcium. The calcium supply cannot be obtained from the calcium carbonate of the animal shells due to the alkaline condition in the gut. Presumably, the calcium source is from the calcium pool of the viscera of the ingested animals.

ACKNOWLEDGMENTS

I thank my thesis committee members, H. D. Ahlberg, B. B. Collette, C. A. Meszoely, and N. W. Riser of the Biology Department of Northeastern University. My deepest appreciation goes to N. W. Riser, Marine Science Institute, Northeastern University, for his encouragement and advice from the very beginning to the completion of this research and to B. B. Collette, Systematics Laboratory, National Marine Fisheries Service, NOAA, for his critical comments and help. In addition, I acknowledge helpful comments on the contents and organization of this paper by R. H. Gibbs, Jr., Division of Fishes, U. S. National Museum, and J. A. Musick and J. D. McEachran, Virginia Institute of Marine Science.

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THE PYGMY WHITEFISH, *PROSOPIUM COULTERI*, IN WESTERN MONTANA

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ABSTRACT

The pygmy whitefish, *Prosopium coulteri*, is a glacial relict which has been considered to be the most primitive of coregonines. It is relatively abundant in lakes of western Montana and is undoubtedly an important source of food for Dolly Varden and lake trout. Compared to other members of its subfamily, it is characterized by low meristic counts. These counts differ somewhat in populations from Montana, Alaska, and Lake Superior.

Major food items consumed by the pygmy whitefish shift with availability but the main reliance is on cladocera and chironomid larvae and pupae. The annual growth in Flathead Lake, Mont., is greater than that in Lake Superior but below that in some Alaskan lakes. No males were found older than age III and no females beyond age IV. Many of the males mature at age I, a year earlier than most females. The spawning season is in December and January when the fish move into tributary streams. The species spawns in successive years. The fecundity of the Montana fish is similar to that of pygmy whitefish from other areas.

The pygmy whitefish successfully competes with other coregonines in reproduction by spawning at a later date and earlier age, and by having smaller eggs which yield more eggs per unit weight of fish. The small size and early age at maturity are considered adaptations developed for survival in cold and nutrient-poor water during glaciation.

The pygmy whitefish, *Prosopium coulteri*, is considered a glacial relict that survived in deep lakes after the retreat of the Wisconsin glaciation. Until the past 20 years the species was infrequently captured, or recognized when it was. It usually inhabits depths of over 30 ft and, because of its small size, escapes capture by most fishing gear. The present distribution is given as the Columbia, Fraser, Skeena, Yukon, and MacKenzie River systems, and both the Pacific Ocean and Bering Sea drainages of southwest Alaska (Heard and Hartman, 1966). In 1955 the report of this little fish from Lake Superior disclosed a remarkable case of disjunct distribution (Eschmeyer and Bailey, 1955).

Only in recent years has it been recognized how ubiquitous the pygmy whitefish is in western Montana. It was first reported in Montana by Schultz in 1941 from tributaries of Lake McDonald in Glacier National Park. The next report was from Bull Lake, a tributary to the Kootenai River (Weisel and Dillon, 1954). In the past 10 years it has been taken with small-mesh gill nets from Flathead, Ashley, Swan, Seeley, and the Little Bitteroot Lakes—all tributary to the Clark Fork River (Brown, 1971). Careful collecting will undoubtedly show the species to be present in many other glacially formed lakes in western Montana.

Our studies show the pygmy whitefish to be one of the most abundant fishes in Flathead Lake. According to Hanzel's 1968-71 extensive nettings, this species constituted 4.8% of the total catch; it ranked in order only below lake whitefish (*Coregonus clupeaformis*), peamouth (*Mylocheilus caurinus*), kokanee (*Oncorhynchus nerka*), northern squawfish (*Ptychocheilus oregonensis*), Dolly Varden (*Salvelinus malma*), and yellow perch (*Perca flavescens*).

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Manuscript accepted October 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

Because of the small size and abundance of the pygmy whitefish, it must be important as a primary carnivore available to species next in the food chain. The only extensive detailed publications on pygmy whitefish, however, are those of Eschmeyer and Bailey (1955) dealing with Lake Superior populations and of Heard and Hartman (1966) and McCart (1970) with Alaskan populations. Our work is concerned with populations from Flathead Lake and Bull Lake in the upper Columbia River drainage but involves comparisons where applicable to the Lake Superior and Alaskan forms. Some comparisons are also made with the mountain whitefish, *Prosopium williamsoni*, a closely related sympatric species.

ASSOCIATED FISHES AND DESCRIPTION OF THE LAKES

Flathead Lake is a large oligotrophic lake covering 126,000 surface acres and reaching a depth of 365 ft. Its major tributaries are the Flathead and Swan Rivers. Its outlet, the Flathead River, joins the Clark Fork River of the Columbia River.

Like many glacial lakes, Flathead Lake is depauperate in native fishes. Indigenous fishes in the lake are cutthroat trout (*Salmo clarki*), Dolly Varden, pygmy whitefish, mountain whitefish, longnose sucker (*Catostomus catostomus*), largescale sucker (*C. macrocheilus*), peamouth, redside shiner (*Richardsonius balteatus*), northern squawfish, and slimy sculpin (*Cottus cognatus*).

Around the turn of the century a number of other species were introduced. The exotic forms presently in the lake are rainbow trout (*Salmo gairdneri*), lake trout (*Salvelinus namaycush*), brook trout (*S. fontinalis*), kokanee, lake whitefish, black bullhead (*Ictalurus melas*), yellow perch, pumpkinseed (*Lepomis gibbosus*), and largemouth bass (*Micropterus salmoides*). Plants of other exotics, including a 1969 plant of coho salmon, *Oncorhynchus kisutch*, were not successful. The northern pike, *Esox lucius*, thrives in Flathead River below the hydroelectric dam at the lake's outlet but is not reported from the lake. Fish species most often taken in the same net settings with pygmy whitefish are lake whitefish, lake trout, and Dolly Varden.

Bull Lake is comparatively small and shallow and is somewhat eutrophic. The total surface is 1,250 acres and the maximum depth is 64 ft. Ross Creek, where the pygmy whitefish were captured during their spawning runs, is the largest tributary.

No thorough studies have been made of the fish species in Bull Lake but, besides pygmy whitefish, it is known to contain rainbow trout, cutthroat trout, brook trout, Dolly Varden, kokanee, mountain whitefish, redside shiner, northern squawfish, peamouth, longnose sucker, largescale sucker, largemouth bass, and a sculpin.

MATERIALS AND METHODS

Pygmy whitefish were collected from Flathead Lake during an investigation on fish populations by the Montana Fish and Game Department. A 35-ft former commercial fishing boat modified to handle specialized fishing gear and provided with a recording sonar was used to set and pull nets from 11 sample areas during 4 seasons from November 1967 through August 1971. Six hundred feet of gill netting ranging from ⅝-inch to 4-inch stretched mesh were laid in 165 settings. Except for spawning populations practically all pygmy whitefish were caught in the ⅝-inch and 1¼-inch mesh portion and were taken within 3 ft of the bottom. The largest collections were taken during the late summer at depths of 60 to 270 ft. Unfortunately, too few pygmy whitefish were taken to interpret an overall distributional pattern.

The Bull Lake collections were taken with seines from spawning aggregations in the lake's inlet during December of 1952, 1955, and 1967.

Counts on scales, gill rakers, and vertebrae followed the methods outlined by Hubbs and Lagler (1964). Gill raker counts included rudimentary rakers and sutures in the hypural complex were regarded as separating vertebrae. Specimens used for vertebral counts were eviscerated, filleted, cleared in KOH, and stained in alizarine red S according to the procedure of Evans (1948).

Standard lengths were measured in millimeters and weights in tenths of grams. To compare our results with the data of other authors who used fork length or total length, it was necessary to use conversion factors. Total length was considered equal to 0.21 plus 1.19 standard length, and the standard length equal to -0.09 plus 0.83 total length. The conversion of fork length to total length used was that given by Heard and Hartman (1966) where fork length times 1.0777 equals total length for specimens shorter than 100 mm and times 1.0845 for the larger specimens.

Scales for age and growth studies were removed from an area above the lateral line just posterior to the dorsal fin. Plastic impressions were made of the scales and projected to an enlargement of 67 times for measurement.

SOME MERISTIC CHARACTERS

Lateral-Line Scales

A striking character of the pygmy whitefish is its large scales. In its northern range the lateral-line scales number 50 to 73, in Lake Superior 54 to 62, in Flathead Lake 52 to 65, and Bull Lake 54 to 63 (Table 1). The mean number of scales varies somewhat among different populations. A low mean of 54.29 is given for fish from Chadburn Lake, Yukon, and a high of 71.57 for low-rakered fish from Lake Aleknagik (McCart, 1970). Pygmy whitefish from Flathead Lake and Bull Lake are intermediate. The closely related mountain whitefish possesses lateral-line scales ranging from 73 to 92 in the Columbia River drainage (Holt, 1960).

TABLE 1.—Frequency distribution of the lateral-line scale counts in pygmy whitefish.

Number of scales	Flathead Lake	Bull Lake
52	3	—
53	4	—
54	3	1
55	5	2
56	12	1
57	14	3
58	14	6
59	15	11
60	9	10
61	6	4
62	4	6
63	6	4
64	1	—
65	3	—
Mean	58.2	59.5

Gill Rakers

The number and length of gill rakers have proved useful in the systematics of coregonines. The range in gill rakers is considerable in pygmy whitefish, from 12 to 21. On the basis of gill raker number and other meristic and morphological data, McCart (1970) distinguished two forms of pygmy whitefish which occur sympatrically in some Alaskan lakes. One form has high raker counts and the other has low raker counts. McCart suggested a western refugium south of the ice sheet for the origin of the Alaskan low gill raker form, a Yukon-Bering Sea refugium for the Alaskan high gill raker form, and a Mississippian refugium for the Lake Superior form.

Pygmy whitefish from Flathead Lake have a range of 14 to 18 gill rakers (mean 15.83); those from Bull Lake range from 15 to 18 (mean 16.28). These means are considerably lower than the 18.28 mean of fish from Lake Superior (Table 2). According to McCart's figures, the Flathead Lake and Bull Lake populations would be classified as high-rakered in comparison with Lake Aleknagik populations,

TABLE 2.—Frequency distribution of gill raker counts in pygmy whitefish.

Locality	Number of gill rakers							
	14	15	16	17	18	19	20	Mean
Lake Superior[1]	—	—	1	6	17	13	3	18.28
Columbia River drainage:								
Lake McDonald[1]	—	2	5	5	3	5	—	17.20
Bull Lake[1]	—	2	6	10	2	1	—	16.71
Flathead Lake	4	15	24	8	3	—	—	15.83
Bull Lake	—	4	13	5	3	—	—	16.28
Alaska:								
Lake Aleknagik:[2]								
High raker			range 14-17					15.28
Low raker			range 12-15					13.46
Naknek Lake:[2]								
High raker			range 16-19					17.33
Low raker			range 13-16					14.54
Chignik Lake:[2]								
High raker			range 17-21					19.21
Low raker			range 13-16					14.16

[1] From Eschmeyer and Bailey (1955).
[2] From McCart (1970).

but intermediate compared to Naknek Lake and Chignik Lake populations. Our counts, as well as those on Lake McDonald fish, do not support McCart's contention that the low-rakered form persisted in the vicinity of the Columbia River Basin during the Pleistocene glaciation.

Vertebrae

As with other meristic characters, the vertebral count of the pygmy whitefish is low for a coregonine. The number of vertebrae is variable however—from 49 to 55. The plasticity of this character is within individual populations as the species exhibits similarity in the mean count of vertebrae throughout its range. The Flathead Lake fish have a mean number of 52.3 and the Bull Lake specimens, a mean of 52.7 (Table 3). Mean vertebral count of the fish from Lake Superior was given as 52.9 by Eschmeyer and Bailey (1955). The lowest mean is 51.5 for Chignik Lake (McCart, 1970).

It appears that most of the variation in the vertebral number is in the caudal rather than precaudal vertebrae. The number of caudal vertebrae ranges from 21 to 26 whereas the precaudals vary from 27 to 31 in Flathead Lake and Bull Lake fish. The number of caudals individually plotted with their respective total number have means that nearly increase by the value of one with each increase in similar value in total number of vertebrae (Table 4).

Although low, the total number of vertebrae of the pygmy whitefish overlaps the lower range of the mountain whitefish. Holt (1960) gave a range of 53 to 61 for the mountain whitefish in the Columbia River drainage. Twenty specimens of the mountain whitefish from Lolo Creek used in our study had caudal vertebrae ranging from 25 to 27, again a slight overlap.

TABLE 3.—Frequency distribution of total number of vertebrae in pygmy whitefish.

No. of vertebrae	Flathead Lake	Bull Lake
50	2	—
51	6	3
52	24	16
53	26	18
54	2	7
55	—	1
Mean	52.3	52.7

TABLE 4.—Relation of number of caudal vertebrae to total number of vertebrae in pygmy whitefish.

Item	Total vertebrae				
	51	52	53	54	55
Caudal vertebrae:					
Range	21-24	21-25	21-25	24-25	26
Mean	21.86	22.82	23.39	24.43	26.00
Number of specimens	7	33	33	7	1

AGE AND GROWTH

Age was determined for 494 pygmy whitefish taken from Flathead Lake during April 1967 through May 1971. Sex was determined on 272 specimens, mostly from mature fish captured in November and December.

Only one fish of age 0 was collected. Fish of this age are so small that they are unlikely to be captured in the collecting gear we used. The percentage of the total fish by age group was: 0, 0.2% ; I, 47.2% ; II, 46.1% ; III, 5.9% ; and IV, 0.6%. Overlap was considerable in the length-frequency distribution between adjacent age groups and between the sexes (Table 5).

Growth rate was calculated by establishing the relationship between the body length and the anterior scale radius. The value of 0.9854, the coefficient of variation r, developed on the 493 measurements, suggests a strong degree of linearity between the body-scale measurements. This linearity differs from the sigmoid body-scale relationship found for pygmy whitefish from Alaskan waters by Heard and Hartman (1966).

The equation fitted from the individual pairs of body and scale measurements was: Total body length = 0.913 anterior scale radius + 61.63. Mean body lengths from each scale radius were plotted against the calculated regression line shown in Figure 1. Total lengths were back calculated by direct proportion (Table 6).

Annual growth of females in Flathead Lake exceeded growth reported for Brooks Lake (Alaska), Lake McDonald (Montana), and Lake

TABLE 5.—Length frequency of age groups of pygmy whitefish from Flathead Lake, 1967-71.

[F, females; M, males.]

Total length (mm)	I M	I F	II M	II F	III M	III F	IV M	IV F	Total M	Total F
84	—	1	—	—	—	—	—	—	—	1
89	1	—	—	—	—	—	—	—	1	—
91	—	—	—	—	—	—	—	—	—	—
94	1	—	—	—	—	—	—	—	1	—
99	1	—	—	—	—	—	—	—	1	—
102	1	—	—	—	—	—	—	—	1	—
104	2	—	1	—	—	—	—	—	3	—
107	4	1	—	—	—	—	—	—	4	1
109	8	3	1	1	—	—	—	—	9	4
112	8	2	—	—	—	—	—	—	8	2
114	31	2	—	3	—	—	—	—	31	5
117	21	3	1	—	—	—	—	—	22	3
119	18	2	5	—	—	—	—	—	23	2
122	10	—	2	1	—	—	—	—	12	1
124	6	1	5	1	—	—	—	—	11	2
127	5	—	7	1	—	—	—	—	12	1
130	—	—	5	—	—	—	—	—	5	—
132	2	—	12	8	—	1	—	—	14	9
135	1	—	4	3	—	—	—	—	5	3
137	—	3	7	6	—	—	—	—	7	9
140	—	—	1	5	1	—	—	—	2	5
142	—	—	2	5	—	1	—	—	2	6
145	—	—	3	7	—	—	—	—	3	7
147	—	—	3	4	—	—	—	—	3	4
150	—	—	1	4	—	1	—	—	1	5
152	—	—	—	4	—	2	—	—	—	6
155	—	—	—	3	—	2	—	—	—	5
157	—	—	—	1	—	1	—	—	—	2
160	—	—	—	1	—	4	—	—	—	5
163	—	—	—	—	—	—	—	2	—	2
170	—	—	—	—	—	—	—	1	—	1
Mean length	116	116	129	140	132	153	—	165	121	138
Total number	120	18	60	58	1	12	—	3	181	91

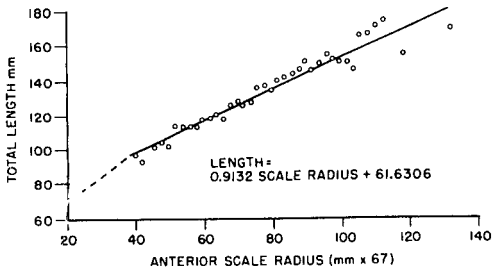

FIGURE 1.—Body length-scale radius relation of pygmy whitefish from Flathead Lake. Solid line is calculated equation; circles represent mean body lengths for given scale radii; dashed line connects estimated intercept at 25 mm length at scale formation.

Superior. Growth was nearly the same in Bull Lake. The initial growth of the Flathead Lake population was exceeded in Wood Lake, Alaska, and after the third year in MacLure Lake, British Columbia, where the fastest growth rate has been reported for the species (Figure 2).

Both Bull Lake and Flathead Lake collections indicate that few males live beyond their third growing year whereas some females reach the fifth growing year. Data from Wood River and the Naknek River systems in Alaska and from Lake Superior also show that females are longer lived. Females in Wood River can attain age VI and those in Lake Superior attain age VII.

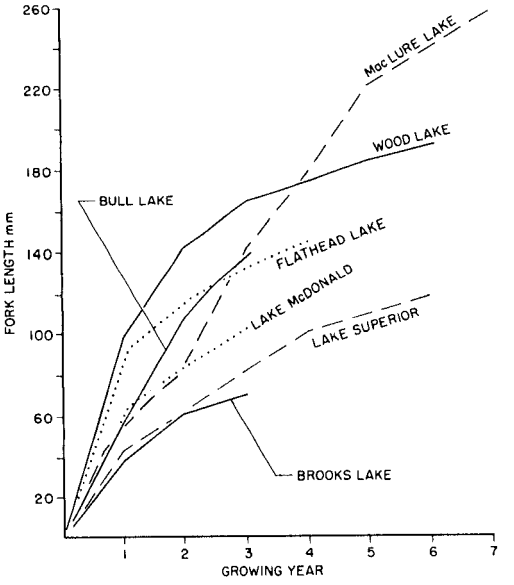

FIGURE 2.—Calculated growth of female pygmy whitefish from Flathead Lake compared with data from Bull Lake and Lake McDonald, Mont., and Lake Superior (Eschmeyer and Bailey, 1955); Wood Lake, Alaska (Rogers, 1964); Brooks Lake, Alaska (Heard and Hartman, 1966); and McLure Lake, British Columbia (McCart, 1963).

FOOD HABITS

The importance of major food items of the pygmy whitefish of Flathead Lake shifts from month to month, undoubtedly according to availability. Chironomid larvae and pupae were the most important items consumed both by

TABLE 6.—Average calculated length and average length at capture of pygmy whitefish, from Flathead Lake, 1967-71.

[F, females; M, males; U, unknown sex.]

Age group	Sex	Number of fish	Average total length at capture (mm)	Calculated length at annulus formation			
				I	II	III	IV
0	U	1	79	—	—	—	—
I	M	120	117	100	—	—	—
	F	18	116	99	—	—	—
	U	95	110	95	—	—	—
II	M	60	128	98	116	—	—
	F	58	140	98	122	—	—
	U	110	134	101	123	—	—
III	M	1	140	100	124	142	—
	F	12	154	100	124	141	—
	U	16	150	101	122	137	—
IV	F	3	168	99	130	145	155
			Average increment				
	M	181	122	99	18	25	—
	F	91	138	98	24	20	13
	U	221	—	98	22	14	—
			Average length				
	M			99	117	142	—
	F			98	122	142	155
	U			98	123	137	—
	Combined			99	121	139	155

TABLE 7.—Percentage frequency of occurrence of food items in stomachs containing food and (in parentheses) percentage estimate of volume for pygmy whitefish from Flathead Lake.[1]

[The two percentage figures are the same or approximate because most stomachs contained only one kind of food.]

Food	May	June	July	Aug.	Sept.	Oct.	Nov.	Average
Cladocera: (including ephippia)	—	—	50 (50)	80 (80)	13 (15)	47 (48)	53 (56)	35
Diptera: Tendipedidae (chironomid larvae and pupae)	67 (67)	89 (95)	33 (37)	20 (20)	69 (71)	44 (45)	10 (8)	47
Trichoptera: (Hydroptilidae and Hydropsychidae)	11 (11)	4 (2)	2 (1)	—	3 (2)	—	—	3
Unknown insect parts	—	4 (2)	6 (4)	—	5 (4)	—	—	2
Fish eggs	—	—	—	—	—	—	6 (6)	1
Detritus and sand	22 (22)	3 (3)	9 (8)	—	10 (8)	9 (7)	31 (30)	12
Empty/full	3/12	0/27	14/68	1/6	5/44	12/44	26/77	61/278

[1] Items appearing in only one or two stomachs included: diatoms, copepods, Podocopa (Ostracoda), Mayfly nymphs (Ephemerotera), midge adults (Tendipedidae), leaf hopper (Cicadellidae), ants (Hymenoptera), terrestrial beattle (Coleoptera), and water mites (Hydracarina). All of these items composed only a small part of stomach contents.

volume and frequency of occurrence; cladocerans were close second (Table 7). No cladocera was consumed during May and June when chironomids were the main food source. Crustaceans became the prime food in July and August, but in September the reliance returned to dipterans. Cladocera apparently became more available in October and November and once more were the important source of food, particularly in November. Other foods were of minor importance during the months when stomachs were collected. The frequent presence of detritus and sand in the guts is evidence that this whitefish feeds at or near the bottom as visually confirmed by Heard and Hartman (1966).

Crustacea identified from the guts of pygmy whitefish from Flathead Lake included an ostracod; the cladocerans *Daphnia thorata*, *D. rosea*, *D. longiremis*, *Bosima longirostris*, and *Leptodora kindtii*; and the copepods *Diaptomus ashlandi*, *Epischura nevadensis*, and a cyclopoid copepod.

A December collection of spawning pygmy whitefish from Ross Creek demonstrates that these fish feed actively during their spawning period. Fish eggs, laid by fellow spawners, were the most frequently ingested food and made up by far the greatest volume. Chironomids were still taken in numbers, however, along with a few other insects (Table 8).

The feeding habits of this whitefish in other lakes are usually similar to those of fish in Flathead Lake. In Lake Superior, crustacea, mostly ostracods and amphipods, occurred in 95% of the stomachs. Chironomids were taken frequently but made up only 8% of the total volume. Fish eggs, presumably coregonine, occurred in collections of May and January (Eschmeyer and Bailey, 1955). Pygmy whitefish from a tributary of Lake Aleknagik, Alaska, fed on the larvae and pupae of chironomids (Rogers, 1964). In the Naknek River system the relative importance of food items differs between lakes. Chironomids accounted for 88% of the stomach volume in some lakes but only 5% in other waters. Plecopteran nymphs were important as food in some lakes or outlets. Periphyton never accounted for more than 4% of stomach contents. Fish eggs, probably from salmon, were taken in November (Heard and Hartman, 1966). Low-rakered Alaskan forms fed predominantly on bottom fauna and the high-rakered fish were almost exclusively plankton feeders (McCart, 1970).

TABLE 8.—Percentage frequency of occurrence of food items in stomachs containing food. Pygmy whitefish from Ross Creek during spawning run, 12 December 1967. The number of fish eggs eaten ranged from 1 to 21 per fish with an average of 6.

Cladocera	8
Diptera:	
Tendipedidae (chironomid larvae)	38
Ceratopogonidae larvae	3
Ephemeroptera:	
Heptagenia nymph	3
Unknown insect remains	8
Fish eggs	75
Detritus and sand	33
Empty stomachs	9 of 50

REPRODUCTION

Age and Size at Maturity

Collections of pygmy whitefish were made from the inlet of Bull Lake during the spawning runs in December of three different years. Only the last collection (1967) included a large number of fish—280, all but 4 were males. The predominance of males in the three collections may be explained by the earlier arrival of males to the spawning aggregation. None of the gonads examined was spawned out.

In the three combined collections, 50% of the males were in their second growing season (age I), 47% at age II, and only 3% at age III. In the small sample of females, none was age I, 64% were age II, and 36% were age III. Except for one large male with three annuli, the females were consistently larger than the males in each age group (Table 9). The smallest ripe male was 86 mm standard length and the largest was 130 mm; the smallest female was 120 mm and the largest was 139 mm.

In late November and December large numbers of pygmy whitefish move from the deep water of Flathead Lake and congregate at the mouths of the Swan and Flathead Rivers before they enter the river systems presumably to spawn. The males outnumber the females 6.7:1 in these concentrations. Of the age I males,

TABLE 9.—Frequency distribution according to standard length of three age groups of ripe pygmy whitefish taken from Ross Creek in three different years.

Sex and standard length (mm)	2 Dec. 1952		10 Dec. 1955			20 Dec. 1967		
	I	II	I	II	III	I	II	III
Males:								
86- 90	4	—	—	—	—	2	—	—
91- 95	4	—	16	—	—	4	—	—
96-100	2	2	7	—	—	4	1	—
101-105	—	5	1	5	—	—	2	—
106-110	—	4	—	12	—	—	8	—
111-115	—	—	—	2	—	—	—	—
116-120	—	—	—	—	2	—	—	—
126-130	—	—	—	—	—	—	—	1
Females:								
116-120	—	1	—	—	—	—	—	—
121-125	—	—	—	1	—	—	1	—
126-130	—	1	—	2	—	—	—	—
131-135	—	—	—	1	1	—	—	2
135-140	—	—	—	—	—	—	—	1

74.5% were sexually mature. All males age II or older were mature. As in the Bull Lake population, the females mature more slowly than the males. The percentage maturity of the females was 27.8 at age I, 90.2% at age II, and 100% for older fish. Younger breeding age in the males and the larger size of mature females characterize the other widely separated populations (Eschmeyer and Bailey, 1955; Heard and Hartman, 1966).

Female pygmy whitefish obviously spawn in consecutive years. Mature ripe eggs were present in the abdominal cavity while smaller eggs, 1 mm in diameter, were developing in the ovaries of ages II and III females.

Sex Ratio

The predominance of males in Bull Lake collections has been discussed previously. Although variable from sample to sample the sex ratio of all pygmy whitefish taken from Flathead Lake in 1969 was nearly equal (Table 10). When collections for 1967 through 1971 were combined, however, males exceeded females by a ratio of 2:1 (Table 5). The sexes were about equal at age II but many more males were taken at age I.

Fecundity

The fecundity of individual fish from Lake Superior and Alaska varied widely. In Flathead Lake egg counts of 28 females ranged from 156 to 918 and averaged 588. The larger fish tended generally to have the most eggs, but exceptions were frequent (Table 11). Four large spawners from Bull Lake had from 1,027 to 1,136 eggs. In Lake Superior egg counts ranged from 93 to 597 and averaged 362 (Eschmeyer and Bailey, 1955); those from the Naknek River system ranged from 103 to 1,153 (Heard and Hartman, 1966).

Conversion of our lengths to total lengths in inches and comparison with Eschmeyer and Bailey's length-fecundity curve shows that pygmy whitefish from Flathead Lake produce more eggs for their size than do the Lake Superior fish and that those from Bull Lake are even more productive. Fish from Bull Lake with total lengths from 6.0 to 6.5 inches have egg counts slightly more than 1,000 compared with about 650 for the Lake Superior fish. If the length-fecundity curve of Heard and Hartman is projected, the Bull Lake population was about the same as fish from South Bay in the Naknek River system, but the Flathead fish produced fewer eggs. Fish in the 5.4- to 5.7-inch range from Flathead Lake had 560 eggs whereas those from South Bay had about 700 eggs. Heard and Hartman explained the differences in fecundity among populations as adaptations to different environmental conditions that produce higher or lower survival opportunities for the species.

TABLE 10.—Length and weight of pygmy whitefish from Bull Lake and Flathead Lake.

[Ranges in parentheses.]

Locality	Number of fish	Sex	Standard length (mm)	Weight (g)
Ross Creek: 10 Dec. 1955	45	male	102 (90-120)	15.8 (10.3-25.0)
	5	female	130 (125-135)	39.6 (30.7-44.0)
12 Dec. 1967	53	male	107 (90-130)	20.7 (9.3-27.5)
	17	female	137 (125-160)	36.0 (26.8-55.6)
Flathead Lake: May-Nov. 1969	102	male	99 (75-116)	11.8 (4.8-22.8)
	117	female	109 (70-140)	18.0 (3.0-42.6)

TABLE 11.—Production of eggs of pygmy whitefish.

Locality	Number of fish	Average weight (g)	Range in standard length (mm)	Number of eggs	
				Range	Mean
Bull Lake	4	43.5	130-135	1,027-1,136	1,084
Flathead Lake	5	16.7	107-110	414-700	547
	11	20.7	111-120	227-733	558
	10	24.9	122-133	156-918	564

Time and Locality of Spawning

No fully mature pygmy whitefish has been found in Bull Lake in November, but ripe fish were readily collected from Ross Creek, the inlet, on 26 December and 12 January 1952, 10 December 1955, and 20 December 1967. Also, fisherman were observed catching ripe fish from the mouth of Stanley Creek, a tributary at the opposite end of the lake, on 3 January 1952 (Weisel and Dillon, 1954). Although milt and roe were easily stripped, the appearance of the gonads indicated that most of the fish had not spawned. The spawning period in Bull Lake must extend from mid-December well into January. All evidence indicates pygmy whitefish spawn in streams rather than in the lake. As previously stated, mature fish were congregated at the mouths of the two major inlets of Flathead Lake in late November and December.

The species spawns in Alaska apparently between mid-November and mid-December in rivers and at the mouths of rivers during the night. In Lake Superior, Glacier National Park, and British Columbia the fish is believed to spawn in November or December in shallow water.

DISCUSSION

The pygmy whitefish is typified by low meristic counts. In gill raker counts the populations from Flathead and Bull Lakes are intermediate compared to Alaskan populations. This does not support McCart's (1970) contention that the low-rakered form persisted in the Columbia River Basin during Pleistocene glaciation. Vertebral counts range widely even within individual populations. Most of the vertebral variation is in the caudal rather than in the precaudal vertebrae.

The pygmy whitefish is flexible in diet and feeding behavior. Depending on the season and locality, the species may feed primarily on insects and zooplankton or on macrobenthic crustaceans. In any one habitat, however, the diet is either highly selective or restricted compared to many other species of fishes.

The pygmy whitefish must be important in the trophic system of Flathead Lake. They are a small, abundant primary carnivore and consequently must be an important food source for the secondary carnivores such as lake trout and Dolly Varden which frequent the deeper water. Its primary food competitor is undoubtedly the lake whitefish. The lake whitefish feeds extensively on molluscs but also includes chironomids and copepods as main dietary items in Flathead Lake (Brunson and Newman, 1951).

The species is short-lived. In the Montana populations no male was found older than age III and no female beyond age IV. In growth rate and fecundity the Montana populations are similar to those from Alaska and Lake Superior.

The pygmy whitefish exists successfully with sympatric salmonoids in spite of its small size and relatively low egg production. The mountain whitefish in Montana, its closest rival in respect to reproduction, produces an average of 4,400 eggs; the largest pygmy whitefish produces a quarter of this number. However the pygmy whitefish produces more eggs per pound of fish—10,000 eggs for Bull Lake specimens compared with 5,340 for mountain whitefish (Brown, 1952). This production is made possible by the reduced size of the eggs of the pygmy whitefish, which are 2.4 to 2.6 mm in diameter when water hardened compared with

3.1 to 4.2 mm for mountain whitefish. Booke (1970) postulated that the large-egg coregonine species gave rise to small-egg types. He admitted that the small-egg size of the pygmy whitefish does not fit his hypothesis because the species is considered to be the most primitive of the subfamily Coregoninae but that this may be a specialized character; and if the pygmy whitefish had the growth potential of the other species in the genus, it would probably have a larger egg. Also compensating for the low egg number per female, the pygmy whitefish spawns at an earlier age. Most mountain whitefish do not mature until their third or fourth year (Sigler, 1951; Brown, 1952), 1 to 2 years later than female pygmy whitefish and 2 years later than male pygmy whitefish. The early maturation and shorter life span of the male pygmy whitefish ensures greater fecundity and abundance of the species at lower consumption of food.

Evidence suggests strongly that direct competition between the two whitefish species on the spawning grounds is avoided by a difference in spawning time. Booke (1970) noted that large-egg coregonines spawn earlier than those with small eggs. From the information available, it appears that in Montana the large-egg mountain whitefish spawns about a month earlier than the small-egg pygmy whitefish.

The small size and consequential small egg diameter of the pygmy whitefish may be explained by the rigors of the glacial period. The known range of the species is restricted to recently glaciated areas. During the glacial period it probably retreated less than other coregonines from the glacial margins. The small size and early spawning age were very possibly adaptations for survival in cold and nutrient-poor waters.

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NOTES

OCCURRENCE OF MATURE REDFISH, *SEBASTES MARINUS*, IN SPORT FISHERY OF THE NEW YORK BIGHT

In the 1971 sport fishery survey of the New York Bight waters, party boat captains reported catching redfish, *Sebastes marinus*, along the edges of the Hudson Canyon. Specimens obtained and examined later were found to be sexually mature fish. This is the first record of redfish being caught in the marine sport fishery off New York, and is a substantial extension of the southern and western breeding range for *Sebastes* in the north Atlantic.

Redfish occur on both sides of the north Atlantic and Goode and Bean (1895) listed the southernmost limit in the western Atlantic off the northern coast of New Jersey (lat 39°48′N; long 71°49′W). Schroeder (1955) reiterated this limit when he reported catching redfish between long 70°00′W and 71°59′W in water deeper than 394 m. Davis and Joseph (1964) reported one specimen (330 mm SL) off Virginia (lat 37°38′N; long 74°15′W) but did not include details on maturation. Prior to my find, the southernmost extent of a breeding population in the western Atlantic was that reported by Bigelow and Schroeder (1953) from Great South Channel off Nantucket Island.

Redfish exist in commercial concentrations from the Gulf of Maine and Georges Bank north to southern Greenland. Although an excellent table fish, redfish are not actively sought by New England anglers because they are usually found in deep water and provide little sporting action. They are caught regularly by anglers at Eastport, Maine (Kelly and Barker, 1961) and occasionally elsewhere along the Maine coast, but few are caught by sportsmen south of there.

During July and August 1971, I collected 14 specimens (13 ripe males and 1 gravid female containing well-developed larvae) from party boat captains. These redfish had an average length of 208 mm, ranging from 188 to 222 mm and averaged 257 g, ranging from 190 to 309 g. Ages ranged from 7 to 11 years with 8-year-old fish being the dominant age group. Their physical characteristics are like those described and pictured by Bigelow and Schroeder (1953) for *Sebastes marinus* from the Gulf of Maine. Each fish had a well-developed bony protuberance on the lower jaw and the anterior preopercular spine projected anteroventrally (Figure 1). The average ratio of horizontal diameter of orbit to head length was 29.5%.

Party boat captains caught these specimens incidentally while fishing for red hake, *Urophycis chuss*; tautog, *Tautoga onitis*; and black sea bass, *Centropristis striata*; on wrecks in 55 to 69 m in the upper end of the Hudson Canyon (general area: lat 40°12′N; long 73°44′W) (Figure 2). Party boat captains also reported

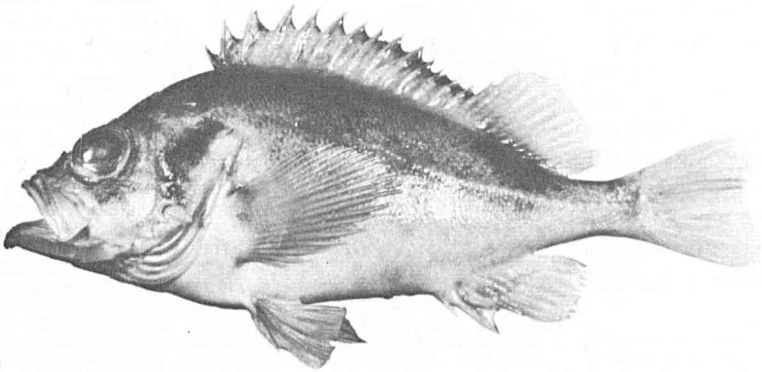

FIGURE 1.—A mature male redfish, 222 mm SL, caught at the northern end of the Hudson Canyon.

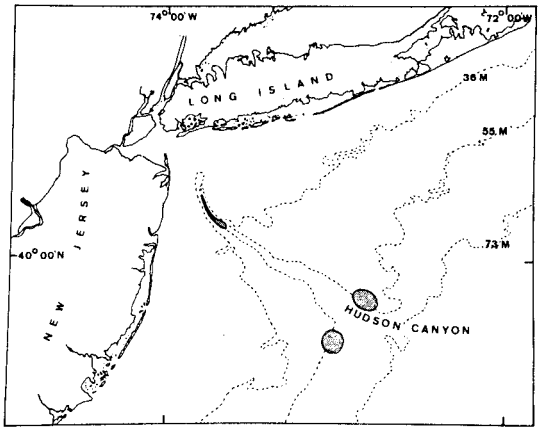

FIGURE 2.—The three areas (cross hatch) where sport fishermen caught redfish in the New York Bight.

catching redfish while fishing for Atlantic cod, *Gadus morhua*, and pollock, *Pollachius virens*, on wrecks deeper than 55 m in the general vicinities of lat 39°48′N, long 72°50′W and lat 39°36′N, long 73°03′W (Figure 2). I did not inspect these fish for positive identification. I received no reports of redfish being caught in water shallower than 55 m or any reports of redfish being caught over natural habitats. Party boat captains reported catching redfish during February, March, June, July, and August, mostly during the latter 2 months.

Several party boat captains reported catching redfish during the last 10 years. Although some captains said they caught up to 35 redfish during at least one trip in past years, I estimate that the total sportsmen's catch in 1971 was less than 100 fish.

Acknowledgments

I would like to thank George Kelly (Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, Mass.) for aging the specimens and critically reviewing the manuscript. I also wish to thank Anthony Pacheco (Middle Atlantic Coastal Fisheries Center, National Marine Fisheries Service, NOAA, Highlands, N.J.) for his assistance in preparing this paper and the party boat captains of Manasquan Inlet, N.J., who collected the specimens, David Bogan, Howard Bogan, John Bogan, and Jack Endean.

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OPTIMUM LIGHT AND TEMPERATURE REQUIREMENTS FOR *GYMNODINIUM SPLENDENS*, A LARVAL FISH FOOD ORGANISM[1,2]

In recent years, it has been possible to substitute the marine dinoflagellate *Gymnodinium splendens* for wild natural plankton as a food source for first-feeding larval anchovies, *Engraulis mordax* (Lasker et al., 1970). *G. splendens* is ideal for this larval marine fish at this developmental stage because the alga's size (approximately 53 μm diameter) is similar to the size range of natural food particles. Reasonably lengthy larval survival (up to 19 days) can be achieved in the laboratory by first using this dinoflagellate and later supplementing with veligers (Lasker et al., 1970). The alga has also been used in combination with the rotifer *Brachionus plicatilis* as a larval food source (Theilacker and McMaster, 1971).

These developments have made possible new studies of anchovy larval behavior (Hunter, 1972) and nutrition (Conklin, unpublished data). Furthermore, the use of *G. splendens* may be of help in rearing other larval fish.

G. splendens is easily grown in an enriched seawater medium that was developed by Sweeney (1951, 1954) and Sweeney and Hastings (1957). The organism was first cultured with soil extract in the medium (Sweeney, 1951) which was later replaced with vitamin B_{12} (Sweeney, 1954). However, for routine culturing soil extract suffices and also provides trace metals and unknown organic factors.

The dinoflagellate has been cultured at 16°C and a light intensity of 60-70 footcandles (Sweeney, 1951); at 20°C and 200-400 footcandles (Sweeney, 1954) and at 20°C and 500 footcandles (Lasker et al., 1970), but optimum physical conditions for growth were not determined. Such information would be of value in setting up continuous cultures of *G. splendens* or in further improving conditions for mass cultures. The purpose of this paper is to establish the optimum conditions of light and temperature for *G. splendens* culture—conditions that result in a maximum growth rate.

Materials and Methods

Our culture of *G. splendens* was isolated from a water sample taken from the Scripps Institution pier in March 1969. It is unialgal but not bacteria-free. *Gymnodinium* is maintained in the enriched seawater medium of Sweeney and Hastings (1957) plus the Fe solution of Rodhe (1948). One liter of medium contains 750 ml seawater, 10 ml 0.1% EDTA (disodium ethylenedinitrilo tetra-acetate), 2 ml 1 M KNO_3, 2 ml 0.1 M K_2HPO_4, 20 ml of soil extract (prepared by autoclaving equal weights of untilled loam and glass distilled water followed by filtration through Whatman[3] No. 4 paper), 0.25 ml Rodhe Fe solution (prepared by dissolving 1.33 g ferric citrate and 1.33 g citric acid in 100 ml of double distilled water) and 216 ml (glass) distilled water. Autoclaving the medium results in a precipitate, which can be avoided by sterile filtration. Stock cultures of *G. splendens* were maintained at 500 footcandles (5,000 lux) and 21°C.

Experimental cultures were grown in this same medium. Cells were concentrated from exponentially growing stock cultures by gentle reverse filtration (Dodson and Thomas, 1964) and inoculated into 65-ml bottles containing 50 ml of medium to give an initial cell count of 200-500 cells/ml.

The culture bottles were then placed in temperature gradient block A of Thomas, Scotten, and Bradshaw (1963). This apparatus consisted of an aluminum block containing 30 holes. Prior to starting the experiment, thermostatted cold water was pumped through one end of the block and warm water was pumped through the other end. This set up a thermal gradient so that there were six rows

[1] Contribution from the Scripps Institution of Oceanography.

[2] This work was part of the STOR (Scripps Tuna Oceanography Research) Program. It was supported by the Oceanography Section, National Science Foundation Grant No. GA-32529X and by Marine Research Committee (California Department of Fish and Game) Grant No. M-13 to Reuben Lasker. The work was performed in the Southwest Fishery Center, National Marine Fisheries Service, NOAA.

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

of five holes each at a given temperature. The bottles were illuminated from below through plastic windows in each hole. The continuous fluorescent light was attenuated with fogged photographic film filters placed below each window. Thus, at each of six temperatures, five light intensities were achieved. The light intensity in each hole was measured by an International Rectifier I2BM silicon photocell which was calibrated against a Weston Model 756 footcandle meter and an Eppley radiometer using the same fluorescent light source.

Counts of cells in each culture were made at daily intervals by taking 1-ml aliquots and counting all the cells in a 0.1-ml portion using a Palmer-Maloney counting chamber. Cell numbers were plotted against time in days on semilogarithmic paper. Growth rates during the exponential phase of growth were calculated by the equation:

$$\mu_2 = \frac{\log_2 N_2 - \log_2 N_1}{t_2 - t_1}$$

where N_1 and N_2 are cell counts at times t_1 and t_2. μ_2 is expressed as doublings of cell numbers per day.

Results and Discussion

Three experiments were performed. The first two were terminated after only 4 days of growth because of failure of the temperature-controlling equipment and because of contamination of some of the cultures with a small, colorless flagellate. Nevertheless, these preliminary experiments served to establish that growth of *G. splendens* was optimum at moderate temperatures and light intensities.

This result was confirmed in the third experiment in which growth was followed for 8 days. Figure 1 shows the growth rates that were achieved during the exponential phase of growth at different temperatures and intensities in this experiment. No growth occurred at 10° and 30°C and was suboptimal at 15°C. Growth was maximal at 20-27°C and at a light intensity of 2-9 kilolux. These are rather wide ranges of

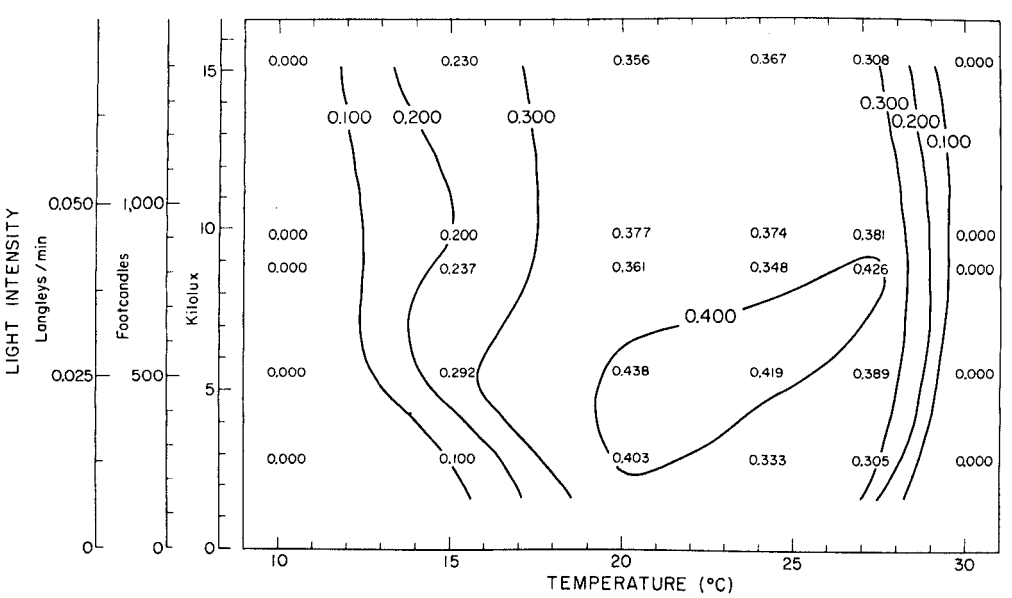

FIGURE 1.—Growth rates of *Gymnodinium splendens* at various light intensities and temperatures. The numbers are rates in doublings per day at each intensity and temperature and the data are also contoured to show similar rates.

TABLE 1.—Optimum temperatures and light intensities for growth of marine dinoflagellates.

Organism	Optimum temperature range (°C)	Optimum light intensities (kilolux)	(ly/min)	Reference
Peridinium sp.	18-20	—	>0.023	Barker (1935)
Prorocentrum micans	25	—	>0.023	Barker (1935)
Prorocentrum micans	—	>6	>0.03	Kain and Fogg (1960)
Prorocentrum gracile	18	—	>0.023	Barker (1935)
Amphidinium carteri	20-30	—	0.1-0.4	Jitts et al. (1964)
Gonyaulax polyedra	25	5-10	—	Hastings and Sweeney (1964) Sweeney (unpublished data)
Gymnodinium simplex	23-28	6-20	—	Thomas (1966)
Gymnodinium splendens	20-27	2-9	0.01-0.04	This paper

temperature and light, but it was surprising that rates were reduced slightly at higher light intensities.

Optimum temperatures and intensities for some other marine dinoflagellates are given in Table 1. *G. splendens* has temperature optima that are close to those of other dinoflagellates, but its light intensity requirements are somewhat lower.

These results are useful in providing proper conditions for mass cultures. Normal room temperatures are proper and optimum light intensities (about 5 kilolux) can be provided with banks of 40-W fluorescent lights placed about 5-10 cm away from culture flasks. At a growth rate of 0.4 doublings per day, a culture inoculated with a few hundred cells per milliliter will increase 10 fold in about 8 days.

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ERRATA

Fishery Bulletin, Vol. 71, No. 1

HIDA THOMAS S., "Food of tunas and dolphins (Pisces: Scombridae and Coryphaenidae) with emphasis on the distribution and biology of their prey *Stolephorus buccaneeri* (Engraulidae)," p. 135-143.

1) Page 139, right column, line 1, correct line to read:
   Majuro and Arno Atolls in February 1972 were feed-

LINDALL, WILLIAM N., JR., JOHN R. HALL, AND CARL H. SALOMAN, "Fishes, macroinvertebrates, and hydrological conditions of upland canals in Tampa Bay, Florida," p. 155-163.

1) Page 158, left column, line 12, delete:
   linity at the control station was 9.0‰ higher than

PRISTAS, PAUL J., AND RANDALL P. CHEEK, "Atlantic thread herring (*Opisthonema oglinum*) - movements and population size inferred from tag returns," p. 297-301.

1) Page 300, right column, line 3 and subsequent lines in this paragraph, correct lines to read:
   of the population. This effect would produce an underestimate of the stock size. On the other hand, this calculation might overestimate population size because we were unable to determine rate of recruitment and no adjustment has been made for tag loss due to shedding or mortality.
2) Page 301, left column, first author line, correct line to read:
   PAUL J. PRISTAS[2]

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NOAA FSYB-A 71-3

A UNITED STATES DEPARTMENT OF COMMERCE PUBLICATION

Fishery Bulletin

U. S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Seattle, Wash.
JULY 1973

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MERCURY IN TUNAS: A REVIEW

C. L. PETERSON, W. L. KLAWE, AND G. D. SHARP[1]

ABSTRACT

Mercury in the aquatic environment comes from both natural processes and industrial activities. The latter probably have not significantly altered the mercury content of the high seas where most tunas are captured.

Mercury compounds enter aquatic organisms through the food web and/or by direct extraction from solution. The relative importance of these pathways in tunas is unknown. Mercury occurs in tuna principally in the form of methylmercury.

Generally, tunas appear to have higher mercury levels than those fish species which occupy a lower level in the food chain.

Mercury content of tunas varies according to fish size. However, other factors such as area of capture, differential growth rates, varying analytical techniques, and different sampling methods may account for some of the observed variation.

The U.S. Food and Drug Administration has established an "in-house" standard of 0.5 ppm of mercury for fishery products sold in the United States. Other countries have established limits as high as 1.0 ppm.

Seawater contains a wide array of dissolved elements and salts including mercury. Some of these occur in quantities that can be recovered on a commercial scale whereas the minute concentrations of others can be detected only by highly sophisticated techniques. Mercury does not play a prominent role among the metals dissolved in seawater because it occurs there only in very small quantities. Mercury in its various forms is also present in the earth's crust from which it can be dissolved by water. In the absence of water, especially under conditions of increased heat, mercury will enter the atmosphere in the form of vapor, from which it can dissolve in water at the water-air interfaces, i.e., rain or the sea surface. It is difficult to conceive that life could have evolved on this planet in an environment devoid of this ubiquitous element so it is of no great surprise that mercury is present in the bodies of living organisms. Furthermore, as is the case with many elements and their compounds, living organisms are even capable of concentrating mercury within or outside of their bodies. Tunas are no exception—mercury occurs in various parts of these pelagic species in concentrations substantially exceeding those dissolved in the waters of the world oceans.

An epidemic of deaths and serious physical impairment among Japanese during the 1950's and 1960's (which was later related to the ingestion of seafood contaminated by mercury from local industries), the discovery of high levels of mercury in freshwater fishes and wildlife in Sweden in the 1960's, and the discovery of unusual mercury concentrations in fishes from parts of the Great Lakes system in 1970 led investigators to examine mercury in tunas and billfishes. The findings resulted in the seizure of some tunas and swordfish in the United States whose mercury content exceeded government standards, and significantly affected fishing strategy and marketing of these species.

SOURCES OF MERCURY IN THE MARINE ENVIRONMENT

Mercury is most often encountered in nature as mercury sulfide or cinnabar. Other compounds and metallic mercury contribute a small percentage of the total available mercury.

[1] Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, La Jolla, CA 92037.

Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

A number of natural processes release a continuous but relatively minor amount of mercury into the soil, groundwater, and air around deposits of mercury compounds. This effusion and volatilization of mercury is the first of many steps in the generation of its compounds and their subsequent entry into bodies of water including the oceans. This mercury is oxidized or recompounded in the environment, deposited in the sediments if insoluble or dispersed in the water if soluble. Rainfall causes erosion of soils and facilitates the mobilization of the mercury into the aquatic environment.

The second (and controllable) source of mercury in rivers, lakes, and oceans stems from the activities of man. Mercury compounds have been used for millennia as a coloring agent, as medicine, and for a multitude of industrial uses. The most common industrial sources of mercury contamination can be divided into several classes. Fossil fuels, i.e., coal and oil, have relatively low levels of mercury, but as millions of tons of these fuels are used each year, they release a substantial amount of mercury into the atmosphere which eventually enters the aquatic environment. Factories producing plastics, chlorine, caustic soda, and/or caustic potash have been charged with one of the more obvious and largest discharges of mercury and its compounds into rivers, lakes, and oceans. The fungicidal properties of mercury compounds have made it useful in preservation of paint and as a coating for seeds used in planting of crops. Mercury compounds also have slimicide properties which have brought about their extensive use in pulp mills and other industries. Gold, silver, and rare metals can be and are extracted by using metallic mercury in an amalgamation process in which the final step is driving off the mercury by heat to leave the other metals behind. The subsequent condensation of the mercury vapors is not 100% effective, and thus some of it enters the environment. Mercury contamination also results from many other industrial processes. However daily household, laboratory, and small business activities contribute considerable quantities of mercury and its compounds to sewage and sludge stores by the breakage of thermometers and electric switches, discarding of or excretion of mercurials used for medication, and other seemingly unimportant events.

Studies show that the contaminant mercury is usually concentrated near the sites of outfall and that the levels decrease with distance from the sources.

MERCURY IN FISHES

Methylmercury is one of the mercury compounds most often found in the bodies of fishes and other aquatic organisms (Westöö, 1966; Johnels et al., 1967). This compound is known to be readily derived from inorganic or metallic forms usually by biological intermediaries (Jernelöv, 1972a). Ionic mercury binds readily to organic materials and can be converted to methylmercury through bacterial activity. Generally speaking, mercury in sediments of water bodies is converted faster under aerobic conditions than in sediments with low oxygen levels or where anaerobic conditions prevail. Methylmercury can readily enter the complex aquatic food chain which may include many levels of concentration.

Mercury compounds, regardless of whether they originate from natural activities or are introduced into the aquatic environment as contaminants, can enter fish via two pathways (Raeder and Snekvik, 1941; Jernelöv, 1972b). The most easily understood path is through the food chain or the food web. All studies on the food chain show a stepwise mercury concentration increase at each subsequent level, culminating in the large predatory organisms, i.e., tunas, billfishes, and sharks. The complexity of the food webs, i.e., number of steps and number of interrelations, and the metabolic requirements of the various members, usually limit the amount of mercury found at each level.

Another pathway, the relative importance of which is poorly understood, is direct extraction of mercury from solution in the aqueous media due to the affinity of mercury ions for proteins. The possibility of the direct absorption of mercury from water was postulated back in 1941 by two Norwegian scientists, Raeder and Snekvik (1941). The most obvious type

of absorption would be through the gills, but it was also found that methylation of inorganic mercury takes place in the slime of some fishes (Jensen and Jernelöv, 1969). The ultimate fate of methylmercury formed this way has not been investigated to the best of our knowledge, but because the organic forms of mercury have an affinity for lipids, perhaps the methylated form also enters the tissues of the fish. It should be pointed out that research on freshwater fishes demonstrates that methylation in fish slime is accomplished mainly, if not exclusively, by certain microorganisms.

Tunas and billfishes, which have high metabolic rates and are extremely mobile species, filter many thousands of liters of water over a short period of time. Thus the possibility of branchial extraction of mercury may be of importance to the buildup of this substance in tunas, especially in regions where the relative concentrations of dissolved mercury are high. The existence of specific oceanic areas with high concentrations of mercury throughout the water column has been demonstrated (Weiss et al., 1972). As food organisms would also tend to have greater mercury content in such regions, it is readily conceivable that a disproportionate increase in mercury levels could be detected in tunas from such regions. Although areas with high volcanic activity would be suspected of having higher amounts of dissolved mercury, there are no data to verify this. Indeed very little is known about geographic variations in concentration of mercury in the world oceans. Furthermore, it is not yet known which of the two pathways responsible for the presence of mercury in tunas is more important. From experiments with other fishes it has been demonstrated that the mercury in some species originates principally from their food whereas in other fishes the mercury originates mainly from mercury dissolved in water (Jernelöv, 1972b).

Research dealing with types of mercury in fishes indicates that in most instances practically all of the mercury accumulated is in an organic form, namely methylmercury (Westöö, 1966, 1967). The same seems to be true of the tunas and swordfish, *Xiphias gladius*. A recent analysis (Kamps, Carr, and Miller, 1972) of the total mercury/methylmercury relationship, based on 11 samples of canned tuna and 20 samples of frozen swordfish steak from the U.S. market, shows that mercury in the edible portions of these fish is essentially all methylmercury. However, it should be noted that Pacific blue marlin, *Makaira mazara*, from Hawaii were found to have total mercury levels ranging from 0.35 to 14.0 ppm[2] whereas the organic mercury for the same samples ranged from 0.23 to 1.79 ppm (Rivers, Pearson, and Shultz, 1972). Furthermore, studies on the methylmercury and total mercury relationship in lake trout, *Salvelinus namaycush*, from Cayuga Lake, N.Y., indicate that 31-35% of total mercury in 1-year fish is methylmercury (Bache, Gutenmann, and Lisk, 1971). By the fourth year, methylmercury in lake trout made up 70% of the total. In 12-year olds, values ranged from 67 to 88%. These findings, as well as some other studies undertaken by a Japanese researcher (Ui, 1971), indicate that the organic to total mercury ratio may not be consistent among or within species and that the relative quantities of the two forms should be further studied.

Not all mercury which enters the body of a fish is retained. For example, the uptake of mercury from food ingested by northern pike, *Esox lucius*, a freshwater fish, does not exceed 20% (Jernelöv, 1972b). Experiments carried out recently by the National Marine Fisheries Service indicate that an even lower figure is applicable to skipjack tuna, *Katsuwonus pelamis*, (Lasker and Leong, 1972).[3] It has been shown that some fish have the ability to rid themselves of some of the mercury which enters the tissues of their body. The mercury excretion rate for tuna is unknown, but for some other species of fish the biological half-life for methylmercury is known to be on the order of 2 yr (Järvenpää, Tillander, and Mietinen, 1970; Lockhart et al., 1972).

[2] Parts per million by wet weight, i.e., 1 mg of metallic mercury per kilogram of wet weight corresponds to 1.0 ppm.

[3] Lasker, R., and R. L. Leong. 1972. Uptake and excretion of mercury by skipjack tuna in aquaria. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92037. (Unpubl. manuscr.)

LEVELS OF MERCURY IN TUNAS AND OTHER LARGE PELAGIC MARINE FISHES

Published data on levels of mercury in tunas and other large pelagic fishes are scarce and difficult to interpret. For example, it has been shown for skipjack tuna caught off Hawaii that the amount of mercury in the red muscle is about 1.6 times greater than that in the white muscle (Lasker and Leong, see footnote 3), and for swordfish caught off the Canadian and U.S. Atlantic coast the amount of mercury in the red muscle is about 1.4 times greater than in the dorsal muscle (Beckett and Freeman, in press), but the majority of published data do not name the parts of the fish which were analyzed.

Table 1 summarizes information on mercury levels in tunas and billfishes, obtained principally from data published within the last 2 yr. The area designations marked with a 4 or 5 refer to museum specimens all of which date from the period 1878-1901 (except for the swordfish which was captured in 1946) and thus predate the period in which mercury pollution became important. It is evident that there is no significant difference in mercury levels between the museum tuna samples captured 62-93 years ago and the tunas caught within about the last 5 yr. The mercury level from the single museum specimen of swordfish falls within the range of the six "modern" specimens caught off California.

The similarity in mercury levels of tunas collected prior to 1900 and those captured in the last several years is substantiated by similar findings in other types of marine fishes. For example, in a recent study of mercury in benthopelagic fishes it was found that mercury

TABLE 1.—Amounts of total mercury expressed as parts per million (wet weight), in tunas and billfishes.

Species and area	No. of specimens	Weight (kg)	Fork length (cm)	Mercury (ppm) Range	Mercury (ppm) Mean	Reference
Yellowfin tuna, *Thunnus albacares:*						
Gulf of Guinea	88	2-105	—	0.07 -1.20	0.42	Ivory Coast Fisheries Service, 1972[1]
Hawaii	22	31-98	—	0.24 -1.32	0.54	Rivers et al., 1972
Pacific	6	4-37	—	0.20 -0.76	—	Unpublished data
Atlantic (Africa)	3	4.5-40.0	—	0.29 -0.77	0.49	Establier, 1972
Skipjack tuna, *Katsuwonus pelamis:*						
Hawaii	26	0.6-1.8	—	[2]0.15 -0.35	—	Lasker and Leong, 1972[3]
	20	—	—	0.27 -0.52	0.38	Rivers et al, 1972
Gulf of Guinea	5	2-6	—	0.11 -0.20	—	Ivory Coast Fisheries Service, 1972[1]
Pacific	1	—	—	—	0.18	Miller et al., 1972
Massachusetts[4]	2	—	—	0.27 -0.64	0.46	Miller et al., 1972
Philippines[4]	1	—	—	—	0.26	Miller et al., 1972
Pacific	1	—	—	—	0.18	Miller et al., 1972
San Diego, Calif.[4]	1	—	—	—	0.45	Miller et al., 1972
Hawaii	1	—	—	—	0.42	Miller et al., 1972
Albacore, *Thunnus alalunga:*						
California[4]	1	—	—	—	0.27	Miller et al., 1972
	1	—	—	—	0.13	Miller et al., 1972
	2	—	—	0.183-0.209	0.193	Knauer and Martin, pers. comm.
Bluefin tuna, *Thunnus thynnus:*						
Gulf of Cádiz	6	—	200-271	0.46 -0.91	0.68	Establier, 1972
Western Atlantic	1	—	172	—	0.80	Beckett and Freeman, in press
Massachusetts[4]	1	—	—	—	0.38	Miller et al., 1972
Bigeye tuna, *Thunnus obesus.*						
Gulf of Guinea	5	30-70	—	0.23 -0.75	—	Ivory Coast Fisheries Service, 1972[1]
Swordfish, *Xiphias gladius:*						
Western Atlantic	210	—	74-247	0.05 -4.90	1.15	Beckett and Freeman, in press
California	6	—	—	0.23 -1.27	—	Miller et al., 1972
Gibraltar Strait	5	—	—	0.99 -2.01	1.36	Establier, 1972
Gulf of Guinea	4	—	—	0.95 -1.25	—	Ivory Coast Fisheries Service, 1972[1]
Baja California[5]	1	—	—	—	0.52	Miller et al., 1972
Pacific blue marlin, *Makaira mazara:*						
Hawaii	27	44-355	—	0.35 -14.0	4.78	Rivers et al., 1972
White marlin, *Tetrapturus albidus:*						
Western Atlantic	1	—	187	—	1.34	Beckett and Freeman, in press

[1] See text footnote 4.
[2] White meat only.
[3] See text footnote 3.
[4] Museum specimens collected from 1878 to 1901.
[5] Museum specimen captured in 1946.

levels in specimens taken in 1971-72 do not differ significantly from those in the same species captured in the same area 85-90 yr ago (Barber, Vijayakumar and Cross, 1972). Also, mercury levels in eight fish, between 1605 and 2100 yr old, discovered in Michigan and Illinois archeological sites, were found to be as high as 0.515 ppm; and nine marine fish from a pre-Inca site in Peru contained as much as 9.5 ppm (Medical World News, 1972).

By way of comparison, mercury levels of some other selected marine fishes are shown in Table 2. These data seem to support the general concept that larger predatory fishes, including tunas, have higher mercury levels than those fish species which occupy a lower level in the food chain.

RELATIONSHIP BETWEEN MERCURY LEVELS AND FISH SIZE

Swedish investigators (Johnels et al., 1967) reported that mercury levels in northern pike increase with the age of the fish. A similar relationship has been reported for freshwater fishes from Wisconsin (Kleinert, 1972).

Mercury content is also known to vary with fish size in some marine species, e.g., in swordfish captured off the Atlantic coast of Canada and the United States (Beckett and Freeman, in press), in Pacific halibut, *Hippoglossus stenolepis*, of the North Pacific coast of Canada and the United States (Bernard E. Skud, International Pacific Halibut Commission, pers. commun.), in a benthopelagic morid *Antimora rostrata* from the U.S. east coast (Barber et al., 1972), in spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia (Forrester, Ketchen, and Wong, 1972), and in Pacific blue marlin from Hawaii (Rivers et al., 1972).

A similar relationship has also been demonstrated in some species of tunas. One of the most detailed studies (Ivory Coast Fisheries Service, 1972)[4] is that for 88 yellowfin tuna, *Thunnus albacares*, captured in the Gulf of Guinea between July 1971 and July 1972 (Figure 1). The large amount of scatter in

[4] Ivory Coast Fisheries Service. 1972. La contamination mercurielle des thons. [Mercury contamination in tuna fish.] Ivory Coast Fish. Serv., Abidjan, 5 p. (Engl. transl. by U.S. Embassy, Abidjan, 7 p.)

TABLE 2.—Amounts of total mercury, expressed as parts per million (wet weight), in some selected marine fishes.

Area Species	No. of specimens	Fork length (cm)	Mercury (ppm) Range	Mercury (ppm) Mean	Reference
Hawaii:					
Squirrel fish, *Myripristis arayomus*	14	—	0.10 -0.43	0.21	Rivers et al., 1972
Red goat fish, *Mulloidichthys auriflamma*	10	—	—	<0.05	Rivers et al., 1972
Bigeyed scad, *Trachurops crumenophthalmus*	10	—	0.07 -0.11	0.09	Rivers et al., 1972
Mullet, *Mugil cephalus*	10	—	—	<0.05	Rivers et al., 1972
Monterey Bay, Calif.:					
Myctophid, *Tarletonbeania crenularis*	29	—	0.013-0.096	0.030	Knauer and Martin, 1972
Myctophid, *Diaphus theta*	5	—	0.032-0.078	0.060	Knauer and Martin, 1972
Pacific saury, *Cololabis saira*	2	—	0.008-0.011	0.009	Knauer and Martin, pers. comm.
Northern anchovy, *Engraulis mordax*	3	—	0.055-0.076	0.063	Knauer and Martin, 1972
Oregon:					
Rex sole, *Glyptocephalus zachirus*	82	—	0.05 -0.24	0.119	Childs and Gaffke, 1973
Petrale sole, *Eopsetta jordani*	94	—	0.05 -0.32	0.114	Childs and Gaffke, 1973
Starry flounder, *Platichthys stellatus*	42	—	0.08 -0.50	0.235	Childs and Gaffke, 1973
Yellowtail rockfish, *Sebastes flavidus*	24	—	0.19 -0.53	0.371	Childs and Gaffke, 1973
Rougheye rockfish, *Sebastes aleutianus*	30	—	0.06 -0.11	0.080	Childs and Gaffke, 1973
Lingcod, *Ophiodon elongatus*	48	—	0.06 -0.73	0.351	Childs and Gaffke, 1973
Sablefish, *Anoplopoma fimbria*	52	—	0.03 -0.65	0.138	Childs and Gaffke, 1973
Pacific hake, *Merluccius productus*	24	—	0.06 -0.18	0.102	Childs and Gaffke, 1973
Arrowtooth flounder, *Atheresthes stomias*	26	—	0.01 -0.33	0.154	Childs and Gaffke, 1973
Spiny dogfish, *Squalus acanthias*	88	—	0.20 -1.14	0.602	Childs and Gaffke, 1973
British Columbia:					
Spiny dogfish, *Squalus acanthias*	206	[1]25-120	0.1 -1.96	—	Forrester and Ketchen, 1972
Atlantic coast, Canada and United States:					
Basking shark, *Cetorhinus maximus*	2	382	0.03 -0.14	0.08	Beckett and Freeman, in press
Blue shark, *Prionace glauca*	14	69-190	0.40 -1.17	0.70	Beckett and Freeman, in press
Sickle shark, *Carcharhinus falciformis*	4	101-199	0.75 -3.28	1.43	Beckett and Freeman, in press
Mackerel shark, *Lamna nasus*	4	78-234	0.62 -5.43	2.08	Beckett and Freeman, in press

[1] Total length.

the points among fish weighing more than about 65 kg is borne out by the following data on white muscle of eight yellowfin tuna taken by a single vessel during one day's fishing in the Gulf of Guinea:

Fish weight (kg)	*Mercury level (ppm)*
66	0.78
67	0.39
70	0.86
70	0.29
70	0.44
75	0.45
75	0.19
75	0.58

The large variation in mercury levels among tunas of the same size may be due to a differential growth rate between sexes. For example, Forrester et al. (1972) noted that for any given length above 65 cm, the mercury content was higher among male spiny dogfish than among females. They pointed out that since mercury has been shown to be cumulative with age in some species (Johnels et al., 1967) the difference in mercury levels between sexes may reflect differences in growth rates since it is probable that males grow slower than females beyond a certain age. Moreover, large differences in growth rates among individuals of the same sex may further complicate the relationship.

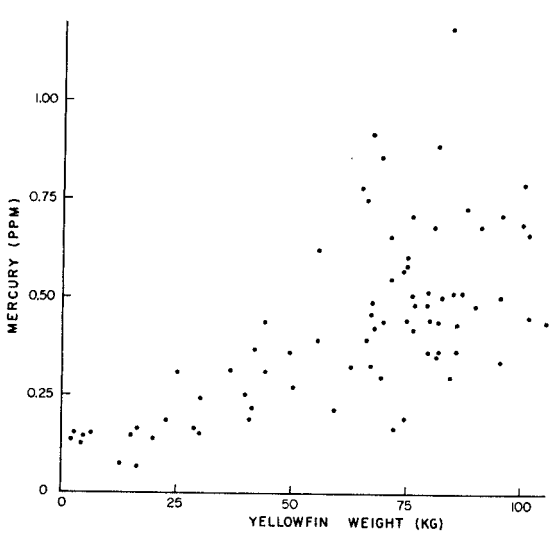

FIGURE 1.—Relation between mercury (ppm) and fish weight (kg) for 88 yellowfin tuna captured in the Gulf of Guinea between July 1971 and July 1972 (from Ivory Coast Fisheries Service, 1972, see footnote 4).

In a study of 22 yellowfin tuna captured off Hawaii (size range 31-98 kg; mercury level 0.24-1.32 ppm) a relationship was found between fish weight and total mercury level (r = 0.47; P = 0.05) (Rivers et al, 1972).

Also, in a study of 26 Hawaiian skipjack tuna it was found that mercury levels in the white muscle of the smaller specimens (18 fish), weighing from 0.6 to about 1.4 kg, were at a nearly constant level of about 0.15 ppm, whereas mercury in the larger fish (8 specimens), weighing about 1.5 to 1.8 kg, ranged from approximately 0.15 to 0.35 ppm (Lasker and Leong, see footnote 3).

GEOGRAPHIC VARIATION IN MERCURY CONTENT OF FISHES

Geographic variations in the mercury levels of fishes have been demonstrated in many cases. Some of these variations have been related to mercury pollution by man such as that observed in some Swedish lakes, Minamata Bay in Japan, and some of the Great Lakes and connecting waters between the United States and Canada.

Other cases of geographic variation have been observed, but it is not known whether they are related to human activities. For example, an investigation of north Pacific halibut has shown that there is a south-north cline in mercury levels, i.e., halibut from the southern areas (off Oregon and Washington States) have higher levels than those from the more northern areas. Also it was found that there are localized "hot spots" in the halibut fishery where the fish have significantly higher mercury levels on the average than halibut in the surrounding area (Bernard E. Skud, pers. commun.). Also Childs and Gaffke (1973) found significant geographic variation in mercury levels of some groundfish (rex sole, *Glyptocephalus zachirus;* dover sole, *Microstomus pacificus;* sand sole, *Psettichthys melanostictus;* starry flounder, *Platichthys stellatus;* lingcod, *Ophiodon elongatus;* and sablefish, *Anoplopoma fimbria*) from three areas off the Oregon coast. However it is interesting to note

that this variation was inconsistent among the species examined, e.g., mercury concentration in some species was highest in the northern area while for other species from the same area it was lowest.

A proper understanding of the cause(s) of geographic variations in mercury levels of fishes is confounded by the possibility that a complex of factors may be involved. For example, Beckett and Freeman (in press) in a study of 210 swordfish from six areas extending from the Caribbean Sea to the Grand Banks found that the average mercury level of this species varied significantly from area to area. They suggested that this variation may be related to (1) the passage of time, i.e., the mercury content appeared to decrease with time in the northern part of the area of investigation; (2) a higher rate of mercury uptake and/or excretion in the southern areas; (3) differences in size composition of swordfish among areas; and (4) the occurrence of forage fishes of high mercury content near the Grand Banks.

Furthermore, Forrester et al. (1972), in a study of about 200 spiny dogfish from four areas in the Strait of Georgia, British Columbia, found differences in mercury content of this species among areas. Mercury level was highest in the Point Grey—U.S. Border area. The authors suggest that contamination by effluents from industrial plants along the Fraser River and its estuary may be a contributing factor. They go on to point out that "The differences in mercury content among areas suggest that dogfish in Georgia Strait are not a homogeneous stock or, if they are, that mercury uptake is very rapid." The authors also state that "If uptake is rapid the extreme variation in mercury content for dogfish of a given length may indicate time spent by various fish in the region of apparent high mercury contamination. On the other hand, there may be large differences in growth rates among individuals, reflecting differences in accumulation with time."

Finally, it is interesting to note that mercury levels in *Aldrovandia macrochir*, a benthopelagic fish captured off the U.S. Atlantic coast, were about an order of magnitude lower than those of several other benthopelagic fishes—macrourids and morids (*Antimora rostrata, Bathysaurus agassizi, Chalinura brevibarbis,* and *C. carapina*)—from the same area-time stratum and of about the same average length, even though their feeding habits and ecological requirements appear to be very similar (Barber et al., 1972). The authors suggest the existence of fundamental metabolic differences to account for the great differences in mercury concentration.

We were unable to find any published data on geographical variations in the mercury levels of tunas, but it is reasonable to suppose that they do occur in view of (1) the geographic variation of mercury concentrations in seawater (Weiss et al., 1972); (2) the geographic exposure of tunas—they are known to occur in all of the major temperate and tropical oceans of the world, and some species migrate many thousands of miles; and (3) the fact that tunas are known to be quite nonselective in their feeding habits (Alverson, 1963).

MERCURY CONTAMINATION AND TOXICOLOGY

As stated earlier, although mercury has been present in our environment since the beginning of time, there are indications that man has been adding significant amounts of this metal to the atmosphere, land, and waters. An analysis of mercury in ice in Greenland has revealed a substantial increase in deposition since 1940 (Weiss, Koide, and Goldberg, 1971). In Sweden, concentrations of mercury in bird feathers were measured, and it was found that mercury levels were low in museum specimens of fish-eating birds collected from 1840 to 1880-90. In the years following, the level has been continuously on the rise. An analysis of seed-eating birds and birds which prey upon them did not show a corresponding rise in levels of mercury until 1946 (Berg et al., 1966). The increase in mercury in the fish-eating birds has been associated with the period when Sweden started to industrialize whereas the marked increase in the seed-eating birds and terrestrial birds of prey has been related to the introduction of organomercurial dressing for

grain. Since 1965 the mercury levels in the feathers of Swedish seed-eating birds have decreased coinciding with the prohibition of alkyl mercury dressings for seed (Johnels and Westermark, 1969).

It should be noted that the increase of mercury in fish-eating birds in Sweden, based on the examination of museum specimens and those of more recent times, is at variance with the situation noted earlier concerning museum specimens of tunas and swordfish. This seeming contradiction may be due to the fact that these fish species are high-seas animals inhabiting waters which are normally far removed from the concentrated effects of mercury pollution caused by man. Furthermore it has been calculated that if the total amount of mercury processed by man since 1900 were put into the world's oceans and well mixed, it would increase the average mercury concentration of seawater (approximately 0.1 part per billion) by at most 1% (Hammond, 1971). Other investigators (Weiss et al., 1971) have calculated that even if the atmospheric mercury load resulting from man's activities equaled the natural degassing rate (which is very unlikely) it would add annually only 15% to the mercury burden of the upper 100 m of the oceans (the mixed layer). With a residence time of mercury in this layer of as much as 5 yr, the mercury content would be increased by a factor of only 0.75. The increased mercury content in surface waters, if transmitted through the food web to the large predatory fishes such as tunas and billfishes, would, at most, double the mercury content in these animals.

Under circumstances whereby large amounts of mercury enter the aquatic environment, freshwater and marine fishes as well as invertebrates will accumulate large amounts of organic mercury, mostly in the form of methylmercury (Hannerz, 1968). Ingestion of substantial quantities of such contaminated aquatic organisms may lead to toxicological symptoms ranging from temporary or permanent afflictions to death. Fortunately, it appears that the contamination caused by industrial discharges and agricultural use of grain treated with mercury compounds, although persistent, tends to become localized.

MERCURY POISONING AND ITS EFFECTS

Methylmercury poisoning resulting from ingestion of contaminated aquatic organisms became evident in 1953 when an epidemic of neurological debility and deaths in people and animals which had eaten fish and other seafood from Minamata Bay in Japan was traced to dumping of large amounts of inorganic mercury into the sea and subsequent microbial methylation of that mercury (Ui, 1971).

It is of no surprise that health authorities around the world became concerned about the possible presence of mercury contamination in their waters. In 1967, Sweden became alarmed to the extent that it closed about 40 contaminated freshwater areas to commercial fishing. At the same time Swedish health authorities established a legal limit of 1.0 ppm as the maximum permissible concentration of mercury in the flesh of fish destined for human consumption. In 1970, fishes of the Great Lakes region were investigated and found to have high mercury levels. A survey of fishes in various lakes showed a direct correspondence between mercury levels in fishes and their relative proximity to industrial mercury sources. Fish-eating birds from the same areas were collected for study. Some of the species of aquatic birds were found to have levels of mercury much higher than in the fishes, which has been related to their relative position within the food chain.

When the clinical aspects of mercury poisoning are considered (Katz and Krenkel, 1972) it becomes more evident why such great concern exists in many parts of the world about the occurrence of unduly high amounts of methylmercury in food. All indications are that mercury, in the form of its methyl compound, readily crosses the blood-brain barrier. As with most toxic substances, the effect of methylmercury varies from person to person. Symptoms can manifest themselves gradually so that the afflicted individual scarcely notices, or they can manifest themselves rapidly in agitation, convulsions, or even coma. In extreme cases of poisoning, destruction of the central nervous system can be so rapid that serious,

irreversible damage is done before the cause of the symptoms is diagnosed. Other manifestations of methylmercury poisoning are concentric restriction of the visual field or even blindness, inability to coordinate voluntary muscular movements, and paralysis. As methylmercury readily crosses the blood-placenta barrier, even an unborn child can be poisoned if its mother is exposed to methylmercury poisoning. Very little is known about the subclinical effects of methylmercury.

It is interesting to note that Ganther et al. (1972) found that the increase in mercury content between two lots of canned tuna examined, one of low mercury content (0.32 ppm average) and the other of high mercury content (2.87 ppm), was in an approximate 1:1 molar ratio with the increase in selenium. Furthermore they found that selenium added to the diet of rats in quantities comparable to that found in tuna, decreased methylmercury toxicity in the rats. These authors suggest that selenium in tuna may actually lessen the danger to man of mercury in tuna.

MERCURY STANDARDS FOR FISH AND FISH PRODUCTS

Currently, only about 13 countries have established standards for the allowable amount of mercury in fish and fishery products for human consumption. These standards, ranging from 0.5 to 1.0 ppm, are expressed in parts per million by wet weight and refer to total metallic mercury (the organic and inorganic compounds of mercury are reduced to metallic mercury during the analysis).

The acceptable limits of mercury in fishes and other aquatic organisms are based on investigations (Berglund et al., 1971) of clinically detectable poisoning of adults sensitive to methylmercury which indicate that manifestations appear at a blood level of 0.2 μg/g (expressed as metallic mercury per gram of whole blood). This level is attained by exposure to 0.3 mg of mercury (as methylmercury) per day taking into account the fact that the human body excretes methylmercury at a rate which eliminates half of the amount present in 70-90 days (Aberg et al., 1969; Berglund et al., 1971). A prestigious Expert Panel appointed by the Swedish Board of the National Institute of Health, in consultation with the Swedish National Board of Health and Welfare and the Swedish National Veterinary Board, applied a safety factor of 10 to arrive at 0.02 μg/g as an acceptable level of mercury (as methylmercury) in whole human blood and 0.03 mg as an acceptable daily intake of methylmercury (Lambou, 1972).

It is generally accepted by researchers and health authorities that with the exception of contaminated wildlife, grain, etc., food of terrestrial origin is relatively free of mercury in general and of methylmercury specifically, and that the only significant source of methylmercury in the human diet is fish and other aquatic organisms (Nelson et al., 1971). In calculations of dietary intake of methylmercury and in the formulation of mercury standards, generally only this class of food is taken into consideration. Therefore, to evaluate the risk of mercury to the general population it is necessary to know the daily or weekly consumption of fish and other aquatic animals.

The Swedish Commission on Evaluating the Toxicity of Mercury in Fish recommended an allowable weekly intake of mercury equivalent to 210 g of fish containing 1.0 ppm of mercury. However, some experts are cautioning that a level of 1.0 ppm in fish might result in a high mercury intake in some individuals eating more fish than the average for the Swedish population, thus attaining the lowest levels shown clinically to be present in persons sensitive to methylmercury poisoning.

The Swedish findings on mercury contamination of fish from some lakes and rivers caused the Food and Drug Administration (FDA) of the U.S. Government to begin its own evaluation, and an "in-house" standard of 0.5 ppm was adopted in May of 1969. If all fish and shellfish contained 0.5 ppm mercury, the daily limit of 0.03 mg of mercury could be reached by eating 420 g of fish and shellfish per week. A. C. Kolbye of FDA, during a hearing before a Congressional Subcommittee, stated that the average weekly intake of fish in the United States is 280 g. However, a survey of the U.S. Department of Agriculture states that the

average is only 168 g. Regardless of the differences between the two estimates of intake, it is evident that even if we assume that all the fish flesh consumed in the United States has 0.5 ppm of mercury, the average daily intake of methylmercury from that class of dietary items should be below 0.03 mg.

A very recent study (Finch, 1973) based on a computer model indicates that FDA's present interim guideline of 0.5 ppm for mercury in fish could be raised to 1.5 ppm without compromising public safety. The computer model uses the results of a survey of fish consumption patterns of about 1,500 U.S. families, together with known levels of mercury in 52 kinds of fish, to predict the distribution of the daily intakes of mercury from fish, among the survey participants.

In 1970, FDA began to test many fish species for mercury content. In a period of a few months they found that nearly 4% of the canned tuna on the wholesale market contained amounts of mercury in excess of the FDA guideline of 0.5 ppm, ranging up to approximately 1.0 ppm. Species of tuna primarily involved were yellowfin tuna, albacore, *Thunnus alalunga*, bigeye tuna, *T. obesus*, and bluefin tuna, *T. thynnus*. Approximately 12,500,000 standards cans of domestic tuna were voluntarily removed from the U.S. market. At about the same time FDA recalled from the market nearly all swordfish because of high levels of mercury. In May 1971, FDA announced that a 3-mo study showed that all but 42 of 853 samples of swordfish contained mercury at or above the guideline of 0.5 ppm. The U.S. Commissioner of Food and Drugs specifically recommended that the public not eat swordfish.

Although the contamination of fish and aquatic organisms has been clearly demonstrated in a number of countries, including the United States, so far there is no evidence that the mercury in tunas, swordfish, marlins, and some other of the high-seas pelagic fishes can be attributed to contamination resulting from human activities. When FDA introduced the safety guidelines, which eventually were instrumental in removing nearly all swordfish and substantial quantities of canned tuna from the market, it acted essentially under the assumption that the fish product was "adulterated" by an "added substance." Legal aspects of this action have been thoroughly discussed in an article which appeared in Harvard Law Review (1972).

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NOTE

An important paper on mercury in fishes and shellfishes, including tunas, reached our hands after submission of our manuscript for publication:

SUN, C. T., AND W. H. CHANG.
1972. A survey of mercury residue in fish caught by Taiwan's fishing vessels. J. Fish. Soc. Taiwan 1(2):31-40.

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EFFECTS OF REGULATORY GUIDELINES ON THE INTAKE OF MERCURY FROM FISH—THE MECCA[1] PROJECT

ROLAND FINCH[2]

ABSTRACT

The MECCA program applies a survey of the fish consumption habits of a sample of over 4,500 individuals, representative of the U.S. population, to build a computer model, which uses known levels of microconstituents in 52 kinds of fish to predict the distribution of the daily intakes of the microconstituents from fish among the survey participants. The model was applied to mercury levels in fish to estimate the effects of guidelines (maximum permitted levels) for fish in protecting the population against excessive intake. The study indicated that, for the sample population, intakes of mercury from fish would remain safe if the guideline for mercury in fish were raised from the present level of 0.5 ppm to 1.5 ppm. The effect of such an increase would be of benefit to both the consumer and the fishing industry. This model can be used to predict the distribution of consumer intakes from fish of any constituent present in the fish, whether nutritious or potentially hazardous, for which the levels in the edible portion of the 52 kinds of fish used in the model are known.

Following incidents of methyl mercury poisoning reported from Japan and Sweden, the U.S. Food and Drug Administration (FDA) in 1970 established an interim guideline permitting a maximum level of 0.5 part per million (ppm) for methylmercury in fish, determined in practice through total mercury. This level was based on a careful review of the limited information available to the FDA at that time, but it was noted that this was an interim action and the level would be subject to amendment if subsequent information indicated this should be done. The level was based on the following assumptions:

1. Fish is the sole significant contributor of methylmercury in the U.S. food supply. Traces of mercury are sometimes found in other foods but are present in the substantially less toxic inorganic form.
2. Almost all of the mercury present in marine fish, which compose most of the U.S. supply, is present in the form of methylmercury.
3. Man can safely consume up to 30 μg methylmercury daily (see Peterson, Klawe, and Sharp, 1973).
   Continued consumption of larger average intakes increases his body burden and can result in harmful effects.
4. An average high consumption level of fish in the United States does not normally exceed 60 g (just over 2 oz) daily. This figure can be compared with the calculated national average of approximately 14 g daily.
5. Limiting the methylmercury level of fish to 0.5 ppm would limit the intake provided by 60 g fish to 30 μg/day.

It was pointed out at the time that the greater part of the fish supply in the United States contains considerably less than 0.5 ppm mercury and suggested that it would be more realistic to use a weighted average of the mercury levels of all species consumed in calculating a guideline. This average, calculated to be below 0.20 ppm, would give a guideline of 1.2 ppm or higher. Such an approach was not regarded as acceptable by the FDA, since

[1] MECCA is an acronym for Model for the Estimation of the Consumption of Contaminants from Aquatic Foods.

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Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

some consumers can be expected to eat disproportionately large amounts of species which they prefer and which in some cases will contain more than this average. This interim level is still in effect.

The application of the 0.5 mercury interim guideline has led to serious operational and economic hardship for some segments of the fishing industry. The swordfish industry has been virtually eliminated, at least for the present. The tuna and halibut industries are operating voluntary self-regulation schemes involving extensive testing, elaborate and expensive handling procedures, and product loss. Press reports on other species have alarmed consumers and adversely affected sales. It is therefore worth examining this present guideline level to see if evidence exists that would provide a basis for upward modification which, while ensuring adequate consumer protection, would alleviate the burden on the fishing industry.

Apart from reexamination of the assumptions, such as the proportion of total mercury present as methylmercury in fish, two key figures can be reviewed which together establish the basis for the 0.5-ppm level. The first of these, the so-called acceptable daily intake (ADI) of 30 μg methylmercury/day, has been reviewed recently by the World Health Organization (WHO)/Food and Agriculture Organization of the United Nations (FAO) Expert Committee of Food Additives, but no information has thus far emerged which will permit a modification of this figure. The second figure is the high average consumption level of 60 g fish daily.

In order to examine the second assumption more carefully, a computer program was written to apply the results of a survey of fish consumption patterns of over 1,500 families to estimate the distribution of individual intakes of any microconstituent for which the levels in different species of fish are known. This was then applied to predict the effect of alternative regulatory guidelines (maximum permitted levels) on reducing the mercury intake of consumers. The same program is directly applicable to estimating the distribution of individual intakes of any microconstituent, whether nutritious or potentially toxic, provided that the levels are known in all the species of fish consumed.

The following report details the procedures used and discusses the results as applied to methylmercury.

MARKET FACTS INC. SURVEY

Commencing February 1969, Market Facts Inc. of Chicago, Ill., under contract with the National Marine Fisheries Services (NMFS), carried out a 1 yr survey of fish consumption patterns of 1,586 U.S. households with a total of 4,864 persons. The participants were selected at random from a large panel designed to parallel census data for the United States with respect to population density and degree of urbanization, geographic region, household income, and age of panel members, providing a reasonable cross section of other demographic characteristics.

The head of each household completed a diary of fish purchases twice monthly for 12 mo. These diaries reported purchases of fish and shellfish products by item, weight and cost, numbers of fish meals eaten away from home by item, and the number of meals consumed at home prepared from sport fish by species. Purchases of meat, meat products, and meat substitute foods were also recorded.

This survey was undertaken to provide information for economic analysis. Results have been reviewed by Nash (1971) and by Miller and Nash (1971).

APPLICATION OF THE SURVEY TO INTAKE ESTIMATES

General Procedure

In order to organize the data in the Market Facts survey to enable intakes to be estimated, they were first transformed into a data base which lists for each family, estimates of the total weights of each kind[3] of fish consumed

[3] The term kind of fish is used here rather than species since, although most of the kinds of fish in the data base are identifiable species in the biological sense, some refer to common names representing mixed species

for the period reported. A computer model was then constructed to scan the data base, using for each run a given set of microconstituent levels for the 52 kinds of fish reported in the data base, and to calculate the average daily intake of the microconstituent for each family in turn, based upon its consumption by species. From this a distribution of the estimated intake levels of all the individuals in the survey was calculated and printed out, with other data to be described. This model was applied to calculate mercury intakes from fish of individuals in the sample on the basis of average levels of mercury for the 52 kinds of fish in the data base. Further computer runs were then made using alternative input mercury levels. These were calculated assuming the effects of different regulatory guidelines upon the mercury levels in the available supply. The program readouts enabled the mercury intakes of the population average, or of any given fraction of the population, to be estimated under any of the input conditions. By comparing results, the extent to which different guidelines reduced the intakes of mercury was estimated. This process is described in detail in the following sections of the report.

Transformation of Survey Information to Data Bases

The estimates of consumption of kinds of fish which comprised the data base were developed as follows:

1. Records were selected from those families who reported for a minimum of 12 periods (6 mo). The number of reporting periods was noted for each family.
2. The purchases of each item by each family during all reporting periods were totaled.
3. These amounts were transformed into corresponding figures for weights of each kind of edible fish consumed by multiplying the total for each item by an appropriate factor for that item. Table 1 lists these factors and provides a note on their derivation.
4. The next step was to estimate the amounts of fish items consumed in meals away from home. The records showed for each item the number of times it was consumed in the reporting period, and how many family members participated in each meal out. From this, the total number of servings of each item for each family was determined for the total reporting period.
5. This number of servings was then converted to the weight consumed, using a factor for the item representing the average weight in ounces usually provided in one serving. Table 1 lists the factors used.
6. The estimated weights for each kind of sport fish consumed by each family was obtained by multiplying the number of events for each kind by the number in the family and then by a factor representing the estimated average weight of the edible portion of this kind usually consumed by an average individual. These factors shown in Table 1 are the same as those used for meals away from home.
7. The total weight of each kind of fish consumed by each family was obtained by adding the edible weights purchased to the weights provided by meals away from home and the sports catch consumption. In a number of cases, several separately reported items were aggregated to provide total estimates of the consumption of a given kind of fish from all sources. For example, the total for the light meat tuna category included canned light meat tuna, tuna sandwiches, tuna salad, and tuna pies. In this way over 150 different classes of fish and products, many of them specialty items, were reduced to 52 kinds. The finished data base displays the estimated amounts of each of these 52 kinds of fish consumed from all sources by each family during the reporting period, the length of reporting period, the number in in the family, and coded socioeconomic data provided by the original survey.

used in the survey and better understood by the average consumer. For example, light meat tuna can legally consist of several species, although in the United States it commonly includes yellowfin tuna, *Thunnus albacares*; bluefin tuna, *Thunnus thynnus*; and skipjack tuna, *Katsuwonus pelamis*. Also for convenience of calculation, some fish products, such as fish sticks, were identified as kinds of fish in the data base rather than reassigning them to component species.

TABLE 1.—Factors used to convert purchased weight, events of meals away from home and home consumption of sport catch to weight of edible portion consumed.[1]

Original item code	Name of item	Purchase/ consumed	Meals away from home and sport catches (oz/event)
001	Tuna pie	0.18	—
002	Clam chowder	.13	—
003	Oyster stew	.30	—
004	Shrimp creole	.14	—
005	Shrimp, stuffed	.90	—
006	TV or prepared fish dinners	.25	—
007	Smoked fish (not canned)	.75	—
008	Cured fish (not canned)	1.00	—
009	Kippered fish (not canned)	.35	—
010	Salted fish (not canned)	1.00	—
011	Pickled fish (not canned)	1.00	—
012	Other specialty items	.50	—
014	Shrimp — size unspec.	.70	3.00
015	Shrimp — jumbo size	.70	3.00
016	Shrimp — large size	.70	3.00
017	Shrimp — medium size	.70	3.00
018	Oysters	1.00	4.00
019	Alaska king crab, unspec.	.20	2.25
020	Alaska king crab, hard	.20	2.25
021	Alaska king crab, soft	.20	2.25
022	Alaska king crab, other	.20	2.25
023	Dungeness crab, unspec.	.24	4.00
024	Dungeness crab, hard	.24	4.00
025	Dungeness crab, soft	.24	4.00
026	Dungeness crab, other	.24	4.00
027	Blue crab, unspec.	.15	4.00
028	Blue crab, hard	.15	4.00
029	Blue crab, soft	.55	4.00
030	Blue crab, other	.15	4.00
031	Deviled crab	1.00	4.00
032	Other crabs, unspec.	.15	4.00
033	Lobster (not Crayfish)	.25	6.00
034	Lobster tail (rock lobster)	.50	6.00
035	Clams (excluding clam chowder)	1.00	4.00
036	Scallops	1.00	4.00
037	Fish sticks	.50	2.00
038	Other	1.00	4.00
039	Haddock	1.00	5.00
040	Flounder and/or sole	1.00	4.00
041	Halibut (Pacific)	1.00	5.00
042	Ocean perch	1.00	4.00
043	Cod	1.00	6.00
044	Salmon	.90	5.50
045	Red snapper	.40	8.00
046	Catfish	.90	5.00
047	Whiting	.40	6.00
048	Scup, porgy	.40	6.00
049	Mullet	.50	6.00
050	Bullhead	.80	6.00
051	Herring	.40	6.00
052	Mackerel	1.00	6.00
053	Buffalo fish	1.00	6.00
054	Yellow perch, Lake perch	.90	4.00
055	Striped bass	.35	6.00
056	Swordfish	1.00	6.00
057	Carp	.40	6.00
058	Crappie	.40	6.00
059	Shad	.40	6.00
060	Alewife	.35	6.00
061	Pollock	1.00	6.00
062	Lake trout	.90	6.00
063	Lake whitefish	.90	6.00
064	Smelt	.80	6.00
065	Jack mackerel	.40	6.00
066	Rockfish (Pacific)	1.00	6.00
067	Pompano	.40	6.00
068	Pike	.80	6.00
069	Butterfish	.50	6.00
070	Trout (other than lake)	.50	6.00
071	Perch (other than yellow or lake)	.50	4.00
072	Bass (other than striped)	.50	6.00
073	Fish sticks	.50	2.00
074	All other	1.00	6.00
075	Canned pink salmon	1.00	—
076	Canned red or sockeye	1.00	—
077	Canned silver or coho	1.00	—
078	Canned chum	1.00	—
079	Canned chinook	1.00	—
080	Canned salmon, unspec.	1.00	—
081	Canned other	1.00	—
082	Canned white meat, unspec.	1.00	—
083	Canned white meat, chunk	1.00	—
084	Canned white meat, solid	1.00	—
085	Canned light meat, unspec.	1.00	—
086	Canned light meat, chunk	1.00	—
087	Canned light meat, solid	1.00	—
088	Canned dark meat, unspec.	1.00	—
089	Canned dark meat, chunk	1.00	—
090	Canned dark meat, solid	1.00	—
091	Canned grated tuna	1.00	—
092	Canned tuna chunk, unspec.	1.00	—
093	Canned other	1.00	—
094	Canned tuna, unspec.	1.00	—
095	Canned Maine	1.00	—
096	Canned Imported	1.00	—
097	Canned Pacific	1.00	—
098	Other sardines, other unspec.	1.00	—
099	Canned shrimp	1.00	—
100	Canned oysters	1.00	—
101	Canned mackerel	1.00	—
102	Canned anchovies	1.00	—
103	Canned clams (minced)	1.00	—
104	Canned lobster	1.00	—
105	Canned crab/crabmeat, unspec.	1.00	—
106	Canned Alaska king crab	1.00	—
107	Canned crab dungeness	1.00	—
108	Herring	.90	—
109	Gefilte fish	1.00	—
110	Shrimp, unspec.	—	3.00
111	Fried shrimp	—	3.00
112	Shrimp cocktail	—	1.50
113	Stuffed shrimp	—	4.00
114	Shrimp royale	—	3.00
115	Other shrimp	—	4.00
116	Lobster, unspec.	—	6.00
117	Lobster tail	—	6.00
118	Other lobster (boiled, etc.)	—	6.00
119	Clams, unspec/fried	—	4.00
120	Clam chowder	—	1.50
121	Other clams	—	2.00
122	Crab/crabmeat, unspec.	—	4.00
123	Crab dungeness	—	4.00
124	Crab Louis	—	2.00
125	Alaska/king crab	—	2.25
126	Other crabs (soup)	—	1.50
127	Perch, unspec.	—	4.00
128	Ocean perch	—	4.00
129	Fried perch	—	4.00
130	Other perch	—	4.00
131	Oysters	—	4.00
132	Scallops	—	4.00
133	Other oysters	—	4.00
134	Flounder	—	5.00
135	Haddock	—	5.00
136	Catfish	—	5.00
137	Halibut	—	5.00
138	Trout	—	6.00

TABLE 1.—*Continued.*

Original item code	Name of item	Purchase/ consumed	Meal away from home and sport catches (oz/event)
139	Red snapper	—	8.00
140	Tuna	—	2.50
141	Tuna casserole/salad/ a la king	—	2.50
142	Salmon, all	—	5.50
143	Swordfish	—	6.00
144	Fish sticks	—	2.00
145	Fish & chips	—	3.00
146	Fish & fries	—	3.00
147	Seafood plate/platter Fish dinner	—	4.00
148	Fish sandwich	—	2.00
149	Fish croquettes	—	2.00
150	Sole	—	4.00
151	Chinese dinners	—	0.75
152	Fish fry	—	4.00
153	Fish, unspec.	—	6.00
154	Other	—	6.00
155	Mackerel	—	6.00
156	Herring	—	5.00
157	Whitefish	—	6.00
158	Cod	—	6.00
159	Pike	—	6.00

[1] These data were derived by reviewing the commonly sold forms of the species involved, available data on the yield of edible portions from purchased forms, and amounts used in standard recipes. For meals away from home, data on amounts of fish served in various dishes was obtained from major institutional caterers. All these figures are somewhat variable, and the factors used represent best estimates of the averages in each case.

A review was made of the defective records in the survey, i.e., those with incomplete data. It was decided that these might be compensated in two ways. One would be to eliminate all defective records. This would give a smaller base but one which might be atypical since more records were defective in some categories. The second approach would be to include all records and develop a recovery procedure for these. It was decided to develop two data bases, one using each procedure. If these compared well, it would indicate the acceptability of both treatments. A detailed description of the consideration, the procedures used, and a comparison of results using the two data bases, are shown in the Appendix. Both methods gave comparable results, thus adding confidence that the methods used were valid. Runs were usually made using Data Base 1.

Application of Data Bases to Estimate Mercury Intakes

The computer program is designed to use the data base to estimate the intake of a microconstituent, in this case mercury, for each family in turn and to display the distribution of these estimated intakes among families and individuals. This is accomplished as follows:

1. The input for each run is a set of microconstituent levels for each of the 52 kinds of fish.
2. Using this set of levels, the program calculates the estimated average microconstituent intake of each family in micrograms per day (I_f) by aggregating the intakes calculated for each kind of fish, and prorating from the number of periods reported (P) to 24 (1 yr, semimonthly) as follows:

$$I_f = \frac{24}{P} \Sigma\ W_s \times L_s \times 0.0777$$

where: W_s = estimated total weight (ounces) consumed of species s.

L_s = level of microconstituent (ppm) in species s.

3. The intake for each family is divided by the number in the family to give individual daily intake levels.
4. The results from all families and individuals are ranked in intervals of 1 μg/day. The results are printed out in two forms. One shows the number and percentage of individuals and families falling into each interval. The second is a histogram which displays the percentage of individuals by tenths falling into each interval.
5. The program also prints out the coded identity of each of the families in the five highest intake intervals occurring and the level of their individual intakes.
6. In addition, the average daily intake for all individuals is calculated and printed out.

Mercury Levels in Fish

In order to apply methylmercury data to the program, a review was made of analytical results available for total mercury on different

species of fish, including results obtained by the NMFS, and those made available by the FDA and the Canadian Government Inspection Service. The data were all obtained using variations of the following procedures: Armstrong and Uthe (1971); Uthe (1971) and Uthe, Armstrong, and Stainton (1970). Difficulty was experienced in cross referencing in some cases since the Market Facts survey used common names for fish which did not always represent unique species. For example, the survey lists mackerel. This could include Spanish mackerel, *Scomberomorus maculatus*; king mackerel, *Scomberomorus cavalla*; or Atlantic mackerel, *Scomber scombrus*. It would not refer to jack mackerel, *Trachurus symmetricus*, which would appear under canned mackerel. In this case, average mercury levels were calculated for mackerel by weighting levels for each of the three species referred to above according to the 1969 U.S. landings (Riley, 1970).

In the case of mixed categories, levels were calculated for each, making assumptions on their frequency of use. Thus in the case of fish sticks, it was assumed that these consisted of 40% cod, 40% haddock, and 20% sole. The risk of introducing serious errors by this somewhat arbitrary procedure was not considered high since all the species likely to be involved in these grouped categories have relatively low mercury levels (0.1 ppm) and do not differ greatly from each other. The case of light meat tuna presents a particular problem since the consumption is relatively high and the levels both within and between species vary considerably.

In other cases also it is difficult to be sure of the extent to which the analytical data for particular kinds of fish is representative of mercury levels in the corresponding commercial supply since methylmercury levels in fish may vary substantially with biological and environmental factors and since there are practical limits to the number and range of samples which may be obtained and analyzed and to their application to the market supply. Moreover, sampling for regulatory purposes may be concentrated on those segments of the catch whose size and catch location may give reason to believe they are most likely to exceed the guideline, e.g., large fish, so that the results obtained in the course of regulatory activities may be unrepresentative of the whole catch. For this study the sources of all available data for each species were reviewed and, to the extent possible, data believed to be unrepresentative were eliminated. The mercury data used also reflect that in the fishery resource, not that in the market place, since FDA controls have eliminated much, if not all, of the high level fish. The figures used cannot therefore be regarded as indicators of levels found in the present supply, but rather that which would exist under various guideline conditions.

To assess the effects of possible errors in the mercury levels used, the sensitivity of the estimates produced by the program to variations in input levels of each species in the program was tested. Preliminary runs were made in which the input mercury levels were increased for each kind of fish in turn. In the case of kinds of fish having low levels initially, the level was increased by 100%. Where the initial levels were over 0.20 ppm, the levels were increased by 25-70% with actual increases no less than 0.10 ppm. Sensitivity was judged by differences from the standard run in the level of intake not exceeded by 99% of the sample (99% level), by changes in the intakes of the highest family. The preliminary runs showed that increases in 40 of the kinds of fish in the survey had no measurable effect on the higher intake levels. This means that relatively large errors in the mercury input data for these kinds of fish data would not be critical to the reliability of the end result. Of the remainder, only variations in the input data of white meat tuna, light meat tuna, and swordfish showed marked effects on the end results. These were subjected to further sensitivity testing using revised data as were also mackerel, red snapper and the "all other fish" category since mercury data available for these was limited. The results of these tests, shown in Table 2, confirms that only the input levels of light meat tuna, white meat tuna, and swordfish markedly affect the end results.

Finally, in order to estimate the effects of guidelines on the mercury consumption pattern,

average mercury levels were calculated for each kind of fish, under five assumptions:

1. All the commercial catch is marketed (base line).
2. Fish containing over 1.5 ppm mercury are removed from the market (guideline 1.5 ppm).
3. Fish containing over 1.0 ppm mercury are removed from the market (guideline 1.0 ppm).
4. Fish containing over 0.75 ppm mercury are removed from the market (guideline 0.75 ppm).
5. All fish containing over 0.5 ppm mercury are removed from the market (present FDA guideline).

For most kinds of fish no sample exceeded 0.5 ppm, and the averages were the same under different assumptions. A list of the levels used under the assumptions is given in Table 3. It is reiterated that these are not intended in all cases to represent levels in fish now available in the market.

TABLE 2.—Sensitivity test.[1]

Run identity	Mercury level input (ppm)		Readouts (μg/day)[2]			
	Standard	Test	0.1%	1.0%	Highest reading	Average
Standard run	—	—	30	17	31.8	2.57
Light meat tuna	0.31	0.41	30	18	32.7	2.85
White meat tuna	0.30	0.35	30	18	31.8	2.69
Swordfish	1.10	0.00	19	12	20.8	1.94
Mackerel	0.51	0.71	30	17	31.8	2.58
Red snapper	0.43	0.54	30	17	31.8	2.58
All other fish	0.15	0.30	30	17	31.8	2.62

[1] The tests were run using Data Base 2 and preliminary data. They may therefore differ slightly from the final run data. Sensitivity to the increase or decrease in mercury level input shown in the test column may be seen by comparing the corresponding readouts with the standard run.
[2] Columns marked 0.1% and 1.0% refer to the level of daily intake in μg/day exceeded only by 0.1% and 1.0%, respectively, of the individuals in the sample.

TABLE 3.—Mercury levels[1] used in MECCA runs.

Code	Kind of fish	Alternative guideline levels (ppm)				
		none	1.5	1.0	0.75	0.5
01	Tuna — light	0.31	0.26	0.26	0.26	0.22
02	Tuna — white	0.30	—	—	—	—
03	Clam	0.04	—	—	—	—
04	Oyster	0.03	—	—	—	—
05	Shrimp	0.06	—	—	—	—
06	Whitefish	0.05	—	—	—	—
07	Herring	0.07	—	—	—	—
08	Cod	0.10	—	—	—	—
09	King crab	0.06	—	—	—	—
10	Dungeness crab	0.16	—	—	—	—
11	Blue crab	0.08	—	—	—	—
12	Lobster	0.24	0.24	0.24	0.19	0.19
13	Lobster tail	0.09	—	—	—	—
14	Scallops	0.03	—	—	—	—
15	Other shellfish	0.06	—	—	—	—
16	Haddock	0.05	—	—	—	—
17	Flounder/sole	0.10	—	—	—	—
18	Halibut	0.23	0.21	0.21	0.20	0.17
19	Ocean perch	0.08	—	—	—	—
20	Salmon	0.03	—	—	—	—
21	Snapper	0.42	0.37	0.37	0.36	0.32
22	Catfish	0.14	—	—	—	—
23	Whiting	0.07	—	—	—	—
24	Scup porgy	0.19	—	—	—	—
25	Mullet	0.14	—	—	—	—
26	Bullhead	0.30	0.30	0.30	0.30	0.14
27	Mackerel	0.51	0.44	0.37	0.33	0.25
28	Buffalo fish	0.23	0.21	0.21	0.21	0.21
29	Yellow, lake perch	0.35	0.35	0.26	0.24	0.21
30	Striped bass	0.35	0.35	0.26	0.23	0.21
31	Swordfish	1.10	0.92	0.80	0.63	0.49
32	Carp	0.31	0.31	0.22	0.19	0.17
33	Crappie	0.11	—	—	—	—
34	Shad	0.12	—	—	—	—
35	Alewife	0.10	—	—	—	—
36	Pollock	0.22	—	—	—	—
37	Lake trout	0.35	—	—	—	—
38	Smelt	0.07	—	—	—	—
39	Jack mackerel	0.04	—	—	—	—
40	Rockfish (Pacific)	0.20	0.20	0.20	0.19	0.19
41	Pompano	0.41	0.25	0.25	0.25	0.25
42	Pike	0.56	0.56	0.43	0.37	0.25
43	Butterfish	0.05	—	—	—	—
44	Trout	0.16	0.16	0.15	0.15	0.13
45	Bass	0.44	0.44	0.37	0.33	0.27
46	Fish sticks	0.06	—	—	—	—
47	All other fish	0.15	—	—	—	—
48	Seafood plate	0.06	—	—	—	—
49	Other specialties	0.06	—	—	—	—
50	Sardine, not Maine	0.02	—	—	—	—
51	Anchovies	0.04	—	—	—	—
52	TV dinners	0.05	—	—	—	—

[1] Figures are only shown for guidelines where there are differences from the unconstrained averages.

PROGRAM RUNS AND READOUTS

Following a number of preliminary experiments, including data base comparisons and sensitivity tests, the computer program was run using Data Base 1 with the following mercury levels:

1. Base-line level, i.e., average calculated for each species assuming no guidelines.
2. Average levels calculated for each species assuming each of the guidelines referred to above (Table 3).
3. Base-line level with the level for swordfish set at zero (to simulate the effect of removing swordfish from the fish supply).

From the printouts for each run, the following figures were tabulated:[4]

1. The estimated daily intake level exceeded by only 1% of the individuals in the sample (referred to as the 1% level).
2. The estimated daily intake level exceeded by only 0.1% of individuals in the sample (referred to as the 0.1% level).
3. The coded identity and estimated daily intake level of the four families with the highest intakes.
4. The average estimated daily intake of all individuals in the survey.

SUMMARY OF RESULTS

The results are summarized in Table 4. They show:

1. Based on the input levels used, 99.9% of the sample population had an intake of less than 30 μg/day, the acceptable daily intake (ADI) which forms the basis of FDA's present 0.5 ppm guideline (99.9% level).
2. The maximum intake was 31.7 μg/day, and this level was reached by one family comprising four individuals, the only family which exceeded 30 μg/day.
3. Ninety-nine percent of the test group had intakes below 17 μg/day, just over one-half of the present ADI (1% level).
4. The average intake was 2.48 μg/day, around 8% of the present ADI.
5. The application of guidelines reduced the higher estimated intakes substantially but reduced the average intake by a proportionately smaller amount.
6. The application of the present 0.5 ppm guideline reduced the highest intake to 21.3 μg/day, the 99.9% level to 20 μg/day, and the average level to 1.99 μg/day.
7. The application of a 1.0 ppm guideline reduced the highest intake to 24.6 μg/day, the 0.1% level to 25.0 μg/day, and the average level to 2.23 μg/day.
8. The application of a 1.5 ppm guideline reduced the highest intake to 27.2 μg/day, the 0.1% level to 26 μg/day, and the average level to 2.28 μg/day.

TABLE 4.—Summary of intake estimates using Data Base 1 (μg/day).[1]

Guideline base	0.1% level	1.0% level	Average level	Intake levels of individuals in the four highest families			
None	30	17	2.48	31.7	29.2	26.6	26.4
1.5 ppm	26	15	2.28	27.2	25.5	24.1	23.0
1.0 ppm	25	15	2.23	24.6	24.0	23.4	23.0
0.75 ppm	21	15	2.17	23.5	22.9	20.9	20.6
0.5 ppm	20	14	1.99	21.3	20.1	20.0	19.0

[1] Intake levels in μg/day exceeded by only 0.1% and 1.0% of the test group.

Swordfish are found to have mercury levels considerably higher than those of other common marine food species. This species has in consequence been largely eliminated from the U.S. market. The effect of this upon mercury intakes was investigated by making a run in which swordfish was eliminated by putting a level of zero into the program. The results are shown in Table 5.

It may be seen that elimination of swordfish gives intake levels which are substantially lower.

This reflects the substantial contribution that swordfish makes to the mercury intake in the diets of high fish consumers. These estimates indicate that if swordfish were to be eliminated from the diet, and no guideline applied, 99.9% of the sample would have a daily intake not exceeding 19 μg/day and the highest intake

TABLE 5.—Effect of eliminating swordfish in intakes (μg/day).[1]

Basis	0.1% level	1.0% level	Average level	Intake levels of individuals in the four highest families			
No guideline	30	17	2.48	31.7	29.2	26.6	26.4
As above but eliminate swordfish	24	15	2.22	26.6	26.4	23.5	23.2

[1] Intake levels in μg/day exceeded by only 0.1% and 1.0% of the test group.

[4] Preliminary runs had shown that one family consisting of a single individual had a mercury intake around 50% higher than the next highest family under all conditions. This individual had reported for a period of 6 mo a total consumption of lake trout of 891 oz (equivalent to 4.9 oz/day). Review of the associated data showed him to have an annual income of $500, a 4th-grade education, and to have purchased 62 lb during a single 2-week reporting period, and none at other times. His total expenditure for the lake trout was given as $8.00, which is much less than the usual retail value of this amount. This report was judged to be returned or entered erroneously and was omitted.

would be 26.3 ppm, less than 90% of the present ADI.

CONCLUSIONS AND DISCUSSION

These results provide evidence which would permit FDA to raise the present interim guideline for mercury in fish to 1.5 ppm without compromising public safety.

At the higher level, it would still be necessary to monitor some fisheries such as swordfish, and perhaps big eye tuna, but the expensive controls on tuna, halibut, and other species would be unnecessary. The benefits of such an action would be:

1. To assist in price stabilization or possible reduction of the affected products.
2. To remove a heavy cost and administrative burden from the processors. While no precise estimate is available, this is believed to run into several millions of dollars of unproductive costs annually.
3. To increase the fish supply by avoidance of rejection, with the corresponding nutritional benefits which this unique food supplies to the U.S. consumer.
4. To offer a probability of restoring the swordfish industry, since an FDA's market survey on swordfish made in 1971, showed that nearly 90% of swordfish samples taken then did not exceed 1.5 ppm. Swordfish at a higher mercury level might be exported to countries which, because of their differing consumption patterns, may not have limiting mercury requirements.

In order to justify the application of the results of the MECCA program to modify present regulatory guidelines, several limitations of the program must be considered. These include:

1. There are limitations on the accuracy of returns received for any survey involving over 40,000 mailed returns. Since families at all levels of education participate, errors in entries will be numerous. When entries are missing, the error is apparent and may be treated, but otherwise there is not usually any way to check. This is especially true in this case where the survey was performed for a different purpose than the present application and was completed 2 yr previously. In addition, there may be key punch errors in transcribing the written report forms received to cards.
2. It is assumed that all the fish purchased was consumed. Any errors in this respect would mean real levels lower than those shown by the program, and so provide a safety factor.
3. The transposition of common names understood by the consumer to particular species with identified mercury levels can give rise to error.
4. In some cases available mercury data are limited.

However, even with these potential shortcomings, we believe that the results of this program present a much more realistic concept than can be obtained from the present simple assumption of a high level daily intake of 60 g/day fish. Particularly it may be noted that, while the absolute values of intakes may be in some error, the relative figures showing the effects of guidelines are likely to be considerably more precise since the same errors in each run will tend to cancel in comparisons. Thus it may be noted in the data base comparison that, while the average intake level estimated for each type of run shown in Table 2 varies from 1.79 to 2.66 μg/day, the difference between the figures produced from the two bases for the same runs varies only from 0.15 to 0.19 μg/day with Data Base 2 being always higher. It may further be noted that the daily consumption of fish in the United States averages 14 g/day. Assuming a weighted average mercury content of around 0.15 ppm for U.S. species, this would provide 2.10 μg/day, which is less than the unconstrained average of 2.48 μg/day predicted by the model. The model figure includes consumption of sport catch but, although no figures exist, this is considered to be relatively small compared with consumption of commercial catch. The model results then are consistent with the

national average derived externally and may indeed show a measure of conservatism, further strengthening the model solidity.

Probably the most important consideration is philosophical. How much of the population can be protected? While it seems likely that the Market Facts survey covers the broad fish purchase pattern in the United States there may be people who for reasons of religion, diet, ethnic considerations, etc. do not fall into the Market Facts pattern. Their interests, if threatened, may best be protected by an education program. It is hard to see how abnormal consumers, i.e., those outside the typical broad fish consumption pattern reviewed, such as weight watchers, can be protected realistically by any guideline that does not seriously restrict the food fish supply and the considerable nutritional benefits it has to offer the U.S. consumer. This is probably true of other guidelines based on a normal consumption pattern. For example, it should be noted that the MECCA results demonstrate that adequate protection would be provided to the entire population using a 1.5 ppm guideline. Applying the more simplistic basis of a 60-g high daily consumption originally used by FDA to the same population demonstrates less protection since 1.8% of the participants in the survey consumed an average of more than 60 g/day, and therefore on a 0.5 ppm guideline, which assumes all fish are at least at this level, these consumers could have exceeded 30 μg/day. In fact, 1% of the participants in the survey consumed 77 g daily, and 0.1% consumed 165 g daily. The MECCA program therefore demonstrates that a greater degree of protection would actually exist using a 1.5 ppm guideline than was planned for in the original calculation which established the present guideline. But in no case under the 1.5 ppm guideline did any participant exceed 27.2 μg/day, nearly 90% of the ADI.

A final note is that the MECCA program is applicable to estimating the distribution of intakes from fish of any nutritional or potentially toxic microconstituent for which the levels in the fish are known. However, its application to potential toxins is limited to mercury since other elements and compounds occur in the whole food supply. The development of a wider survey is now being considered covering the full food spectrum. Participation by FDA and U.S. Department of Agriculture is being investigated. Such a survey could be addressed to any nutrient or constituent in the same manner as MECCA to determine the distribution of the intakes of, say, available iron, vitamin A, DDT, radionuclides, etc.

ACKNOWLEDGMENT

The substantial and willing assistance of David Weiss of NOAA Computer Division and many other staff members of the College Park Fishery Products Technological Laboratory and the Economics Research Laboratory of NMFS and NOAA Computer Division, is gratefully acknowledged.

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APPENDIX

TECHNIQUES USED TO RECOVER DEFECTIVE RECORDS

While editing the Market Facts data, in preparation for creating the MECCA data base, 13,377 records were identified which qualified for inclusion, but which had critical information missing. The missing information was found to be confined to four data elements:

1. Number of individuals in family.
2. Number of meals eaten away from home.
3. Weight of fish purchased.
4. Item code (species identification).

The majority of the 13,377 records had two or more of these items missing. Because of certain redundant information in each record it was felt that many of these records could be recovered without substantial distortion of the true distribution of fish consumption.

The most easily recoverable data item was "number of individuals in family." For each record with this defect, the file of good records was searched until a match on family identity was obtained. The number of individuals shown in the good record was then inserted into the defective record.

Records of meals eaten away from home were supposed to contain the number of meals eaten on that occasion (not necessarily equal to number in family). To recover records in which this information was missing, the file of good records was read. A tally was kept of the number of "meals away from home" records, and the total number of meals eaten on those occasions was tallied. From those two figures the average number of meals eaten away from home on each occasion was computed (1.7). This value was then inserted into the defective records.

Records which had only the above two defects were reintroduced into the file of good records following recovery. The two remaining types of defects presented a more difficult problem of recovery. Not only was there no redundant information of any use, but also it was determined that nearly all of the remaining defective records had neither purchase weight nor species identification. The only usable data in the record, other than family-specific items, was an indication of fish category such as "fresh or frozen finfish," "specialty items," etc. There were 10 such categories. Balancing the desire to account for all fish products consumed against the possibility of introducing distortion of the distribution of consumption, it was decided to create two separate data bases: one with only good records and the records already recovered and the other to include all records, following the recovery of these more serious defects.

These remaining records were recovered in the following manner:

1. The file of good records was first sorted by fish category.
2. The percentage of each category represented by each item code (species identification) was calculated.
3. A cumulative percentage table was constructed for each category, giving the relative frequencies of each item code among the good records on a scale of 1 to 10,000.
4. Each defective record without an item code was read sequentially. A random number in the range 1 to 10,000 was generated and used as the subscript to the appropriate cumulative percentage table. The corresponding item code was then assigned to the record.

This processing resulted in the random assignment of item codes to the defective records with essentially the same relative frequency found in the good records.

The final phase of the recovery process involved assigning a "consumption weight" to each record without a "purchase weight" entry. The good records had already been processed to convert "weight purchased" to "weight consumed" by use of ratio figures supplied by NMFS. The good records were sorted by item code, and the average consumption weight for

each item was calculated. These average weights were placed in an array in item code order. The records which were defective in purchase weight were then read sequentially, and the item code in each record was used as a subscript to access the proper average weight figure in the array. The average weight figure thus located was inserted into the defective record, completing the recovery process.

A comparison of results obtained on different types of runs using both data bases shows little difference (Appendix Table 1).

APPENDIX TABLE 1.—Comparison of data bases using four indices (all figures in μg/day).[1]

Run	0.1% level		1.0% level		Average level		Maximum individual level	
	[2]DB1	[2]DB2	DB1	DB2	DB1	DB2	DB1	DB2
Standard run	29	30	17	17	2.39	2.57	31.7	31.8
Sensitivity LM tuna	30	30	18	18	2.66	2.85	32.6	32.7
Guideline 1.0	26	26	15	15	2.18	2.34	26.9	27.0
Guideline 0.5	21	21	13	14	1.94	2.10	20.7	20.8
Swordfish 0	21	21	14	14	2.13	2.30	26.2	26.3
Guideline 0.5 + swordfish 0	17	19	12	12	1.79	1.94	20.7	20.8

[1] Intake levels in μg/day exceeded only by 0.1% and 1.0% of the test group.
[2] DB1—using Data Base 1. BD2—using Data Base 2. These figures were obtained using preliminary mercury data and may differ slightly from the final results, but the comparative data will not be significantly different.

EVALUATION OF CAUSES FOR THE DECLINE OF THE KARLUK SOCKEYE SALMON RUNS AND RECOMMENDATIONS FOR REHABILITATION[1]

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ABSTRACT

The continued decline of the Karluk River sockeye salmon, *Oncorhynchus nerka*, runs indicated the need for review of their condition. We reviewed the literature on the Karluk sockeye salmon and the different explanations for their decline. Unpublished material from the Auke Bay Fisheries Laboratory, National Marine Fisheries Service, was studied along with published and unpublished observations of Karluk sockeye salmon by the Fisheries Research Institute. Recent reports showing the behavioral differences between fry from one of the side streams and from the Karluk River, combined with studies of the genetic basis of similar behavioral differences in Fraser River sockeye salmon populations indicate that the sockeye salmon of the Karluk system are separated into a number of different races. The spawner-recruit relationship was examined over the 50 yr during which the numbers of spawners and resulting returns have been estimated. The combination of all evidence including peculiarities of sockeye salmon life history, derived from the work of the International Pacific Salmon Fisheries Commission on the Fraser River, and from the material on the Karluk, leads to the conclusion that the Karluk River below Karluk Lake is the largest and most productive spawning area in the system. We conclude that the productivity of the races spawning on these grounds could be restored by removal of all weirs from the Karluk system, by restricting the study of these fish in freshwater to methods which do not involve interfering in any way with the free movement of adults or young, and by protecting the adult Karluk sockeye salmon that move through the fishery in midseason, i.e., during July and August each year.

The year 1973 marks the 53d year since a weir was first installed on the lower end of the Karluk River by the U.S. Fish Commission to count the number of sockeye salmon, *Oncorhynchus nerka*, which escaped the commercial fishery to spawn in the Karluk watershed. While sporadic observations of the fishery and of the spawning grounds had been made before then, a program of management was established in 1921 to assure the escapement of an adequate number of spawners. Gilbert and Rich (1927) began more frequent visits to the spawning areas after 1921 which were extended in 1927 to annual surveys lasting from about May to September each year.

Beginning shortly after 1900, a decline was noticed in the numbers of sockeye salmon returning each year to the Karluk, which was reflected in the annual catch. This decline has continued in spite of the increasing severity of restrictions imposed on the fishery to allow a greater proportion of the run to spawn. In 1971, the fishery was closed although an incidental catch of 14,000 Karluk sockeye salmon resulted. Nevertheless, only 144,660 sockeye salmon escaped through the weir. Using the factor of 10% of the total run used by the Auke Bay Fisheries Laboratory staff of the National Marine Fisheries Service (NMFS), NOAA, since 1963 to estimate the numbers spawning in the Karluk River below the weir, the total run that year must have been about 175,000 fish, the smallest

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Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

run of sockeye salmon ever recorded for the Karluk. Since the total run was estimated to have been about 5,600,000 (Rounsefell, 1958, Table 2) in 1901 it is obvious that the management program during the past 50 yr has not been effective. The results of research made available to us indicate that agreement has not been reached on the reasons for the continued decline of the Karluk sockeye salmon runs.

Examination of published papers and unpublished material made available to us by William A. Smoker, Director of the Auke Bay Fisheries Laboratory, NMFS, NOAA, by the Alaska Division of Fish and Game, and by various members of the staff of the Fisheries Research Institute and comparison with information on the sockeye salmon of the Fraser River, has led us to the following conclusions:

1. The Karluk River below the outlet of Karluk Lake is the largest and the most productive sockeye spawning ground in the Karluk system.
2. It must be the principal spawning ground of the midseason sockeye salmon that Thompson (1950) showed had been fished down by a management program which protected only the early and late races.
3. While depletion of these midseason races was the first cause of the decline in the Karluk sockeye salmon runs, the weir, built each year since 1945 just below the outlet of the lake, must have been the final cause of the decline and has driven the productivity of the Karluk sockeye salmon runs to the low level reached in 1950.

Removal of all weirs from the Karluk watershed is recommended as the first and most necessary step toward rehabilitating the Karluk sockeye salmon runs. The midseason races which appear in the fishery between mid-July and late August should also be protected by an effective management program. In addition the research program should be restricted to observations which do not interfere with the movements of either adult migrants, fry, fingerlings, or smolts in any way in the Karluk River, Lake, or tributary streams.

The foundation for these conclusions is developed in the following pages and is summarized in Summary and Discussion.

ACKNOWLEDGMENTS AND SOURCES OF INFORMATION

We wish to acknowledge the assistance of Dorothy D. Beall who has made available the material in the Fisheries Research Institute archives and has checked our bibliography. We also wish to thank William A. Smoker, Director, Auke Bay Fisheries Laboratory, NMFS, NOAA, Alaska, for age and length frequencies of Karluk sockeye salmon samples from 1946 to 1969, and for permission to quote manuscript reports of his Laboratory. Fruitful criticisms of other members of the staff of the College of Fisheries are also acknowledged. Thanks are also extended to the staff of the Kodiak Office, Alaska Department of Fish and Game, for information concerning the 1971 run as well as for historical information on regulations and the valued criticism of the manuscript. John F. Roos of the International Pacific Salmon Fisheries Commission, Charles E. Walker of the Canadian Fisheries Service, Milo C. Bell and Robert L. Burgner of the College of Fisheries, and Richard Gard, formerly of the Auke Bay Fisheries Laboratory, have all contributed valuable comments on the text. We wish to acknowledge especially the excellent work of Charles E. Walker who made some of the most significant observations of the Karluk young and adults during his work with the Fisheries Research Institute.

HYPOTHESES CONCERNING DECLINE

A number of theories have been put forward to explain the decline of the Karluk sockeye salmon runs. Bean (1891), reporting on his visit to Karluk in 1889, noted the large numbers of smolts destroyed by the fishery then operating in the lower end of the Karluk River and indicated that this practice would have to be stopped. Accordingly, the commercial fishery was excluded from the river sometime after 1889 although fishermen were still working in the river as late as 1898 (Moser, 1899). As the run continued to decline commercial fishing was excluded from the Karluk Lagoon in 1918 (Smith, 1920) after it had demonstrated that with longer beach seines than were used in the

river, and with sufficient effort, the seines could block the upstream movement of spawners just as effectively by operating in the lagoon as they had in the river itself. Gilbert and Rich (1927) thought that the downward trend could be reversed if an adequate number of fish were allowed to escape the fishery each year to spawn. Their objective was to make sure that at least 1 million sockeye salmon spawned each year.

Barnaby (1944) found that the relative numbers of fish which had migrated to sea as smolts in their third and fourth years had changed. From this, and from the small amount of phosphorous and nitrogen he found in Karluk Lake compared with that in the spawning streams, as well as from an increase in the proportion of 4-yr smolts, he concluded that the length of freshwater residence had increased, and thus that the productivity of Karluk Lake had decreased.

Thompson (1950), using the number of cases of Karluk red salmon packed each day by one packer, between 1900 and 1919, showed that during the period of 1900 to 1904 the Karluk run had a single peak which occurred early in August (Thompson, 1950, Figure 10). During the next 5 yr (1905-09), this midseason peak decreased and while the run seemed to slack off in early July, the daily pack remained almost constant at an average of about 7,000 cases (4,000 to 11,000) up to mid-September (Thompson, 1950, Figure 11). Thompson's Figure 12 for 1910 to 1914 showed an almost uniform daily pack for the entire season from early June to mid-September with a slight indication of peaks in June and September. These "spring" and "fall" peaks had become well marked in his Figure 13, which showed the total daily case pack for 1915 to 1919. The catch during that period was depressed from 30 June to late August, and the configuration of the run found in 1921 had been established. Thompson (1950) concluded that the midseason fish, which had supported most of the catch in the early fishery and hence were the most productive segments of the run, had been fished out by the fishery which concentrated most of its effort on the middle part of the run. Furthermore, he stated that the productivity of the entire Karluk run of sockeye salmon had been reduced as the run was cut back to the less productive early and late fish. On the basis of this analysis, Thompson and Bevan (1954) advocated managing the Karluk sockeye salmon fishery so as to fish only the early (June) and late (September) segments of the run, allowing all the midseason fish to spawn.

Discussing the similarity in the history of the decline of Karluk sockeye salmon to that of the chinook salmon runs of the Columbia River, and the sockeye salmon runs of the Fraser, Thompson (1950) stated:

> In each case the change took place relatively early in the history of the rivers. A large degree of independence must exist between the different sections of the runs in both cases. And the most productive part of the season has been least protected, so that the best part of the run has vanished. The independence of different sections of the runs is strongly corroborated by what we know of the red salmon runs in a third river, the Fraser in Canada. Here tagging operations have clearly shown that the early runs pass far into the upper Fraser. The late runs spawn mostly in streams near the mouth. Radical reduction of the early runs occurred due to railroad construction along the main river, but other and later runs continued. Even where the early and late runs used the same streams, as in the Adams River, they were depleted and rebuilt independently of each other. It is not only logical but inescapable that a run can be over-fished in one part and under-fished in another, and I can see no other explanation of the peculiar present character of the runs in the Columbia, the Karluk, and the Fraser.

Rounsefell (1958) concluded that the decline since 1900 was not associated with fluctuations in rainfall or temperature, but found reason to believe that predatory fishes such as Dolly Varden, *Salvelinus malma*, and Arctic char, *S. alpinus*, might have been a factor. He disagreed with Thompson that different races of sockeye salmon could exist in the Karluk watershed and concluded that only one population of fish exists in the Karluk by a study of the occurrence of different ages of fish in different years.

Rounsefell has suggested that "the Karluk sockeye salmon comprise one population, since the number of fish of the same brood running at different seasons, and even in different years, are significantly correlated." Unfortunately, he does not point out that the correlations presented concern only a few of the possible age combinations involved and those that he does show as being correlated make up only a minute frac-

tion of the run. The 4_3's amount to a little over 1% and the 7_3's less than 0.1% of the total run. Rounsefell relies on correlations between fish returning at different times of the season to prove one population. It would seem entirely possible that the total returns from two groups of discrete populations that run prior to and after a given date could be negatively correlated.

Rounsefell (1958:142) used his Figure 54 to show that "one can not compare pack during one period with escapement in another period as escapement was not uniform in different parts of the season." This figure actually shows that the percentages of the annual salmon catch that was packed during different portions of the season for 1895 to 1919 and for 1921 to 1950 were almost identical and in reality demonstrated that the catch has been taken mostly from the midseason runs as was shown by Thompson (1950) and by Thompson and Bevan (1954) in the early 1950's. Rounsefell (1958:143) however concluded that the Karluk runs had not been overfished: ". . . . It is not the rate of exploitation that has changed, but the ability of the populations to withstand even a greatly diminished rate." This in effect was the same as Thompson's conclusion except that Rounsefell offered no explanation for this decline in productivity. He recommended in part: 1) control of predatory species of fish in Karluk Lake, after demonstrating that partial control of predators can result in increased predation, and 2) regulation to protect more midseason fish, etc.

Owen, Conkle, and Raleigh (1962),[4] after studying the distribution of spawners of different ages at different times each season, concluded that:

> (14) Based on information and analyses now on hand: (a) A change in the lacustrine environment has not been demonstrated. (b) Long-term physical changes in the spawning habitat have not been demonstrated. (c) Changes in the proportion of the total escapement utilizing the different specific spawning areas are indicated, inasmuch as the fishery over the years has been concentrated on the midseason portion of the run, and the specific spawning areas are occupied in season sequence. (d) Changes in the biological characteristics of the spawners have been suggested, principally in the prolonged lake residence indicated by a higher proportion of 4-freshwater sockeye salmon. Other associated changes are the disappearance of the formerly predominant 5-year cycle and the appearance of larger relative numbers of 4-freshwater grilse.
>
> (15) Changes (c) and (d) above can both be explained as possible effects of the concentrations of the commercial fishery on the midseason Karluk sockeye salmon run, leaving spawning escapement to occur in the fall and in the spring. It has recently been shown that the age composition of returning sockeye salmon is chiefly determined by the age composition of their parents.

They recommended that research be directed at evaluating the productive quality of the season escapements themselves.

Ricker (1972) discussed Rounsefell's conclusions concerning the existence of separate races of sockeye salmon in Karluk Lake on the basis of his interpretation of variations in abundance of the different combinations of freshwater and saltwater ages in different segments of the Karluk run. Ricker concluded that:

> . . . . As I see it, however, none of the information presented precludes the possibility of considerable discreteness of stocks arriving at different seasons, provided the stocks are distinguished by having different proportions of the different life-history types, as is actually the case (personal communication from Dr. J. B. Owen). [Ricker, 1972:41.]
>
> . . . . Thus the balance of local evidence, as well as the analogy with other areas, favours the existence of a number of separate sockeye stocks at Karluk Lake. [Ricker, 1972:42.]

Gard and Drucker (1972)[5] demonstrated the existence of these races by significant differences between early sockeye salmon spawners in the lateral tributaries of Karluk Lake, in the upper Thumb, O'Malley River, and Canyon Creek and those which spawn later in these terminal streams, and on the Thumb Beach in Karluk Lake near the outlet of the lower Thumb River. The late spawners showed greater mid-eye to fork length and greater fecundity at comparable lengths. Gard and Drucker did not include comparison with fish spawning in the Karluk River but concluded that ". . . . Difference in length, age and fecundity among spatial and temporal segments of red salmon have been

[4] Owen, J.B., C. Y. Conkle, and R. F. Raleigh. 1962. Factors possibly affecting production of sockeye salmon in Karluk River, Alaska. U.S. Bur. Commer. Fish., Auke Bay Biol. Lab., Manuscr. Rep. 62-8, 57 p.

[5] Gard, R., and B. Drucker. 1972. Differentiation and cause of decline of sockeye salmon of the Karluk River system, Alaska. Unpubl. manuscr. Auke Bay Fish. Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

demonstrated. These findings support the theory that distinct subpopulations of red salmon separated by space and time exist in Karluk Lake and that these subpopulations possess widely varying reproductive capacities. . . ." These results confirmed the hypothesis of separate races put forward by Thompson (1950), Thompson and Bevan (1954), and Owen et al. (see footnote 4).

In Bulletin No. 10 of the International North Pacific Fisheries Commission (1962:91), the annual escapement and return of sockeye salmon to Karluk Lake were shown in Table 8. These figures were taken from Rounsefell's Table 12 (Rounsefell, 1958:112) which were "corrected for climate, for odd- and even-numbered years, and for density of young in the lake, 1890-1948" although that density had never been measured. The principal result of such "corrections" based upon hypothetical relationships was to reduce the variability of the observed figures.

Rounsefell (1958, Append. D) calculated the total run into the Karluk for each year before 1921 by multiplying the catch by 1.538, on the following basis: Rich (in Gilbert and Rich, 1927) says, "The spawning escapement [of 1926] was the best in many years, and in all probability was the best that has ever been observed by the few white men who have visited the lake."[6] Rounsefell then assumed that if Rich's statement were correct, he could conclude that earlier escapement must have been proportionately smaller than in more recent years and therefore he (Rounsefell) used the number of sockeye salmon (15,000) which Shuman (1950) said spawned in Moraine Creek in 1947 and the number of fish Rutter (quoted by Chamberlain, 1907) estimated to be in Moraine Creek in 1903, to obtain a ratio of 22/15 of the escapement in 1947. Since the escapement in 1947 was 485,000 fish, the escapement in 1903 was estimated as 22/15 of 485,000 or 711,000 fish. The catch in 1903 was 1,320,000 fish, which would make the escapement only 35% of the total run. Rounsefell admitted that the calculation was probably not valid, but used it nevertheless to compute the number of fish in the total run each year before 1921 as the catch divided by 0.65 or multiplied by 1.538.

Since Shuman's count for Moraine Creek escapement was obtained by a weir, while Rutter's estimate was from a stream survey, Rounsefell's factor was too small. In 1952, Bevan and Walker (1955) counted the spawners in Moraine Creek on weekly stream surveys and obtained a peak count of 2,730. The total count through a weir maintained in Moraine Creek in 1952 gave an escapement of 7,921. From this it can be inferred that Rutter's estimate of escapement in 1903 may have been as little as one-third of the actual numbers. In 1948, Shuman counted 62,000 fish into Moraine Creek. Calculations similar to Rounsefell's for 1948 and 1952 produce an escapement to Moraine Creek of 17% and 54% of the total run. While Moraine Creek does not appear to be representative of the entire run as Rounsefell himself suggested, Rounsefell's conversion factor is about the average of these two extremes.

A careful reading of Gilbert and Rich (1927) also shows that they felt that Rutter's estimate of the total number that spawned in Moraine Creek in 1903 was about one-half as large as the true figure.

The assumptions involved in the above "corrections" and conversion of catch to total run undoubtedly make them too conservative so that the sizes of total runs before 1921 must have been larger. However these figures were used in Figure 10 of International North Pacific Fisheries Commission (1962:92) to calculate the average relationship between spawners and returns, and thus give a conservative picture of the decline in the Karluk sockeye salmon runs. The lower rate of return per spawner shown for 1929-1948 compared with 1870-1928 would indicate that the actual reduction in the Karluk run must have been much greater than was shown by Rounsefell. No basis has been found for the division of the data into two parts in 1928. This division was apparently an arbitrary decision by Rounsefell. There is no question that the return per spawner after 1928 was less than before 1928, and the decline in productivity is obvious, but there was no reason to separate the earlier from later periods at 1928.

The Karluk system was compared with the

[6] This was certainly a rhetorical statement with little foundation other than Rich's impression of a "big" run.

other major river systems in southwestern Alaska which produce sockeye salmon, by Burgner et al. (1969). Using special surveys made in 1961 and 1962, as well as other data on the Karluk runs, they concluded that: "restoration of the Karluk runs to former high levels will require considerably more than mere manipulation of numbers of spawners in the escapement. Evidence suggests that the average reproductive capacity of the sockeye salmon in the Karluk system was reduced while the run was in decline. Current research at Karluk is directed toward determination of the cause of this reduction."

OTHER INFORMATION BEARING ON KARLUK RUNS

In addition to the above discussions of the decline of the Karluk runs, a wealth of other information is available in the published and unpublished records of surveys and research on the Karluk sockeye salmon.

Chamberlain (1907) first mentioned the single peak in the Karluk run. On page 70 of his report he states:

> . . . . The Karluk is said similarly to have two runs, one maximum about the last of June and one the first of August, but this was not true in 1903 when the River was under study. . . . In the Karluk in 1903 [page 75] the first sockeyes entered the lake about the middle of June; they continued to arrive in numbers until the latter part of July. They spawn during August.

Thus, even though Thompson's analysis of the catch in his 1950 paper was based upon that of a single cannery, it agreed with this earlier observation and proved that the spring and fall peaks evident in 1921 were artifacts.

The intensity of the fishery that eliminated the middle portions of the Karluk run is well documented in the reports of the U.S. Fish Commission. McDonald (1894:2) noted that:

> . . . . The enormous production of this year [of red salmon from the Karluk River] was secured by entirely obstructing the river by running a fence across so that no fish could pass up, . . .

He also described the destructive methods of fishing used at Karluk at this time, as well as throughout Alaska:

> . . . . One seine follows another in such rapid succession as to cover all approaches to fresh water, and the movement of the salmon into the rivers is as effectually arrested as if permanent barriers were maintained across the entire width of the stream. [McDonald, 1894: 11.]

Moser (1899), in his report for the year 1898, described the use of barricades in salmon streams in Alaska as follows:

> It was a matter of great surprise to discover, . . . the large number of streams which were either actually barricaded, or which showed indications of having been barricaded, notwithstanding the strict law forbidding such obstructions, the maximum penalty being $1,000 fine, three months' imprisonment, and a fine of $250 per day for every day the obstruction remains.

A law prohibiting the erection of barricades in streams or to fish in such a manner as to prevent salmon from moving upstream, was passed by Congress in 1896, but it was undoubtedly some years before it could have been enforced effectively.

Moser (1899) also remarked on the inability of the Karluk hatchery to obtain fish for spawning purposes from 20 July to 5 August, due to the heavy net fishery in the lower end of the lagoon.

> Few salmon were taken at the hatchery for spawning purposes from the 20th of July to the 5th of August. An abundance of fish entered the lower river, but as river fishing was being carried on, only an occasional salmon was observed as far upstream as the hatchery. Consequently the fishing gang, which was stationed on a projecting point making out from the southern bank of the river, watched for days for favorable signs, making repeated hauls with little or no success. The highest number of fish taken in one day was 83. This catch was made on the 5th of August, the day of our departure. The cause of this remarkable scarcity of salmon at the hatchery was attributable to the frequent seine hauls made inside the mouth of the river near the canneries, from 8,000 to 10,000 being taken there daily. Fish which escaped the seines off the spit were almost certain of capture before they could get very far up the river, thereby minimizing the chances of many being secured at the hatchery. . . . It was subsequently learned that during the latter part of August a number of good hauls of salmon were made off the hatchery.

In any event, the continued decline in the Karluk sockeye salmon runs after 1900 resulted in the exclusion of commercial fishing from the Karluk Lagoon in 1918 as indicated above. Thompson's (1950) description of the loss of the midseason spawners from the Karluk run

cannot be disputed. Thompson and Bevan (1954) studied the average weekly number of salmon in the catch each year, from 1937 through 1952. Comparison of the number caught each week with the numbers that escaped in the same period showed that the catch in 1950 was taken between 7 June and 19 July and between 2 and 16 August. A few were taken between 27 September and 4 October, but most of the spawners escaped between 14 June-12 July and 6 September-4 October. Few escaped during the fishing season in early August (Thompson and Bevan, 1954, Figure 5). Thus, as late as 1950 the midseason Karluk sockeye salmon were still being heavily fished.

SPAWNING IN THE KARLUK RIVER

During the entire history of the investigation of the Karluk sockeye salmon beginning in 1921 it is remarkable that the large numbers of fish spawning in the Karluk River below the lake received only passing attention until the observations of Walker and Bevan in 1950. One would think that large numbers of fry and fingerlings must have been seen by those tending the weir after it had been moved to the outlet of the lake in 1945. However, no doubt the rigors of establishing the weir and making it "fish tight" each year, combined with other demands of the yearly observations gave added credibility to Gilbert and Rich's (1927) hypothesis that the sockeye salmon eggs spawned in the Karluk River were wasted. A measure of the small importance attached to the Karluk spawners is that all reports including Gilbert and Rich (1927) do not include the Karluk River on their maps of the watershed. In view of the relatively small proportion of the total numbers of fish escaping through the weir which were accounted for each year in the spawning streams around and above the lake, an examination of the number of fish that have been seen spawning in the river below the lake becomes necessary. The entire Karluk watershed is shown in Figure 1.

The Karluk River is difficult to navigate by shallow draft outboard, and is not easily observed from the bank. The general practice of those visiting the spawning grounds has been to spend practically all of their time on Karluk Lake and on the streams above the outlet. Other factors contributing to the neglect of the spawning activity in the Karluk were listed by Rounsefell (1958) in his Appendix L as: (1) Spawning in the Karluk is late and hence was only partially observed by the summer field parties visiting the lake. (2) Spawning fish intermingled with migrating fish. (3) Only a small percentage of returning adults have stream-type nuclei. Hence Gilbert and Rich (1927) suggested that the spawning below Karluk Lake might be a waste.

Nevertheless, it is surprising that so little effort seems to have been expended studying this part of the Karluk population. Rounsefell (1958:169) summarized the observations to 1932 in his Table A-16, which is reproduced below as Table 1.

Further evidence of the importance of spawning in the Karluk River is provided by observations of large numbers of sockeye salmon fry

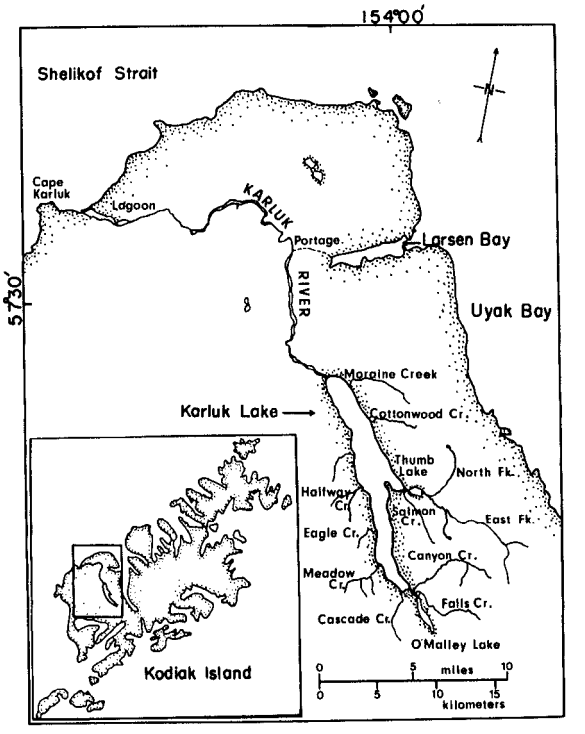

FIGURE 1.—The Karluk system. True north is indicated in the upper right.

TABLE 1.—Sockeye salmon spawning in Karluk River below Karluk Lake in certain years from 1917 to 1932 (from Rounsefell, 1953).

Year of spawning	Observer	Source of data	Area of spawning	Estimated number
1917	Edward M. Ball	Gilbert and Rich (1927)	Upper 2 miles	Large.
1918	No survey			
1919	O'Malley and Gilbert	Gilbert and Rich (1927)	At foot of lake	10,000.
1920	No survey			
1921	O'Malley and Gilbert	Gilbert and Rich (1927)	None up to Aug. 12	
1922	Gilbert and Rich	do	Upper ¼ mile	Greater abundance than pinks.
1923	No survey			
1924	Fred R. Lucas	Gilbert and Rich (1927)	Upper ½ to ¾ mile	Considerable numbers.
1925	No survey			
[1] 1926	Gilbert and Rich	Gilbert and Rich (1927)	Upper 2 miles	50-100 thousand and more coming on Aug. 27.
1926	Howard H. Hungerford	Warden report	1. Between lower weir and weir near Larsen Bay.	Many.
			2. Above Larsen Bay weir	150,000.
			3. Lower weir to lake total	250,000.
1927	Seymour P. Smith	Field notebooks	Upper 1½ miles	10-15 per 10 sq. yards, plus many already dead (158-238 thousand).
1928	S. P. Smith and Alan C. Taft	do	None mentioned	
1929	Merrill Brown (Boucher and Sundberg).	do	do	
[2] 1930	J. T. Barnaby	do	Lake down to Deep Hole	50-100 thousand on Sept. 10.
[3] 1931	do	do	Below lake	15,000 on Sept. 19, but one-third dead so is an underestimate.
1932	do	do	For 2 to 3 miles below lake	Two-thirds of 5,000 spawners on Aug. 31.

[1] Considerable numbers not yet ascended when weir removed on Oct. 14.
[2] Weir removed Oct. 9 with a few sockeye still in lagoon and river very low.
[3] Weir removed Oct. 8 with a few sockeye still in lagoon.

and fingerlings. Chamberlain (1907) said Cloudesly Rutter had recorded that throughout May and June 1903 the sloughs of the upper part of the Karluk River contained many sockeye salmon fry or small fingerlings.

The upstream movement of the fry in the Karluk River was observed by Walker in 1950 and is reported as follows in his manuscript (Walker, 1954a)[7]:

> In the Karluk River the fry were engaged in an upstream movement along both river banks. They were temporarily halted by the adult counting weir. Passage through the weir was difficult under certain flow conditions. *On occasion fry removed above the weir appeared to have bruised bodies and broken skin.* [Italics ours.] At such a time the fry were extremely scarce above the weir and could not be taken in sufficient numbers to allow a size comparison between those above and below. [Walker, page 14, paragraph 4, and page 15, paragraph 1.]

In 1951, the following observation was made by Walker:

> Two fry migrations into Karluk Lake were witnessed. The one which appeared to be of greater magnitude was that in the Karluk River. More fry were seen there than in all the other areas combined. They were engaged in an upstream movement along both river banks. These fish were, on the average, three millimetres longer and had heavier bodies than those seen elsewhere. The second migration was from Thumb to Karluk Lake. [Walker, page 25, paragraph 2.]
>
> In the Karluk River the fry reappeared in numbers at the weir in the latter part of July. They became very abundant in August, then decreased in September and were absent in October. In this second upstream migration they were larger by an average of 20 mm.+, and like their predecessors they followed the river banks. . . . [Walker, page 41, paragraph 4.]
>
> Fry moved up the Karluk River in two peaks, the first through May and the early part of June, and the second from the latter part of July to the end of August. The first migration was of 28 mm. (average) fish and the second of 46 mm. fish. It is believed that these fish are the progeny of the river spawners, and that upon emergence part of the group move lakeward immediately while the remainder stay in the river, probably in the slow weedy part by Barnaby Ridge, until the later date (Table 8). As in 1950, a check was put down on some of the scales of the late-running fry. [Walker, page 45, paragraph 2.]

And in 1952,

> The Karluk fry migration again appeared in two peaks, the first which was composed of 28-mm fish was in May and early June, and the second which was made up of 47-48 mm was in late July and well into September . . . . [Walker, page 56, paragraph 2.]

[7] Walker, C. E. 1954a. Karluk young fish study, 1950-1953. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

Walker and Bevan (1955)[8] noted that the largest spawning population of sockeye salmon in the Karluk watershed was found in the Karluk River. They also observed that the decline in size of the Karluk River race could explain the decrease in size of smolts observed by Barnaby (1944) who was later quoted by Rounsefell. They also maintained that the decrease in Karluk River spawning could explain the increase in relative numbers of 4-yr smolts, since the river spawners were predominantly of 5_3 age. Barnaby interpreted these events as evidence of a decline in productivity of the lake, but Walker and Bevan maintained that since fry from the Karluk River are largest at the time of emergence, they should also be largest at the time of seaward migration if they retain their size difference during lake residence. Moreover, the second migration of fingerlings up the Karluk River into the lake which extended through late July and August consisted of fish ranging from 39 to 72 mm long with a mode at 51 mm. They were not certain where these fish came from, but said that some no doubt were from the Karluk River spawners and after emerging from the gravel in May had remained in the river to feed and grow before migrating upstream to Karluk Lake (Walker and Bevan, see footnote 8, page 16).

The slow-moving section of the river just above the portage which appears in all the descriptions of the Karluk River, would be an ideal location for a sockeye nursery area comparable to those areas in the Chilko, South Thompson Rivers, and Little Shuswap Lake, which are used for the same purpose by different races of Fraser River sockeye salmon fry.

Bevan (1951),[9] in his notes on the Karluk Lake stream surveys made in 1948 through 1951, said that in the Karluk River sockeye salmon spawn almost exclusively in the first mile below the outlet where the current is moderate and the water shallow. He recorded that large numbers of fry migrate upstream into the lake and are most noticeable behind the weir and 1 mile below where they are blocked by fast water. In 1951, large numbers of fry were seen as far downstream as "Barnaby Ridge." He also stated that between Barnaby Ridge and Larsen Bay Portage the current is slow and the water is choked with *Potamogetan* and *Ranunculus* in the summer. The sockeye salmon spawn in the river in the second or third week of September.

The upstream movement of the fry was also noted by Burgner et al. (1969:427).

> Recently emerged fry behave in such a way in the Karluk system that the total escapement is assignable to Karluk Lake for consideration of rearing areas. The progeny of spawners that use the outlet (Karluk River) move upstream into the lake, and progeny of spawners from areas above O'Malley and Thumb Lakes move down into Karluk Lake early in their first summer of life.

This upstream movement of fry and small fingerlings into the nursery lake was also observed by the senior author in several rivers in the Fraser River system, i.e., the South Thompson River, Little River, and the Chilko River. Fry and fingerlings from the South Thompson move upstream into Little Shuswap Lake and then with the fry already accumulated in that lake from spawning in Little River and Adams River they move up Little River into Big Shuswap Lake, Little Shuswap Lake and slowly flowing sections of the South Thompson River provide shelter for the fry until they gain sufficient strength to swim upstream. The same function is performed by the slower section of the Chilko River near Canoe Cross. The slow section of the Karluk River near the portage opposite the head of Larsen Bay must serve the same purpose for many of the Karluk River fry.

Although Rounsefell's (1958) demonstration of a negative effect of the even-year pink salmon, *O. gorbuscha*, runs on the sockeye salmon returns is of marginal significance, competition between the two species for spawning room in even years would emphasize the importance of the sockeye salmon race which spawns in the Karluk River.

Further study of this relationship would require a restudy of the ages assigned to the Karluk sockeye salmon to improve the accuracy of

[8] Walker, C. E., and D. E. Bevan. 1955. Observations on the biology of the red salmon in the Karluk watershed. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

[9] Bevan, D. E. 1951. Karluk Lake stream surveys, 1948-1951. Unpubl. manuscr. Kodiak Isl. Res. Group, Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

estimated returns. Walker (1956)[10] attempted to check the age readings made from Karluk sockeye salmon using the objective technique developed by Koo (1962). Walker (see footnote 10) presented the results of a comparison of age readings he had made with the U.S. Fish and Wildlife Service on the same fish as follows:

> The year 1952 offered the only data that were comparable. The escapement was sampled by both research groups; actually the same fish were handled by each. The catch data taken by the Fisheries Research Institute were shared, and hence the sampling was identical. The discrepancy in the final results (table 6) [Walker's Table 6 is reproduced as our Table 2.] must be due to the method of age interpretation and calculation.
>
> From this study and a review of 1947 and 1948 Fish and Wildlife Service Karluk smolt samples, it is suggested that the Fish and Wildlife Service favors the older age classes, particularly in the fresh-water ages. Two policies may account for this: (1) The recording of an annulus on the outside of plus growth, and (2) recording an annulus wherever there is a departure from a uniform circulus.

This attempt to reconcile the age readings of two organizations was given up for Karluk fish, but has been pursued later for other stocks of salmon under the International North Pacific Fisheries Commission. However, so far as we can determine, this coordination has not been extended to the Karluk data and in particular has not been used to review the age determinations prior to 1950, which were the basis for Rounsefell's estimates of the numbers of fish which returned from different spawning years. The process of reconciling age readings on sockeye salmon scales is particularly difficult because of the distinct fields of freshwater and saltwater growth found in each scale, each of which requires separate interpretation. We do not know if the ages of Karluk sockeye salmon have been checked by the Koo technique since 1952.

The relative importance of the Karluk River as a spawning ground is further emphasized by the estimated number of potential redd sites shown in Table 13 of Burgner et al. (1969:424), which is partially reproduced below as Table 3. The spawning capacity of the Karluk system is given as follows on page 425:

> *Karluk system.* — Estimates of the size of a redd site for several tributaries in the Karluk system are about 2 m.^{2}, and because estimates are not available for other areas, 2 m.^{2} is used for all. The estimated number of redd sites for streams and lake beaches is 174,000 (table 13), and (assuming a 1:1 sex ratio) the capacity is 348,000 adults. This estimate is only approximate—the situation in the Karluk system is complicated by the occurrence of successive waves of spawners in most streams and incomplete information on the amount of potential spawning ground, especially on lake beaches. Escapements to Karluk neared or exceeded 1 million fish for many years during the early 1900's.

The conclusion is inescapable that the Karluk River must have been the most important spawning area in the Karluk system but the only data directly substantiating this conclusion is found in the report by Bevan (1962) on the sockeye salmon tag recoveries in 1948 and 1949.

TABLE 2. — ["Table 6 Comparison of 1952 Adult Age Analysis"]

Year of return	4_2	5_2	4_3	5_3	6_3	5_4	6_4	7_4	2 SW	3 SW
				F.R.I. figures for the year 1952						
Percent of total run	0.3	0.5	1.8	52.3	5.2	3.1	12.0	22.1	64.6	27.8
				F.W.S. figures for the year 1952						
Percent of total run		0.2	1.8	28.0	10.2	1.0	18.9	38.7	46.9	49.1

TABLE 3.—Estimated numbers of potential redd sites in various types of spawning grounds of the Karluk system (from Burgner et al., 1969).

Type of spawning ground	Area of potential spawning ground (hectares)	Area required per female (m^2)	Redd sites[1] (number)
Terminal streams	1.67	2	8,000
Lateral streams	6.71	2	34,000
Lake beaches	1.25	2	6,000
Outlet river	25.28	2	126,000
Total	34.91	—	174,000

[1] Does not take into consideration successive waves of spawners.

[10] Walker, C. E. 1956. Age analysis of the Karluk red salmon runs. Unpubl. manuscr. Univ. Wash. Fish. Res. Inst., Seattle, WA 98195.

While these recoveries were not designed to identify the times and areas of spawning, they indicate that sockeye salmon which spawn in late August and early September use the Karluk River. These fish would have optimum conditions for survival in the Karluk River in the fall where the eggs would have excellent conditions for development, with both temperature and floods moderated by the lake so that productivity of the spawn deposited late in the season in this area should be high.

Why then has this part of the Karluk run continued to decline?

The decline in earlier periods, i.e., before 1940, must have been due to overfishing as indicated by Thompson (1950). However, the decrease has continued in later years even when the entire run has been given protection. This is seen in the spawner-recruit relationship shown in Figure 2. Different symbols are used to identify the returns from different periods in the Karluk history which correspond to 1) before 1921, i.e., before a weir was installed at the lower end of the Karluk River, 2) 1921 to 1941, when the weir was located at the lower end of the Karluk River, 3) 1942 to 1944, a brief period during which the weir was located at the portage opposite the head of Larsen Bay, and 4) 1945 and later, when the weir was located just below the outlet of Karluk Lake.

Interest in the location of the weir was aroused by Schaefer's (1951) reports of attempts in the Birkenhead River to hold sockeye salmon for spawning, by the effects of delays of sockeye salmon in their migration up the Fraser River as reported by Thompson (1945) and Talbot (1950), and by Walker's reports (Walker, see footnote 7, 1954,[11,12] 1959[13]) of the effects of the weir of sockeye salmon fry migrating up the Karluk River to the lake. Walker also indicated that the smolts migrating downstream were delayed and he and Bevan replaced the wooden weir pickets with round metal bars to increase flows and thereby to induce the smolts to move through the weir.

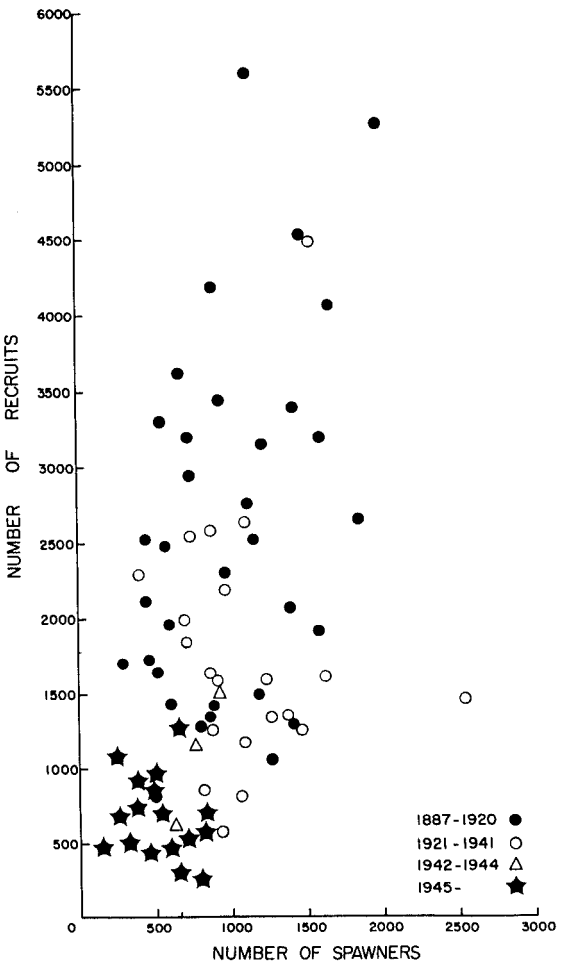

FIGURE 2.—Spawner-recruit relationship for Karluk sockeye salmon 1887 to 1961.

The loss of over 50% of the adult sockeye salmon held for spawning in the Karluk hatchery is recorded by Bower (1912:75). Lest this be considered to be the result of rough handling, we must recall the history of the hatchery operation on the Birkenhead River above Harrison Lake in the Fraser River system. This history is briefly recounted by Schaefer (1951) as follows:

> The Birkenhead River is frequented by sockeye as far up as Poole Creek. During the period of our studies,

[11] Walker, C. E. 1954b. The red salmon smolt migration at Karluk Lake, 1954. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

[12] Walker, C. E. 1954c. Size and age analysis of the red smolt migration—Part II of the red salmon smolt migration at Karluk Lake, 1954. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst.

[13] Walker, C. E. 1959. The enumeration of the Karluk red salmon smolt run in 1954. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst.

however, no sockeye were seen beyond seven miles upstream, and nearly the entire spawning population confined itself to the lowest mile of the stream. . . . [Schaefer 1951:26.]

The Birkenhead sockeye supported a hatchery from 1905 to 1935, when all the British Columbia hatcheries were closed. Here eggs were taken and the fry held until absorption of the yolk sac. They were not reared beyond the yolk-sac stage. . . . It is apparent that although the egg-takes fluctuated considerably they are of about the same size in the later years as in the earlier years of operation. This record, however, is somewhat misleading as an index to the relative sizes of the populations from year to year, since a variable fraction was taken by the hatchery men. From examination of the remains of structures on the river banks, and from conversations with local inhabitants and employees of the Dominion Fisheries Department, it has been possible to ascertain that the take of eggs was maintained by the expedient of including an ever increasing share of the population in the operation. The first fence for capturing sockeye was placed some distance above Owl Creek. As the eggs became harder to get, fences were erected at successively lower points until the last fence was located at the lowest practicable place for establishing the conventional type of fence for capturing upstream migrants (see Figure 9). In the last few years of operation the captures at this fence fell so low that they were supplemented by gaffing ripe fish out of the stream below. At the time of our study the preponderate majority of sockeye were found spawning well below the former site of the lowest fence, and the number of sockeye ascending above that point could by no means supply as many eggs as were taken by the hatchery in its last years of operation. [Schaefer, 1951:32-33.]

Schaefer's statement that the number of eggs from the Birkenhead sockeye salmon was only maintained by taking a larger and larger percentage of the spawning stock is not quite true. In fact, the weir seemed to kill off most sockeye salmon that spawned above it, except for those that must have escaped upstream, and after about 4 yr in each location an insufficient number came up to the weir to provide the numbers of eggs required to fill the hatchery. When this happened, the weir was moved downstream to a new location where the process of taking eggs was continued until the spawning stock had been killed off and it was necessary to move the weir again. When sockeye salmon hatcheries were closed in British Columbia in 1935, Schaefer found that the weir had been moved downstream as far as it could be conveniently built on the Birkenhead. But, even though no weir had been installed on that stream after 1935, most sockeye salmon spawning was still confined to the lower end of the Birkenhead River until after 1947. Between 1947 and 1950 the Canadian Prairie Farm Rehabilitation Administration attempted to divert the lower Birkenhead River into a newly dug channel. In addition Lilloet Lake was lowered 6 feet in 1950. One result of the changes made by the Prairie Farm Rehabilitation Administration was to destroy a part of the original spawning grounds of the lower Birkenhead River. (Memorandum 7 November 1959, M. C. Bell to L. A. Royal, International Pacific Salmon Fisheries Commission.)

Bell concluded from his study of the Birkenhead that the upper part of that river is inhabited by an early run of fish ". . . that are from 8 to 10 cm less in length than the late fish . . . ." which occupied the lower river. He stated that some way would have to be found to stabilize a spawning area for this late run to correct the harm resulting from the work of the Prairie Farm Rehabilitation Administration.

The implications of the effect of the Birkenhead weir are many. Of course the death of the runs above the weir was due partly to the lack of eggs, but then, if this killed off the run to a particular section of a straight stretch of river, this must mean that an independent "race" of salmon inhabited, i.e., spawned, in that particular section of the stream. In other words, it indicates that different parts of a continuous section of a stream can be inhabited by distinct races of sockeye salmon which are closely adapted to the different conditions they encounter during the spawning and subsequent rearing of eggs and young. This was substantiated by Bell's report of 1959.

While the Karluk weir has always been provided with gates through which the fish are counted upstream, no study has ever been made of the length of time sockeye salmon have been delayed in finding their way through. Again work at Hell's Gate by the International Pacific Salmon Fisheries Commission has indicated that such delays can be fatal. Talbot (1950) concluded that 14 days' delay at Hell's Gate was sufficient to prevent successful completion of migration of sockeye salmon to any of the streams above. Construction of the fish ladders at Hell's Gate eliminated this cause of mortality

of upper Fraser sockeye salmon which Talbot estimated must have been as high as 70 to 80% of the total run reaching Hell's Gate in some years. Thompson (1945) also felt that the effects of delays in migration would increase as the time of spawning was reached. Thus, as each run approached its spawning grounds, and as the time for spawning approached, a shorter delay would be fatal. Even a short delay at the Karluk weir could have been as fatal to some sockeye salmon races as the longer delay at Hell's Gate on the Fraser River was to the upriver spawners which in the Fraser had several hundred miles to go to the nearest spawning ground.

A more important effect of the weir, located just below the outlet of Karluk Lake could have been the same as that observed by W. F. Royce in 1957 at the Brooks Lake weir (Royce, pers. comm.). In 1957, Royce noted that a school of salmon that had migrated into Brooks Lake, and had been holding in the lake not far from the outlet, moved down against the upper side of the Brooks Lake weir. On removal of some pickets in the weir this entire school of salmon moved down into the Brooks River where it spawned. Nothing similar to this has been reported in the literature on the Karluk River, but Bevan has observed similar behavior of schools of adult sockeye salmon above the Karluk weir. The same behavior has been observed by John Roos (pers. comm.) in Chilko Lake and River. The Karluk weir thus could have prevented salmon from returning down river to spawn after moving into the lake. Richard Gard has informed us (pers. comm., 1972) that some time after 1957 sockeye salmon were being counted downstream through the Karluk weir during the end of the season. Nevertheless the weir has been a barrier to the free movement of sockeye salmon adults up and downstream and has prevented easy access of the young to the lake. Thus it must have reduced the productivity of the Karluk River spawning grounds.

Gard and Drucker (see footnote 5) determined the number of "red salmon" spawning in the upper Karluk River by marking sockeye salmon at a weir installed at the portage and recovering the tags and establishing a ratio of tagged to untagged fish as they passed through the Karluk weir. The number spawning in the river was calculated to be about 10% of the total escapement to the Karluk watershed.

The chain of events noted on the Birkenhead River and at Hell's Gate in the Fraser River system indicate that sockeye salmon which are prevented from spawning in their ancestral grounds do not do so successfully elsewhere. While all of the young derived from eggs taken from the Birkenhead run were planted in other streams, the absence of fish from the upper Birkenhead River for a number of years after the weir had been removed indicates that the fish which formerly spawned above it were not casual strays which spawned in the upper Birkenhead because it happened to be a good spawning ground and was available for occupation. While there seems to have been no occasion for study of the degree to which the homing of sockeye salmon is specific for different sections of any spawning ground, the recent work of Hara, Ueda, and Gorbman (1965) supports the investigations of the International Pacific Salmon Fisheries Commission on the Fraser River, which indicate that specific streams are occupied by individual races of sockeye salmon.

This was also indicated by the experiments reported by Hartman and Raleigh (1964) in Meadow Creek, a tributary of Karluk Lake which proved that the sockeye salmon refused to spawn in other streams when transported from Meadow Creek and died unspawned when denied access to what was obviously their natal spawning ground.

The adaptation of sockeye salmon to a specific type of spawning ground has been further verified by Raleigh (1967) who pointed out the different migratory behavior of fry spawned in the outlet stream, Karluk River, and in Meadow Creek, a tributary of Karluk Lake. When tested in an experimental apparatus only 1% of the Meadow Creek fry moved upstream while 98% moved downstream which would take them into Karluk Lake, their nursery lake. When tested, 30% of fry from the Karluk River moved upstream while 66% moved downstream. Moreover the Meadow Creek fry were found to move almost entirely at night while Karluk River fry moved in either the day or night. Raleigh concluded that this behavior must be genetically

controlled but was unable to explain satisfactorily the variability in behavior of outlet fry.

The nature and mechanisms controlling these movements of sockeye salmon fry have been investigated by Brannon (1967, 1972) who found that these movements are basically genetically controlled though they are subject to environmental factors which require flexibility in the response of the newly emerged fry. The genetic nature of these movements was proven by crossing two races, one in which the fry moved downstream to their nursery lake with another in which the fry must move upstream. The progeny of these crosses showed intermediate behavior. Thus the behavior of fry in the Karluk River agrees with that shown by progeny of the Little River and Chilko races in the Fraser River. The immediate movement of some fry into Karluk Lake followed some time later by the upstream movement of larger fingerlings is in complete agreement with similar activities described by Brannon (1972) for the Fraser River sockeye salmon.

The more complicated behavior of Weaver Creek fry mentioned by Ricker (1972) and studied in detail by Brannon (1972) is only an extended variation of behavior found in similar form but under slightly different conditions in Chilko River, Little River, and the South Thompson in the Fraser River system and in the Karluk River. Those fry which move or are carried downstream on emergence are found resting in more quiet water below and later are seen as a wave of larger fingerlings which move upstream along the margins of their spawning grounds into their nursery lakes.

The genetic basis of this behavior leaves no basis for doubt that the Karluk watershed is inhabited by several races of sockeye salmon. The insistence of adults upon entering a particular stream indicates that the fish spawning in the different streams must belong to separate races. The behavior of sockeye salmon in the Brooks River and the evidence presented by the progressive elimination of sockeye salmon spawning in different sections of the Birkenhead River gives further substance to the probability of the existence of individual races of sockeye salmon that spawn in different sections of the Karluk River itself.

Ricker (1972:30) also discussed the "overshooting" and "proving" of spawning grounds by salmon, an aspect of homing that has been noted in the past but which has received little attention until recently. He includes in this activitiy the return of most transplanted sockeye salmon to the vicinity of the stream from which they were removed by Hartman and Raleigh (1964) and the overshooting of Sweltzer Creek sockeye salmon up the Chilliwack River at least 0.5 km reported by Ricker and Robertson (1935) as well as the movement of sockeye salmon through the Brooks River into Brooks Lake, described by Hartman and Raleigh (1964), where they remained until ready to spawn when they dropped downstream into the Brooks River. The latter incident is mentioned above as it was first discovered by W. F. Royce. Moreover, similar movements of sockeye salmon have been noted in Chilko Lake and in the Karluk River (see above). The establishment of a barrier, such as a weir, in the middle of a spawning ground or above it, as at Karluk, in limiting this movement of sockeye salmon therefore must reduce the productivity of those grounds.

Whatever the causes, by the time the size of the Karluk River race of spawners was estimated by tagging in the late 1950's it had been reduced to 10% of the total escapement to the Karluk watershed. The total returns from each year's spawning computed from ages obtained from samples taken at the weir are shown in Figure 3 and indicate that these returns reached a low point in 1950 and 1951 of about 250,000 fish. While the possible errors involved in using samples taken at the weir to determine the distribution of ages of fish taken in the catch as well as the errors in estimating age mentioned by Walker are unknown, the dominance of 5- and 6-yr-old fish is sufficient to give credence to these returns.

As a result of these recommendations attempts were made to protect these midseason sockeye salmon especially in the odd-numbered years when pink salmon are scarce. Apparently the total returns from the spawning years of 1950 to 1957 responded to these regulations as well as to efforts to improve passage at the weir, and increased from about 250,000 in 1951 to 1,100,000 in 1957. But to accomplish this the catch was

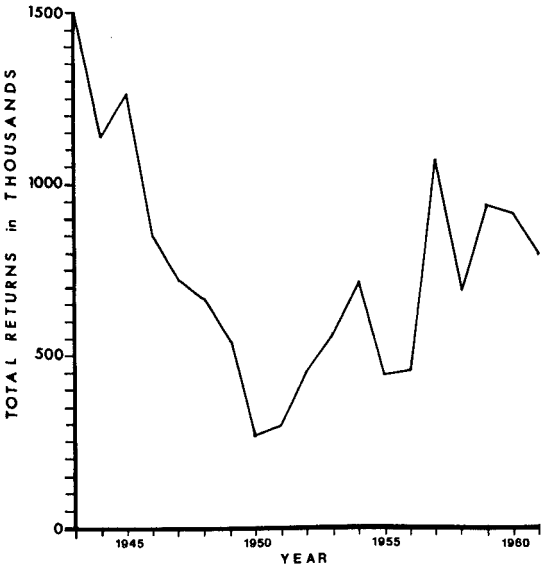

FIGURE 3.—Total Karluk sockeye salmon returns from each year's spawning computed from ages obtained from samples taken at the weir, 1943-61. Both catch and escapement included.

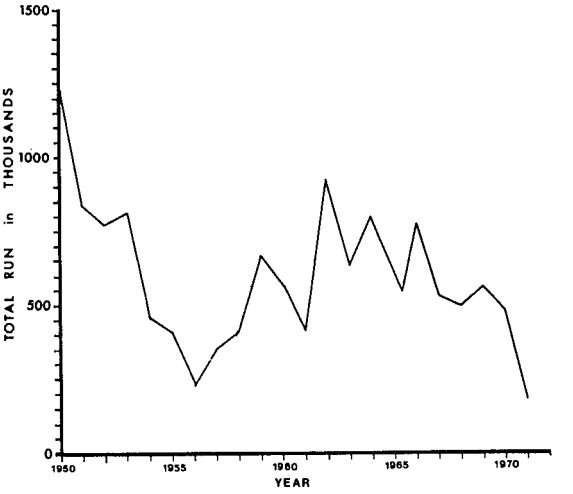

FIGURE 4.—Total Karluk sockeye salmon run, including spawning escapement and catch for each year from 1950 to 1971.

reduced to 76,834 in 1953 and to 21,000 in 1955. Finally, fishing of Karluk sockeye salmon was prohibited in 1971. Nevertheless the Karluk weir count of about 143,000 sockeye salmon in that year was the lowest on record.

Beginning in 1950, the total number of fish returning from each year's spawning increased, reaching a high of about 1,100,000 from the 1957 spawning. Thereafter the returns fell. This is shown on a different time scale in Figure 4 in which the total run including both the spawning escapement and catch are plotted. This shows a decline in total Karluk run to a low point in 1956 with a subsequent rise to 1962 after which the run declined again to the present. This figure agrees with the former and also illustrates the dominance of the 5-yr-old fish in the returns.

As indicated above there are many causes of the changes in size of the Karluk runs, but one obvious factor must be the amount of fishing in the Karluk area along the beach on either side of the mouth of the Karluk River and about 1 mile offshore. The open fishing periods are plotted in Figure 5 from 1941 through 1972 to show periods closed to fishing in June, July, August, and September.

The greatest numbers of consecutive closed days were in the latter half of August and in all of September in 1929, 1930, 1934, 1935, 1936, 1938, 1939, 1941, 1944, 1946, 1947, and 1949. None occurred in 1928 and 1931 and none occurred in August in 1932, 1933, 1937, 1940, 1943, and after 1960. The period of 1928 to 1950 shows a declining run. From 1951 to 1957 the Karluk run increased in total numbers of fish returning from those spawning years as shown in Figure 3 (i.e., from 1956 to 1962 in total size of run in Figure 4). The primary difference between the fishing season in the years 1950 through 1956 and all other years is the increased number of consecutive days of closure shown in Figure 5, especially in August and September in 1951 through 1956 and in July in 1951 through 1955. Beginning in 1956 escapement was obtained by reducing the weekly fishing time and increasing the length of weekly closures except that closed periods of 12 to 34 days were used in 1965 and 1967, respectively. In 1971 only 14,000 Karluk sockeye salmon were taken from a total run of about 175,000 fish, so that this method of control apparently was not effective in arresting the decline in runs.

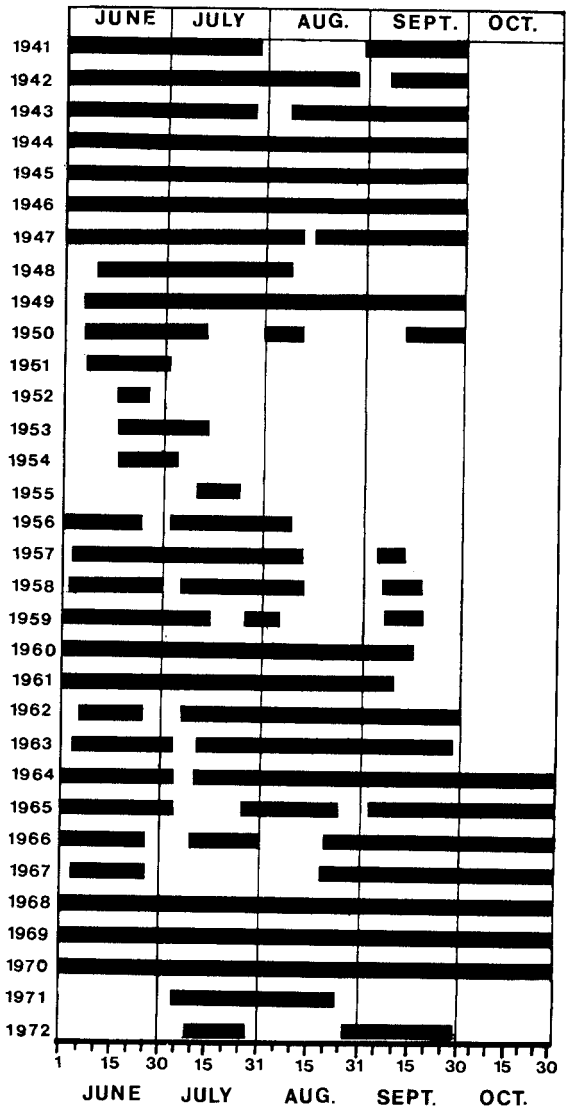

FIGURE 5.—Karluk district fishing season, 1941-72. Open seasons shown in black.

Of course other factors such as too heavy sampling on the spawning grounds, the presence of the weir or other activities which might have interfered with the free movement and migration of adult or young sockeye salmon in the Karluk watershed may have added to the effect of the fishery. Moveover varying numbers of Karluk adults were also taken in the Uyak extension of the Karluk district which was left open in 1953 and 1954 and probably also in other years after the Karluk district had been closed.

Nevertheless the fact that the size of the returns from individual spawning years as well as the total size of runs responded to the added protection afforded them in 1951 through 1956 in July and August supports the hypothesis of the greater productivity of the races which pass through the fishery during these months.

Moreover the continued decline after the 1957 spawning (total run size in 1962) indicates that regulation by weekly closed periods in the Karluk district is not sufficient alone to cause recovery of the runs.

The Karluk weir with heavy fishing on those races must therefore have reduced those segments of the Karluk run, which in former years migrated into the lake and when ready to spawn dropped downstream below the lake and below the present location of the weir to spawn. It could also have imposed an additional mortality on adults headed for some of the spawning grounds above the weir by delaying them and by preventing the free movement of adults which overshoot their spawning area and wish to move downstream. This would be especially true for those which were ready to spawn when they reached the weir and had little margin of time to avoid physical deterioration characteristic of this period of sockeye salmon life history.

Another important effect was indicated by the observations of Walker (see footnote 7) quoted above which indicated that the weir must take an unknown toll of sockeye salmon fry by blocking their movement up the Karluk River into the lake and by injuring those that try to fight their way through it. In 1950 M. C. Bell of the College of Fisheries, University of Washington designed a small Denil type fishway which Bevan and Walker constructed out of corrugated galvanized roofing to help the sockeye salmon fry surmount the barrier presented by the weir. Bevan also persuaded those responsible for the weir to modify the shape of the weir pickets to create a more favorable flow pattern to induce the smolts to move downstream more quickly. As far as can be determined, however, no effort has been made to improve the movement of sockeye salmon fry upstream through

the weir in recent years. Moreover, Bell's fish ladder was only tried on the eastern end of the weir and the numbers of fry and small fingerlings injured and blocked by the rest of the weir were not studied.

The blocking action of such a weir to fry is confirmed by M. C. Bell (1972) who finds that the maximum darting speed of small salmonids is about equal to 1 ft/s per inch of length. This speed can be maintained for only a few seconds. The 28- to 72-mm fry and fingerlings observed by Walker in the Karluk River would be able to dart through maximum velocities of 1.1 ft/s for the smaller fish to 1.9 ft/s for the small fingerlings Walker found moving upstream in the Karluk River between late July and September. These velocities correspond to a drop in water level of ¼ to 1½ inches through the weir pickets which are smaller drops than could be expected when the weir is clean. Passage through the weir would be impossible if only a few dead spawned-out fish rested against the weir pickets.

Predation has been a favorite explanation for the decline of sockeye salmon runs. Rounsefell (1958: 142) discussed efforts to control predators in the Karluk system:

> At Karluk the destruction of predators was confined to attempting to destroy large numbers of Dolly Varden charrs by seining or trapping at the salmon-counting weir during their annual downstream migration in May and June. In the 21 years from 1922 to 1942 the annual reports of the Alaska Division mention the destruction of Dolly Vardens during 15 years. During the 9 years in which the numbers destroyed are recorded they vary from 3,000 to 81,500. The work was hampered by high water and by the desire to avoid harming the downstream sockeye migrants. These migrants commence their seaward migration soon after that of the Dolly Vardens and there is considerable overlap.
>
> DeLacy and Morton (1943) have shown that many Dolly Vardens are found in the tributaries of Karluk Lake during the season when those that have migrated downstream are at sea, so it is obvious that not all the Dolly Vardens were subject to capture at the weir.

Evaluation of the predacity of Dolly Varden in the Karluk system led DeLacy (1941) and DeLacy and Morton (1943) to the conclusion that they are not a significant consumer of sockeye salmon fry or smolts. The relationship described by Rounsefell and by Delacy and Morton is complicated by the presence of two species of char described by the latter two authors in Karluk Lake. The presence of the two species is discussed in a later paper by McPhail (1961). The arctic char are described as lake dwellers while the Dolly Varden are anadromous. While DeLacy and later DeLacy and Morton did not find large numbers of sockeye salmon young in the char stomachs they examined, they sampled only at the weir, which was located then at the lower end of the Karluk River, and in Karluk Lake above its outlet. As in most studies of char predation, this investigation was carried out as a personal effort by DeLacy and Morton in addition to their primary duties concerned with the study of the sockeye salmon. It is not surprising therefore that sampling of stomach contents in their programs was designed to interfere as little as possible with the sockeye salmon work rather than to provide a complete picture of the char feeding habits.

Roos (1959) also indicated that Dolly Varden are not serious predators of sockeye salmon in the Chignik system since he found only an average of 0.1 sockeye salmon per stomach in 5,050 Dolly Varden stomachs examined. However, he did find that 31.1% of the Dolly Varden taken in swift water below the outlet of Chignik Lake were feeding on sockeye salmon. Moreover John Rogers and John Wells in 1970 encountered a school of Dolly Varden in the Black River above Chignik Lake that were feeding on sockeye salmon fry as they emerged from the gravel and dropped out of the Chiaktuak Creek. Roos had not sampled in that location. On the other hand no char were seen at that same location and under comparable circumstances in 1971 (Rogers and Wells, pers. comm., 1972).

Large losses suffered by migrating sockeye salmon smolts to Arctic char are reported by Rogers (1972) in the Wood River system where the char school at the lower ends of each connecting river in the system and feed on the smolts as they move downstream. A loss of at least 4,000,000 smolts was estimated in 1971 in Lake Aleknagik alone and a total loss to char of 27% of the total number of smolts produced in the Wood River system was estimated.

The relationship found between Arctic char, Dolly Varden, and sockeye salmon varies widely in different locations and times of sampling. Ricker (1941) found that Dolly Varden were

heavy predators of young sockeye salmon in Cultus Lake, Roos (pers. comm.) has noted Dolly Vardens preying on sockeye salmon smolts as they leave Chilko Lake. While the normal productivity of sockeye salmon runs must adjust to this mortality, these losses could become critical in populations subjected to other extraordinary pressures. Under such circumstances an objective evaluation of the effects of Dolly Varden and Arctic char on the productivity of different sockeye salmon races in the Karluk system warrants more attention than it has been accorded so far.

INTERPRETATION OF DECLINE IN CATCH

The information recorded above has been developed from observations which have been made almost accidentally. However, the decline in catch is real and it is evident that it must be the result of two factors. The first and major cause has been the fishing out of the middle portion of the Karluk run noted by Thompson (1950) and by Thompson and Bevan (1954). This process continued until the 1950's and in the even years it still continues because the pink salmon run must be harvested and this run overlaps the midseason sockeye salmon runs in the Karluk system. This depletion of the midseason Karluk sockeye salmon runs was responsible for the change of the sockeye salmon run from a single mode to one with a mode in June and another in August. It also was one factor which reduced the annual catch of Karluk fish from an average of 3,195,000 fish in 1889-94 to an average of 107,000 fish in 1953-58 and to 14,000 fish in 1971.

But, along with this reduction of the most productive segments of the Karluk spawning run, there has been the additional effect since 1945 of the weir on both adult and young salmon. The weir, located at the lower end of the Karluk River from 1921 to 1941 might not have affected adults, but after 1945 and in its location just below the lake it must have affected both adults and blocked the migration of fry and fingerling sockeye salmon out of the Karluk River. At any rate, the peak run in 1934 was much smaller than in 1926 (see Rounsefell, 1958, Figure 4). After the weir was moved to the upper end of the Karluk River in 1945, however, the size of the Karluk sockeye salmon runs fell more rapidly than before and have finally been reduced to present minimal size.

The correspondence between the location of the weir and the drop in productivity is clearly demonstrated in Figure 2 which relates the number of spawners to the number of returns. While the data prior to 1921 are not reliable measures of the size of the total run, they are related to the size of catch and serve to show that in this early period the level of productivity of the Karluk run was much greater than it has been since 1921. There is also some question as to the accuracy of age readings (Walker, see footnote 10) but we have used the age readings used before by Rounsefell and the age distributions in data given to us by W. A. Smoker of the Auke Bay Fisheries Laboratory for the years since 1946 as the best information that is available. The level of productivity shown in Figure 2 since 1945 is but a fraction of the earlier level, and while the data are too widely scattered to provide a reliable basis for calculating a production curve, it is interesting that the maximum of such a curve for 1946 to 1961 inclusive is at 345,000 spawners, which could be expected to return a total of 720,000 fish. The curve for 1921 through 1939 peaks at 1,050,000 spawners, with a return of 1,875,000 fish. Obviously, the earlier level of productivity is more desirable than the current one which seems to have an ultimate end point of zero. The curve for the years before 1921 must have been higher still with a correspondingly higher expected return.

SUMMARY AND DISCUSSION

It is evident that the spawning of sockeye in the Karluk River has not been observed except incidentally. Rounsefell (1958:168) explains that:

> The extent of spawning in the main river below Karluk Lake may not have received as much attention as it may deserve because (1) such spawning often occurred rather late in the season and so was only partially observed by summer field parties visiting the lake, (2) since spawning fish would often be intermingled with fish migrating into the lake it was somewhat difficult to distinguish spawners from upstream migrants, and (3) because of the extremely small percentage of mature fish

found that had stream-type scale nuclei indicating they had entered the sea as fry, it has been rather generally considered that the great majority of the offspring of these below-the-lake spawners perish.

Rounsefell in 1958 was apparently unaware of the work of the International Pacific Salmon Fisheries Commission on the Fraser River sockeye salmon that had revealed the peculiar life history of several of the largest runs in that system which spawn below the lakes where the young are reared so that the fry have to migrate upstream into the nursery lakes either immediately after emergence or after a brief period of growth to small fingerlings. However, he did express doubt that the progeny of these fish were wasted as Gilbert and Rich (1927) thought.

The Karluk River for the most part is difficult to observe and would require much more effort to study than the lake and its tributaries. However, evidence of the importance of spawning in the Karluk River is overwhelming. The different estimates of numbers of sockeye salmon spawning in the Karluk River below Karluk Lake listed by Rounsefell (1958) and shown in Table 1, for between 1917 and 1932, are as great as 400,000 in 1926, i.e., more fish than were recorded for any other part of the watershed. Rutter, quoted by Chamberlain (1907) observed large numbers of fry and small fingerlings in the upper Karluk River and 47 yr later in 1950, 1951, and 1952, Walker saw fry and fingerlings moving up the Karluk River through the weir. He noted two upstream migrations. The first was of fry which averaged 40 mm or less in length and occurred in late June and early July. The second was of fingerlings which varied from 48 to 72 mm in length and began in late July and continued through August. Moreover, Walker and Bevan (see footnote 8) stated that the sockeye salmon population spawning in the Karluk was the largest population in the system. They also said that the decline in this race could explain the decline in size of smolts and increase in numbers of 4-yr smolts mentioned by Barnaby (1944) as evidence of a decrease in productivity of Karluk Lake. Bevan considered the negative correlation between the number of sockeye returning from the even year runs, which compete with pink salmon for spawning room mostly in the river below Karluk Lake, as evidence of the importance of the Karluk River spawning. While Bevan's tagging experiments of 1948 and 1949 were not designed to identify the spawning location with the time the fish were in the fishery, the recoveries did show the presence of spawners in the Karluk River in late August and early September. Finally, Burgner et al. (1969) estimated there are 126,000 redd sites in the Karluk River as opposed to 48,000 in the rest of the watershed. While the total spawning capacity of 348,000 they estimated is far below the numbers known to have spawned in the Karluk system in the past, the capacity of the river is still about three times greater than that of the rest of the system. Furthermore, the slow-moving section of the Karluk opposite the portage must provide an ideal location for the growth of the fry to fingerlings as similar localities do in the Chilko and South Thompson Rivers in the Fraser River system.

The loss of the midseason races of sockeye salmon in the Karluk is well authenticated. Chamberlain (1907) mentioned that the Karluk run had a single peak in 1903 and earlier reports of McDonald (1894) and Moser (1899) described the intensity of the fishery that finally depleted the run. Evidence of its decline came early and was met by increasingly severe regulation of the commercial fishery which was prevented from using barricades in about 1890, was excluded from the Karluk River in 1889 or 1890, and was excluded from the Karluk Lagoon in 1918. The gradual loss of the midseason peak was demonstrated by Thompson (1950) but Thompson and Bevan (1954) showed that the fishery was still concentrated in late July and early August, as late as 1950. Rounsefell disagreed with Thompson's conclusions, that different races of sockeye salmon exist in the Karluk basin, but in effect agreed with Thompson by recommending added protection of the midseason fish. Rounsefell's conclusions have been refuted by Owen et al. (see footnote 4) and later by Hartman and Raleigh (1964) and by Gard and Drucker (see footnote 5). Owen et al. showed that no change had occurred in either Karluk Lake or in the spawning habitat which might have caused the decline in the Karluk sockeye salmon runs, but demonstrated that changes had occurred in different sections of the spawning population, especially in the midsea-

son races. Gard and Drucker (see footnote 5) showed that distinct races of sockeye salmon do exist in the Karluk system.

The decline in productivity of the Karluk runs was shown in Bulletin 10 of the International North Pacific Fisheries Commission (1962) by comparing spawner-recruit curves calculated for the periods of 1870 to 1928 and 1929 to 1948. Productivity in the latter period was of course much lower than the former. This is more clearly shown by the returns plotted in Figure 2 for the period of 1945 through 1961. The effect of the weir is also shown by Figure 2 which demonstrates the low-level of productivity to which the Karluk runs have been driven since the weir was moved to the outlet of Karluk Lake in 1945.

Walker in 1950 was the first to record injuries to fry and fingerlings as they struggled to swim through the weir. Bevan and Walker tried to reduce the block by installing a miniature fishway in the eastern end of the weir which they built from a design by M. C. Bell. Bevan also tried to reduce the delay to downstream migrating smolts by having the shape of the weir pickets altered to increase the flow of water through it. Rounsefell's note of the method used in early times to destroy predatory Dolly Vardens by seining at the weir mentions that it was found difficult to do this without injuring larger numbers of sockeye salmon smolts which apparently were mixed with Dolly Vardens. Such schools of smolts as well as fry and fingerlings above and below the weir must have provided unparalleled opportunity for predation since Rogers (1972) showed that without a barrier such as a weir, a school of 15,000 Arctic char which lay below the outlet of the Agulowak River in Lake Aleknagik must have consumed about 4,000,000 sockeye salmon smolts during the 30-day migration. This was about 27% of the total number of smolts he estimated were produced in the Wood River system above Lake Aleknagik in 1971.

The effect of the weir on adults has never been measured and may not have been great. But Thompson (1945) and later Talbot (1950) estimated that sockeye salmon delayed for 14 days at Hell's Gate never reached their spawning grounds. Moreover, at least half the sockeye salmon held for ripening at the old Karluk hatchery died before they were ready for spawning. The weir must also have prevented adults from moving back downriver to spawn after ripening in the lake. Such was observed by W.F. Royce in 1957 at Brooks Lake on the Naknek system. Bevan and also Walker have seen schools of sockeye salmon move out of Karluk Lake and try to swim downstream through the Karluk weir. Roos has also observed schools of sockeye salmon which had ripened in Chilko Lake move downstream in the Chilko River to spawn.

It is obvious that the Karluk weir has imposed increased mortalities on sockeye salmon—fry, fingerlings, and smolts—and by blocking the river to free movement of adults has reduced the productivity of the Karluk River spawning ground.

The effect of the weir on the sockeye salmon runs has never been studied, hence the conclusion that it, along with the improperly regulated fishery, has been one of the basic causes of the decline of the Karluk runs can only be supported by indirect evidence. Yet, this evidence is so convincing to us that the elimination of the Karluk weir assumes a primary place in any program for restoration of these runs. With other methods for enumeration of salmon runs, such as towers for counting and well-planned tagging operations, much more could be learned about the Karluk sockeye salmon than has ever been learned from the weir. Of course the study of spawning and fry emergence and migration would have to be extended from Karluk Lake into the Karluk River—provided these studies are carried out without interfering in any way with either young or adult salmon.

Finally, adjustment of the regulations to protect the midseason spawners, recommended by Thompson and Bevan (1954), is a second requirement. The immediate reversal of the downward trend in the returns from individual spawning years when the fishery was closed for extended periods in the Karluk district from 1951 through 1956 demonstrated that protection of the midseason fish is essential to recovery of the run. It is impossible to say how far this recovery would have gone with the weir still in place just below the lake. The present critical state of the run since 1957 has resulted at least in part from increased fishing pressure.

Six salmon fisheries are now being managed successfully on bases which can be judged from published reports. These are the sockeye and pink salmon fisheries of the Fraser River, the red (sockeye) salmon fisheries of Bristol Bay, the pink salmon fisheries of Kodiak Island and Prince William Sound, and the sockeye salmon fishery at Chignik. Since the Bristol Bay runs move through the inshore fishery within 2 or 3 wk at most, on their way to the spawning grounds, they cannot serve as a guide to the management of the Karluk runs which historically enter the river beginning in early June and continue until October. The Karluk sockeye salmon run is therefore more similar in its extent to that of the Chignik River or the Fraser River which also may begin in June and usually continues until October or later.

The recent successful management of the Chignik fishery has come about with the realization that the two lakes in the Chignik watershed contain independent populations of sockeye salmon and that escapement to the more productive Black Lake must be provided from the early season run.

The Fraser River system is, of course, much larger than the Karluk and its complexity and actual as well as potential productivity of sockeye salmon is correspondingly greater. Moreover, the Fraser sockeye salmon runs originate in a number of completely independent rivers and lakes between which interbreeding of sockeye salmon populations is virtually impossible except through straying of fish from overlapping runs. There is no way of knowing from available data if this happens in the Fraser, but the maintenance of the individual characters in time, abundance, and seeming identity indicates that if it occurs, such straying must be unimportant. On the other hand, except for differences in environmental effects on survival, there appear to be no natural barriers to stop Karluk fish from spawning wherever they please in the watershed. Yet from the life history and peculiarities shown by both the Karluk runs and the Fraser River sockeye salmon within individual segments of the watersheds, and from the work of Hartman and Raleigh (1964) and of Gard and Drucker (see footnote 5) there is no reason to doubt that the Karluk watershed is inhabited by an unknown number of separate races and there is now no reason for support of Rounsefell's assumption that all segments of the run interbreed, i.e., that escapement from any part of the run is equally desirable.

The information required for effective management of this fishery should not involve unnecessary assumptions concerning the nature of the managed population which could nullify the benefit from that management, if the assumptions are false. The importance of the return of different races or segments of a run to different spawning grounds should be obvious if these different segments have varying reproductive capacities, pass through the fishery at different times, and are independent in reproduction. Therefore, the fundamental requirements of management of the Karluk sockeye salmon are: (a) recognition of the existence of different and independent races in the run, (b) adjustment of regulation to the time these different races move through the fishery, and (c) adjustment to the length of time different races remain available to the fishery as a basis for determining the total numbers taken from each race by the fishery, (d) consideration of the nature of the fishery, and its potential for expansion or contraction of effort, (e) adjustment of regulations to the productivity of each race, i.e., the numbers of fish which can be profitably accommodated on its spawning ground, and if possible (f) optimizing the methods of controlling the fishery to obtain the escapement desired of each race.

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COMMENTS ON "EVALUATION OF CAUSES FOR THE DECLINE OF THE KARLUK SOCKEYE SALMON RUNS AND RECOMMENDATIONS FOR REHABILITATION," BY R. VAN CLEVE AND D. E. BEVAN

GEORGE A. ROUNSEFELL[1]

The causes for the decline of the Karluk River sockeye salmon runs are many and diverse. Van Cleve and Bevan oversimplify the case, stressing but a few factors and ignoring others without adequate explanation of their omission. Their paper also contains several obvious misstatements, e.g.,

> Rounsefell in 1958 was apparently unaware of the work of the International Pacific Salmon Fisheries Commission on the Fraser River sockeye that had revealed the peculiar life history of several of the largest runs in that system which spawn below the lakes where the young are reared so that the fry have to migrate upstream into the nursery lakes . . . .

In my report (Rounsefell, 1958:85), I specifically refer to this habit in the sockeye salmon that spawn below both Chilco Lake and Babine Lake. On the same page I refer to Philip Nelson observing the young of these river spawners at Karluk working upstream through the weir pickets. This habit was well documented long before the Salmon Commission existed.

Again they state,

> . . . there is now no reason for support of Rounsefell's assumption that all segments of the run interbreed, i.e., that escapement from any part of the run is equally desirable.

On page 147 of my report I state,

> . . . . On the average, neither the very early nor the very late spawners are as successful as those spawning in midseason. The analyses showed that because of the deleterious effects on survival of low autumn (11 out of 48 years) and late spring (about 14 out of 47 years) temperatures, survival depends to some extent on the season of spawning. It would be best then to abandon the idea of obtaining a spring and fall group of spawners, but rather to encourage the canning of the early and late fish, and insist on a higher percentage of the summer fish being in the escapement. . . .

They state that the estimate of 400,000 sockeye salmon spawning in Karluk River in 1926 is " . . . more fish than were recorded for any other part of the watershed." If the 400,000 is compared with the 1926 escapement of 2,500,000 it comes to only 16% compared with 84% in the lake and its tributaries. I assume that Van Cleve and Bevan are not trying to say that while those that enter the lake consist of a large number of subpopulations, the river spawners are only one subpopulation. If they do mean this they obviously invalidate their comments about the Birkenhead River spawners consisting of different races spawning along the same stream at different distances from its mouth. Rich (Gilbert and Rich, 1927:23) states on 18 July 1926 that

> . . . . Any estimate of the number of spawning fish was difficult but it was thought that certainly not less than 300,000 fish, and probably about half a million, had entered Upper Thumb River up to this time.

This was far too many spawners for the exceptionally dry year of 1926, and the returning progeny numbered only 1,460,000. This can be compared with the 1931 escapement of only 870,000 which produced a return of 2,600,000, with but 22% of summer spawners.

Van Cleve and Bevan also state,

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Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

> A measure of the small importance attached to the Karluk [River] spawners is that all reports including Gilbert and Rich (1927) do not include the Karluk River on their maps of the watershed.

To this one might reply that neither do the available manuscript reports of the junior author (Bevan and Walker, 1955; Bevan, 1957) or the unpublished manuscript reports of W. F. Thompson (Thompson, 1951; Thompson, Bevan, and Thorsteinson, 1954; Thompson and Bevan, 1954) include the river on their maps. The map in my report (Rounsefell, 1958) does show the river, just as does that of Van Cleve and Bevan. As a matter of far more importance, I do not find any attempt to measure the number of sockeye spawning in the Karluk River in any of the manuscripts just mentioned. My report, showing that in some years a number of mid- to late-season sockeye salmon spawned in the river below the lake, apparently stimulated the authors into hypothesizing one cause for the decline of the runs. In this connection I should like to mention that Bevan and Walker (1955) tabulate the results of their Karluk sockeye salmon spawning ground observations in 1954. They total 138 observations (101 by Bevan and Walker themselves) between 18 May and 29 September. Very surprisingly not a single observation is recorded for the Karluk River despite the fact that they camped at the weir site at the foot of the lake.

Van Cleve and Bevan attempt to explain the importance of the Karluk River spawners by saying that the river spawners were predominately of age 5_3 and that their decline in numbers could explain the increase in relative numbers of 4-yr smolts in the total runs. An examination of the basic data on which they base their conclusions (Barnaby, 1944) finds (Figure 1) that for the brood years 1922 and 1924 through 1929 that the rate of decrease of the 5_3 age group is similar in both the spring and summer-fall groups of spawners. The latter group of spawners, with the slightly greater decrease in the 5_3 age group shows a somewhat higher rate of return, quite the contrary of the theory advanced by Van Cleve and Bevan concerning the superiority of the 5_3 spawners.

The assumption of two seasonal modes in the Karluk run (or merely one mode depleted in the center as these authors claim) is not borne out by the weekly data on runs accumulated since 1921. Thus in the 30-yr period from 1921 through 1950 (Rounsefell, 1958; see also Figure 2) three modes are evident. The first mode, peaking in mid-June, falls off rapidly with a low point in the week ending 12 July. The second mode peaks from the first to the ninth of August. The second low point is not as distinct as the first because of overlapping between the second and third modes but it is about August 16th. The third mode peaks in

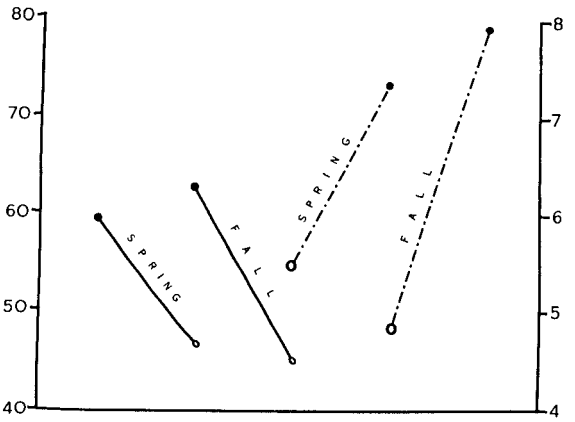

FIGURE 1.—Relation of age 5_3 fish to brood years and return date (Barnaby, 1944). Showing the geometric mean (left hand scale) of the percent 5_3 age fish in the spring and fall runs (solid lines). Dots are for the spawners, open circles for the returns. Geometric mean of number (-00000) of spawners (dot-dash lines) in brood years (open circles) and geometric mean of number in returns (dots).

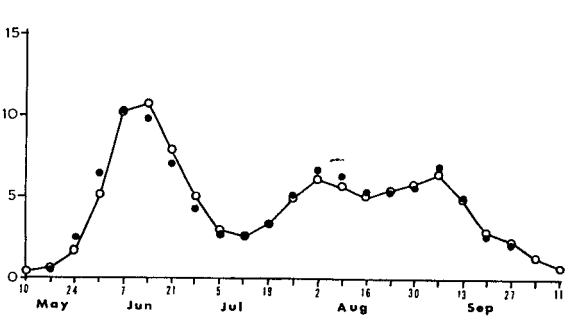

FIGURE 2.—Percentage seasonal occurrence of the Karluk sockeye salmon runs 1921-50 (open circles) and percentage seasonal occurrence of age 5_3 fish 1922 and 1924-49 (dots).

early September. Van Cleve and Bevan cite Walker and Bevan (1955),[2]

> . . . . They also maintained that the decrease in Karluk River spawning could explain the increase in relative numbers of 4-yr smolts, since the river spawners were predominantly of 5_3 age.

To refute this claim one has only to look at Figure 2 showing the seasonal occurrence of the total runs and of the 5_3 age group during the 30-yr period in which this alleged reduction in Karluk River spawners was supposed to have taken place. In other parts of their paper they state that the center of the run, which they claimed spawned in the main river, was supposed to have been depleted before 1921; you cannot have it both ways. Very obviously the decrease in the proportion of fish of 5_3 age has been occurring almost equally in all segments of the runs.

The authors place undue emphasis on a quotation from Chamberlain (1907), which they suggest proves that in the early years there was only one peak in the run. As I shall mention later, Cloudsley Rutter actually said that there were two runs, but that only one occurred in the year (1903) he visited the lake. Chamberlain was not personally acquainted with Karluk but was paraphrasing field notes by Rutter. In discussing the egg take of the Karluk hatchery for 1898 (the parent brood year for most of the 1903 run described in Rutter's notes) Moser (1901:342) says,

> Of the season's take the spring run therefore amounted to 50.4 per cent as against 49.6 per cent for the fall run . . . . the monthly percentages of fish spawned are as follows: June, 0.5 per cent; July, 47.9 per cent; August, 2.9 per cent; September, 41.5 per cent; October, 6.8 per cent; November, 0.4 per cent.

In discussing the hatchery operations for 1899 Moser (1901:343) lists the eggs taken as coming from the spring run and from the fall run. Again, on page 344 Moser states,

> It would appear from the above that the eggs eye very much faster with the spring run, and that the hatching range covers a much longer period. It is also apparent that in considering the hatching of redfish at Karluk the two runs must be treated separately—*the runs are so marked* and the prevailing conditions so radically different . . . . the early run in 1899, under natural conditions of temperature, hatched in an average of 129 days, whereas the fall run required 198 days. [Italics mine.]

The constant reiteration by Van Cleve and Bevan of the notion of a former run with only one mode is quite contrary to their insistence that the run consists of subpopulations and that only the main river spawners are of any importance in maintaining the run.

If we concede for the moment that there are strong tendencies for most sockeye salmon to attempt to spawn in their natal area (within reasonable limits), then we can make a separate assessment of the relative reproductive success of different portions of the run. For the 25-yr period from 1921 to 1945 I have compared the spring, summer, and fall escapements (only spring escapement was available for 1934) with the size of the run returning 5 yr later during the same respective seasons. The resulting returns per spawner for all three periods (73 comparisons) are shown in Figure 3. Table 1 shows which of the three groups of spawners was most successful for the same number of spawners, and on odd- and even-numbered years.

This table shows that if the theory of independent seasonal subpopulations at Karluk advanced by Van Cleve and Bevan is correct, the spring and summer spawners are about equally successful; the fall spawners are much less successful. It also shows that fall spawners, while successful on the odd-numbered years, are very unsuccessful on the even-numbered years. This analysis therefore strongly suggests that it is chiefly the fall spawners (not the summer spawners as Van Cleve and Bevan contend) that use the main river and are thus in direct competition with the large even-year pink-salmon, *O. gorbuscha*, runs.

Concerning the question of races and seasonal races I should like to emphasize the lack of factual data in the report of Van Cleve and Bevan. They quote liberally and at length from various unpublished manuscripts and inhouse mimeographed memoranda. Thus they cite an unpublished manuscript by Gard and Drucker

[2] Walker, C. E., and D. E. Bevan. 1955. Observations on the biology of the red salmon in the Karluk watershed. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

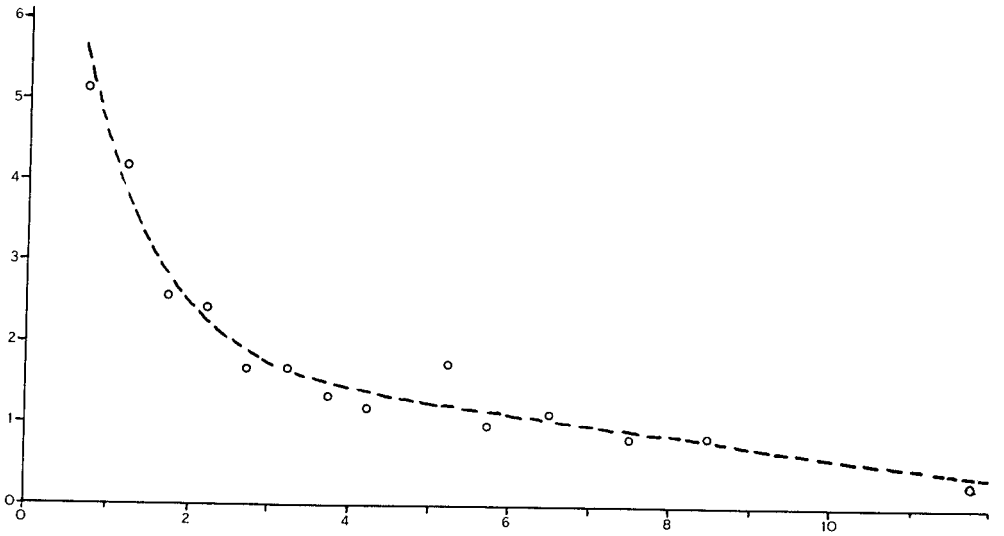

FIGURE 3.—Ratio of returns to number of spawners for the spring, summer, and fall groups of spawners (see text) on the ordinate scale against hundreds of thousands of spawners (abscissa).

TABLE 1.—Showing the number of odd- and even-numbered years on which each group of spawners produced returns falling above or below the curve of Figure 3.

Spawning group	Odd years			Even years			All years		
	Above	Below	Percent above	Above	Below	Percent above	Above	Below	Percent above
Spring:									
to 21 June	6½	6½	50	7	2	78	13½	8½	61
Summer:									
22 June-16 Aug.	9½	3½	73	4½	6½	45	14	10	58
Fall:									
17 Aug. on	6	7	46	1½	8½	15	7½	15½	33
All seasons	22	17	56	13	17	43	35	34	51

(1972)[3] and say (data not given) that Gard and Drucker demonstrated the existence of these races by comparing early spawning sockeye salmon in the lateral tributaries of the lake, in the upper Thumb, O'Malley River, and Canyon Creek with later spawners in these terminal streams, and on the Thumb Beach in Karluk Lake. The late spawners were said to show greater mideye to fork length, and greater fecundity at comparable lengths.

According to this statement Van Cleve and Bevan show, not a comparison between geographical localities (the same localities in each season were not used) but merely between early and late spawners. The validity of the quoted comparison is open to serious question. In my published report on the fecundity of North American Salmonidae (Rounsefell, 1957) I note that for Karluk sockeye salmon, over a 4-yr period, that 60-cm sockeye with 2 yr at sea showed a consistently and statistically significant higher fecundity than Karluk sockeye with 3 yr at sea. These data were for fish running throughout the season.

Davidson and Shostrom (1936:9) showed that late-running salmon have longer heads and that the distance from the eye socket (equivalent to Gard and Drucker's center of the eye for general

[3]Gard, R., and B. Drucker. 1972. Differentiation and cause of decline of sockeye salmon of the Karluk River system, Alaska. Unpubl. manuscr. Auke Bay Fish. Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

anatomical position) to the back of the head in 36 days increased in percentage of body length (measured from the back of the head) by 5.08%. Thus we do not need to postulate races on the basis of the unpublished findings of Gard and Drucker.

If we were to assume (as done by Van Cleve and Bevan) that the early and late spawners in the same tributary are of separate races, then there is no plausible explanation of why large numbers of late-running 4_3 grilse should presage a large total run of 5_3 age fish in the following year, yet the coefficient of correlation between them over a 25-yr period is 0.956 and highly significant. Rich describes these 4_3 grilse (Gilbert and Rich, 1927:32-33),

> A larger size of grilse, belonging to group 3, is one year older than those above mentioned and returns in its second season in the sea as 4-year fish. These are still largely, but not exclusively, males, and are undersized fish of little value . . . . conspicuously deficient in color of flesh and amount of oil, ...

I question the quotation concerning fry from river spawners (the report says it was a 1951 observation but from what field notes or unpublished manuscript is not divulged) in which Walker is purported to state concerning these river-derived fry that,

> . . . . These fish were, on the average, three millimeters longer and had heavier bodies than those *seen* elsewhere. [Italics mine.]

Such a supposedly exact comparison between two or more sets of data without divulging the source is questionable. Did he compare actual measured and weighed samples with fry from spring, summer, or fall spawners in lateral or terminal tributaries of Karluk Lake? Or with beach spawners, or with fry from Thumb or O'Malley Lakes?

Van Cleve and Bevan follow this by stating,

> . . . .Walker and Bevan maintained that since fry from the Karluk River are largest at the time of emergence, they should also be largest at the time of seaward migration if they retain their size difference during lake residence.

This statement apparently infers that biologists should believe that fry from eggs spawned in June are smaller when they emerge from the gravels in the spring than are fry from eggs spawned in the fall. Such a statement requires carefully gathered data for substantiation. It is more likely that if data exists showing smaller fry descending into the lake from tributary streams, the fry were from the late spawners in those streams and that the fry from the early spawners descended into the lake in the very early spring, probably unobserved.

The probability of a very early lakeward migration of the fry from the early spawners is suggested by records of the Karluk hatchery (Moser 1901:345-346),

> According to a report from the hatchery, under date of November 3, 1900, all the June eggs and part of the July eggs had hatched out, producing an excellent lot of healthy fry. It was found (1900) that the earlier eggs and the September eggs were the best, while a portion of those taken during the middle of the season were of indifferent quality. . . .
>
> After the fry are hatched out they escape to the bottom of the trough, ... As they age they require more space, but they are usually held in the parent trough until the egg—or umbilical—sac is absorbed, a period of about ten weeks, depending upon the temperature of the water.

This suggests that the spring fry would be ready to emerge from the gravel of the redd by the middle of January.

At another point Van Cleve and Bevan paraphrase an additional unpublished manuscript by Walker and Bevan saying,

> . . . . Walker and Bevan (1955)[8] noted that the largest spawning population of sockeye salmon in the Karluk watershed was found in the Karluk River.

This type of generalized statement, without presentation of data is unconvincing, especially as in the second paragraph of the whole paper Van Cleve and Bevan used the factor of 10% of the total run to estimate the numbers spawning below the lake in 1971, as determined by the National Marine Fisheries Service in 1963. In fact, it means almost nothing for them to say "largest" when in another place they say 400,000 (out of an escapement of 2,600,000) was "more fish than were recorded for any other part of the watershed."

They quote from the Karluk River report of Gilbert and Rich (1927) a statement by Rich,

> . . . . The spawning escapement [of 1926] was the best in many years, and in all probability was the best that has ever been observed by the few white men who have visited the lake.

They then append the following footnote,

> This was certainly a rhetorical statement with little foundation other than Rich's impression of a "big" run.

Actually Van Cleve and Bevan are wrong. The total run of 1926 was exceeded only by those of 1901 and 1906. The escapement in 1926 of over 2½ million sockeye salmon was certainly larger than in either of the two earlier years. In 1901 for instance the egg take for the Karluk hatchery was less than in all but 7 of the 20 yr the hatchery operated. They admit themselves that despite regulations to the contrary fishermen were still operating in the river itself as late as 1899, and were not officially excluded from the lagoon until 1918. Furthermore, there is no record of anyone visiting Karluk Lake in either 1901 or 1906.

Van Cleve and Bevan have devoted far too much space to trying to prove that my assumption of a 35% escapement before installation of a counting weir in 1921 is much too conservative, apparently in order to substantiate their theory of one large seasonal run overfished in the center. Yet there are no records in existence by which one can make a truly sound estimate and the exact proportion is of little consequence. When one considers, however, the numerous closed fishing seasons that had to be imposed from time to time each year after 1921 in order to achieve a 50% escapement through the weir it is wholly unreasonable to expect more than a 35% escapement in the earlier years of almost unrestricted fishing in the river and the lagoon. They go so far as to credit Gilbert and Rich (1927) as supporting their view (despite their earlier reflections on the validity of Rich's statements), saying,

> A careful reading of Gilbert and Rich (1927) also shows that they felt that Rutter's estimate of the total number that spawned in Moraine Creek in 1903 was about one-half as large as the true figure.

Van Cleve and Bevan perhaps failed to note that Rutter kept a careful count of spawners in Moraine Creek over a full month from 5 August to 5 September. Rutter also stated that in 1903 the spawning season was practically over early in September. Far from supporting the view of Van Cleve and Bevan, Rich says,

> In 1926 Moraine Creek was well seeded by this early run and was also used extensively by the later runs—those that spawned in the early part of August, at the same time Rutter's observations were made. . . . It is quite probable that conditions were vastly different in 1903 than in 1926, and that the early escapement was very much smaller. Certainly, if Moraine Creek in 1903 had received anything like the early spawning run it had in 1926 the remains of the dead fish would have attracted the attention of a well-trained observer such as Mr. Rutter.

In this connection it should be noted that Van Cleve and Bevan also use Rutter's statement (Chamberlain, 1907) to prove that the early years had only one peak in the runs. However, Rutter actually said,

> The Karluk is said similarly to have two runs, one maximum about the last of June and one the first of August, but this was not true in 1903 when the river was under study.

It is thus quite clear that Rutter had been well informed on the usual two runs, the first one being the larger. The use of what happened in only one year (1903) to prove the usual nonexistence of a large early run is poor extrapolation on the part of Van Cleve and Bevan in my opinion.

It should be noted that Van Cleve and Bevan in claiming to believe my admittedly rough assumption of a 35% escapement during the early years of the fishery is too conservative, base their argument partially on the lower return per spawner in the 1929-48 period as contrasted with the earlier period. Nevertheless they have not challenged my calculations (Rounsefell, 1949) showing escapements of sockeye salmon in the Fraser River from 1894 to 1921 as amounting to only 18% of the runs (only 6% in the heavily fished war year of 1917), and its increase to 27.4% of the run in the 1922-45 period of stricter law enforcement and longer closed seasons.

Concerning their theory that in the earlier

years of the fishery there were no early or late runs, Van Cleve and Bevan also state,

> . . . . even though Thompson's analysis of the catch in his 1950 paper was based upon that of a single cannery [the actual cannery was not named although the Alaska Packers Association operated three canneries at Karluk and usually did not operate them all for the entire season], it agreed with this earlier observation [referring to Rutter's statement concerning lack of a large early run in 1903, even though Rutter also said that the Karluk is said to have two runs] and *proved that the spring and fall peaks evident in 1921 were artifacts.* [Italics mine.]

My Figure 2 clearly shows that over a 30-yr period the existence of spring, summer, and fall runs was not an artifact, even though the catch was taken from almost exactly the same portion of the seasonal runs as in the earlier years. Why then do they assume that the seasonal runs differed between the two periods? And if, as they state, the midseason fish were so badly depleted by fishing in the earlier years, how was this midseason run, which by their reasoning should have been wiped out, still furnishing the largest share of the catch? It would appear from the actual data on hand that the only "artifact" is their hypothetical large midseason run.

On the point of the weir at the foot of Karluk Lake obstructing the downstream migration onto river spawning areas of some adults in occasional years, I agree with Van Cleve and Bevan that this is undesirable. I went through the same problem in Maine where the hatchery personnel insisted on fish tight weirs below every lake before planting landlocked salmon. They mistakenly thought that the salmon were escaping when they dropped downstream to spawn, often in the only spawning area available. I do not agree that the weir has been any serious obstacle to upstream migrating salmon, but in Karluk with the often enormous pink salmon runs it is difficult to maintain a weir downstream because of the dead carcasses of spawned-out salmon.

This habit of late-running sockeye salmon spawning in an outlet river is well known. The very late salmon may seldom reach the lake. In some rivers the earlier portion of the late spawners may enter the lake until their gonads are ready for spawning and then drop downstream, but I note that even Van Cleve and Bevan do not claim that this is an annual occurrence at Karluk, being able to cite but one instance. There is no good reason, however, why the Karluk weir cannot be easily converted into an upstream and downstream weir.

I do not agree that obtaining most of the escapement in midseason is the panacea. To begin with it appears that the main river spawners (contrary to Van Cleve and Bevan) are recruited chiefly from rather late-running fish. Secondly, the large pink salmon runs in the even years will continue to handicap the even-year river spawners more than those in Karluk Lake tributaries. In their Table 3 Van Cleve and Bevan show a table from Burgner et al. (1969) that shows only 126,000 redd sites in the main river. When such a spawning area is also used by thousands of pink salmon on the even years (Bevan in his 1956 survey shows 700,000 spawning pink salmon actually observed) the competition between pink salmon and late-running sockeye salmon in the main river is obvious. In earlier years the pink salmon runs varied greatly in numbers since insufficient harvesting when the runs were large caused cataclysmic declines in following cycles. Under present conditions of better harvesting of pink salmon runs it would appear unwise to count on good sockeye production from the main river in most even years.

I did point out (Rounsefell, 1958) that after the weir was moved to the lake outlet in 1945 it was discovered that some pink salmon passed into the lake every year, varying from less than a hundred to 16,000 in odd years, and from 37,000 to 87,000 in even years.

Van Cleve and Bevan minimized the spawning areas in Karluk Lake and its tributaries while maximizing the spawning areas below the lake. Thus the table of Burgner et al. (1969) is presented without adequate explanation. Burgner et al. show:

Karluk system	*Hectares*	*Redd sites* (based on 2 m²)
Terminal streams	1.67	8,000
Lateral streams	6.71	34,000
Lake beaches	1.25	6,000
Outlet river	25.28	126,000
Total	34.91	174,000

The text of the report by Burgner et al., however, says that in the shallow torrential lateral streams in the Karluk system, space requirements were often substantially less than 2 m^2. They also say their figure is only an approximation complicated by the occurrence of successive waves of spawners in successive streams. They also admit incomplete information on the amount of potential spawning ground, especially on lake beaches, and their figure includes only the beach spawning areas of Thumb and O'Malley Lakes. Observations of beach spawning have been published, mentioning Tent Point, Meadow Point, Cascade Creek, Moraine Creek, Canyon Creek, Halfway Creek, off Boulder Point, off Grassy Point Creek, etc.

Fred Lucas estimated in 1924 that sockeyes spawning in O'Malley River would average a pair to each square yard. (Gilbert and Rich, 1927:20).

The estimate of the area (Burgner et al., 1969) of river spawning beds is quite meaningless in my opinion without information on the location of these beds along the 30-mile course of the Karluk River. Furthermore, in the estimates of main river spawning areas for other systems redd sites range from 3 to 8 m^2 rather than the 2 m^2 used for Karluk.

Burgner et al. (1969:457) also say,

> The individual spawning areas in the Karluk system are occupied continuously for about 5 weeks to 5 months by a succession of spawners, with the result that many more spawners are accommodated than could be if they all spawned in 2 or 3 weeks. This occupation by successive waves of spawners introduces questions as to the effect of superimposition of redd sites on the success of spawning. *We do not know the answers.* [Italics mine.]

Since the sources of Van Cleve and Bevan's spawning area data readily admit that they do not have the answers to many of the questions raised in attempting to convert spawning area into redd sites, I believe that their figures need considerable qualification and cannot be taken seriously.

From the above discussion I suggest that the number (ignoring the main river since there is no locality information given) of redd sites would be more like the following:

Terminal streams	32,000
Lateral streams	144,000
Lake beaches	60,000
Total	236,000

That is, the lake and its tributaries should, have, and can accommodate about half a million spawners without overcrowding.

It is apparent that the Karluk sockeye salmon run is continuing the decline that was accelerated by destruction, since 1921, of the natural cyclic character of the runs. Restoration of the runs at this stage can scarcely be expected from merely assuring a more even seasonal distribution of spawners.

Two important factors I stressed 15 yr ago were the control of both density-dependent and density-independent predators in order to raise the number of smolts per spawner leaving the lake, and hopefully to raise the biomass of smolts in the lake to a level where eventually it would lower the threshold size of the migrating smolts, so that we would have a reversal of the trend toward more 4-yr and fewer 3-yr smolts.

In this regard I note that Van Cleve and Bevan refrain from mentioning the high mortality of spawning salmon by Kodiak bears. Shuman (1950) reported a bear kill of unspawned salmon of 94,000 or 19.4% of the 1947 spawning escapement of 485,000. If this quantity has been lost annually since I recommended control 15 yr ago it means a loss of 1,400,000 spawning salmon.

I also recommended (Rounsefell, 1958) that an attempt be made to restore the cyclic character of the runs, stating,

> The attempt to stabilize the runs by obtaining a high number of spawners in every year has largely destroyed and obscured the former cyclic character of the runs. During the period when these cycles were present the number of spawners fluctuated in a more or less regular manner from very high to very low (lower than most recent years). This wide variation in number of spawners resulted in wide oscillations in the numbers of young sockeye present in the lake and therefore available as food for predator fishes. These regular oscillations in the supply of available prey may have acted as a control on the abundance of predators.

I then explained more fully its purpose as follows:

> . . . by restoring insofar as practicable the former cyclic character of the runs in order to lessen competition between the older young and fry, and perhaps give some measure of natural control of predators. Because of the present low state of the runs this should be accomplished by providing a higher proportion of spawners on big runs rather than by decreasing the proportion on smaller runs, ...

This recommendation was concurred in by Thompson, Bevan (junior author of the present paper), and Thorsteinson (1954) in which they state,

> The assumption is made, under this quota system, that by allowing a larger escapement in poor years, these years can be built up to a level of good years. This is probably in error. Poor cycle years are now known to be due to natural conditions which limit production and attempts to rebuild these poor years in Bristol Bay and elsewhere by radical restrictions have failed . . . . The cycles in the Karluk and elsewhere seem to have broken down, possibly due to efforts to increase escapement ratios in poor years, thus probably destroying natural conditions favorable to the big-cycle years.

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REPLY TO ROUNSEFELL'S "COMMENTS ON 'EVALUATION OF CAUSES FOR THE DECLINE OF THE KARLUK SOCKEYE SALMON RUNS AND RECOMMENDATIONS FOR REHABILITATION,' BY R. VAN CLEVE AND D. E. BEVAN"

RICHARD VAN CLEVE[1] AND DONALD E. BEVAN[2]

A detailed reply to Rounsefell's comments on our paper would involve repetition of those sections in which we have corrected misconceptions and errors in his paper of 1958. He has repeated many of the arguments he used in 1958 and has quoted parts of ours out of context. For a detailed reply to Rounsefell's "rebuttal" we refer you again to our paper. In it we have brought relevant information from older publications together with factual unpublished material from a number of agencies and some of the most recent knowledge of sockeye biology and behavior that has demonstrated the genetic basis of the racial structure of their populations. This has been described for both the Karluk and Fraser River stocks. We have used this information to interpret the past history of the Karluk sockeye salmon runs and from it have explained their continued decline. In view of the papers by Thompson (1950, 1951), Thompson and Bevan (1954), Hartman and Raleigh (1964), Raleigh (1967), Brannon (1967, 1972), and Gard and Drucker (1972),[3] there is no question that the Karluk sockeye salmon runs are divided into many races. It is unfortunate that this was not recognized earlier.

It is also unfortunate that while spawning sockeye were noted in the Karluk River and the upstream movement of fry was noted, that the Karluk River spawning races have not been studied. So far as we know the observations of Walker (1954)[4] were the first detailed observations of the upstream movement of fry through the weir and of the injuries sustained in that struggle. However, soon after those observations were made Bevan and Walker shifted from studying sockeye salmon to studying pink salmon, so they did not continue working on the Karluk River spawning or on the movements of the young sockeye salmon.

In repeating his disbelief in the existence of the races in the Karluk sockeye salmon as well as his recommendation of added protection of the midseason runs "because they are more productive," Rounsefell is not only inconsistent but confuses the time the fish enter the river or lake with the time they spawn. Those sockeye salmon that spawn in the side streams above the lake move up the river and spawn in their special spawning areas after a delay of several weeks in the lake. Karluk River spawners, however, wait in the river while others move into Karluk Lake and rest there until they are ready for spawning; consequently the average time between their passage and spawning is shorter for river spawners than for those which spawn in tributary streams. The movement of fish out of the lake and into the river noted by Bevan (1951)[5] was not a single observation but has been seen several times. Since the

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[3] Gard, R., and B. Drucker. 1972. Differentiation and cause of decline of sockeye salmon of the Karluk River system, Alaska. Unpubl. manuscr. Auke Bay Fish. Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

[4] Walker, C. E. 1954. The red salmon smolt migration at Karluk Lake, 1954. Unpubl. manuscr. Univ. Wash., Fish Res. Inst., Seattle, WA 98195.

[5] Bevan, D. E. 1951. Karluk Lake stream surveys, 1948-1951. Unpubl. manuscr. Kodiak Isl. Res. Group, Univ. Wash. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

Manuscript accepted March 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

same action has been observed to occur regularly at Brooks and Chilko Lakes it is obviously a regular part of the spawning behavior of sockeye salmon that spawn in rivers below lakes. It has not been observed regularly at Karluk Lake but it must occur, since the weir was made to pass fish downstream as well as upstream sometime in the late 1950's.

Thompson (1950, 1951) proved conclusively that the bimodal structure of the Karluk sockeye runs after 1921 was an artifact caused by the fishery. He provided a series of figures from the total weekly Karluk pack of the largest canner in that area, that showed the transition from a run with a single mode in the late 1890's through the gradual destruction of the center of the run, finally ending before 1921 with the two modes representing the spring and fall remnants. These had not been fished as hard as the center and after 1921 they were protected by federal regulations of the catch. Rounsefell's Figure 2, based upon runs since 1921, is therefore of no significance concerning the original runs.

The reports of the International Pacific Salmon Fisheries Commission document the variability in age at which fish of the same race return from the sea to spawn. Every peak cycle of the major Fraser River races is normally preceded by a large run of 3-yr-old jacks that are almost all males. The peak years are also usually followed by a large run of 5-yr-old fish. This is shown in the annual reports of the Commission which describe the returns from the large Adams River run or from the Chilko run. This variability in age of return is part of the normal variability within any race of sockeye and represents the adaptability of each race to environmental variations. The age of return of each race is never fixed, though in the successful ones most fish usually return at a certain age. The variation in age of return provides protection against disasters such as occurred at Hells Gate on the Fraser River in 1913, and increases the probability of survival of each race. Of course if a number of different races are lumped together as Rounsefell has done for both the Karluk and Fraser Rivers and the variations in returning age classes are studied without regard for the individual variation of each race, the results are meaningless. Correlations between the main age group and inconsequential segments of any group of races such as those mentioned by Rounsefell on page 655 of his comments are of no significance and certainly do not prove that races do not exist in the Karluk. Variations in time and space of the numbers of 5- and 4-yr-old fish must be expected though the returning fish of each race to be most successful conform in time within each season with limits imposed upon it by the composite of environmental factors that race encounters during its entire life history. We would expect the most successful portions of the run to produce the most "strays" that return at odd times and places.

It is difficult to appreciate Rounsefell's dismissal of the numbers of redds estimated for the terminal streams, lateral streams, and lake beaches in the Karluk watershed by the biologists who have been working on the Karluk (see Rounsefell page 658 and compare with Burgner et al., 1969). Rounsefell multiplied the number of potential redd sites noted by Burgner et al., in terminal streams by 4, in lateral streams by about 4.2 and on the lake beaches by 10 with no apparent justification other than his statement that the estimates made by Burgner et al. cannot be taken seriously. Using his most conservative factor of 4, he should also have increased the number of potential redd sites in the Karluk which would then exceed 500,000. The Karluk River could be expected to accommodate about 1,000,000 spawners. This would in fact agree with 3 times the 400,000 estimated to have spawned there in 1926, i.e., when that figure is multiplied by the difference observed by Bevan and Walker (1955) between stream estimates of spawners and weir counts which they established on Moraine Creek (see our paper page 631). This also agrees with the factor of about 3.0 established for Forfar Creek, one of the small streams in the Stuart Lake system of the Fraser River when the senior author was chief biologist for the International Pacific Salmon Fisheries Commission. Much as we have always admired the pioneering biological work of Rutter we cannot conceive that his stream counts would be more accurate than those of our modern salmon biologists. How-

ever, it is useless to argue about the relative numbers of sockeye that spawn in the Karluk River since the weir was moved to its present location in 1945. As noted in our paper this reduced the productivity of the Karluk runs to a new low level (see our Figure 2) and altered the relative numbers of the different races in the system. The weir must have had an especially adverse effect on the Karluk River spawners so that the proportion of 10% of the total run established by the Auke Bay Fisheries Laboratory staff after 1950 must have been far below the original proportion.

Shuman's (1950) estimate of high mortality of sockeye salmon due to Kodiak bears introduced by Rounsefell could have been associated with the large population of Kodiak bears resulting from lack of hunting during World War II. With more intensive hunting since then it is probable that predation is not as heavy as Shuman observed. We agree that this is a factor that should be studied.

It is probable if the sockeye salmon runs could be rebuilt in the Karluk system that natural cycles would again appear. However, artificial manipulation of the size of the sockeye salmon runs as Rounsefell (1958) recommends to restore the "cyclical abundance," which was characteristic of the period after 1921, should not be attempted before restoration of their abundance has been accomplished since they seem already to have been overburdened with manipulation and experimentation.

Testing the conclusions reached in our paper would be the height of simplicity: merely remove the weir from the upper Karluk River (as well as from all the other streams in the Karluk watershed) and maintain the present fishing intensity on the Karluk sockeye salmon. The cost would be minimal, especially if the biological work on the Karluk runs were restricted to observation of the adults and young from the stream banks and lake shore. Modern acoustical gear could be used on the lake to estimate numbers of both adults and young without harming them and stream counts of spawners would serve as a basis for comparison with past years. Concern with "complete counts" such as is theoretically obtained from the weir is fallacious because the weir counts do not include sockeye that remain in the Karluk River below it and as we have indicated the weir must have a major adverse effect on both young and adults.

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GROWTH, RECRUITMENT, AND DISTRIBUTION OF THE LITTLENECK CLAM, *PROTOTHACA STAMINEA*, IN GALENA BAY, PRINCE WILLIAM SOUND, ALASKA

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ABSTRACT

Specimens of the littleneck clam, *Protothaca staminea*, were collected in Galena Bay, Prince William Sound, Alaska, during the summer months of 1971 for a study of recruitment, growth, and distribution.

The average size of *P. staminea* in Galena Bay at the end of the first growing season is approximately 2 mm in length. At any given age, littleneck clams from Galena Bay are smaller than those from British Columbia. In Galena Bay 8 yr are needed for *P. staminea* to reach a length of 30 mm as compared with 3 yr for individuals from British Columbia.

In Galena Bay the intertidal distribution of *P. staminea* generally follows a bell-shaped curve with upper and lower extremes occurring between the tidal heights of +0.73 and -0.76 m. The young-of-the-year are essentially epifaunal, and the majority of the specimens of all age classes are found within 4 cm of the sediment surface.

The number of individuals surviving annual recruitment into the populations studied was variable.

Protothaca staminea (Conrad), commonly called the littleneck clam, is frequently encountered on beaches in Prince William Sound, Alaska. It is a clam of commercial importance in the State of Washington, and was harvested in southeastern Alaska until 1946 when the presence of toxic clams in Alaska resulted in regulatory action halting commercial production (M. Hayes in Felsing, 1965). Feder and Paul (1973) and R. Nickerson (Alaska Department of Fish and Game, pers. comm.) suggested that a small clam fishery is feasible in Prince William Sound since paralytic shellfish poison (P.S.P.) does not seem to be a problem there, and many beaches with sizable populations of *P. staminea* from beaches near Victoria, British *giganteus*, occur in the area.

Considering the extensive distribution of the littleneck clam along the Pacific coast of North America, few papers on the basic biology of the species are available. The most extensive paper is that of Fraser and Smith (1928) which provides information on size at age, sex ratios, size at maturity, and time of spawning for *P. staminea* from beaches near Victoria, British Columbia. Smith (1928) compared the different types of normally available food and the effects of these food types on growth rates of *P. staminea*. The only paper providing detailed information on reproduction of *P. staminea* is that of Quayle (1943) for clams of Ladysmith Harbour, British Columbia. General, but brief reviews of the species are included in Marriage (1954) for Oregon, Fitch (1953) primarily for California, and Amos (1966) for the entire range of the species. Toxicity of *P. staminea* from P.S.P. is considered by Felsing (1965) and Quayle (1967, 1969). No intensive work on littleneck clams from Alaskan waters is available.

The major purpose of this investigation was to study age and growth of *P. staminea* in Galena Bay, Prince William Sound, Alaska. The material collected also provided information on recruitment, distribution, and abundance of *P. staminea*. This project was conducted with funds provided by the University of Alaska's Sea Grant Program for a study of

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Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

shellfishes in Prince William Sound, Alaska (Grant No. 1-36109).

METHODS

Field work was accomplished from June 1971 through October 1971 in Galena Bay, a small embayment in the northeastern portion of Prince William Sound (lat. 60°58′N, long. 146°44′W), 20 miles from the town of Valdez. Two gravel beaches and one mud flat were sampled on the north side of Galena Bay (Figure 1); all were completely covered by water at the highest spring tides. The major features of the study sites are summarized in Table 1 and Figure 2.

The weather conditions in the study area were, in general, typical of south-central Alaska with overcast skies and considerable precipitation. Summer air temperatures were generally on the order of 7.5° to 10°C (also see Searby, 1969). Longshore surface-water temperatures in Galena Bay ranged from 8° to 18.2°C during the study period. No extended winter water temperatures are available for Galena Bay; however, we observed the freezing of shallow tidal pools in Galena Bay in January 1973 (Feder and Paul, unpubl. data). The National Ocean Survey (1970) recorded mean surface-water temperatures in the Cordova region (approximately 60 miles from Galena Bay) as a minimum of 2°C in February and a maximum of 11°C in August. Beach-surface temperatures during the study period ranged from 9°C in October to 32°C in July with the latter value 15°C higher than longshore seawater temperatures measured at the same time.

Sampling was accomplished by transecting; the actual positions of the transects on the beaches were arbitrarily selected. Collections

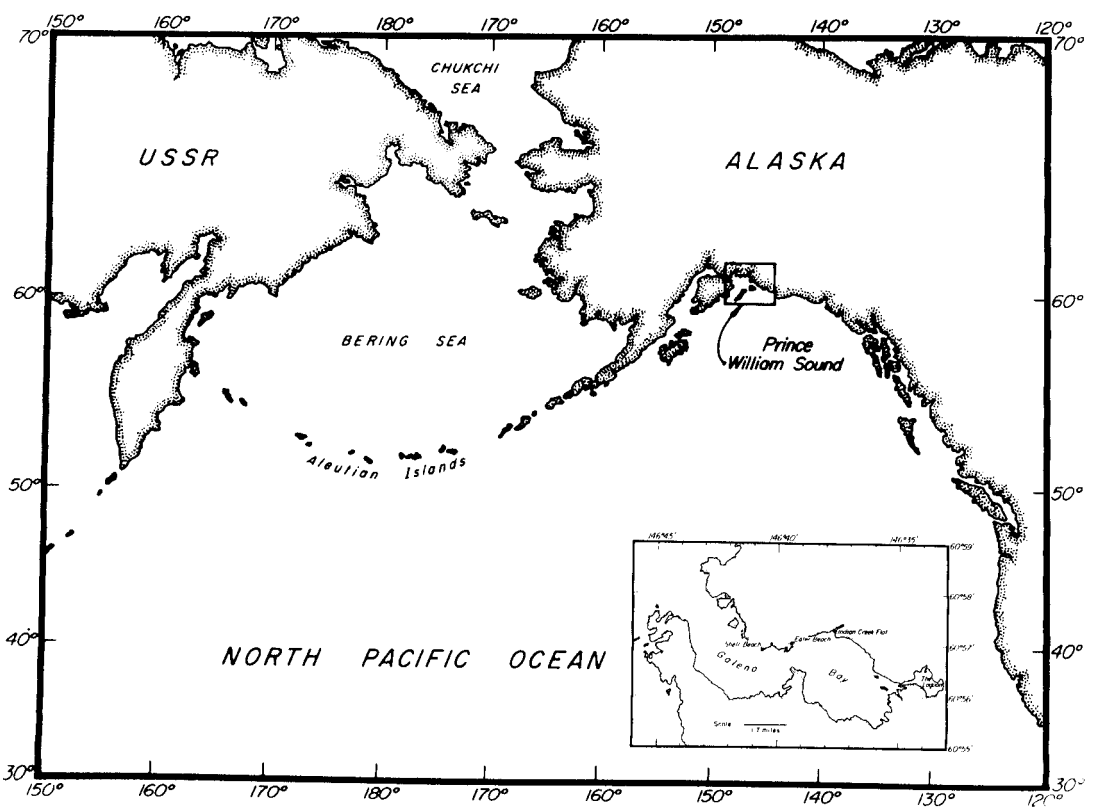

FIGURE 1.—Galena Bay, Prince William Sound, Alaska. The study area for the investigation.

TABLE 1.—A description of the three study areas in Galena Bay, Prince William Sound. Description of the beach and its biota refers to appearance at low water.

Item	Shell Beach	Eater Beach	Indian Creek Flat
Wave and wind exposure	Most exposed	Well protected	Protected but exposed to occasional rain squalls
Longshore currents	Obvious	Not obvious	Not obvious
Study area:			
Size (feet)	190 × 70	220 × 100	900 × 900
(m)	57.6 × 21.2	66.7 × 30.3	272.7 × 272.7
Slope	6°47′	6°3′	0°21′
Substratum	Fine gravel for first few centimeters overlying fine sediment	Fine gravel intermingled with large rocks scattered over beach; fine sediment closer to surface than on Shell Beach	Mixture of gravel and fine sediment
Freshwater drainage	Minimal	Typically minimal; strong outwash after persistent rains dissects center of beach	Located at mouth of permanent stream; flat; dissected by numerous tributaries
Flora and fauna	No *Fucus*; no *Mytilus edulis*; *Balanus* spp. very sparse	Light cover of *Fucus*; moderate cover of *M. edulis*; *Balanus* cover over entire beach	Light cover of *Fucus* at upper edge; moderate cover of *M. edulis*; moderate cover of *Balanus*.

from each transect were made from a series of stations, with each station defined by a 0.25-m² (115 × 22 cm) frame. The sediment within each station was sampled to a depth of 15 cm. The first collection made along a transect (Station 1) was positioned 1 m up the beach from the location of the first *P. staminea* encountered in a preliminary trench dug directly adjacent to the proposed sampling transect. The number of stations on a transect was dependent on the width and slope of the beach and the tidal range at the time of collection. On the two gravel beaches all stations sampled were contiguous; however, on the mud flat, a much larger area was involved, and collections here were made at 5.75-m intervals.

Utilizing reference points from a standard tide table (U.S. Coast and Geodetic Survey, 1970), a hand level, and a stadia rod, the tidal heights were determined for the midpoint of each station.

Prior to sampling, distribution of *P. staminea* was determined by removing sediment in 2-cm layers to a depth of 8 cm from selected plots (36 × 15 cm) along each transect. Samples collected were examined in the laboratory under a 2× lens for the presence of *P. staminea*, and sediments from these samples were then used for sieve analysis of grain-size distribution (Morgans, 1956).

Vertical distribution studies indicated that most of the smaller *P. staminea* (1.5 to 20 mm in length) were restricted to the upper 2 cm of sediment; thus, sampling was accomplished in two steps at each transect station. The young clams were collected with the upper 2 cm of sediment; the larger clams were collected with the remaining sediment.

Each surface sample was washed through a series of screens, the smallest mesh being 1.5- × 1.5-mm window screening. Screens of 3.5- and 6.5-mm² mesh were used for washing deep samples. Seawater used for the washing process was furnished by a portable Homelite Pump (Model XL5).[2] The sediment trapped in the finest screen was returned to the laboratory and examined for small individuals with a 2× lens.

Standard measurements taken on all clams were greatest length and height (width) (see Fraser and Smith, 1928 for details on measurement technique). In an older *P. staminea* an increase in shell height is often apparent when the increase in shell length is so small that it is difficult to measure. Therefore, shell height is the most sensitive measurement for describing

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

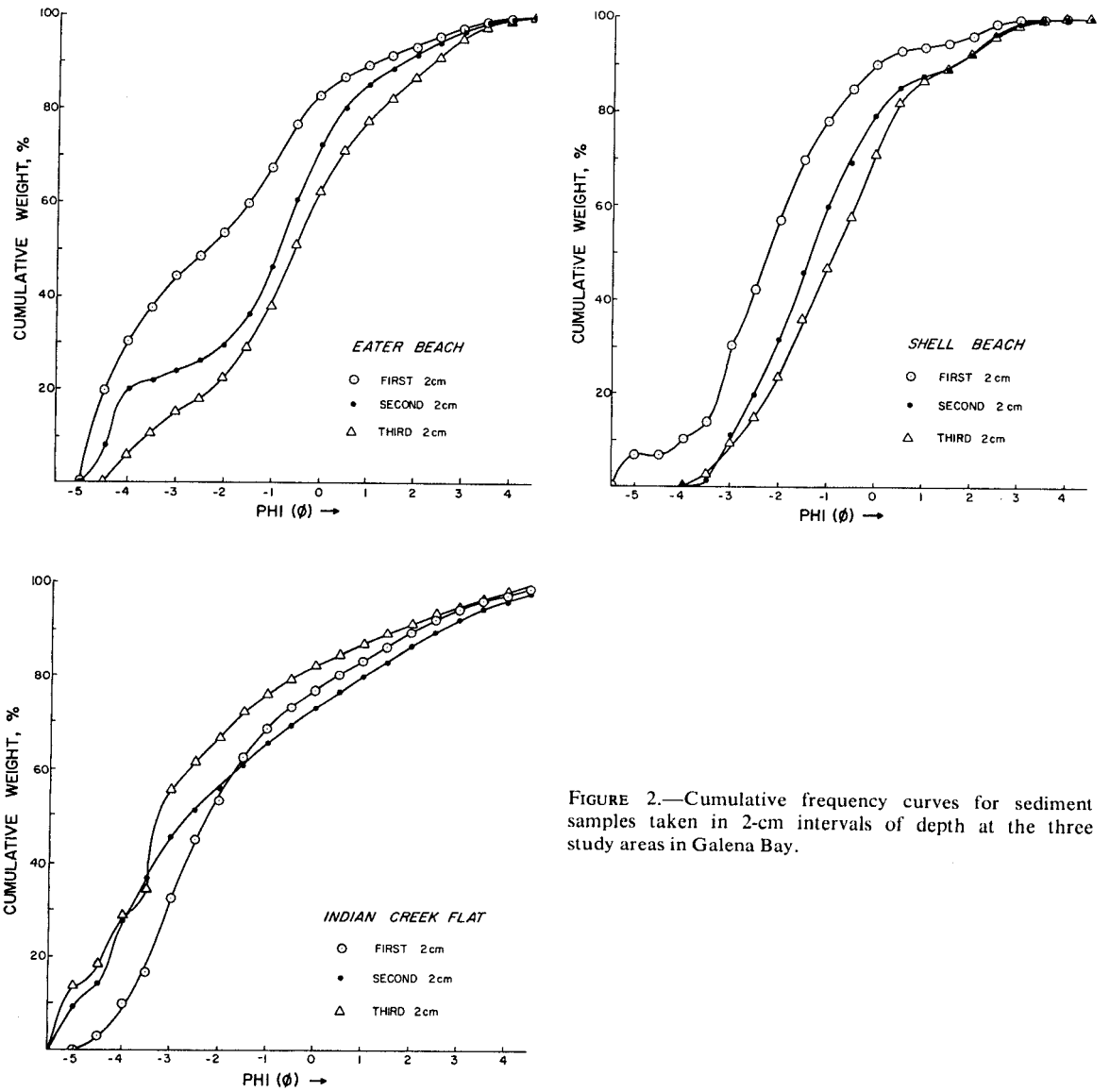

FIGURE 2.—Cumulative frequency curves for sediment samples taken in 2-cm intervals of depth at the three study areas in Galena Bay.

the growth of these clams. In this paper length data is included for comparative purposes.

Age was estimated for all clams less than 20 mm in length utilizing the annular method (Weymouth, 1923). All the larger clams from Shell Beach, one station on Eater Beach, and one station on Indian Creek Flat were also aged. In the aging procedure the distance between annuli[3] was measured along the radial sculpture line that originated at the approximate center of the umbonal region and roughly bisected the ventral margin of the shell (Figure 3).

BIOMED programs BMDOID, BMDO5D, and BMDO1V were adapted for this investigation (Dixon, 1965), and data were processed

[3] Annulus-A series of closely spaced concentric growth rings; the result of slow growth at low winter temperatures.

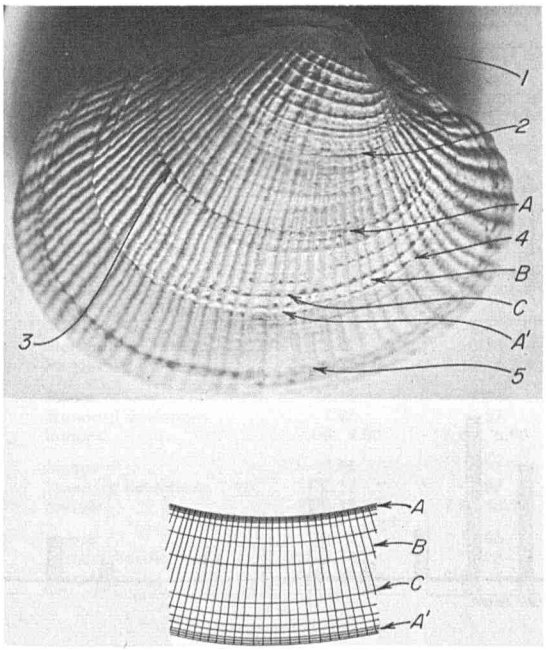

FIGURE 3.—The use of shell sculpture as a means of aging *Protothaca staminea*. Above: Photograph of a 5-yr-old *P. staminea* illustrating shell sculpture. Below: Graphic illustration of the shell sculpture between two annuli A = annulus (winter growth). B = radial sculpture line. C = concentric growth line. A′ = annulus. A to C = increasing distances between concentric growth lines C to A′ = decreasing distances between concentric growth lines during late summer and fall growth. 1, 2, 3, 4, and 5 = successive annuli. Clam length = 11 mm.

with an IBM 360 Computer. Several additional programs were designed to arrange and plot the data. A one-way analysis of variance was used to test the accuracy of the annular aging technique.

RESULTS

Aging

Annuli on valves less than 20 mm in length were quite distinct. False checks[4] which superficially resemble annuli (see first section under Discussion for comments), although present, could be readily distinguished from true annuli. Although false checks and shell abrasion made aging more difficult for clams greater than 20 mm in length, specimens from all three study sites were aged. The oldest clam collected in Galena Bay was 15 yr old with a length of 47.6 mm.

The validity of the annular aging method was examined with a standard one-way analysis of variance, utilizing the individual shell heights within each age class from Shell Beach as a basis for comparison (Snedecor, 1956). The calculated F ratio indicates that, in general, age classes, as defined by shell heights, are statistically distinguishable ($P = 0.01$; $N = 368$). Similar data plotted for Eater Beach further indicate the integrity of the aging method used (Figure 4). In addition, annuli for 3 yr of growth have been validated by the recovery and subsequent examination of over 100 marked *P. staminea* from Galena Bay (Feder and Paul, unpubl. data).

Histograms plotting size and age indicate that age classes form fairly distinct but overlapping groups (Figure 5).

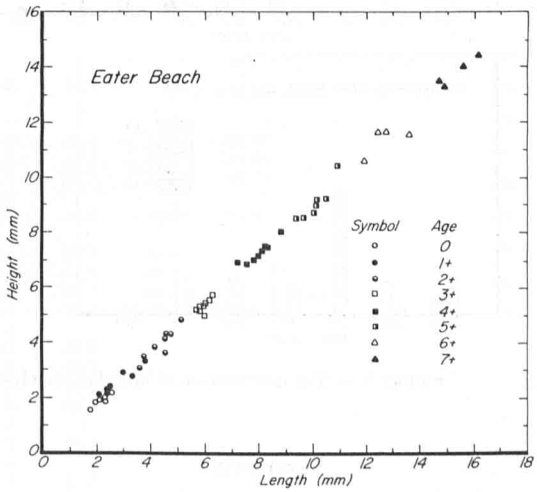

FIGURE 4.—Average length and height plotted as a function of age for specimens collected on the Eater Beach transect, Galena Bay. Each point represents a mean value for specimens of a given age group collected at a single station.

[4] False checks are series of concentric growth rings, resembling annuli, formed in spring and summer when growth is normally most active. These checks are also termed disturbance checks.

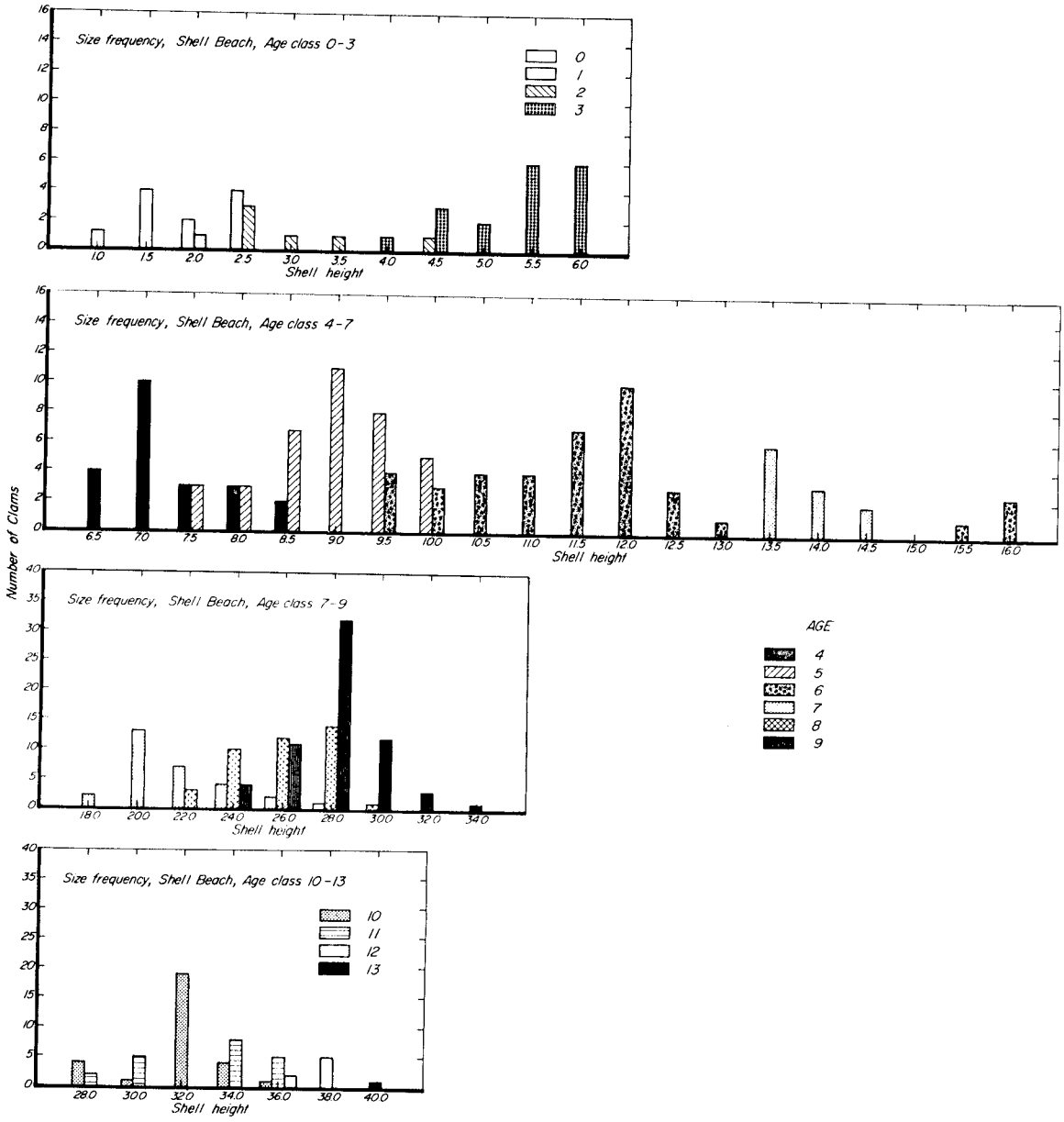

FIGURE 5.—Size distribution of annular age classes of *Protothaca staminea* from Shell Beach, Galena Bay.

Growth

The littleneck clams in Galena Bay (Table 2) at a given age are smaller than those collected by Fraser and Smith (1928) in British Columbia (Table 3). The annual increase in shell length for the various size classes in Galena Bay is typically 2 to 5 mm. As a result, 8 to 9 yr are needed for *P. staminea* to reach a length of 30 mm, the minimum size generally harvested in the sport fishery in Prince William Sound (J. Van Hyning, Wildlife Department, Univer-

TABLE 2.—Average size at age of littleneck clams from Shell Beach (N = 368).

Age (yr)	Item	Length (mm)	Height (mm)	Age (yr)	Item	Length (mm)	Height (mm)
0	Means	2.06	1.84	7	Means	21.56	18.63
	Standard deviations	0.37	0.28		Standard deviations	5.04	3.99
	Ranges	1.60- 2.60	1.50- 2.30		Ranges	14.50-37.20	12.50-32.60
1	Means	2.88	2.68	8	Means	28.84	25.70
	Standard deviations	0.40	0.33		Standard deviations	4.52	4.07
	Ranges	2.20- 3.20	2.10- 2.90		Ranges	15.00-36.00	12.90-30.90
2	Means	3.78	3.35	9	Means	32.68	29.06
	Standard deviations	0.90	0.70		Standard deviations	1.99	1.96
	Ranges	2.90- 5.10	2.70- 4.60		Ranges	27.80-38.50	24.50-34.30
3	Means	6.53	5.63	10	Means	36.44	32.59
	Standard deviations	1.59	0.73		Standard deviations	1.89	1.83
	Ranges	4.40- 7.30	4.10- 6.50		Ranges	32.00-39.70	28.90-37.90
4	Means	8.10	7.54	11	Means	37.19	34.74
	Standard deviations	1.97	0.63		Standard deviations	8.09	2.25
	Ranges	7.00- 9.80	6.60- 8.90		Ranges	33.00-46.00	29.30-37.30
5	Means	10.95	9.71	12	Means	42.08	37.68
	Standard deviations	2.13	1.87		Standard deviations	2.52	1.69
	Ranges	9.00-18.90	7.60-16.30		Ranges	37.80-45.50	34.50-39.90
6	Means	14.70	12.86				
	Standard deviations	3.74	3.26				
	Ranges	19.90-29.30	9.60-26.00				

TABLE 3.—Length in millimeters at end of each year for clams collected in Victoria, British Columbia (based on Fraser and Smith, 1928).

Year									
1	2	3	4	5	6	7	8	9	10
12.6	25.4	35.3	43.1	48.2	52.7	54.6	55.9		
12.9	23.2	33.4	39.9	44.3	46.3	49.4	52.3	53.8	
13.0	25.7	37.0	44.0	48.0					
13.9	25.7	27.5	43.6	48.7	54.1				
13.9	28.2	38.6	48.3						
—	—	—	—						
15.7	27.4	37.2	44.2	49.0	52.8	55.8			
13.2	24.8	35.3	42.9						
11.8	30.0								
13.5	25.8	34.9	41.4	46.3	50.0	52.6	55.8	58.9	
12.6	23.6	30.6	36.2	40.9	44.2	47.4	48.7	49.9	
12.2	22.9	33.5	41.7	47.7	51.8	55.7	57.8	59.1	
13.4	25.9	35.7	42.9	48.5	52.5				
14.0	24.5	33.6	38.7	43.2	45.9	48.0	49.5	51.3	53.8
25.4	34.2	39.3	43.2	47.1					
13.4	25.2	32.5	38.8	43.6	46.1	50.3	52.6		
12.2	24.5	35.1	42.8	48.9	54.1	57.8	60.7		
13.1	26.3	37.0	45.6	50.6	54.6	57.7	60.3	62.2	63.4
12.4	23.0	31.6	38.3	42.9	46.4	49.0	50.1	53.6	
11.2	25.4	35.4	44.4	51.1	54.3				
11.3	22.1	31.3	37.3	42.1	45.8	48.8			
11.2	22.0	31.3	38.6	43.6	46.8	49.9	51.1		
12.7	27.4	36.0	42.4	47.2	50.0	52.0			
14.8	28.4	36.6	42.9	47.8	52.0	54.5			
13.3	26.9	37.2	44.1	47.5	49.7				
13.1	29.5	40.2	47.3	52.0	57.3	59.5			
13.4	24.7	33.7	40.0	44.7	48.4				
11.1	26.5	36.0	43.4	49.4	52.9	55.7			
13.6	28.4	38.6	45.8	50.9	54.2	57.3	58.7		
14.6	30.8	41.5	48.8	54.1	57.0	59.9			
17.0	32.7	44.4	50.6	54.9					
12.5	22.9	32.6	40.0	45.2	49.3	57.0			

sity of Alaska, pers. comm.; Feder and Paul, 1973).

A comparison of growth rates in the three study areas indicates that differences in length at age are less than 2 mm by the end of the sixth year (Figure 6). In older clams the difference in growth rates between individuals from the three study sites is more pronounced. The annual increase in size for individuals 6 to 12 yr of age was generally greatest on Shell Beach, and by age 12 specimens from this beach were, on the average, 12 mm longer than those from Eater Beach and 9.5 mm longer than specimens from the Indian Creek Mudflat.

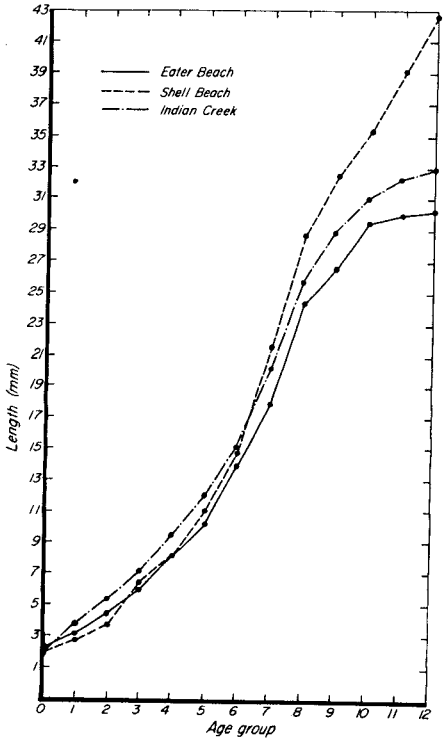

FIGURE 6.—Cumulative growth in shell length for clams from Shell (N = 368) and Eater Beaches (N = 554) and Indian Creek Flat (N = 642). Plotted points represent mean values.

Recruitment and Distribution

The number of recruits surviving in a littleneck clam population varies considerably from year to year. This is indicated in Figures 7 and 8 where the number of clams surviving as a function of year of settlement are plotted. On the beaches examined, individuals of the 1966, 1967, and 1968 year classes are more abundant than those of the 1970 or 1971 year classes, even after surviving 3 to 5 yr of natural mortality. It is also evident that the 1964 year class, which represented the newest recruits to the sport fishery in 1971, was not very abundant.

The total number of young littleneck clams found on the Eater Beach transect (352 clams on a 12-station transect) as compared with the number found on the Indian Creek transect (528 clams on a 10-station transect) indicates

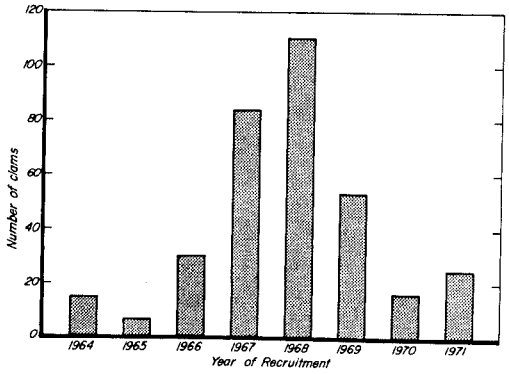

FIGURE 7.—Abundance of clams 0 to 7 yr of age on a 12-station transect from Eater Beach, Galena Bay.

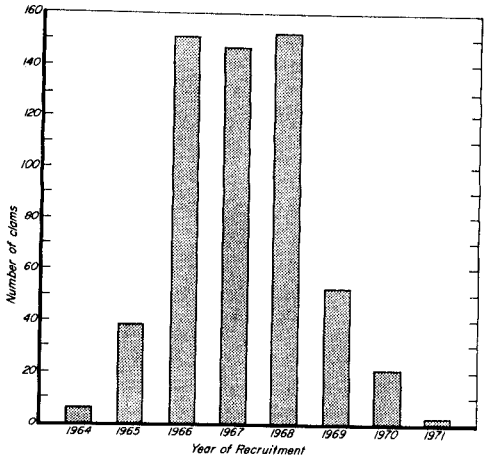

FIGURE 8.—Abundance of clams 0 to 7 yr of age on a 10-station transect from Indian Creek Flat, Galena Bay.

a greater density of young littleneck clams per unit area on the latter site. On the other hand, a comparison of the average number of older *P. staminea* per 0.25-m² station along these same transects reveals 55 littleneck clams per station on Eater Beach and 25 per station on the mud flat.

The intertidal distribution of *P. staminea* is influenced by tidal height; Figure 9 provides a general picture of the intertidal distribution of two size groups of *P. staminea* in Galena Bay. The distribution and frequency of age classes 0[5] through 6 for different tidal heights along one transect on Eater Beach are shown in Figure 10.

The intertidal distribution of *P. staminea* in Galena Bay in 1971 was similar to that reported for pre-earthquake Kodiak Island (Nybakken, 1969) and pre-earthquake Olsen

[5] The term 0 age group refers to those individuals of the settling year class that have undergone only one growing season (5 to 6 mo) before forming their first winter annulus. Thus, individuals referred to as 1 yr of age are actually 17 or 18 mo old and have lived through two growing seasons.

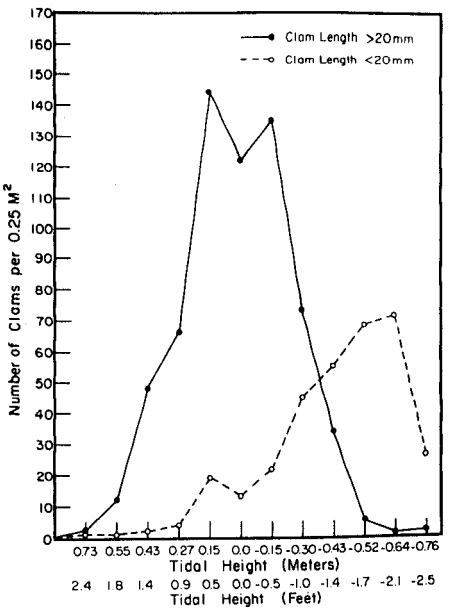

FIGURE 9.—An example of the typical intertidal distribution of *Protothaca staminea* as observed in Galena Bay. Data plotted here is from Eater Beach. Clams less than 20 mm in length are primarily ages 0-7; those larger than 20 mm in length are mainly ages 8-12.

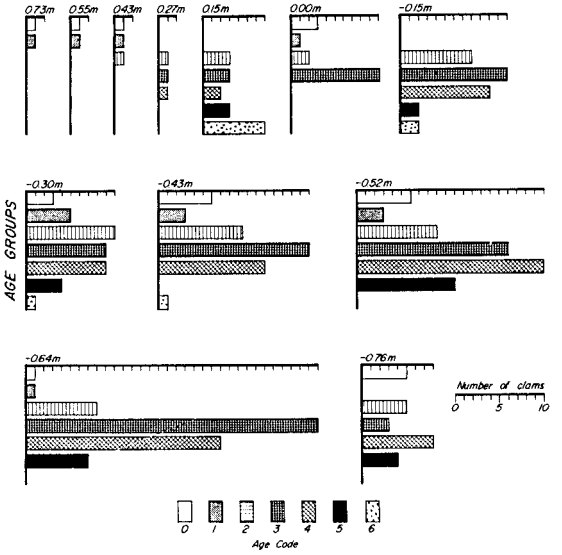

FIGURE 10.—The horizontal distribution of *Protothaca staminea*, age groups 0-6, grouped according to tidal height. Specimens were collected on Eater Beach, Galena Bay. Numbers above each plot refer to tidal height.

Bay (Hubbard, 1971), with the upper and lower extremes of this distribution occurring between the tidal heights of + 0.73 and -0.76 m, respectively. On the three study beaches the maximum density for clams larger than 20 mm in length, primarily individuals 8 to 12 yr of age, occurred between the tidal heights of +0.43 and -0.43 m, while the greatest density for smaller individuals occurred between -0.43 and -0.64 m (Figure 9).

The maximum depth in the sediment at which *P. staminea* was observed in Galena Bay was 8 cm. Clams of ages 0 through 7 consistently occurred in the upper 2 cm with most individuals of all age groups within 4 cm of the surface. Clams as large as 10 mm in length were often clearly visible between or just under small rocks. There was no apparent difference in vertical distribution of *P. staminea* on the gravel beaches or the mud flat.

DISCUSSION

Aging

Aging by the annular method is a time-consuming process best accomplished with a

dissection microscope. The patterns created by the radial sculpture and the concentric growth lines of the valves are invaluable aids for aging *P. staminea* by the annular method (Figure 3).

During the winter increase in shell size is negligible, and growth at the shell margin consists of a series of closely spaced concentric lines which form a winter annulus. Spring growth results in a progressively increasing distance between these lines; as summer progresses the distance between these lines gradually decreases until a new annulus is formed the following winter. True annuli extend from near the umbo anteriorly and merge with the hinge structure posteriorly. False checks may also appear as an aggregation of fine concentric lines; however, such checks generally fail to merge dorsally, and do not fit within the pattern of gradually increasing and decreasing distances between the concentric growth lines mentioned above.

Size-frequency distribution histograms cannot be used to accurately age *P. staminea* from Galena Bay (Figure 5). The individual differences in yearly growth within age groups, even when taken from a single 0.25-m^2 plot, result in a considerable overlap in size distribution. As a result, an aging error of 1 or 2 yr may occur if a clam were assigned an age based on size alone. Fraser and Smith (1928) found a similar disparity in the range of sizes within annular age groups for *P. staminea* from British Columbia, and Quayle (1952) reports that length-frequency distributions could not be used to determine age groups for *Venerupis pullastra* in Scotland.

Growth

Our study indicates that *P. staminea* grows much more slowly in Galena Bay, Prince William Sound, than in British Columbia (Fraser and Smith, 1928). The average length for *P. staminea* at the end of its first year in Galena Bay is approximately 2 mm (Table 2, Figure 6) while in British Columbia it is approximately 12 mm (Table 3). Slow growth in Alaskan waters is probably the result of severe winter conditions which reduces clam-feeding activities at this time. The adverse effect of low-water temperatures on growth rate has been reported for a number of bivalve molluscs including *Pinctada martensii* (Kobayashi and Watabe, 1959), *Crassostrea virginica* (Loosanoff, 1958), *Mytilus edulis* and *Mercenaria mercenaria* (Pratt and Campbell, 1956).

Both Fraser and Smith (1928) and Smith (1928), working in Canadian waters, observed that the most favorable growth occurred on beaches near strong tidal currents while poor growth took place on beaches at the heads of quiet bays. An examination of older specimens of *P. staminea* from Galena Bay supports this observation (Feder, unpubl. data). The cumulative growth curve (shell length) for littleneck clams from Shell Beach is nearly a linear expression (Figure 6). This beach, the most exposed study site, is subject to strong tidal currents (Table 1). On the other hand, cumulative growth plots for Eater Beach and Indian Creek Flat, protected locations with little current or wave action, provide more standard growth curves which become asymptotic at about age 10 (Figure 6).

Recruitment and Distribution

The differences in year-class strength of *P. staminea* noted in Galena Bay (Figures 7, 8) have also been observed for other bivalve species, e.g., *Saxidomus giganteus* (Fraser and Smith, 1928), *Cardium edule* (Hancock, 1970), and *Venerupes pullastra* (Quayle, 1952). There are a number of interrelated factors affecting larval production in bivalve molluscs, but in general the most important ones appear to be the number and physical condition of mature females and the temperature requirements necessary for the liberation of the larvae (Hancock, 1970). Survival of larvae in the plankton and successful settlement are also affected by several environmental conditions, especially temperature, adequate food supply, predation, and favorable conditions for settlement (Thorson, 1966, 1971; Christensen, 1970; Hancock, 1970). Data on most of these conditions are not available for *P. staminea* in Prince William Sound.

Hancock (1970) working in England noted

that the number of 0-age group cockles (*C. edule*) appeared to be poorly correlated with abundance of spawning stock. He also observed that poor to moderate settlements followed years of good to exceptional recruitment. If larval production and settlement of *P. staminea* is affected by year-class densities in a similar manner, it is possible that the strong year classes of 1966, 1967, and 1968 are responsible for the moderate to poor recruitment observed in Galena Bay during the following years (Figures 7, 8).

P. staminea does not move horizontally (Feder and Paul, unpubl. data); therefore, the only source of recruitment of this species to an area is the annual settlement of veligers. Thus, the large number of clams 20 mm in length and longer that are found between the tidal heights of +0.43 and -0.43 m must be the result of relatively good survival of these larvae (Figure 9).

Very few littleneck clams were located above the tidal height of +0.43 m (Figure 9); the number of clams observed is probably the result of environmental stresses which act on young clams at the upper, more frequently exposed portions of a beach. The 2-foot uplift of land in Galena Bay following the Alaska Earthquake in March 1964 (National Research Council, 1971) may have affected settlement and/or survival of clams at the upper limits of their intertidal distribution during that year (Figures 7, 8). The time of the year for settlement of *P. staminea* veligers in Prince William Sound is not known.

Strong tidal currents may affect the numbers of settling veligers in the intertidal zone (Fraser and Smith, 1928). On Shell Beach, the study site with the strongest currents (Table 1), the number of clams under 5 yr of age (seven clams per 0.25 m^2) was consistently lower than that found on the Indian Creek Mudflat (23 clams per 0.25 m^2) where the shore was relatively undisturbed by wave action and currents.

On most beaches and flats of Prince William Sound, there are many temporary and permanent streams fed by rain, melting snow, and glacial ice. *P. staminea* is rarely encountered in areas where permanent freshwater streams flow over or percolate through beach sediments at low tide (Feder and Paul, unpubl. data). Mortality resulting from rainfall on exposed beaches is negligible; however, heavy rainfall affects distribution of *P. staminea* by altering beach topography. Freshwater runoff after a period of prolonged rainfall is often responsible for the active transport of beach sediments; in such areas clams are washed away with these sediments (Feder and Paul, unpubl. data).

Throughout its range *P. staminea* is found within 15 cm of the sediment surface and occasionally at the surface (Amos, 1966). In areas of Prince William Sound examined by us, clams 0 through 4 yr of age are essentially epifaunal in their distribution while older individuals are subsurface dwellers. Siphon length is almost certainly the limiting factor in determining the depth at which various sizes of clams occur. Sieve analysis of sediment from Eater and Shell Beaches shows that coarse gravel at the beach surface covers medium gravel and finer sediment (Figure 2). The geology of such gravel beaches affords young *P. staminea* protection from predation, exposure, and ice scouring by providing spaces between the gravels in which the clams can lodge themselves. These spaces, filled with water at high tide, provide a haven for young clams. Here they can remain and feed below the level of the beach surface at a depth greater than their siphon length. On the Indian Creek Flat, sediment fills the intergravel spaces (Figure 2), thereby forcing young *P. staminea* to remain closer to the surface for longer periods of time than if they had settled on a gravel beach. Clams on mud flats such as Indian Creek are then more vulnerable when young, and this may, in part, explain better survival of clams on gravel beaches.

In Galena Bay few individuals that settle between the tidal heights of -0.43 and -0.76 m survive beyond their fourth year, despite the fact that it is here that the heaviest concentrations of young clams occur (Figure 10). This distribution may be the result of selective settlement by veliger larvae (Thorson, 1957, 1966), hydrographic concentrations of larvae in the plankton at time of settlement (see Ryther, 1968 for discussion), or some form of selective mortality such as predation (see

Newcombe, 1935; Paine, 1969, 1971; Feder, 1970; Birkeland and Chia, 1971 for discussion).

SUMMARY AND GENERAL COMMENTS

The results of this paper provide information on growth rates of *P. staminea* in northeastern Prince William Sound, Alaska. Growth rates for this species in Galena Bay are considerably less than those reported for British Columbia (Fraser and Smith, 1928). *P. staminea* in Galena Bay reach a harvestable size (length = 30 mm) in 8 to 9 yr.

Examination of recruitment and distribution on three beaches studied suggests that the number of recruits entering and/or surviving recruitment on an annual basis in Prince William Sound is extremely variable. On each of the beaches examined, recruitment was at its maximum between the tidal heights of -0.43 and -0.64 m while survival was best between the tidal heights of +0.43 and -0.43 m. The majority of *P. staminea* were found within 4 cm of the sediment surface.

Based on the large number of beaches in Prince William Sound having populations of littleneck clams, this species undoubtedly represents a potential, although probably limited fishery resource in Prince William Sound (R. Nickerson, pers. comm.; Feder and Paul, 1973). Since the variable recruitment and slow growth rates observed for Galena Bay appear to apply throughout Prince William Sound (Feder and Paul, unpubl. data), such a fishery would probably require that beaches be harvested on an 8- to 10-yr rotational basis.

The large port facility proposed for Valdez to receive crude oil from Prudhoe Bay, Alaska will undoubtedly result in some degree of oil contamination as a result of accidental spillages, ballast treatment, and shipboard operations (Arthur, 1968; Dudley, 1968; Nelson-Smith, 1970; Blumer, 1971; U.S. Department of the Interior, 1972:64). Therefore, beyond its potential as a commercially harvestable species, *P. staminea* may have additional value as an indicator of environmental change since this clam is the only intertidal invertebrate whose natural history has been examined in detail in Prince William Sound.

ACKNOWLEDGMENTS

We would like to thank R. T. Cooney (University of Alaska) for valuable advice; Rosemary Hobson (Institute of Marine Science, University of Alaska) for invaluable advice on computer programming techniques; Shirley Wilson (Institute of Marine Science, University of Alaska) for drafting all the figures; Richard B. Nickerson (Alaska Department of Fish and Game) for discussions and for use of an Alaska Department of Fish and Game boat; Carol Anderson, George Perkins, David Roseneau, and Frederick Smith for technical assistance.

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SURVIVAL, MATURITY, ABUNDANCE, AND MARINE DISTRIBUTION OF 1965-66 BROOD COHO SALMON, *ONCORHYNCHUS KISUTCH*, FROM COLUMBIA RIVER HATCHERIES

ROBERT H. LANDER AND KENNETH A. HENRY[1]

ABSTRACT

Data are presented estimating the survival, maturity, and abundance of marked coho salmon, *Oncorhynchus kisutch*, of the 1965-66 broods from 18 to 20 Columbia River hatcheries. Also presented are data depicting the distribution of these fish as caught in the northeastern Pacific Ocean. Compared to fish from hatcheries on the upper reaches of the river, coho salmon from hatcheries near the estuary had a better survival until recruitment to the ocean fishery, a greater proportion maturing as jacks (2-yr olds), and an apparent differential migration pattern in the ocean. For hatcheries from all river sections combined, the parameter estimates differed little between broods. Estimates for both broods are as follows: 9-10% surviving during the 6.0 mo between release of smolts and the return of young males or jacks to the Columbia River; 3-4% of survivors maturing as jacks; 10-12% surviving during the last 12.0 mo of ocean life; 5-6% of the original number of smolts surviving until the time of recruitment to ocean fishing 13.5 mo after release; and exploitation rates of 68-70% in the ocean fishery during the last 4.5 mo of life at sea.

A cooperative program was undertaken among the various Pacific coast fishery agencies in the United States and Canada to estimate the contribution to various fisheries of coho salmon, *Oncorhynchus kisutch*, produced by 20 Columbia River hatcheries. The hatcheries were placed into four groups according to their locations on the river (Figure 1). About 10% of the fish released from each of the hatcheries on each of the four river sections were identified with section-specific marks (certain fins or bones excised) for the 1965-66 brood years:

Group	*Location boundaries*	*Fins or bones excised*
Lower River	Mouth of Columbia River to mouth of Cowlitz River	Adipose-right maxillary (Ad-RM)
Middle River	Mouth of Cowlitz River to Bonneville Dam	Adipose (Ad)
Upper River	Bonneville Dam to The Dalles Dam	Adipose-left maxillary (Ad-LM)
Uppermost River	Above The Dalles Dam	Dorsal-adipose (D-Ad) Dorsal-adipose-left maxillary (D-Ad-LM) Dorsal-adipose-right maxillary (D-Ad-RM)

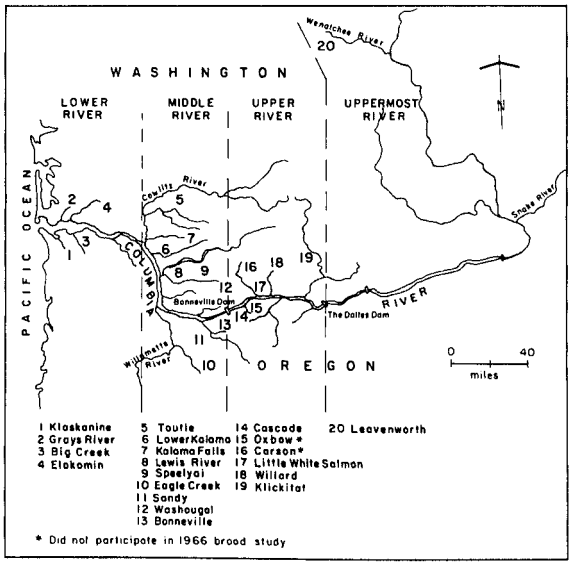

FIGURE 1.—Grouping of Columbia River hatcheries by release area and marks applied to evaluate the contribution of 1965-66 brood coho salmon.

Such studies are needed to determine the economic justification for the large scale hatchery program that has been developed for the

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Manuscript accepted January 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

Columbia River to supplement natural spawning and to compensate for loss of and damage to natural spawning areas by construction of dams.

A brief resume of the life history of these coho salmon may be helpful. Most of the salmon used in these studies were released as small fish during April and May, approximately 1 yr after hatching in the hatcheries. About 10% of them were marked just before release. The young salmon then migrated to the ocean. After a few months in the ocean a relatively small portion of the fish—mainly 2-yr-old males called jacks—matured and returned to their hatcheries in the Columbia River. At that time, a few were captured in the Columbia River sport and commercial fisheries. Most of the fish, however, remained in the ocean over the winter. During the following summer, many were captured in the ocean commercial troll and sport fisheries. During late August through October, all the remaining fish (3-yr olds) from each brood then began to mature and reenter the Columbia River, where some were captured in the commercial gill net and sport fisheries. Those escaping these fisheries returned in the late fall to their hatchery streams, where their eggs were taken artificially for rearing in the hatchery. Coho salmon, like all Pacific salmon, die after spawning and the cycle is then complete.

In a report by Wahle, Vreeland, and Lander,[2] the economic contributions of all hatcheries combined have been analyzed for these two broods of fish. These benefit/cost calculations rely mainly on release and recovery data. Such biological parameters as fishing and natural mortality, age at maturity, abundance, and time/area distribution were not considered. These are important in developing a proper management plan for these fish, so we have developed estimates of them for these two brood years. These will be timely supplements to the benefit/cost analysis of Wahle et al. (See footnote 2.)

The estimates of survival, maturity, and abundance in the present report mainly are average values for all hatcheries combined. Limitations in the basic data reduce the reliability of separate evaluations for hatcheries on each of the four sections of the Columbia River, particularly for the 1966-brood data. The distribution of hatchery fish in marine fisheries is compared between the four river sections for each brood.

PROBLEMS OF ESTIMATING PARAMETERS

To aid in understanding the various parameters we wish to estimate, in Figure 2 we have portrayed graphically certain features of the coho salmon's life history, particularly as they pertain to the various parameters for the period from release as smolts until their return to the Columbia River as adults—approximately 18 mo. The time sequence shown in Figure 2 is accurate to approximately 0.5 mo. It readily can be seen from Figure 2 that there are four known values: 1) number of smolts released (N_0), 2) number maturing as jacks (E_1), 3) number caught by the ocean troll and sport fisheries (C), and 4) number returning as adults (E_2). From these four known values we wish to estimate: 1) fishing mortality rate over the last 4.5-mo period (F), 2) proportion maturing as jacks (m), 3) natural mortality rate for the 6.0-mo period from release of smolts until the jacks mature (M_1), 4) natural mortality rate for the 12.0-mo period from the time jacks mature until the adults return to the Columbia River (M_2), 5) number of coho remaining at sea when the jacks have returned (N_1), and 6) number of coho

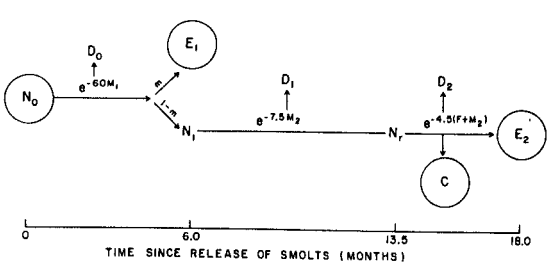

FIGURE 2.—Diagram depicting the life history of the coho salmon for the period from release of smolts until their return to the Columbia River as adults—approximately 18 mo (circled items indicate observed data).

[2] Wahle, R. J., R. R. Vreeland, and R. H. Lander. Bioeconomic contribution of 1965-66 brood coho salmon from Columbia River hatcheries. Columbia Fish. Program Off., Natl. Mar. Fish. Serv., NOAA, Portland, Oreg., and Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash. [Unpubl. manuscr.]

available at the start of the commercial troll fishery (N_r). The D_i represent the number of fish dying naturally.

The known data for the two brood years are listed in Tables 1 and 2. The catch data shown are estimated numbers based on sampling (see footnote 2). Each escapement value is the sum of the river catch and returns to the hatchery for a given mark. In making our computations we have made some additional assumptions: 1) the data in Tables 1 and 2 are accurate, 2) adipose only marks (Ad) were not regenerated, 3) all recoveries of fish with appropriate marks were hatchery fish, and 4) all pertinent hatchery marks in catch samples and hatchery returns were detected and reported.

The events in Figure 2 can be depicted by a multinominal model with the N_0 smolts falling

TABLE 1.—Estimated total recapture of 1965 brood marked Columbia River hatchery coho salmon, grouped by river section.

Year of life	Ocean catch (C)	River catch	Number spawning	River total (E)	Grand total
Lower River (Ad-RM) 508,294 released; 2.92% recovered					
2	—	155	1,568	1,723	1,723
3	10,435	841	1,864	2,705	13,140
Total	10,435	996	3,432	4,428	14,863
Middle River (Ad) 845,674 released; 9.83% recovered					
2	—	346	4,391	4,737	4,737
3	63,829	5,197	9,399	14,596	78,425
Total	63,829	5,543	13,790	19,333	83,162
Upper River (Ad-LM) 837,829 released; 1.41% recovered					
2	—	—	1,125	1,125	1,125
3	7,933	846	1,882	2,728	10,661
Total	7,933	846	3,007	3,853	11,786
Leavenworth Uppermost River (D-Ad) 101,734 released; 2.82% recovered					
2	—	7	38	45	45
3	2,448	238	138	376	2,824
Total	2,448	245	176	421	2,869

TABLE 2.—Estimated total recapture of 1966 brood marked Columbia River hatchery coho salmon, grouped by river section.

Year of life	Ocean catch (C)	River catch	Number spawning	River total (E)	Grand total
Lower River (Ad-RM) 385,630 released; 3.98% recovered					
2	—	88	2,067	2,155	2,155
3	9,802	1,639	1,771	3,410	13,212
Total	9,802	1,727	3,838	5,565	15,367
Middle River (Ad) 764,262 released; 9.30% recovered					
2	—	666	2,191	2,857	2,857
3	53,967	8,501	5,769	14,270	68,237
	53,967	9,167	7,960	17,127	71,094
Upper River (Ad-LM) 493,110 released; 2.43% recovered					
2	—	103	624	727	727
3	7,691	2,505	1,075	3,580	11,271
Total	7,691	2,608	1,699	4,307	11,998
Leavenworth (D-Ad) 174,735 released[1]; 1.07% recovered					
2	—	6	8	14	14
3	1,570	283	—	283	1,853
Total	1,570	289	8	297	1,867

[1] Includes 92,250 D-Ad-LM and 73,011 D-Ad-RM, and 9,474 D-Ad.

into the observed categories with certain probabilities θ_i ($i = 1 \cdot\cdot 4$) as follows:[3]

$$\text{Probability of } E_1 = \theta_1 = me^{-6M_1} . \quad (1)$$

$$\text{Probability of } C = \theta_2 = (1 - m)e^{-6M_1}e^{-7.5M_2}\left[\frac{F}{F + M_2}\right]\left[1 - e^{-4.5(F + M_2)}\right] . \quad (2)$$

$$\text{Probability of } E_2 = \theta_3 = (1 - m)e^{-6M_1}e^{-7.5M_2}e^{-4.5(F + M_2)} . \quad (3)$$

$$\text{Probability of } D = \theta_4 = 1 - \theta_1 - \theta_2 - \theta_3 , \text{ where } D = D_0 + D_1 + D_2 . \quad (4)$$

The maximum likelihood estimators of the θ_1 are:

$$\hat{\theta}_1 = E_1/N_0. \quad (5)$$

$$\hat{\theta}_2 = C/N_0. \quad (6)$$

$$\hat{\theta}_3 = E_2/N_0. \quad (7)$$

$$\hat{\theta}_4 = 1 - \hat{\theta}_1 - \hat{\theta}_2 - \hat{\theta}_3 . \quad (8)$$

A maximum likelihood estimator of a function of the parameters θ_i is obtained by replacing the parameter values by the corresponding maximum likelihood estimates, $\hat{\theta}_i$. Beyond that, however, there exists no unique transformation or function to obtain maximum likelihood estimates of M_1, m, M_2, and F: any given set of observed data can generate a variety of combinations of parameter estimates.

METHODS OF ESTIMATING PARAMETERS

Estimations Based on Selection of m or M_2

Since no unique solution exists, the only practical solution is to assume some values for one of the unknown parameters and solve the equations for the remaining parameters. This in effect is what Cleaver (1969) and Henry (1971) did for hatchery chinook salmon, *O. tshawytscha*, (with 3-4 spawning escapements from a given release group). In their calculations, however, they assumed various values for M_2 (natural mortality during the last year of life) and then calculated values for the remaining parameters. In applying this method to the 1965-66 brood coho salmon data, the appropriate equations, based on the time periods and notations shown in Figure 2, would be:

$$C/E_2 = \frac{F}{F + M_2}\left(e^{4.5F + 4.5M_2} - 1\right) \quad \text{solve for } F \quad (9)$$

$$N_r = E_2 e^{4.5M_2 + 4.5F} \quad \text{solve for } N_r \quad (10)$$

$$\frac{E_2}{E_1} = \frac{e^{-12M_2 - 4.5F}(1 - m)}{m} \quad \text{solve for } m. \quad (11)$$

The resulting values for these computations at six different levels of natural mortality for all hatcheries combined for each brood year are listed in Table 3. It is apparent from these data that the changes in natural mortality have a relatively greater effect on the proportion maturing as 2-yr-old fish (m), and on the number of recruits to the third year of life (N_1) and to the fishery (N_r), than on the fishing mortality (F).

As mentioned previously, it is difficult to analyze the data separately from the four sections of the river. For the 1966 brood two additional groups of marked fish were released —approximately 92,000 D-Ad-LM in the Middle River areas and about 73,000 D-Ad-RM in the Uppermost River area (see footnote 2). Obviously, any fin regeneration or fins missed in sampling from this group would confound data from the other marked groups, making a comparison of individual markings for the 1966 brood much more questionable. Nevertheless, in Table 4 are listed the parameter values for

[3] We are indebted to Jerome Pella who, as editorial referee, suggested that the relationships affecting the coho salmon be depicted in this manner and pointed out a relation between the proportion maturing as jacks (m) and the rates of natural mortality that we had not considered earlier. Pella's suggestions greatly improve the understanding and description of the actual situation.

TABLE 3.—Values of F, m, N_1, N_r, and N_r/N_0 at various levels of natural mortality for 1965-66 broods of marked Columbia River coho salmon (F is summed for 4.5 mo, data from all hatcheries combined).

$12M_2$	F	m	N_1	N_r	N_r/N_0
1965 brood:					
0.24	1.594	0.056	127,585	109,861	0.0479
.45	1.554	.048	151,378	114,247	.0498
.48	1.549	.047	155,055	114,917	.0501
.60	1.526	.043	171,020	117,532	.0512
.72	1.504	.039	188,629	120,261	.0524
.96	1.406	.032	229,472	125,966	.0549
1966 brood:					
.24	1.437	.048	115,244	99,175	.0546
.45	1.400	.040	137,010	103,413	.0569
.48	1.395	.039	140,478	104,020	.0572
.60	1.374	.036	155,097	106,579	.0586
.72	1.353	.033	171,237	109,151	.0600
.96	1.312	.027	208,941	114,639	.0631

TABLE 4.—Values of F, P, N_1, N_r, and N_r/N_0 for 1965-66 broods of marked coho salmon from various Columbia River locations (F is summed for 4.5 mo; M_2 = 0.06).

Area	F	m	N_1	N_r	N_r/N_0
1965 brood:					
Mouth to Cowlitz River (Lower)	1.449	0.068	23,667	15,091	0.0297
Cowlitz River to Bonneville (Middle)	1.545	.033	140,576	89,620	.1060
Bonneville to The Dalles (Upper)	1.243	.055	19,425	12,385	.0148
Above The Dalles (Uppermost)	1.865	.009	4,987	3,179	.0312
Combined	1.504	.039	188,629	120,261	.0524
1966 brood:					
Mouth to Cowlitz River (Lower)	1.235	.082	24,088	15,356	.0398
Cowlitz River to Bonneville (Middle)	1.434	.023	122,997	78,401	.1026
Bonneville to The Dalles (Upper)	1.040	.034	20,809	13,273	.0269
Above The Dalles (Uppermost)	1.733	.004	3,289	2,098	.0120
Combined	1.353	.033	171,237	109,151	.0600

hatcheries from these four sections as well as for the combined data for $12M_2$ = 0.72 for the 1965-66 brood years, respectively. The quite different results for the Middle River releases are believed due primarily to the maxillary and dorsal fins either regenerating or being overlooked in the sampling (see footnote 2). Ignoring the Middle River releases for the moment and assuming that the effect of fin regeneration or sampling equally affects the other marks, certain trends in the data are of interest. Thus, the estimated proportion maturing (m) at age 2 consistently decreases from the Lower River to the Uppermost River hatcheries for both brood years. In other words, these data suggest that at the end of their second year, a greater portion of the Lower River coho salmon matured as jacks, and the proportion maturing as jacks consistently decreased for coho salmon released farther and farther upriver.

Another statistic of interest in Table 4 is the estimated proportion of released fish that survived to enter the fishery (N_r/N_0). The results were not consistent for the two brood years in that the Uppermost releases showed the highest estimated recruitment to the fishery for the 1965 brood and lowest recruitment to the fishery for the 1966 brood. However, in com-

paring only the two groups of similarly marked fish (Ad-RM, Lower River; Ad-LM, Upper River) the Upper River marked fish had a lower estimated recruitment to the fishery for both brood years. Also, recruitment was higher for the 1966 brood from both these river sections. Few hatchery returns of the 1966 brood, Leavenworth (Uppermost) marked coho salmon, were obtained because of passage difficulties at John Day Dam due to construction of fish ladders and mortalities caused by trapping at Priest Rapids Dam. This factor undoubtedly contributed to the relatively low estimated recruitment for the 1966 brood from this area.

Instead of assuming a certain value for M_2 as we have done using the Cleaver model, as pointed out by Jerome Pella (see footnote 3), assuming a fixed value for the proportion maturing (m) permits unique solutions to Equations 1-4, combined with Equations 5-8, so that with:

$$m = m \text{ (fixed) } (\hat{\theta}_1 < m < 1). \tag{12}$$

$$M_1 = -\frac{1}{6} \ln\left(\frac{\hat{\theta}_1}{m}\right) \tag{13}$$

$$\left[\frac{\ln k_2 + 12M_2}{\ln k_2 + 7.5M_2}\right]\left[1 - e^{-(\ln k_2 + 7.5M_2)}\right]$$

$$e^{-7.5M_2} = k_1 \tag{14}$$

$$\text{where } k_1 = \left(\frac{\hat{\theta}_2}{1 - m}\right) e^{6M_1}$$

$$k_2 = \left(\frac{\hat{\theta}_3}{1 - m}\right) e^{6M_1}$$

$$F = -\left[\frac{\ln k_2 + 12M_2}{4.5}\right] \tag{15}$$

The derivations of Equations 12-15 are verified in the Appendix. For a particular value of m (Equation 12), one solves Equation 13 explicitly for M_1. Then using these values of m and M_1, M_2 in Equation 14 is found by iteration. Finally, one obtains the proper F from Equation 15.

Using Equations 12-15, we again calculated values for the various parameters for the 1965-66 broods, based on selected values of the proportion maturing (m). These values are listed in Table 5 and graphed in Figure 3. Only values of m that gave non-negative values of M_1, M_2, and F were used. Values of the average monthly rate during all 18.0 mo, Z_T, were calculated from the relation, $Z_T = (6.0M_1 + 12.0M_2 + 4.5F)/18.0$. Other rates of monthly mortality that can be calculated from these data are:

Average total mortality during last 12.0 mo of ocean life:

$$Z_2 = (12.0M_2 + 4.5F)/12.0.$$

Average natural mortality from time of smolt release until beginning of commercial troll fishing:

$$M_r = (6.0M_1 + 7.5M_2)/13.5.$$

Total mortality during last 4.5 mo of ocean life:

$$F + M_2.$$

Comparison of Two Methods

Before examining Figure 3 in detail, we would like to compare briefly these two possible approaches: 1) assuming selected values for M_2 (natural mortality during second year) and 2) assuming selected values for m (proportion maturing as jacks). First of all, it should be recognized that the values obtained by either method as used here (Cleaver applied an approximation formula noted before his Equation 20) are identical because Equation 9, used in the calculation for a given value of M_2, is simply $\frac{\text{Equation 2}}{\text{Equation 3}}$ used in calculations based on a fixed value of m. Furthermore, whenever a fixed value for either M_2 or m is selected, all the other unknown parameters are uniquely determined.

Although either of these approaches give identical results, their conceptual basis differs. In selecting a fixed value for M_2, one starts at the end of the life cycle and work backwards; by selecting m values, one more closely parallels the actual life history of the coho salmon. Furthermore, a wide range of selected values for

TABLE 5.—Calculated values of m (proportion maturing as jacks), M_1 (natural mortality rate during first 6 mo after release of smolts), M_2 (natural mortality rate during last 12 mo of ocean life), F (fishing mortality during last 4.5 mo of ocean life) and Z_T (average total mortality for 18 mo after release of smolts) for 1965-66 brood Columbia River hatchery coho salmon.

m	M_1	M_2	F	Z_T
1965 brood:				
0.0033	0.0	0.3101	0.2218	0.2622
.0050	.0679	.2697	.2384	.2620
.0100	.1834	.2003	.2685	.2618
.0106	.1939	.1939	.2713	.2617
.0200	.2990	.1295	.3008	.2612
.0300	.3665	.0874	.3209	.2606
.0400	.4145	.0570	.3357	.2601
.0500	.4517	.0331	.3475	.2595
.0600	.4821	.0133	.3574	.2589
.0677	.5022	.0	.3641	.2584
1966 brood:				
.0032	.0	.2935	.2023	.2462
.0050	.0762	.2487	.2197	.2461
.0096	.1844	.1844	.2459	.2459
.0100	.1917	.1800	.2477	.2458
.0200	.3073	.1100	.2780	.2453
.0300	.3748	.0684	.2968	.2447
.0400	.4228	.0383	.3106	.2441
.0500	.4600	.0147	.3218	.2435
.0573	.4828	.0	.3287	.2431

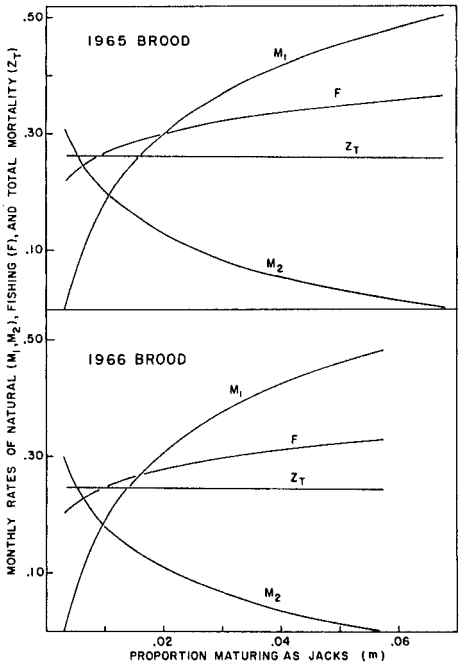

FIGURE 3.—Relations of monthly natural mortality (M_1, M_2), fishing mortality (F), and total mortality (Z_T) rates to the fraction maturing as jacks (m), for 1965-66 brood coho salmon from Columbia River hatcheries. For any particular value of m, the corresponding rates operated as follows: M_1-first 6.0 mo after release of smolts, M_2-last 12.0 mo of ocean life, F-last 4.5 mo of ocean life, and Z_T-all 18.0 mo from release of smolts to end of ocean life.

M_2 have a relatively lesser effect on the estimated values of m than the effect on M_2 by a corresponding range of selected values of m (Figure 3). For example, if the selected value of M_2 is increased four times, the estimated value of m is reduced by about one-half. On the other hand, if the selected values of m are increased four times the estimated value of M_2 is decreased to about one-fourth. Finally, the use of selected values of m (Equations 12-15) is based on a logical, probablistic, portrayal of the life history of the coho salmon whereas the use of selected values of M_2 is a more deterministic approach.

ANALYSIS OF 1965-66 BROOD DATA BASED ON SELECTION OF m

Let us return briefly to the estimates in Table 4. It might be argued that since m and M_2 are inversely related (this will be discussed in greater detail later), the declining estimates for m as one moves upriver are merely the result of using a fixed value for M_2 when in fact M_2 is different for the various sections of the river. To examine this possibility in greater detail, we assumed the proportion maturing as jacks (m) was the same for all river sections and again calculated the pertinent estimates of the parameters relating to these data. The results are listed in Table 6. In making these calculations we discovered that m had to be less than 0.008 before it was applicable to the data from all four river sections. Furthermore, again ignoring the Middle River data for reasons previously discussed, the estimates of M_2 (natural mortality in the last 12 mo) decreased from the Lower River to the Uppermost River.

We find these results based on an assumption of a constant m for all river sections difficult to accept for a number of reasons. The decreasing M_2 (natural mortality) as one moves upriver is suspect in view of the unobserved natural mortality that probably occurs during the upriver migration, as it does for chinook salmon (Merrell, Collins, and Greenough, 1969). Also,

TABLE 6.—Calculated monthly values of F, M_1, and M_2 for 1965-66 broods of marked coho salmon from Columbia River hatcheries — river sections combined (m = 0.0006).

Area	F	M_1	M_2
1965 brood:			
Mouth to Cowlitz River (Lower)	0.2130	0.0952	0.3084
Cowlitz River to Bonneville (Middle)	.2613	.0115	.2341
Bonneville to The Dalles (Upper)	.1878	.2495	.2816
Above The Dalles (Uppermost)	.3912	.4346	.1022
1966 brood:			
Mouth to Cowlitz River (Lower)	.1719	.0118	.3231
Cowlitz River to Bonneville (Middle)	.2570	.0789	.1954
Bonneville to The Dalles (Upper)	.1704	.2339	.2291
Above The Dalles (Uppermost)	.4047	.7193	.0235

the relatively low value of m (<0.008) needed to be comparable with all the data is considerably lower than we feel it should be because the calculated values of M_2 greatly exceed those for M_1 for the lower river areas as they also do for all coho salmon combined in Figure 3. This is contrary to all previously published data as discussed in the next section. On the basis of these analyses, we believe that the proportion maturing as jacks for these two brood years consistently decreased for coho salmon released farther and farther upriver.

Returning to Table 5 and Figure 3, these data show the same pattern for both broods as m increases. Thus M_1 and F both increase (M_1 much more rapidly), M_2 decreases sharply, and (the linear function) Z_t decreases so slightly as to be nearly independent of m. Figure 3 also shows that the lower limit of m (when $M_1 = 0$) is about 0.003 for both broods: $\hat{\theta}_1 = E_1/N_0 = 0.00333$ (1965 brood) and 0.00316 (1966 brood). The upper limit of m (when $M_2 = 0$) is about 0.068 for the 1965 brood but only about 0.057 for the 1966 brood. These latter values again agree with data in Table 1. Of course, when $M_2 = 0$, $m = E_1/(E_1 + C + E_2)$. This is the highest possible value of m.

Figure 3 emphasizes that a unique set of nominally unbiased estimates would be available if m were estimated independently. It is now evident from Cleaver's (1969) model and Equations 12-15 here that the same applies to hatchery chinook salmon, or indeed to any salmon stock or species with two or more returns when the offshore catch from a group of smolts is known by origin. Thus, for I returns one would use assigned values of m_i ($i = 1, 2 \cdots I-1$) and solve the extended counterparts of Equations 12-15 to estimate the various parameters (however, this gets to be very complicated to display graphically). Unfortunately, independent estimation of m_1 (m for coho salmon) is not feasible on a practical scale under present management of most ocean fisheries for coho and chinook salmon on the Pacific coast because minimum size limits are imposed.

Before turning to summary estimates with unknown bias, we emphasize that unique estimates could be obtained also if the present data included estimates of the sex ratio of the N_0 smolts and E_2 adults (Example 5 of Paulik and Robson, 1969). Change-in-ratio estimates for hatchery coho salmon are to be recommended highly: not only is the field work relatively inexpensive and straightforward, but these nominally unbiased estimates would provide definitive tests of other methods.

ANALYSES BASED ON CONSIDERATION OF INDEPENDENT ESTIMATES OF LIMITS FOR M_2

It is useful at this stage to note some published values (or derivatives thereof) which may help to 1) delimit from the possibilities shown for M_1 and M_2 in Figure 3 the actual time distribution of natural mortality in 1965-66 brood coho salmon, and 2) justify assumptions leading to unique estimates (other than in Tables 4 and 6) with unknown bias. The following include corrections for marking mortality; data in Table 1 (see footnote 2) and all our estimates are for marked fish.

Source	*Species*	*Value and explanation*
Parker (1962)	All *Oncorhynchus* except *O. masu*	$M_2 \simeq 0.026$/mo, a rough average for all species during offshore life only.
Ricker (1962)	*O. nerka*	M_1(lower) > M_2(upper) = 0.038/mo during last 2 yr at sea.

Fredin (1964)	*O. nerka*	M_1(lower) > M_2(upper) = 0.042/mo after the first few months or first year at sea. Value is from Model 1 (constant natural mortality during all of ocean life), averaged for smolts migrating in their third third and fourth years.
Parker (1968)	*O. gorbuscha*	$M_1 \simeq$ 0.781/mo during first 40 days in coastal waters and M_2(upper) = 0.169/mo during last 410 days of ocean life (hence $M_1/M_2 \simeq 4.0$). Reported daily rates are averaged here for the 1961-63 broods and multiplied by 30.

In contrast to the situation for 1965-66 brood coho salmon, offshore fishing had a negligible effect on data from which the foregoing values were derived. Thus Ricker (1962) and Fredin (1964) demonstrated sharp decreases in the total and monthly average rates of natural mortality during all of ocean life as the size of smolts increased; they correctly emphasized that the actual risk of death is much greater during the first part of ocean life when fish are smallest. Their values for M_2(upper)—0.038/mo and 0.042/mo—are compatible with Parker's (1962) value of $M_2 \simeq$ 0.026/mo which excludes mortality on small, juvenile fish before they leave coastal waters. Although Lander (1973) contrasted the assumptions of Ricker's (1962) mortality computation and Model 1 of Fredin (1964), the distinction is mainly academic: natural mortality is the overwhelming agent of removal for salmon smolts and values calculated from a given set of real data differ little between the two models.

Parker's (1968) results appear to be the only ones which determine with reasonable success the real time distribution of natural mortality in salmon from direct marking/recovery at sea. Thus Parker's value of $M_1 \simeq$ 0.781/mo greatly exceeds the highest possible values in Figure 3: M_1(upper) is about 0.50/mo for the 1965 brood and 0.48/mo for the 1966 brood. This is not surprising since relatively higher natural mortality is associated with smaller sockeye salmon smolts as just noted (Ricker, 1962; Fredin, 1964). The pink salmon in Parker's analysis were tiny when marked during their first 40 days at sea—roughly 0.3-8.0 g judging from LeBrasseur and Parker (1964)—compared with average release weights of about 14.6-33.1 g (at different hatcheries) for 1965-66 brood coho salmon. Beyond this initial size difference, Parker's value of $M_1 \simeq$ 0.781/mo is for only the first 40 days at sea, but values of M_1(upper) for the coho data of about 0.50 (1965 brood) and 0.48 (1966 brood) are for the first 6.0 mo after release. With respect to M_2(upper) = 0.169/mo, Parker (1968) emphasized that his reported escapement was considerably low.

The foregoing evidence, although indirect so far as 1965-66 brood coho salmon are concerned, does suggest that $M_1 > M_2$, and further that M_2 is closer to the lower limit ($M_2 = 0$) than to $M_2 = M_1$ (Figure 3). Assuming $M_2 < M_1$, one can choose any value of M_2 in this range to get a reasonable idea of the relative magnitudes of survival during the first 6.0 mo (s_1) and last 12.0 mo (s_2) after smolts were released. Based on the observation that M_2(upper) = 0.038/mo (Ricker, 1962) or 0.042/mo (Fredin, 1964), we chose M_2 = 0.03/mo to illustrate relative magnitudes of s_1 and s_2. Values for M_1 and F were approximated from Figure 3, and values for s_1 and s_2 were calculated from the relations given below.

Relation	*1965 brood*	*1966 brood*
$s_1 = e^{-6.0M_1}$	0.06	0.08
$s_2 = e^{-12.0M_2 - 4.5F}$	.14	.17

To present unique point estimates with unknown bias for all parameters, we applied the limit-mean model; its basic assumption is that s_1 (upper) = s_2 (lower) = s (Lander, 1973). Its possible effect on estimates is discussed in the Appendix, where the scheme for calculating is summarized also.

The resulting estimates for all parameters are in Table 7. The exploitation rate (μ) in offshore fisheries evidently was slightly higher for the 1965 brood (70%) than the 1966 brood (68%). The proportion of smolts recruited to oceanic fishing was slightly lower for the 1965 brood (5%) than the 1966 brood (6%), as noted earlier. The estimates indicate also that slightly more of the surviving smolts matured as jacks in the

TABLE 7.—Estimates of mortality (monthly), maturity, survival, and abundance parameters for 1965-66 brood coho salmon from Columbia River hatcheries—river sections combined.

Parameter	Estimated value	
	1965 brood	1966 brood
m	0.0373	0.0321
M_1	.4029	.3862
M_2	.0644	.0613
F	.3320	.3000
μ	.6969	.6670
N_1/N_0	.0858	.0954
N_r/N_0	.0530	.0602
s_1	.0891	.0985
s_2	.1037	.1243

1965 brood (4% compared with 3%). In general, estimates of all parameters are very similar for both broods. It should be remembered that despite the similarity between broods for all river sections combined, there was considerable variation between sections (Tables 4, 5).

DISTRIBUTION

Distribution by Area

Figure 4 depicts the calculated recoveries of the different groups of marked coho salmon in the different fisheries for both the 1965-66 broods. Because any fish which had a regenerated maxillary mark, or for which the maxillary mark was not observed, would be listed with the adipose only marked fish, in all probability this Ad-only group of recoveries actually includes many fish from the other groups of marks. This also is suggested by the large number of recoveries of Ad-only marks compared with the other groups (see footnote 2).

Despite these difficulties, however, it is possible to compare directly the Ad-LM (Upper River) and Ad-RM (Lower River) recoveries. There appears to be a tendency for a greater percentage of the Lower River marks (Ad-RM) to be recovered in the California troll fishery, indicating a greater tendency to migrate south from the Columbia River; this was particularly evident for the 1965 brood fish. Also, there appears to be a tendency for a greater percentage of the Lower River fish to be caught in the Oregon ocean fisheries compared with the Washington ocean fisheries, whereas the reverse

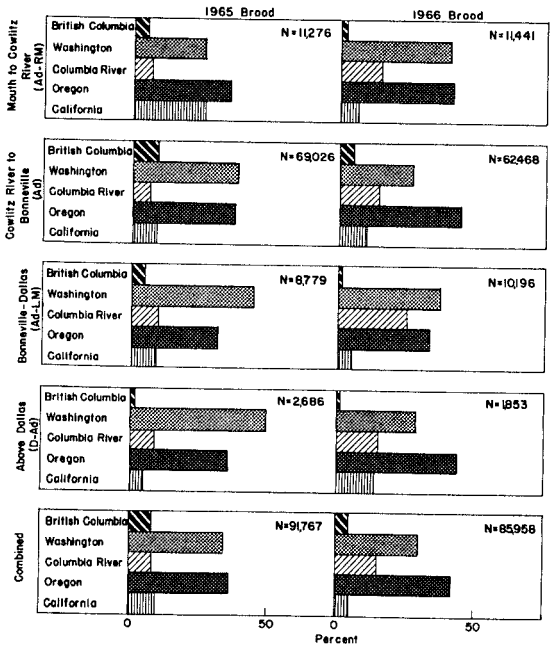

FIGURE 4.—Calculated recoveries (in percent) in various fishing areas of marked 3-yr-old coho salmon from Columbia River hatcheries.

was true for the Upper River (Ad-LM) marks. Again this would be consistent with the possibility that a greater portion of the Lower River fish (Ad-RM) tend to migrate south from the Columbia River compared with the Upper River fish (Ad-LM). As might be expected from the greater exposure to river fishing, a greater percentage of Upper River fish were recovered in the Columbia River fisheries.

The marks from above The Dalles (D-Ad) were not consistent in this respect, although they did show a greater percentage recovery in California fisheries than in British Columbia fisheries. This possibly indicates a greater portion of these fish also migrated south from the Columbia River.

Finally, when the recoveries from all hatcheries are combined, the data indicate that the percentage of these fish caught in the British Columbia and California ocean fisheries is about equal (less than 10%), whereas the percentage recovered in the Oregon ocean fisheries is somewhat greater (from less than 1 to over 12%) than that recovered in the Washington fisheries.

TABLE 8.—Tests of the hypothesis that recoveries of 1965-66 brood coho salmon in ocean troll and sport fisheries are independent of hatcheries of origin. Chi-square was tested at the 95% level.

Fishery	1965 brood LR[1]	1965 brood UR[2]	1965 brood Total	1966 brood LR	1966 brood UR	1966 brood Total
Washington:						
Sport	1,206	1,809	3,015	526	482	1,008
Commercial	1,716	2,051	3,767	356	432	788
Total	2,922	3,860	6,782	882	914	1,796
χ^2	—	—	21.06	—	—	9.93
Test result	—	—	Reject	—	—	Reject
Oregon:						
Sport	420	265	685	107	86	193
Commercial	3,564	2,530	6,094	911	622	1,533
Total	3,984	2,795	6,779	1,018	708	1,726
χ^2	—	—	2.04	—	—	1.12
Test result	—	—	Accept	—	—	Accept
California:						
Sport	331	30	361	22	14	36
Commercial	2,617	789	3,406	158	102	260
Total	2,948	819	3,767	180	116	296
χ^2	—	—	42.33	—	—	0.002
Test result	—	—	Reject	—	—	Accept

[1] LR = number of Lower River mark (Ad-RM) recoveries.
[2] UR = number of Upper River mark (Ad-LM) recoveries.

Distribution by Ocean Commercial and Sport Fisheries

It also is possible to compare the recovery of marks from the Lower River (Ad-RM) and the Upper River (Ad-LM) hatcheries in the ocean commercial and sport fisheries for the different states. This is done in Table 8 for both the 1965-66 broods by means of Chi-square tests. The commercial fishery usually operates farther from shore than the sport fishery, so the analysis also may test differences in offshore distribution between these two marks. In Table 8 we see the hypothesis of independence is rejected for the Washington fisheries for both brood years. In other words, the recovery of marks in the Washington commercial and sport fisheries was different for these two groups of marked coho salmon for both brood years. For Oregon, on the other hand, the differences were not significant for either brood year. For California recoveries, the difference in the recoveries between the two marks and two fisheries was significant for the 1965 brood but not for the 1966 brood. As was pointed out earlier, it was these 1965 brood recoveries of Ad-RM marks in California which showed the high percentage recovery in Figure 4. To summarize these analyses, the two marks (Ad-RM; Ad-LM) showed no significant difference in recoveries in the Oregon ocean sport and commercial fisheries, were significantly different for the Washington fisheries, and were significantly different for the 1965 brood for the California fisheries. This suggests a definite differential distribution pattern north of the Columbia for both broods and also a differential distribution pattern south of the Columbia River, at least for the 1965 brood fish.

Distribution by Time

The Upper River (Ad-LM) and Lower River (Ad-RM) mark recoveries also can be examined to see if the data indicate any difference in time of recovery in certain fisheries. In Table 9 are listed the calculated seasonal recoveries (in percent) for selected ports along the Pacific coast. In general, data for most of the ports not listed either showed a similar pattern or had insufficient sampling data for this analysis.

The data listed in Table 9 clearly indicate that there was a definite difference in timing between these two groups of fish for both the British Columbia and Washington recoveries for both brood years, the Upper River fish (Ad-LM) disappearing first from the ocean fisheries. This difference in time of capture also persisted for

TABLE 9.—Calculated recoveries (in percent), by time, of Upper River (UR) and Lower River (LR) marked, 1965-66 brood coho salmon in the various ocean fisheries.

Brood	California				Br. Columbia		Washington				Oregon			
	Fishing period	Ft. Bragg		Fishing period	Area 40		Neah Bay		Westport		Tillamook		Newport	
		UR[1]	LR[2]		UR	LR	UR	LR	UR	LR	UR	LR	UR	LR
1965	Month ending			Two weeks ending										
	30 May	9.8	16.0	15 June	0.3	—	—	—	0.2	—	0.6	0.3	2.1	1.4
	30 June	43.8	29.1	29 June	5.3	1.1	13.0	2.4	12.3	5.8	10.7	4.5	22.5	14.4
	31 July	46.4	42.3	13 July	22.2	3.3	2.9	0.0	5.3	13.1	11.3	7.7	21.1	14.1
	31 Aug.	—	12.0	27 July	5.0	3.3	15.9	4.7	11.9	8.5	56.8	48.7	36.8	23.0
	30 Sept.	—	0.7	10 Aug.	14.9	10.0	11.6	4.7	16.2	6.6	15.8	31.0	17.5	37.4
				24 Aug.	21.5	10.5	14.5	11.8	25.6	9.0	4.8	5.2	—	7.8
				7 Sept.	26.5	44.5	42.0	68.2	23.1	28.2	—	0.6	—	2.0
				21 Sept.	4.3	20.9	—	8.2	5.7	19.7	—	—	—	—
				5 Oct.	—	6.5	—	—	—	9.2	—	—	—	—
Number of fish[3]		153	719		302	449	69	85	438	412	336	310	280	348
1966														
	30 June	19.3	18.9	28 June	13.0	16.2	34.3	10.0	3.6	—	6.1	11.9	27.1	20.1
	31 July	75.4	76.2	12 July	10.4	12.6	11.4	17.5	4.1	9.8	26.3	11.9	30.3	37.7
	31 Aug.	5.3	4.9	26 July	9.1	7.9	0.0	0.0	8.0	3.2	9.5	7.7	13.8	14.2
				9 Aug.	26.0	28.5	0.0	0.0	12.6	13.5	31.3	34.5	16.0	14.7
				23 Aug.	41.6	12.6	17.1	7.5	28.8	29.7	24.6	34.0	8.3	8.3
				6 Sept.	—	14.2	37.1	65.0	28.6	21.6	2.2	—	4.4	5.1
				20 Sept.	—	7.9	—	—	11.3	15.0	—	—	—	—
				4 Oct.	—	—	—	—	3.0	7.3	—	—	—	—
Number of fish[3]		285	391		77	253	35	40	364	468	179	194	587	1,042

[1] UR = Upper River mark (Ad-LM) recoveries.
[2] LR = Lower River mark (Ad-RM) recoveries.
[3] Calculated number of marked fish recovered during the fishing season.

recoveries in the Oregon and California ocean fisheries for the 1965 brood but was not evident for the 1966 brood data. We also can look at recoveries in the Zone 1 (lowest) fishery in the Columbia River (Table 10). For both brood years the Upper River marks (Ad-LM) peaked earlier and disappeared first from the catches when compared with the Lower River marks (Ad-RM). Of course, in view of the longer migration up the Columbia River for the Upper River fish, this phenomenon might be expected.

TABLE 10.—Calculated recoveries (in percent) by time of marked Upper River and Lower River coho salmon in the Columbia River Zone 1[1] fishery.

Brood	Fishing record	Upper River	Lower River
	Week ending		
1965	8/24	13.8	2.1
	8/30	—	—
	9/7	68.6	27.7
	9/14	6.3	4.0
	9/21	11.4	38.5
	9/28	0.0	0.0
	10/5	0.0	27.7
	10/12	—	—
Calculated number of fish		414	325
1966	8/23	—	—
	8/29	0.0	0.7
	9/6	—	—
	9/13	—	—
	9/20	74.5	58.1
	9/27	25.5	30.7
	10/4	0.0	10.5
	10/11	0.0	0.0
Calculated number of fish		545	602

[1] Zone 1 extends from the mouth of the Columbia River to the Elokomin River (see Figure 1).

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APPENDIX

Derivations of Text Equations 12-15

As pointed out in the text,

The probability of E_1: $\theta_1 = m\,e^{-6M_1}$. (1)

The probability of C: $\theta_2 =$

$$(1 - m)e^{-6M_1}e^{-7.5M_2}\left(\frac{F}{F + M_2}\right)e^{-4.5(F + M_2)}. \quad (2)$$

The probability of E_2: $\theta_3 =$

$$(1 - M)e^{-6M_1}e^{-7.5M_2}\,e^{-4.5\,(F + M_2)} \quad (3)$$

and maximum likelihood estimators of the θ_i are:

$$\hat{\theta}_1 = \frac{E_1}{N_0} \text{ or } \hat{\theta}_1 = m\,e^{-6M_1} \text{ from (1).} \quad (4)$$

$$\hat{\theta}_2 = C/N_0 \text{ or } \hat{\theta}_2 = (1 - m)\,e^{-6M_1}e^{-7.5M_2}\left(\frac{F}{F + M_2}\right)e^{-4.5\,(F + M_2)} \text{ from (2).} \quad (5)$$

$$\hat{\theta}_3 = E_2/N_0 \text{ or } \hat{\theta}_3 = (1 - m)e^{-6M_1}e^{-7.5M_2}e^{-4.5\,(F + M_2)} \text{ from (3).} \quad (6)$$

Then for $m = m$ (fixed) ($\hat{\theta}_1 < m < 1$), text Equation 12, by rearranging Equation 4 and taking natural logarithms we obtain

$$-\frac{1}{6}\ln\left(\frac{\hat{\theta}_1}{m}\right) = M_1 \quad \text{(text Equation 13).}$$

Then, Equation 6 can be rewritten as

$$\frac{\hat{\theta}_3}{(1 - m)}\,e^{6M_1} = e^{-7.5M_2}e^{-4.5\,(F + M_2)}$$

$$= e^{-7.5M_2 - 4.5F - 4.5F - 4.5M_2}$$

$$= e^{-(4.5F + 12M_2)}$$

$$= k_2.$$

The natural logarithm of k_2

$$\ln k_2 = -(4.5F + 12M_2) \quad (7)$$

which can be solved for F as follows:

$$-4.5F = \ln k_2 + 12M_2$$

$$F = -\left[\frac{\ln k_2 + 12M_2}{4.5}\right] \text{(text Equation 15).} \quad (8)$$

Equation 5 can be written

$$\frac{\hat{\theta}_2}{(1 - M)}\,e^{6M_1} = e^{-7.5M_2}\left(\frac{F}{F + M_2}\right)\left(1 - e^{-4.5\,(F + M_2)}\right) = k_1 \quad (9)$$

and since

$$e^{-4.5\,(F + M_2)}$$

$$= e^{-4.5F - 12M_2 + 7.5M_2}$$

$$= e^{-(4.5F + 12M_2) + 7.5M_2}$$

$$= e^{\ln k_2 + 7.5M_2} \quad \text{(from Equation 7)}$$

and

$$\left(\frac{F}{F + M_2}\right) = \frac{-\left(\frac{\ln k_2 + 12M_2}{4.5}\right)}{-\left(\frac{\ln k_2 + 12M_2}{4.5}\right) + M_2} \quad \text{(from Equation 8)}$$

$$= \frac{-(\ln k_2 + 12M_2)}{-(\ln k_2 + 12M_2) + 4.5M_2}$$

$$= \frac{\ln k_2 + 12M_2}{\ln k_2 + 12M_2 - 4.5M_2}$$

$$= \frac{\ln k_2 + 12M_2}{\ln k_2 + 7.5M_2}$$

then Equation 9 becomes

$$\frac{\theta_2}{(1 - m)} e^{6M_1} = \left[\frac{\ln k_2 + 12M_2}{\ln k_2 + 7.5M_2}\right] e^{-7.5M_2}$$

$$1 - e^{(\ln k_2 + 7.5M_2)} = k_1$$

(text Equation 14).

Failure of the Basic Assumption in the Limit-Mean Model

The basic assumption of the limit-mean model is that survivial (s_1) from the time N_0 smolts start seaward until E_1 jacks return from the ocean does not exceed survival (s_2) thereafter until E_2 adults return. For sockeye and pink salmon not fished in offshore waters, the text discusses certain evidence (Ricker, 1962; Fredin, 1964; Parker, 1962, 1968) indicating almost incontrovertibly that $M_1 > M_2$, i.e., the monthly natural mortality rate during the "early" part of ocean life exceeds the rate thereafter. The same probably applies to coho salmon and to all other anadromous salmonids. Coho salmon smolts are about the same size as most sockeye salmon smolts when they enter the sea; on general grounds we would expect relatively little difference, on the basis of smolt size alone, in the values of M_1 and M_2 between these two species for a common time base. (By contrast, text Figure 3 shows for coho salmon that monthly M_1, as averaged for the first 6.0 mo after release, is much less than monthly $M_1 \simeq$ 0.781/mo for tiny pink salmon during only the first 40 days at sea.) Fredin (1964, Table 2) reported about 13-15 mo as the time between the outmigration of sockeye salmon smolts and the first return. For our data, coho salmon first returned as jacks after only 6 mo; furthermore, those that stayed at sea were fished quite heavily in offshore waters but the sockeye salmon in Fredin's analysis suffered natural mortality alone until they entered the coastal fishery. Even if $M_1 > M_2$ in hatchery coho salmon, the shorter time for s_1 and the effect of oceanic fishing on s_2 might conceivably result in $s_1 > s_2$ —instead of $s_1 \leq s_2$ as assumed in the limit-mean model.

Bias in estimates from the limit-mean model (text Table 7), or in any model giving a single set of estimates where in fact only various possible sets can be determined (as in text Figure 3), must be evaluated with hypothetical data. To get a fairly realistic notion of how the assumption, $s_1 \leq s_2$, might have affected the estimates in text Table 7, we 1) used the same time intervals as in the text, 2) chose hypothetical values of m, s_2, and M_2 (hence F) which were quite close to the estimates, then 3) varied s_1 so that $s_1 = 0.5\ s_2$, $1.0\ s_2$, and $1.5\ s_2$. Values for the data as observed in practice (E_1/N_0, C/N_0, and E_2/N_0) were calculated from relations given in the text.

Estimates of all parameters in Appendix Table 1 contain less relative bias in Example 2, where $s_1 = s_2$ ($= 0.10$), than in Example 1 ($s_1 = 0.5\ s_2$) or Example 3 ($s_1 = 1.5\ s_2$). In Example 3, estimates of m and s_2 are too large and the estimate of s_1 is too small. The converse happens in Example 1. The direction of bias in these three estimates is the same in Examples 1 and 2. It is interesting to note in all examples the decrease in relative bias (estimate minus parameter value/parameter value) as one proceeds (in the life of a cohort) from $\hat{N}_1/N_0$ to $\hat{N}_r/N_0$:

	Relative bias (%) in abundance estimate	
Example	$\hat{N}_1/N_0$	$\hat{N}_r/N_0$
1	+29	+6
2	-4	-2
3	-18	-4

Applicable values in Appendix Table 1 were rounded to three places before calculating the above percentages.

This result is perhaps not surprising because 1) N_r/N_0 is actually the target parameter in estimation by the limit-mean model when the offshore catch is known and 2) the lower and upper limits for N_r/N_0 were found during calculation to bracket the true values quite closely in all three examples despite the fact

APPENDIX TABLE 1.—Comparison of "actual" values, as calculated from assigned input parameters, with estimates from the limit-mean model. For m, s_2, and M_2 (hence F) fixed near the estimates for 1965-66 brood coho in Table 7 of the text, the three hypothetical examples show how the basic assumption of $s_1 \leqq s_2$, which Example 3 violates, might have biased the estimates.

Input parameters with fixed values in all examples	Items with values that vary between examples		Example 1		Example 2		Example 3	
	Data	Parameter	Actual	Estimated	Actual	Estimated	Actual	Estimated
m = 0.0350000	—	—	—	0.027	—	0.036	—	0.042
s_2 = .1000000	—	—	—	.077	—	.104	—	.122
M_2 = .0600000	—	—	—	.086	—	.056	—	.040
F = .3516856	—	—	—	.339	—	.354	—	.362
—	E_1/N_0	—	0.001750	—	0.003500	—	0.005250	—
—	C/N_0	—	.022176	—	.044352	—	.066528	—
—	E_2/N_0	—	.004825	—	.009650	—	.014475	—
—	—	s_1	.0500000	.064	.1000000	.096	.1500000	.124
—	—	M_1	.4992887	.458	.3837642	.390	.3161867	.348
—	—	N_1/N_0	.0482500	.062	.0965000	.093	.1447500	.119
—	—	N_r/N_0	.0307656	.033	.0615312	.061	.0922967	.088

$s_1 \neq s_2$ in Examples 1 and 3. The latter comparison and estimates are summarized below:

Example	*Lower limit*	N_r/N_0	*Upper limit*	N_r/N_0
1	0.0270	0.0308	0.0394	0.033
2	.0540	.0615	.0689	.061
3	.0810	.0923	.0962	.088

Noting finally that absolute bias (estimate minus parameter value) is not excessive for any estimate or example in Appendix Table 1, the foregoing analysis leads us to believe that estimates in text Table 7 of the text are quite close to reality for 1965-66 brood coho salmon from Columbia River hatcheries (data from all river sections combined).

Procedure for Calculating Estimates

The estimating scheme is described elsewhere (Lander, 1973). That account may not be available to the reader; furthermore, it discusses also the situations where offshore catch is not known and an offshore fishery does not occur, and therefore is not a compact summary. Appendix Table 2 briefly reviews the assumptions and calculating methods for the case where offshore catch is known by origin.

APPENDIX TABLE 2.—Assumptions and calculating procedure for the limit-mean model when the offshore catch is known by origin.

Known values			Assumptions and a calculating sequence
N_0	=	number of smolts	Noting $E_2 = N_0 s_1 (1 - m) s_2 = N_0 s_1 s_2 - E_1 s_2$, *assume* s_1(upper) = s_2(lower) = s.
C	=	number in offshore catch	Solve $s^2 - (E_1/N_0)s - (E_2/N_0) = 0$ and find $s + (E_1/N_0) = N_1$(upper). Evaluate X in $(C + E_2)/N_1$
E_i	=	number of jacks (i = 1) and adults (i = 2) in inshore and river fishery plus escapement to spawning site.	(upper) $= e^{-(t_2 + t_3)X}$, then note and find (N_r/N_0)(upper) = (N_1/N_0)(upper)$e^{-t_2 X}$. *Assume* $M_2 = 0$ during t_3 and find (N_r/N_0)(lower) = $(C + E_2)/N_0$. Find $(\hat{N}_r/N_0) = [(N_r/N_0)$(upper) X
t_1	=	months between outmigration of smolts and return of jacks.	(N_r/N_0)(lower)$]^{1/2}$ as the geometric mean of limits used here or take another abitrary and intermediate value as the estimate. Find $\hat{\mu} = C/\hat{N}_r$ and evaluate $(\widehat{F + M_2})$ in $E_2/\hat{N}_r = e^{-t_3 (\widehat{F + M_2})}$. Rearranging the
t_2	=	months between return of jacks and start of offshore fishing.	general definition of μ, find $\hat{F} = \hat{\mu}(\widehat{F + M_2})/[1 - e^{-t_3 (\widehat{F + M_2})}]$, then $\hat{M}_2 = (\widehat{F + M_2}) - \hat{F}$. Find $\hat{Z}_2 =$
t_3	=	months between start of offshore fishing and return of adults.	$\hat{M}_2 + [t_2/(t_2 + t_3)]\hat{F}$ and $\hat{N}_1/N_0 = (E_2/N_0)/e^{-t_2 + t_3)\hat{Z}_2} = (\hat{N}_r/N_0)/e^{-t_2 \hat{M}_2}$. Find $\hat{s}_2 = E_2/\hat{N}_1$, $\hat{m} = 1/(1 + E_2/E_1\hat{s}_2)$, and $\hat{s}_1 = (E_1/N_0)/\hat{m}$. Evaluate $\hat{M}_1$ in $\hat{s}_1 = e^{-t_1 \hat{M}_1}$. If desired, $\hat{M}_r$, $\hat{M}_T$, and $\hat{Z}_T$ can be found from relations noted near Table 7 of the text.

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ABUNDANCE AND DISTRIBUTION OF LARVAL FISHES IN WATERS OFF OREGON, MAY-OCTOBER 1969, WITH SPECIAL EMPHASIS ON THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

SALLY L. RICHARDSON[1]

ABSTRACT

Quantitative information on larval fishes in waters off Oregon is presented. Three hundred fifty-four samples, containing 55,049 larvae, were taken from lat. 42°00′ to 46°30′N and from the coastline to long. 129°30′W during six cruises, May to October 1969. Catches by three types of gear—bongos, meter net, and Isaacs-Kidd midwater trawl—are compared. The midwater trawl captured the greatest number of taxa and had the greatest frequency of occurrence of major taxa while overall the bongos caught the most larvae per 1,000 m^3 of water filtered. Shallow tows compared with deep tows from the same stations showed small anchovy larvae were concentrated near the surface while larvae of myctophids and scorpaenids were more common in deeper waters.

Species composition (40 taxa in 22 families from deep tows), frequency of occurrence, abundance, and dominance are discussed. Northern anchovy, *Engraulis mordax*; northern lampfish, *Stenobrachius leucopsarus*; blue lanternfish, *Tarletonbeania crenularis*, and *Sebastes* spp. were the most dominant taxa. Distributional features of species in the most important families are described. *E. mordax* larvae were concentrated in Columbia River plume waters from June to August.

Species composition, abundance, seasonal occurrence, and areal distribution of larval fishes in ocean waters of the northeast Pacific off Oregon are virtually unknown (Ahlstrom, 1968). Pearcy (1962)[2] and LeBrasseur (1970)[3] listed larval fishes from these waters collected only incidentally to major sampling goals. Waldron (1972) provided the first quantiative data on larvae off Oregon collected from 12 April to 11 May 1967. No additional comprehensive, quantitative information has been published.

From 10 May to 31 October 1969, the Department of Oceanography of Oregon State University conducted a series of cruises off Oregon to quantitatively study the chemical, physical, and biological interrelationships involved with two major oceanographic phenomena—the Columbia River plume and coastal upwelling. The area surveyed extended from lat. 42°00′ to 46°30′N and from the coastline to long. 129°30′W.

This extensive sampling effort yielded much quantitative information on abundance and distribution of larval fishes off Oregon. Three types of gear are compared for their effectiveness in catching fish larvae. Shallow tows are compared with deep tows made at the same stations on two cruises. Species composition, frequency of occurrence, abundance, and dominance are discussed. Occurrence and distribution patterns are described for species in the most important families.

MATERIALS AND METHODS

Six cruises were conducted at approximately monthly intervals from 10 May to 31 October 1969 in waters off Oregon. Inclusive cruise dates and stations occupied during these cruises are shown in Figure 1.

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Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

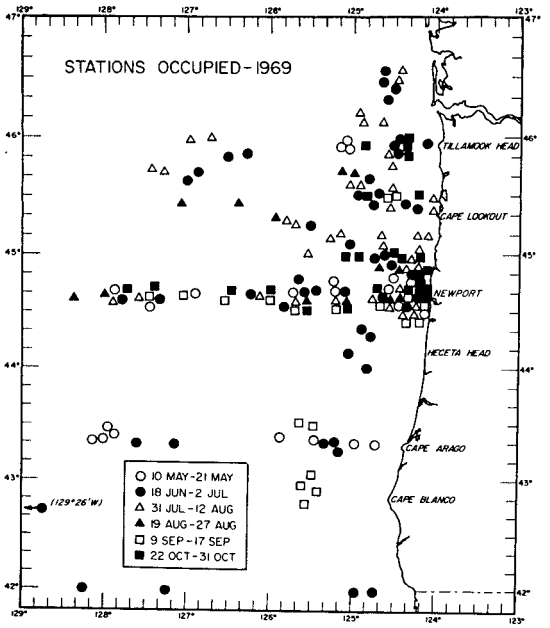

FIGURE 1.—Stations occupied during survey of waters off Oregon, May to October 1969.

Micronekton and zooplankton were sampled with a 6-foot Isaacs-Kidd midwater trawl (IKMT) equipped with a 5-mm mesh liner and a 0.571-mm mesh cod end, paired 0.7 m (mouth diameter) bongos with 0.571-mm mesh nets, and a 5-m long 1.0-m-mouth diameter net (MN) with a 0.571-mm mesh.

The bongos were located 3 m above the bridle of the IKMT on the same tow line. Hauls were made obliquely, usually from 200 m, depth permitting, to the surface at a tow speed of 5 knots. Eight hundred meters of wire, assuming a 4:1 wire length to depth fished ratio, was let out at 50 m/min and retrieved at 30 m/min. A usual haul required about 40 min effective towing time. Surface tows (upper 10-20 m) were made horizontally at the same stations as deep (200 m) oblique tows on the June and July-August cruises for comparison. Three of these surface tows did not have paired samples from deep hauls. For MN hauls, the ship remained stationary as the net was lowered at 10 m/min to 200 m on 200 m of wire, depth permitting, and hauled vertically to the surface at 30 m/min. Effective tow time was usually about 8 min. At depths < 400 m only the upper half of the water column was sampled by the IKMT and bongos. Bongos were not used on the May or August cruises. MN samples were not always taken in conjunction with IKMT samples. All tows were made between dusk and dawn.

A flow meter was situated inside the mouth of each net to record volume of water filtered. A depth distance recorder (Pearcy and Laurs, 1966) was also used in the IKMT to record the distance travelled vs. depth.

Temperature (BT) and salinity (induction salinometer) of surface waters were determined at each station.

All biological samples were preserved at sea in 10% buffered seawater Formalin.[4] Later the IKMT samples were transferred to 36% isopropyl alcohol. Fish larvae were sorted from bongo (one side only), MN (some of which had been split a varying number of times with a Folsom plankton splitter), and IKMT samples (not split). They were later identified and measured. Measurements, reported to the nearest millimeter, refer to standard length (SL = snout tip to notochord tip preceding development of caudal fin, then to end of hypural plate). For convenience, the term larvae in this paper sometimes includes early juvenile stages, e.g., anchovies, scorpaenids, and osmerids.

The taxonomic listings follow the scheme of Greenwood et al. (1966). Species names correspond to those listed by the American Fisheries Society (Bailey, 1970). The following discussion is based on the deep tows of the bongos and IKMT unless indicated otherwise.

RESULTS AND DISCUSSION

Comparison of Gear

The three types of gear were compared for the number of taxa taken, estimates of larval abundance, and frequency of occurrence of major taxa. The IKMT samples contained the greatest number of taxa followed by the bongos and MN (Table 1). Many of the bongo and MN samples, but not IKMT samples, had been split prior to removal of fish larvae. This process

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

TABLE 1.—Number of deep hauls taken, number of positive hauls, number of taxa taken, volume of water filtered, numbers of larvae originally in samples, number of larvae/1,000 m³ of total volume of water filtered according to type of gear and cruise.

		Cruise						
	Gear	May	June	July-Aug.	Aug.	Sept.	Oct.	Total
Number of hauls taken	Bongo	—	23	23	—	8	8	62
	MN[1]	14	20	10	13	17	25	99
	IKMT[2]	19	34	23	14	14	22	127
	Total	33	77	56	35	39	47	287
Number of positive hauls	Bongo	—	17	15	—	6	6	44
	MN	9	17	7	7	6	1	47
	IKMT	19	29	20	14	14	20	116
	Total	28	63	42	21	26	27	207
Number of taxa taken	Bongo	—	20	12	—	8	7	25
	MN	11	11	7	6	4	2	18
	IKMT	16	23	29	21	20	12	38
	Total	27	27	30	21	22	16	40
Volume of water filtered (1,000 m³)	Bongo	—	44.58	43.30	—	17.11	20.56	125.55
	MN	1.59	2.54	1.02	1.52	1.90	2.80	11.37
	IKMT	173.49	469.21	312.23	154.08	193.43	636.38	1,938.82
	Total	175.08	516.33	356.55	155.60	212.44	659.74	2,075.74
Numbers of larvae originally in samples	Bongo	—	499	13,138	—	214	15	13,866
	MN	159	295	43	45	42	4	588
	IKMT	691	343	10,100	2,184	438	279	14,035
	Total	850	1,137	23,281	2,229	694	298	28,489
Numbers of larvae per 1,000 m³ of total water filtered	Bongo	—	11.19	303.42	—	12.50	0.72	110.44
	MN	100.00	116.14	42.15	29.60	22.10	1.42	51.71
	IKMT	3.98	0.73	32.35	14.17	2.26	0.43	7.24
	Total	4.85	2.20	65.29	14.32	3.27	0.45	13.72

[1] MN = Meter net.
[2] IKMT = Isaacs-Kidd midwater trawl

results in a loss of rare taxa in the split fraction. The IKMT was towed the longest and filtered the greatest volume of water which increased the probability of capturing rare taxa. This factor outweighed the loss of larvae by escapement through the 5-mm mesh liner which would be expected to be great.

Bongo samples gave the largest estimate of larval abundance (individuals/1,000 m³) for combined cruises. (Although not done in this paper, subsequent data on larval fishes will be standardized to numbers under a unit area of sea surface as encouraged by E. H. Ahlstrom.) Bongos captured a large number of anchovies on the July-August cruise which mainly accounted for the large estimate for combined cruises. MN samples gave the largest estimates of abundance for five of the six periods sampled. The bongos were towed at a speed of 5 knots which may have resulted in extrusion of small larvae. This would explain the low estimates of abundance on three of the four cruises compared with the MN which was hauled more slowly and primarily took small larvae. The IKMT gave the smallest estimates of abundance of larval fishes for each cruise and for the combined cruises probably because of a high degree of escapement through the net by small forms.

Numbers of taxa occurring in 5% or more of the samples for each gear were: 7 for the bongos, 5 for the MN, and 19 for the IKMT (Table 2). For each gear the four taxa taken most frequently were northern anchovy, *Engraulis mordax*; northern lampfish, *Stenobrachius leucopsarus*; blue lanternfish, *Tarletonbeania crenularis*, and *Sebastes* spp. (*Sebastes* spp. was fifth in bongo samples preceded slightly by *Promyctophum thompsoni*.) However, percent frequency of occurrence of each of the four, except *S. leucopsarus*, varied considerably among types of gear (Table 2). Percent occurrence of *E. mordax* was similar in bongo and IKMT samples but much lower in MN samples. The IKMT took *T. crenularis* and *Sebastes* spp. much more often than either the bongos or the MN. The greater frequency of occurrence of

TABLE 2.—Frequency of occurrence (%) of fish larvae in deep samples according to type of gear and cruise.

Taxa	Bongos					Meter net							Isaacs-Kidd midwater trawl						
	June	July-Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total
EEL LEPTOCEPHALUS																			
Unidentified 1	0	0	0	0	0	0	0	0	0	0	0	0	5.3	0	0	0	0	0	0.8
ENGRAULIDAE																			
Engraulis mordax	8.7	56.5	75.0	12.5	35.5	0	25.0	40.0	30.8	0	0	13.1	0	0	69.6	92.8	64.3	54.8	39.7
OSMERIDAE																			
Undetermined spp.	4.3	4.3	0	0	3.2	0	0	0	0	0	0	0	0	2.9	17.4	7.1	0	18.2	7.9
BATHYLAGIDAE																			
Bathylagus milleri	4.3	0	0	0	1.6	0	0	0	0	0	0	0	0	8.8	4.4	0	0	0	3.2
Bathylagus ochotensis	8.7	0	12.5	0	4.8	28.6	5.0	10.0	7.7	0	0	7.1	21.0	11.8	22.2	14.3	7.1	0	12.7
Bathylagus pacificus	8.7	0	0	0	3.2	7.1	5.0	0	0	0	0	2.0	0	5.9	4.4	7.1	7.1	0	4.0
Leuroglossus stilbius	0	0	0	0	0	0	0	0	0	0	0	0	5.3	0	0	0	0	0	0.8
GONOSTOMATIDAE																			
Danaphos sp.	4.3	0	0	0	1.6	0	0	0	0	0	0	0	5.3	0	0	0	0	0	0.8
Diplophos sp.	0	0	0	0	0	0	0	10.0	0	0	0	1.0	0	0	0	0	0	0	0
MELANOSTOMATIDAE																			
Tactostoma macropus	0	0	0	0	0	0	0	0	0	0	0	0	5.3	0	4.4	7.1	14.3	0	4.0
CHAULIODONTIDAE																			
Chauliodus macouni	8.7	4.3	0	12.5	6.4	7.1	5.0	0	7.7	0	0	0	15.8	14.7	26.1	57.1	14.3	0	19.0
ALEPOCEPHALIDAE																			
Sagamichthys abei	0	0	0	0	0	0	0	0	0	0	0	0	5.3	0	0	0	0	0	0.8
PARALEPIDIAE																			
Lestidium ringens	4.3	4.3	0	0	3.2	0	0	0	0	0	0	0	47.4	8.8	22.2	14.3	0	0	15.1
SCOPELARCHIDAE																			
Benthabella dentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.4	7.1	7.1	0	2.4
MYCTOPHIDAE																			
Diaphus theta	0	4.3	0	0	1.6	0	0	0	0	0	0	0	0	0	13.0	14.3	7.1	0	4.8
Lampanyctus regalis	0	13.0	0	0	4.8	0	20.0	0	0	0	0	4.0	0	2.9	30.4	28.6	14.3	0	11.1
Lampanyctus ritteri	0	0	0	0	0	0	10.0	0	0	0	0	2.0	0	0	0	0	0	0	0
Protomyctophum crockeri	0	4.3	12.5	0	3.2	0	0	0	0	0	0	0	10.5	5.9	4.4	21.4	0	0	6.3
Protomyctophum thompsoni	21.7	4.3	37.5	12.5	16.1	0	5.0	10.0	0	0	0	2.0	15.8	29.4	26.1	57.1	35.7	0	25.4
Stenobrachius leucopsarus	26.1	47.8	62.5	0	35.5	50.0	70.0	50.0	38.5	29.4	0	36.4	21.0	41.2	65.2	92.8	71.4	0	44.4
Tarletonbeania crenularis	21.7	17.4	62.5	12.5	24.2	28.6	45.0	0	30.8	11.8	0	19.2	15.8	26.5	56.5	85.7	64.3	0	36.5
MACROURIDAE																			
Unidentified 1	0	0	0	0	0	0	0	0	0	0	0	0	5.3	0	0	0	0	0	0.8
MELAMPHAEIDAE																			
Melamphaes sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9	4.4	0	0	0	2.4
TRACHIPTERIDAE																			
Trachipterus sp.	0	0	0	12.5	1.6	0	0	0	0	0	0	0	0	0	13.3	0	0	0	2.4
SCORPAENIDAE																			
Sebastes spp.	8.7	8.7	37.5	25.0	14.5	28.6	30.0	10.0	15.4	5.9	4.0	15.2	84.2	29.4	43.5	57.1	64.3	45.4	50.0
Sebastolobus spp.	0	0	0	12.5	1.6	0	0	0	0	0	0	0	5.3	5.9	4.4	0	14.3	18.2	7.9
COTTIDAE																			
Undetermined spp.	4.3	0	0	0	1.6	0	0	0	0	0	0	0	21.0	2.9	4.4	14.3	0	0	6.3
AGONIDAE																			
Undetermined spp.	0	0	0	0	0	0	0	0	0	0	0	0	15.8	0	0	0	0	0	2.4
CYCLOPTERIDAE																			
Undetermined spp.	21.7	8.7	0	0	11.3	0	0	10.0	0	0	0	1.0	31.6	35.3	34.8	42.8	21.4	9.1	29.4
STICHAEIDAE																			
Plectobranchus evides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13.3	14.3	7.1	0	4.8
NOMEIDAE																			
Icichthys lockingtoni	0	0	0	0	0	0	5.0	0	0	0	4.0	2.0	0	5.9	8.7	0	0	9.1	4.8
BOTHIDAE																			
Citharichthys sordidus	8.7	0	0	0	3.2	0	0	0	0	5.9	0	1.0	21.0	8.8	4.4	7.1	0	4.5	7.9
Citharichthys stigmaeus	13.0	0	0	0	4.8	7.1	0	0	0	0	0	1.0	21.0	17.6	8.7	0	35.7	22.7	12.5

TABLE 2.—*Continued.*

Taxa	Bongos					Meter net						Isaacs-Kidd midwater trawl					
	June	July-Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total
PLEURONECTIDAE																			
Eopsetta jordani	0	0	0	0	0	0	0	0	0	0	0	0	21.0	0	0	0	0	0	3.2
Glyptocephalus zachirus	13.0	0	0	0	4.8	0	0	0	0	0	0	0	5.3	2.9	4.4	7.1	21.4	27.3	10.3
Isopsetta isolepis	0	0	0	0	0	7.1	0	0	0	0	0	1.0	15.8	2.9	0	0	0	0	3.2
Lyopsetta exilis	4.3	0	0	0	1.6	14.3	0	0	0	0	0	2.0	10.5	5.9	4.4	14.3	7.1	4.5	7.1
Microstomus pacificus	4.3	0	12.5	0	3.2	0	0	0	0	0	0	0	10.5	5.9	4.4	0	7.1	4.5	5.6
Parophrys vetulus	0	0	0	0	0	7.1	0	0	0	0	0	1.0	10.5	0	0	0	0	0	1.6
Psettichthys melanostictus	4.3	0	0	0	1.6	7.1	0	0	0	0	0	1.0	5.3	0	4.4	0	7.1	9.1	4.0
Miscellaneous fragments																			
Unidentified myctophid	0	0	12.5	0	1.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pleuronectid	0	0	0	12.5	1.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified fragments	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.4	0	0	0	0.8

taxa in the IKMT samples is probably due to the greater volume of water filtered.

Shallow vs. Deep Tows

Shallow tows of the IKMT and bongos made on the June and July-August cruises were compared with the standard deep tows from the same stations. Volume of water filtered was approximately the same for each shallow and deep pair. In shallow tows, positive samples (47 out of 64) yielded 20,629 fish larvae compared with 18,087 larvae in 50 out of 64 samples from deep tow pairs (Table 3). A total of 31 taxa were taken; 17 occurred in both shallow and deep samples, 3 occurred only in shallow samples, and 11 were only in deep samples (Table 4). Ninety-eight percent of all larvae were distributed in three families for shallow and deep tows:

Shallow tows:
- 89.4% Engraulidae in 35.9% of all samples
- 5.7% Myctophidae in 31.2% of all samples
- 2.9% Osmeridae in 14.1% of all samples

TABLE 3.—Comparison of shallow and deep hauls from June and July-August cruises according to gear.

		Cruise					
		June		July-August		Total	
	Gear	Shallow	Deep	Shallow	Deep	Shallow	Deep
Number of hauls taken	Bongo	15	15	16	16	31	31
	IKMT[1]	17	17	16	16	33	33
	Total	32	32	32	32	64	64
Number of positive hauls	Bongo	8	12	10	10	18	22
	IKMT	15	15	14	13	29	28
	Total	23	27	24	23	47	50
Number of taxa taken	Bongo	7	17	5	11	9	21
	IKMT	11	15	14	23	18	25
	Total	16	21	14	24	20	28
Volume of water filtered (1,000 m^3)	Bongo	35.73	28.87	30.26	27.35	65.99	56.22
	IKMT	304.12	245.40	222.94	199.46	527.06	444.86
	Total	339.85	274.27	253.20	226.81	593.05	501.08
Numbers of larvae originally in samples	Bongo	1556	257	13,823	10,668	15,379	10,925
	IKMT	93	81	5,157	7,081	5,250	7,162
	Total	1649	338	18,980	17,749	20,629	18,087
Numbers of larvae per 1,000 m^3 of total water filtered	Bongo	43.55	8.90	456.81	390.05	233.05	194.32
	IKMT	0.30	0.33	23.13	55.50	9.96	16.10
	Total	4.85	1.23	74.96	78.82	34.78	36.10

[1] IKMT = Isaacs-Kidd midwater trawl.

TABLE 4.—Frequency of occurrence (%) of fish larvae in shallow vs. deep samples taken in June and July-August.

Taxa	Bongos						Isaacs-Kidd midwater trawl						Grand total	
	June		July-Aug.		Total		June		July-Aug.		Total			
	Shal.	Deep	Shal.	Deep	Shal.	Deep	Shal.	Deep	Shal.	Deep	Shal.	Deep	Shal.	Deep
ENGRAULIDAE:														
Engraulis mordax	13.3	6.7	56.2	56.2	35.5	32.2	—	—	75.0	62.5	36.4	30.3	35.9	31.2
OSMERIDAE:														
Undetermined spp.	6.7	6.7	6.2	6.2	6.4	6.4	17.6	5.9	43.8	43.8	21.2	15.2	14.1	10.9
BATHYLAGIDAE:														
Bathylagus milleri	—	6.7	—	—	—	3.2	—	5.9	—	6.2	—	6.1	—	4.7
Bathylagus ochotensis	—	6.7	—	—	—	3.2	—	—	—	18.8	—	9.1	—	6.2
Bathylagus pacificus	—	13.3	—	—	—	6.4	—	11.8	—	6.2	—	9.1	—	7.8
GONOSTOMATIDAE:														
Danaphos sp.	—	6.7	—	—	—	3.2	—	—	—	—	—	—	—	1.6
CHAULIODONTIDAE:														
Chauliodus macouni	—	—	—	6.2	—	3.2	—	—	—	18.8	—	9.1	—	6.2
PARALEPIDIDAE:														
Lestidium ringens	—	—	—	6.2	—	3.2	5.9	11.8	6.2	18.8	6.1	15.2	3.1	9.4
MYCTOPHIDAE:														
Diaphus theta	—	—	—	6.2	—	3.2	—	—	—	12.5	—	6.1	—	4.7
Lampanyctus regalis	—	—	—	12.5	—	6.4	—	—	12.5	25.0	6.1	12.1	3.1	9.4
Protomyctophum crockeri	—	—	—	—	—	—	—	5.9	—	6.2	—	6.1	—	3.1
Protomyctophym thompsoni	—	20.0	—	6.2	—	12.9	—	17.6	12.5	25.0	6.1	21.2	3.1	17.2
Stenobrachius leucopsarus	26.7	26.7	12.5	43.8	19.4	35.5	11.8	29.4	37.5	56.2	24.2	42.4	21.9	39.1
Tarletonbeania crenularis	—	13.3	—	25.0	—	19.4	—	5.9	12.5	43.8	6.1	24.2	3.1	21.9
TRACHIPTERIDAE:														
Trachipterus sp.	—	—	—	—	—	—	—	—	6.2	18.8	3.0	9.1	1.6	4.7
SCORPAENIDAE:														
Sebastes spp.	—	6.7	—	12.5	—	9.7	35.3	47.0	12.5	31.2	24.2	39.4	12.5	26.0
Sebastolobus spp.	—	—	—	—	—	—	—	—	—	6.2	—	3.0	—	1.6
COTTIDAE:														
Undetermined spp.	—	6.7	6.2	—	3.2	3.2	5.9	5.9	12.5	6.2	9.1	6.1	6.2	4.7
CYCLOPTERIDAE:														
Undetermined spp.	—	20.0	—	6.2	—	12.9	23.5	47.0	—	25.5	12.1	36.4	6.2	25.0
BATHYMASTERIDAE:														
Ronguilus jordani	—	—	—	—	—	—	5.9	—	—	—	3.0	—	1.6	—
STICHAEIDAE:														
Plectobranchus evides	—	—	—	—	—	—	—	—	—	6.2	—	3.0	—	1.6
Unidentified 1	6.7	—	—	—	3.2	—	—	—	—	—	—	—	1.6	—
AMMODYTIDAE:														
Ammodytes hexapterus	6.7	—	—	—	3.2	—	—	—	—	—	—	—	1.6	—
NOMEIDAE:														
Icichthys lockingtoni	—	—	—	—	—	—	—	—	12.5	6.2	6.1	3.0	3.1	1.6
BOTHIDAE:														
Citharichthys sordidus	—	13.3	—	—	—	6.4	23.5	11.8	—	—	12.1	6.1	6.2	6.2
Citharichthys stigmaeus	20.0	20.0	—	—	9.7	9.7	58.8	17.6	6.2	6.2	33.3	12.1	21.9	10.9
PLEURONECTIDAE:														
Glyptocephalus zachirus	—	13.3	—	—	—	6.4	5.9	—	—	—	3.0	—	1.6	3.1
Isopsetta isolepis	6.7	—	—	—	3.2	—	11.8	5.9	6.2	—	9.1	3.0	6.2	1.6
Lyopsetta exilis	—	6.7	—	—	—	3.2	—	—	—	—	—	—	—	1.6
Microstomus pacificus	—	—	—	—	—	—	—	5.9	—	6.2	—	6.1	—	3.1
Psettichthys melanostictus	—	6.7	6.2	—	3.2	3.2	—	—	12.5	6.2	6.1	3.0	4.7	3.1
Unidentified	6.7	—	—	—	3.2	—	—	—	—	6.2	—	3.0	1.6	1.6

Deep tows:

73.1% Engraulidae in 31.2% of all samples
23.8% Myctophidae in 95.3% of all samples
1.7% Scorpaenidae in 26.6% of all samples

Deep tows consistently yielded a greater number of taxa because they sampled more completely the vertical range of larval fishes. The taxa most frequently taken (>20% of samples) in shallow tows were *E. mordax*, *S. leucopsarus*, and speckled sanddab, *Citharichthys stigmaeus*. In deep tows they were *S. leucopsarus*, *E. mordax*, *Sebastes* spp., Cyclopteridae, and *T. crenularis*. Frequency of occurrence of *E. mordax* in samples was generally higher in shallow tows than in deep tows (the same in shallow and deep bongo samples from July-August). On both the June and July-August cruises the bongos took more anchovies in surface tows than in deep tows. The IKMT took no anchovy larvae in June and in July-August captured more anchovies in deep tows than in surface tows. The IKMT is more selective for larger forms because small larvae can escape through the net. Thus small anchovy larvae appear to be concentrated in surface waters, with larger larvae

occurring deeper. Myctophids, scorpaenids, bathylagids, and cyclopterids had a much higher frequency of occurrence in deep tows.

Species Composition

Positive samples (207 out of 287) yielded 28,489 fish larvae from all deep tows (Table 1). Of the 40 taxa, 28 were identified to species and 6 to genus. Twenty-two families were represented.

Ninety-eight percent of all larvae (individuals/1,000 m^3) in combined samples were in four families:

68.4% Engraulidae in 29.6% of all samples
25.3% Myctophidae in 96.9% of all samples
4.2% Scorpaenidae in 34.1% of all samples
0.4% Osmeridae in 4.2% of all samples

Other families represented in over 5% of the samples were: Pleuronectidae, 19.5% of all samples; Cyclopteridae, 15.7%; Bathylagidae, 14.3%; Bothidae, 13.6%; Chauliodontidae, 9.8%; and Paralepididae, 7.3%.

During the sampling period, abundance of larvae per 1,000 m^3 estimated from combined samples (Table 1) peaked in July-August and was lowest in October. Results from the MN indicated greatest abundance in May and June. The MN collected many small *E. mordax* in June and *S. leucopsarus* in May and June (Table 5). By the July-August cruise, larvae of these two species were still abundant, however the larger specimens were not as readily captured by the more slowly hauled MN.

Dominance

Dominant taxa for each type of gear during each cruise were determined by a ranking system (biological index, BI) modified from Fager (1957). By this method, the most numerous species in each sample is given 5 points, the next 4, etc. Scores for each taxa are summed for all positive samples for each cruise and each type of gear and divided by the total number of samples (positive and negative) on that cruise by that gear. Both abundance and frequency of occurrence are considered in this determination.

BI values from each type of gear and all gear combined for combined cruises indicated the same four taxa were most dominant, *E. mordax*, *S. leucopsarus*, *T. crenularis*, and *Sebastes* spp., although not necessarily in that order (Table 6). *S. leucopsarus* had a higher BI value than *E. mordax* in MN samples and combined samples. *Sebastes* spp. ranked above *T. crenularis* in IKMT samples. A drop in BI value, indicating a lower degree of dominance, existed between the fourth and fifth highest ranked taxa for each gear, particularly MN and IKMT, and combined gears. Only the bongos agreed with taxa shown to be in the top 11 by combined gears, although not in the same order.

Some of the discrepancy among gear types may be explained by size of organisms captured. The high BI values of osmerids; rex sole, *Glyptocephalus zachirus;* and *Lestidium ringens* in IKMT samples was in part due to the large size of most specimens which would avoid the smaller types of gear. None of these taxa was captured by the MN and generally few were taken by the bongos. Some of the higher ranked taxa from bongo and MN samples, Pacific viperfish, *Chauliodus macouni*, and *Bathylagus ochotensis*, are very slender forms which may escape readily through the IKMT net. Specimens of pinpoint lampfish, *Lampanyctus regalis*, taken by the MN in June were small, mostly 3 to 4 mm, and may have been extruded out of the bongos because of the fast tow speed. BI values indicate that the IKMT captured more large organisms, the MN captured more small or slender forms, and the bongos were intermediate.

The most dominant (BI) taxa in May (all gear combined) were *Sebastes* spp. and *S. leucopsarus*; in June, *S. leucopsarus* and *T. crenularis*; in July-August, *E. mordax* and *S. leucopsarus*; in August and September, *S. leucopsarus*, *E. mordax*, *T. crenularis*; and in October, *Sebastes* spp. and *E. mordax* (Table 7). All had a $BI > 1$. All taxa below these had a $BI < 1$, usually with a considerable drop in BI value from the most dominant taxa. *S. leucopsarus*, *T. crenularis*, and *Sebastes* spp. consistently ranked in the top five from May through September (Table 5). *E. mordax* became the most dominant species in July-August and remained dominant through October.

TABLE 5.—Numbers of larvae per 1,000 m³ of total volume of water filtered in deep hauls according to type of gear and month of cruise. (M = <0.01/1,000 m³.)

Taxa	Bongos					Meter net							Isaacs-Kidd midwater trawl						
	June	July-Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total
EEL LEPTOCEPHAULUS:																			
Unidentified 1	0	0	0	0	0	0	0	0	0	0	0	0	M	0	0	0	0	0	M
ENGRAULIDAE:																			
Engraulis mordax	3.61	204.13	7.94	0.19	72.79	0	26.77	13.72	3.94	0	0	7.73	0	0	28.69	5.65	1.24	0.25	5.28
OSMERIDAE:																			
Undetermined spp.	0.04	0.37	0	0	0.14	0	0	0	0	0	0	0	0	M	0.26	M	0	0.01	0.05
BATHYLAGIDAE:																			
Bathylagus milleri	0.02	0	0	0	0.01	0	0	0	0	0	0	0	0	0.01	M	0	0	0	M
Bathylagus ochotensis	0.40	0	0.05	0	0.15	6.91	0.78	0.98	1.31	0	0	1.40	0.04	0.01	0.01	0.04	M	0	0.02
Bathylagus pacificus	0.02	0	0	0	0.01	2.51	0.78	0	0	0	0	0.52	0	M	M	M	M	0	M
Leuroglossus stilbius	0	0	0	0	0	0	0	0	0	0	0	0	M	0	0	0	0	0	M
GONOSTOMATIDAE:																			
Danaphos sp.	0.36	0	0	0	0.13	0	0	0	0	0	0	0	M	0	0	0	0	0	M
Diplophos sp.	0	0	0	0	0	0	0	0.98	0	0	0	0.08	0	0	0	0	0	0	0
MELANOSTOMATIDAE:																			
Tactostoma macropus	0	0	0	0	0	0	0	0	0	0	0	0	M	0	M	M	0.01	0	M
CHAULIODONTIDAE:																			
Chauliodus macouni	0.11	0.05	0	0.04	0.06	1.25	1.57	0	1.31	0	0	0.70	0.02	0.02	0.04	0.10	0.01	0	0.02
ALEPOCEPHALIDAE:																			
Sagamichthys abei	0	0	0	0	0	0	0	0	0	0	0	0	M	0	0	0	0	0	M
PARALEPIDIDAE:																			
Lestidium ringens	0.02	0.76	0	0	0.27	0	0	0	0	0	0	0	0.06	0.01	0.04	0.01	0	0	0.01
SCOPELARICHIDAE:																			
Benthabella dentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	M	M	M	0	M
MYCTOPHIDAE:																			
Diaphus theta	0	0.02	0	0	0.01	0	0	0	0	0	0	0	0	0	0.01	0.01	M	0	M
Lampanyctus regalis	0	2.48	0	0	1.03	0	4.33	0	0	0	0	0.96	0	M	0.18	0.03	0.01	0	0.01
Lampanyctus ritteri	0	0	0	0	0	0	2.36	0	0	0	0	0.52	0	0	0	0	0	0	0
Protomyctophum crockeri	0	0.02	0.05	0	0.02	0	0	0	0	0	0	0	0.01	M	0.01	0.01	0	0	M
Protomyctophum thompsoni	0.25	0.05	0.35	0.04	0.15	0	0.39	0.98	0	0	0	0.17	0.04	0.03	0.07	0.23	0.04	0	0.05
Stenobrachius leucopsarus	5.34	84.57	2.45	0	31.39	59.74	55.51	23.52	13.81	15.78		27.35	0.02	0.35	0.41	6.23	0.47	0	1.02
Tarletonbeania crenularis	0.16	5.24	1.28	0.04	2.05	3.77	10.23	0	5.92	1.57	0	3.86	0.04	0.11	0.37	0.94	0.23	0	0.19
MACROURIDAE:																			
Unidentified 1	0	0	0	0	0	0	0	0	0	0	0	0	M	0	0	0	0	0	M
MELAMPHAEIDAE:																			
Melamphaes sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	M	0	0	0	M
TRACHIPTERIDAE:																			
Trachipterus sp.	0	0	0	0.04	0.01	0	0	0	0	0	0	0	0	0	0.02	0	0	0	M
SCORPAENIDAE:																			
Sebastes spp.	0.04	5.17	0.23	0.09	1.98	15.72	12.59	0.98	3.28	4.21	1.07	6.50	3.32	0.07	0.09	0.73	0.08	0.10	0.43
Sebastolobus spp.	0	0	0	0.04	0.01	0	0	0	0	0	0	0	M	M	M	0	0.03	M	0.01
COTTIDAE:																			
Undetermined spp.	0.02	0.01	0	0	0.01	0	0	0	0	0	0	0	0.03	M	0.01	0.01	0	0	M
AGONIDAE:																			
Undetermined spp.	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	M
CYCLOPTERIDAE:																			
Undetermined spp.	0.18	0.05	0	0	0.08	0	0	0.98	0	0	0	0.08	0.05	0.05	0.03	0.07	0.01	M	0.03
STICHAEIDAE:																			
Plectobranchus evides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.01	M	0	M
NOMEIDAE:																			
Icichthys lockingtoni	0	0	0	0	0	0	0.78	0	0	0	0.35	0.26	0	M	0.02	0	0	M	M

TABLE 5.—*Continued.*

Taxa	Bongos					Meter net							Isaacs-Kidd midwater trawl					
	June	July-Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total	May	June	July-Aug.	Aug.	Sept.	Oct.	Total
BOTHIDAE:																			
Citharichthys sordidus	0.04	0	0	0	0.02	0	0	0	0	0.52	0	0.08	0.06	0.01	M	M	0	M	0.01
Citharichthys stigmaeus	0.07	0	0	0	0.02	0.62	0	0	0	0	0	0.08	0.03	0.02	0.01	0	0.02	0.01	0.02
PLEURONECTIDAE:																			
Eospetta jordani	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0	M
Glyptocephalus zachirus	0.07	0	0	0	0.02	0	0	0	0	0	0	0	0.04	M	M	M	0.02	0.01	0.01
Isopsetta isolepis	0	0	0	0	0	2.50	0	0	0	0	0	0.35	0.04	M	0	0	0	0	M
Lyopsetta exilis	0.02	0	0	0	0.01	3.77	0	0	0	0	0	0.52	0.01	0.01	M	0.01	M	M	0.01
Microstomus pacificus	0.02	0	0.05	0	0.02	0	0	0	0	0	0	0	0.01	0.01	M	0	M	M	M
Parophrys vetulus	0	0	0	0	0	2.51	0	0	0	0	0	0.35	0.01	0	0	0	0	0	M
Psettichthys melanostictus	0.02	0	0	0	0.01	0.62	0	0	0	0	0	0.08	M	0	M	0	M	M	M
Miscellaneous fragments:																			
Unidentified myctophid	0	0	0.05	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pleuronectid	0	0	0	0.19	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified fragments	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	M
Total	11.9	303.42	12.50	0.72	110.44	100.0	116.14	42.15	29.60	22.10	1.42	51.71	3.98	0.73	32.35	14.17	2.26	0.43	7.24

Comments on Major Families

Discussion is limited to the most important families. Numbers of larvae refer to total numbers taken during the sampling period. Comments on distribution focus on inshore-offshore aspects as no north-south differences were evident except for *E. mordax*. Trends in seasonality can be determined from Tables 2 and 5.

Engraulidae (43,191 larvae in 110 samples)

E. mordax larvae were taken first on the June cruise. At that time, larval lengths ranged from 3 to 12 mm with a median at 8 mm (Figure 2A). Some were newly hatched. Spawning probably occurred from June until August in 1969 if growth rates (to 10.2 mm in 20 days after fertilization) given by Lasker et al. (1970) are comparable for this area. Surface water temperatures were cooler (14°-17°C) than the 17.5°C temperature used in their experiments and would result in a longer development time. The smallest larvae collected after August were 18 mm which suggests the spawning period was limited. Larval growth throughout the study period is indicated in Figure 2. Ranges of SL overlapped considerably in July-August and August, probably because of continued spawning into August. By September spawning appeared to be over and a marked increase in median length was shown from September to October.

Ranges, medians, and median quartiles of SL of larvae differed somewhat according to gear type for each cruise (Figure 2A). Some of the apparent differences may be a result of small numbers of larvae measured. The IKMT did not catch any anchovies until July-August when larvae were larger. The MN did not catch any after August probably because the larger forms avoided the net. By October, only the IKMT took anchovies (except for one specimen taken by the bongos) which had a median length of 43 mm.

Anchovy larvae were most abundant in Columbia River plume waters in June and July-August. Larvae were not taken north of the Columbia River or south of the major influence of plume waters. They were not abundant near

TABLE 6.—Ranks (biological index) of most dominant taxa by gear for each cruise and for all cruises combined, and for combined gears and cruises. (*denotes top 10 taxa for each gear, cruises combined, and combined gears and cruises.)

	Bongos					Meter net						
Taxa	June	July-Aug.	Sept.	Oct.	Combined cruises	May	June	July-Aug.	Aug.	Sept.	Oct.	Combined cruises
Engraulis mordax	0.22	2.74	3.44	0.63	1.86*	—	1.12	1.80	1.46	—	—	0.73
Stenobrachius leucopsarus	1.30	2.04	2.00	—	1.34*	2.32	3.32	2.35	1.88	1.41	—	1.88*
Tarletonbeani crenularis	0.70	0.48	2.19	0.63	1.00*	0.86	1.62	—	1.15	0.53	—	0.69*
Sebastes spp.	0.20	0.22	0.64	1.19	0.56*	1.00	1.10	0.35	0.23	0.24	0.20	0.52*
Protomyctophum thompsoni	0.67	0.02	0.64	0.33	0.42*	—	0.18	0.35	—	—	—	0.09*
Cyclopteridae	1.02	0.13	—	—	0.29*	—	—	0.50	—	—	—	0.08*
Chauliodus macouni	0.39	0.02	—	0.63	0.26*	0.21	0.22	—	0.12	—	—	0.09*
Bathylagus ochotensis	0.20	—	0.32	—	0.13*	0.93	0.18	0.40	0.12	—	—	0.27*
Glyptocephalus zachirus	0.50	—	—	—	0.12*	—	—	—	—	—	—	—
Osmeridae	0.22	0.22	—	—	0.11*	—	—	—	—	—	—	—
Citharichthys stigmaeus	0.43	—	—	—	0.11*	0.36	—	—	—	—	—	0.06*
Sebastolobus spp.	—	—	—	0.33	0.08	0.08	—	—	—	—	—	0.01
Lampanyctus regalis	—	0.30	—	—	0.08	—	0.78	—	—	—	—	0.13*
Cottidae	0.20	—	—	—	0.05	—	—	—	—	—	—	—
Citharichthys sordidus	0.24	—	—	—	0.04	—	—	—	—	0.29	—	0.05
Lestidium ringens	—	0.09	—	—	0.02	—	—	—	—	—	—	—
Isopsetta isolepis	—	—	—	—	—	—	—	—	—	—	—	—

	Isaacs-Kidd midwater trawl							
Taxa	May	June	July-Aug.	Aug.	Sept.	Oct.	Combined cruises	Combined gears
Engraulis mordax	—	—	3.43	3.57	2.66	2.50	2.03*	1.54*
Stenobrachius leucopsarus	0.45	1.68	2.65	4.11	2.78	—	1.94*	1.72*
Tarletonbeania crenularis	0.42	1.00	1.48	2.34	2.14	—	1.40*	1.03*
Sebastes spp.	4.03	1.15	0.51	1.36	1.78	2.00	1.80*	0.96*
Protomyctophum thompsoni	0.47	1.09	0.26	1.04	0.52	—	0.56*	0.36*
Cyclopteridae	0.63	1.26	0.65	0.39	0.51	0.11	0.59*	0.32*
Chauliodus macouni	0.16	0.25	0.04	0.38	0.16	—	0.16	0.17*
Bathylagus ochotensis	0.66	0.21	0.16	—	—	—	0.17	0.19*
Glyptocephalus zachirus	0.21	0.06	—	—	0.46	1.04	0.30*	0.14*
Osmeridae	—	0.13	0.76	0.14	—	0.59	0.27*	0.13
Citharichthys stigmaeus	0.42	0.63	0.15	—	0.97	0.75	0.49*	0.22*
Sebastolobus spp.	0.10	0.15	—	—	0.43	0.73	0.22	0.10
Lampanyctus regalis	—	0.02	0.43	—	—	—	0.08	0.10
Cottidae	0.46	0.13	0.17	0.50	—	—	0.21	0.09
Citharichthys sordidus	0.71	0.25	—	—	—	0.16	0.19	0.09
Lestidium ringens	1.22	0.18	0.28	—	—	—	0.28*	0.10
Isopsetta isolepis	0.79	0.12	—	—	—	—	0.15	0.06

TABLE 7.—Ranks (biological index) of most dominant taxa by cruise, all gear combined. (* denotes top 5 taxa for each cruise.)

Taxa	May	June	July-Aug.	Aug.	Sept.	Oct.
Engraulis mordax	—	0.45	2.66*	2.52*	2.03*	1.04*
Stenobrachius leucopsarus	1.39*	2.10*	2.36*	3.00*	2.06*	—
Tarletonbeania crenularis	0.64*	1.11*	0.65*	1.75*	1.62*	0.21
Sebastes spp.	2.52*	0.82*	0.36*	0.80*	0.89*	1.13*
Protomyctophum thompsoni	0.24	0.65*	0.21	0.52*	0.39*	0.11
Cyclopteridae	0.32	0.83*	0.43*	0.20	0.17	0.04
Chauliodus macouni	0.19	0.29	0.02	0.25	0.05	0.21
Bathylagus ochotensis	0.80*	0.20	0.19	0.06	0.11	—
Glyptocephalus zachirus	0.11	0.19	—	—	0.15	0.35*
Osmeridae	—	0.12	0.33	0.07	—	0.20
Citharichthys stigmaeus	0.39	0.35	0.05	—	0.32	0.25*
Sebastolobus spp.	0.04	0.05	—	—	0.14	0.35*
Lampanyctus regalis	—	0.27	0.24	—	—	—
Cottidae	0.23	0.11	0.06	0.25	—	—
Citharichthys sordidus	0.36	0.16	—	—	0.10	0.05
Lestidium ringens	0.61*	0.06	0.12	—	—	—
Isopsetta isolepis	0.45	0.04	—	—	—	—
Psettichthys melanostictus	0.26	0.01	—	—	0.09	0.05

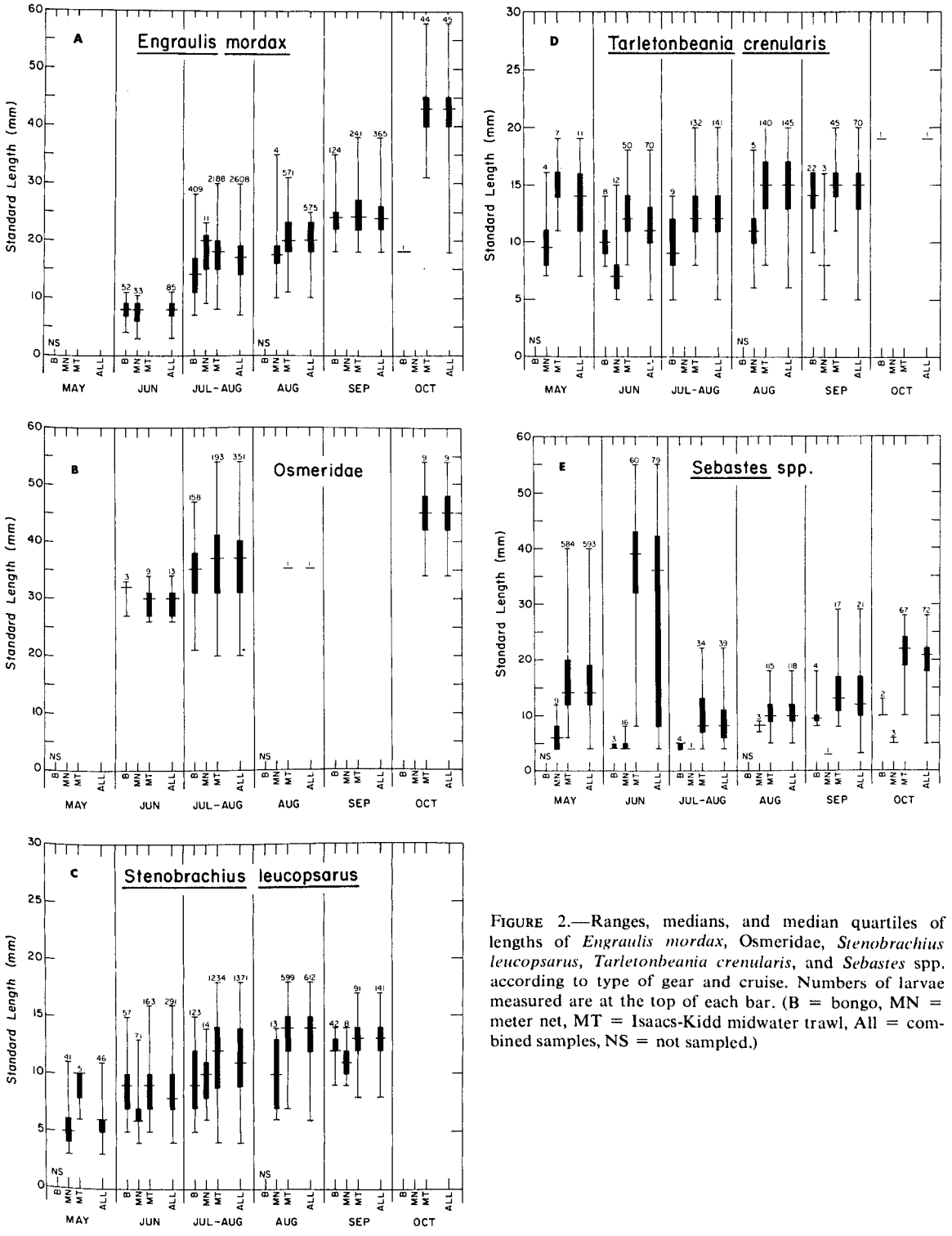

FIGURE 2.—Ranges, medians, and median quartiles of lengths of *Engraulis mordax*, Osmeridae, *Stenobrachius leucopsarus*, *Tarletonbeania crenularis*, and *Sebastes* spp. according to type of gear and cruise. Numbers of larvae measured are at the top of each bar. (B = bongo, MN = meter net, MT = Isaacs-Kidd midwater trawl, All = combined samples, NS = not sampled.)

the coastline or offshore beyond the bounds of the plume. Their distribution showed a closer correlation with temperature than salinity. Plots of larval abundance, which ranged from <1 to 62/1,000 m³, 210 to 451/1,000 m³, and 14 to 252/1,000 m³ in positive tows in deep bongo, shallow bongo, and MN samples respectively in June, are in Figure 3. Larvae were associated with water >14°C which agrees with Ahlstrom's (1959) findings off California. Plots of abundance (2 to 840/1,000 m³ and <1 to 4,493/1,000 m³ in deep and shallow bongo samples) for July-August (Figure 4) again show larvae concentrated in water >14°C. Upwelling was prevalent at that time with colder water near shore. The Columbia River plume was not clearly distinguishable although the warm waters offshore were probably a result of the plume (Pearcy and Mueller, 1969). After the July-August cruise, fewer larvae were taken and distribution was scattered throughout the area sampled.

Small anchovy larvae were concentrated in surface waters which agrees with Ahlstrom's (1959) results on vertical distribution of anchovies off California.

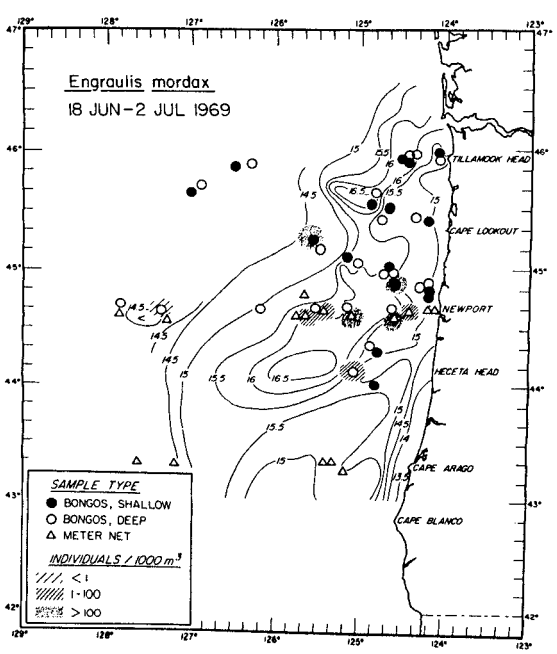

FIGURE 3.—Distribution of *Engraulis mordax* larvae and surface temperature, June 1969.

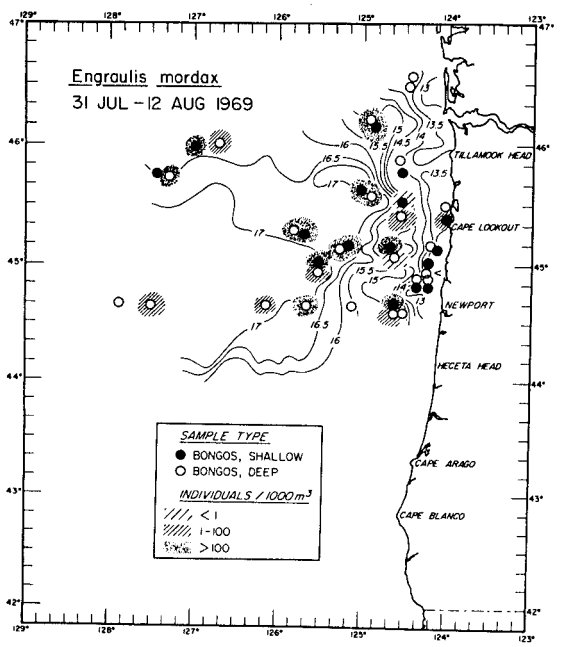

FIGURE 4.—Distribution of *Engraulis mordax* larvae and surface temperature, July-August 1969.

Results of meristics and blood genetics studies have indicated at least three distinct anchovy subpopulations exist off Oregon, California, and Baja California (Vrooman and Smith, 1972). The present results together with previous studies offer support for the existence of a separate stock off Oregon. Anchovy larvae were abundant in Columbia River plume waters in the upper 10 to 20 m in 1969. Waters of the Columbia River plume have a strong vertical density gradient and a shallow mixed layer depth (Owen, 1968). Anchovies spawn mostly in the upper 10 m at temperatures >14°C (Ahlstrom, 1959). Adult anchovies were reported in unusually large concentrations near the coast of northern California and Oregon in 1969 (Frey, 1971). The adults were probably spawning. CalCOFI (California Cooperative Oceanic Fisheries Investigations) sampling has indicated a high abundance of anchovy larvae off southern California with a substantial drop in abundance from southern to northern California. In 1949 and 1950, anchovy larvae were found in moderate abundance off Oregon (Ahlstrom, 1968). Thus, a separate spawning stock of an-

chovies seems to exist off Oregon associated with the warm, near surface waters of the Columbia River plume. The spawning period seems to be correlated with the time when warm plume water is a dominant oceanographic feature, before the rest of the ocean surface water warms to >14°C. Additional sampling for eggs as well as larve with even more extensive coverage is needed to determine areal extent of spawning and extent of yearly variation caused by changing oceanographic conditions.

Osmeridae (687 larvae in 21 samples)

Larvae of osmerids were collected in June, July-August, August, and October at the nearshore stations shown in Figure 5. The nearshore area was heavily sampled on the July-August cruise, perhaps explaining why few or no specimens were taken on other cruises. Similarly, no samples were taken near shore south of Newport (Figure 1). Distribution appears to be restricted to near shore when upwelling was prominent.

All specimens have not yet been identified to species, although some are known to be *Thaleichthys pacificus*. The trend in growth in Figure 2B might indicate all the larvae were products of one major spawning and therefore one species.

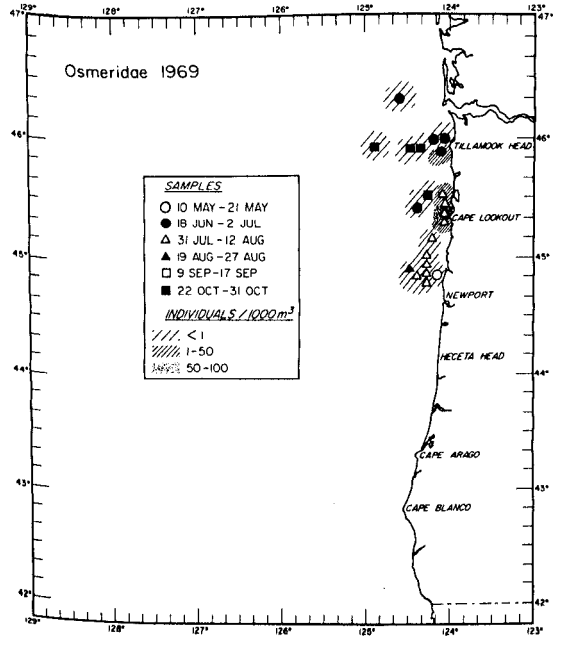

FIGURE 5.—Distribution of osmerids collected from June to October 1969.

Mycthophidae (8,694 larvae in 152 samples)

Larvae of *S. leucopsarus* (7,683 specimens) were taken from May to September in moderate numbers. Capture of 3-mm individuals in May (Figure 2C) indicated spawning may have occurred recently, although early growth rates have not yet been established. The occurrence of 4-mm larvae as late as July-August appears to extend the spawning period off Oregon beyond the December to March range estimated by Smoker and Pearcy (1970). The smallest larvae taken in September were 8 mm. No larvae were taken in October which supports the idea that *S. leucopsarus* does not spawn throughout the year off Oregon.

The IKMT generally captured larger larvae than the bongos or MN (Figure 2C). An increase in median length of larvae occurred from May through August. Individuals about to undergo metamorphosis, which occurs around 18 mm (Smoker and Pearcy, 1970), were taken from July-August to September. By October, all larvae apparently had begun the process of metamorphosis, which takes place at depths greater than we sampled (Fast, 1960).

Larvae of *S. leucopsarus* were more abundant west of long. 124°30′W(about 20 nautical miles off Newport, Oreg.) than closer to shore (Table 8) although a few specimens did occur in nearshore samples. North-south distribution was scattered. Larvae were never taken around the mouth of the Columbia River where lower salinity water fans out into the ocean. Larvae were more frequently taken in deep (200 m) tows than in shallow tows (Table 4) during the June and July-August cruises.

Larvae of *T. crenularis* (714 specimens) were collected on all cruises. Larval lengths ranged from 5-7 mm to 19-20 mm on each cruise from May to September (Figure 2D). From these data, *T. crenularis* appears to spawn at least throughout the period sampled, although collection of only one specimen in October cannot be explained.

TABLE 8.—Numbers of individuals/1,000 m³ of water filtered in deep hauls of *Stenobrachius leucopsarus* and *Tarletonbeania crenularis* taken east (near shore) and west (offshore) of long. 124°30′W.

Species		Bongos		Meter net		Isaacs-Kidd midwater trawl	
		East	West	East	West	East	West
Stenobrachius leucopsarus	May	—	—	0	65.97	0	0.03
	June	0	6.04	25.00	57.76	0.02	0.40
	July-Aug.	0	89.95	0	26.67	0.15	2.72
	Aug.	—	—	11.76	14.07	0.14	6.84
	Sept.	0	2.58	0	17.86	0	0.49
	Oct.	0	0	0	0	0	0
Tarletonbeania crenularis	May	—	—	0	4.17	0	0.04
	June	0	0.20	0	10.92	0	0.12
	July-Aug.	0	5.90	0	0	0	0.42
	Aug.	—	—	11.76	5.19	0.14	1.03
	Sept.	0	0.01	0	1.79	0	0.24
	Oct.	0	0.05	0	0	0	0

Distribution of *T. crenularis* larvae was more predominantly offshore than that of *S. leucopsarus* (Table 8). In August, two specimens each were collected with the IKMT and MN at long. 124°24.5′W. No additional *T. crenularis* were found closer to shore than long. 124°30′W. Distribution was scattered from north to south within the area sampled. During the June and July-August cruises, capture of *T. crenularis* larvae was almost entirely restricted to deep tows (Table 4.)

Other myctophids were captured in smaller numbers. *Lampanyctus regalis* (151 specimens) ranged from 3 to 19 mm in length and occurred mainly west of long. 125°W; only one specimen was taken nearer shore. Six *L. ritteri*, all 5 mm, were taken in two samples west of long. 127°30′W in June. *Protomyctophum thompsoni* (117 specimens, 6-20 mm) occurred somewhat closer to shore than *L. regalis*, with a moderate number between long. 124°30′W and 125°W. None was found closer to shore than long. 124°30′W. The distribution of flashlightfish, *P. crockeri*, (11 specimens, 6-20 mm) was similar to that of *P. thompsoni*. All 12 California headlightfish, *Diaphus theta*, (8-13 mm) were taken west of long. 125°30′W.

Scorpaenidae (1,205 larvae in 102 samples)

Sebastes spp. (1,189 specimens) were captured throughout the sampling period. Individual species were not identified so interpretation of data is limited. In May and June products of an earlier spawning were captured (individuals 40-55 mm) along with newly hatched (4 mm) larvae (Figure 2E). Growth of the smaller larvae can be observed from June to October in Figure 2E. Distribution of *Sebastes* spp. larvae was scattered throughout the area studied with no discernible pattern.

Larvae of *Sebastolobus* spp. (16 specimens, 10-40 mm) exhibited a scattered distribution similar to that of *Sebastes* spp.

Bothidae (93 larvae, 48 samples)

Pacific sanddab, *Citharichthys sordidus*, (25 specimens, 8-45 mm) occurred from long. 124°30′W to farther offshore. Distribution of *C. stigmaeus* (68 specimens, 17-44 mm) was concentrated closer to shore than that of *C. sordidus*, although some specimens were taken west of long. 126°W.

Pleuronectidae (123 larvae in 52 samples)

Four petrale sole, *Eopsetta jordani*, (13-21 mm) were collected in May: one off Tillamook Head at long. 125°W, one off Newport at long. 125°W, and two off Cape Arago—one at long. 125°W and the other at long. 126°W. *Glyptocephalus zachirus* (31 specimens, 22-89 mm) occurred throughout the sampling period from near shore to far offshore in no discernible pattern. All 33 butter sole, *Isopsetta isolepis*,

(12-22 mm) were captured east of long. 125°W. Most larvae were close to shore. Slender sole, *Lyopsetta exilis*, (21 specimens, 10-23 mm) occurred east of long. 125°30′W, but were not concentrated as close to shore as *I. isolepis*. Dover sole, *Microstomus pacificus*, (10 specimens, 12-61 mm) were all collected west of long. 125°W. The six English sole, *Parophrys vetulus*, (18-22 mm) taken in May occurred off Newport (2) and Cape Arago (4) between the coast and long. 125°W. Sand sole, *Psettichthys melanostictus*, (18 specimens, 15-26 mm) also occurred mainly between the coast and long. 125°W; two of the specimens were taken at long. 125°30′W.

ACKNOWLEDGMENTS

I thank Sharon Myers for her help with identification of fish larvae and Michael Richardson and William G. Pearcy for their helpful comments and review of the manuscript. This research was supported in part by NOAA (maintained by the U.S. Department of Commerce) Institutional Sea Grant 2-35187.

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MERCURY CONTENT OF OREGON GROUNDFISH[1]

E. A. CHILDS AND J. N. GAFFKE[2]

ABSTRACT

The mercury content of Oregon groundfish was determined. The mercury content of rex sole, *Glyptocephalus zachirus*; Dover sole, *Microstomus pacificus*; petrale sole, *Eopsetta jordani*; English sole, *Parophrys vetulus*; sand sole, *Psettichthys melanostictus*; starry flounder *Platichthys stellatus*; canary rockfish, *Sebastes pinniger*; flag rockfish, *Sebastes rubrivinctus*; yellowtail rockfish, *Sebastes flavidus*; rougheye rockfish, *Sebastes aleutianus*; sablefish, *Anoplopoma fimbria*; lingcod, *Ophiodon elongattus*; Pacific hake, *Merluccius productus*; and arrowtooth flounder, *Atheresthes stomias*; was significantly lower than 0.50 ppm mercury. All spiny dogfish, *Squalus acanthias*, samples contained >0.50 ppm. No highly significant relationship in those species appropriately examined between (a) catch location, (b) time of catch, (c) weight and length of fish, or (d) sex and mercury content was observed.

Although the possibility of seafood organisms containing large amounts of mercury has been of recent concern, no systematic survey of a major American marine fishery has been published. A number of freshwater studies in the United States (Willford, 1971), Canada (Uthe and Bligh, 1971; Bligh, 1972), England (Taylor, 1971), and Sweden (Ackefors, 1971), and marine studies in Canada (Zitko et al., 1971) and Sweden (Ackefors, 1971) are found in the literature. The present study was undertaken to determine the extent of mercury contamination of commercially important groundfish in the Oregon fishery, with data being obtained which would allow evaluation of the effect of species, location of catch, size of fish, time of catch, and sex on mercury content.

MATERIALS AND METHODS

Fish were obtained from each of the three major fishing areas off the Oregon Coast (Figure 1). Specimens were immediately dissected, packed in evacuated film, and held at -40°C until mercury analyses were performed. Five-gram samples of the epaxial musculature on both the right and left sides were taken for analysis, and thoroughly ground and mixed. The digestion apparatus consisted of a 250-ml flat-bottom distilling flask connected to a 45-cm cold-water condenser. The homogeneous samples were digested for 10 min in 20 ml of 1:1 (v/v) concentrated sulfuric and nitric acid, with 5-10

FIGURE 1.—Commercial fishing areas along Oregon coast from which samples for mercury analysis were obtained. N. - Northern coast C. - Central coast S. - Southern coast.

[1] Technical Paper No. 3422, Oregon State University Agricultural Experiment Station.

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Manuscript accepted December 1972.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

mg V_2O_{53} added to catalyze the digestive reaction. After digestion, 10 ml of distilled, deionized water were added; the samples were allowed to cool; and 3-5 drops of hydrogen peroxide solution (30% w/w) and another 10 ml of deionized, distilled water were added. The digests were then brought to 100 ml with distilled, deionized water. The amount of mercury in the digested samples was determined by flameless atomic absorption spectroscopy (AAS) (Hatch and Ott, 1968). The method was accurate (>95% recovery) and precise (standard error of mean for duplicates <5% of mean) in this laboratory for samples containing 0.05-6.0 μg mercury (i.e., based on a 5-g sample, the method is precise and accurate for 0.01-1.2 ppm Hg). The data obtained were a measure of total mercury, and stated in ppm wet weight.

Fish were obtained at various times from August 1971 to June 1972. All data represent catches from at least two different time periods. Duplicate analyses of samples were performed, and if the duplicates varied by greater than 0.05 ppm, the data were discarded, and new analyses performed. Reagent purity, glassware cleanliness, and AAS performance were scrutinized daily.

RESULTS AND DISCUSSION

The mercury content of groundfish caught off the Oregon coast is summarized in Table 1. The only species with a mean mercury content greater than the U.S. Food and Drug Administration's guideline of 0.50 ppm was spiny dogfish, *Squalus acanthias*. The *t*-function significance tests indicated the mean mercury content of arrowtooth flounder, *Atheresthes stomias*; sablefish, *Anoplopoma fimbria*; Pacific hake, *Merluccius productus*; starry flounder, *Platichthys stellatus*; rex sole, *Glyptocephalus zachirus*; Dover sole, *Microstomus pacificus*; petrale sole, *Eopsetta jordani*; English sole, *Parophrys vetulus*; sand sole, *Psettichthys melanostictus*; canary rockfish, *Sebastes pinniger*; flag rockfish, *Sebastes rubrivinctus*; and rougheye rockfish,

TABLE 1.—Mercury content of Oregon groundfish.

Species	Number of samples	Mean Hg content (ppm) ($\bar{x}$)	Range	Standard deviation	99% confidence interval (ppm)	*t*-function sig. levels for $\bar{x}$ <0.3 ppm	*t*-function sig. levels for $\bar{x}$ <0.5 ppm
Rex sole, *Glyptocephalus zachirus*	82	0.119	0.05-0.24	0.050	0.10-0.14	0.005	0.005
Dover sole, *Microstomus pacificus*	46	0.122	0.01-0.29	0.076	0.09-0.17	0.005	0.005
Petrale sole, *Eopsetta jordani*	94	0.114	0.05-0.32	0.045	0.10-0.13	0.005	0.005
English sole, *Parophrys vetulus*	128	0.108	0.06-0.21	0.032	0.10-0.12	0.005	0.005
Sand sole, *Psettichthys melanostictus*	48	0.083	0.03-0.16	0.036	0.06-0.10	0.005	0.005
Starry flounder, *Platichthys stellatus*	42	0.235	0.08-0.50	0.102	0.18-0.29	0.005	0.005
Canary rockfish, *Sebastes pinniger*	18	0.197	0.08-0.50	0.123	0.08-0.32	0.025	0.005
Yellowtail rockfish, *Sebastes flavidus*	24	0.371	0.19-0.53	0.095	0.30-0.45	NS[1]	0.005
Flag rockfish, *Sebastes rubrivinctus*	40	0.136	0.06-0.43	0.091	0.08-0.19	0.005	0.005
Rougheye rockfish, *Sebastes aleutianus*	30	0.080	0.06-0.11	0.012	0.07-0.09	0.005	0.005
Lingcod, *Ophiodon elongatus*	48	0.351	0.06-0.73	0.240	0.26-0.49	NS	0.010
Sablefish, *Anoplopoma fimbria*	52	0.138	0.03-0.65	0.148	0.07-0.21	0.005	0.005
Pacific hake, *Merluccius productus*	24	0.102	0.06-0.18	0.035	0.07-0.13	0.005	0.005
Arrowtooth flounder, *Atheresthes stomias*	26	0.154	0.01-0.33	0.089	0.08-0.22	0.005	0.005
Spiny dogfish, *Squalus acanthias*	88	0.602	0.20-1.14	0.275	0.52-0.71	NS	NS

[1] NS means not significant.

[3] The use of V_2O_5 to catalyze the digestion was originally developed by Robert Munns, Food and Drug Administration, Denver, Colo.

Sebastes pinniger; flag rockfish, *Sebastes rubrivinctus*; and rougheye rockfish, *Sebastes aleutianus* were significantly lower than 0.30 ppm at the 0.005 level. The means of all species were significantly lower than 0.50 ppm at the 0.005 significance level, with the exception of lingcod (the significance level was 0.01) and spiny dogfish (not significantly lower). Spiny dogfish were further investigated to determine if there was any difference in mercury content with regard to sex. The mean of all male samples was 0.58 ppm with a 99% confidence interval of 0.41-0.76 ppm, and the mean for female samples was 0.65 ppm with a 99% confidence interval of 0.53-0.77 ppm. The confidence interval ranges overlapped considerably and *t*-function analysis revealed no significant difference in mercury content based on sex.

Numerous species of soles and rockfishes were obtained. The mercury content of all soles was similar suggesting that their degree of exposure and metabolism of mercury may be similar. However, the mercury content of rockfishes varied widely, with yellowtail rockfish having a 99% confidence interval of 0.30-0.45 ppm, canary rockfish 0.08-0.32 ppm, and flag rockfish 0.08-0.19 ppm. These data make it difficult to predict the mercury content of marine fish on a phylogenetic basis.

For species of fish which were available along the entire coast, data were analyzed separately for each area (Table 2). There was variation among the coastal areas. Lingcod from the northern coast had a mean mercury content of 0.403 ppm, from the central coast 0.274, and from the southern coast 0.400. Conversely, sand sole from the central coast had more mercury than samples from the southern coast and Dover sole from the northern coast was lower than either of the other coastal areas. Thus, no relationship is immediately discernible between catch area and mercury content.

In freshwater fish it has been noted that there is a correlation between length and mercury content (Bligh, 1972). All present data were scrutinized by regression analysis to determine if a similar correlation existed in Oregon groundfish (Table 3). No highly discernible linear correlation (i.e., correlation coefficient greater than 0.90) between either length or weight and mercury content was noted. Graphs of mercury concentration vs. length are pre-

TABLE 2.—Mercury content of Oregon groundfish according to coastal area.

Species	Northern coast		Central coast		Southern coast	
	Mean	99% confidence interval	Mean	99% confidence interval	Mean	99% confidence interval
Rex sole	0.122	0.10-0.14			0.122	0.08-0.16
Dover sole	0.076	0.06-0.09	0.094	0.04-0.15	0.193	0.13-0.25
Sand sole			0.102	0.07-0.13	0.060	0.04-0.08
Starry flounder	0.266	0.18-0.35	0.194	0.12-0.27		
Lingcod	0.403	0.27-0.53	0.274	-0.21 to 0.76	0.400	-1.63 to 2.42
Sablefish	0.143	0.06-0.22			0.098	-0.07 to 0.27

TABLE 3.—Regression analysis of mercury content of Oregon groundfish vs. length and weight.

Species	Length correlation coefficient	Length range (cm)	Weight correlation coefficient	Weight range (kg)
Rex sole	0.546	27.0- 39.0	0.638	0.09- 0.46
Dover sole	0.254	34.0- 56.0	-0.065	0.30- 1.95
Sand sole	0.675	29.0- 50.0	0.609	0.22- 1.30
Starry flounder	-0.012	23.0- 55.5	-0.012	0.30- 2.80
Canary rockfish	0.307	40.0- 51.0	0.516	1.40- 3.20
Yellowtail rockfish	-0.517	39.0- 49.0	-0.443	1.30- 2.52
Flag rockfish	0.659	31.0- 44.0	0.479	0.22- 0.93
Rougheye rockfish	0.372	32.0- 37.0	0.353	0.55- 0.80
Lingcod	0.572	43.0-102.0	0.585	0.85-10.62
Sablefish	0.793	35.0- 88.0	0.728	0.38- 6.35
Pacific hake	0.462	26.5- 64.0	0.241	0.75- 1.25
Arrowtooth flounder	0.318	41.9- 53.3	0.230	0.64- 1.25
Spiny dogfish	0.469	65.0-108.6	0.486	0.42- 5.60

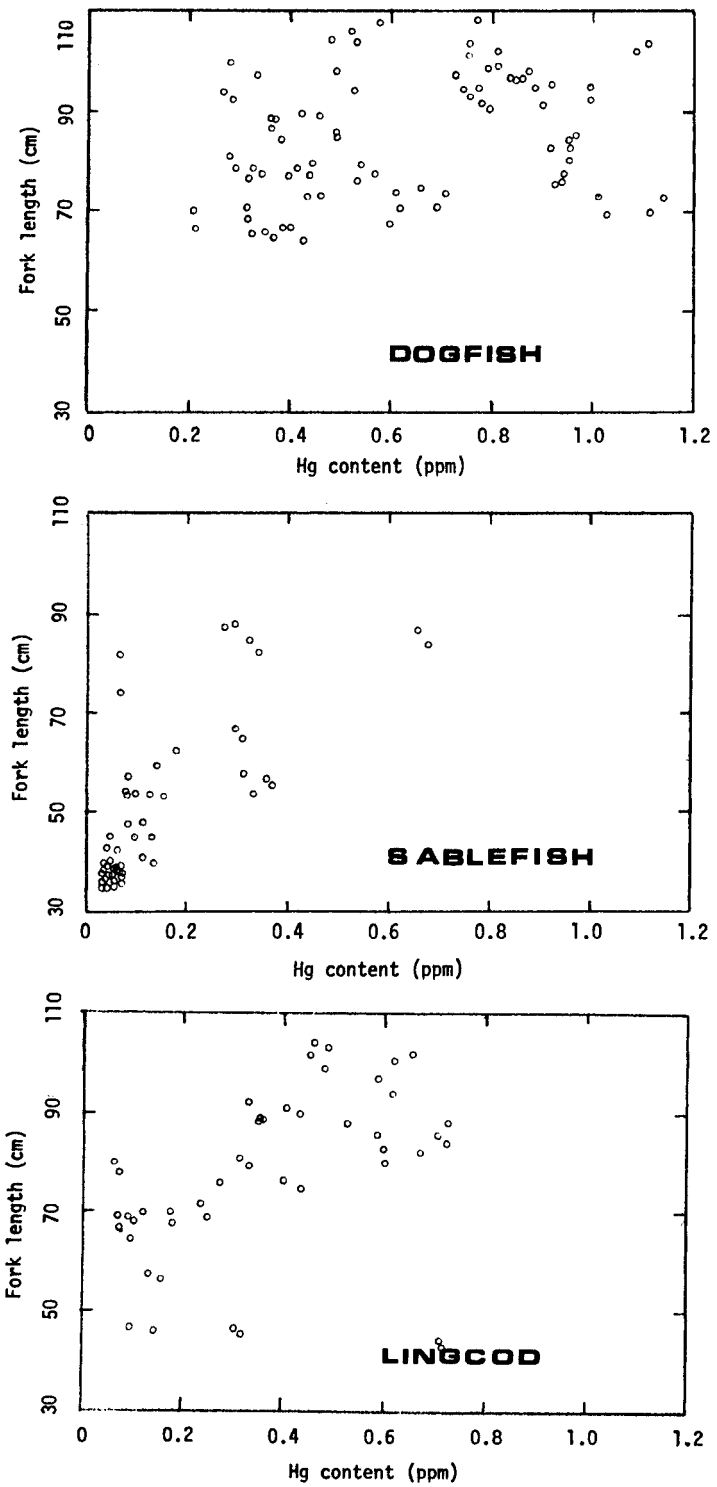

FIGURE 2.—Relation of mercury content to fork length in spiny dogfish, sablefish, and lingcod.

sented for samples of spiny dogfish, sablefish, and lingcod in Figure 2. The graphs of spiny dogfish and lingcod show a random spread. Since this study was concerned with commercially important fish, no attempt was made to acquire extremely small or large individuals. Naturally, the lack of linear correlation observed cannot be extended beyond the noted size ranges. It was thought there might be correlations within specific catch areas which were obliterated when the data were pooled; however, regression analysis of each catch area also showed no highly discernible linear correlation between length or weight and mercury content.

Fish taken at different times of the year did not contain greatly different amounts of mercury, with the exception of sablefish. In this species, 20% of the samples taken in August 1971 had a mercury content greater than 0.50 ppm, while samples obtained later in the study contained no fish with greater than 0.20 ppm mercury.

When these data were compared with those for the Bay of Fundy and Nova Scotia Banks (Zitko et al., 1971), Oregon groundfish were found to contain, on the average, slightly more mercury. However, the mean mercury content of Oregon groundfish was less than that reported for a number of Swedish coastal areas (Ackefors, 1971). In summary, Oregon groundfish contain small amounts of mercury, and the 99% confidence intervals suggest there is little probability of normal commercial catch samples exceeding the 0.50 ppm guideline established by the U.S. Food and Drug Administration.

ACKNOWLEDGMENTS

This study was financed in part by the National Oceanic and Atmospheric Administration (maintained by the U.S. Department of Commerce) Institutional Sea Grant No. 04-3-158-4. We thank D. L. Crawford, program director of the Seafoods Laboratory, for his administrative direction; V. L. Parsons for superior technical assistance; and Paul Heikkila, Ken Hilderbrand, Dean Murray, Joe Fenander, Fred Anderson, and the Otter Trawl Commission of Oregon for aid in collecting samples.

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PRELIMINARY ANALYSES OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, MIGRATIONS, POPULATION STRUCTURE, SURVIVAL AND EXPLOITATION RATES, AND AVAILABILITY AS INDICATED FROM TAG RETURNS

ROBERT L. DRYFOOS, RANDALL P. CHEEK, AND RICHARD L. KROGER[1]

ABSTRACT

Over 1 million adult Atlantic menhaden, *Brevoortia tyrannus*, were tagged from Long Island Sound to Florida between 1966 and 1969. Tag recoveries indicate these fish migrated northward in spring and early summer and southward in fall. As the fish grew older and larger, they also migrated farther northward each spring. Calculation of rates of interchange between fishing areas indicated that 21% of the recoveries from fish released in Chesapeake Bay in 1967 and 1968 accounted for 72% of the catch of tagged fish 1 yr later in New York and New Jersey.

Preliminary estimates of population parameters were made from tag-recovery and catch data. Survival rates determined yearly from ratio of recoveries, however, varied due to fluctuations in availability. Annual survival rates averaging 0.23 were calculated with Robson-Chapman catch curve analysis and age composition of catch methods. From tag recoveries, exploitation rate was estimated to be 50%, instantaneous fishing mortality rate (F) was 0.95, and instantaneous natural mortality (M) was 0.52. Tag returns also indicated that significant fluctuations in availability of Atlantic menhaden occurred in Chesapeake Bay.

Menhaden, genus *Brevoortia*, are distributed along the Atlantic and Gulf coasts of the United States and constitute the source of the largest U.S. fishery by weight. Prior to 1966 knowledge of population structure and migrations was determined by analysis of meristics, age and size composition and catch-effort data. In the summer of 1966, the Bureau of Commercial Fisheries (now the National Marine Fisheries Service), Beaufort, N.C., began tagging Atlantic menhaden, *Brevoortia tyrannus*, to obtain direct information about population structure, movements, growth, and survival. In 1967, the program was expanded to encompass the Atlantic fishing areas from New York to Florida. Through 1969 a total of 1,066,357 adult menhaden were tagged with an internal ferromagnetic tag and 202,943 were recaptured. In 1969 we began tagging juvenile Atlantic menhaden and adult Gulf menhaden, *B. patronus*, and reduced efforts to tag adult Atlantic menhaden. This paper describes the results of Atlantic menhaden tagging and recovery from 1966 through 1969.

TAGGING METHOD

Preliminary experiments were conducted at the laboratory, Beaufort, to determine the best method of tagging menhaden. After experimenting with several sizes of internal ferromagnetic tags for menhaden larger than 100-mm fork length, we selected a rectangular stainless steel tag with rounded corners, 14.0 by 3.0 by 0.5 mm, identified with a prefix letter and five numbers (Carlson and Reintjes, 1972). From subsequent experiments, Kroger and Dryfoos (1972) found that clean untreated tags were shed less than tags treated with a germicide. Tags were also shed less when inserted anteriorly rather than posteriorly into the body cavity. Tagging guns, manufactured by Bergen-Nautik, a Norwegian firm, were selected over the scalpel-forcep method of insertion because they are safer to use in the field and increase the speed of tagging without increasing mortality or tag shedding.

[1] Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

Estimates of tagging mortality and tag shedding were also obtained from the experiments. Because these estimates are based on fish acclimated to holding tanks, they are probably minimum estimates of losses experienced in the field. The combined loss was 10 to 20% for menhaden averaging 110 to 160 mm in length. The combined loss for menhaden less than 100 mm was approximately 50%. Most tagging mortality occurred within 3 days and most tag shedding within 2 wk.

A smaller version of the tag was developed for juvenile menhaden. These fish can be tagged most effectively by inserting a 7.0 by 2.5 by 0.4 mm tag posteriorly into the body cavity from the base of the pectoral fin.

The menhaden purse seine fishery provided most of the fish for our work. We also tagged fish obtained from commercial pound nets and our own pound net, purse seines, and haul seines before the purse seine fishery began or where there was no menhaden fishery.

When working with the commercial purse seine fishery, two methods of obtaining and holding fish were used. We accompanied commercial vessels in our own small boats and dipped fish from the purse seine into our holding nets, or we tagged directly from the commercial vessel, keeping the fish alive in holding boxes supplied with flowing seawater. Data were recorded for each group of fish released. A percentage of the fish released were measured to the nearest millimeter and the age determined by counting scale annuli. We recorded the condition of fish, size of catch and time it was made, time tagged fish were released, surface-water temperature, and name of tagger (Pristas and Willis).[2]

TAG RECOVERY

All tags were recovered from menhaden reduction plants because there is no satisfactory way of recovering them from menhaden used for bait or for other reasons precluding their passage through a reduction plant. About 99% of the tags recovered were taken from magnets inside the plants. Primary magnets were placed in the plant's conveyor system between the fish scrap drier and the scrap storage area (Figure 1). About 75% of the tags pass over these magnets the same day the tagged fish are processed. The following day an additional 10% pass the primary magnet. More than 95% of the tags pass the primary magnet within 2 wk from the time they enter the plant. Secondary magnets installed at other locations in the system may not recover tags until months after the fish are landed when the fish scrap is ground into meal or is shipped out of the plant. Whole tagged fish were recovered by using electronic detector-recovery systems which shunted fish past a section of the plant's conveyor. Tagged fish were ejected, and untagged fish continued through processing (Parker, 1972).

Primary and secondary magnets were usually cleaned daily (Parker).[3] Thus, tags recovered on primary magnets indicated the approximate date of capture. Precise recapture locations are not obtained from magnet recoveries, but along the Atlantic coast the fishery in each area was localized and area of recapture could usually be determined.

We tested the efficiency of the recovery system in each plant by putting tags in whole fish in the catch and noting the percentage of these tags recovered. Estimates of the number of tagged fish recaptured were obtained using these primary recovery efficiencies. Tables 1 through 8 give the estimated numbers of tagged fish recaptured by area and season of release and by area and season of recovery. A precise description of tagging and release areas is given in the section on migrations. We estimate that 202,943 tagged fish, or 19% of those released, have been recaptured. Actual recoveries by area and month of release are given by Coston (1971).

MIGRATIONS

We tagged Atlantic menhaden in the estuaries and major fishing areas to test the following

[2] Pristas, P. J., and T. D. Willis. Field tagging methods for menhaden. Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516. Manuscript in preparation.

[3] Parker, R. O., Jr. Magnetic recovery of internal ferromagnetic tags applied to menhaden (*Brevoortia* spp.) Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516. Manuscript in preparation.

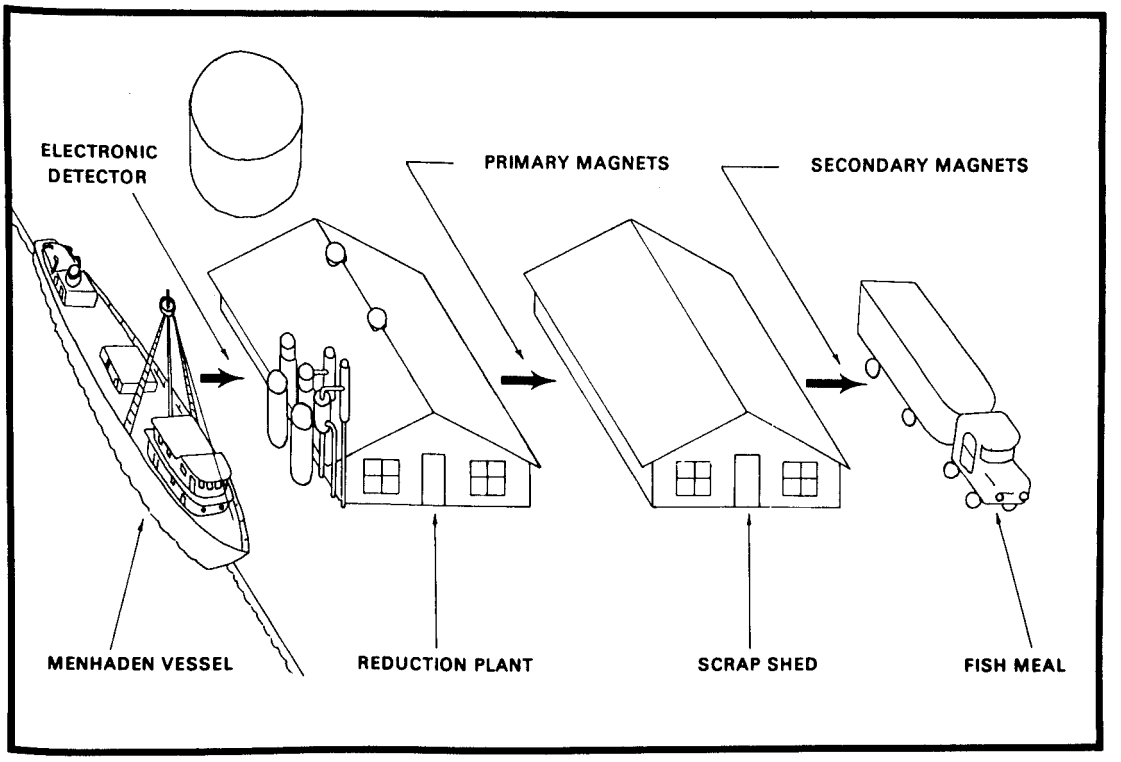

FIGURE 1.—Schematic diagram of a typical menhaden reduction plant showing general areas of tag recovery stations.

hypotheses (first inferred by Roithmayr, 1963):

1. Adult menhaden migrate northward in spring and early summer and southward in fall.
2. Adult menhaden migrate farther northward each spring as they grow larger and older.
3. Juvenile menhaden migrate southward in fall.

The Atlantic coast was divided into five tagging areas based on activities of the commercial fishery (Figure 2). Boundaries between areas are drawn through waters where little fishing occurs, and each area is generally limited to the range of menhaden vessels fishing within that area.

New York Area: Waters along the southern coast of Long Island east of a line due south of Moriches Inlet (lat. 40°46′N and long. 72°44′W), Long Island Sound, and waters northward.

New Jersey Area: Waters north of a line due east of the Maryland-Virginia line (lat. 38°02′N and long. 75°15′W) to the southern boundary of area 1.

Chesapeake Bay Area: Chesapeake Bay proper and coastal waters outside the Bay lying between False Cape, Va., (lat. 36°35′N and long. 75°53′W) and the southern boundary of area 2. Purse seine fishing is prohibited in Maryland waters of Chesapeake Bay.

North Carolina Area: Waters north of a line running due east from the South Carolina-Georgia line at the mouth of the Savannah River (lat. 32°02′N and long. 80°53′W) to the southern boundary of area 3.

Florida Area: Waters south of the southern boundary of area 4.

Our records of the movements of tagged adult menhaden support the above hypotheses. Figure 3 shows the generalized pattern of migration as obtained from tag recoveries.

Northward migration occurs in spring and early summer. Menhaden tagged early in the

TABLE 1.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the summer of 1966.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	%
N.C.	74,906	1966 S	*	*	*	5,316	*	5,316	7.1
		F	---	---	*	984	---	984	1.3
		1967 S	---	152	548	138	52	890	1.2
		F	---	---	44	140	---	184	0.2
		1968 S	49	107	229	3	0	388	0.5
		F	---	---	32	107	---	139	0.2
		1969 S	17	13	12	1	0	43	<0.1
		F	---	---	0	21	---	21	<0.1
		Total recaptured						7,965	10.6

[1]S indicates spring and summer; F indicates fall.
[2]* indicates menhaden fishing but no tag recovery was attempted.
-- indicates no menhaden fishing.

TABLE 2.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the fall of 1966.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	%
N.C.	21,721	1966 F	--	--	*	424	--	424	2.0
		1967 S	--	79	1,305	131	63	1,578	7.3
		F	--	--	48	124	--	172	0.8
		1968 S	46	146	584	11	3	790	3.6
		F	--	--	41	171	--	212	1.0
		1969 S	11	21	57	0	0	89	0.4
		F	--	--	2	30	--	32	0.1
		Total recaptured						3,297	15.2

[1]S indicates spring and summer; F indicates fall.
[2]* indicates menhaden fishing but no tag recovery was attempted.
-- indicates no menhaden fishing.

fishing season in Florida, North Carolina, and Chesapeake Bay have been recovered in fishing areas north of the release area in the same season of their release. Some fish tagged in Florida in April have been recaptured near Southport, N.C., in May and near Beaufort in June. Few Florida tags were recovered in North Carolina from those released in midseason, and none were recovered in North Carolina from those released late in the season. Menhaden tagged in North Carolina from pound nets early in the spring have been recaptured in pound nets in Chesapeake Bay as early as May and in the purse seine fishery in New Jersey and New York in July. Fish tagged in Chesapeake Bay in April and early May occurred in New Jersey and New York catches as soon as the fisheries began in early June. Again, the amount of movement decreased through the spring, and there appeared to be relatively little movement between fishing areas after June. There appeared to be little northward movement in the spring and early summer of fish tagged in the Maryland portion of Chesapeake Bay. Only a few have been recaptured in New Jersey and none in New York.

Southward migration does not begin until late summer. The North Carolina fall fishery

TABLE 3.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released from New York to Florida in the spring and summer of 1967. [Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	*%*
N.Y.	2,093	1967 S	--	270	0	0	0	270	12.9
		F	--	--	0	58	--	58	2.8
		1968 S	134	68	3	1	0	206	9.8
		F	--	--	0	4	--	4	0.2
		1969 S	14	31	0	0	0	45	2.2
		F	--	--	0	2	--	2	0.1
			Total recaptured					585	28.0
N.J.	13,660	1967 S	--	1,313	17	0	0	1,330	9.7
		F	--	--	139	863	--	1,002	7.3
		1968 S	102	423	247	6	0	778	5.7
		F	--	--	26	126	--	152	1.1
		1969 S	14	46	7	1	0	68	0.5
		F	--	--	5	9	--	14	0.1
			Total recaptured					3,344	24.4
Chesapeake Bay	100,128	1967 S	--	360	13,770	0	0	14,130	14.1
		F	--	--	1,419	2,944	--	4,363	4.4
		1968 S	691	3,533	11,480	10	0	15,714	15.7
		F	--	--	849	3,212	--	4,061	4.1
		1969 S	158	517	810	21	0	1,506	1.5
		F	--	--	0	505	--	505	0.5
			Total recaptured					40,279	40.3
N.C.	112,428	1967 S	--	35	1,221	12,522	0	13,778	12.3
		F	--	--	133	7,553	--	7,686	6.8
		1968 S	16	523	2,664	832	46	4,081	3.6
		F	--	--	317	1,418	--	1,735	1.5
		1969 S	27	106	281	21	0	435	0.4
		F	--	--	0	148	--	148	0.1
			Total recaptured					27,863	24.7
Fla.	95,832	1967 S	--	0	0	425	5,958	6,383	6.7
		F	--	--	0	0	--	0	0
		1968 S	0	128	626	596	477	1,827	1.9
		F	--	--	70	381	--	451	0.5
		1969 S	0	25	102	18	9	154	0.2
		F	--	--	0	47	--	47	<0.1
			Total recaptured					8,862	9.4
Combined	324,141	1967 S	--	1,978	15,008	12,947	5,958	35,891	11.1
		F	--	--	1,691	11,418	--	13,109	4.0
		1968 S	943	4,675	15,020	1,445	523	22,606	7.0
		F	--	--	1,262	5,141	--	6,403	2.0
		1969 S	213	725	1,200	61	9	2,208	0.7
		F	--	--	5	711	--	716	0.2
			Grand total recaptured					80,933	25.0

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 4.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the fall of 1967.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	%
N.C.	38,920	1967 F	--	--	0	5,188	--	5,188	13.3
		1968 S	213	725	1,662	538	172	3,310	8.5
		F	--	--	185	909	--	1,094	2.8
		1969 S	46	87	268	39	0	440	1.1
		F	--	--	2	127	--	129	0.3
		Total recaptured						10,161	26.0

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 5.—Estimated number of tagged fish recaptured, by area and season, from Atlantic menhaden released from New York to Florida in the spring and summer of 1968.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	%
N.Y.	2,370	1968 S	344	200	0	0	0	544	23.0
		F	--	--	0	10	--	10	0.4
		1969 S	35	72	5	0	0	112	4.7
		F	--	--	0	20	--	20	0.8
		Total recaptured						686	28.9
N.J.	21,789	1968 S	321	5,460	18	0	0	5,799	26.6
		F	--	--	188	970	--	1,158	5.3
		1969 S	68	311	57	4	0	440	2.0
		F	--	--	0	85	--	85	0.4
		Total recaptured						7,482	34.3
Chesapeake Bay	132,596	1968 S	10	144	26,822	0	0	26,976	20.3
		F	--	--	2,076	7,525	--	9,601	7.2
		1969 S	158	410	3,333	63	0	3,964	3.0
		F	--	--	38	1,611	--	1,649	1.2
		Total recaptured						42,190	31.7
N.C.	103,483	1968 S	3	25	643	13,070	0	13,741	13.3
		F	--	--	150	1,575	--	1,725	1.7
		1969 S	3	41	1,003	482	5	1,534	1.5
		F	--	--	11	400	--	411	0.4
		Total recaptured						17,411	16.9
Fla.	118,295	1968 S	0	0	0	1,498	10,994	12,492	10.6
		F	--	--	3	61	--	64	<0.1
		1969 S	0	21	495	1,732	329	2,577	2.2
		F	--	--	0	162	--	162	0.1
		Total recaptured						15,295	13.0
Combined	378,533	1968 S	678	5,829	27,483	14,568	10,994	59,552	15.7
		F	--	--	2,417	10,141	--	12,558	3.3
		1969 S	264	855	4,893	2,281	334	8,627	2.3
		F	--	--	49	2,278	--	2,327	0.6
		Grand total recaptured						83,064	21.9

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 6.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina and Florida in the fall of 1968. [Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	*%*
N.C.	6,937	1968 F	--	--	0	480	--	480	6.9
		1969 S	16	25	184	99	0	324	4.7
		F	--	--	2	72	--	74	1.1
			Total recaptured					878	12.7
Fla.	524	1968 F	--	--	0	0	--	0	0
		1969 S	0	0	0	0	0	0	0
		F	--	--	0	0	--	0	0
			Total recaptured					0	0
Combined	7,461	1968 F	--	--	0	480	--	480	6.4
		1969 S	16	25	184	99	0	324	4.3
		F	--	--	2	72	--	74	1.0
			Grand total recaptured					878	11.7

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 7.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released from New York to Florida in the spring and summer of 1969. [Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	*%*
N.Y.	8,468	1969 S	1,310	301	0	0	0	1,611	19.0
		F	--	--	0	419	--	419	4.9
			Total recaptured					2,030	23.9
N.J.	700	1969 S	2	7	0	0	0	9	1.3
		F	--	--	0	2	--	2	0.3
			Total recaptured					11	1.6
Chesapeake Bay	75,581	1969 S	0	0	4,261	0	0	4,261	5.6
		F	--	--	54	1,875	--	1,929	2.6
			Total recaptured					6,190	8.2
N.C.	24,685	1969 S	0	0	98	2,429	0	2,527	10.2
		F	--	--	7	529	--	536	2.2
			Total recaptured					3,063	12.4
Fla.	108,150	1969 S	0	0	0	117	4,828	4,945	4.6
		F	--	--	--	4	--	4	0.0
			Total recaptured					4,949	4.6
Combined	217,584	1969 S	1,312	308	4,359	2,546	4,828	13,353	6.1
		F	--	--	61	2,829	--	2,890	1.3
			Grand total recaptured					16,243	7.4

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 8.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the fall of 1969.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture: N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.	Tagged fish recaptured	
	Number		*Number*[2]					*Number*	%
N.C.	3,091	1969 F	--	--	0	402	--	402	13.0

[1] F indicates fall.
[2] -- indicates no menhaden fishing.

begins in November and, as the season progresses, fish tagged in more northern areas enter the fishery. The first recoveries from releases of the previous summer are from fish tagged in North Carolina. Then fish from Virginia, Maryland, Delaware, and New Jersey enter the North Carolina fishery before the end of November. During the first week of December, tags are recovered from fish tagged in Long Island Sound. In 1969 we tagged as far north as Narragansett Bay, R.I., and tags from that area were not recovered in the fall fishery before December 18. Consequently, it appears that the fish enter the North Carolina fall fishery progressively; those from farther north enter last.

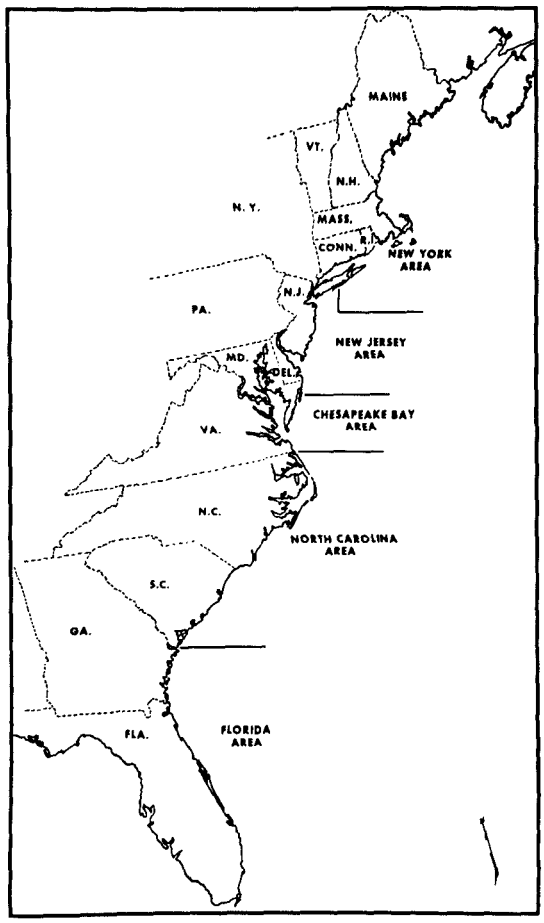

FIGURE 2.—Commercial fishing areas for Atlantic menhaden along Atlantic coast of the United States.

Rates of interchange between fishing areas can be inferred from recoveries of the 1967 and 1968 releases. Two important aspects of interchange between areas have been considered: 1) where did tagged fish recaptured in a particular area come from, and 2) where did fish released in a particular area go?

To determine the relative contributions of fish from one area to another, it is necessary to either tag in proportion to abundance (with equal tagging survival rates in each area) or to adjust the returns to compensate for disproportionate tagging in the different areas. In general we attempted to tag in proportion to abundance, but in practice this is impossible since relative abundances are not known until after the fact of tagging. Consequently, we have attempted to adjust the returns in relation to the achieved density of tags in each area.

There are several possible approaches to equalizing tag density (number of tags per million individual fish landed) in the different areas. We examined three approaches for the 1967 spring and summer tagging season:

1. Season-average density: Total number of recoveries from fish re-

leased within the area and season divided by total number of individual fish landed within the area and season.

2. Maximum-monthly density: Highest monthly ratio of number of recoveries from releases within the area and season to the total number of individual fish landed during the month.

3. Last-month-of-season density: Number of recoveries during the last month of fishing from releases within the area and season divided by the total number of individual fish landed during the month.

If the areas were truly closed to recruitment, immigration and emigration, and if there were rapid dispersal of tagged fish throughout the population in each area, any one of these approaches would provide adequate density indices.

We observed that the maximum density was not always achieved at the end of the season and believe that the effects of recruitment and migration near the end of the fishing season confound the third approach. We believe that selecting the month with the highest density may also be misleading due to nonrandom distribution of tags within each area. We selected the season average as a robust statistic for determination of an index of achieved tag density.

After obtaining the index of density (the season-average density) for each area, we determined the standardization factor necessary for each area to achieve an arbitrarily selected

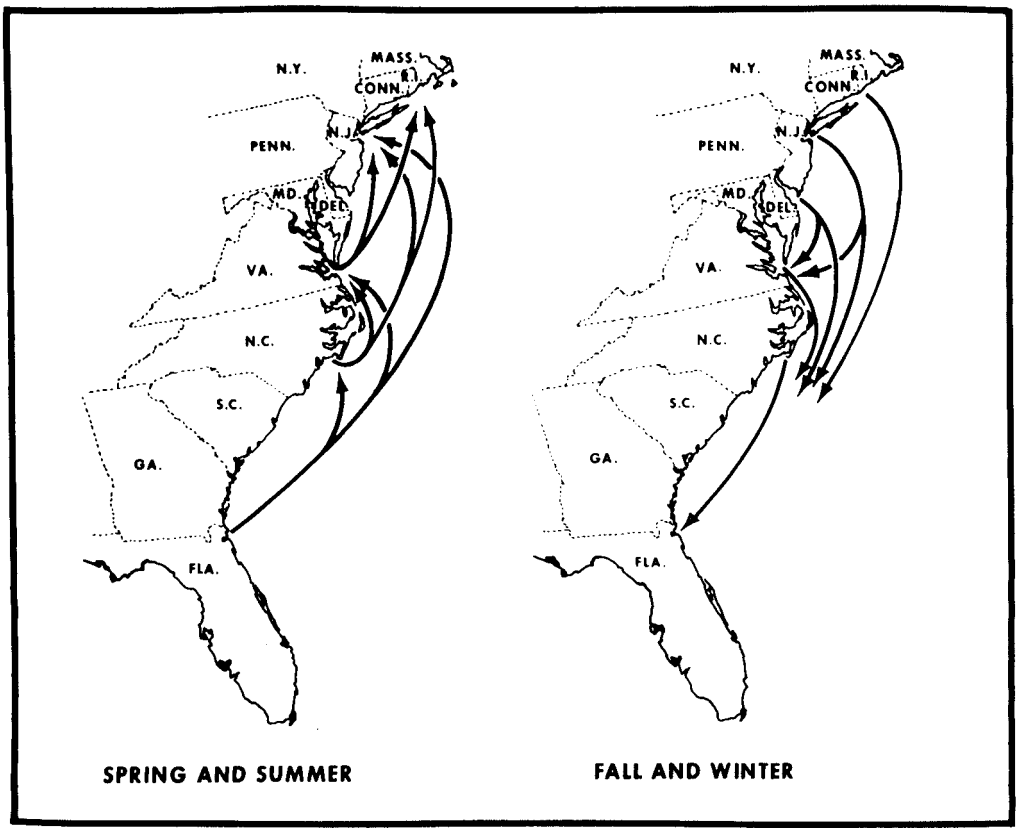

FIGURE 3.—Generalized movements of tagged Atlantic menhaden.

density of 50 tags per million individual fish (Table 9). Multiplying the number of recaptures in subsequent fishing season by the appropriate standardization factor will equalize tag densities from each tagging area so that meaningful comparisons can be made of the relative contribution of fish from different areas in succeeding seasons.

Fish tagged in Chesapeake Bay and the Florida areas contributed most to landings in other areas (Table 10). In New York and New Jersey, 83.2% of the 1968 tag recoveries came from fish tagged in Chesapeake Bay in 1967. In Chesapeake Bay, 85.6% of the 1968 recoveries were from fish tagged in that area in 1967. Fish tagged in Florida the previous year made up 75.3% of the recoveries in North Carolina and 97.9% of the recoveries in Florida. The pattern of migration was similar for fish tagged in 1968 and recaptured in 1969 (Table 11).

Selection of either of the other two alternative approaches for determining the index density for each area had little effect in changing the relative contributions from the different areas. Table 12 shows the differences in relative contributions from spring and summer releases recaptured in 1968.

We have determined the destination of fish tagged in each area based on the distribution of recoveries in successive summers. The adjustments of ratios do not in any way affect this analysis. These percentages are based upon the numbers of recaptures in the different areas from all the releases in an area. For example, Table 3 and Table 10 show that of the fish tagged in Florida in 1967 and recaptured in the summer of 1968, 26% were recovered in Florida, 33% in North Carolina, 34% in Chesapeake Bay,

TABLE 9.—1967 adjustments of tags per million individual fish landed to achieve equal density of tags (50 tags per million individual fish) in each area.

Area	Tags recaptured (within season and area) *a*	Individual fish caught *b*	*a/b*	Standardization factor
	Number	*No.* × 10^6		
North & Middle Atlantic	1,583	32	49.5	1.01
Chesapeake Bay	13,770	410	33.6	1.49
North Carolina	12,522	118	106.1	0.47
Florida	5,958	256	23.3	2.15

TABLE 10.—Calculated numbers of tags recovered and percentage distributions for 1967 summer releases recovered in summer 1968.

Tagging area	Standardization factor	Recovery area: N.Y. and N.J.	Chesapeake Bay	N.C.	Fla.	Total
		Number[1]				
N.Y. and N.J.	1.01	734	252	7	0	993
Chesapeake Bay	1.49	6,294	17,105	15	0	23,414
N.C.	0.47	253	1,252	391	22	1,918
Fla.	2.15	275	1,346	1,281	1,026	3,928
Total		7,556	19,955	1,694	1,048	30,253
Distribution of recoveries by area of recovery (where tagged fish came from).						
		Percent				
N.Y. and N.J.		9.7	1.3	0.4	0	
Chesapeake Bay		83.2	85.6	0.9	0	
N.C.		3.4	6.4	23.4	2.1	
Fla.		3.6	6.7	75.3	97.9	
Distribution of recoveries by area of release (where tagged fish go).						
		Percent				
N.Y. and N.J.		73.8	25.4	0.7	0	
Chesapeake Bay		26.9	73.0	0.1	0	
N.C.		13.2	65.3	20.4	1.1	
Fla.		7.0	34.2	32.6	26.1	

[1] Adjusted numbers from Table 3.

TABLE 11.—Calculated numbers of tags recovered and percentage distributions for summer 1968 releases recovered in summer 1969.

Tagging area	Standardization factor	Recovery area: N.Y. and N.J.	Chesapeake Bay	N.C.	Fla.	Total
		Number[1]				
N.Y. and N.J.	0.54	262	33	2	0	297
Chesapeake Bay	0.85	483	2,833	54	0	3,370
N.C.	0.88	39	883	424	4	1,350
Fla.	0.84	18	416	1,455	276	2,165
Total		802	4,165	1,935	280	7,182
Distribution of recoveries by area of recovery (where tagged fish came from).						
		Percent				
N.Y. and N.J.		32.5	0.8	0.1	0	
Chesapeake Bay		60.4	68.0	2.8	0	
N.C.		4.9	21.3	22.0	1.5	
Fla.		2.2	10.0	75.2	98.5	
Distribution of recoveries by area of release (where tagged fish go).						
		Percent				
N.Y. and N.J.		88.2	11.2	0.6	0	
Chesapeake Bay		14.3	84.1	1.6	0	
N.C.		2.9	65.4	31.4	0.3	
Fla.		0.8	19.2	67.2	12.8	

[1] Adjusted numbers from Table 5.

TABLE 12.—Comparison of percentage distributions of recoveries by area of recovery (where fish came from) calculated from three different indices of achieved density of tagging. Method 1 is based on season-average density; Method 2 on maximum-monthly density; Method 3 on last-month-of-season density. Data are for spring and summer 1967 releases recaptured in spring and summer 1968.

Tagging area	Recovery area: New York and New Jersey			Chesapeake Bay			North Carolina			Florida		
	Method 1	2	3	Method 1	2	3	Method 1	2	3	Method 1	2	3
New York and New Jersey	10	20	8	1	3	1	<1	4	4	0	0	0
Chesapeake Bay	83	79	91	86	93	98	1	4	11	0	0	0
North Carolina	3	1	<1	6	2	1	23	26	23	2	3	2
Florida	4	1	<1	7	2	<1	75	67	61	98	97	98

and 7% in New York and New Jersey. These data are not adjusted for different exploitation rates in the different areas; however, we believe the basic pattern would not change with adjustment.

These data point up the importance of fish from Chesapeake Bay. An average of 21% of the recoveries 1 yr later from fish released in Chesapeake Bay in 1967 and 1968 occurred in the New York and New Jersey areas. Thus 21% of the fish from the Bay made up 72% of the total catch of tagged fish in the New York and New Jersey areas. The patterns of movement observed for 1967 and 1968 releases are similar. In the second year after release, there is even more northward displacement from each tagging area (Table 13).

Peak migration speeds estimated from one area to another along the coast ranged from 11 to 16 km/day. A fish tagged off St. Augustine, Fla., in April traveled to Beaufort in no more than 53 days or 14 km/day. The shortest migration time from Chesapeake Bay to New Jersey in the spring was 29 days or 11 km/day.

TABLE 13.—Calculated numbers of tags recovered and percentage distributions for summer 1967 releases recovered in summer 1969.

Tagging area	Standardization factor	Recovery area: N.Y. and N.J.	Chesapeake Bay	N.C.	Fla.	Total
		Number[1]				
N.Y. and N.J.	1.01	105	7	1	0	113
Chesapeake Bay	1.49	1,006	1,207	31	0	2,244
N.C.	0.47	63	132	10	0	205
Fla.	2.15	54	219	39	19	331
Total		1,228	1,565	81	19	2,893
Distribution of recoveries by area of recovery (where tagged fish came from).						
		Percent				
N.Y. and N.J.		8.6	0.5	1.8	0	
Chesapeake Bay		81.9	77.1	38.2	0	
N.C.		5.1	8.6	12.7	0	
Fla.		4.4	13.8	47.3	100	
Distribution of recoveries by area of release (where tagged fish go).						
		Percent				
N.Y. and N.J.		92.2	6.5	1.3	0	
Chesapeake Bay		44.8	53.8	1.4	0	
N.C.		30.2	64.7	5.0	0	
Fla.		16.4	65.9	11.8	5.9	

[1] Adjusted numbers from Table 3.

In the fall the shortest migration time from the Chesapeake Bay to Cape Hatteras, N.C. was 25 days indicating a rate of 12 km/day. A fish tagged near Fire Island Inlet on the south side of Long Island, N.Y., in October was recaptured near Cape Hatteras 41 days later. This fish traveled at a rate of 16 km/day. There was no apparent difference in maximum rates of travel between spring and fall migrations.

Juvenile menhaden were first tagged in Rhode Island in October 1969. Of 1,020 juveniles tagged, 3 have been recovered in North Carolina and 1 in Florida as of July 1970 (Kroger, Dryfoos, and Huntsman, 1971). The first North Carolina recovery was in January 1970 during the fall fishery, and the remaining recoveries were in June 1970. The lone Florida recovery was in July 1970.

In general our recoveries of tagged fish support all three hypotheses: Adult menhaden migrate northward in spring and early summer and southward in fall, and menhaden migrate farther northward as they grow older. Juveniles also migrate southward in fall.

POPULATION STRUCTURE

Previous conjecture by Hildebrand (1948) and from work based on morphology of Atlantic menhaden by June (1958), Sutherland (1963) and June (1965), summarized by Reintjes (1969), led to the conclusion that at least two subpopulations occur along the coast, one north of Long Island and one to the south. Nicholson (1972a) differed with previous interpretations of the morphometric data and has presented an alternative interpretation suggesting a single population.

Recoveries of tagged fish also indicate that Atlantic menhaden constitute a single population. Adult fish tagged in Florida, North Carolina, Cheapeake Bay, and New Jersey have been recovered north of the release sites in subsequent years. Fish tagged in each area during the summer have subsequently been recovered in the North Carolina fall fishery. Juvenile menhaden tagged north of Long Island show a southward displacement from their estuarine rearing areas. The pattern of recoveries suggests an intermingling and mixing of menhaden from various areas during the winter and a resegregating by size during the following spring and summer. This inference also agrees with previous analyses of changes in age and size distribution (Nicholson, 1971a). All recent work has tended to negate the existence of a

hypothetical northern subpopulation. Tagging of known sexually active fish in the north in the spring or summer followed by their recapture in the North Carolina fall fishery, where they could be assumed to be sexually active again, would confirm this conclusion. For the present, with such significant mixing of fish from the various areas, the Atlantic menhaden resource should be considered as one population.

SURVIVAL AND EXPLOITATION RATES

Tag recoveries can provide estimates of survival and exploitation rates that are independent of those obtained from catch and effort data (Widrig, 1954), and with such data can provide measures of changes in resource availability. Estimates of annual survival rates were calculated for releases of each season by determining the ratio of recoveries in successive years. These estimates vary considerably because of fluctuations in availability. Survival rates also were obtained using the Robson-Chapman catch curve analysis (Paulik, 1962). The latter rates for the entire recovery period were the most consistent (Table 14). Better estimates of survival rates will be possible when we have a longer series of recovery data. Survival rates based on analyses of the age composition of the catch for 1966 to 1968 average 0.22 and are in good agreement with the average estimate of 0.24 from tag returns. Using an average value of 0.23 corresponds to a total instantaneous mortality rate of $Z = 1.47$.

Exploitation rates can be obtained from the estimated percentage of tags recaptured from early season releases after corrections are made for tagging mortality and tag shedding (Table 15). Tagging mortality and shedding losses for 1967-69 are thought to be about 10% for New York and New Jersey, 20% for Virginia, 25% for North Carolina, and 40% for Florida releases. The differences in percentage result primarily from differences in fish size. The average exploitation rate along the Atlantic coast, weighted by the catch in numbers of fish and preliminary estimates of tagging mortality, varied between 42 and 54%. Estimates for 1967 and 1968 from North Carolina fall fishery releases agree with values obtained from the weighted average summer releases. This indicates that most menhaden occurring in the fall fishery also occur within the fishery during the summer. The best single estimate of exploitation rate obtained from these tagging data is 50%.

Fishing and natural mortality rates can be obtained from exploitation rates and total mortality rates. Using our estimates of the instan-

TABLE 15.—Exploitation rate by area and year of release.

Release area	Year of release		
	1967	1968	1969
New York	33.6	47.1	55.7
New Jersey	52.9	52.9	--
Chesapeake Bay	48.2	65.4	21.7
North Carolina	33.5	49.1	57.6
Florida	66.7	33.3	32.0
Average (weighted by catch)	49.3	53.9	41.8
North Carolina fall fishery	42.9	48.0	--

TABLE 14.—Survival rates for all releases by season and by year, 1966-69.

Releases	Annual survival rates[1]					Robson-Chapman annual survival rate[2]
	Fall 67/66	Summer 68/67	Fall 68/67	Summer 69/68	Fall 69/68	
1966						
Summer	0.187	0.436	0.755	0.111	0.151	0.23
Fall	--	0.501	1.232	0.113	0.151	.33
1967						
Summer	--	--	0.488	0.098	0.112	.37
Fall	--	--	--	0.133	0.118	.13
1968						
Summer	--	--	--	--	0.185	.15
Average	0.187	0.468	0.825	0.114	0.143	.24

[1] Survival rate is ratio of recoveries in either fall or summer fishery 1 yr to recoveries in the same season the previous year.
[2] Robson-Chapman annual survival rate calculated from combined summer and fall recoveries. For fall releases recoveries were only considered for subsequent summer and fall seasons.

taneous total mortality rate (Z = 1.47) and exploitation rate (μ = 0.50), the instantaneous fishing mortality rate (F) is calculated to be 0.95 and the natural mortality rate (M), 0.52. Each year 50% of the fish in the fishery are being caught and 24% are dying from natural causes. This estimate of rate of fishing is in general agreement with the others based on an analysis of the catch and effort data in earlier years (Schaaf and Huntsman, 1972) at a higher level of fishing effort. We are continuing to analyze and to add additional years of data to reduce the effects of fluctuating availability upon the estimates.

AVAILABILITY

Tagging studies suggest that in Chesapeake Bay there are significant fluctuations in availability of Atlantic menhaden within and between years. Since most of the summer catch of Atlantic menhaden is landed in Chesapeake Bay (60% to 75%, 1967 through 1970) and since our movement data suggest that in the summer the stocks in different areas are relatively stable, we made a special study of the fluctuations in availability there. Fluctuations in availability may be caused by factors making the fish more or less accessible, such as weather and horizontal or vertical distribution of the fish or by differences in vulnerability brought about by changes in fish behavior, gear selectivity, or numbers of fish (Cushing, 1968). Murphy (1966) developed a population model for the Pacific sardine, incorporating the idea of variation in availability. In his model:

$$\frac{N_i + 1}{N_i} = e^{-M-(rvf)_i} = S_i$$

where

N_i is the number of fish present in the population in years;
e is the base of the natural logrithms;
M is the instantaneous natural mortality rate;
f is fishing effort;
r is an index of availability;
v is a residual constant; and
S_i is the annual survival rate of the population.

As Murphy indicated, errors in measuring f also contribute to r but in the menhaden fishery in Cheasapeake Bay we use a vessel week as the unit of effort (Nicholson 1971b), and there is little error in this measurement.

The factor v includes changes in vessel efficiency or fishing power which are separable from effects of availability. Schaaf and Huntsman (1972) concentrate on changes in the catchability coefficient (rv) resulting from changes in vessel efficiency and changes in distribution of effort. Over a number of years and major fishing innovations, efficiency of the vessels has increased markedly. However, for the limited number of years in our analysis (1967-70) and in consideration of only the Chesapeake Bay area, we believe it is reasonable to assume that unit efficiency and consequently v, may be considered constant. The quantity rv is a variable catchability coefficient and, since v is assumed constant, relative estimates of r can be obtained from the percentage of tags recaptured per unit of fishing effort (Gulland, 1963).

Fluctuations in availability, or percent tag recaptures per unit of fishing effort, in Chesapeake Bay were observed in 1967 through 1970. Estimates in 1970 were even more striking than those obtained in the earlier years. The data used for this analysis are based upon tags released during the first 2 wk of the purse seine fishery in Chesapeake Bay by our best taggers. The number of tags released varied by year, i.e., 1967, 4,290 tags; 1968, 10,387 tags; 1969, 2,147 tags; and 1970, 21,189 tags. Table 16 shows the actual and relative values, compared with the base year 1967, of catch, effort, catch per unit effort (CPUE), percent recapture, availability index, and population size. The percentage of tagged fish recaptured, shown in Table 16, is not comparable to the exploitation given for Chesapeake Bay in Table 15 because no adjustment was made in Table 16 for tagging mortality and tag shedding which we assume to be constant each year, nor were recoveries considered at plants outside of Chesapeake Bay during the summer or fall. Consequently, the data shown in Table 16 for population size are relative estimates and cannot be considered true estimates of the number of fish. Table 16 shows that while the CPUE increased almost

TABLE 16.—Actual and comparative values of catch, effort, catch per unit effort (CPUE), percent recapture, availability index and population size for menhaden landings in Chesapeake Bay, 1967-70 using 1967 as the base year. (Comparative values are in parentheses.)

Year	Catch (Millions of individual fish) C	Effort (Number of vessel weeks) f	CPUE C/f	Percent recaptured R	Availability index R/f	Population size $100\ C/R$
1967	384 (1.00)	757 (1.00)	0.507 (1.00)	24.1 (1.00)	0.0318 (1.00)	1,593 (100.)
1968	449 (1.17)	601 (0.79)	0.747 (1.47)	34.3 (1.42)	0.0571 (1.80)	1,309 (82.)
1969	255 (0.66)	519 (0.69)	0.491 (0.97)	14.3 (0.59)	0.0276 (0.87)	1,783 (112.)
1970	791 (2.06)	501 (0.66)	1.579 (3.11)	45.8 (1.90)	0.0914 (2.87)	1,727 (108.)

threefold between 1969 and 1970, the availability index more than tripled, so the difference in the population size was relatively small. Table 16 suggests that most of the variation in catch during 1967-70 in Chesapeake Bay results from the reduction in effort and the fluctuations in availability rather than actual changes in fish abundance.

Anomalies in survival rates calculated from tagged fish or age composition data provide another indication of fluctuation in availability. When availability is high and a larger than normal catch is made, a correspondingly large number of fish are recaptured. Then, compared to a normal year, the survival rate is overestimated when the high number is the numerator and underestimated when it is the denominator. Such an anomaly was noted in our estimates of survival rate based on tag recoveries and also in age composition data for Chesapeake Bay in the summer of 1968 (Henry, 1971).

Differences in monthly catches between 1967 and 1968 from June to September also suggest changing rates of availability. The catch for these months in 1968 was up to 28% over the previous year, but nearly three-fourths of the difference occured in July. Most of these fish were caught near the Maryland border in the vicinity of Tangier Island. Since the time and location of large catches was so restrictive, the large catch probably resulted from fish moving from Maryland to Virginia, rather than a general increase in the number of fish in the Bay.

Vulnerability appears to have varied in recent years in Chesapeake Bay. The proportion of the weekly catch made on Mondays in Chesapeake Bay has increased since 1962, coinciding with an increase in fishing effort in the early 1960's and a decrease in relative abundance during the decade (Nicholson, 1972b). Although this phenomenon had not generally been observed in other areas, it demonstrates one type of fluctuation in availability.

SUMMARY

From 1966 through 1969, over 1 million adult Atlantic menhaden were tagged in the major fishing areas from Long Island Sound to Florida. We estimate that more than 200,000 tags have been recaptured.

Tag recoveries demonstrate a seasonal migration of menhaden along the coast: Northward in spring and early summer and southward in fall. As the fish grow older and larger they migrate farther northward each spring. Maximum migration speeds from one area to another along the coast vary from 11 to 16 km/day.

Rates of interchange between fishing areas were determined from recoveries of the 1967 and 1968 releases. An important feature of the data is that 21% of the recoveries from fish released in Chesapeake Bay in 1967 and 1968 occurred off the coasts of New York and New Jersey 1 yr later. These fish from Chesapeake Bay made up 72% of the catch in New York and New Jersey.

Preliminary estimates of population parameters were made from tag-recovery data. Survival rates were estimated by several methods; i.e., ratio of recoveries in successive years, Robson-Chapman catch curve analysis technique, and age composition of catch for 1966 to 1968. Rates determined yearly from ratio of recoveries varied due to fluctuations in availability. Annual survival rates were based upon Robson-Chapman catch curve analysis and age composition of catch. Both use several years data and agree closely, averaging 0.23. Better

estimates of survival rates will be possible when a longer series of recovery data is available.

Exploitation, fishing, and natural mortality rates are estimated from tag recaptures. The best estimate of exploitation rate from these data is 50%. Instantaneous fishing mortality rate (F) is estimated to be 0.95 and instantaneous natural mortality (M) is 0.52.

Tagging studies suggest that there are significant fluctuations in availability of Atlantic menhaden in Chesapeake Bay.

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LARVAE AND YOUNG OF WESTERN NORTH ATLANTIC BOTHID FLATFISHES *ETROPUS MICROSTOMUS* AND *CITHARICHTHYS ARCTIFRONS* IN THE CHESAPEAKE BIGHT[1, 2]

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ABSTRACT

Development of smallmouth flounder, *Etropus microstomus*, and Gulf Stream flounder, *Citharichthys arctifrons*, is illustrated and described from larval to adult stages. Adults occur along the Atlantic coast, mainly from Cape Cod, Mass., to Cape Hatteras, N.C. Larvae of these two species were the most numerous of all flatfishes collected from 1959 to 1963 in the Chesapeake Bight by the Virginia Institute of Marine Science.

Changes in pigmentation, changes in morphology, sequences of ossification, and developmental osteology are described and compared. Occurrence of both species as larvae and adults in the Chesapeake Bight, their spawning times, abundance, and economic importance are noted. Taxonomic problems involving the validity of the generic separation of *Etropus* and *Citharichthys* are mentioned.

This paper presents the first descriptions of larvae of smallmouth flounder, *Etropus microstomus* (Gill), and Gulf Stream flounder, *Citharichthys arctifrons* Goode. The larvae of these two species were the most numerous of all flatfishes collected in the Chesapeake Bight plankton by the Virginia Institute of Marine Science (VIMS) from 1959 to 1963.

Adult *E. microstomus* and *C. arctifrons* are found principally from Cape Cod, Mass., to Cape Hatteras, N.C. The reported northern limit for *E. microstomus* is New England (Parr, 1931; Norman, 1934). The southern limit may extend to the Gulf coast of Florida and Mississippi (Springer and Bullis, 1956; Gutherz, 1967). *C. arctifrons* is found from the southwest part of Georges Bank (Bigelow and Schroeder, 1953) to the Gulf coast of Florida and Yucatan, Mexico (Gutherz, 1967). *E. microstomus* is most common at depths of 4-27 m (2-15 fm) and is generally not in the tidal zone or greater than 46 m (25 fm) (Parr, 1931). *C. arctifrons* occurs mainly at depths of 46-366 m (25-200 fm) (Goode and Bean, 1895; Gutherz, 1967) and infrequently in waters as shallow as 22 m (12 fm) (Bigelow and Schroeder, 1953). Little additional information is available on the life history of either species.

MATERIALS AND METHODS

Specimens

Several thousand larvae of each species, fixed and stored in 3-5% Formalin,[5] were examined. Juveniles and adults had been fixed in 10% Formalin and transferred to 40% isopropyl alcohol for storage.

Larvae used in this study came mainly from VIMS collections made with the RV *Pathfinder* during three series of Atlantic plankton cruises: monthly from December 1959 through December 1960 (October excluded) and from March 1961 through March 1962, and seasonally from July 1962 to April 1963 (winter excluded). The pattern of stations at which col-

[1] Contribution No. 510, Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[2] Part of a dissertation submitted by the senior author to the Faculty of the College of William and Mary in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

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

lections were made (Figure 1) changed for each of the three series of cruises (Joseph, Massmann, and Norcross, 1960; Massmann, Norcross, and Joseph, 1961; Massmann, Joseph, and Norcross, 1962). All collections were made in the Chesapeake Bight between lat. 36° and 38°N and from near shore to 80 nautical miles offshore. Gear, depths of sampling, and tow times were modified throughout the cruises (Joseph et al., 1960; Norcross, Massmann, and Joseph, 1961; Wilson, 1962). Meter and half-meter nets and the Gulf III high speed plankton sampler (Gehringer, 1952, 1962; Bridger, 1958) were the main types of gear used.

Larvae collected in the Chesapeake Bight by the Sandy Hook Sport Fisheries Marine Laboratory in New Jersey were examined also. The specimens were taken with Gulf V high speed plankton samplers (Arnold, 1959) during an offshore survey ranging from Martha's Vineyard, Mass., to Cape Lookout, N.C. The survey consisted of eight cruises made from December 1965 to December 1966. Clark et al. (1969) give details of the survey area and sampling procedures.

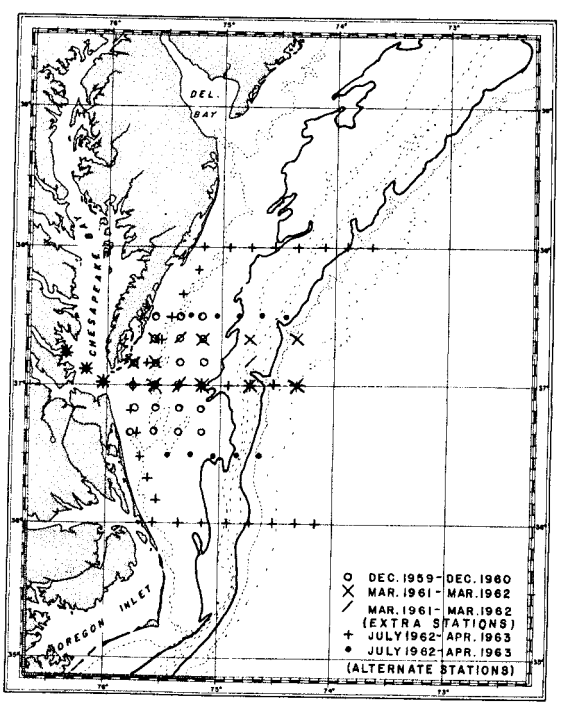

FIGURE 1.—Stations sampled by the RV *Pathfinder* of the Virginia Institute of Marine Science during three series of Atlantic plankton cruises from 1959 to 1963. The 37-m (20-fm) and 183-m (100-fm) depth contours are emphasized.

Additional larvae were collected in Norfolk Canyon (approximately lat. 37°04′N, long. 74°40′W), 13-14 August 1969, by VIMS personnel on board the National Marine Fisheries Service RV *Albatross IV*. Four plankton tows, each 1 h long, were made at 6-h intervals. Each tow consisted of four Miller plankton samplers (Miller, 1961), a pair of 0.2-m bongos (McGowan and Brown, 1966), all without closing mechanisms, and a 2-foot Braincon depressor. Estimated fishing depths for the Miller samplers were 2, 50, 100 and 275 m for each tow. The bongos fished at nearly the same depth as the deepest Miller sampler.

Juvenile and adult specimens were examined from various trawl collections taken between Cape Cod and Cape Hatteras by VIMS or by the National Marine Fisheries Service Laboratory at Woods Hole, Mass.

Measurements

Measurements were made on 100 unstained larvae of each species with an ocular micrometer and on 100 unstained adults of each species with dividers and a wooden millimeter scale. The larvae were selected from the VIMS 1962 plankton collections to represent the available size range. The adults were taken from trawl collections made from 1954 to 1967 (mostly 1965-67) between lat. 35°58′N and 40°09′N. Lengths reported in this study refer to standard length (SL). Fish were measured with the left side uppermost. The following body measurements, some of which were modified from Hubbs and Lagler (1958), were made:

Standard length - snout tip to notochord tip preceding development of caudal fin, then to end of hypural plate.

Head length - snout tip to anterior edge of cleithrum where it meets posterior opercular edge (larvae) or to posteromost margin of opercular membrane (juveniles and adults).

Snout length - snout tip to anterior margin of orbit of left eye.

Snout to anus length - distance along body midline from snout tip to vertical through center of anus.

Eye diameter - greatest diameter of left eyeball.

Upper jaw length - snout tip to posterior margin of maxillary.

Depth at anus - vertical distance from base of dorsal finfold or fin to anus.

Depth behind anus - vertical distance from base of dorsal finfold or fin to base of ventral finfold or fin immediately behind anus at the angle where body depth decreases greatly (larvae) or where body depth is greatest (juveniles and adults).

Peduncle depth - least depth of caudal peduncle (in larvae, body depth at posteromost myomere before formation of caudal fin).

Meristics

Meristic counts were made on 192 selected larvae of both species taken from the VIMS 1962 plankton collections. The larvae had been stained with Alizarin Red S by a method modified slightly from that described by Hollister (1934). Faded larvae were restained using Taylor's (1967) enzyme method. Counts were made of dorsal fin rays, anal fin rays, caudal fin rays, left and right pectoral fin rays, branchiostegal rays, vertebral centra, neural spines, and hemal spines. Fin rays and vertebrae were counted even if they were tinted only slightly with alizarin.

Meristic data on fin rays of adults of both species were obtained from specimens in VIMS collections. Fifty specimens of *E. microstomus* came from lower Chesapeake Bay in 1955, and 27 had been collected offshore from Wachapreague, Va., in 1965. Fifty-two specimens of *C. arctifrons* had been trawled near lat. 40°N in 1967, and 33 had been taken from approximately lat. 36°N in 1966. Fifty adults of each species were x-rayed for vertebral counts. Half of these specimens came from lat. 36°N and half from lat. 38°N, an area encompassing that of the VIMS larval collections. For comparison, additional meristic data were gathered from the literature (Gutherz, 1967).

Illustrations

Illustrations were made with the aid of a camera lucida. Penciled halftones (Figures 2-8) show the external morphology of larval to adult stages. Line drawings of osteological features (Figures 9-11) were made from alizarin stained specimens.

The illustrations were made from specimens representative of general trends, as considerable variation may be found.

EGGS AND LARVAE OF OTHER SPECIES OF *ETROPUS* AND *CITHARICHTHYS*

Norman (1934) listed 6 species of *Etropus* and 14 species of *Citharichthys;* all but one are found along the Atlantic and Pacific coasts of North, Central, and South Americas. Very little has been published about early stages of any of these species.

Goode and Bean (1895) illustrated (Plate CIV, Figure 361) a larval stage (size not given) of what they thought to be *E. rimosus.* Hsiao (1940) illustrated a 6.5-mm larva and described larvae from 6.5 mm to 15 mm which he called *E. crossotus.* None of these larvae resemble those of *E. microstomus.* They more closely resemble those of *Bothus* sp. figured and described by Kyle (1913), Padoa (1956), Colton (1961), and Jutare (1962).

Kyle (1913) illustrated two larvae labelled *?Citharichthys* sp. A and *?Citharichthys* sp. B. Pigmentation on Kyle's *Citharichthys* A is similar to that of *Paralichthys dentatus* (Smith and Fahay, 1970; Plates 9, 10); fin ray and vertebral counts of *Citharichthys* A are within the range for this species and agree with no other North Atlantic species of *Paralichthys* (Gutherz, 1967). Kyle's *Citharichthys* B were collected in the northwestern part of the Gulf Stream (lat. 42°12′N, long. 62°15′W). Vertebral counts (plus urostyle) and fin ray counts of Kyle's *Citharichthys* B lie within the range for *C. arctifrons* (Gutherz, 1967); however, Kyle's illustrated specimen closely resembles

the 10.6-mm SL larva of *E. microstomus* figured here (see Figure 4A) in pigmentation, stage of development, and mouth size. Kyle's specimens are probably *Citharichthys* or *Etropus* as Gutherz (1970) suggests, but lack of knowledge of larval bothids prevents identification.

Ahlstrom (1965) figured several stages of *C. stigmaeus*, *C. sordidus*, and *C. xanthostigma*. However, he provided only a small amount of descriptive information on the larvae of these species together with larvae of *C. fragilis* and *C. gilberti*.

VERIFICATION OF IDENTIFICATION OF LARVAL *E. MICROSTOMUS* AND *C. ARCTIFRONS*

The larvae of *E. microstomus* and *C. arctifrons* were identified using the series method of Schmidt (1905). Developmental series of larvae of each of two distinguishable but similar flatfishes were taken from VIMS collections made in the Chesapeake Bight. Larvae in each series were linked together primarily by pigment patterns and meristics. Migration of the right rather than the left eye in the largest specimens indicated they were members of the Scophthalmidae or Bothidae rather than the Pleuronectidae. VIMS records of adult sinestral flatfishes other than cynoglossids taken in the Chesapeake Bight (Table 1) listed one scophthalmid and seven bothids. Descriptions of larvae of *Scophthalmus aquosus* (Moore, 1947), *Bothus ocellatus* (Colton, 1961; Jutare, 1962), *Hippoglossina oblonga* (Agassiz and Whitman, 1885; Miller and Marak, 1962; Leonard, 1971b), *Paralichthys dentatus* (Deubler, 1958; Smith and Fahay, 1970) revealed differences from the larvae in question.

The unknown larvae were the most numerous flatfishes collected by VIMS in the Chesapeake Bight from 1959 to 1963. The great numbers of larvae in each series comprised large size ranges which indicated they were progeny of adults of two species which also should be fairly abundant in the same area. *E. microstomus* and *C. arctifrons*, constituting well over half of the total number of bothid and scophthalmid flatfishes taken in spring and summer of 1966 (Table 2), were prime candidates; other possible candidates, *C. macrops* or *E. crossotus*, occur only rarely in the bight.

Most of the unknown larvae were collected between July and October and were assumed to be products of summer spawnings. We have obtained gravid *E. microstomus* in July and August and *C. arctifrons* in August and September from the Chesapeake Bight.

Dorsal and anal fin ray and vertebral counts (Table 1) of the largest larvae in each series correspond to those of adult *E. microstomus* and *C. arctifrons*.

TABLE 1.—Abundance, spawning season, and meristics of adult bothid and scophthalmid flatfishes which occur in the Chesapeake Bight.[1]

Species	Relative abundance	Spawning season	Dorsal fin rays	Anal fin rays	Vertebrae	
					Abdominal	Caudal
Etropus microstomus	Numerous	Summer	67-82 [2](72-76-84)	50-63 [2](54-57-62)	[2]10	[2]24-35
Citharichthys arctifrons	Numerous	Summer	75-86 [2](75-81-87)	58-67 [2](60-65-71)	[2]10-11	[2]26-28
Bothus ocellatus	Rare	Summer	76-91	58-68	10	25-27
Citharichthys macrops	Very rare	Unknown	80-85	56-64	10	24-25
Etropus crossotus	Rare	Summer	75-87	58-68	10	25
Hippoglossina oblonga	Numerous	Summer	71-86	58-72	11	30-31
Paralichthys dentatus	Numerous	Fall and winter	80-96	61-74	11	30-31
Scophthalmus aquosus	Numerous	Summer	63-71	46-55	11	23-25

[1] Compiled from Jordan and Evermann, 1898; Parr, 1931; Norman, 1934; Moore, 1947; Ginsburg, 1952; Bigelow and Schroeder, 1953; Deubler, 1958; Colton, 1961; Jutare, 1962; Gutherz, 1967.
[2] Data from studies conducted at the Virginia Institute of Marine Science.

TABLE 2.—Total numbers of adult *Etropus microstomus* and *Citharichthys arctifrons* (and percentage of these two species combined in parentheses) compared with total numbers of bothids and scophthalmids and all flatfishes collected in the Chesapeake Bight during 1966.[1]

Species	February and March	May	August and September	November
Bothidae and Scophthalmidae:				
Etropus microstomus	52	29	36	141
Citharichthys arctifrons	103	1,146	230	100
Subtotal	155	1,175	266	241
Hippoglossina oblonga	286	148	71	191
Paralichthys dentatus	145	46	41	111
Scophthalmus aquosus	38	119	41	90
Total Bothidae and Scophthalmidae	624 (24.8%)	1,488 (79.0%)	419 (63.5%)	633 (38.1%)
Pleuronectidae:				
Glyptocephalus cynoglossus	7	3	2	0
Limanda ferruginea	17	17	33	35
Pseudopleuronectes americanus	29	440	98	272
Soleidae:				
Trinectes maculatus	0	0	11	2
Cynoglossidae:				
Symphurus plagiusa	0	0	2	0
Total Pleuronectidae, Soleidae, and Cynoglossidae	53	460	146	309
Grand total flatfishes	677 (22.9%)	1,948 (60.3%)	565 (47.1%)	942 (25.6%)

[1] From Virginia Institute of Marine Science trawl data.

DISTINGUISHING FEATURES OF *E. MICROSTOMUS* AND *C. ARCTIFRONS* LARVAE

Characters useful in distinguishing and separating larvae of *E. microstomus* and *C. arctifrons* taken in the Chesapeake Bight are listed in Table 3. Larvae <4 mm are most easily separated by the presence of preopercular spines in *E. microstomus*. Larvae >4 mm are best separated by pigment patterns (*C. arctifrons* has less pigment in general than *E. microstomus*) and the presence of three elongated anterior dorsal fin rays in *C. arctifrons*.

The number of myomeres, which usually corresponds to the number of vertebrae, is frequently a valuable character for identification of larvae. In this study, myomeres were usually impossible to count on specimens <4 mm because the segments, especially those on the most anterior and posterior parts of the body, were indistinct. The same was true of many larger specimens. When accurate counts were possible, the number was always less than vertebral numbers, i.e., *E. microstomus*—31-33 myomeres (34-35 vertebrae) and *C. arctifrons*—34-35 myomeres (36-39 vertebrae). Specimens selected for illustration were the best representatives and all had rather well-defined myomeres. Myomeres are still visible in juveniles of 40 mm (see Figure 7) mainly because of the deciduous nature of the scales. However, scales or scale pockets, particularly in the anterior abdominal region, tend to obscure them.

EGGS AND YOLK SAC LARVAE OF *E. MICROSTOMUS* AND *C. ARCTIFRONS*

Eggs of *E. microstomus* and *C. arctifrons* have not yet been identified in plankton samples. Attempts to strip, fertilize, and rear eggs of both species have been unsuccessful.

None of the ovaries examined of several hundred mature specimens of *E. microstomus* was running ripe. Eggs taken from the ripest ovaries were still hard, opaque, and quite small. They were approximately spherical with no apparent oil globule. Eggs stripped from *C. arctifrons* which were approaching spawning condition were pliable and almost transparent. They were spherical to slightly ovoid, with a

TABLE 3.—Distinguishing features of larvae of *Etropus microstomus* and *Citharichthys arctifrons* from the Chesapeake Bight.[1]

Character	*Etropus microstomus*	*Citharichthys arctifrons*
Pigmentation:		
Head	Internal spot below hindbrain (8 mm).	No.
	Stellate melanophore on operculum (10-11 mm).	No.
Abdomen	1-2 stellate melanophores on pectoral fin.	No.
	Internal spots along notochord (4 mm).	No.
Tail	3 postanal horizontal bars (3-4 mm).	Similar (4-5 mm).
	Internal spots along length of notochord (4 mm).	Internal spots along notochord only in region of postanal bar (5 mm).
	2 prominent ventral clusters between anus and postanal bars (4 mm).	No.
Morphology:		
Size at metamorphosis	10-12 mm.	13-15 mm.
Preopercular spines	Prominent from 2.5-8 mm, disappear by 10 mm.	None.
Elongated fin rays	None.	3 elongated anterior dorsal rays (4-5 mm to 11-12 mm).
Body depth	Depth at anus/SL and depth behind anus/SL usually greater for *E. microstomus* than *C. arctifrons* of equal size.	
	Depth behind anus/depth at anus related to SL greater for *E. microstomus* than *C. arctifrons* of equal size (8 mm).	
Meristics:		
Anal fin rays	Usually <60 (8 mm)	Usually >60 (10 mm).
Vertebrae	10 abdominal	10-11 abdominal.
	24-25 caudal (9 mm) including urostyle	26-28 caudal (10 mm) including urostyle.

[1] Sizes in parentheses indicate size at which the character is attained.

deviation of ±0.04 mm between major and minor axes. The eggs had a smooth surface; no oil globule was apparent although most bothid eggs have a small one. Diameters of these *C. arctifrons* eggs ranged from 0.70 to 0.82 mm ($\bar{X}$ = 0.74 mm). Diameters of fertilized eggs may differ.

The smallest larvae examined of both species were 2.3 mm. At that size, a small amount of yolk material is still present. These larvae are similar in appearance to the 2.5-mm larvae (Figure 2) described in the next section. No additional information is available on earlier stages. Because larvae of the two species are comparable in size (under 5 mm) and developmental stage, they probably hatch at about the same size, estimated to be about 2 mm.

DEVELOPMENT OF *E. MICROSTOMUS* AND *C. ARCTIFRONS* - LARVAE TO ADULTS

Descriptions of the development of *E. microstomus* and *C. arctifrons* are patterned after workers who followed the dynamic approach, e.g., Ahlstrom and Ball (1954), Ahlstrom and Counts (1955, 1958), Kramer (1960), Moser and Ahlstrom (1970), and others. Three major aspects of development are discussed: pigmentation changes, morphological changes, and osteological changes. Descriptions are based primarily on the left (eyed) side. A length designation of 4 mm implies a range of values from 4.0 to 4.9 mm. The term metamorphosis is used to describe the period of eye migration until the right eye rests in its final position on the left side of the head. The term larva is used to define all stages from yolk sac absorption until all fins are formed after completion of metamorphosis. The term juvenile refers to all stages from completion of fin formation to adult. Comparative development is followed through to the adult stage.

Pigmentation Changes

Changes in pigmentation of *E. microstomus* and *C. arctifrons* are described as they occur

throughout development in three body regions: head, abdominal, and tail.

E. microstomus - Head Region

The eyes of the smallest specimens examined (2.3 mm) are pigmented. The head of early stage larvae, 2-3 mm, is marked by a few melanophores scattered along the lower jaw and on the ventral body margin from the angle of the lower jaw to the cleithrum (Figure 2A). The concentration of ventral pigment increases with age to about 8-9 mm (Figure 3) and then decreases (Figure 4), although it may vary considerably among individuals. A group of melanophores is usually noticeable on the postero-ventral angle of the lower jaw and sometimes at the tip of the cleithrum in larvae over 3 mm (Figures 3, 4). Melanophores occur over the hindbrain and midbrain singly or in groups in larvae from 3.5 mm up to metamorphosis (Figures 3, 4). Larvae over 8 mm have additional scattered melanophores around the snout and upper jaw and on the operculum. An internal pigment spot may be seen beneath the lobe of the hindbrain by about 8 mm (Figure 3D). A single stellate melanophore appears on the operculum anterior to the base of the pectoral fin at about 10-11 mm (Figure 4A, B).

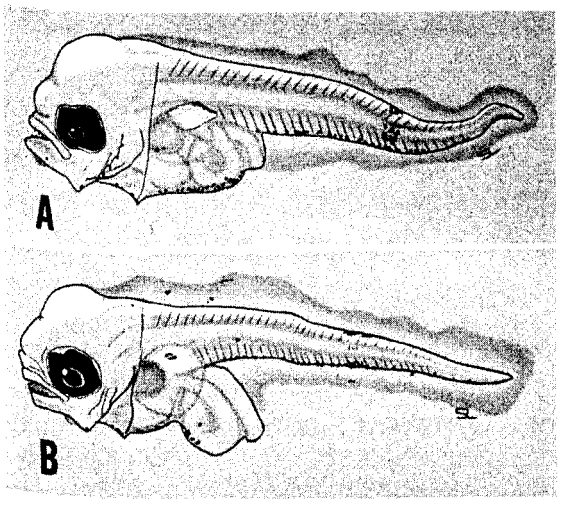

FIGURE 2.—Early stage larvae of A) *Etropus microstomus* (2.5 mm SL) and B) *Citharichthys arctifrons* (2.5 mm SL).

After metamorphosis and with scale formation, head pigmentation becomes less pronounced. A general darkening occurs on the lips and over the brain (see Figure 7A). Later the snout darkens and pigmentation increases on the operculum.

E. microstomus - Abdominal Region

Most conspicuous is the pigmentation, which persists until metamorphosis, on the gas bladder (Figures 2A, 3). This pigment area spreads out onto the hindgut with the disappearance of the gas bladder (Figure 4B, C). Melanophores line the ventral body margin from the cleithrum to the hindgut in early stage larvae (Figure 2A). After the pelvic fin begins to form (5-7 mm), melanophores no longer line the ventral body margin at the base of the fin but increase in concentration under the gut (Figures 3D, 4A). Several diffuse melanophores, the number increasing with age, appear over the end of the hindgut at about 3 mm (Figure 3A). One or two stellate melanophores are visible on the pectoral fin near its ventral origin throughout the larval period. Scattered melanophores appear on the distal margin of the pelvic fin after it forms. Two or three characteristic internal pigment spots appear along the dorsal surface of the notochord above the gut cavity at about 4 mm and remain until metamorphosis. A pigment spot appears on the dorsal body margin above the gut cavity at about 3 mm (Figure 3A). It persists until metamorphosis, although later it is located on the proximal margin of the interneural musculature (Figure 4A, B). As the larva approaches metamorphosis, pigmentation appears and increases along the myosepta of the body (Figure 4B, C).

After metamorphosis, the gut cavity becomes darkened on the eyed side. Pigmentation increases on the pectoral and pelvic fins (Figures 7A, 8A). Pigmentation along myosepta disappears on the body but increases on the interneural and interhemal regions in juveniles.

E. microstomus - Tail Region

Larvae of 2.3 mm have a band of pigment about two-thirds the distance from the anus to

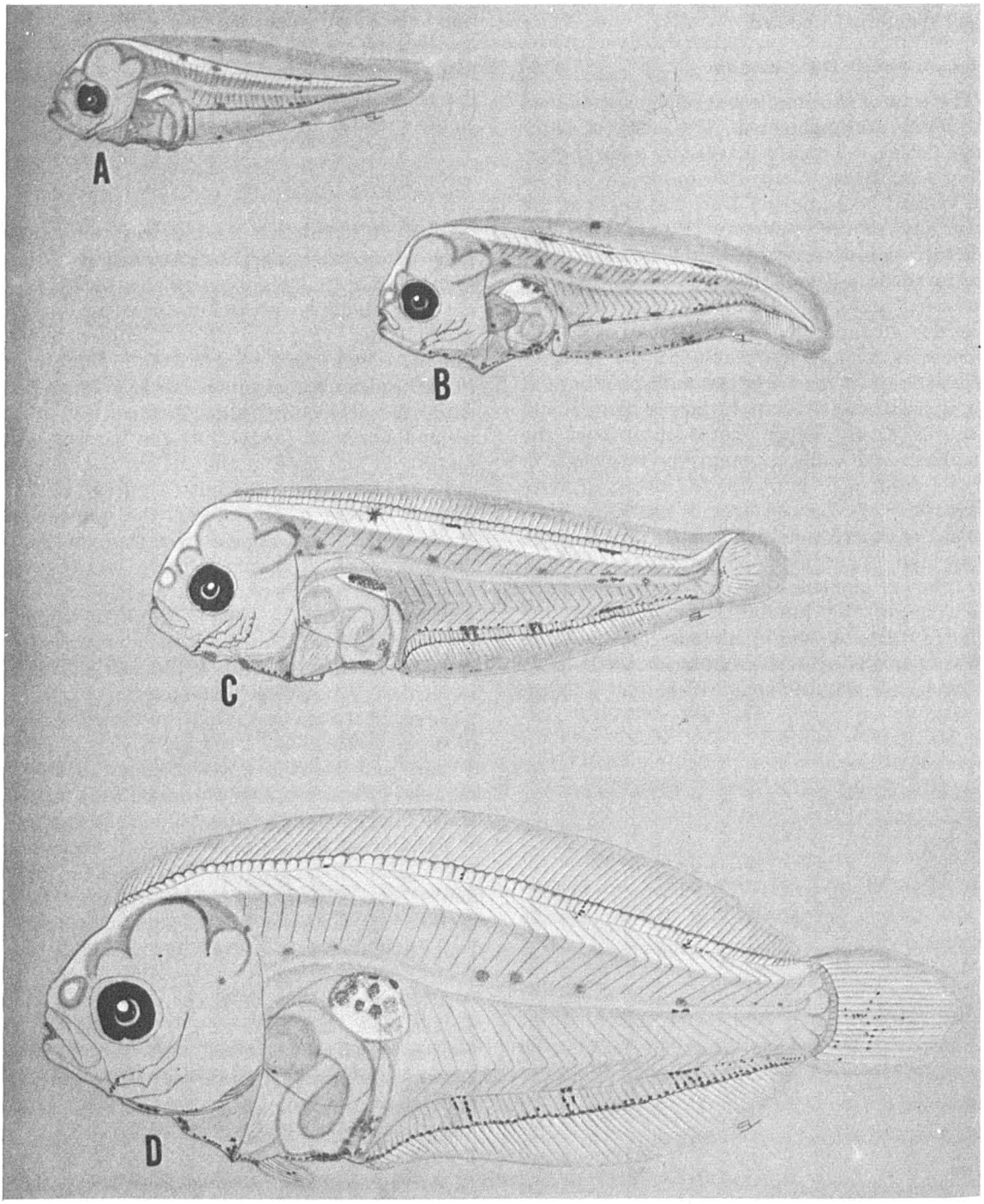

FIGURE 3.—Early stage larvae of *Etropus microstomus*. A) 3.5 mm SL; B) 4.5 mm SL; C) 5.9 mm SL; D) 8.3 mm SL.

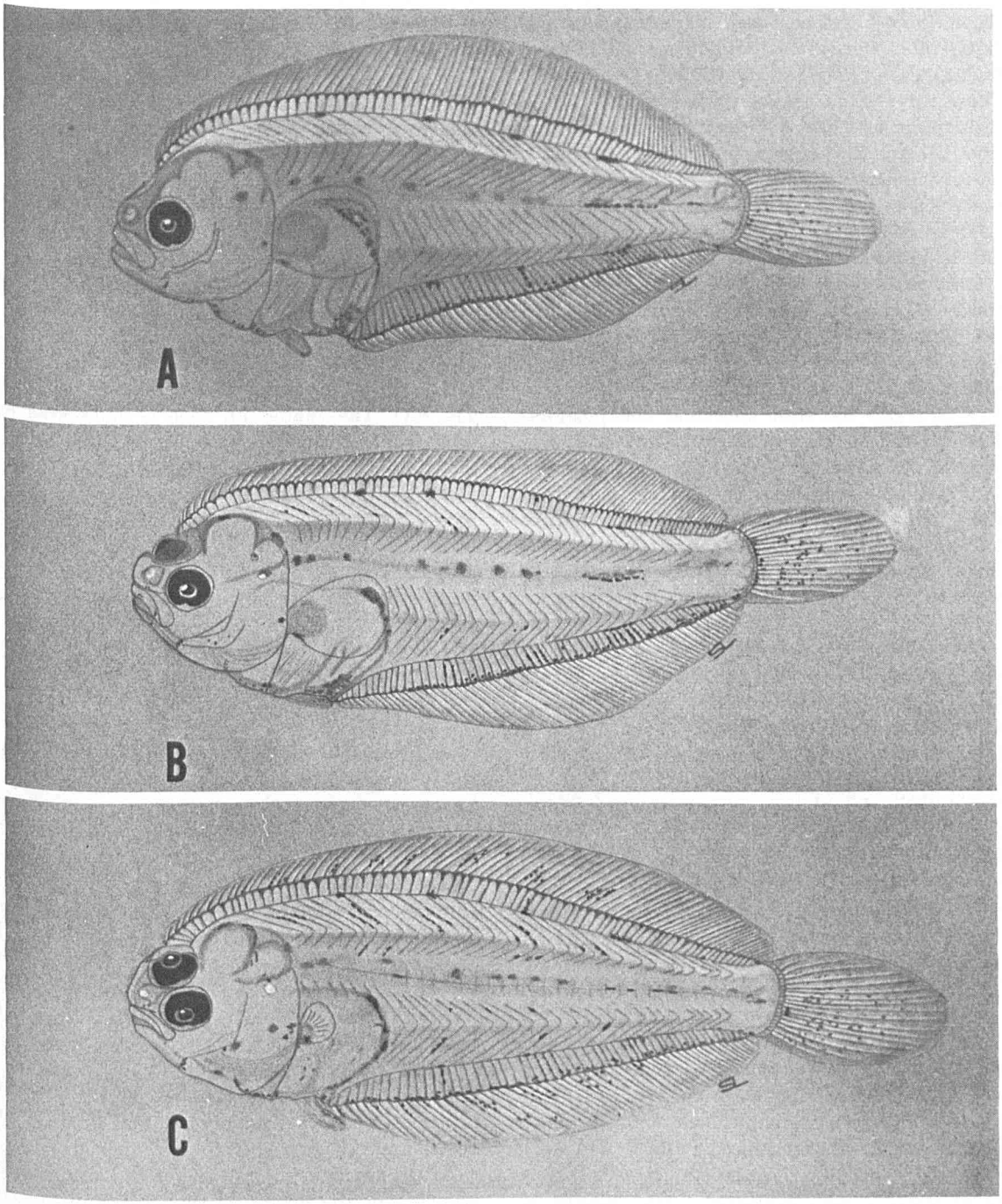

FIGURE 4.—Late stage larvae of *Etropus microstomus*. A) 10.6 mm SL; B) 10.9 mm SL (early transformation); C) 11.4 mm SL (late transformation).

the notochord tip (Figure 2A). By about 3 mm, sometimes before, this band differentiates to become two horizontal lines of pigment on the dorsal and ventral body margin, and a third line appears along the notochord (Figure 3A). These three lines persist until metamorphosis. Melanophores line the ventral body margin from the gut to the notochord tip on the smallest specimens (Figure 2A). As development proceeds, this ventral pigmentation shifts from its original position to the distal margin of the interhemal musculature (Figure 3C, D). One prominent ventral pigment spot appears in larvae of about 3 mm (Figure 3A), one-third the distance from the hindgut to the postanal pigment bars. A second prominent ventral spot appears by about 4 mm (Figure 3B), halfway between the first spot and the postanal bars. At the location of these two ventral pigment spots and the ventral postanal pigment bar, melanophores form several vertical lines along the septa of the interhemal musculature from proximal to distal margin (Figure 3C, D), beginning at about 5 mm. These vertical pigment lines persist until metamorphosis (Figure 4).

By about 4 mm, characteristic internal pigment spots begin to appear along the dorsal margin of the notochord from the abdominal region to the tail. These spots number 3 to 5 at first and may increase to about 8 to 10 by metamorphosis (Figure 4C).

Along the dorsal body margin one prominent pigment spot appears at about 3 mm (Figure 3A), and another by about 6-7 mm (Figure 3D) between the gut cavity and the tail tip, opposite those on the ventral margin. Up to metamorphosis these spots may appear as a cluster of melanophores (Figure 3A), a horizontal line (Figure 3C), or vertical line (Figure 3D), extending onto the interneural musculature. An increase in pigmentation occurs along the myosepta on the eyed side as the larva begins to metamorphose (Figure 4B, C).

One to three prominent melanophores may be seen on the distal edges of the finfold dorsally and ventrally (Figure 3A, B), on larvae up to about 5 mm. Scattered melanophores of less prominence may be seen in some specimens, depending on state of preservation, along the ventral finfold from the anus to the three postanal pigment bars (Figure 3B). These melanophores disappear with fin formation at about 6-8 mm. When the urostyle turns upward and the caudal fin begins to form at about 5-6 mm, scattered melanophores appear along its base (Figure 3C). Later, melanophores become scattered throughout the caudal fin and sometimes delineate its base (Figure 4B). Melanophores begin to dot both dorsal and anal fins at about metamorphosis (11-12 mm), first appearing in groups (Figure 4C) and later scattered throughout.

After metamorphosis, concentrated blotches of pigment become prominent along the proximal portions of the dorsal and anal fins (Figures 7A, 8A). The caudal fin base is delineated by pigment. An increase in pigmentation occurs along interneural and interhemal myosepta and along the lateral line. In adults, this pigment is partially obscured by scales. Pigment along body myomeres tends to disappear, but scale pockets are outlined with pigment which accounts for the general darkening of the eyed side. In females, an increase in pigmentation occurs over the ovarian cavity.

C. arctifrons - Head Region

The eyes are heavily pigmented by 2.3 mm. Early stage larvae of 2-5 mm (Figures 2B; 5A, B, C) have melanophores scattered along the ventral body margin from the angle of the lower jaw to the cleithrum. This pigment becomes less conspicuous with age (Figure 6). Clusters of melanophores are usually noticeable on the posteroventral angle of the lower jaw and at the tip of the cleithrum from about 5 mm throughout larval development. Pigment begins to appear over the brain at about 6-7 mm. At metamorphosis, the amount of pigment increases on the head (Figure 6C). Concentrations of melanophores develop on the tips of the three elongated anterior dorsal fin rays at about 8 mm (Figures 5D, 6A).

After metamorphosis, a general darkening occurs over the brain, on the lips (Figure 7B) and later over the operculum (Figure 8B).

C. arctifrons - Abdominal Region

A heavy concentration of pigment occurs over the gas bladder in larvae of 2.5 mm (Figure 2B) and persist until metamorphosis. Additional melanophores appear over the dorsal surface of the hindgut beginning at about 4 mm (Figure 5B). Scattered melanophores occur along the ventral body margin from the cleithrum to the hindgut. When the pelvic fin forms (5-7 mm), this pigment becomes less concentrated at its base. The concentration of pigment over the ventral part of the gut cavity increases with age (Figure 5C, D), and several diffuse melanophores appear near the end of the hindgut by 8-10 mm (Figures 5D; 6A, B). Pigment becomes noticeable on the tip of the pelvic fin by about 5-6 mm (Figure 5C, D). As the larva approaches metamorphosis, one to three prominent pigment spots appear along the proximal margin of the interneural musculature (Figure 6B, C). After these spots appear, a general increase in pigmentation occurs along the myosepta of the body (Figure 6B, C) on the eyed side.

Pigmentation over the gut cavity increases greatly after metamorphosis (Figure 7B) and the pectoral and pelvic fins become dotted with melanophores. The amount of pigment lining myosepta tends to decrease on the body and increase in the interneural and interhemal regions.

C. arctifrons - Tail Region

Larvae of 2-3 mm may have a postanal band of pigment, which becomes a dorsal and anal bar of pigment (Figures 2B, 5A), on the body margins about two-thirds the distance from the anus to the notochord tip. A distinct horizontal pigment bar appears intermediate to the dorsal and anal bars by 4-5 mm (Figure 5C). The three postanal pigment bars remain until metamorphosis (Figure 6C).

Melanophores appear scattered along the ventral body margin from the hindgut to the tail tip at 2-3 mm (Figures 2B, 5A). This pigmentation shifts to the distal margin of the interhemal musculature as development proceeds (Figure 5D). By about 10-11 mm, two clusters of melanophores develop along the proximal margin of the interhemal musculature between the hindgut and the ventral horizontal pigment bar (Figure 6A, B). These clusters increase in prominence until metamorphosis (Figure 6C).

Internal pigment spots appear along the dorsal surface of the notochord immediately above the intermediate postanal pigment bar by about 5 mm (Figure 5C). These internal spots remain apparent until metamorphosis.

Along the proximal margin of the interneural musculature, several (usually three) clusters of pigment become prominent by 12-13 mm, two between the abdominal region and the dorsal postanal pigment bar and one posterior to the dorsal bar (Figure 6B, C). After the appearance of the dorsal and anal pigment clusters, as metamorphosis proceeds, pigmentation increases along the myosepta of the body on the eyed side (Figure 6C).

Scattered pigment may occur on the finfold from 2 to 4 mm, but in no set pattern (Figures 2B; 5A, B). Melanophores begin to delineate the base of the caudal fin by about 10 mm (Figure 6A) and later appear scattered over the fin (Figure 6C). Pigmentation appears on the dorsal and anal fins, first in clusters (Figure 6C) and then scattered throughout, as the larva nears the completion of metamorphosis at around 14 mm.

After metamorphosis, pigmentation becomes less pronounced along the body myomeres but increases along the septa of the interneural and interhemal musculature (Figure 7B). Pigmentation appears along the lateral line on both eyed and blind sides. In females, pigmentation increases over the ovarian cavity. In adults, the most prominent pigmentation is that of the scale pockets which results in a general darkening of the eyed side (Figure 8B).

Comparative Morphological Changes

Nonmorphometric changes are described for both species together as they are quite similar. Differences are noted.

Body shape of the earliest stage larvae of both species is characteristic of flatfishes. The head and abdominal region are deep and later-

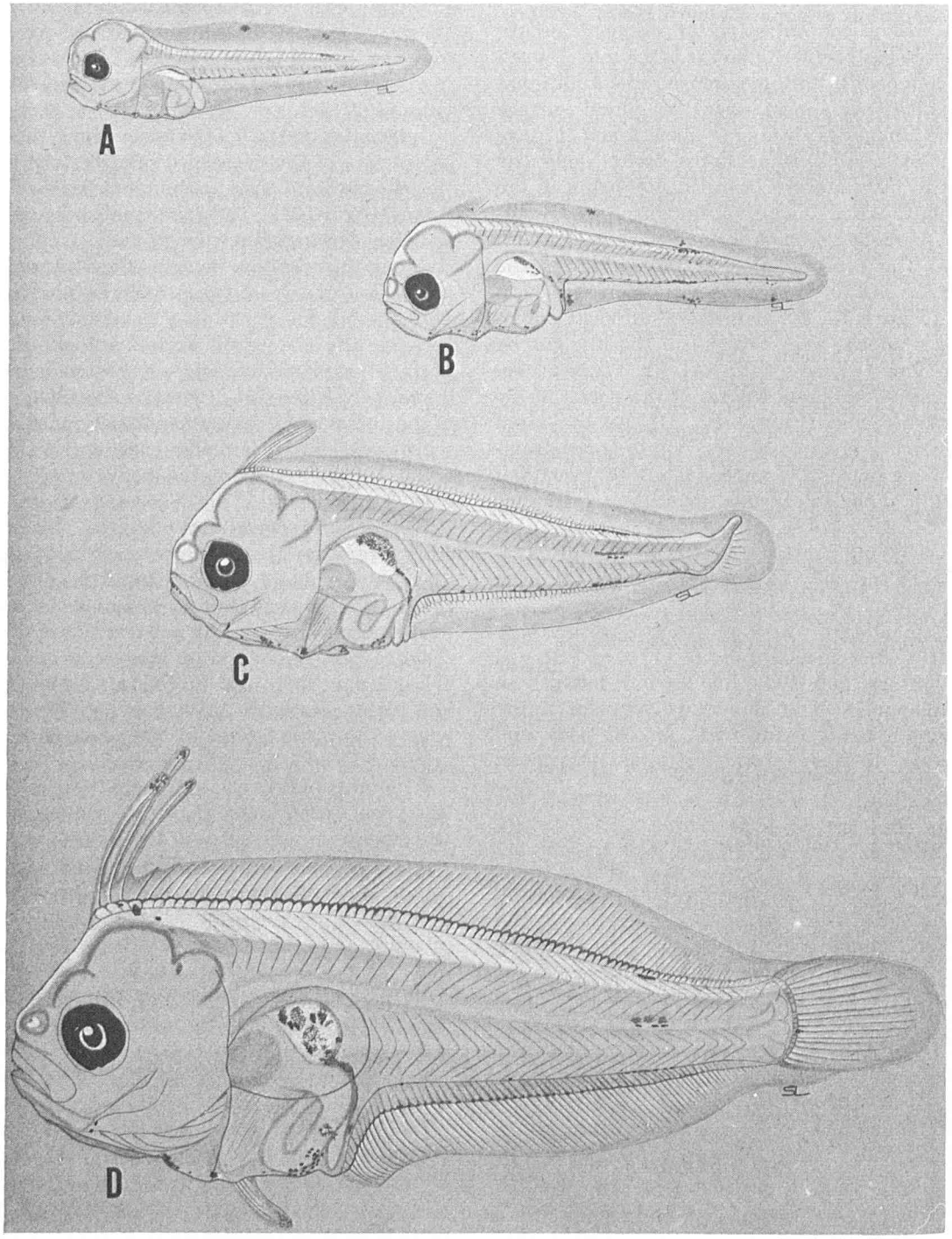

FIGURE 5.—Early stage larvae of *Citharichthys arctifrons*. A) 3.5 mm SL; B) 4.5 mm SL; C) 5.9 mm SL; D) 8.3 mm SL.

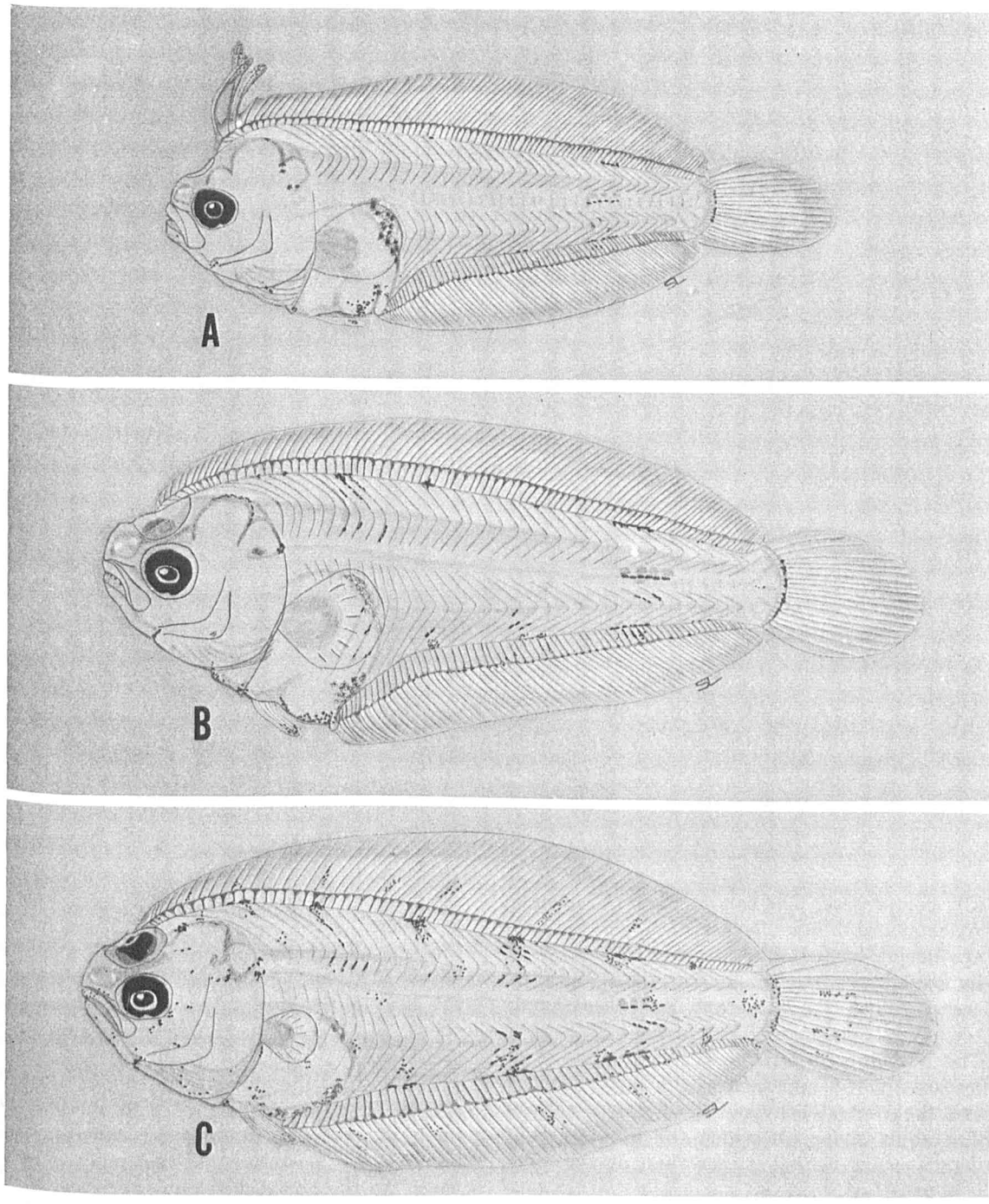

FIGURE 6.—Late stage larvae of *Citharichthys arctifrons*. A) 11.2 mm SL; B) 13.8 mm SL (soon before transformation); C) 14.4 mm SL (transformation).

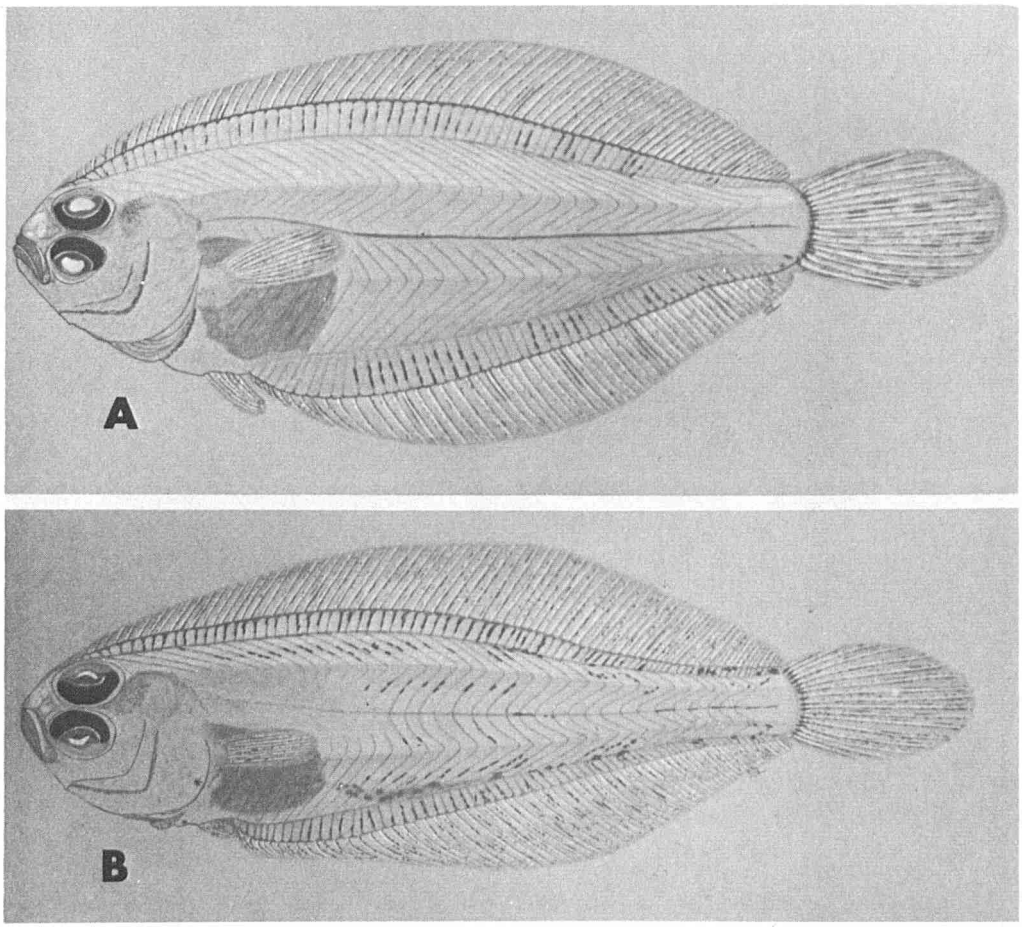

FIGURE 7.—Juvenile stages of A) *Etropus microstomus* (41 mm SL) and B) *Citharichthys arctifrons* (40 mm SL).

ally compressed. The caudal region is slender. At comparable sizes, larvae of *E. microstomus* are deeper-bodied than those of *C. arctifrons* immediately posterior to the anus. With increasing age, the head and peritoneal cavity occupy proportionately less of the body length. The dorsal body outline becomes convex. As metamorphosis approaches, the body deepens, and the ventral body outline becomes convex. The adult shape, in which the greatest body depth occurs behind rather than at the anus, is approached.

The fore-, mid-, and hindbrain are distinctly outlined in 2.5-mm larvae of both species and remain so until metamorphosis. A nasal capsule is evident on the snout at about 3 mm in both species and remains prominent until metamorphosis. The left otolith becomes noticeable in the head on the eyed side of *E. microstomus* at about 10-11 mm. It is not observable in *C. arctifrons*.

The coils of the alimentary tract can be seen clearly in 2.5-mm larvae of both species with the hindgut ending in a nearly vertical position immediately posterior to the main visceral mass. As the larval development proceeds, the position of the anus shifts anteriorly until it rests adjacent to the base of the left pelvic fin

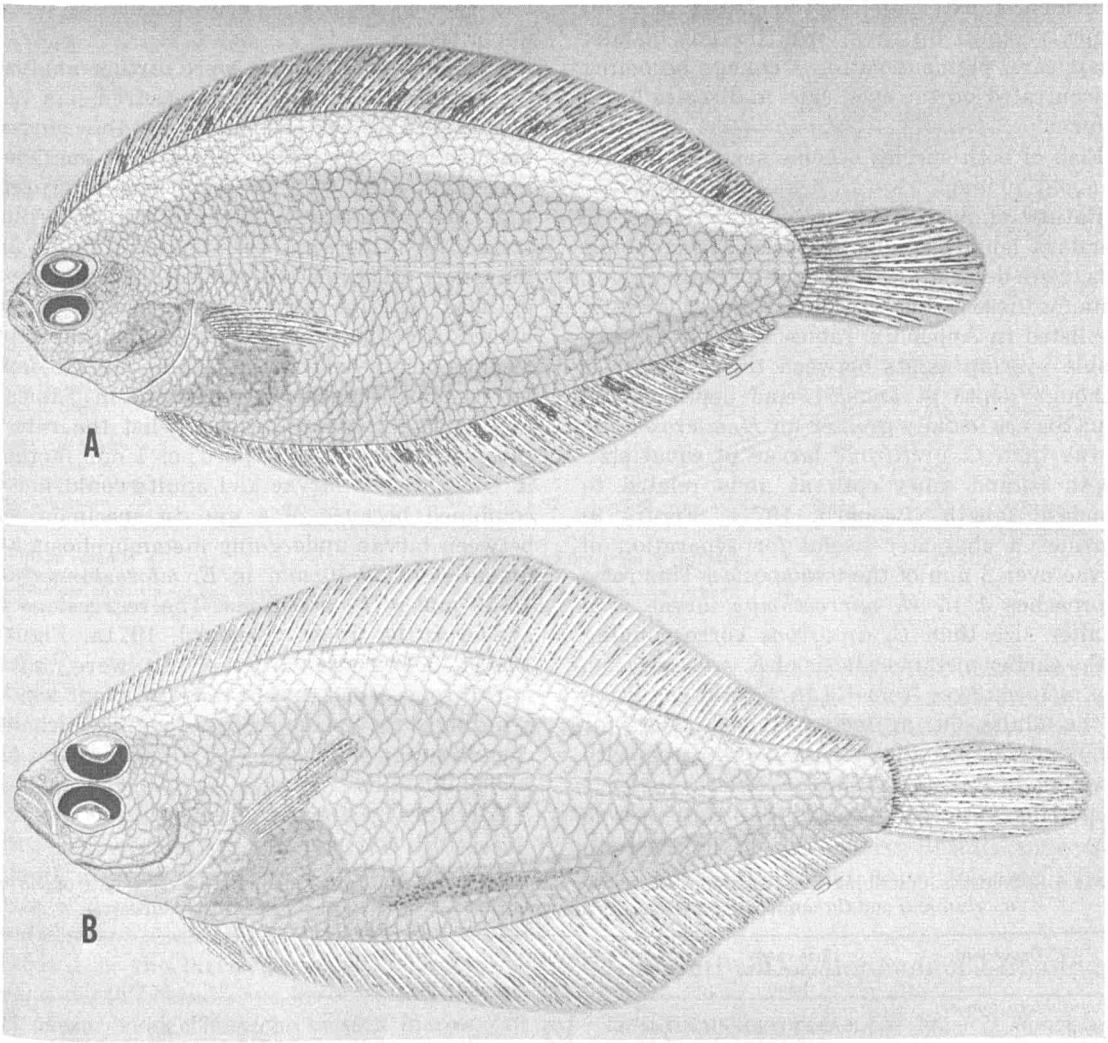

FIGURE 8.—Adult stages of A) *Etropus microstomus* (64 mm SL) and B) *Citharichthys arctifrons* (69 mm SL).

and lies beneath the center of the gut cavity. As metamorphosis approaches, the coils of the gut become obscured by overlying musculature.

Eye shape tends to be roughly spherical becoming more smoothly rounded with increasing age. A ventral cleft of the eye is apparent in larvae of both species from 3.0 mm up to metamorphosis.

The gas bladder is developed dorsal to the gut region in the smallest specimens of both species. It becomes increasingly prominent during larval development, but disappears during metamorphosis.

Metamorphosis occurs at 10-12 mm in *E. microstomus* and at 13-15 mm in *C. arctifrons*. Some variation was found in that a few specimens of *E. microstomus* were not transformed by 12 mm and some specimens of *C. arctifrons* had begun to do so at 12 mm. During metamorphosis, the right eye moves over the dorsal ridge of the head in front of the dorsal fin, the body deepens, the facial bones become distorted

as evidenced externally by the change in snout shape, pectoral fin rays form, the gas bladder disappears, pigment patterns change becoming concentrated on the eyed side, and scales begin to form.

Fish of both species become sexually mature by about 50 mm.

Ratios of body measurements related to standard length, frequently used as taxonomic aids, were determined for larvae of both species. Data for these ratios, which change with growth, are listed in Appendix Tables 1 and 2. Considerable overlap exists between the two species although depth at anus/SL and depth behind anus/SL are usually greater for *E. microstomus* larvae than *C. arctifrons* larvae of equal size. Depth behind anus/depth at anus related to standard length (Leonard, 1971a, Figure 9) provides a character useful for separation of larvae over 8 mm of the two species. This ratio approaches 1 in *E. microstomus* larvae of a smaller size than *C. arctifrons* corresponding to the earlier metamorphosis of *E. microstomus*. The ratio changes from <1 to >1, the condition in the adults, during metamorphosis. Data for the adults (Appendix Tables 3, 4) agree with those given by Parr (1931). *E. microstomus* is proportionately deeper bodied than *C. arctifrons* but the latter has a proportionately longer upper jaw.

Changes in body form were further analyzed for growth patterns. Body measurements (Appendix Tables 1-4) were used for this purpose because methods using ratios "are inefficient and may often lead to erroneous interpretation" as explained by Marr (1955) and illustrated by Ahlstrom and Counts (1955) and Mansueti (1958). Statistics for the regressions of head length, snout length, snout to anus length, eye diameter, upper jaw length, depth at anus, depth behind anus, and peduncle depth on standard length are presented in Tables 4 and 5. The columns headed *b* list the rate of increase in size of body part per 1 mm increase in SL. Data on larvae and adults could not be combined because of a gap in specimen size between larvae undergoing metamorphosis and juveniles of 30-40 mm in *E. microstomus* and 40-50 mm in *C. arctifrons*. The regressions all appear to be linear (Leonard, 1971a, Figures 10-17). Correlation coefficients were >0.93 for all regressions except those of snout length, eye diameter, and upper jaw length which had correlation coefficients >0.87 in larvae and >0.80 in adults.

All body parts measured increase more in

TABLE 4.—Statistics describing the regressions of body measurements on standard length for larval stages of *Etropus microstomus* and *Citharichthys arctifrons*. The independent variable X is standard length in all cases.

Dependent variable Y	Size range of specimens (mm)	$\bar{X}$	$\bar{Y}$	N	b	a	S_y	r
Etropus microstomus:								
Head length	3.53-12.60	7.44	1.95	100	0.267	-0.039	0.208	0.987
Snout length	3.53-12.60	7.44	0.47	100	0.068	-0.040	0.155	0.895
Snout to anus	3.53-12.60	7.44	2.93	100	0.321	0.538	0.428	0.960
Eye diameter	3.53-12.60	7.44	0.49	100	0.048	0.127	0.127	0.875
Upper jaw length	3.53-12.60	7.44	0.66	100	0.076	0.096	0.178	0.890
Depth at anus	3.53-12.60	7.44	2.57	100	0.482	-1.017	0.450	0.980
Depth behind anus	3.53-12.60	7.44	2.08	100	0.481	-1.498	0.418	0.982
Peduncle depth	3.53-12.60	7.44	0.76	100	0.162	-0.441	0.244	0.950
Citharichthys arctifrons:								
Head length	4.54-14.36	7.55	2.06	100	0.304	-0.236	0.275	0.984
Snout length	4.54-14.36	7.55	0.51	100	0.080	-0.098	0.155	0.931
Snout to anus	4.54-14.36	7.55	3.10	100	0.378	0.248	0.605	0.974
Eye diameter	4.54-14.36	7.55	0.55	100	0.063	0.072	0.084	0.954
Upper jaw length	4.54-14.36	7.55	0.77	100	0.099	0.028	0.095	0.933
Depth at anus	4.54-14.36	7.55	2.31	100	0.462	-1.177	0.152	0.991
Depth behind anus	4.54-14.36	7.55	1.69	100	0.403	-1.352	0.260	0.991
Peduncle depth	4.54-14.36	7.55	0.68	100	0.168	-0.591	0.236	0.962

$\bar{X}$ - Mean value of X
$\bar{Y}$ - Mean value of Y
N - Number of specimens examined
b - Rate of increase of Y with respect to X
a - Y-intercept of regression line
S_y - Standard deviation of the regression
r - Correlation coefficient

TABLE 5.—Statistics describing the regressions of body measurements on standard length for juvenile and adult stages of *Etropus microstomus* and *Citharichthys arctifrons*. The independent variable X is standard length in all cases.

Dependent variable Y	Size range of specimens (mm)	$\bar{X}$	$\bar{Y}$	N	b	a	S_y	r
Etropus microstomus:								
Head length	29-123	73.70	17.13	100	0.200	2.388	1.592	0.972
Snout length	29-123	73.70	3.33	100	0.036	0.653	0.876	0.805
Snout to anus	29-123	73.70	17.13	100	0.200	2.388	1.592	0.972
Eye diameter	29-123	73.70	4.85	100	0.049	1.250	0.886	0.875
Upper jaw length	29-123	73.70	4.74	100	0.047	1.268	0.761	0.897
Depth at anus	29-123	73.70	26.37	100	0.378	-1.475	2.874	0.974
Depth behind anus	29-123	73.70	33.30	100	0.511	-4.350	2.937	0.977
Peduncle depth	29-123	73.70	8.35	100	0.114	-0.073	1.100	0.960
Citharichthys arctifrons:								
Head length	47-135	93.07	22.18	100	0.214	2.226	1.615	0.980
Snout length	47-135	93.07	4.29	100	0.034	1.102	0.779	0.852
Snout to anus	47-135	93.07	22.18	100	0.214	2.226	1.615	0.980
Eye diameter	47-135	93.07	7.18	100	0.063	1.283	1.193	0.891
Upper jaw length	47-135	93.07	7.19	100	0.046	2.895	1.130	0.834
Depth at anus	47-135	93.07	28.77	100	0.319	-0.925	2.652	0.976
Depth behind anus	47-135	93.07	34.63	100	0.439	-6.251	2.701	0.986
Peduncle depth	47-135	93.07	8.92	100	0.091	0.464	1.282	0.934

$\bar{X}$ - Mean value of X
$\bar{Y}$ - Mean value of Y
N - Number of specimens examined
b - Rate of increase of Y with respect to X
a - Y-intercept of regression line
S_y - Standard deviation of the regression
r - Correlation coefficient

relation to SL in *C. arctifrons* than in *E. microstomus* larvae except depth at anus and depth behind anus. Thus larval growth patterns support the fact that, as adults, *E. microstomus* is the deeper-bodied of the two, while *C. arctifrons* has larger eyes and a larger mouth.

In larvae of both species, the rate of increase of depth at anus is greater than the rate of increase of depth behind anus. Yet depth behind anus/depth at anus approaches and eventually exceeds 1 as the larvae undergo metamorphosis and depth behind anus becomes the deepest part of the body. Thus, the rate of increase of depth behind anus should be greater than depth at anus.

For juveniles and adults, head length, eye diameter, upper jaw length, and snout to anus length increase at a faster rate in *C. arctifrons* while all components of body depth (depth at anus, depth behind anus, peduncle depth) increase more rapidly in *E. microstomus*. Snout length in both species increases at about the same rate.

The data indicate decreases in rates of growth of head length, snout length, snout to anus length, upper jaw length, peduncle depth from larvae to adults of both species. Rate of growth of eye diameter is nearly the same in larvae and adults of both species. Depth at anus decreases and depth behind anus increases in growth rate from larvae to adults of both species.

Some degree of error exists in these calculations because of specimen shrinkage, wide area of collection, and varying lengths of time of preservation of specimens. Results presented here may differ from those obtained from newly preserved material.

Comparative Developmental Osteology

The discussion presented here is based entirely on stained material of approximately 100 larvae and of 10 juveniles and adults of each species. No dissections were made. The smallest stained larvae examined were 4 mm SL.

Sequences of ossification are consistent within each species, but the size at which specific bones begin to ossify may vary from specimen to specimen. The sizes given here indicate general trends of the larval specimens examined from VIMS 1962 collections.

This study is not intended to be a descriptive osteology of each species but rather a comparison of development of the two. Discussion of skull bones is mainly limited to those of the branchiocranium which are identifiable in early

stages. Most bones of the neurocranium cannot be distinguished in stained larvae.

Terminology is based on Gregory (1933), Lagler, Bardach, and Miller (1962), Fraser (1968), and Wolcott, Beirne, and Hall (1968).

Fin Formation

A large finfold surrounds the body of early stage larvae from the head, around the tail tip, to the anus. The first fins to form are larval pectorals. Fin rays begin to ossify in larvae of 5-6 mm in dorsal, anal, caudal, and pelvic fins in both species (Table 6). Fin rays do not appear in the pectoral fins until metamorphosis. Fin formation in both species is completed in the following order: caudal, dorsal and anal, pelvic, and pectoral.

Incipient caudal fin rays become visible in the posteroventral region of the finfold as early as 4 mm in *E. microstomus*. Fin rays ossify after the urostyle begins to turn dorsad at about 5 mm in both species. The first rays to take up alizarin stain are in the center of the fin. Development proceeds dorsally and ventrally until the full complement of 17 caudal fin rays is attained by 7 mm in *E. microstomus* and 9 mm in *C. arctifrons*.

The proximal portions of incipient dorsal fin rays may appear in the center of the dorsal finfold as early as 4 mm in *E. microstomus*. Ossification of rays in the dorsal fin begins centrally at about 5 mm and proceeds anteriorly and posteriorly. The full complement is achieved by 8 mm. In *C. arctifrons*, a notch appears dorsally in the anterior portion of the finfold at about 4 mm. By 5 mm, three elongated fin rays become ossified in this region. These rays persist until the onset of metamorphosis, although they appear to get proportionately shorter with increasing age. Formation of the rest of the dorsal fin is similar to that of *E. microstomus*. Ossification of fin rays begins centrally at about 6 mm and proceeds anteriorly and posteriorly. The full complement is attained by 10 mm. During dorsal fin formation in *C. arctifrons*, one fin ray appears anterior to the three elongated rays, which then become the 2d, 3d, and 4th rays. The 1st ray is inconspicuous and is best seen on the blind side. Only its base takes up alizarin stain until the three elongated anterior rays become reduced in size. With development, the dorsal fin moves progressively anteriorad in both species. As the right eye moves over the ridge

TABLE 6.—Ranges of meristic counts in early stages of *Etropus microstomus* and *Citharichthys arctifrons*.

Size group (mm)	Number of specimens	Dorsal fin rays	Anal fin rays	Caudal fin rays	Pelvic fin rays		Vertebral column					Branchiostegal rays (left)
							Neural spines		Hemal spines	Centra		
					Left	Right	Abdominal	Caudal	Caudal	Abdominal	Caudal + urostyle	
Etropus microstomus:												
4.00- 4.99	10	—	—	—	—	—	0-6	—	0-4	—	—	0-5
5.00- 5.99	15	0-60	0-40	0-15	0-3	LB[1]	0-9	0-22	0-23	0-9	0-1	5-7
6.00- 6.99	20	17-68	17-50	5-17	0-4	0-3	9-10	8-23	6-23	0-10	0-23	[1]7
7.00- 7.99	16	49-72	34-55	[2]17	2-4	2-5	9-10	16-23	13-23	8-10	2-25	7
8.00- 8.99	12	[2]68-80	[2]50-60	17	3-5	3-5	9-10	21-24	21-24	7-10	3-25	7
9.00- 9.99	10	72-83	55-62	17	4-6	4-6	[2]10	[2]23-24	[2]23-24	[2]10	[2]24-25	7
10.00-10.99	6	70-80	53-58	17	5-6	5-6	10	23-24	23-24	10	24-25	7
11.00-11.99	2	74	54	17	5-6	[2]6	10	23-24	23-24	10	24-25	7
12.00-12.99	7	77-79	58-60	17	[2]6	6	10	23-24	23-24	10	24-25	7
Citharichthys arctifrons:												
4.00- 4.99	6	—	—	—	—	—	—	—	—	—	—	0-3
5.00- 5.99	25	0-3	—	0-5	LB	LB	0-10	0-15	0-15	—	—	4-7
6.00- 6.99	23	3-68	0-52	6-17	0-3	0-4	3-10	9-26	3-26	—	0-1	[2]7
7.00- 7.99	12	45-74	31-57	9-17	2-4	3-4	9-10	19-25	23-25	0-10	0-27	7
8.00- 8.99	9	67-75	49-57	16-17	3-5	3-5	[2]10	23-25	23-25	6-10	1-26	7
9.00- 9.99	7	66-82	49-65	[2]17	3-5	3-5	10	[2]25-26	[2]25-26	[2]10	6-27	7
10.00-10.99	4	[2]82-83	[2]66-67	17	4-5	3-6	10	25-26	25-26	10	[2]27	7
11.00-11.99	5	77-81	62-66	17	4-6	5-6	10	25-27	25-26	10	26-28	7
12.00-12.99	3	77-82	64-66	17	5-6	[2]6	10	26	26	10	27	7

[1] Larval bud.
[2] Size range in which final or adult count is consistently achieved.

of the head, the anterior part of the fin is deflected to the blind side.

The anal fin forms similarly to the dorsal fin. Rays become ossified centrally first, with formation progressing both anteriorly and posteriorly. Ossified fin rays are evident by 5 mm in *E. microstomus* and 6 mm in *C. arctifrons*. The full complement of rays is achieved by 8 mm in *E. microstomus* and 10 mm in *C. arctifrons*.

Pelvic fin buds appear at 5 mm in both species. Ossification of fin rays begins from 5 to 6 mm in *E. microstomus* and at 6 mm in *C. arctifrons*. The right pelvic fin completes formation before the left fin. The full complement of six rays is consistently attained by 11-12 mm in *E. microstomus* and 12+ mm in *C. arctifrons* (Table 6). By about 8 mm in *E. microstomus* and 10 mm in *C. arctifrons*, the right pelvic fin base is located noticeably above the body midline on the blind side. Its origin is slightly anterior to that of the left pelvic fin base which is located on the body midline. These relative positions of pelvic fin bases become more obvious after the basipterygium ossifies (12 mm in *E. microstomus*, later in *C. arctifrons*) and are difficult to detect on unstained specimens until a larger size.

With metamorphosis, the larval pectoral fins transform to much smaller fins in relation to body size, as incipient fin rays form. The size at which pectoral fins are completely formed could not be determined because of a lack of specimens in the size range between those undergoing metamorphosis and juveniles of 20+ mm.

Vertebral Column and Median Fin Supports

Sequence of ossification of the vertebral column is the same for both species. Neural spines of the abdominal region ossify first, followed by neural and hemal spines of the caudal region. Development progresses posteriorily (Leonard, 1971a, Figure 18). Vertebral centra then begin to ossify in the posterior abdominal region with development progressing anteriorly. Centra of the caudal region ossify from anterior to posterior. The urostyle ossifies before the several centra immediately preceding it. The abdominal rod, which extends from the anteromost hemal spine to the position of the anus and supports the interhemal spines ventral to the gut cavity, begins to ossify before the elements of the hypural plate and after most centra are ossified. Ribs become evident on abdominal centra about the time the abdominal rod begins to ossify (7 mm for *E. microstomus* and 8-9 mm for *C. arctifrons*). Interneural and interhemal spines probably ossify near the completion of metamorphosis.

C. arctifrons generally lags behind *E. microstomus* in development (Table 6). Neural and hemal spines appear by 4 mm in *E. microstomus* and 5 mm in *C. arctifrons*. Centra may begin to ossify at 5 mm in *E. microstomus* and 6-7 mm in *C. arctifrons*. The adult vertebral complement, including neural and hemal spines and abdominal and caudal centra, is achieved by 9 mm in *E. microstomus*. Neural and hemal spines are all ossified by 9 mm in *C. arctifrons*, but not all centra are consistently stained until about 10 mm.

Structure of the vertebral column and dorsal, anal, and caudal fin supports is essentially the same in juveniles and adults of both species (Leonard, 1971a, Figures 19-21). The anterior interneural spines are inclined forward such that the first interneural spine, which is bifurcated (sometimes trifurcated in *C. arctifrons*), lies in a horizontal position. The abdominal rod, the distal portion of which is bifurcated, provides support for the 6-9 most anterior interhemal spines. The 17 rays of the caudal fin occur in a 4-5-4-4 sequence, supported by four hypural elements. Neural and hemal spines of the penultimate vertebra support no caudal fin rays.

Pectoral and Pelvic Girdles

The cleithrum (Leonard, 1971a, Figure 22) is ossified in the smallest stained specimens and observable as early as 2.3 mm in unstained larvae. The supracleithrum appears early in both species (Table 7). The posttemporal and postcleithrum ossify next, appearing first in *E. microstomus*. Ossification of the basipterygium (Figure 9) seems to coincide with achieve-

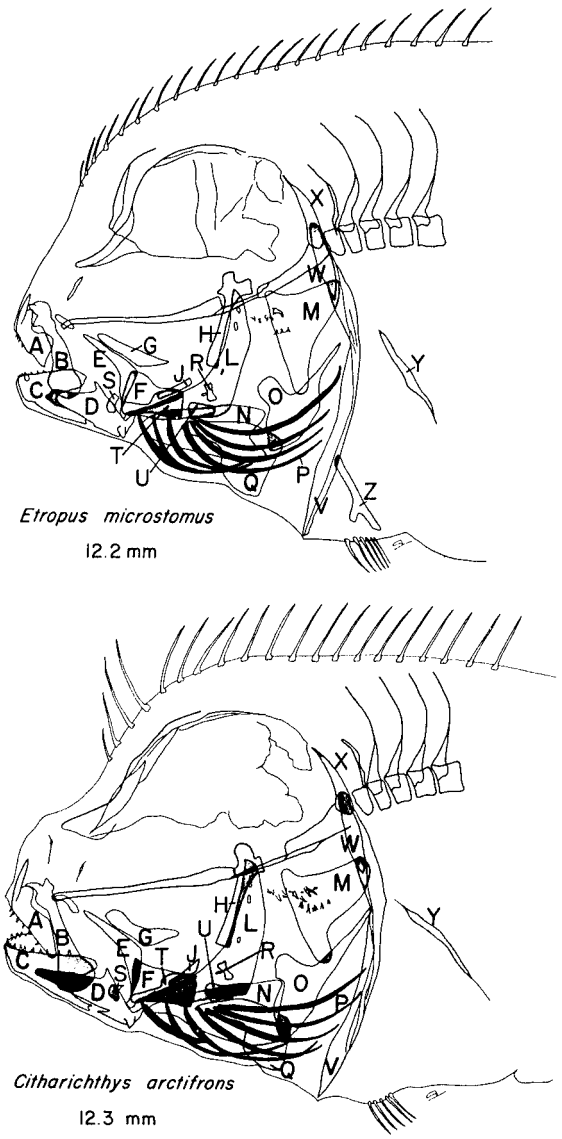

FIGURE 9.—Composite illustration of bones of the branchiocranium and of the pectoral and pelvic girdles (shaded) of young *Etropus microstomus* and *Citharichthys arctifrons*. The ossified part of the neurocranium including the parasphenoid is outlined. Upper and lower jaws: A - premaxillary, B - maxillary, C - dentary, D - articular and angular process. Oromandibular region: E - ectopterygoid, F - quadrate, G - endopterygoid, H - hyomandibular, J - symplectic. Opercular series: L - preopercle, M - opercle, N - interopercle, O - subopercle. Hypobranchial region: P - branchiostegal rays, Q - urohyal, R - interhyal, S - hypohyal, T - ceratohyal, U - epihyal. Pectoral and pelvic girdles: V - cleithrum, W - supracleithrum, X - posttemporal, Y - postcleithrum, Z - basipterygium.

TABLE 7.—Size in millimeters at which certain bones begin to ossify in *Etropus microstomus* and *Citharichthys arctifrons*.

Item	Bone[2] type	*Etropus microstomus*	*Citharichthys arctifrons*
Upper and lower jaws:			
A Premaxillary	D	?- 4.9	?- 4.9
B Maxillary	D	?- 4.9	?- 4.9
C Dentary	D	?- 4.9	?- 4.9
D Articular	C	?- 4.9	?- 4.9
Angular process	D	8.0- 8.9	7.0- 7.9
Oromandibular region:			
E Ectopterygoid	D	4.0- 5.9	4.0- 5.9
F Quadrate	C	5.0- 5.9	5.0- 6.9
G Endopterygoid	D	5.0- 6.9	6.0- 7.9
H Hyomandibular	C	5.0- 6.9	6.0- 7.9
J Symplectic	C	7.0- 7.9	8.0- 8.9
K Palatine	C	9.0- 9.9	11.0-11.9
K′ Metapterygoid	C	A M[3]	A M
Opercular series:			
L Preopercle	D	?- 4.9	?- 4.9
M Opercle	D	?- 4.9	?- 4.9
N Interopercle	D	5.0- 6.9	6.0- 7.9
O Subopercle	D	5.0- 6.9	6.0- 7.9
Hypobranchial region:			
P Branchiostegal rays	D	4.0- 5.9	4.0- 5.9
Q Urohyal	D	6.0- 6.9	7.0- 7.9
R Interhyal	C	7.0- 7.9	7.0- 7.9
S Hypohyals	C	7.0- 7.9	8.0- 8.9
T Ceratohyal	C	7.0- 7.9	8.0- 8.9
U Epihyal	C	7.0- 7.9	8.0- 8.9
U′ Basihyal	C	A M	A M
Pectoral and pelvic girdles:			
V Cleithrum	D	?- 4.9	?- 4.9
W Supracleithrum	D	4.0- 5.9	4.0- 5.9
X Posttemporal	D	5.0- 6.9	6.0- 7.9
Y Postcleithrum	D	5.0- 6.9	6.0- 7.9
Z Basipterygium	C	11.0-12.9	A M
Z′ Scapula	C	A M	A M
Z″ Coracoid	C	A M	A M
Z‴ Radials	C	A M	A M

[1] The smallest stained larvae examined were 4 mm.
[2] D - Dermal bone.
C - Cartilage replacement bone.
[3] A M - After metamorphosis.

ment of the adult complement of pelvic fin rays (Table 6) and possibly completion of metamorphosis—about 12 mm in *E. microstomus* and sometime before 16 mm in *C. arctifrons*. Time and sequence of ossification of the scapula, coracoid, and radials are unknown. They are ossified in juveniles of 40 mm. Ossification probably corresponds with pectoral fin formation.

Structurally, bones in these girdles are similar in both species. The posterior extension of the basipterygium on both sides is longer in juvenile and adult *E. microstomus* (Figures 10,11). The posttemporal of the eyed and blind side is relatively smaller in adult *C. arctifrons*.

Upper and Lower Jaws

By 4 mm, parts of the premaxillary, maxillary, dentary, and articular have begun to ossify in both species (Table 7). Development of the upper jaw (Leonard, 1971a, Figure 23) is similar to that described for other highly evolved forms of fishes (Berry, 1964). The toothless maxillary ossifies to a greater degree than the premaxillary in early stages and is included in the gape. As development proceeds, the premaxillary continues to grow posteriad and eventually eliminates the maxillary from the gape in *C. arctifrons* and nearly so in *E. microstomus* (Figures 9-11). Ossification of the jaw bones appears to be more advanced in *C. arctifrons* than in *E. microstomus* of equal size. This tendency is evident in the dentary and articular in *C. arctifrons* larvae of 4 mm. The angular process on the articular appears first in *C. arctifrons* (about 7 mm) and later (about 8 mm) in *E. microstomus*.

The fact that *C. arctifrons* has a larger jaw becomes evident by about 7 mm. The maxillary and premaxillary are longer than in *E. microstomus* and the processes of the dentary extend farther posteriorly. The anteromost process located laterally on the anterior knob of the maxillary becomes noticeably more elongate in *C. arctifrons* by about 12 mm (Figure 9). This maxillary process forms the osseous protuberance of the snout characteristic of adults (Figure 10). The premaxillary process, which occurs medially in the upper jaw, appears longer and narrower in *C. arctifrons* of about 12 mm, but not in juveniles and adults.

Teeth, distributed evenly in single rows on the left and right sides of the anterior portion of the premaxillary and dentary, are evident in the smallest stained larvae (in 3 mm unstained larvae) of both species. Teeth in adult *E. microstomus* are distributed mainly on the blind side (Figures 10, 11). This unequal distribution becomes apparent on the eyed side during metamorphosis (Figures 9, 10) as larval teeth are replaced. On the eyed side of juvenile and adult *E. microstomus*, teeth are more numerous on the lower jaw, e.g.:

	Upper jaw	*Lower jaw*
40 mm SL	7	13
60 mm SL	6	16

In juvenile and adult *C. arctifrons*, teeth on the eyed side are more numerous on the upper jaw, e.g.:

	Upper jaw	*Lower jaw*
40 mm SL	30	23
60 mm SL	40	25

Teeth on the blind side of the lower jaw are about equal in number to those of the upper jaw for each species. *C. arctifrons* has a greater total number of teeth corresponding to its larger mouth.

Oromandibular Region

The ectopterygoid is the first bone to ossify in this region, usually between 4 and 5 mm in both species (Leonard, 1971a, Figure 24). The quadrate, endopterygoid, hyomandibular, and symplectic become ossified in that order and at an earlier stage in *E. microstomus* than *C. arctifrons* (Table 7). By about 12 mm, degree of ossification of bones in this region is similar in both species (Figure 9). The palatine and metapterygoid become ossified sometime after metamorphosis (Figures 10, 11).

Structure of bones in this region is similar in the two species. The anterior wing of the hyomandibular extends farther ventrally along the central shaft of the bone in juvenile and adult *E. microstomus*, particularly on the eyed side.

Opercular Series

The opercle and preopercle are partly ossified in both species by 4 mm (Leonard, 1971a, Figure 25). The interopercle and subopercle ossify first in *E. microstomus* (Table 7) between 5 and 6 mm and by 7 mm in *C. arctifrons*.

Within this series, a major structural difference exists between larvae of these two species. Spines are present on the posterior preopercular margin of *E. microstomus* by 4 mm. (They may be seen on unstained larvae of 2.5 mm.) With development, the number of spines increases over the lateral surface of the preopercle. They begin to disappear at around 8 mm and can no longer be seen by 10 mm. *C. arctifrons* has no preopercular spines.

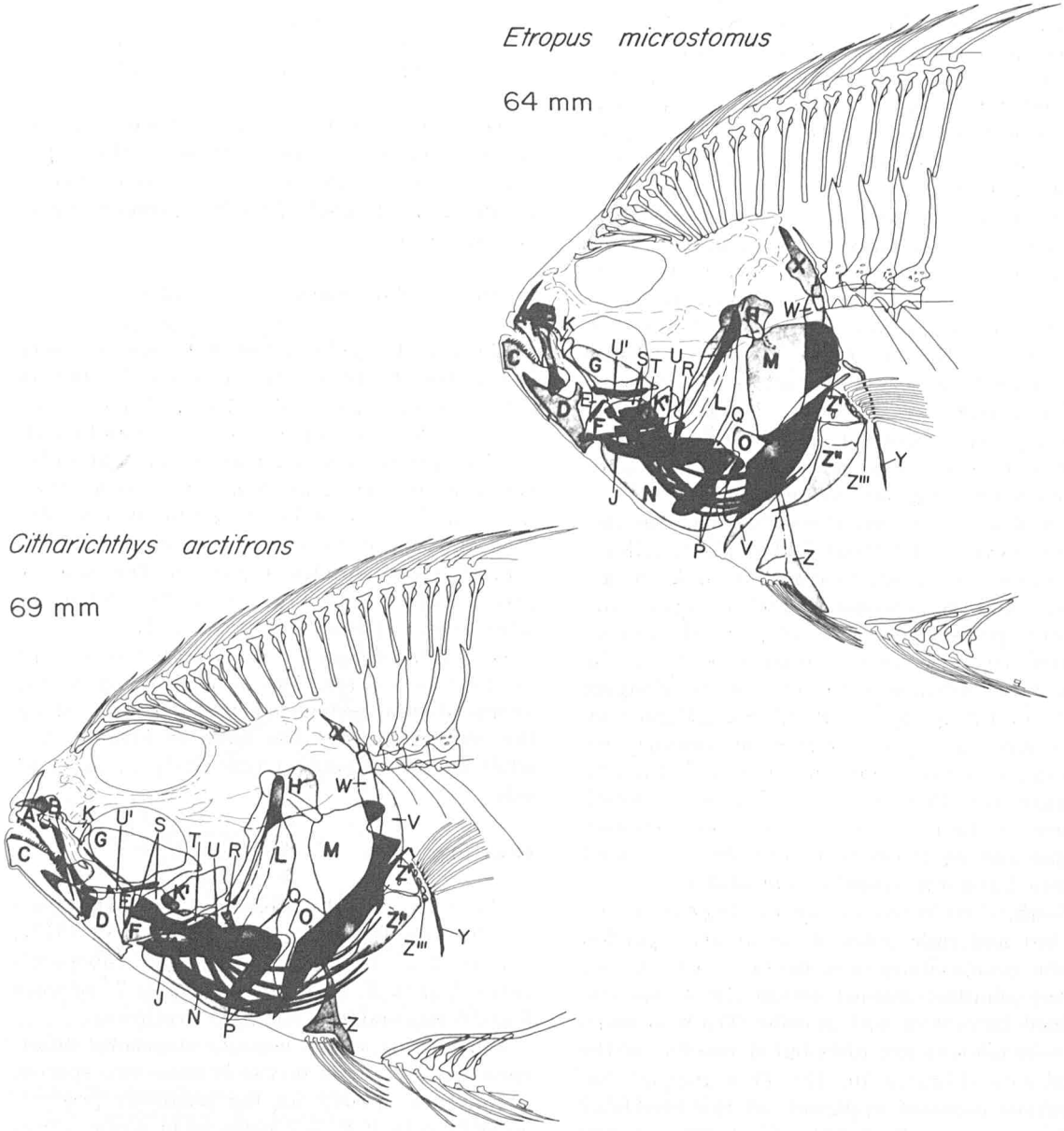

FIGURE 10.—Composite illustration of bones of the branchiocranium and of the pectoral and pelvic girdles (shaded) of the eyed side of adult *Etropus microstomus* and *Citharichthys arctifrons*. Upper and lower jaws: A - premaxillary, B - maxillary, C - dentary, D - articular and angular process. Oromandibular region: E - ectopterygoid, F - quadrate, G - endopterygoid, H - hyomandibular, J - symplectic, K - palatine, K′ - metapterygoid. Opercular series: L - preopercle, M - opercle, N - interopercle, O - subopercle. Hypobranchial region: P - branchiostegal rays, Q - urohyal, R - interhyal, S - hypohyals, T - ceratohyal, U - epihyal, U′ - basihyal. Pectoral and pelvic girdles: V - cleithrum, W - supracleithrum, X - posttemporal, Y - postcleithrum, Z - basipterygium, Z′ - scapula, Z″ - coracoid, Z‴ - radials.

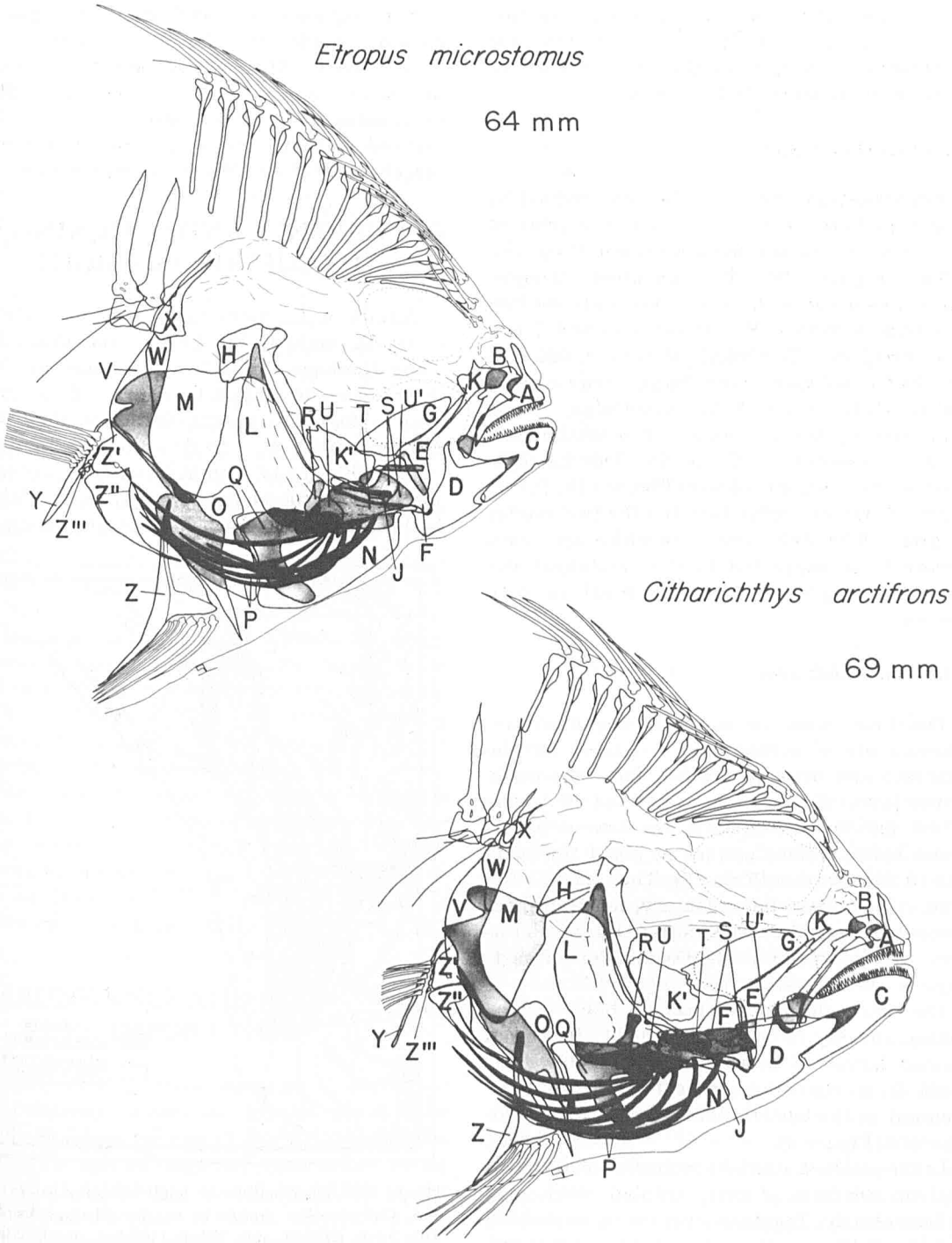

FIGURE 11.—Composite illustration of bones of the branchiocranium and of the pectoral and pelvic girdles (shaded) of the blind side of adult *Etropus microstomus* and *Citharichthys arctifrons*. See Figure 10 legend for the key.

The opercular bones in adults are structurally similar in both species except that the posterodorsal margin of the opercle may be more deeply indented in *C. arctifrons*.

Hypobranchial Region

Branchiostegal rays may become ossified by 4 mm in both species, although the total of seven may not be stained until 6 mm (Leonard, 1971a, Figure 26). The unpaired urohyal, which lies beneath the branchiostegals, ossifies at around 6 mm in *E. microstomus* and 7 mm in *C. arctifrons*. The interhyal is next, followed by the hypohyals, ceratohyal, and epihyal which ossify at about the same time. These bones usually become ossified at a smaller size in *E. microstomus* (Table 7). The basihyal ossifies after metamorphosis (Figures 10, 11).

Structural similarity between the two species is great. The first three branchiostegal rays appear to be supported by the ceratohyal and the remaining four by the epihyal in both species.

Additional Comments

The first bones to ossify in the branchiocranium are of dermal origin. Except for the quadrate and articular, which form the angle of the jaws, the only bones ossified in larvae of 4-5 mm in both species are dermal bones. These bones become ossified at about the same size in both species (Table 7). They include the premaxillary, maxillary, dentary, ectopterygoid, preopercle, opercle, branchiostegal rays, cleithrum, and supracleithrum. Ossification of cartilage bones follows.

The parasphenoid, a dermal bone of the neurocranium, is also prominent in 4-mm stained larvae of both species. This bone extends from the ethmoid region to the basioccipital in the basicranial region of the neurocranium (Figure 9).

In the smallest stained specimens, pharyngeal teeth in the form of sharp pointed cones, may be seen clearly. Together with the parasphenoid and the cleithrum, they are prominent features in 4-mm larvae of both species. They are still apparent in 12-mm larvae (Figure 9).

The sequences of ossification of bones discussed are the same for *E. microstomus* and *C. arctifrons*. Most bones become ossified at an earlier stage in *E. microstomus*. Major differences are the preopercular spines of *E. microstomus* and the small size at which the larger jaw of *C. arctifrons* becomes evident.

OCCURRENCE AND SPAWNING IN THE CHESAPEAKE BIGHT

Adults of *E. microstomus* and *C. arctifrons* occur throughout the Chesapeake Bight from Cape Henlopen, Del., to Cape Hatteras. Their distribution is limited by depth. *E. microstomus* is found in waters shallower than 37 m (20 fm) while *C. arctifrons* occurs in depths >37 m (Figure 12). Slight distributional overlap may occur around depths of 37 m. Adults of both species are present in the bight throughout

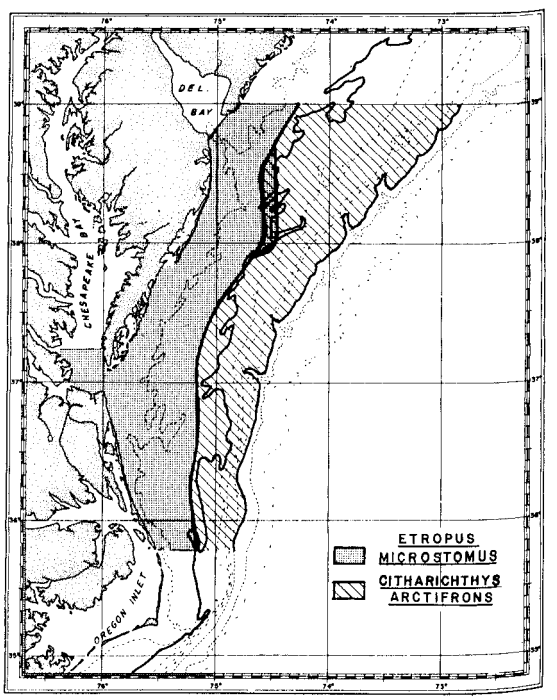

FIGURE 12.—Distribution of adult *Etropus microstomus* and *Citharichthys arctifrons* in the Chesapeake Bight. The 37-m (20-fm) and 183-m (100-fm) depth contours are emphasized. [From data collected by Virginia Institute of Marine Science in 1966. No tows were made beyond 183 m (100 fm).]

the year. Insufficient information is available to determine whether north-south or inshore-offshore movements occur, seasonal or otherwise.

Areal distribution of larvae, based on VIMS collections, is not as clearly defined. While most *E. microstomus* larvae were collected at stations inside the 37-m (20-fm) isobath, some were found out as far as the 183-m (100-fm) line. Most *C. arctifrons* larvae were taken outside the 37-m curve, but some were found near the 18-m (10-fm) line. Many samples contained larvae of both species. A greater number of *C. arctifrons* larvae were taken during 1962 when the sampling program was expanded to cover a greater offshore range.

Depths at which larvae occur in the water column may be a specific character (Simpson, 1956 Ahlstrom, 1960 Rae, 1965). Data from VIMS collections indicated that *E. microstomus* larvae were more common in the upper layers (0-12 m) while *C. arctifrons* larvae were more abundant in tows made at 12-18 m. Data from the Norfolk Canyon Collections (refer to section on Materials and Methods) showed *E. microstomus* larvae most abundant in the net towed at 2 m and *C. arctifrons* larvae most numerous in the net towed at 50 m. Additional sampling is needed to give accurate profiles of depth distribution for the two species.

The spawning peak for both species ranges from July through October, but spawning may occur sporadically through much of the year. Larvae have been taken as early as May and as late as December. Examination of ovaries of adults supports these conclusions.

ABUNDANCE AND ECONOMIC IMPORTANCE

Adults of *E. microstomus* and *C. arctifrons* are relatively numerous in the Chesapeake Bight. Seasonal records (Table 2) indicate that these two species together constituted about half of all flatfishes collected by VIMS in the spring and summer of 1966. Comparison of numerical catches of *E. microstomus* and *C. arctifrons* (Table 2) and the major commercially important flatfish species in the bight (*Paralichthys dentatus* and *Pseudopleuronectes americanus)* is noteworthy.

Larvae of *E. microstomus* and *C. arctifrons* were the most numerous of all flatfish species taken in VIMS plankton collections. Ahlstrom (1965) reported larvae of *Citharichthys* spp. (as a group) were similarly the most abundant of all flatfishes taken in the California Current System from 1955 to 1958. He stated, "Larvae of . . . sanddabs (*Citharichthys* spp.) are . . . [species] that represent present or potential commercial resources."

Despite the relative abundance of *E. microstomus* and *C. arctifrons* in the Chesapeake Bight, the two species alone do not represent sufficient biomass to make exploitation economically feasible. Lengths probably rarely exceed those given by Parr (1931) of 120 mm for *E. microstomus* and 150 mm for *C. arctifrons*. However, they could become part of the catch of miscellaneous trash fishes used for reduction into fish meal as has *E. rimosus* (Beaumariage, 1968), a species very similar to *E. microstomus*.

TAXONOMIC PROBLEMS

Original descriptions of the genera *Etropus* (Jordan and Gilbert, 1882) and *Citharichthys* (Bleeker, 1862) offer few characters to separate the two. The major difference between *Etropus* and *Citharichthys*, according to the original descriptions, is dentition. In *Etropus* "the teeth . . . [are] mostly on the blind side" while in *Citharichthys* the teeth on the eyed and blind sides of both jaws are well developed. Jordan and Evermann (1898) pointed out that " . . . this genus [*Etropus*] is very close to *Citharichthys*, from which it differs only in the very small size of the mouth, and in the correspondingly weak dentition."

The separation of 10 western Atlantic species of *Etropus* and *Citharichthys* into two genera has been disputed by Parr (1931). He claimed that length of the maxillary did not adequately segregate the species that he considered into two groups. He placed them all in the genus *Citharichthys*, apparently disregarding the dentition. Norman (1934) retained the separation of *Etropus* and *Citharichthys* in his

monograph. He stated *Etropus* is "very close to *Citharichthys*," the major difference being the smaller mouth and more feeble dentition with teeth mostly on the blind side of *Etropus*.

Transitory larval characters may provide clues to taxonomic relationships. *Syacium*, *Cyclopsetta*, *Citharichthys*, and *Etropus* are four closely related genera of bothid flatfishes (Norman, 1934). *Syacium* and *Cyclopsetta* can be separated from *Citharichthys* and *Etropus* on the basis of transitory larval characters (Gutherz, 1970). Similarly, *Syacium* can be separated from *Cyclopsetta* (Gutherz, 1970). Such characters could yield new evidence to substantiate or discredit the validity of the generic separation of *Etropus* and *Citharichthys*. However, as yet too few life histories have been described for species of *Etropus* and *Citharichthys* to permit meaningful conclusions.

ACKNOWLEDGMENTS

We acknowledge the Medical College of Virginia for use of its x-ray facilities, the Sandy Hook Sport Fisheries Marine Laboratory of the National Marine Fisheries Service for use of its larval fish collections, and George C. Grant for use of his Norfolk Canyon plankton collections. We are grateful to Jane Davis for her guidance in the preparation of the illustrative material contained herein. We thank Jackson Davis, George C. Grant, John J. Norcross, and Marvin L. Wass for their review of the manuscript. Special thanks are given to Elbert H. Ahlstrom for reviewing and commenting on the paper.

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APPENDIX TABLE 1.—Body measurements and their proportions in percent SL (standard length) of larval stages of Etropus microstomus.

	Measurements (mm)								Ratios (percent SL)							
SL (mm)	Head length	Snout length	Snout to anus	Eye diameter	Upper jaw length	Depth at anus	Depth behind anus	Peduncle depth	Head length	Snout length	Snout to anus	Eye diameter	Upper jaw length	Depth at anus	Depth behind anus	Peduncle depth
3.53	0.76	0.25	1.39	0.25	0.25	0.88	0.50	0.13	21.4	7.1	39.3	7.1	7.1	25.0	14.3	3.6
3.78	.88	.13	1.64	.25	.25	1.01	.63	.13	23.3	3.3	43.3	6.7	6.7	26.7	16.7	3.3
4.03	.88	.25	1.51	.25	.25	.88	.50	.13	21.9	6.3	37.5	6.3	6.3	21.9	12.5	3.1
4.28	1.01	.25	1.76	.25	.38	1.01	.63	.13	23.5	5.9	41.2	5.9	8.8	23.5	14.7	2.9
4.28	1.01	.25	1.64	.25	.25	.88	.50	.13	23.5	5.9	38.2	5.9	5.9	20.6	11.8	2.9
4.28	1.01	.25	1.76	.25	.38	1.13	.63	.25	23.5	5.9	41.2	5.9	8.8	26.5	14.7	5.9
4.54	1.13	.25	1.76	.25	.38	1.01	.63	.13	25.0	5.6	38.9	5.6	8.3	21.8	13.9	2.8
4.79	1.13	.25	1.76	.38	.38	1.26	.76	.25	23.7	5.3	36.8	7.9	7.9	26.3	15.8	5.3
4.79	1.13	.25	1.76	.38	.38	1.26	.88	.25	23.7	5.3	36.8	7.9	7.9	26.3	18.4	5.3
4.79	1.13	.25	1.76	.25	.38	1.01	.63	.25	23.7	5.3	36.8	5.3	7.9	21.1	13.2	5.3
4.79	1.13	.25	1.76	.25	.38	.88	.63	.13	23.7	5.3	36.8	5.3	7.9	18.4	13.2	2.6
4.79	1.26	.25	2.14	.38	.50	1.39	1.01	.25	26.3	5.3	44.7	7.9	10.5	28.9	21.1	5.3
5.04	1.26	.25	2.02	.38	.38	1.51	1.01	.38	25.0	5.0	40.0	7.5	7.5	30.0	20.0	7.5
5.04	1.26	.25	1.89	.38	.50	1.01	.63	.25	25.0	5.0	37.5	7.5	10.0	20.0	12.5	5.0
5.29	1.26	.38	2.02	.38	.50	1.51	1.01	.38	23.8	7.1	38.1	7.1	9.5	28.6	19.0	7.1
5.29	1.26	.25	1.89	.38	.38	1.39	.88	.25	23.8	4.8	35.7	7.1	7.1	26.2	16.7	4.8
5.29	1.51	.25	2.14	.38	.50	1.39	1.01	.38	28.6	4.8	40.5	7.1	9.5	26.2	19.0	7.1
5.29	1.51	.38	2.39	.38	.50	1.51	1.01	.38	28.6	7.1	45.2	7.1	9.5	28.6	19.0	7.1
5.29	1.26	.25	2.14	.38	.50	1.13	.63	.25	23.8	4.8	40.5	7.1	9.5	21.4	11.9	4.8
5.29	1.39	.25	2.14	.38	.50	1.39	.88	.38	26.2	4.8	40.5	7.1	9.5	26.2	16.7	7.1
5.29	1.26	.25	2.27	.38	.50	1.39	.88	.38	23.8	4.8	42.9	7.1	9.5	26.2	16.7	7.1
5.54	1.51	.50	2.39	.38	.63	1.64	1.26	.50	27.3	9.1	43.2	6.8	11.4	29.5	22.7	9.1
5.80	1.64	.38	2.39	.38	.63	1.76	1.26	.63	28.3	6.5	41.3	6.5	10.9	30.4	21.7	10.9
5.80	1.39	.25	2.27	.38	.50	1.64	1.13	.38	23.9	4.3	39.1	6.5	8.7	28.3	19.6	6.5
5.80	1.76	.38	2.52	.50	.63	2.14	1.64	.63	30.4	6.5	43.5	8.7	10.9	37.0	28.3	10.9
5.80	1.51	.50	2.14	.50	.63	2.02	1.39	.50	26.1	8.7	37.0	8.7	10.9	34.8	23.9	8.7
5.80	1.51	.38	2.39	.38	.63	1.89	1.39	.50	26.1	6.5	41.3	6.5	10.9	32.6	23.9	8.7
6.05	1.51	.38	2.27	.38	.50	1.64	1.13	.50	25.0	6.3	37.5	6.3	8.3	27.1	18.8	8.3
6.05	1.76	.50	2.90	.50	.63	2.27	1.64	.76	29.2	8.3	47.9	8.3	10.4	37.5	27.1	12.5
6.05	1.51	.38	2.52	.50	.63	1.76	1.26	.50	25.0	6.3	41.7	8.3	10.4	29.2	20.8	8.3
6.05	1.64	.38	2.39	.50	.63	1.76	1.26	.63	27.1	6.3	39.6	8.3	10.4	29.2	20.8	10.4
6.05	1.51	.38	2.52	.38	.50	1.89	1.26	.50	25.0	6.3	41.7	6.3	8.3	31.3	20.8	8.3
6.30	1.51	.38	2.39	.38	.50	1.51	1.13	.50	24.0	6.0	38.0	6.0	8.0	24.0	18.0	8.0
6.30	1.76	.50	2.52	.50	.63	2.14	1.64	.50	28.0	8.0	40.0	8.0	10.0	34.0	26.0	8.0
6.30	1.64	.50	2.90	.38	.50	2.02	1.64	.63	26.0	8.0	46.0	6.0	8.0	32.0	26.0	10.0
6.30	1.76	.38	2.77	.50	.50	2.14	1.64	.63	28.0	6.0	44.0	8.0	8.0	34.0	26.0	10.0
6.30	1.51	.38	2.39	.38	.50	1.76	1.26	.50	24.0	6.0	38.0	6.0	8.0	28.0	20.0	8.0
6.30	1.64	.38	2.65	.50	.50	2.14	1.76	.63	26.0	6.0	42.0	8.0	8.0	34.0	28.0	10.0
6.30	1.64	.38	2.65	.38	.63	2.02	1.64	.50	26.0	6.0	42.0	6.0	10.0	32.0	26.0	8.0
6.30	1.51	.25	2.65	.38	.50	1.76	1.39	.50	24.0	4.0	42.0	6.0	8.0	28.0	22.0	8.0
6.55	1.76	.38	3.02	.50	.63	2.14	1.64	.63	26.9	5.8	46.2	7.7	9.6	32.7	25.0	9.6
6.55	1.76	.38	2.90	.50	.76	2.27	1.64	.63	26.9	5.8	44.2	7.7	11.9	34.6	25.0	9.6
6.55	1.89	.50	2.77	.50	.76	2.52	1.89	.76	28.8	7.7	42.3	7.7	11.5	38.5	28.8	11.5
6.55	1.76	.25	2.65	.50	.63	1.89	1.51	.63	26.9	3.8	40.4	7.7	9.6	28.8	23.1	9.6
6.80	2.02	.50	3.28	.50	.63	2.78	2.14	.88	29.6	7.4	48.1	7.4	9.3	40.7	31.5	13.0
6.80	1.89	.38	2.90	.50	.63	2.14	1.76	.63	27.8	5.6	42.6	7.4	9.3	31.5	25.9	9.3
6.80	1.76	.38	2.65	.50	.63	2.27	1.64	.63	25.9	5.6	38.9	7.4	9.3	33.3	24.1	9.3
7.06	1.89	.50	3.15	.50	.63	2.52	1.89	.76	26.8	7.1	44.6	7.1	8.9	35.7	26.8	10.7
7.06	1.89	.38	2.90	.38	.63	2.27	1.64	.63	25.0	5.4	41.1	5.4	8.9	32.1	23.2	8.9
7.06	1.89	.50	2.90	.50	.63	2.39	1.89	.76	26.8	7.1	41.1	7.1	8.9	33.9	26.8	10.7

APPENDIX TABLE 1.—Continued.

SL (mm)	Measurements (mm)								Ratios (percent SL)							
	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth
7.06	1.89	.50	3.02	.50	.63	2.52	1.89	.76	26.8	7.1	42.9	7.1	8.9	35.7	26.8	10.7
7.06	1.89	.50	2.90	.50	.63	2.27	1.89	.76	26.8	7.1	41.1	7.1	8.9	32.1	26.8	10.7
7.13	2.02	.50	3.28	.50	.76	2.52	2.02	.88	27.6	6.9	44.8	6.9	10.3	34.5	27.6	12.1
7.13	2.14	.50	2.90	.50	.63	3.15	2.52	.76	29.3	6.9	39.7	6.9	8.6	43.1	34.5	10.3
7.13	1.89	.50	2.90	.50	.76	2.65	2.27	.88	25.9	6.9	39.7	6.9	10.4	36.2	31.0	12.1
7.13	2.02	.50	3.28	.50	.76	2.65	2.02	.88	27.6	6.9	44.8	6.9	9.4	36.2	27.6	12.1
7.13	1.89	.38	2.90	.50	.76	2.39	1.89	.76	25.9	5.2	39.7	6.9	8.6	32.8	25.9	10.3
7.13	2.02	.50	3.02	.50	.63	2.65	2.14	.88	27.6	6.9	41.4	6.9	8.6	36.2	29.3	12.1
7.56	2.02	.63	3.28	.50	.63	2.65	2.14	.88	27.7	8.3	43.3	6.7	8.3	35.0	28.3	11.7
7.56	1.89	.38	3.15	.50	.50	2.39	1.89	.76	25.0	5.0	41.7	6.7	6.7	31.7	25.0	10.0
7.56	1.89	.38	3.02	.50	.63	2.52	1.89	.76	25.0	5.0	40.0	6.7	8.3	33.3	25.0	10.0
7.81	2.27	.63	3.28	.50	.76	2.77	2.27	.88	29.0	8.1	41.9	6.5	9.7	35.5	29.0	11.3
7.81	2.02	.63	2.90	.50	.76	3.15	2.52	.88	25.8	8.1	37.1	6.5	9.7	40.3	32.3	11.3
8.06	2.27	.50	3.40	.63	.76	2.90	2.27	.88	28.1	6.3	42.2	7.8	9.4	35.9	28.1	10.9
8.06	2.27	.50	3.28	.63	.76	3.15	2.52	1.01	28.1	6.3	40.6	7.8	9.4	39.1	31.3	12.5
8.06	2.01	.50	3.28	.50	.63	2.39	1.89	.76	25.0	6.3	40.6	6.3	7.8	29.7	23.4	9.4
8.06	2.14	.50	3.02	.50	.76	2.77	2.27	.88	26.6	6.3	37.5	6.3	9.4	34.4	28.1	10.9
8.32	2.27	.50	3.15	.63	.76	3.15	2.52	1.01	27.3	6.1	37.9	7.6	9.1	37.9	30.3	12.1
8.32	2.27	.50	3.53	.50	.76	3.15	2.65	1.01	27.3	6.1	42.4	6.1	9.1	37.9	31.8	12.1
8.32	2.14	.50	3.28	.50	.76	2.77	2.39	.88	25.8	6.1	39.4	6.1	9.1	33.3	28.8	10.6
8.32	2.27	.50	3.28	.50	.76	3.28	2.77	1.01	27.3	6.1	39.4	6.1	9.1	39.4	33.3	12.1
8.82	2.27	.63	3.53	.63	.76	3.28	2.52	.88	25.7	7.1	40.0	7.1	8.6	37.1	28.6	10.0
8.82	2.39	.63	3.28	.63	1.01	3.65	3.02	1.13	27.1	7.1	37.1	7.1	11.4	41.4	34.3	12.9
8.82	2.39	.50	3.53	.50	.76	3.28	2.77	1.01	27.1	5.7	40.0	5.7	8.6	37.1	31.4	11.4
8.82	2.27	.50	3.02	.50	.76	3.15	2.65	1.01	25.7	5.7	34.3	5.7	8.6	35.7	30.0	11.4
9.07	2.39	.50	3.28	.63	.88	3.40	2.90	1.13	26.4	5.6	36.1	6.9	9.7	37.5	31.9	12.5
9.07	2.52	.63	3.40	.63	.76	3.78	3.15	1.13	27.8	6.9	37.5	6.9	8.3	41.7	34.7	12.5
9.07	2.14	.63	3.28	.50	.76	3.15	2.65	1.01	23.6	6.9	36.1	5.6	8.3	34.7	29.2	11.1
9.32	2.52	.50	3.53	.63	1.01	3.65	3.15	1.01	27.0	5.4	37.8	6.8	10.8	39.2	33.8	10.8
9.32	2.52	.63	3.65	.63	.88	3.28	2.77	1.13	27.0	6.8	39.2	6.8	9.5	35.1	29.7	12.2
9.32	2.52	.63	3.78	.63	.88	3.65	3.40	1.26	27.0	6.8	40.5	6.8	9.5	39.2	36.5	13.5
9.32	2.39	.50	3.65	.50	.76	3.28	2.90	1.13	25.7	5.4	39.2	5.4	8.1	35.1	31.1	12.2
9.58	2.65	.63	3.65	.63	.88	3.65	3.15	1.26	27.6	6.6	38.2	6.6	9.2	38.2	32.9	13.2
9.58	2.52	.63	3.78	.63	.88	3.78	3.40	1.39	26.3	6.6	39.5	6.6	9.2	39.5	35.5	14.5
9.83	2.52	.63	3.78	.63	.76	3.40	2.77	1.13	25.6	6.4	38.5	6.4	7.7	34.6	28.2	11.5
10.33	2.65	.63	4.03	.63	.88	3.78	3.28	1.26	25.6	6.1	39.0	6.1	8.5	36.6	31.7	12.2
10.33	2.65	.63	3.78	.63	.88	4.16	3.65	1.26	25.6	6.1	34.9	6.1	8.5	40.2	35.4	12.2
10.33	2.65	.50	3.78	.50	.88	4.28	3.78	1.26	25.6	4.9	34.9	4.9	8.5	41.5	34.9	12.2
10.33	2.65	.76	3.91	.50	.88	3.91	3.40	1.26	25.6	7.3	37.8	4.9	8.5	37.8	32.9	12.2
10.58	2.77	.76	4.16	.63	.88	3.91	3.40	1.26	26.2	7.1	39.3	6.0	8.3	36.9	32.1	11.9
10.84	2.77	.76	4.03	.50	1.01	4.16	3.78	1.26	25.6	7.0	37.2	4.6	9.3	38.4	34.9	11.6
11.09	2.90	1.01	4.03	.50	.76	4.41	4.03	1.39	26.1	5.7	36.4	6.8	9.1	39.8	36.3	12.5
11.59	2.90	.76	4.28	.63	.88	4.41	4.03	1.39	25.0	6.5	37.0	5.4	7.6	38.0	34.8	12.0
12.10	3.15	.63	4.28	.76	1.13	5.04	4.54	1.51	26.0	5.2	35.4	6.3	9.4	41.7	37.5	12.5
12.10	3.15	.76	4.03	.63	.88	4.79	4.16	1.51	26.0	6.3	33.3	5.2	7.3	39.6	34.4	12.5
12.35	3.15	.63	4.28	.76	.88	4.91	4.54	1.64	25.5	5.1	34.7	6.1	7.1	39.8	36.8	13.3
12.35	3.15	.76	4.28	.63	.88	4.54	3.91	1.39	25.5	6.1	34.7	5.1	7.1	36.7	31.6	11.2
12.60	3.40	.88	4.28	.76	.88	5.04	4.79	1.01	27.0	7.0	34.0	6.0	7.0	40.0	38.0	8.0
12.60	3.28	.76	4.16	.76	.88	4.79	4.66	1.13	26.0	6.0	33.0	6.0	7.0	38.0	37.0	9.0
12.60	3.28	.88	4.16	.76	1.13	4.79	4.41	1.64	26.0	7.0	33.0	6.0	9.0	38.0	35.0	13.0

APPENDIX TABLE 2.—Body measurements and their proportions in percent SL (standard length) of larval stages of Citharichthys arctifrons.

	Measurements (mm)								Ratios (percent SL)							
SL (mm)	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth
4.54	0.88	0.13	1.64	0.25	0.38	0.88	0.50	0.13	19.4	2.8	36.1	5.6	8.3	19.4	11.1	2.8
4.54	1.01	.13	1.76	.38	.38	.88	.50	.13	22.2	2.8	38.9	8.3	8.3	19.4	11.1	2.8
4.79	1.13	.13	2.02	.38	.50	1.13	.63	.25	23.7	2.9	42.1	7.9	10.5	23.7	13.2	5.3
4.79	1.13	.38	1.89	.38	.50	1.01	.63	.25	23.7	7.9	39.5	7.9	10.5	21.1	13.2	5.3
4.79	1.01	.25	1.89	.38	.38	1.01	.50	.13	21.1	2.9	39.5	7.9	7.9	21.1	10.5	2.6
4.79	1.13	.25	1.89	.38	.38	.88	.38	.13	23.7	5.3	39.5	7.9	7.9	18.4	7.9	2.6
5.04	1.13	.38	1.89	.38	.50	1.13	.76	.25	22.5	7.5	37.5	7.5	10.0	22.5	15.0	5.0
5.04	1.26	.13	2.14	.38	.38	1.13	.76	.25	25.0	2.5	42.5	7.5	7.5	22.5	15.0	5.0
5.04	1.26	.38	2.14	.38	.63	1.26	.88	.25	25.0	7.5	42.5	7.5	12.5	25.0	17.5	5.0
5.04	1.13	.25	1.89	.38	.63	1.01	.50	.13	22.5	5.0	37.5	7.5	12.5	20.0	10.0	2.5
5.29	1.39	.38	2.14	.38	.63	1.26	.76	.25	26.2	7.1	40.5	7.1	11.9	23.8	14.3	4.8
5.29	1.39	.38	2.27	.38	.63	1.13	.63	.13	26.2	7.1	42.9	7.1	11.9	21.4	11.9	2.4
5.29	1.39	.38	2.14	.38	.50	1.26	.88	.38	26.2	7.1	40.5	7.1	9.5	23.8	16.7	7.1
5.29	1.39	.38	2.27	.38	.63	1.26	.88	.38	26.2	7.1	42.9	7.1	11.9	23.8	16.7	7.1
5.29	1.39	.38	2.14	.38	.50	1.39	.88	.25	26.2	7.1	40.5	7.1	9.5	26.2	16.7	4.8
5.29	1.13	.25	2.27	.38	.50	1.13	.63	.13	21.4	4.8	42.9	7.1	9.5	21.4	11.9	2.4
5.29	1.39	.38	2.39	.38	.63	1.26	.88	.25	26.2	7.1	45.2	7.1	11.9	23.8	16.7	4.8
5.54	1.39	.38	2.14	.50	.50	1.39	.88	.38	25.0	6.8	38.6	9.1	9.1	25.0	15.9	6.8
5.54	1.51	.38	2.39	.50	.63	1.51	1.01	.38	27.3	6.8	43.2	9.1	11.4	27.3	18.2	6.8
5.54	1.39	.25	2.27	.38	.63	1.39	.88	.13	25.0	4.5	40.9	6.8	11.4	25.0	15.9	2.3
5.54	1.39	.38	2.27	.38	.50	1.39	.76	.25	25.0	6.8	40.9	6.8	9.1	25.0	13.6	4.5
5.54	1.39	.38	2.27	.38	.50	1.26	.88	.25	25.0	6.8	40.9	6.8	9.1	22.7	15.9	4.5
5.54	1.51	.25	2.27	.38	.50	1.26	.76	.38	27.3	4.5	40.9	6.8	9.1	22.7	13.6	6.8
5.54	1.13	.25	1.89	.38	.50	1.13	.76	.25	20.5	4.5	34.1	6.8	9.1	20.5	13.6	4.5
5.54	1.26	.25	2.02	.38	.50	1.13	.76	.25	22.7	4.5	36.4	6.8	9.1	20.5	13.6	4.5
5.54	1.39	.38	2.27	.38	.50	1.51	.88	.25	25.0	6.8	40.9	6.8	9.1	27.3	15.9	4.5
5.54	1.39	.38	2.14	.38	.63	1.39	.88	.25	25.0	6.8	38.6	6.8	11.4	25.0	15.9	4.5
5.54	1.26	.38	2.27	.38	.50	1.26	.76	.25	22.7	6.8	40.9	6.8	9.1	22.7	13.6	4.5
5.80	1.39	.25	2.39	.50	.50	1.39	1.01	.38	23.9	4.3	41.3	8.7	8.7	23.9	17.4	6.5
5.80	1.64	.38	2.52	.50	.76	1.51	1.01	.38	28.3	6.5	43.5	8.7	13.0	26.1	17.4	6.5
5.80	1.39	.38	2.27	.38	.63	1.39	.88	.25	23.9	6.5	39.1	6.5	10.9	23.9	15.2	4.3
6.05	1.51	.38	2.39	.50	.50	1.39	1.01	.38	25.0	6.3	39.6	8.3	8.3	22.9	16.7	6.3
6.05	1.64	.38	2.52	.50	.63	1.51	1.01	.25	27.1	6.3	41.7	8.3	10.4	25.0	16.7	4.2
6.05	1.64	.50	2.39	.38	.76	1.64	1.13	.38	27.1	8.3	39.6	6.3	12.5	27.0	18.8	6.3
6.30	1.64	.38	2.52	.50	.76	1.76	1.13	.50	26.0	6.0	40.0	8.0	12.0	28.0	18.0	8.0
6.30	1.64	.38	2.52	.38	.63	1.76	1.13	.38	26.0	6.0	40.0	6.0	10.0	28.0	18.0	6.0
6.30	1.64	.38	2.52	.50	.63	1.64	1.13	.38	26.0	6.0	40.0	8.0	10.0	26.0	18.0	6.0
6.30	1.89	.50	2.77	.50	.63	1.89	1.26	.50	30.0	8.0	44.0	8.0	10.0	30.0	20.0	8.0
6.30	1.64	.38	2.52	.50	.63	1.76	1.26	.50	26.0	6.0	40.0	8.0	10.0	28.0	20.0	8.0
6.30	1.76	.38	2.65	.38	.63	1.51	1.01	.25	28.0	6.0	42.0	6.0	10.0	24.0	16.0	4.0
6.55	1.64	.38	2.65	.50	.63	1.76	1.13	.50	25.0	5.8	40.4	7.7	7.6	26.9	17.3	7.7
6.55	1.86	.38	2.65	.50	.76	2.02	1.39	.63	28.8	5.8	40.4	7.7	11.5	30.8	21.2	9.6
6.55	1.76	.50	2.65	.50	.63	1.64	1.13	.50	26.9	7.7	40.4	7.7	9.6	25.0	17.3	7.7
6.55	1.76	.50	2.65	.50	.76	1.89	1.39	.50	26.9	7.7	40.4	7.7	11.5	28.8	21.2	7.7
6.55	1.76	.50	2.65	.50	.63	1.89	1.26	.63	26.9	7.7	40.4	7.7	9.6	28.8	19.2	9.6
6.55	1.76	.50	2.65	.50	.63	1.76	1.13	.50	26.9	7.7	40.4	7.7	9.6	26.9	17.3	7.7
6.55	1.76	.38	2.90	.50	.63	1.89	1.26	.50	26.9	5.8	44.2	7.7	9.6	28.8	19.2	7.7
6.55	1.89	.50	2.77	.50	.76	1.89	1.26	.50	28.8	7.7	42.3	7.7	11.5	28.8	19.2	7.7
6.55	2.02	.50	3.02	.50	.76	1.89	1.39	.50	30.8	7.7	46.2	7.7	11.5	28.8	21.1	7.7
6.80	1.89	.50	3.02	.50	.76	1.89	1.26	.63	27.8	7.4	44.4	7.4	11.1	27.8	18.5	9.3

APPENDIX TABLE 2.—Continued.

SL (mm)	Measurements (mm)								Ratios (percent SL)							
	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth
6.80	1.89	.50	2.90	.50	.76	2.14	1.64	.63	27.8	7.4	42.6	7.4	11.1	31.5	24.1	9.3
6.80	1.89	.50	3.02	.50	.63	2.14	1.51	.76	27.7	7.4	44.4	7.4	9.3	31.5	22.2	11.1
6.80	1.89	.38	2.90	.50	.63	1.76	1.26	.50	27.8	5.6	42.6	7.4	9.3	25.9	18.5	7.4
6.80	2.02	.50	2.90	.50	.63	1.89	1.39	.50	29.6	7.4	42.6	7.4	9.3	27.8	20.4	7.4
7.06	2.14	.50	3.15	.50	.88	2.27	1.76	.76	30.4	7.1	44.6	7.1	12.5	32.1	25.0	10.7
7.06	2.14	.50	3.15	.50	.76	2.27	1.64	.76	30.4	7.1	44.6	7.1	10.7	32.1	23.2	10.7
7.06	2.02	.50	2.90	.50	.63	2.14	1.51	.63	28.6	7.1	41.1	7.1	8.9	30.4	21.4	8.9
7.31	2.14	.38	3.15	.63	.76	2.39	1.76	.76	29.3	5.2	43.1	8.6	10.3	32.8	24.1	10.3
7.31	2.27	.63	3.28	.63	.88	2.39	1.86	.88	31.0	8.6	44.8	8.6	12.1	32.8	25.9	12.1
7.31	2.14	.50	3.02	.50	.63	2.27	1.76	.76	29.3	6.9	41.4	6.9	8.6	31.0	24.1	10.3
7.31	2.02	.50	3.15	.63	.76	2.27	1.64	.76	27.6	6.9	43.1	8.6	10.3	31.0	22.4	10.3
7.31	1.89	.50	3.28	.63	.76	2.14	1.64	.76	25.9	6.9	44.8	8.6	10.3	29.3	22.4	10.3
7.31	2.14	.63	3.15	.63	.76	2.27	1.64	.76	29.3	8.6	43.1	8.6	10.3	31.0	22.4	10.3
7.50	2.14	.50	3.28	.50	.76	2.52	2.02	.88	28.3	6.7	43.3	6.7	10.0	23.3	26.7	11.7
7.56	2.14	.50	3.40	.50	.76	2.27	1.51	.63	28.3	6.7	45.0	6.7	10.0	30.0	20.0	8.3
7.81	2.02	.50	3.15	.63	1.01	2.52	1.76	.76	25.8	6.5	40.3	8.1	12.9	32.3	22.6	9.7
8.06	2.27	.38	3.40	.63	.88	2.52	1.76	.76	28.1	4.7	42.2	7.8	10.9	31.3	21.9	9.4
8.06	2.39	.50	3.65	.63	.76	2.52	1.76	.76	29.7	6.3	45.3	7.8	9.4	31.3	21.9	9.4
8.06	2.27	.50	3.40	.63	.88	2.77	1.89	.76	28.1	6.3	42.2	7.8	10.9	34.4	23.4	9.4
8.32	2.27	.50	3.28	.63	.88	2.65	1.89	1.01	27.3	6.1	39.4	7.6	10.6	31.8	22.7	12.1
8.32	2.52	.63	3.78	.63	.88	2.52	1.89	.88	30.3	7.6	45.5	7.6	10.6	30.3	22.7	10.6
8.32	2.27	.50	3.40	.63	.88	2.52	1.89	.63	27.3	6.1	40.9	7.6	10.6	30.3	22.7	7.6
8.32	2.39	.63	3.53	.63	1.01	2.77	1.89	.88	28.8	7.6	42.4	7.6	12.1	33.3	22.7	10.6
8.57	2.39	.50	3.91	.63	.88	2.90	2.27	1.13	27.9	5.9	45.6	7.4	10.3	33.8	26.5	13.2
8.57	2.65	.63	3.78	.63	.76	2.65	2.02	.88	30.9	7.4	44.1	7.4	8.8	30.9	23.5	10.3
9.07	2.77	.76	3.78	.63	1.13	3.40	2.65	1.13	30.1	8.3	41.7	6.9	12.5	37.5	29.2	12.5
9.07	2.52	.63	4.03	.63	.88	2.90	2.27	.88	27.8	6.9	44.4	6.9	9.7	31.9	25.0	9.7
9.07	2.52	.63	4.16	.63	.88	3.28	2.27	1.01	27.8	6.9	45.8	6.9	9.7	36.1	25.0	11.1
9.32	2.52	.63	3.78	.63	1.13	3.40	2.39	1.01	27.0	6.8	40.5	6.8	12.2	36.5	25.7	10.8
9.32	2.65	.63	4.03	.63	1.01	3.02	2.27	1.01	28.4	6.8	43.2	6.8	10.8	32.4	24.3	10.8
9.58	2.77	.63	4.28	.63	1.01	3.28	2.65	1.13	28.9	6.6	44.7	6.6	10.5	34.2	27.6	11.8
9.83	3.02	.63	4.28	.63	.88	3.78	2.90	1.13	30.8	6.4	43.6	6.4	9.0	38.5	29.5	11.5
10.33	3.15	.76	4.41	.76	1.01	3.53	2.77	1.26	30.5	7.3	42.7	7.3	9.8	34.1	26.8	12.2
10.58	3.02	.76	4.16	.88	1.13	4.03	3.02	1.26	28.6	7.1	39.3	8.3	10.7	38.1	28.6	11.9
10.58	3.02	.76	4.41	.76	.88	3.78	2.65	1.26	28.6	7.1	41.7	7.1	8.3	35.7	25.0	11.9
10.58	2.90	.63	4.54	.76	1.26	3.91	2.90	1.26	27.4	6.0	42.9	7.1	11.9	37.0	27.4	11.9
11.09	3.15	.88	4.54	.76	1.26	3.91	3.15	1.51	28.4	8.0	40.9	6.8	11.4	35.2	28.4	13.6
11.09	3.02	.76	4.41	.76	1.26	3.91	3.02	1.26	27.3	6.8	39.8	6.8	11.4	35.2	27.3	11.4
11.34	3.02	.63	4.54	.88	1.13	4.16	3.28	1.39	26.7	5.6	40.0	7.8	10.0	36.7	28.9	12.2
11.34	3.28	.88	4.16	.76	1.26	4.16	3.53	1.39	28.9	7.8	36.7	6.7	11.1	36.7	31.1	12.2
11.59	3.28	.76	4.41	.76	1.13	4.28	3.15	1.39	28.3	5.6	38.0	6.5	9.8	37.0	27.2	12.0
12.10	3.28	.88	4.79	.76	1.26	4.16	3.40	1.26	27.1	7.3	39.6	6.3	10.4	34.4	28.1	10.4
12.35	3.40	.88	4.41	.76	1.26	4.41	3.65	1.39	27.6	7.1	35.7	6.1	10.2	35.7	29.6	11.2
12.35	3.53	1.01	4.91	.76	1.13	4.54	3.65	1.39	28.6	8.2	39.8	6.1	9.2	36.7	29.6	11.2
12.35	3.53	.76	4.91	.88	1.26	4.28	3.53	1.51	28.6	6.1	39.8	7.1	10.2	34.7	28.6	12.2
12.35	3.28	.88	4.41	.88	1.26	4.41	3.65	1.39	26.5	7.1	35.7	7.1	10.2	35.7	29.6	11.2
12.60	3.78	1.01	5.04	.88	1.26	4.54	3.53	1.51	30.0	8.0	40.0	7.0	9.0	36.0	28.0	12.0
13.36	3.78	1.13	4.66	.88	1.39	4.66	4.03	1.15	28.3	8.5	34.9	6.7	10.4	34.9	30.2	11.3
13.86	3.65	.88	5.42	.88	1.26	5.42	4.28	1.64	26.4	6.4	39.1	6.4	9.1	39.1	30.9	11.8
14.36	3.78	1.01	5.17	1.01	1.13	5.04	4.41	1.64	26.3	7.0	35.8	7.0	7.9	35.1	30.7	11.4

APPENDIX TABLE 3.—Body measurements and their proportions in percent SL (standard length) of selected juvenile and adult specimens of *Etropus microstomus*.

	Measurements (mm)								Ratios (percent SL)							
SL (mm)	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth
29	8	2	8	2	2	10	12	3	27.6	6.9	27.6	6.9	6.9	34.5	41.4	10.3
40	10	2	10	3	3	13	16	4	25.0	5.0	25.0	7.5	7.5	32.5	40.0	10.0
45	11	2	11	3	3	16	18	5	24.4	4.4	24.4	6.7	6.7	35.6	40.0	11.1
50	12	2	12	3	3	17	20	5	24.0	4.0	24.0	6.0	6.0	34.0	40.0	10.0
56	13	3	13	4	4	18	23	6	23.2	5.4	23.2	7.1	7.1	32.1	41.1	10.7
60	14	3	14	4	5	21	25	6	23.3	5.0	23.3	6.7	8.3	35.0	41.7	10.0
65	16	3	16	5	5	22	27	7	24.6	4.6	24.6	7.7	7.7	33.8	41.5	10.8
70	17	3	17	5	5	26	34	8	24.3	4.3	24.3	7.1	7.1	37.1	48.6	11.4
75	17	3	17	5	5	25	31	8	22.7	4.0	22.7	6.7	6.7	33.3	41.3	10.7
80	19	3	19	6	5	32	38	10	23.8	3.8	23.8	7.5	6.3	40.0	48.8	12.5
85	20	4	20	5	5	29	39	10	23.5	4.7	23.5	5.9	5.9	34.1	45.9	11.8
90	21	4	21	6	6	32	43	10	23.3	4.4	23.3	6.7	6.7	35.6	47.8	11.1
95	22	4	22	6	6	34	46	11	23.2	4.2	23.2	6.3	6.3	35.8	48.4	11.6
104	22	4	22	6	6	37	47	12	21.2	3.8	21.2	5.8	5.8	35.6	45.2	11.5
115	24	4	24	6	6	40	51	13	20.9	3.5	20.9	5.2	5.2	34.8	44.3	11.3
123	27	5	27	7	7	44	58	14	22.0	4.1	22.0	5.7	5.7	35.8	47.2	11.4

APPENDIX TABLE 4.—Body measurements and their proportions in percent SL (standard length) of selected juvenile and adult specimens of *Citharichthys arctifrons*.

	Measurements (mm)								Ratios (percent SL)							
SL (mm)	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth	Head length	Snout length	Snout to anus	Eye diam-eter	Upper jaw length	Depth at anus	Depth behind anus	Pedun-cle depth
47	12	2	12	5	6	14	15	5	25.5	4.3	25.5	10.6	12.8	29.8	31.9	10.6
55	13	3	13	5	5	16	19	5	23.6	5.5	23.6	9.1	9.1	29.1	34.5	9.1
63	16	3	16	5	6	19	22	6	25.4	4.8	25.4	7.9	9.5	30.2	34.9	9.5
66	17	4	17	5	6	19	22	6	25.8	6.1	25.8	7.6	9.1	28.8	33.3	9.1
70	17	3	17	5	6	23	25	7	24.3	4.3	24.3	7.1	8.6	32.9	35.7	10.0
75	18	4	18	6	6	22	25	7	24.0	5.3	24.0	8.0	8.0	29.3	33.3	9.3
80	19	4	19	6	7	24	27	7	23.8	5.0	23.8	7.5	8.8	30.0	33.8	8.8
85	20	4	20	6	6	24	29	8	23.5	4.7	23.5	7.1	7.1	28.2	34.1	9.4
90	20	4	20	6	7	27	32	9	22.2	4.4	22.2	6.7	7.8	30.0	35.6	10.0
95	23	4	23	7	8	30	37	11	24.2	4.2	24.2	7.4	8.4	31.6	38.9	11.6
101	25	5	25	9	9	31	38	10	24.8	5.0	24.8	8.9	8.9	30.7	37.6	9.9
105	25	5	25	8	8	36	41	11	23.8	4.8	23.8	7.6	7.6	34.3	39.0	10.5
110	27	5	27	9	8	36	44	10	24.5	4.5	24.5	8.2	7.3	32.7	40.0	9.1
115	26	5	26	9	8	37	45	10	22.6	4.3	22.6	7.8	7.0	32.2	39.1	8.7
119	27	5	27	8	8	36	48	11	22.7	4.2	22.7	6.7	6.7	30.3	40.3	9.2
123	29	6	29	9	8	37	45	10	23.6	4.9	23.6	7.3	6.5	30.1	36.6	8.1
135	31	5	31	10	10	42	53	13	23.0	3.7	23.0	7.4	7.4	31.1	39.3	9.6

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DESCRIPTIONS OF PREZOEAE AND STAGE I ZOEAE OF *CHIONOECETES BAIRDI* AND *C. OPILIO* (OXYRHYNCHA, OREGONIINAE)

EVAN HAYNES[1]

ABSTRACT

Prezoeae and stage I zoeae of *Chionoecetes bairdi* and *C. opilio* from larvae of known parentage are described. The prezoeae of the two species are essentially identical, and the stage I zoeae differ only in minor detail. The larvae are similar to others of the subfamily Oregoniinae but are separable from them by slight differences in morphology and size.

Snow crabs, genus *Chionoecetes*, are fished commercially in Bristol Bay, Alaska, by three nations—the United States, the Soviet Union, and Japan. Catches of snow crabs in Bristol Bay by all three nations have increased markedly in recent years and in 1970 totaled nearly 85 million pounds. Most of the catches consist of *C. bairdi* Rathbun, but some *C. opilio* (O. Fabricius) are caught also. In 1968 the National Marine Fisheries Service began an intensive investigation into the biology of the snow crabs in Bristol Bay, which includes studies on the early life history stages, especially larval distribution and abundance. Positive identification of larvae of *C. bairdi* and *C. opilio* is important in these studies.

The morphology of prezoeae and stage I zoeae of *C. bairdi* and *C. opilio* (subfamily Oregoniinae) from the Bering Sea are described in this report. The larval forms of the two species are so similar that only the larvae of *C. bairdi* are described in detail; for *C. opilio*, only those morphological features that differ from *C. bairdi* are described. Larvae of the two species from the Bering Sea are compared with larvae of the same subfamily from the North Pacific Ocean.

MATERIALS AND METHODS

During a National Marine Fisheries Service trawling survey for snow crabs in Bristol Bay in May 1970, I obtained two females of *C. bairdi* and two of *C. opilio* that were releasing larvae. The *C. bairdi* were caught May 9 in 55 fathoms at lat. 55°22′N, long. 164°35′W. Their carapace widths (greatest width excluding lateral spines) were 99 mm and 105 mm. One of the *C. opilio* (77-mm carapace width) was caught May 9 in 51 fathoms at lat. 55°40′N, long. 164°37′W, and the other (82-mm carapace width) was caught May 12 in 46 fathoms at lat. 56°01′N, long. 162°25′W. My identification of the two species is based on characters used by Garth (1958).

Larvae were obtained in the following manner. Each gravid female was kept in about 20 liters of filtered sea water with a temperature of about 2.5°C. Hatching began immediately, and the first samples, which consisted mostly of prezoeae, were taken after about 2 h. Other samples were collected about 24 h later, when most of the larvae had molted to stage I. Only prezoeae and stage I zoeae were obtained because it was not practical to keep the zoeae alive at sea long enough to allow molting to the next zoeal stage. The larvae were preserved in a 5% solution of Formalin[2] and sea water.

Drawings of whole animals and appendages (Figures 1 and 2) were made from preserved specimens cleared in lactic acid; the illustrations were prepared with the aid of a camera

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Manuscript accepted November 1972.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

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

lucida. The left appendage is shown in the figures. When setae were plumose, the fact is noted in the text but is not always shown in the drawings; this omission made it possible to show other details. At least 10 specimens each of prezoeae and stage I zoeae of *C. bairdi* and *C. opilio* were dissected and studied in detail with respect to appendage setation and other characteristics.

An ocular micrometer was used to measure the following body dimensions of the larvae: Carapace length—straight-line distance from posterior margin of orbit to middorsal posterior margin of carapace; dorsal-rostral length—straight-line distance from tip of dorsal spine to tip of rostral spine; width between tips of lateral spines of carapace—horizontal straight-line distance between tips of spines; total body length—distance from tip of rostrum to posterior margin of telson, not including telson spines (except in prezoeae, in which it is distance from folded rostrum to posterior margin of telson). Total body length is difficult to measure accurately in preserved larvae because the abdomen is generally flexed beneath the carapace; the measurement therefore requires the summation of several straight-line measurements or chords of the arch formed by the dorsal margin of the body.

Nomenclature of the larval appendages follows that of Gurney (1942). The setation formula of the endopodite is the number of setae per segment from the distal to the proximal segment.

DESCRIPTION OF LARVAL STAGES

Chionoecetes bairdi

Prezoeae (Figure 1a)

Cuticle of antennules, antennae, and telson delicately plumed. Antennule (Figure 1b) has two projections, one appreciably shorter than the other; shorter projection nonpulmose. Exopodite of antenna (Figure 1c) has four plumose projections; endopodite has a simple nonplumose projection, no projection arising from area of rudimentary flagellum. Endopodites and exopodites of first maxilliped (Figure 1d) and second maxilliped (Figure 1e) consist of simple sheaths. Telson (Figure 1f) has seven projections on each side; following Lebour (1928), these are numbered from the inside 1 to 7; fourth projection short and nonplumose and covers spine that in zoea forms tip of telson fork; seventh projection also nonplumose but may occasionally have a few hairs.

The average carapace length (50 specimens) is 0.39 mm (range 0.32 to 0.46 mm) and the average total body length is 2.48 mm (range 2.22 to 2.80 mm).

Stage I Zoeae

General shape (Figure 2a, b) characteristic of larvae of subfamily Oregoniinae. All spines well developed and armed with fine spinules on at least the distal half of their length. Dorsal and rostral spines long, tapering, and usually slightly "s" shaped; dorsal spine slightly longer than rostral. Lateral spines large; at right angles to carapace and curved downward slightly. Eyestalks short, not articulated, and each bears a minute protuberance about midway between eye and carapace. Carapace has slight medial crest with noticeable hump on front of head. Distinct protuberance on carapace posterior to dorsal spine. A minute hair on each side of carapace between lateral spine and base of dorsal spine. Total of six setae along posterior edge of carapace all arising from inner side of carapace; posterior three setae longer and stouter than anterior three setae. Lateral margin of carapace strongly indented just posterior to eye.

The averages for the following measurements (50 specimens) are: carapace length 0.54 mm (range 0.45 to 0.73 mm); dorsal-rostral length 4.17 mm (range 3.96 to 4.55 mm); width between tips of lateral spines 2.73 mm (range 2.52 to 2.97 mm); and total body length 5.15 mm (range 4.96 to 5.60 mm).

ANTENNULE (FIGURE 2c).—Antennule conical and uniramous, with five terminal processes—three long aesthetes and two shorter setae; two aesthetes about equal in length, but third only slightly longer than longest setae.

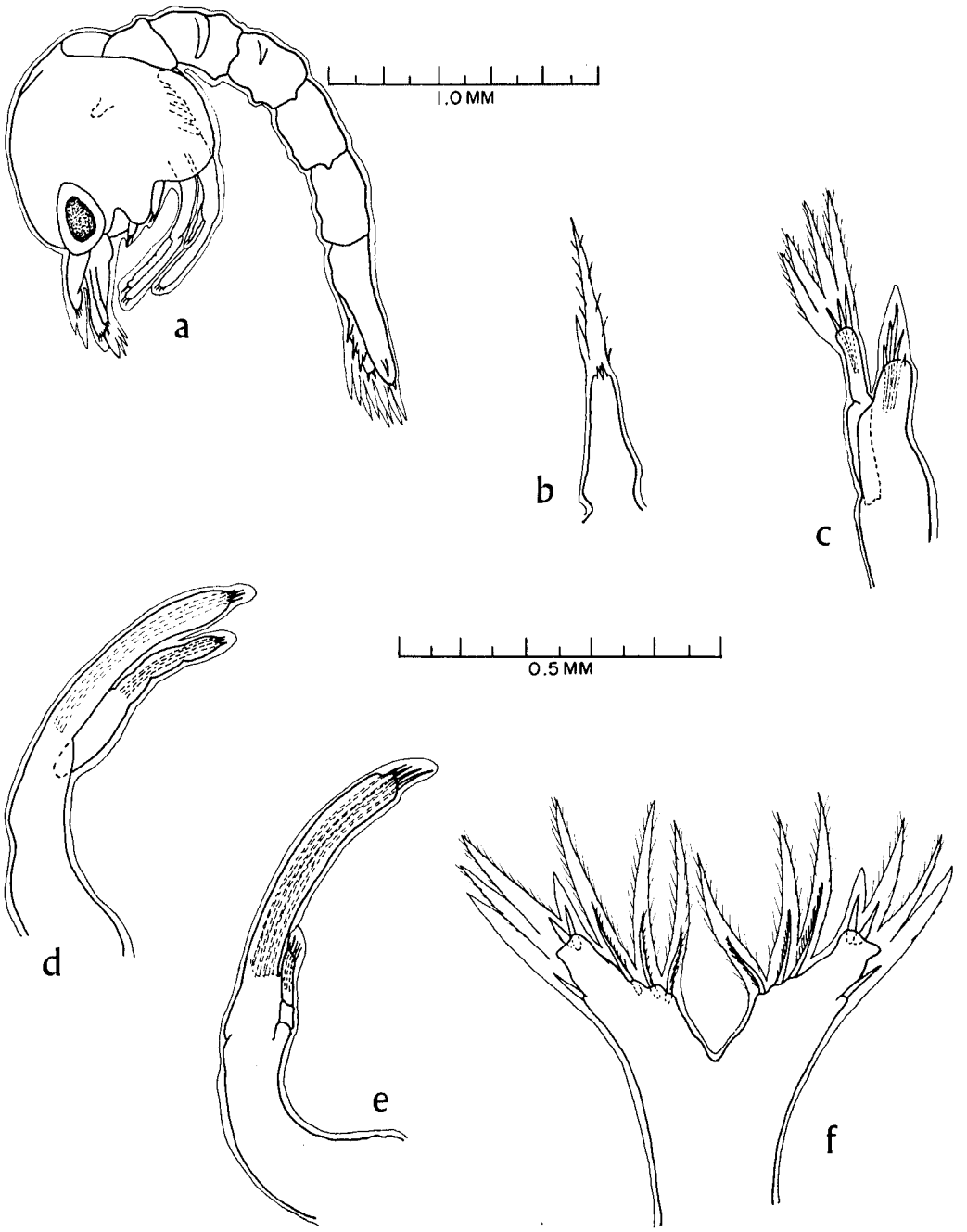

FIGURE 1.—(a) Prezoea of *Chionoecetes bairdi*, (b) antennule, (c) antenna, (d) first maxilliped, (e) second maxilliped, (f) telson.

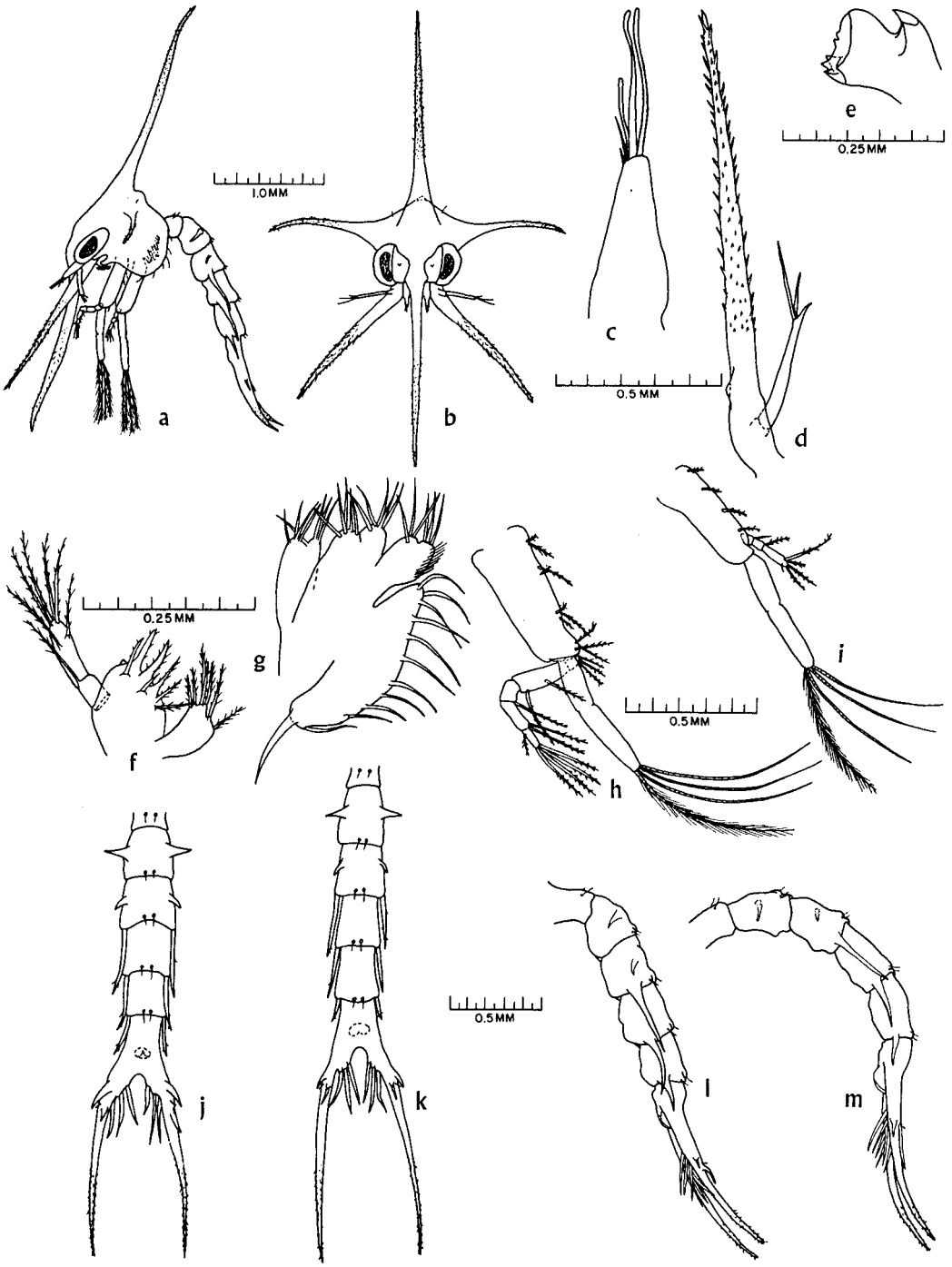

FIGURE 2.—Stage I zoea of *Chionoecetes bairdi* and two views of abdomen of *C. opilio* for comparison: (a) lateral view, (b) anterior view, (c) antennule, (d) antenna, (e) mandible, (f) maxillule, (g) maxilla, (h) first maxilliped, (i) second maxilliped, (j) abdomen (dorsal)—*C. bairdi*, (k) abdomen (dorsal)—*C. opilio*, (l) abdomen (lateral)—*C. bairdi*, (m) abdomen (lateral)—*C. opilio*.

ANTENNA (FIGURE 2d).—Protopodite (spinous process) of antenna elongate; slightly shorter than rostral spine and 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 with two rows of many fine setules. Endopodite (flagellum) rudimentary (represented by small protuberance near proximal end of protopodite).

MANDIBLES (FIGURE 2e).—Mandibles without palps. Incisor composed of two large pointed processes. A subterminal denticle that arises from ventral side of mandible occurs on molar process of right mandible but not on left mandible.

MAXILLULE (FIGURE 2f).—Endopodite two segmented, with six setae on terminal segment (arranged in pairs, one pair being terminal) and one seta on distal end of basal segment. Basal endite bears seven setae at distal end (two setae are especially stout). A bluntly pointed projection one-eighth the height of nearest seta occurs between basal endite setae and endopodite. Coxal endite bears seven setae at distal end. All setae on maxillule plumose.

MAXILLA (FIGURE 2g).—Maxilla bears large platelike exopodite (scaphognathite) with 11 (rarely 12) long, evenly spaced plumose setae along outer margin and one longer and thicker seta at proximal end. Endopodite only slightly bifurcate; bears many fine hairs along outer margin and three setae on each lobe. There are two endites, both slightly bifurcate; basal endite (distal) has five setae on each lobe, and coxal endite (proximal) has four setae on each lobe. All setae sparsely plumose except those on exopodite, which are heavily plumose.

FIRST MAXILLIPED (FIGURE 2h).—Exopodite appears to have two segments but segmentation not complete; four heavily plumose segmented (natatory) setae on distal end. Endopodite five segmented—setation formula is 5, 2, 1, 2, 3. Basis has 10 setae along posterior edge—setation formula is 3, 3, 2, 2. All setae except natatory setae sparsely plumose.

SECOND MAXILLIPED (FIGURE 2i). — Exopodite not completely segmented; four long, heavily plumose segmented (natatory) setae on distal end. Endopodite three segmented—setation formula is 5, 1, 1. Basis has four setae along posterior edge. All setae except natatory setae sparsely plumose.

THIRD MAXILLIPED (FIGURE 2a). — Developing third maxilliped small, rudimentary, and nonsegmented; tip bilobed.

PEREIOPODS (FIGURE 2a).—Five developing pereiopods beneath carapace; they are small, rudimentary, and not segmented or bilobed.

ABDOMEN AND TELSON (FIGURE 2j, l).—Abdomen consists of five segments and telson (somite six is fused with telson in stage I). Each segment has pair of hairs near dorsal posterior margin; second and third segments both have pair of slightly curved lateral knobs —pair on third segment about half the length of pair on second; pairs of long well-developed spines, which become progressively shorter posteriorly, on posterior lateral margin of third, fourth, and fifth segments; those on third and fourth segments extend beyond posterior margins of adjacent segments; those on fifth segment extend posteriorly to level of anus; lateral spines may or may not have few minute hairs. Telson bifurcate; furcations long, slender, and finely spinulate and have upcurved tips; each furcation bears three articulated telson setae on inner side, a prominent spine laterally on outer margin, a smaller dorsal spine posterior to telson setae, and a minute spinule[3] about midway between the lateral and dorsal spines; lateral and dorsal spines on furcations minutely spinulate. Each telson seta bears two rows of spinules, and each row has two types of spinules. First type short but wide at base, resembling row of

[3] The spinule was first described by Kurata (1963) for *C. o. elongatus* and is best seen in stained specimens under high (400X) magnification.

"teeth"; second type small and hairlike; first type extends about three-fourths the length of the seta and decreases in size proximally; second type covers distal one-fourth of seta; spinules in both rows fit this description, although those on one row are considerably smaller than those on the other. Pleopods and uropods developing, but not evident at this stage.

Chionoecetes opilio

Prezoeae of *C. opilio* are identical in all respects to those of *C. bairdi*. Stage I zoeae are identical except for a few subtle differences in abdominal morphology. The most obvious difference is in the length of the posterior lateral spines on the third and fourth abdominal segments. In *C. bairdi* (Figure 2j, l), the spines overlap the adjacent segments by about one-third the length of the spines. In *C. opilio* (Figure 2k, m), the spines on third segment barely extend past the posterior margin of the fourth segment, and those on the fourth segment do not quite reach the posterior margin of the fifth segment. Another, but small, difference is the thickness and shape of the abdomen. In *C. bairdi* the abdomen appears slightly deeper than in *C. opilio*, especially in the areas of the developing pleopods. Finally, the telson furcations of *C. opilio* are about one-sixth longer than those of *C. bairdi*. This last difference may be difficult to distinguish clearly because the degree of curvature of the furcations may vary considerably among specimens of both species.

COMPARISON OF NORTH PACIFIC ZOEAE OF THE SUBFAMILY OREGONIINAE

The subfamily Oregoniinae comprises three genera, *Oregonia*, *Hyas*, and *Chionoecetes* (Garth, 1958). Zoeae of only a few species of the Oregoniinae that occur in the North Pacific are known. Hart (1960) reared and described the zoeae of *O. gracilis* and *H. lyratus* and showed that they were separable from each other by slight differences in size, color, and spinulation. Aikawa (1937) and Kon (1967) described prezoeae and Kurata (1963) described the first zoeal stage of *C. o. elongatus*, all from specimens of known parentage. Kurata also described zoeal stages of *H. coarctatus alutaceus*, but the specimens were obtained from the plankton. In the following discussion, I compare the morphology of the first zoeal stages of *C. bairdi* and *C. opilio* with the first zoeal stages of each of the species mentioned above, emphasizing the differences among them.

Kon's (1967) prezoeae of *C. o. elongatus* were nearly identical to my prezoeae of *C. bairdi* and *C. opilio* except that he described the short embryonic spine of the antennule as plumose, whereas I did not. Aikawa's (1937) prezoeae differed in several respects from mine and from Kon's: his specimens did not have an embryonic cuticle; the appendages and carapace spines were partially or fully extended; and a lateral knob was present only on the second abdominal somite. Apparently, Aikawa described a prezoea that had just cast its embryonic cuticle and was in the process of metamorphosing to stage I.

The stage I zoeae of *C. o. elongatus* described by Kurata (1963) differed slightly from my stage I zoeae of *C. bairdi* and *C. opilio*: the lateral knobs on the third abdominal segment of Kurata's stage I zoeae almost reached the posterior margin of the segment, but in my larvae they were considerably shorter. Also, in Kurata's specimens the posterior lateral spines on the abdomen were covered with spinules, whereas I found only one or two minute spinules on the lateral spines. Finally, the maxilla of Kurata's larvae had 15 setae along the outer margin of the exopodite in addition to the single stout seta at the proximal end; the larvae I studied had only 11 setae (rarely 12) along the outer margin in addition to the stout setae. This last difference may include phenotypic variation. J. Watson of the Fisheries Research Board of Canada (pers. comm.) has informed me that *C. opilio* in Atlantic waters have 12 (rarely 13) setae in addition to the stout seta. Unfortunately, Kurata did not mention whether any variation of the number of setae on the exopodite of the maxilla occurred in his specimens.

A comparison of Hart's (1960) specimens of *O. gracilis* and *H. lyratus* with my specimens of *C. bairdi* and *C. opilio* shows that morpho-

logical differences among the zoeae were slight. The most obvious difference was size—my stage I zoeae were nearly twice as large as Hart's stage I zoeae. Another difference is the morphology of the antennule: According to Hart (1960) zoeae of *O. gracilis* and *H. lyratus* had two aesthetes and one seta (although in specimens of *O. gracilis* sent me by Hart, the antennule had two setae instead of one), whereas in *C. bairdi* and *C. opilio* the antennule had three aesthetes and two setae. A third difference was the length of the posterior lateral spines: In stage I *C. bairdi* and *H. lyratus*, the spines extended beyond the posterior margin of the adjacent segment about one-third the length of the spine, but in *C. opilio* and *O. gracilis* they barely reached the posterior margin of the adjacent segment. In addition to the above differences, Hart did not describe the protuberances on the eyestalks or the minute spinule located between the dorsal and lateral spines on the telson furcations; on the specimens sent me by Hart, I found no minute protuberances on the eyestalks but did find the minute spinule.

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FEEDING ORIENTED MOVEMENTS OF THE ATHERINID FISH *PRANESUS PINGUIS* AT MAJURO ATOLL, MARSHALL ISLANDS

EDMUND S. HOBSON AND JAMES R. CHESS[1]

ABSTRACT

The feeding behavior of the atherinid *Pranesus pinguis* was studied in the lagoon at Majuro Atoll, Marshall Islands, during March 1972.

During the day, individuals larger than about 35 mm (standard length) assemble in relatively inactive schools along the shore. Shortly after sunset the schools migrate offshore to feeding grounds in the lagoon, following the same route night after night. Once out in the lagoon the schools disperse, and individuals 2 to 4 m apart feed on plankton at the water's surface throughout the night. Their prey include hyperiid amphipods, caridean shrimp larvae, myodocopid ostracods, the tretomphalus stage of foraminiferans, and calanoid copepods. Most of their prey are at the surface at night, but at greater depths in daylight. At first morning light the silverside begin to concentrate in the shoreward part of their feeding ground. Then about 45 min before sunrise, having reached daytime proportions, the school moves inshore over the same route it had taken outward the night before and at about 20 min before sunrise arrives at its diurnal schooling site to take up its relatively inactive daytime mode.

In contrast, limited evidence indicates that individuals smaller than about 30-mm standard length feed by day but not at night.

The silverside *Pranesus pinguis* (Lacépède) is widespread in the western Pacific and Indian Oceans (Schultz, 1953) and is a potential baitfish for tuna fishermen (Hida, 1971). Because biological information of the species does not exist, we studied its feeding activity in the lagoon at Majuro Atoll, in the southeastern Marshall Islands, from 16 to 25 March 1972.

Majuro Atoll is a ring of shallow coral reefs and low islands encircling a lagoon about 40 km east to west and 10 km north to south (Figure 1). Around the perimeter of the lagoon a narrow shelf of sand and isolated coral heads extend offshore under 1 to 6 m of water. At the outer edge of this shelf, several hundred meters from shore, the sea floor falls abruptly to a depth of 40 m, which is the approximate water depth over most of the lagoon.

The study was centered on silverside that schooled during the day (Figure 2) along the shore of Arniel Island (Figure 3). The behavior of fish in this school was judged typical of that seen in other members of the species during a limited survey along the shores of other islands bordering the lagoon.

Movements and other behavior of this fish were observed directly using a face plate and snorkel at all hours of day and night over the 10 days we spent at Majuro. Specimens were collected for analysis of gut contents, and plankton samples were taken in the lagoon during both day and night. Sampling methods and procedures are described below where pertinent. All lengths given for the silverside are standard length. Because the horizon frequently was obscured by clouds, times of sunrise and sunset were calculated using the Nautical Almanac, U.S. Naval Observatory.

ACTIVITY PATTERN

The Diurnal School

During each day, individuals about 35 to 65 mm long hovered in a quiet school that was strung out along the shore. Here, where it is 1 to 2 m deep, the school occupied most of the water

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Manuscript accepted December 1972.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

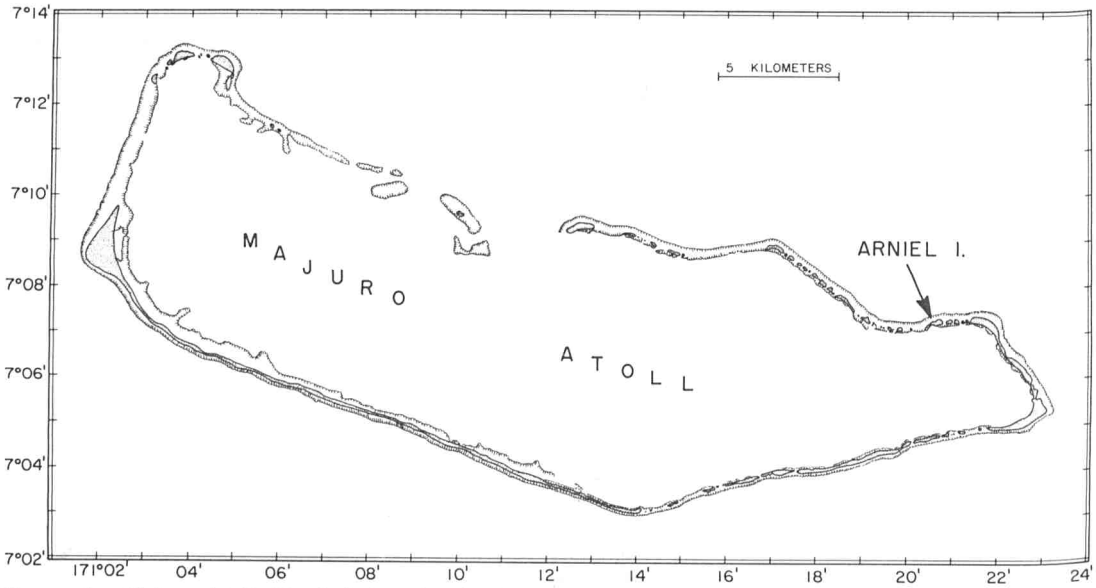

FIGURE 1.—Majuro Atoll, Marshall Islands, showing Arniel Island. Adapted from U.S. Hydrographic Office chart 6087.

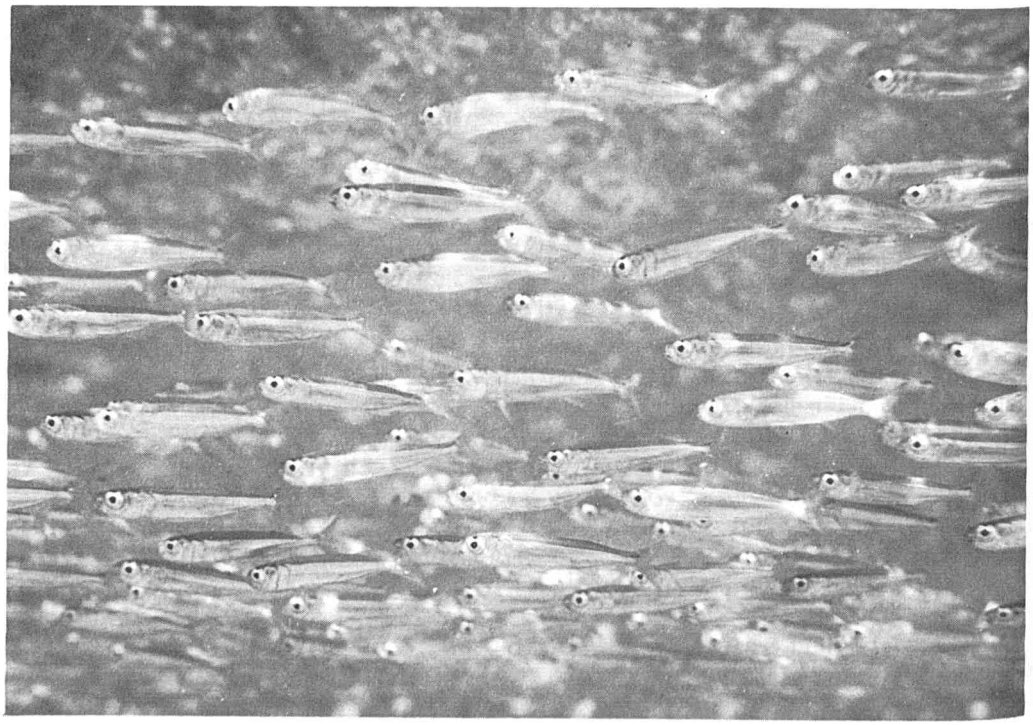

FIGURE 2.—*Pranesus pinguis* schooling during the day along the lagoon beach of Arniel Island.

FIGURE 3.—The lagoon shore of Arniel Island, viewed from the point at the western end of the bay in which this study was centered.

column. Perhaps the outstanding characteristic of the school at this time was the inactivity of its members.

The situation began to change late in the afternoon, when fish in the school gradually drew together at a point in the center of the bay. By sunset the school was a compact unit, concentrated just beneath the surface of the water.

As evening approached, the fish became increasingly restless, and often the school was briefly in motion, only to return to its original position. The fish were highly responsive to disturbances at this time. Repeatedly a segment of the school exploded from a point within, so that a void suddenly appeared. Sometimes this maneuver could be traced to a predator—usually a carangid or a belonid—but more often no basis for the action was noted.

The Offshore Migration

Shortly after sunset the silverside migrated away from their daytime schooling site. We recorded this phenomenon on all three occasions when observations were made at this time of day.

The school could not be seen effectively from out of water at this time of day, owing to the fading light and wind-waves on the water's surface. Consequently, we watched from underwater: once (21 March) from the center of the school, when the fish around us began to migrate 14 min after sunset; once (22 March) at the eastern edge of the school, when the fish in view began moving out at 9 min after sunset; and once (24 March) at the western edge, when the observed fish got underway at 4 min after sunset. Because we made observations from three widely separated parts of the school, these times are not directly comparable. Nevertheless, on each occasion the last of the silverside had left the schooling site about 10 min after the first individuals moved out.

When the migration was recognized to be underway, one of us remained at the schooling

site to follow developments there, while the other accompanied the migration. The major segment of the school did not move directly offshore; rather, each evening it headed westward along the beach. It continued in this direction until reaching the point of land at the western end of the bay (Figure 4) and then veered offshore over the deeper water of the lagoon, where contact with it was lost.

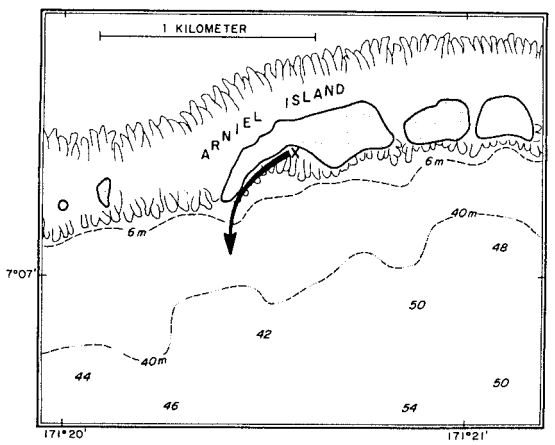

FIGURE 4.—Route taken by the silverside when migrating offshore from Arniel Island. The diurnal schooling site of this fish is marked by "X." Soundings are in meters. Adapted from U.S. Hydrographic Office chart 6087.

Nocturnal Activity

Later during the night the silverside were found offshore in the lagoon, spread out just below the surface of the water, with 2 to 4 m between each fish. They remained there throughout the night, feeding on plankton (discussed below); although some of them ranged as much as 2 km out into the lagoon, most occurred within 1 km of the beach. Their distribution at 0400 h on 24 March, more than 2 h and 30 min before sunrise, is illustrated in Figure 5. The method used to obtain the distribution of silversides in Figure 5 is as follows: Running a skiff along Arniel Island, we established a speed that took us the length of the Island in precisely 4 min. Maintaining this speed, we then headed out into the lagoon from the center of the bay, using a light on the opposite side of the atoll to stay on course. Upon passing over the dropoff

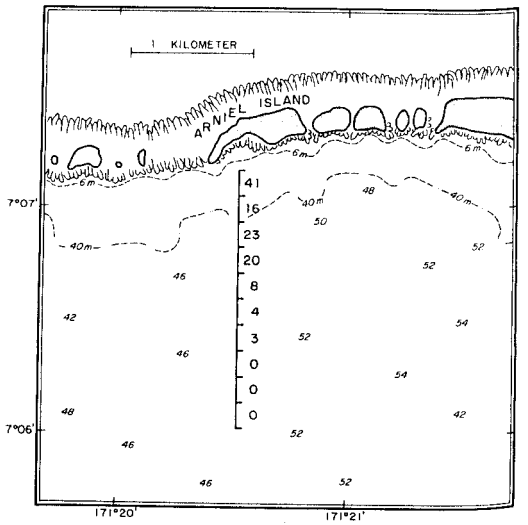

FIGURE 5.—Distribution of silverside at the surface along a transect running offshore from Arniel Island at 0400 h on 24 March 1972 (see text for method used). Adapted from U.S. Hydrographic Office chart 6087.

into deeper water, we used a hand light to count the number of silversides in our path during each minute of a 10-min run. These fish are readily seen using this method owing to the characteristic reflections from their silvery bodies when struck by the light.

At first morning light, about 1 h and 15 min before sunrise, the silverside began to concentrate in the shoreward part of their feeding ground. Soon it was apparent that the silverside were regrouping directly offshore from where they had departed the island the previous evening.

The fish continued to regroup until about 30 min before sunrise, by which time the school had attained daytime proportions and was ready to return to its diurnal location.

The Inshore Migration

The lagoon was glassy-calm on each of the three consecutive mornings that we witnessed the inshore migration (23-25 March) so that observations could be made from above the surface of the water near the daytime schooling site. By noting agitation on the water's surface, the school was seen arriving each morning

off the point at the western end of the bay, and then progressing steadily eastward along the shore. Thus, in the morning the silverside reversed the route they had taken offshore the night before. The vanguard of the school arrived at the diurnal schooling site on each of the three mornings at 20, 18, and 16 min before sunrise, respectively. Because these observations, unlike those of the evening, were made from the same vantage point, they are directly comparable.

For a while after arriving inshore, the silverside remained in a compact school but progressively strung themselves out along the beach until the midday situation prevailed.

P. pinguis is another example of a fish that assembles in relatively inactive schools in shallow water during the day and then migrates to feed elsewhere at night. This phenomenon is known in certain clupeids, pomadasyids, carangids, sciaenids, and lutjanids in the Gulf of California (Hobson, 1965, 1968), and has also been reported for many species in the tropical Atlantic (Starck and Davis, 1966). Obviously it is a widespread activity pattern among shore fishes in tropical seas.

FEEDING HABITS

The inactivity of silverside (>35 mm long) that hover in their inshore schools during the day indicates that they do not feed at this time. To obtain more data on this question, specimens were collected for gut-content analysis three times during the day (19 March). The first collection was made early in the day (0700 h); the second collection, during midday (1030 h); and the third collection, late in the day (1600 h). Ten specimens from each collection were examined.

All 10 specimens (61 to 73 mm long) examined from the early collection had material in their guts, which on the average were about 20% full. Composition of these gut contents, ranked as the mean percent (by volume) of each item in all silverside specimens, were as follows: hyperiid amphipods, 49.6%; caridean shrimp larvae, 6.7%; calanoid copepods, 6.2%; ostracods, 5.5%; crab megalops, 2.3%; mollusk veliger larvae, 1.0%; polychaetes, 0.5%; foraminiferans (tretomphalus stage), 0.4%; and unidentified, well-digested material 27.8%. Digestion had damaged all of this material so that identifications could be made only to major groups.

Of the 10 specimens (61 to 70 mm long) examined from the midday collection, three were empty; the guts of the remaining seven were on the average about 15% full, but digestion had reduced this material to a soup of unidentifiable fragments.

Finally, the guts of all 10 specimens (58 to 64 mm long) from the collection made late in the day were empty.

The data clearly demonstrate that the silverside in these inshore schools do not feed during the day. But even in those individuals taken during early morning, digestion had damaged the gut contents beyond the point where a precise analysis could be made. Being small themselves, the silverside take tiny prey, mostly under 2 mm long, whose identifying features do not resist digestion well.

To obtain material for a detailed analysis of food habits, we went 200 to 800 m offshore from Arniel Island between 0400 and 0500 h on 23 and 24 March. Here, using a dip net and flashlight from a moving skiff, we collected 64 specimens between 35 and 69 mm long, which were immediately placed into a 10% Formalin[2] solution. With this procedure, we obtained fish that were actively feeding, and whose gut contents (Table 1) included fresh material. In Table 1, the items are ranked by a "ranking index," which is computed by multiplying the mean percent (by volume) of each item in the gut contents of all silverside specimens by the ratio of silverside containing that item to total silverside sampled. Thus, for *Hyperia bengalensis* found in silverside collected on 23 March, the ranking index is $46.71 \times 30/31 = 45.20$. To increase the precision of the ranking index, the mean percent of each item in the gut contents is carried to two decimal places. The actual observed values for individual fish were estimated to the nearest percent, except where the estimate was <1.00, in which case the estimate was to > or <0.50%. For purpose of calculating the mean percent,

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

TABLE 1.—Gut contents of 64 silversides collected on 23 and 24 March 1972.

Rank	Item	Size (mm) Mean	Size (mm) Range	Number of silverside with this item	Mean percent (vol.) of each item in all silverside specimens	Ranking index
	Gut contents of 31 silversides 35 to 67 mm long, collected on 23 March 1972					
1	*Hyperia bengalensis* (hyperiid amphipod)	1.6	(1.0-2.0)	30	46.71	45.20
2	Tretomphalus stage of foraminiferan(s)	0.3	(0.2-0.7)	14	18.43	8.32
3	Caridean shrimp larvae	1.7	(0.5-6.0)	18	7.84	4.55
4	Myodocopid ostracods	1.3	(0.5-2.0)	18	6.61	3.83
5	*Undinula vulgaris* (calanoid copepod)	1.5	(1.0-2.0)	11	1.94	0.69
6	Crab megalops	2.0	(1.0-3.0)	4	3.70	0.48
7	*Lucifer* (sergestid shrimp)	7.0	(4.0-16.0)	3	4.03	0.39
8	*Candacia discaudata* (calanoid copepod)	1.6	(1.0-2.0)	8	1.19	0.31
9	Insects	3.0	(2.0-5.0)	3	1.77	0.17
10	Mysids	5.0		2	1.77	0.11
11	Veliger larvae (mollusks)	0.9	(0.5-1.5)	5	0.22	0.04
12	Zoea larvae (crabs)	1.5	(1.0-2.0)	2	0.32	0.02
13	"Other" calanoid copepods	1.0		2	0.13	0.008
14	Polychaetes	—		1	0.13	>0.004
15	*Saphirella* sp. (cyclopoid copepod)	0.9	(0.7-1.0)	2	0.06	<0.004
16	*Oncaea* sp. (cyclopoid copepod)	0.3		1	0.03	<0.001
17	Larvaceans	1.0		1	0.03	<0.001
	Also, unid. amorphous material	—		8	5.09	1.27
	Gut contents of 33 silversides 35 to 69 mm long, collected on 24 March 1972					
1	*Hyperia bengalensis* ((hyperiid amphipod)	1.9	(1.0-3.0)	24	28.28	20.57
2	Myodocopid ostracods	1.5	(0.5-2.0)	21	14.75	9.39
3	Tretomphalus stage of foraminiferan(s)	0.3	(0.1-0.8)	20	12.00	7.27
4	*Candacia discaudata* (calanoid copepod)	1.5	(0.5-2.0)	15	4.46	2.02
5	Caridean shrimp larvae	2.2	(1.0-4.0)	12	4.88	1.77
6	*Undinula vulgaris* (calanoid copepod)	1.6	(1.0-2.5)	12	2.73	0.99
7	Mysids	5.5	(2.0-7.0)	5	5.60	0.85
8	"Other" calanoid copepods	0.9	(0.8-1.0)	8	2.25	0.54
9	Insects	2.5	(1.5-3.0)	7	1.89	0.40
10	Veliger larvae (mollusks)	0.7	(0.3-1.0)	9	1.45	0.39
11	Polychaetes	—		4	0.88	0.11
12	*Labidocera acuta* (calanoid copepod)	2.0	(1.5-2.5)	3	0.64	0.06
13	*Lucifer* (sergestid shrimp)	3.0	(1.0-5.0)	2	0.60	0.04
14	Crab megalops	5.0		1	1.20	0.04
15	*Oncaea* sp. (cyclopoid copepod)	0.7	(0.5-1.0)	3	0.36	0.03
16	*Saphirella* sp. (cyclopoid copepod)	0.8	(0.5-1.0)	4	0.17	>0.02
17	Stomatopod larvae	5.0		1	0.60	<0.02
18	Alphaeid shrimp	4.0		1	0.30	0.009
19	Zoea larvae (crabs)	3.0		1	0.30	0.009
20	Gammarid amphipods	1.0		1	0.20	0.006
21	*Globigerina* sp. (foraminiferan)	1.0		1	0.03	<0.001
	Also, unid. amorphous material	—		10	12.57	3.81
	unid. crustacean fragments	—		5	3.86	0.59

>0.50 was considered to be 0.75, and <0.50 was considered to be 0.25.

A few forms predominated in the silverside diet when these observations were made. The hyperiid amphipod *Hyperia bengalensis* was especially important, with other major prey including: the tretomphalus stage of a foraminiferan(s); myodocopid ostracods; caridean shrimp larvae; and two calanoid copepods: *Candacia discaudata* and *Undinula vulgaris*. These forms constituted over 90% of the food in the guts of the silverside that were sampled.

PLANKTON AS PREY FOR THE SILVERSIDE

To determine whether these forms were selected by the silverside or were taken only in numbers relative to their abundance in the plankton, net hauls were made concurrently with the fish collections. The plankton sampled were from the lagoon between 22 and 24 March 1972. Additional plankton collections were made in the same location during daylight, thus

providing a comparison of the plankton between day and night. These data (Table 2) demonstrate the importance of sampling the plankton right along with the fish. The methods of collecting were as follows: Seven tows were made over one 500-m course (duration approximately 15 min), about 600 m offshore from Arniel Island using a 1-m net with a 0.333-mm mesh. Night tows were made on 23 and 24 March at the same time that the fish were collected for gut-content analysis (Table 1). Day tows were made at 1600 h on 22 March and at 1200 h on 24 March. Six of the tows were paired: on both nights and during the day of 24 March one tow at 4 to 5 m deep was immediately followed by a second tow with the net breaking the water's surface. On the day of 22 March only the 4- to 5-m depth was sampled. The analysis is of 10% subsamples, one taken from each collection. Significantly, except for a lone alphaeid shrimp in one gut, every prey species found in the silverside occurred in the night plankton samples.

Clearly there was a great difference in the composition of the plankton between day and night, and a lesser though significant difference from one day or night to the next. Furthermore, these differences are reflected in the feeding habits of the silverside.

The daytime samples had greater volume (measurements by displacement: day volume—mean 16 ml, range 11-26 ml; night volume — mean 13 ml, range 10-15 ml), but this was due mostly to there being more chaetognaths in those collections. As shown in Table 2, there were many more species in the plankton samples taken at night, and most of the species present in both day and night collections were more numerous in the night collections. This is especially true of forms taken as prey by the silverside. Nevertheless, although many forms taken by silverside were relatively numerous, they contributed relatively little to the total volume of the plankton samples, even at night.

Major Prey Organisms

The habits of the silverside are better understood after a closer look at some of its major prey.

Hyperia bengalensis

This amphipod was the major prey of the silverside at the time of this study. Our collections indicate that it is present at the surface in greater numbers at night. This widespread species has been found elsewhere to move toward the surface after dark, and retreat to deeper water in daylight (G. J. Brusca, Humboldt State College, Calif., pers. comm.). It was equally numerous at the surface and at the 4- to 5-m depth in all night collections, but occurred in only 1 day collection, here in lesser numbers (Table 2).

Although *H. bengalensis* was the top-ranked prey on both nights, it was considerably more numerous in the gut samples on 23 March than on 24 March. Significantly, it was also more numerous in the plankton samples taken on the 23d (Table 2).

Tretomphalus Stage of Foraminiferans

Perhaps several species are represented here, but all are characterized by a calcareous, gas-filled float that buoys them at the surface (Myers, 1943). Undoubtedly, this habit accounts for this form's high incidence among prey of the surface-feeding silverside. One would not expect the tretomphalus to migrate vertically between day and night, and the data indicate they do not (Table 2).

Although the tretomphalus were well represented in the plankton collections on both nights, they were more numerous on 24 March; nevertheless, although their importance as prey on the two nights was similar, they were the third-ranked prey on the 24th and second-ranked prey on the 23d.

Myodocopid Ostracods

Being relatively numerous in the night plankton collections, but absent from the day plankton collections, these forms, like the hyperiid, apparently rise toward the surface in darkness, and descend to deeper water in daylight. Myodocopids were prominent among the gut contents on both nights, but whereas they ranked only fourth on the 23d, they ranked second on

TABLE 2.—Plankton samples 22, 23 and 24 March 1972.

Organism	Size (mm)	Number of individuals							Rank in silversides gut contents	
		Night				Day				
		Surface		4-5 m depth		Surface	4-5 m depth			
		23 Mar.	24 Mar.	23 Mar.	24 Mar.	24 Mar.	22 Mar.	24 Mar.	23 Mar.	24 Mar.
Foraminiferans										
Globigerinids	0.2- 1.0	130	130	68	160	48	5	147	—	21st
Tretomphalus	0.2- 0.6	18	58	0	2	10	12	2	2d	3d
"Other" forams	0.6- 2.0	18	6	0	41	2	1	8	—	—
Coelenterates										
Siphonophores	3.0-10.0	9	3	16	0	7	37	14	—	—
Flatworms										
Turbellarians	1.0	0	1	0	0	0	0	0	—	—
Annelids										
Polychaete larvae	0.5- 4.0	35	6	12	18	0	16	2	14th	11th
Polychaete post larvae	4.0	3	0	0	0	0	0	0	—	—
Brachiopod larvae	0.5- 2.0	8	0	4	3	0	20	0	—	—
Mollusks										
Veligers	0.2- 0.5	36	47	25	70	15	84	40	11th	10th
Heteropods (1 sp.)	0.5- 3.0	12	2	6	1	1	21	8	—	—
Pteropods (2 sp.)	1.0- 8.0	6	6	3	5	1	17	0	—	—
Crustaceans										
Myodocopid ostracods	0.4- 2.0	50	150	160	190	0	0	0	4th	2d
"Other" ostracods	—	4	18	35	20	24	27	0	—	—
Cladocerans	0.5	0	1	0	0	0	0	0	—	—
Calanoid copepods										
Candacia discaudata	1.5- 3.0	19	370	16	330	0	0	0	8th	4th
Undinula vulgaris	1.0- 3.0	173	90	200	180	11	192	191	5th	6th
Labidocera acuta	1.0- 3.0	24	2	15	1	1	0	8	—	12th
"Other" calanoids	0.5- 2.0	54	1,304	90	390	34	130	60	13th	8th
Cyclopoid copepods										
Oncaea sp.	0.5	3	4	1	2	2	3	1	16th	15th
Corycaeus sp.	0.5	0	1	0	1	0	0	0	—	—
Sapphirina sp.	0.5	0	1	0	1	0	0	0	—	—
Saphirella	0.5	1	1	0	0	0	0	0	15th	16th
Caligoid copepods	3.0	0	1	0	0	0	0	0	—	—
Hyperiid amphipods										
Hyperia bengalensis	0.2- 2.5	282	24	238	29	0	10	0	1st	1st
Gammarid amphipods	1.0	1	1	1	0	0	0	1	—	20th
Isopod larvae	—	0	2	0	0	0	0	0	—	—
Mysids	2.0- 7.0	2	15	15	16	0	0	0	10th	7th
Stomatopod larvae	3.0- 8.0	3	1	1	0	0	0	0	—	17th
Caridean shrimp larvae	0.5-10.0	243	630	330	130	70	214	35	3d	5th
Panaeid shrimps										
Lucifer	3.0-12.0	8	4	10	10	0	0	0	7th	13th
Crab zoea	0.2- 3.0	26	162	55	280	55	65	0	12th	19th
Crab megalops	0.3- 2.0	3	12	0	3	0	0	0	6th	14th
Lobster puerulus	4.0	0	1	0	0	0	0	0	—	—
Lobster phyllosome	—	0	1	0	0	0	0	0	—	—
Insects	1.0	0	0	0	1	0	0	0	9th	9th
Echinoderms										
Echinopluteus larvae	0.2- 1.0	>4,000	>1,000	>2,000	>3,000	—	>100	>1,000	—	—
Holothurian larvae	0.2- 1.5	3	0	2	1	0	0	1	—	—
Ophiuroid larvae	—	3	0	2	0	0	0	0	—	—
Chaetognaths										
Sagitta enflata	4.0-12.0	~120	~180	~150	~350	~900	~440	~600	—	—
S. neglecta	4.0- 8.0	4	30	~100	~ 40	~ 80	~100	~100	—	—
S. regularis	3.0- 6.0	0	6	50	10	28	10	30	—	—
Chordates										
Larvaceans	0.5- 3.0	30	36	50	100	35	9	682	17th	—
Fish eggs	0.2- 1.0	26	80	40	55	200	14	60	—	—
Fish larvae	1.0- 5.0	20	22	25	9	—	4	22	—	—

the 24th. Significantly, they were three times more numerous in the surface plankton samples on the 24th (Table 2).

Caridean Shrimp Larvae

Our data suggest an increase in caridean shrimp larvae at the surface after dark, even though many are present in daylight (Table 2). Based on the collections, caridean larvae were more numerous in the plankton than were the forms discussed above, but many were too large to be taken as prey by the silverside (see below). It remains undetermined how many of those individuals in the plankton were, in fact, suitably sized prey, so that numbers in the gut samples cannot be related to numbers in the plankton, as is done above.

Candacia discaudata

The greater numbers of this copepod in the diet of the silverside on 24 March, when it ranked fourth, compared to 23 March, when it

ranked eighth, is consistent with its relative numbers in the plankton on these two dates (Table 2). As with other prey of the silverside, the presence of *C. discaudata* in the night collections, and its absence from the day collections (Table 2), probably can be attributed to a diel vertical migration.

Undinula vulgaris

In the samples from 4 to 5 m deep, *U. vulgaris* was equally abundant day and night; however, it was numerous in the surface collections only at night (Table 2). Thus, although this copepod swims at the surface after dark, it seems to be at least a few meters deeper during the day. This conclusion is in agreement with Johnson (1949), who found *U. vulgaris* abundant at or above 2 m only at night and concluded that it descends to deeper water in daylight.

Based on the plankton hauls, *U. vulgaris* was present in similar numbers on both nights—with perhaps more at the surface on 23 March. Consistent with this, it was ranked fifth in the gut contents on the 23d, and sixth on the 24th.

Other Prey

The silverside preyed on many other forms at the time of this study, but in fewer numbers than the above (Table 1). Probably various of these lesser prey, though of secondary importance here, assume major status under appropriate conditions. In general, these other prey have many of the characteristics of the major prey: most are crustaceans or larval forms of other groups, and generally they seem to rise into the surface waters at night, then descend to deeper water during the day (Table 2).

Prey Size

Undoubtedly size is important in determining whether or not a given organism is suitable prey for the silverside. Based on the gut-content analysis, most prey are between 0.5 and 3 mm in their greatest dimension. Nevertheless, other factors are also important. For example, the size range of the abundant larvaceans in the plankton samples was precisely the size range of most prey—0.5 to 3 mm—and yet only a single larvacean was found among the gut contents. Obviously some characteristic of the larvaceans, apart from size, excluded them as prey for the silverside.

BEHAVIOR OF SMALL SILVERSIDE

Limited observations indicate that individuals smaller than about 30 mm behave differently than the larger fish, discussed above. During the day the smaller fish do not school with the larger individuals along the beach; instead, they occur in small schools 1 m or so in diameter that swim in the upper part of the water column 20 m or more away from shore. The fish in these schools appear to be actively feeding, as individuals are continually breaking away from the school, snapping at objects in the water that were too small to be seen by us, and then immediately dashing back to the school—all in one rapid, continuous movement. None of these small active individuals were collected during the day for gut-content analysis; however in the collections offshore at night, in which the 64 larger individuals were collected for the gut-content analysis (Table 1), 5 individuals less than 30 mm long also were taken (3 on 23 March; 2 on 24 March). Significantly, although the guts of all 64 larger individuals contained food, the guts of all 5 small individuals were empty.

These limited data suggest that the small silverside may feed during the day but not at night.

CONCLUSIONS

1. During the day in the Majuro Atoll lagoon silverside larger than 35 mm long assemble in relatively inactive schools along the beaches. These fish do not feed at this time.
2. Shortly after sunset these schools migrate away from shore, following the same route day after day.
3. Once out into the lagoon the schools disperse, and the fish spread out just under the water's surface. They feed throughout the night,

operating as individuals 2 to 4 m apart. Some occur as far as 2 km off the beach.

4. The prey of the silverside are zooplankton, mostly crustaceans between 0.5 and 3 mm in greatest dimension, that occur right at the water's surface after dark. Generally they are species that rise to the surface at night, and descend to deeper waters during the day, and are selected by the silverside from among other organisms of similar size that are not taken.

5. Major prey include a hyperiid amphipod, myodocopid ostracods, the tretomphalus stage of foraminiferans, caridean shrimp larvae, and calanoid copepods.

6. At first morning light, about 1 h and 15 min before sunrise, the silverside begin to concentrate in the shoreward part of their feeding ground. The school continues to develop for about 45 min, then having attained daytime proportions, it moves inshore over the same route it had taken when moving outward the night before. About 20 min before sunrise it arrives at its diurnal schooling site, and the daytime period of inactivity begins.

7. The behavior of silverside less than 30 mm long is in contrast to that of large individuals. Limited evidence indicates that these small fish feed by day and not at night.

ACKNOWLEDGMENTS

We are grateful to Frank Hester and his staff at the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA—especially Thomas S. Hida and Everett C. Jones—for the cooperation and logistic support. We also thank Gary J. Brusca, Humboldt State College, and Abraham Fleminger, Scripps Institution of Oceanography, for help in identifying the planktonic organisms. Finally, we thank Carl L. Hubbs and Richard H. Rosenblatt, Scripps Institution of Oceanography, as well as Abraham Fleminger, for helpful comments on a draft of the manuscript. Kenneth Raymond, Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service, NOAA, drew the figures.

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DISTRIBUTION, SEASONAL ABUNDANCE, AND SOME BIOLOGICAL FEATURES OF STEELHEAD TROUT, *SALMO GAIRDNERI*, IN THE NORTH PACIFIC OCEAN

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ABSTRACT

Cruise and catch data of Canadian, Japanese, and United States research vessels for 1953 and 1955-67, together with information from published literature, were used to investigate the distribution, age, and size of steelhead trout, *Salmo gairdneri*, in the North Pacific Ocean.

Steelhead trout were distributed virtually throughout the entire North Pacific Ocean, north of about lat. 42°N. Their abundance was greatest in the Gulf of Alaska and eastern North Pacific, decreased to the westward, and was lowest in the western North Pacific and the western Aleutian Islands area. The relative abundance in all areas sampled was far less than that of Pacific salmon, *Oncorhynchus* spp. The distribution of steelhead trout at sea appears to be influenced by surface water temperatures, apparently conforming closely to the 5°C isotherm on the north and the 15°C isotherm on the south. Definite seasonal shifts of abundance were associated with changes in water temperature. Northward and westward movement began in late winter and early spring and became most extensive in summer; it shifted to a southward and eastward movement in late summer, fall, and early winter.

Ages of steelhead trout caught at sea ranged from 2 to 8 yr. The majority of fish were 3, 4, or 5 yr old and belonged to either the 2.1, 3.1, or 3.2 age groups.

The length of time spent in salt water had a marked effect on size of fish. In their first summer in the ocean, they grew in average size from about 15 to 36 cm in length and to 0.8 kg in weight. At the end of the first year at sea (age .0 to .1), their average size was 57 cm and 2 kg; in the second year (age .1 to .2), it was 70 cm and 3 kg.

This paper summarizes the considerable information available from field data obtained by research vessels of Canada, Japan, and the United States on the distribution, relative abundance, age, and size of steelhead trout, *Salmo gairdneri*, in the North Pacific Ocean. The steelhead, or sea-run rainbow trout, is a highly prized sport fish on the Pacific Coast of North America. Since World War II the sport fishery for steelhead trout has increased manyfold. Because of its value as a sport fish, and to a lesser extent as a commercial fish, the fishery agencies of the Pacific Coast states and British Columbia have research and development programs for managing the stocks (Pautzke and Meigs, 1940; Larson and Ward, 1955). Management of the fisheries, however, is based almost entirely on the knowledge of the freshwater life history of the fish, which has been described by a number of authors (Pautzke and Meigs, 1940; Shapovalov and Taft, 1954; Larson and Ward, 1955; Maher and Larkin, 1955; Bali, 1958; Chapman, 1958; Hartman, 1965; Withler, 1966).

Spawning stocks of steelhead trout are widely distributed along the Pacific Coast of North America. Carl, Clemens, and Lindsey (1959) described their distribution as ranging from southern California to Bristol Bay, Alaska. The true limit of their range may extend no farther than central or northern California to the Alaska Peninsula. They are virtually extinct in streams south of San Louis Obispo County, Calif., and research vessels fishing in Bristol Bay over a period of several years have not confirmed their presence in that area. Also, scales from many adult *S. gairdneri* taken from Bristol Bay streams and examined by personnel of the Fisheries Research Institute, University of Washington, have without

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Manuscript accepted January 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

exception failed to show a saltwater growth pattern characteristic of steelhead trout (R. L. Burgner, Fisheries Research Institute, University of Washington, Seattle, pers. comm.).

The distribution of steelhead trout is not known to include coastal streams of Asia. The literature on Asian fishes does not list *S. gairdneri* as a native species. Some fish identified as steelhead trout, however, have been taken close to Asia. Steelhead trout were reported in the catches of Japanese research vessels in the Okhotsk Sea near the coast of southwest Kamchatka in 1962, 1964, and 1967 (Appendix Figures 11, 12). The locality of the catches may, therefore, represent an extension of the range of steelhead trout of North American origin, or the fish might possibly have been misidentified. The latter appears most likely as the taxonomy of the genus *Salmo* in Asia is unresolved. For example, Behnke (1966) considered two species of trout in the Far East, *S. mykiss* and *S. penshinensis*, to be a single species, *S. mykiss*, with both anadromous and nonanadromous populations. Behnke further stated that the single species is most clearly related to the rainbow trout, *S. gairdneri*. In his opinion, "The only apparent distinction between *S. mykiss* and *S. gairdneri* is the number of vertebrae." Berg (1948) described *S. mykiss* and *S. penshinensis* as separate species, but he noted that *S. mykiss* is related to *S. penshinensis* as *S. trutta* is related to *S. salar*. Taxonomic study of the Far Eastern species is complicated by the rarity of specimens. Shmidt (1950) emphasized the lack of specimens of *S. penshinensis* and said, " . . . all attempts to receive it from Kamchatka have hitherto been of no avail." Behnke's (1966) review also pointed out the lack of samples of both *S. mykiss* and *S. penshinensis*. Thus, although steelhead trout are not recorded in the Far East, species taxonomically similar to the steelhead trout have been described.

Steelhead trout hatch in freshwater streams, migrate to sea to grow and mature, and return to their natal streams to spawn as adults after usually spending one or more summers in the ocean. The young steelhead trout may migrate to sea soon after emerging from the gravel of their home stream or delay migration for several years. The period of residence in salt water is similarly indefinite. Some return to fresh water after a short stay and others remain in salt water for several years. Scale studies of adult steelhead trout indicate few fish survive that migrate to sea in the year of emergence. Residence in salt water is an essential part of their life history. Anadromy among *S. gairdneri* is optional, however (Rounsefell, 1958). The progeny of steelhead trout are not certain to follow the anadromous habits of their parents; instead some may spend their entire lives in fresh water.

The anadromy of steelhead trout is similar in some respects to that of Pacific salmon, *Oncorhynchus* spp. Both reside temporarily in fresh water after hatching, migrate to sea, and return to their home streams on reaching maturity. Steelhead trout do not always die after spawning, as do Pacific salmon, but may survive to repeat the migration, maturation, and spawning process in the manner of Atlantic salmon, *S. salar* (Bureau of Sport Fisheries and Wildlife, 1962).

Because of incomplete catch and escapement statistics, agencies that manage steelhead trout fisheries rely primarily on annual indices of abundance derived from commerical and sport landings, hatchery returns, counts at fish-passage facilities, and spawning ground surveys (Larson and Ward, 1955 Washington Game Department, 1968). Individually or collectively, the indices generally do not accurately estimate the total population size. Therefore, no attempt was made in this study to relate annual fluctuations of the apparent relative abundance of steelhead trout in offshore waters to inshore "runs."

The commercial landings of steelhead trout have declined substantially in the United States in recent years. The annual landing in the Pacific Coast states averaged 247,000 kg (543,000 lb.) in 1964-67 compared to 485,000 kg (1,068,000 lb.) during 1960-63 (Power, 1962, 1963; Power and Lyles, 1964; Lyles, 1965, 1966, 1967, 1968, 1969). By state, about 71% were landed in Oregon, 25% in Washington, and 4% in Alaska. The decline may be attributed in part to changes in fishing regulations that limit the commercial catch and increase the availability of the fish to sport fishermen. The steel-

head trout fishery in California is exclusively a sport fishery. In Oregon and Washington it is open to commercial fishermen. Although in Washington, the commercial fishery is limited to Indians fishing in treaty waters. In British Columbia, where steelhead trout are fished commercially, landings have ranged from 59,000 kg (130,000 lb.) to 141,000 kg (310,000 lb.) during 1961-67; no pronounced trend towards decreasing or increasing landings is evidenced (Department of Fisheries of Canada, 1967).

Sport fishery catches of steelhead trout have increased substantially in recent years. In Washington, for example, angler catches have increased from an average of approximately 137,000 fish during the 1951-52 to 1960-61 fishing seasons to approximately 268,000 fish during the 1961-62 to 1965-66 seasons (Washington Game Department, 1968).

Little has been published about the distribution and biology of steelhead trout in the oceanic environment. Since 1953, Canada, Japan, and the United States, as member nations of the International North Pacific Fisheries Commission (INPFC), have engaged in extensive research in the North Pacific Ocean, Gulf of Alaska, Bering Sea, Okhotsk Sea, and Sea of Japan on species of mutual interest. Their vessel operations have extended over all seasons and to most areas of the North Pacific Ocean and Bering Sea occupied by salmon and steelhead trout. They have included catches of steelhead trout in their reports to the Commission (the Canadians and Japanese did not do this in all years), although steelhead trout was not considered a species of mutual interest. In 1955, the Fisheries Research Institute (FRI) began tagging experiments on salmon and steelhead trout in the North Pacific Ocean, Gulf of Alaska, and Bering Sea under contract to the National Marine Fisheries Service (NMFS), formerly the Bureau of Commercial Fisheries. Research reports of FRI that describe these experiments have been included in the reports of investigations by the United States in the Annual Reports of INPFC. Neave and Hanavan (1960) used data from catches by Canadian and United States research vessels in 1956 and 1957 to describe the summer distribution of steelhead trout in the Gulf of Alaska and along the eastern Aleutian Islands. Larkins (1964) reported steelhead trout as common in gill net catches of NMFS research vessels operating in the Gulf of Alaska, North Pacific, and Aleutian Island areas. The occurrence of steelhead trout in the Gulf of Alaska in the winter was noted by Manzer (1968). The purpose of my study was to make additional information available on the life history of steelhead trout in the ocean. Some of this information may be of value in the future in managing the fisheries. For example, steelhead trout are vulnerable in offshore waters to gill net and longline fisheries such as are now carried out by Japan in the western North Pacific Ocean; a gill net or longline fishery in the eastern North Pacific would probably be a serious threat to some stocks.

FISHING GEAR AND METHODS

The fishing gear and methods used aboard research vessels of Canada, Japan, and the United States have been described in various publications. Canadian high-seas fishing was reported in detail by Neave, et al. (1962) and that of Japan was described by the Fisheries Agency of Japan (1962). The methods used by the United States in 1953 in pioneering efforts of the RV *John N. Cobb* were reviewed by Schaefers and Fukuhara (1954). Later reviews were made by Powell and Peterson (1957), Hanavan and Tanonaka (1959), Hartt (1962), and French (1964). Gill nets, longlines, and purse seines were the types of gear used.

Gill nets of several mesh sizes, synthetic materials, lengths, and depths were fished by the research vessels in daylight and darkness for various periods. The net string most commonly used consisted of mesh sizes ranging from 50.8 to 139.7 mm and was constructed of multifilament nylon. It generally varied from about 2,928 to 3,221 m (1,600-1,700 fm) in length and 7.3 to 9.1 m (4-5 fm) in depth. The net string was usually set at dark, allowed to drift free through the night, and hauled after dawn the following morning.

The basic unit of the longline is a skate (basket) consisting of 49 hooks, one each on 1-m drop lines, spaced 2.3 m apart; the total length of the skate is 138 m (75.5 fm). The number of

skates jointed together as a longline varies but probably average 30 to 40. Anchovy, herring, and squid are preferred bait. The gear is usually set just before dawn and hauled after about 45 min of fishing.

The purse seine was used to capture fish for tagging and migration studies by FRI and by the Fisheries Research Board of Canada (FRBC). The net and method of fishing were described by Hartt (1962). Basically, the net measures 732 m (400 fm) long and 36 m (20 fm) deep and has a bunt section of 50.8-mm mesh nylon near one end. A power skiff holds one end of the net while the vessel sets the net in a wide arc. After about 30 min the net is closed and hauled on board the vessel. The bunt section containing the fish remains in the water until the fish are brailed from the net. The operation may be repeated up to 4 times a day if the catches are small and the seas relatively calm.

The catch data obtained by the various fishing gears were reviewed for information on the distribution and abundance of steelhead trout on the high seas. Biological data—age, length, and weight—were taken from specimens collected by NMFS. Some of the observations were made at sea on fresh specimens and others on frozen specimens returned to the laboratory for subsequent analysis. Information on steelhead trout migrations was obtained from tagging and recovery data provided by FRBC, FRI, and state agencies.

The catch data were not obtained in a manner that precludes objectionable sources of bias. The majority of sets, for instance, were made within 10 m of the surface, and the effort was primarily in the spring and summer. Set and haul times varied daily and seasonally. Loss of gilled fish by dropout and predation varied with sea state, type of enmeshment, time of day, and distance from shore. In nearshore gill net sets, predation by sea lions occasionally reduced the catch per set to zero.[2]

Interpretation of the gill net catch data is particularly difficult because of the variations in the gear. The U.S. research vessels have routinely fished with mesh sizes of 64, 83, 115, and 133 mm, but occasionally fished with 51- and 98-mm mesh sizes. The total shackles in a net string have varied from 4 to 40. Monofilament and multifilament nylon has been used in net construction. The Japanese gill nets have similarly varied in mesh size, in length and number of shackles, and in type and color of net materials. For this reason Mason (1965), after reviewing the Japanese mothership and research vessel catch data for distribution and abundance of chinook salmon, *O. tshawytscha*, concluded that trends and conclusions can be indicated only very generally.

Much of the above criticism of gill net data also applies to longline catch data. Furthermore, the efficiency of longlines depends on the surface feeding activity of the fish, kind of bait used, size of hooks, and number of baited hooks available to passing fish.

Most of the purse seine fishing was done within a day's cruising range offshore. This fact alone limits the value of the data for describing either the distribution or abundance of steelhead trout on the high seas. But, since much of the effort centered about the Aleutian Islands, the data provide some valuable information on the relative abundance of steelhead trout in that area.

The selection of a standard unit of effort involved consideration of the many problems which have been discussed. Ideally, a population should be sampled with one kind of gear so that all units of effort would be of comparable value (Ricker, 1958). Because of the relatively small steelhead trout catches and the variations in gear, the catch per set was chosen as the comparative unit of effort.

OFFSHORE FISHING EFFORT AND CATCHES OF STEELHEAD TROUT

The catches of steelhead trout by research vessels of the United States, Japan, and Canada are summarized in Table 1. A summary of the salmon catches and the ratio of salmon to steelhead trout is also given. Assuming equal catchability, the apparent abundance of steelhead trout in relation to salmon is provided by the catch data. As indicated, the greatest ratio of

[2] D. R. Craddock. Comparison of gill net and purse seine catches of salmon in the North Pacific Ocean. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash. [Unpubl. Manuscr.]

TABLE 1.—Numbers of salmon and steelhead trout and ratios of salmon to steelhead trout in gill net, longline, and purse seine catches by research vessels of Canada, Japan, and the United States, 1953 and 1955-67.

Gear and country	Catches							Ratio of salmon/steelhead trout in catches					
	Chinook salmon	Chum salmon	Coho salmon	Pink salmon	Sockeye salmon	Total salmon	Steelhead trout	Chinook salmon	Chum salmon	Coho salmon	Pink salmon	Sockeye salmon	All salmon
Gill nets:													
Japan[1]	6,173	671,981	79,797	1,454,977	138,217	2,351,145	171	36:1	3,930:1	467:1	8,509:1	808:1	13,743:1
United States[2]	554	50,876	5,134	16,038	68,523	141,125	1,341	0.4:1	38:1	3.8:1	12:1	51:1	105:1
Total	6,727	722,857	84,931	1,471,015	206,740	2,492,270	1,512	—	—	—	—	—	—
Longlines:													
Canada[3]	106	12,610	1,965	26,118	36,963	77,762	1,426	0.07:1	8.8:1	1.4:1	18.3:1	26:1	54:1
Japan[4]	800	97,756	4,464	632,493	8,969	744,482	15	53:1	6,517:1	298:1	42,166:1	598:1	49,632:1
United States													
NMFS[5]	0	123	1	31	388	543	18	—	6.8:1	0.1:1	1.7:1	21.6:1	30:1
FRI[6]	27	2,940	478	7,429	8,614	19,488	286	0.09:1	10:1	1.7:1	26:1	30:1	68:1
Total	1,033	133,429	6,908	666,071	54,934	842,275	1,745	—	—	—	—	—	—
Purse seines:													
United States[7]	2,085	88,250	11,398	19,805	73,758	195,296	193	10.8:1	457:1	59:1	103:1	382:1	1,012:1

1 Fisheries Agency of Japan, 1956-57, 1962-67.
2 National Marine Fisheries Service (NMFS), 1953, 1955-67.
3 Fisheries Research Board of Canada, 1961-67.
4 Fisheries Agency of Japan, 1962-67.
5 National Marine Fisheries Service, 1964-65.
6 Fisheries Research Institute (FRI), 1963-66.
7 Fisheries Research Institute, 1956-67.

steelhead trout to salmon was 1 steelhead trout per 30 salmon in longline catches by NMFS vessels fishing primarily in the eastern North Pacific Ocean. The lowest ratio was 1 steelhead trout per 49,632 salmon in longline catches by Japanese vessels fishing primarily in the western North Pacific Ocean. The catch by all vessels in all years averaged 1 steelhead trout per 1,023 salmon. Fishing effort and catches in coastal waters of British Columbia, Washington, and Oregon were omitted, since the data add little to the subject of oceanic distribution of steelhead trout. Sets of experimental gear were also omitted unless the effort was repeated 2 or more years and sufficient numbers of fish were caught to justify consideration.

United States Research Vessels

National Marine Fisheries Service

In 1953 and annually since 1955, NMFS assigned one to five vessels to fisheries research in the North Pacific Ocean and Aleutian Islands area; in some years, NMFS vessels were also in the Gulf of Alaska and the Bering Sea. No research was conducted in 1954. The fishing area was from about lat. 41°N northward to lat. 60°N and from the coast of the United States and Canada westward to about long. 170°E. The fishing period was limited to spring and summer in 1953, 1955-62, and 1966. In 1963-65 and 1967, fishing extended from early winter (January or February) to early or late summer.

In the 14 yr of operation the vessels fished 33,319 shackles of gill net in 1,282 sets and caught 1,341 steelhead trout for an average catch of 1.05 steelhead trout per set (Table 2). The catch per set ranged from a high of 2.3 in 1963 to a low of none in 1964. The latter figure possibly resulted from a limited effort of only 13 sets, all west of long. 170°W. The relative abundance of steelhead trout in relation to salmon (as measured by the ratio of steelhead trout to salmon in the gill net catches) averaged 1:105 over the 14 yr (Table 1).

NMFS first experimented with longlines in 1953. The 1953 catch data were not included in this report because of limited fishing and

TABLE 2.—Catch of steelhead trout and catch per gill net and longline set by research vessels of the National Marine Fisheries Service, 1953, 1955-67.

			Gill net catches			Longline catches		
Year	Date	Number of vessels	No. of sets	No. of steelhead trout	Catch/set	No. of sets	No. of steelhead trout	Catch/set
1953	6/9 - 7/28	1	25	2	0.08	—	—	—
1955	6/25-10/23	3	102	67	0.66	—	—	—
1956	5/24- 9/24	5	195	110	0.56	—	—	—
1957	5/8 - 9/12	3	75	116	1.53	—	—	—
1958	5/28- 8/27	2	78	79	1.01	—	—	—
1959	4/24- 8/12	2	76	63	0.83	—	—	—
1960	5/8 - 8/26	2	82	57	0.70	—	—	—
1961	5/5 - 9/29	4	127	127	1.00	—	—	—
1962	2/10- 9/21	2	100	185	1.85	—	—	—
1963	1/28- 9/13	2	118	271	2.30	—	—	—
1964	2/12-10/11	1	13	0	—	19	18	0.95
1965	2/5 -11/5	2	76	19	0.25	5	0	—
1966	6/20- 9/3	2	155	222	1.43	—	—	—
1967	1/30- 8/18	1	60	23	0.38	—	—	—
Total or average			1,282	1,341	1.05	24	18	0.75

negligible catch. Longline fishing was repeated on a larger scale in 1964 and again in 1965. The results are summarized in Table 2. In the 2 yr, 24 sets were made and 18 steelhead trout caught. They were taken in two sets in 1964 in the Gulf of Alaska east of long. 143°W, where steelhead trout frequently occur in considerable abundance. The catch per set averaged 0.75 fish in the 2 yr. The ratio of steelhead to salmon in longline catches averaged 1:30 (Table 1), or 3½ times more steelhead trout (in relation to salmon) than indicated by gill net catches in all years.

Fisheries Research Institute

FRI has assigned two to four vessels to high-seas fisheries research annually during 1956-67. Their fishing areas have been primarily in the eastern North Pacific Ocean, Gulf of Alaska, and the Aleutian Islands area. In some years, fishing was extended to the western North Pacific, Bering Sea, and Bristol Bay. The operations usually were limited to the spring and summer seasons, beginning in April or May and ending in August or September. In 1959, fishing began in late March and ended in mid-October; in 1967, it ended in late October.

The main objective of the research was to study migrations of salmon and steelhead trout by tagging captured live fish. Purse seines were used each year for that purpose; the longlines also were used in 1963-66. The catch and effort data for both gears are given in Tables 1 and 3.

Steelhead trout catches by purse seines were substantially smaller than by either longlines or gill nets. The largest average catch of steelhead trout in any year was only 0.21 fish per set (1958). None were caught in either 1959 or 1960 in 292 sets. The average purse seine catch in 12 yr of operation was 0.07 steelhead trout per set. By comparison, gill net catches by NMFS average 0.82 per set in 1959, 0.70 in 1960, and 1.05 in 14 yr of fishing. The ratio of steelhead trout to salmon in the purse seine catches averaged 1:1,012 in 12 yr of fishing, or about one-tenth of the steelhead trout (in relation to salmon) indicated by gill net catch of NMFS (Table 1).

Longline catches of steelhead trout in 4 yr of fishing averaged 0.81 fish per set and exceeded catches per set by purse seines in all years. The average catch per set was comparable to that of gill nets but exceeded that of gill nets in some years. In 1964, when NMFS failed to catch a steelhead trout in 13 sets in the Aleutian Islands area, FRI caught 49 in 87 longline sets in the Gulf of Alaska for a catch per set of 0.56. The ratio of steelhead trout to salmon was 1:68 in longline catches, about 1½ times more steelhead trout (in relation to salmon) than the ratio (1:105) indicated by gill net catches of NMFS.

In comparing purse seine and gill net catches,

TABLE 3.—Catch of steelhead trout and catch per purse seine and longline set by research vessels of the Fisheries Research Institute, University of Washington, 1956-67.

			Purse seine catches			Longline catches		
Year	Date	Number of vessels	No. of sets	No. of steelhead trout	Catch/set	No. of sets	No. of steelhead trout	Catch/set
1956	5/2 - 9/14	2	159	5	0.03	—	—	—
1957	5/23- 9/14	3	295	11	0.04	—	—	—
1958	5/12- 9/13	3	224	47	0.21	—	—	—
1959	3/28-10/12	2	124	0	—	—	—	—
1960	4/19- 8/23	2	168	0	—	—	—	—
1961	5/3 - 9/29	4	347	15	0.04	—	—	—
1962	5/2 - 8/13	4	386	25	0.06	—	—	—
1963	5/3 - 8/19	4	291	26	0.09	41	16	0.39
1964	5/2 - 9/24	2	129	7	0.05	87	49	0.56
1965	4/12- 9/25	3	150	15	0.10	124	155	1.25
1966	4/29- 9/26	3	279	27	0.09	100	66	0.66
1967	6/13-10/25	2	188	15	0.08	—	—	—
Total or average			2,740	193	0.07	352	286	0.81

French (1964) found the efficiency of the two gears differed with size of fish. The purse seines caught relatively more small fish and the gill nets relatively more large fish. The difference in steelhead trout catch per set for purse seines compared to gill nets or longlines may be attributed to the ability of the large fish to escape the purse seines or the lesser chance that the relatively scarce steelhead trout had in encountering the purse seine with its limited coverage in time and space. Because of the bias in the catch data previously discussed and the vast difference in dates and locations of fishing, the catch per set may be of little comparative value between gears.

Japanese Research Vessels

The Fisheries Agency of Japan has engaged in fisheries research on the high seas for INPFC since 1955. The research centered chiefly in the western North Pacific Ocean from the Asian coast eastward to long. 180° and from lat. 40°N northward to the Aleutian Islands. In some years the investigations extended eastward along the Aleutian Islands to about long. 160°W and throughout most of the Bering and Okhotsk Seas and the Sea of Japan.

The research during 1955-61 was of about the same intensity as that of NMFS, with one to three vessels operating over a wide ocean area. Fishing effort was substantially increased in subsequent years, with 16 to 19 vessels given research assignments primarily in the Japanese land-based fishery area west of long. 170°E and south of lat. 48°N. Before 1967 the vessels were operated only in the spring and summer: April or May to August. In 1967 the operations began in early February and ended in late August.

Catches of steelhead trout by Japanese research vessels were few in all years and in all areas surveyed. The data show a 9-yr total catch of 186 steelhead trout—171 by gill nets and 15 by longlines (Table 4). The catch per set for the 9 yr averaged 0.048 fish by gill nets and 0.007 by longlines. The apparent abundance of steelhead trout in relation to salmon was very low in the areas fished, as indicated by the catch ratios in Table 1. In 9 yr of fishing directed toward salmon, the catch of salmon exceeded steelhead trout in gill nets by an average ratio of 13,743:1 and in longlines by a ratio of 49,632:1.

Canadian Research Vessels

Gill net catches of steelhead trout by FRBC were not included in the catch data submitted to INPFC before 1960. A single steelhead trout was reported in 1960, and some were listed in 1963 catch data from inshore sets. FRBC began longline fishing in 1961 to catch live fish for tagging experiments; steelhead trout as well as salmon were included in their catch reports.

TABLE 4.—Catch of steelhead trout and catch per gill net and longline set by research vessels of the Fisheries Agency of Japan, 1955-57 and 1962-67 (no information available for 1958-61).

			Gill net catches			Longline catches		
Year	Date	Number of vessels	No. of sets	No. of steelhead trout	Catch/set	No. of sets	No. of steelhead trout	Catch/set
1955[1]	5/20-8/21	1	63	4	0.063	—	—	—
1956[1]	5/12-8/11	3	135	7	0.052	—	—	—
1957[1]	5/18-8/8	2	78	3	0.038	—	—	—
1962[2]	4/6 -9/2	17	457	0	—	212	1	0.005
1963[2]	4/5 -8/10	16	450	28	0.049	286	0	—
1964[2]	4/13-8/17	19	479	19	0.040	471	2	0.004
1965[2]	4/13-8/7	19	614	3	0.005	509	0	—
1966[2]	4/12-8/2	18	594	45	0.076	394	7	0.018
1967[2]	2/6 -8/27	17	704	62	0.088	401	5	0.012
Total or average			3,574	171	0.048	2,273	15	0.007

[1]Effort and gear for 1955-57 from Fisheries Agency of Japan (1956-58). Catch for 1955 and 1957 from personal communication, Fisheries Agency of Japan; for 1956 from Fisheries Agency of Japan (1957).
[2] Data from Fisheries Agency of Japan (1962-1967).

The longline fishing by the Canadians in 1961 and subsequent years covered most of the Gulf of Alaska and the eastern North Pacific Ocean east of long. 170°W and north of lat. 42°N. Fishing effort was well dispersed over this area in all years except 1961, when it was concentrated near Kodiak Island. The period of operation extended from early spring to midsummer in 4 of 7 yr and from early winter to midspring in 3 of 7 yr. From one to four vessels were assigned to the investigations.

The Canadian longline catches in the Gulf of Alaska and eastern North Pacific averaged one steelhead trout per set over the 7-yr period, 1961-67 (Table 5). The annual catch varied from a high of 1.75 per set in 1965 to a low of 0.29 per set in 1967. Individual sets yielded up to 41 steelhead trout. Catches of from 5 to 20 steelhead trout per set were not uncommon. The ratio of steelhead trout to salmon in longline catches averaged 1:54 for all years (Table 1).

TABLE 5.—Catch of steelhead trout and catch per longline set by research vessels of the Fisheries Research Board of Canada, 1961-67.

			Longline catches		
Year	Date	Number of vessels	No. of sets	No. of steelhead trout	Catch/set
1961	5/29-8/5	1	41	28	0.68
1962	4/10-7/26	4	324	256	0.79
1963	1/5 -6/3	4	164	252	1.54
1964	1/7 -5/28	2	94	122	1.30
1965	1/14-6/7	4	169	295	1.75
1966	3/31-8/23	4	457	422	0.92
1967	5/5 -7/26	2	176	51	0.29
Total or average			1,425	1,426	1.00

AGE, LENGTH, AND WEIGHT OF STEELHEAD TROUT CAUGHT AT SEA

The age, length, and weight of steelhead trout caught at sea by research vessels of NMFS in 1955-67 are shown in Table 6.

Age

Age determinations were made from projected images of plastic impressions of scales (Mosher, 1950). Of those collected and examined, 78% or 323 scales had well-defined winter annuli for each year of fresh- and saltwater life. The other 22% were unreadable for age because of regeneration of scale features at some stage in the life history of the fish.

The formulae of Koo (1962) were followed for designation of age. Briefly described, the number of winters in fresh water is expressed by an appropriate numeral followed by a dot; the number following the dot denotes winters in salt water. Total winters of life are derived by adding the two numerals; for steelhead trout, which spawn in the spring, this sum represents total age. Thus, a 1.2 age steelhead trout that has spent one winter in fresh water

TABLE 6.—Age, length, and weight of steelhead trout caught by research vessels of the National Marine Fisheries Service, 1955-67. The data are grouped by the number of winters spent in salt water.

Age[1] group	Age		Length (cm)		Weight (kg)			
					Male		Female	
	Number	Percent	Number	Average	Number	Average	Number	Average
2.0	6	1.9	3	34	—	—	1	0.4
3.0	11	3.4	8	37	—	—	3	1.3
4.0	4	1.2	4	37	—	—	—	—
Total or average	21	6.5	15	36	—	—	4	0.8
1.1	2	0.6	2	55	2	1.0	1	2.5
2.1	70	21.7	34	57	20	2.3	12	2.5
3.1	97	30.0	80	58	10	2.0	9	2.1
4.1	35	10.8	32	59	—	—	3	2.5
5.1	6	1.9	7	57	—	—	—	—
Total or average	210	65.0	155	57	32	1.8	25	2.4
1.2	1	0.3	1	67	—	—	2	3.9
2.2	19	5.9	14	71	5	3.5	6	2.8
3.2	40	12.4	41	71	1	2.3	4	3.8
4.2	14	4.3	10	69	—	—	3	2.9
5.2	3	0.9	3	72	—	—	—	—
Total or average	77	23.8	69	70	6	2.9	15	3.4
2.3	8	2.5	3	82	2	2.1	3	3.7
3.3	2	0.6	2	73	1	5.1	—	—
4.3	2	0.6	2	79	—	—	—	—
Total or average	12	3.7	7	78	3	3.6	3	3.7
2.4	—	—	1	91	—	—	—	—
3.4	1	0.3	1	68	—	—	1	5.6
Total or average	1	0.3	2	79	—	—	1	5.6
2.5	1	0.3	1	89	—	—	1	5.1
2.6	1	0.3	1	90	—	—	1	6.7
Grand total	323	100	250		41		50	

[1] Freshwater age precedes dot; saltwater age follows dot.

and two winters in the ocean is now a 3 yr-old fish.

Ages of steelhead trout caught at sea ranged from 2 to 8 yr with 20 different life history categories represented. Those categories included various combinations of freshwater ages of 1 to 5 yr and saltwater ages of 0 to 6 yr. The majority, however, belonged to three categories: 2.1 (22%), 3.1 (30%), and 3.2 (12%) and were 3, 4, or 5 yr old. Most of the steelhead trout sampled spent 2 or 3 yr in fresh water before migrating to the sea. None were age 0. and less than 1% were age 1. A large percentage had migrated to sea at age 2. (33%) or at age 3. (47%). A substantial number of the fish had remained in fresh water to age 4. (17%) and some to age 5. (3%) before first entering salt water. The ages of those fish at initial entry into salt water differed markedly from those returning to Waddell Creek, Calif., as observed by Shapovalov and Taft (1954). Of 383 adult first spawners examined from Waddell Creek, 3% had migrated to sea; at age 1., 79% at age 2., 14% at age 3., and 4% at age 4. The age composition of the high-seas catches did not differ appreciably from that of steelhead trout taken from the Chilliwack River, British Columbia. A majority of steelhead trout taken from that stream had migrated to sea at age 2. or 3. (Maher and Larkin, 1955).

The number of years steelhead trout caught by NMFS spent at sea ranged from .0 to .6. Because of a minimum gill net mesh size of 51 mm, steelhead trout in their first year at sea were not caught by the sampling gear in proportion to their theoretical abundance; it is unlikely, however, that age .0 fish were available in much of the area sampled, since it is

assumed that, like salmon, they remain in coastal waters in their first summer at sea. Of 323 steelhead trout caught in several years of fishing on the high seas and whose age was determined, only 21 (6%) were ocean age .0. Presumably, this age group made up a substantial part of the total oceanic steelhead trout population. After having advanced to ocean age .1 and having increased in size from 36 cm at ocean age .0 to an average length of 57 cm (Table 6), they were readily caught by the sampling gear. In the same of 323 steelhead trout caught over several years, 65% were age .1, 24% age .2, and 4% age .3. The older age groups, .4, .5, and .6, contributed less than 1% to the population sampled.

Data on the age composition of returning adults, together with tag and recovery information, indicate that most steelhead trout spent two summers at sea before returning to fresh water.

Length and Weight

The average lengths and weights of steelhead trout of various age groups caught at sea by NMFS research vessels are shown in Table 6. The bulk of the samples from which length and weight data were taken were in ocean ages .1 and .2. Although the number of samples in the other ocean ages was small, particularly for weight data, some observations on length and weight can be made.

On entering salt water, juvenile steelhead trout vary in size among the freshwater age groups represented, by season of migration, and by geographical area. For the freshwater groups 0. to 4., Shapovalov and Taft (1954) found that the average lengths of these seaward migrants from Waddell Creek, Calif., ranged from 6.0 to 27.0 cm. Sumner (1953), in a study at Sand Creek, Oreg., found average fork lengths of 16.0, 14.2, and 15.2 cm, with ranges from 3.0 to 23.4 cm, for migrants in three seasons. In British Columbia, studies by Maher and Larkin (1955) in the Chilliwack River showed the average fork length of migrants in five seasons (1948-53) for ages 1., 2., 3., and 4. were 11.1 cm, 16.5 cm, 20.0 cm, and 22.9 cm, respectively. The average length for all ages combined was 17.6 cm.

The average length of steelhead trout taken at sea in gill nets ranged from 34 to 90 cm among the various age groups (Table 6). Those fish caught after a few months in salt water (age .0) had an average length of 36 cm. The increase in length amounted to a gain of about 100-150% from the average of 14-17 cm observed by various authors (Sumner, 1953; Shapovalov and Taft, 1954; Maher and Larkin, 1955) for seaward migrants of all age groups. The greatest difference in the average length of all freshwater age groups of ocean age .0 caught offshore was only 3 cm. During the first year at sea (age .0 to .1) the average length of those steelhead trout caught had increased by 58% to 57 cm, in the second year (age .1 to .2) by 23% to 70 cm, and in the third year (age .2 to .3) by 11% to 78 cm. The length range of the various age groups increased with ocean age but not progressively from the youngest to the oldest. With the added variability due to age, the maximum differences averaged only 4 cm within age group .1 and 5 cm within age group .2. The samples of older age categories were too small to yield realistic average lengths, although growth apparently continues at a substantial rate in succeeding years. One steelhead trout caught after 4 yr at sea had attained a length of 91 cm and another after 6 yr at sea was 90 cm.

The number of steelhead trout weighed was inadequate for a detailed analysis of this growth parameter for all ocean ages except .1 and .2. Females weighed more than males in all age categories. At age .1 the females averaged 2.4 kg compared with 1.8 kg for males. At age .2 the average weight of females increased to 3.4 kg compared with 2.9 for males. The oldest fish, an age .6 female, weighed 6.7 kg when caught.

OCEANIC DISTRIBUTION AND SEASONAL ABUNDANCE OF STEELHEAD TROUT

The research vessel catch and effort data described above are used here to describe the oceanic distribution and seasonal abundance

of steelhead trout. Summaries of the data are presented in Figures 1-4 to show the relative abundance of steelhead trout throughout their ocean range by season, as measured by the fishing effort (number of sets) and the catch per set within INPFC statistical areas (2° lat. by 5° long.). Appendix Figures 1-15 show in detail the fishing stations, locations where steelhead trout were caught, and the number caught at each location by all vessels.

Oceanic Distribution

The oceanic range of steelhead trout as revealed by the catch and effort data extended generally north of lat. 42°N (the approximate southern limit of effort) from the coast of North America to about long. 152°E in the western North Pacific Ocean and Okhotsk Sea. The northern limits were about lat. 60°N in the Gulf of Alaska, lat. 56°N in the Bering Sea, and lat. 53°N in the Okhotsk Sea. The trout were not uniformly dispersed over this range, however. Broad areas of concentration and seasonal shifts of the population were revealed by the data.

The Japanese reported catches of 10 steelhead trout in 3 of 6 yr of fishing in the Okhotsk Sea off southwest Kamchatka, USSR. The catches each year were made in the summer near the mouths of productive salmon streams. The time and place of capture suggest that the fish originated in those streams and were either seaward migrants or returning adults. Other information suggests they may have originated elsewhere. By virtue of the similarity of *S. gairdneri* to *S. mykiss*, mentioned previously, the Japanese report of steelhead trout in the Okhotsk Sea may be in error. It is not entirely unlikely, however, that steelhead trout of North American origin migrate to the Okhotsk Sea, for west Kamchatkan chum salmon stocks are known to range to long. 152°W in the central North Pacific Ocean.

Steelhead trout catches in the Bering Sea were negligible. Extensive salmon fishing by the Fisheries Agency of Japan, NMFS, and FRI over a period of several years resulted in catches of only two steelhead trout. One was caught in a set by the Fisheries Agency of Japan about 361 km (195 miles) north of Buldir Island, and the other by NMFS in a set about 167 km (90 miles) north of Amchitka Island. None was caught by FRI in many sets in Aleutian Islands passes, along the north side of the islands, or in Bristol Bay.

Steelhead trout apparently do not occur in the Sea of Japan; none was caught by the Fisheries Agency of Japan in 3 yr of operations in that area.

Seasonal Abundance

The catch and effort data showed a definite seasonal shift of steelhead trout. In the winter (Figure 1) they were not caught north of lat. 57°N in the eastern Gulf of Alaska, and the northern limit decreased in latitutde diagonally across the Gulf of Alaska to lat. 45°N in the central North Pacific Ocean and lat. 42°30′N in the western North Pacific Ocean. The latter limit was based on a single fish caught by the Japanese in late winter (April). To the south, catches were made westward from the coast of Oregon along approximately lat. 42°N to the location of the Japanese steelhead trout catch (long. 157°E, lat. 42°30′N). The greatest concentration of steelhead trout appeared to be between lat. 44°N and 52°N from the coasts of British Columbia, Washington, and Oregon to long. 155°W. Within this area the catch averaged 2.4 steelhead trout per set and was more than 10 steelhead trout per set in two subareas. In all other areas combined, the catch averaged slightly less than 0.04 steelhead trout per set.

Because of restricted vessel operations in the winter, the true distribution of steelhead trout may differ from that revealed by the catch data. Steelhead trout tagged in the eastern North Pacific Ocean and Gulf of Alaska were recovered as far south in the eastern North Pacific Ocean as California (lat. 36°30′N) in the winter. Similar information was not available on the movement of steelhead trout in the western North Pacific.

The northward and westward movement of steelhead trout evidently begins in late winter and early spring, for they were well dispersed throughout the Gulf of Alaska and across most

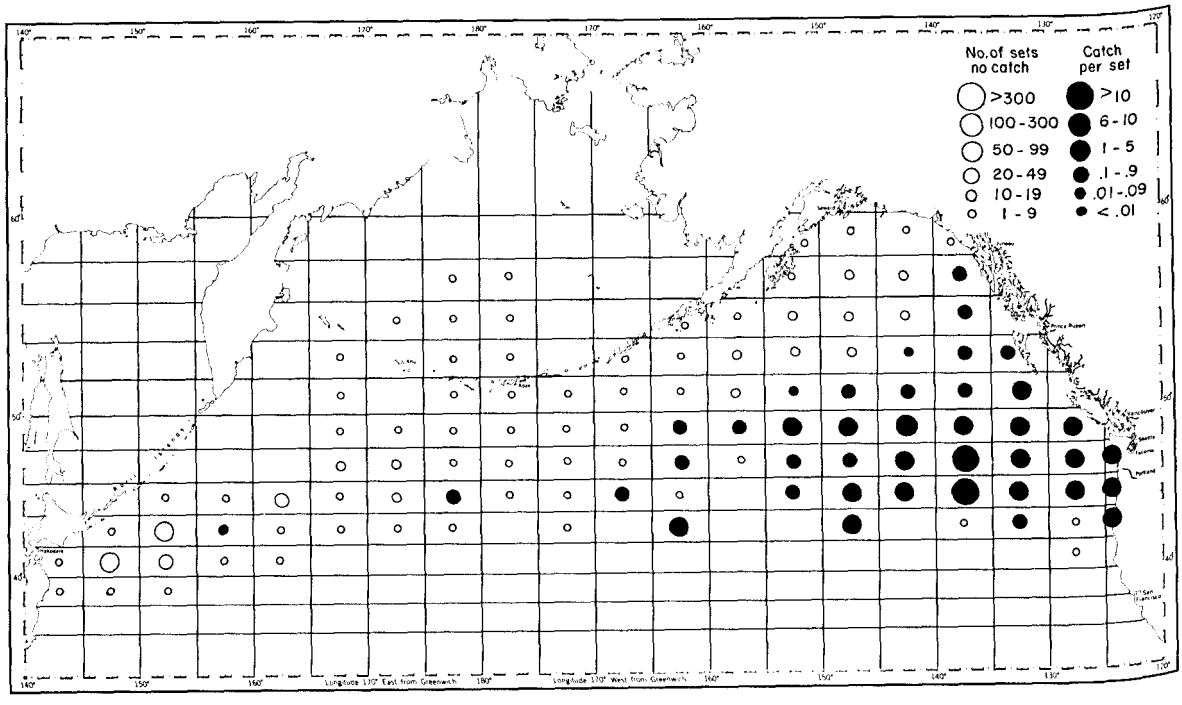

FIGURE 1.—Oceanic distribution and relative abundance of steelhead trout in winter (January-April). Catch and effort data from gill net, longline, and purse seine sets by research vessels of Canada (1961-67), Japan (1955-57), and the United States (1953, 1955-67).

of the North Pacific Ocean in May and June (Figure 2). They occurred in limited numbers along the Aleutian Islands to about long. 180° and the Okhotsk Sea off southwest Kamchatka. The movement resulted in catches in the area of winter concentration being reduced from 2.4 to 1.5 fish per set. The greatest spring concentration of steelhead trout (0.72 per set) appeared to be off the coasts of southeast Alaska, British Columbia, Washington, and Oregon, west to about long. 165°W, north of lat. 44°N. In the central North Pacific Ocean, the Aleutian Islands area (west of long. 165°W) and the Okhotsk Sea catches averaged only 0.02 steelhead trout per set. None were caught in the Bering Sea during spring in 418 sets.

The most extensive movement of steelhead trout northward occurs in the summer (Figure 3). Their oceanic range at this time extends westward across the North Pacific Ocean from the coasts of the United States and British Columbia to the Kuril Islands in Asia north of lat. 44°-46°N and may extend northward to about lat. 52°N in the Okhotsk Sea, lat. 56°N in the Bering Sea, and lat. 59°N in the Gulf of Alaska. The bulk of the fish, however, were found north of lat. 44°N; the catch averaged 0.86 steelhead trout per set. As a result of the summer shift, the steelhead trout catch in the area where they were concentrated in the winter declined 89% from 2.4 fish per set to 0.27 fish per set.

West of long. 175°W to near southeast Kamchatka and south to lat. 44°N, the catch of steelhead trout averaged 0.16 per set in the summer. In the Okhotsk Sea, the Japanese reported three steelhead trout caught in 349 sets for a catch per set of 0.009 fish. Some movement of steelhead trout through the Aleutian Island passes in the summer was indicated by two catches of one steelhead trout each in the Bering Sea.

The fall distribution and abundance of steelhead trout is described from a total of only 48 sets made by Canadian and United States vessels. Those sets were scattered over a vast ocean

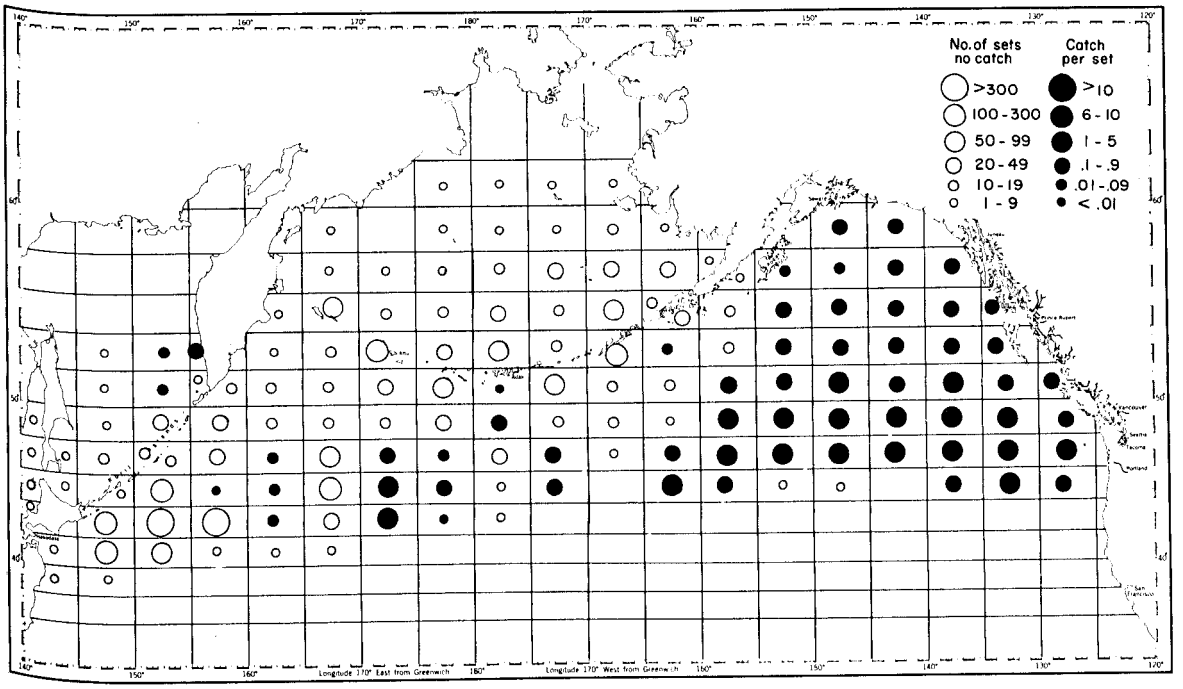

FIGURE 2.—Oceanic distribution and relative abundance of steelhead trout in spring (May-June). Catch and effort data from gill net, longline, and purse seine sets by research vessels of Canada (1961-67), Japan (1955-57, 1962-67), and the United States (1953, 1955-67).

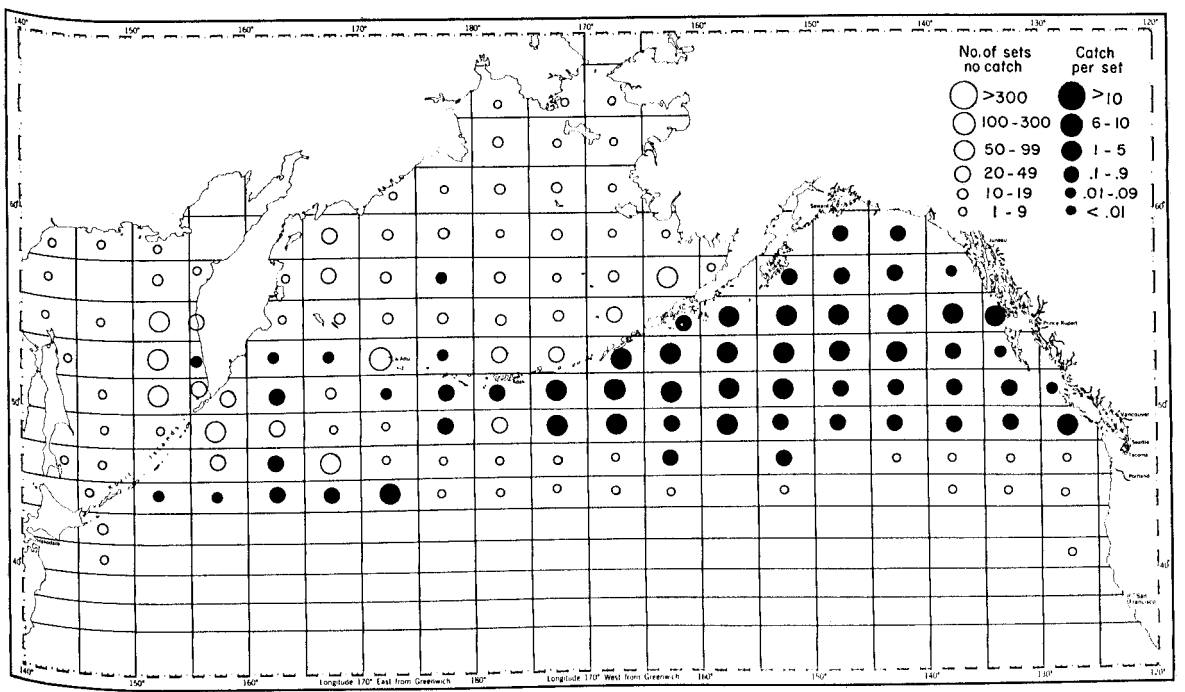

FIGURE 3.—Oceanic distribution and relative abundance of steelhead trout in summer (July-September). Catch and effort data from gill net, longline, and purse seine sets by research vessels of Canada (1961-67), Japan (1955-57, 1962-67), and the United States (1953, 1955-67).

area and, for the most part, restricted to early fall. The areas fished and the catch per set are shown in Figure 4. The Japanese did not engage in any fishing activity on the high seas in the fall. As a result, no information was available on steelhead trout in the far western North Pacific Ocean or Okhotsk Sea in that season.

Although the data are meager, steelhead trout continued to be found as far north and west as the central Aleutian Islands area in early fall. The catch of 0.90 steelhead trout per set in that area was only slightly less than the NMFS 14-yr catch average of 1.03 steelhead trout per gill net set.

Larger catches were made in the northeastern Pacific (east of long. 150°W, south of lat. 54°N) than in the Aleutian Islands area, averaging 2.9 fish per set and exceeding somewhat the relative abundance of steelhead trout in the same area in the winter. The increased catches in the northeastern Pacific area, together with the return of spawning adults to the coastal waters and streams from southeast Alaska to central California, indicate a general shift of the population south and east in the late summer, fall, and early winter.

OCEANIC DISTRIBUTION OF STEELHEAD TROUT IN RELATION TO SURFACE TEMPERATURE

Catch records and temperature data from Canadian, Japanese, and the United States (NMFS and FRI) research vessels showed a relation of ocean distribution of steelhead trout to surface water temperatures. Catches were made in areas with surface water that ranged in temperature from 5° to 14.9° C the majority (61%) were in areas with surface water of 8° to 11.4°C (Table 7.). The data strongly suggest that the limits of steelhead trout distribution conform closely to the 5°C isotherm on the north and the 15°C isotherm on the south. Very few steelhead trout were caught in areas where

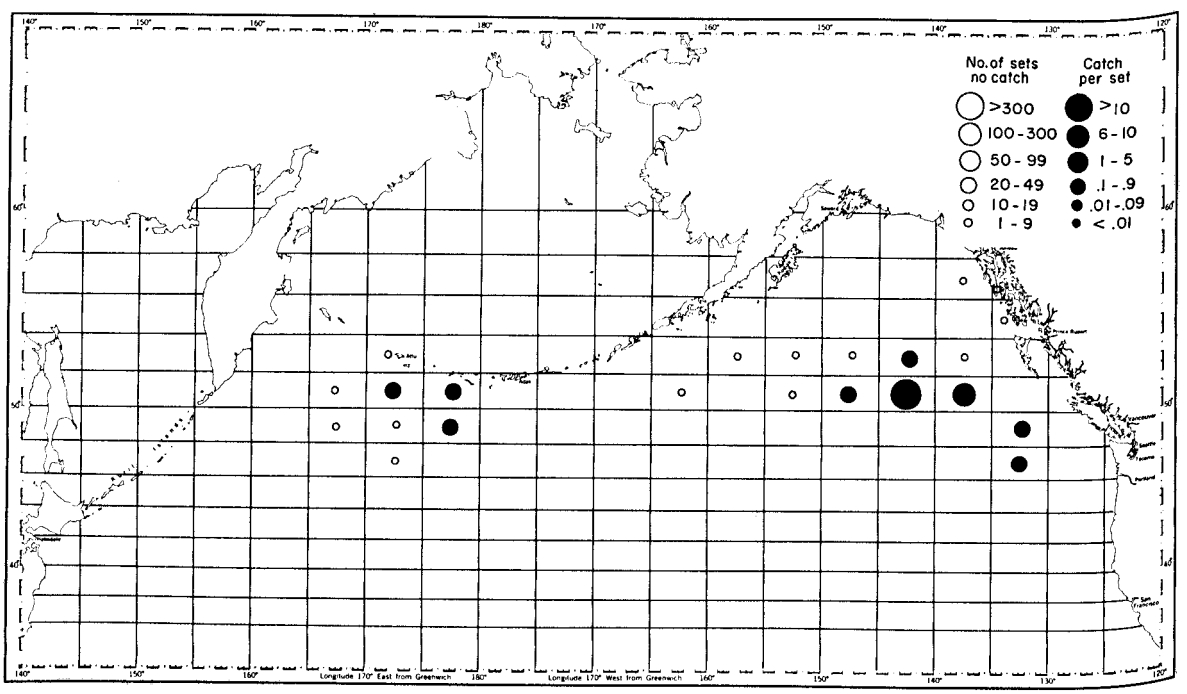

FIGURE 4.—Oceanic distribution and relative abundance of steelhead trout in fall (October-December). Catch and effort data from gill net, longline, and purse seine sets by research vessels of Canada (1961-67), Japan (1955-57, 1962-67), and the United States (1953, 1955-67).

TABLE 7.—Ocean surface temperatures and catches of steelhead trout by research vessel of the United States, Japan, and Canada.

Surface temperature (°C)	Number of steelhead caught				
	United States[1]	Japan	Canada	Total	Percent
5.0- 5.4	4	1	5	10	0.3
5.5- 5.9	9	1	32	42	1.4
6.0- 6.4	26	4	83	113	3.8
6.5- 6.9	19	2	146	167	5.6
7.0- 7.4	23	17	117	157	5.3
7.5- 7.9	24	12	157	193	6.5
8.0- 8.4	54	27	125	206	6.9
8.5- 8.9	85	28	142	255	8.6
9.0- 9.4	116	10	187	313	10.5
9.5- 9.9	187	2	106	295	9.9
10.0-10.4	263	0	78	341	11.5
10.5-10.9	114	8	61	183	6.2
11.0-11.4	182	—	54	236	7.9
11.5-11.9	100	—	18	118	4.0
12.0-12.4	70	—	22	92	3.1
12.5-12.9	103	—	8	111	3.7
13.0-13.4	83	—	2	85	2.9
13.5-13.9	54	—	0	54	1.8
14.0-14.4	2	—	1	3	0.1
14.5-14.9	—	—	1	1	0.1
Total	1,518	112	1,345	2,975	100.0

[1] Combined catches of National Marine Fisheries Service and of Fisheries Research Institute.

surface water was warmer than 13.9°C (0.2% of the total catch) or colder than 6°C (1.7%).

Seasonal shifts of the isotherms undoubtedly result in shifts of the steelhead trout populations. Neave and Hanavan (1960), reviewing catch data for 1956-57 for a number of fish species (including steelhead trout), concluded that distribution patterns in the Gulf of Alaska conformed with the general pattern of near-surface isotherms. On the basis of 2 years' data, they believe that the total area of surface distribution of steelhead trout shrank by some 770,000 km² (300,000 square miles) in the Gulf of Alaska between early and late summer. Analysis of steelhead trout catch records of Canada, Japan, and the United States shows that the two steelhead trout reported from all fishing in the Bering Sea were caught in the summer, the period of highest surface temperature. Analysis of temperature charts of Eber, Saur, and Sette (1968) for part of the years (1953-62) included in this report shows surface temperatures in the Bering Sea generally were higher than 5°C from July to October and were 5°C or less from November to June. One steelhead trout was caught by NMFS in July 1958 (lat. 53°00′N, long. 179°48′E) where the Bering Sea surface temperature was 7.2°C. The other steelhead trout from the Bering Sea was taken by the Japanese in August 1967 (lat. 56°29′N, long. 176°00′E), but the temperature at the location was not reported.

The true horizontal distribution of steelhead trout may not be indicated by surface or near-surface catches because, as Neave and Hanavan (1960) noted, the fish may be present at depths below the fishing range of surface gill nets. Neave and Hanavan observed that when the surface temperatures in the Gulf of Alaska exceeded 15°C, water of that temperature was usually present within 25 m of the surface. Significant numbers of steelhead trout have been caught in gill nets in summer at depths of 15 to 23 m (French et al., 1970), although over 85% of the catch had been gilled in the upper 7 m of the nets. It is not unlikely that some steelhead trout react to excessive cooling of surface water in the fall and winter by seeking warmer strata at depths below the surface. Similarly, they may seek cooler waters at depths in summer to avoid warmer surface waters. The catch and effort data are inadequate to demonstrate the occurrence or absence of steelhead trout below the surface isothermal layer in either case.

Although the limits of distribution of steelhead trout in relation to surface temperature appear to be shown by the catch data, ocean distribution of steelhead trout should not be assumed to be related to temperature alone. As pointed out by Favorite and Hanavan (1963) in a study of salmon distribution, "Until we know more of the reaction of salmon to changes or extremes of temperature and salinity, we must consider the environment as a whole." Similar limitations should be applied to data on steelhead trout distribution.

MIGRATIONS OF TAGGED STEELHEAD TROUT

Tagging experiments furnish some information about the migrations of steelhead trout. Although it is limited, the information is of value in describing routes, rates, and timing of ocean migrations. It also confirms some of the inferences on oceanic movement of steelhead trout drawn from catch data.

The information on tagging was taken from studies conducted by Canada, fishery agencies of the States of Oregon and Washington, and FRI (Appendix Tables 1, 2). Canadian steelhead trout tag and recovery data were taken from an unpublished summary provided by FRBC. Tag recovery data for the States of Oregon and Washington and FRI for 1956-60 were summarized by Hartt (1962, 1966). Subsequent data were taken from unpublished records of FRI.

Figures 5 and 6 show the distribution of recoveries of steelhead trout tagged in 1957-69. Of the steelhead trout marked or tagged in inshore waters by the state fishery agencies, only two are known to have been recovered in offshore waters (Figure 6). In contrast, 63 of those tagged offshore by FRBC and FRI were recovered in inshore waters, and those tagged fish, with one exception, had been released in the eastern North Pacific Ocean east of long. 160°W. A single steelhead trout tagged in offshore waters was later recovered in offshore waters (Hartt, 1962).

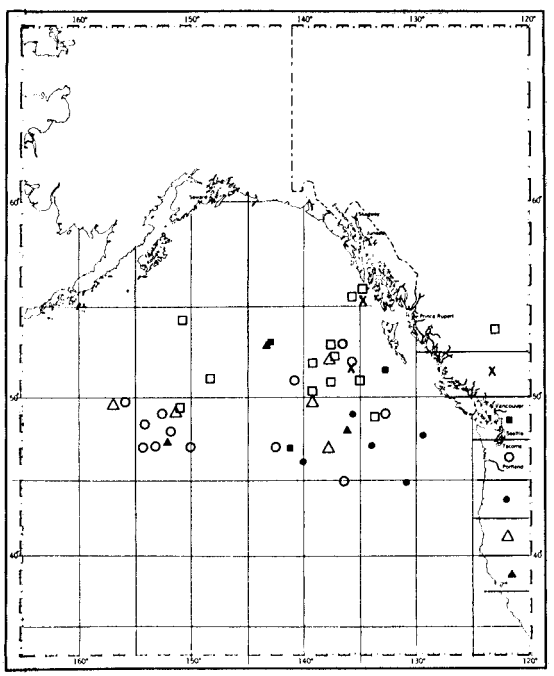

FIGURE 5.—Tagging locations and recovery area (like symbols) of individual steelhead trout tagged by Canadian research vessels, 1961-67.

Tagging experiments show that some steelhead trout of North American origin make extensive migrations. The directional movement of steelhead trout in the spring and summer is exemplified by the successive catches of a single identifiable fish (Hartt, 1966). This fish, marked by a fin clip, was released in the Alsea River, Oreg., in April 1958. On 5 September of the same year, it was caught and tagged just off the Albatross Bank south of Kodiak (lat. 52°42′N, long. 151°49′W). In 5 mo this steelhead trout had traveled some 2,963 km (1,600 miles) to the northwest at a minimum speed of 19.8 km (10.7 miles) per day. On 5 February 1960, 17 mo later, it was caught at Alsea River Hatchery. This return demonstrates the capability of steelhead trout to undertake extensive feeding migrations in the open ocean and still find their home streams when ready to spawn. The recovery of another tagged fish indicates that some steelhead trout migrate westward across the North Pacific Ocean at least as far as the Japanese fishery area in the western North Pacific (Hartt, 1962). The fish was tagged on 16 August 1957, 40 nautical miles south of Amlia Island (lat. 51°26′N, long. 173°47′W) and recaptured at sea 1 yr later in July 1958, about 1,126 km (700 miles) to the southwest (lat. 47°12′N, long. 167°35′E) by a Japanese gill net vessel. The origin of that fish is not known, although another steelhead trout tagged in the same general vicinity on 19 July 1957 was recaptured in the Chehalis River, Wash., on 13 March 1958 (Hartt, 1962). Additional evidence that some steelhead trout of North American origin make extensive westward migrations was obtained in 1969. A steelhead trout tagged and released by the Washington Department of Fisheries in the Stillaguamish River, Wash., in April 1968, had traveled some 4,213 km (2,275 miles) westward when I recaptured it south of Adak Island (lat. 50°00′, long. 176°22′W) in the central Aleutian Islands in August 1969 on a cruise of the NMFS research vessel *George B. Kelez*.

Recoveries in coastal streams of steelhead trout tagged offshore provided clear evidence of extensive intermingling of North American stocks in the eastern North Pacific Ocean and the Gulf of Alaska. Some fish recovered in

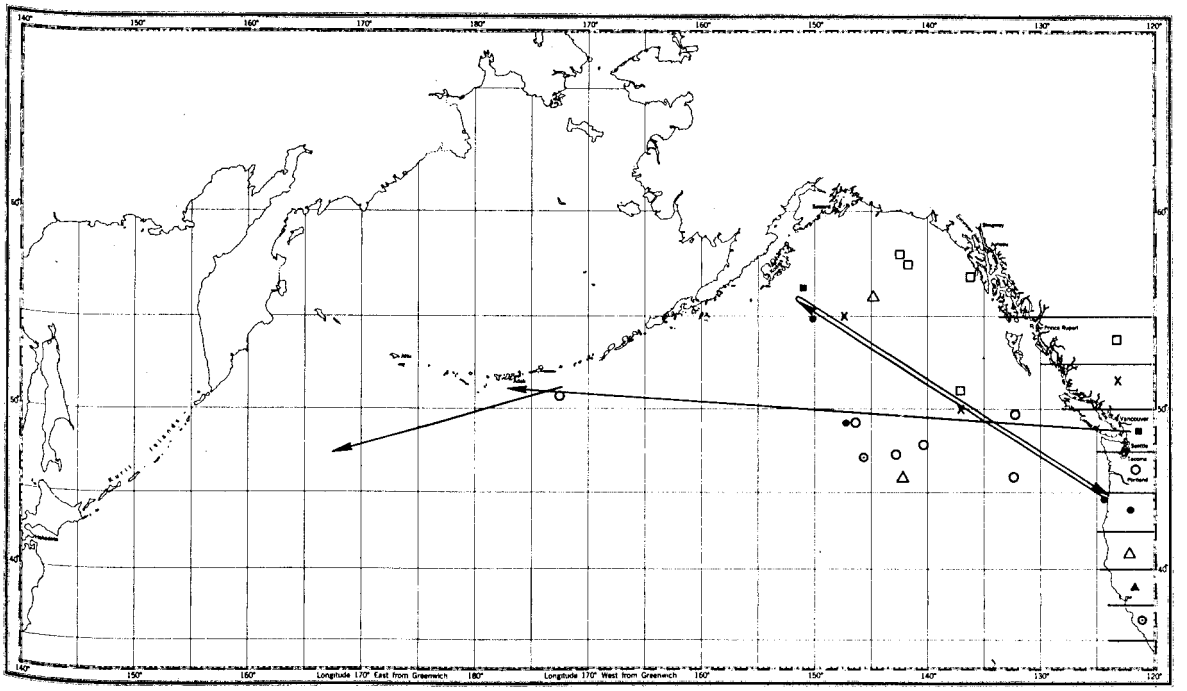

FIGURE 6.—Tagging locations and recovery areas (like symbols) of individual steelhead trout tagged by U.S. agencies, 1957-69. Directional movements of three individual fish are shown by arrows.

northern British Columbia were tagged as far south as lat. 50°N, and some that were recovered in California were tagged as far north as lat. 53°N. Thus the two widely separate stocks intermingled over at least 3° of latitude. Stocks from the area that includes the Columbia River were tagged over the latitudinal range of 45°N to 53°N and west to long. 174°45′W. Recoveries from other streams were well represented within this range.

The directional movement of steelhead trout from offshore to inshore varied among the stocks of the various geographical regions. In interpreting migration routes, it is assumed that the fish travel in a direct route from tagging site to point of recovery. All fish recovered in California and southern Oregon were tagged north of the point of recovery, indicating a southeasterly directional movement. The migration routes of fish recovered in northern Oregon and Washington were essentially easterly to southeasterly. Two fish, however, were tagged south of the point of recovery, indicating movement in a northeasterly direction. Fish recovered in British Columbia were tagged in nearly equal numbers north and south of the points of recovery. The directional movement of these fish, therefore, varied from southeasterly to northeasterly.

Timing of recoveries indicates that both "summer-run and winter-run" steelhead trout were tagged. Withler (1966) described summer steelhead trout as those which enter and ascend streams during May through August and winter steelhead trout as those which enter from mid-October to as late as May. Based on the percentage composition of the tagged fish recovered in coastal streams, summer steelhead trout stocks predominated in British Columbia and winter steelhead trout stocks predominated in Washington, Oregon, and California. Of the 23 tagged fish recovered in British Columbia, 20 (87%) were captured from May through September and 3 (13%) from January through March. Of the 41 tagged fish recovered in Washington, Oregon, and California, 29 (71%) were captured from December through March and 12 (29%) from May through September.

These results are in general agreement with the known timing and composition of steelhead runs on the west coast of North America (Withler, 1966). Although major stocks of summer and winter steelhead trout are known to spawn in British Columbia streams, little information is available on their comparative abundance. Winter steelhead trout stocks predominate in Washington, Oregon, and California (J. D. Ayerst, Washington Department of Game, pers. comm.).

The precise timing of arrival or the seasonal composition of the run cannot be judged solely on the basis of the time of catpture in coastal streams, however. Some time lapse between arrival and capture is to be expected. Many of the tagged fish returned to British Columbia were recovered before ascending coastal streams; whereas, most of those returned to Washington, Oregon, and California were recovered after ascending coastal streams. Those captured in the summer are presumably summer-run fish that arrived shortly prior to capture. Recoveries in the winter may be either winter runs or summer runs because both spawn in late winter through spring.

The tag recoveries indicate that, on the average, Canadian steelhead trout spend more time at sea than do Washington, Oregon, and California steelhead trout, as was also shown by Withler (1966) in his analysis of the age composition of the stocks. (It should be noted, however, that my evidence is based on a rather small number of fish.) In comparing the time that fish recovered in northern spawning streams spent at sea with the time that fish in southern streams spent at sea, tagged fish recovered in May through March are considered as belonging to the same spawning run. Of the 15 tagged steelhead trout (with readable scales) recovered in British Columbia, 6 (40%) were age .1 at the time of tagging; 5 (33%) were age .2; and 4 (27%) were age .3. Of the 22 recovered in Washington, Oregon, and California, 17 (77%) were age .1 at the time of tagging, and 5 (23%) were age .2.

SUMMARY

1. Cruise and catch data of United States, Japanese, and Canadian research vessels in the North Pacific Ocean for 1953 and 1955-67 and the scientific literature were analyzed for information on distribution, age, and size of steelhead trout in the ocean. Data are not available from all nations in all years, but considerable information was obtained.

2. Catches were made with gill nets, longlines, and purse seines. U.S. catches were with gill nets and longlines by the National Marine Fisheries Service (NMFS) and with purse seines and longlines by the Fisheries Research Institute (FRI), University of Washington. Japanese and Canadian vessels used gill nets and longlines. The catch per set was chosen as the comparative unit of effort because of the great variation in types of gear used and variation in construction and in methods of fishing gill nets.

3. Catches by research vessels showed steelhead trout to be distributed virtually throughout the Gulf of Alaska and the North Pacific Ocean north of about lat. 42°N to the Aleutian Islands chain and west from the coast of North America to about long. 152°E. Steelhead trout rarely were found north of the Aleutian Islands in the southern Bering Sea and in the southeastern Okhotsk Sea (catch reported by the Japanese). None were reported in fishing sets in the Bristol Bay area, central and northern Bering Sea, central and western Okhotsk Sea, or the Sea of Japan.

4. The relative abundance of steelhead trout could be indicated only in a general way. Because the fishing gear often varied between years and between areas and because catches were relatively small, the catch per set was chosen as the comparative unit of effort. Data on the catch per set indicated that the abundance of steelhead trout was greatest in the Gulf of Alaska and eastern North Pacific Ocean, decreased westward, and reached a low level in the western North Pacific and western Aleutian Islands area. Fishing primarily east of long. 180°, NMFS research vessels averaged 1.05 steelhead trout per gill net set. In the same general area research vessels of NMFS, FRI, and FRBC averaged 0.75, 0.81, and 1.00 steelhead trout per longline set, respectively. Fishing primarily west of long. 175°W, the Japanese

research vessels averaged 0.007 steelhead trout per longline set. Purse seine catches by FRI averaged 0.07 fish per set.

5. The relative abundance of steelhead trout in all areas sampled was far less than that of salmon. In NMFS gill net catches, salmon exceeded steelhead trout by the average ratio of 105:1. The average ratio of salmon to steelhead trout in Japanese gill net catches was 13,743:1. The longline catch ratios averaged 30:1 in NMFS catches, 54:1 in Canadian catches, 68:1 in FRI catches, and 49,632:1 in Japanese catches. In purse seine catches by the FRI, the ratio was 1,012:1.

6. Ages of steelhead trout caught at sea ranged from 2 to 8 yr. Twenty different age groups, including various combinations of freshwater ages of 1 to 5 yr and saltwater ages of 0 to 6 yr, were represented. The majority belonged to three age categories—2.1 (22%), 3.1 (30%), and 3.2 (12%) — and were 3, 4, or 5 yr old.

7. Age, length, and weight data reinforce previous knowledge that the number of years steelhead trout spend in fresh water has little or no effect on their ultimate length and weight. The period in salt water has a profound effect on growth, which is particularly rapid in the first and second years. The average length of all freshwater age groups differed by no more than 4 cm after the second summer of feeding in salt water. Maximum growth is achieved by prolonged residence in salt water. In the first summer in the ocean, the steelhead trout grew from an average length of about 14-17 cm as seaward migrants to an average size of about 36 cm in length and 0.8 kg in weight. The average size increased to 57 cm and 1.8 kg for males and to 2.4 kg for females in the second summer. Growth continued at a substantial, but less rapid, rate in succeeding years. One female in its seventh summer (six winters at sea) measured 90 cm and weighed 6.7 kg.

8. The catch and effort data showed a definite seasonal shift of steelhead trout in the ocean. A northward and westward movement began in late winter and early spring. The most extensive movement northward occurred in summer. Data on fall distribution are limited. Larger catches south of lat. 54°N and the return of spawning adults to North American streams in the fall, however, indicated a general shift of the populations southward and eastward in late summer, fall, and early winter.

9. Catch records showed a relation between ocean distribution of steelhead trout and surface water temperatures. Catches were made in surface water that ranged from 5° to 14.9°C. The majority of catches (61%) were in areas with surface water of 8° to 11.4°C. Very few steelhead trout were caught in water warmer than 13.9°C or colder than 6°C. The data suggest the limits of distribution in the ocean conform closely to the 5°C isotherm on the north and the 15°C isotherm on the south.

10. The vertical distribution of steelhead trout has not been adequately investigated. Over 85% of the gill net catch by NMFS in experimental deep nets was in the upper 7 m of net. Significant numbers have been caught in summer at depths of 15 to 23 m. If steelhead trout in significant numbers range to depths greater than 7 m, the true horizontal distribution may differ from that described from gill net and longline catches.

11. Tagging studies showed that some steelhead trout make extensive oceanic migrations. Individuals tagged in the eastern North Pacific Ocean, including the Gulf of Alaska and south of the central Aleutian Islands, were recovered in streams of Washington and Oregon 1 to 2 yr after release. A steelhead trout marked by a fin clip in Oregon was caught and tagged 5 mo later south of Kodiak, Alaska, after traveling a minimum distance of 2,963 km (1,600 miles) at a minimum speed of 19.8 km (10.7 miles) per day. Seventeen months after tagging, the fish was recaptured in the home stream in Oregon. Another fish, tagged and released in Washington, in April 1968 had migrated some 4,213 km (2,275 miles) northwestward when recaptured south of the central Aleutian Islands in August 1969.

12. Time of return of tagged fish to coastal streams and time spent at sea varied by geographic area. The majority of tagged steelhead trout returning to British Columbia were recovered in July-September the majority of returns to Washington, Oregon, and California were recovered in Decmember-March. Steel-

head trout from northern streams tended to spend more time at sea than those from southern streams.

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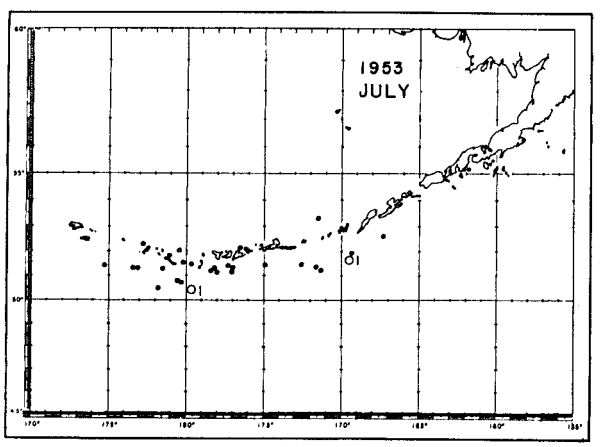
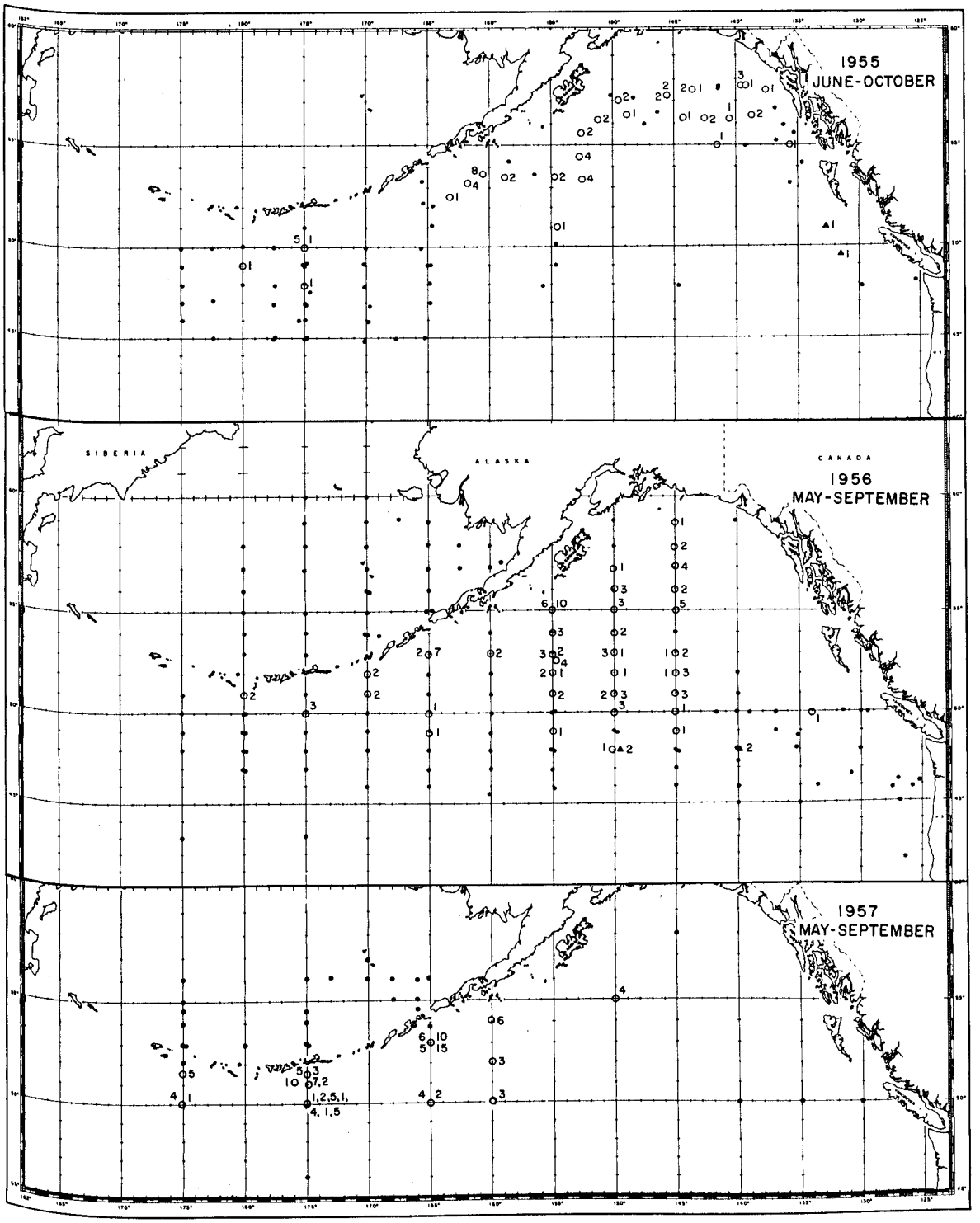
APPENDIX FIGURES 1-6.—Stations fished and locations where the research vessels of the National Marine Fisheries Service caught steelhead trout, 1953, 1955-67.

Key: • Stations fished
△ January-April
▲ May - June
○ July - September
□ October - November

No.= steelhead caught per set



Appendix Figure 1.



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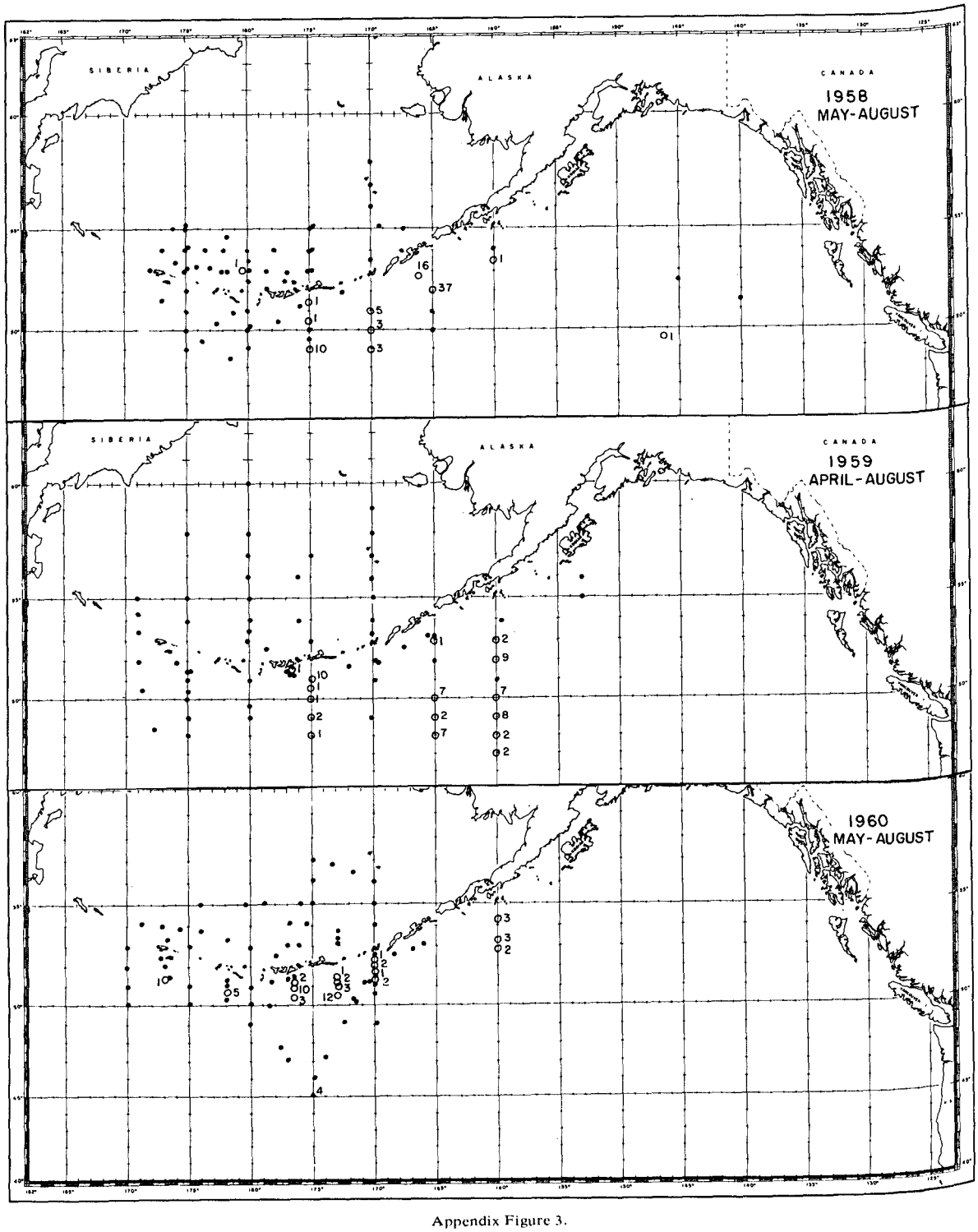

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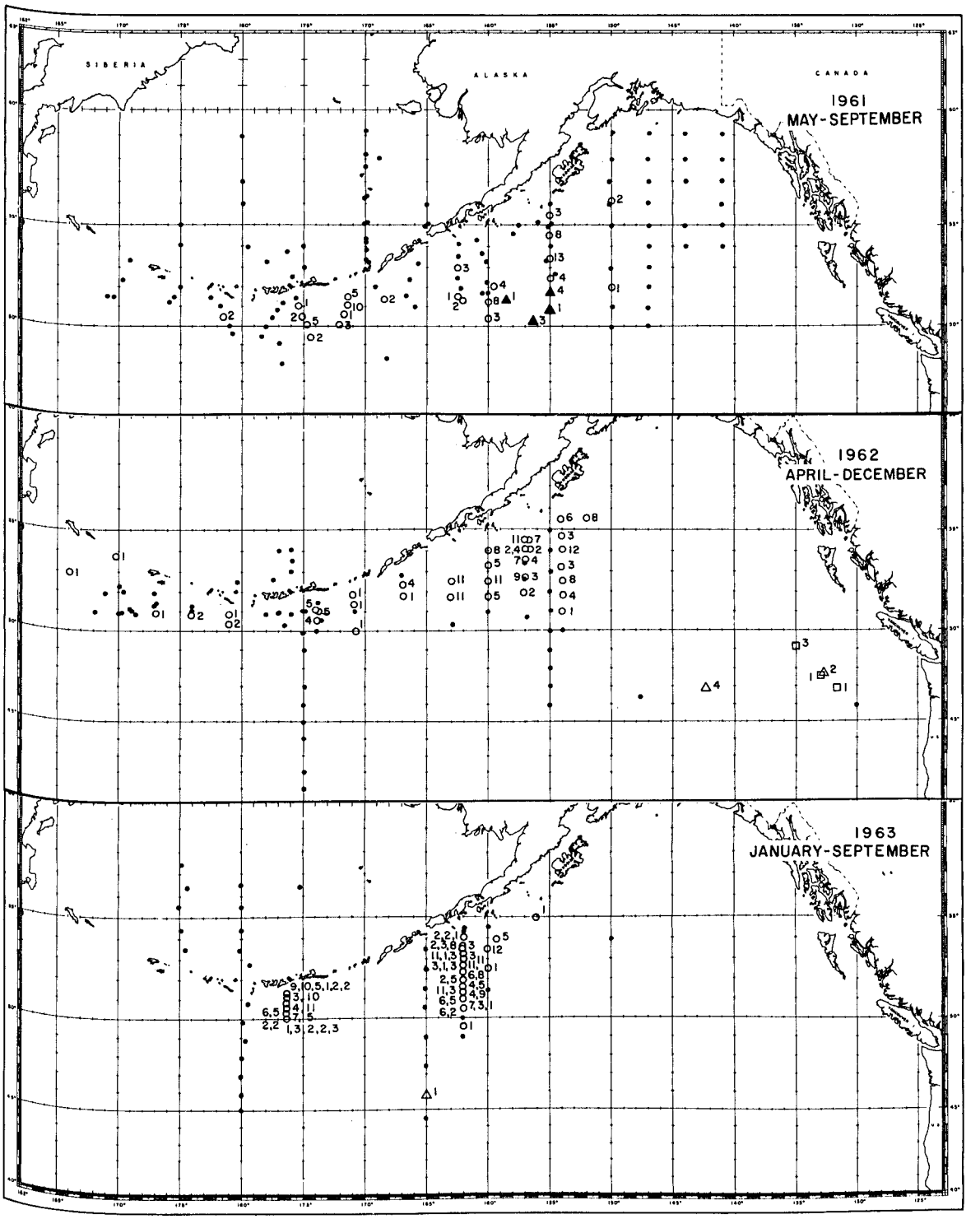

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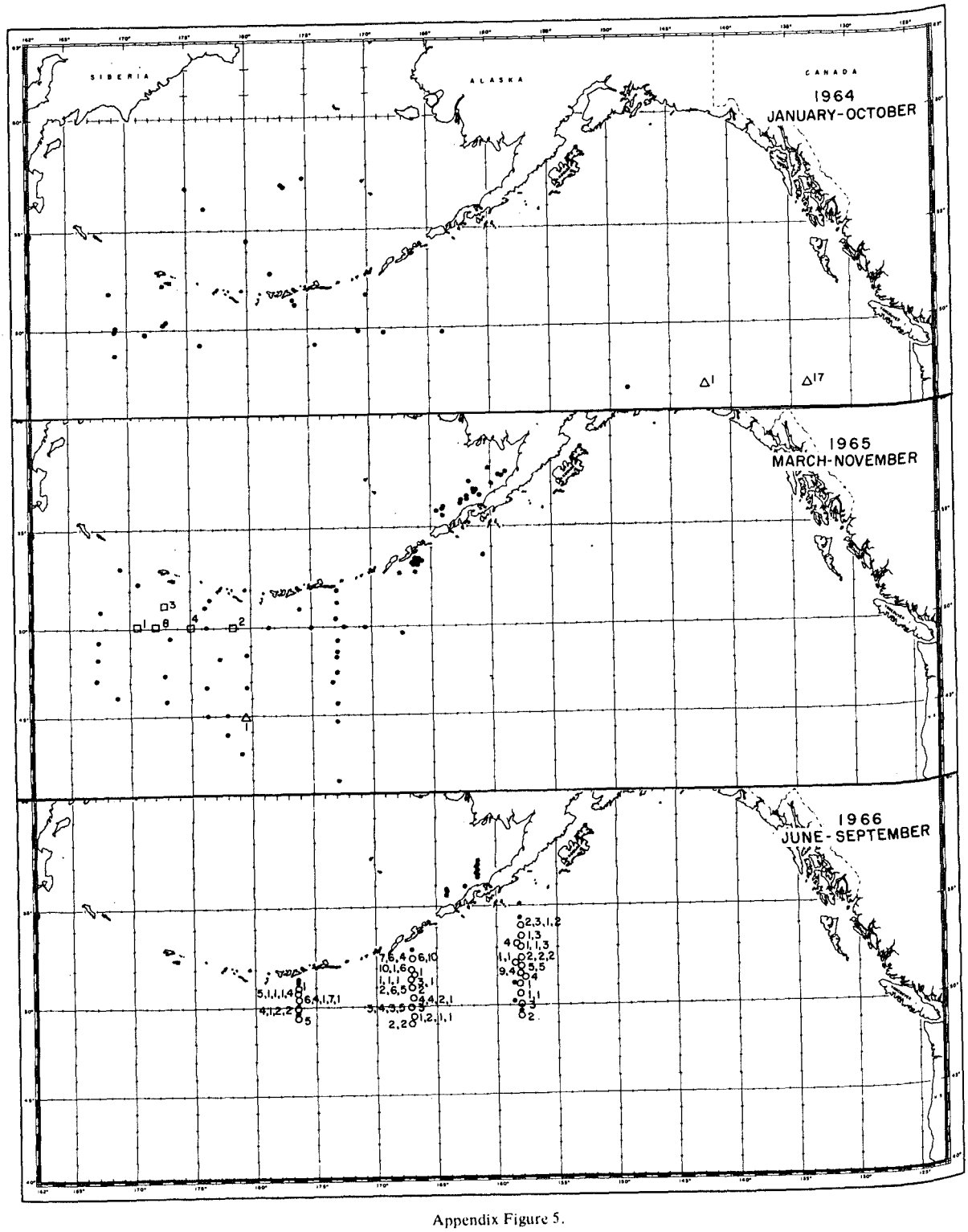

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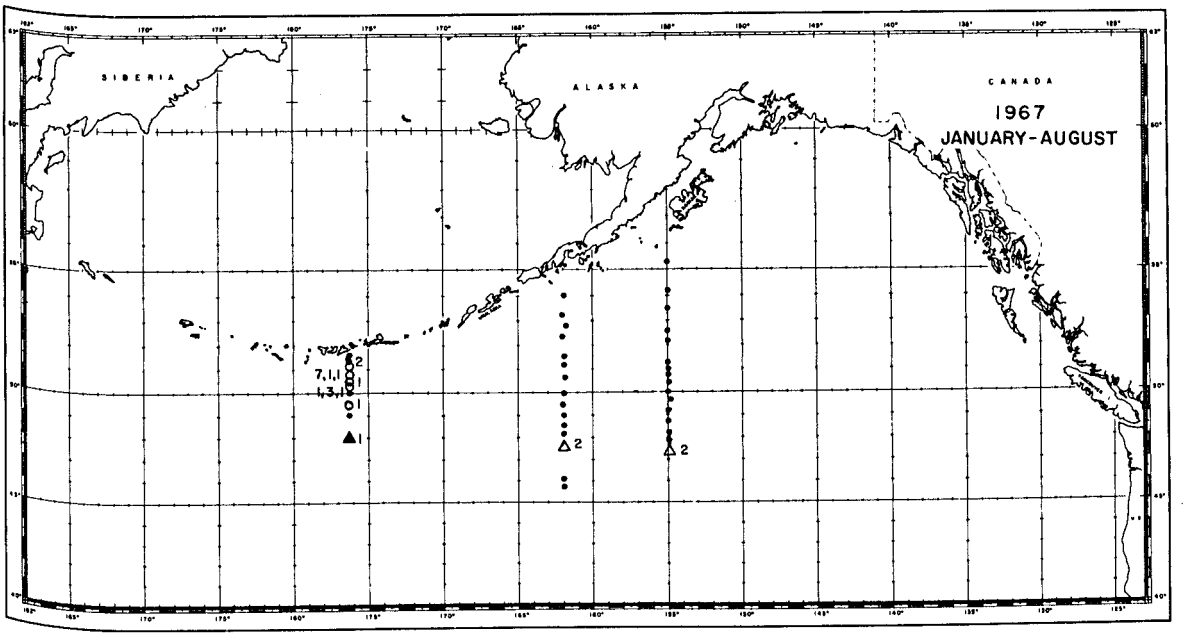
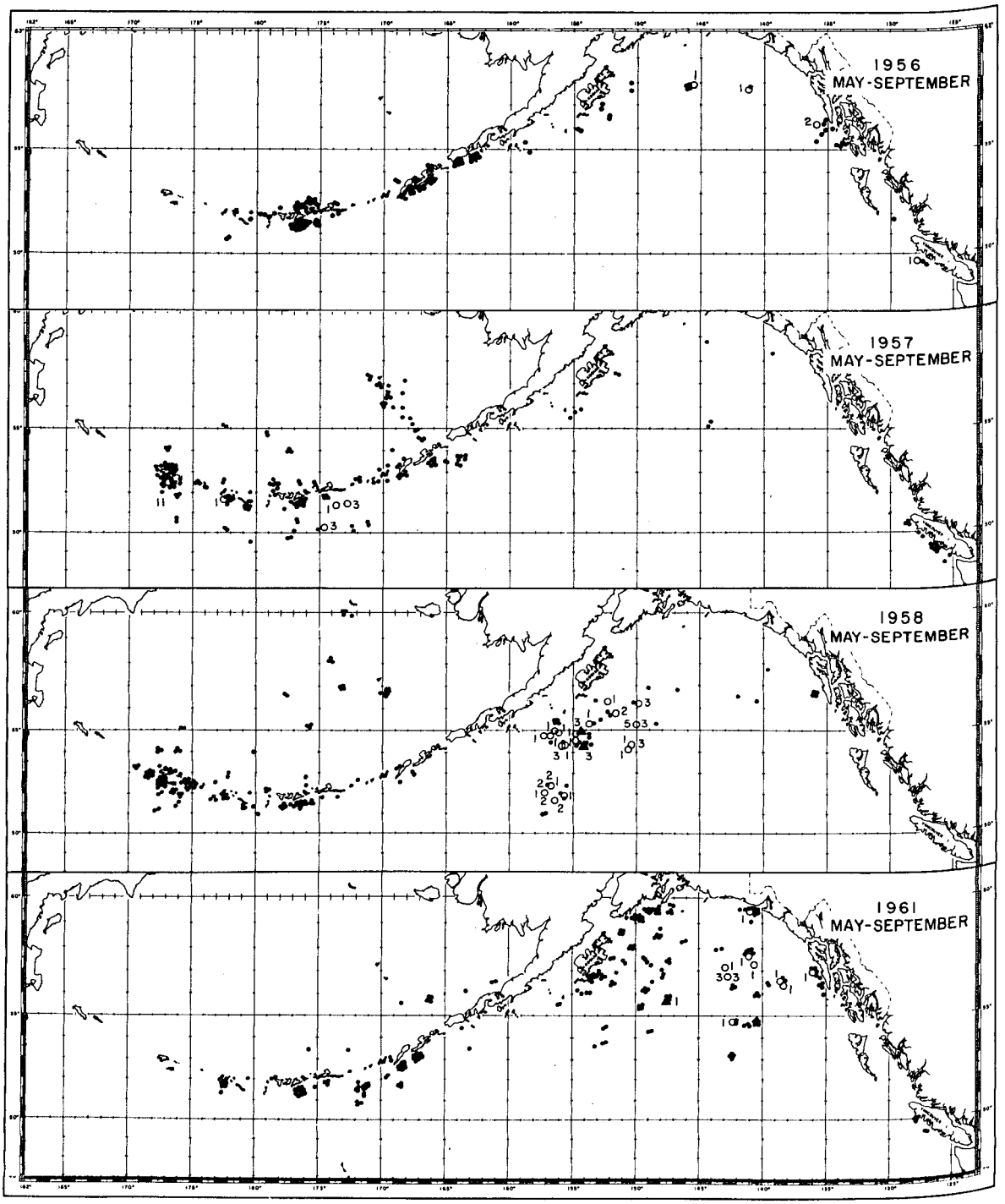


Appendix Figure 6.

APPENDIX FIGURES 7-9.—Stations fished and locations where the research vessels of the Fisheries Research Institute, University of Washington, caught steelhead trout, 1956-58, 1961-67.

Key: • Stations fished
△ January - April
▲ May - June
○ July - September
□ October - November

No.= steelhead caught per set



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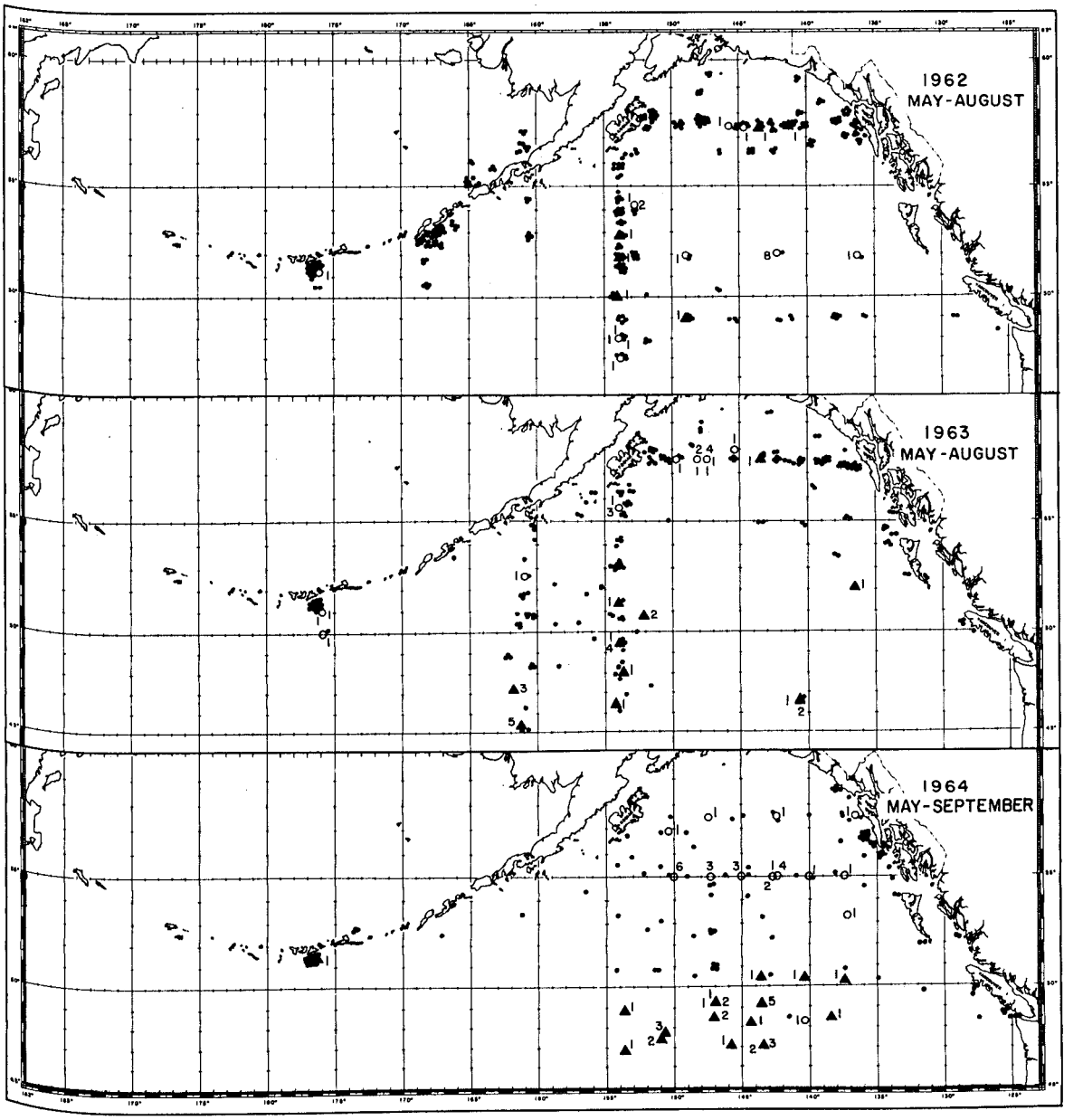

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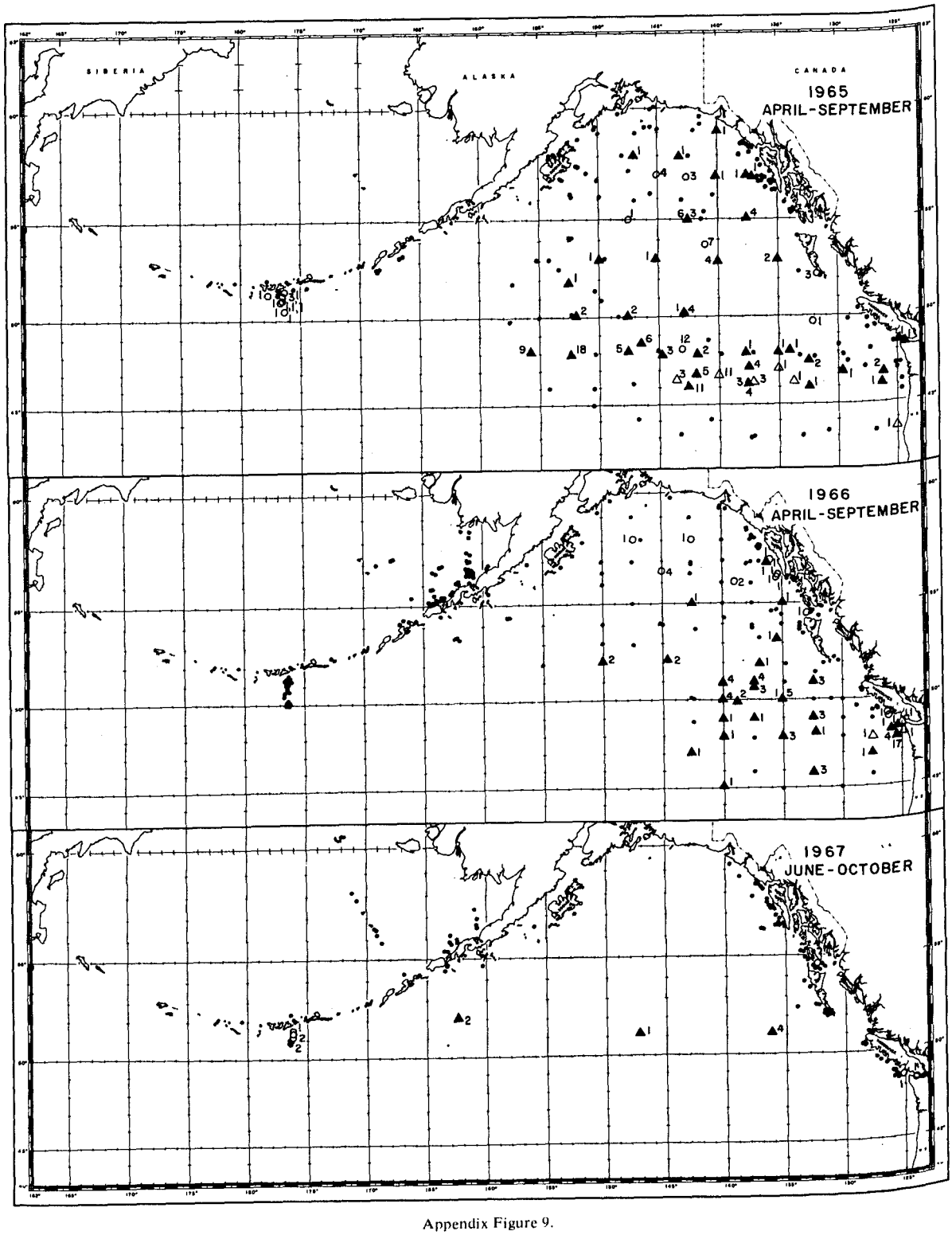
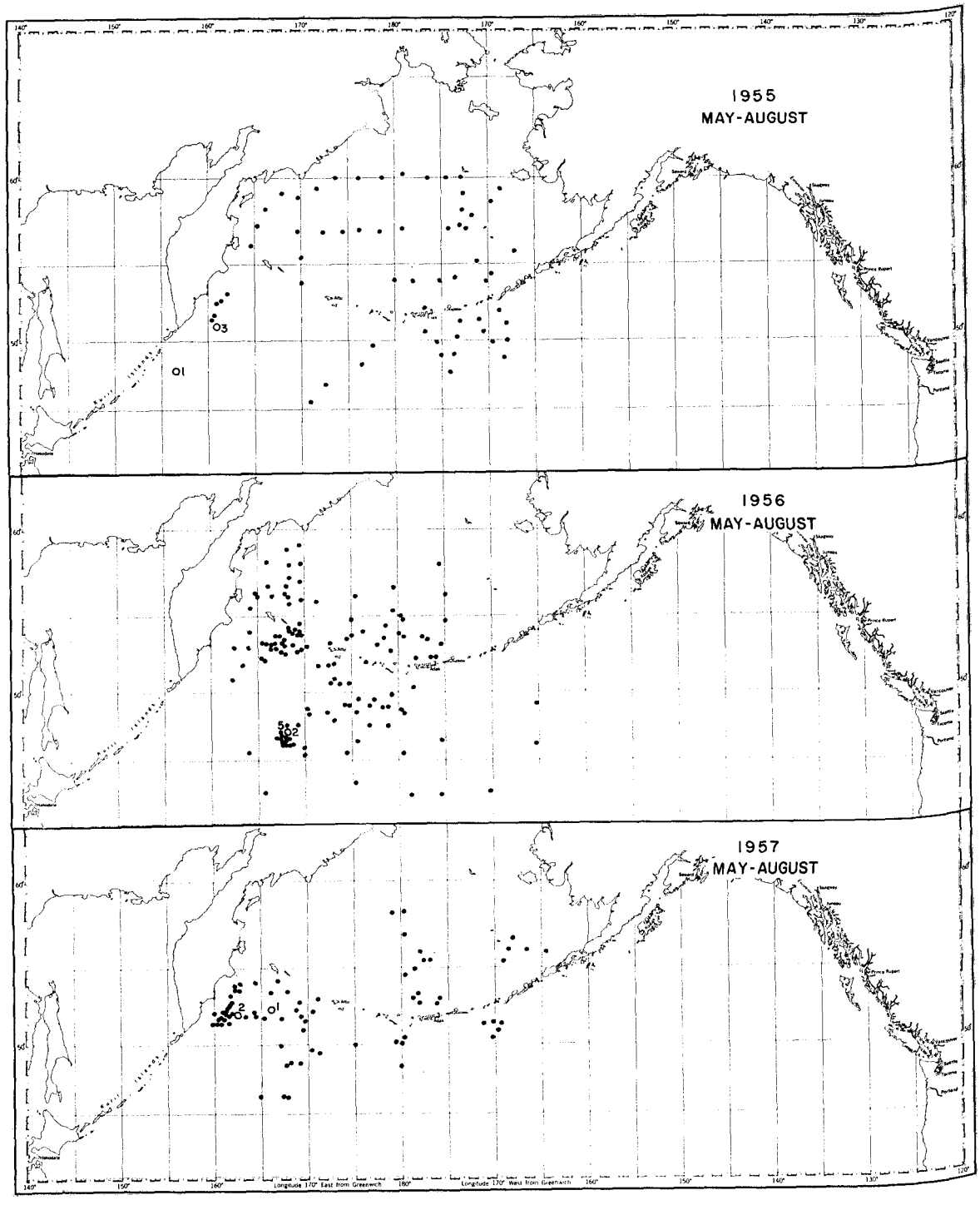


Appendix Figure 9.

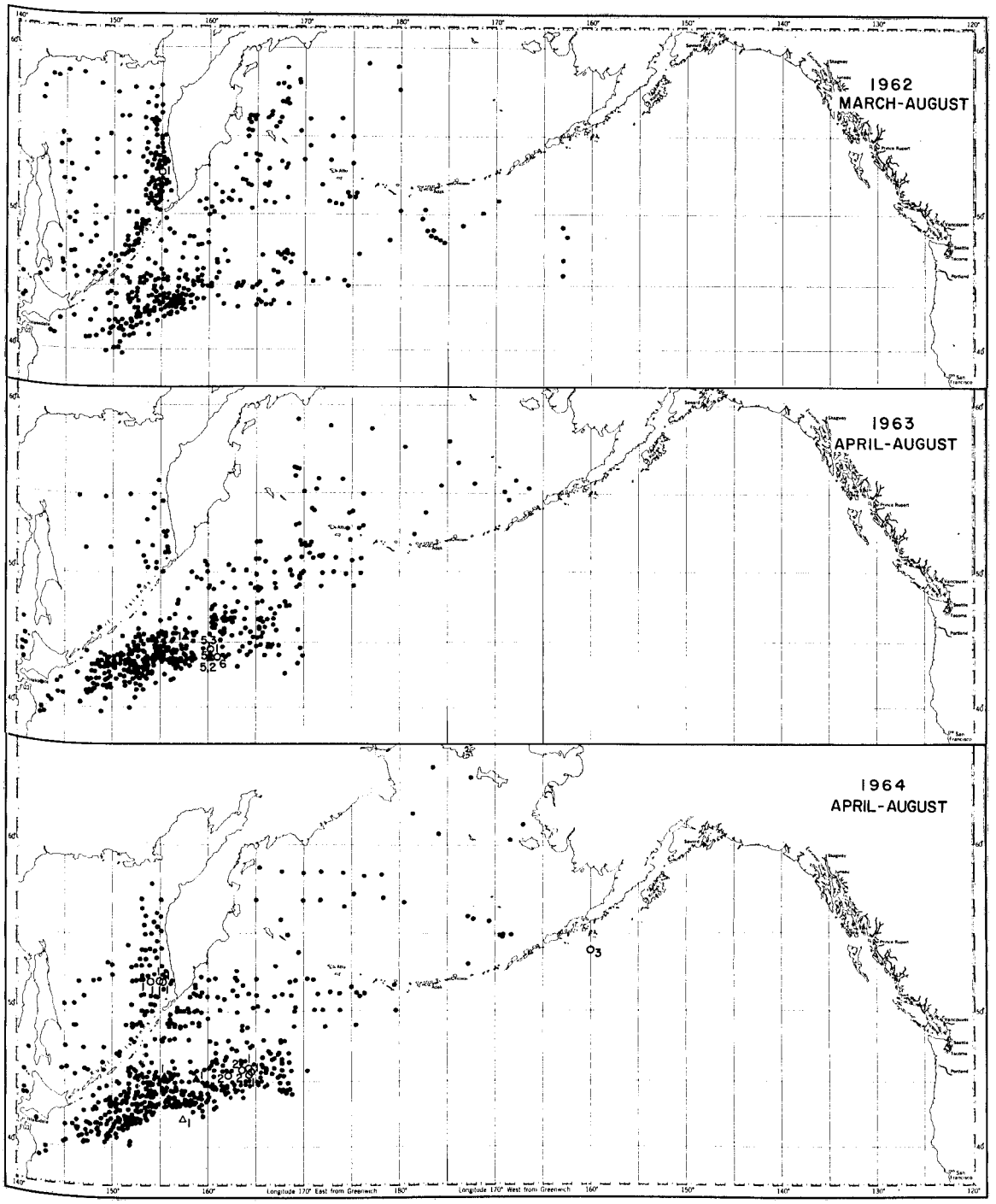
APPENDIX FIGURES 10-12.—Stations fished and locations where the Japanese research vessels caught steelhead trout, 1955-57, 1962-67.

Key: • Stations fished
△ January-April
▲ May - June
○ July - September
□ October - November

No.= steelhead caught per set



Appendix Figure 10.



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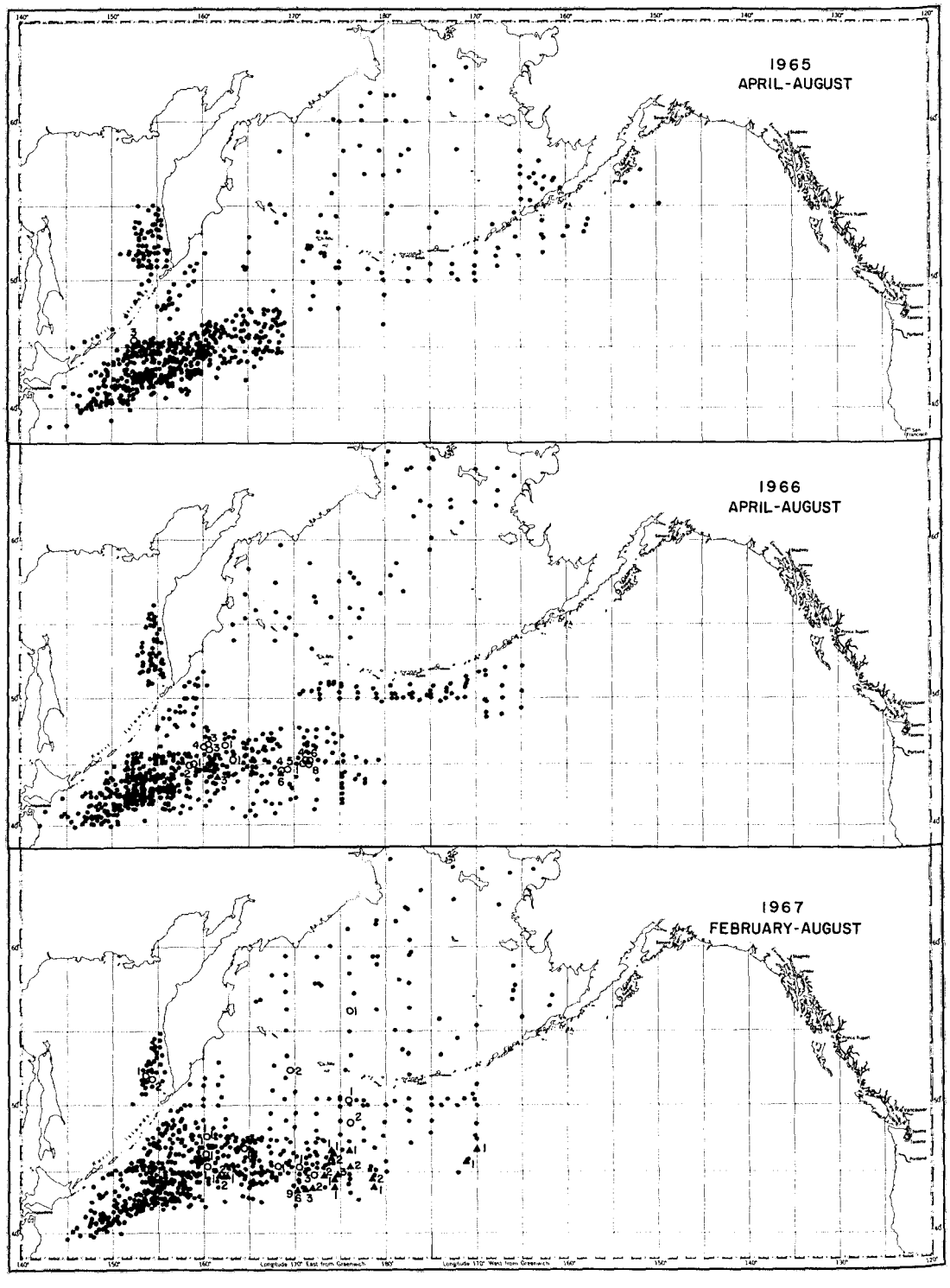
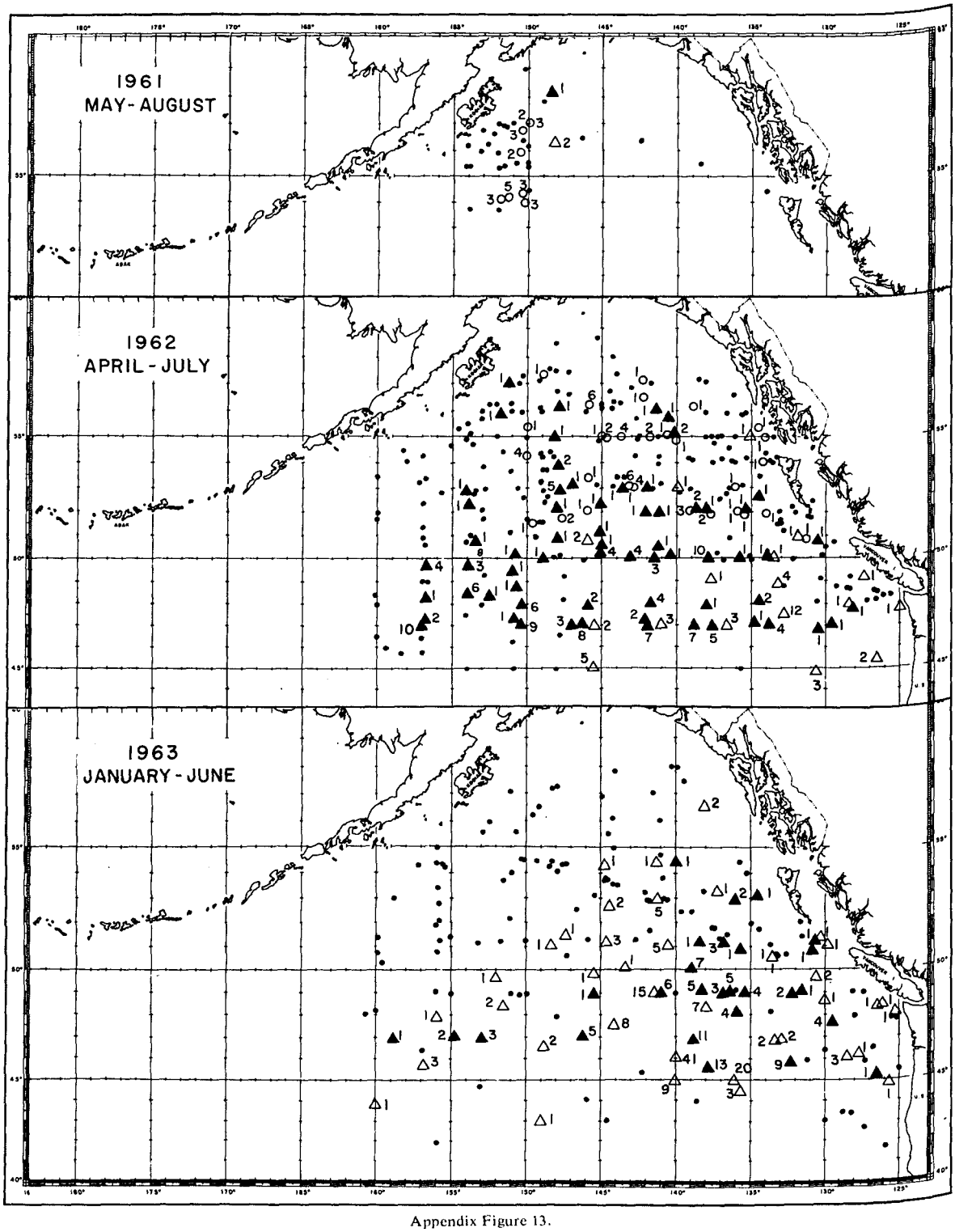


Appendix Figure 12.

APPENDIX FIGURES 13-15.—Stations fished and locations where the Canadian research vessels caught steelhead trout, 1961-67.

Key: • Stations fished
△ January-April
▲ May - June
○ July - September
□ October - November

No.= steelhead caught per set



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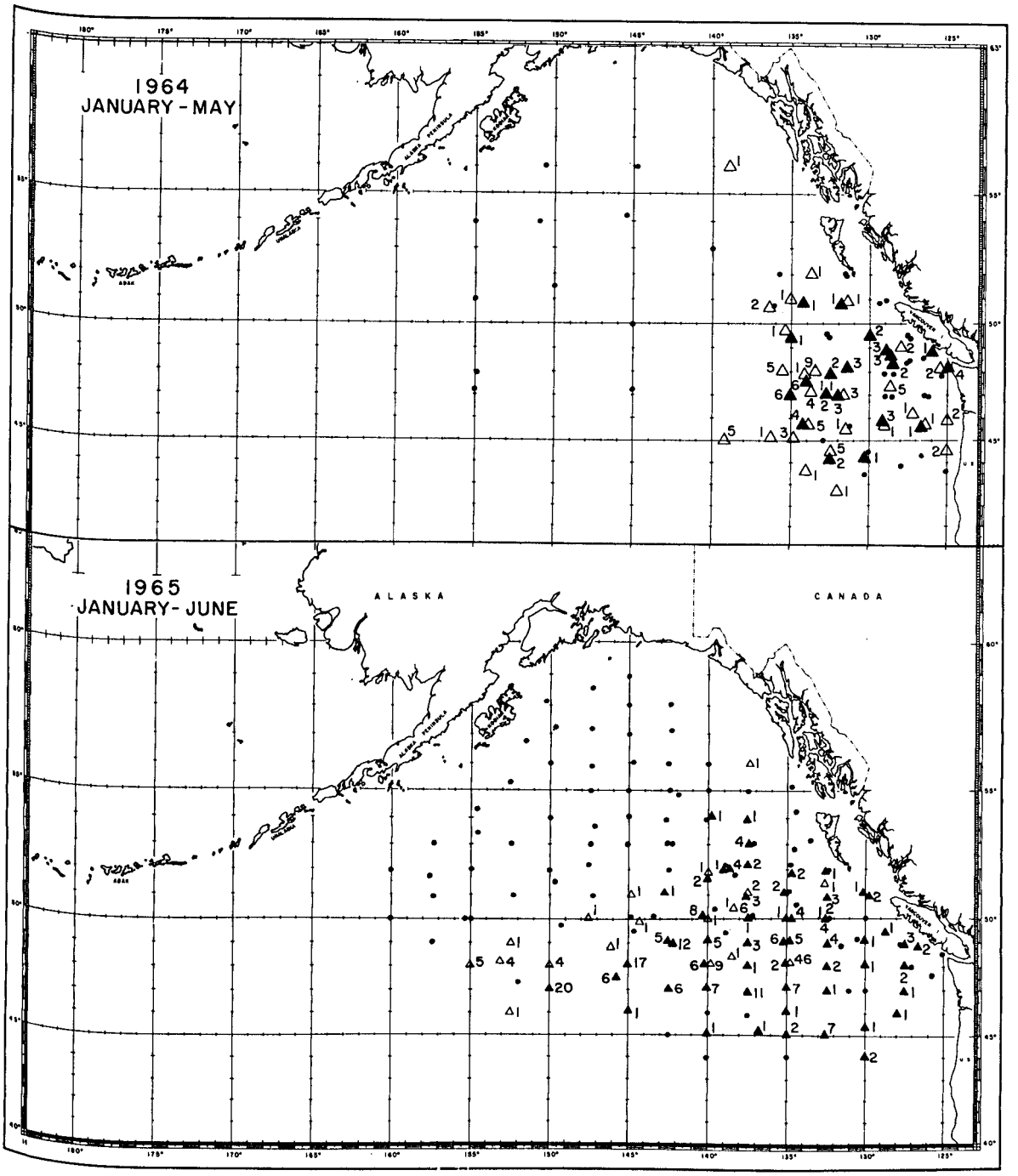

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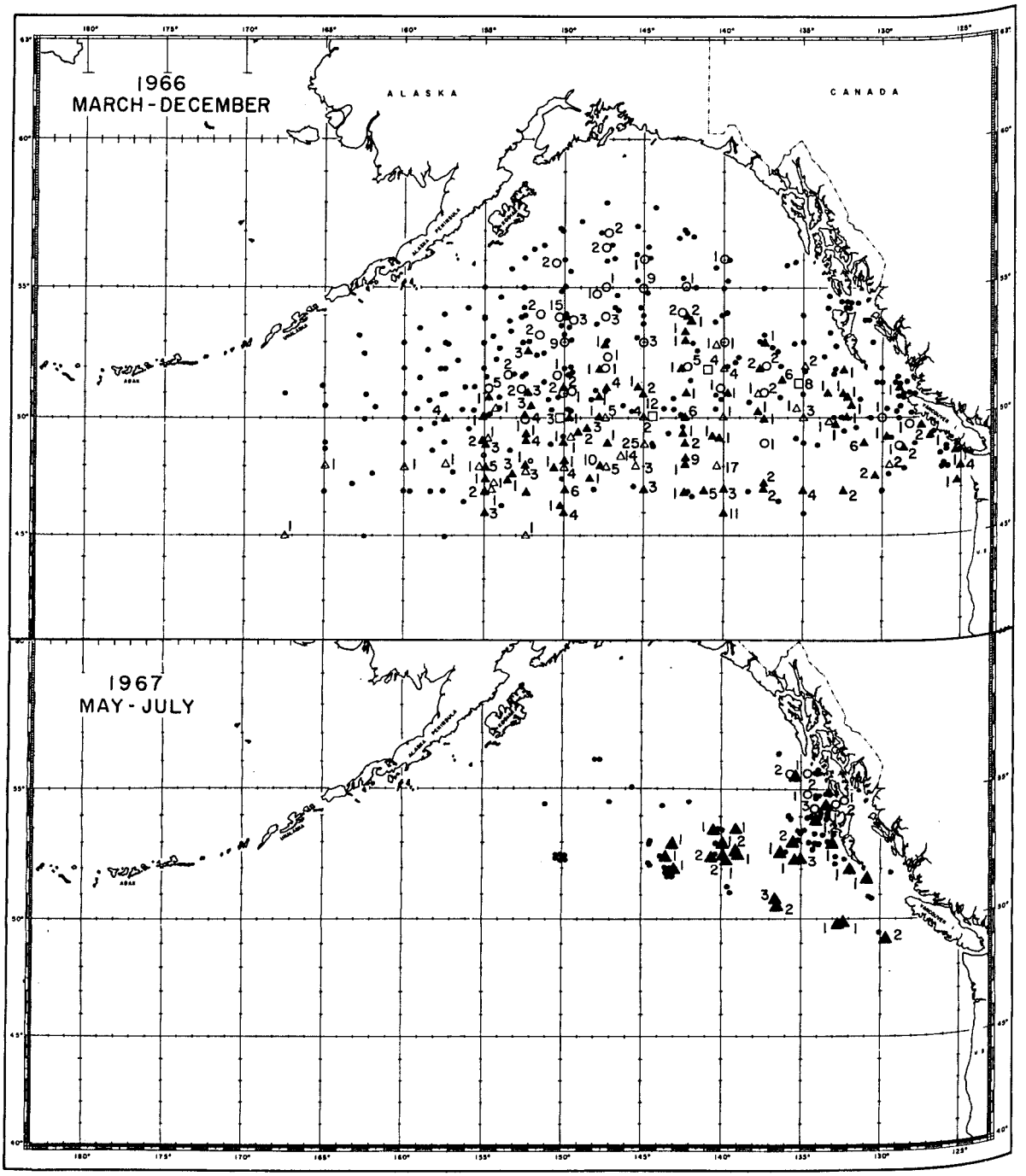

Appendix Figure 15.

APPENDIX TABLE 1.—Recovery of steelhead trout tagged by Canada, 1961-67.[1]

Tagging data			Tag recovery data		
Date of tagging	Latitude N	Longitude W	Date of recovery	Latitude N	Longitude W
		Recovered Year of Tagging			
7/23/61	54°21′	150°32″	8/29/61	54°05′	130°08′
4/12/62	44°55′	130°40′	9/06/62	42°51′	124°34′
4/18/62	47°00′	141°05′	8/20/62	48°40′	125°40′
5/02/62	49°35′	151°00′	8/14/62	54°34′	130°28′
6/23/62	52°05′	135°20′	7/10/62	46°16′	123°45′
7/09/62	51°58′	135°30′	8/05/62	52°15′	128°20′
7/11/62	53°00′	136°10′	8/13/62	46°17′	123°39′
7/19/62	55°13′	134°35′	7/31/62	51°19′	127°48′
4/10/63	44°55′	136°08′	7/11/63	46°15′	123°35′
4/27/63	48°06′	136°00′	12/25/63	39°29′	123°46′
4/28/63	45°56′	137°52′	7/10/63	41°50′	124°25′
5/11/63	47°39′	129°35′	/ /63	44°25′	124°00′
5/16/63	49°00′	135°30′	12/27/63	43°20′	123°30′
5/22/63	47°00′	159°00′	12/29/63	46°55′	122°35′
5/31/63	51°00′	140°35′	7/10/63	46°15′	123°40′
1/13/64	51°00′	135°00′	9/22/64	55°26′	126°41′
4/11/65	49°00′	152°30′	8/20/65	46°10′	123°50′
5/01/65	47°00′	150°00′	8/11/65	45°57′	124°00′
5/05/65	52°00′	139°00′	7/27/65	55°02′	130°00′
5/18/65	50°57′	137°33′	8/12/65	52°45′	128°40′
5/27/65	49°00′	132°30′	8/16/65	46°12′	123°25′
6/01/65	53°01′	137°20′	8/20/65	56°45′	131°45′
7/05/67	55°33′	134°40′	8/24/67	55°05′	127°50′
7/06/67	55°30′	135°30′	7/29/67	54°38′	130°52′
		Recovered First Year After Tagging			
4/10/62	48°53′	133°15′	3/ /63	54°25′	126°45′
6/01/62	48°00′	151°50′	1/16/63	46°11′	122°54′
6/21/62	49°42′	156°50′	1/01/63	47°20′	123°15′
6/22/62	47°15′	156°57′	12/26/63	39°05′	123°12′
6/25/62	48°25′	154°00′	2/06/63	47°13′	122°20′
7/20/62	53°01′	142°52′	5/26/63	47°33′	124°20′
4/12/63	46°08′	140°00′	2/23/64	43°05′	123°15′
5/15/63	50°00′	139°00′	1/25/64	55°26′	126°41′
5/15/63	50°00′	139°00′	2/29/64	40°37′	124°15′
5/20/63	47°00′	153°08′	2/25/64	47°20′	124°18′
5/20/63	47°00′	153°08′	2/13/64	46°05′	123°43′
5/26/63	49°00′	151°04′	1/10/64	40°55′	124°06′
1/14/64	47°13′	133°50′	2/06/65	43°40′	123°40′
4/04/65	51°35′	132°30′	1/15/66	46°10′	122°55′
5/29/65	47°00′	142°30′	12/31/66	45°27′	122°18′
6/26/65	52°08′	137°33′	1/22/66	54°10′	127°25′
7/07/67	54°27′	134°18′	7/17/68	54°59′	130°02′
		Recovered Second Year After Tagging			
6/21/62	49°42′	156°50′	2/22/64	40°30′	124°00′
6/28/62	56°10′	148°00′	7/13/64	54°09′	130°05′
7/20/62	53°01′	142°52′	1/25/64	39°00′	123°41′
5/24/65	47°00′	137°30′	1/13/67	40°06′	123°48′
6/02/65	52°08′	137°33′	1/07/67	42°08′	124°11′

[1] Data from unpublished summary, Fisheries Research Board of Canada.

APPENDIX TABLE 2.—Recovery of steelhead trout tagged by the States of Oregon and Washington and Fisheries Research Institute, University of Washington, 1957-68.[1]

Tagging data			Tag recovery data		
Date of tagging	Latitude N	Longitude W	Date of recovery	Latitude N	Longitude W
Recovered Year of Tagging					
7/14/61	56°56′	136°03′	7/27/61	54°06′	130°29′W
6/17/62	57°33′	141°40′	9/01/62	54°10′	130°00′W
5/26/64	49°10′	147°00′	12/10/64	46°00′	124°00′W
7/09/65	49°45′	132°05′	8/06/65	45°38′	121°31′W
5/10/66	52°00′	137°00′	6/21/66	50°40′	126°10′W
5/24/66	50°58′	137°28′	10/01/66	55°02′	127°21′W
7/05/66	58°00′	142°30′	9/16/66	55°15′	129°05′W
Recovered First Year After Tagging					
7/19/57	50°17′	174°45′	3/13/58	47°00′	126°00′W
8/16/57	51°26′	173°47′	7/12/58	47°12′	167°35′ E
8/08/58	56°17′	150°08′	3/30/59	48°32′	122°25′W
5/25/64	47°05′	145°45′	1/27/65	36°30′	123°00′W
5/26/64	49°10′	147°00′	/ /65	44°22′	124°00′W
7/15/64	55°00′	147°25′	7/13/65	51°15′	127°50′W
5/15/65	46°00′	142°25′	6/30/66	42°29′	124°31′W
7/08/66	56°30′	145°00′	1/10/67	42°03′	124°16′W
4/ /68	48°35′	121°45′	8/08/69	51°00′	176°22′W
Recovered Second Year After Tagging					
9/05/58	55°42′	151°49′	2/05/60	44°26′	124°05′W
7/14/64	55°00′	150°05′	2/16/66	43°20′	123°15′W
5/07/65	48°06′	143°05′	1/08/67	45°44′	122°24′W
5/17/65	46°02′	137°30′	1/15/67	46°01′	122°53′W

[1] Data from Hartt (1962, 1966) and from unpublished records of the States of Oregon and Washington, and Fisheries Research Institute.

ARGYRIPNUS BROCKI, A NEW SPECIES OF STOMIATOID FISH FROM HAWAII, WITH OBSERVATIONS ON *A. EPHIPPIATUS* AND *A. IRIDESCENS*

PAUL STRUHSAKER[1]

ABSTRACT

Argyripnus brocki is proposed as a new species, and new observations on *A. ephippiatus* from the Hawaiian Islands and *A. iridescens* from Australia are presented. *A. brocki* differs from *A. atlanticus*, *A. ephippiatus*, and *A. iridescens* in possessing fewer photophores in the VAV + anterior AC series, fewer photophores in the posterior AC series, fewer gill rakers, fewer vertebrae, and a greater interorbital distance. A single small specimen of *Argyripnus* from the Indian Ocean is tentatively assigned to *A. brocki*. Evidence is presented that *Argyripnus* is primarily an inhabitant of the near-bottom community. In Hawaii, *A. brocki* and *A. ephippiatus* exhibit nonoverlapping vertical distributions.

The stomiatoid genus *Argyripnus* is poorly known. At the time of Grey's (1961, 1964) treatments of the group, only 47 specimens of the three nominal species were available for study. Because *Argyripnus* was not present in the open-sea collections of the RV *Dana*, Bruun (according to Grey, 1964) had earlier suggested that members of this genus may live near the bottom. All but 3 of the previously reported 47 specimens have been taken with bottom-fishing gear. The holotype of *Argyripnus atlanticus* Maul 1952 was taken alive at the surface off Madeira, and two specimens were collected after being killed by a lava flow entering the sea from the island of Hawaii (Gosline et al., 1954; Grey, 1961). The later specimens are the only record of *A. atlanticus* from the Indo-Pacific region.

During recent bottom trawling surveys by the NMFS (National Marine Fisheries Service, formerly the Bureau of Commercial Fisheries) in the Hawaiian Islands, numerous individuals of *Argyripnus* were taken and provide additional evidence that the members of this genus are primarily demersal. The material consists of about 460 specimens of *Argyripnus ephippiatus* Gilbert and Cramer 1897 and about 145 specimens of a new species, *A. brocki*, proposed herein. Additional observations on *A. ephippiatus* and *A. iridescens* McCulloch 1926 are also presented. I did not find specimens of *A. atlanticus* in the new Hawaiian material, and taxonomic judgments relative to this species are based on data presented by Grey (1961, 1964).

METHODS

Most sampling was done with 12.5-m (headrope) shrimp trawls (ST) constructed of 38-mm mesh (stretched) webbing in the body and cod end. Limited sampling was also done with similarly constructed 7-m and 21.5-m shrimp trawls. A discussion of the sampling effort and ichthyological results of the surveys is given by Struhsaker (1973).

Measurements were made point to point and generally are as defined by Hubbs and Lagler (1958). Measurements and counts of paired structures are usually the average of both sides. The first and second anal fins are separated at the third photophore of the middle AC series. The last two dorsal and anal rays are counted as two.

Photophore terminology is that of Grey (1964), except that in this case I follow Ahlstrom and Moser (1969) in dividing the IV

[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

Manuscript accepted December 1972.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

series into the IP (isthmal) and PV (abdominal) groups. All photophores, regardless of how rudimentary, were counted. There are two closely associated gill rakers at the angle of the first arch: The upper one is associated with the epibranchial and is included in the count for the upper limb, while the lower raker is included in the count for the lower limb. The pelvic rays of most specimens of *Argyripnus* I have examined are usually split and can only be counted accurately when submerged in fluid. Most vertebral counts were obtained from radiographs.

As an aid in the analysis of the morphometric characters, measurements obtained for the various body parts of all the specimens of *Argyripnus* I examined were plotted as functions of the standard length (SL) in both original units and as percent of SL.

ARGYRIPNUS BROCKI NEW SPECIES

(Figure 1)

Holotype.—U.S. National Museum (USNM) No. 207653, female, 81.5 mm SL, collected by the NMFS RV *Townsend Cromwell* at station TC-36-24 (*Townsend Cromwell* cruise 36, station 24); north edge Penguin Bank, Hawaiian Islands, lat. 21°09.7′N, long. 157°29.3′W (start of haul), 2235-0028 (local time), 4-5 May 1968, 183 m, 12.5-m shrimp trawl (ST).

Paratypes.—Four specimens (of 10 from station), USNM 207654, 46.5, 50, 52.5, and 56 mm SL, station TC-35-33, north edge Penguin Bank (lat. 12°09.7′N, long. 157°25.0′W) 1912-2052, 7 April 1968, 183 m, 12.5-m ST. One specimen, USNM 207655, 51.2 mm SL, station TC-35-34, north edge Penguin Bank (lat. 21°09.7′N, long. 157°25′W), 2225-2353, 7 April 1968, 183 m, 12.5-m ST. One specimen, USNM 207656, 54 mm SL, station TC-35-35, north edge Penguin Bank (lat. 21°09.7′N, long.157° 24.9′W), 0127-0307, 8 April 1968, 183 mm, 12.5-m ST. One specimen, USNM 207657, 84 mm SL, station TC-35-39, Kalohi Channel (lat. 20°59.3′ N, long. 157°03′W), 1902-2007, 8 April 1968, 274 m, 12.5-m ST. Four specimens (of 21, including holotype), USNM 207658, 64.5, 70.5, 83, and 91.5 mm SL, station TC-36-24, same data as for holotype. Four specimens (of 51) USNM 207659, 64, 65, 80, and 91 mm SL, station TC-36-26, north edge Penguin Bank (lat. 21°09.7′N, long. 157°29.7′W), 0336-0521, 5 May 1968, 183 m, 12.5-m ST. Two specimens, USNM 207660, 66.5 and 75 mm SL, station TC-40-2, north edge Penguin Bank (lat. 21°09.9′N, long. 157°24.1′W), 2144-2344, 6-7 November 1968, 183 m, 12.5-m ST. One specimen, USNM 207661, 77.5 mm SL, station TC-40-16, north edge Penguin Bank (lat. 21°09.8′N, long. 157° 24.5′W), 2021-2205, 8 November 1968, 179 m, 12.5-m ST. One specimen, USNM 207662, 70 mm SL, station TC-40-20, north edge Penguin Bank (lat. 21°09.8′N, long. 157°24.3′W), 2025-2222, 9 November 1968, 12.5-m ST.

Additionally, specimens of *A. Brocki* not included in the type series were taken at the following stations during the surveys: TC-33-15 (1 specimen), Pailolo Channel (lat. 21°01.5′N,

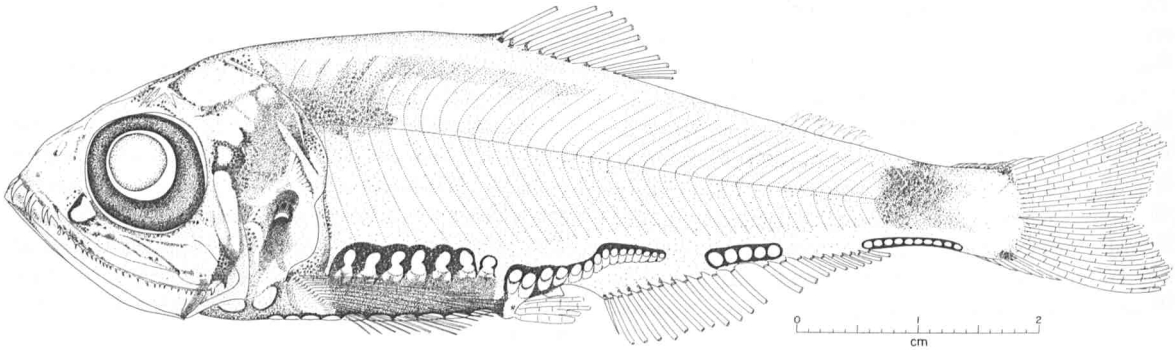

FIGURE 1.—Holotype of *Argyripnus brocki*, USNM 207653.

long. 156°45.9′W), 2028-2228, 31 October 1967, 248 m, 12.5-m ST. TC-33-25 (3), Kealaikahiki Channel (lat. 20°43.3′N, long. 156°48.6′W), 0150-0250, 4 November 1967, 224 m, 8-m ST. TC-33-37 (2), Kealaikahiki Channel (lat. 20° 41.7′N, long. 156°39.8′W), 1747-1836, 9 November 1967, 276 m, 8-m ST. TC-35-8 (1), northeast coast Hawaii Island (lat. 19°54′N, long. 155°03.1′W), 1804-1930, 29 March 1968, 280 m, 12.5-m ST. TC-35-36 (1), north edge Penguin Bank (lat. 21°10.2′N, long. 157°24.9′W), 0435-0625, 8 April 1968, 183 m, 12.5-m ST. TC-36-23 (22), north edge Penguin Bank (lat. 21°09.7′N, long. 157°25.2′W), 2019-2149, 4 March 1968, 183 m, 12.5-m ST. TC-36-35 (20), north edge Penguin Bank (lat. 21°09.7′N, long. 157°24.9′W), 0114-0245, 5 May 1968, 183 m, 12.5-m ST. TC-40-10 (7), north edge Penguin Bank (lat. 21°09.8′N, long. 157°24.4′W), 2021-2211, 7 November 1968, 181 m, 12.5-m ST. TC-40-26 (1), north edge Penguin Bank (lat. 21° 09.8′N, long. 157°24.2′W), 2023-2124, 10 November 1968, 183 m, 12.5-m ST. TC-40-61 (5), Pailolo Channel (lat. 21°02.1′N, long. 156° 44.4′W), 2026-2126, 18 November 1968, 238 m, 12.5-m ST. These specimens, and those taken at the same stations as specimens in the type series, are in the collections of the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA.

Diagnosis

A. brocki is morphologically closest to *A. ephippiatus* and *A. iridescens*. These three species differ markedly from *A. atlanticus* in having fewer photophores in the VAV + anterior AC series and the posterior AC series. They usually have fewer gill rakers, pectoral rays, and vertebrae (Table 1). They have shorter snouts and longer upper jaws than *A. atlanticus*. The anal fins in *A. brocki*, *A. ephippiatus*, and *A. iridescens* originate below the posterior half of the dorsal fin bases, whereas the anal fin in *A. atlanticus* originates nearly below the origin of the dorsal fin.

Counts. — *A. brocki* exhibits clearcut differences from the three nominal species of this genus in having fewer photophores in the VAV + anterior AC series (17 or less in specimens 40 mm SL or longer, Figure 2, as compared with 18-28), fewer photophores in the posterior AC series (9-11 as compared with 12-18), fewer gill rakers (15-17 as compared with 18-26), and fewer vertebrae (41-43 as compared with 44-46).

Measurements. — *A. brocki* differs from *A. ephippiatus* in possessing a smaller bony orbit, greater interorbital distance, and (in specimens longer than 70 mm SL) a greater distance from snout to anal fin origin. It differs from *A. atlanticus* in possessing a greater interorbital distance, longer snout, longer upper jaw (and accordingly, a longer premaxillary and maxillary), a greater body depth, longer dorsal fin base, and a greater snout to anal fin origin distance. It differs from *A. iridescens* in that it possesses a greater interorbital distance.

Description

Meristics. — The meristics for the 20 specimens in the type series are summarized below and in Table 1. Supplementary counts for certain characters were obtained from specimens not included in the type series. The number of specimens having a particular count is given in parentheses. Occasionally, only one side of bilaterally symmetrical structures could be counted.

Gill rakers on first arch (counts for the right upper and lower limbs given first): 4/4 + 11/11(1), 4/4 + 11/12(1), 4/4 + 12/12(12), 4/5 + 12/12(2), 4/4 + 12/3(2), 5/5 + 12/12(2). The four specimens with five gill rakers on the upper limb were small, being 41-56 mm SL. Pelvic rays: 7(19). Caudal rays (primary): 10 superior, 9 inferior (20). Branchiostegals: 7 + 3 = 10(20).

Only the combined VAV + anterior AC and the posterior AC series of photophores exhibit variation. ORB: 1/1(20). OP: 3/3(20). BR: 6/6(44). IV series — IP: 6/6(43), PV: 10/10 (43). OA: 7/7(44). Middle AC: 5/5(44). Posterior AC 9-11 (Table 1). There is no obvious relation between specimen size and numbers of posterior AC photophores. The number of photophores in the VAV + anterior AC series increases with size until the full complement

TABLE 1.—Summary of meristics of four species of *Argyripnus*. Frequency data are not available for *A. atlanticus* except one vertebral count (Grey, 1964).

Total gill rakers	15	15.5	16	16.5	17	17.5	18	18.5	19	19.5	20	20.5	21	21.5	22	23	24	25	26
A. brocki	1	1	12	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. ephippiatus	—	—	—	—	—	—	2	4	20	4	—	—	—	—	—	—	—	—	—
A. iridescens	—	—	—	—	—	—	—	—	—	—	—	1	6	1	1	—	—	—	—
A. atlanticus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+

Posterior AC photophores	9	9.5	10	10.5	11	11.5	12	12.5	13	13.5	14	15	16	17	18
A. brocki	1	2	26	5	7	—	—	—	—	—	—	—	—	—	—
A. ephippiatus	—	—	—	—	—	—	2	2	15	1	10	—	—	—	—
A. iridescens	—	—	—	—	—	—	5	—	2	—	1	—	—	—	—
A. atlanticus	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+

Pectoral rays	13	13.5	14	14.5	15	15.5	16	16.5	17	18	19
A. brocki	1	—	9	5	18	—	2	—	—	—	—
A. ephippiatus	—	—	2	3	20	2	1	—	—	—	—
A. iridescens	—	—	—	—	—	—	3	1	5	—	—
A. atlanticus	—	—	—	—	—	—	—	—	+	+	+

Dorsal rays	10	11	12	13
A. brocki	1	21	8	—
A. ephippiatus	—	10	1	—
A. irridescens	—	1	6	2
A. atlanticus	—	+	+	—

First anal rays	10	11	12	13	14	15
A. brocki	1	18	11	—	—	—
A. ephippiatus	—	2	24	3	—	—
A. iridescens	—	—	—	1	6	—
A. atlanticus	—	—	—	+	+	+

Total anal rays	19	20	21	22	23	24	25
A. brocki	2	3	11	12	1	1	—
A. ephippiatus	—	—	1	7	16	5	—
A. iridescens	—	—	—	—	1	2	4
A. atlanticus	—	—	—	+	+	+	+

Second anal rays	8	9	10	11	12
A. brocki	1	4	20	4	1
A. ephippiatus	—	—	8	18	3
A. iridescens	—	—	3	4	—
A. atlanticus	—	+	—	—	—

Total vertebrae	41	42	43	44	45	46
A. brocki	5	17	1	—	—	—
A. ephippiatus	—	—	—	16	2	—
A. iridescens	—	—	—	—	12	5
A. atlanticus	—	—	—	—	—	1

of 14-17 photophores is attained in specimens longer than about 65 mm SL (Figure 2). Counts for specimens in which the two sides varied are given as the average of the two.

Vertebral counts were obtained from the 20 specimens in the type series and three cleared and stained specimens. Frequency of occurrence was as follows (including urostyle): 41 vertebrae (15 precaudal + 26 caudal), 5 specimens; 42 (15 + 27), 17 specimens; 43 (15 + 28), 1 specimen. Of the five specimens with 41 vertebrae, three exhibited double neural and/or haemal spines on the penultimate vertebra. Vertebral counts for *A. ephippiatus* and *A. iridescens* are given below. Only one vertebral count (46 total) is available for *A. atlanticus* (Grey, 1964).

The number of teeth on the maxillary bone of *A. brocki* (as well as *A. ephippiatus* and *A. iridescens*) increases with growth, there being 15-16 teeth at a SL of about 50 mm and 22-30 at about 90 mm. Although *A. brocki*

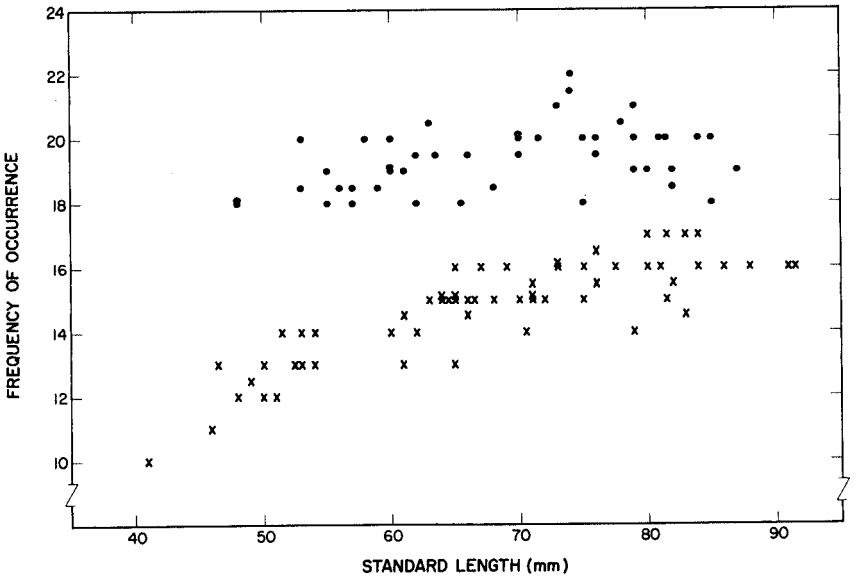

FIGURE 2.—Distribution of VAV + anterior AC photophores by standard length for 60 specimens of *Argyripnus brocki* (X) and 47 specimens of *A. ephippiatus* (dots).

exhibits a significant regression coefficient ($P < 0.001$) for this character, there is much variation ($r^2 = 0.503$) and considerable overlap with the other two species.

In addition to possessing diagnostically fewer VAV + anterior AC photophores, posterior photophores, gill rakers, and vertebrae, *A. brocki* exhibits further differences in numerical characters from the other three nominal species. The range in pectoral-ray numbers (13-16) for *A. brocki* although similar to *A. ephippiatus* (14-16) only slightly overlaps that of *A. iridescens* (16-17) and is less than that of *A. atlanticus* (17-19). The dorsal-ray counts are modally 11 for *A. brocki* and *A. ephippiatus*, while they are 12 for *A. iridescens*. The rays of the first anal fin of *A. brocki* (10-12) are fewer than for *A. iridescens* (13-14) and *A. atlanticus* (13-15), while they are modally one less than for *A. ephippiatus* (11-13). The number of rays in the second anal fin of *A. brocki* is modally one less than those of *A. ephippiatus*. Accordingly, *A. brocki* usually has one to two fewer total anal rays than *A. ephippiatus*.

Measurements.— The original measurements of the 20 specimens in the type series and their range as percent of SL are given in Table 2. Linear regressions were calculated and values for y-intercept, regression coefficient, and r^2 are also presented.

A. brocki does not differ greatly from the other species in most of the other body proportions not mentioned in the diagnosis. It does exhibit a strong tendency to be more deeply bodied than *A. ephippiatus*. Comparison with *A. iridescens* is difficult because only larger specimens are available for that species. The adipose fins of *Argyripnus* spp. exhibit considerable variation in the lengths of their bases and distances between their origins and the dorsal fins; much of this variation appears due to mechanical damage. In some specimens the adipose fin is completely missing.

The length-frequency distribution for 123 specimens of *A. brocki* is given in Figure 3. Females longer than 65-70 mm seem to be mature.

Color. — All three species examined have the same basic pigmentation pattern. The patch of black pigmentation on the upper portion of the body just behind the head is very seldom entire in specimens of *A. brocki* and *A. ephippiatus* because of chafing in the trawl, but it still appears that this patch is best developed in

TABLE 2.—*Argyripnus brocki*: Measurements (mm), ranges of proportions (percent SL), *y*-intercept (*a*), regression coefficient (*b*), and r^2 for the type series.

Standard length (mm)	46.5	50	51.2	52.5	54	56	64	64.5	65	66.5	70	70.5	75
Head length	14.5	16.6	16.0	16.0	16.5	16.5	19.0	20.6	20.6	20.0	21.0	21.8	21.5
Snout length	4.4	4.0	4.6	4.4	4.4	5.0	5.0	5.6	5.8	5.8	5.5	6.0	5.9
Orbit diameter	6.0	6.6	6.5	6.5	6.4	6.4	7.8	8.1	8.0	7.8	8.7	9.0	9.2
Interorbit width	3.8	4.0	4.2	3.8	3.8	4.2	5.0	5.2	5.0	5.2	5.2	5.9	5.4
Length of upper jaw	11.0	11.4	11.5	11.2	12.0	12.2	14.5	15.6	15.0	15.0	16.0	16.5	17.0
Length of premaxillary	5.0	5.8	5.0	5.5	5.5	6.0	6.5	6.5	7.0	7.6	7.8	7.0	7.5
Length of maxillary (toothed portion)	7.0	7.4	8.0	7.2	8.0	7.8	9.2	10.0	9.6	9.0	10.2	11.5	11.2
Greatest body depth	13.4	14.8	16.0	14.2	15.0	15.0	19.0	18.2	19.0	19.0	21.0	21.0	22.5
Least depth caudal peduncle	4.9	5.0	5.2	4.9	5.6	5.5	7.0	6.6	6.8	7.0	7.0	7.5	7.2
Length of pectoral fin	11.8	14.0	13.0	12.8	13.6	13.4	15.0	16.6	16.2	16.0	16.0	18.0	17.0
Length dorsal fin base	6.6	7.8	7.2	7.4	7.2	7.5	9.1	8.8	8.8	9.0	9.5	9.8	10.0
Length anal fin base	14.5	16.2	16.4	16.2	16.0	17.2	17.2	20.0	18.2	19.5	18.6	20.5	21.0
Length adipose fin base	5.0	5.2	4.0	—	—	4.0	—	5.8	4.4	—	3.6	—	—
Distance: dorsal to adipose	6.0	9.0	7.0	—	—	10.5	—	11.6	13.5	—	15.2	—	—
Snout to:													
Pectoral fin origin	13.2	14.8	15.5	15.0	15.0	16.0	19.0	19.0	19.0	19.4	20.0	20.4	22.0
Dorsal fin origin	22.0	24.0	24.5	25.5	25.0	26.0	31.5	31.0	32.0	31.0	32.8	34.4	35.0
Anal fin origin	26.0	28.0	28.6	28.8	29.5	31.0	35.0	38.0	36.5	39.0	40.0	40.5	46.0

Standard length (mm)	77.5	80	[1]81.5	83	84	91	91.5	Range percent SL	*a*	*b*	r^2
Head length	24.0	23.6	25.4	27.0	25.0	28.0	28.2	28.7-33.2	0.44	0.301	0.970
Snout length	6.5	6.4	7.0	7.0	7.4	7.8	7.8	7.8- 9.5	0.19	0.082	0.948
Orbit diameter	8.9	9.0	10.0	10.6	9.6	11.0	10.4	11.3-13.2	0.85	0.109	0.948
Interorbit width	6.2	6.0	6.0	6.6	6.8	7.2	7.0	7.0- 8.4	-0.03	0.078	0.952
Length of upper jaw	19.0	18.0	19.0	20.0	20.0	22.0	21.5	21.3-24.5	-1.60	0.255	0.983
Length of premaxillary	8.0	7.0	7.9	8.1	8.0	9.0	8.8	8.8-11.6	1.33	0.082	0.897
Length of maxillary (tooth portion)	12.2	12.0	12.6	13.6	13.2	14.8	14.2	13.5-16.4	-1.57	0.17	0.964
Greatest body depth	23.0	23.5	23.0	27.0	26.0	27.5	27.0	26.8-32.5	-2.02	0.324	0.967
Least depth caudal peduncle	7.2	8.0	7.8	8.5	8.2	8.8	9.0	9.3-10.9	0.55	0.092	0.954
Length of pectoral fin	19.0	17.5	19.5	18.5	20.0	21.0	21.5	21.9-28.0	2.90	0.198	0.939
Length dorsal fin base	11.0	11.5	11.9	11.5	12.0	12.5	13.0	13.3-15.6	-0.04	0.140	0.973
Length anal fin base	23.4	22.0	23.0	23.2	23.0	25.0	25.0	26.6-32.4	4.15	0.228	0.947
Length adipose fin base	5.5	6.1	6.0	8.1	6.0	5.0	7.0	5.1-10.8	2.07	0.047	0.349
Distance: dorsal to adipose	14.5	15.0	15.0	13.5	15.0	16.6	19.0	12.9-21.7	6.94	0.114	0.205
Snout to:											
Pectoral fin origin	23.0	23.0	24.0	25.2	26.0	28.0	27.2	27.8-31.0	-1.58	0.317	0.989
Dorsal fin origin	38.0	39.5	40.8	42.0	41.0	45.0	45.0	46.3-50.6	-2.52	0.521	0.990
Anal fin origin	46.0	47.0	49.5	50.2	50.0	55.8	55.0	54.6-61.3	-6.52	0.677	0.992

[1] Holotype.

A. iridescens. The black patch on the caudal peduncle is best developed in *A. brocki*, less so in *A. ephippiatus*, and is weakest in *A. iridescens*. Some specimens of *A. iridescens* possess pigmentation on the distal portions of the dorsal rays, a condition not observed in the other two species. In fresh specimens of *A. brocki* and *A. ephippiatus*, the body musculature is translucent.

Etymology. — Named for the late Vernon E. Brock in recognition of his contributions to marine biology and his encouragement and support of my studies on Hawaiian bathyal fishes.

ARGYRIPNUS EPHIPPIATUS GILBERT AND CRAMER

Measurements and counts were obtained from the following material: 12 specimens (of 256), USNM 207663, 53-87 mm SL, station TC-33-29, Kealaikahiki Channel (lat. 20°35.0′ N, long. 156°50.9′W), 1915-2100, 4 November 1967, 412 m, 7-m ST. Three specimens (of 189) USNM 207664, 62-78 mm SL, station TC-33-30, Kealaikahiki Channel (lat. 20°34.1′N, long. 156°52.2′W), 0010-0210, 5 November 1967, 400 m, 7-m ST. *A. ephippiatus* was taken at eight

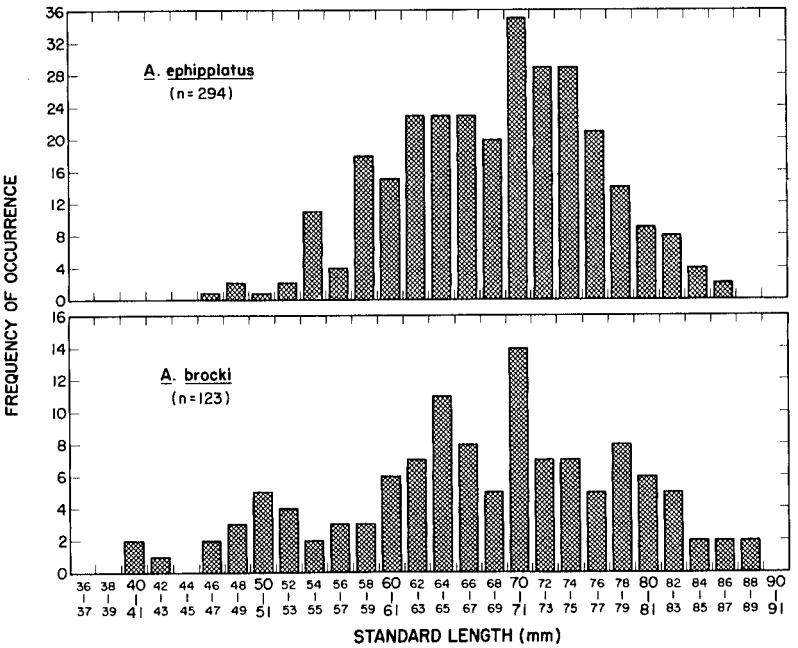

FIGURE 3.—Length-frequency distributions for 123 specimens of *Argyripnus brocki* and 294 specimens of *A. ephippiatus*.

additional stations (2-8 specimens per station), all in the 325- to 450-m depth range.

Measurements obtained from the 15 specimens are given in Table 3, while some of the counts (supplemented by randomly selected individuals from the same stations) are summarized in Table 1. The length-frequency distribution for 294 specimens is given in Figure 3. As in the case of *A. brocki*, *A. ephippiatus* females longer than 65-70 mm seem to be mature.

Gill rakers on the first arch: 5/5 + 13/13(2), 5/5 + 13/14(4), 5/5 + 14/14(20), 5/5 + 14/15(2), 6/5 + 14/14(2). Pelvic rays: 7(13). Caudal rays (primary): 10 superior and 9 inferior (9). Branchiostegals: 7 + 3 = 10(15).

ORB: 1/1(15). OP: 3/3(15). BR: 6/6(15). IV series — IP: 6/6(12), PV: 10/10(12). OA: 7/7(15). Middle AC: 4/4(1), 5/5(28). Posterior AC: 12-14: (Table 1). There was no obvious relation between specimen size and number of posterior AC photophores. The number of VAV + anterior AC photophores (18-22) also increases with growth in *A. ephippiatus*, although the variation within the observed size range is not as pronounced as for *A. brocki*. The linear regression coefficient obtained for the photophore-SL relations for 47 specimens of *A. ephippiatus* (Figure 2) is significant ($P < 0.01$, but r^2 is only 0.145).

Total vertebrae for 18 specimens ranged from 44 to 45: 14 precaudal + 30 caudal, 2 specimens; 15 + 29, 14 specimens; 15 + 30, 2 specimens.

ARGYRIPNUS IRIDESCENS McCULLOCH

I have examined nine specimens of McCulloch's type series deposited in The Australian Museum. Each specimen is individually tagged, and the measurements I obtained from them are given in Table 4. Some of the counts are summarized in Table 2.

Gill rakers: 6/6 + 14/15(1), 6/6 + 15/15(6), 7/7 + 15/15(1), 6/6 + 15/16(1). Pelvic rays: 7(9). Caudal rays: 10 superior, 9 inferior (9). Branchiostegal rays: 7 + 3 = 10(9).

TABLE 3.—*Argyripnus ephippiatus:* Measurements (mm), range of proportions (percent SL), *y*-intercept (*a*), regression coefficient (*b*), and r^2 for 15 specimens.

Standard length (mm)	53	62	63	65.5	66	70	71.5	73	74	75	76	78	79	81.5	87	Range percent SL	*a*	*b*	r^2
Head length	17.4	20.6	22.0	21.0	20.0	20.4	24.0	22.0	22.2	24.4	23.5	24.0	27.0	24.0	27.0	29.1-34.9	3.57	0.266	0.787
Snout length	5.0	5.0	5.2	5.2	5.2	5.5	5.8	5.6	6.0	6.6	6.2	5.8	6.4	6.1	6.5	7.4- 9.4	1.29	0.055	0.761
Orbit diameter	7.6	9.0	9.3	9.4	9.0	9.6	10.2	10.0	10.0	10.2	10.7	11.0	11.6	11.5	12.0	13.5-14.8	0.70	0.131	0.945
interorbit width	3.3	3.8	3.5	3.6	3.6	3.9	4.7	4.6	4.2	5.0	4.8	5.0	4.5	5.1	—	5.5- 6.7	-0.78	0.071	0.787
Length of upper jaw	12.8	15.2	15.8	15.5	15.9	16.8	17.0	16.8	16.8	18.1	17.5	17.6	18.6	19.0	21.0	22.6-25.1	1.74	0.212	0.945
Length of premaxillary	6.3	7.0	7.6	7.0	7.0	7.8	8.0	8.0	8.0	8.2	8.0	8.0	8.5	8.0	8.4	9.7-12.1	3.14	0.064	0.804
Length of maxillary (toothed portion)	8.0	10.1	10.2	10.0	10.9	11.0	11.5	11.0	10.8	11.2	11.2	12.2	12.5	13.0	14.0	14.6-16.5	0.03	0.156	0.907
Greatest body depth	14.6	17.8	18.0	17.0	17.8	20.0	20.0	20.0	19.5	20.0	20.0	21.0	22.6	21.6	25.2	26.0-28.9	-0.05	0.275	0.909
Least depth caudal peduncle	4.9	5.8	6.2	5.8	6.2	6.3	6.8	6.8	7.0	6.3	6.4	7.2	7.7	7.8	7.5	8.4- 9.8	0.63	0.083	0.828
Length of pectoral fin	13.0	14.5	16.2	16.5	17.0	18.0	17.2	18.0	17.8	17.0	18.5	17.0	19.6	19.0	21.0	21.8-25.8	2.58	0.206	0.845
Length dorsal fin base	—	7.8	7.5	8.4	8.0	9.5	8.4	9.0	9.0	10.0	9.2	10.0	10.0	11.0	—	11.7-13.6	-1.77	0.151	0.841
Length anal fin base	17.0	20.0	20.0	21.0	21.5	22.0	23.0	24.0	22.0	24.5	23.0	26.0	25.5	25.5	27.0	29.7-33.3	1.25	0.301	0.930
Length adipose fin base	—	—	—	—	—	—	6.2	—	—	—	—	8	—	—	—	8.7-10.3	—	—	—
Distance:dorsal to adipose	—	—	—	—	—	—	13.0	—	—	—	12	—	—	—	—	15.4-18.2	—	—	—
Snout to:																			
Pectoral fin origin	16.0	18.0	19.3	18.8	20.0	20.0	21.0	20.6	22.4	22.0	22.8	22.2	23.8	23.9	27.0	28.2-31.0	-0.63	0.305	0.945
Dorsal fin origin	24.5	29.0	29.0	29.6	30.0	32.2	33.5	33.0	35.5	36.0	34.5	36.0	38.8	37.5	41.5	45.2-49.1	-2.49	0.499	0.965
Anal fin origin	29.0	33.5	35.0	36.0	36.5	38.0	39.5	40.0	41.5	40.0	41.8	42.4	42.0	44.0	47.5	53.0-56.5	1.38	0.527	0.985

Counts for the ORB, OP, BR, IP, and PV series are as for other species of *Argyripnus*. VAV + anterior AC: 19.5(2), 20(7). Middle AC: 5(9). Posterior AC 12-14 (Table 1).

Total vertebrae for 17 specimens (radiographs obtained for 8 unexamined specimens) ranged from 45 to 46: 15 precaudal + 30 caudal, 12 specimens (including holotype); 15 + 31, 3 specimens; 16 + 30, 2 specimens.

McCulloch (1926) stated that *A. iridescens* was so similar to *A. ephippiatus* that he separated the two species with hesitation. The new counts presented here for the two species indicate that they should continue to be recognized.

ARGYRIPNUS SPP.

I have examined the following three specimens of *Argyripnus:* (1) 51 mm SL, USNM 207984. RV *Anton Bruun* cruise 9, station 422, Indian Ocean, lat. 6°51′N, long. 39°54′E, 19 November 1964, 100 m, midwater trawl. (2) 64 mm SL, SIO 69-19-10 (Scripps Institution of Oceanography Circe Expedition, Celebes Sea), lat. 06°00′N, long. 122°36′E, 21 April 1968, midwater trawl. (3) USNM 135402, 78 mm SL. This is the same Philippine specimen treated by Grey (1961).

Measurements obtained on selected body parts are given in Table 4. Counts that were obtained on characters that show variation in other species of *Argyripnus* are as follows (values given are for the respective specimen number). VAV + anterior AC photophores: 15, 16, 18. Posterior AC photophores: 10, 11, 12. Gill rakers: 4/4 + 11/11, 4/4 + 12/12, 2/4 + 9/12. There is no indication that the right gill arch has been damaged on the third specimen, but the higher count is taken to be "correct." Pectoral rays: 15, 17, 15. Dorsal rays: ca. 13, 12, 10. First anal rays: ca. 11, 13, 11. Second anal rays: ca. 9, 10, not available.

TABLE 4.—Measurements (mm) of nine *Argyripnus iridescens*, one *A. brocki* from the Indian Ocean (USNM 207984), and two specimens of undetermined species of *Argyripnus* (last two columns).

Specimen number	IA1347	IA1346	E4369	IA1345	E6586	E6584	IA1344	IA1349	IA1348	Range percent SL	USNM 207984	SIO 69-19-10	USNM 135402
Standard length (mm)	83.5	85	98	98	98.5	101	104	108	112	—	51	64	78
Head length	26.0	26.0	28.0	31.0	29.5	30.5	32.0	32.3	34.0	28.6-31.6	16.5	19.7	27.0
Snout length	7.0	6.6	7.5	7.0	7.6	8.0	8.0	8.2	9.5	7.1- 8.5	4.4	5.2	7.0
Orbit diameter	10.0	11.0	12.0	11.6	12.4	12.2	13.0	12.8	14.0	11.8-12.9	6.9	7.8	11.8
Interorbit width	5.4	5.2	5.9	6.0	6.0	6.0	6.8	7.0	7.0	5.9- 6.5	3.2	4.1	5.8
Length of upper jaw	18.6	18.0	21.8	21.0	21.5	23.0	23.0	23.6	25.0	21.2-22.8	12.5	15.0	19.0
Length of premaxillary	8.0	8.0	9.0	8.5	7.8	10.0	9.8	9.4	9.5	7.9- 9.9	6.0	5.8	9.0
Length of maxillary (toothed portion)	12.6	12.6	14.5	14.9	15.0	15.0	16.0	16.2	17.0	14. -15.4	8.0	11.0	13.0
Greatest body depth	21.5	23.0	27.5	27.0	26.0	30.0	30.0	31.9	32.5	25.7-29.5	15.0	18.0	22.0
Least depth caudal peduncle	7.8	8.0	9.0	8.1	8.8	—	9.2	9.6	10.0	8.3- 9.4	5.0	6.1	7.4
Length of pectoral fin	20.0	21.0	23.0	23.0	22.5	23.0	24.0	24.5	26.5	22.8-24.7	12.0	—	17.0
Length dorsal fin base	11.3	11.0	12.2	13.0	13.0	13.0	13.0	15.0	14.2	12.4-13.9	9.0	9.0	12.0
Length anal fin base	27.7	27.0	29.5	32.0	31.0	31.0	30.0	35.0	37.0	28.8-33.2	15.0	20.0	26.0
Length adipose fin base	4.2	7.0	6.2	6.0	9.0	9.0	8.0	6.8	5.5	4.9- 9.1	—	—	—
Distance: dorsal to adipose	14.6	14.0	18.0	15.0	17.0	18.0	19.0	17.0	18.0	15.3-18.4	—	—	—
Snout to:													
Pectoral fin origin	23.0	23.0	29.0	29.0	27.5	29.5	28.5	30.0	32.2	27.1-29.6	15.0	19.2	25.0
Dorsal fin origin	40.0	41.0	48.0	48.0	48.5	50.0	52.0	51.0	55.0	47.2-50.0	23.5	29.0	39.0
Anal fin origin	46.5	47.0	55.0	57.0	56.0	57.0	61.0	61.0	64.0	55.3-58.7	27.0	—	45.0

Vertebrae: 42 (15 precaudal + 27 caudal), 44 (15 + 29), 44 (15 + 29).

I tentatively assign the 51-mm specimen from the Indian Ocean to *A. brocki*. The specimen shares in common with the Hawaiian type series 19 of 23 morphological and meristic characters, including the four diagnostic counts (VAV + anterior AC photophores, posterior AC photophores, gill rakers, and vertebrae). It does not agree with the range of interorbital measurements obtained from the type series (a diagnostic character), but this may be due to geographical variation or distortion of the small specimen. Thus, the distribution of *A. brocki* may extend from Hawaii to the Indian Ocean.

Although the remaining two specimens certainly do not represent *A. atlanticus*, I cannot definitely assign them to a species because, to varying extents, they share characters with *A. brocki*, *A. ephippiatus*, and *A. iridescens*. For example, the Philippine specimen exhibits 10 body proportions similar to both *A. ephippiatus* and *A. brocki*, 3 proportions characteristic of *A. ephippiatus*, and 3 proportions characteristic of *A. brocki*. With regard to counts, there are two characters common to both *A. ephippiatus* and *A. brocki*, one common to *A. ephippiatus*, two common to *A. brocki*, and one shared by both *A. ephippiatus* and *A. iridescens*.

While this report was in press I had the opportunity to examine an approximately 60-mm SL specimen of an undetermined species of *Argyripnus* taken from the stomach of a specimen of *Etelis* captured at a depth of 280 m outside of "Grand Récif," New Caledonia. The specimen is in poor condition and only the vertebrae and gill rakers may be counted with certainty. The total vertebral count of 42 (14 + 28) places this specimen within the range of vertebral counts for *A. brocki*. However, the only *Argyripnus* specimens I have examined that possess 14 precaudal vertebrae are two individuals representing *A. ephippiatus* (all other specimens have 15 or 16 precaudal vertebrae). The gill raker count of 3 + 10 = 13 (for both sides) is two less than the lowest count obtained for *A. brocki* (which has the lowest gill raker counts of the four species treated here). The stomach of the New Caledonia *Argyripnus* specimen contains an undetermined myctophid. I thank P. Fourmanoir and Robert K. Johnson for making this specimen available for study.

ECOLOGY

The capture of large numbers of *Argyripnus* in bottom-fishing gear strongly indicates that the genus is essentially a member of the near-bottom (demersal, engybenthic) bathyal ichthyofauna. In the case of the Hawaiian specimens reported here, it seems improbable that such large numbers of *Argyripnus* would be taken during the short periods of time that the bottom-fishing trawls are effectively sampling the midwater environment. This premise is argued for by the absence of the genus in the numerous midwater trawl stations occupied by NMFS and the University of Hawaii (Thomas A. Clarke, pers. comm.) within a few miles of the Hawaiian Islands. Additionally, if the species were pelagic and being captured during the setting and hauling of the trawl, then they would be expected to be present in all the deeper hauls, including those exceeding the apparent optimal depths of the two species as indicated by the data presented here. The two specimens taken in the Indian Ocean and the Celebes Sea by midwater trawls are most likely individuals that have been displaced from the bathyal environment. If the young of this genus are pelagic like other stomiatoids, it should not be surprising to occasionally encounter a small specimen offshore. However, the possibility of established breeding populations of the genus in the oceanic realm cannot be ruled out at present.

A. brocki and *A. ephippiatus* were never taken in the same trawl haul. The capture records show that the vertical distributions of the two species do not overlap: *A. brocki* was taken at 17 stations in depths of 180-280 m, while *A. ephippiatus* appeared at 10 stations in depths of 325-450 m. This must be one of the few examples of sympatric congeneric bathyal fish species not exhibiting some degree of overlap in their vertical distributions.

A. brocki and *A. ephippiatus* were never taken between dusk and dawn. Possibly this species undergoes diel vertical migrations over the sea bottom as has been hypothesized for several other species of Hawaiian bathyal fishes (Struhsaker, 1973). Because of the relatively small numbers of specimens taken, however, the effect of net avoidance during daylight hours cannot be discounted at present.

ACKNOWLEDGMENTS

I thank John C. Marr and Richard S. Shomura for the opportunity to examine the study material. John R. Paxton made available specimens and radiographs of *A. iridescens* from The Australian Museum. Other radiographs were provided by Scripps Institution of Oceanography and the Systematics Laboratory, NMFS. Richard H. Rosenblatt and Robert K. Johnson loaned the specimen of *Argyripnus* from the Celebes Sea and reviewed the manuscript. I am indebted to Robert H. Gibbs, Jr., and Stanley H. Weitzman for review of the manuscript. The illustrations are by Tamotsu Nakata. Much of this work was supported by the Hawaii Institute of Marine Biology, University of Hawaii, and is HIMB contribution No. 393.

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DIGITAL HYDROACOUSTIC DATA-PROCESSING SYSTEM AND ITS APPLICATION TO PACIFIC HAKE STOCK ASSESSMENT IN PORT SUSAN, WASHINGTON[1]

RICHARD E. THORNE[2]

ABSTRACT

A digital hydroacoustic data-processing system was developed at the University of Washington utilizing the general-purpose computer PDP/8L. The system, which functions as a 20-channel squared voltage integrator, was applied to the annual assessment of the spawning stock of Pacific hake, *Merluccius productus*, in Port Susan, Wash. Four surveys were conducted between 14 and 16 March 1971. The population estimates based on calibration by net hauls ranged from 15.9 to 18.8 million lb. An estimate of 18.2 million lb was obtained with an analog voltage integrator for one of the surveys. The digital system provided more detailed information on the horizontal and vertical distribution of the fish and resulted in a much smaller variance of the estimated mean fish density than the analog system.

Echo sounders have been used extensively since 1950 as a means of studying the distribution and relative abundance of fish populations, but only during the last decade has the tedious interpretation of echograms begun to be obviated by the development of electronic devices for automated signal processing. These are basically of two types, echo counters (Mitson and Wood, 1961; Carpenter, 1967; Dowd, 1969) and echo integrators (Dragesund and Olsen, 1965). The principles governing the application of acoustics to fish abundance estimation are described in Parrish (1969).

An analog echo integrator was designed and built at the University of Washington (Lahore, 1969) as part of a general study of acoustic methods of resource assessment in the University's Sea Grant Marine Acoustics Program. It was used in investigations of the relationship between integrated echo voltage and fish density (Thorne, 1971) and of the population size of juvenile sockeye salmon, *Oncorhynchus nerka*, in Lake Washington in 1969 (Thorne and Woodey, 1970) and of Pacific hake, *Merluccius productus*, in Port Susan in 1969 and 1970 (Thorne, Reeves, and Millikan, 1971). It became apparent during these investigations that integration with analog echo integrators had several disadvantages, such as instability and limited dynamic range, which could be eliminated by suitable digital circuitry. Consequently, a digital processing system was designed and built around a small general-purpose computer. A preliminary report of the Digital Data-Acquisition and -Processing System (DDAPS) was reported in Moose, Thorne, and Nelson (1971). A detailed description of the system and its initial application to the population assessment of Pacific hake in Port Susan, Puget Sound, Wash., in 1971, is presented here.

MATERIALS AND METHODS

The Digital Data-Acquisition and -Processing System

The DDAPS is constructed for use with the general-purpose computer PDP/8L, 4 K memory, manufactured by Digital Equipment Company. A block diagram is shown in Figure 1. The amplified signals from either one or two echo sounder transducers are envelope detected, low pass filtered, multiplexed (should two sounders be in use), A/D converted into 8-bit binary words, and then digitally squared in a

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Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

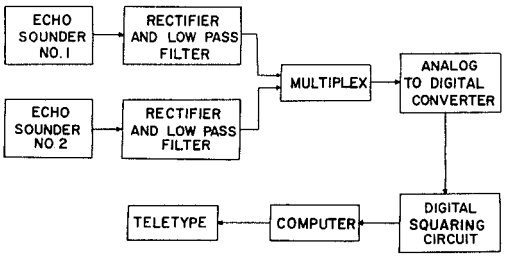

FIGURE 1.—Block diagram of Digital Data-Acquisition and -Processing System (DDAPS).

hardwired 8- × 8-bit multiplier. Squaring results in an output that is proportional to acoustic intensity (Thorne, 1971). Conversion to digital form before squaring eliminates the problems with dynamic range associated with analog voltage squared integrators. The 12 most significant bits of the square are retained and transmitted to the PDP/8L central processing section.

The processing section adds the squared data words to the appropriate integrator. Ten contiguous depth intervals are provided for each sounder, so that a maximum of 20 integrations may be operating simultaneously.

Overall timing for the system comes from the echo sounders. An initiation pulse signals the computer to begin data processing. A bottom signal indicates to the computer that the sea floor has been reached. Thus the bottom can be tracked and integration terminated a short distance above it. The magnitude of this distance is an input value to the computer and generally depends on the steepness of the slopes. Typical values are 2 to 3 m. If occasional bottom echos are too weak to activate the bottom indicator signal, the computer automatically terminates integration just above the last known bottom depth. The bottom can also be tracked manually under circumstances, such as extremely steep slopes, where the bottom signal is consistently too weak to be followed automatically.

The program keeps count of the transmitted signals, and when the count reaches the input value for "number of pings," processing terminates. Alternately, the operator may terminate processing by setting a sense switch.

In the output section, the integrator value is teletyped for each depth interval for each sounder. Using input constants relating integration to fish density, the program then calculates the fish density from the integrator values, automatically correcting for depth. An example of the output is given in Figure 2. The mathematical relationship between integration and fish density is detailed in Thorne (1970), Moose and Ehrenberg (1971), and Moose, Ehrenberg, and Green (1971). The constant relating fish density to integration from any echo sounder can be calculated when the target strength of the fish and absolute calibration of the sounder and transducer are known. Alternately, the constant may be determined indirectly by calibration of the integration against other measures of fish density, such as net hauls or echo counts (Thorne, 1971, 1972).

The hardware of the DDAPS, with the exception of the teletype, is contained in a 4-foot-high, 19-inch relay rack. The special circuitry is packaged on 4- × 6-inch, plug-in, wire-wrapped cards. All digital circuitry is integrated circuit, TTL logic. The system is highly portable and is easily moved from laboratory to ship in several hours. It is intended for processing data aboard ship in real time, and in

Number of Pings

P = 145

Upper limit of Depth interval (m)	Integration	Density (fish/m^3)	Number of Samples
20	4334	+0.650E-03	78445
60	26948	+0.885E-02	58870
90	32777	+0.174E-01	44940

FIGURE 2.—Sample DDAPS output for one echosounder and three depth intervals.

the laboratory from either digital or analog magnetic tape.

Survey Area and Methods

Port Susan (Figure 3) is exceptionally well suited to hydroacoustic assessment studies. It is a long, narrow basin with steep sides and relatively uniform depth (between 100 and 120 m). Each winter large concentrations of Pacific hake enter Port Susan to spawn. They occupy depth strata below 50 m and make up over 90% of the biomass in these depths. An industrial fishery was initiated in Puget Sound in 1965. Annual landings have ranged from 6.3 to 10.6 million lb, over 80% of which have come from Port Susan (Millikan, 1970). Acoustical censusing of Pacific hake in Port Susan was undertaken in 1969 and 1970 by the use of analog echo integrators (Thorne et al., 1971).

During 13 to 16 March 1971, 4 surveys and 21 net hauls were made for evaluation of the DDAPS. Each survey consisted of nine oblique transects spaced evenly throughout Port Susan (Figure 3). The net hauls and three of the surveys were conducted aboard the research vessel *John N. Cobb*, operated by the Northwest Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, Seattle. The fourth survey was conducted with a 23-foot inboard-outboard cruiser, *Research 1*, of the Washington State Department of Fisheries. Both vessels

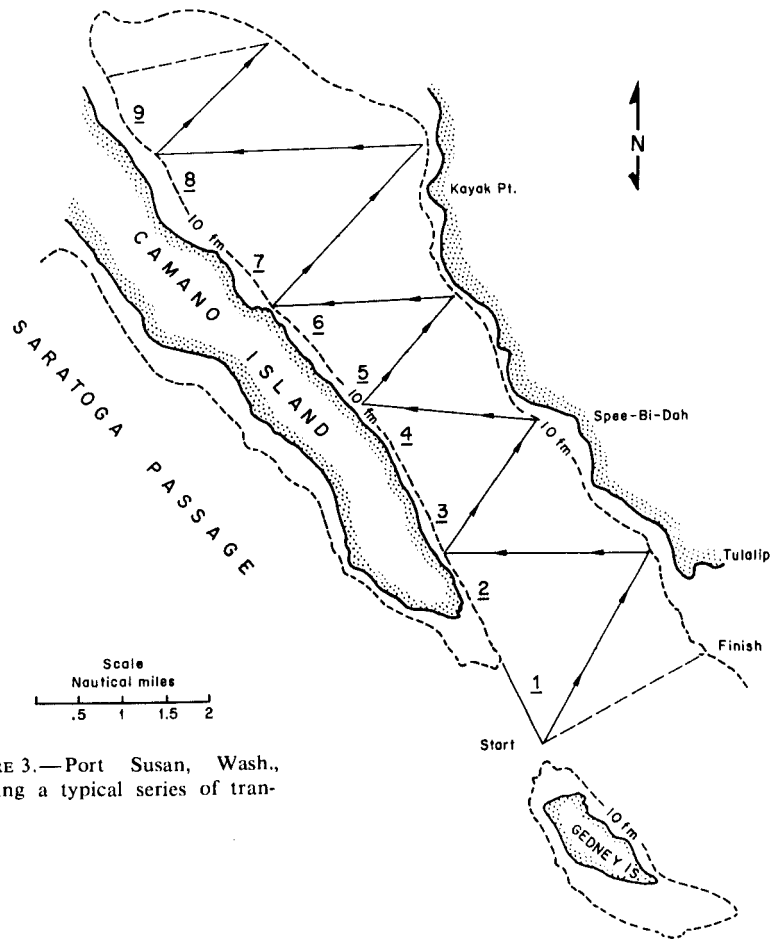

FIGURE 3.—Port Susan, Wash., showing a typical series of transects.

were equipped with Ross 200A Fineline echo sounders,[3] with a frequency of 105 kHz and a pulse length of 0.6 msec. The transducers produced circular beams approximately 8° full beam angles to the -6 dB points. The echo sounding data were heterodyned to 6 kHz and recorded on analog magnetic tape for later analysis. Details of the data-acquisition system are given in Thorne, Nunnallee, and Green (1972). Net hauls were made with the pelagic trawl described in Thorne (1971). The net filtered approximately 30,000 m^3 in a 10-min tow.

Data Analysis and Calibration

The echo data collected on magnetic tape during both the surveys and the net hauls were analyzed with the DDAPS. Integrated squared voltages were determined in 10-m depth strata from 60 m to 120 m. The relationship between integration and fish density was computed from the net catches as in previous surveys (Thorne et al., 1971). Integrated squared voltages were determined over the duration (10 min) of the net hauls, and fish densities were found from the net catches with an assumption of 100% net efficiency and regressed against the integrations from the corresponding 10-m depth strata including the mean depths of the net. The depths of the net were determined by the use of an electrical telemetry system (Lusz, 1967). Then this relationship was used to determine fish densities from the integrations along transects. During analysis of the data collected on transects, integrated voltages and corresponding densities were usually put out every one-third of each transect.

Data from one of the surveys (14 March) and the net hauls were also analyzed with an analog voltage integrator for comparison. The integrator used was the unsquared voltage integrator described by Thorne (1971). Integrated voltages were determined over 10-m intervals centered on the mean depths of the net. The relationship between integrated voltage and fish density was computed as above. Integrated voltages and corresponding densities were found over the complete duration of each transect in each of the depth intervals 60-75 m, 75-90 m, and 90 m to the bottom.

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

RESULTS

Relation Between Integrated Voltage and Net Catch

Net catches of Pacific hake and corresponding integrated voltages from the DDAPS are shown in Figure 4. The corresponding data from the analog echo integrator are shown in Figure 5. The integrated voltages from both systems are definitely linearly related to respective fish density as represented by catch. A linear regression model was fitted to the data from each integrator. The model was

$$D = bI$$

where D is catch in pounds of hake per 30,000 m^3, and I is the integrated voltage.

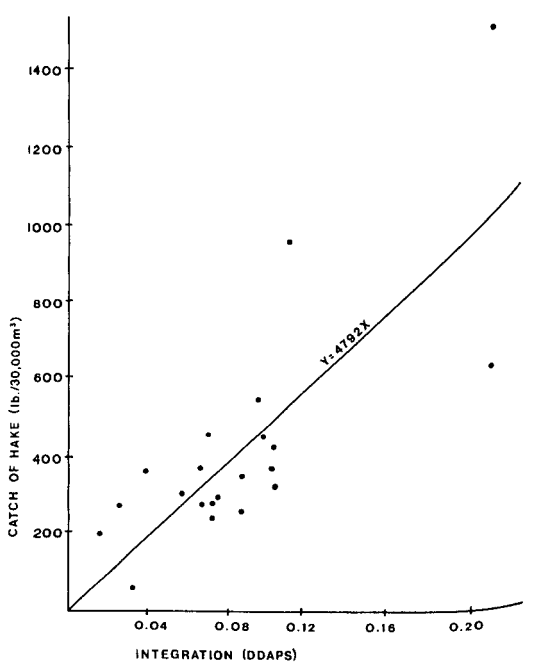

FIGURE 4.—Relation between catch of Pacific hake and integration output from DDAPS.

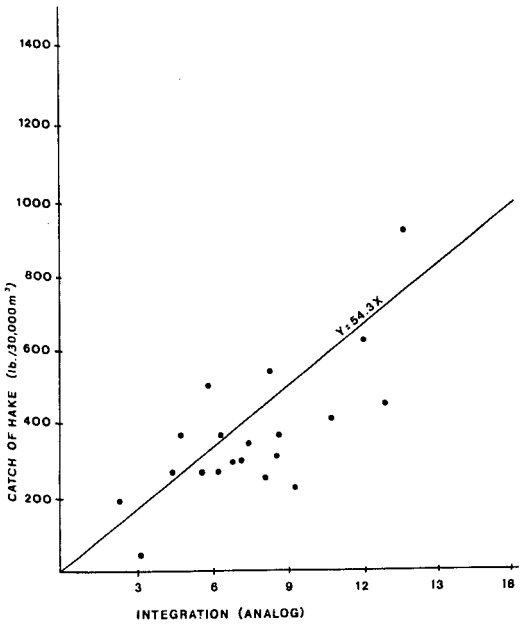

FIGURE 5.—Relation between catch of Pacific hake and integrated voltage from analog echo integrator.

The relative error of the beta coefficient was 8.0% for the analog integration data and 9.4% for the DDAPS, where relative error is defined as the ratio of the standard deviation of beta to beta expressed as a percentage.

Population Estimate

The number of integrated voltages and corresponding density observations from the DDAPS varied from 125 to 145 per survey. A weighted mean density of Pacific hake was determined for each survey and for all surveys combined. Each observation was weighted in proportion to the associated number of samples in the DDAPS output (Figure 2), which depended on the number of pings and the depth interval (10 m or less, depending on depth of bottom). The population of Pacific hake in Port Susan was estimated by multiplication of the estimated mean density of Pacific hake by the volume of water covered by the various surveys, expressed as the surface area at the 60-m contour (50×10^6 m^2) times the average depth interval. The average depth interval was obtained directly from the number of samples. Since the DDAPS reads the integrated voltages at a rate of 10,000 per second, or each 0.073 m of depth, the average depth surveyed during a transect series was the average number of samples per ping times 0.073 m. The weighted mean densities, associated variances, volumes, and estimated total biomasses for the four series and for all series combined are given in Table 1. The population estimates for the four series ranged from 15.9 to 18.8 $\times 10^6$ lb. These estimates are higher than the preliminary results reported in Moose, Thorne, and Nelson (1971) because of the greater area involved (50×10^6 m^2).

A weighted mean density was also determined for the survey analyzed with the analog echo integrator. The densities along each transect were weighted by the duration of the transect. Since depth was not determined directly, the volume was assumed to be the same as that determined with the DDAPS analysis of the same survey. The results of the analysis are also given in Table 1. The population estimate was 18.2 $\times 10^6$ lb.

TABLE 1.—Results of data analysis for various transect series.

Series		Mean density (lb/10^4 m^3)	Variance of mean	Volume (10^9 m^3)	Population estimate (10^6 lb)	Number of observations
DDAPS:						
John N. Cobb,	14 March	81	13.5	1.96	15.9	125
	16 March	98	13.3	1.76	17.2	142
	16 March	105	15.0	1.75	18.4	137
Research I,	16 March	83	18.8	2.26	18.8	145
All series grouped		93	3.96	1.90	17.7	549
Analog:						
John N. Cobb,	14 March	93	41.2	1.96	18.2	26

DISCUSSION

A major advantage of the digital processing system is the ability to estimate fish densities in a number of depth strata simultaneously. This ability allows detailed examination of the variation of density with depth. During the 1971 surveys in Port Susan the Pacific hake were uniformly distributed over both depths and transects, so that it was possible to consider all observations as estimates of the mean fish density. A slightly different distribution was found during the 1970 acoustic surveys, when two density strata were identified (Thorne et al., 1971). During the acoustic surveys in Port Susan in 1969 and 1970, integration was done directly off the sounders and a single output was obtained, including the entire depth range of interest. Thus only one estimate of density was obtained for each transect, and only 9 observations were made over a standard set of nine transects; whereas 26 observations were obtained from the 1971 survey processed with the analog integrator and 125-145 observations were taken with the DDAPS from 10-m depth strata and three outputs per transect. The increased number of outputs greatly decreased the variance of the estimated mean density. For example, Thorne et al. (1971) calculated that 36 transects (18 per stratum) were required to reach a precision of ±15% in 1970, neglecting variance in the calibration relationship. This level was reached in nine transects processed in three depth intervals with the analog integrator from magnetic tape in 1971, whereas precisions of about ±8% were shown for nine transects processed by the DDAPS, and a precision less than 5% for the combined four series (549 observations).

The estimates of total population from the four series processed with the DDAPS varied even less than the estimates of mean density because of an apparent inverse relationship between density and average bottom depth. It is possible that shallower areas had slightly higher fish densities. It is interesting to note that the range in estimated fish density for the four series was not much greater than the range in estimated average depth of Port Susan (mean 98 m, range 95-105 m).

A good linear relationship was obtained between catch and integrated voltage for both the digital and analog systems in 1971. The relative error of the beta coefficient for the relationship between integration and catch obtained in 1970 was quite large, 29% compared to less than 10% for both systems in 1971. Part of the variability in the 1970 results probably was associated with instability in the analog voltage-squared integrator.

The highly linear relationship between catch and integration from the 1971 analog voltage integrator was somewhat surprising. Since the integrated voltages were unsquared, the relationship should have deviated from linearity at higher densities (Thorne, 1971). However, densities were relatively low compared to the resolution of the system. The pulse resolution volume at the mean haul depth (80 m) was about 40 m^3, if an 8° cone and 0.6 msec pulse length are assumed. Thus a catch of about 525 lb (750 fish) would be equivalent to an average density of one fish per pulse resolution volume. Only four catches were greater than 525 lb. There is some indication that the highest two observations may be deviating from linearity. The ratio of fish density to integrated voltage associated with multiple targets would be greater and would tend to increase the magnitude of the beta coefficient over that expected from all single targets. This effect may account for the greater population estimate derived from the survey processed with the analog echo integrator.

Estimates of density of fish from an echo integrator are dependent upon determination of the individual fish's mean target strength (Moose, Ehrenberg, and Green, 1971). In acoustic studies of Pacific hake populations in Port Susan since 1969, the mean target strength has been determined indirectly from comparison of integrated voltage with net catches, on the assumption of 100% net efficiency. The procedure provides a valuable relative index for annual comparisons, but suffers from a large variability associated with the net catch and from possible bias in the assumptions concerning net efficiency. A relative error of 9.4% was associated with the calibration relationship between the catches from the 21 net hauls and

the integrated voltages from the DDAPS in 1971. The theoretical variance of the relationship should be considerably less according to the model of Moose and Ehrenberg (1971). The greater part of the observed variability is undoubtedly associated with the catching process. Further development and understanding of methods of target strength measurement are needed so that this variability may be reduced and absolute densities can be directly estimated.

ACKNOWLEDGMENTS

The digital data acquisition and processing system (DDAPS) was developed under the University of Washington Sea Grant Marine Acoustics Program in cooperation with the Northwest Fisheries Center, NMFS, Seattle. Both Sea Grant and NMFS are agencies of the National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

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LOSS OF SALMON FROM HIGH-SEAS GILLNETTING WITH REFERENCE TO THE JAPANESE SALMON MOTHERSHIP FISHERY

ROBERT R. FRENCH AND J. RICHARD DUNN[1]

ABSTRACT

Studies by the National Marine Fisheries Service on the loss (i.e., dropouts, those salmon that become unmeshed or otherwise escape from drifting gill nets; and fallouts, those salmon observed falling from gill nets as the gear is hauled aboard the vessel) of salmon due to high-seas gillnetting were conducted in the North Pacific Ocean and Bering Sea from 1964 to 1969. Losses attributed to dropouts and to predators and scavengers, as determined by indirect methods, were estimated as 32% for immature salmon for fishing periods up to 12.5 h (1964) and 27% for maturing salmon for a 3-h fishing period (1965). Loss estimates derived from direct observations in 1966-69 were 6, 14, and 41% for fishing periods up to 1, 2½, and 11 h, respectively. Estimates of losses of immature salmon were 46% up to 11 h and 20% for maturing salmon for the same time period. No losses were recorded for fishing periods of 3 h in an inshore commercial gill net fishery in Puget Sound, Wash., in August 1967.

Losses attributed to fallouts from U.S. research vessels during 1965-70 amounted to about 1.4% of the total number of salmon landed, a figure similar to that reported for Japanese research vessels.

The estimated annual loss from dropouts (including predators and scavengers) by the Japanese mothership fishery would range from 5.5 to 10.8 million fish in applying an estimated average loss of 20% (for maturing salmon) to 33% (for maturing and immature salmon combined) to the average annual catch of 22 million salmon by the mothership fleet. It was estimated that an average of 0.6 to 1.8 million sockeye salmon, *Oncorhynchus nerka*, of Bristol Bay, Alaska, origin would be lost annually from the Japanese mothership fishery (depending on total catch). The estimated annual loss due to fallouts (1% of landings) would average over 200,000 fish each year, of which 25,000 sockeye salmon of Bristol Bay origin would be lost on the average.

The estimated large numbers of salmon lost from gill nets (and probable high mortality of those fish escaping) indicate a relatively large waste of resources due to a high-seas gill net fishery.

For many years, Pacific salmon, *Oncorhynchus* spp., with gill net marks have been observed in coastal waters and in spawning streams, indicating they had escaped from gill nets. Percentages of net-marked salmon in some river systems have been substantial. For example, from 1944 to 1952, counts of gill net-marked salmon at a weir near Brooks Lake, Bristol Bay, Alaska, showed 6.3% of the annual escapement of salmon were net-marked (Nelson and Abegglen, 1955). Hanson, Zimmer, and Donaldson (1950) reported about 4% of the sockeye, *O. nerka*, and 6% of the chinook, *O. tshawytscha*, salmon on the Columbia River showed gill net wounds and scars in 1946. Talbot (1950) showed that the percentage of net-marked sockeye salmon in the daily catch below Hells Gate on the Fraser River during 1943-47 ranged from 0 to 75%.

With the advent of the Japanese offshore gill net fishery in 1952, Japan and the USSR have reported net injuries to salmon in coastal waters. Thus, Petrova (1964) reported that up to 15% of the salmon ascending the Bolshaya River (USSR) in recent years had gill net injuries. She observed that these net-marked fish were less effective as spawners; net-marked chum salmon, *O. keta*, retained more than 20% of their eggs and many died before spawning. Konda (1966) noted that as early as 1934, drift net fishing off the Kuril Islands was caus-

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Manuscript accepted January 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

ing a problem of net-injured salmon in the streams of Hokkaido Island, Japan. He also reported that up to 5% of the salmon in some streams in 1960 were gill net-marked.

These net-marked or injured salmon that are observed in coastal waters or in river systems are, of course, only the surviving salmon that have encountered and escaped either a high-seas or an inshore gill net fishery. The loss or dropout of salmon from high-seas gill nets has been recognized as a potentially serious loss to the resource by scientists of all nations concerned; however, neither the rates of fish dropping from the nets nor the number which perish are known. Doi (1962), in experiments on the high seas, estimated the rate of dropouts from examination of the catch in gill nets at 30-min intervals. He concluded that the rate of dropouts is a function of the time the fish are in the nets; that is, dropouts increase with time in the net. In Doi's experiments, dropout rates ranged up to 55% for coho salmon, *O. kisutch*, and 47% for sockeye salmon after periods of 5½ h. Miyazaki and Taketomi (1963, as cited by Konda, 1966) estimated a 20% loss of pink salmon, *O. gorbuscha*, from gill nets. Semko (1964), in discussing the irrationality of a high-seas salmon fishery, stated that a large mortality is inflicted in salmon by the drift nets and that the loss may amount to 30% of the catch. Konda (1966), while commenting on the loss of salmon from gill nets during hauling, stated that the ratio of live to dead fish is closely related to the length of time needed to haul the net. He further stated ". . . not only when hauling in the set, but even while setting the gillnet, no small number of fish will leave the net after having once been gilled, . . . " and ". . . as is well known, the gillnet is effective for high seas salmon fishing, however, it is always accompanied with a large loss of resources." Ishida et al. (1969) found salmon dropout rates of 4.2 to 24.1% in four experiments in the Okhotsk Sea. Thus, there is recognition of loss of resources due to dropouts during the drift of gill nets and due to fallouts during hauling of the fishing gear.

Because of the possible deleterious effects on U.S. salmon stocks by the Japanese high-seas gill net fishery, the former Seattle Biological Laboratory of the Bureau of Commercial Fisheries (now National Marine Fisheries Service) undertook studies on the loss of salmon owing to a gill net fishery in 1964.

Progress on these studies has been reported in Annual Reports of the International North Pacific Fisheries Commission (French, 1966; French, Craddock, and Dunn, 1967; French, Craddock, Bakkala, Dunn, and Thorson, 1967; French et al., 1969, 1970, 1971). Progress on determining the fate of salmon which escape from gill nets has been reported by Thompson, Hunter, and Patten (1971); by Hunter, Patten, and Thompson (1972); and by Thompson and Hunter (1972)[2].

Reported here are the results of 6 yr of experiments to determine: (1) the rate of dropout; (2) the effect of varying length of fishing time on dropout loss rate; (3) the effect of different types of gill net materials and mesh sizes on dropout rates of maturing and immature salmon; and (4) rate of fallouts during hauling operations. Included are estimates of loss of salmon from high-seas and inshore gillnetting.

In this report we use the term "dropouts" as those salmon that become unmeshed or otherwise escape from drifting gill nets; the term "fallouts" is used to describe those salmon seen to fall from gill nets as the gear is hauled aboard the vessel.

EXPERIMENTAL METHODS

Dropout Studies

Experimental methods used in 1964 and 1965 differed from those used in 1966-69. The former methods were based on indirect observations of the fish, whereas, the more recent studies were based on direct observation of the fish. Experimental methods will be described separately below for the indirect and direct methods of observation.

[2] Thompson, R. B., and C. J. Hunter. 1972. Viability of adult sockeye salmon that disentangle from gill nets. *In* Investigations by the United States for the International North Pacific Fisheries Commission—1971, p. 95-105. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash. [Processed.]

Indirect Observations (1964 and 1965)

1964.—The 1964 studies of dropouts were carried out while conducting exploratory fishing for salmon in the western North Pacific Ocean in September and October. The method used to estimate the rate of dropouts was to determine the differences in numbers of salmon caught in gill nets fished for a long period compared to the cumulative catch of salmon caught in a series of short sets fished at the same time and place. Any decrease in catch of the nets fished continuously would be attributed to dropouts. In this procedure, gill nets were set, hauled, and reset at intervals throughout the night (Figure 1).

Conventional multifilament nylon gill nets (1 shackle was 91.5 m long and 7.3 m deep)[3] were fished in individual units of shackles, with each unit connected by a 55-m line. Each unit of gear consisted of 2 shackles of 114-mm and 2 shackles of 83-mm mesh—sizes that would capture most sizes of salmon present. There was a security snap on each gear unit for easy connection and disconnection of the units. Lighted buoys and radio buoys were attached to the net string to ensure finding the gear during hours of darkness.

The time and fishing procedure during the night were as follows:

2000 Set gear units No. 1, 2, 3, and 4.
2300 Haul unit No. 1, remove salmon, and reset.
0200 Haul units No. 1 and 2, remove salmon, and reset 2.
0500 Haul units No. 2 and 3, remove salmon, and reset 3.
0800 Haul unit No. 3 and the last unit, No. 4.

This fishing routine allowed comparison of the different 3-h periods during the night (2000-2300, 2300-0200, 0200-0500, and 0500-0800). Additionally, comparisons were possible for catches of nets fished continuously with the sum of the catches of the individual gear units for various time periods. For example, unit No. 4 fished for 12 h, from 2000 to 0800, and catches in these nets were compared to the cumulative catch of the four individual units hauled at the end of each 3-h period.

1965.—Procedures used in 1965 were extensions of those used in 1964 but on a larger scale employing two vessels full time. Fishing was conducted in the North Pacific Ocean (near long. 166°W) and in the Bering Sea (near long. 160°W) in June and early July, concentrating on maturing sockeye salmon.

Two experimental designs were used to estimate dropout rates of salmon. In the first design, the nets were fished at night; one unit of gear (four 91.5-m shackles of 133-mm mesh gill nets per unit) was fished for 6 h, a second unit for the first 3 h, and a third for the second 3 h (Figure 2). The fishing was repeated over three different time periods during the night. The dropout rate was computed by comparing the catch of the 6-h unit with those of similar

[3] Details of net construction (and fishing procedure) were given by Craddock (1969).
Multifilament nylon gill nets were 100% nylon—330 Starrlock type E (or equivalent) of plied or cable laid salmon twine and dark green in color. Ply size ranged from 3 to 12, depending on mesh size; numbers of body meshes ranged from 57 to 123 (plus guard meshes), depending on mesh size. Each shackle was 183-m long, stretched measure, so that each gill net made a full 91.5-m shackle when hung in 50% on the cork line. Monofilament nylon gill nets were of identical construction to multifilament nylon gill nets, except for net material. Monofilament nets were constructed of light green single strand filament, double selvage, with body meshes of 0.30-, 0.40-, 0.50-, and 0.50-mm diameter for mesh sizes 64, 83, 114, and 133 mm (stretched measure, knot to knot), respectively. [Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.]

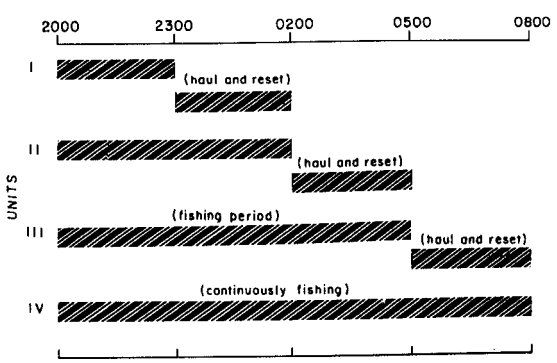

FIGURE 1.—Fishing plan for study of dropouts, 1964. Each unit of gear is identical; length of shaded area refers to fishing time.

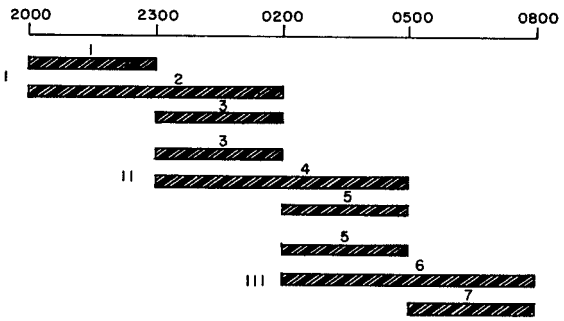

FIGURE 2.—Fishing plan (nighttime) for study of dropout, 1965. Each unit of gear is identical; length of shaded area refers to fishing time.

units fished during the first and second 3-h intervals. Loss of salmon from gill nets was estimated by regression analysis based on data from the catches in the various time periods (a 6-h catch vs. two 3-h catches).

In the second experimental design, four units of gill nets were set before daylight and fished for various lengths of time until noon. Additional units were fished concurrently as shown in Figure 3. In this design, we expected that in the event fish did not enter gill nets fished during daylight the dropout rate of fish caught before daylight could be measured directly by comparing catches of the gear units fished before daybreak with those units fished for various periods after daybreak.

The indirect methods described above have certain inherent limitations and potential sources of error. These methods assume that: a) each gill net is equally efficient; b) each net fishes the same amount of time; and c) the same number of fish are available to each unit of net.

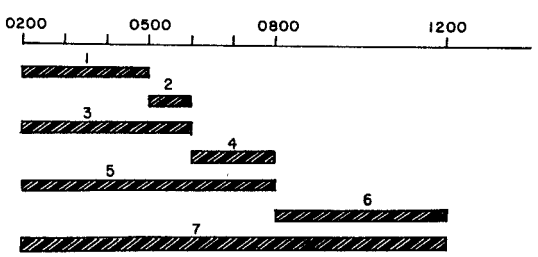

FIGURE 3.—Fishing plan (night-day) for study of dropout, 1965. Each unit of gear is identical; length of shaded area refers to fishing time.

Additionally, it is not possible to differentiate between losses due to dropout and losses due to predators and carrion eaters.[4] Thus, all losses of salmon from gill nets must be attributed to dropout and predation.

Direct Observations (1966-69)

Loss of salmon in gill nets was estimated by direct observation during experiments in 1966-69. The experimental procedure was to patrol the nets at night from small boats (when sea conditions permitted), mark the locations of gilled salmon, and determine their presence or absence at later patrols and when the gear was hauled in the morning. Portable spotlights were used to observe the salmon at night; reflected light made fish in the net visible. The position of an enmeshed salmon was noted by fastening a colored marker to the corkline directly over the fish.

The time and procedure are described below; some variation in timing occured during various sets.

2000 Put out 24-36 shackles of gill net.

2100 First patrol: Examine the nearest 7-14 shackles; mark positions of gilled salmon with colored pins.

2130 Second patrol: Repeat the patrol and record the presence or absence of salmon at locations marked at the first patrol; mark locations of newly observed salmon with pins of a second color.

2330 Third patrol: Repeat the above procedure, again marking locations of newly observed salmon with pins of a third color.

0800 Haul the gill net string; record presence or absence of salmon for all marked locations.

Variations in timing and frequency of observations occurred among years. For example, in 1967, an additional observation at 0230

[4] Total loss due to predators and carrion eaters is designated as loss due to predation in the remaining part of our report.

was made. Additionally, because the study required the use of small boats from the research vessel at night, some patrols were not made in rough seas.

These studies, with minor modifications, were conducted during high-seas gillnetting in 1966-69 and in Puget Sound in 1967. Details of these modifications are explained in the analysis section.

The direct method of observation also contained potential sources of error. For example, salmon marked on one patrol may drop out but be replaced by another fish, thus causing the observer to miss an actual dropout. Moreover, some fish may be inadvertently missed on subsequent patrols and erroneously recorded; upon hauling the net, the observer may then attribute the presence of a fish to replacement. Furthermore, as was the case with the indirect methods, it was not possible to differentiate losses due to dropout and losses due to predation.

Fallout Studies

Observations of the number of fish falling out of gill nets during net hauling operations (fallouts) were made from 1965 to 1970. Fish falling from nets of known mesh sizes were tallied and expressed as a percentage of the total catch. The number of fallouts are believed to be reasonably accurate, although some may have been missed during inclement weather or during very large catches.

SALMON DROPOUT RATES DURING GILLNETTING

Offshore Fishing

Indirect Observations (1964 and 1965)

1964.—Studies of the loss of salmon from gill nets by indirect methods were conducted in September and October. Four sets for these studies were made south of the western Aleutian Islands (one set along long. 178°W and three sets along long. 173°E); catches were principally of immature salmon.

The fishing procedure provided catch data for approximately four 3-h periods throughout the night and for approximately one 6-, 9-, and 12-h period. Precise gear hauling and setting schedules could not be maintained, and usually units of gear scheduled for a 3-h fishing period were fished for shorter time periods. Results of two experiments were unusable because of a combination of weather and tidal currents affecting the net string and because of the difficulty encountered in hauling the nets. The two successful experiments, however, provided data on catches in 6, 9, and 12 h compared to the cumulative catches in nets fished for 3-h periods.

The two sets caught 257 and 239 salmon, respectively. Catches were predominately age .1 immature sockeye salmon.[5] Catches by age and species of fish and by mesh size in each unit of gear are listed in Table 1.

The catches in gill net units fished continuously for periods of 6, 9, and 12 h, and the cumulative catch in individual units fished for short intervals (2.0-3.5 h) are compared in Figure 4. Less fish were landed each day in nets fished continuously for 9 and 12 h than for the 9- and 12-h cumulative catches of individual units fished for three and four short intervals. The catches each day were similar between fishing methods for approximately the first 6 h. Thereafter, in both experiments, the gear that fished continuously caught comparatively fewer fish.

The loss from the continuously fishing units (difference in total catch of the two fishing methods divided by the total catch during short intervals of fishing) for the two sets was 16 and 24% in 10 h and 43 and 20% in 12.5 h. No loss was shown after 6 h. The average for the two sets was 20% for 10 h and 32% for 12.5 h (Table 2). The loss was attributed to dropouts and predation.

1965.—In the spring of 1965, a concentrated effort was directed toward indirect methods of estimating the rate of dropout of salmon from gill nets. Two research vessels fished on maturing sockeye salmon (primarily

[5] Age designation follows that of Koo (1962); numerals indicate numbers of ocean annuli.

TABLE 1.—Catch of salmon by species, age of fish, and unit of gear, 30 September and 2 October 1964.

Sampling location	Date	Unit	Time fished	Total hours fished	Sockeye 83 mm .1	Sockeye 83 mm .2	Sockeye 114 mm .1	Sockeye 114 mm .2	Chum 83 mm .1	Chum 83 mm .2	Chum 114 mm .1	Chum 114 mm .2	Coho 83 mm .0	Coho 83 mm .1	Chinook 114 mm .1	Chinook 114 mm .2	Total catch
Lat. 50°10′N, long. 173°00′E	9/30	1	2025-2330	3.1	14	0	0	3	5	6	0	8	0	0	0	0	36
		2	2025-0230	6.1	20	0	0	1	5	17	0	9	0	0	0	0	52
		3	2025-0625	10.0	28	0	0	3	4	5	0	27	0	0	0	1	68
		4	2025-0855	12.5	29	1	0	3	6	15	0	4	0	0	0	0	58
		5	0010-0233	2.4	3	1	0	0	1	0	1	3	0	0	0	0	9
		6	0335-0535	2.0	8	0	0	4	1	1	0	1	1	0	0	0	16
		7	0635-0855	2.3	9	0	0	0	0	4	0	5	0	0	0	0	18
			Total		111	2	0	14	22	48	1	57	1	0	0	1	257
Lat. 50°10′N, long. 173°00′E	10/2	1	2000-2330	3.5	17	0	2	3	1	2	0	3	0	0	0	0	28
		2	2000-0250	6.8	25	0	3	3	4	5	0	7	0	0	0	0	47
		3	2000-0650	10.1	40	0	1	2	1	3	1	5	0	0	0	0	53
		4	2000-0825	12.4	47	2	1	2	2	7	1	3	0	0	0	0	65
		5	2350-0250	3.0	7	1	3	0	1	0	0	3	0	0	0	0	15
		6	0255-0525	2.5	14	0	0	1	1	2	1	0	0	0	0	0	19
		7	0630-0855	2.4	9	2	0	0	0	0	0	1	0	0	0	0	12
			Total		159	5	10	11	10	19	3	22	0	0	0	0	239

of Bristol Bay origin) south of the Alaska Peninsula and in the eastern Bering Sea in June and early July.

Fishing gear consisted of multifilament gill nets of 133-mm mesh. Four 91.5-m nets, 7.3-m deep, were joined together to form a basic unit of gear 366-m long. For some sets in areas where large catches were expected, the basic unit was reduced to 2 shackles (183 m).

Dropout of salmon from gill nets was estimated by regression analysis of catch ratio obtained from the catch for a 6-h period and the catches for the first and second halves of the same period (Figure 5). Assuming N_1 and N_2 are the numbers of fish available to the gill nets during the first and second halves of a given 6-h period, the expected catches of the three units of gear are:

$$c_1 = s_0\, u_1\, N_1 \text{ for the first 3-h unit,}$$
$$c_2 = s_0\, u_1\, N_2 \text{ for the second 3-h unit,}$$
$$C = s_1\, s_0\, u_1\, N_1 + s_0\, u_2\, N_2 \text{ for the 6-h unit.}$$

Where u_1 is the fraction of the fish available during a 3-h period which are captured by the unit of gear, s_0 is the fraction of those captured which are retained by the gear until the time of hauling, and s_1 is the fraction of the fish captured and retained by the 6-h unit of gear during the first half of the period, which are

TABLE 2.—Catch of salmon in gill nets fished continuously and in gill nets hauled at intervals, and estimated loss of salmon from nets fished continuously.

Nets fished continuously			Nets fished for short intervals						
Date and time period	Hours fished	Catch (no.)	Time period	Hours fished	Catch (no.)	Cumulative catch (no.)	Catch[1] per hour	Adjusted cumulative catch[2]	Estimated loss[3] (%)
30 September									
2000-2300	3.1	36	2000-2300	3.1	36	36	11.6	36	
2000-0200	6.1	52	2300-0200	2.4	9	45	8.2	50	0.0
2000-0500	10.0	68	0200-0500	2.0	16	61	8.1	81	16.0
2000-0800	12.5	58	0500-0800	2.3	18	79	8.1	101	42.6
2 October									
2000-2300	3.5	28	2000-2300	3.5	28	28	8.0	28	
2000-0200	6.1	47	2300-0200	3.0	15	43	6.6	45	0.0
2000-0500	10.1	53	0200-0500	2.5	19	62	6.9	70	24.3
2000-0800	12.4	65	0500-0800	2.4	12	74	6.5	81	19.8

[1] Cumulative catch divided by cumulative hours fished.
[2] Adjusted to equal time period of nets fished continuously; catch per hour times number of hours fished of nets fished continuously.
[3] Total in adjusted cumulative catch for nets fished short intervals minus total for nets fished continuously, divided by adjusted cumulative catch.

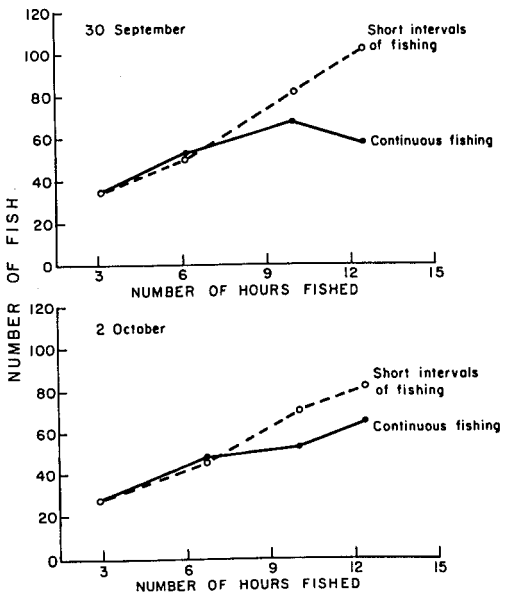

FIGURE 4.—Comparison of salmon catch in gill nets fished continuously with the cumulative catch in nets fished for short intervals (2.0-3.5 h), 1964. Data for short intervals of fishing have been adjusted to allow for comparable fishing hours.

also retained during the second half of the period. Rewriting C in terms of c_1 and c_2 we have

$$C = s_1 c_1 + (u_2/u_1) c_2$$

or

$$C/c_1 = s_1 + (u_2/u_1)(c_2/c_1).$$

By substituting the observed values of C, c_1, and c_2 for each 6-h fishing period, the regression of (C/c_1) on (c_2/c_1) will be linear with intercept equal to s_1 and slope equal to (u_2/u_1).

In the application of this model, it is assumed that over the totality of the 6-h-fishing periods, the average number of fish available to two units of gear fishing simultaneously is the same. The loss from gill nets, $1 - s_1$, applies to the fraction of fish disappearing from a gill net unit during a 3-h interval which is assumed to begin 1½ h after the fish enter the net. The loss from the time of entry to the beginning of the 3-h interval is not included in the estate of s_1.

Salmon catches (sockeye, chum, and pink salmon) by time periods and gear units of the usable experimental dropout sets are listed in Table 3. The total of column c_1 (the catches in the first 3-h unit) includes appropriate catches of c_2 where the second 3-h unit also constituted the first unit of the second or third time periods (see Figure 2). Sockeye salmon were the principal species taken in these sets; species totals were 4,327 sockeye, 353 chum, and 4 pink salmon.

A plot of the catch ratios, C/c_1 on c_2/c_1 is shown in Figure 5. In computing the regression constants, each point was weighted according to the weighting function shown in the Figure 5. This weighting function arose from two considerations. First, in those instances where the difference in catch between the 6-h unit and the sum of catches of the two 3-h units is large, there is some reason to suspect that the number of fish available to units of gear fishing simultaneously is not the same. Hence, those points should receive less weight in the regres-

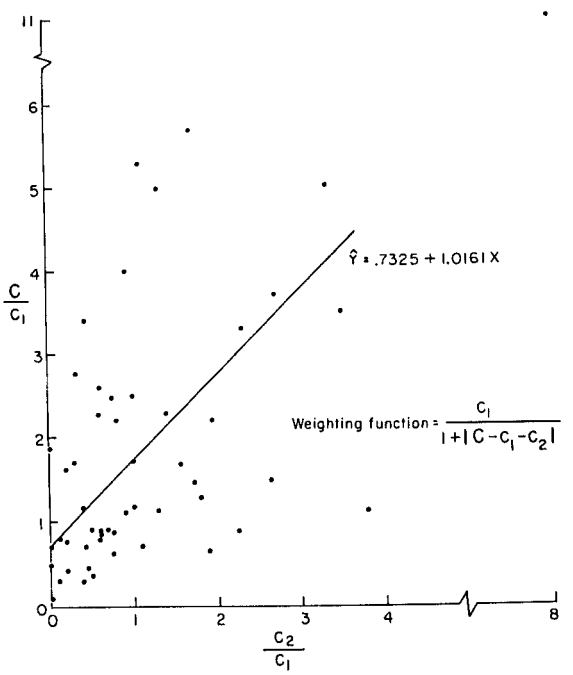

FIGURE 5.—Regression of C/c_1 on c_2/c_1. C is the catch in the 6-h unit, c_1, the catch in the first 3-h unit and c_2, the catch in the second 3-h unit.

TABLE 3.—Salmon catches by time periods, 1 June to 2 July 1965.

Research vessel and date	Sampling location		Time period (see Fig. 2)	Catch		
	Lat. N	Long. W		1st 3-h unit (c_1)	6-h unit (C)	2d 3-h unit (c_2)
RV *George B. Kelez:*						
6/6	53°23′	166°05′	I	8	1	0
			III	2	7	7
6/7	53°01′	166°03′	I	49	92	0
			III	18	50	6
6/8	53°06′	166°00′	I	13	69	14
			II	14	16	18
			III	18	21	7
6/14	53°07′	166°37′	I	38	44	38
			II	38	87	22
			III	22	38	6
6/15	52°55′	167°43′	I	100	107	91
6/22	55°50′	164°00′	I	73	65	36
			II	36	13	18
			III	18	9	0
6/23	56°10′	162°31′	I	22	49	17
			II	17	28	3
			III	3	17	5
6/25	57°01′	159°58′	I	25	57	35
			II	35	23	67
			III	67	112	105
7/2	56°24′	162°00′	II	44	40	30
			III	30	38	54
MV *Paragon:*						
6/1	53°43′	160°44′	I	3	10	7
			II	7	12	7
			III	7	24	3
6/7	53°20′	165°52′	I	167	129	19
			II	19	13	0
6/8	53°26′	165°57′	I	170	147	105
6/12	52°52′	166°12′	I	5	13	3
			II	3	15	4
			III	4	10	3
6/14	53°15′	166°38′	III	67	21	7
6/15	52°57′	167°41′	I	53	33	40
			II	40	160	37
			III	37	27	40
6/18	53°16′	166°15′	I	9	4	2
6/21	55°48′	160°31′	I	61	18	23
			II	23	20	14
			III	14	11	8
6/22	55°55′	164°00′	I	3	15	10
6/23	56°06′	162°30′	I	44	50	166
			II	166	130	31
			III	31	14	14
6/25	56°37′	161°30′	I	89	132	235
6/28	57°06′	161°56′	II	7	5	3
			III	3	11	8
6/29	56°47′	161°25′	I	15	22	26
7/1	56°30′	161°05′	I	1	11	8
			II	8	7	6
			III	6	15	6
7/2	56°17′	162°00′	II	8	7	18
			III	18	40	35
		Total	52	1,778	2,109	1,467

sion analysis. Secondly, since the measure of dropout refers to the fish which enter the 6-h unit during the first 3-h period and disappear during the second 3-h period, it seems reasonable to weight more heavily those points in which large numbers of fish entered during the first 3-h period.

The resulting weighted regression line is shown in Figure 5. In spite of the apparent wide scattering of points, the relation is significant at the 5% level (t = 8.48). The estimate of loss of salmon from the gill nets is 27% for the 3-h period; the 80% confidence interval is from 5 to 48%.

In the model used in estimating dropouts during a 3-h interval, we have assumed that

salmon entered the nets 1½ h prior to the beginning of the second 3-h interval. If, on the other hand, we postulate that the majority of the salmon entered the nets either prior to or after the assumed 1½ h, an increased or decreased time interval is available for salmon to drop from nets during the 3-h period. Our estimate of dropouts now would be either lower or higher than that of the original model. A test of these hypotheses was inconclusive. Dropout rates were estimated at 15 and 35% for the two new assumptions of time of entry into the nets, but in neither instance was the rate significant.

When fishing the experimental dropout sets, we frequently observed northern fur seals, *Callorhinus ursinus*, and Steller sea lions, *Eumetopias jubatus*, swimming along the nets and taking fish. We frequently observed seabirds near the nets and we often took salmon sharks, *Lamna ditropis*, in the gill nets. Removal of fish from the nets by these animals was a factor we could not differentiate from actual salmon dropouts from the nets. Both factors, however, lead to loss of salmon from gill nets. As a matter of fact, the gill nets served to collect and hold salmon for predators and carrion eaters. We do not know if sea lions and fur seals could catch salmon as easily through their own efforts compared to having gill net-caught fish available. We concluded from these experiments, therefore, that there was loss of salmon from gill nets that was due to predation (removal of fish by predators and carrion eaters) and dropouts.

In the experiments to determine dropouts in 1964 and 1965, our technique involved indirect methods and assumptions of equal availability of salmon to units of gill nets fished during varying time periods and that all nets fished with equal efficiency. In 1965, the experiments were limited to estimates of dropouts over a 3-h period. To overcome these limitations, we attempted in subsequent experiments to observe salmon in the nets and determine dropouts by direct observation.

Direct Observations (1966-69)

1966.—In the summer of 1966, the loss of salmon from gill nets was estimated by direct observation. Three vessels fished with gill nets in July, August, and in early September along three sampling lines: long. 176°22′W, 167°W, and 158°W. In this technique, as outlined under the section of "Experimental Methods," we observed fish in the net from small boats, marked their position in the net with colored tags, and determined their presence or absence at subsequent time periods and at haul.

The experimental gill nets included 4 shackles of 133-mm, 3 of 114-mm, 4 of 83-mm, and 3 of 64-mm nets when the first 14 shackles of the string were observed. The net sequence was 133, 83, 114, 64 mm. In some sets not all nets were observed because of inclement weather or other factors. In any event, however, a range of mesh sizes was observed to include observations on age .1 immature salmon and on the larger .2 and older immatures.

In 1966 we made 28 observations for dropouts (Table 4). Each observation entailed one to three patrols of the net, some of which were not completed because of rough seas. There were 28 first patrols, 27 second patrols, and 16 third patrols.

Combining data from all observations, the overall dropout rate was substantial, 42.5% (95% confidence interval ±5.6) for periods up to 11 h (Table 5). After 1 h the rate was 3.7% (±5.1), and 14.9% (±7.9) for periods up to 2½ h. The rates for varying time periods were generally similar for the two combinations of mesh sizes. An exception was the 8% (±7.7) dropout rate of the large mesh sizes for periods up to 2½ h compared with 22.7% (±14.6) for the smaller mesh sizes. Typically, the large mesh nets take age .2 and older salmon with immature sockeye and chum salmon dominating catches in the summer. The small mesh sizes take mainly age .1 immature sockeye and chum salmon in the summer. Thus, overall dropout rates appeared to be about the same for small fish as for large fish.

The data suggested little difference in loss rates among the three vessels. The total rate of loss in the large mesh nets ranged from 42.3% (MV *Paragon*) to 48.1% (MV *St. Michael*). In the small mesh nets, overall loss rates were 39.6% for the *Paragon* and 45.7% for the *St. Michael* (and was 22.2% for RV *George B. Kelez*, but only 10 fish were marked).

TABLE 4.—Number of salmon marked and observed in gill nets over varying periods of time by mesh size, summer 1966.

Vessel and date	Sets	Position Lat. N	Position Long. W	Observation no.	114- and 133-mm mesh: No. fish marked	114- and 133-mm mesh: Number of fish observed after marking: Up to 1 h	114- and 133-mm mesh: Up to 2½ h	114- and 133-mm mesh: Up to 11 h[1]	64- and 83-mm mesh: No. fish marked	64- and 83-mm mesh: Number of fish observed after marking: Up to 1 h	64- and 83-mm mesh: Up to 2½ h	64- and 83-mm mesh: Up to 11 h[1]	Total marked fish	Total recovered fish
RV *George B. Kelez:*														
7/20	24	51°30′	166°59′	(a)	3	—	3	3	1	—	—	0	4	3
				(b)	2	—	—	2	1	—	—	1	3	3
7/29	32	51°31′	167°00′	(a)	0	—	—	—	0	—	—	—	0	0
				(b)	1	—	1	0	2	—	2	1	3	1
				(c)	0	—	—	—	0	—	—	—	0	0
8/19	48	49°29′	167°00′	(a)	0	—	—	—	3	3	—	3	3	3
				(b)	0	—	—	—	1	—	—	1	1	1
9/01	56	49°30′	167°01′	(a)	1	1	—	0	[2]2	2	—	1	3	1
				(b)	4	—	—	0	0	—	—	—	4	0
9/02	57	49°02′	167°04′	(a)	1	1	—	1	0	—	—	—	1	1
				(b)	1	—	—	1	0	—	—	—	1	1
MV *Paragon:*														
6/27	2	51°15′	176°22′	(a)	0	—	—	—	3	3	2	0	3	0
				(b)	0	—	—	—	0	—	—	—	0	0
				(c)	1	—	—	0	3	—	—	0	4	0
6/28	3	51°00′	176°22′	(a)	2	2	2	1	0	—	—	—	2	1
				(b)	0	—	—	—	0	—	—	—	0	0
				(c)	5	—	—	3	0	—	—	—	5	3
6/29	4	50°45′	176°22′	(a)	0	—	—	—	0	—	—	—	0	0
				(b)	1	—	1	1	1	—	1	0	2	1
				(c)	3	—	—	3	1	—	—	1	4	4
6/30	5	50°30′	176°25′	(a)	0	—	—	—	1	0	0	0	1	0
				(b)	0	—	—	—	0	—	—	—	0	0
				(c)	0	—	—	—	2	—	—	0	2	0
7/14	15	50°22′	176°22′	(a)	0	—	—	—	0	—	—	—	0	0
				(b)	2	—	2	0	4	—	3	1	6	1
				(c)	2	—	—	2	0	—	—	—	2	2
7/15	16	50°37′	176°22′	(a)	0	—	—	—	0	—	—	—	0	0
				(b)	2	—	—	2	1	—	—	1	3	3
7/18	19	51°22′	176°22′	(a)	3	2	2	0	1	1	0	0	4	0
				(b)	1	—	0	0	4	—	3	0	5	0
				(c)	0	—	—	—	1	—	—	0	1	0
7/24	23	51°30′	176°22′	(a)	9	9	9	6	1	1	1	1	10	7
				(b)	0	—	—	—	1	—	1	0	1	0
				(c)	9	—	—	5	35	—	—	32	44	37
7/26	25	51°00′	176°22′	(a)	0	—	—	—	0	—	—	—	0	0
				(b)	0	—	—	—	0	—	—	—	0	0
				(c)	2	—	—	1	4	—	—	2	6	3
8/05	33	50°45′	176°22′	(a)	1	1	1	1	1	1	1	0	2	1
				(b)	1	—	1	0	1	—	1	1	2	1
				(c)	3	—	—	2	4	—	—	2	7	4

TABLE 4.—*Continued.*

Vessel and date	Sets	Position		Observation no.	114- and 133-mm mesh				64- and 83-mm mesh				Total marked fish	Total recovered fish
		Lat. N	Long. W		No. fish marked	Number of fish observed after marking			No. fish marked	Number of fish observed after marking				
						Up to 1 h	Up to 2½ h	Up to 11 h[1]		Up to 1 h	Up to 2½ h	Up to 11 h[1]		
8/11	37	51°30′	176°22′	(a)	2	—	—	0	0	—	—	—	2	0
				(b)	2	—	—	0	1	—	—	1	3	1
8/12	38	51°15′	176°22′	(a)	1	—	1	0	5	—	4	4	6	4
				(b)	5	—	—	2	13	—	—	7	18	9
8/15	41	50°30′	176°22′	(a)	0	—	—	—	0	—	—	—	0	0
				(b)	1	—	0	0	0	—	—	—	1	0
				(c)	2	—	—	0	0	—	—	—	2	0
8/16	42	50°15′	176°22′	(a)	7	7	7	7	3	3	3	1	10	8
				(b)	3	—	3	3	1	—	1	1	4	4
				(c)	3	—	—	3	2	—	—	1	5	4
8/17	43	50°00′	176°22′	(a)	2	2	—	2	3	3	—	3	5	5
				(b)	0	—	—	—	1	—	—	0	1	0
8/24	47	51°30′	176°22′	(a)	0	—	—	—	0	—	—	—	0	0
				(b)	0	—	—	—	0	—	—	—	0	0
				(c)	3	—	—	1	3	—	—	2	6	3
MV *St. Michael*														
7/18	6	49°20′	158°00′	(a)	1	1	—	1	0	—	—	—	1	1
				(b)	0	—	—	—	1	—	—	1	1	1
7/19	7	50°37′	158°01′	(a)	1	1	1	0	0	—	—	—	1	0
				(b)	3	—	—	2	1	—	—	1	4	3
				(c)	2	—	—	2	2	—	—	2	4	4
7/21	9	52°32′	158°00′	(a)	1	1	1	1	5	5	5	4	6	5
				(b)	1	—	1	1	2	—	1	1	3	2
				(c)	4	—	—	2	1	—	—	1	5	3
7/22	10	53°30′	158°00′	(a)	2	2	2	2	0	—	—	—	2	2
				(b)	0	—	—	—	0	—	—	—	0	0
				(c)	5	—	—	5	1	—	—	1	6	6
7/24	12	55°07′	158°00′	(a)	0	—	—	—	2	—	0	0	2	0
				(b)	18	—	—	0	7	—	—	0	25	0
8/25	28	52°00′	158°00′	(a)	9	—	8	7	6	—	5	3	15	10
				(b)	3	—	—	2	6	—	—	4	9	6
8/26	29	51°05′	158°00′	(a)	8	—	—	[3]3	13	—	—	[2]7	21	10

[1] A dash (—) indicates the net was not examined at the time interval.
[2] One tag missing at haul; treated as missing observation and not included in totals.
[3] Four tags missing at haul; treated as missing observation and not included in totals.

TABLE 5.—Number of salmon marked and observed in multifilament gill nets over varying periods of time by mesh size and area, 1966.

Nets and area (long.)	Vessel	No. fish marked during patrols	Number of fish observed after marking[1]		
			Up to 1 h later	Up to 2½ h later	Up to 11 h later
114- and 133-mm mesh:					
176°W	MV *Paragon*	78	23	29	45
			(24)	(32)	(78)
	Percentage loss		4.2	9.4	42.3
167°W	RV *George B. Kelez*	13	2	4	7
			(2)	(4)	(13)
	Percentage loss		0	0	46.2
158°W	MV *St. Michael*	58	5	13	28
			(5)	(14)	(54)
	Percentage loss		0	7.1	48.1
	Total	149	30	46	80
			(31)	(50)	(145)
	Percentage loss and 95% confidence interval		3.2 ± 6.4	8.0 ± 7.7	44.8 ± 8.2
64- and 83-mm mesh:					
176°W	MV *Paragon*	101	12	21	61
			(13)	(27)	(101)
	Percentage loss		7.7	22.2	39.6
167°W	RV *George B. Kelez*	10	5	2	7
			(5)	(2)	(9)
	Percentage loss		0	0	22.2
158°W	MV *St. Michael*	47	5	11	25
			(5)	(15)	(46)
	Percentage loss		0	26.7	45.7
	Total	158	22	34	93
			(23)	(44)	(156)
	Percentage loss and 95% confidence interval		4.3 ± 8.6	22.7 ± 14.6	40.4 ± 7.7
	Grand total (both mesh sizes)	307	52	80	173
			(54)	(94)	(301)
	Percentage loss and 95% confidence interval		3.7 ± 5.1	14.9 ± 7.9	42.5 ± 5.6

[1] Number of possible observations (figures in parentheses) for the time periods; difference from the number marked is because some observations were not made during rough weather.

1967.—Studies of loss from gill nets fished on the high seas were continued in 1967 in the same manner as in 1966. Because of inclement weather, only five gill net sets were observed for dropouts; however, the number of patrols during each set was increased over 1966.

Observations were made from one research vessel operating south of Adak Island (long. 176°W) in June-August. Eleven nets were patrolled: two each of 133-mm monofilament and 133-mm multifilament nets, two each of 114-mm monofilament and 114-mm multifilament nets, two 83-mm multifilament nets, and one 64-mm multifilament net. This combination of mesh sizes and net materials allowed comparisons of loss rates of small and large fish and comparisons between large mesh multifilament and monofilament gill nets. Not all of the 14 nets were patrolled during each set because of weather or mechanical problems. The large mesh multifilament nets were patrolled five times as opposed to three times for the small mesh nets.

Results of the dropout experiments in 1967 are listed in Table 6. Overall loss rates were nearly 11% (± 6.8) for periods up to 1 h, 17% (± 10.1) for up to 2½ h, 58% (± 18.0) for up to 5 h, and 64% (± 9.7) for up to 10 h. The loss rates for large mesh nets (multi- and monofilament combined) were nearly 58% (for up to 10 h) as opposed to 83% for small mesh nets (although sample sizes for the latter were small).

The dropout rates of monofilament and multi-

TABLE 6.—Numbers of salmon marked and observed in gill nets of varying periods of time, July-August 1967.

Nets and set no.	Date hauled	Set position	No. fish marked during patrols	Number of fish observed after marking[1]			
				Up to 1 h later	Up to 2½ h later	Up to 5 h later	Up to 10 h later
114- and 133-mm mesh nets (multifilament):							
6	6/29	Lat. 48°00′N Long. 176°22′W	6	3	—	3	1
			1	1	—	1	1
			4	—	4	4	—
12	7/13	Lat. 50°45′N Long. 176°22′W	1	—	—	—	1
21	8/01	Lat. 51°40′N Long. 176°22′W	1	1	1	0	0
25	8/05	Lat. 50°45′N Long. 176°22′W	2	2	1	—	0
			1	1	1	—	0
			3	3	3	—	0
			4	3	—	—	0
26	8/15	Lat. 51°30′N Long. 176°22′W	2	2	2	—	0
			1	0	—	—	0
		Total	26	16 (21)	12 (13)	8 (12)	3 (22)
		Percentage loss and 95% confidence interval		23.8 ± 17.9	7.7 ± 15.2	33.3 ± 26.8	86.4 ± 11.2
114- and 133-mm mesh nets (monofilament):							
12	7/13	Lat. 50°45′N Long. 176°22′W	1	—	—	—	1
21	8/01	Lat. 51°40′N Long. 176°22′W	2	2	2	0	0
25	8/05	Lat. 50°45′N Long. 176°22′W	2	2	1	—	1
			2	2	1	—	1
			1	1	1	—	0
			1	1	—	—	1
26	8/15	Lat. 51°30′N Long. 176°22′W	9	9	8	—	6
			13	11	10	—	7
			2	2	—	—	2
			4	4	—	—	3
		Total	37	34 (36)	23 (29)	0 (2)	22 (37)
		Percentage loss and 95% confidence interval		5.6 ± 7.7	20.7 ± 14.9	100	40.6 ± 15.3
64- and 83-mm mesh nets (multifilament):							
21	8/01	Lat. 51°40′N Long. 176°22′W	1	1	1	0	0
			4	4	—	0	0
25	8/05	Lat. 50°45′N Long. 176°22′W	1	1	0	—	0
			4	3	3	—	0
			1	1	1	—	0
			2	2	—	—	0
26	8/15	Lat. 51°30′N Long. 176°22′W	5	5	5	—	3
		Total	18	17 (18)	10 (12)	0 (5)	3 (18)
		Percent loss and 95% confidence interval		5.6 ± 10.9	16.7 ± 21.0	100	83.3 ± 12.8
		Grand total (all mesh sizes)	81	67 (75)	45 (54)	8 (19)	28 (77)
		Percentage loss and 95% confidence interval		10.7 ± 6.8	16.7 ± 10.1	57.9 ± 18.0	63.6 ± 9.7

[1] A zero (0) indicates that the net was examined, but no marked fish were observed; a dash (—) indicates that the net was not examined. Numbers in parentheses indicate number of possible observations for the time period; difference from the number marked is because some observations were not made in some periods.

filament nets are also listed in Table 6. Loss rates for fish observed up to 10 h were 86% in the large multifilament nets as opposed to 41% for monofilament nets of the same mesh size.

1968.—Studies on the loss of salmon from gill nets in 1968 were concentrated on maturing fish in May and June, south of Unalaska Island (long. 164°W). The procedures used to estimate loss of salmon were the same as used in 1966 and 1967. The net string consisted of five mesh sizes (64-, 83-, 98-, 114-, and 133-mm mesh) of multifilament net, all of which were observed for dropouts. Two shackles of monofilament nets (133-mm mesh) were also observed for comparison with multifilament nets.

Overall loss rates were zero up to 1 h, 4.7% (±6.3) up to 2 h, and 20.4% (±7.8) for up to 10 h (Table 7). Rates of loss for periods up to 10 h were nearly 18% (± 9.9) for multifilament nets and 22% (± 14.5) for monofilament nets; the difference was not significant. This similar loss rate for monofilament nets as opposed to multifilament nets contrasts to the loss rate of the two types of gear in 1967 on immature fish (41% loss for monofilament nets and 86% for multifilament nets).

Compared to the 1966 and 1967 studies of losses of primarily immature salmon, the dropout rates of maturing fish in 1968 were much smaller. Possibly this reduction in dropout rate in 1968 was due to unusually calm seas and partly to the fact that the experiments were on maturing fish taken in large mesh nets as opposed to immature salmon in large and small mesh nets in 1966 and 1967.

1969.—Studies of the loss of salmon from gill nets in 1969 were conducted in April and May on maturing salmon and in July on immature salmon.

Because of inclement weather in April and May, we were able to patrol the net string and mark the position of salmon in the nets in only four different sets. Eight nets were observed: one each of 114- and 133-mm monofilament nets and two each of 98-, 114-, and 133-mm multifilament nets (in one set, a single 64-mm multifilament net was also observed). Only 13 salmon were marked in the four sets; no loss was observed up to 1, 2, or 5 h (Table 8). A loss of two fish (15.4%) was recorded for periods up to 10 h.

In July, experiments on immature salmon were conducted south of Adak Island (long. 176°W) during three sets. Eight nets were patrolled: two 114-mm monofilament nets and three each of 114- and 133-mm multifilament nets. Comparison of loss rates was made between monofilament and multifilament nets (Table 9).

The loss rate in the monofilament nets was over twice that of the multifilament nets for the relatively small sample sizes (46% vs. 22% for periods up to 10 h). The combined loss was 35% (±14.8) up to 10 h; it was 15% (±13.6) up to 1 h and 25% (±21.4) up to 2 h. The total loss rate in the large nets was smaller than that observed in 1966 and 1967.

SUMMARY.—The total number of salmon marked and observed by direct methods over varying periods of time, by mesh size and year, are presented in Table 10. In 4 yr of experiments, 534 fish were marked. Overall loss rates for periods up to 11 h were about 41% (±4.0). Loss rates were about 6% (±3.4) up to 1 h and 14% (±4.4) up to 2½ h. The loss rate of about 52% (±16.2) for periods up to 5 h was greater than the rates for up to 11 h. However, this loss rate for up to 5 h was based on only 21 fish marked, whereas the loss rate for up to 11 h was based on 524 fish marked. The data indicated that losses of salmon continued with time in the net.

Losses from small mesh (64- and 83-mm) multifilament nets, which capture mainly the small age .1 immature salmon, were similar to losses from the large mesh multifilament nets (45% vs. 41%). Loss rates from the small mesh nets were similar to those of large mesh nets for periods up to 1 h (5 and 6%, respectively) and were greater than for the large mesh multifilament nets up to 2½ h (21 and 7%, respectively).

Comparisons of the loss rates of large mesh multifilament nets as opposed to large mesh monofilament nets indicated that, for periods

TABLE 7.—Number of salmon marked and observed in gill nets over varying periods of time, May and June 1968.

Nets and set no.	Date hauled	Set position	No. fish marked during patrols	Number of fish observed after marking[1]		
				Up to 1 h later	Up to 2 h later	Up to 10 h later
Multifilament nets (98-, 114-, and 133-mm mesh)[2]:						
17	5/28	Lat. 50°25′N Long. 168°43′W	1	1	1	1
			3	3	3	3
19	5/31	Lat. 50°59′N Long. 164°01′W	1	1	1	1
			3	3	—	3
			5	—	—	4
20	6/03	Lat. 52°58′N Long. 164°00′W	3	3	—	3
			4	—	—	3
22	6/05	Lat. 53°30′N Long. 164°00′W	15	15	15	12
			18	18	—	15
			4	—	—	2
		Total	57	44 (44)	20 (20)	47 (57)
		Percentage loss and 95% confidence interval		0	0	17.6 ± 9.9
Monofilament nets (133-mm mesh):						
17	5/28	Lat. 50°25′N Long. 168°43′W	1	1	—	1
19	5/31	Lat. 50°59′N Long. 164°01′W	1	1	1	1
20	6/03	Lat. 52°58′N Long. 164°00′W	5	—	—	3
22	6/05	Lat. 53°30′N Long. 164°00′W	21	21	19	17
			2	2	—	2
			2	—	—	1
		Total	32	25 (25)	20 (22)	25 (32)
		Percentage loss and 95% confidence interval		0	9.1 ± 12.7	21.9 ± 14.5
Multifilament nets (64- and 83-mm mesh):						
17	5/28	Lat. 50°25′N Long. 168°43′W	1	1	1	0
			1	1	—	1
19	5/31	Lat. 50°59′N Long. 164°01′W	1	—	—	1
20	6/03	Lat. 52°58′N Long. 164°00′W	1	—	—	0
		Total	4	2 (2)	1 (1)	2 (4)
		Percentage loss		0	0	50.0
		Grand total (all mesh sizes)	93	71 (71)	41 (43)	74 (93)
		Percentage loss and 95% confidence interval		0	4.7 ± 6.3	20.4 ± 7.8

[1] A zero (0) indicates that the net was examined, but no marked fish were observed; a dash (—) indicates that the net was not examined. Numbers in parentheses indicate number of possible observations for the time period; difference from the number marked is because some observations were not made in rough weather.
[2] Only one fish was marked in the 98-mm mesh nets.

up to 11 h, loss rates from the former exceeded the latter (41% vs. 33%) although the difference was not statistically significant.

Comparisons of rates of loss of immature and maturing salmon present some difficulty because we do not know the maturity status of those fish initially marked which are subsequently lost from the nets. We may rationally

TABLE 8.—Number of salmon marked and observed in gill nets over varying periods of time, April and May 1969.

Nets and set no.	Date hauled	Set position	No. fish marked during patrols	Number of fish observed after marking[1]			
				Up to 1 h later	Up to 2 h later	Up to 5 h later	Up to 10 h later
98,-114-,and 133-mm mesh nets (multifilament):							
1	4/25	Lat. 55°10′N Long. 155°00′W	1	1	—	—	0
11	5/09	Lat. 51°00′N Long. 165°00′W	3	—	3	1	2
12	5/10	Lat. 52°10′N Long. 165°00′W	1	—	—	—	1
		Total	5	1 (1)	3 (3)	1 (1)	3 (5)
		Percentage loss		0	0	0	40.0
114- and 133-mm mesh nets (monofilament):							
1	4/25	Lat. 55°10′N Long. 155°00′W	1	—	—	—	1
9	5/07	Lat. 49°00′N Long. 165°00′W	3 1	3 —	3 —	— —	3 1
11	5/09	Lat. 51°00′N Long. 165°00′W	1	—	1	1	1
12	5/10	Lat. 52°10′N Long. 165°00′W	1	—	—	—	1
		Total	7	3 (3)	4 (4)	1 (1)	7 (7)
		Percentage loss		0	0	0	0
64- and 98-mm mesh nets (multifilament):							
9	5/07	Lat. 49°00′N Long. 165°00′W	1	—	—	—	1
		Total	1	— (—)	— (—)	— (—)	1 (1)
		Percentage loss		0	0	0	0
		Grand total	13	4 (4)	7 (7)	2 (2)	11 (13)
		Percentage loss		0	0	0	15.4

[1]A zero (0) indicates that the net was examined, but no marked fish were observed; a dash (—) indicates that the net was not examined. Numbers in parentheses indicate number of possible observations for the time period; difference from the number marked is because some observations were not made in rough weather.

assume, however, that the overwhelming majority of salmon caught in the small mesh nets (64- and 83-mm) are immature fish. The larger mesh nets (98-, 114-, and 133-mm), however, capture both maturing and immature salmon, depending on the season and availability of each group. The studies conducted in the spring of 1968 and 1969 were primarily on maturing salmon. By comparing the rate of loss of salmon from small mesh nets in 1966 and 1967 (and in July 1969) with the loss rates of salmon from large mesh nets in the spring of 1968 and 1969, we may effectively compare the loss rates of immature and maturing salmon (Table 11).

Overall loss rates for mature salmon were 0, 4% (±8.9), and 0 for three periods (1, 2½, and 5 h) and about 20% (±7.5) for periods up to 11 h (Table 11). Immature losses were 9% (±4.3), 17% (±5.6), 58% (±18.0), and 46% (±4.6) for the corresponding time periods. Overall loss rates were similar for mature fish in large mesh mono- and multifilament nets (19 and 18%), as were the rates for immature salmon in the same nets (48 and 42%, respectively). Loss rates of immatures in small mesh multifilament nets (45%) were also similar to the loss rates of immatures in the large mesh mono- and multifilament nets (42 and 48%, respectively).

TABLE 9.—Number of salmon marked and observed in gill nets over varying periods of time, July 1969.

Nets and set no.	Date hauled	Set position	No. fish marked during patrols	Number of fish observed after marking[1]		
				Up to 1 h later	Up to 2 h later	Up to 10 h later
Multifilament nets (114- and 133-mm mesh):						
17	7/21	Lat. 51°32′N Long. 176°22′W	2	2	—	0
21	7/25	Lat. 50°10′N Long. 176°22′W	9 6	8 6	8 —	8 6
25	7/29	Lat. 51°35′N Long. 176°22′W	1	—	—	0
		Total	18	16 (17)	8 (9)	14 (18)
		Percentage loss and 95% confidence interval		5.9 ± 12.0	11.1 ± 23.7	22.2 ± 11.3
Monofilament nets (114-mm mesh):						
17	7/21	Lat. 51°32′N Long. 176°22′W	3	2	2	0
21	7/25	Lat. 50°10′N Long. 176°22′W	4 2	2 2	2 —	2 2
25	7/29	Lat. 51°35′N Long. 176°22′W	13	—	—	8
		Total	22	6 (9)	4 (7)	12 (22)
		Percentage loss and 95% confidence interval		33.3 ± 35.5	42.9	45.5 ± 19.8
		Grand total	40	22 (26)	12 (16)	26 (40)
		Percentage loss and 95% confidence interval		15.4 ± 13.6	25.0 ± 21.4	35.0 ± 14.8

[1] A zero (0) indicates that the net was examined, but no marked fish were observed; a dash (—) indicates that the net was not examined. Numbers in parentheses indicate number of possible observations for the time period; difference from the number marked is because, some observations were not made in some periods.

The results showed that for many of the 1-h and 2-h time periods the 95% confidence interval included zero indicating that the estimated loss rates were not significantly greater than zero. Similarly, the width of the confidence intervals indicated that the estimated losses for some adjacent time periods would not be considered to be significantly different. The point estimates, however, showed an increase in loss rates with time indicating that in general the longer the fish were in the nets the greater likelihood there was for the fish to drop out.

Because we could not determine species readily during the process of marking the location of salmon in the nets, we could not identify dropouts as to species. During the 1966-69 experiments, sockeye and chum salmon made up over 70% of the catches and thus these species most likely were the species escaping the nets. Undoubtedly, in a salmon gill net fishery, dropout rates would be applicable to those species which make up the bulk of the catches.

The above summary of dropout rates for all experiments includes losses due to predation as well as to dropouts. The effect on predation on dropout loss is examined in the next section.

Effects of Predation on Dropout Rates

The methods used in this study to estimate the loss of salmon due to gillnetting fail to differentiate between losses due to predation and losses due to disentanglement. The subject of losses due to predation apparently has not been considered by other authors (e.g., Doi, 1962; Konda, 1966; Ishida et al., 1969).

There is evidence, however, that predators

TABLE 10.—Total number of salmon marked and observed over varying periods of time by mesh size, material, and year, 1966-69.

Mesh size and year	Maturity	No. fish marked during patrols	Number of fish observed after marking[1]			
			Up to 1 h later	Up to 2½ h later	Up to 5 h later	Up to 11 h later
98-, 114-, and 133-mm mesh (multifilament):						
1966	Immature	149	30	46	—	80
			(31)	(50)	—	(145)
1967	Immature	26	16	12	8	3
			(21)	(13)	(12)	(22)
1968	Mature	57	44	17	—	47
			(44)	(17)	—	(57)
1969	Mature	5	1	3	1	3
			(1)	(3)	(1)	(5)
	Immature	18	16	8	—	14
			(17)	(9)	—	(18)
	Total	255	107	86	9	147
			(114)	(92)	(13)	(247)
	Percentage loss and 95% confidence interval		6.2 ± 4.4	6.5 ± 5.2	30.8 ± 27.1	40.5 ± 5.7
114- and 133-mm mesh (monofilament):						
1967	Immature	37	34	23	0	22
			(36)	(29)	(2)	(37)
1968	Mature	32	25	20	—	25
			(25)	(22)	—	(32)
1969	Mature	7	3	4	1	7
			(3)	(4)	(1)	(7)
	Immature	22	6	4	—	12
			(9)	(7)	—	(22)
	Total	98	68	51	1	66
			(73)	(62)	(3)	(98)
	Percentage loss and 95% confidence interval		6.9 ± 5.4	17.8 ± 9.3	(66.7)	32.7 ± 9.0
64- and 83-mm mesh (multifilament):						
1966	Immature	158	22	34	—	93
			(23)	(44)	—	(156)
1967	Immature	18	17	10	0	3
			(18)	(12)	(5)	(18)
1968	Mature	4	2	1	—	2
			(2)	(1)	—	(4)
1969	Mature	1	—	—	—	1
			(—)	(—)	(—)	(1)
	Total	181	41	45	0	99
			(43)	(57)	(5)	(179)
	Percentage loss and 95% confidence interval		4.7 ± 6.5	21.1 ± 10.8	100	44.7 ± 7.1
	Grand Total	534	216	182	10	312
			(230)	(211)	(21)	(524)
	Percentage loss and 95% confidence interval		6.1 ± 3.4	13.8 ± 4.4	52.4 ± 16.2	40.5 ± 4.0

[1] A zero (0) indicates that the net was examined, but no marked fish were observed; a dash (—) indicates that the net was not examined. Numbers in parentheses indicate number of possible observations for the time period; difference from the number marked is because some observations were not made in rough weather.

TABLE 11.—Total number of salmon marked and observed over varying periods of time by maturity, mesh size, material, and year, 1966-69.

Mesh size and maturity	Years	No. fish marked during patrols	Number of fish observed after marking[1]			
			Up to 1 h later	Up to 2½ h later	Up to 5 h later	Up to 11 h later
Large mesh multifilament nets (98-, 114-, and 133-mm mesh):						
Mature	1968-69	62	45 (45)	20 (20)	1 (1)	50 (62)
	Percentage loss and 95% confidence interval		0	0	0	19.4±9.9
Immature	1966-67, 1969	193	62 (69)	66 (72)	8 (12)	97 (185)
	Percentage loss and 95% confidence interval		10.1±6.9	8.3±6.5	33.3±29.7	47.6±6.9
Large mesh monofilament nets (114- and 133-mm mesh):						
Mature	1968-69	39	28 (28)	24 (26)	1 (1)	32 (39)
	Percentage loss and 95% confidence interval		0	7.7±10.7	0	17.9±12.1
Immature	1967, 1969	59	40 (45)	27 (36)	0 (2)	34 (59)
	Percentage loss and 95% confidence interval		11.1±8.9	25.0±14.3	100	42.4±12.9
Small mesh multifilament nets (64- and 83-mm mesh):						
Mature	1968-69	5	2 (2)	1 (1)	— —	3 (5)
	Percentage loss		0	0	—	40.0
Immature	1966-67	176	39 (41)	44 (56)	0 (5)	96 (174)
	Percentage loss and 95% confidence interval		4.9±6.8	21.4±10.9	100	44.8±7.2
Total (all mesh sizes):						
Mature	1968-69	106	75 (75)	45 (47)	2 (2)	85 (106)
	Percentage loss and 95% confidence interval		0	4.3±8.9	0	19.8±7.5
Immature	1966-67, 1969	428	141 (155)	137 (164)	8 (19)	227 (418)
	Percentage loss and 95% confidence interval		9.0±4.3	16.5±5.6	57.9±18.0	45.7±4.6

[1] A zero (0) indicates that the net was examined, but no marked fish were observed; a dash (—) indicates that the net was not examined. Numbers in parentheses indicate number of possible observations for the time period; difference from the number marked is because some observations were not made in rough weather.

and carrion eaters could affect dropout rates. During the haul of gill nets, and in early morning hours, we often observe Steller sea lion, northern fur seal, and seabirds along the net string feeding on enmeshed salmon. Obviously, these animals could affect the results of the dropout experiments if they took marked salmon. An example of suspected sea lion predation was observed when, on one occasion in 1966, 25 salmon were marked between hours of 2254 and 2320; not a single salmon was present at the marked positions when the nets were hauled at 0730. Sea lions were observed along the nets on this occasion. On other occasions, while patrolling the gill nets at night during dropout studies, we have observed sea lions cruising the net and taking salmon.

Steller sea lions are probably the most flagrant predators. Although examination of their stomach contents has shown only occasional salmon (Pike, 1958; Mathisen, Baade, and Lopp, 1962; Thorsteinson and Lensink, 1962; Fiscus and Baines, 1966), there

TABLE 12.—Decoy loss rates in relation to distance from shore, spring and summer 1968-70.

Year	Season	No. of sets	No. of decoys set	No. of decoys recovered	Percentage loss	% sets predators observed[1]
		≤145 km from shore				
1968	Spring	4	92	46	50.0	100
	Summer	21	394	71	82.0	81
1969	Spring	8	147	55	62.6	88
	Summer	34	663	317	52.2	94
1970	Spring	6	108	46	57.4	100
	Summer	16	320	209	34.7	94
Total		89	1,724	744	56.9	91
		>145 km from shore				
1968	Spring	10	183	149	18.6	80
	Summer	10	196	114	41.8	70
1969	Spring	13	260	195	25.0	77
	Summer	9	180	124	31.1	89
1970	Spring	14	266	215	19.2	93
	Summer	4	80	68	15.0	25
Total		60	1,165	865	25.8	78
Overall total or mean		149	2,889	1,609	44.3	86

[1]Potential predators or carrion eaters include: fur seal, sea lion, albatross, shark, porpoise.

TABLE 13.—Numbers of salmon marked and observed for varying periods of time for sets far offshore (>145 km).

Years	Number marked	Number observed after marking[1] Up to 1 h	Up to 2½ h	Up to 5 h	Up to 11 h
1966-69	181	62	56	9	121
		(66)	(62)	(12)	(173)
Percentage loss		6.1	9.7	25.0	30.1

[1] Number of possible observations for time period indicated in parentheses.

is evidence that sea lions rob salmon from gill nets and trolling gear (Pike, 1958; Thorsteinson, Nelson and Lall, 1961) and cause damage to gear. Furthermore, some authors (Mathisen, 1959; Tikhomirov, 1964) feel that sea lions may be attracted to areas where fishing boats are operating.

During our experimental gillnetting in the central Aleutians over a number of years, sea lions have been observed around gill nets much more frequently at inshore (within 145 km) than at offshore stations (Table 12). During studies of predation (French et al., 1970, 1971, 1972) in which frozen "decoy" salmon were tied to the nets when they were set and the numbers remaining counted at haul, the percentage loss of decoys was smaller at distances greater than 145 km than at stations closer to shore (26% vs. 57%, see Table 12).

These studies, though, were not conclusive when applied to the dropout data. For example, the mean decoy loss rate for all stations (44%) was similar to the average loss (40.5%) of salmon marked in gill nets (Tables 10, 12). In addition, the decoy loss rate beyond 145 km (26%) was similar to the dropout loss (30%) for the same area (Tables 12, 13).

As French et al. (1970, 1971, 1972) pointed out, the results of the decoy studies are difficult to relate to actual gill net catches. For example, the decoy fish normally were exposed to predators and carrion eaters from the time the gear was set (at about 2000 h) until completion of haul at about 1000 h, whereas salmon are not normally caught in gill nets on the high seas until dark and would, therefore, be subjected to predation for fewer hours than the decoy fish. The food preference of some animals may also vary between the dead decoy fish and the live gill net-caught salmon. Percentages of decoy fish removed by these animals therefore, may not be directly comparable to predation upon fish captured by gill nets. The

possibility exists that the presence of decoy fish attached to the gill nets when they are set may attract predators and carrion eaters and, therefore, increase the incidence of predation.

To study further the relation between decoy losses and dropouts, we examined losses of decoys and salmon marked for dropout studies in 10 gill net sets in which dropout and decoy loss studies were conducted simultaneously. In these sets the decoys were generally attached near the distal end of the net string from the vessel, and salmon were marked for dropout studies at the proximal end of the string. Of these 10 sets, three showed no decoy loss but did have a mean total dropout loss of 11.8% (Table 14). The remaining seven sets had a mean total dropout loss of 27.3%, but also had a mean decoy loss rate of 36.4% (Table 14). Thus, if we accept a zero loss of decoy fish as evidence of no predation, we have evidence of dropout loss independent of predation.

Additionally, Thompson et al. (1971) studied the viability of salmon that disentangled from gill nets in a predator-free controlled environment. In the 1968 studies, nearly 46% of the 180 sockeye salmon exposed to the gill nets became disentangled.

Thompson et al. (1971) also studied the loss of dead salmon which became unmeshed from gill nets during high-seas fishing in 1968-69. These studies involved the placement of identifiable dead salmon in the net (i.e., "gilling" them in as natural a manner as possible) at the time of set and counting the retained carcasses when the net was hauled the following morning. Although it was not possible to establish whether a missing fish had dropped out of the net passively or had been extracted by an animal, these authors estimated the passive loss by comparing the loss of dead carcasses to the loss of decoy salmon during the same sets. The conditional estimate of passive loss (independent of predation) was 12.5%.

Admittedly, this is not extensive evidence. We must, therefore, attribute the loss of salmon from gill nets to both predation and disentanglement, and we cannot accurately separate the two.

It is pertinent, however, to draw analogies between the Japanese mothership fishery and our research vessel fishing. Both vessels fish gill nets in a similar manner, and both types of fishing would be subject to predation. The presence of Stellar sea lions in abundance in the area of the Japanese mothership fishery (from the central Aleutians to the Kuril Islands) has been documented (Mathisen, 1959; Tikhomirov, 1964). Estimates of abundance of Steller sea lions ranged up to 40,000 animals in the western Aleutians and up to 20,000 in the Kuril Islands (Kenyon and Rice, 1961; Tikhomirov, 1964).

Thus the estimates of loss of salmon from

TABLE 14.—Summary of loss from gill nets when "decoy" and dropout studies were conducted concurrently.

			Dropout studies			Decoy studies		
Year	Season	Set no.	Number marked	Number recovered	Percentage loss	Percentage loss	Total catch	Distance offshore (km)
Loss from nets when no decoys were lost:								
1968	Spring	19	11	10	9.1	0	71	342
1969	Spring	12	2	2	0	0	23	161
	Summer	21	21	18	14.3	0	296	143
Total			34	30	11.8	0	—	
Loss from nets when decoys were lost:								
1968	Spring	17	7	6	14.3	47.6	58	228
	Spring	20	13	9	30.8	25.0	110	151
	Spring	22	62	49	20.9	47.4	283	100
1969	Spring	9	5	5	0	10.0	56	438
	Spring	11	4	3	25.0	5.0	50	255
	Summer	17	5	0	100.0	100.0	0	19
	Summer	25	14	8	42.9	20.0	154	15
Total			110	80	27.3	36.4	—	

gill nets (attributable to predation and disentanglement) based on research vessel data presented here would apply equally to the Japanese mothership fishery in areas where the fishery is exposed to sea lions. In other areas far offshore, loss of salmon attributable to predators would be minimal, but losses would still be expected from fish becoming disentangled.

Effects of Weather on Dropout Rates

Weather is one factor which should affect the dropout rate. Normally one would expect greater losses of fish from gill nets during strong winds and the resultant heavy seas.

The indirect methods of estimating losses from gill nets used in 1964 and 1965 allowed fishing in winds up to 35 knots. The design of the experiments, however, did not provide for an easy comparison of dropout loss and weather conditions, nor were detailed weather measurements recorded.

The direct methods of estimating loss from gill nets used in 1966-69 precluded observations in strong winds and heavy seas. Observations were normally not made in winds greater than 15 knots or in other than nearly calm seas. At times, however, winds would increase during the dropout observations, necessitating the canceling of the experiment.

Routine weather observations made aboard the vessel while setting and hauling the gill nets in 1966-69 included wind speed and direction, wave height, sea swell conditions, and barometric pressure. These data were compared to the percentage loss of salmon from gill nets (Table 15).

Because of the relatively small changes in most of the weather variables between set and haul times, no apparent relation with percentage loss of salmon was found. The weather measurement exhibiting the largest variation was wind speed at haul. This measurement was compared with the total loss of salmon (Figure 6), but little correlation was found (r = 0.125).

In a number of sets the loss rate was high (up to 40% or more) when wind speed at haul was 10 knots or less. In an attempt to determine whether or not these losses were due primarily

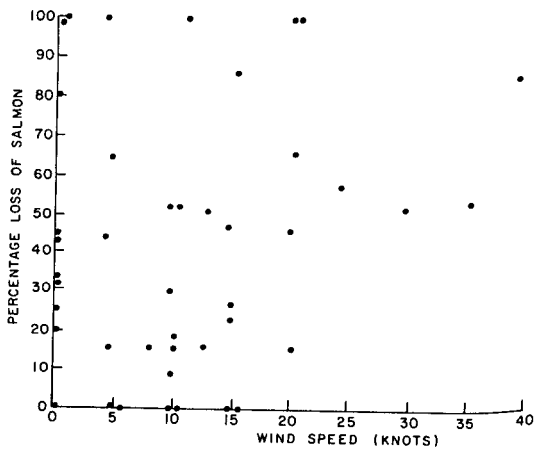

FIGURE 6.—Percentage loss of salmon in relation to wind speed at haul.

to predation as opposed to dropouts and, therefore, more independent of weather, all sets less than 145 km from shore were eliminated from further analysis to reduce the effects of predation. Twenty dropout sets remained for analysis; the correlation between percentage loss of salmon and wind speed at haul remained poor (r = 0.362).

Although it seems obvious that weather conditions (at least sea state) should influence the rate of loss of salmon from gill nets, the available data fail to demonstrate any relation. Effects of sea state must therefore remain as an unknown influence on the rate of salmon loss from gill nets. If, however, we assume that dropout of fish increased with increased agitation of the nets, the rates as measured (due to selectivity of experimental conditions) are probably low. Ishida et al. (1969) also were unable to evaluate the effect of sea state on dropout rate during their experiments from 1963 to 1967.

Inshore Fishing

The loss of salmon from gill nets fished on maturing salmon in inshore waters was studied by direct observation in Puget Sound in August 1967. The same basic experimental methods used on research vessels were applied to a commercial salmon fishing vessel. Because the commercial fishermen in Puget Sound

TABLE 15.—Loss of salmon from gill nets and weather conditions at set and haul, 1966-69.

Year	Cruise	Set	Date	Number of fish		Percentage loss	Weather conditions							
							At set (2000-2200)				At haul (0800-1000)			
				Marked	At haul		Barometer	Wind direction	Sea height	Swell height	Barometer	Wind direction	Sea height	Swell height
1966	37	24	7/20	7	6	14.2	30.02	SSE/5	0	1	30.00	S/10	1	1
		32	7/29	3	1	66.7	—	SW/15	2	6	30.01	SW/20	4	6
		48	8/19	4	4	0.0	30.02	SW/15	2	4	30.06	0	calm	—
		56	9/1	7	1	85.7	29.92	NW/5	2	5	29.94	W/15	2	6
		57	9/2	2	1	50.0	—	—	—	—	30.00	NW/35	5	6
1966	38	2	6/27	7	0	100.0	30.34	calm	0	2	30.37	calm	—	long
		3	6/28	7	4	42.9	30.25	NE/5	1	—	30.11	NW/5	1	long
		4	6/29	6	5	16.7	30.10	calm	—	—	29.89	NW/5	1	0
		5	6/30	3	0	100.0	29.81	calm	—	—	29.75	SW/20	2	—
		15	7/16	8	3	62.5	30.04	W/10	2	—	30.17	S/5	1	—
		16	7/17	3	3	0.0	—	—	—	—	30.90	S/5	1	—
		19	7/18	10	0	100.0	30.12	NE/5	—	—	30.14	0	—	—
		23	7/24	55	44	20.0	30.04	NE/5	2	—	29.88	0	—	—
		25	7/26	6	3	50.0	30.01	SW/15	2	—	30.05	SW/10	2	—
		33	8/5	11	6	45.5	29.90	calm	—	—	29.96	calm	—	—
		37	8/11	5	1	80.0	29.65	NE/10	2	4	29.69	calm	—	—
		38	8/12	24	13	45.8	29.65	W/10	2	low	29.58	W/30	6	8
		41	8/15	3	0	100.0	30.20	SW/5	1	low	30.20	W/5	1	—
		42	8/16	19	16	15.8	30.20	calm	1	—	30.26	W/20	3	—
		43	8/17	6	5	16.7	30.27	SW/10	3	—	30.20	SW/10	3	—
		47	8/24	6	3	50.0	30.12	W/5	calm	—	30.16	S/10	calm	—
1966	39	6	7/18	2	2	0.0	30.20	SE/5	calm	—	30.20	NE/5	calm	—
		7	7/19	9	7	22.2	30.17	NW/10	calm	—	30.16	NW/15	calm	—
		9	7/21	14	10	28.6	30.17	W/5	calm	—	30.16	W/10	calm	—
		10	7/22	8	8	0.0	30.20	NE/10	calm	—	30.22	E/15	choppy	—
		12	7/24	27	0	100.0	30.29	E/20	calm	—	30.23	E/20	choppy	—
		28	8/25	24	16	33.3	30.23	SW/5	calm	—	30.25	calm	—	—
		29	8/26	21	10	52.4	30.15	E/5	calm	—	30.14	SE/25	choppy	5-10
1967	41	6	6/29	11	6	45.5	30.20	calm	—	—	30.15	SE/15	4	5
		12	7/13	2	2	0.0	30.18	SW	1	3	30.10	SW/10	4	5
		21	8/1	8	0	100.0	30.07	SW/calm	2	5	30.04	0	1-2	4
		25	8/5	24	3	87.5	29.86	W/17	—	—	29.68	WSW/40	—	—
		26	8/15	36	21	41.7	29.59	SW/10	—	—	29.54	SW/20	—	—
1968	43	17	5/28	7	6	14.3	30.04	E/5	0	2	30.06	SE/10-15	1	2
		19	5/31	11	10	9.1	30.13	NNE/10-15	1	2	30.10	NNE/10	1-2	4
		20	6/3	13	9	30.8	29.59	WNW/5	1	3	29.63	calm	0	3
		22	6/5	62	49	20.9	29.85	ESE/10	1	3	29.87	ESE/15	1	3
1969	46	1	4/25	2	1	50.0	29.65	NW/10	—	3	29.63	NW/10-15	1	3
		9	5/27	5	5	0.0	29.91	0	—	3	29.93	E/10	1	3
		11	5/29	4	3	25.0	30.21	0	0	3	30.24	0	0	3
		12	5/30	2	2	0.0	30.28	W/10	1	3	30.18	SW/15	2	4
1969	47	17	7/20	5	0	100.0	30.15	NE/18	1	2	30.23	NE/12	1	2
		21	7/24	21	18	14.3	30.22	S/8	1	3	30.24	NE/8	1	3
		25	7/28	14	8	42.9	30.34	0	0	2	30.40	0	0	2

generally do not drift longer than 3 h at a time, our inshore observations were limited to a maximum of 3 h. These inshore observations provided a basis of comparison with loss rates determined on the high seas.

Commercial salmon gill nets used in Puget Sound were 549 m long and about 15 m deep. Our observations covered the entire string. Mesh sizes used were 130 mm and 143 mm.

Observations were conducted during eight sets (Table 16). Fifty-nine fish (primarily sockeye and pink salmon) were marked. No dropouts were recorded for periods up to 3 h. Although the observations were limited, it appears that loss of salmon from gill nets of 130- and 143-mm mesh is not a serious problem in the commercial fishery of Puget Sound.

Similar conclusions were reached by the Washington State Department of Fisheries after studies on dropouts in Puget Sound in 1968 and 1969.[6] During 2 yr of experiments, 245 salmon were observed or marked in commercial type gill nets; only 3 of these (1.2%) were dropouts. In a special experiment involving sockeye salmon native to Lake Washington (near Seattle, Wash.), 38 fish were marked (located by observation in the nets), and 11 (29%) had dropped out by the time the gear was hauled. In this experiment, however, the gill nets used were 121 to 140 mm in mesh size and were considered too large for the salmon which averaged less than 5 lb. per fish.

These studies in Puget Sound, in a gill net fishery generally conducted in comparatively calm and protected waters, show that dropouts were much reduced from dropout rates on the open seas. They further indicate that dropouts from gill nets may be mainly related to open-seas fishing.

[6] Jewel, E. D. 1970. Gill net dropout study. Wash. Dep. Fish., Prog. AFC-14, 5 p. [Unpubl. Rep.]

TABLE 16.—Numbers of salmon marked and observed in gill nets (130- and 143-mm mesh) over varying periods of time, Puget Sound, Wash., August 1967.

Set	Number of fish marked during patrols	Number of fish observed after marking: Up to 1 h later	Up to 2-3 h later
1	1	—	—
2	2	2	—
	2	2	—
3	8	8	—
	2	—	—
4	2	—	—
	1	—	—
5	3	3	—
	3	—	—
6	3	—	3
	2	2	2
	5	—	—
7	9	9	9
	4	—	4
	9	9	9
8	3	3	3
Total	59	38	30
		[1](38)	[1](30)
Percentage loss		0	0

[1] Number of possible observations for the time period; different from the number marked because some net drifts were of short duration and observations were not made over the entire period. Dash (—) indicates no observation.

SALMON FALLOUTS FROM GILL NETS DURING HAUL

In the process of hauling gill nets aboard fishing vessels during high-seas salmon fishing, salmon are frequently observed falling from the nets before they can be taken aboard. These fish have been termed fallouts to distinquish them from the dropouts or those salmon that become disentangled from the gill nets during fishing. We have examined the catch records of research vessels from 1965 to 1970 to determine the number of fallouts by season of fishing, size of vessel, and mesh size.

The total number of fallouts during hauling of gear amounted to about 1.4% of the total number of salmon landed (Table 17). The greatest number of fallouts occurred on the RV *Miller Freeman*, the vessel having the highest lift of the nets from the water surface to the net roller where the nets are brought aboard the vessel; the least number occurred on the chartered vessels *Paragon* and *St. Michael*, vessels with the shortest lift distance between the water and roller. The fallouts from the *George B. Kelez*, with an intermediate distance from water to roller, were intermediate between those of the smaller and larger vessels.

Only one vessel, the *George B. Kelez*, fished over the four seasons. Results of fallout tabulations indicated relatively little difference by

TABLE 17.—Salmon fallouts from gill nets during hauling operations, by vessel and season.

Vessel	Vessel length (m)	Height from water to net roller (m)	Season	Number of fish falling out of nets	Total number of fish landed	Percent fallout of number of fish landed
RV *George B. Kelez*	54	2.4-3.0	Summer	264	18,725	1.41
			Fall	11	1,012	1.09
			Winter	67	3,357	2.00
			Spring	116	7,880	1.47
RV *Miller Freeman*	65	7.0-9.0	Summer	141	6,739	2.09
MV *Paragon*	27	1.5-2.0	Spring	20	3,492	0.57
MV *St. Michael*	23	1.5-2.0	Summer	25	3,611	0.69
Total				644	44,816	1.44

season of fishing, although slightly more fallouts were observed during the winter cruises—the season of generally poor weather and rough sea conditions.

Results of tabulating fallouts by mesh size are given in Table 18. In winter there was not a large difference in fallouts by mesh size with the exception of the 133-mm mesh. In general, however, during winter fishing operations (1967, 1969, 1970), the large salmon (predominantly sockeye) that were normally taken by 133-mm mesh nets in the spring were not as numerous as the smaller salmon. In the spring, when maturing salmon predominated in the catches and the catches were primarily in the large meshes (98, 114, and 133 mm), fallouts were mainly from those mesh sizes. Summer catches were primarily of immature salmon (sockeye and chum); the largest number of fallouts were from the small meshes (64 and 83 mm).

Konda (1966) examined data from Japanese research vessels for 1961-63 and estimated the escapement of salmon from gill nets during haul at 2%, a figure similar to our findings for U.S. research vessels. He further concluded that the number of fish surviving from falling out of the nets at haul is related to the length of time needed to haul the nets and that in commercial operations most fish will die because of the large number of gill nets fished in a day.

We concluded from our experimental fishing that the number of fallouts was small in relation to the number of fish hauled aboard the vessels and that there was little difference in percentage of fallouts by size of vessel.

If our findings are comparable to the catch and fallout of a large high-seas gill net fleet and unless remedial action is taken to retrieve lost fish, a sizeable number of salmon would be lost by the fleet over a season.

POTENTIAL LOSS OF SALMON RESOURCES FROM HIGH-SEAS GILLNETTING

The evidence of loss of salmon from gill nets (due either to dropouts, predation, or both) fished on the high seas in test fishing by research vessels indicated that the potential for substantial waste of the resource was due to the harvesting technique. Although the mortality of salmon escaping from gill nets (dropouts) is not known, there is evidence in the literature that losses are relatively large. Nelson and

TABLE 18.—Salmon fallouts according to mesh size.

Season	Sample size[1]	Percent fallouts by mesh size					
		51 mm	64 mm	83 mm	98 mm	114 mm	133 mm
Winter	71	18.6	18.6	22.5	18.3	17.9	4.2
Spring	114		8.8	13.9	38.6	26.2	12.5
Summer	459		30.4	36.6		17.9	15.1

[1] Totals by mesh size are equated to equal number of shackles of each mesh size as fished by season in 1970.

Abegglen (1955) studied the survival and spawning of sockeye salmon marked by gill nets in the Karluk Lagoon (Alaska). In experiments on maturing salmon entering Karluk River, fish were induced to enter gill nets, tagged, and recovered at upriver weirs or on the spawning grounds. Nelson and Abegglen estimated that from 10 to 20% of the gill net-marked fish escaping commercial gill nets die because of injuries inflicted by the webbing.

More conclusive evidence of high mortality of salmon which escape from gill nets in salt water comes from controlled experiments in 1968 and 1970. These experiments indicated that an average of 73% of the dropouts died in 6 days compared with 10% for control fish (Thompson and Hunter, see footnote 2).

Recoveries in inshore areas of gill net-caught salmon which had been tagged and released at sea have been far fewer than recoveries of gill net-caught fish tagged in rivers or estuaries. For example, from 1952 to 1957, Japanese scientists tagged 6,155 salmon that had been captured in gill nets on the high seas; only 26 (0.4%) were recovered (Fisheries Agency of Japan, 1959). In another example, U.S. scientists tagged 378 salmon captured with gill nets on the high seas, and none were recovered. At the same time as these experiments, salmon were captured by longlines and purse seines and were tagged and released; recoveries amounted to 7.3%. From inshore tagging during these same series of experiments (fish were captured in gill nets and tagged primarily in Bristol Bay, east of long. 165°W), recoveries were 6.9%, whereas recoveries from fish captured with longline and purse seines averaged 29% (Lander et al., 1967). The poor recovery of tagged salmon led Japanese, Canadian, and United States scientists to abandon gill nets as a means of capturing salmon for tagging experiments.

There is evidence, on the other hand, that recoveries of salmon captured in gill nets and tagged in fresh water may be relatively high. Salmon captured in gill nets at Hells Gate (Fraser River, B.C.) were tagged in 1939 and 1940; upstream recoveries were 40% in 1939 and 31% in 1940 (Thompson, 1945).

If we assume similar care in handling fish for offshore and inshore experiments and assume that the fish were in the nets for approximately equal time periods, these examples illustrate that salmon upon reaching estuaries and fresh water are likely to be much hardier than their offshore counterparts and apparently are much more able to survive the effects of gillnetting.

From the evidence of tagging experiments and from studies on the viability of salmon escaping gill nets, we concluded that the survival of salmon escaping gill nets on the high seas is relatively low. Furthermore, we may assume that losses of salmon due to predation result in 100% mortality of the extracted fish. Therefore, the potential loss of salmon and waste of the resource due to dropouts and predation amount to large numbers of salmon.

Japan engages in a major high-seas gill net fishery for Pacific salmon in the North Pacific Ocean and Bering Sea. The Japanese mothership fishing area, governed by agreements with Canada and the United States (International North Pacific Fisheries Convention) and with the USSR (International Convention for Northwest Pacific Fisheries), lies west of long. 175°W and extends generally from lat. 46° to 60°N (International North Pacific Fisheries Commission, 1968). In addition, a land-based gill net fishery for salmon is pursued by Japan in areas of the North Pacific Ocean south of the mothership fishing area (Figure 7).

Fukuhara (1971) analyzed the Japanese mothership fishery, the details of which follow. The fishing effort of the fleet since 1961 has numbered 11 motherships and 369 catcher boats, fishing between 5 and 7.5 million tans[7] (cumulative effort) of nylon gill nets during a season. West of long. 170°E, the maximum allowable number of tans per boat is 264 and 330 east of that longitude. On a given day, therefore, the fleet is capable of fishing 4,900 to 6,100 km of gill nets, depending on its east-west distribution. Two sizes of mesh are used, 121 mm and 130 mm, stretched measure. The ratio of large mesh to small mesh must be 6:4 west of long. 170°25′E and may be 4:6 east of

[7] A tan is approximately 50 m long.

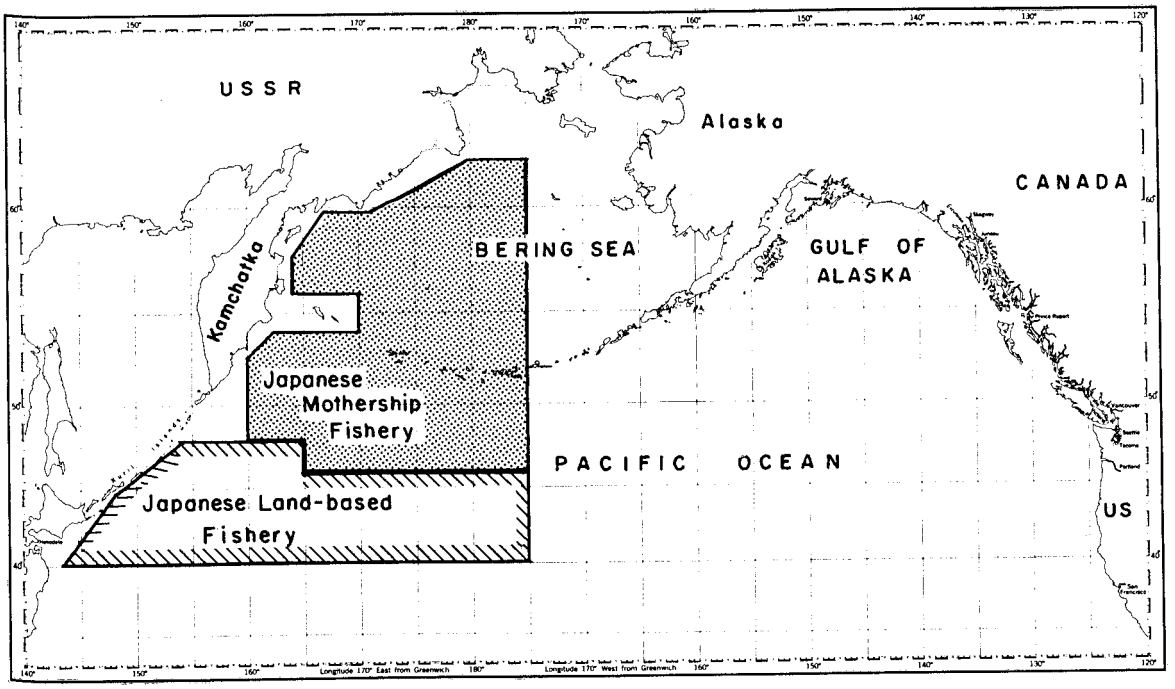

FIGURE 7.—Fishing area of Japanese mothership and land-based fishery.

long. 170°25′E. In recent years the fleet has been changing the gill nets to monofilament netting in lieu of multifilament netting. Our most recent information is that most, if not all, of the catcher boats now use the monofilament gear.

Although our experiments on dropouts and fallouts have been conducted on research vessels, the results are applicable to fishing practices as carried out by the mothership fleet. The webbing for the gill nets used by our research vessels originated from Japan, and construction of the gill nets was generally copied from the construction of Japanese gear. The leadline of the Japanese gear has heavier cordage and is slightly shorter than the corkline, whereas in the U.S. gear the corkline is slightly shorter than the leadline and is of heavier cordage; therefore, while the gear is soaking and during the hauling, the tension is on the leadline in Japanese commercial gear and on the corkline in U.S. research gear. The mesh sizes of 114 mm and 133 mm, as used by our research vessels for capturing maturing salmon and the larger immature salmon were similar in size to the mesh sizes (121 and 130 mm) of the commercial nets of the fishing fleets. The modal selection length for 114-mm and 121-mm meshes are 53 cm and 56 cm, respectively, and for 130 mm and 133 mm, 60 and 62 cm, respectively, which is a very slight disparity in selection lengths (Fukuhara, 1971).

Salmon catches by the Japanese mothership fleet have ranged from about 19 to 26.5 million fish and have averaged about 22 million salmon annually for 1960 through 1968 (International North Pacific Fisheries Commission, 1965-1968). An annual estimated average of about 2.5 million sockeye salmon (maturing and immature) of Bristol Bay origin have been taken by the mothership fishery; the catch has ranged from approximately 0.3 to 7.2 million fish for 1956-69 (Fredin and Worlund).[8] Loss

[8] Fredin, R. A., and D. D. Worlund. 1972. Estimates of the catches of sockeye salmon of Bristol Bay origin by the Japanese mothership salmon fishery, 1956 to 1970. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., 82 p. [Unpubl. Manuscr.]

rates as determined from the dropout studies, therefore, indicated substantial numbers of salmon lost during high-seas gillnetting.

To summarize the loss rates obtained, for large mesh nets of monofilament construction, the percentage loss of immature and mature salmon was approximately 33% (Table 10). For mature fish and for multifilament and monofilament nets the loss rate was about 20% (Table 11). These estimates of loss due to gillnetting are similar to those reported by Semko (1964) and by Miyazaki and Taketomi (1963, as cited by Konda, 1966), are smaller than those reported by Doi (1962), and are somewhat larger than the losses reported by Ishida et al. (1969).

Applying a loss rate of 33% to the average catch of 2.5 million sockeye salmon of Bristol Bay origin taken by the Japanese mothership fleet results in an estimated average of about 1.2 million sockeye salmon lost from the gill net fishery annually, with a range of 0.15 to 3.5 million fish yearly, depending upon the size of the catch. A loss rate of 20% would indicate that 0.6 million Bristol Bay sockeye salmon are lost annually on the average (with a range of 0.08 to 1.8 million fish).

Calculation of the total loss of salmon (of North American and Asian origin) from the mothership operation, based on annual catches, resulted in an estimated loss of about 10.8 million salmon at a 33% loss rate and 5.5 million fish at a 20% loss rate. The range of losses, depending upon the annual catch by the mothership fleet, was from 9.4 to 13.1 million fish and 4.8 to 6.6 million fish for the two respective loss rates.

In experiments in which no decoys were lost and in which losses from gill nets were attributable only to dropouts (Table 14), the disentanglement rate of about 12% also indicated substantial losses of salmon. This loss rate applied to the average annual catches by the mothership fishery, resulted in estimated annual losses of 0.3 million sockeye salmon of Bristol Bay origin (with a range of 0.04 to 1.0 million fish, depending upon the catch) and an average total loss of 3.0 million salmon of all origins (range of 2.6 to 3.6 million fish depending upon catch).

We have no way of determining the actual mortality of salmon lost from gill nets. We know that some fish survive as evidenced by net-marked salmon observed in spawning streams. In the experiments on viability of adult sockeye salmon that disentangle from gill nets, which were carried out in an enclosed area in relatively calm waters of Puget Sound, it was shown that approximately 73% of fish that disentangled from gill nets died within 6 days compared with 10% for control fish. These particular fish were held in a protected enclosure throughout the experiments; mortalities of gill net dropouts could be even greater in the open ocean. Therefore, at any likely mortality level that we might assign to salmon dropping out of gill nets on the high seas, the resultant waste of the resource is substantial.

In addition to losses due to dropouts and predation, there is the attendant loss of salmon during the haul of gear aboard vessels. It was estimated for U.S. research vessels that about 1.4% of the number of fish landed fell out of the gill nets at haul. If we consider a 1% fallout rate (the approximate fallout rate of the smallest of U.S. research vessels), the resultant loss of salmon during the Japanese mothership fishery would average over 200,000 fish annually. The estimated loss of sockeye salmon of Bristol Bay origin by the mothership fishery would amount to an average annual loss of 25,000 fish.

From the indirect methods of determining rates of losses, we obtained rates of approximately 32% for immature fish and 27% for maturing fish. Either of these rates indicated losses of salmon on the order of or even greater than that estimated from direct observation. As with the majority of direct observations, however, we were unable to differentiate the effect of predators on dropout rates and losses were considered as due to a combination of dropouts and predation.

The estimated large numbers of salmon lost from gill nets in a high-seas fishery and the probable large mortality of these salmon indicate the relatively large waste of part of the resource. In contrast, inshore experiments in Puget Sound indicated that there is not the loss of salmon from gill nets or potential waste of

the resource as associated with an open sea fishery.

SUMMARY AND CONCLUSIONS

Studies by U.S. scientists on the loss of salmon from gill nets fished on the high seas commenced in 1964. The indirect methods of determining losses used in 1964 and 1965 resulted in the estimates of loss of immature salmon of 32% for periods up to 12.5 h in 1964 and an estimated average loss of maturing salmon of 27% for a 3-h period in 1965. These losses were attributed to disentanglement and to extraction by predators.

Direct methods of observation were initiated in 1966. These studies permitted estimates of rate of loss of salmon for periods up to 1, 2½, and 3 h (and in some years up to 5 h) as well as periods up to 10-11 h. These studies were directed toward both maturing and immature salmon; comparisons were also made between large and small mesh gill nets and between monofilament and multifilament gill nets.

In the 4 years' experiments, 534 salmon were marked. Overall loss rates for periods up to 11 h was 41%. Loss rates were nearly 6% up to 1 h and 14% up to 2½ h, and it was shown that losses continued with time in the net.

Losses from small mesh (64- and 83-mm) multifilament nets, which capture mainly the small age .1 immature salmon, were similar to losses from large mesh nets (45% vs. 41%). Loss rates from the small mesh nets were similar to those of large mesh multifilament nets for periods up to 1 h (5 and 6%, respectively) and greater than the losses in large mesh multifilament nets for periods up to 2½ h (21 and 7%, respectively).

Comparisons of the loss rates of large mesh (98-, 114-, and 133-mm) multifilament nets as opposed to large mesh (114- and 133-mm) monofilament nets indicated that for periods up to 11 h, loss rates from the multifilament nets exceeded the monofilament nets (41% vs. 33%), although the difference was not statistically significant.

The loss rates of primarily immature salmon in the summers of 1966 and 1967 were compared with the catches of primarily maturing salmon in the spring of 1968 and 1969. Loss rates for the immatures for the three time periods (1, 2½, and 11 h) were 9, 17, and 46%; for maturing salmon the loss rates for the three time periods were 0, 4, and 20%.

It was not possible to determine accurately species during the process of marking the locations of fish in the nets. It was concluded that dropout rates would be applicable to those species which make up the bulk of the catches (sockeye and chum salmon made up over 70% of the catch during these experiments).

The losses were attributed to both disentanglement (dropout) and to extraction by predators. Attempts at differentiating between losses due to dropout and losses due to predation were not entirely conclusive. Estimates of the loss of salmon due only to dropout was about 12%, although the data from which this estimate was derived are limited. It was concluded that the estimates of losses from gill nets based on research vessel data apply equally to the Japanese mothership fishery because of similarity of fishing methods, gill net construction, and susceptibility to predation.

Weather (wind and sea state) was expected to influence gill net loss, but the available data failed to demonstrate any relation, primarily because the experiments were generally conducted in comparatively calm weather.

Direct observation of the loss of maturing salmon from gill nets was extended to an inshore fishery (Puget Sound) in August 1967. No losses were recorded for periods up to 3 h. Subsequent studies by the Department of Fisheries, State of Washington, also failed to demonstrate significant losses, suggesting that losses from gill net fisheries were mainly related to high-seas fishing.

Additional losses in high-seas gillnetting were attributed to fallouts, those salmon lost while hauling the nets aboard the vessel. Examination of U.S. research vessel catches from 1965 to 1970 indicated that fallouts amounted to about 1.4% of the total number of salmon landed. There was relatively little difference in percentage of fallouts by size of vessel. Although the number of fallouts did not form a substantial part of the total number of salmon landed, if the percentage loss was

similar in a large gill net fishing fleet, substantial numbers of salmon would be lost over a fishing season.

Based on the data reported herein, it was concluded that a substantial loss of salmon could occur in the Japanese high-seas fishery. Applying an estimated loss of from 20% (for maturing salmon) to 33% (for maturing and immature salmon combined) to the average annual catch of 22 million salmon by the mothership fishery, the estimated annual loss from gill nets would range from 5.5 to 10.8 million fish. Of this loss, it was estimated that an average of 0.6 to 1.8 million sockeye salmon of Bristol Bay origin would be lost annually by the Japanese mothership fishery.

In addition to losses due to dropouts, there is an attendent loss due to fallouts. If 1% of the total landings of the Japanese mothership fleet were lost, this would average over 200,000 fish each year, of which 25,000 sockeye salmon of Bristol Bay origin would be lost on the average.

Although the ultimate fate of salmon dropping out of gill nets is not known, evidence from the literature suggests that the mortality of salmon escaping from gill nets is high. The potential loss of salmon (due to dropout and predation) and waste of the resource, therefore, amount to substantial numbers of salmon.

ACKNOWLEDGMENTS

We thank all of the following who helped patrol the gill nets at night in the North Pacific Ocean in small boats during wind, rain, and fog: R. Bakkala, N. Budnick, R. Carlson, D. Craddock, T. Dunatov, W. Gronlund, F. Lund, W. Peterson, D. Sutherland, and R. Thompson of the Northwest Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, Seattle, Wash.; M. Berg, J. Svendsen, and E. Tveit from the NMFS charter vessel *Paragon*; and R. Ware from NMFS charter vessel *St. Michael*.

R. Fredin, D. Worlund, and G. Hirschhorn, Division of Fisheries Data and Management Systems, Northwest Fisheries Center, NMFS, NOAA, Seattle, provided the experimental design used in 1965.

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ECOLOGY AND PRODUCTION OF JUVENILE SPRING CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN A EUTROPHIC RESERVOIR[1,2]

DUANE L. HIGLEY AND CARL E. BOND[3]

ABSTRACT

Juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, were reared in a central Oregon reservoir of 7.5 hectare. The reservoir is strongly eutrophic, as shown by its heavy sedimentation, summer stratification, and chemical qualities (total dissolved solids over 200 ppm, total phosphorus to 0.4 ppm, and summer pH between 9 and 10). Surface water temperatures ranged from 3° to 29°C. Salmon were apparently confined to the upper 3 m during the summer because of low dissolved oxygen below this depth. In 1961, epilimnion conditions of high pH, high temperatures, decreasing oxygen concentrations, and possibly algal toxins caused condition loss and deaths among salmon. Fry planted in 1961 (75,300) and in 1962 (150,000) suffered first-summer mortalities in excess of 80%, primarily due to predation by older salmon. Summer growth was rapid, but dependent on population densities. Coho salmon, *O. kisutch*, and chinook salmon remaining from a 1959 plant averaged 280 and 215 g after 30 mo. The 1961 year class averaged 62 g at 10 mo and 89 g at 22 mo. The 1962 year class averaged 22 g at 9 mo. Average condition factor values rose above 1.20 in the summer. Net production by the 1961 year class was 159 kg/hectare in 1961 and 35.5 kg/hectare in 1962. The 1962 year class produced 170 kg/hectare in 1962. Potential December yield of first-year salmon was 98 kg/hectare in 1961 and 73.5 kg/hectare in 1962. First-year salmon ate primarily Entomostraca and chaoborid larvae. Apparently competition from the 1962 year class caused the 1961 year class to feed more on littoral and terrestrial forms and to grow and produce less in their second year. Age class I and age class II salmon weighing from 25 to 189 g emigrated via spillway outflows. In 1963, migrations occurred only at temperatures above 10°C; this relationship was not observed in 1962. This reservoir, or others with similar limnological conditions, cannot be recommended as a rearing site for chinook salmon because of the severe summer conditions.

Reduction in natural rearing sites available to Pacific salmon, *Oncorhynchus* spp., has led to a search for ways of augmenting the smolt production of various stream systems in the Pacific Northwest. One possibility is to rear the young salmon in impoundments where they presumably would develop into naturally fed, vigorous smolts. The smolts could then be released into nearby streams suitable for downstream migration. Various pond, lake, and estuarial habitats have been utilized as rearing impoundments. This paper describes the results of the rearing of chinook salmon, *O. tshawytscha* (Walbaum), of the spring race in Happy Valley Reservoir, a eutrophic impoundment located on the Warm Springs Indian Reservation in central Oregon. The research correlated reservoir limnology with the growth, survival, food habits, and migratorial tendencies of salmon planted in the reservoir. The project period was February 1961 to June 1963.

The reservoir was the site of an earlier study on the survival and growth of 30,000 coho salmon, *O. kisutch* (Walbaum), and 23,000 spring chinook salmon, which were planted in January 1959. Shelton (pers. comm.) reported that growth was rapid in both species, coho salmon averaging 41 g and chinook salmon 32 g, after an 18-mo

[1] Technical Paper No. 3439, Oregon Agricultural Experimental Station.

[2] This research was supported by United States Department of the Interior contracts 14-17-0001-374 and 14-17-0001-544.

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Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973

residence. In June 1960, the reservoir was treated with rotenone in an attempt to remove both salmon and resident rainbow trout, *Salmo gairdneri* Richardson. Survival of the salmon, to this time, was estimated to have been 90%.

In the present study, the reservoir received two plantings of spring chinook salmon fry: on 8 February 1961, 75,300 unfed fry at 3,300/kg from the Bureau of Sport Fisheries and Wildlife hatchery at Carson, Wash.; and on 22 March 1962, 150,000 advanced fry at 2,200/kg from the Bureau of Sport Fisheries and Wildlife Eagle Creek hatchery at Estacada, Oreg.

A fry planted in 1961 is called a 1961 year class fish; it is designated as 0-age from February 1961 to February 1962 and as age class I from February 1962 to February 1963, so that the Roman numeral corresponds to the number of winters spent in freshwater life (Koo, 1962).

METHODS AND MATERIALS

A stadia survey and depth sounding provided data from which a hydrographic map was made. Area and volume were computed from this map. Temperature patterns of the upper strata of water were recorded with a maximum-minimum thermometer and constant-recording thermographs. A transistorized thermometer was used to take vertical temperature series. Light penetration was measured with a Secchi disc.

A Kemmerer water bottle was employed to take water samples in vertical series for pH and dissolved oxygen determinations. The Winkler method was used for oxygen determinations, and either a color-comparator or portable conductivity meter was used to measure pH.

Other determinations made were total dissolved solids, volatile dissolved solids, total phosphorus, and methyl orange alkalinity. The same water sample sufficed for the first two; after the suspended solids were removed by centrifugation, the sample was evaporated at 60°C and ashed at 600°C for these measurements. The phosphorus analyses were conducted by the analytical laboratory of the Department of Soils at Oregon State University. A 0.02 N sulfuric acid solution was used in the titration for methyl orange alkalinity.

From 14 to 59 chinook salmon were collected at approximately 1 mo intervals for food and growth studies. These collections, in addition to the more extensive ones for survival estimates, were made by means of gill nets and beach seines, and by angling. Each fish in a monthly sample was measured for fork length to the nearest millimeter and weighed on a double-pan balance to the nearest 0.1 g. Fish to be used in the food analyses were preserved in 10% Formalin[4] after their body cavities had been slit open. The exception to this procedure involved the recently planted fish, which were preserved in 70% ethyl alcohol or 5% Formalin prior to measurement.

The condition factor for each fish was computed from the following formula, as modified from Rounsefell and Everhart (1953):

$$K = 100W/L^3$$

where K = a condition factor near unity
W = weight in grams
L = fork length in centimeters.

In preparation for stomach analyses, the preserved fish were transferred to 5% Formalin and eventually to 20% isopropyl alcohol. Ten fish from each sample were chosen for analysis. Only the contents of the anterior halves of the stomachs were removed in order to reduce error caused by partially digested foods. The stomach contents were pooled and thoroughly mixed, and a random subsample was extracted for dry-weight analysis.

Population estimates were determined through the mark-and-recapture method. Fish were captured with seines, anesthetized in a solution of quinaldine (8 to 12 ppm), marked with a fin-clip, and then distributed over the reservoir in accordance with the apparent distribution of the population. Fins clipped included both pelvics and anterior third of the anal fin on the 1961 year class, and adipose and posterior third of the anal on the 1962 year class.

Salmon which migrated from the reservoir via spillway outflows were captured in an

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

inclined-plane trap. Screens on the spillway forced emigrating fish to enter the trap. After spill had ceased, additional outflows of 0.071 m^3/s [2.5 cfs (cubic feet per second)] were produced by using a U-shaped iron tube as a siphon. The time or amount of outflow was otherwise uncontrolled.

Many of the measurements were taken in English units, and these occasionally are presented for clarity.

DESCRIPTION OF RESERVOIR

Happy Valley Reservoir (Figure 1) lies behind an earth-filled dam constructed on Quartz Creek in the Warm Spring River watershed. The stream flowed at rates up to 1.13 m^3/s (40 cfs) during the winters of the study. These inflows replaced water used for summer irrigation and produced spillway outflows of up to 0.56 m^3/s (20 cfs). Summer inflows dropped to less than 0.028 m^3/s (1 cfs).

At full pool, the reservoir covers 7.5 hectares and has a maximum depth of 12.8 m (42 feet). For most of the 1961 and 1962 summers these dimensions were reduced to 6.1 hectares and 10.7 m (35 feet) by irrigation drawdown. Minimal dimensions were 4.9 hectares and 9.1 m (30 feet), occurring from late summer to early winter.

The reservoir receives a heavy sediment load; Secchi disc visibility was 10 cm after a 1961 rainstorm and did not exceed 2.1 m during the study. The flat central plain region of the reservoir is a mixture of this sediment and organic deposits capable of releasing large gas bubbles.

Air temperatures of −34°C and ice cover to 18-cm thick occurred under winter conditions; summer temperatures exceeded 27°C at 0.8 m (Figure 2). Thermal stratification was evident from May to September. In July and August, when temperatures were high and stratification most severe, the upper 1.5 m was frequently 21° to 27°C, and only at depths of 2 m or more could temperatures below 20°C be found. Figure 3 illustrates the seasonal patterns in temperature profiles.

The concentration of dissolved oxygen was greatly affected by thermal stratification and by decomposition occurring in the organically rich bottom of the reservoir. During July and August, measurable amounts of dissolved oxy-

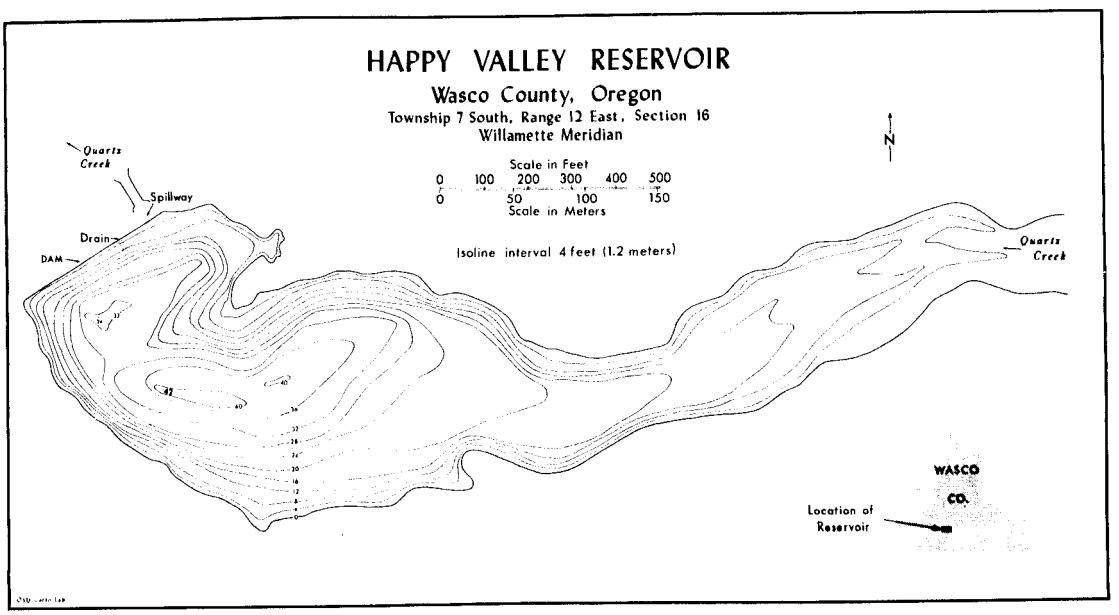

FIGURE 1.—Contour map of Happy Valley Reservoir. The 42-foot depth was sampling station 1, and 45 m directly off the spillway was sampling station 2.

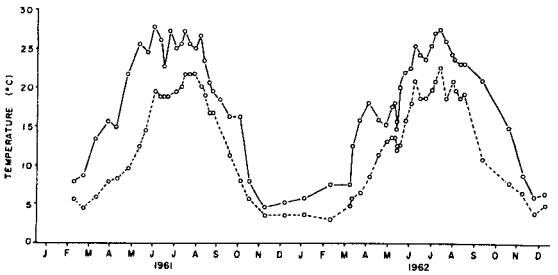

FIGURE 2.—Maximum-minimum temperatures at 0.8 m (2.5 feet) taken with reversing thermometer at station 2, 1961-62.

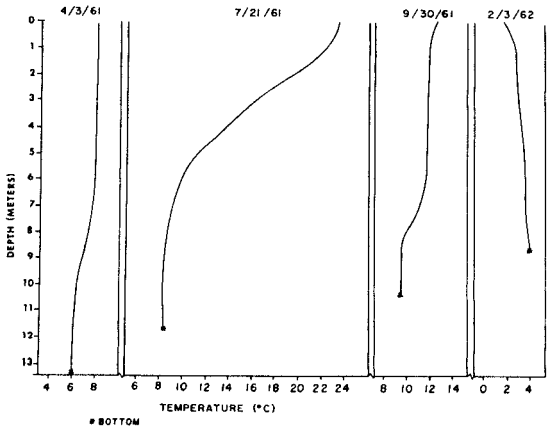

FIGURE 3.—Representative temperature profiles for station 1 on 3 April, 21 July, and 30 September 1961 and 3 February 1962. Changes in depth were caused by irrigation drawdown.

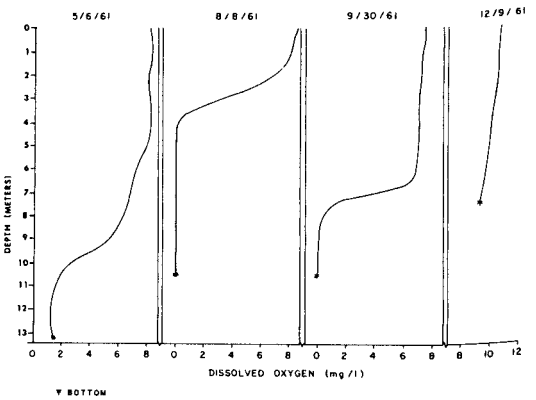

FIGURE 4.—Representative dissolved oxygen profiles for station 1 on 6 May, 8 August, 30 September, and 9 December 1961.

gen were usually absent in the nearly stable water mass below 4.3 m (e.g., the 8 August 1961 profile in Figure 4). Upward from this depth, concentrations increased to maxima of 6 to 13 mg/liter, depending upon algal activity. After fall turnover and the second irrigation drawdown (in late September), dissolved oxygen concentrations exceeded 6 mg/liter at all depths, even during periods of ice cover, until the following spring (Figure 4, profiles for 30 September and 9 December 1961).

Chemical analyses of water indicated a high basic fertility for the reservoir. Total dissolved solids generally exceeded 80 ppm and occasionally were as high as 220 ppm on the bottom; and early-to midsummer volatile dissolved solids mostly varied between 80 and 100 ppm (Figure 5). Total phosphorus concentrations exceeded 0.4 ppm at the bottom and 0.2 ppm at the surface (Figure 5). Surface pH (Figure 6) rose to 10.0 during algal blooms, although it generally varied between 7.0 and 8.5 for all depths. Methyl orange alkalinity usually exceeded 60 ppm and approached 130 ppm expressed as $CaCO_3$ (Figure 7).

The reservoir supported high summer densities of plant and animal life. Sago pond weed, *Potomogeton pectinatus* L., choked the inlet until water drawdown stranded the plants. Much less rooted aquatic vegetation grew outside the inlet area because of limited shallow water. Blue-green algae of the genera *Aphanizomenon* and *Microcystis* dominated the phytoplankton and gave a characteristic copper-blue stain to the shoreline. Cladocera and lesser numbers of other Entomostraca composed the bulk of the zooplankton and were noted to be abundant at various times of the year. Native rainbow trout were kept at low numbers by the chemical treatment (made several months before fry were introduced) and by subsequent gillnetting. The littoral zone was well populated with larvae of Ephemeroptera, Odonata (mostly Coenagrionidae), Trichoptera, and Diptera (Chironomidae). Amphipods (Gammaridae) were numerous, and some crayfish (*Pacifasticus*) and snails (*Physa*) were observed. The deeper benthic zones were inhabited primarily by oligochaetes and by *Chironomus* and *Chaoborus* larvae. At times during the summer, large

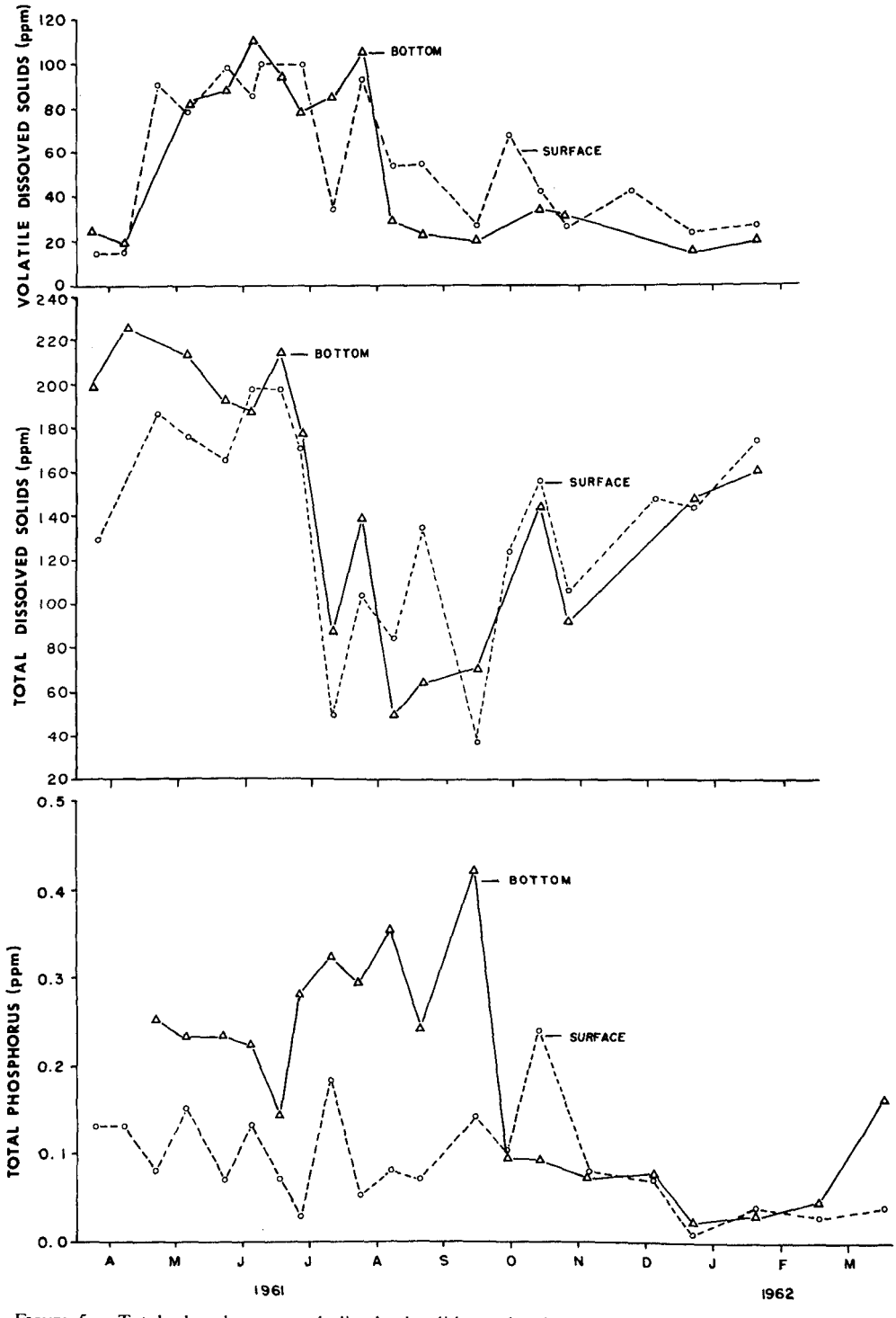

FIGURE 5.—Total phosphorus, total dissolved solids, and volatile dissolved solids at station 1, April 1961 to March 1962.

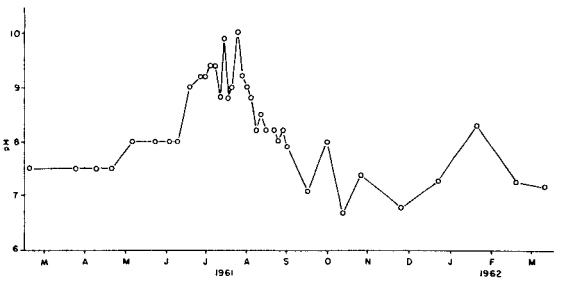

FIGURE 6.—Surface pH at station 1, March 1961 to March 1962. Summer increases reflect blooms of blue-green algae.

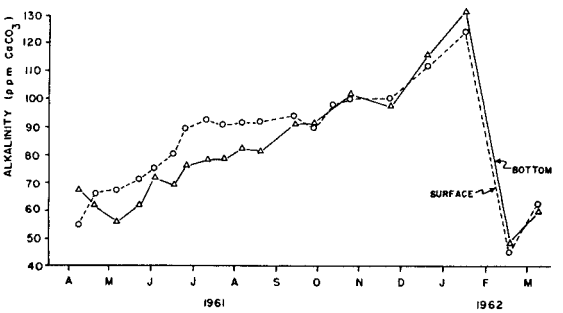

FIGURE 7.—Methyl orange alkalinity expressed as ppm $CaCO_3$ at station 1, April 1961 to March 1962.

swarms of adult Diptera hovered above the reservoir.

EFFECTS OF RESERVOIR CONDITIONS ON SALMON

Happy Valley Reservoir, a eutrophic impoundment with warm summer conditions, is markedly different as a rearing site from the streams naturally inhabited by juvenile chinook salmon. Spring chinook salmon normally make the parr-to-smolt transformation during the spring after 1 yr of freshwater residence. Salmon reared 1 yr in the reservoir met severe midsummer conditions. They were driven upward by low oxygen concentrations and downward by high temperatures, high pH, and possibly by algal toxins released by decomposing blue-green algae. As an example of midsummer conditions, temperature and dissolved oxygen profiles are presented in Figure 8 for 1 August 1961. Under these conditions, which likely did not represent the extreme for that day, fish

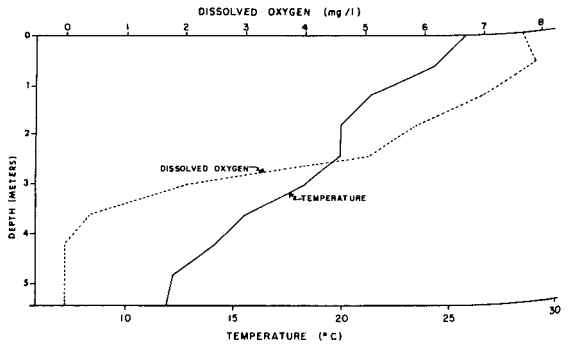

FIGURE 8.—Midday conditions of temperature and dissolved oxygen on 1 August 1961 at station 1. Fish die-off occurred on this date.

seeking temperatures below 20°C would have had to accept dissolved oxygen concentrations below 5 mg/liter. The preferred temperature is 12° to 13°C (Brett, 1952), at which depth oxygen levels would not have sustained life.

Scores of observations of fish "echoes" on the dial of a depth-sounder indicated that the fish sought the least extreme combination of these low oxygen and high temperature stresses and congregated near the 1.7-m (5- to 6-foot) depth. Similarly, gill nets set at various depths in August 1962 captured fish almost exclusively at depths of 1.8 m (6 feet) or less (Table 1). Water at 1.8 m usually held 5 mg/liter or more oxygen and was just above the zone of rapid oxygen decline (Figure 9). These observations are in accord with those by Whitmore, Warren, and

TABLE 1.—Frequency of capture by gill net at approximate depth of capture, 8 to 15 August 1962. Surface 0.6 m was not fished. Most sets were made in waters more than 4.6 m deep.

Depth of capture (m)	(feet)	Number of fish caught per hour	Number of hours fished at depth
0.6	(2)	0.25	22
0.9	(3)	0.18	22
1.2	(4)	0.96	22
1.5	(5)	0.77	22
1.8	(6)	0.27	22
2.1	(7)	0.00	22
2.4	(8)	0.10	95
2.7	(9)	0.08	95
3.0	(10)	0.01	95
3.4	(11)	0.00	95
3.7-4.3	(12-14)	0.00	74
4.6-5.2	(15-17)	0.00	144
5.5-7.3	(18-24)	0.00	71

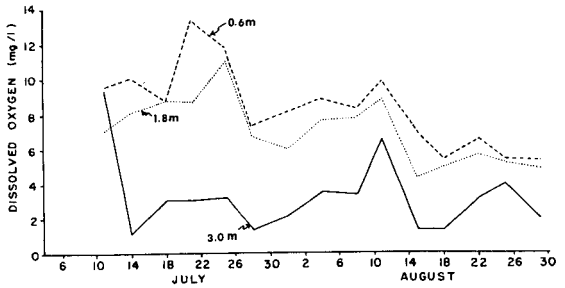

FIGURE 9.—Dissolved oxygen concentrations at 0.6, 1.8, and 3 m (2, 6, and 10 feet) during July and August 1961. Salmon typically inhabited water 1.2 to 1.8 m deep during this period. Samples taken midday at station 1.

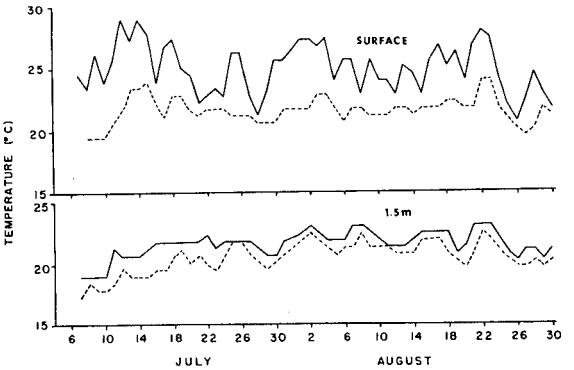

FIGURE 10.—Daily maximum-minimum temperatures at surface and at 1.5 m (5 feet) during July and August 1961. Maxima at the surface exceeded the lethal limit (25.1°C) for chinook salmon fry, and reached 23°C at 1.5 m. Data from thermograph records for station 2.

Doudoroff (1960), who state that at 16.5° to 25.5°C, under controlled conditions, juvenile chinook salmon directly avoided oxygen concentrations of 4.5 mg/liter and below.

Conditions in the upper 1.8 m of water were sometimes marginal for survival of the salmon because of 18° to 29°C temperatures (Figure 10), varying oxygen concentrations, and other stresses. Between 31 July and 3 August 1961, 65 dead salmon (50 of 1959 year class and 15 of 1961 year class) were collected at the water surface. Fish broke water in obvious distress at various hours of the day. At this time, a heavy bloom of *Aphanizomenon* was decomposing, accompanied by declines in surface pH (Figure 6) and oxygen concentrations (Figure 9). Oxygen concentrations remained at 5 to 8 mg/liter in the upper 1.5 m of water during a 24-h series taken 31 July-1 August. During the die-off, daily temperature maxima were reaching 23°C at 1.5 m (Figure 10). Brett (1956) estimated that 25.1°C is the upper lethal limit for chinook salmon acclimated to 20°C. The combination of low oxygen, high temperature, high pH, and possibly algal toxins apparently formed untenable conditions for some of the fish.

During the extreme conditions of midsummer 1961, the 0-age class salmon lost condition (see later section on Condition). Herrmann, Warren, and Doudoroff (1962) observed progressively lower food consumption and growth rates among juvenile coho salmon held at 20°C and exposed to decreasing oxygen concentrations. The most rapid decline in these rates occurred at concentrations decreasing below 4 mg/liter and weight losses occurred at 2 mg/liter. Salmon in Happy Valley Reservoir, on the whole, grew rapidly during the summer despite occasionally critical conditions. They surface-fed in the mornings and evenings in water as warm as 21° to 23.5°C. Brett (1952) also noted that his experimental salmon fry would move up through strong temperature gradients and into temperatures near their lethal level to feed at the surface.

During the summer, salmon generally congregated along the dam face and in the southwest corner. The reason for this is not known; oxygen concentrations and temperatures were similar to those in other areas of the reservoir. However, when a freshet brought a cooler (and probably more highly oxygenated) water mass into the inlet, the salmon quickly congregated there. On 14 August 1962, surface temperature was 24.5°C in the lower reservoir and 19°C in the inlet. The temperature difference soon disappeared, but the salmon remained abundant in the inlet until late September when fall turnover began.

The salmon were less frequently captured and were more uniformly distributed about the reservoir during the winter than in the summer. No vertical limitation was evident. Cold water caused no observed deaths, but apparently reduced the activity of the fish, and

this reduced gill-net catches. The lower lethal temperature was estimated by Brett (1956) as 0.8°C for chinook salmon fry acclimated to 10°C. Cold tolerance, Brett indicated, is gained slowly by fish. Winter temperatures of 7°C and below were reached at Happy Valley only after about a 2-mo period of decreasing temperatures (Figure 2). This period seems sufficient for the salmon to have acclimated to cold.

SURVIVAL

Mortality of 0-age salmon exceeded 80% for both the 1961 and 1962 year classes. This contrasted with the light losses among 1959 0-age salmon, which did not face predation by older salmon at planting.

Predation rate in 1962 was estimated in two ways. In the first method, stomach contents from 1961 year class salmon were studied. A total of 29 0-age salmon were found in the stomachs of 299 salmon collected between 26 May and 29 June 1962. There were about 10,000 of the 1961 year class present during this period (Figure 11). Assuming that the stomach contents represented daily consumption, the daily consumption rate was on the order of 1 prey per 10 predators, and mortality was about 1,000 fry per day. Predation rate by the 1961 year class was also estimated using growth and food habits data (see sections on Growth and Food Habits). Relative growth of the 1961 year class was 1.4 mg/g per day from 15 May to 15 June 1962. Experimental evidence, provided by Davis and Warren (1968) for chinook salmon fry held at 10°C, indicated that at 1.4 mg/g per day, food consumption was about 40 mg/g per day. The total 1961 year class biomass was about 700,000 g (10,000 fish times 70 g average weight). Thus, consumption was 28,000 g per day. According to food studies on the 1961 year class, 21% of this consumption, or 5,880 g per day, was fry. At 4 g per fry, 1,470 fry per day were consumed by the older salmon. A similar calculation for 18 June to 20 July gave a mortality rate estimate of 1,125 fry per day.

The two estimates agree on a predation rate sufficiently high to account for most of the losses in 1962 and, by inference, in 1961. The heaviest losses actually would have occurred when the fry were smallest and most abundant, i.e., close to planting time as shown by the survival curves in Figure 11. More specific information about the fates of the 1961 and 1962 year classes is given below.

The 75,300 fry planted on 8 February 1961 (1961 year class) met severe predation by 1959 year class salmon and rainbow trout surviving chemical treatment. Additional losses occurred when a flash flood on 11 February carried many of the fry over the spillway. A mark-and-recapture operation indicated population size was 28,600 fish (38% survival) on 22 March 1961 (Table 2). According to a second estimate, the population contained 6,800 fish (9% survival) in late August 1962. Continued losses were caused by predation, harmful summer water conditions, and a transplantation program which removed 2,500 salmon to Beaver Creek, a tributary of the Warm Springs River.

The second plant of chinook salmon (1962 year class) was made on 22 March 1962. Because predation was expected, a large, fine-mesh seine was used to impound and protect the fry in a cove of about 0.05 hectare, while gill nets were set to deter predator movement. These measures reduced predation at planting, but also produced a high fry density in the cove and this caused the fry to grow relatively slowly. Some fry escaped from the cove; these fish were substantially larger than fry still in the cove

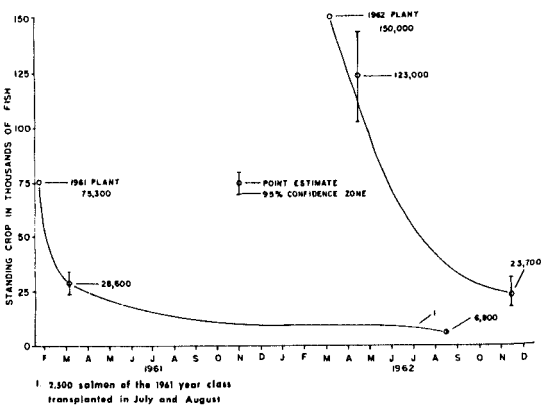

FIGURE 11.—Survival curves for 1961 and 1962 year class salmon. Curves were fit by eye according to population estimates and information on predation rates described in text.

TABLE 2.—Statistics used in estimating the standing crop in numbers of the 1961 and 1962 year classes.

Date	Fins marked	Number marked	Marks recovered	Total catch	Estimate of population at marking time	95% Confidence limits	
						Lower	Upper
1961 year class							
22 Mar. 1961	Both pelvics	984	133	3,871	[1]28,640	23,760	33,520
30 Aug. 1962	Anterior one-third of anal	1,203	131	739	[1] 6,786	5,710	7,862
1962 year class							
1 May 1962	Adipose	5,080	143	3,461	[1]122,950	102,810	143,090
30 Nov. 1962	Posterior one-third of anal	1,793	59	1,261	[2]23,722	[3]18,900	31,845

[1] Direct-proportion estimate.
[2] Schnabel estimate (Rounsefell and Everhart, 1953).
[3] Limits set with Poisson distribution (Rounsefell and Everhart, 1953).

(0.79 g vs. 0.48 g) on 28 April, when the seine was removed. The reduced growth evidently extended the period during which the fry were susceptible to predation, and losses were again high. Population size was estimated at 123,000 (82% survival) on 1 May and 23,700 (16% survival) in late November 1962.

GROWTH

The salmon grew rapidly, especially under conditions of low population density. During their initial 18-mo residence (January 1959 to June 1960), the 48,000 members of the 1959 year class grew to average weights of 32 g (chinook salmon) and 41 g (coho salmon). Chemical treatment of the reservoir in June 1960 drastically reduced population size, and surviving salmon grew at very rapid rates. By August 1961, chinook salmon averaged 215 g and coho salmon 280 g. These salmon were captured less and less frequently during the 1961 summer, apparently because of deaths brought on by sexual maturation and water conditions. By fall 1961, the population was virtually extinct.

Growth by the 1961 and 1962 year class salmon also appeared density-regulated. About 30,000 of the 1961 year class escaped initial predation and other losses. By December 1961, population size was about 10,000 fish, which averaged 17 cm in fork length (Figure 12) and 62 g (Figure 13). In December 1962, 5,000 of these salmon remained. They then averaged 21 cm and 89 g, which represented relatively small 12-mo increases. Rapid second-year growth, such as occurred in the 1959 year class, appears to have been prevented by the introduction of the 1962 year class. Of the 150,000 fry planted in March 1962, about 23,000 remained in December 1962, when they averaged 13 cm and 22 g (Figures 12 and 13). Thus, slower growth occurred among first-year salmon in 1962 than in 1961 due to the higher density in 1962. Other influences may have been the later planting date in 1962 and the protective enclosure of the 1962 year class in a relatively small area for 5 wk.

Ricker and Foerster (1948) studied competition and population size in juvenile sockeye salmon, *O. nerka* (Walbaum), of Cultus Lake.

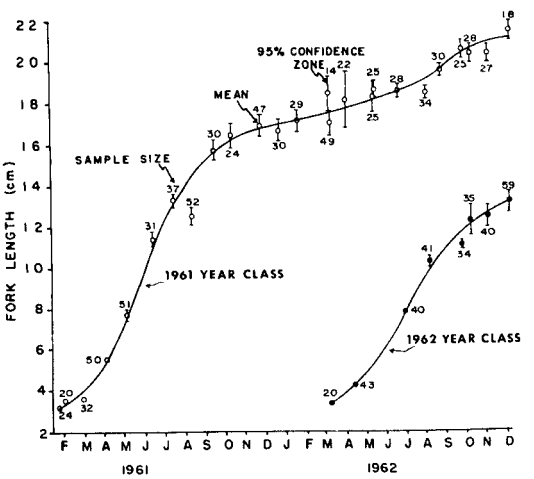

FIGURE 12.—Growth in length of 1961 and 1962 year class salmon. Some confidence zones were omitted because of their small size.

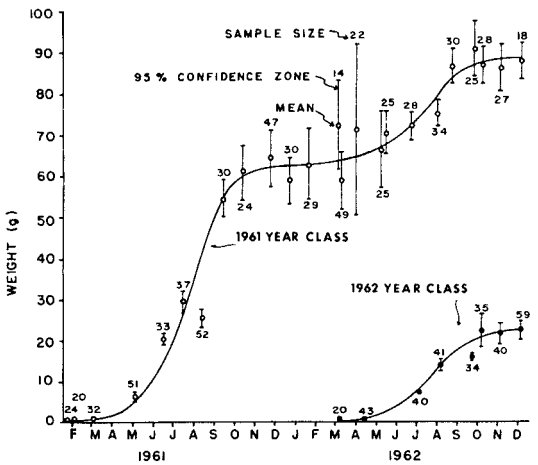

FIGURE 13.—Growth in weight of 1961 and 1962 year class salmon. Confidence zones for the first three samples of 1961 year class were too small to be shown. Those for the first three samples of 1962 year class were not calculated because the fish were weighed in groups.

They postulated, "a very nice regulatory mechanism: the more fry present, the less each eats, hence the slower it grows, and hence the longer it remains at a size especially vulnerable to predator attack." A similar mechanism probably produced the heavy losses and comparatively slow growth in the 1962 year class in Happy Valley Reservoir.

Hoover (1936) described the growth achieved by chinook salmon in New Hampshire Lakes. The fish generally matured at 4 yr, when they averaged about 2.3 kg. Where rainbow smelt, *Osmerus mordax*, were abundant, however, the salmon averaged 4.5 to 5.4 kg and one reached 7.3 kg. Hoover thus also implied a food regulation of growth, with these impounded salmon being capable of growth approaching that of sea-run fish when abundant foods were present. Similarly, Johnson and Hasler (1954) depicted food and the space over which it was concentrated as a primary factor limiting trout growth in the lakes they studied. At Happy Valley, under circumstances of low competition, growth by first-year and second-year chinook salmon was rapid; increased size as obtained in the New Hampshire lakes, however, would likely not have occurred in the absence of a forage fish or other large foods.

The average weight of 62 g attained by members of the 1961 year class at the end of their first summer represented a more rapid growth rate than usually found in stream-living chinook salmon juveniles. The 22 g average of the 1962 year class, however, is close to that estimated by Breuser (1961) for chinook salmon in the Willamette River of western Oregon, which grew from an average of 2.35 g in May to 20.17 g in November.

CONDITION

The salmon gained condition during the spring, and lost condition during the midsummer when temperatures were highest (Figures 14 and 2). In 1961, condition increased again in the fall to the highest level measured (1.38). Neither age class gained condition in fall 1962, likely because of more slowly decreasing temperatures and the presence of a higher fish density. The 1962 year class lost condition during the 5-wk period after planting when they were concentrated behind the seine.

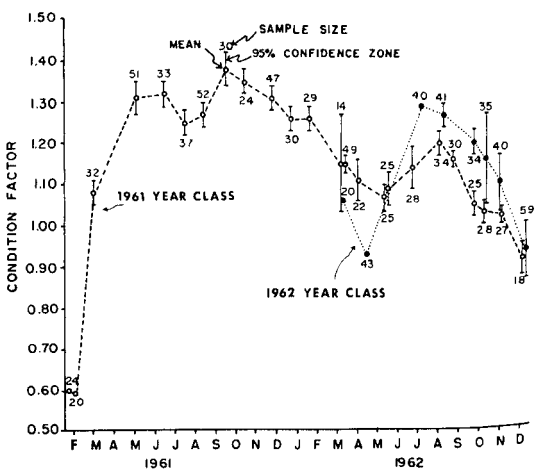

FIGURE 14.—Changes in condition factor of 1961 and 1962 year class salmon. Confidence zones of some samples were omitted for reasons stated for Figure 13.

During the winter, average weight increased little, and may have decreased (Figure 13). Average length slowly increased (Figure 14) resulting in decreasing condition factor values.

NET PRODUCTION AND YIELD

The production of a given group of organisms was defined by Ivlev (1966) as the total elaboration of tissue by that group over a given time period, regardless of the fate of the tissue. Ricker and Foerster (1948) used this viewpoint with mathematical formulation to calculate the production of juvenile sockeye salmon in Cultus Lake. Allen (1951) described the graphical method of computation which was used here.

Allen's method uses survival and growth information in plotting estimated population size against average weight at successive intervals. The area under the curve between plottings (month intervals were used here) represents the net production for that period. Survival data are usually more difficult to obtain than growth data, and deficiencies may introduce considerable error into production estimates. For example, estimated annual production in Happy Valley by the 1962 year class would be increased by one-half if mortalities were assumed to have occurred later in the summer. Despite such limitations, production estimates are valuable measures for comparing the rearing capacities of various bodies of water (Ricker and Foerster, 1948).

Both net production and potential yield were computed for salmon impounded in Happy Valley during 1961 and 1962, and compared with values obtained for fish in other bodies of water. Extrapolation of survival and growth curves through December 1962 was required to make the 1962 computations. Annual production for first-year salmon was considered to be the tissue produced from planting until 31 December. Production by rainbow trout and 1959 year class salmon was not computed. Because production was concentrated in the summer, the average summer surface area of 6.1 hectares was used in comparisons with other bodies of water.

Total production by the 1961 year class in its first year was 972 kg (159 kg/hectare). A similar biomass—1,039 kg (170 kg/hectare)—was elaborated by the 1962 year class in its first year, with less individual growth being attained by larger numbers of fish. In 1962, production by yearling salmon was only 217 kg (35.5 kg/hectare), or 22% of their production in 1961. Reduced population size and slower growth created by competition from the 1962 year class apparently caused this low production. Much of the 217 kg elaborated depended on the consumption of foods different from those used by the younger salmon and on the consumption of the younger salmon themselves. Total production by both age classes in 1962 was 1,256 kg (206 kg/hectare). In both years, about 75% of the production occurred from June through September. Similarly, two-thirds to three-quarters of the sockeye salmon production in Cultus Lake occurred between 15 June and 15 September (Ricker and Foerster, 1948). Gerking (1962) stated that, "production is an event of the summer," for the bluegill, *Lepomis macrochirus* Rafinesque, of the Indiana lake he studied. These observations simply assert the importance of the limited growing season in temperate waters.

The potential yield of salmon tissue from Happy Valley is here defined as production surviving to the end of the year. This was calculated as the biomass introduced at planting subtracted from the standing crop present on 31 December. Standing crop was estimated by multiplying the number of surviving fish (Figure 11) times their average weight (Figure 13). Potential yield of first-year salmon on 31 December 1961 was 98 kg/hectare, and on 31 December 1962 was 73.5 kg/hectare. These yields amounted to 61% in 1961 and 43% in 1962 of the tissue produced. Coche (1967) estimated 59.4% was the yield of first-year steelhead trout, *S. gairdneri* from a western Oregon reservoir. Survival in Coche's experiment was 38.4% as compared with 13% and 15% for the two year classes in this study.

Coche (1967) has summarized net production values for a variety of streams and impoundments. Salmonids studied in oligotrophic lakes produced from 0.6 to 65 kg/hectare/yr, those in dystrophic lakes 19 to 84 kg/hectare/yr, and those in North American streams 41 to 198 kg/hectare/yr. Brown trout, *S. trutta* Linnaeus, in a New Zealand stream produced 275 to 837 kg/hectare/yr. Largemouth bass, *Micropterus salmoides* (Lacépède), in fertilized ponds

of western Oregon produced up to 128 kg/hectare/yr. The maximum first-year production of 170 kg/hectare/yr and the total 1962 production of 206 kg/hectare/yr by salmon in Happy Valley rank this reservoir as high among impoundments studied and apparently comparable to some of the more productive streams studied.

The yield of juvenile salmonids from 10 impoundments has also been summarized by Coche (1967). The lowest value (2.3 kg/hectare/yr) was for sockeye salmon in a large oligotrophic lake in Canada. Most values ranged between 20 and 100 kg/hectare/yr; the highest was 143 kg/hectare/yr. Ellis, Pressey, and Smith (1958), citing Washington Department of Game figures, stated that Washington lakes yield 45 to 209 kg/hectare/yr (average 112) in rainbow trout. Although covering a wide range, these figures suggest that yields of 100 kg/hectare/yr may be expected of fertile impoundments. This was true for Happy Valley which, despite high mortality rates, yielded 98 and 73.5 kg/hectare/yr of first-year salmon in the 2-yr of this study. Both net production and yield estimates corroborate chemical evidence that the reservoir is highly fertile.

FOOD HABITS

Studies such as those by Johnson and Hasler (1954) and Ricker and Foerster (1948) have shown Entomostraca to be the primary food type eaten by many lake-resident juvenile salmonids. The coho salmon of the small lake in Kamchatka Penninsula studied by Dvinin (1949), however, fed on insects (midges and mosquitoes), although older fish took some zooplankton. In food-habit studies of stream-inhabiting coho and chinook salmon juveniles, Brueser (1961) and Chapman et al. (1961) found mainly Diptera and Trichoptera larvae, Ephemeroptera nymphs, and terrestrial insects. Availability very likely played a major role in these differences of food habits; for example, planktonic forms in a stratified lake and "drift" organisms in a stream would be available forms, with salmonids capable of eating a variety of foods.

Food habits of the 1961 year class in Happy Valley Reservoir were determined by dry-weight analyses of stomach contents from 17 samples of fish taken between April 1961 and November 1962. The results (Table 3) indicated a heavy utilization of Entomostraca (mostly Cladocera) and chaoborid larvae in both summer and winter until the 1962 year class was released. These foods averaged 97% of the stomach contents for the samples taken before the 1962 salmon were released, and only about 6% of the sample contents taken thereafter. The planktonic Entomostraca and vertically migrating chaoborid larvae were apparently both abundant and available to the salmon, which probably fed in the upper 3 m of water during the summer. Competition from the 1962 year class, however, evidently forced a shift in food habits and led to the slow growth already mentioned. A variety of benthic forms (crayfish, snails, damsel fly naiads, and amphipods) as well as chironomid pupae, terrestrial insects, and members of the 1962 year class were then eaten.

Meanwhile, the 1962 year class was utilizing Entomostraca, as shown by field checks of stomach contents. In a 23-member sample of these fish taken on 21 August 1962, Entomostraca were found in all stomachs and made up roughly 80% of the total contents identified. In another sample of 10 fish taken on 2 September 1962, 9 stomachs contained Entomostraca, which formed 45% of the total contents. Most of the remaining food in both samples was chironomids.

Increased size does not seem to have been the direct cause of the change in food preference by the 1961 salmon because their size (Figures 12 and 13) did not appreciably increase from fall 1961 to spring 1962, when the apparent food shift occurred. That fish of their size are capable of feeding upon the Entomostraca was shown by an earlier analysis of the stomach contents from 25 salmon of the 1959 year class. These fish averaged 193 g when collected on 8 April 1961. Entomostraca were found in 13 of the stomachs and constituted 90% of the combined sample on a settle volume basis. The high production by first-year salmon in Happy Valley Reservoir apparently was supported chiefly by entomostracan foods.

TABLE 3.—Contents of stomachs taken from chinook salmon of the 1961 year class, April 1961 to November 1962. Contents were subjected to dry weight analysis; results are presented according to percentage contribution of each food type.

	1961							1962									
	4-22	7-1	8-10	8-28	10-1	10-29	12-10	1-1	2-4	3-23	5-29	7-5	8-14	9-6	10-6	10-29	11-18	Av. %
Aquatic organisms:																		
Entomostraca	18.72	55.88	30.77	91.72	98.26	99.28	90.61	96.07	100.00	29.24				39.04				44.1
Gastropoda															100.00		80.01	10.6
Zygoptera	0.52	0.73		0.45	1.59	0.72						3.15	68.97	60.96			8.11	8.5
Chaoboridae																		
Larvae	74.91	24.18	69.23	7.83			9.39	3.93		70.76								15.3
Pupae												6.49	6.92					0.8
Chironomidae																		
Larvae	5.33	3.07									79.02	6.98	24.11					0.5
Pupae		1.22										52.59						6.6
Crayfish																		3.1
Hemiptera		14.92																0.9
Annelida																	3.50	0.2
Juvenile salmon (1962 year class)											20.98	30.35						3.0
Amphipoda	0.52											0.44				31.31	8.38	
Terrestrial organisms:																		2.4
Hymenoptera																64.54		3.8
Coleoptera																4.15		0.2
Lepidoptera					0.15													0.0

MIGRATION OF SALMON FROM RESERVOIR

Intrinsic factors suggested as influencing the downstream migration of salmonid juveniles include size and age of fish (Elson, 1957) although these apparently are variable in migrating spring chinook salmon juveniles (Wallis, 1968; Wagner, Conte, and Fessler, 1969). Changes in water flow and temperature may be associated with movements. Wallis (1968) in reviewing literature concerning this subject found a number of authors who cited elevations in water temperature as correlated with downstream movements of Pacific salmon smolts. Emigration of sockeye salmon juveniles from Cultus and other lakes typically follows ice break up and rising temperatures (Foerster, 1968).

Migrants from Happy Valley Reservoir varied in size from 25 to 188.9 g and included fish of both age class I and class II (Table 4). The migrants appeared similar in size and condition to fish taken from the reservoir for growth studies. Migrations occurred between February and May of 1962 and 1963 at varying temperatures and outflow volumes. In 1962, no temperature relation was evident; but migrations in 1963 occurred only at temperatures above 10°C.

In 1962, 196 fish of age class I emigrated. On different days during a 6-wk period, groups of 30, 37, and 33 left when temperatures were 3.5° to 5°C, and outflows were 0.141 to 0.283 m^3/s (5 to 10 cfs). During an 18-day period when temperatures were increasing from 6° to 15°C and outflows were less than 0.056 m^3/s (2 cfs), migrations of 5 to 15 fish occurred on 7 nights. Outflow through the iron tube, used on 13 days when temperatures were 11.5° to 24°C, attracted one migration of 17 fish at a temperature of 13°C.

In 1963, a mid-February to mid-March spill volume of 0.141 m^3/s (5 cfs) maximum, at temperatures below 5°C, brought no migration. By late April, water temperatures were 10° to 13°C, and a new spill of 0.141 to 0.283 m^3/s (5 to 10 cfs) occurred. Approximately 500 salmon including both age classes exited. An additional 56 age class II and 498 age class I

TABLE 4.—Comparison of size and condition of migrating salmon with salmon in reservoir population.

Year of migration	Year class	Sample size	Migrants: Fork length (cm) Mean	Fork length (cm) Range	Weight (g) Mean	Weight (g) Range	Condition factor Mean	Condition factor Range	Reservoir population[1]: Fork length (cm) Mean	Weight (g) Mean	Condition factor Mean
1962	1961	[2]117	16.5	13.2-28.2	55.7	25.0-188.9	1.10	0.67-1.37	17.5	65	1.15
1963	1961	[3]13	20.0	19.1-22.2	—	—	—	—	[4]22.5	—	—
	1962	[3]13	14.1	13.3-15.9	—	—	—	—	[4]14.5	—	—

[1] From Figures 12, 13, and 14; mean is for midpoint of sampling period.
[2] Taken between 2/27/62 and 5/27/62.
[3] Taken 5/7/63.
[4] By extrapolation of Figure 12.

salmon left when temperatures were 11° to 14.5°C, and spill was 0.014 to 0.056 m^3/s (0.5 to 2 cfs).

CONCLUSIONS

The high productive capacity of the reservoir was seen in the rapid growth, high condition factor, and high net production achieved during the summer by planted chinook salmon. High mortalities were caused primarily by predation. Severe summer conditions also caused deaths, indicating that the reservoir and others similar to it in thermal and chemical qualities should be considered marginal for use in natural rearing of salmon smolts.

Emigration by salmon was limited, but indicated that substantial voluntary movement may occur at appropriate temperatures and outflows, and that migrations by both age classes I and II including fish in excess of 100 g in weight are possible.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to the following who assisted in the preparation of this manuscript: Jay B. Long directed field operations in summer 1961. James Shelton advised on field work and assisted during transplanting operations. John Edgington, David Vincent, and other students assisted in field and laboratory work. Donald W. Chapman helped interpret the biological data. James D. Hall, John R. Donaldson, and Anthony J. Gharrett reviewed the manuscript.

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NOTES

OLFACTORY ELECTROENCEPHALOGRAPHIC RESPONSES OF HOMING COHO SALMON, *ONCORHYNCHUS KISUTCH*, TO WATER CONDITIONED BY CONSPECIFICS[1]

Experimental determination of the home stream of migrating salmon is an important technique for elucidating possible orienting cues. Responses are observed in the fish that are specific to the home-stream water and weaken with increasing dilution.

Two techniques have been employed with some success: Idler et al. (1961) and Fagerlund et al. (1963) found that homed salmon made consistent unconditioned behavioral responses to the water to which they homed. Hara, Ueda, and Gorbman (1965) could electrophysiologically demonstrate unconditioned reponses of the olfactory bulb to the home stream. Hara (1970) in his review states that "this electric response is specific in the sense that it cannot be evoked by water from spawning sites of other groups of breeding salmon."

We undertook an investigation of lake-run coho salmon, *Oncorhynchus kisutch*, to determine whether these fish exhibited specific olfactory bulb responses to home water. We tested salmon from two different home streams, examining responses to waters both on and off the migration routes. Furthermore, our field situation allowed us to assess the effects of the returning adult spawners upon the olfactory quality of the home stream.

Materials and Methods

The experimental fish were hatched from eggs obtained from a Michigan fish hatchery and raised in a Wisconsin hatchery for 1.5 yr. In the spring of 1969 approximately 1 mo prior to smolting, they were placed in small impoundments in tributaries of the Ahnapee River and the Kewaunee River (Kewaunee County, Wis.) to which numerous fish have returned in previous years. After initiation of smolting, they were allowed to leave the ponds and make their way downstream to the rivers and thence to Lake Michigan (Figure 1). In the fall of 1970, the mature fish were trapped in weirs on their return up the respective tributaries. The EEG (electroencephalographic) experiments were conducted within 1 km of the trap at the Ahnapee site.

Our experimental procedure was similar to that used by Hara et al. (1965). The fish was paralyzed with gallamine triethiodide (2 mg/kg), and water was perfused continually over the gills. An electrode was placed near the rear margin of the exposed olfactory bulb. The responses, evoked by perfusion of the ipsilateral naris, were amplified (Bio-electric Instruments, model DS2C[2]) and recorded on a two-channel oscillograph (Hewlett Packard, model 7712B) for later analysis. This oscillograph was equipped with an integrating preamplifier for efficient quantification of bulbar activity. Responses reported later are expressed as the sum of the positive areas under the response wave.

Our procedure differed from that of previous workers in two ways:

1. A monopolar stainless steel microelectrode (Transidyne General, model 415100K) was used instead of a bipolar one. The indifferent electrode was clipped to the contralateral operculum.
2. Instead of direct introduction of stimuli to the naris via a wash bottle, a perfusion apparatus allowed one of four samples to be interspersed between a continuous tap water rinse (1 ml/s). Every 75 s, test water (10 ml) was introduced into the interrupted tap water flow. The median response to each stimulus was then

[1] This work was completed under financial support from the National Science Foundation (Grant No. GB 7616X) to Prof. A. D. Hasler and the University of Wisconsin Sea Grant Program, which is a part of the National Sea Grant Program maintained by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce.

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

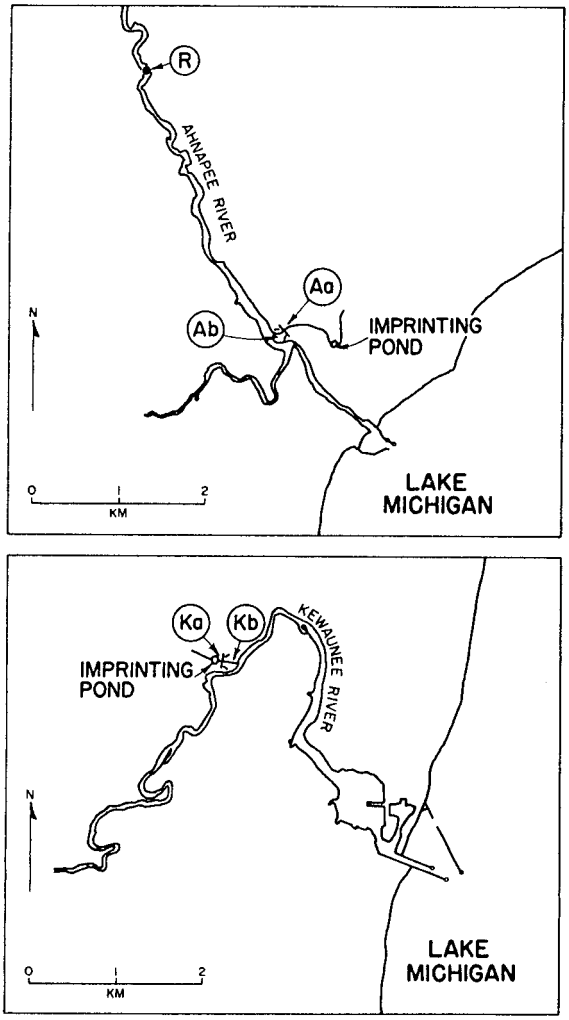

FIGURE 1.—Map of area. Water from Lake Michigan (L) was collected upwind of river mouth.

used in the later analysis. A control series with the same stimulus in each of the four holders demonstrated that delivery through any one of the four sample holders gave comparable results.

Water samples for testing responses of coho salmon were collected from the two home streams (a tributary to the Ahnapee River (A) and a tributary to the Kewaunee River (K)), the Ahnapee River (R) 4 km above the entrance of the home-stream tributary, and Lake Michigan (L) (Figure 1). Samples from the home streams were taken above (Aa, Ka) and below (Ab, Kb) barrier fish traps so that Aa and Ka were home-stream waters while Ab and Kb were home-stream water plus the scents from the returning migrants. Both home streams (A, K) had similar physical features and coho salmon stocking histories; but the tributary to the Kewaunee River (K) contained a greater proportion of well water than stream water compared with the tributary to the Ahnapee River (A).

All sample presentations were made in groups of four to each fish, and responses were quantified as a ratio to the response to water from station Ab. This water sample was included as one of the four presentations for all fish and was chosen as a base because it evoked intense responses. Nineteen Ahnapee fish were tested: 11 with water samples from Aa, Ab, R, and L; 3 with Aa, Ab, R, and water from an unrelated source; 1 with Aa, Ab, and 2 samples from unrelated sources; and 4 with water from Aa, Ab, Ka, and Kb. Six fish from Kewaunee were tested with water from Aa, Ab, Ka, and Kb. (The water samples from other sources showed no consistent patterns and will not be discussed.)

Results

For the Ahnapee fish, samples from the terminus of the return migration evoked greater responses than the sample from the origin (L). But this result is probably not an example of Hara's (1970) "specific electric" response to the home stream: (1) One-half of the "stimulus strength" was added at the trap, although water collected above the trap (Aa) must be considered home stream (Table 1). (2) Agreement on order of responses to each water (Ab>Aa>R>L) was good among fish [$W = 0.87$, $k = 11$, $N = 4$, $P<0.01$ Kendal coefficient of concordance test (Siegel, 1956)], but the absolute difference in responses between presumably nonhome water from the Ahnapee River (R) and home water (Aa) was small. (3) Six fish collected from the Kewaunee River and four controls from the Ahnapee site were tested with water collected at Ab and Aa and from the corresponding stations from Kewaunee, Kb, and Ka. Kewaunee fish responded to their home-stream water more

TABLE 1.—Median EEG response ratios of coho salmon[1] from two different spawning sites to waters collected both on and off their migration route.

Water sample collection point	Number of fish	Quartile Responses		
		1st	2d	3d
Ahnapee fish:				
Aa	19	0.40	0.50	0.67
R	14	.14	.37	.47
L	11	0	.07	.21
Kb	4	.16	.28	.35
Ka	4	.04	.10	.18
Kewaunee fish:				
Aa	6	.36	.46	.55
Kb	6	.19	.25	.55
Ka	6	0	.06	.12

[1] Response ratio $\left[\frac{\text{response to sample}}{\text{response to Ahnapee tributary below (Ab)}}\right]$.

strongly if the water was taken from below the traps (Kb) than from above the traps (Ka). Furthermore, Kewaunee fish responded to Ahnapee home-stream water more than to their own (Table 1). Yet the Kewaunee fish did home correctly — three of the six Kewaunee fish carried fin clips unique to that site (the other three were unmarked).

Discussion

Hara (1970) in his recent review of electrophysiological studies of olfactory discrimination by homing salmon, concluded that "each spawning area has its own specific stimulant, or special combination of stimulants, recognized and responded to by the anadromous salmon." He acknowledged both that EEG responses of returning salmon adults can indicate a recognition of a chemical factor from conspecifics and that recent exposure of mature salmon to nonhome-stream water can result in strong EEG responses to that water (Oshima, Hahn, and Gorbman, 1969). Therefore olfactory responses to the home stream could result from (1) natal imprinting (a long-term memory), (2) recent exposure to the water (a short-term memory), (3) recognition of chemical factors from conspecifics, (a genetic (?) memory), and (4) the presence of stimulatory products not in any way specific to the home stream, transient, and incidental to the salmon's appearance, past or present, in the stream (responses independent of memory).

Our work appears to be the first to separate responses to conditioned home-stream water (other conspecifics were present) from responses to "pure" home-stream water. Conditioning of water by conspecifics appeared to double the EEG response to the home stream.

Perception of factors in the home stream other than those contributed by conspecifics is indicated in the greater responses of the Ahnapee coho salmon to "pure" home-stream water (Aa) than to other waters (R, M) not strongly conditioned by conspecifics. But this result does not necessarily imply natal imprinting (long-term memory) or recent exposure (short-term memory). Perception of nonspecific odoriferous products is indicated since (1) responses to water from the home stream (Aa) and nonhome river (R) by Ahnapee fish differ little, and (2) Kewaunee fish responded more to "pure" water from the Ahnapee tributary than to their own home-stream water.

The consistence of ranking of the four test waters (Ab>Aa>R>L) by 11 fish indicates some degree of reliability of the electrophysiological technique. Nevertheless, there seems to be an inherent lack of precision associated with evoked bulbar recordings. Sutterlin and Sutterlin (1971) found that EEG responses varied greatly among and within fish when compared to simultaneous olfactory epithelium recordings. Furthermore, our collection stations for water samples were subject to seiches (reversed current flow in the river and stream) and variable rates of river and stream discharge that made the water inconstant.

In conclusion, our experiments with lake-run coho salmon indicate the need to clearly differentiate between responses to "pure" home-stream water and water conditioned by presence of conspecifics. An intense and apparently specific response to home-stream water is not necessarily indicative of juvenile olfactory imprinting.

Acknowledgments

Special thanks go to Ralph Schmiling, Francis "Toots" Wenniger, and Jack Haegele of Algoma, Wis., for help with the specimens, boats, tools, housing, and storage.

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A TEMPORARILY ANOXIC WATER MASS IN AN ALASKA ESTUARY

Anoxic marine waters have been reported to exist in the Black Sea, in many fjords in Norway, in British Columbia, and in a few tropical basins (Richards, 1965a). Anoxic estuaries in nontropical areas are usually characterized by the existence of a very shallow sill that restricts horizontal water movement and a strong pycnocline that restricts vertical water movement. When these conditions exist, and a water mass below the biological compensation depth is not mixed with water above or outside of its basin, the dissolved oxygen is eventually depleted and remains so until there is an intrusion of oxygenated waters. An anoxic condition may be temporary where the isolation of the water mass is temporary. A fortuitous observation of temporary anoxia in Little Port Walter on southern Baranof Island, Alaska, in October 1971 suggests the possibility of other temporarily anoxic estuaries in Alaska. This is the first reported occurrence of a naturally anoxic estuary in Alaska.

Powers (1963) provides a detailed description of the physical and hydrographic features of the Little Port Walter estuary (Figure 1).

> The estuary is located near the [southern] tip of Baranof Island in southeastern Alaska. . . . A stream, Sashin Creek, enters the inner end over a small waterfall which marks the limit of salt-water intrusion. At its seaward end the estuary connects with Chatham Strait and Port Walter Bay . . . .
>
> The distance from the waterfall to Chatham Strait is 1.5 kilometers (km.); the distance across the widest part of the estuary is about 0.4 kilometer (km.). A peninsula . . . extends from the south shore and divides the estuary into two bays of approximately equal area, Inner Bay and Outer Bay. These are connected by a short channel . . . between [the peninsula] and the north shore.
>
> The maximum observed depth of Inner Bay was 21 meters (m.) and of Outer Bay, 44 m. (referred to mean lower low water). The depth of . . . [the channel], where a shallow sill is present, was almost 5 m. Because of this sill, Inner Bay has the structural characteristics of a fiord; Outer Bay does not, since it connects

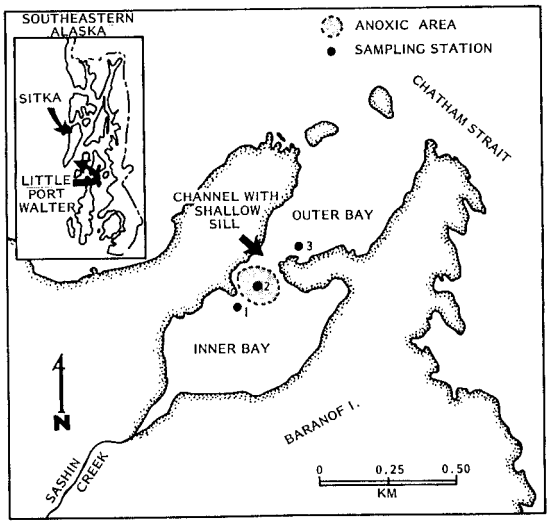

FIGURE 1.—Little Port Walter estuary, Baranof Island, southeastern Alaska.

directly with Chatham Strait through a channel approximately 36 m. deep.

The basins of both Inner and Outer Bays are steep sided, with practically no shelf formation except for a small shoal area at the head of Inner Bay. The surface area of the estuary consequently undergoes little change between low and high waters. Basins of this type are characteristic of Baranof Island as well as much of the rest of southeastern Alaska. The coastline is frequently indented by long narrow, deep embayments from which mountains rise sharply to heights of several thousand feet.

Tides in the estuary exhibit the exaggerated diurnal inequality typical of the west coast of North America. The range of spring tides at Little Port Walter is as much as 4.6 m., the range of neap tides less than half of this. Within the estuary, the tide has the characteristics of a standing wave, with high and low slack waters occurring at about the same time over the entire basin.

The surface area of Inner Bay, where the anoxic condition was observed, is about 0.25 km², and the approximate area of the affected water was about 0.02 km² (Figure 1).

Observations During Anoxic Period

The first time the anoxic condition was observed was on 4 October 1971, when two biologists (including the senior author) from the Auke Bay Fisheries Laboratory made a night dive in Inner Bay. The purpose of the dive was to count shrimp along underwater transects close to the shallow sill that separates Inner and Outer Bays. In a restricted area near the sill and below a depth of 12 m, the divers saw numerous dead animals on the bottom; most of them were shrimp, but there were also numerous chitons, limpets, clams, anemones, sea stars, crabs, and a few fish. No animals definitely known to be living were seen in the anoxic zone. No indication of the deeper affected zone was evident at the surface or in the water column at depths less than 12 m.

During the next 2 days (5 and 6 October) additional dives were made into the affected area to make more observations and to collect water samples. The water mass in the area of the die-off was obviously different from that in the rest of the bay; the water was milky, and visibility within the area ranged from a few centimeters to a meter. Outside of that area the water was clearer, and visibility was 6 m or more. Within the milky water of the die-off area, there was an odor of hydrogen sulfide—strong enough, in fact, to be smelled by the divers under water.

Three stations (Figure 1) were set up at which measurements of salinity, temperature, and dissolved oxygen were taken. Two of the stations were within the Inner Bay—station 2 in the affected area and station 1 in an unaffected area immediately adjacent to the affected water mass. The third station (station 3) was in the Outer Bay. Water samples collected on the third day of observations (6 October) in the area where the die-off had occurred had extremely low levels of dissolved oxygen (less than 0.08 to 0.45 mg O_2/liter); those collected outside of this area had much higher levels (4.23 to 8.29 mg O_2/liter). Approximate contours of distribution of dissolved oxygen are shown in Figure 2. The affected water mass had higher salinity than the surrounding waters within the Inner Bay; near the bottom salinity was 30.4‰ in the anoxic water and 30.1‰ in the adjacent oxygenated water (Figure 3). Similarly, temperature was higher in the anoxic water—9.2°C compared

with 8.4° to 8.7°C in the adjacent oxygenated water in the Inner Bay (Figure 4). Calculated density values (Figure 5) show that the water within the affected mass was more dense (σ_t, 23.6) than the overriding water within the Inner Bay (σ_t, 22.6 to 23.4). The two features common to anoxic situations in fjords were present —a shallow sill and an adjacent pycnoline. The situation at Little Port Walter was typical of

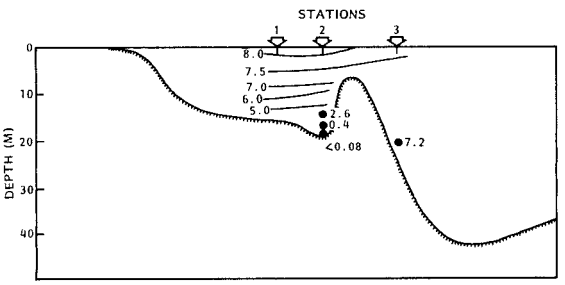

FIGURE 2.—Dissolved oxygen (mg/liter) contours in anoxic estuary, Inner Bay, Little Port Walter, 6 October 1971.

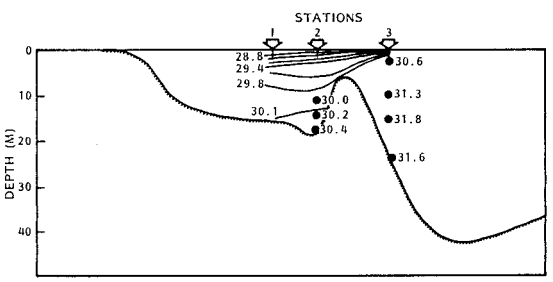

FIGURE 3.—Salinity (‰) contours in anoxic estuary, Inner Bay, Little Port Walter, 6 October 1971.

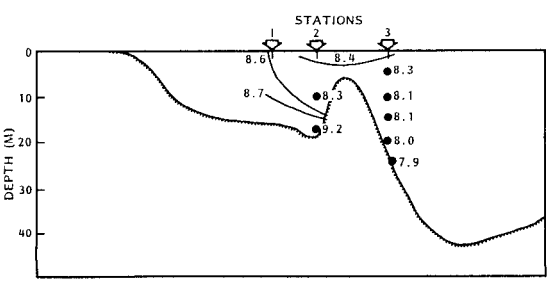

FIGURE 4.—Temperature (°C) contours in anoxic estuary, Inner Bay, Little Port Walter, 6 October 1971.

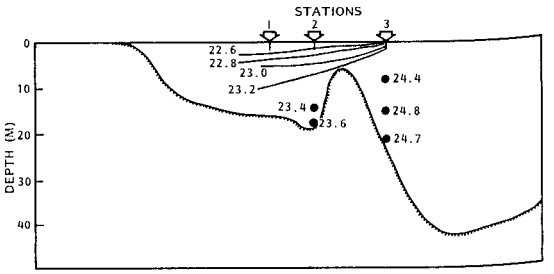

FIGURE 5.—Density (σ_t) contours in anoxic estuary, Inner Bay, Little Port Walter, 6 October 1971.

anoxic fjords; the pycnocline existed because of a strong halocline.

The mass of anoxic water was abruptly flushed out of the bay sometime between midday of 6 October and early evening of 7 October. On the evening of the 7th, divers found that the water was clear. Live benthic animals (mostly shrimp) were seen, although not abundantly, in the area where none had been seen the previous 3 days. Also, most of the dead organisms had disappeared.

Possible Causes of Formation and Destruction of Anoxic Condition

Depletion of dissolved oxygen to the point of anoxia in Little Port Walter is probably the result of the biochemical oxidation of organic matter (mainly salmon carcasses) both in Sashin Creek and in the Inner Bay. Richards (1965b) explains a mechanism which could account for the situation observed at Little Port Walter.

> As long as appreciable quantities of dissolved oxygen are present in the water, it is the preferred hydrogen acceptor for the biochemical oxidation of organic matter, being the richest available source of free energy. The decomposition can be pictured as the hydrolytic release of ammonium and phosphate ions, and the oxidation of the organic residues to carbon dioxide and water. The released ammonia is a transient form, because in oxygen-bearing waters it enters upon nitrification and is oxidized through nitrite to nitrate—the most abundant form of combined inorganic nitrogen in the ocean.
>
> When all, or nearly all, of the dissolved oxygen is consumed, nitrate and nitrite ions become the

richest available source of free energy, and denitrification ensues. Again, phosphate and ammonium ions can be pictured as being hydrolytically released, and the organic residues are oxidized, by denitrifying bacteria, to carbon dioxide and water, with the concurrent reduction of nitrate and nitrite ions to free nitrogen. [The ammonia released during this process accumulates.]

Following the disappearance of nitrate and nitrite ions, the next richest source of free energy in seawater is sulfate ions, which then take their place as hydrogen acceptors, being reduced to sulfides in the process. Again, phosphate and ammonium ions are hydrolytically released and accumulate while the organic residues are oxidized to carbon dioxide and water.

Brickell and Goering (1972) reported that on 29 September 1969, ammonia concentrations near the mouth of Sashin Creek were as high as 7.80 μg-atoms N/liter. This figure was 10 times higher than the concentrations in late August and early September before carcasses had begun to accumulate from the escapement of 30,000 pink salmon, *Oncorhynchus gorbuscha*. Dissolved organic nitrogen was at a peak concentration of 10.3 μg-atoms N/liter in the Inner Bay surface waters on 28 October—twice the concentration measured by Brickell and Goering in a control area lacking salmon carcasses. They did not report the presence of oxygen or sulfide, but their reported high levels of ammonia and dissolved organic nitrogen clearly indicate that chemical conditions were leading to sulfide formation at that time.

We did not measure ammonia and dissolved organic nitrogen in October 1971, but the escapement of 72,000 pink salmon, over twice that at the time of Brickell and Goering's study in 1969, would make the presence of excess ammonia and dissolved organic nitrogen even more likely in 1971. The detection of the odor of hydrogen sulfide by divers and in water samples implies that the reduction of organic materials had proceeded through oxidation and denitrification stages; i.e., in some parts of the water anoxic conditions were present.

The milky appearance of the water could have been due to the formation of colloidal sulfer when sulfide-bearing waters formed near the bottom mixed with oxygenated waters higher in the water column (Cline and Richards, 1969).

The sudden disappearance of the anoxic water from the bay was probably associated with extreme spring tides that immediately preceded the flushing. The large volume of exchange and relatively greater current velocities during the large tides probably caused a gradual reduction of the pycnocline. When the pycnocline was reduced sufficiently, mixing occurred throughout the water column, and the anoxic water was flushed out of the bay.

The coincident sudden disappearance of the dead organisms may have resulted from one or a combination of factors: use by scavengers such as amphipods, which moved back into the affected area after the flushing, or physical removal of many of the decaying organisms by water movements in the area.

Applicability of Observations of Anoxic Conditions

It seems probable that other estuaries in Alaska may also develop temporary anoxic conditions. Likely estuaries could be identified by studying the morphometry of the basin for presence of a shallow entrance sill and by determining the presence of periodically or chronically high biological oxygen demand. A capability for predicting formation of anoxic conditions in estuaries would aid in determining the proper management of susceptible bays which might be subjected to artificial introduction of large quantities of organic material.

Acknowledgments

Thanks are due to Robert J. Ellis, William R. Heard, and Roy Martin who assisted in the underwater observations and to Melford Bony who collected the water samples and oceanographic field data.

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TARACTES RUBESCENS AND *TARACTICHTHYS STEINDACHNERI* FROM HAWAIIAN WATERS

The various species of the family Bramidae are mostly high-seas fishes with the possible exception of *Eumegistus*. Although capture records of adult *Taractes rubescens* (Jordan and Evermann, 1887) and *Taractichthys steindachneri* (Döderlein, 1883) are few, Mead (1972) surmises that they are probably widespread in the tropical oceanic Pacific. Most of the documented accounts of the occurrence of these two species in the Pacific Ocean are of juvenile stages taken from stomachs of large predators. In the Pacific, *Taractes rubescens* has been recorded from a few widely separated localities between lat. 05°48′N and 02°26′S and long. 88°46′ and 155°W. All except one of the documented captures are of juveniles smaller than 120 mm. The only adult specimen was taken by a Japanese longliner at lat. 05°48′N, long. 126°00′W. *Taractichthys steindachneri* is also known mostly from juveniles. They have been captured at widely separated localities between lat. 40° 48′N and 04°46′S and long. 165°35′W and 98° 28′E. Although adult specimens of this species are also taken incidentally by Japanese longliners, documented capture localities are available in the Pacific for only four specimens. This note records the capture of the adults of 10 *Taractes rubescens* and 2 *Taractichthys steindachneri* from Hawaii and also provides some observations on the ecology of the two species.

Within the area around the Hawaiian Islands bounded by lat. 10°-30°N and long. 150°-170°W, *Taractes rubescens* was previously known from one juvenile measuring 27.5 mm in standard length (SL) and *Taractichthys steindachneri* was known from three juveniles measuring 17.0, 42.5, and 130.0 mm SL (Mead, 1972). The latter species was also known from an adult specimen (*Taractes longipinnis* = *Taractichthys steindachneri*) "about 2 feet long" (Gosline and Brock, 1960). However, *T. steindachneri* is probably more common than indicated: Mead (1972) cites a personal communication from W. A. Gosline (December 1963) in which it is indicated that fishermen in Hawaii are familiar with this species. The 12 bramids reported here were captured on longline gear at nine fishing stations during cruise 101 of the NOAA vessel *Charles H. Gilbert* between 17 May and 6 June 1967 (Table 1). The fishing stations were from 14 to 30 km off the coast of Waianae, Oahu, over depths of 1,800-3,000 m. The surface water temperature ranged from 25.5° to 27.4°C and the salinity from 34.5‰ to 34.9‰ at the fishing stations. Other fishes caught together with the bramids, in order of abundance, were *Alepisaurus* sp., *Prionace glauca*, *Thunnus obesus*, *Tetrapturus audax*, *Xiphias gladius*, *Alopias* sp., *Gempylus serpens*, *Katsuwonus pelamis*, *Acanthocybium solandri*, *Thunnus albacares*, *Tetrapturus angustirostris*, and *Isurus* sp.

Three of the *Taractes rubescens* and both of the *Taractichthys steindachneri* were frozen after capture. Approximately 5 yr later, body measurements and counts on two *Taractes rubescens* and two *Taractichthys steindachneri* were made in the laboratory after the specimens thawed out (Table 2). The five preserved specimens are presently in the Southwest Fisheries Center, Honolulu Laboratory's fish collection.

TABLE 1.—Capture locality of *Taractes rubescens* and *Taractichthys steindachneri*.

Date 1967	Position		*Taractes rubescens*			*Taractichthys steindachneri*		
	Lat. N	Long. W	Number	Length	Sex[1]	Number	Length	Sex[1]
				mm			*mm*	
18 May	21°26′	158°22′	1	729	M	—	—	—
19 May	21°34′	158°34′	1	749	M	—	—	—
20 May	21°19′	158°22′	2	781	M	1	611	F
				635	F			
21 May	21°23′	158°24′	2	522	F	—	—	—
				662	F			
22 May	21°16′	158°15′	1	713	M	—	—	—
26 May	21°17′	158°17′	1	730	M	—	—	—
28 May	21°16′	158°16′	1	[2]—	[2]—	—	—	—
3 June	21°21′	158°18′	—	—	—	1	644	F
6 June	21°20′	158°26′	1	760	M	—	—	—

[1] M = male, F = female.
[2] Not determined.

The primary purpose of cruise 101 of the *Charles H. Gilbert* was to determine if longline catch rates for *X. gladius* around Hawaii could be improved by fishing at night. Also included in the fishing experiment was a comparison of Pacific saury, *Cololabis saira*, and squid, *Loligo opalescens*, as bait, and a comparison of the effect of 9.1-, 18.3-, and 36.6-m float lines on the catch rates. Although the number of specimens taken was small, it was interesting to examine the fishing results as they pertain to the bramids.

During cruise 101 longline fishing operations were conducted in two general areas: one off the coast of Hilo, Hawaii, and the other, as noted earlier, off the coast of Waianae, Oahu. The 3 days of fishing off Hilo did not produce any bramids. Off Waianae, bramids were taken on 9 of the 19 days fished in that area. Although the data are too few to make definitive conclusions, it is of interest that slight environmental differences existed in the two areas, which may in part account for the fact that no bramids were taken off Hilo. The surface water temperature was slightly cooler off Hilo, ranging from 24.7° to 25°C as compared with 25.5° to 27.4°C off Waianae. The salinity of the water at the surface ranged from 34.4‰ to 34.6‰ off Hilo and 34.4‰ to 34.9‰ off Waianae.

As far as I know, *Taractichthys steindachneri* and *Taractes rubescens* are not commonly caught by the Hawaiian longline fishermen. This may be because longlines are usually set and retreived during daylight hours. The fact that they were taken on cruise 101 of the *Charles H. Gilbert* when the longlines were fished at night suggests that they may be nocturnal feeders. The results of the experimental use of the float lines of different lengths suggest that they may also be subsurface feeders: More were taken when the longline gear fished deeper, i.e., had longer float lines. Considering only the stations off the Waianae coast, 2,340

TABLE 2.—Measurements and counts on two specimens of *Taractes rubescens* and two specimens of *Taractichthys steindachneri*.

Measurements and counts	*Taractes rubescens*		*Taractichthys steindachneri*	
Standard length (mm)	660	663	538	568
Measurements (in percent of standard length)				
Head length	31.8	32.3	29.2	30.8
Depth of body at origin of dorsal fin	40.0	40.3	45.7	48.9
Least depth of caudal peduncle	7.7	7.5	6.5	7.2
Horizontal diameter of eye	6.4	6.6	6.3	6.5
Snout to origin of dorsal fin	38.6	39.5	36.0	41.9
Snout to origin of anal fin	62.7	60.5	51.1	51.6
Snout to origin of pectoral fin	32.6	31.7	29.4	31.7
Length of pectoral fin	42.7	43.4	42.4	42.1
Length of ventral fin	[1]—	15.2	7.4	8.4
Length of longest dorsal ray	34.1	32.1	38.8	[1]—
Length of longest anal ray	28.8	27.3	30.5	37.8
Counts:				
Dorsal fin	30	30	35	35
Anal fin	20	20	29	28
Pectoral fin	21	20	20	20
Gill rakers	2+8	2+8	4+7	2+8
Scales in horizontal series	[2]45	[2]47	37	37

[1] Damaged.
[2] Excluding the enlarged keel scales.

hooks were fished on longline baskets with 9.1-m float lines, 2,160 hooks on baskets with 18.3-m float lines, and 2,340 hooks on baskets with 36.6-m float lines. No specimens were taken on longline gear with 9.1-m float lines. One *Taractichthys steindachneri* and seven *Taractes rubescens* were taken on longline gear with 18.3-m float lines. One *Taractichthys steindachneri* and three *Taractes rubescens* were taken on longline gear with 36.6-m float lines.

Saury and squid were used as bait on alternate baskets on each fishing station. More bramids were taken on hooks baited with saury than with squid. Nine *Taractes rubescens* were caught on hooks baited with saury, and two on hooks baited with squid. Both of the *Taractichthys steindachneri* were caught on hooks baited with saury. These results would indicate that fish constitute an important part of the diet of these bramids. However, only one of five stomachs (4 *Taractes rubescens* and 1 *Taractichthys steindachneri*) had fish remains. Squid and shrimp remains were more frequent in the stomachs.

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UPWELLING INDICES AND ANNUAL CATCHES OF DUNGENESS CRAB, *CANCER MAGISTER*, ALONG THE WEST COAST OF THE UNITED STATES[1]

The Pacific Coast Dungeness crab, *Cancer magister*, fishery shows yearly fluctuations in the catch. For example, since the 1948-49 season, the Oregon catch averaged 8.3 million pounds, with a range of 3.1 to 15.0 million pounds. Variations between seasons are characteristic of the fishery, however, long persistence of below average catches causes alarm in the industry. The years 1962-64 were such a period of low catches. The Pacific Marine Fisheries Commission (1964) noted that these fluctuations in abundance occurred uniformly along the entire west coast of the United States. Therefore, they concluded that some coast-wide environmental changes were responsible for the fluctuating crab catches.

Cleaver (1949) felt that the fishery had a strong dependence upon the survival of the young and that the abundance of the adult animals will fluctuate widely with conditions affecting the earlier stages. The Pacific Marine Fisheries Commission (1964) suggested that perhaps seasonal changes in water circulation patterns could sweep the pelagic crab larvae into unfavorable settling habitats, causing high larval mortality, thus accounting for fluctuations in abundance of the marketable adult crabs. Reed (1969) looked into the effects of temperature and salinity on survival of crab larvae. He concluded that these factors were unable to cause large fluctuations in larval survival.

Upwelling is a coastwide environmental phenomenon that varies from year to year. It has not been mentioned in any reports discussing the Dungeness crab fishery and its fluctuations. Yearly strength of upwelling is known to fluctuate (Hubbard and Pearcy, 1971). It is hypothesized that annual upwelling fluctuations are related to annual variations in fishery strength, since the west coast's resident commercial species (bottom fishes, shrimp, Dungeness crab, and mollusks) must depend in large part upon the increased food production during summer upwelling for their growth and sur-

vival. If several years of poor upwelling occur in a row, there may be several years of poor commercial catches, after some lag time. The converse should be true as well, assuming food is limiting. This paper will examine these possibilities by attempting to relate catches of Dungeness crab from the coasts of Washington, Oregon, and northern California to an upwelling index.

Certain aspects of the crab fishery make it uniquely suited for direct comparison to coastal upwelling. At the winter start of any crab fishing season, a finite number of legal-sized male crabs exist. The season essentially ends when virtually all of these animals are harvested. Tagging studies at Grays Harbor, Wash., in 1947 and 1948 found that minimally 79 and 87%, respectively of the available males were harvested (Cleaver, 1949. In California, research has indicated (Pacific Marine Fisheries Commission, 1964) that between 90 and 100% of the male crabs have been taken annually since 1928 or 1929. I am assuming that the intensity of the Oregon fishery has been similar. The Pacific Marine Fisheries Commission noted in 1964 that " . . . a few years ago, it took probably seven months to remove 90-95% of the available crabs. Now it takes hardly seven weeks." Fishing effort data are not required, since very few of the available animals escape capture. Therefore, total pounds landed in a given season is an excellent indicator of population size and possibly growth rate.

Reproduction is unaffected by the fishery, since males have several opportunities to mate, and females are not legally harvested. In Oregon and Washington, reproduction can occur at age 2. By age 3 probably most males have mated at least once during the summer mating season (Cleaver, 1949). These animals may reproduce again the following summer before entering the winter fishery at age 4½ yr. In California, mating occurs earlier, during late winter and spring. Males 1½ yr old have been observed mating, but generally do not until 2½ yr of age. At age 3½ males enter the fishery (Poole and Gotshall, 1965), 1 yr earlier than Washington and Oregon crabs. All along the west coast, females rarely, if ever, attain the legal size for males of 6¼-inch carapace width, and thus they are not generally retained in crab pots. The crab population may even be benefited by removal of those 4-yr-old males who have fulfilled their copulatory obligations, since this may reduce intraspecific competition for food required by growing 2- and 3-yr-old males, and egg-bearing females.

Coastal Upwelling and Dungeness Crabs

Ekman's theory (Bakun, in press) states that the net mass transport of water set in motion by sea surface winds will be 90° to the right of the direction in which the wind is blowing, in the northern hemisphere. The intensity of this water transport (referred to as Ekman transport) is a function of the intensity and duration of the wind stress.

Along the Oregon coast for example, winds generally blow from the north and northwest from April to September. The effect is a transport of surface water away from the coastline. This offshore near-surface transport is balanced by an onshore deep transport of cool, nutrient-rich water, coming to the surface. This phenomenon is called upwelling.

Strong upwelling off Oregon occurs when strong winds have a northerly component. The opposite phenomenon, downwelling, can occur if the winds have a southerly component. In this case warm surface waters are carried onshore, and cooler deep water moves offshore. Both phenomena occur in any given summer. The result of continuous steady northerly winds would be a summer of strong upwelling. A relative increase in the frequency of weak northerly and/or southerly winds would result in a summer of weak upwelling.

There is evidence that one of the biological effects of upwelling (i.e., increased production of copepods) is felt primarily along a rather narrow band paralleling Oregon's coastline, only a few miles wide, in close proximity to the shore. Zooplankton samples collected with fine-mesh nets off Newport, Oreg. (lat. 44°40′N), during periods of upwelling show the greatest abundances of phytoplankton and microcopepods at stations 1, 3, and 5 nautical miles from the beach. Microcopepod numbers drop rapidly farther offshore. Dungeness crabs are found

only on sandy bottoms within this food-rich area of intense upwelling, from the 4-m contour out to about the 75-m contour (about 10 nautical miles offshore). The fishery is usually confined to less than 50-m depth (Waldron, 1958). If crabs are dependent upon food produced in the pelagic environment, their survival and thus their fishery may be influenced by annual variations in upwelling and food production.

Materials and Methods

Bakun (in press) has generated quantitative indices of upwelling based upon monthly mean wind stress on the sea surface at points near the coast. The indices are calculated for each 3° of latitude ranging from Baja California (lat. 18°N) to the Gulf of Alaska (lat. 60°N). Knowing wind stress one can compute the expected offshore Ekman transport and resolve the component of Ekman transport perpendicular to the coast. Bakun's data are derived from analyses of monthly mean atmospheric pressure fields, rather than from numerous but generally spotty direct wind observations. For an explanation of the methods used to convert pressure fields into geostrophic wind fields, see Bakun (in press).

The magnitude of the offshore component of the Ekman transport is considered by Bakun to be an index of the amount of water upwelled to replace that driven offshore. Negative values of the index are possible and indicate net onshore transport of water (downwelling) for that particular month. Negative values occur only during the winter months. A low positive value would indicate either weak offshore transport or alternating periods of upwelling and downwelling within that particular month. Positive values occur during summer months, and some spring and fall months. Maximum positive values (i.e., most intense upwelling) occur in July at all points north of San Francisco. I will refer to the upwelling season as the summer upwelling season since monthly indices are highest in June, July, and August.

Data on total pounds of Dungeness crab landed in Oregon and Washington were taken from the annual reports of the Pacific Marine Fisheries Commission (1959-70). The pre-1959 data were read from graphs in the same reports. Northern California data were taken from annual reports of the California Department of Fish and Game (1948-70). Data for 1970-71 and 1971-72 seasons were obtained from C. Dale Snow, Oregon Fish Commission (pers. comm.).

Monthly upwelling index data were summed for those months representing the upwelling season (as defined by Bakun) at the selected latitudes. These months are the only ones which may have positive values of the index. In some years, negative values occurred during certain spring and autumn months. Nevertheless these negative values are included in the summed upwelling season index. For Washington, upwelling indices calculated for lat. 48°N, long. 125°W were used. The May through September values were summed, thus generating an upwelling-season index. For Oregon, indices for lat. 45°N, long. 125°W were summed over April through September. For northern California, indices calculated for lat. 42°N, long. 125°W were summed over March through September. Only the California data representing the Eureka region will be considered here because the San Francisco region crab fishery has apparently collapsed since the 1961-62 season, as will be shown later.

Although upwelling index data are available for as early as 1946, west coast crab data for only as early as 1948-49 are considered because of the nature of the Oregon data. Until the 1948-49 season, both males and females could be harvested in Oregon, at 6-inch carapace width. Since then, only males of 6¼-inch carapace width have been legal. Therefore to make all data sets comparable, the 1948-49 season was chosen as the starting point.

Results

Figure 1 is a plot of crab catches in Washington. Oregon, and the Eureka and San Francisco regions of California. Since 1954-55, seasonal catch trends are quite similar for all three states. In each state, a trend of declining catches over the seven seasons from 1957-58 until 1963-64 is apparent, with the exception of high catches in northern California from 1958-59 through 1960-61, and in Oregon for 1959-60 and 1960-61

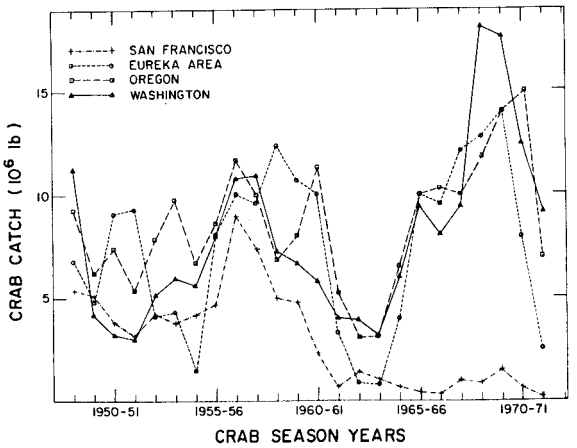

FIGURE 1.—Crab landings, in millions of pounds, for Washington, Oregon, northern California (Eureka area), and San Francisco area, by season, for the 25-yr period 1947-48 through 1971-72.

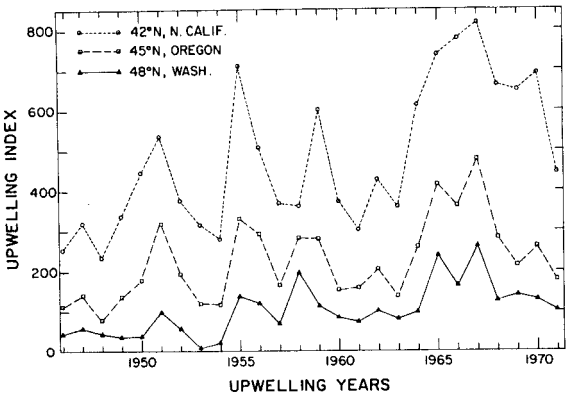

FIGURE 2.—Bakun's upwelling indices for Washington, Oregon, and northern California. The units of the index are cubic meters of water upwelled per second per 100 m of coastline. The northern California values represent summed March through September index values calculated by Bakun for lat. 42°N. The Oregon data were summed over April through September at lat. 45°N and the Washington data were summed over May through September at lat. 48°N.

seasons. The latter resulted from high catches in newly exploited crab grounds off Brookings, Oreg. (Pacific Marine Fisheries Commission, 1960, 1961). Perhaps the high catches in northern California during the same period were due to exploitation of these or other newly discovered beds.

The coastwide trend from 1963-64 until 1969-70 has been one of steadily improving catches climaxing in record catches for nearly all areas. What might have been termed a collapse of the Eureka and San Francisco region fisheries in 1962-63 and 1963-64 has become a reality for the San Francisco area ports. All other areas recovered from this depressed period.

Figure 2 shows the summed upwelling index values for lat. 48°N, 45°N, and 42°N. The units of the indices are cubic meters of water upwelled per second per 100 m of coastline. Absolute values of the indices were always lowest in Washington, intermediate in Oregon, and highest in northern California.

A uniform coastwide pattern of annual variability of the upwelling index is apparent in all three states, over the periods of 1948-57 and 1960-71. No coastwide trend is apparent for the summers of 1958 and 1959. Deviations from the agreement pattern do appear in other years (1949, 1954, 1961, 1966, 1969, and 1970) but they are small and probably insignificant.

Figures 3, 4, and 5 are time-series plots of upwelling index and crab catch, in Washington, Oregon, and northern California, respectively. Washington winter crab catches are plotted opposite the preceeding summer's upwelling index (½-yr lag). Oregon and northern California crab catch data are plotted with a 1½ yr lag (upwelling plotted opposite catch of the winter 1½ yr later). Reasons for the differing lag times will be discussed later.

The Oregon data (Figure 4) follows trends in upwelling index values remarkably well, since 1955. Notable is the weak upwelling period of 1960-63 followed 1½ yr later by the poorest crab catches in 1961-62 through 1964-65, and the high values of the upwelling index in 1964-68 followed 1½ yr later by record and near-record crab landings in 1965-66 through 1970-71. The record catch of 1970-71 would seem anomalous but very likely reflects the long-term effect that prolonged periods of very strong upwelling can have on the population. The three record years of upwelling in 1965-67, as well as strong upwelling in 1968, may have generated enough food reserves to keep the crab population supplied with a food surplus, thus contributing to a good catch 2½ yr later.

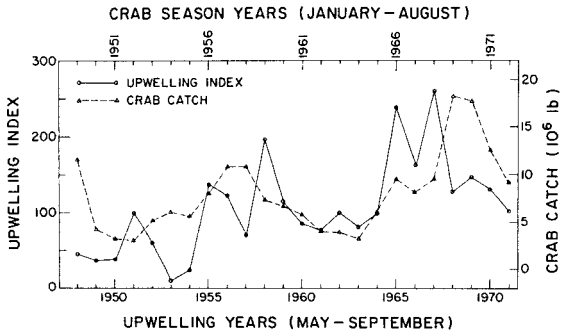

FIGURE 3.—Upwelling index values compared with crab catch in Washington. Crab catches are plotted opposite summer upwelling ½ yr earlier.

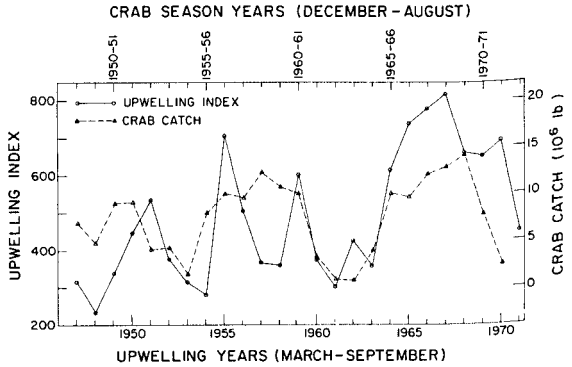

FIGURE 5.—Upwelling index values compared with crab catch in northern California. Crab catch is lagged 1½ yr.

The northern California upwelling-crab data (Figure 5) have paralleled Oregon's since the summer of 1959. The upwelling data for the summers of 1949-55 would match crab catch better if the crab data were lagged ½ yr (i.e., crab data shifted to the right 1 yr) instead of 1½ yr. The high crab catches of the 1958-59 and 1960-61 seasons may have resulted from exploitation of newly discovered crabbing areas, as suggested earlier.

In Washington State (Figure 3) trends are not apparent in the 1949-59 data set, but from the 1960-61 fishing season until 1971-72 the trend is similar to Oregon's trend.

Each upwelling-crab catch data set can be tested statistically for associations between the magnitude of the upwelling index and crab catch. Scatter diagrams of upwelling index vs. crab catch were prepared for lagtimes of ½ to 4½ yr for Washington and Oregon, and ½ to 3½ yr for northern California. (California crabs mature 1 yr earlier than those from more northerly points (Poole and Gotshall, 1965).)

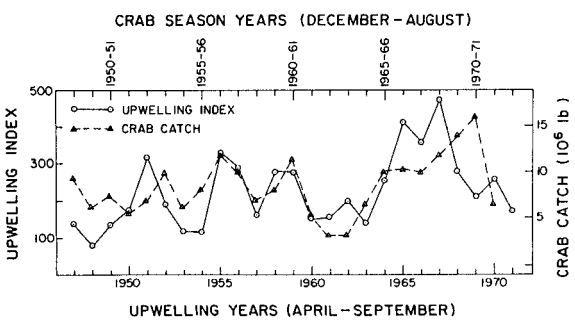

FIGURE 4.—Upwelling index values compared with crab catch in Oregon. Crab catch, in millions of pounds, is plotted opposite upwelling 1½ yr previous.

Figure 6 is Oregon's set of upwelling-crab catch scatter diagrams for the indicated lag times. (The Washington and northern California scatter diagrams are not illustrated but results of statistical tests performed upon the scatter are summarized in Table 1.) The median values of the upwelling index and crab catch partition each scatter diagram into quadrants. The first and third quadrants (upper right and lower left) represent strong upwelling-good crab catch and weak upwelling-poor crab catch, respectively. The second and fourth quadrants contain data points with the inverse relationship.

A number of statistics can be applied to these scatter diagrams to test the null hypothesis of independence, i.e., no relations between upwelling and crab catch. One of the tests is the corner test (Tate and Clelland, 1957:67). This test is useful in exploring general associations in a scatter diagram. Results of the test (Table 1) indicate that at the 5% level, a significant association exists between upwelling and crab catch ½ yr later in Washington, 1½ and 2½ yr later in Oregon, and ½, 1½, and 2½ yr later in northern California. Such a close time link between an environmental factor (upwelling) and its hypothesized effect upon a fishery implies that the fishery is dependent upon survival of older individuals, rather than juvenile individuals.

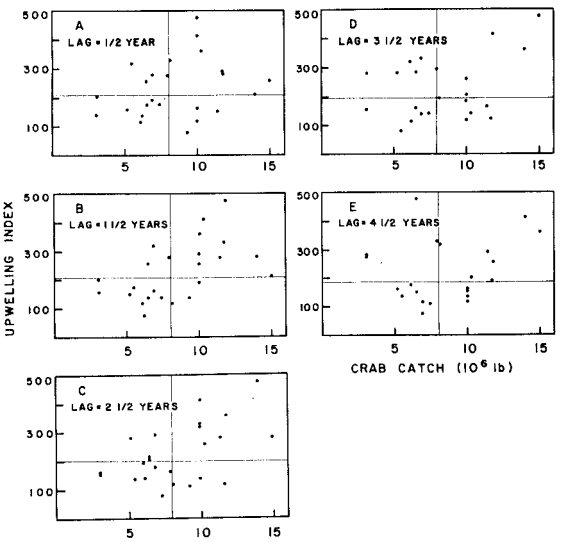

FIGURE 6.—Scatter diagrams of upwelling and crab catch for various lag times, for Oregon. The median values of upwelling index and crab catch divide each scatter diagram into quadrants.

The null hyphothesis of independence cannot be rejected for lag times of from 1½ to 4½ yr in Washington, 3½ and 4½ yr in Oregon, and 3½ yr in northern California. Nonsignificance at lag times of 4½ yr in Washington and Oregon and 3½ yr in northern California implies that the crab fishery is not strongly dependent upon the survival or growth of recently metamorphosed crabs, or upon the survival of crab larvae. Thus, even if abundance and survival of crab larvae in one year are important to a successful crab fishery some years later, upwelling has no strong influence upon these factors.

Another statistical test lends stronger support for this conclusion. Contingency tables (2 × 2) were set up from each scatter diagram. The tables were defined by the number of data points in each quadrant. For example, the 1½-yr lag scatter diagram for Oregon (see Figure 6) reduces to a

3	9
9	3

median value of crab catch

median value of upwelling index

TABLE 1.—Results of certain statistical tests performed upon scatter diagrams of upwelling index vs. crab catch in Washington, Oregon, and northern California. The Corner Test was performed on the scatter alone, while the absolute probabilities were calculated from 2 × 2 contingency tables set up from each scatter diagram. Quadrants were defined by the median value of the upwelling index and crab catch. The number of data points in each quadrant were the frequencies entered in each cell of the contingency table. The null hypothesis tested was independence of crab catch from the upwelling index. The absolute probability calculations indicate rejection of this hypothesis for the 1½-yr lag periods in Oregon and northern California, and the ½-yr lag period for Washington; i.e., crab catch and upwelling index are related at these lag times.

State or region	Lag time (Yr)	Corner test: Sum	Corner test: Level of significance	2 X 2 contingency tables: *A*	*B*	*C*	*D*	Absolute probability
Wash.	½	18	0.01	2	10	10	2	0.003
	1½	8	>.10	4	8	8	4	.22
	2½	7	>.10	4	8	8	4	.22
	3½	6	>.10	4	7	8	4	.22
	4½	5	>.10	5	6	6	5	1.00
Oreg.	½	10	~.08	4	8	8	4	.22
	1½	17	.01	3	9	9	3	.04
	2½	11	.05	4	8	8	4	.22
	3½	8	>.10	5	6	6	6	1.00
	4½	5	>.10	4	7	7	4	.39
N. Calif.	½	14	.01	4	8	8	4	.22
	1½	15	.01	3	9	9	3	.04
	2½	10	~.08	6	6	6	6	1.00
	3½	4	>.10	6	6	6	5	1.00

contingency table, symbolically represented by

A	*B*
C	*D*

Where $N = A + B + C + D$.

The chi-square test can be applied to contingency tables but the results tend to be unreliable when N is less than about 40 ($N = 24$ in my examples). In such cases, if reliable results are desired, the exact probability of a particular contingency table given the null hypothesis can be calculated from

$$P_0 = (A + B)!(C + D)!(A + C)!(B + D)! \div N!A!B!C!D!$$

(Tate and Clelland, 1957:73). To obtain a two-

tailed significance level, P_0 and the probabilities of each more extreme table with the same row and column totals which might have occurred, are summed and multiplied by 2. For example, the significance calculation for the 1½-yr lag table, for Oregon, is

$$P_0 \begin{array}{c|c} 3 & 9 \\ \hline 9 & 3 \end{array} = 0.0179 \qquad P_2 \begin{array}{c|c} 1 & 11 \\ \hline 11 & 1 \end{array} = 0.0006$$

$$P_1 \begin{array}{c|c} 2 & 10 \\ \hline 10 & 2 \end{array} = 0.0016 \qquad P_3 \begin{array}{c|c} 0 & 12 \\ \hline 12 & 0 \end{array} = 0.0001$$

where significance level, $\alpha = 2(P_0 + P_1 + P_2 + P_3) = 0.0404$. The significance levels for different lag times for all three states are presented in Table 1. (The null hypothesis of independence was rejected at the 5% significance level.)

The results indicate that crab catch and upwelling are related as hypothesized. The relationship is that summers of strong upwelling generally produce a good crab catch 1½ yr later along the coasts of northern California and Oregon. Along the coast of Washington, summers of strong upwelling almost always produce a good crab catch the following winter. The converse is also true (weak upwelling results in poor crab catches). It must be emphasized here that a qualitative statement is all that these statistics will allow.

Discussion

The observed lag times probably are a direct result of slow energy transfer through the pelagic environment to the benthos. The benthic predators may not experience upwelling-induced increases in food resources until many months after the onset of upwelling. Stephens, Sheldon, and Parsons (1967) determined that deposition of phytogenous material did not occur until 2 months after commencement of the annual spring phytoplankton bloom, in Departure Bay, British Columbia. Several times the generation time of the dominant copepods would be required after commencement of the bloom before copious amounts of fresh copepod faecal material would begin settling to the sea floor. Population increases of the benthic filter feeders and deposit feeders would lag additionally by the generation time of each species. Some of these animals (amphipods, polychaetes, clams, and shrimp) are known Dungeness crab prey. Other preys include small fish and small crabs (MacKay, 1942; Waldron, 1958).

Two-year old and older crabs moult annually. This event occurs during the summer off northern California, late summer-early fall off Oregon, and late fall off Washington (Poole and Gotshall, 1965, for northern California; Snow, pers. comm., for Oregon; Cleaver, 1949, for Washington). It is hypothesized that the California and Oregon crabs moult before benefitting from increased food resources, so their response to a summer of strong upwelling is not exhibited until the next summer's moult. Washington crabs however moult several months after the end of the upwelling season, and therefore must benefit from the increased production since the lag between strong upwelling and a good fishery is only ½ yr.

This hypothesis implies that a summer of strong upwelling off California and Oregon serves to maintain a large crab population throughout the coming year by both increasing food availability and decreasing competition for the food. Although lower food availability resulting from a summer of weak upwelling implies increased competition for food, increased mortality of sublegal adults need not be the only outcome of such competition. Another possibility is decreased moulting success. If a crab has not accumulated enough food reserves during a year of feeding, it need not shed its carapace. Numerous workers have observed from tagging studies and observations on the degree of fouling of the carapaces that Dungeness crabs can wait 2 yr before moulting (MacKay, 1942; Cleaver, 1949; Waldron, 1958; Butler, 1961; Snow and Wagner, 1965; Poole, 1967). The prevalence in the field is unknown. Poole (1967) believes that as many as 10-15% of the male crabs may miss moults. If moults are missed, animals would not enter the fishery until an additional year later, i.e., 1½ yr after a particular upwelling season in Washington and 2½ yr after in Oregon and California.

Graphically, I have shown (Figures 3, 4, 5) that trends of annual variability of crab catch

were closely correlated with trends of annual variability of an upwelling index, for the period 1959-71. Poor correlations during the period 1950-58 may have resulted from one or a combination of at least four causes. First, if the fishery were not as intense in these earlier years so that fewer than 90-95% of the available males were taken during a particular season, each seasons catch may be higher than an upwelling index might suggest. Second, if at any time during this period some previously unexploited areas were fished, the statewide catch data would be higher than one might predict, if one could predict catch. For valid comparison of the raw catch data to environmental factors, all crab beds must be "cleaned-out" each year. Third, the upwelling index may be in error during this period. Earlier atmospheric pressure data may not be as reliable, or sparce data coverage may have yielded erroneous indices. A fourth alternative may be that all data are adequate, and that only the extreme conditions influence crabs. Four summers of poor upwelling occurred together from 1960 to 1963, followed by five summers of good upwelling in 1964-68. Crab catch trends were well established during this period. Prior to the 1960's no such persistent trends were found, except with the Oregon data.

To my knowledge, this study represents the first published attempt to relate Bakun's (in press) upwelling index to fisheries data. Although the physical meaning of the index is clear (index value proportional to the volume of water upwelled) it must be remembered that it expresses a monthly mean condition. A low value of the index does not necessarily imply that upwelling-induced production was low in a particular month. For example, if during a particular month, there were 5-day periods of alternating northwest and southwest winds, the upwelling index would be low, but biological production may still have been reasonably high. In this light then, perhaps only persistent summers of either high or low values have biological meaning.

Whatever the reasons might be for certain anomalous data points occurring during the period 1950-58, the data from the past 13 yr lend strong support to the hypothesis that upwelling is responsible for fluctuations in the crab catches of the west coast, and that the catches show response to the upwelling 1½ yr later off northern California and Oregon, and ½ yr later off Washington.

Acknowledgments

This study has been supported by a NOAA Institutional Sea Grant to Oregon State University (Contract No. 2-35187). I am indebted to Andrew Bakun of the Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, Calif., for supplying a copy of his manuscript on upwelling indices. I am also indebted to Charles Miller for assistance with the statistical tests, for reviewing this manuscript, and for many helpful discussions. William Pearcy read an earlier manuscript and offered valuable comments. C. Dale Snow of the Oregon Fish Commission, Newport, Oreg., supplied the recent crab catch data. We had several mutually informative discussions.

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NOAA FSYB-A 71-4

A UNITED STATES DEPARTMENT OF COMMERCE PUBLICATION

Fishery Bulletin

U. S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Seattle, Wash.
OCTOBER 1973

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Seattle, Washington

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PRODUCTIVITY GAINS IN U.S. FISHERIES

FREDERICK W. BELL AND RICHARD K. KINOSHITA[1]

ABSTRACT

Changes in productivity or annual landings per fisherman help to determine the economic welfare of the fishing industry. Although a study of productivity gains in various U.S. fishing fleets over the last 20 yr showed variations between fisheries, many sectors of the fishing industry experienced substantial increases in labor productivity in recent years. Of the 17 fisheries studied, 11 exhibited positive trends in output (landings) per fisherman. A productivity index was constructed which indicated that, in the aggregate, fishing labor productivity increased by approximately 2.5% per year during the 1950-69 period, compared with 3% for the entire U.S. economy. Upon comparison of the fishing industry with those of meat and poultry, the fisheries' chief competitors, it was shown that labor productivity advances in the U.S. fishing industry were the lowest. A similar analysis for selected foreign fishing sectors revealed that the United States had fallen behind other countries with respect to productivity gains. A detailed quantitative study of three selected fisheries showed that increases in aggregate fishing pressure significantly reduced labor productivity; however, this force was more than offset by increases in fishing effort per worker and technological progress in many fisheries. The quantitative impact of environmental, technological, and regulatory factors was also identified.

The growth in productivity or annual landings per fisherman is an important determinant of the economic welfare for the U.S. fishing industry.[2] Small or negative productivity gains in a fishery are often associated with lagging profits, wages, and employment because U.S. fishermen must compete with foreign fishery imports and other protein substitutes where productivity is a main ingredient of competitive advantage. Moreover, rising productivity in the fishery sector has helped reduce inflationary tendencies that have been most prevalent in meat and fish products. Productivity gains, in the long run, raise standards of living or reduce the amount of time we must work to produce a pound of fish or a television set or an automobile.

Generally, gains in productivity are determined by the increasing efficiency of our vessels and gear; the education, training, experience, and morale of our fishermen; and, of course, the condition of the fishery stock and other environmental factors.

This article will survey the gains in productivity experienced by various U.S. fishing fleets over the last two decades. Comparisons will be made between gains in fishing productivity and those in competing sectors. We shall also explore some of the reasons behind the gains in productivity for selected fisheries.

LABOR PRODUCTIVITY TRENDS IN SELECTED U.S. FISHERIES

Before we discuss productivity trends in selected U.S. fisheries, it will be instructive to look at the statistical definition of labor productivity that will be employed in this article. Productivity or annual landings per fisherman is obtained by dividing aggregate landings (for a year) by the number of fishermen employed.[3]

[1] Economic Research Division, National Marine Fisheries Service, NOAA, Washington, D.C. 20235.

[2] Productivity is usually measured in terms of output per man-hour. These data are not available for the U.S. fishing industry; we must therefore rely on annual landings per fisherman as a rough measure.

[3] As economists define it, productivity is simply a ratio of physical output to physical input. Higher productivity means getting more output with the same effort or the same output with less effort. "Total-factor productivity" can be calculated by dividing output by a figure that represents all the resources used, including plant and equipment, labor, and land. Theoretically, this is the true mea-

Manuscript accepted May 1973.
FISHERY BULLETIN: Vol. 71, No. 4, 1973.

For any particular fishery, the accuracy of data on aggregate annual landings is fairly reliable. However, the number of fishermen reported by the National Marine Fisheries Service is not adjusted for the extent of utilization during the year. For example, the U.S. Bureau of Labor Statistics collects detailed data on hours worked for most industries in the economy. This makes it possible to compute productivity on the output per man-hour basis. No universally comparable data are available on the fishing industry. Hence, our statistical base is something less than perfect.[4] Systematic variations in days and hours worked per year may be a biasing factor, but it is hoped that they are random. In addition, the reader should note that we are comparing rates of growth in productivity among fisheries and other industries and not absolute differences in productivity.

Table 1 shows the compound annual growth rate of labor productivity for 17 of the nation's major fisheries over the 1950-69 period.[5] Notice that the Gulf of Mexico blue crab, Atlantic clam, and Gulf of Mexico menhaden fisheries all had rates of productivity advance over 5%. Unfortunately, some of our largest fisheries such as Gulf of Mexico shrimp, Atlantic sea scallop, Atlantic and Gulf of Mexico oysters, and Alaskan salmon exhibited negative trends in productivity.

One interesting aspect of the growth in labor productivity is its year-to-year fluctuation. This is important for a variety of reasons. Many fishermen are paid according to the "lay" agreement where fishermen and vessel owners share the value of the catch on some predetermined basis. Short-run oscillations in labor productivity may contribute to an unstable earnings pattern.[6] Other industries have fixed wage agreements that depend on secular rather than short-run changes in productivity. To get some idea of which fisheries are more subject to oscillations in labor productivity, we constructed an index of instability which measures the percentage fluctuations around the long-run time trend in annual landings per fisherman.[7] Table 2 shows the 17 fisheries discussed earlier ranked according to cyclical instability in labor productivity. Using the most unstable as a base (i.e., Gulf of Mexico blue crab pot fishery), we see that 13 of the fisheries have less than one-half the instability of the base fishery.

Although the performance of individual fish-

TABLE 1.—Ranking of fisheries by the rate of growth in output per fisherman, 1950-69.

	Fishery	Rate of growth[1]
1.	Gulf of Mexico blue crab pot fishery	[2]+7.8
2.	North-Middle Atlantic and Chesapeake Bay dredge clam fishery	[2]+7.0
3.	Gulf of Mexico menhaden	[2]+6.8
4.	Pacific yellowfin-skipjack tuna	[2]+4.5
5.	Pacific halibut	[2]+3.8
6.	North Pacific groundfish	[2]+3.1
7.	Atlantic menhaden	[2]+2.4
8.	Atlantic blue crab pot fishery	[2]+1.3
9.	Pacific albacore	+0.8
10.	Atlantic shrimp	+0.7
11.	North Atlantic groundfish	+0.5
12.	Pacific (excluding Alaska) Dungeness crab	−0.4
13.	Inshore American lobster	−0.5
14.	Gulf of Mexico shrimp	[2]−1.3
15.	Atlantic sea scallop (subarea 5Z)	−1.5
16.	Atlantic and Gulf of Mexico oyster	[2]−2.0
17.	Alaska salmon	[2]−3.1

[1] Linear least squares trends of the logarithms of output per fisherman.
[2] Trend was statistically significant at the 5% level.

sure of efficiency, but statisticians have trouble constructing the index number that serves as the divisor. They have to combine unlike quantities—hours of work and units of capital investment—into a single index. And while statisticians never hesitate to add apples to oranges, the results are questionable. Economists, therefore, usually work with a simpler concept, "partial productivity." This is the ratio of physical output to a single input, usually labor. In most discussions, "productivity" means "labor productivity" or real output per hour, day, or year of work. It is a rough measure of the effectiveness with which we use our most important productive resource-labor.

[4] See Appendix to this article on employment figures in the U.S. fishing industry.

[5] The growth rate in labor productivity was computed by fitting a logarithmic function, i.e. fitting a linear time trend to the logarithm of output per fishermen. The 17 fisheries represent 68, 71, and 58% by landings, value, and employment, respectively, for the United States.

[6] Generally, a contraction in landings—due to a decline in productivity—will reduce income per fisherman if prices do not change appreciably. Prices may not increase if foreign imports are significant and/or price elasticity is large (i.e., a large percentage drop in landings results in a small percentage increase in price).

[7] The formula used to construct the index was:

$$CV_y = \frac{\sum_{i=1}^{N} \left| 1 - \frac{Y_{c_i}}{Y_{o_i}} \right|}{N}$$

where CV_y = cyclical variation in labor productivity; Y_o = observed labor productivity; Y_c = computed labor productivity from the time trend; and N = number of years.

eries is important, we do want some summary measure to tell us how the entire fishery sector is doing with respect to the rate of growth in labor productivity. If so, we can compare this summary measure with other important sectors in the U.S. economy. Fortunately, we can construct an aggregate index of labor productivity. The construction of this index is rather technical in nature and will not be discussed in detail here.[8] Suffice it to say we cannot add the total pounds of fish landed in the United States and divide by the number of fishermen employed when constructing an aggregate index over a period of time. This is true since there may be appreciable shifts in the production of various species with differing absolute productivity, thereby biasing the index. (Therefore, the constructed index controls product mix.)

Constructing an index based on the 17 fisheries shown in Table 1, we find that aggregate productivity grew at an annual rate of 0.7%. To obtain a more representative figure for all fisheries, we added an 18th fishery, which represents the group of remaining U.S. fisheries not included in the original 17. The aggregate index showed productivity growth at an annual rate of 2.5% over the 1950-69 period.[9] However, there seems to be a noticeable tendency for the growth rate of fishermen's productivity to decline over the observed period; i.e., the annual growth rate over 1950-59 was 4.7%, but it slackened to 0.5% in the last 10 yr. This was probably a result of increasing fishing pressure in established fisheries (see section below on factors behind productivity advances). This index is plotted in Figure 1. On the average, the American fisherman has been able to raise his productivity significantly over the last 19 yr. This is especially encouraging when we realize that the fishermen, as opposed to their counterparts in manu-

TABLE 2.—Ranking of fisheries by the cyclical variation in output per fisherman, 1950-69.

	Fishery	Cyclical variation in labor productivity	Percent of largest
1.	Gulf of Mexico blue crab pot fishery	0.448	100.0
2.	Atlantic sea scallop (subarea 5Z)	0.298	66.5
3.	Pacific (excluding Alaska) Dungeness crab	0.242	54.0
4.	Pacific albacore	0.234	52.2
5.	Gulf of Mexico menhaden	0.204	45.5
6.	Atlantic shrimp	0.188	42.0
7.	Atlantic menhaden	0.157	35.0
8.	North-Middle Atlantic and Chesapeake Bay dredge clam fishery	0.148	33.0
9.	Alaska salmon	0.147	32.8
10.	Atlantic blue crab pot fishery	0.104	23.2
11.	Pacific yellowfin-skipjack tuna	0.104	23.2
12.	North Pacific groundfish	0.100	22.3
13.	Gulf of Mexico shrimp	0.095	21.2
14.	Pacific halibut	0.093	20.8
15.	North Atlantic groundfish	0.082	18.3
16.	Atlantic and Gulf of Mexico oyster	0.081	18.1
17.	Inshore American lobster	0.055	12.3

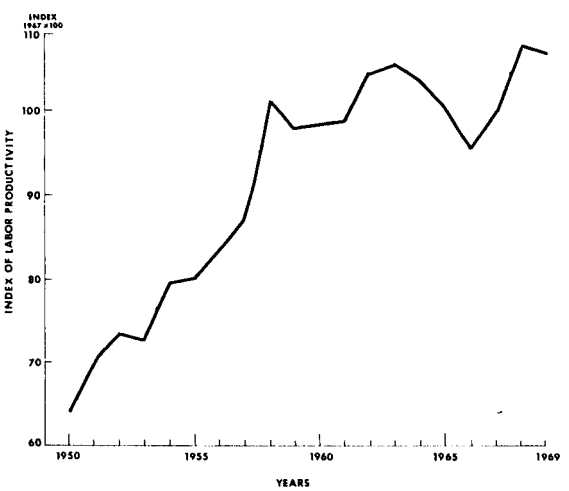

FIGURE 1.—Index of labor productivity for the fishing sector, 1950-69. (Productivity index is based on 17 individual fisheries and 18th residual category.)

[8] See "Output per man-hour measures: industries," (Bureau of Labor Statistics, 1966). Because of the problems with our data, it should be said that it was implicitly assumed that the work year is approximately the same for each fishery; a biasing factor may be introduced in the index to account for errors as a result of this assumption. However, as long as the difference in work years remains constant from fishery to fishery, this factor should not appreciably influence the time trend in the productivity index.

[9] The 18th fishery contained all residual fisheries or mostly minor fisheries that were too numerous to analyze separately. However, the rate of growth of labor productivity of the residual was fairly high. The reasons behind this finding are numerous. First, some of the residual fisheries are latent or newly developing, resulting in high productivity. Second, some duplication of fishermen operating in a number of fisheries is implicit in some of the data. That is, fishermen included in the 17 individual fisheries should also be counted in the residual. However, they were not since we merely subtracted the total number of fishermen in the 17 fisheries from aggregate employment (i.e., with no duplication). This would bias labor productivity in the 18th fishery upward. The reader should be aware of this technical problem that could not be solved with existing information.

facturing and service industries, must exploit a resource which has a fixed biological maximum that has a tendency to depress labor productivity (see discussion below).

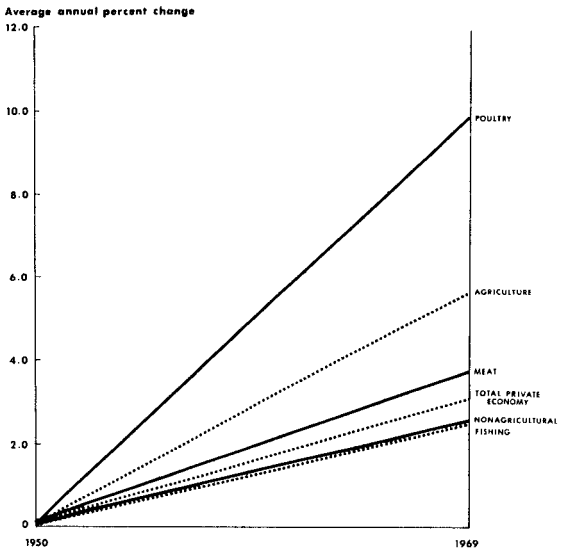

FIGURE 2.—A comparison of the rates of growth in labor productivity for the total private economy, agriculture, meat, poultry, nonagricultural, and fishing industries, 1950-69. (Source: U.S. Department of Labor, Bureau of Labor Statistics; U.S. Department of Agriculture, "Agricultural Statistics"; and Economic Research Division.

COMPARISON OF PRODUCTIVITY IN FISHING WITH OTHER SECTORS OF THE ECONOMY

Figure 2 shows a comparison of the growth in labor productivity over the 1950-69 period in the total economy, and specific categories encompassing all agriculture, meat, poultry, nonagriculture, and fishing industries.[10] The rate of growth in fishing was less than that for the U.S. economy as a whole. However, the rate of growth of labor productivity in agriculture was nearly twice that of the entire economy. Of special significance, changes in productivity in fishing lagged considerably behind that in the poultry industry and over one percentage point (per annum) in the meat industry. Since labor productivity is a prime ingredient in relative price changes, it may be concluded that these trends were generally adverse to the fishing industry.[11] That is, the more rapid advance in agriculture (including meat and poultry) lowered the price ratio of agricultural to fishery products. For example, the annual rate of growth (1950-69) in the wholesale price index of processed finfish was 3.9% while the wholesale price index for processed foods and feeds was 0.9%, partially reflecting the differential gains in productivity.[12] The consumer may then substitute the less expensive agricultural products for fishery products, and the share of the total food markets will decline for fish. This is reflected in the data that show 0.8 and 3.6% increase in per capita consumption of meat and poultry, respectively, while the per capita consumption of fish remained constant over the 1960-69 period.

Data are not readily available on fishing labor productivity in other countries. For illustrative

[10] The aggregate productivity index based upon 18 fisheries will be used throughout the remainder of this article. Furthermore, we are comparing annual productivity in other sectors (as opposed to output per man-hour) with that in U.S. fisheries.

[11] Some have contended that the relatively lower price of poultry has resulted from a reduction in cost of feed. According to the Economic Research Service of the U.S. Department of Agriculture, feed grain and high protein feeds have increased over 31% over the last decade. Of course, technical improvements in genetics, breeding, nutrition, and feed formulation have increased feed conversion ratios in broilers, and this has been the proximate cause of the striking rise in labor productivity in the poultry industry. Hence, labor productivity is the prime factor or indicator which is used to assess the impact of changing technology in changing relative prices. This is the reason labor productivity is monitored so closely in each sector of the economy in our battle against inflation.

[12] Some have suggested that price support programs in agriculture have been a factor in lowering the price advance of agricultural commodities. Admittedly, agricultural price support programs have had an effect on agricultural prices, but the major effect has been reducing price fluctuations and stabilizing prices rather than a direct effect on the fundamental change in agricultural costs and price structures. Trends in any statistical series will depend to a certain extent on when the series is started. In the case of agriculture, prices were low in 1950 and picked up with the Korean conflict and dropped in 1953-54. Agricultural policy was to support prices starting in 1953-54—a continuation of their earlier policy in 1950. Prices in 1951-52, however, received little or no support. Consultation with the Economic Research Service of the U. S. Department of Agriculture indicated that the lower rate of advance in processed foods and feeds has been due to sizeable increases in agricultural production (from 1950), attributable largely to the rapid increase in agricultural labor productivity contrasted with a reduction in aggregate farm inputs (i.e., farm output grew at 1.8% per annum while inputs remained constant).

TABLE 3.—Comparisons of the growth rate in labor productivity for selected fisheries and countries.

Fishery	United States	Other country	Period[1]
Menhaden (Atlantic and Gulf of Mexico)	-0.4	[2] +2.8	1960-68
Northeast groundfish	-1.9	[3] +4.0	1959-69
Inshore American lobsters	-0.3	[4] −3.8	1959-69

[1] Periods are different than shown in Table 1 because of lack of data in foreign countries for earlier periods.
[2] Peruvian anchoveta.
[3] Canada.
[4] Canada.

purposes, however, we do have some information for the groundfish, menhaden, and lobsters as shown in Table 3. For this limited sample, it is quite apparent that U.S. fishermen are *not* holding their own with their foreign counterparts in menhaden and groundfish. More research is needed in this area.

FACTORS BEHIND THE GROWTH IN LABOR PRODUCTIVITY IN FISHING

Why has labor productivity increased at a lower rate in fisheries than in competing sectors such as meat and poultry? Has it been because fishermen are technologically backward or are not working harder? To answer these questions, we have selected three fisheries for examination. As indicated in the introduction, there are many factors that influence the trends in the productivity of fishermen. Probably, there are two important opposing forces. First, fishermen attempt to improve their technology, training, and experience so that their capability to catch fish will be enhanced. This tends to raise productivity. Second, the fishermen, unlike their counterparts in agriculture, are characterized by finite limitations to production. The buildup of aggregate fishing effort (i.e., vessels, gear and fishermen) tends to lower the productivity (catch per unit of effort) of those fishing the resource because more people share a fixed pie. This is a paradoxical result in that improvements in technology increase gear efficiency but also increase effective fishing effort, which in turn depresses the catch per unit of effort. Unless the level of effective fishing effort is controlled (e.g., through limited entry and not merely making gear less efficient or maintaining constant gear efficiency), the fishermen will remain on a constant treadmill attempting to balance changes in technology against the finite productivity of the resource. This is why fishery management may be one of the more important solutions to the problem. In addition there are other factors that influence labor productivity in the fisheries such as changes in the environment and institutional changes (e.g., gear regulations).

In an attempt to quantify the influence of these important factors on labor productivity, for each fishery we computed the statistical relation between annual landings per fisherman and the following factors:

1. Aggregate fishing effort
2. Fishing effort per fisherman
3. Secular time trend
4. Environmental factors
5. Institutional or regulatory changes.

It is hypothesized that increases in *aggregate* fishing will depress productivity; increases in fishing effort per worker (e.g., traps fished per fisherman, standard days fished per fisherman, or other gear used per fisherman) will increase productivity; a secular time trend represents all other factors such as changes in technology that may raise productivity; environmental change may either raise or lower productivity depending on individual factors; and regulatory changes will hopefully raise productivity.

Eastern Tropical Pacific Yellowfin and Skipjack Tuna

The fishery for tropical tunas in the eastern Pacific Ocean developed shortly after the turn of the century. The degree of exploitation increased steadily as the U.S. fleet, which lands the major portion of the catch, grew, and as the fleets of Latin America and Japan developed. Prior to 1959, the catch of yellowfin and skipjack tunas from the eastern tropical Pacific Ocean was taken by bait fishing vessels that use live bait and pole. After 1959, many fishermen converted their bait vessels to purse seiners

which have subsequently proved to be more efficient fishing vessels. Over the 1935-69 period, annual landings per tuna fisherman showed an upward time trend, growing at a rate of 2.1% per year.[13]

To analyze the growth in labor productivity in the eastern tropical Pacific tuna fishery, we specified the following explanatory variables: fishing effort, or the aggregate number of standard fishing days; fishing effort per worker (i.e., standard units of fishing effort expended per worker); secular trend variable; crew size; and a variable to reflect any residual increase in labor productivity because of the switch from bait fishing to purse seining.[14] As expected, the statistical analysis revealed that the buildup in fishing effort displayed a negative impact on labor productivity; fishing effort per worker exhibited a positive influence on labor productivity; and the other factors were not statistically important. The Inter-American Tropical Tuna Commission apparently did a good job in adjusting its effort series for the switch in technology over the 1960-67 period. Therefore, it must be concluded that the switch in technology is primarily reflected in the effort-per-worker variable. A look at the effort-per-worker series reveals that it increased from approximately 13 to 20 standard units of effort per worker from 1959 to 1960. Prior to 1959, the standard unit of fishing effort per worker increased gradually, owing presumably to more efficient use of labor in searching and catching tuna. Although fishing effort increased appreciably over the period, its negative effect was greatly offset by increases in effort per fisherman, resulting in an annual growth rate of 2.1% over 1935-69. The actual and computed (using a statistical equation) yellowfin landings per fisherman are shown in Figure 3.

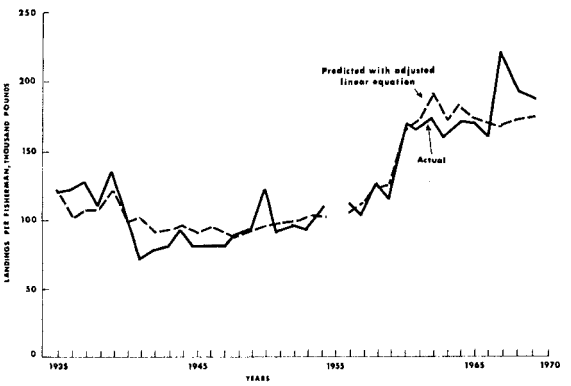

FIGURE 3.—Observed and predicted labor productivity (annual landings per fisherman) for the eastern tropical Pacific tuna fishery, 1935-54 and 1956-69. Estimating equation: $Q/L = -50615 - 2.524E + 7406E/L + 13501L/K$. Variables: E = effort in fishing days; E/L = effort per fisherman in days; L/K = crew size. R^2 = 0.82; D-W = 1.22; t values—E = 2.81; E/L = 8.04; L/K = 1.76. Annual compound rate of growth = 2.1%. Data source: Inter-American Tropical Tuna Commission.

Pacific Halibut

Early commercial fishing for Pacific halibut is considered to have commenced in 1888 when three sailing vessels from the New England States started to fish Cape Flattery on the northwest coast of Washington Territory. The rapid development of the Pacific halibut fishery did not occur until the 1920's. Initially, the fishery for the larger vessels was conducted over 12 mo of the year. Because of the possibility of overfishing, the season was legally restricted by a 3-mo winter closure in 1924. Since then the season has been regulated by the International Pacific Halibut Commission (IPHC). The fishery is presently carried on by a mixture of Canadian and U.S. longline vessels.

Unlike other fisheries, an analysis of changes in labor productivity is complicated by institutional factors (i.e., control by IPHC of gear and length of season) as well as economic and biological forces. Considering the entire fishery, it is hypothesized that annual labor productivity is heavily influenced by the following factors:

1. Length of fishing season
2. Aggregate fishing effort
3. Fishing effort per worker
4. Crew size on halibut vessels
5. Secular time trend.

In the Pacific halibut fishery, we used average landings per man-day at sea as a measure of

[13] Catch quotas of yellowfin tuna were not a factor in productivity until 1969.

[14] The number of fishermen employed is a series which was estimated by Bruno G. Noetzel of the Economic Research Division with the help of material published in various years of the Annual Report of the Inter-American Tropical Tuna Commission.

labor productivity.[15] Over the 1927-68 period, landings per fisherman-day increased by 2.5% a year. The use of landings per fisherman-day eliminates the influence of shorter seasons due to regulations. According to the IPHC, an adjustment has already been made to the effort series to include improvement in technology. Therefore, the time trend will reflect any residual influence of secular improvement in labor productivity not specifically measured as part of the effort series. In addition, since the skates series[16] is really a skates-per-day series, we can create a fishing-effort-per-worker series. This would measure the amount of fishing effort exerted per worker and should have a positive influence on labor productivity, holding other factors constant. The statistical results reveal that both fishing effort and gear used per worker are statistically important determinants of productivity and exhibit the hypothesized sign. Crew size and the time trend were not statistically important. Figure 4 shows the actual and computed annual landings per fisherman-day in the Pacific halibut fishery.

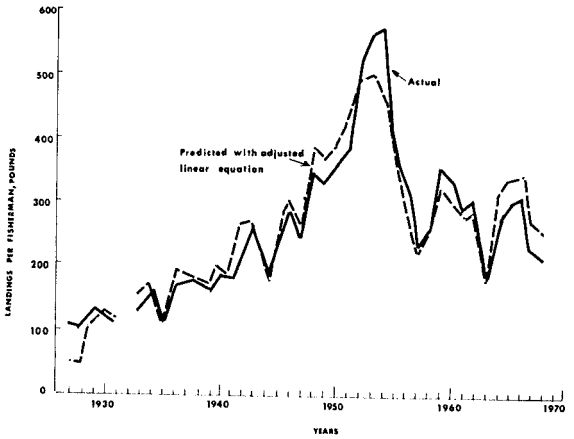

FIGURE 4.--Observed and predicted labor productivity (landings per fisherman *day*) for the Pacific halibut fishery, 1927-31 and 1933-68.
Estimating equation: $Q/(L \times S) = 50.654 - 0.254(E_2 + E_3) + 167.161\ (E_2' + E_3')/(L \times S) + 2.112\ T$. Variables: $(E_2 + E_3)$ = total effort in number of skates; $(E_2' + E_3')/(L \times S)$ = U.S. effort per fisherman day in number of skates; T = secular trend. $R^2 = 0.91$; D-W = 0.66; t values—$(E_2 + E_3) = 4.41$; $(E_2' + E_3')/(L \times S) = 12.71$; $T = 2.99$. Annual compound rate of growth = +2.5%. Data source: International Pacific Halibut Commission.

The Inshore American Lobster Fishery

The inshore American lobster fishery is largely based upon fishing with wooden traps or pots; most lobsters are caught off the coast of Maine. Based upon previous studies such as that done by Dow (1961), it was hypothesized that changes in lobster productivity are due to the following factors:

1. Total number of traps fished per annum
2. Traps fished per fisherman
3. Crew size
4. Mean annual seawater temperature, Boothbay Harbor, Maine
5. Secular time trend.

According to our statistical analysis, the secular decline in seawater temperature and increase in aggregate fishing effort produced a decided negative effect on labor productivity. The computed and actual labor productivities are shown in Figure 5. Holding all other factors constant, the *increase* in fishing effort and secular *decline* in seawater temperature lowered annual landings per fisherman. However, increases in fishing effort per fisherman and the secular trend offset the negative factors, thereby producing a negligible downward trend in lobsterman productivity. In conclusion, despite drastic changes in fishing effort and seawater temperature in the inshore American lobster fishery, labor productivity did not change appreciably over the 1950-69 period.

MAJOR FINDINGS

1. Of the 17 fisheries studied, 11 exhibited positive time trends in output (landings) per fisherman. Based upon available data, therefore, it is quite apparent that many sectors of the fishing industry experienced substantial increases

[15] This variable was formed by dividing the actual annual halibut catch by an estimate of the number of man-days expended in producing that catch. The estimate was derived by multiplying the halibut employment by the average number of days in a halibut season per annum.

[16] In Pacific halibut, fishing pressure is measured in terms of a skate of setline gear. "The groundline in a skate of gear is usually 250 to 300 fathoms long. Short lines called gangions are attached to the groundline at regular intervals and each gangion carries a hook." (Skud, 1972, p. 5).

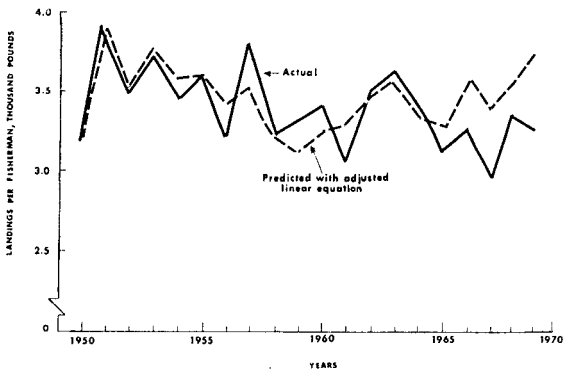

FIGURE 5.—Observed and predicted labor productivity (annual landings per fisherman) for the inshore American lobster fishery, 1950-69. Estimating equation: $Q/L = -1290 - 0.003\ E + 16.886\ E/L - 2840 L/K + 158.435°\ F + 76.930T$. Variables: E = number of traps fished; E/L = traps fished per fisherman; L/K = crew size; $°F$ = seawater temperature; T = secular trend. $R^2 = 0.69$; D-W = 2.20; t values—$E = 2.15$; $E/L = 1.73$; $L/K = 1.60$; $°F = 2.99$; $T = 1.85$. Annual compound rate of growth = -0.5%. Data source: Fishery Statistics of the United States.

in labor productivity over the 1950-69 period. Also, the annual fluctuation of labor productivity varied significantly among the fisheries from the Gulf of Mexico blue crab to the North Atlantic groundfish fisheries.

2. The construction of a productivity index for *all* fisheries indicated that, for U.S. fisheries as a whole, labor productivity increased by approximately 2.5% per year over 1950-69. The growth rate slackened, however, in recent periods.

3. Of great importance, labor productivity in the U.S. fishing sector grew at a lower rate (i.e., 2.5%) than the entire U.S. economy. However, it was significantly below levels of labor productivity advances in poultry (9.8%) and meat (3.8%), which are fish's chief competitors for the consumer's protein dollar. Preliminary international comparisons revealed that U.S. advances have not been keeping pace with labor productivity advances in other countries for the groundfish and menhaden fisheries.

4. In our detailed study of three selected fisheries, it was generally found that two forces were at work: (a) increasing pressure on the resource base and (b) attempts to increase the fishing effort per worker. We were successful in isolating the quantitative effect of each factor. Generally, it was found that increases in fishing effort per worker offset the negative impact of rising aggregate fishing effort on the resource, thereby producing a rise in output per fisherman over the period of analysis. We were also quite successful in identifying the quantitative impact of such other productivity determinants as environmental, technological, and regulatory factors. The productivity function developed to explain changes in output per fisherman were quite successful in explaining the trend in the actual data.

ACKNOWLEDGMENT

We are greatly indebted to Fred Olson of the Economic Research Division for his helpful comments and suggestions dealing with the comparisons between fishing and agricultural productivity made in this article.

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APPENDIX

Employment Figures in the U. S. Fishing Industry

The employment data utilized are from "Fishery Statistics of the United States" compiled by the Division of Statistics and Market News, National Marine Fisheries Service. The numbers of fishermen employed separated by the type of fishing craft they work. The number of fishermen on vessels are gathered by field personnel

through interviews, while fishermen on boats (craft of less than 5 net tons) are obtained from State conservation agencies through licensing and by contract with firms purchasing fish or shellfish from fishermen.

Except for problems of duplication brought about by fishermen and fishing craft shifting from one fishery to another and from one region to another, the Division of Statistics and Market News report data on total numbers are very reliable. Problems arise when one is interested in the time spent in fishing by fishermen and their craft. The number of hours, days, weeks, or months worked is not reported. Most fisheries are highly seasonal, lasting as little as several weeks, while others are year around, although they may have seasonal peaks.

Except for Pacific halibut, the number of fishermen is the total number engaged in fishing regardless of the fishing craft employed, and length of employment. In most areas, fishermen not on vessels have been divided into regular and casual. Regular fishermen are defined as those who receive more than one-half their annual income from fishing, whereas casual are those who receive less than one-half their earnings from fishing. It has not been possible to separate regular from casual fishermen on the Pacific coast. When information on casual or part-time fishermen was available, the ratio of part-time to full-time fishermen was tested by including it as an independent variable in "explaining" changes in labor productivity. The variable was significant in only two fisheries, indicating the higher percent of part-time fishermen tended to lower annual landings per fishermen.

Therefore, although the employment figures are somewhat less than optimal and the reader should be warned against many of these data problems, the rate of growth in labor productivity published in this article is probably fairly accurate. For a further discussion of these problems, the reader may write the Economic Research Division, National Marine Fisheries Service, NOAA, U.S. Department of Commerce, Washington, D.C. 20235 for a draft manuscript entitled "The Measurement and Analysis of Labor Productivity Changes in United States Fisheries."

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EFFECT OF p,p′-DDT ON DEVELOPMENTAL STABILITY OF PECTORAL FIN RAYS IN THE GRUNION, *LEURESTHES TENUIS*

DAVID W. VALENTINE[1] AND MICHAEL SOULÉ[2]

ABSTRACT

Experiments are described that test the validity and utility of using bilateral asymmetry for the early detection of environmental deterioration. The first experiment, using a continuously flowing water system, was designed to test the effects of a ubiquitous pollutant, p,p′-DDT, on the pectoral fin ray asymmetry of grunion, *Leuresthes tenuis*, fry. Toxicant concentrations ranged from a low of 0.001 to a high of 500 parts per billion. The two highest p,p′-DDT concentrations, 100 and 500 parts per billion, proved lethal to grunion fry. For the other concentrations, increases in pectoral fin ray asymmetry with increasing toxicant concentration were observed. Increases in asymmetry were statistically significant.

The second experiment, which utilized a recirculating static water system, was designed to determine inherent differences in the level of pectoral ray fin asymmetry in fish from different localities. Results for grunion fry paralleled previously published results for adult grunion. Grunion from the relatively polluted southern California region had higher asymmetry levels than did those from Baja California. The significance of these results as they relate to the general question of asymmetry as a statistical indicator of environmental stress is discussed.

Asymmetry of bilateral characters has been proposed as a morphological measure of environmental stress in fish populations (Valentine, Soulé, and Samollow, 1973). The theory underlying such an analysis is that various environmental stresses may reduce the efficiency of developmental homeostatic mechanisms, thus leading to an average increase in the within-individual variation of morphological structures (Adams and Niswander, 1967). An asymmetry index, then, might provide a relative estimate of the physiological stress to which a population is being subjected.

Data from three wild-caught fish species supporting this hypothesis have previously been presented (Valentine, Soulé, and Samollow, 1973). We now present experimental results supporting the theory.

METHODS AND MATERIALS

Grunion, *Leuresthes tenuis*, were chosen as our experimental organism. Grunion are small, rapidly maturing, marine atherinids endemic to the Californias. They possess many features which make them attractive as a laboratory organism. Grunion spawn biweekly on sandy beaches during the high tides from late February or early March through August or September, and wild-spawned eggs may be easily collected by digging in wet sand after such a spawning run. The eggs mature into fry in about 10 days (Walker, 1952). Fry are large and easily maintained in the laboratory.

The approximate straight-line distances in miles to the localities mentioned in this paper from Point Fermin, the prominent point located adjacent to the entrance of the Los Angeles Harbor, are Belmont Shore, 9; Del Mar, 87; La Jolla Shores, 91; San Diego, 101; and Bahia San Quintin, 270. All of these localities are south of Point Fermin.

The toxicant chosen was p,p′-DDT(1,1,1-trichloro-2,2-bis(p-chlorophenyl) ethane), the metabolic products of which are known to be ubiquitous in the world ecosystem (Risebrough, Hugget, Griffin, and Goldberg, 1968). Such compounds are found in fairly high concentrations in marine organisms from California waters

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Manuscript accepted May 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

(Risebrough et al., 1967; Anas and Wilson, 1970; Wolman and Wilson, 1970; Burnett, 1971; Shaw, 1971, 1972; Castle and Woods, 1972; Munson, 1972; Risebrough, Menzel, Martin, and Olcott[3]).

Two types of apparatus were used: a flowing water system and a static water system. The flowing water apparatus was used for experiments in which fish were subjected to different toxicant concentrations. Flowing water mitigates differential toxicant uptake in experimental aquaria where unequal numbers of organisms are present. The static water apparatus was used to examine differences in congenital (untreated) asymmetry in populations; it employed filters to remove metabolic by-products.

Flowing Water Experiments

The experimental apparatus used consisted of 10 pairs of 6-liter, solid, molded, all-glass aquaria. One pair of aquaria was used as a control, the other nine pairs had the following p,p′-DDT concentrations: 0.001, 0.01, 0.1, 0.4, 0.7, 1, 10, 100, and 500 ppb (parts per billion). Water was gravity-fed from an 18-liter seamless all-glass reservoir tank to a pair of aquaria, thus ensuring that each experimental pair received the same quantity of toxicant. Water levels in the aquaria were maintained at 4 liters by individual all-glass, air-lift water pumps, each pump having the capacity to remove more water from the aquaria than was entering from the reservoir. Aquaria were covered with a ¼-inch plastic cover, and air was removed by vacuum (discharged to the outside of the building) to prevent contamination between tanks. Waste water from each tank was discharged into a central collecting tube and deposited into a sealed drain. The water flow to each tank was such that its water was completely replaced daily.

To obtain the desired toxicant concentrations, as mentioned above, standard solutions of p,p′-DDT in pesticide quality acetone were prepared. The quantity of p,p′-DDT in each standard solution was such that when 100 μl of acetone was dissolved in 18 liters of seawater (the size of our reservoir tanks), the concentration of p,p′-DDT in each reservoir tank was brought to one of the desired experimental concentrations. Filtered seawater was used for these experiments (obtained from the Scripps Institution of Oceanography Aquarium supply).

Grunion eggs for this experiment were collected from Belmont Shore. The eggs were obtained by digging in the sand the morning after a major grunion run. Clutches of eggs were placed in damp sand for an incubation period of 10 days. Eggs were hatched by placing handfuls of egg-bearing sand in seawater and agitating for a short period of time.

The flowing water experiments were begun with two control tanks and two replicate tanks for each treatment. Each tank initially contained approximately 400 fry. Thirty-eight days after hatching (48 days after being spawned), fish in one of the control tanks and one each of the replicate treatment tanks were killed. Fifty-one days after hatching (61 days after being spawned), the remaining fish were killed.

Static Water Experiments

The static water experiments consisted of raising grunion fry from different localities in continuously filtered recirculating seawater. Seawater in these tanks was changed weekly. Approximately 400 fry were used from each of three localities, Belmont Shore, Del Mar, and Bahia San Quintin, 200 fry being placed in each of two replicate tanks. Collection of eggs, hatching, and experiment termination periods were identical to those previously described.

All grunion were fed several times weekly on a diet consisting of newly hatched brine shrimp nauplii. Dead brine shrimp were removed from all tanks daily. Water temperature was ambient (ca. 20°C). No attempt was made to adhere to a light-dark cycle.

Analyses

Upon termination of each experiment, live

[3] Risebrough, R. W., D. B. Menzel, D. J. Martin, and H. S. Olcott. 1970. DDT residues in Pacific marine fish. Unpubl. manuscr., 32 p. Bodega Bay Mar. Lab., Bodega Bay, CA 94923.

specimens were placed in a 10% Formalin[4] solution. The fish died with their pectoral fins spread. After a minimum of 24 h in the fixative, specimens were rinsed in fresh water and stained for several hours in a 5% KOH-alizarin red solution. Pectoral fin rays were scored using a binocular dissecting microscope. The standard length of each specimen was determined by placing individuals on a flat plastic ruler.

We have chosen to use the variance, V_a, of the right (R) minus left (L) values to quantify the amount of asymmetry. This statistic is simply $\Sigma(d - \bar{d})^2/N - 1$, where d is an individual's asymmetry (right minus left value), d is the mean of the asymmetry distribution, and N is the sample size. In our previous paper we used a similar statistic, the squared coefficient of asymmetry variation,

$$CV_a^2 = (s_d \times 100/\bar{x}_{R+L})^2,$$

where the scale correction, $\bar{x}_{R+L}$, is the mean value of the character itself. In contrast to the earlier study, we found that the amount of asymmetry was uncorrelated with the mean character state, probably because the fins of the grunion in this study were still developing. Even though smaller grunion fry had fewer fin rays, they were not less asymmetrical in an absolute sense.

The use of CV_a^2 would, in fact, give misleading results. For example, examination of Table 1 will show that fry in untreated tanks have pectoral fin ray means varying from a low of 13.491 (Control) to a high of 23.220 (Del Mar). The V_a values are 0.554 and 0.596, respectively. The corresponding CV_a^2 values are 30.5 and 11.0.

RESULTS

One-half of the replicates were killed at 38 days after hatching because we were uncertain how long the fry would live. The remaining replicates were terminated 51 days after hatching. This latter time period was chosen because examination of grunion fry from Bahia San Quintin at that age (this experiment was started 2 wk before the others) indicated that the number of pectoral fin rays was near the same mean as was found in wild adults. Mortality, due to an unknown cause, was also reducing the numbers of fry in some tanks. The 38-day experiments were terminated too early to yield useful data as many fish had not yet begun to develop ossified pectoral fin rays.

Grunion fry receiving the largest dose of p,p'-DDT, 500 ppb, began showing signs of neuromuscular dysfunction the day after the experi-

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

TABLE 1.—Grunion statistical information.

Treatment	N	Mean length ± standard error	Pectoral fin rays: Mean count (right + left) ± standard error	Pectoral fin rays: [1]V_a
		Static water experiments		
Bahia San Quintin	75	13.811 ± 0.084	22.800 ± 0.332	0.132
Del Mar	82	14.734 ± 0.096	23.220 ± 0.267	0.596
Belmont Shore	79	12.457 ± 0.099	16.684 ± 0.296	0.590
		Flowing water experiments		
Control[2]	53	11.728 ± 0.122	13.491 ± 0.557	0.554
0.001 ppb DDT	66	12.625 ± 0.105	20.303 ± 0.381	0.519
0.01 ppb DDT	7	13.486 ± 0.531	22.714 ± 1.266	0.576
0.1 ppb DDT	64	12.358 ± 0.114	19.031 ± 0.442	1.499
0.4 ppb DDT	65	12.602 ± 0.127	20.154 ± 0.473	0.898
0.7 ppb DDT	78	12.096 ± 0.088	17.679 ± 0.384	0.918
1.0 ppb DDT	51	11.402 ± 0.137	11.409 ± 0.737	2.401
10.0 ppb DDT	65	12.409 ± 0.139	18.985 ± 0.606	2.902

[1] Asymmetry variance.
[2] Control for the flowing water experiments.

ment began. Fry began swimming erratically, moving jerkily and, unlike untreated fry, swam on or near the bottom of the tank, sometimes upside down. Within a week all fry died. After 1 wk, fry in the 100-ppb treatment tanks began showing similar signs. Mortality reached 100% after 2 wk.

Asymmetry data are presented in Table 1. Grunion from Bahia San Quintin have the lowest variance of all groups examined. Fish from Del Mar and Belmont Shore, as well as the Control 0.001 and 0.01 fish, have intermediate variances (the 0.01-ppb sample should perhaps be eliminated because of its small size). Slightly greater variances are found in the 0.1-, 0.4-, and 0.7-ppb treatments. Finally, the 1- and 10-ppb treatment fish have the highest variances. It should also be pointed out that while the progression of asymmetry variances for p,p′-DDT-treated fish in the flowing water experiments is not perfect, the trend is statistically significant. Applying the Tau coefficient (Sokal and Rohlf, 1969) to these data (Control through 10-ppb treatment) yields $0.05 > P > 0.02$.

Comparing the V_a values for fry from Belmont Shore and Bahia San Quintin with the V_a values for adult fish (from data presented by Valentine, Soulé and Samollow, 1973) indicates that the ratio of asymmetry for adults is nearly the same as it is for fry (Table 2).

TABLE 2.—Comparison of pectoral fin ray V_a values for experimental and wild-caught grunion.

Locality	Wild adults			Experimental fry (untreated)		
	Date	N	V_a	Date	N	V_a
Bahia San Quintin	1970	57	0.070	1972	75	0.132
Belmont Shore	1969-70	27	0.286	1972	79	0.590

DISCUSSION

Egg and Adult DDT Burdens

We have measured the chlorinated hydrocarbon body burdens of several wild-caught grunion. These data will be published in a later paper and are here offered only for comparative purposes. Our small sample suggests that Belmont Shore grunion contain almost twice as much DDT as do La Jolla Shores grunion: Belmont Shore females 2.45 ppm ± 0.97, $N = 5$; La Jolla Shores females 1.40 ± 0.77, $N = 2$ (values on a whole body, wet weight basis, and include all isomers and metabolic products). DDT values reported here for Belmont Shore fish were obtained from specimens caught during the first grunion run of the season, whereas the experimental eggs were collected almost 6 wk later, from the third run.

Circumstantial evidence supports the hypothesis that eggs spawned early in the season have relatively high levels of DDT. Walker (1952) states that older fish spawn first. If larger fish have higher body burdens of DDT than smaller fish, then eggs spawned by large fish might have more DDT. Alternatively, if the amount of DDT deposited in eggs is a constant proportion of the amount of DDT in the female body, then the first spawn would contain more DDT in absolute terms than the later spawns. We lay some stress on these possibilities because of our enigmatic observation that eggs from the first Belmont Shore run all failed to hatch, dying at an advanced stage of development.

If DDT increases asymmetry, then the low V_a values for grunion fry from Bahia San Quintin might be attributed to low adult and egg DDT burdens. Although we have no data on pesticides concentrations in adult grunion from Bahia San Quintin, we have gathered such data in barred sand bass, *Paralabrax nebulifer* (pertinent life history data for this species are given in Valentine, Soulé, and Samollow, 1973). DDT concentrations in barred sand bass from Bahia San Quintin are 0.199 ± 0.038 ppm (N = 16), from San Diego, 2.150 ± 0.184 ppm (N= 28), a difference of roughly an order of magnitude.

DDT and Asymmetry

In our earlier report we showed that adult grunion from Belmont Shore were 4.08 times as asymmetrical as San Quintin fish. In the present study, the ratio of asymmetry variances in untreated fry is almost the same, 4.46. This consistency may be more than coincidence. This result and our experimental data support our hypothesis based on data from wild-caught fish that environmental stress may produce statistically detectable changes in asymmetry (Valentine, Soulé, and Samollow, 1973). Perhaps the most important result is that extremely low concentrations of DDT (< 1 ppb) cause a very significant deterioration in the symmetry of fin rays. When it is noted that in all probability the control fry from Belmont Shore were already carrying a stressful load of DDT, the significance of the results is enhanced.

Our rationale for utilizing p,p'-DDT as a stressant was that it (and its metabolic products) are known to occur in high concentrations in southern California marine organisms (Burnett, 1971; Castle and Woods, 1972; Duke and Wilson, 1971; Munson, 1972; Risebrough et al., 1967). The White's Point outfall, situated about a mile north of Point Fermin, was shown to be releasing effluent containing DDT approaching 100 ppb in late 1970, and also similar quantities of polychlorinated biphenyls (Schmidt, Risebrough, and Gress, 1971). These polychlorinated biphenyls may themselves produce increases in asymmetry since they have properties similar to DDT (Risebrough, Reiche, Peakall, Herman, and Kirven, 1968; Gustafson, 1970; Peakall and Lincer, 1970). We would, in any case, expect to find a diversity of agents in southern California's marine waters capable of producing increases in asymmetry, among them DDT.

Grunion fry exposed to increasing levels of p,p'-DDT in water yielded results in accord with our environmental stress hypothesis (Valentine, Soulé, and Samollow, 1973). At p,p'-DDT levels greater than 0.01 ppb, asymmetry values increased. Increases in the asymmetry of bilateral structures are easily quantified and monitored. We hope other workers will test this system with other pollutants that may affect calcium metabolism. The funding situation precludes our doing so.

ACKNOWLEDGMENTS

We dedicate this paper to our colleague, E. W. Fager, a constructive and creative critic and a good friend. This research was supported by a contract from the Southern California Coastal Water Research Project (NO. 02304). The second author, Michael Soulé, was supported by National Science Foundation Grants GB-27358 and GB-8525.

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ACANTHASTER (ECHINODERMATA, ASTEROIDEA) IN THE GULF OF CALIFORNIA

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ABSTRACT

Possible invasion of the coral-rich Caribbean by eastern Pacific populations of *Acanthaster*, which might follow on construction of a sea-level Central American canal, directed our attention to *Acanthaster* in the Gulf of California. Based on the literature, field notes, and a study of tagged specimens, the distribution, density, and behavior of this little known asteroid are discussed.

The population extends through some 300 miles of the southern half of the Gulf, mainly along the western shore, and appears to be geographically isolated from eastern Pacific *Acanthaster* populations known at lower latitudes. It is sparse and, even where common, average density estimates are of the order of 1/200 m^2. Through the northern part of its range, the sea star feeds primarily on small encrusting growths of *Porites californica*, but in the most southerly regions, *Pocillopora* is a frequent prey. The change in prey preference appears to be related to the distribution of the coral species and to changes in their dominant growth forms.

During a 48-h study of nine tagged specimens, 70% of the observed activity involved feeding, 20% resting, and 10% traveling. There was no clear-cut diurnal behavior, and no tendency to aggregate or to migrate as a population.

Measurements and behavioral traits indicate that *Acanthaster ellisii* is a valid binomen for the Gulf of California. We conclude that, if there is ground for concern over transoceanic invasion, it should shift to the more southerly population.

The alarm which followed early reports (Barnes, 1966; Endean, 1969; Chesher, 1969) of the devastation of South Pacific coral reefs by the crown-of-thorns sea star, *Acanthaster planci*, appears to have subsided, although interpretation of the phenomenon is still being debated (Dana, 1970; Newman, 1970; Vine, 1970; Weber and Woodhead, 1970; Dana, Newman, and Fager, 1972). However, the events have served to highlight our ignorance of the eastern tropical Pacific representatives of the genus. Furthermore, the possible construction of a Central American sea-level canal through which eastern Pacific *Acanthaster* might gain access to the coral-rich, but *Acanthaster*-free tropical Atlantic, has raised the question of the predation-potential of the American population (Newman and Dana, in press; David Pawson, pers. comm.).

The long-standing questions surrounding the taxonomic status of *Acanthaster* in the Gulf of California and adjacent regions have been further confused by the discovery of large numbers in the Secas and Contreras Islands adjacent to the Gulf of Panamá (Glynn, 1970a, b; 1972), and it is not at present clear whether any or all of the American *Acanthaster* are assignable to *A. ellisii* (Gray, 1840), to *A. ellisii pseudoplanci* Caso, 1962, or to *A. planci* (L., 1758). However, we consider *A. ellisii* a valid binomen for the populations we have observed in the Gulf of California, and shall adhere to it for purposes of this report.

As recently as 1955, *A. ellisii* was known from less than a dozen lots, mostly of single

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Manuscript accepted March 1973
FISHERY BULLETIN: VOL. 71, NO. 4, 1973

TABLE 1.—Numbers, distribution, and feeding behavior of *Acanthaster ellisii* in the Gulf of California.

Location	Reference[1]	Stations	Date	Number of specimens	Observation: Not feeding	Observation: Feeding	Observation: Prey
B. San Carlos	1	S side, Pta. Dobles	Jan. 1966	1	No data		
Pta. Sta. Inez	1	SW side	Nov. 1966	Few	No data		
Pta. Sta. Inez	1	SW side	July 1967	Few	No data		
Pta. Sta. Inez	1	SW side	Nov. 1968	Few	No data		
Pta. Concepción	1	1 mile S of B. Concepción	Nov. 1966	Few	No data		
Pta. Concepción	1	1 mile S of B. Concepción	Nov. 1968	Few	No data		
Pta. Concepción	1	1 mile S of B. Concepción	Nov. 1970	2	0	2	*Porites*
Pto. Escondido	1	SW side, Coyote Pt.	Nov. 1966	Few	No data		
Pto. Escondido	1	SW side, Coyote Pt.	Nov. 1968	Few	No data		
Pto. Escondido	1	SW side, Coyote Pt.	Nov. 1970	5	0	5	*Porites*
I. San Ignacio	1	SE side	Mar. 1971	1	0	1	*Porites*
I. San José	2	Stn. 6, SW end	Apr. 1970	5	3	2	*Pacifigorgia* (1); *Padina* (1)
I. San José	3	Stn. 6, SW end	Oct. 1971	3	No data		
I. San Francisco	4	Stn. 4, cove on S side	Apr. 1970	12	6	6	*Porites*
I. San Francisco	3	Stn. 4, cove on S side	Oct. 1971	12	7	5	*Porites*
I. San Francisco	4	Stn. 3, SW anchorage	Apr. 1970	7	No data		
I. San Francisco	2	Stn. 1-5, S side	Apr. 1970	48	Incomplete, but:		*Porites* (30); *Pacifigorgia* (1)
I. Partida	1	Pink Cliff station	Nov. 1970	4	[2]4	[2]12	*Porites*
I. Partida	1	Pink Cliff station	Mar. 1971	9	[2]18	[2]38	*Porites* (30); *Pocillopora* (2); coralline algae (2); ? (4)
I. Partida	4	Stn. 1, SW end	Apr. 1970	1	No data		
I. Partida	3	Stn. 2	Apr. 1970	1	No data		
I. Partida	3	Stn. 2	Apr. 1972	2	2		
I. Partida[3]	2	Stn. 7, 8 SW end	Apr. 1970	16	0	16	*Porites* (14); *Psammacora* (1); *Pocillopora* (1—presumed)
I. Espíritu Santo	2	Stn. 10, in B. San Gabriel	Apr. 1970	1	0	1	*Pocillopora* (1—presumed)
I. Espíritu Santo	3	Stn. 7, N. side San Gabriel	Oct. 1971	4	0	4	*Pocillopora*
I. Espíritu Santo	3	Stn. 7, N. side San Gabriel	Apr. 1972	2	1	1	*Pocillopora*
Ens. de los Muertos	3	Stn. 8, NW side P. Arena	Apr. 1972	9	4	5	*Pocillopora* (4); *Porites* (1)
Cabo Pulmo	3	Stn. 9, seaward of inner reefs	Apr. 1972	3	2	1	*Porites*
B. Frailes	3	Stn. 10, NE side	Apr. 1972	1	0	1	*Pocillopora*

[1] 1 = Authors.
2 = Dana and Wolfson (1970).
3 = Faulkner, unpublished notes.
4 = Faulkner, cited in Dana and Wolfson (1970).
[2] Based on multiple observations of same specimens (See text and Table 3).
[3] Cited as Espíritu Santo.

specimens (Madsen, 1955). The fact that the sea star inhabits rocky subtidal substrates has made it generally unavailable to shore collectors and impossible to dredge; only with the increased use of diving techniques has it become accessible. Accordingly, the literature is sparse.

Since Madsen's review (1955), *A. ellisii* has been described and contrasted to *A. ellisii pseudoplanci* by Caso (1962), and Barham and Davies (1968) and Glynn (1972) have mentioned it. Only Dana and Wolfson (1970) have dealt with any aspects of its biology. It is apparent from recent field observations (Dana and Wolfson, 1970; D. J. Faulkner, pers. comm.; and the material to be presented here) that the scanty records reflect our poor knowledge of the invertebrate fauna of the Gulf of California, rather than the prevalence of the sea star. This paper aims at adding to our understanding of the habits and habitats of *Acanthaster* in the Gulf of California.

We present information based on three distinct types of observations: 1) Presence and absence of *A. ellisii* noted in the course of our ecological surveys in the Gulf of California between 1965 and 1968, prior to a defined interest in the species; 2) numbers of *A. ellisii* and its prey observed by us at various locations during specifically directed surveys in November 1970 and by D. J. Faulkner in 1970, 1971, and 1972; 3) studies of tagged specimens at "Pink Cliff" station, Isla Partida, in November 1970 and March 1971.

Distribution of *Acanthaster* in the Gulf of California

The early records contribute little information on distribution. According to Madsen (1955), the collection site of Gray's type specimen was simply given as South America, and the two specimens described under the name of *ellisii* by Perrier were of unknown origin. Verrill (1869) listed La Paz as the locality for his *A. ellisii*, but the reference may be to the port from which it was shipped (Squires, 1959), and it was probably collected elsewhere. Thus, prior to 1970, the only valid records for *Acanthaster* in the Gulf of California are for Puerto Escondido, where Steinbeck and Ricketts (1941) collected several specimens, and where Madsen's (1955) type specimen was taken by an Allan Hancock Expedition. Some of Caso's specimens were also collected there by an Allan Hancock Expedition in 1940 (Caso, 1962).

Table 1, showing the distribution patterns of *A. ellisii* in the Gulf of California, combines our notes, the data given by Dana and Wolfson (1970), and the information contributed by Faulkner (cited in Dana and Wolfson, 1970). The known range of the species, extending through some 300 miles along the western shore of the Gulf of California, is shown in Figure 1.

No *Acanthaster* have been reported on the eastern shores of the Gulf, and our extensive search of the three areas which appear to offer suitable environments produced only two specimens: one at Bahía San Carlos, north of Guaymas, in January 1966 (we found none there in November 1968 and November 1970); the other, after a lengthy search, at Farallon San Ignacio. This small rocky islet offshore from Topolobampo represents one of the few likely environments for the asteroid for hundreds of miles along that part of the coast. No specimens were observed at the southeast end of I. Tiburon or on the adjacent mainland at Pta. Sargento.

Within its known range, *A. ellisii* is most often found on the south sides of islands and points, or in small embayments in the lee of northerly winds and partially protected from the south (Table 1). Note from Table 2, however, that although present at adjoining locations, it is not found in the more thoroughly protected bays and coves, such as Bahía Coyote, Pichilinque, and the inner bay at Puerto Escondido. Apparently the asteroid prefers habitats with some degree of wave action, but protected from violent wave shock and strong surge.

With two exceptions, there appears to be a good degree of correspondence in the distributions of *A. ellisii* and corals. The first exception is Bahía San Gabriel, where heavy growths of *Pocillopora* and other corals occur in a reeflike formation, and where Dana and Wolfson (1970) found only one *A. ellisii* in a thorough search of some 1,500 m^2. The second is El Pulmo, where by far the most extensive stands of branching

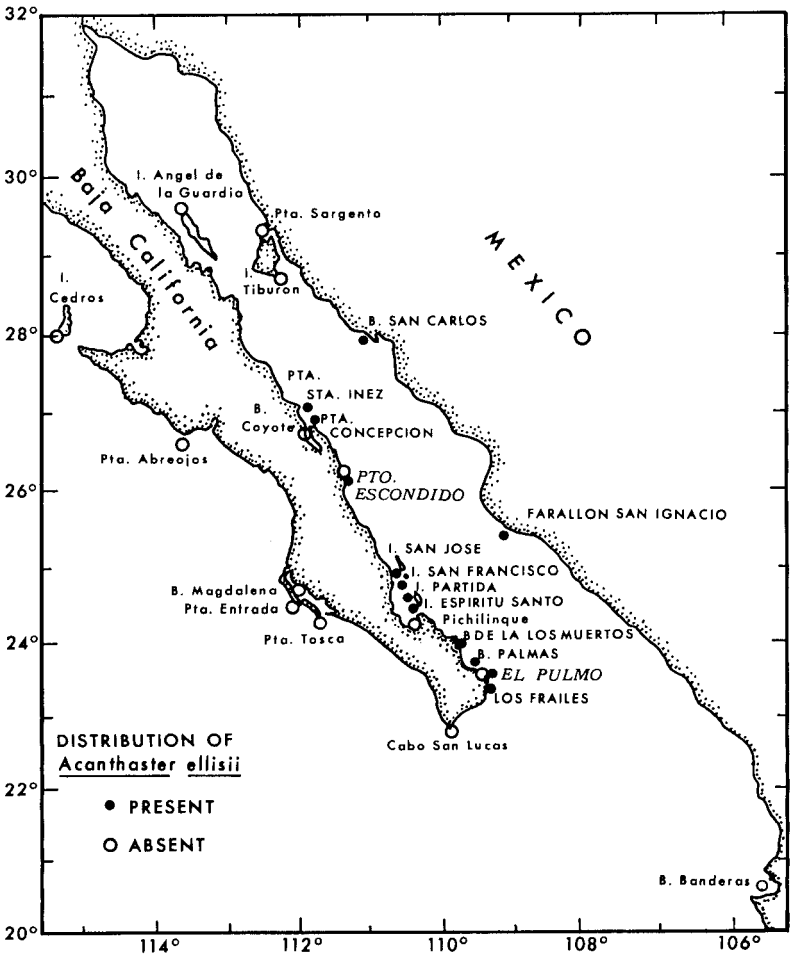

FIGURE 1.—Distribution of *Acanthaster ellisii*.

stony corals in the Gulf occur. We found no *Acanthaster* there on two visits, although we dove over large areas of the two shallower reefs and were towed behind a skiff over extensive regions of the deeper reefs. Sport divers have reported *A. ellisii* there, but the species is not easily identifiable on casual observation, and confusion with other asteroids, particularly with the similarly sized, heavy-spined, and abundant *Nidorellia armata*, is common. Faulkner's report (pers. comm.) of two specimens taken in relatively deep water outside the main reefs at El Pulmo represents an anomaly in the distribution of *A. ellisii* as otherwise observed.

Density

Except at the islands near La Paz (Islas San José, San Francisco, Partida, and Espíritu Santo, to which we shall refer as the "island complex") low densities of *A. ellisii* are suggested by the numbers in Table 1. Dana and Wolfson (1970) give 0.0045/m^2 (1/222 m^2) for those islands, and the nine specimens we found in the thoroughly searched area of approximately 2,000 m^2 at "Pink Cliff" station on Isla Partida translate to an identical average. The high density at Pto. Escondido, 0.005/m^2 (1/200 m^2), is deceptive, as we searched a preselected area where the sea stars were con-

TABLE 2.—Locations in the Gulf of California and adjacent areas where *Acanthaster ellisii* was not observed.

Location	Station	Date	Man hours underwater observation
Gulf of California			
I. Ángel de la Guardia	S. side of Arch Rock in P. Refugio	July 1967	8
I. Ángel de la Guardia	S. side of Arch Rock in P. Refugio	Nov. 1970	4
Pta. Sargento	SW side	July 1967	4
I. Tiburon	SE end	July 1967	4
B. San Carlos	S. side Pta. Dobles	Nov. 1968-Nov. 1970	16
B. Coyote	4 stations on or near I. Blanca	Nov. 1966	60
B. Coyote	4 stations on or near I. Blanca	July 1967	4
B. Escondido	Inner bay, S and E sides	Nov. 1966-Nov. 1968 Nov. 1970	8
P. Pichilinque	Bay on S. shore	Nov. 1966, Jan. 1968, Nov. 1968, Nov. 1970	50
B. Los Palmos	NW Shore	Jan. 1968	4
C. Pulmo	Lagoon and inner reef	Jan. 1968	6
C. Pulmo	Lagoon, inner and outer reefs	Mar. 1971	12
C. San Lucas	Sheppard's Rock area	Jan. 1965, Jan. 1968	20
West coast Baja California			
I. Cedros	SW end	Jan. 1965	8
Pta. Abreojos	SW end	Jan. 1965	2
B. Magdalena	NE shore	Jan. 1965	2
Pta. Entrada	Inside passage	Jan. 1965	8
Pta. Tosca	SW end	Jan. 1965	8
West coast Mexico			
Banderas Bay	5 stations E and S regions	Nov. 1968	40
Banderas Bay	1 station E region	Mar. 1971	4

centrated. The nine specimens reported by Faulkner (pers. comm.) at Ensenada de los Muertos constitute the only sizeable population known to the south of the La Paz island complex, but density figures are not available.

"PINK CLIFF" STUDY

Observations at Pink Cliff station provide an insight into the behavior of *A. ellisii*. We made preliminary observations there on four specimens in November 1970; a further study was conducted over a 48-h period in March 1971.

Study Area

The Pink Cliff study area covers about 2,000 m^2 in the northeast corner of El Cardonal Bay on the west side of Isla Partida (lat. 24°32′10″ N; long 110°23′30″W). The pink-pumice cliff extends about 3 m underwater and then curves into a wave-cut platform which interfaces at about 10 m with the sand bottom. Several large monument-like rocks with truncated tops stand isolated from the cliff. A few reeflike ledges lie farther seaward, and an extensive pile of large boulders is located near the northern edge of the platform. (Figure 2, based on underwater sketches and substrate measurements, gives a schematic picture of the area.)

Coralline algae predominate on rock and cliff faces. A rich growth of sessile organisms, dominated by sponges, tunicates, hydroids, and gorgonians, is concentrated on and near the vertical cliff and monument rocks. The upper rock surfaces and much of the platform are covered with a thin veneer of filamentous algal material. At the deepest levels, on the inshore sides of the rock pile, there is a luxuriant stand of the brown alga, *Padina*.

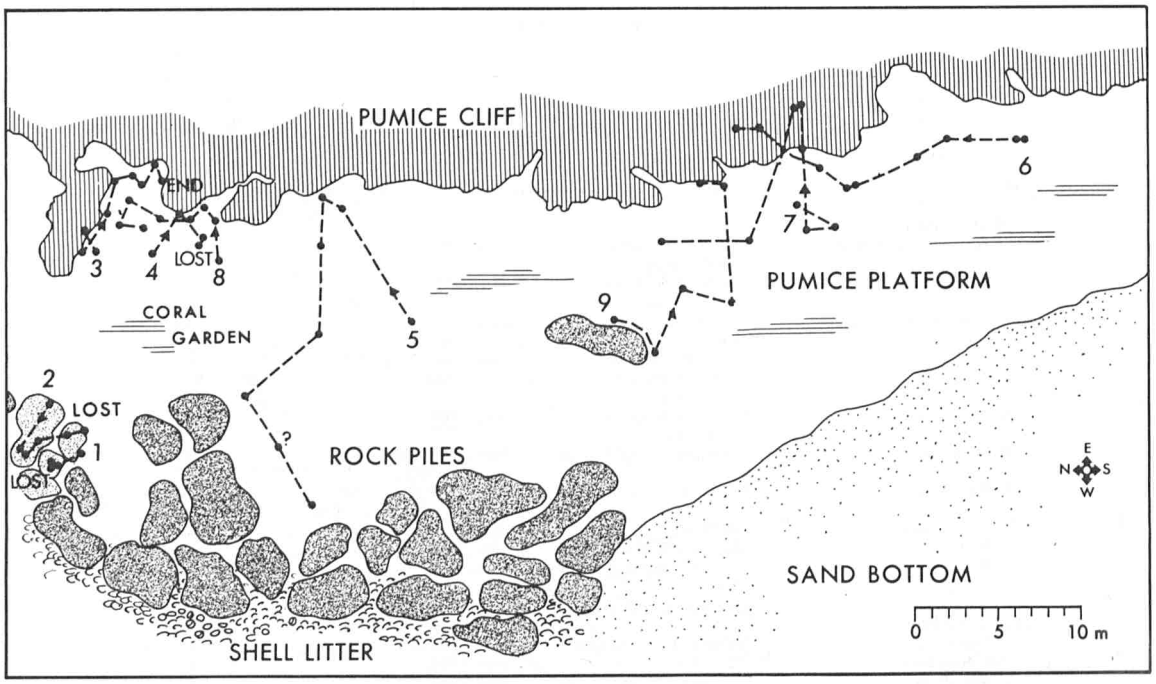

FIGURE 2.—Schematic diagram of Pink Cliff study area, Isla Partida, showing the relative positions and movements of the nine tagged *Acanthaster ellisii* during the 48-h study period. Depth of water at the interface between hard and soft bottoms is about 10 m.

Daytime underwater visibility in 1970 was about 20 m; in 1971, it varied between 6 and 15 m. Night visibility was reduced by swarms of mysids, polychaetes, and larval fishes which concentrated in the beams of our hand-held lights. Water temperatures were 27°C during the fall visit, 18°-21°C in the spring.

The Coral Fauna

Pocillopora is the conspicuous coral, although there are less than 20 large heads; the majority stand as scattered individuals in the "coral garden" near the cliff base in the northeast part of the platform. Several are inhabited by hawkfish (see Figure 3) and anomuran crabs. A few small *Pocillopora* grow on the lower vertical surfaces of the cliffs and monument rocks. Scattered small colonies of the dendrophyllid coral, *Tubastrea aurea*, are restricted to the deeply shaded sides of the monument rocks and cliff walls.

The large number of small encrusting *Porites californica* contradicts the first impression of a sparse coral fauna. In the deeper regions, these scablike coralla (see Figure 4) are about 4-5 cm in diameter and well separated from one another; with increasing height, they become progressively larger and less regular in outline, encrusting the pits and crevices, or covering small protuberances to form knobs.

The abundant *Porites* on the cliff face is so highly irregular in outline that it was impossible to distinguish individual colonies, but we attempted to count the coralla within a 0.5 m-diameter ring placed in five locations on each of two transects along the platform. Numbers increased from 50 coralla/m^2 on the seaward edge of the platform to 100 coralla/m^2 at the cliff base. In the surge shadow cast by a 3 m-high rock, and on the adjacent region of the platform which is protected from surge by the reef, there were as few as 10 coralla/m^2.

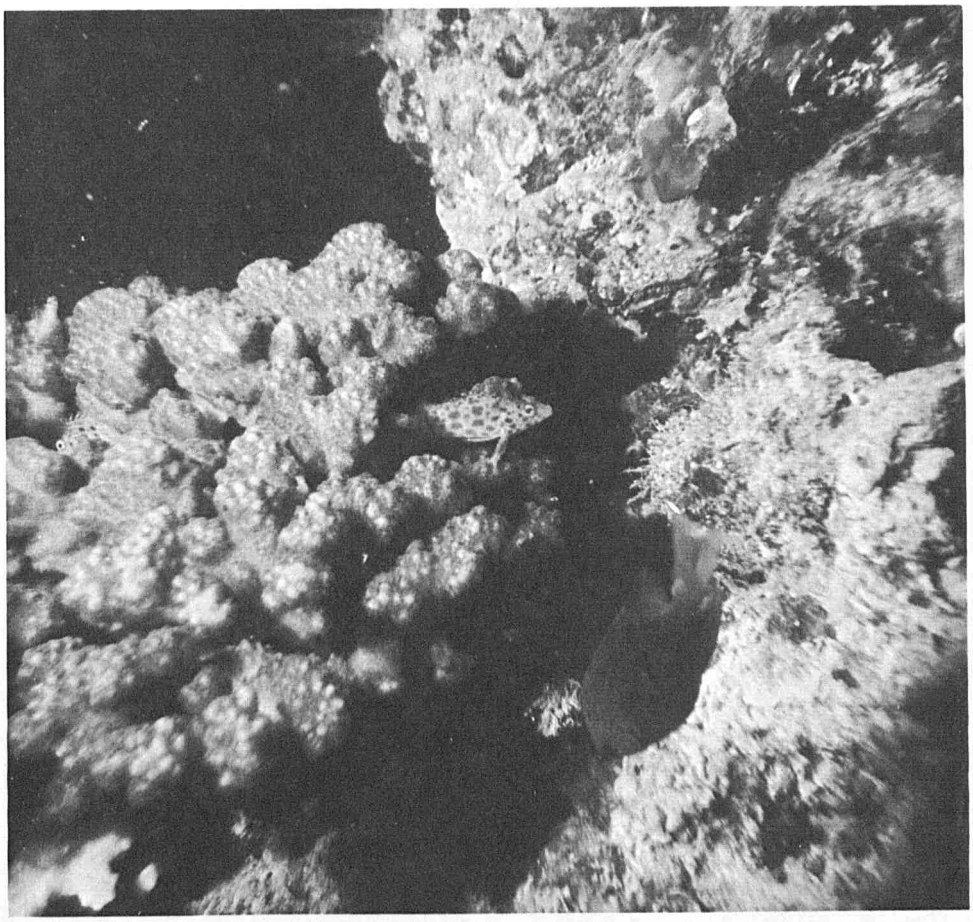

FIGURE 3.—An isolated head of *Pocillopora* sp. harboring two hawkfish (family Cirrhitidae), photographed near the base of a monument rock in the Pink Cliff study area. Only minor blemishes are evident on the distal regions of the branches.

Methods and Procedures

On 1 November 1970, we tagged four *Acanthaster ellisii* in situ by threading monofilament, to which numbered tapes were knotted, through the body wall and under the dermal ossicles with a curved upholstery needle. The operation was particularly awkward because of the necessity of wearing heavy gloves and entailed considerable manipulation of the animals, causing one specimen to react in an abnormal manner. The 16 observations made in this preliminary study are summarized in Table 1.

For the 1971 survey, the nine specimens located within the search area were tagged by simply tying numbered tapes to a ray (Figure 5). (This procedure also required great care and has additional drawbacks. If the monofilament is tied too tightly, the sea star may autotomize the insulated arm, as one of our specimens did after 40 h. Conversely, two loosely tied tags snagged and pulled free. Fortunately, they were found near animals whose characteristics corresponded to originally tagged individuals, and the tags were retied.)

The position of each specimen was marked with a short length (approximately 30 cm) of

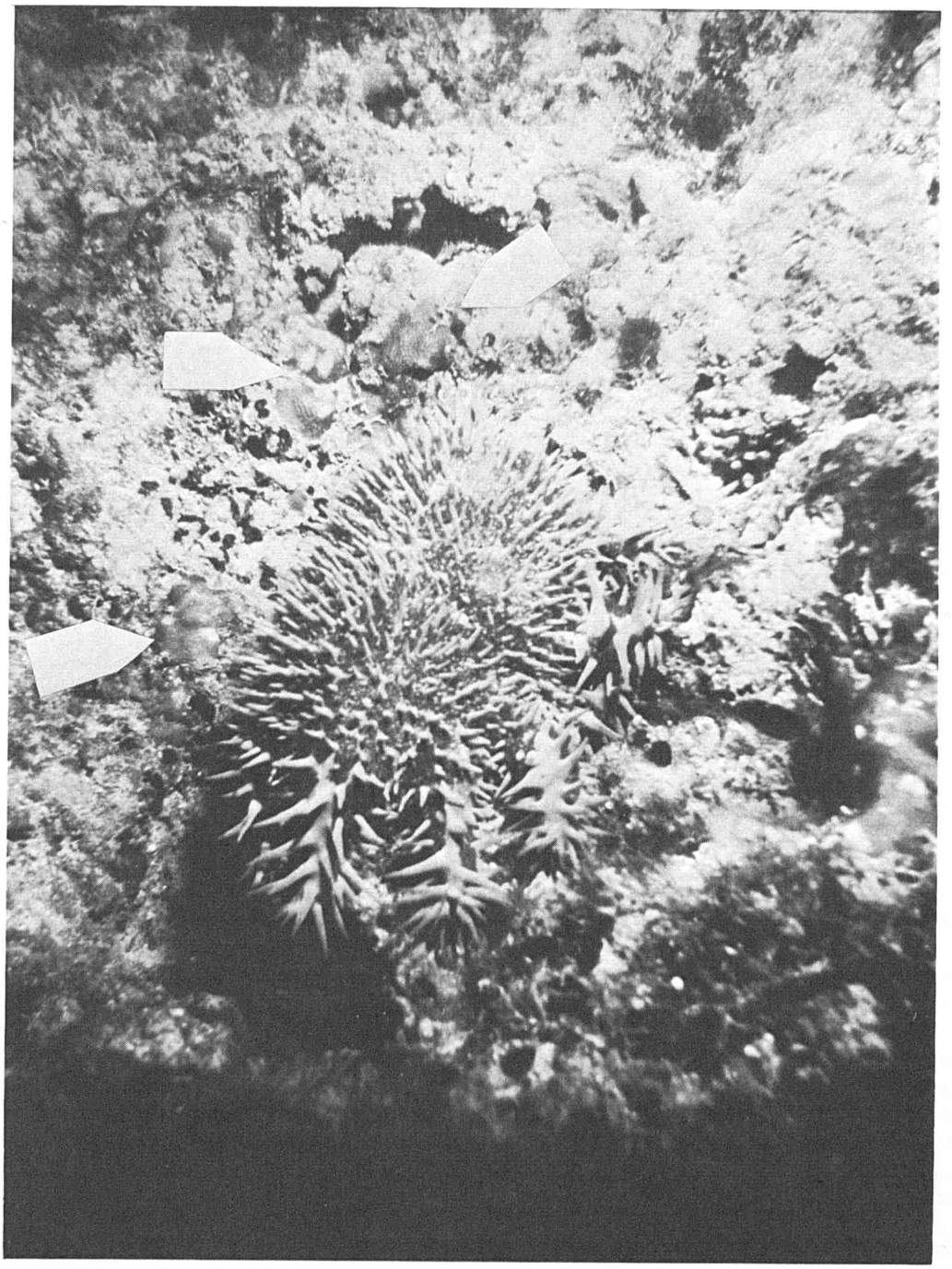

FIGURE 4.—A. *Acanthaster ellisii* in feeding posture on the cliff wall at the Pink Cliff study area. Several of the numerous small *Porites californica* encrustations are indicated by the arrows. The two small coralla in the upper left show damage more characteristic of fishes than of *Acanthaster*. B. The same specimen pulled back to expose the *Porites* nodule (indicated by the arrow) on which it was feeding.

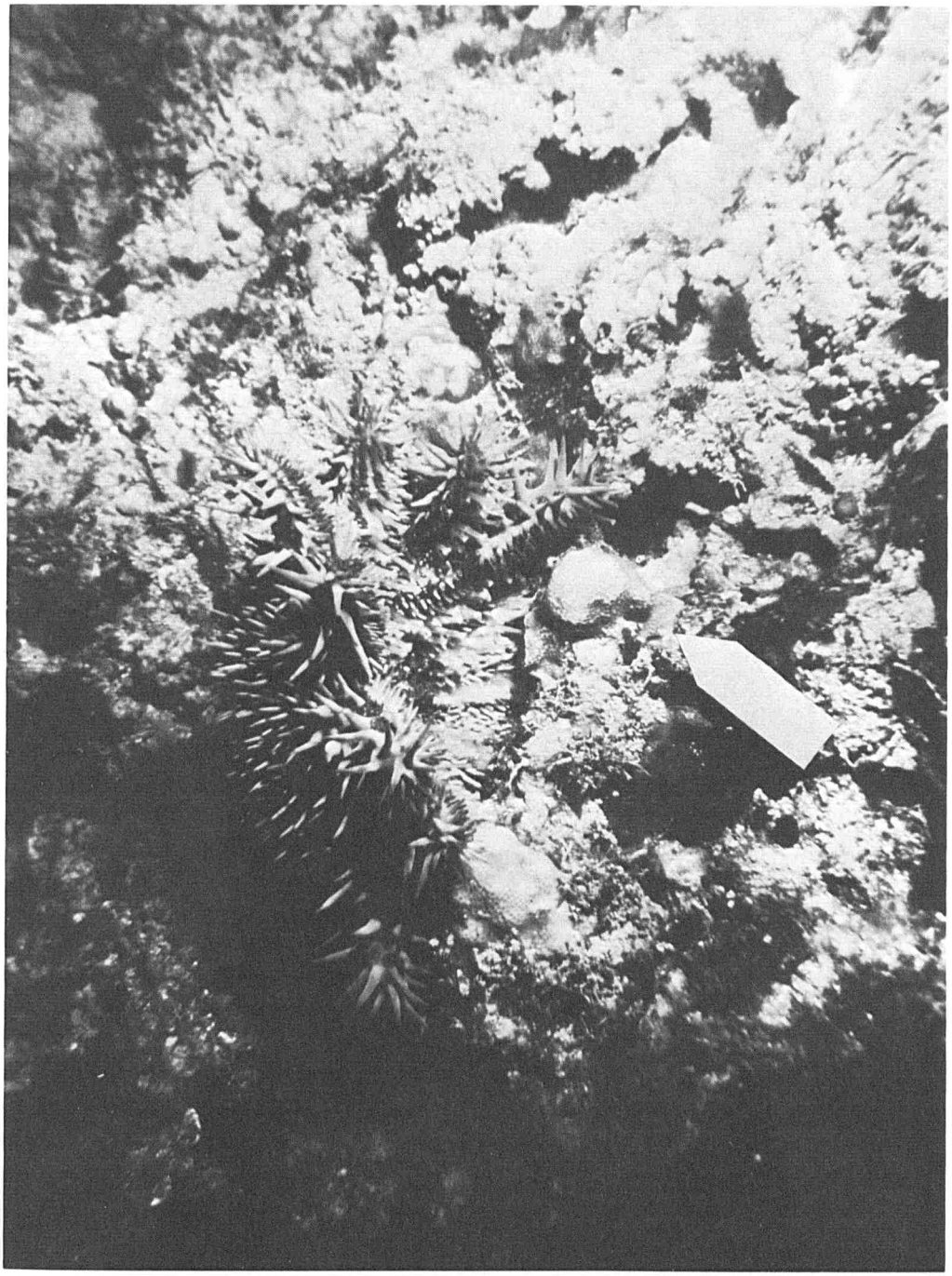

TABLE 3.—Tagging experiment, Pink Cliff station, Isla Partida, March 1971. Behavior, prey, and distances moved between observations.[1]

Specimen	0830-1130 Original location	27 March 1971								28 March 1971						29 March 1971		Total	
		Move (m)	*1* 1415-1515	Move (m)	*2* 1615-1645	Move (m)	*3* 1930-2030	Move (m)	*4* 0920-1015	Move (m)	*5* 1115-1145	Move (m)	*6* 1430-1510	Move (m)	*7* 2030-2130	Move (m)	*8* 0915-1000	Time (h)	Dist. (m)
1	Rock pile	0.6	F/?	0	F/P	0	F/P	—	—	—	—	—	—	—	—	—	—	12	0.6
2	Rock pile	3.7	F/P	0	F/P	0.5	R	1.3	F/P	0	F/P	0.7	T	—	—	—	—	29	6.2
3	Coral gardens	1.4	F/P	0.2	F/P	2.2	R	2.2	F/P	1.7	F/A	0.5	R	0.8	R	3.0	F/P	48	12.0
4	Coral gardens	3.6	F/P	2.6	F/P	0	F/P	—	—	—	—	—	—	—	—	—	—	12	6.2
5	Platform	6.6	F/P	0.5	F/?	1.9	F/P	2.9	F/P	4.5	T	(/)	(/)	6.0	R	2.2	R	48	24.0
6	Platform	0	F/PP	4.9	R	1.8	R	4.2	F/PP	0	F/PP	1.7	T	6.0	R	6.0	T	48	24.6
7	Cliff base	1.9	R	1.3	T	4.2	F/?	2.7	F/P	0	F/P	7.0	F/P	2.0	F/P	3.0	F/P	48	22.1
8	Coral gardens	2.5	F/Pc	1.0	F/P	(/)	(/)	1.0	T	2.2	R	2.4	R	1.3	F/PA	1.3	F/Pc	48	11.7
9	Reef rock	(2)			F/P	2.0	F/?	3.0	F/P	0	F/P	4.6	F/A	(/)	(/)	6.0	F/P	42	15.6
																		330	123.0

[1] F = feeding
? = undetermined
P = *Porites*
— = lost
R = resting
T = traveling
A = coralline algae
(/) = missed
Pc = *Pocillopora*
[2] Not tagged until Period 2.

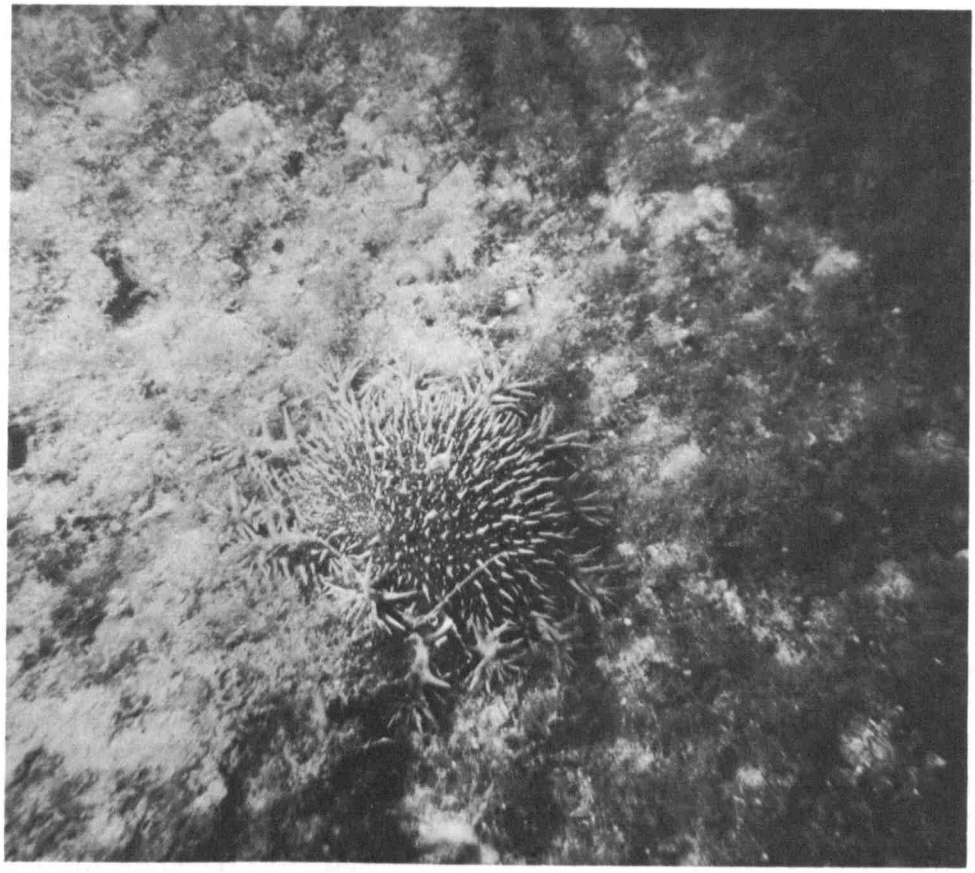

FIGURE 5.—*Acanthaster ellisii*, specimen no. 1, photographed while moving over a large rock in the Pink Cliff study area. The tag is tied to the proximal part of the arm nearest the camera.

plastic PVC (polyvinyl chloride) pipe weighted with lead strips to stand vertically. Small surface buoys equipped with life-jacket lights were anchored near each location to aid in night operations.

Observation and search periods are given in Table 3. Time on the bottom was dependent on our scuba air supply. The greatest care was taken to minimize disturbance of the animals. Specimens on the move were not touched and, to prevent interruption of their activity by stimulating the "shadow reflex" (Hyman, 1955), we tried to avoid swimming over them. The activity of animals at rest was investigated by gently lifting a part of the body with a knife blade. Distance of movement was measured with a meter stick; direction was determined by compass bearings. Following each observation, the pipes and buoy anchors were transferred to the new position.

Specimens in the open were recovered with relative ease; locating them on the rock pile or in its interstices was difficult or even impossible, especially at night. During the course of the study, we failed to recover individuals on six occasions. Three times the "lost" specimen was found on the succeeding search; we suspect that no. 1 and 2 specimens, which were last seen close to their original position (see Figure 2), had moved out of the search area.

Behavior

Table 3 summarizes the 56 observations made during the 48 h of the Pink Cliff study. In 38 instances (68%), the specimen was feeding, that is, it was immobile, hunched or puffed up (Figure 4a), with stomach everted and covering the prey. Feeding was observed in 31 of the 43 daytime observations (72%) and 7 of the 13 night observations (54%). On 12 occasions, 6 at night and 6 during the day, the asteroids were "resting," i.e., they were immobile and the stomach was within the gastric cavity. Six times the observed specimen was "traveling," moving over the substrate on tube feet, one slightly lifted arm leading (Figure 5). Traveling was only observed during the day, but the evidence is insufficient for postulating a diurnal rhythm.

Feeding

Analysis of the 38 feeding observations indicates a definite prey preference. *Porites* comprised 79% of the food (29 observations, plus one of simultaneous feeding on *Porites* and coralline algae). *Pocillopora* was fed on two times (5%) and coralline algae two times (5%). On four occasions (11%) it was impossible to determine the prey.

Specimen no. 8, which fed simultaneously on coral and alga, was also the sole predator on *Pocillopora*. Unusual behavior was also exhibited by no. 6 which, on three occasions, displayed the singular habit of feeding on two or three *Porites* colonies at once.

Movement

The sequence of behaviors observed suggests a general pattern of movement. The individual remains for one or more hours over a small *Porites* encrustation, and then moves off, usually to another corallum which may be several meters distant. A series of feeding stops is followed by a resting period, which may also last for several hours, or by several rest stops interspersed with short moves. It should be noted that, even though specimen no. 3, 5, 6, and 8 were at rest in consecutive observations separated by intervals of 3-13 h, in each case the individual had moved between the observation periods.

The specimen which reacted abnormally to the 1970 tagging operation provides some evidence for the rate at which *A. ellisii* is capable of moving: when returned to the substrate, it immediately embarked on a continuous journey, covering a distance of approximately 10 m in a little over an hour. More refined observations are necessary for estimation of rate of movement, but a rough idea can perhaps be gained from the Pink Cliff study. Dividing the total elapsed time between midpoints of the first and last observation periods (33 h) by the summed distances moved (123 m) gives an average ground coverage of 0.373 m/h. A higher figure is derived from considering the two cases (between period 2-3 and 5-6) in which the intervening intervals were approximately equal (about 3½ h), Distances covered between those periods ranged from 0 to 7.0 m and averaged 2.1 m, giving a rate of 0.6 m/h. Furthermore, average rate in the rock pile and coral gardens, where coral are most abundant, was 0.246 m/h, approximately half of that on the relatively coral-poor platform (0.464 m/h), suggesting correlation with density of the corals.

ACANTHASTER ELLISII AS PREDATOR

Crucial to an evaluation of *A. ellisii* as a potentially destructive coral predator is its foraging behavior throughout its range. North of the island complex, small crustose colonies of *Porites* are the only positively identified prey of *A. ellisii*. In the island complex, which falls in the middle of its known range, *Porites* apparently remains the major food item, with gorgonians, algae, and *Pocillopora* attaining minor importance. (It might be mentioned here that feeding by *A. ellisii* on *Pocillopora* was inferred, rather than actually observed, by Dana and Wolfson (1970).) The few observations which have been made farther to the south suggest that *Pocillopora* is more frequently fed on than *Porites*.

This apparent shift in prey preference may

reflect the distribution of corals in the Gulf of California. From an ecological standpoint, the ranges for coral genera given in the most recent treatment of the subject (Squires, 1959) can be misleading. For example, Squires shows the northern limit for extant *Pocillopora* species as a line extending across the Gulf from about the level of Santa Rosalía to Guaymas. The line is based on a single specimen of *Pocillopora robusta* (= *elegans*) collected by an Allan Hancock Expedition at Isla San Marcos (Durham and Barnard, 1952). John Garth of the Hancock Foundation informs us that the specimen was dredged in 20 fathoms south of Isla San Marcos (lat. 27°09′05″N; long. 112°04′25″W) and appears to have been taken alive. In our experience, the only common coral north of the island complex is *Porites*, and this Isla San Marcos specimen must represent an isolated outpost of *Pocillopora*. Squires' Table 1, summarizing the diminution of the hermatypic coral fauna in the northern regions of the Gulf, gives a more accurate picture of the situation as we have seen it. It seems obvious, then, that if *A. ellisii* is primarily an obligate coral feeder, its major prey through the northern part of its range must be *Porites*.

The varying growth forms of the corals may also enter into the prey preference of *A. ellisii*. In gross morphology, *Porites* is highly plastic, showing phenotypic gradation from encrusting colonies in the northern part of its range to columnar, branched, or nodular forms in the south. However, the influence of latitude is cancelled in protected situations in the lower mid-Gulf, such as Bahía Coyote and the inner bay at Puerto Escondido, and *Porites* tends to assume the dome-shaped heads and large nodular form typical of the southern type. We have never seen *A. ellisii* in these quiet-water environments.

It is noteworthy that we have never seen *A. ellisii* on large or ramose corals at any locality. The *Porites* being preyed on in all of our observations were so small that the sea stars appeared to be sitting on a coral-free substrate; only when the animal was lifted could the coral be seen and identified. Furthermore, our observations of predation on *Pocillopora* all involved feeding at substrate level. In a crude field trial, a traveling specimen immediately began to feed on a broken branch that we had placed in its path; and the three observations at Pink Cliff station (all by specimen no. 8) involved one instance of feeding on the underside of a low branch and two on broken branches. However, at the end of the study, no. 8 fed on a ramose *Pocillopora* when dropped directly on top of it, and Faulkner (pers. comm.) reports that south of La Paz, where *Pocillopora* assumes a densely packed, reeflike formation, *A. ellisii* feeds on top of the colonies. It thus appears that some factor or factors may prevent the asteroid from mounting upright, solitary corals.

Weber and Woodhead (1970) reported that fish and crabs living among the branches of *Stylopora*, a close relative of *Pocillopora*, defend that coral from attack by *A. planci*. *Pocillopora's* symbionts (Figure 3) perhaps serve a similar function.

The experimental work of Barnes, Brauer, and Jordan (1970) and Brauer, Jordan, and Barnes (1970) may explain the marked preference of *A. ellisii* for discrete, low coralla. Working with *A. planci*, these investigators demonstrated that, while the tube feet are sensitive to nematocysts, the stomachs respond positively to nematocyst-containing tissue. From these experiments, and from the observation that the sea star uses its arms and spines as much as possible when climbing coral heads, they infer that the humped feeding position of *A. planci* may serve to keep the tube feet free of the prey's stinging polyps. If *A. ellisii* responds to nematocysts in the same ways, small, isolated, crustose coralla that can be easily straddled and then covered by the stomach would constitute more acceptable prey and would be selected over larger growths.

Examination of small *Porites* fed upon by *A. ellisii* suggests that the entire colony is not necessarily destroyed; white patches, which indicate that the zooxanthellae have been digested, are left mainly on regions that protrude above the general level of the substrate. We consistently observed, however, that the entire corallum appears to be covered with a mucous film, and suggest that the extent of the damage inflicted on small *Porites* by *A. ellisii* bears further investigation.

It should be borne in mind that not all coral damage can be attributed to *A. ellisii*. The report of predation by *Pharia pyramidata* (Dana and Wolfson, 1970) is the first indication that the smaller asteroid, which occurs throughout the coral areas of the Gulf, is also a coral-feeder. And, of course, certain fishes are well known to be coral-browsers and commonly leave gouge marks on the coralla.

The amount of *Porites* available to *A. ellisii* in the preferred small form is difficult to evaluate. The vast numbers of small encrustations have, perhaps, been unappreciated by coral workers in the Gulf. Dana and Wolfson (1970) estimate approximately 3% coral coverage in their survey areas. While our attempt to count the numbers of *Porites* at Pink Cliff station does not warrant critical treatment, we estimated that the encrustations covered roughly 10% of the substrate.

The important question of how much coral is necessary to maintain the *A. ellisii* population in the Gulf of California must await some definitive information on coral growth rates in that physical regime. Dana and Wolfson (1970) calculated that an average-sized specimen would consume 5.3 m^2 of coral per year. Our rough estimate of 10% coral coverage at Pink Cliff station would provide 20 m^2 of *Porites* per individual. If that can be extrapolated to the Gulf as a whole, even with an allowance for competition, it would appear that *A. ellisii* is living well within the available resources of its environment.

Miscellaneous Observations

In its natural environment, *A. ellisii* reacts to a touch or a cast shadow with a rapid retraction of the dermal papulae, resulting in an overall color change from dark red (or orange or yellow) to dull gray. If not further disturbed, the papulae are soon extruded, restoring the original color; if removed from the water, however, the gray persists. This habit reconciles the conflicting descriptions of the species as gray (Steinbeck and Ricketts, 1941) and as rufous (Ziesenhenne, 1937). Madsen (1955) mentions the same phenomenon for *A. planci*.

When feeding or at rest, the aboral spines are partly hidden in the papulae, and *A. ellisii* presents a deceptively harmless appearance. Although it can be more easily removed from the substrate than most asteroids, it should be handled with caution. Ziesenhenne (1937) was uncertain of the toxicity of the spines, but two of us (Barham and Wolfson) can attest to the painful and long-lasting effects of a puncture.

To augment the meager morphological data available for *A. ellisii*, we collected and measured six specimens at the termination of the 1971 study. Number of arms varied from 12 to 15, madreporic bodies from 5 to 9. Overall diameters ranged from 10.7 to 15.4 cm, disk diameters from 7.6 to 9.1 cm. Ratios of disk diameter to arm length (calculated from overall diameter minus disk diameter) ranged from 1.3 to 1.6.

(In comparing specimens, it should be noted that their general appearance will differ markedly, depending on the method of preservation. Dried specimens tend to "collapse" and appear less spiny, much flatter, and more bat-armed than if either fixed in preservative before drying or maintained in the preservative. Our specimens were preserved in Formalin[3] and then dried.)

Distribution of *Acanthaster* adjacent to the Gulf of California

We have found no *Acanthaster* at Banderas Bay, our most southerly station, although the environment seems ideal for the sea star. Specimens designated as *A. ellisii* have been reported at Clarión, Roca Partida, and Socorro Islands in the Revillagigedo Group, some 24° south of the tip of Baja California (Ziesenhenne, 1937), and the subspecies, *A. ellisii pseudoplanci*, was described (Caso, 1962) from specimens collected at various locations in those islands. Whether these identifications will survive taxonomic review of the genus remains, of course, to be seen.

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

It would be of considerable interest to know if *Acanthaster* is present on the Tres Marías Islands and along the great stretch between Farallon, San Ignacio, and Panamá, or if the distribution of the genus is indeed as discontinuous as it now appears.

CONCLUSION

Our adherence to the taxon, *Acanthaster ellisii*, stems from the conviction that the binomen is valid for the Gulf of California. Regardless of final decisions on the taxonomy of the more southerly, oceanic populations of *Acanthaster*, we believe that the Gulf populations constitute a distinct form.

Dana and Wolfson (1970), who have observed both *A. planci* and *A. ellisii* in the field, point out that the behavior of the two species is strikingly different. The information presented here indicates that, unlike *A. planci*, *A. ellisii* is not cryptic during daylight hours and feeds both night and day. Even where its population densities are similar to those given by Chesher (1969) for infestation levels of *A. planci*, *A. ellisii* does not appear to aggregate or to migrate as a population.

In gross morphology, *A. ellisii* also appears to be quite distinct from *A. planci*. Madsen (1955) stresses the disk-diameter to arm-length ratio as the most conspicuous difference between the American and Indo-West Pacific forms; our ratios fall well below the 1.9:2.2 ratio established for *A. planci*. (Other taxonomic characteristics appear to be too subtle and variable for comment by a nonspecialist.)

In conclusion, from the evidence presented in this paper, *A. ellisii* gives every appearance of living in harmony with its environment. There is nothing to suggest that it represents a threat to the coral fauna within its geographic range or a potential threat to any area beyond it.

ACKNOWLEDGMENTS

We thank John Faulkner, Scripps Institution of Oceanography, for generously contributing his notes and observations. David Pawson, Smithsonian Institution; John Garth, Allan Hancock Foundation; and Peter Glynn, Smithsonian Tropical Research Institute, have forwarded literature and information. John Hall, Steven Leatherwood, I. E. Davies and, particularly, George Pickwell of the Naval Undersea Center have aided in the field work. Chief Warrant Officer Russell Ludwig and the crew of the U.S. Navy yawl, *Saluda*, rendered logistic support. Our investigations in Mexican waters were made possible through the courtesy of the Mexican Government, Department of Industry and Commerce, National Institute of Biological Fishery Research. The work was initiated under Task No. 0588 supported by the U.S. Naval Ships System Command but was brought to conclusion as independent research in the spirit of the Navy's Environmental Protection Program.

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SOME METAZOAN PARASITES OF THE EASTERN PACIFIC SAURY, *COLOLABIS SAIRA*

STEVEN E. HUGHES[1]

ABSTRACT

Parasite composition of the eastern Pacific saury, *Cololabis saira*, and severity of infections were investigated to determine their possible effects on potential food fish markets and to assist in determining population structure of the stock. Infection data from two copepods and one acanthocephalan are presented and examined for host dependent factors, temporal and spacial variation, and variation between saury with different scale features (hypothesized spring- and autumn-born fish). The acanthocephalan infecting saury was also identified in the steelhead trout, *Salmo gairdneri*, which is reported as a second definitive host. It is concluded that because of parasites, only 30 to 60% of marketable-sized saury occurring off the Washington-Oregon coast would be acceptable as fresh-food fish sold in the round although most would be acceptable as canned products. The parasite data do not indicate that fish with the two different patterns of growth on the scales are independent sub-populations.

The eastern Pacific saury, *Cololabis saira*, is a pelagic teleost occurring in offshore waters along the Pacific coast of North America. Although previously recognized mainly as a food source for albacore, *Thunnus alalunga*, the saury resource in the eastern Pacific attracted the interest of foreign and domestic fishermen during the late 1960's. Potential domestic markets included fresh, frozen, and canned products for human consumption. Studies to determine the parasite composition and severity of infections, believed an important consideration in assessing the potential value of saury as a food fish, were undertaken by the National Marine Fisheries Service at the Northwest Fisheries Center. Parasite data were also examined for their possible use in determining the population structure of saury in the sampled area. Preliminary growth and scale studies (Hughes, in press; Mosher[2]) suggested two spawning groups of saury, spring- and autumn-born.

Initial samples collected off California in 1969 and limited information from two previous reports (Eberhardt, 1954; Sokolovskii, 1969) indicated that the eastern Pacific saury were primarily parasitized by two species of copepods and one acanthocephalan. Results of a detailed study by Baeva (1970) indicated the eastern Pacific saury are infected by at least 10 species of parasites. Eberhardt reported the copepod *Pennella* sp. parasitized more than 20% of 250 saury captured off California in 1950-52. Although several *Pennella* species infecting marine fish have been described and partial life histories determined, detailed work on the saury parasite appears lacking. My preliminary studies and a recent Soviet study by Sokolovskii indicated that up to 90% of the eastern Pacific saury were infested by the copepod *Caligus macarovi* Gussev. This copepod also infects the western Pacific saury, but Sokolovskii and Baeva reported that *Pennella* sp. is peculiar to the eastern Pacific stock. The acanthocephalan detected in the preliminary studies was described by Laurs and McCauley (1964) as a new species, *Rhadinorhynchus cololabis*. Further reports on this species also appear lacking.

This report presents data on the numbers and incidence of infestation for *Pennella* sp., *Caligus*

[1] Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2] Mosher, K. H. Age determination procedures for saury (*Cololabis saira*) from the northeastern Pacific Ocean, using scales. Manuscr. in preparation. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

Manuscript accepted February 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973

macarovi, and *Rhadinorhynchus cololabis* infections found on and in Pacific saury captured off the Oregon, Washington, and British Columbia coasts during August-September 1970-71. Incidence of infestation and numbers of scars resulting from previous copepod infestations are presented by geographical areas and correlated to size, age, and possible racial composition of the host species. Sex ratio and length data are included for *R. cololabis* recovered from saury; a second definitive host infected by this acanthocephalan is reported.

MATERIALS AND METHODS

A total of 4,396 saury sampled from 13 individual fish schools captured in offshore waters along the Pacific coast of North America between lat. 44°01′N and lat. 49°16′N were involved in this study. Fish were captured with a modified purse seine-artificial light attraction system (Ellis and Hughes, 1971). Random samples were collected and frozen for processing at shoreside facilities. In the laboratory, fish samples were examined for copepod parasites and scars from previous copepod infestations. Simultaneously, host length, weight, sex, maturity, and age indicators were collected. Digestive tracts from 20 saury randomly subsampled from 12 of the 13 samples were placed in 10% Formalin[3] and later examined for metazoan parasites with the aid of a dissecting microscope (7 × – 50×). Each *R. cololabis* was measured (trunk length) to the nearest 0.5 mm, and its sex determined by dissection and examination of the posterior portion. Females were generally swollen with bipolar eggs, and the uterus was easily distinguished from cement glands in the males. Host age was determined from scales. Patterns of growth displayed on the scales were used to identify the two hypothesized spawning groups, spring- and autumn-born fish.

Specimens were photographed in a circumilluminated lightbox, using standard techniques and materials.

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

RESULTS

Two copepods, *Pennella* sp. and *Caligus macarovi*, and the acanthocephalan *Rhadinorhynchus cololabis* made up the major macroparasitic fauna of the eastern Pacific saury. Other than an occasional nematode located in the body cavity, additional metazoan parasites were not detected.

Incidence and intensity of infection of parasites recovered on and in saury throughout the study are presented by sample in Table 1.

Pennela sp.

An adult fish heavily parasitized by this large copepod is shown in Figure 1. In addition to three mature females (one with broken egg strings), two juveniles are shown — one posterior to the pectoral fin and the other posterior to the pelvic fin and above the anal finlets. Figure 2 shows an entire mature female (A), with a juvenile (B), after removal from the host. The external portion of this parasite usually protruded from the host at some point below the darkly colored dorsal surface but above the lateral line; and the head was usually lodged in or adjacent to the host's heart or major blood vessels. The tissue invading portion ends where the trunk diameter increases notably. Infected hosts weighed as much as 17% less than uninfected hosts of equal length, and extensive destruction of host tissue occurred during degeneration of the parasite.

Pennella sp. was frequently encountered in each of the six samples collected in 1970 but was detected in only one of seven samples collected in 1971. Incidence of infection for schools sampled in 1970 ranged from 17.0 to 21.6% (mean 18.4%) off Oregon and 11.5 to 18.4% (mean 14.5%) off Washington. Multiple infections were common. Only 2.1% of one school was infected in 1971 and no multiple infections were detected.

The 1970 data showed a trend toward increasing incidence of infection with increasing host size. To determine whether this noted increase was a function of increasing host age, length, or both, Washington and Oregon *Pennella* sp. data were analyzed by host age groups, length

TABLE 1.—Parasites recovered from Pacific saury, *Cololabis saira*, captured off the Oregon and Washington coasts in 1970 and the Oregon and Washington-southern British Columbia coasts in 1971.

Year and coastal area	Location		No. of fish examined	*Pennella* sp.				*Caligus macarovi*				*Rhadinorhynchus cololabis*			
	Lat. N.	Long. W		Total no.	No. per infected fish: Range	No. per infected fish: Mean	Incidence of infection (%)	Total no.	No. per infected fish: Range	No. per infected fish: Mean	Incidence of infection (%)	Total no.	No. per infected fish: Range	No. per infected fish: Mean	Incidence of infection (%)
1970:															
Oregon	45°03′	125°50′	300	93	1-6	1.82	17.0	21	1-2	1.10	6.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	98	1-14	7.0	70.0
	44°33′	125°11′	300	96	1-5	1.48	21.6	57	1-2	1.19	16.0	—	—	—	—
			20	—	—	—	—	—	—	—	—	74	1-20	4.1	90.0
	44°30′	125°08′	300	94	1-4	1.74	18.0	61	1-4	1.15	17.7	—	—	—	—
			19	—	—	—	—	—	—	—	—	47	1-13	3.4	73.9
Washington	47°43′	126°02′	284	47	1-5	1.20	13.7	158	1-5	1.44	38.7	—	—	—	—
			20	—	—	—	—	—	—	—	—	16	1-4	2.0	40.0
	47°41′	125°58′	191	25	1-4	1.14	11.5	81	1-4	1.36	42.4	—	—	—	—
			20	—	—	—	—	—	—	—	—	20	1-4	1.8	55.0
	47°39′	126°00′	192	44	1-3	1.26	18.4	62	1-5	1.35	24.0	—	—	—	—
			20	—	—	—	—	—	—	—	—	27	1-9	2.7	50.0
1971:															
Oregon	44°01′	125°01′	419	0	—	0	0	20	1-2	1.11	4.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	1	1	1.0	5.0
	43°55′	124°59′	508	0	—	0	0	34	1	1.00	6.7	—	—	—	—
			20	—	—	—	—	—	—	—	—	0	—	0	0
	43°54′	125°00′	508	0	—	0	0	37	1	1.00	7.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	2	1	1.0	10.0
	44°02′	125°02′	268	0	—	0	0	18	1-2	1.06	6.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	4	1-2	1.3	15.0
	43°58′	125°04′	507	0	—	0	0	14	1	1.00	2.8	—	—	—	—
Washington-British Columbia	48°21′	126°04′	513	11	1	1.00	2.1	41	1-2	1.03	7.8	—	—	—	—
			19	—	—	—	—	—	—	—	—	109	1-13	6.4	89.5
	49°16′	127°06′	106	0	—	0	0	24	1-3	1.26	17.9	—	—	—	—
			20	—	—	—	—	—	—	—	—	21	1-5	2.3	45.0
Total			4,396	410				628				419			

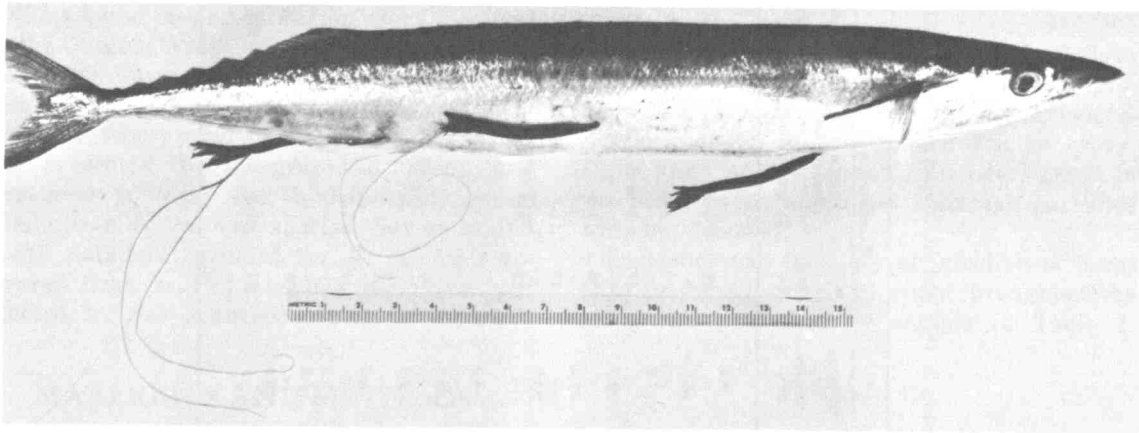

FIGURE 1.—Pacific saury with three adult female and two juvenile copepods, *Pennella* sp. Oken.

groups, and length groups within age. The increasing incidence of infection was found to be a function of age (Table 2) but not length. A chi-square test was employed to test the null hypothesis that the occurrence of infected II-, III-, and IV-year-old-fish was the same in potential harvest areas off Washington and Oregon (0.05 level). This hypothesis was rejected (0.025 level) for II-year-olds and accepted for III- and IV-year-olds.

Caligus macarovi

Incidence of infection by *C. macarovi* (Figure 3) showed both annual and geographic variability (Table 1). The proportion of infected saury in 1970 samples ranged between 6.3 and 17.7% (mean 12.8%) off Oregon and between 24.0 and 42.4% (mean 35.0%) off Washington. Infections were less common in 1971 samples, 2.8 to 7.3% (mean 5.5%) off Oregon and 7.8 to 17.9% (mean 12.9%) off Washington. These percentages, however, are certainly minimum estimates of the rate of infection of the sampled population because some *C. macarovi* dropped off captured fish.

Both 1970 and 1971 Washington and Oregon data were separately examined for changes in infection rate with increasing host size and age. No trends of change related to those factors

TABLE 2.—Numbers and percent incidence of *Pennella*-infected saury in different host age groups in samples taken in September 1970 from off the Washington and Oregon coasts.

Fishing area and type of data	Host age (years)					
	I	II	III	IV	V	VI
Washington coast:						
No. fish examined	9	326	244	22	4	1
No. fish infected by *Pennella* sp.	0	55	98	7	2	1
Incidence of infection (%)	0	16.87	40.16	31.81	50.00	100
Oregon coast:						
No. fish examined	314	322	70	10	—	—
No. fish infected by *Pennella* sp.	26	80	32	5	—	—
Incidence of infection (%)	8.26	24.84	45.71	50.00	—	—

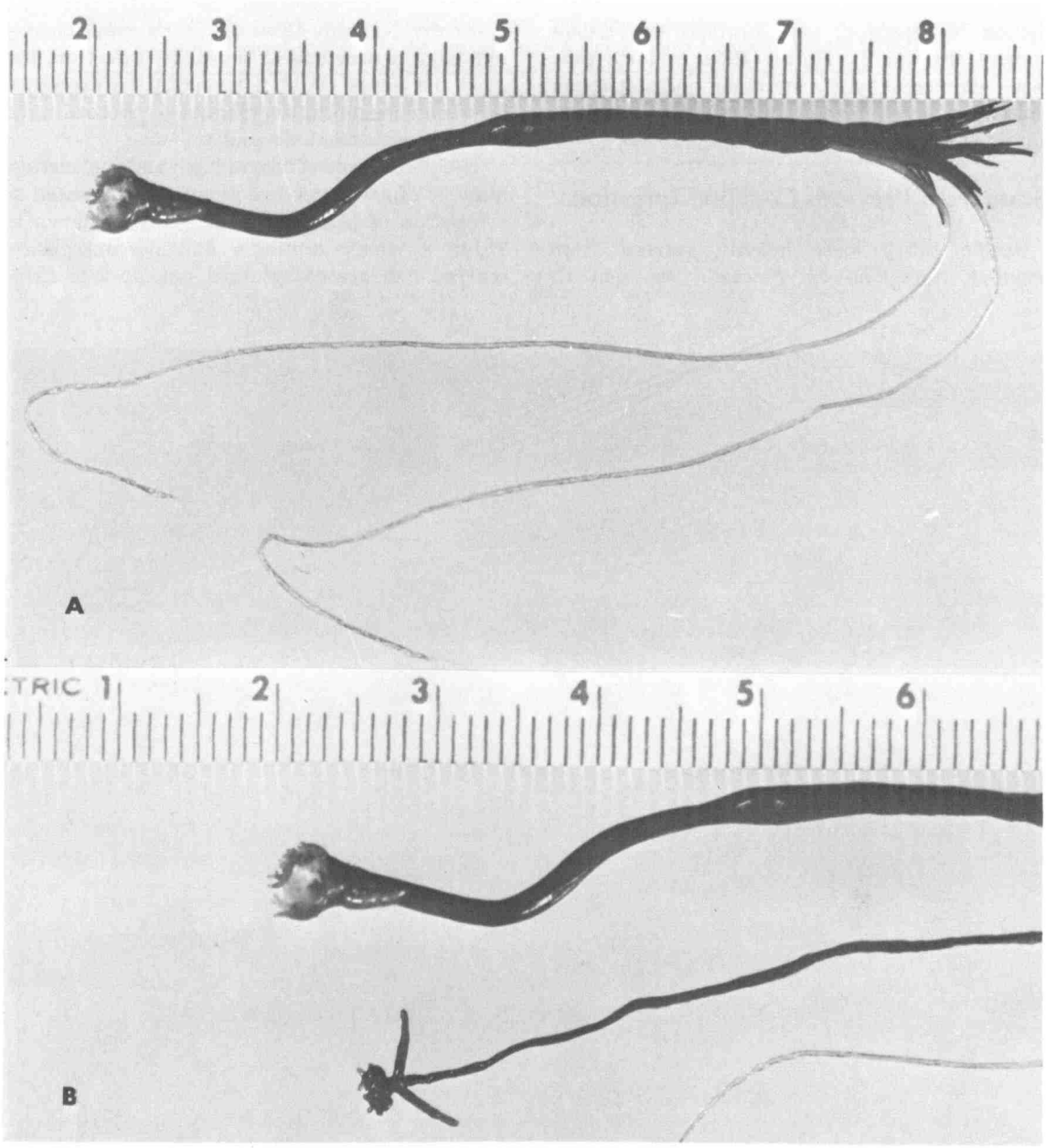

FIGURE 2.—Mature female *Pennella* sp. (A), with a juvenile (B), after removal from the host.

were detected. Accordingly, fish from individual schools captured in each area and year were combined and tested by chi-square analysis between areas. In both 1970 and 1971, numbers of fish infected with *C. macarovi* were significantly higher (0.05 level) off Washington than off Oregon.

This ectoparasitic copepod usually occurred more frequently than *Pennella* sp., but was considered less burdensome due to small size,

method of infection, and minimal host-tissue damage (Figure 3). Hotta (1962) reports that tissue damaged by *C. macarovi* infestation is limited to the epidermis and mucosa while the muscle is not penetrated.

Scars from Previous Copepod Infections

Pacific saury were heavily scarred from previous infections by *Pennella* sp. and *C. macarovi*. In many cases the scar's shape clearly indicated a previous *C. macarovi* infection, but most old scars could not readily be discerned between specific causes (Figure 4). Accordingly, all scars were treated equally.

The percentage of scarred fish and the average number of scars per fish generally increased as a function of increasing age. This is shown in Table 3 where numbers and percentages of scarred fish are categorized by age into three

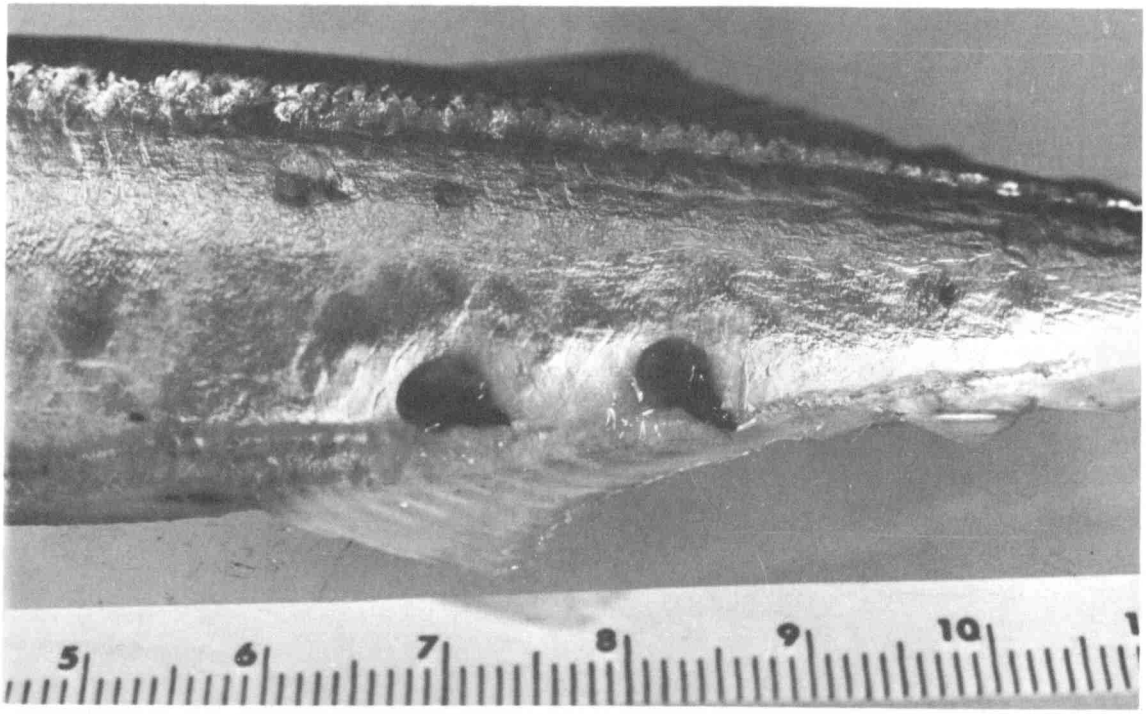

FIGURE 3.—Pacific saury infected by the copepod, *Caligus macarovi* Gussev.

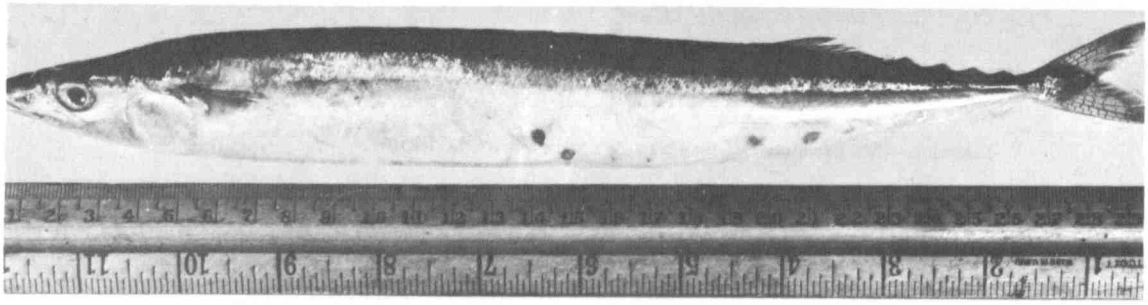

FIGURE 4.—Examples of scars resulting from previous infections by copepods on Pacific saury.

TABLE 3.—Pacific saury scarred from infections with the copepods *Pennella* sp. and *Caligus macarovi* as sampled off the Pacific coast of North America during August-September 1970-71.

Year and coastal area	Fish age (years)	No. fish examined	Fish with 1-3 scars		Fish with >3 scars		Total scarred fish	
			No.	%	No.	%	No.	%
1970:								
Oregon	I	314	224	71.3	20	6.4	244	77.7
	II	320	232	72.5	40	12.5	272	85.0
	III	70	47	67.1	15	21.4	62	88.5
	IV	10	5	50.0	5	50.0	10	100
Washington	I	9	5	55.6	4	44.4	9	100
	II	326	150	46.0	163	50.0	313	96.0
	III	244	68	27.9	196	80.3	237	97.2
	IV	22	5	22.7	17	77.2	22	100
1971:								
Oregon	I	576	172	29.9	1	0.2	173	30.1
	II	729	356	48.8	7	1.0	363	49.8
	III	137	79	57.7	3	2.2	82	59.9
Washington-southern British Columbia	II	26	13	50.0	2	7.7	15	57.7
	III	104	62	59.6	8	7.7	70	67.3
	IV	277	157	56.7	26	9.4	183	66.1
	V	97	54	55.7	7	7.2	61	62.9

groups—those fish with one to three scars, those with more than three scars, and total number of scarred fish. In 1970 when scarred fish were more prevalent (77.7-100%), the percentage of fish with one to three scars decreased with increasing age whereas those with more than three scars increased. The fact that 1971 fish were less severely scarred than 1970 fish is puzzling.

Rhadinorhynchus cololabis

This acanthocephalan was associated primarily with the lower digestive tract although worms were also found attached in the midstomach area (Figure 5). Tissue damage around the point of attachment appeared minimal, and the worm's proboscis rarely protruded through the wall of the digestive tract. Female *R. colo-*

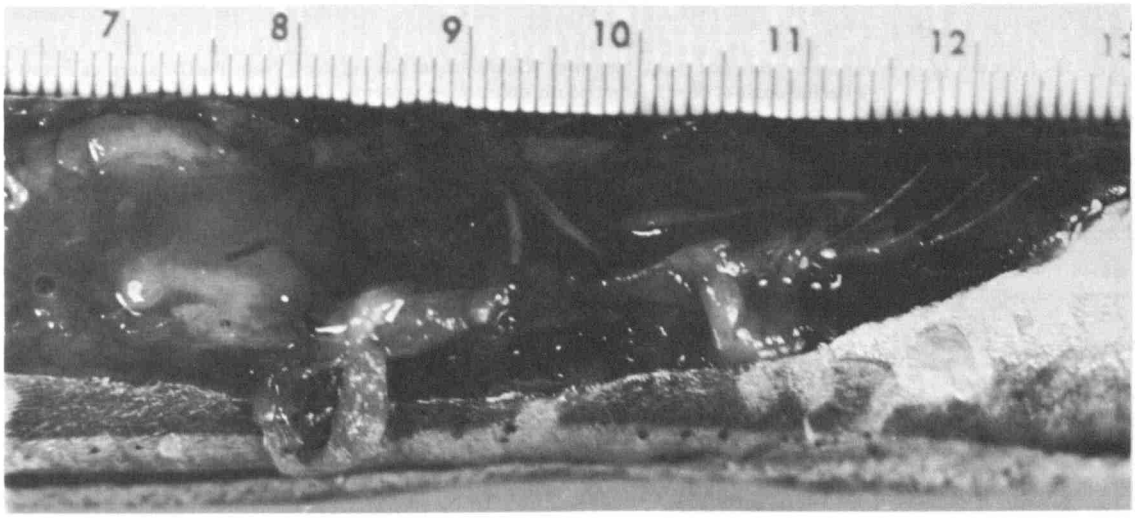

FIGURE 5.—Lower digestive tract of a Pacific saury typically infected by the acanthocephalan, *Rhadinorhynchus cololabis* Laurs and McCauley.

labis were much larger than males and occurred less frequently (Table 4). The range of trunk lengths for both males and females is increased from the original reporting—females 18.0 to 26.7 mm, now 13.5 to 35.0 mm, and males 9.20 to 12.16 mm, now 7.5 to 14.0 mm. All females with trunk lengths exceeding 15.0 mm were swollen with bipolar eggs.

Occurrence of this parasite as presented in Tables 1 and 4 was minimal since worms were often squeezed from the host's anus as fish were brailed aboard the ship. Occurrence of *R. cololabis* showed inconsistent geographic and annual variability precluding further meaningful analysis. Proportions of infected saury in 1970 samples ranged between 70.0 and 90.0% (mean 78.0%) off Oregon and between 40.0 and 55.0% (mean 48.3%) off Washington. Like the parasitic copepods, incidence of infection was generally lower in 1971, ranging between 0 and 15.0% (mean 7.5%) off Oregon and between 45.0 and 89.5% (mean 67.2%) off Washington. Rates of infection were found to be independent of host size and age.

R. cololabis in Steelhead Trout

The steelhead trout was found bearing the adult form of the same acanthocephalan identified in Pacific saury. Steelhead trout had previously been reported with an acanthocephalan identified as *Rhadinorhynchus* sp., Shaw (1947); however, more recent or specific reports have not been located.

C. M. Senger, Professor of Biology, Western Washington State College, Bellingham, Wash., recovered two Acanthocephala from steelhead trout captured in Skagit County, Wash., in 1967-68. He later compared these with specimens I supplied from Pacific saury and concluded both hosts carried *R. cololabis*. Additional steelhead trout from Skagit County (1969-72) and from high-seas areas of the northwestern Gulf of Alaska (August 1970) were subsequently examined. Nine of 28 steelhead trout from Skagit County and 4 of 22 steelhead trout from the northwestern Gulf of Alaska were infected with *R. cololabis*. Multiple but not severe infections were noted from hosts collected in both areas. The heavy egg load carried by female *R. cololabis* indicated the steelhead trout to be a second definitive host.

Copepod Infections in Two Possible Subpopulations of Saury

Chi-square analysis was applied to test the null hypothesis that no significant differences (0.05 level) in numbers of infected fish existed between the two possible subpopulations (spring- and autumn-born saury) that were classified by means of scale features. The two indicators

TABLE 4.—Intensity of infection, sex ratio, and trunk length of *Rhadinorhynchus cololabis* from Pacific saury captured off the Pacific coast of North America during August-September 1970-71.

Year and coastal area	Location		No. fish examined	Incidence of infection (%)	Sex ratio (%)		Trunk length (mm)			
							Males		Females	
	Lat. N	Long. W			M	F	Range	Mean	Range	Mean
1970:										
Oregon:	45°03′	125°50′	20	70.0	64.3	35.7	8.0-13.0	10.1	16.0-27.0	21.0
	44°33′	125°11′	20	90.0	77.0	23.0	7.5-12.0	9.4	16.0-32.0	23.0
	44°30′	125°08′	19	73.9	66.0	34.0	8.5-13.0	10.4	17.5-28.0	21.5
Washington	47°43′	126°02′	20	40.0	81.2	18.8	8.5-12.0	10.1	22.0-23.0	22.5
	47°41′	125°58′	20	55.0	55.0	45.0	9.5-12.0	10.6	13.5-27.5	22.8
	47°39′	126°00′	20	50.0	63.3	36.7	8.5-12.5	10.5	15.0-33.0	22.8
1971:										
Oregon	44°01′	125°01′	20	5.0	100.0	—	12.0-	12.0	—	—
	43°55′	124°59′	20	0	—	—	—	—	—	—
	43°54′	125°00′	20	10.0	50.0	50.0	10.0-	10.0	17.0-	17.0
	44°02′	125°02′	20	15.0	75.0	25.0	10.0-14.0	12.0	21.0-	21.0
Washington-southern British Columbia	48°21′	126°04′	19	89.5	69.3	29.7	10.0-13.0	11.0	15.0-35.0	23.8
	49°16′	127°06′	20	45.0	81.0	19.0	10.0-14.0	11.5	16.0-26.0	20.3

were *Pennella* sp. and *C. macarovi* since insufficient data excluded use of the acanthocephalan.

As previously shown, infections by *Pennella* sp. increased with increasing host age, and *C. macarovi* infections were found to be independent of host age or length. Accordingly, chi-square tests of *Pennella* sp. infections were conducted for spring-born versus autumn-born fish by individual age groups for each area during 1970. *C. macarovi* infections were compared after combining all host age groups within each area for 1970 and 1971.

Results of chi-square tests are summarized in Table 5. The only significant difference in numbers of saury infected by *Pennella* sp. occurred between spring- and autumn-born II-year-olds captured off Oregon in 1970. No significant differences between numbers of spring- and autumn-born saury infected by *C. macarovi* existed in either area during 1970 and 1971.

CONCLUSIONS AND SUMMARY

The eastern Pacific saury was found to be infected with two species of copepods and one acanthocephalan, in addition to being scarred from previous copepod infections. Mean incidence of *Pennella* sp. infections was 18.4% off the Oregon coast and 14.5% off the Washington coast in 1970, but this parasite was rarely found

TABLE 5.—Numbers and percentage incidence of copepods (*Pennella* sp. and *Caligus macarovi*) in two possible subpopulations of eastern Pacific saury. Chi-square values are presented testing the null hypothesis that no significant difference in numbers of infections exists (0.05 level) between the hypothesized spring- and autumn-born fish. Fish ages are in parentheses.

Year and area	Pacific saury examined for *Pennella* sp.	Number of saury			Incidence of infection (%)	χ^2	Null hypothesis	
		Noninfected	Infected	Total			Accept	Reject
1970:								
Washington	Spring born (II)	221	47	268	17.5	1.03	X	—
	Autumn born (II)	51	7	58	12.7			
	Spring born (III)	103	45	148	30.4	0.42	X	—
	Autumn born (III)	63	33	96	34.4			
Oregon	Spring born (II)	154	64	218	29.4	6.93	—	0.01
	Autumn born (II)	86	16	102	15.7			
	Spring born (III)	23	13	36	36.1	2.70	X	—
	Autumn born (III)	15	19	34	55.8			

Year and area	Pacific saury examined for *Caligus macarovi*	Number of saury			Incidence of infection (%)	χ^2	Null hypothesis	
		Noninfected	Infected	Total			Accept	Reject
1970:								
Washington	Spring born	329	114	443	25.7	0.58	X	—
	Autumn born	126	37	163	22.7			
Oregon	Spring born	503	71	574	12.4	1.11	X	—
	Autumn born	118	22	140	15.7			
1971:								
Washington	Spring born	368	32	400	8.0	3.16	X	—
	Autumn born	96	15	111	13.5			
Oregon	Spring born	1,211	83	1,294	6.4	2.42	X	—
	Autumn born	150	16	166	9.6			

in 1971. Incidence of infection increased with host age. Mean incidence of *C. macarovi* infections was 12.8% off Oregon and 35.0% off Washington in 1970 and also decreased in 1971 to 5.5% off Oregon and 12.9% off Washington. Infection rates were independent of host size and age. The incidence of scars resulting from previous copepod infections was very high. Mean incidence of *R. cololabis* in 1970 was 78.0% off Oregon and 48.3% off Washington and decreased substantially during 1971. Infection rates were independent of host size and age. Trunk length measurements increased the known length range for both male and female worms.

R. cololabis was also identified in steelhead trout, which is reported as a second definitive host. It seems most likely that both hosts are infected through a common food organism carrying the acanthor stage although steelhead trout are known to feed on saury in ocean waters.

For aesthetic reasons, presence of copepod parasites or scars, and to a lesser extent the acanthocephalan, would undoubtedly limit usage of saury in the round as a fresh fish product for human consumption. Saury infected by the obnoxious appearing *Pennella* sp. and those with multiple infections of *C. macarovi* or numerous scars, would undoubtedly be rejected by consumers. Although western Pacific saury are not infested by *Pennella* sp., Nishimura (1964) reports that saury heavily blemished by *C. macarovi* have a lower commercial value than nonblemished fish. The acanthocephala are not as unsightly as either copepod, although the bright orange worms are often clearly visible protruding from the anus.

Considering apparent annual and age dependent changes in incidence of infection, only 30 to 60% of the market-sized saury occurring in Washington-Oregon coastal waters appear to be acceptable as a fresh-food fish sold in the round. Although some geographical variations of infection rates and occurrence of scars have been noted, the percentage of fish usable as a fresh product appears nearly equal off Washington and Oregon.

Test packs prepared by the Pacific Fishery Products Technology Center, National Marine Fisheries Service, Seattle, have indicated that these parasites have practically no effect on canned saury products. Acanthocephala are removed with the vicsera, and *C. macarovi* can be scraped free with resulting wounds and old scars presenting no qualitative or aesthetic problems. Uninfected portions of saury with pennellids can also be used.

Pennella sp. and *C. macarovi* were also employed as racial indicators by comparing their occurrence between fish displaying spring- and autumn-born growth patterns on their scales. Seven of eight chi-square tests showed no significant differences (0.05 level), between fish of the two scale features; thus, evidence from the parasite data does not indicate the existence of separate populations. Although use of parasites as biological indicators is not a strong test of population structure, particularly without knowledge of the parasites' life history, biochemical and growth studies likewise do not indicate existence of two genetically isolated populations (Hughes, see footnote 2).

ACKNOWLEDGMENTS

I thank Paul L. Illg, Professor of Zoology, University of Washington, for confirming identification of the copepods, and Clyde M. Senger, Professor of Biology, Western Washington State College, for his cooperative work on the acanthocephalan and review of this manuscript.

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AGE, GROWTH, AND REPRODUCTION OF THE NORTHERN PUFFER, *SPHOEROIDES MACULATUS*[1]

JOANNE L. LAROCHE[2,3] AND JACKSON DAVIS[4]

ABSTRACT

Rings on vertebral centra of the northern puffer, *Sphoeroides maculatus*, were shown to be true year marks. Age groups 0 to V were found in 1,128 specimens collected from Chesapeake Bay. Females were significantly larger than males at each age. Most growth in length took place during the first growing season from June through October. Sexual maturity was reached at age I. Peak spawning occurred in June and July.

The northern puffer, *Sphoeroides maculatus* (Bloch and Schneider), occurs on the Atlantic coast of North America from Newfoundland to Flagler County, Fla. (Shipp and Yerger, 1969). It is the only tetraodontid that is abundant along the middle Atlantic coast and that comprises a large part of the spring and fall commercial catches in Chesapeake Bay. During the period 1962 to 1970, total annual landings from Chesapeake Bay ranged from 1 to 12 million pounds. The steady northward progression of commercial landings in the spring from North Carolina to Chesapeake Bay and the southward progression of catches in the fall suggest an annual coastal migration.

There is little published information on the life history of the northern puffer. Welsh and Breder (1922) reported the food habits, larval development, and weight-length relationships of puffers from New Jersey. Shipp and Yerger (1969) reviewed the taxonomy of *S. maculatus*.

This paper describes a technique for determining the age of the northern puffer and reports the rate of growth, weight-length relationships, age at sexual maturity, and spawning time.

This is the first published report of age determination for a tetraodontid.

MATERIALS AND METHODS

Age and growth determinations were based on 123 fish captured during November 1969 and 1,005 fish collected from April through November 1970 from lower Chesapeake Bay, Mobjack Bay, and the mouths of the York and Rappahannock rivers, Va. A homogeneous puffer population in the area sampled is assumed. Fish were primarily obtained from commercial pound nets and haul seines but also with a push net, beach seine, and trawl and from commercial crab pots.

Total length was measured from the tip of the snout to the center of the flared caudal fin. Fish with a distended ventral sac were not weighed because water was retained in the sac. Fish were classified as immature, gravid, running ripe, or spent by gross inspection of the gonads.

In a preliminary study, otoliths, cleithra, opercles, jaw bones, fin rays, and all the vertebrae were removed from a small number of fish. Afterwards only vertebrae No. 2-No. 7 were removed from the fish and were disarticulated and then stained in a solution of 4-8% KOH and Alizarin Red S. The stain reduced glare from the centrum surface and increased contrast

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[2] This paper is adapted from a thesis submitted in partial fulfillment of the degree of Master of Arts, College of William and Mary, Williamsburg, Va.

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Manuscript accepted April 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

between growth bands while KOH removed adherent flesh. Staining techniques of Hollister (1934), Galtsoff (1952), Daiber (1960), and La Marca (1966) were not effective in staining growth marks differentially. Puffer vertebrae have deeply concave centra and had to be sliced lengthwise in order to measure straight-line distances. Vertebrae No. 4 and No. 5 with the neural spines removed were placed dorsal surface up in a V-shaped slit in a wood block and were sliced with a hand-held razor blade. All vertebral measurements were made on vertebra No. 4 using an ocular micrometer in a dissecting microscope at 15× under reflected light. The marginal width or distance between the last annulus and the centrum edge was measured on the posterior segment of vertebra No. 4.

AGE DETERMINATION

Vertebrae and saccular otoliths exhibited growth marks, although only the growth marks on vertebral centra were both distinct and consistent. Growth marks on otoliths were ambiguous and could not be distinguished in larger fish. Cleithra, opercles, jaw bones, and fin rays exhibited no discernible growth marks.

Growth marks on northern puffer vertebrae formed distinct steps on the centrum surface which are best seen when a vertebra is rested on one end at a 45° angle from the vertical and is viewed looking down on the centrum face. The step is more opaque and its surface texture appears coarser under magnification in reflected light than the rest of the centrum. A narrow, dark, translucent ring appears along the inner edge of each step. The step and narrow dark band form a continuous ring on the centrum and constitute the annulus. Broad opaque bands with uniform surface texture lie between the narrower annuli. Together these features represent 1 yr's growth. Season marks on black bullhead, *Ictalurus melas*, vertebrae are narrow, translucent bands associated with a depression in the centrum surface and alternating with broad, opaque bands (Lewis, 1949). In contrast, narrow dark annual bands on channel catfish, *I. punctatus*, were usually associated with a ridge (Appelget and Smith, 1951).

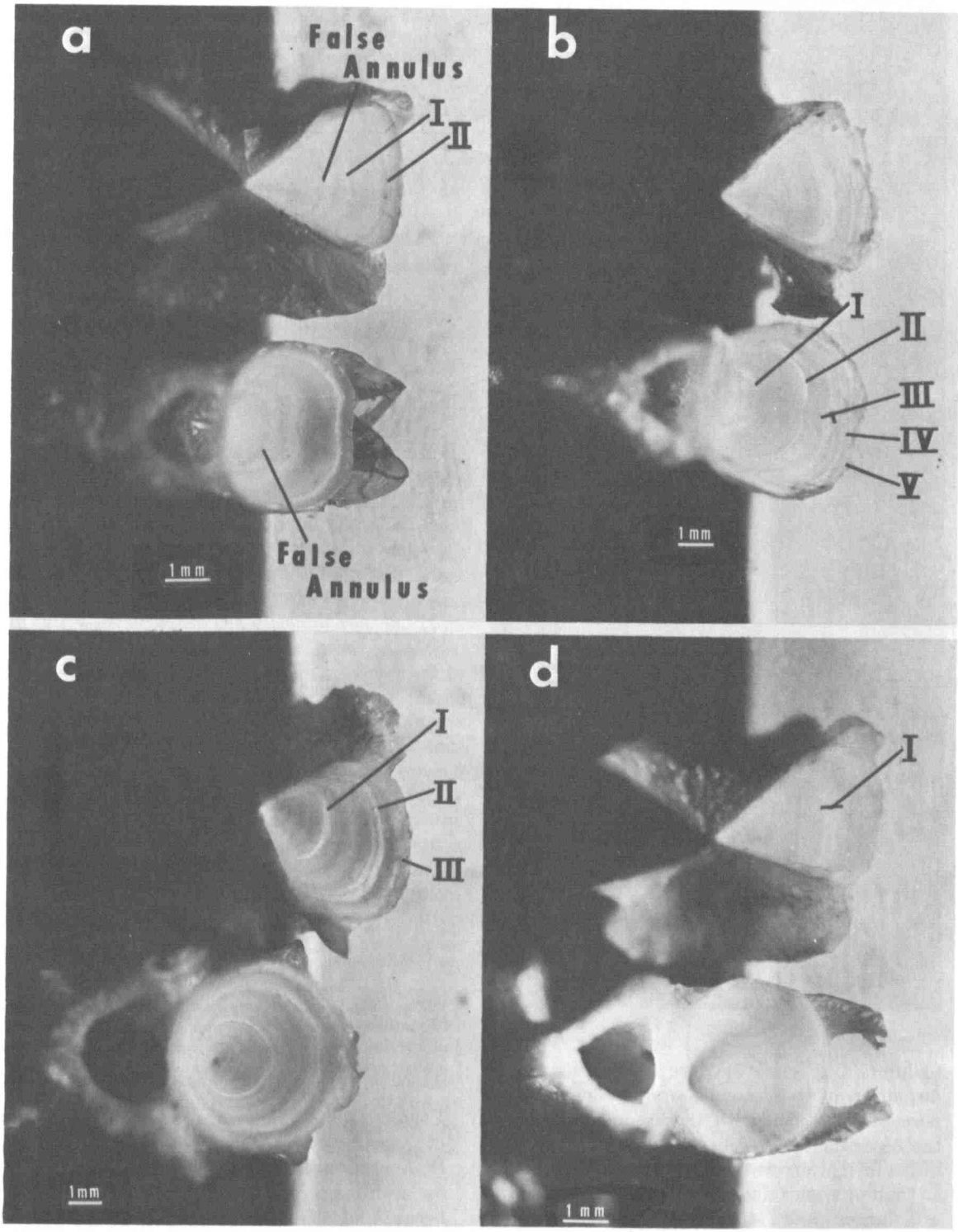
Five age groups of northern puffer were found by considering the marks on vertebrae to be annuli.

There was excellent agreement among vertebrae No. 3-No. 7 in the number and position of annuli. Age could not be assigned because of disagreement in less than 1% of the fish. However, age could not be determined in 7% of the fish because of false annuli, crowding of annuli at the centrum edge, and changes in the surface texture of centra in older fish. False annuli were faint dark bands which were not associated with a distinct step. Another extraneous mark was a shallow depression forming a continuous ring on the centrum which was not a definitive step. This feature was found on black bullhead vertebrae (Lewis, 1949). False annuli were most frequent in the first growth zone (Figure 1a). With increasing age, annuli became crowded at the centrum edge (Figure 1b), and the surface texture of centra became more coarse and irregular, especially near the edge (Figure 1c). However, there was no indication that annuli at the centrum edge were obscured by crowding in the 58 age III and 17 age IV fish examined.

VALIDATION OF THE ANNULUS

The annular step on vertebrae of the northern puffer met four of Hile's (1941) criteria for validating the annulus as a true year mark. First, a single annulus was formed each year. No annuli were present on vertebrae of yearlings in April and early May, but a distinct ring became visible at the outer edge of the centrum late in May when growth resumed (Figure 2). Annulus formation began in May, and by August most yearlings had formed an annulus (Figure 3). The fish taken in April with a single annulus and wide marginal width

FIGURE 1.—Vertebrae of the northern puffer: (a) vertebrae from a 2-yr-old northern puffer showing a false annulus adjacent to the first annulus, (b) vertebrae from a 5-yr-old northern puffer on which the third annulus appears double because of the expanded step, (c) vertebrae from a 3-yr-old northern puffer, (d) expanded annular step on the vertebrae from a 1-yr-old northern puffer.


a
False Annulus
I
II
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1 mm
b
I
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V
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c
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d
I
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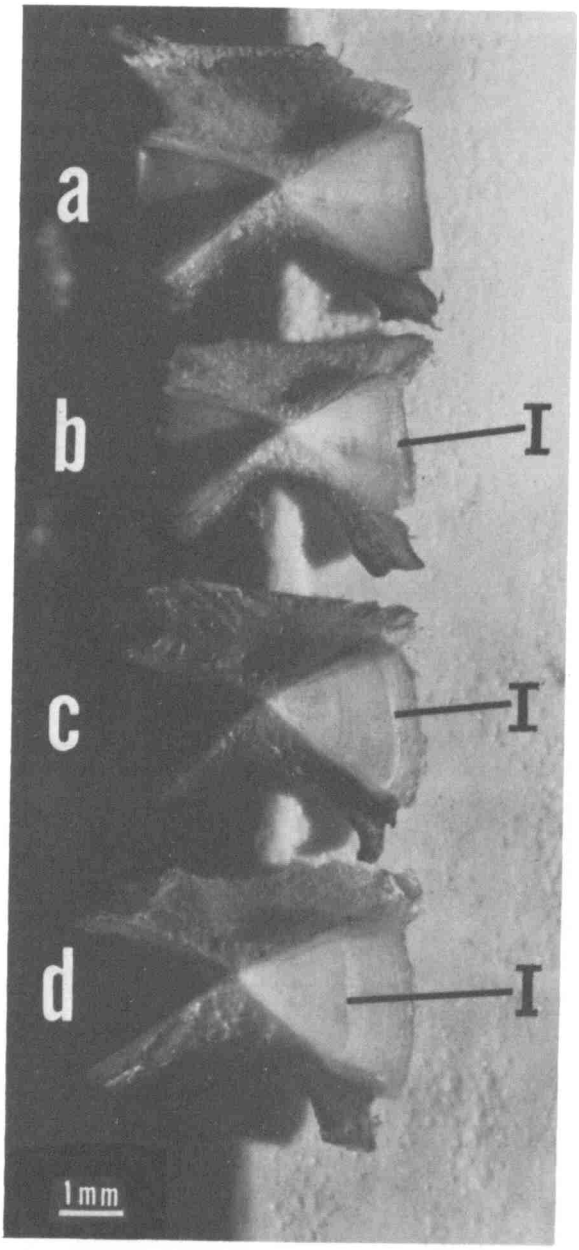

FIGURE 2. (left)—Vertebral sections of the northern puffer showing the increase in margin width after formation of the first annulus: (a) young-of-the-year female captured in November, (b) female captured in May with the first annulus just visible at the centrum edge, (c) age I male captured in September, (d) age I male captured in November.

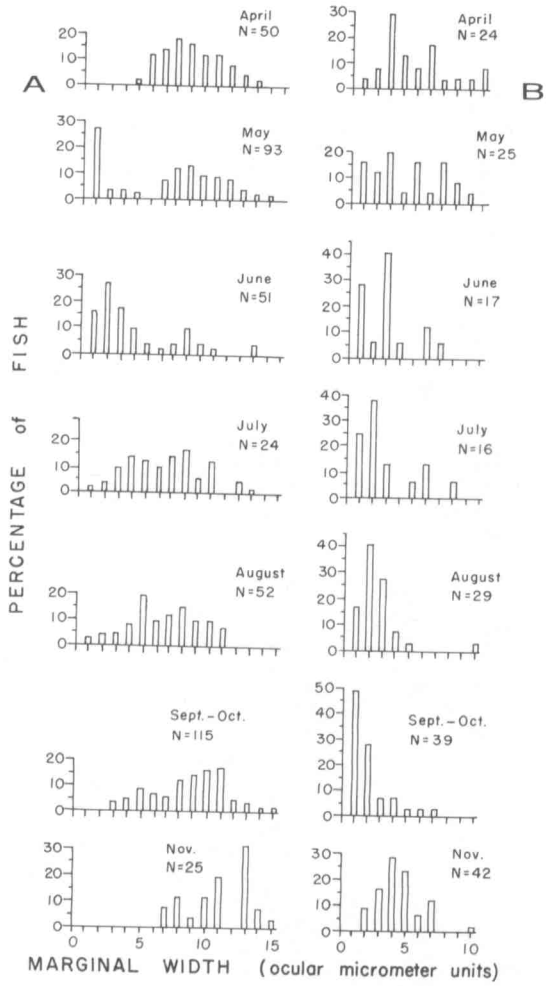

FIGURE 3.—Frequency distributions of margin widths (distance between the last annulus and the centrum edge) of vertebral centra from the northern puffer: (A) with a single annulus, (B) with two annuli.

(column A, Figure 3) were 2-yr-olds prior to formation of the second annulus. The greatest percentage of fish with the second annulus at the centrum edge occurred in September. Annulus formation on the centrum may take longer than on scales and otoliths because vertebrae are larger and structurally more complex. Yasuda (1940) showed that annuli on vertebrae of *Scombrops* sp. were formed 1.5 mo later than on otoliths. In older fish the length of time for annulus formation may be extended further because of the decreasing annual addition to

TABLE 1.—Calculated total length at end of each year of life of male and female northern puffer.

Age group	Number of fish		Mean length at capture (mm)		Mean calculated total length (mm) at end of year of life							
					1		2		3		4	
	M	F	M	F	M	F	M	F	M	F	M	F
I	190	315	181	200	133	151	—	—	—	—	—	—
II	88	99	204	235	125	141	183	208	—	—	—	—
III	22	32	224	256	125	128	178	194	208	237	—	—
IV	7	9	236	274	146	137	185	194	213	238	227	259
Weighted mean length					131	147	182	204	209	237	227	259
$S_{\bar{X}}$ $t_{.05}$					±2.5	±2.2	±3.5	±4.2	±6.8	±6.1	±18.4	±15.6
Length increment					131	147	52	58	27	33	19	22
Calculated length range					93-191	90-203	140-231	161-260	172-246	197-279	201-250	236-289
Measured length range					120-225	125-259	161-232	181-264	199-256	223-292	211-263	246-295

vertebral length as body length increments decrease.

The second criterion was met by the agreement of measured lengths with length at each age as calculated by the Lee method (Lagler, 1956) (Table 1). Mean weighted lengths at each age coincided closely with the measured length for fish 1 yr younger because most fish were taken in the fall after the growing season and in late spring before the growing season. Total vertebral length and distance between annuli across the center of the vertebra were used to calculate lengths. Measurements were made along the shortest straight line connecting the approximate midpoints of annuli and the centrum edge (Figure 4). The distance between annuli could not be measured with certainty in 5% of the fish because the annular step was expanded into a broad, opaque shelf without a distinct end point (Figure 1d). The plot of body length on vertebral length was approximately linear, and the regression equation was $L = 27.52 + 3.28V$ with a significant correlation coefficient of 0.9827 where L is total length in millimeters and V is vertebral length in ocular micrometer units.

The third and fourth criteria were met by the correspondence of peaks in the length-frequency plots for each age group with peaks in the plot of the entire sample and by the regular increase in number of annuli with increasing body length (Figure 5). Overlap in mean body length among age groups was caused by early summer annulus formation in yearlings coupled with an extended period of annulus formation in older age groups. The wide range of lengths attained in the first growing season also contributes to the observed overlap of body lengths. The biomodal distribution of females in age group I was caused by the great number of fish larger than 210 mm taken in April and May from culled and sorted commercial pound net catches. Throughout the rest of the sampling period, the majority of fish came from unculled pound net and haul seine catches.

Therefore, the annulus on northern puffer vertebrae has been validated based on agreement with these criteria.

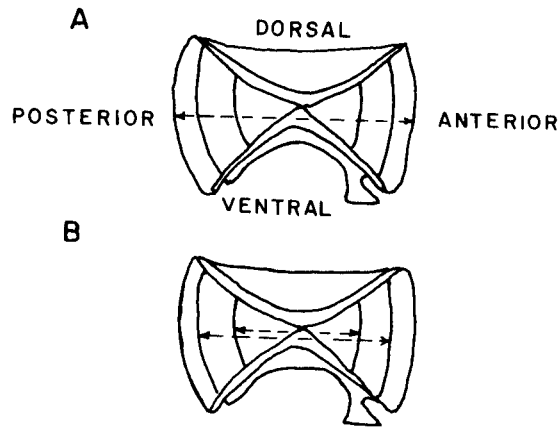

FIGURE 4.—Measurements taken on vertebral sections which were used in calculating length at age: (A) vertebral length, (B) distance between annuli across center of vertebra.

GROWTH

Young-of-the-year which were first collected in June from shallow eelgrass (*Zostera marina*) beds in the York River averaged 28 mm in length. Young-of-the-year in the fall of 1970 ranged from 88 to 184 mm (Table 2). The November sample came from a culled pound net catch; therefore, 160 to 184 mm is not a true indication of the length range after the first growing season. A better estimate is 83 to 195 mm based on lengths of yearlings without an annulus taken in April and May with a trawl and from unculled pound net catches. This corresponds closely to the calculated range of lengths at age I for all fish, 90-203 mm (Table 1). In December a live 37-mm juvenile was found floating at the surface near the mouth of the York River. Several fish of this size were collected in October on the east side of Chesapeake Bay during 1968 and 1969 by personnel of Virginia Institute of Marine Science. It is not known whether these small fish were hatched late in the season in Chesapeake Bay or were southern migrants from more northern spawning stocks.

The von Bertalanffy mathematical expression of growth as outlined by Ricker (1958) closely fits the weighted mean length at each age for age groups I to IV (Figure 6). The weighted mean length for age group I was calculated from age groups II, III, and IV because commercial gear is selective for the larger fish of age group I. Females were larger than males at all ages. Covariance tests (Ricker, 1958; Mottley, 1941; Snedecor, 1956) on the Ford-Walford lines for males and females indicated a significant difference in the lengths attained by males and females in the first growing season, but the difference in growth after the first season was not significant at the 5% level. The decrease in yearly increment of length was similar for both sexes (Figure 6).

REPRODUCTION

Differences between testes and ovaries in vascularization and size became apparent in

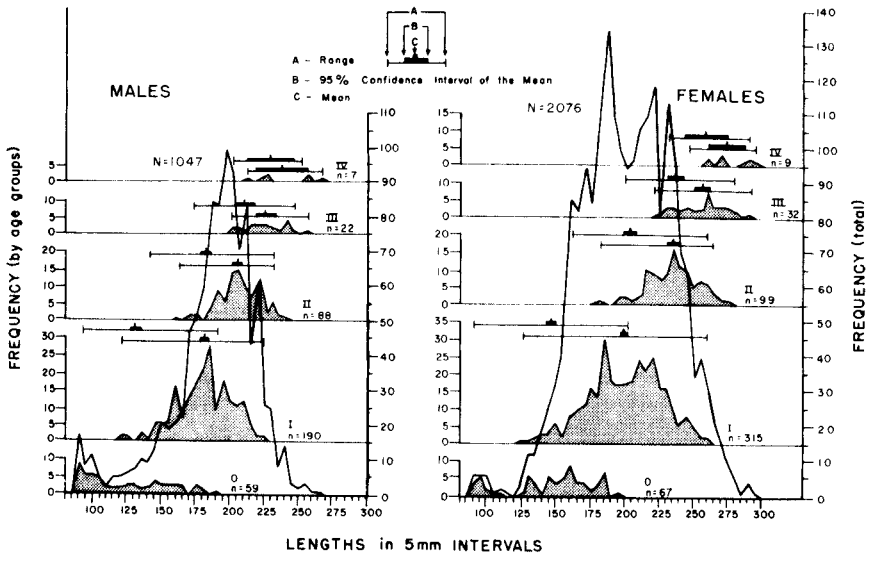

FIGURE 5.—Length-frequency distributions of the northern puffer (shaded polygons for each age group; unshaded polygon represents fish from the entire 1970 collection; distribution characteristics for each age group are shown above polygons with calculated lengths above measured lengths).

TABLE 2.—Length-frequency of young-of-the-year northern puffer.

Total length (mm)	June sex unknown	July sex unknown	Aug. M	Aug. F	Sept. M	Sept. F	Oct. M	Oct. F	Nov. M	Nov. F	Dec. sex unknown
18- 22	1										
23- 27	6										
28- 32	3										
33- 37	1										
38- 42											1
43- 47											
48- 52											
53- 57											
58- 62		1									
63- 67		1									
68- 72		2									
73- 77											
78- 82											
83- 87											
88- 92		2			5	4					
93- 97					2	6					
98-102		3	1		4	2					
103-107					1	1					
108-112			1			1					
113-117					1	1					
118-122					1						
123-127					1						
128-132					1	3					
133-137					2	3					
138-142					2	3					
143-147					1	4	1	1			
148-152						1					
153-157											
158-162									1	1	
163-167						1		1		1	
168-172										2	
173-177										1	
178-182										1	
183-187										2	
N	11	9	2		21	30	1	2	1	8	1

young-of-the-year by early September. Both sexes reached sexual maturity by the second growing season. In the spring the gonads of fish as small as 88 mm contained either milt or ova. Running ripe males were first obtained during the last week of May. Females were gravid during May but from June through the first week of July they were found in all three conditions, gravid, ripe, and spent. Few running ripe females were taken. Males were running ripe longer than females and may spawn a greater number of times.

By late July gonads of most fish taken from the mouth of the York River, Mobjack Bay, and lower Chesapeake Bay were spent and in recovery stages. However, males taken from the mouth of the Rappahannock River in mid-August were still running ripe, and many females were gravid. Welsh and Breder (1922) took ripe females along the New Jersey coast from July 30th to August 27th. Wheatland (1956:296-297) reported northern puffer spawning from late May until August in Long Island Sound. Time and duration of northern puffer spawning appears variable within Chesapeake Bay and along the middle Atlantic coast. By September gonads of puffers from lower Chesapeake Bay were in various stages of recovery. Neither milt nor developing ova were visible during October and November.

The ratio of males to females in May and November was approximately 1:1. However, females were consistently more abundant throughout the summer and early fall. During this period the ratio of males to females was 1:3. Males were least abundant during the peak of spawning in June and July. This change in the sex ratio may be related to reproductive behavior.

WEIGHT-LENGTH RELATIONSHIP

Logarithmic functions describing the exponential increase in weight with increasing length according to sex and gonadal condition were calculated (Figure 7). These plots indicate that logarithmic transformation of weight and length give a linear relation. About 89 to 99% of the variation in weight is associated with variation in length of pre- and post-spawning puffers of each sex. Puffers of both sexes were heavier after recovery from spawning (late July to November) than fish of comparable length before spawning (April to early July). Covariance tests (Mottley, 1941) indicated that this difference in weight was not significant in females but was in males at the 5% level. A large increase in muscle and liver tissue occurred during the growing season but was not quantified. By November fish appeared more robust and had larger livers than in April.

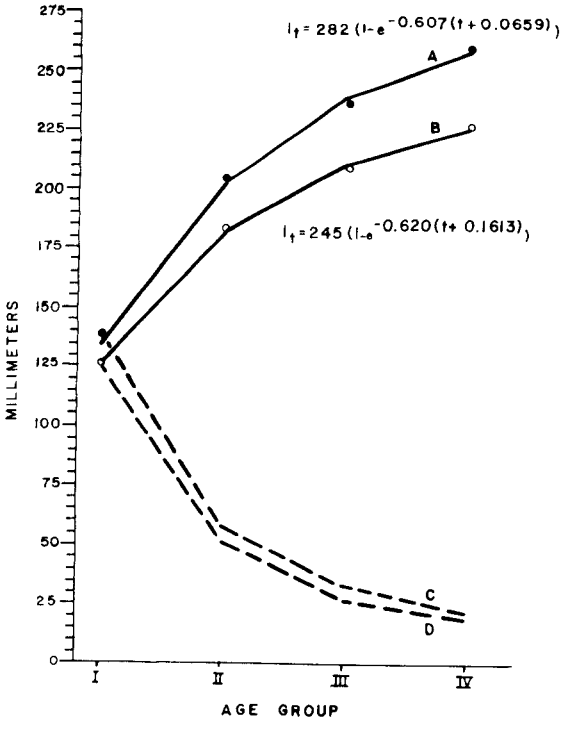

FIGURE 6.—Growth curves of female (A) and male (B) northern puffer fitted by the von Bertalanffly growth equation and plots of increments in length of females (C) and males (D) (circles represent calculated lengths).

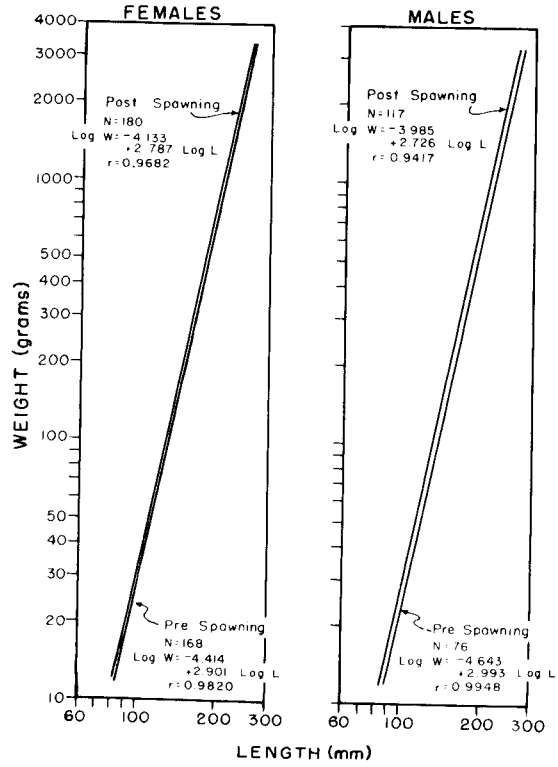

FIGURE 7.—Weight-length relationships for northern puffers in postspawning condition (late July to November) and in prespawning condition (April to early July).

ACKNOWLEDGMENTS

The authors express their appreciation to John V. Merriner, Mark Chittenden, Jr., Joseph G. Loesch, George C. Grant, and John J. Norcross for their counsel and criticism of the manuscript.

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PATTERN, NUMBER, VARIABILITY, AND TAXONOMIC SIGNIFICANCE OF INTEGUMENTAL ORGANS (SENSILLA AND GLANDULAR PORES) IN THE GENUS *EUCALANUS* (COPEPODA, CALANOIDA)

ABRAHAM FLEMINGER[1]

ABSTRACT

Methods for study of bilaterally symmetrical, serially homologous sets of integumental organs comprising hair, peg, and pit sensilla and the pores of integumental glands as well as their number and distribution in the genus *Eucalanus* are described.

A survey of these organs was carried out on geographically representative samples of the 17 discrete populations I recognize as valid species in the genus. The survey concentrated on adult females, but smaller numbers of adult males and some younger copepodid stages were also examined. Numbers and arrangement of these organs, estimates of variability, and their relationship to total length were established for each species. Phenetic similarity in integumental organ arrangement is shown to concur with other morphological features within the genus. Comparison is also made between number and arrangement of integumental organs and the geographical relationships among the members in each species group. Several new species in the attenuatus group are described on the basis of integumental organs and geographical distribution. A preliminary study of geographical variation in the circumglobal, broadly tropical species *E. subtenuis* is used to estimate the general complexity of genetic control and the use of these organs to study gene flow and population variability in planktonic species.

The integument of arthropods bears numerous organs that fall into two general classes: sensory receptors or sensilla, and glands. Sensilla are composed of one to several sensory neurons and generally two accessory cells, the latter forming the external features which may be in the form of an outgrowth, i.e., a hair, a cone, or a peg, or an ingrowth such as a pit or plate organ with sensory cell bodies located underneath (Laverack, 1969; Schneider, 1969; Stürckow, 1970). The regular presence of sensilla containing nerve fibers has been demonstrated histologically in a variety of different copepods (e.g., Fahrenbach, 1962; Elofsson, 1971).

In terrestrial arthropods integumental glands are highly variable in number, in distribution, and in morphological detail (Eisner and Meinwald, 1966). Integumental glands described from copepods tend to be rather simple sacs underlying the integument and communicate with the environment via a simple pore penetrating the integument (e.g., Clarke et al., 1962; Fahrenbach, 1962; Park, 1966).

On the body of copepods as in mystacocarids and other arthropods, sensilla and glands are in general distributed in bilaterally symmetrical patterns that are somewhat redundant on successive body segments, i.e., they appear to be serially homologous (Sewell, 1929, 1932, 1947; Fahrenbach, 1962; Hessler, 1969). It is highly probable that chemical communication via integumental organs, a widespread means for exchanging information among arthropods and vertebrates (e.g., cf. Johnston, Moulton, and Turk, 1970) is essential to copepods. Dioecious and nonparthenogenetic copepods must locate and correctly identify a potential mate without visual aids. This search and contact procedure is mediated by pheromones in *Eurytemora* and called "mate-seeking behavior" (Katona, 1973). Moreover successful culmination of the mating act requires attachment of the spermatophore

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Manuscript accepted May 1973
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

that permits passage of the sperm into the female's seminal receptacles (Wolf, 1905; Neubaur, 1913; Heberer, 1932; Fahrenbach, 1962).

Integumental organ systems are used widely in arthropod systematics. Indeed, in some groups, as for example, mosquitoes, dependence upon chaetotaxy is essential. A unique and particularly interesting application devised to permit identification of the fossilized remains of chydorid cladocerans in extinct lake sediments utilizes the number, size, and arrangement of integumental pores (Frey, 1959, 1962).

Despite repeated mention of integumental organs in the early copepod literature, attempts to apply them to study of marine species are rare. Notable exceptions must include With's (1915) detailed accounts of the sensilla surrounding the oral region for a number of species collected in North Atlantic samples. Sewell showed considerable interest in the general distribution of body integumental organs in planktonic copepods. His observations made on a broad variety of species are presented in scattered notes, remarks, and illustrations within the context of his faunal studies on Indian Ocean calanoids (1929, 1932, 1947). Unfortunately, the diminutiveness of these organs, Sewell's omission of methods for study, and a critical estimate of their reliability contributed to their neglect by subsequent workers. Two studies on bioluminescence in planktonic copepods (David and Conover, 1961; Clarke et al., 1962) call attention to the potential value of luminescing integumental glands for identifying the species of living specimens.

Conventional taxonomic systems organizing diversity among calanoid copepods are strongly dependent upon sexually modified structures of the adult (copepodid stage VI) sometimes assisted by nonsexual morphological or meristic features in the adult condition, as for example, spination and setation of appendages, segmentation of appendages, and segmentation of body tagmata. These sources of diagnostic information serve all hierarchial levels, species to family. Due to the nature of calanoid ontogeny, all of these structures assume their definitive state only in sexually mature adults. Thus, juveniles lie outside of existing systems, males and females are only rarely served by the same system, and genera that are relatively undistinguished in sexually modified structures tend to be "taxonomically difficult."

The primary purpose of this paper is to demonstrate the potential significance of sensilla and the pores of integumental glands on the body tagmata to the systematics and phylogeny of calanoid copepods. From a survey of these organs in the genus *Eucalanus*, their numbers and arrangements provide an objective basis for grouping related species, for distinguishing between sibling species, for relating adults of either sex to their respective species despite the elimination of other common characters by sexual dimorphism, for aiding in the specific identification of late immature copepods, and for the determination of regionalized cohorts that apparently lack unrestricted gene flow with morphologically similar cohorts in other regions.

REMARKS ON THE GENUS *EUCALANUS* DANA, 1853

Eucalanus is a universally familiar marine genus of eucalanid copepods. It contains primary consumers that form a conspicuous part of the epiplanktonic and uper mesoplankton in low to middle latitudes; some of the species are primarily oceanic, others are neritic. Within its habitat many of the species tend to be among the most abundant and largest (adult total length ranges from about 3 to 7 mm) of the regional copepod fauna. Since the inception of the genus for *E. attenuatus* (Dana, 1853), about 25 nominal species have been proposed. Contributions by Giesbrecht (1892), Johnson (1938), and Vervoort (1946, 1963) provide the framework for the genus and its taxa. The current world literature indicates 12 nominal species in active use. Two are represented by two subspecies each, yielding a total of 14 widely accepted taxa.

Though *Eucalanus* is a morphologically distinctive genus and its species are widespread and relatively abundant, frequent questions and confusion about the validity and rank of its nominal species and subspecies tarnish its literature. Difficulties with the identification

of the species emanate largely from the absence of distinctive sexually modified appendages, the few available meristic characters in setation and the widespread dependence of the existing taxonomic system upon relatively subtle shapes and proportions of segments and tagmata unsupported by rigorous estimates of variability. Difficulties and inconsistencies associated with the rank of the taxa in the genus *Eucalanus*, notably in the elongatus group, might be the product of several factors: e.g., the lack of accurate data on geographical distribution, uncertainties about the significance of morphological differences among the subspecies, the widespread lack of an adequate basis for viewing the planktonic taxon in the perspective of a biological population.

For example, questions or expressed doubts challenge the validity of separating *E. pileatus* from *subcrassus*, and the two have often been confused with *monachus* (Deevey, 1960; Grice, 1962; Vervoort, 1963; Lang, 1965). Confusion about *subtenuis* appears to trouble some (Fukase, 1957). Awareness of variation and taxonomic complexity within the nominal species *attenuatus* has been noted frequently (Sewell, 1947; Tanaka, 1956; Brodsky, 1962; Lang, 1965; Park, 1968), and similar questions must be raised regarding *dentatus* (Fleminger, unpublished data). Finally, a point must be made with regard to the elongatus complex. Three decades have passed since Johnson's (1938) perspicacious revision based on so few data, decades of increasing oceanographic activity and the accumulation of geographical and morphological observation on these common forms. Considering our increased experiences and understanding the logic of justification for the general practice of regarding *inermis* as a full species but continuing the two subspecies of *elongatus* and the two subspecies of *bungii* escapes me. On the basis of both morphology and geography the known similarities and differences between *inermis* and its two cognates and those between the subspecies of each of these cognates are about equal.

As part of an unpublished doctoral dissertation, Lang (1965) presented a taxonomic review and study of the distribution of *Eucalanus* in the Pacific Ocean based on plankton samples from the Scripps Institution of Oceanography Zooplankton Collections. Lang's data on the elongatus complex, published in 1967, contributed appreciably to our knowledge of geographical relationships among its populations. Though providing considerable evidence favoring extension of the revision initiated by Johnson (1938), his use of subspecies was retained. Expressed dissatisfaction with separation of *pileatus* and *subcrassus* and the considerable variation encountered in *attenuatus* s.l. were noted in the unpublished portion of Lang's dissertation.

My attempts to strengthen the *Eucalanus* section of Lang's manuscript for publication using the material on hand to clarify unresolved issues were unsuccessful. Two issues emerged: Resolution of the difficulties depended on 1) expanding geographical representation to encompass the world ocean and 2) the need to develop more reliable morphological characters for distinguishing the reproductively isolated populations within the genus. As conditions permitted, I gathered geographic records and specimens of *Eucalanus* in conjunction with global studies on other calanoid genera including *Clausocalanus* and *Pontellina* (Frost and Fleminger, 1968; Fleminger and Hulsemann, in press). In addition, I began to examine various structures of *Eucalanus* at relatively high magnifications (200× to 600×). Useful characters were found in the female genital segment, especially in the shape and arrangement of the seminal receptacles, and in the male fifth legs. For example, general similarities in the seminal receptacles provided a promising basis for phylogenetic groupings within the genus and a dependable means for separating at least some of the species of the pileatus group (Figure 1).

In the course of my survey, distinctive patterns in the distribution of integumental organs on the urosome became apparent. Recall of Sewell's (1947) use of these features to support his separation of *attenuatus* and *pseudattenuatus* prompted development of procedures described below to map integumental organs on dorsal and lateral surfaces of all body segments. The results provided the means for separating regional populations, species, and species

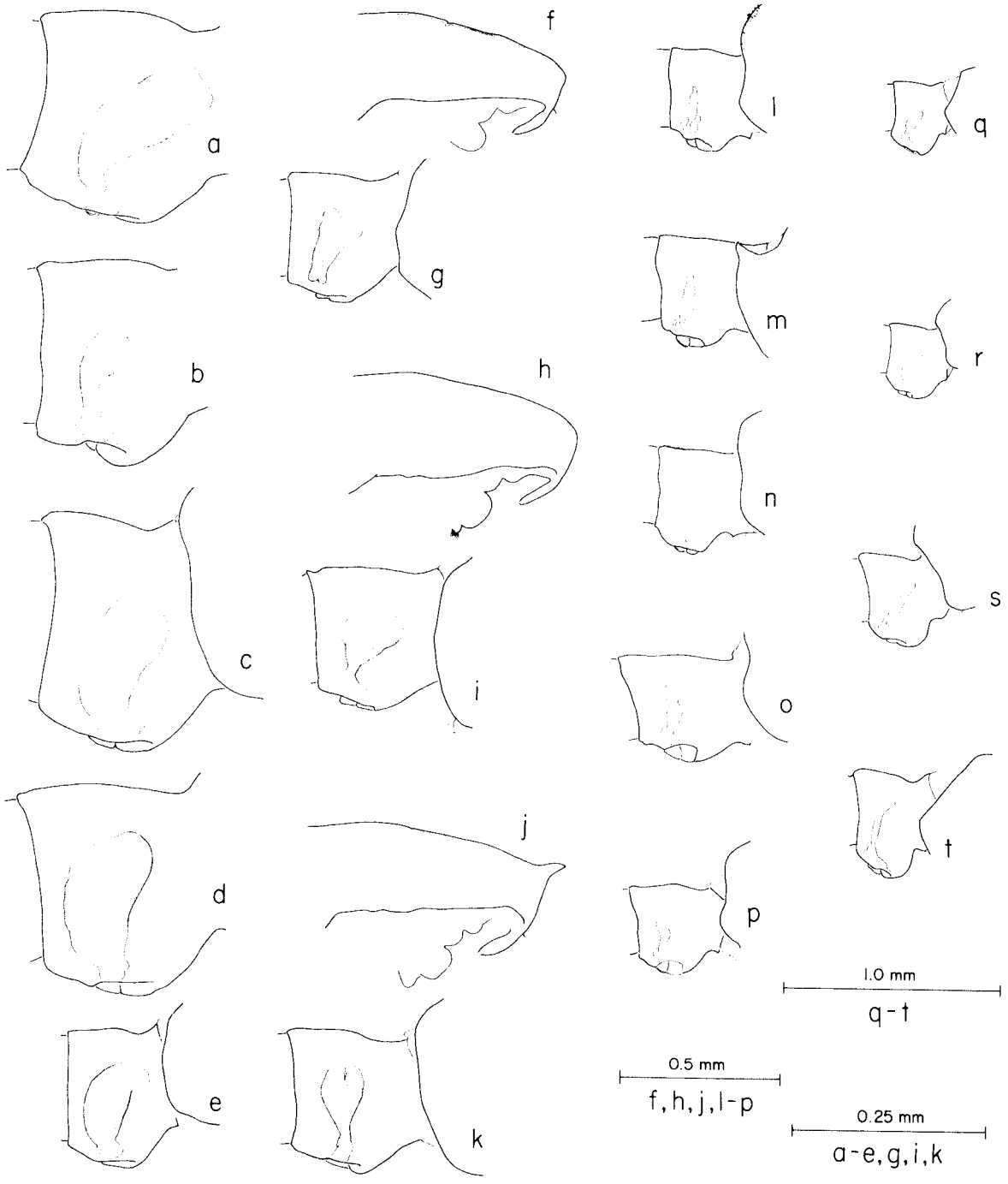
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FIGURE 1.—Genus *Eucalanus*. Genital segment, lateral view, female—**a**. *subtenuis* (Downwind 28); **b**. *mucronatus* (Monsoon 11); **c**. *crassus* (*Alaska* 4-36); **d**. *longiceps* (Monsoon 24); **e**. *monachus* (*Alaska* 5-7); **g**. *pileatus* (Lusiad VII Freetown); **i**. *subcrassus* (Lusiad II H-1); **k**. *dentatus* (Naga S11A 61-198); **l**. *elongatus* (Naga S11A 61-127); **m**. *hyalinus* (TRANSPAC 10 B); **n**. *inermis* (Muddauber 137-1); **o**. *bungii* (TRANSPAC 65 B); **p**. *californicus* (5606 50.80); **q**. *attenuatus* (EASTROPAC A 207); **r**. *sewelli* (*Atlantis* II-31-119); **s**. *parki* (Boreas 19); **t**. *langae* (Monsson 24). Anterior portion of head, lateral view, female—**f**. *pileatus* (Lusiad VII Freetown); **h**. *subcrassus* (Lusiad II H-1); **j**. *dentatus* (Naga 61-198). The shaded areas indicate the extent of sperm in the seminal receptacle. Positions for stations mentioned are listed in Snyder and Fleminger (1965, 1972).

groups within the genus and concurred with the evidence derived from study of the seminal receptacles. Greater appreciation of the reproductively isolated populations within *Eucalanus* (Table 1) also revealed the compelling need for much additional work on finer details to complete a satisfactory account of each species. The four geographical forms of *attenuatus* s.l. require comparative study of conventional morphological features in both sexes. Their geographical distributions should be amplified by reexamination of the great number of records and sorted specimens now in hand recorded collectively under *attenuatus* s.l.

Evidence of geographical variation in *subtenuis*, described below, requires additional study and should be examined in the context of co-occurrence with its sibling congener, *mucronatus*. Also, closer geographical scrutiny should be made of other widely ranging species showing broadly neritic habitat preferences such as *crassus* and *pileatus*.

Realization that the significance of integumental organs in copepods overshadows and holds more widespread interest than the genus *Eucalanus* is the basis for presenting the survey of sensilla and pores within the framework of an incomplete taxonomic review. Completing the global account of *Eucalanus* first would impose a long and unnecessary delay. Based on seminal receptacles, geography, and integumental organs, the essential diversity within the genus is now unmistakably clear. Details still

TABLE 1.—Author's provisional list of valid species and phylogenetic groupings comprising the genus *Eucalanus*. Summarized distribution and biogeographic assignment based on records confirmed by author.

subtenuis group:
1. *E. subtenuis* Giesbrecht, 1888. Broadly Tropical, circumglobal[1] in eutrophic oceanic waters; epiplanktonic. Figure 9e.
2. *E. mucronatus* Giesbrecht, 1888. Tropical, Indian Ocean to western Pacific in equatorial circulation systems[2]; epiplanktonic. Figure 9d.
3. *E. crassus* Giesbrecht, 1888. Tropical-subtropical, circumglobal in eutrophic broadly neritic waters; epiplanktonic. Figure 9a.
4. *E. longiceps* Matthews, 1925. Boreal-temperate, circumglobal, Southern Hemisphere West Wind Drift system (= Southern Ocean Transition zone); epiplanktonic? Figure 9b.
5. *E. monachus* Giesbrecht, 1888. Tropical-subtropical, Atlantic, broadly neritic; subsurface epiplanktonic. Figure 9c.

pileatus group:
6. *E. pileatus* Giesbrecht, 1888. Tropical-subtropical, circumglobal, coastal- neritic; epiplanktonic. Figure 11a.
7. *E. subcrassus* Giesbrecht, 1888. Tropical, Indo-Pacific, broadly neritic; epiplanktonic. Figure 11c.
8. *E. dentatus* Scott, 1909. Tropical, Austral-Asian seas; coastal epiplanktonic. Figure 11b.

elongatus group:
9. *E. elongatus* (Dana, 1849). Tropical, Indian Ocean to western Pacific in equatorial circulations; epiplanktonic? Figure 13b.
10. *E. hyalinus* (Claus, 1866). Tropical-subtropical, circumglobal especially in eutrophic, oxygenated waters adjacent to boundary currents; deep epiplankton to upper mesoplankton. Figure 13c.
11. *E. inermis* Giesbrecht, 1892. Eastern Tropical Pacific in eutrophic, low oxygen water; deep epiplankton to upper mesoplankton. Figure 13a.
12. *E. bungii* Giesbrecht, 1892. Boreal-subpolar, North Pacific, and Bering Sea; epiplanktonic to upper mesoplanktonic.
13 *E. californicus* Johnson, 1938. Temperate, North Pacific, West Wind Drift system (= North Pacific Transition zone); deep epiplanktonic to upper mesoplanktonic. Figure 13d.

attenuatus group:
14. *attenuatus* (Dana, 1849). Tropical, Indo-Pacific equatorial circulation systems; epiplanktonic. Figure 15d.
15. *sewelli* sp.n. Tropical-subtropical, circumglobal; epiplanktonic. Figure 15c.
16. *parki* sp.n. Temperate, North Pacific, West Wind Drift system (= North Pacific Transition zone); deep epiplanktonic to upper mesoplanktonic. Figure 15a.
17. *langae* sp.n. Temperate, circumglobal, Southern Ocean West Wind Drift system (= Southern Ocean Transition zone); deep epiplanktonic and upper mesoplanktonic. Figure 15b.

[1] Evidence of three regionalized populations: Eastern Tropical Pacific; Tropical Indian Ocean to western Tropical Pacific; Tropical Atlantic.
[2] Two questionable records from Tropical Atlantic: Florida Current (Owre and Foyo, 1967) and Gulf of Mexico (Fleminger, unpublished data). Forehead pointed but basal segment of mandible with two setae.

TABLE 2.—Adult female *Eucalanus*: collecting localities and numbers of specimens surveyed for sensilla and pores. All samples taken with open nets ½ m or larger in diameter at the mouth and towed horizontally or obliquely at epiplanktonic depths.

Cruise or ship	Station	Latitude	Longitude	Date	Species*																
					A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
Afram[1]	F-1	14°00′N	17°30′W	?			5		2												
Alaska[2]	4-36	23°31′N	86°44′W	24 Jan 52	2																
	5-9	26°00′N	87°32′W	26 May 52																2	
	11-5	29°07′N	88°47′W	30 May 53					3	2											
Arctic Exped.	1310(4)	38°49′N	168°03′W	19 Jul 47													5				
Atlantis II-31[3]	15	24°42′N	49°42′W	19 Jan 67																1	
	31	20°07′N	20°36′W	27 Jan 67			3														
	33	19°21′N	16°52′W	28 Jan 67					3												
	34	18°35′N	16°59′W	28 Jan 67	4		2			2											
	35	17°54′N	17°20′W	28 Jan 67			5														
	36	15°45′N	17°45′W	29 Jan 67					7												
	43	08°08′N	19°48′W	9 Feb 67					5											7	
	45	05°41′N	21°29′W	11 Feb 67																1	
	46	04°09′N	22°45′W	11 Feb 67											1					1	
	48	00°56′N	25°20′W	12 Feb 67					2												
	51	00°07′N	28°43′W	14 Feb 67					2												
	74	29°11′S	40°06′W	12 Mar 67																3	
	80	26°20′S	46°05′W	28 Mar 67																2	
	119	30°23′N	64°17′W	30 Apr 67																1	
	122	35°12′N	67°15′W	2 May 67																2	
	123	36°59′N	68°50′W	2 May 67											3						
Azul I	F-1	23°38′N	109°36′W	5 Sep 62					4												
Boreas	19	41°57′N	165°06′W	2 Feb 66													1	2			
	64	58°21′N	168°57′E	15 Feb 66												5					
	148	48°55′N	157°55′E	12 Mar 66												4					
Bureau of	F1832	34°02′S	17°44′E	8 May 62					1										1		
Sea Fisheries[4]	A2000	33°04′S	17°16′E	8 Sep 62											3						
	A2003	33°05′S	17°47′E	8 Sep 62					1												
	90.28D	33°28′N	117°47′W	13 Jun 52													3				
CalCOFI 5206	120.50	27°33′N	115°52′W	18 Apr 55													5				
5504	144G.15	24°28′N	110°28′W	24 Aug 57																2	
5708	137.30	25°20′N	112°45′W	10 Jul 58									2								
5807	PT 18	22°31′N	105°53′W	26 Aug 61						5		5									
6108	27	03°30′S	121°54′W	9 Feb 53					2												
Capricorn	31	06°31′S	124°41′W	13 Feb 53																	3
	32	07°58′S	124°11′W	14 Feb 53									1								
	5	15°41′N	64°12′W	14 Jun 65					2												
Chain 49[3]	9	19°52′N	69°57′W	16 Jun 65					7												
	13	14°48′N	68°09′W	26 May 66																1	
Chain 60[3]	15	12°58′N	73°34′W	28 May 66			5														
	4	42°33′N	162°09′W	17 Jul 56											1			4			
Chinook	8	40°28′N	173°04′W	3 Aug 56											2			4			
	NT 3	22°28′N	177°21′E	5 Apr 68					1												
Circe	NT 8	17°29′N	141°38′E	16 Apr 68					1												
	NT 11	05°11′N	123°58′E	20 Apr 68																1	1
	NT 14	08°28′N	118°24′E	23 Apr 68				5						2							
	NT 15	07°16′N	115°20′E	24 Apr 68					4												
	NT 16	05°39′N	112°39′E	25 Apr 68											2						
	NT 25	19°04′N	87°47′E	17 May 68																	1
	NT 27	09°46′N	83°31′E	23 May 68																	2
	NT 30	07°27′N	77°42′E	27 May 68																4	
	NT 33	19°42′S	63°12′E	28 Aug 68					2												
	Camera 3	26°28′S	46°04′E	29 Sep 68					1												
	Dm 2.75.63	11°00′S	110°00′E	26 May 63							2										
Diamantina[5]	36	06°05′N	49°53′E	16 Aug 64																	3
Dodo VI	49	10°19′N	53°11′E	20 Aug 64								2									
	54	10°23′N	51°43′E	22 Aug 64	2																
	55	10°14′N	51°19′E	22 Aug 64				4						5							
	55-15	09°45′N	51°31′E	23 Aug 64					1											1	
	60	11°58′N	55°11′E	26 Aug 64					2	1		7		1						2	
	86	12°00′S	55°55′E	5 Sep 64								5									
Downwind	19B	46°25′S	123°38′W	4 Dec 57		7															
	20C	44°36′S	112°08′W	10 Dec 57															1		
	22A	40°39′S	92°02′W	17 Dec 57															1		
	24	34°30′S	79°30′W	20 Dec 57																2	
	28	27°08′S	72°02′W	31 Dec 57					3				3							3	
EASTROPAC	J 087	01°34′N	105°00′W	26 Feb 67					3												
	A 207	13°23′S	126°00′W	19 Feb 67																	3
Eastropic	82	08°00′N	104°00′W	9 Dec 55									6								

TABLE 2.—*Continued*

Cruise or ship	Station	Latitude	Longitude	Date	Species* A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
El Golfo I	I CN2	24°38′N	109°22′W	14 Nov 63									2								
	II CD1	25°35′N	110°14′W	17 Nov 63									1								
	VI AN2	28°37′N	112°56′W	25 Nov 63																1	
El Golfo II	XIV B2D1	26°31′N	111°03′W	22 May 65																1	
EQUAPAC	H 20	10°00′S	163°00′E	17 Aug 56																	3
	S 1	20°43′N	158°27′W	21 Aug 56				5													
	S 20	00°51′N	167°14′W	29 Aug 56					10												
	S 21	00°02′N	166°59′W	29 Aug 56																	1
	S 23	01°55′S	166°52′W	30 Aug 56																	2
Gascoyne[5]	G1.24.63	15°31′S	110°00′E	10 Feb 63																	2
	G1.28.63	21°26′S	110°01′E	12 Feb 63					3											2	
	G1.29.63	23°10′S	110°00′E	12 Feb 63					2												
Gill[6]	2-74	34°24′N	75°36′W	10 May 53					2												
	8-9	28°20′N	79°48′W	12 Sep 54					3												
Lusiad II	H 1	01°16′N	103°52′E	28 Jun 62							6										
	H 7	06°58′N	79°50′E	28 Aug 62						3											
	29	05°02′N	53°01′E	31 Jul 62										1							
	45	05°00′S	62°00′E	14 Aug 62						1		4									
	51	00°57′S	62°19′E	17 Aug 62										1							
Lusiad V	46	00°02′N	58°52′E	30 Mar 63					4												2
	48	00°01′S	63°00′E	1 Apr 63																	
	50	00°00′	67°02′E	2 Apr 63					4												
	54	00°08′N	74°59′E	4 Apr 63				2	2					1							
	64	04°54′N	92°02′E	19 Apr 63										1							
	94	02°01′N	53°02′E	5 May 63										1							
Lusiad VII	75 H 7	00°28′S	10°51′W	4 Jul 63					6												
	MWT 14	32°29′S	09°04′E	6 Jun 63		1													4		
	MWT 19	31°11′S	00°56′E	9 Jun 63											2				5		
	MWT 79	00°55′N	11°29′W	6 Jul 63																1	
	Freetown	08°30′N	13°17′W	11 Jul 63						3											
Monsoon	7	09°11′S	127°33′E	22 Oct 60				2			2			2							
	9	13°19′S	109°35′E	7 Nov 60										2							
	11	11°15′S	103°32′E	20 Nov 60										2	1						
	13	17°01′S	93°29′E	25 Nov 60					1												
	22	37°50′S	85°22′E	26 Dec 60		2									2				1		
	24	39°18′S	119°51′E	9 Jan 61		2									2				1		
	26	64°11′S	165°56′W	13 Feb 61																	1
	31	32°35′S	160°56′W	8 Mar 61											2						
Naga	61-13	08°18′N	104°42′E	13 Jan 61								4									
	61-124	10°12′N	103°50′E	10 Feb 61								2									
	S10 61-107	09°19′N	103°58′E	10 Feb 61						4		4									
	S11A 61-198	09°11′S	115°33′E	27 Mar 61				2			11									2	2
	S11B 61-268	03°20′S	127°21′E	26 Apr 61																2	1
NORPAC	1 H	45°58′N	134°22′W	30 Aug 55												2	2				
	24-42H	40°26′N	146°37′W	21 Aug 55											1			6			
Scan	IV-1	33°49′N	139°10′E	15 Jun 69					5												
Shellback	90	06°01′S	95°46′W	26 Jun 52											2						
	109	03°41′S	81°30′W	4 Jul 52									1								
T. Washington	13	11°16′N	64°10′W	2 Jan 66					6												
TO-58-1 (Scot)	35	09°45′N	96°04′W	7 May 58																	4
Transpac	10 B	38°22′N	141°23′W	31 Jul 53											3						
	32 B	52°29′N	176°09′W	15 Aug 53												3					
	64 B	46°54′N	153°55′E	15 Sep 53												1					
Troll	40	31°10′N	128°48′E	10 Apr 55	3							2									
	45 A	31°17′N	137°29′E	12 Apr 55													7			1	1
	56	34°21′N	138°29′E	13 Apr 55					3												
Zetes	14	39°00′N	154°58′W	17 Jan 66														2			

* Species code:

A *crassus*	G *dentatus*	M *californicus*
B *longipceps*	H *subcrassus*	N *parki*
C *monachus*	I *inermis*	O *langae*
D *mucronatus*	J *elongatus*	P *sewelli*
E *subtenuis*	K *hyalinus*	Q *attenuatus*
F *pileatus*	L *bungii*	

Unless identified by footnotes the samples are from the Marine Invertebrate Collections of Scripps Institution of Oceanography.

[1] University of Rhode Island.
[2] National Marine Fisheries Service, Galveston Laboratory.
[3] Woods Hole Oceanographic Institution.
[4] Bureau of Sea Fisheries, Cape Town, Republic of South Africa.
[5] Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
[6] National Marine Fisheries Service, Beaufort Laboratory.

remaining to be analyzed will not affect basic conclusions to be drawn about the sensilla and pores in *Eucalanus*. For purposes of this paper nomenclatural recommendations have been limited to an essential minimum. The species I recognize are summarized in Table 1. Aside from the integumental organs and dorsal and lateral views of the body, description of other characters is restricted to a few basic features (Figure 1).

Functional significance aside, the diagnostic qualities of body patterns of pores and sensilla should be examined in the Copepoda on a broad front.

MATERIALS AND METHODS

Systematic analysis of sensilla and pores was carried out routinely on adult females of all *Eucalanus* populations known to me (Table 1). Numbers of specimens and collecting localities are shown in Table 2. Sample size varied for each species according to its geographical distribution, the overall frequency of variation, number and arrangement of sensilla and pores, and the availability of specimens. The number of regularly occurring pores and sensilla on the body of a specimen is large, ranging from 80 to 140 depending on the species, and their unvarying arrangement in strongly patterned, bilaterally symmetrical arrays eliminated the need for examining large numbers of specimens in all but one case. Specimens were selected at random from within each zooplankton sample, but collecting localities were deliberately chosen to represent the known distribution of the species; i.e., as material on hand permitted representative specimens of each species were selected for examination from peripheral, intermediate, and central localities. Observations on adult males and on copepodite stages IV and V were also made on all species but were ordinarily limited to only two to four specimens each.

Sensilla and pores are exceedingly difficult to observe in *Eucalanus* using conventional light microscopy without staining and clearing specimens. Two simple methods were employed in this study. One served in examining general external features of the various types of sensilla and their proximity to glandular pores. Specimens were immersed for about 24 h in a combined clearing agent and stain, consisting of 9 parts lactic acid and 1 part of a 1% solution of chlorazol black E (CBE) in 70% ethanol. Specimens were then transferred directly to a drop of glycerol on a glass slide for microscopic examination.

More intensive clearing is necessary for accurate and systematic tabulation of body pores and sensilla. All tissue was removed from within the integument by heating specimens in a 10% aqueous KOH solution at 80° to 100°C for 2 to 4 h. Rapid boiling should be avoided to prevent the integument from breaking apart. The ratio of KOH solution to specimens was about 50 cc per individual. The KOH digestion was repeated using fresh solution if precipitates or fatty substances remained within the integument. The concentration of KOH has been increased on occasion to 25% with satisfactory results. For ease in viewing during microscopic analysis, it is essential in preparing the specimen to digest all tissues and eliminate precipitates from within the integument.

Following digestion the empty, still intact, exoskeleton is prepared for staining by a rinse in distilled water for 1 to 2 min and transfer to 70% ethanol for 1 to 2 min. These rinses should be repeated if flocculent precipitates remain within the integument. Immersion for about 30 sec in a solution of 1% CBE dissolved in 70% ethanol stains specimens intensely. Staining is terminated by flooding the preparation with distilled water and transfer of the specimen through a brief rinse in water to a drop of glycerol placed on a glass microscope slide for examination. Stained specimens suspended in glycerol may be stored indefinitely in appropriate slide storage boxes.

Washing and staining were carried out under a stereomicroscope using 3-spot deep depression slides and with solutions changed with the aid of finely drawnout glass pipettes equipped with rubber bulbs. Sensilla are usually lost in this process, leaving the stained cuticle punctured by clear perforations. Glandular pores also appear as clear perforations permitting light to stream through, but differ in shape and appearance of the margin as described below (p. 973).

Length measurements were carried out with the aid of a stereomicroscope at 24× and 40× magnifications depending on the size of the species. The microscope was equipped with a mechanical stage and an eyepiece reticle bearing a ruled scale of 100 divisions. Total length (TL) was taken from the right lateral view in two steps: one measurement along an imaginary line extending from the anteriormost tip of the forehead to the dorsalmost juncture between prosome and urosome (Fleminger, 1967) and the second along an imaginary straight line from the dorsalmost juncture of prosome and urosome to the posteriormost point on the right furcal ramus omitting the setae.

Examination of specimens for perforation number and distribution was carried out with the aid of a compound microscope equipped with a mechanical stage at magnifications of 150× to 600×. A camera lucida was used in the preparation of drawings to approximate spatial arrangement of perforations in each form.

The outline drawing with perforations was reproduced by electrostatic duplicating machine for use on subsequent specimens of the species as a data recording form. Allowance was made for small variations in the distance between regularly occupied perforation sites; all missing and additional perforations were recorded on the form together with length measurements, sample, and specimen number. No attempt was made to estimate variability in the distance between adjacent perforations.

GENERAL OBSERVATIONS

Three general types of sensilla were found in *Eucalanus* (Figures 2, 3). They resemble relatively simple types found in other arthropods (e.g., see Snodgrass, 1935; Bullock and Horridge, 1965; Schneider, 1969) and are as follows:

1. Hair (trichodea) sensilla (Figure 2d); slender, elongated, uniformly attenuated, and unarmed; roughly 20 to 150μ in length and 1 to 5μ in diameter at the base; observed only on thoracic segments II to V.

2. Peg (basiconica) sensilla (Figure 2g); with pointed or rounded apex, ranging from 14 to 27μ in length, 1 to 3μ in diameter; they are widely distributed over the prosome and usually occur adjacent to the pore of an integumental gland.

3. Pit (coeloconica) sensilla (Figure 2i): shallow circular depressions in the integument, 3 to 6μ in diameter, the center raised in a nipple-like protuberance that stains intensively in CBE-lactic acid; they were observed in few species and only on the cephalon and anterior thoracic segments.

As a rule the sensilla are lost during the course of tissue digestion and staining. Perforations representing the sites of sensilla in prepared specimens appear under the light microscope as simple round openings. The innermost margin stains noticeably lighter than the surrounding integument. Large perforations ($\geqslant 4\mu$) from large hair sensilla may have a craterlike margin on the outer surface (Figure 2e). Under the light microscope the walls of the perforation may slope to form a larger elliptical outline on the inner surface of the integument. Perforations derived from pegs are simple and about 1 to 2μ across (Figure 2h). Perforations derived from pit sensilla appear as a pair of very small openings separated by a slender ridge (Figure 2j). One or more of the three types of sensilla were found on all segments of the cephalon and thorax. One aesthetask-like sensillum, usually weakly plumose, is present distoventrally on the furcal rami in all species. No other sensilla were observed on the urosome.

The other class of cuticular perforations are formed by the ducts of underlying integumental glands (Figure 2b). The glandular pore tends to vary from a semicircular to a slitlike opening of 4 to 7μ across the maximum dimension when viewed from above (Figure 2f-j). The margin stains as intensely as the surrounding cuticle and at least a section of the circumference turns inward toward the underlying hypodermis.

My use of the term pore in connection with integumental glands does not imply relationship to a different integumental feature, pore canals (Richards, 1951) discussed below.

Microscopic examination (300× to 600× magnification) of intact specimens, especially those belonging to the elongatus group (treated

with CBE-lactic acid), frequently confirmed the connection between the pore and a single, gland-like, spherical to ovoid sac, roughly 30 to 75μ across the maximum dimension (Figure 2b), and not unlike the glands noted in other copepods (Fahrenbach, 1962; Clarke et al., 1962; Park, 1966). Integumental glands may occur on all the segments of the body (Figure 3).

A notable feature of the perforations (both sensilla and gland duct types) is their relationship to formation of the integument. Resembling that described in other arthropods (Dennell, 1960), the exoskeleton in *Eucalanus* has been observed in the present study to consist of prisms apparently laid down over individual cells of the hypodermis. The prisms are joined by interprismatic septa presumably of secreted procuticle that stains darker with CBE than the prisms. The organ-forming and neural cell extensions pass between cells of the hypodermis. Hence passage of these features through the integument occurs in the interprismatic septa, a feature frequently observed in this study in all of the species. In specimens with well differentiated prisms, numerous minute perforations formed by the pore canals (~0.1 to 0.3μ) may be seen within each prism. As Dennell (1960, p. 461) states, perforations observed on the surface of the cuticle formed by integumental organs and pore canals cannot be confused; the latter are numerous, minute, and within the margins of individual prisms; the former are an order of magnitude larger and lie in the septa between prisms. Pore canals were not considered in the analysis of *Eucalanus* perforations.

LIMITATIONS

Failure to obtain total elimination of tissue and precipitates in the hot alkali treatment and insufficient staining were the commonest sources of difficulties in carrying out microscopic examination of the perforations. Specimens that had moulted shortly before fixation and species in which the exoskeleton is relatively flabby (e.g., species of the elongatus group) require greater care in staining and handling.

Occasionally, areas of perforation size fail to take up as much stain as the surrounding

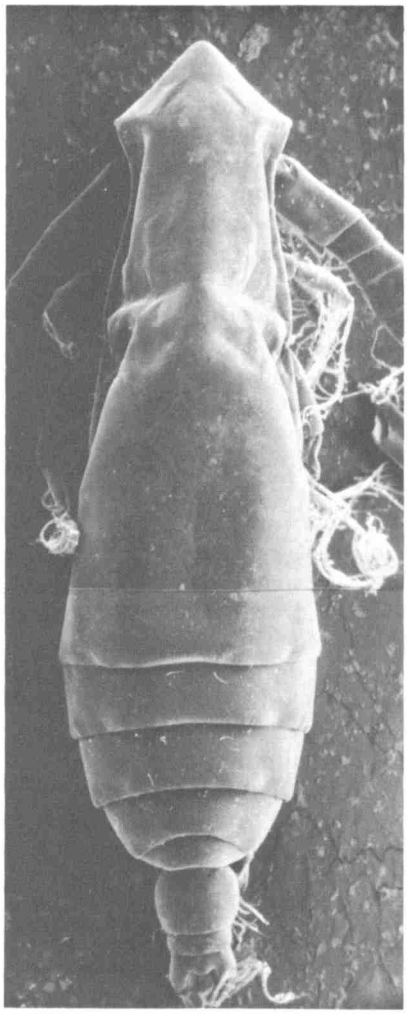
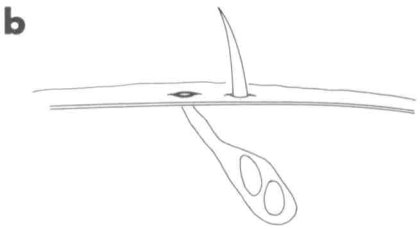
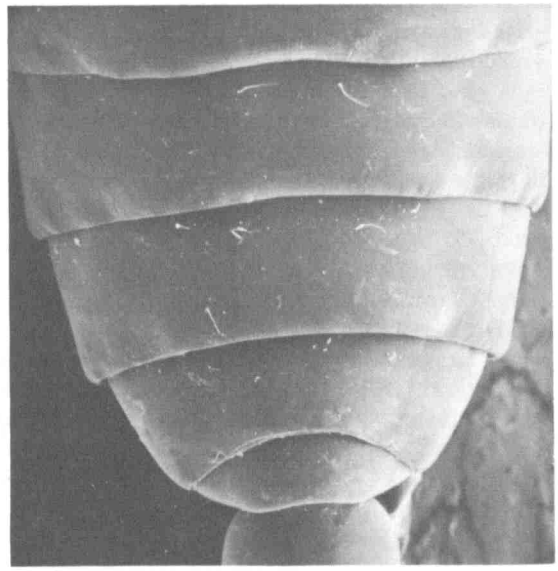
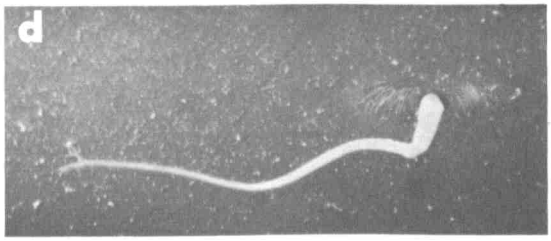
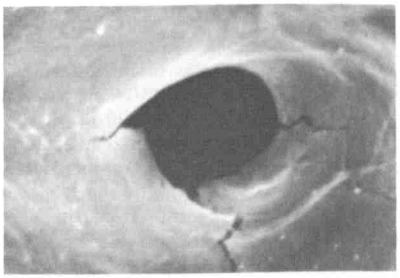


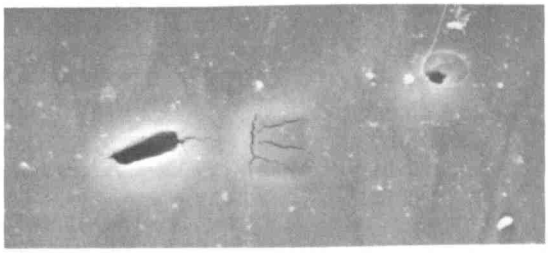
FIGURE 2.—Appearance of intact integumental organs and the perforations left by these organs in the integument of KOH-treated specimens of *Eucalanus subtenuis* (adult females). Specimens prepared for scanning electron microscope by Freon critical-point drying, vacuum coating with gold-palladium and examined with the aid of a Cambridge Stereoscan S.E.M. **a.** entire specimen in dorsal view; 1 mm ≅ 24.4 μ. **b.** schematic sectional view of typical combination of peg (basiconicum) sensillum and integumental gland with pore. **c.** thorax in dorsal view; 1 mm ≅ 8.5 μ. **d.** hair (trichodeum) sensillum; 1 mm = 1 μ. **e.** perforation in integument left by hair sensillum in KOH-treated specimen; 1 mm = 0.25 μ. **f.** pore of integumental gland; 1 mm = 0.25 μ. **g.** typical arrangement of peg sensillum (right) and pore (left). **h.** perforations in integument left by peg sensillum (right) and pore (left) in KOH-treated specimen. **i.** pit (coeloconicum) sensillum (left) and pore (right) of integumental gland. **j.** perforations in integument left by pit sensillum (left) and pore (right) in











KOH-treated specimen. Figures g-j: scale, 1 mm = 0.5 μ. (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.)

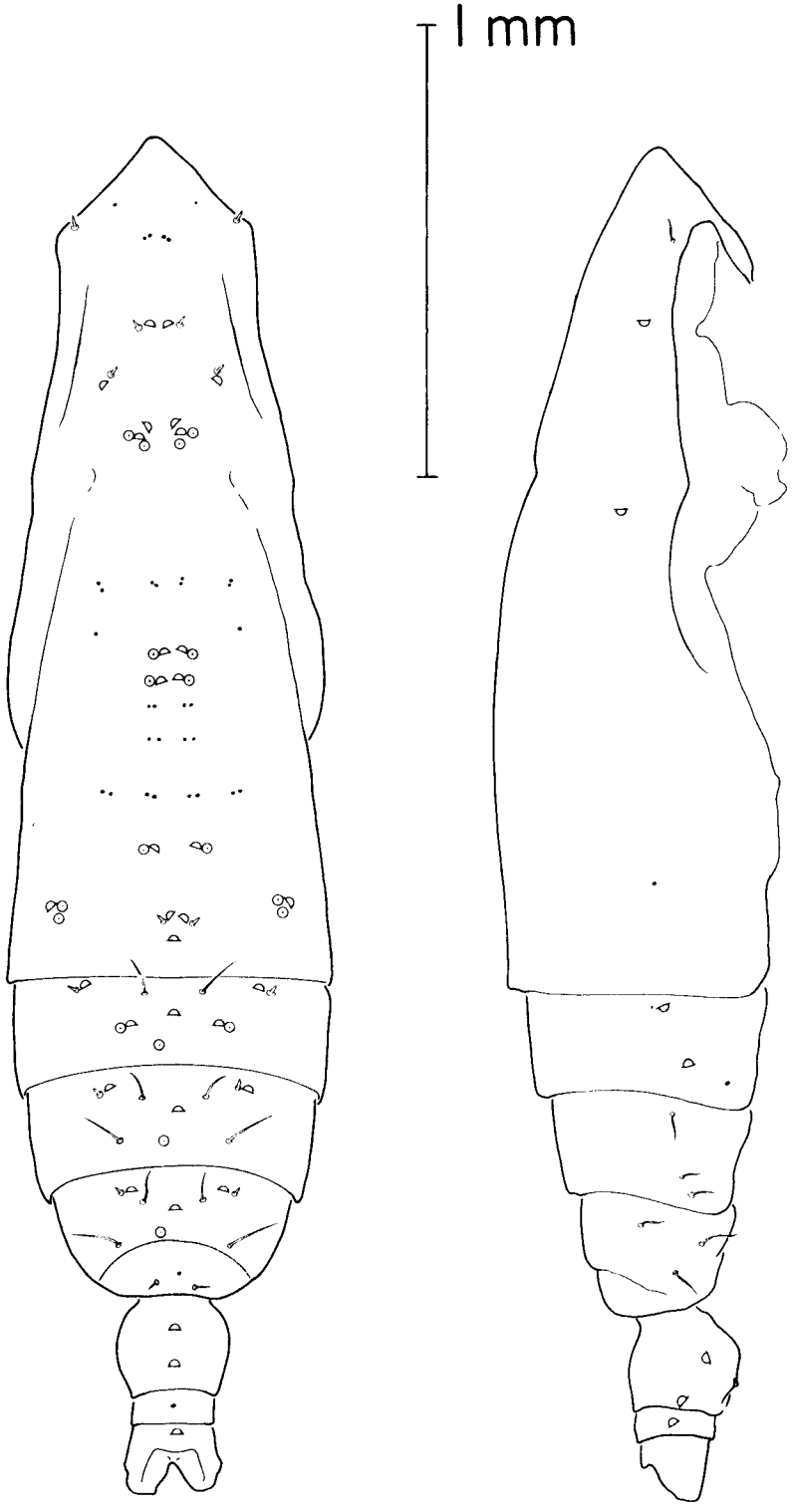


FIGURE 3.—Distribution of sensilla and pores of integumental glands in an adult female specimen of *E. subtenuis*; dorsal view on left, lateral view on right. Hair sensilla are shown as curving, attenuated, and varying in length; peg sensilla are short, straight and blunt; pit sensilla are shown as an open circle with a dot in the middle. Pore of integumental glands shown as a half circle. Solid dots represent perforation sites observed in specimen after KOH-CBE treatment and represent organs missed during microscopic examination of the specimen before digestion of tissues; intact specimen cleared in CBE-lactic acid solution for 24 h prior to examination. All organs shown enlarged and schematically, though position is based on records obtained from camera lucida drawings; microscopic examination carried out at magnifications of from 150x to 600x.

integument and appear as light spots that may be mistaken for perforations. Direct comparison with a true perforation is helpful to note the reduced intensity of illumination passing through the light spot. Light spots tend to occur in the vicinity of usual perforation sites found in the genus and may represent incomplete or arrested development of a gland or sensillum. Light spots were not recorded as perforations.

A number of perforations relatively difficult to observe were not examined systematically. They include the dorsal surface of the furcal rami and cephalolateral sites in the vicinity of the first and second maxillae and the maxilliped. The ventral surfaces of the prosome appear to have few perforations but were not examined systematically.

DISTRIBUTION OF INTEGUMENTAL ORGANS

In each species the three types of sensilla and pores of integumental glands maintain essentially constant topographic relationships in arrangement and number on both the dorsal and lateral surfaces of the body, as seen for instance in *subtenuis* (Figure 3). One notable pattern appearing in all of the species for example is the distribution of dorsal hair sensilla, two appearing on the second thoracic segment, four on the third, and four on the fourth, the hairs always being arranged in transverse symmetrical rows, two hairs in each row (Figure 3). Another type of persistent pattern is the regular occurrence of the peg sensillum adjacent to the pore of an integumental gland (Figure 2). The organs are distributed in bilaterally symmetrical patterns that exhibit serial homologies. Serial homology is indicated by the partial to complete repetition of patterns in adjacent segments. As is shown below in the account of the different species, the closer the general morphological similarities between individual pairs of species the more similar the overall perforation patterns.

Every morphological type of sensillum or gland pore occupies a topographically unique position, i.e., a designated site within the framework of the overall bilaterally symmetrical pattern. The designated sites appear in KOH-treated specimens as morpholigically distinctive perforations in the integument. Each body segment has a constant number of organs (Table 3) arranged in a distinctive pattern that is repeated with negligible variation within the series of specimens representing the species. Hence on an empirical basis the appearance of the same type of perforation in approximately the same topographic relationship in the series of specimens representing the species is compelling evidence that similarly positioned organs of the same type are homologous among individuals of the same species. That is, they appear to bear the morphogenetic relationships that are a primary basis for regarding the same cephalic or thoracic appendage among individuals of a population as being homologous. Thus the array of regularly appearing integumental organs (designated sites) among the individuals of the species is assumed to comprise a homologous set characteristic of the species.

Among the species of a species group, integumental organs appearing in topographically similar positions on the same body segment in all of the species are viewed as comprising a homologous set characteristic of the species group. The integumental organs common to the various species groups comprise the homologous set characterizing the genus. The implication of phylogenetic redundancies is seen in comparing perforation patterns among the species (see Figures 9, 11, 13, 15) presented below and in a segment-by-segment comparison of the number of regularly appearing sites in the species and species groups (see Table 3 and Figures 8, 9, 11, 13, 15).

In the case of a fused series of somites, i.e., a tagma such as the cephalosome, the patterns are arranged in accord with the sets of body appendages in the tagma. The number of homologous sites within the members of a species group is relatively high (cf. Figure 8 with Figures 9, 11, 13, 15) and the number of homologous sites within the genus (55) is remarkably high (Figure 6) considering that the species range from a low of 83 sites in *longiceps* to a high of 131 shared by *bungii* and *californicus* (Table 3).

TABLE 3.—Total number of lateral and dorsal perforation sites, by body and abdominal segments in ≥80% of *Eucalanus* specimens examined. Body segments indicated by corresponding appendages.

	Anterior body segments								Midbody segments					Abdominal segments					
Genus & species	A1	A2	Mnd	Mx1*	Mx2*	Mxp*	P1	Total	P2	P3	P4	P5	Total	Abd 1+2	Abd 3	Abd 4	Abd 5	Total	Grand total
Eucalanus:																			
Number of homologous sites in genus	8	6	4	4	2	4	1	29	5	6	6	2	19	2	2	—	1	5	53
subtenuis group:																			
subtenuis	12	6	10	10	4	4	17	63	14	18	15	3	51	6	2	1		9	122
mucronatus	8	6	6	6	4	4	9	43	12	14	13	3	42	6	2	1		9	94
crassus	8	6	8	6	—	4	5	37	11	13	13	3	40	4	2	1		7	84
longiceps	8	6	6	6	—	4	5	35	11	13	13	3	40	5	2	1		8	83
monachus	8	6	6	6	—	4	5	35	13	15	13	3	44	5	2	3		10	89
Number of homologous sites in group	8	6	6	6	—	4	5	35	11	13	13	3	40	4	2	1		7	82
pileatus group:																			
pileatus	8	6	6	8	—	4	5	37	11	14	14	3	42	5	2	3		10	89
suberassus	8	6	6	10	4	4	9	47	15	18	14	3	50	7	4	1		12	109
dentatus	8	6	6	8	4	4	9	45	15	18	14	3	50	7	4	3		14	109
Number of homologous sites in group	8	6	6	8	—	4	5	37	11	14	14	3	42	5	2	1		8	87
elongatus group:																			
elongatus	10	6	4	6	2	8	7	43	7	10	10	4	31	8	4	4	1	17	91
hyalinus	12	6	8	6	10	16	9	67	9	11	10	4	34	7	4	4	1	16	117
inermis	14	6	8	4	6	12	11	61	7	10	9	3	29	4	2	—	3	9	99
bungii	12	6	6	4	12	16	15	71	13	14	12	4	43	8	4	4	1	17	131
californicus	12	6	6	4	12	16	15	71	13	14	12	4	43	8	4	4	1	17	131
Number of homologous sites in group	10	6	4	4	2	8	7	41	5	7	9	3	24	4	2	—	1	7	72
attenuatus group:																			
attenuatus	12	6	4	6	4	12	11	55	13	16	16	6	51	8	2	7		17	123
sewelli sp.n.	12	6	4	6	4	12	11	55	13	12	12	6	43	6	2	5		13	111
parki sp.n.	12	6	4	6	4	12	11	55	13	12	12	4	41	7	3	5		15	111
langae sp.n.	12	6	4	6	4	12	11	55	13	12	12	4	41	8	3	10		21	117
Number of homologous sites in group	12	6	4	6	4	12	11	55	13	12	12	4	41	6	2	3		11	107

*Lateral perforation not counted.

VARIATION AT DESIGNATED SITES

As described above designated sites are those topographic positions on each segment occupied by an integumental organ of a morphologically specified type that occur within the context of a relatively fixed pattern on each segment. The pattern on each segment is primarily characteristic of the species and includes elements characteristic of the species group and of the genus as well.

No variation was observed in the morphological nature of the organ occupying the designated site during occasional examination of randomly selected intact specimens or in the characteristic type of perforation observed at the site in the sample of the species that was examined. Small differences in the relative distance between adjacent sites within the pattern of a segment were observed frequently. They are negligible, however, with respect to influencing the accuracy of recording details for each specimen. Replicate counts of the same specimens taken on subsequent days usually yielded similar results; the few departures from zero variation ranged from 1 to 3%. Spatial variation was not examined closely. Better understanding of its significance should be developed, as it probably reflects individual morphogenetic and possibly genetic differences.

Quantitative variation in terms of failure to find a perforation at a designated site or finding a perforation in excess of the regular number characterizing the segment (Table 3) is remarkably low. To the extent that spatial variability does occur, it may be argued that the basic

scoring of individual perforations as representing particular sites contains an element of judgment on the part of the observer.

Constant repetition of pattern (per body segment per species) in the distribution of perforations (see Figures 9, 11, 13, 15) and the small amount of variation in the total number of perforations observed in each species (Table 4) indicate that personal judgment by an experienced observer introduces negligible bias. The range about the mean number of perforations per species (Table 4) does not exceed 10% with exception of *subtenuis*, a special case actually representing three allopatric populations occupying separate regions of the world's tropical belt. Indeed, perusal of Table 4 indicates that quantitative variation is not a simple function of either sample size or total number of perforations.

With respect to presenting variation scored for each species, the frequency of a perforation appearing at each designated site is presented symbolically in three categories: sites occupied in all specimens, sites represented in 80 to 99% of the specimens, and sites represented in 10 to 79% of the specimens (see Figures 9, 11, 13, 15).

TABLE 4.—Number of localities, size of pooled sample, and number of observed perforations in species of *Eucalanus*.

Species	Localities	Specimens	Perforations Range	$\bar{x}$	s
subtenuis group:					
subtenuis					
Atlantic Ocean	15	50	125-141	134.8	3.2598
Indian Ocean	10	24	119-139	130.0	4.9111
Pacific Ocean	10	36	114-135	123.6	4.9750
mucronatus	6	20	86-91	89.4	1.5355
crassus	4	11	83-85	84.0	0.4713
longiceps	4	12	79-83	82.7	1.1572
monachus	5	17	87-91	88.8	0.8106
pileatus group:					
pileatus	8	21	85-94	90.5	2.0384
subcrassus	9	34	109-117	110.1	2.4722
dentatus	5	24	109-115	111.5	1.3313
elongatus group:					
elongatus	11	19	90-101	94.9	3.3154
hyalinus	14	25	109-121	114.8	3.2490
inermis	7	16	94-106	99.7	2.7500
bungii	5	15	127-133	130.1	1.8086
californicus	6	23	125-135	131.2	2.1829
attenuatus group:					
attenuatus	16	26	117-126	122.0	2.0703
sewelli sp.n	24	43	107-113	110.3	1.2070
parki sp.n.	5	18	109-114	111.5	1.3323
langae sp.n.	7	14	115-121	117.6	1.7388

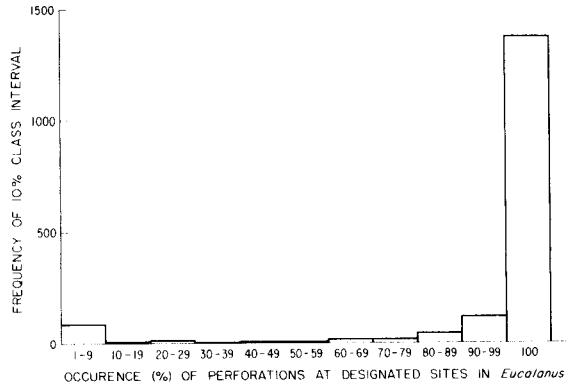


FIGURE 4.—Frequency of occurrence of perforations at designated sites on the dorsal and right lateral integument of *Eucalanus*. The frequencies found in each species are grouped in class intervals of 10% and each class is summed for all species. Each designated site represents the occurrence of a particular type of integumental organ appearing in a KOH-treated specimen as a distinctive perforation in the integument and occupying a topographically unique place within the framework of the overall bilaterally symmetrical pattern found in the species. For purposes of this graph the appearance of such a distinctively placed perforation in only one specimen of the pooled sample for the species is sufficient to include it among the number of designated sites found in the species. Graph based on examination of 448 adult female specimens representing 17 species that yielded a total of 1,709 designated sites as defined above.

Sites found in less than 10% of the sample have been omitted. A general summary of the variability at each site is presented in Figure 4. Roughly 80% of the sites were represented by a perforation in every specimen. In 10% of the sites a perforation was observed in 80 to 99% of the sample. The remaining 10% of the sites were occupied at lower frequencies, but this category includes a number of sites that show remarkable patterns of geographical variation in *subtenuis* that are discussed below.

Designated sites do not vary with respect to type of organ they represent, but one class of variation in topographic relationship is noteworthy. As mentioned above, peg sensilla regularly occur adjacent to the pore of an integumental gland. The peg and pore pairing often varied with respect to the position of the two relative to the orientation of the segment. The peg tends to be lateral to the pore, but this may be completely reversed or appear at any intermediate stage about a 360° arc. As a pair, how-

ever, they occupy a discrete position relative to the remainder of the sites on the segment. This class of variation also deserves increased attention as a potential fine scale indicator of intrapopulation genetic variation.

Thus for application of integumental organs to copepod systematics at or above the rank of species, variation encountered during this study appears to be of no consequence. Moreover, the intraspecific variability observed may on the basis of experience with *subtenuis* provide a dependable, measurable source for studying population homogeneity and gene flow.

PERFORATION SITES IN THE GENUS

Intra- and interspecific comparisons of perforation number and arrangement are facilitated by compelling evidence that sites similar in location and associated organ (i.e., gland pore or sensilla type) within and between species are homologous. Tables 3 and 4 and figures of individual species summarize the evidence that in general perforation number and topographic arrangement are essentially constant and characteristic for each species. Further, all of the available observations indicate that the type of organ found at any particular perforation site is also constant.

As shown below, constant differences in numbers and arrangement of perforations between the morphologically more similar species are small. Quantitative and topographic differences are correspondingly greater between species that are more dissimilar morphologically (e.g., Figures 9, 11, 13, 15). However, the total number of perforation sites in the genus appears to be about two times the number found in any one species (Figure 5).

To construct Figure 5 an assessment of the extent of interspecific homology in sensilla and pores of *Eucalanus* was obtained by rigorous comparison of all the species segment by segment. The tabulation was restricted to designated sites, i.e., those occurring in 10% or more of the specimens of each species. As described above, sites are judged to be homologous if they occur on the same segment in the same general position relative to the pattern characteristic of the segment and represent the same kind of organ (gland pore or type of sensilla). The place of insertion of the segment's paired appendages and the topographic position relative to the other sensilla and gland pores of the segment aid in locating perforation sites. Overlaps of camera lucida sketches were also helpful when allowance was made for relative and absolute differences in size. Allowance was also made for small-scale variation of one or two perforations relative to another one or a set as in peg and pore pairings; small differences in the spacing between adjacent sites and rotation of one site relative to another was observed frequently within the general pattern arrangement of individual species.

The analysis reveals 163 different dorsal pore and sensilla sites and 30 lateral sites on each side of the body. The total number of different sites within the genus (223) is less than twice that of the species with the highest individual score (Table 3). Thus most sites in the genus appear to be common to many of the species and an appreciable number is common to all (Figure 6).

Examination of small numbers of copepodid stages IV and V, adult males of all species and a few specimens of copepodid stage III indicated conformity of each to the pattern characteristic of the species, except for segments that undergo sexual modifications in the process of maturation.

PERFORATION NUMBERS AND PATTERNS AMONG THE SPECIES GROUPS

Interspecific comparison of the perforations observed in *Eucalanus* is, as already mentioned above, greatly simplified by the not unreasonable assumptions that repetitious similarities in pattern are dependent upon and a direct reflection of genetic similarities. With this as a working hypothesis, reducing and assimilating the distribution of perforation sites was enhanced by assembling similarities among the different species and by using for comparisons all other constant topographic features of the integument.

All the species have in common 37 tergal sites, best seen in dorsal view and 9 pleural sites

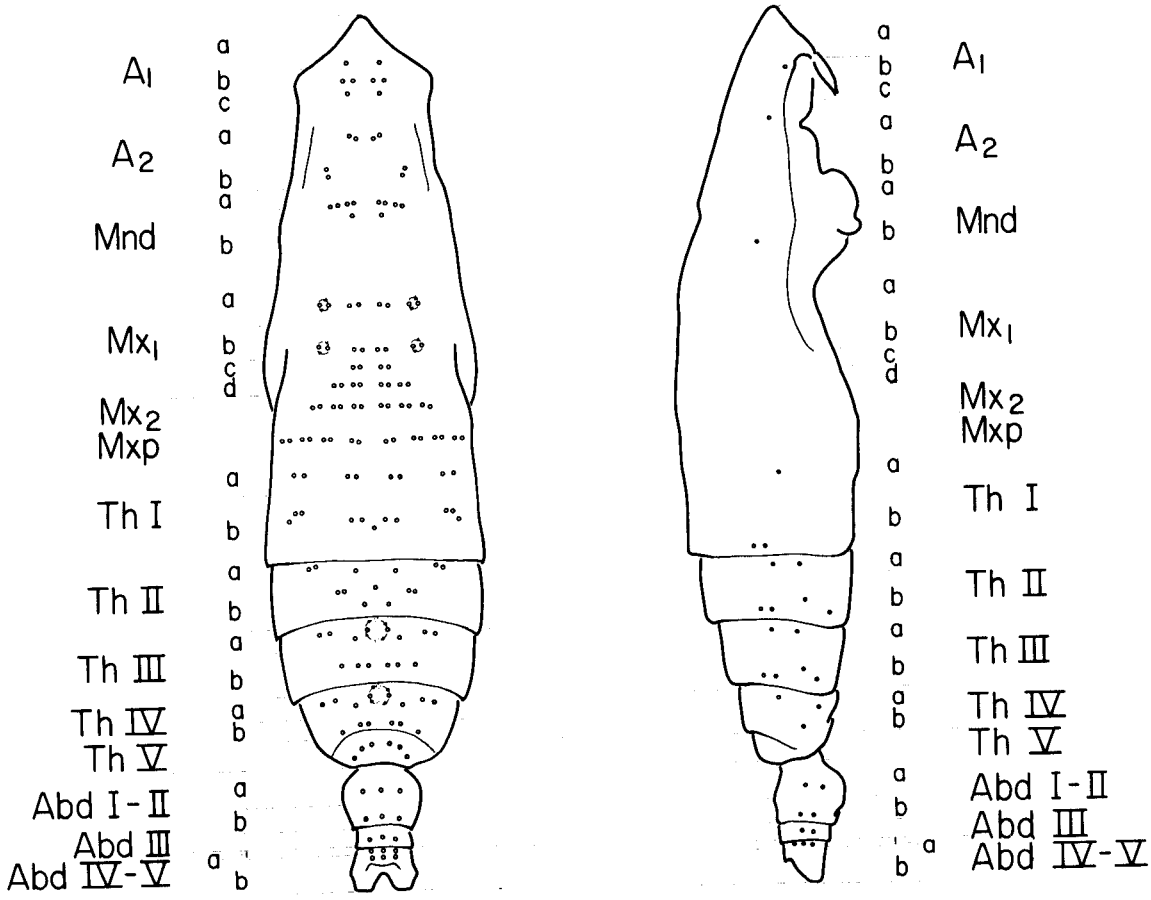


FIGURE 5.—Schematic presentation of all designated sites observed in adult female *Eucalanus*. Open-ended system for designating individual sites provided by abbreviations of appendages or abdominal segments together with row (a, b, . . .) and in dorsal view number to left or right of midline, or in lateral view number in dorsal to ventral order.

Cephalosome in *Eucalanus* contains the cephalon extending from the first antennae (A1) to the second maxillae (Mx2), the maxillipedal somite (Mxp = Th0) and the first pedigerous somite (ThI). Thoracic segments ThII, ThIII, ThIV bearing swimming legs 2, 3, and 4 are separate from one another, but ThV lacking a pair of swimming legs in the female is partially fused to ThIV. In the female abdomen the first two somites are fused (Abd.I-II) during maturation of the genital segment. Abd.III is separate and Abd.IV is separate in the elongatus species group but fused to Abd.V in the other three species groups. The furcal rami are fused to Abd.V in all the species.

on each side, best seen in lateral view (Figure 6). Tergal sites on the cephalosome are pores and peg sensilla; on ThII to ThV, all but two (ThII-mb and Abd.IV-V-m) are hair sensilla; the two exceptions are pores. The pleural sites of the cephalosome appear to include both pores and peg sensilla. Pleural sites on ThII to ThIV are hair sensilla and those of the urosome are pores.

Within the genus four groupings may be distinguished by virtue of additional perforations that appear in common only among the species comprising each group (Figure 8). Additional support for these groupings may be found in other morphological characters of taxonomic value in *Eucalanus* such as segmentation of the abdomen and the shape of the seminal receptacles in females (Figure 1), fifth legs of adult males, and various details in the appearance of the cephalosome. The groupings and their complement of species and geographical forms are listed in Table 1.

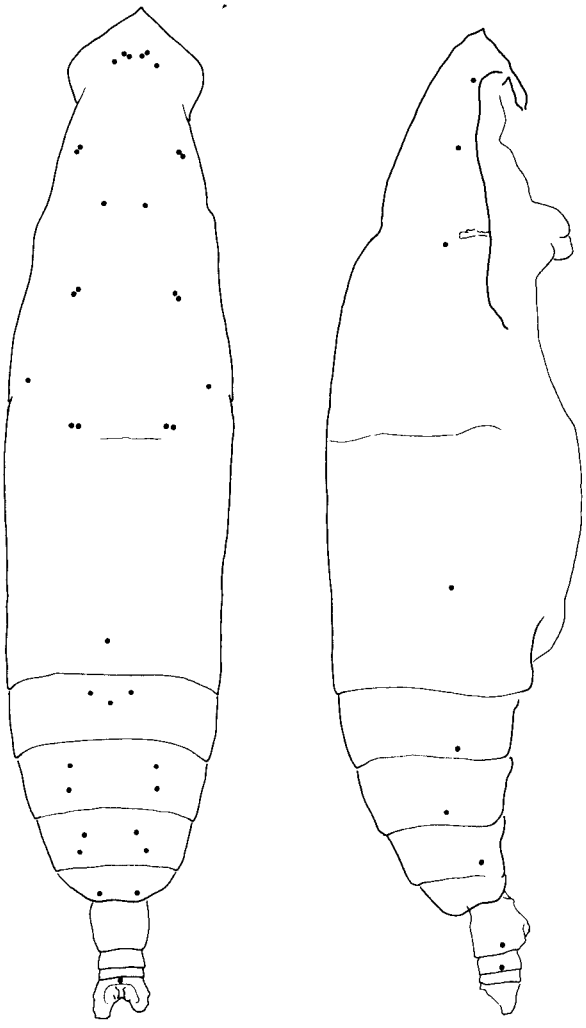


FIGURE 6.—Designated sites (represented by a dot) occurring at frequencies of ≥80% within the pattern of each species and present in every species of the genus *Eucalanus*. Dorsal view on left, lateral view on right; outline of organism based on *elongatus* used solely as vehicle to show topographic relationships of sites.

The Subtenuis Group

Sites distinguishing the subtenuis group (Figure 8c) appear on various portions of the cephalosome and thorax. On the cephalon the mandibular somite bears two pairs of tergal sites. ThI shows only three sites arranged in a transverse row. ThIII and ThIV are similar, both being characterized by bilateral tergal pairs lying outside and anterior to the quadrangle of hair sensilla and a single medial site slightly posterior to the anterior hair sensilla. The subtenuis group contains five generally accepted species that occur typically in eutrophic oceanic waters.

Sites in *E. crassus* (Figure 9a) are identical with the pattern of the species group except that the perforations of row a on the mandibular somite are increased to two pairs (Mnd T-a-*l*1, *l*2 and r1, r2).

E. longiceps differs from the group pattern solely by the presence of a single mediodorsal site on the genital segment (Figure 9b).

E. monachus (Figure 9c) differs from *longiceps* in two features: the occurrence of a transverse row of three tergal sites across Abd.IV-V and three pleural sites on ThII, ThIII, and ThIV.

E. mucronatus (Figure 9d) shows a small increase in the number of sites. On the cephalosome up to six pairs of tergal sites may appear in addition to the group number between the somite of the second maxilla and the maxillipedal somite. ThI shows an additional tergal pair on either side of the middorsal site. ThII and ThIII have an additional site in the posterior row (ThII T-b-*l*1 and ThIII T-b-*l*1) to the left, but the symmetrical homologue to the right of the middorsal axis is absent. On the abdomen the genital segment has two middorsal sites and Abd.III may have one.

E. subtenuis (Figure 9e) has the largest number of regular perforation sites in the genus. Dorsally, in addition to the species group number, two more pairs appear in the somite of the second antenna, up to eight more pairs between the somites of the first and second maxillae, four more pairs on the maxillipedal somite, four more pairs on ThI, and two more pairs on ThII. ThII and ThIII have a single asymmetrical tergal site (pore) within the quadrangle formed by the hair sensilla as in *mucronatus*. Laterally, ThII and ThIII both show one or more pairs on either side.

Within the group, *subtenuis* shows the largest number of perforations (Figure 10) and the most extensive geographical distribution relative to areal extent and sympatry (unpublished). Differences between *subtenuis* and its closest cognate, *mucronatus*, are concentrated in the

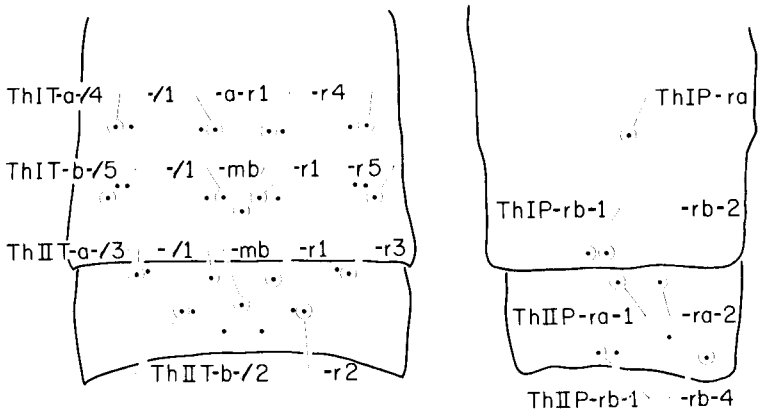


FIGURE 7.—Scheme for codifying designated sites in *Eucalanus*. Left: dorsal view of posterior portion of cephalosome and thoracic segment 2. Right: lateral view of same.

First unit of code for referring to a designated site is reference to the somite, using the appropriate appendage in the case of the cephalosome or the body segment (ThII, ThIII, . . ., Abd.I-II, Abd.III, . . .). Second unit indicates whether it is dorsal, i.e., tergal (T), or lateral, i.e., pleural (P). Tergal sets are grouped in transverse rows. Thus, perforations are designated as being on the right (r) or left (l) of the mid-sagittal plane and are numbered from the medialmost to the lateralmost (1, 2, . . .). Transverse rows are lettered in an anterior-to-posterior sequence (a, b, . . .). Perforations falling on the midsagittal plane are termed medial (m) and lettered in an anterior-to-posterior sequence (a, b, . . .).

Both right (r) and left (l) laterial, i.e., pleural (P), sets are numbered in a dorsal-to-ventral sequence (1, 2, . . .). For convenience anterior-to-posterior division into rows is utilized following the corresponding set of tergal sites and are also lettered in an anterior-to-posterior sequence.

Various sites in dorsal and lateral views in the figures are codified according to the scheme proposed above.

the tagma also showing the most extensive geographical variation. Geographical variation in *subtenuis* distinguishing the Indian, Atlantic, and East Pacific populations is discussed below (p. 999). The other four species fall within a narrow overlapping range (>80 to <95 perforations). Differences in number and arrangement especially in the genital segment characterize *crassus* and *mucronatus*, the two species overlapping geographically in the Indian and West Pacific Oceans. Differences in number and pattern also involving the genital segment distinguish *crassus* and *monachus* which co-occur in the Atlantic Ocean. *E. crassus* also differs from *longiceps*, a temperate species of the Southern Hemisphere, and from *subtenuis* in the sites on the genital segment.

The Pileatus Group

The pileatus group (Figure 8d) consists of three sibling species that are only weakly differentiated in general appearance from that of the subtenuis group. The pileatus group also strongly resembles the subtenuis group in perforation pattern, the primary differences being in a small increase in the number of middorsal sites on the thoracic segments. One additional pair occurs on the somite of the first maxilla, and single anterior middorsal sites are found on ThIII and ThIV. Three tergal sites may appear on the genital segment, but the posterior two of the three sites are irregular in occurrence in *pileatus;* therefore, at the species group level, the genital segment is best characterized by a single middorsal site.

Among the individual species *E. pileatus* is essentially undifferentiated from the pattern in the species group (Figure 11a). It lacks tergal sites on the somite of the second maxilla and on Abd. III, although it has three tergal sites across Abd.IV-V. It also lacks posterodorsal pleural sites on ThI, ThII, and ThIII. The genital segment may have one or two posterotergal sites in addition to the regular middorsal site.

E. dentatus and *subcrassus* share a number of features that separate them from *pileatus*, namely two tergal pairs of sites on the somite of the

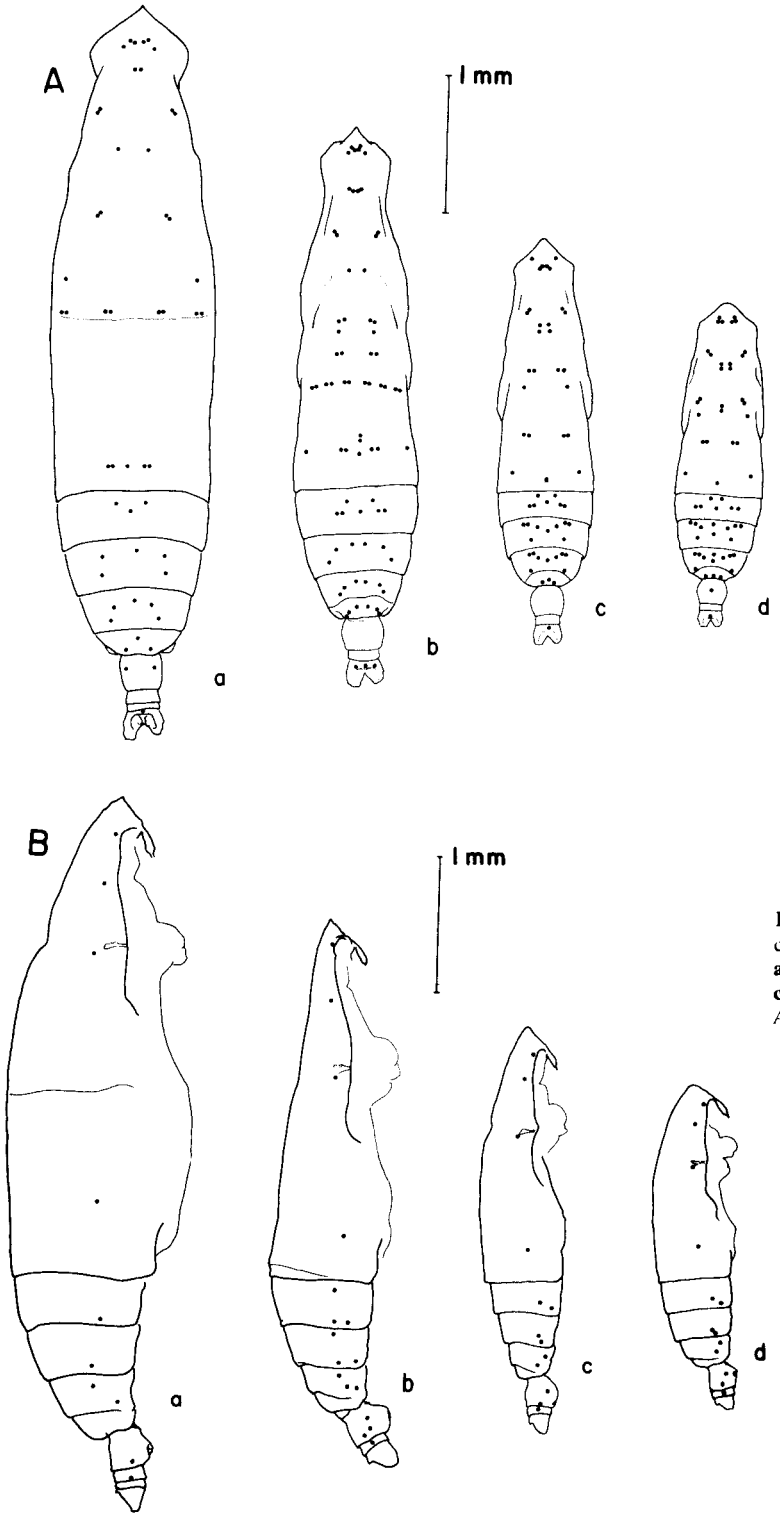


FIGURE 8.—Sites common to each species group of *Eucalanus*. From the left, **a.** elongatus group, **b.** attenuatus group, **c.** subtenuis group, **d.** pileatus group. A, dorsal view. B, right lateral view.

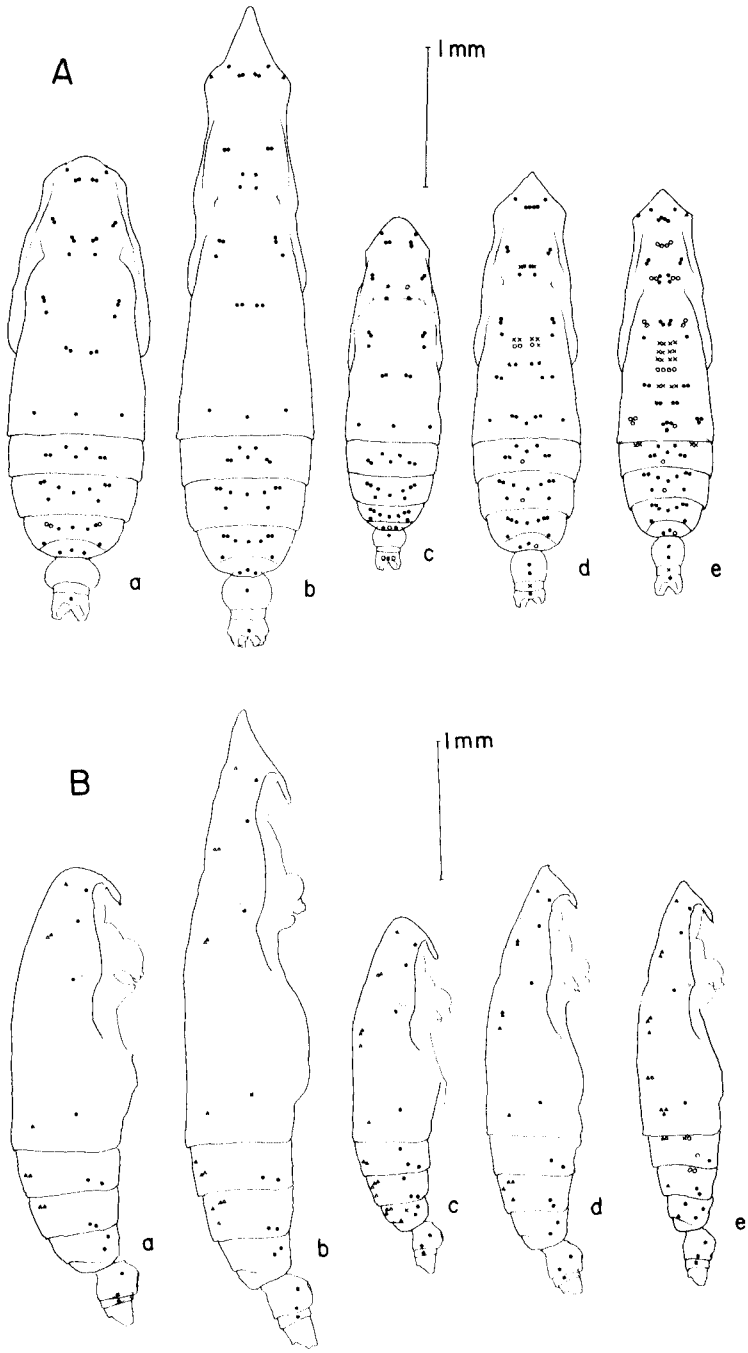


FIGURE 9.—Species of the subtenuis group of *Eucalanus:* **a.** *crassus,* **b.** *longiceps,* **c.** *monachus,* **d.** *mucronatus,* **e.** *subtenuis.* Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. A, dorsal view. B, lateral view. All figures of adult females made with the aid of a camera lucida.

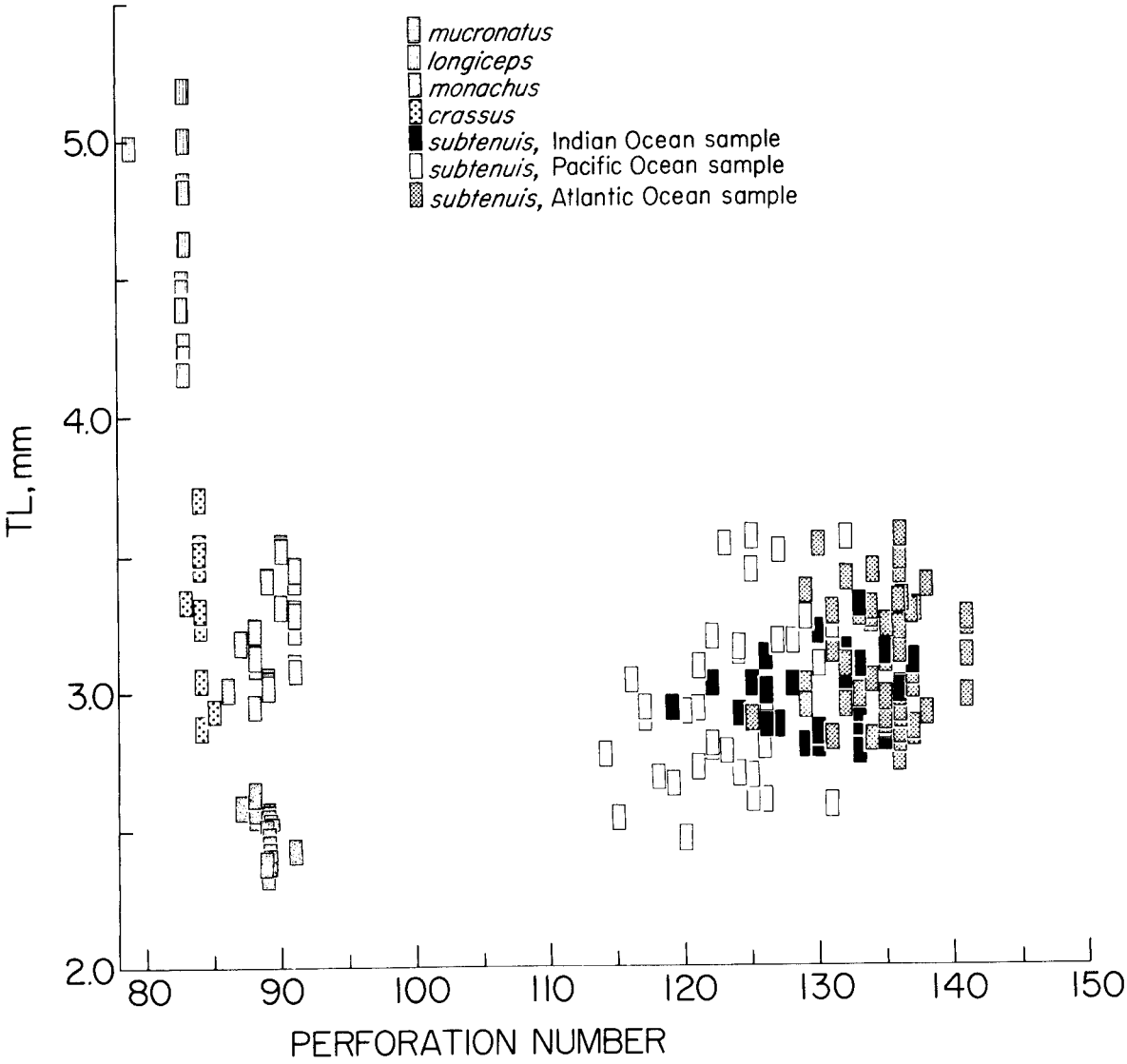


FIGURE 10.—The subtenuis group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

second maxilla, three tergal sites regularly on the genital segment, two or more tergal sites on Abd.III, and, laterally, a pair of posterodorsal pleural sites on each side of segments ThI, ThII, and ThIII. *E. dentatus* (Figure 11b) shows, in addition, three tergal sites across Abd.IV-V while *suberassus* (Figure 11c) has a single mid-dorsal site on Abd.IV-V.

As in the subtenuis group the species with the most extensive geographical range, the circumglobal *pileatus*, shows the most distinctive number of perforations within the species group (Figure 12). Differences between *suberassus*, a broadly neritic species of the Indian and Pacific Oceans, and *dentatus*, a coastal species of Austral-Asian seas, are limited to arrangement, the number of perforations shown by the pooled samples of the two species being equal.

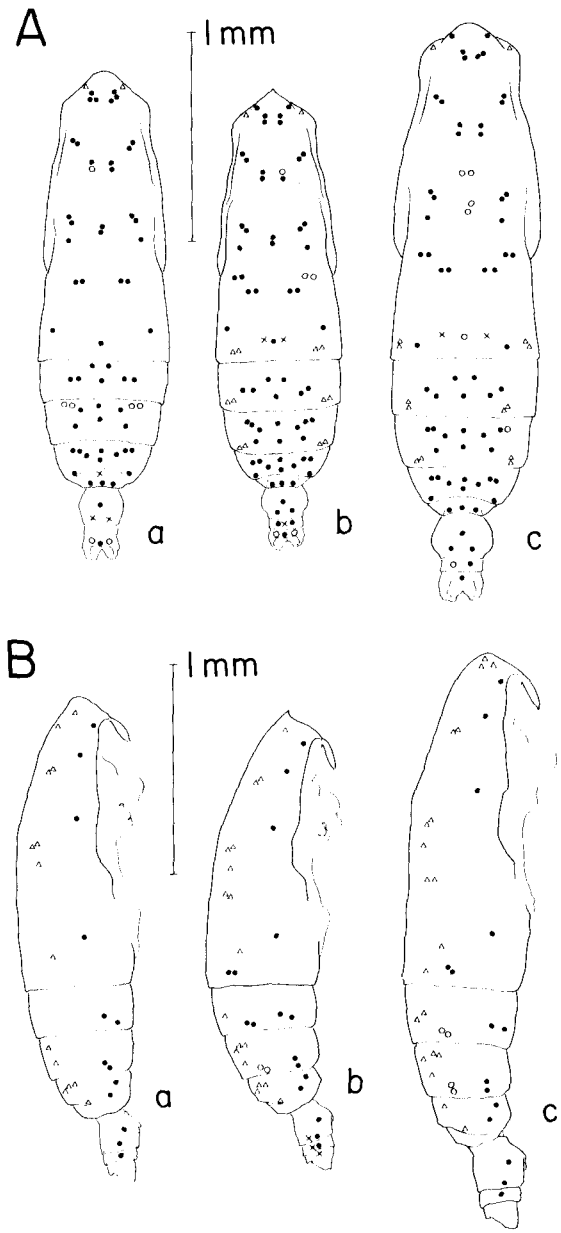


FIGURE 11.—Species of the pileatus group of *Eucalanus*: **a.** *pileatus*, **b.** *dentatus*, **c.** *subcrassus*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view above, lateral view below. All figures of adult females made with the aid of a camera lucida.

The Elongatus Group

Species of the elongatus group are characterized by 1 pleural and 23 tergal sites in addition to the 37 and 9, respectively, present in the genus (Figure 8a). The increase represents the sum of one pair in the forehead (A2T-a-*l*1 and r1), two pairs on the maxillipedal somite (MxpT-*l*3, *l*4 and r3, r4), two pairs on the first free thoracic segment (ThIT-*l*1, *l*2 and r1, r2), one medial site each on ThIII, ThIV, and ThV, two dorsal sites on the genital segment, and one additional pleural site on each side of ThIV.

E. inermis (Figure 13a) is distinguished in dorsal view by the following tergal sites: a set of eight on the A1 somite, five on ThIV, three on ThV, two on the genital segment, none on Abd.-III and Abd.IV, and three on Abd.V. In lateral view diagnostic pleural sites on either side include one on the genital segment and none on Abd.IV.

E. elongatus (Figure 13b) differs from each of the other species in the group in a number of details but only the two anterior tergal sites on the second antennal somite (A2T-a-*l*1 and *r*1 and the tendency for more than two sites on Abd.III and Abd.IV are uniformly diagnostic within the group.

E. hyalinus (Figure 13c). Single tergal sites on ThI (ThIT-a-*l*1 and r1) and the three tergal sites on the genital segment distinguish *hyalinus* from the other species of the group.

E. californicus (Figure 13d). Sites that distinguish *californicus* from the preceding species are the pair middorsal on the somite of the second maxilla, the pair on the first free thoracic segment (ThIIT-a-*l*1, *l*2 and r1, r2), the pair flanking the median site on ThII (ThIIT-b-*l*1, *l*2 and r1, r2), and in lateral view the three pleural sites on either side of ThIV. No consistent difference in number or in arrangement of perforation sites was found that distinguishes *californicus* from *bungii*. Both species are morphologically distinctive in other respects (e.g., setation of the mandibular basis) and share a common boundary across the North Pacific, *californicus* occupying the temperate zone and *bungii* occurring to the north, without any apparent evidence of intergradation or hybridization.

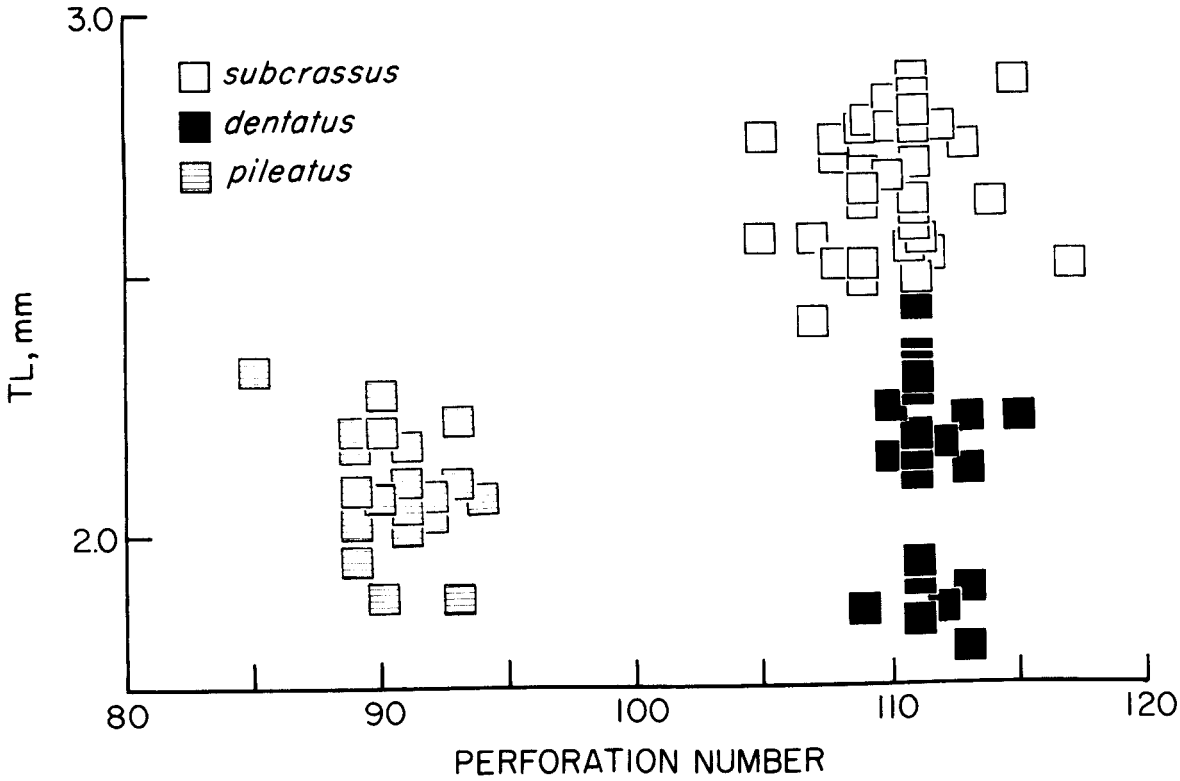


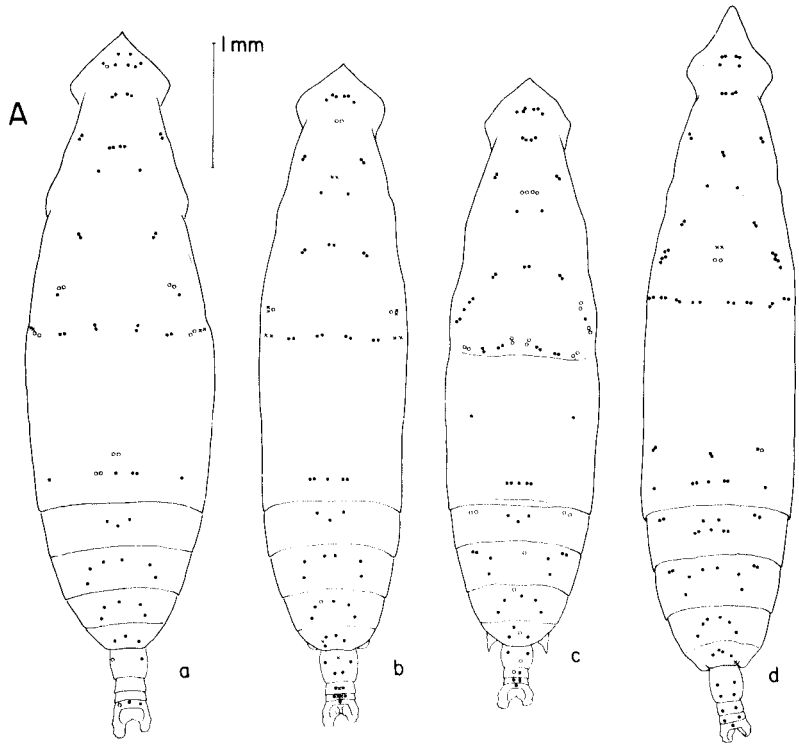
FIGURE 12.—The pileatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

As in the two preceding species groups a relationship between distinctiveness in overall number of perforations and geographical distribution is shown by the elongatus group (Figure 14). The only circumglobal species of the group, *hyalinus*, occupies a distinctive position with respect to perforation number. The two species to the left, *inermis* and *elongatus*, are geographically isolated from one another and the two species to the right, *bungii* and *californicus*, are biogeographically separated from one another. The distribution of *hyalinus* in contrast brings reproductively ripe individuals into contact with all of the other species except *bungii* (unpublished data).

The Attenuatus Group

Members of the attenuatus group have in common 38 tergal and 8 pleural sites added to the primary generic number (Figure 8b). The increase is widely dispersed about the body being found anteriorly on the second antennal somite (A2T-a-*l*1, *l*2 and r1, r2), the somite of the second maxilla (Mx2T-*l*1, *l*2 and r1, r2) and on the maxillipedal somite, where six pairs occur, two pairs more than in the elongatus group. Adding to the characterization are the anterior middorsal pair of ThI, the six symmetrically arranged tergal sites of ThV and the three tergal sites of Abd.IV-V. In lateral view pleural sites are also more numerous, three pleural sites on each side being found on ThII, ThIII, ThIV, and on the genital segment. Every segment except Abd.III bears more sites than the number characterizing the genus, and the group total of 109 sites is the largest among the four groups of species in *Eucalanus*.

Four discrete populations of *attenuatus* s.l. emerge from the present study. They are mor-



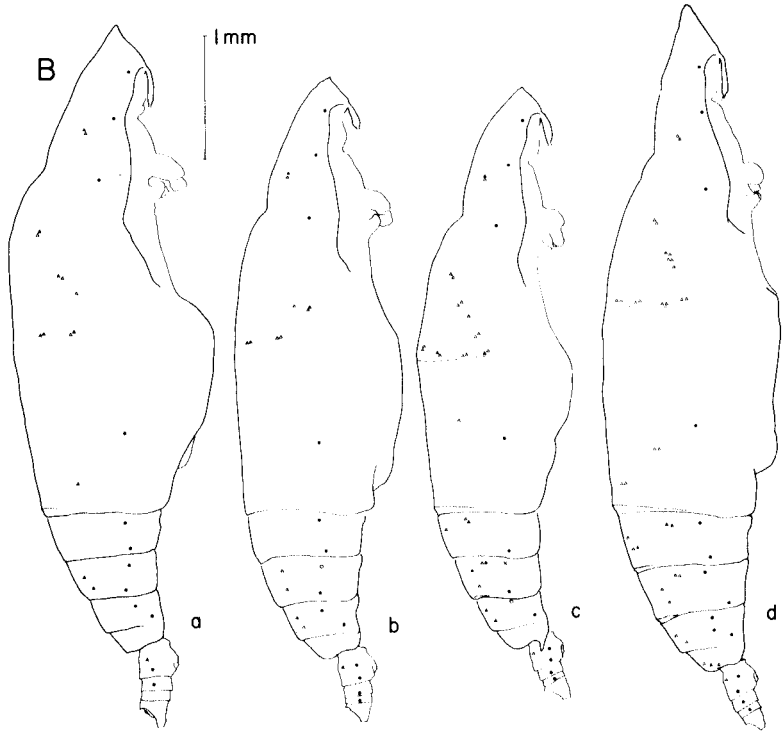


FIGURE 13.—Species of the elongatus group of *Eucalanus:* **a.** *inermis,* **b.** *elongatus,* **c.** *hyalinus,* **d.** *californicus.* Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view above, lateral view below. All figures of adult females made with the aid of a camera lucida.

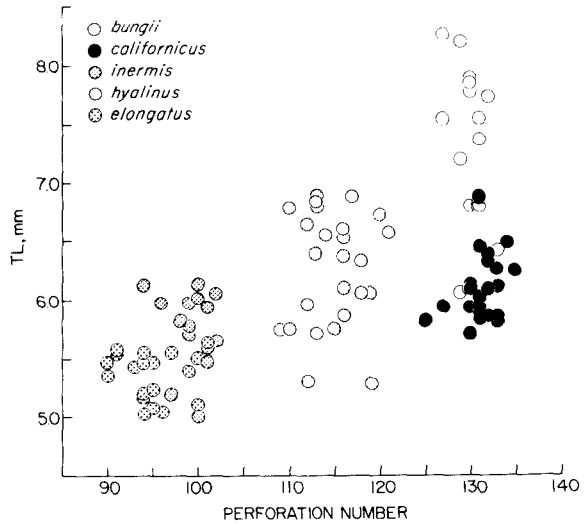


FIGURE 14.—The elongatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

phologically distinguished primarily by the number and arrangement of integumental organs and biogeographically by inferred distributions derived from the very different sets of geographical localities available for each form. In this regard it is important to stress that the sampling localities were chosen to represent the geographical extent of each population from hundreds of localities of *attenuatus* s.l. obtained during the course of global studies on several calanoid genera. In the case of the two unusually large species, *parki* and *langae*, the geographical records represent all that are on hand. A major factor favoring separation of this complex into four distinct species is the pattern seen in the preceding three species groups and repeated in the attenuatus group. That is, the species with the broadest geographical range also shows the most distinctive number or arrangement of sites, especially on the genital segment, and that related allopatric species may show little or no difference in these features.

In each instance the diagnosis is based on the adult female and stresses those designated sites characterizing the species within the group. Thus despite the more formal presentation and the addition of nonperforation data essential to describe each species the information on number and arrangement of designated sites is readily available within the diagnosis for each species.

Eucalanus attenuatus (Dana, 1849), *sensu stricto*

(Figures 1q, 15d, 18a, g, j, k, n, q)

E. attenuatus Dana, 1849, p. 18; 1853, p. 1080, Pl. 75, Figs. 2a-d; Vervoort, 1946, p. 95-103 (pars), Figs. 7a-c.

E. pseudattenuatus Sewell, 1947, p. 39, Test fig. 7A. NEW SYNONYMY.

Diagnosis: Adult female: Characterized by having the largest number of designated sites among the species of the attenuatus group (Figures 15d, 16; Tables 3, 4). Sites in addition to those of the species group include two pairs of tergal sites on ThIII (ThIIIT-b-*l*1, *l*2 and r1, r2), two similar tergal pairs on ThIV, two tergal sites on the genital segment, a single transverse row of three tergal sites on Abd.IV-V and, laterally, three pleural sites on either side of Abd.IV-V (Figure 15d). Length of triangular forehead extending beyond the lateral lobes overlying the first antennae usually shorter than width at origin, apex acute in lateral view and not curving ventrad (Figure 15d). Mandibular basis with two setae.

Adult male: Thoracic tergal sites as in female. Abd.II with two tergal sites (Figure 18j). Mandibular basis with two setae. Forehead weakly produced beyond base of rostrum, apex broadly rounded in dorsal and lateral views (Figure 18g, k).

Additional description: Female lacking fifth pair of legs, abdomen with three separate segments (Figure 15d). Male left fifth legs with four segments, right leg about half as long and trimerous (Figure 18q).

Total length: Adult female: range 3.63 to 4.65 mm, mean = 4.10 mm, s = 0.2900, N = 28 (Figure 16).

Adult male: range 2.93 to 3.50 mm, mean = 3.135 mm, s = 0.1775, N = 7. Specimens selected at random from localities listed in Table 1.

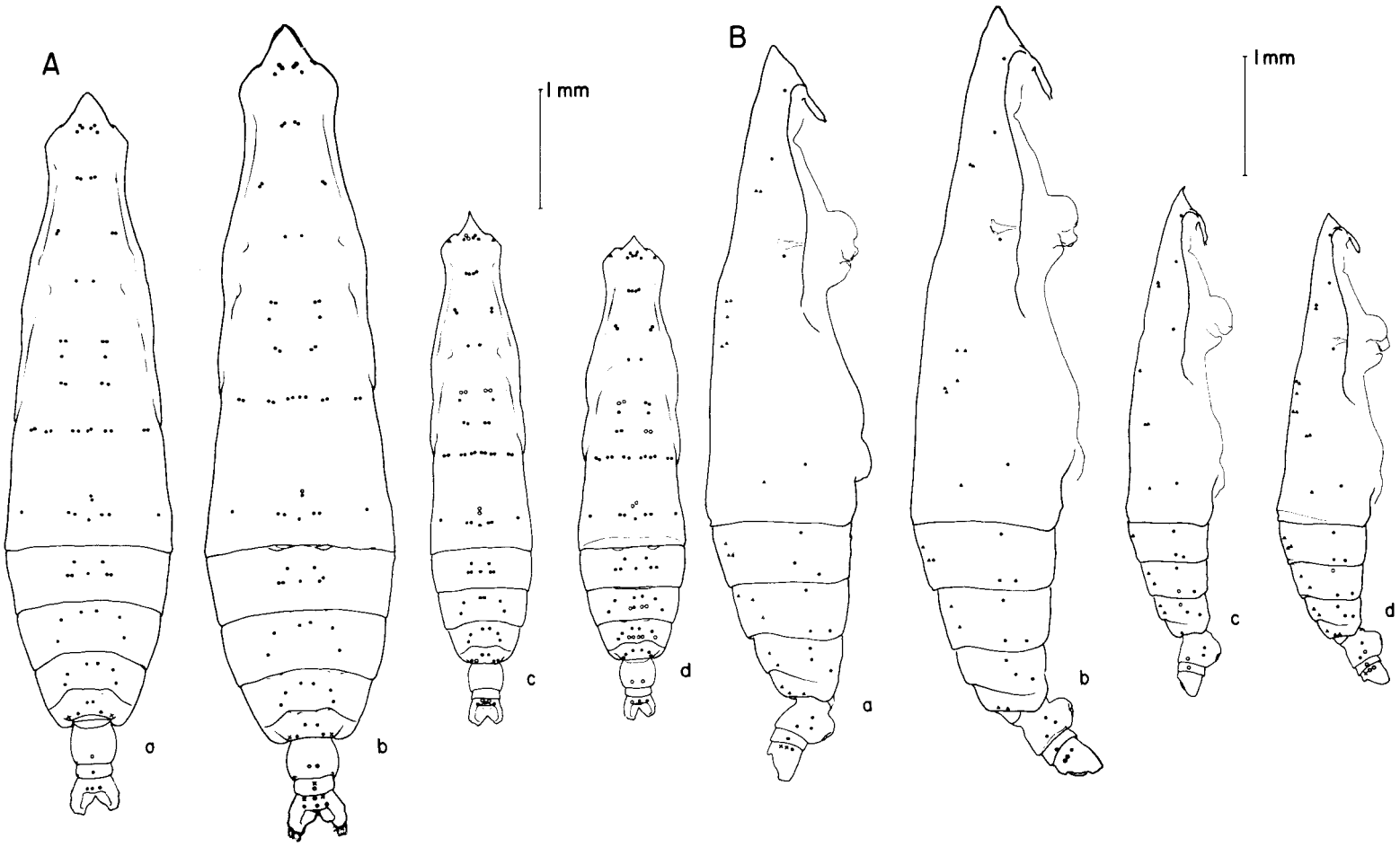


FIGURE 15.—Species of the attenuatus group of *Eucalanus:* **a.** *parki*, **b.** *langae*, **c.** *sewelli*, **d.** *attenuatus*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view on left, lateral view on right. All figures of adult females made with the aid of a camera lucida.

Geographical distribution: Verified localities (Figure 17) suggests a broadly tropical distribution restricted to the Indian and Pacific Oceans. A deliberate search among several hundred plankton samples from Atlantic Ocean localities scattered over the lower latitudes failed to yield a single specimen of *attenuatus* s.s. The species is widespread in tropical latitudes of the Indo-Pacific but appears to be most abundant immediately downstream of eutrophic regions along the equator.

Reference: Three lots of reference specimens deposited in the U.S. National Museum (USNM).

2 ♀♀. USNM 143848. Cruise Dodo VI, stn 49, 1-m net, 0-200 m wire out (MWO); 20 Aug. 1964, 1445-1500 h; 10°19′N, 53°11′E.

3♀♀. USNM 143849. Cruise Dodo VI, stn 47, 1-m net, 0-200 MWO; 19 Aug. 1964, 1825-1840 h; 8°53′N, 53°09′E.

1 ♀. USNM 143850. Cruise Scot (TO58-1), stn 35, 1-m net, surface; 7 May 1958, 0343 h; 9°45′N, 96°04′W.

Remarks: Dana's (1849, p. 18, 19) first locality given for *attenuatus* is from the vicinity of the Kingsmill (= Gilbert) Islands in the western Pacific (13 April 1841). Other U.S. Exploring Expedition localities include the China Sea at about lat. 5° to 10°N (15 February 1842) and the Sulu Sea (2 February and 2 March 1842). All of these localities lie in Indo-Pacific tropical waters, the biogeographical zone and the geographical region that yielded most of the records of *attenuatus* s.s. Moreover, Dana's figures (1853, Figure 2d, e) of *attenuatus*, while crude emphasize a short wide-angled forehead characteristic of the tropical population.

Vervoort (1946) noted two morphological kinds of *attenuatus* s.l. in *Snellius* collections, and his illustration (Figure 7c) probably refers to *attenautus* s.s.

Sewell's (1947) description of *pseudattenuatus* shows a pattern of integumental organs ascribable to the tropical species *attenuatus* s.s. His illustration of *attenuatus* (1947, Text Figure 7B) appears on the basis of an incomplete account of integumental organs and the forehead to be referrable to *sewelli* described below.

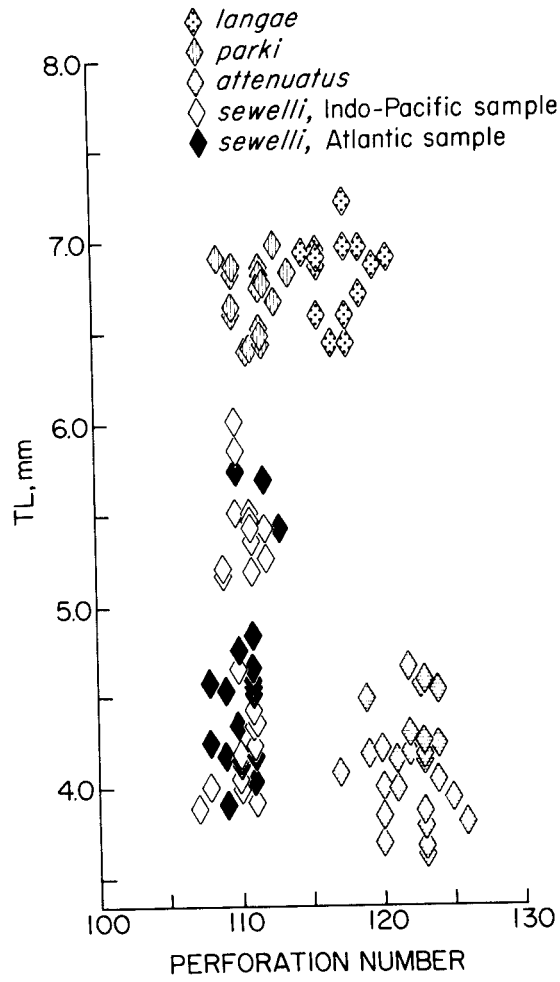


FIGURE 16.—The attenuatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

Brodsky's (1962) description of *pseudattenuatus* may be based on *attenuatus* s.s., but the figures fail to provide adequate details of the forehead and the absence of information on dorsal integumental organs on ThIII and ThIV leave the issue open.

Eucalanus sewelli, n. sp.
(Figures 1r, 15c, 18b-d, o, r)

E. attenuatus: Vervoort 1946, p. 95-103 (pars), Figs. 7d-f; Sewell, 1947, p. 39, Text-fig. 7B; Brodsky 1962, p. 113, Fig. 14.

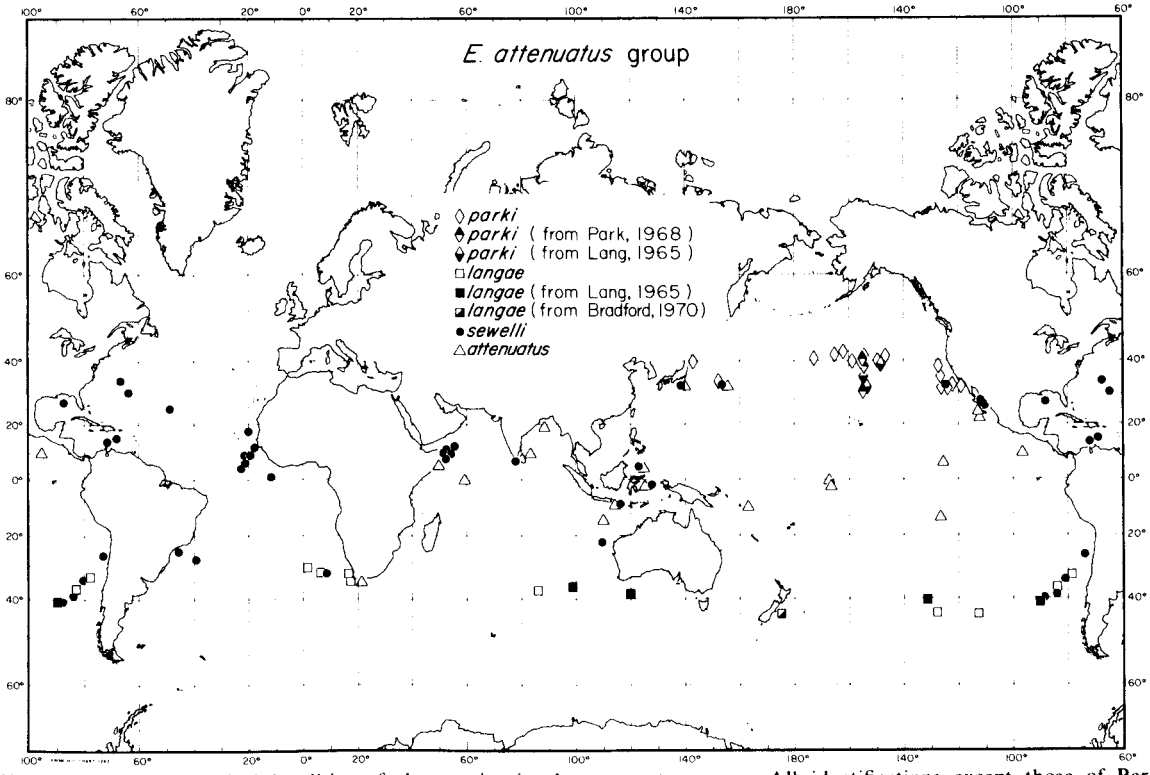


FIGURE 17.—Geographical localities of the species in the attenuatus group. All identifications except those of Park (1968) and Bradford (1970) verified by examination of integumental organs.

Diagnosis: Adult female with mandibular basis bearing two setae as in *attenuatus*. Differs from *attenuatus* in designated sites on ThIII and ThIV, each of which lacks the two pairs of tergal sites enclosed by the outer arc of six tergal sites (Figure 15c). Genital segment lacking integumental organs. Abd.IV-V with two transverse tergal rows and lacking pleural sites (Figure 15c).

Adult male: Tergal sites on ThIII and ThIV as in female. Abd.II lacking dorsal integumental organs (Figure 18i). Mandibular basis with two setae.

Additional description: Adult female with forehead more strongly attenuated and longer than that in *attenuatus* (Figure 15c), apex usually curving weakly ventrad (Figure 18c). In relatively eutrophic regions of the Indo-Pacific *attenuatus* and *sewelli* may co-occur and resemble one another in size and general morphology, but differences in integumental organs persist. In strongly eutrophic tropical regions *sewelli* may exceed 6 mm in TL and exhibit a more prominent conical forehead with rounded apex (Figure 18d). Male with fifth pair of legs as in *attenuatus* (Figure 18o, r).

Total length: Adult female: range 3.89 to 6.10 mm, mean = 4.720 mm, s = 0.6350, N = 43 (Figure 16).

Adult male: range 2.89 to 4.58 mm, mean = 3.195 mm, s = 0.4680, N = 14. Specimens selected at random from localities listed in Table 1.

Geographical distribution: Verified localities (Figure 17) indicate a circumglobal range in eutrophic tropical and subtropical waters extending to the subtropical convergences.

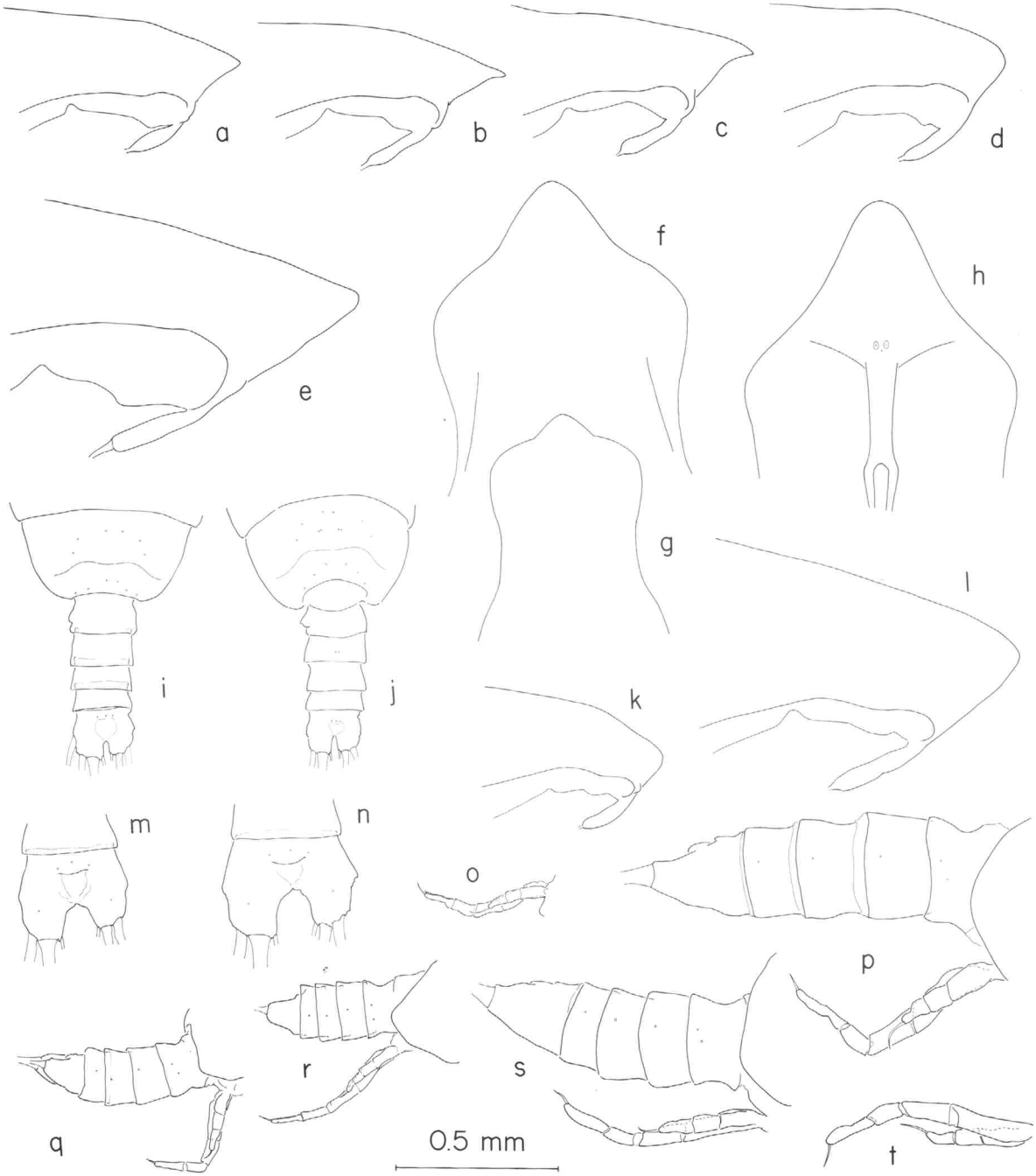


FIGURE 18.—Anterior portion of head, lateral view, female; **a.** *Eucalanus attenuatus* (EQUAPAC S 21); **b.** *sewelli* (*Alaska* 5-9); **c.** *sewelli* (Naga S11A 61-198); **d.** *sewelli* (CalCOFI 5708 144.G15); **e.** *parki* (Boreas 19). Anterior portion of head, dorsal view, male; **f.** *parki* (Zetes 14); **g.** *attenuatus* (EQUAPAC S 21). Anterior of head, ventral view, female; **h.** *langae* (Lusiad 14). ThIV-V and abdomen, dorsal view, male; **i.** *sewelli* (CalCOFI 5708 144.G15); **j.** *attenuatus* (EQUAPAC S 21). Anterior portion of head, lateral view, male; **k.** *attenuatus* (EQUAPAC S 21); **l.** *parki* (Zetes 14). Anal segment and fused furcal rami, dorsal view, male; **m.** *parki* (Zetes 14); **n.** *attenuatus* (Monsoon 24). Fifth pair of legs, male, right lateral view; **o.** *sewelli* (CalCOFI 5708 144.G15); **p.** *langae* (Lusiad VII MWT 19); **q.** *attenuatus* (EQUAPAC S 21); **p.** *sewelli* (*Alaska* 5-9); **s.** *parki* (CalCOFI 5804 80.130); left lateral view; **t.** *parki* (Boreas 19). Positions for stations mentioned are listed in Snyder and Fleminger (1965, 1972).

Types and type locality: Holotype: ♀. USNM 143844. Cruise Downwind, stn 23a, 45-cm net, 0-352 m; 19 Oct. 1957, 0000-0100 h; 38°46′S, 83°20′W.

Reference: 3 ♀♀. USNM 143845. Cruise Downwind, stn 28, 1-m net, 0-283 m; 31 Dec. 1957, 0520-0542 h; 27°08.5′S, 72°02′W.

3 ♀♀. USNM 143846. Cruise Atlantis II-13, stn 8, ¾-m net, depth? 5 Oct. 1964, 1410-1435 h; 41°26′N, 55°45′W.

1 ♀. USNM 143847. Cruise Dodo VI, stn 55, 1-m net, 0-200 MWO; 22 Aug. 1964, 1845-1858 h; 10°14′N, 51°19′E.

Remarks: Brodsky's (1962, p. 113) record of (?) *attenuatus* appears from his illustration (Figure 14) and the locality off northern Japan to be referable to *sewelli*. Other records that appear to be assignable to *sewelli* include Tanaka (1956, p. 266, Figure 4a), Ramírez (1969), and Roe (1972). This species is named to honor R. B. Seymour Sewell who among his many significant contributions to the copepod literature inspired study of their integumental organs and directed attention to the complexity existing in the attenuatus group.

Eucalanus parki, n. sp.
(Figures 1s, 15a, 18e, f, l, m s, t)

E. attenuatus: Park 1968, p. 533, Pl. 1, Figs. 16, 17, Pl. 2, Figs. 1-16, Pl. 3, Figs. 1-13, large form only.

Diagnosis: Adult female: Mandibular basis with four setae. Sites of integumental organs similar to those of *sewelli* except for presence of one medial tergal site on both the genital segment and on Abd.III, one or more pleural sites on Abd.IV-V, and only one transverse tergal row on Abd.IV-V (Figure 15a).

Adult male: Forehead prominent, protruding as an elongate triangle about twice as far beyond base of rostrum as in *sewelli* and *attenuatus* (Figure 18f). Integumental organs on cephalosome and thorax as in female; Abd.II with or without one tergal site (in 11 specimens, 6 with and 5 without). Mandibular basis usually with four setae, one specimen in 11 with three setae.

Additional description: Adult female with conical forehead and rounded apex as in Figure 18e, differs from typical acutely pointed forehead of *sewelli*.

Total length: Adult female: range 6.40 to 7.17 mm, mean = 6.744 mm, s = 0.1982, N = 18 (Figure 16).

Adult male: range 5.20 to 5.96 mm, mean = 5.620 mm, s = 0.2380, N = 10. Localities of specimens listed in Table 1, pooled sample represents all adults on hand.

Geographical distribution: All records (Figure 17) are from the North Pacific Ocean. Most fall within the Transition zone (Brinton, 1962, p. 202) but a number also appear along long. 155°W extending south to lat. 32°N, following the line of division between western and eastern North Pacific Central Water (Sverdrup, Fleming, and Johnson, 1942, Figure 209A) which is supported by the relative elevation of the isotherms in the upper 200 m of the mid-latitudes in the North Pacific relative to those of the South Pacific (Reid, 1965, Figure 2).

Types and type locality: Holotype: ♀. USNM 143841. Cruise Norpac H5508, stn 24-42, 1-m net, 0-200 MWO; 21 Aug. 1955; 1556-1610 PST; 40°26′N, 146°37′W.

Reference: 1 ♀, specimen no. 2. USNM 143842. Cruise Norpac H5508, stn 24 (up), 1-m net, 0-200 MWO; 25 Aug. 1955, 1620 PST; 42°17′N, 146°16′W.

1 ♀, specimen no. 1. USNM 143843. Cruise Norpac H5508, stn 25 (up), 1-m net, 0-200 MWO; 25 Aug. 1955, 1816-1831 PST; 42°17′N, 150°00′W.

Remarks: Large forms of *attenuatus* s.l. have been noted from the North Pacific by several authors (e.g., Tanaka, 1956, p. 266, Figure 4b; Lang, 1965 Park, 1968). Park (1968) fully appreciating its distinctiveness described it in detail. He relinquished his original intention of naming it as a distinct species upon my recommendation, which was based on the apparently extensive variability generally thought to prevail in *Eucalanus*. At that time there was no reliable basis for distinguishing genetic from phenetic variation and reliable capture records

were insufficient to provide an indication of biogeographical affinities. It is a great pleasure to name this species for TaiSoo Park in recognition of his acumen and farsightedness in judging copepod systematics.

Eucalanus langae, n. sp.

(Figures 1t, 15b, 18h, p)

E. attenuatus: Bradford 1970, p. 353, Figs. 6-9.

Diagnosis: Adult female: Closely resembling *parki* in size and appearance including the occurrence of four setae on the mandibular basis. Integumental organs as in *parki* except for significant increase in abdomen (Figure 15b). Genital segment and Abd.III each with two tergal sites. Anal segment (Abd.IV-V) with two transverse rows of tergal sites as well as more regularly occupied pleural sites occurring in copepodid stage V and in adults (Figure 19, Table 5), the mean total number being about twice that of *parki*.

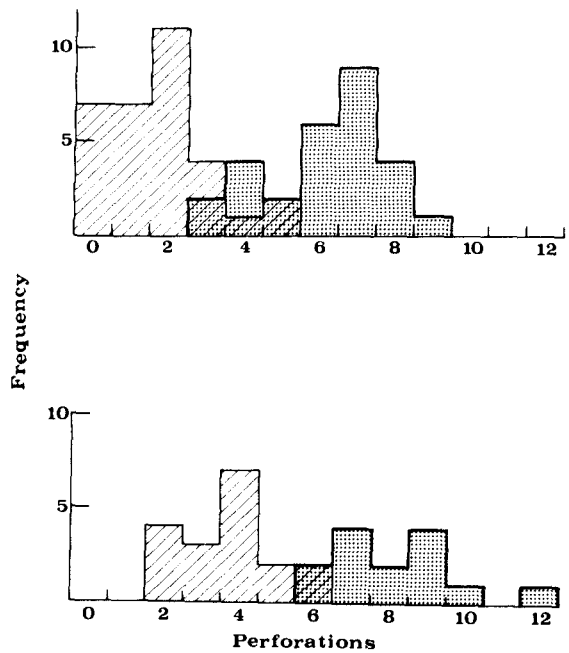


FIGURE 19.—Frequency distribution of the total number of perforations on the anal segment (Abd.IV-V) in stage V female copepodids above and in adult females below. Diagonal hashing represents *Eucalanus parki*, dotted area represents *E. langae*.

Additional description: Adult male: Integumental organs of cephalosome and thorax as in female; Abd.II with two tergal sites as in genital segment of female.

Total length: Adult female: range 6.44 to 7.22 mm, mean = 6.847 mm, s = 0.2235, N = 14 (Figure 16).

Adult male: 6.12 mm and 6.59 mm. Localities of specimens given in Table 1.

Geographical distribution: Available records (Figure 17) indicate that *langae* is a resident of the circumglobal Transition zone in the Southern Hemisphere.

Types and type locality: Holotype: ♀. USNM 143839. Cruise Lusiad VII, stn 14, Isaacs-Kidd midwater trawl; 0-3,400 m; 6 June 1963, 1530-2300 h; 32°30′S, 9°04′E to 32°24′S, 8°25′E.

Reference: 2 ♀♀, specimens no. 4 and 6. USNM 143840. Cruise Monsoon, stn 18, Isaacs-Kidd midwater trawl; 0-2,723 m; 11 Mar. 1961, 2046-0303 h; 25°52′S, 155°44′W to 25°40′S, 155°34′W.

Remarks: Lang (1965) found specimens of this species at several Monsoon and Downwind stations (Figure 17) and noted their resemblance to their North Pacific temperate cognate. Bradford (1970) also noted this similarity in recording it from off the Kaikoura Peninsula, New Zealand, and referring to Tanaka's (1956) mention of a large *attenuatus* s.l. off Japan.

Though data on designated sites are lacking for Bradford's specimens, the probability that they are referable to *langae* is sufficiently great to include them under the species without reservation.

Assignment of the sibling populations *langae* and *parki* to separate species is based on two lines of evidence: 1) significant differences in designated sites involving abdominal segments that undergo modification with sexual maturation (Table 5, Figure 19); 2) apparent restriction of each population to temperate zones in opposite hemispheres (Figure 17).

Although data on actual depth distribution are unavailable for either species, most of the

TABLE 5.—Number of perforations on anal segment of *parki* and *langae* in copepodid stage V and adult females of *Eucalanus*.

Species	Range	$\bar{x}$	s	N	t	P
parki: stage ♀	0-5	1.75	1.4368	32		
adult ♀	2-6	3.7222	1.2744	18		
langae: stage V ♀	3-9	6.1428	1.6036	28		
adult ♀	6-12	8.1428	1.6576	14		
Comparison of sample means of female specimens						
parki stage V and adult ♀				50	4.85	<0.001
langae stage V and adult ♀				42	3.76	<0.001
stage V: *parki* and *langae*				60	11.193	<0.001
adults: *parki* and *langae*				32	8.55	<0.001

records of *langae* and *parki* (Table 1) are based on relatively shallow tows with open nets from 300 m or less to the surface. Following the shortest prevailing surface circulation in the Pacific Ocean, shallow water passage from the temperate zone of one hemisphere to that of the other is at least 9,000 miles long. It would begin necessarily in the eastern boundary currents and continue in the equatorial circulation where crossover to the succeeding western boundary current in the opposite hemisphere might occur. Assuming a high rate of 1 knot and an unrealistic expectation of continuous and direct transport would require a transit time exceeding 1 yr.

Among my unpublished records of *attenuatus* s.l. neither *langae*- nor *parki*-like individuals of any copepodid stage appear in the equatorial localities (cf. Fleminger and Hulsemann, 1973, for geographical distribution of samples that have been examined for *Eucalanus*). Moreover, no specimens that might be attributable to *langae* or *parki* on the basis of unusually large size appear among the published records of *attenuatus* s.l. collected from the vicinity of the Pacific's equatorial circulation.

Transhemispheric passage at subsurface depths would be at transport rates that are probably an order of magnitude less than surface transport. Evidence of tropical submergence by *attenuatus* s.l. is lacking, however, despite widespread studies on the vertical distribution of copepods in the upper 500 m of the Pacific. Also, *attenuatus* s.l. appears to be a fine particle filter-feeder (Mullin, 1966; Samyshev, 1970) and therefore not a likely candidate to survive deep submergence to meso- or bathypelagic depths for periods of one or more years. In the light of this background the relatively small but constant morphological differences and an apparent allopatry, maintained by the formidable barrier of the tropical and subtropical zones separating the ranges of *parki* and *langae*, provide compelling reasons for treating the two biantitropical (Brinton, 1962) populations as separate species.

If *langae* could survive transport to temperate waters of the Northern Hemisphere it could be expected to appear in the North Atlantic Drift. Despite the great intensity of study on oceanic copepods of the North Atlantic no "giant" *attenuatus* s.l. forms have been noted from the region. With (1915, p. 52-53, Pl. 1, Figure 6a-c, Text figure 10a-e) reports several large *attenuatus* s.l. stage V copepodids (♀ = 5.18 mm, ♂ = 5.0 mm) collected at two North Atlantic localities lying roughly between Iceland and Scotland. With notes that "The structure of the mouth appendages . . . scarcely show differences of any importance from Giesbrecht's description . . .". Thus it seems likely that the mandibular basis in his specimens bore two setae as in *sewelli*, a species that reaches a length in accord with With's measurements (Figure 16 and see p. 993 above). The absence of other reports of large *attenuatus* s.l. in excess of 6 mm in TL from the North Atlantic even at considerable depths (e.g., Roe, 1972) further substantiates the lack of a North Atlantic temperate cognate of *parki* and *langae*.

The species is named for Bui Thi Lang to acknowledge her discovery (1965) of morphological and geographical complexity in *attenuatus* s.l.

KEY TO THE SPECIES OF *EUCALANUS*

(Adult Females Only)

Based on integumental organs, all sites are tergal unless specified otherwise.

1. Mxp with four or more pairs of sites; ThIII and IV lacking single middorsal site between anterolateral hair sensilla; ThIV lacking paired sites lying outside of dorsal quadrangle of hair sensilla 2

   Mxp usually with two pairs of sites; ThIII and IV with single middorsal site lying between anterior two hair sensilla; ThIV with one pair of sites lateral to quadrangle formed by four hair sensilla 3

2. Mx1 and Mx2 with total of 10 sites forming a rectangle and arranged anterior to posterior in two bilateral sets of one pair, one single and one pair of sites; ThII and III in lateral view with three sites, Abd.IV-V with at least three tergal sites .....attenuatus group, 4

   Mx1 and Mx2 sites vary from 8 to 18 in number, not arranged in rectangle pattern, posterior sets more lateral than anterior sets; ThII and III with one or two lateral sites; Abd.I-II with at least two tergal perforations .....elongatus group, 5

3. ThIII and IV with one medial site in tergal arc formed by the tergal sites .....subtenuis group, 6

   ThIII and IV with two medial sites in the arc formed by the tergal sites .....pileatus group, 7

4. A. Abd.III with tergal site ..... B

   Abd.III lacking tergal site C

   B. Abd.I-II usually with one site, Abd.IV-V with three tergal and one pleural site ..... *parki*

   Abd.I-II usually with two sites, Abd.IV-V with at least four tergal and three pleural sites ..... *langae*

   C. Abd.I-II lacking tergal sites, Abd.IV-V usually with five tergal and zero pleural sites ..... *sewelli*

   Abd.I-II with two tergal sites, Abd.IV-V with three tergal, usually two or more pleural sites ..... *attenuatus*

5. A. ThII and III with a pair of sites anterolateral to arc formed by tergal sites; Mx1 and Mx2 with at least 16 sites ..... B

   ThII and III lacking a pair of sites anterolateral to arc formed by tergal sites, Mx1 and Mx2 with 12 or fewer sites ..... D

   B. ThI and II each with seven tergal sites; Abd.I-II with three tergal sites ..... *hyalinus*

   ThI with 13, ThII with nine tergal sites; Abd.I-II with four tergal sites C

   C. Mandibular basis with one seta ..... *californicus*

   Mandibular basis with three setae ..... *bungii*

   D. A1 somite with sets of eight and four sites; Mnd somite with six sites; ThV with three sites; Abd.I-II with two sites, Abd.III and IV lacking tergal sites, Abd.IV lacking pleural sites .. *inermis*

   A1 somite with sets of six and two sites; Mnd somite with two to four sites; ThV

with four or more sites; Abd.I-II with four or more sites; Abd.III and IV with two or more sites; Abd.IV with one pleural site ..... *elongatus*

6. A. Mx2 somite with two or more pairs of sites; ThI with seven or more sites; ThII and III with one asymmetrical site within arc of hair sensilla on left of midline; Abd.I-II with two sites ..... B

Mx2 somite lacking sites; ThI with three sites; ThII and III lacking sites within dorsal arc of hair sensilla; Abd.I-II with up to one site C

B. ThI with 15 sites; Mx1 somite with 10 sites including a medial set of four; A1 somite with 10 sites including a posterior set of four; Mnd somite with eight sites . *subtenuis*

ThI with seven sites; Mx1 somite lacking four medial sites; A1 somite lacking four posterior sites; Mnd somite with four to six sites ..... *mucronatus*

C. ThII and III with three pleural sites, Abd.IV-V with three tergal sites ..... *monachus*

ThII and III with two pleural sites, Abd.IV-V with one tergal site ..... D

D. Mnd somite with six sites; Abd.I-II lacking tergal sites .. *crassus*

Mnd somite with four sites; Abd.I-II with one tergal site ..... *longiceps*

7. A. ThII and III with two pairs of pleural sites; Mx2 somite with two pairs of tergal sites; Abd.I-II with three sites; Abd.III with two sites ..... B

ThII and III with one pair of pleural sites; Mx2 somite lacking tergal sites; Abd.I-II usually with one site; Abd.III lacking tergal sites ..... *pileatus*

B. Mx1 somite with two pairs of sites adjacent to the midline; Abd.IV-V with one site ..... *subcrassus*

Mx1 somite with one pair of sites adjacent to the midline; Abd.IV-V with three sites ..... *dentatus*

USE OF INTEGUMENTAL ORGANS IN STUDIES ON GEOGRAPHICAL VARIATION

A relatively high degree of variability in perforation number was noted for the circumglobal, broadly tropical species, *E. subtenuis* (Table 4, Figures 9, 10). The conspicuous variability was noticed after realization that bilateral symmetry and arrangement in regular patterns distinguishing species groups as well as species is characteristic of integumental organs. The variation suggested that these organs are a promising source to search for evidence of genetic variation in field-collected planktonic populations. Thus to carry out a pilot study of this possibility the original sampling of *subtenuis* was supplemented by additional specimens sorted at random from zooplankton samples selected to represent both extreme and intermediate geographical locations within the known distribution in each ocean (Figure 20). For each specimen pleural perforations were tallied from both left and right sides of the entire body and summed with counts of the tergal perforations to obtain a maximum estimate referred to as the perforation number (PN). TL was also measured routinely using procedures described in the section on Material and Methods. It should be noted that no attempt was made to determine the existence of geographical variation in any

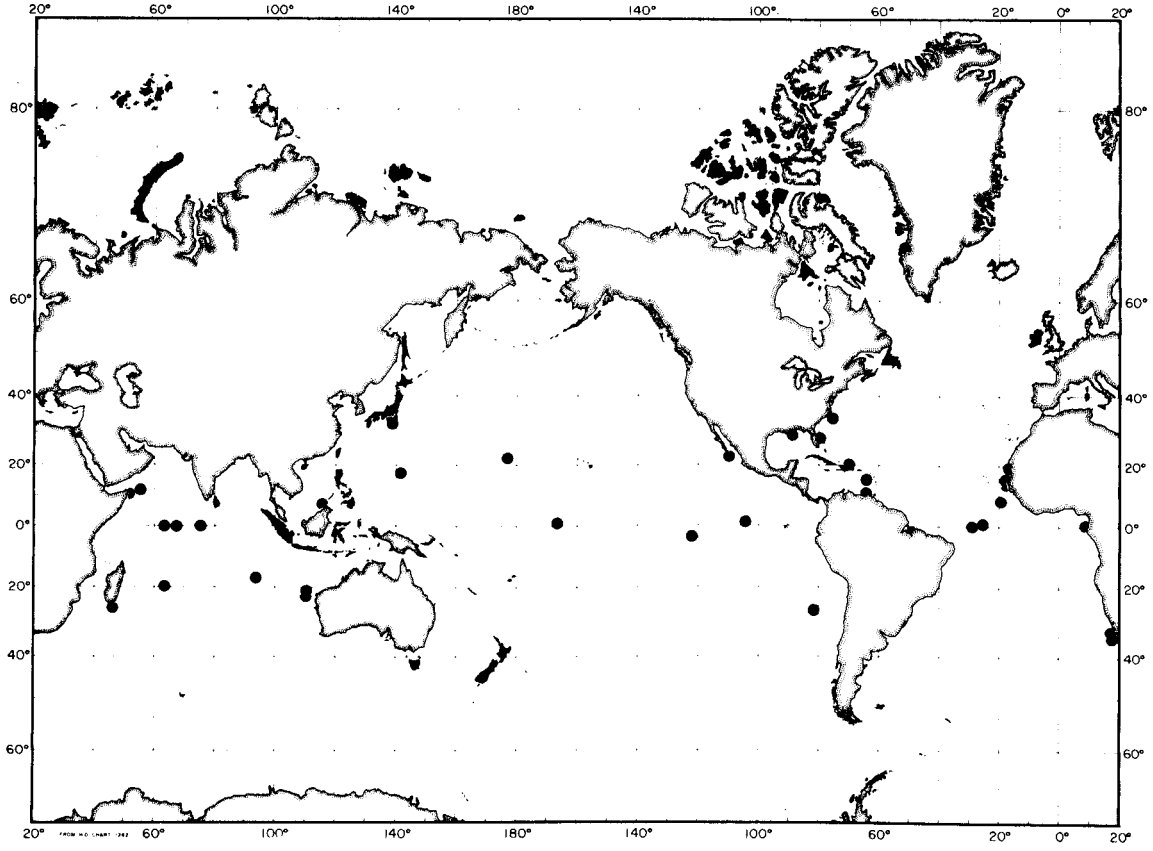


FIGURE 20.—Geographical distribution of *Eucalanus subtenuis*. Localities shown based on records verified by analysis of integumental organs.

other morphological features of *subtenuis* except to confirm that in virtually all specimens from each ocean the mandibular basis bore three setae as found by Fukase (1957).

The data were first examined by pooling the samples from each ocean and comparing the mean number of perforations between oceans. Differences between the pooled samples proved to be highly significant (Table 6), and the mean PN values show a pronounced geographical trend. The lowest mean was obtained from the Pacific Ocean specimens and the highest from the Atlantic Ocean specimens. The pooled sample from the Indian Ocean yielded a mean PN virtually midway between the other two.

The gross indication of clinal variation suggested further consideration at a finer scale.

The PN counts of *subtenuis* were regrouped by geographical source of the specimens in units of 60° of longitude and compared in terms of frequency distribution and mean PN per geographical segment (Figure 21). Grouped samples falling within the hydrographic limits of any one ocean do not differ significantly (Table 7) and serve to emphasize the stepped or discontinuous pattern of the means from the different oceans. The range shown by PN in the two geographical segments between long. 30°E and 150°E (Indian Ocean and westernmost Pacific Ocean) spans the apparent differences in the distribution of PN in the Pacific and Atlantic samples (Figure 21). Thus the Indian Ocean population would appear to be the one genetically and geographically intermediate in

TABLE 6.—Total number (PN) of perforations in samples of *Eucalanus subtenuis* from different oceans.

Sample	Range	$\bar{x}$	s	s^2	N	t	P
Pacific Ocean	114-135	123.6388	4.9750	24.7506	36		
Indian Ocean	119-139	130.0416	4.9911	24.9111	24		
Atlantic Ocean	125-141	134.8400	3.2598	10.6263	50		
Comparison of differences between mean number (Student's t - test)							
Pacific : Indian					60	4.877	<0.001
Indian : Atlantic					74	4.98	<0.001
Atlantic : Indian-Pacific combined					110	9.37	<0.001

position to those of the Pacific and Atlantic populations, a pattern consistent with the prevailing surface circulations of equatorial and western boundary currents.

When the various sets of perforations are analyzed separately, however, the resemblance of the variation to either a zone of intergradation or a stepped cline disappears. The designated sites in *E. subtenuis* fall into 26 tergal and 13 pleural sets based on the scheme described above (Figures 5, 7). More than half of these sets show zero or negligible variability, i.e., typical perforations were observed at these sites in virtually all of the specimens. Most of the variation was in fact concentrated in only nine sets of designated sites (Figure 22a, b).

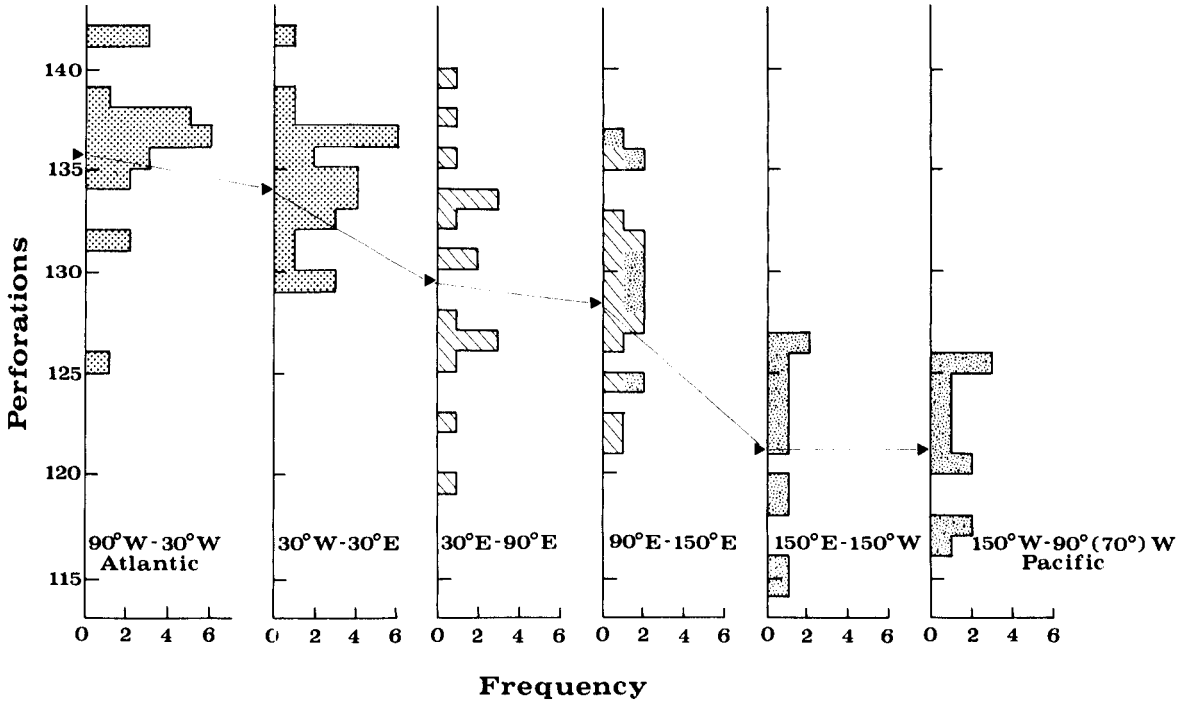


FIGURE 21.—Frequency distribution of total number (PN) of perforations per specimen in samples of adult females of *Eucalanus subtenuis* collected within 60° segments of longitude. Uniform large spot shading represents specimens collected at localities in the Atlantic Ocean; obliquely ruled shading represents specimens collected at localities in the Indian Ocean; irregular finely dotted shading represents specimens collected at localities in the Pacific Ocean. Differences between the means in the second and third histograms and the fourth and fifth histograms counting from the left are highly significant (t-test, Table 7). Black triangle indicates position of mean PN within geographical segment. All specimens selected at random from zooplankton samples located in various sectors of the *subtenuis* range (Figure 20).

TABLE 7.—Comparison by Student's t-test of mean TN values of samples of adult female *subtenuis* grouped regionally as in Figure 21 in segments of 60° of longitude.

Regional segments (longitude)	N_1+N_2	$\bar{x}$	t	P
90°-30°W : 30°W-30°E	52	135.74 : 134.00	1.99	<0.1 P >0.05
30°W-30°E : 30°-90°E	45	134.00 : 129.56	3.59	<0.001
30°-90°E : 90°-150°E	35	129.56 : 128.68	0.54	<0.6 P >0.5
90°-150°E : 150°E-150°W	30	128.68 : 121.18	5.623	<0.001
150°E-150°W : 150°-90°(70°)W	23	121.18 : 121.25	0.064	>0.9
150°-90°(70°)W : 90°-30°W	35	121.25 : 135.74	11.91	<0.001

The nine sets appear to vary independently of one another, some showing unusually high or low frequencies of absence in one or two of the three oceans. In some sets the frequency of absence in one ocean differs significantly from that elsewhere (Figure 22a, b; Table 8). Within each set perforations tend to be absent at similar frequencies. Genetic linkage is suggested by the similar deviations in the Pacific sample affecting the following sets: Mx1-T-a-*l*3, 4, r3, 4; Mxp-T-*l*1, 2, r1, 2; ThII-P-*l*a1, ra1; ThIII-P-*l*a1, ra1; and ThIV-P-*l*a1, ra1.

Also unique to the Pacific sample is the more frequent occurrence of four perforations on the somite of the first maxilla (Mx1-T-d-*l*1, 2, r1, 2). The Indian Ocean sample is distinguished by a relatively infrequent appearance of the set of perforations on the somite of the second antenna (A2-T-a-*l*1, 2, r1, 2). The Atlantic sample shows relatively few absences on the Mx1 somite (Mx1-T-c-*l*1, 2, r1, 2) and on ThII (ThII-T-a-*l*2, 3, r2, 3).

In an individual specimen perforations are often absent in pairs rather than in full sets though right and left pairs in a set tend to show similar frequencies in the sample. Absences of peg and pore combinations are usually bilateral and affect both the right and left sides of a particular set. Absences of pairs consisting of a pit sensillum and a pore may be bilateral but more frequently affect only one side in a specimen. An appreciable portion of the variability in *subtenuis* emanates from losses among such tergal pairs occurring sequentially on the two maxillary somites. An individual specimen may show losses that alternate in successive sets from either left to right or the reverse. A noticeable trend in losses toward unbalanced symmetry was found only in the case of Mx1-T-b-*l*1, 2, r1, 2. Indian and Atlantic samples showed more absences on the right side and Pacific samples had a higher frequency of absence on the left side, but the differences are significant (χ^2 test for homogeneity) only in the case of the Indian Ocean sample (Table 9). Critical examination for patterned variation among specimens using larger samples may prove to be especially useful for genetic studies on natural and laboratory populations of planktonic copepods.

Despite the relatively frequent absences, each of the 110 specimens of *subtenuis* comprising the combined global sample exhibited a representative perforation pattern permitting identification to species by this feature alone. Also noteworthy is the qualitative resemblance in characters distinguishing the geographical populations of *subtenuis* and differences separating *parki* from *langae*. As in *subtenuis* few perforations distinguish these allopatric temperate species of the attenuatus group from one another, and the sites involved are also restricted to a limited portion of the body (i.e., the abdomen and especially Abd.IV-V). The parallels emphasize the likelihood of appreciable genetic discontinuity separating Atlantic, Indian, and Pacific populations of *subtenuis* that deserves more intensive study.

SIZE AND PERFORATION NUMBER

The perforation number (PN), i.e., the number of designated sites in the species observed on each specimen is derived from a meristic complex of integumental organs. The two organ systems, sensilla and glandular pores, are arranged in serially homologous sets that are distributed on all body segments. Showing phylogenetic and species specific patterns, they

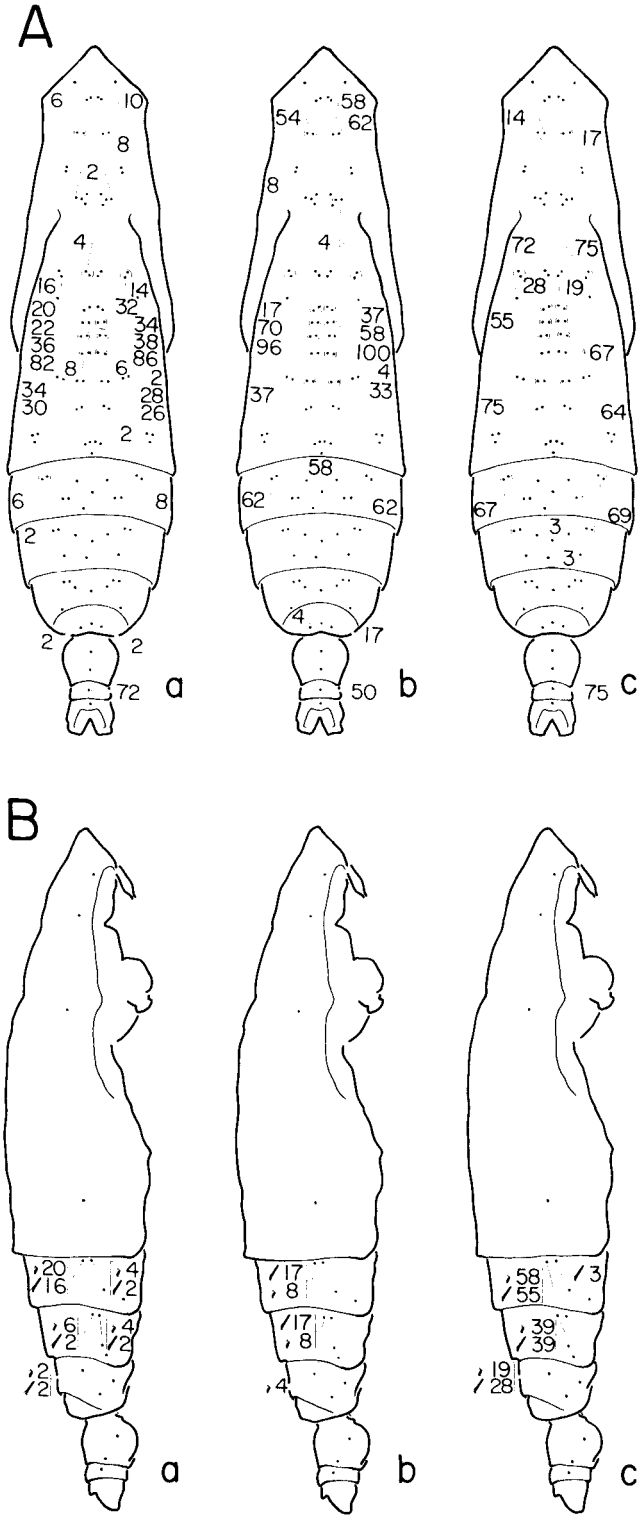


FIGURE 22.—Variation in the occurrence of perforations at designated sites in three regionally pooled samples of *Eucalanus subtenuis* adult females. Sampling localities shown in Figure 20 and geographical grouping based on significant differences between geographical regions shown in Table 7. From the left: Atlantic Ocean sample (N = 50), Indian Ocean sample (N = 24), Pacific Ocean sample (N = 36). Dots represent perforation sites typical of the species. Numbers represent percentage of specimens lacking a perforation at this site; open circles enclose pairs of sites showing the same frequency of absence. Absence of a number indicates perforation found in all specimens of the sample. Dorsal view top; right lateral view bottom.

TABLE 8.—X^2 test for homogeneity of frequency of absence of perforations from designated sites among geographically different samples of *Eucalanus subtenuis* adult females described in Figures 20 and 21.

Regional sample	Frequency of absences			Atl., Ind., Pac. compared		Atl., Ind. compared		Atl., Pac. compared		Ind., Pac. compared		Largest source of X^2
N	Atl. 50	Ind. 24	Pac. 36	X^2	*P*2d.f.	X^2	*P*1d.f.	X^2	*P*1d.f.	X^2	*P*1d.f.	
Designated sites (no.)												
A2-Ta $\Sigma l1,2;r1,2$ (4 sites)	15	55	23	99.8	<0.001	89.2	<0.001	5.28	<0.025 $P>0.01$	44.6	<0.001	Indian
Mx1-Ta $\Sigma l3,4;r3,4$ (4 sites)	29	4	106	179.9	<0.001	6.98	<0.01 $P>0.005$	122.2	<0.001	108.2	<0.001	Pacific
Mx1-Tc $\Sigma l1,2;r1,2$ (4 sites)	75	62	88	27.5	<0.001	19.1	<0.001	18.7	<0.001	0.26	<0.75 $P>0.5$	Atlantic
Mx1-Td $\Sigma l1,2;r1,2$ (4 sites)	168	94	96	39.3	<0.001	12.3	<0.001	14.1	<0.001	29.1	<0.001	Atlantic
Mxp-T $\Sigma l1,2;r1,2$ (4 sites)	59	34	100	57.7	<0.001	1.0	<0.5 $P>0.25$	53.8	<0.001	27.1	<0.001	Pacific
ThII-Ta $\Sigma l2,3;r2,3$ (4 sites)	14	58	98	156.2	<0.001	100.7	<0.001	142	<0.001	1.48	<0.25 $P>0.1$	Atlantic
ThII-Pr,*l* Σal (2 sites)	4	6	28	32.3	<0.001	~0.8	<0.5 $P>0.25$	22.2	<0.001	18.0	<0.001	Pacific
ThIII-Pr,*l* Σal (2 sites)	4	6	28	33.3	<0.001	3.7	<0.1 $P>0.05$	30.2	<0.001	8.3	<0.005 $P>0.001$	Pacific
ThIV-Pr,*l* Σal (2 sites)	2	1	17	26.0	<0.001	0	>0.9	18.7	<0.001	9.5	<0.005 $P>0.001$	Pacific
No. X^2 with $P \leq 0.5$					9		5		9		7	

are the unmistakable phenetic expression of the genotype.

Body size (TL) is a priori also under genetic control, and probably in copepods this control is rigorous (Brooks and Dodson, 1965; Brooks, 1968; Dodson, 1970; June and Carlson, 1971). However, it is known that in addition to selection pressures diet and temperature may strongly influence size determination (Coker, 1933; Deevey, 1960, 1964, 1966; Omori, 1970). A question of immediate concern is whether TL and PN may be sufficiently related to show similar phenetic patterns of variation.

Morphogenesis during the copepodite phase of ontogeny appears to affect PN in a simple predictable fashion. In general, copepodid stages III, IV, and V were found with the same number and arrangement of sites, segment by segment, as they appear in adults of the species with exceptions in abdominal segments as indicated above. The exceptions noted are restricted to ontogenetic modifications in the addition of abdominal segments and subsequent fusion of segments brought on by sexual maturation. Thus at least during the second half of ontogenesis integumental organs maintain numerical and distributional relationships during typical size increases associated with moulting; no observations are available for copepodite stages I and II. If a relationship exists between TL and PN it should be apparent from comparison of the two within a given onto-

TABLE 9.—Frequency of absence of perforations at a designated site in *Eucalanus subtenuis* (%).

Sample	Designated site: Mx1-T-6 left 1, 2	right 1, 2	X^2, 1d.f.	P
Pacific Ocean	28, 28	19, 19	~1.6	<0.25 $P>0.2$
Indian Ocean	17, 17	37, 37	5.28	<0.025 $P>0.02$
Atlantic Ocean	20, 20	32, 32	3.64	<0.1 $P>0.05$

genetic stage. In making such comparisons, however, it should be recalled that considerations limited to the numerical value of PN is meaningful primarily within a species group. Between groups numerical differences in designated sites may not occur, but the species always differ in topographic arrangement of sets of perforations common to their respective group (Figures 9, 11, 13, 15).

Scatter diagrams of TL and PN (Figures 10, 12, 14, 16) show no common pattern of relationship among the 19 distinguishable populations (i.e., including the three geographical populations of *subtenuis*). Pearson's product-moment correlation coefficients were calculated for the available measurements of each population (Table 10). Eleven were positive correlations and eight were negative, a division indicative of the absence of a real relationship between TL and PN in the genus. Only four of the correlations depart significantly from zero (5% level): three are positive correlations and one is negative. All aspects considered, the four significant correlations, i.e., *subtenuis*, Pacific Ocean (+), *mucronatus* (+), *sewelli* (+), and *monachus* (−) are probably spurious. Thus, as a working hypothesis PN and TL may be considered to vary independently in adult female *Eucalanus*.

These data shed light on another vital question involving TL and PN, namely, whether in fact the two characters are related genetically. We may anticipate that such a relationship would be apparent by the correlation of the two characters in each species group.

Figures 10, 12, 14, and 16 in fact clearly show the absence of uniformity in the relationship of TL and PN across the genus. We find that each group presents a different pattern of relationship between TL and PN.

TABLE 10.—Correlation coefficient (r) of TL and PN in adult females of *Eucalanus*. Original measurements shown graphically in Figures 10, 12, 14, 16.

Species	N	r	P
subtenuis:			
Atlantic	50	0.0241	>0.1
Indian	24	.1683	>0.1
Pacific	36	.3586	<0.05 $P>0.02$
mucronatus	20	.4743	<0.05 $P>0.02$
crassus	10	−.3477	>0.1
longiceps	12	−.3311	>0.1
monachus	17	−.5967	<0.02 $P>0.01$
pileatus	20	−.3556	>0.1
subcrassus	34	.1569	>0.1
dentatus	21	−.0543	>0.1
elongatus	19	−.0518	>0.1
hyalinus	25	.0831	>0.1
inermis	16	.2365	>0.1
bungii	15	−.0434	>0.1
californicus	22	.3241	>0.1
attenuatus	26	.0498	>0.1
sewelli	43	.3446	<0.05 $P>0.02$
parki	17	.0407	>0.1
langae	14	.0565	>0.1

It would be of considerable interest to know if PN relates to geographical overlap in the breeding range of species of the same species group. Another related question of ecological significance is whether TL varies with the extent to which the range of a species falls outside of the ecological or biogeographic regions typically occupied by the species group.

REMARKS ON THE FUNCTION OF INTEGUMENTAL ORGANS IN *EUCALANUS*

With so few available retinal cells (Vaissière, 1961; Fahrenbach, 1962, 1964; Park, 1966), copepods must locate appropriate sexual partners, couple, and accomplish spermatophore transfer and attachment in the apparent absence of visual contact with the environment. In nature the available methods appear to be eminently successful in preventing hybrid pairing and in ensuring functional placement of the spermatophore's discharge canal on the female genital pore (Fleminger, 1967; Frost and Fleminger, 1968). External chemical and mechanical receptor-effector systems among the Crustacea appear sufficiently diverse to provide adequate non-visual channels mediating the exchange of information required by a relatively complex and efficient, instinctive mating behavior. As in

terrestrial arthropods microanatomical studies on copepods (Lowe, 1935; Fahrenbach, 1962; Park, 1966) reveal a highly organized central nervous system, one that supports innervated integumental sensilla and glands distributed symmetrically over the body. The receptors may monitor the environment, and the effectors may release information in response to appropriate stimulators.

Among semispecies, i.e., somewhat differentiated populations of a superspecies (Mayr, 1970), the primary reproductive barrier is extrinsic inasmuch as potential hybridizers lack access to one another. Assuming no significant contact since the inception of allopatry, intrinsic reproductive barriers, i.e., prezygotic mechanisms, if any, are untested and probably imperfect or nonexistent. Similar populations of recent common ancestry newly brought together through the expansion of ranges are likely to interact unfavorably across a spectrum of fundamental organismic processes and thereby experience pronounced selection pressures. When sympatry replaces allopatry among sets of semispecies hybridization is often intense in the area of geographical overlap (Remington, 1968; Rising, 1970).

The only stabilizing alternatives for such interacting populations are: 1) elimination of one or both; 2) genetic displacement; or 3) coalescence. Alternatives 1 and 2 will prevail if, in general, hybrid offspring are less fit and at a selective disadvantage and only postzygotic barriers are available. Development of increased efficiency of prezygotic barriers will be at a premium and the rate of their development and distribution will be a function of the rate of interactions and the mobility of the populations. According to MacArthur and Wilson (1967) a computer model by Bossert has indicated that full displacement is achieved rapidly and, under ideal conditions, equilibrium may be achieved in as few as 10 generations.

As seen in each of the species groups of *Eucalanus*, differences in the integumental organs between species groups include features common to all members and those common to members comprising the group. Within a group differences tend to occur on or near the genital segment. Moreover, there is a general trend for differences to be more pronounced in the populations whose distributions are most extensive and bring them into contact with the largest number of other members within the species group. Thus, the pattern of integumental organs in *Eucalanus* show configurations that appear to have been shaped by character displacement (Brown and Wilson, 1956) in the broadest sense or what some (Blair, 1963; Littlejohn, 1965) have referred to as reinforcement. If so, integumental organs in copepods may play a significant role in the mating process.

CONCLUSIONS

1. This study provides unique and compelling evidence of the extensive information content applicable to systematics, phylogenetics, evolution, and population biology present in the integumental sensory and effector organs of planktonic copepods.

2. Integumental organs appearing on the body segments in *Eucalanus* are distributed in bilaterally symmetrical, serially homologous patterns that appear in both dorsal (tergal) and lateral (pleural) sets corresponding to the somites of the body. The organs fall into two basic groups: a) receptors that appear as hairs, pegs, or pits and b) integumental glands that communicate with pores on the surface of the exoskeleton. Within the set of a somite each designated site is constant in position and in morphological type of organ relative to the others comprising the set.

3. Analysis and survey of the gross morphology, distribution, and variation of these integumental organs was facilitated by a combination of techniques including a) digestion of internal tissues and intensive staining for light microscopy, b) clearing and integumental staining of intact specimens for light microscopy, and c) scanning electron microscopy. Processing of relatively large numbers of specimens was accomplished most efficiently using method a.

4. Comparative survey of integumental organs in 17 species recognized in this study as comprising the genus *Eucalanus* indicated that the numbers and arrangement of these structures reflect generic similarities, species group similarities, and individual species patterns, all

species but one pair being sufficiently distinctive in number and arrangement to be identifiable solely on the basis of integumental organs. Species grouped on the basis of integumental organs concur with groupings that utilize the seminal receptacle, segmentation of the abdomen and structure of the male fifth legs. In general, variation was negligible; about 80% of the sites in each species was observed in all specimens examined and an additional 10% appeared in from 80 to 99% of the specimens. The mean number of organs observed in samples of each population ranged from a low of 83 to a high of 135 in a combined total of 448 randomly selected specimens representing the 17 species in the genus.

5. Comparison of geographical relationships and number of integumental organs within each species group indicates that the species with the broadest geographical range is also the one with the most distinctive number or arrangement of integumental organs especially with respect to organs on the genital segment. The combination of species specificity, phylogenetic relationships, and geographical patterns associated with numbers and arrangement of organs indicate that the organs may function in prezygotic mating barriers within the genus.

6. Comparison of total length and number of integumental organs indicates that the two features are unrelated.

7. Variation in integumental organs in the circumglobal broadly tropical species *E. subtenuis* was found to have a strong geographical pattern indicating limited gene flow between the populations of the Eastern Tropical Pacific, the Indo-West Pacific, and the Atlantic Ocean. Some sets of organs were found to vary independently; others appeared to vary similarly providing evidence that the genetic control is complex. Their responses to selection pressures appear to vary sufficiently to warrant detailed study of *subtenuis* in relation to its closest cognate, *mucronatus*, within and outside of their region of co-occurrence.

8. Limited examination of males and copepodid stages III to V indicate that the integumental organs appear in the same numbers and arrangements that characterize the adult female except for structures that have not yet completed sexual maturation or are sexually dimorphic.

9. The attenuatus complex is revised on the basis of integumental organs and geographical distribution. Four biologically discrete populations are recognized, three being described as new species.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation Grants (GB 12412, GA 31092, GB 32076) and by the Marine Life Research Group of Scripps Institution of Oceanography. I am particularly grateful to my two colleagues: K. Hulsemann whose meticulous editing and compilation of the manuscript significantly improved its accuracy and expedited its completion and J. Behrhorst who carried out scanning electron microscopy and prepared Figure 2.

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DIFFERENTIAL BLOOD CELL COUNTS OF ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*

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ABSTRACT

In differential blood counts of 200 herring, *Clupea harengus harengus*, the percentages of white cell types and immature erythrocytes in the blood were found to be different from those previously reported in the literature. Herring were sampled from February 1969 through July 1969 from the Boothbay Harbor, Maine, and Deer Island, New Brunswick, Canada, areas.

Immature erythrocytes in wild herring ranged from 6 to 38% with an average of 21; in captive herring they ranged from 2 to 22% with an average of 11. Thrombocytes were the most common type of leukocyte, followed in decreasing order by lymphocytes, neutrophils, basophils, and eosinophils in both captive and wild herring.

The percentage of each white cell type varied greatly between individual herring, but except in one instance, the mean percentage of each white cell type varied little between samples. One group of wild herring was unusual in that neutrophils averaged 21% of the leukocytes in contrast with an average of 4% neutrophils for three other wild samples and an average of 6.8% neutrophils for four captive samples.

The percentage of immature red cells varied widely between individual herring, but the mean percentage varied little between wild and captive herring within their respective categories.

The blood of herring has been studied at the Boothbay Harbor Laboratory to find physiological indicators of environmental stress that may help us determine causes of fluctuations in success of year classes. In previous published studies Naumov (1959) reported changes in the differential white cell counts of Atlantic herring, *Clupea harengus harengus*, from the Barents Sea and from the Greenland Sea in relation to the sexual cycle; Boyar (1962) reported no differences in the occurrence of blood cell types of Atlantic herring, *Clupea harengus harengus*, from the Gulf of Maine that related to length, or that offered any promise as an aging method. The differential white cell counts of herring I examined were different from those previously reported by Boyar and by Naumov. I shall report the results of my studies and discuss possible reasons for those differences.

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Manuscript accepted April 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

MATERIALS AND METHODS

My analysis is based upon blood samples collected from wild herring obtained from commercial fishermen's catches and captive herring held in a tank at the Boothbay Harbor Laboratory. These data are shown in Tables 1 and 2.

All herring sampled from Boothbay Harbor were immature. Those from Deer Island were nonspawning mature fish and those from Eastport were 95% nonspawning mature fish and 5% immature fish. Captive herring were held in circular tanks having a capacity of 1,325 gallons. These tanks were supplied with unheated seawater which was pumped directly from the ocean. The water temperature was recorded at the site of capture in each instance.

Captive herring were fed a diet of canned cat food and commercial fish pellets. This diet was supplemented with natural food which entered the tanks through the water system. This natural food supply varied with the season; barnacle larvae were available in spring, and mollusk larvae were available in summer.

Slides were made from blood obtained by

TABLE 1.—Wild herring (obtained from commercial fishermen's catches.)

Collection date (1969)	Source	No. of fish	Range	
			Length (cm)	Weight (g)
13 Mar.	Boothbay Harbor, Me.	34	11.6-19	9.4- 46.4
10 June	Eastport, Me.	32	14.5-30.4	18.0-214.5
8 July	Boothbay Harbor, Me.	45	12.5-18.2	12.7- 38.6
16 July	Deer Island, N.B., Can.	30	20 -24.6	56.5-119.3

TABLE 2.—Captive herring (held in a tank at the Boothbay Harbor Laboratory prior to collection of blood samples.)

Collection date (1969)	Months held captive	No. of fish	Range	
			Length (cm)	Weight (g)
25 Feb.	6	16	14 -17.2	14.2-29
24 Mar.	7	17	13.2-17.4	10.6-29.4
21 Apr.	8	18	14.3-17.7	14.9-33.1
23 June	10	8	13.1-18	14.1-34.7

direct heart puncture with a heparinized capillary tube. A small drop of blood from the capillary was placed on a microscope slide and the smear made. Slides were air-dried and stained by either the Wright's or Wright-Giemsa staining method. Distilled water was used as a diluent for the Wright's and Giemsa stains. The air-dried film was covered with Wright's stain for 1½ min, then an equal quantity of distilled water added and the film further stained for 3-4 min; then, either the diluted stain was flooded off with water and the slide dried, or the slide counterstained with diluted Giemsa for 20 min. Staining times varied slightly with different batches of Wright's stain. Each herring was measured for total length, weighed, sexed, marked, examined for gross parasitism, and frozen for reference in case abnormal blood properties were found. Cells were examined under oil immersion at 800 and 1,250 powers.

Differential counts were made of both red and white cells on an area of the slide where the cells were evenly distributed. A leukocyte differential count was made of a random selection of 100 leukocytes and listed under the following categories: lymphocytes, thrombocytes, neutrophils, eosinophils, or basophils. The range and mean percentage of each type of leukocyte present was calculated for each sample. An erythrocytic differential count was made of a random selection of 100 red cells and divided into mature or immature cells based upon their general morphology and staining properties. I classify herring erythrocytes in the peripheral blood according to the stage of development as erythroblasts, early polychromatics, mid-polychromatics, late polychromatics or mature cells. These terms were used by Lucas and Jamroz (1961) in describing the developmental stages of avian erythrocytes. The developmental stages for herring erythrocytes are described in Table 3. There are variations in individual herring in the size and shape between and within cell stages, and the amount of polychromasia present is the best indicator as to the stage to which the cell belongs. The primary morphological criteria I used in this paper were those of Boyar (1962). Additional references were consulted for a more definitive classification of cell types, to clarify the distinction of basophils from basophilic-staining immature erythrocytes, and to resolve confusion regarding the existence of monocytes in herring blood. These additional references were Catton (1951), Davidsohn and Nelson (1969), Jakowska (1956), Lucas and Jamroz (1961), Saunders (1968b), and Watson, Shechmeister, and Jackson (1963).

TABLE 3.—Erthrocytes in the peripheral blood of Atlantic herring, *Clupea harengus harengus*, according to the stage of development.

Stage	Description
Erythroblast	Round cell, similar in size to the early polychromatic. Has a dark blue staining cytoplasm with lightly stained spaces. The round purple-red staining nucleus is larger than that of the early polychromatic and takes up most of the cell. Erythroblasts are scarce in normal samples.
Early polychromatic	The smallest immature red cell that is normally seen in any quantity. Has a light blue to gray staining cytoplasm and appears round. The nucleus takes up most of the cell.
Mid-polychromatic	Round to slightly oval cell with a gray to light gray-orange staining cytoplasm. Cell is larger than the early polychromatic.
Late polychromatic	Slightly oval, has a larger cytoplasm and a smaller nucleus than the mid-polychromatic. The cytoplasm appears light orange-yellow.
Mature erythrocyte	Oval, has a slightly larger cytoplasm and a slightly smaller nucleus than the late polychromatic. The cytoplasm appears orange-yellow to reddish. Late polychromatic and mature erythrocytes have essentially the same appearance with Wright's and Wright-Giemsa stains.

RESULTS

Differential red and white cell counts are listed in Table 4. Blood cell measurements of all cells included in the differential counts are listed in Table 5.

The mean percentage of each white cell type varied greatly between individual herring, but except in one instance, the mean percentage for most white cell types varied little between samples. Thrombocytes were the most common leukocyte, followed in decreasing order by lymphocytes, neutrophils, basophils, and eosinophils in both wild and captive herring. One group of wild herring sampled on 8 July from Boothbay Harbor was unusual in that neutrophils averaged 21% of the leukocytes in contrast to an average of 4% neutrophils for three other wild samples and an average of 6.8% for captive herring. The herring from the 8 July sample were confined in the pocket of a stop seine overnight before being bled, in contrast to other wild herring that were bled immediately after the pocket was made in a purse seine (13 March) or in weirs (10 June and 16 July). The relative neutrophilia in the 8 July sample may be a result of the combination of being held overnight at relatively high water temperatures and crowded conditions. Temperature alone was evidently not the cause of relative neutrophilia in the July wild sample, for captive herring taken from nearly the same water temperature did not show relative neutrophilia.

Basophils and eosinophils were scarce in most herring examined, the greatest average (2% basophils) occurred in a wild sample from Eastport, Maine. Though one captive herring had 16% basophils, one wild herring from Eastport had 32% basophils, and another wild herring from Boothbay Harbor had 5% eosinophils and 17% basophils, no differences were found in those specimens in their red cell morphology or

TABLE 4.—Differential leukocyte and erythrocyte counts of wild and captive herring, *Clupea harengus harengus*, with the mean percentage and range (in parentheses) of each cell type.

Sample source and date	Water temp. (°C)	Number of herring	Type of leukocyte: Thrombocytes	Lymphocytes	Neutrophils	Basophils	Eosinophils	Immature erythrocytes
Wild:								
13 Mar. 1969 Boothbay Harbor, Maine	2.0	34	56.7 (33-75)	39.2 (23-58)	4.0 (0-13)	0.1 (0- 3)	0.0	19.1 (6-38)
10 June 1969 Eastport, Maine	7.7	32	53.3 (33-68)	40.8 (21-61)	3.8 (0-10)	2.0 (0-32)	0.1 (0-1)	21.2 (9-35)
8 July 1969 Boothbay Harbor, Maine	13.8	45	48.5 (21-79)	29.1 (9-62)	21.3 (8-47)	1.0 (0-17)	0.1 (0-5)	22.6 (12-33)
16 July 1969 Deer Island, N.B., Can.	9.8	30	62.7 (42-75)	31.8 (16-55)	4.5 (0-14)	0.9 (0-12)	0.1 (0-2)	19.0 (10-35)
All wild		141	54.6 (21-79)	34.7 (9-62)	9.6 (0-47)	1.0 (0-32)	0.1 (0-5)	20.7 (6-38)
Captive:								
25 Feb. 1969	1.3	16	80.2 (64-95)	13.0 (2-33)	6.6 (0-19)	0.1 (0- 1)	0.1 (0-2)	7.9 (2-19)
24 Mar. 1969	3.3	17	69.2 (29-89)	22.3 (9-51)	8.4 (0-20)	0.1 (0- 1)	0.0	11.2 (2-21)
21 Apr. 1969	4.9	18	67.8 (42-89)	26.3 (5-52)	4.6 (1-13)	1.1 (0-16)	0.2 (0-3)	12.3 (2-22)
23 June 1969	15.2	8	63.1 (35-76)	28.0 (18-48)	8.6 (1-17)	0.3 (0- 2)	0.0	13.2 (7-20)
All captives		59	70.9 (29-95)	21.8 (2-52)	6.8 (0-20)	0.4 (0-16)	0.1 (0-3)	10.9 (2-22)

TABLE 5.—Blood cell measurements in microns of wild Atlantic herring, *Clupea harengus harengus*, with the average size, standard deviation, and size range (in parentheses).

Cell type	Number of herring	Total number of cells measured	Cytosome		Nucleus	
			Length	Width	Length	Width
Erythrocytes:						
Mature RBC	8	200	10.7 ± 0.9 (9.0-14.0)	7.8 ± 0.6 (6.2-9.7)	4.6 ± 0.5 (3.3-6.1)	2.9 ± 0.2 (2.2-3.9)
Late polychromatic	6	150	10.4 ± 0.8 (9.0-12.3)	7.6 ± 0.6 (6.2-9.4)	4.8 ± 0.4 (4.2-6.2)	2.9 ± 0.2 (2.3-4.1)
Mid-polychromatic	6	150	9.5 ± 0.7 (7.8-10.9)	7.1 ± 0.7 (5.0-9.0)	5.0 ± 0.5 (4.4-6.2)	3.0 ± 0.2 (2.3-4.4)
Early polychromatic	6	150	8.2 ± 0.7 (6.2-10.6)	7.1 ± 0.7 (4.7-9.2)	4.9 ± 0.5 (3.7-6.2)	3.4 ± 0.4 (3.0-4.8)
Erythroblast	1	10	8.7 ± 0.9 (7.0-9.4)	7.9 ± 0.4 (7.5-8.6)	6.2 ± 0.2 (5.5-6.2)	5.8 ± 0.6 (4.7-6.2)
Leukocytes:						
Thrombocyte	3	100	8.9 ± 0.9 (7.0-10.9)	4.4 ± 0.5 (3.1-6.1)	7.2 ± 0.6 (5.9-9.0)	3.5 ± 0.5 (2.8-4.8)
Lymphocyte	2	100	7.7 ± 0.9 (5.0-10.1)	7.4 ± 0.8 (5.5-9.4)	6.4 ± 0.6 (4.7-8.6)	6.1 ± 0.6 (4.7-7.8)
Neutrophil	8	100	11.3 ± 1.7 (7.6-17.2)	10.9 ± 1.5 (6.2-15.6)	4.9 ± 0.9 (2.2-6.2)	7.3 ± 1.2 (3.6-10.9)
Basophil	6	100	12.4 ± 1.6 (9.4-17.2)	12.0 ± 1.2 (8.6-14.0)	5.1 ± 1.2 (3.1-8.6)	6.6 ± 1.4 (3.1-9.4)
Eosinophil	1	25	14.1 ± 1.7 (10.1-17.2)	14.3 ± 1.4 (12.5-17.2)	4.6 ± 0.9 (3.1-6.2)	7.5 ± 1.0 (6.2-9.4)

gross parasitism to distinguish them from other herring in their respective samples.

The mean percentage of immature erythrocytes varied widely between individual herring, but the mean percentage of immature erythrocytes varied little between samples of wild and captive herring within their respective categories. Wild herring had a greater percentage of immature erythrocytes at each sampling than did the herring held captive. Immature erythrocytes in wild herring ranged from 6 to 38% with an average of 21; in captive herring they ranged from 2 to 22% with an average of 11. As noted for other fish species (Catton, 1951; Hesser, 1960), films prepared from herring blood were characterized by the presence of more cellular debris and disintegrating cells than is usually found in films prepared from mammalian bloods. Erythroblasts, hemoblasts, and cells showing mitotic division were scarce in the peripheral blood of herring examined in this study.

DISCUSSION

The high variability in differential counts between individual herring is not unusual; such variability was noted in a number of vertebrate species (Altman and Dittmer, 1961:127-128). Lucas and Jamroz (1961) discussed the individual variability in blood values and the problems associated with this characteristic in avian species. Rooney, Roberts, and Dexter (1972), in differential counts of immature Atlantic salmon, found the most individual variability in thrombocytes, followed in decreasing order by lymphocytes and neutrophils.

Though I agree with Boyar (1962) in the general description of cell types in herring, my data differ markedly in the percentage of immature red cells in herring blood, in the percentage of white cell types present, and in the relative size of neutrophils in comparison to other white cell types. I found an average of 21% immature erythrocytes in 141 wild herring ranging in

length from 116 to 304 mm in my study, whereas Boyar reported immature erythrocytes and white cells combined constituted less than 3% of the total blood cells in the 85 wild herring ranging in length from 75 to 300 mm in his study.

Boyar (1962) reported neutrophils were much larger than other white cell types, with an average area twice that of the second largest cells, the eosinophils. However, in the herring I examined, the average area of neutrophils was larger than thrombocytes and lymphocytes, but smaller than basophils and eosinophils. The neutrophils in Boyar's line drawings of blood cell types have the appearance of cells that have been mechanically distorted. This flattening and spreading out would cause an increase in cell dimensions.

The average cell measurements in my studies are larger than those reported by Boyar, except in the case of neutrophils. Naumov (1959) reported ranges but not mean dimensions of leukocytes. My size range for neutrophils was similar to Naumov's, while the maximum sizes of individual lymphocytes and eosinophils were larger than reported by Naumov.

The total 8 July sample consisted of 76 herring. Five contained intracytoplasmic inclusions associated with erythrocytic degeneration (Sherburne, 1973). One herring in the total March wild sample, two herring in the total June captive sample, and two herring in the total 16 July wild sample contained erythrocytic inclusions. Though their white cell differentials did not differ markedly from other herring in their respective samples, the ten herring with inclusions are not included in this report.

Basophils were scarce and were not found in the leukocyte counts of 157 of the 200 herring in my study. Only 7 herring in my study had more than 5% basophils in their blood differentials. In contrast, Boyar (1962) reported basophils were the most abundant leukocyte in herring from brit 75 mm in length to sexually mature herring up to 300 mm. He reported basophils averaged 31% of the less than 3% cells other than mature erythrocytes (47% of the leukocytes) present in herring ranging in length from 101 to 200 mm, the predominant sizes of herring included in my study. Boyar also reported that basophils averaged from 18% to 56% of the leukocyte cell types in other size ranges of herring included in my study.

I have used the same staining method (Giemsa) used by Boyar and found no differences in the relative numbers of basophils compared with those I found using Wright's or Wright-Giemsa stains. Romer (1949) reported basophils are seldom found in fishes. Naumov (1959) found no basophils in sexually mature Murmansk (Atlantic) herring, *Clupea harengus harengus*, collected in 1938-39 from the Barents Sea and 1947 from the Greenland Sea. Saunders (1968a) found no basophils in blood smears of 49 species of teleost fishes from the Red Sea, and Saunders (1966) found basophils in the circulating blood of only 5 species out of 116 species of marine teleosts examined off Puerto Rico. The differences between Boyar's findings and my own may reflect environmental variations between the time of his study and my own. A more likely explanation is that Boyar confused certain basophilic staining immature erythrocytes with basophils. Small basophils are similar in size to basophilic staining immature erythrocytes, but in my slides these cell types were readily distinguished.

Thrombocytes were the most common leukocyte in my study; they constituted an average of 70% of the white cells in captive herring and 54% in wild herring. Boyar (1962) reported thrombocytes (spindle cells) made up 0 to 7% of the less than 3% cells other than mature erythrocytes present in his study. Saunders (1966, 1968a) reported thrombocytes were the most common leukocyte in the circulating blood of 116 species of marine teleosts from Puerto Rico and 49 species of teleost fishes from the Red Sea.

Boyar (1962) reported round, granular ghost cells averaged from 17 to 50% of the less than 3% cells other than mature erythrocytes present in his study. I also found round, anucleated cells occasionally in apparently normal herring, but most cells appeared finely vacuolated. Several blood smears from herring with intracytoplasmic inclusions associated with erythrocytic degeneration (Sherburne, 1973) had up to 50% round, anucleated cells present in the blood films. The anucleated cells appeared pale red with Wright's stain, were similar in size, and ranged from 9.4 x 9.4μ to 10.9 x 10.9μ. Some

of the cells appeared to show diffusion of nuclear material into the cytoplasm.

Naumov (1959) reported that the blood of sexually mature Murmansk (Atlantic) herring, *Clupea harengus harengus*, contained—in decreasing order of relative abundance—lymphocytes, monocytes, polymorphonuclear leukocytes, and eosinophils. Naumov, like many other authors, did not include thrombocytes in his differential counts.

In contrast to Naumov's report, neither Boyar (1962) nor I found monocytes in the Atlantic herring we examined. Jakowska (1956) discussed the confusion regarding the term monocyte, and because of the difficulty of recognizing monocytes with certainty, advised caution in including them as a separate category of teleost blood cell types. Catton (1951), Gardner and Yevich (1969), Hesser (1960), Romer (1949), Saunders (1966, 1968a) and Watson et al. (1963) did not report monocytes in teleost fish species they examined. Romer (1949) stated that monocytes, sometimes regarded as a separate category of white cells, appear to be merely large lymphocytes. I believe Naumov (1959) may have confused monocytes with large lymphocytes or neutrophils for the following reasons: Naumov reported lymphocytes in Atlantic herring ranged from 3.5 to 5.6μ, while monocytes ranged from 8.0 to 10.8μ. The lymphocytes in the herring I examined ranged from small (5μ) to large (10μ). Thus, perhaps Naumov's monocytes were actually large lymphocytes; however, he stated that during the process of regeneration of the gonads after spawning, there is an increasing quantity of monocytes and polymorphonuclear leukocytes in the blood evidently acting as phagocytes. Watson et al. (1963) stated that the neutrophil is a possible cause for some of the confusion regarding the existence of a monocyte within teleost blood, especially a neutrophil with a kidney-shaped nucleus. As the photographs in the translation of Naumov's report available to me are not clear and his monocytes and polymorphonuclear leukocytes have nearly the same range of dimensions (8.0 to 10.8μ and 8.5 to 14.4μ, respectively) perhaps his phagocytic monocytes were neutrophils.

Differential blood counts of herring fry 55-65 mm in total length, sampled in June and July 1971 from Boothbay Harbor, and mature herring 290-320 mm in total length, sampled 28 October 1972, northeast of Nantucket Shoals, confirm the findings of this study in that thrombocytes are the most common type of leukocyte in herring blood followed in decreasing order by lymphocytes, neutrophils, basophils and eosinophils.

This report provides a more accurate description of characteristic blood cell differentials found in Atlantic herring and provides a baseline for a systematic study of leukocyte differentials in physiologically stressed herring.

ACKNOWLEDGMENT

I wish to thank George J. Ridgway for many helpful discussions and constructive criticism of the manuscript.

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A GENERAL LIFE HISTORY EXPLOITED POPULATION SIMULATOR WITH PANDALID SHRIMP AS AN EXAMPLE[1]

WILLIAM W. FOX, JR.[2]

ABSTRACT

A general life history population simulator, GXPOPS, with provisions to exploit any age sector of the population is presented. In addition to the usual fish life history pattern, the model allows simulation of random mating, sex-differential maturation, and stepwise growth found in many crustacean and some fish populations. GXPOPS provides for monthly calculations and all rates may be as general as month specific. The generality of the model is illustrated with an examination of closed season management strategies for a pandalid shrimp population.

The advent of the digital computer has allowed simulation modeling to become the current vogue within nearly all fields of science; fisheries is no exception. The computer has freed mathematically inclined scientists from being able to examine only equilibrium or cursory transitional states and from the need for expressing relations in neat closed analytical forms. Numerical integration schemes and the speed of computation have made possible the examination of large systems of differential equations with feedback mechanisms, both from deterministic and stochastic standpoints. Even the simplest self-regenerating population model of Beverton and Holt (1957), which may be regarded as a simulation model in that it has a feedback mechanism, is largely intractable for looking at transitional states and parameter variability without the aid of a computer.

Paulik (1969) gives a good review of simulation modeling in fisheries. He divided the modeling of fishery systems in an admittedly arbitrary way into two categories, management models and scientific models, depending on the manner in which a model is utilized. Management models are employed for decision making in evaluating or planning strategies for management purposes, while scientific models are constructed to help elicit certain basic knowledge of a biological system. The actual implementation of models in the two categories, however, should be similar in utilizing the model for planning, alternative evaluation, organization, and identifying sensitive areas of the system.

There are at least two fishery simulation models currently in existence which were designed to be generally applicable to most exploited populations. The most comprehensive is GAMES (Gales, 1972). This simulator has seven interacting sectors from the fish stock to the marketing of the final fish product, is modular in structure, and uses the most updated means of input/output. Unfortunately, GAMES is still in a state of development. The other simulator, POPSIM, was written by Walters (1969). POPSIM's major feature is an optimization routine for planning harvesting strategies for a number of harvesting periods. Both of these simulation models are easily adapted to the life history characteristics of fish populations which have been traditionally studied in fisheries science. However, the FORTRAN IV computer simulation model, GXPOPS, was written to allow additionally for the life history pattern of many crustaceans and some fishes that require actual copulation in reproduction and a sex-differentiated maturation schedule.

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Manuscript accepted April 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

MODEL STRUCTURE

A flow-chart of GXPOPS indicating the optional life history sectors is presented in Figure 1. Each sector is described by the equations below. The basic time period for calculations in GXPOPS is monthly with all processes summed or averaged annually. There are three output options: 1) annual summaries only, 2) monthly and annual summaries by age class, and 3) monthly listings by age class as well as monthly and annual summaries.

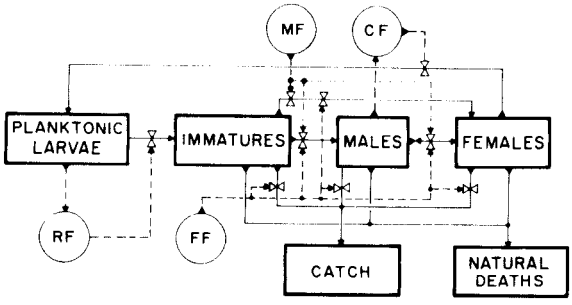

FIGURE 1.—Simplified flow chart of the computer program, GXPOPS. Boxes represent state variable compartments, solid lines represent material flows, dashed lines represent information flows, and circles represent regulatory functions; CF = copulation function, FF = fishing mortality function, MF = sex specific maturation function, and RF = recruitment function.

Mortality

Mortality may be age-specific on a monthly basis and is assumed to be representable by an exponential decline such that

$$N_{i,j+1} = N_{ij} e^{-Z_{ij}} \tag{1}$$

with

$$Z_{ij} = M_{ij} + A_{ij} F_{ij} \tag{2}$$

where N_{ij} is the number of animals belonging to the ith year class at the beginning of month j, M_{ij} is the instantaneous coefficient of natural mortality, A_{ij} is an availability multiplier, F_{ij} is the potential instantaneous coefficient of fishing mortality of a fully available year class, $i = 1 \ldots n$, and $j = 1 \ldots 12$. With natural and fishing mortality so general one can evaluate the effects of seasonal mortality patterns such as mass winter mortalities, closed seasons, etc. The coefficient A allows patterns of selectivity or seasonal availability, etc. to be incorporated. The average number alive of year class i during month j is given by

$$\bar{N}_{ij} = N_{ij} (1 - e^{-Z_{ij}})/Z_{ij}. \tag{3}$$

Growth

The growth in weight of the animals is represented by one of two options, the von Bertalanffy growth equation or a linear segmental growth curve as in POPSIM (Walters, 1969). The von Bertalanffy formulation is

$$w_{ij} = W_\infty [1 - e^{-K(12i + j - 13 - t_0)}]^3 \tag{4}$$

where w_{ij} is the average weight of an individual in year class i at the beginning of the month j, and W_∞, K and t_0 are parameters of the von Bertalanffy growth equation. The segmental growth option is formulated as

$$w_{ij} = a + b \Delta t \tag{5}$$

where $a = w_{i,j-1}$, $b = (w_{ij} - w_{i,j-1})$ and $\Delta t = 1$. Using the segmental option, any shape growth curve may be approximated, including the stepwise growth pattern of crustaceans and many temperate fishes and mollusks.

Yield

Yield is computed monthly both in numbers and weight for each year class under either the von Bertalanffy or linear segmental growth option.

$$Y_{N_{ij}} = A_{ij} F_{ij} \bar{N}_{ij} \tag{6}$$

where Y_{Nij} is the yield in numbers. Under the von Bertalanffy growth option, the yield in weight, Y_{wij}, is computed as

$$Y_{w_{ij}} = A_{ij}F_{ij}N_{ij}W_{\infty} \sum_{u=0}^{3} \frac{\Omega_u e^{-uK(12i+j-13-t_0)}}{Z_{ij}+uK} \times [1 - e^{-(Z_{ij}+uK)}] \quad (7)$$

where $\Omega_u = 1, -3, 3, -1$, respectively. With the linear segmental growth option

$$Y_{w_{ij}} = Y_{N_{ij}} \{w_{ij} + (w_{ij+1} - w_{ij}) [1/Z_{ij} - 1/(e^{Z_{ij}} - 1)]\} \quad (8)$$

Equations (7) and (8) are modified for monthly calculations from Beverton and Holt's (1957) equations 4.4 and 9.5 respectively.

Maturation

A maturity schedule of the sexes is necessary to compute several relationships associated with the reproductive sextor of GXPOPS. This is accomplished in the simulator with two vectors of age-specific values, one denoting the average fraction of mature males in each year class during the breeding season, ϕ_{mi}, and the other denoting the female fractions, ϕ_{fi}. The mean number of mature males, $\overline{N}_{m_j}$, and mean number of mature females, $\overline{N}_{f_j}$, during month j of the spawning season are

$$\overline{N}_{m_j} = \sum_{i=1}^{n} \phi_{mi}N_{ij}(1 - e^{-Z_{ij}})/Z_{ij} \quad (9)$$

and

$$\overline{N}_{f_j} = \sum_{i=1}^{n} \phi_{fi}N_{ij}(1 - e^{-Z_{ij}})/Z_{ij} \quad (10)$$

with

$$s_j = \overline{N}_{m_j}/\overline{N}_{f_j}, \quad (11)$$

where s_j is the mean monthly sex ratio. The mean sex ratio for the breeding season is given by

$$\bar{s} = [\sum_{j=t_s}^{t'_s} s_j]/(t'_s - t_s + 1) \quad (12)$$

where t_s and t'_s are respectively the months that breeding begins and ends.

The maturation fractions, ϕ, are assumed to be constants in the present version of GXPOPS. It is possible that the ϕ may be density-dependent in certain populations. One can investigate the effect of differences in ϕ at equilibrium with the current version of GXPOPS, but it would be a simple matter to reprogram GXPOPS to examine the consequences of any functional hypotheses.

Reproduction

The major components of the reproduction sector of GXPOPS are copulation, egg-carrying (ovigerous period), and hatching. For the common spawing characteristics of freely casting both spermatozoa and eggs, the copulation and ovigerous period sector may be bypassed.

The traditional concept of fertilization success in fisheries population dynamics, excluding the salmonids, is described by Beverton and Holt (1957, p. 61) as:

> . . . if there is free liberation of gametes, with spermatozoa greatly in excess of eggs, and especially if the percentage of successful fertilisations is fairly high, then the number of fertilised eggs would tend to be a constant fraction of the numbers laid. In addition, a large spawning population would tend to distribute eggs over a rather wider area than a small one, so that the number of gametes per unit volume, which in such a situation determines the rate of fertilisation, would not be expected to change much.

Copulation is one mode of ensuring the fertilization of eggs in sexual reproduction. The success of fertilization, therefore, depends on the copulation rate which is at least some function of the sex ratio and density of the mature population. Beverton and Holt recognized this may be the case for a lobster population, in which copulation occurs.

Copulation is a part of reproduction in most commercially exploited crustaceans, and some fishes. With the exception of salmonid studies, where a form of pseudocopulation occurs, population dynamics studies of commercial fisheries have ignored the effects of exploitation on the rate of copulation. Conway (1969) presents the most extensive quantitative treatment of reproduction in insects, whose copulation parallels

that of many crustaceans. He recognizes three types of mathematical models for representing reproduction: 1) derivations from the Lotka-Volterra equations, 2) empirical models (essentially multiple regressions from data sets with a number of variables), and 3) structural models of the causal mechanisms likely to be involved.

Derivations from the Lotka-Volterra equations assume that if mating is random, then the rate of change of copulated females is proportional to the expected rate of contact per female times the number of uncopulated females. The rate of contact per female is assumed to be proportional to the number of males, giving

$$dN_f^*/dt = k_c N_m (N_f - N_f^*) \tag{13}$$

where * denotes copulated females and k_c is the coefficient of copulation. The copulation coefficient may be thought of as consisting of two multipliers — the instantaneous coefficient of males contacting females at random and the fraction of these encounters that result in copulation. Equation 13 has the solution

$$N_f^* = N_f(1 - e^{-k_c N_m}) \tag{14a}$$

or

$$p = (1 - e^{-k_c N_m}) \tag{14b}$$

where p is the fraction of mature females that, at the end of the breeding season (scaled to be of one unit length for convenience), have been copulated. Equation (14b) may also be derived probabilistically by assuming the number of copulations is Poisson distributed such that k_c is the mean rate of contact resulting in copulation per male, then

$$P_r\,[x \text{ copulations}] = e^{-k_c N_m} \frac{(k_c N_m)^x}{x!}$$

with equation (14b), therefore, expressing the probability that at least one copulation per female has occurred in one unit of time (Klomp, Montfort, and Tammes, 1964 [cited in Conway, 1969]). This assumes that the population is not aggregated but is randomly distributed over the breeding grounds regardless of the size of the population. Philip (1957) has also derived equation (14b) under slightly different circumstances. Writing equation (14a) in terms of the sex ratio (males: females), s, and total mature population, N_a, we have

$$N_f^* = \left(\frac{1}{1+s}\right) N_a \left[1 - e^{-k_c \left(\frac{s}{1+s}\right) N_a}\right]. \tag{15}$$

Therefore, as the total mature population decreases, or as the sex ratio increases, the number of females being copulated with decrease under this model for reasonable values of s in the virgin state.

With the aid of equation (15) one can easily follow the reasoning of Beverton's and Holt's conclusions for large, long-lived fish populations with essentially a constant sex ratio. The maximum sustainable average yield (MSAY) in these populations is likely to occur at relatively low rates of fishing, hence there would be only a small reduction in population size from the virgin state. If k_c were high, then the reduction in N_f^* would be negligible. On the other hand, if the population is short-lived, the MSAY is likely to occur at a relatively lower population level. If fishing also increases the sex ratio, the deleterious effects on the size of N_f^* are compounded.

Equation (13) may be extended to become more realistic for a multiage population under exploitation. Often the mortality during breeding is neglected; however, exploitation may increase the mortality significantly and the breeding season may be protracted. Therefore, with the additional assumption that males make no distinction between year classes of females, for any year class i during month j

$$dN_{fi}^*/dt = k_c N_m(t)\,[N_{fi}(t) - N_{fi}^*(t)] - Z_i N_{fi}^* \tag{16}$$

where

$$N_m(t) = \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij} t} \tag{17}$$

and

$$N_{fi}(t) = \sum_{i=1}^{n} \phi_{fi} N_{ij} e^{-Z_{ij} t} \tag{18}$$

Rewriting equation (16) in terms of the ratio of

copulated females to total mature females, $p(t)$, giving

$$dp(t)/dt = k_c \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij}t} [1 - p(t)], \quad (19)$$

the solution obtained is

$$p_j = [1 - e^{-k_c \sum_{i=1}^{n} \phi_{mi} N_{ij} (1 - e^{-Z_{ij}})/Z_{ij}}] \quad (20)$$

with $t = (0, 1)$ months and $p_0 = 0$. Equation (20) may be further simplified by substitution from equation (9) to give

$$p_j = [1 - e^{-k_c \bar{N}_{mj}}]. \quad (21)$$

Therefore, the fraction of the females in any year class that are copulated is the same for all year classes *provided that k_c is not age specific*. Given the fraction copulated in the previous month, p_{j-1} [where $p_{t_s - 1} = 0$], the fraction copulated at the end of the month j is

$$p_j = [1 - (1 - p_{j-1}) e^{-k_c \bar{N}_{mj}}]. \quad (22)$$

The total number of females in the population bearing fertile eggs at the end of the breeding season is then

$$N^*_{ft'_s} = p_{t'_s} \sum_{i=1}^{n} \phi_{fi} N_{it'_s}, \quad (23)$$

further assuming that one copulation results in fertilization.

Recounting the assumptions implicit in the simple model, equation (23), they are:

1. The instantaneous copulation rate per female is linear and proportional to the number of males.
2. The copulation coefficient is independent of the age of the males and females.
3. The copulation coefficient is independent of population size.
4. A single copulation results in fertilization.
5. Multiple copulations, if they occur, do not alter the fraction of each egg clutch that is fertilized from the first copulation.

In developing a reproduction model for insects, Conway (1969) criticized the first assumption as being unrealistic. Empirical evidence and biological induction suggest that the copulation rate should be concave downwards, rising to a maximum at some intermediate density and declining at very high densities owing to interference. Conway (1969) dismissed the second type of models (empirical) as lacking generality for a critical examination of reproduction, and developed three structural models based on nearest neighbor distances. Given the population size, density, and sex ratio, four parameters are contained in his models as compared with only one for the simple model. Conway fits each of his models to data obtained from the literature on insects. The fits he obtained are hardly remarkable considering that four parameters were estimated, and a number given, for only eight points. However, the fits are an indication of the flexibility and possible validity of Conway's structural concepts—especially since an irregularity in the data with biological significance was predicted with the fitted model. The decline in copulation rate in the data, however, occurs at very high population densities. The major use of GXPOPS will likely be for examining the dynamics of populations under exploitation, hence at less than virgin population densities. Also, since the two data sets given by Conway are adequately described by a straight line for the observations at population densities before the decline in copulation rate occurred, and lacking other empirical evidence to the contrary, equation (22) was adopted as the copulation model in GXPOPS.

Many exploited animals carry their fertilized eggs so that the number of eggs reaching the hatching period is intimately tied to the survival of the females during the ovigerous period. If it is assumed that all female mortality results in the loss of the eggs as well, then the number of copulated females reaching the hatching period is given by

$$N^*_{ft'_h} = p_{t'_s} \sum_{i=1}^{n} \phi_{fi} N_{it_h} \quad (24)$$

where t_h is the time at hatching. Instantaneous

hatching is assumed, so t_h represents the mean hatching time.

Individual fecundity (eggs per female) is usually correlated with the size of the individual. Many plots of fecundity on length appear to be concave upward, which indicates that fecundity is closely proportional to the weight of the individual. In order to be more useful generally, however, fecundity in GXPOPS is represented by a vector of mean viable eggs per female at hatching by age class, λ_i, such that the total number of larvae hatched, L_h, is given by

$$L_h = p_{t_s'} \sum_{i=1}^{n} \lambda_i \phi_{f_i} N_{it_h}. \qquad (25)$$

Recruitment

Any equilibrium point achieved with the population model as now formulated is likely to be unstable, such that with a sustained increase or decrease in mortality the population will decrease to extinction or increase to infinite size. Most successful natural populations are believed to achieve equilibrium through any of a number of homeostatic mechanisms associated with density-dependent reproduction or mortality. One such mechanism already mentioned is a decrease in copulation rate at high densities. Others include a lack or destruction of oviposition sites at high densities as in insects or salmonid fishes, an overutilization or competition for a fixed food supply, cannibalism, predator-prey interactions, etc. The usual mode of population regulation assumed in fisheries studies is through density-dependent early stage (or larval) mortality. Treatises on this subject can be found in Ricker (1954, 1958) and Beverton and Holt (1957).

Two models have been widely used in fishery population dynamics; GXPOPS allows the selection of one or the other. The first model, owing to Beverton and Holt (1957), states that the simplest assumption one can make is that the larval mortality coefficient can be expressed as a simple linear function of larval population size

$$dL_t/dt = -(\mu_1 + \mu_2 L_t) L_t \qquad (26)$$

where μ_1 and μ_2 are the density-independent and density-dependent larval mortality coefficients. Equation (26) integrates to

$$L_j = [\mu_2/\mu_1 (e^{\mu_1} - 1) + e^{\mu_1} / L_{j-1}]^{-1} \qquad (27)$$

for the survival of larvae from month $j - 1$ to j. Collecting the constants we have

$$L_j = 1/(\alpha_1 + \alpha_2/L_{j-1}),$$

or

$$L_{h+t_r} = 1/(\alpha_1 \sum_{r=0}^{t_r - 1} \alpha_2^r + \alpha_2^{t_r}/L_h) \qquad (28)$$

for t_r months of larval existence. Equation (28) is a concave downward function that increases monotonically with L_j for a constant period of larval existence and it approaches an asymptote of $\sum_{r=0}^{t_r - 1} \alpha_2^r/\alpha_1$ at an increasing rate as α_2 increases.

The second model, owing to Ricker (1954, 1958), simply assumes that the density-dependent coefficient, μ_2, may operate only until some critical size is reached and that the time to attain this critical size may be proportional to the size of the larval population at hatching, L_h, which gives

$$dL_t/dt = -(\mu_1 + \mu_2 L_h) L_t$$

or on integrating

$$L_{h+t_r} = L_h e^{-(\mu_1 t_r + \mu_2 L_h)} \qquad (29)$$

for t_r months of larval existence. Equation (29) is also concave downwards, but monotonically increases to a maximum at $L_h = 1/\mu_2$, and then monotonically decreases approaching zero as L_h becomes infinite.

Both equations (28) and (29) allow a population to achieve stability over a range of sustained mortality rates. Equation (29), additionally, will produce oscillations in the population (Beverton and Holt, 1957), the criteria for which are given by Paulik and Greenough (1966).

Constant recruitment of size $1/\alpha_1$ may be simulated with GXPOPS by selecting equation (28) and setting $\alpha_2 = 0$.

Timing in the Simulator

Reference in this study is made to a year divided into 12 mo because the reproductive cycles of many exploited fish populations are annual. It is just as easy to consider the "year" as a reproductive cycle (16 days, 3 yr, etc.) divided into 12 time periods of equal length.

The conventional notation, for numbering timestream entities, is for the initial or first instance to be denoted as 0. The computer, however, begins with 1 in executing "DO" loops, etc., therefore, the ordinal numbering system is used in GXPOPS. The first month and year are denoted as 1, as are the initial numbers and yields of the first month and year, and the young of the year. The simulator takes the hatching time, t_h, as time 1 (i.e., $L_h = L_1$) and the year is carried on a biological fiscal basis. For example, if hatching occurs on April 1, recruitment to the main population on July 1 of the first year of life, and breeding begins October 1 and ends December 1; then

$$t_h = 1, t_r = 3, t_s = 7, \text{ and } t_s' = 8,$$

respectively. If recruitment does not occur until July 1 of the third year of life, then $t_r = 27$.

EXAMPLE: A PANDALID SHRIMP POPULATION

GXPOPS was designed to be useful for examining the responses of many life history patterns to exploitation. The impetus, however, was to examine the response to exploitation of a pandalid shrimp life history (Fox, 1972). Pandalid shrimps are protandric hermaphrodites—i.e., individuals mature as males but later transform to function as females (Berkeley, 1930), fertilization is accomplished through copulation, the females carry fertilized eggs 3-9 mo until hatching, and they exhibit pronounced stepwise growth. While the extensive simulation studies investigating the effects and management implications of all sectors of the pandalid shrimp model will be published subsequently, one particular study of the effect of season length on the simulated fishery is useful for illustrating the utility of GXPOPS.

Table 1 contains the parameters of the simulated pandalid shrimp population which 1) consists of six year classes, 2) is fully recruited to the fishable population during the third year of life (at 2 yr old), 3) breeds over 2 mo, 4) carries its eggs 5½ mo until hatching, 5) recruits to the main population during the fourth month of life (3 mo after hatching), 6) matures as males during the third year of life (at 2 yr old), and 7) transforms into females during the fourth year of life (at 3 yr old). The stepwise growth in weight is given in Figure 2.

Exploiting the simulated pandalid shrimp produced the relationship between equilibrium yield and fishing effort (= instantaneous fishing mortality coefficient since the catchability coefficient was assumed to be 1.0) given in Figure 3. An equilibrium yield was achieved with fishing effort up to 1.4, with the maximum equilibrium yield occurring at about 1.0. Fishing above a level of 1.4 did not result in equilibrium within 25 yr of simulated fishing, and continued fishing somewhere between 1.4 and 2.0 would eventually result in extinguishing the population. By not including the effect of random mating (copulation), i.e., $k_c = \infty$, the simulated population achieved equilibrium out to nearly $F = 1.8$ (Fox, 1972). This exhibits some need for considering the implications of copulation success in evaluating management alternatives.

The equilibrium yields given in Figure 3 are for an annual pandalid shrimp fishery. Several states, however, have closed seasons during that part of the year when females are carrying fertilized eggs — ovigerous period — (Dahlstrom, 1970). For the simulated pandalid shrimp population, the ovigerous period lasts 6 mo (months 7-12). It is of interest to compare the results of the closed ovigerous season strategy with other possible season lengths, all beginning subsequent to hatching and running continuously until reaching the closed season.

TABLE 1.—Parameters of the simulated pandalid shrimp population.

Parameter	Symbol	Value
1. Number of year classes	n	6 (i = 1-6)
2. Instantaneous natural mortality coefficient	M_{ij}	0.06 (for all i and j)
3. Availability multipliers	A_{ij}	0.0 (for $i < 3$) 1.0 (for $i \geqslant 3$)
4. Month breeding begins	t_s	7
5. Month breeding ends	t'_s	8
6. Year of first maturity	t_m	3
7. Age (mo) at first recruitment	$t_r + 1$	4
8. Copulation coefficient	k_c	10^{-9}
9. Recruitment parameters of the Beverton and Holt model	α_1 α_2	3.2851×10^{-11} 1.01
10. Fecundity coefficients	λ_i	0.0 (for i = 1-3) 1314 (for i = 4) 1679 (for i = 5) 1997 (for i = 6)
11. Male maturity fractions	ϕ_{mi}	0.0 for i = 1, 2 and 4-6 1.0 for i = 3
12. Female maturity fractions	ϕ_{fi}	0.0 for i = 1-3 1.0 for i = 4-6

FIGURE 2.—Arbitrary growth curve exhibiting the stepwise growth pattern of pandalid shrimps.

The simulated pandalid shrimp population was fished for six different season lengths, from 12 to 2 mo after the hatching period (Table 2). The maximum equilibrium yield for each season length occurred with an *annual* fishing mortality coefficient, F, of 1.0. This means that the monthly fishing effort must increase proportionally to the inverse of the season length to obtain the maximum equilibrium yield (column 2, Table 2). Of those seasons simulated, the greatest equilibrium yield and catch per unit effort were obtained with the 8-mo season (columns 3 and 4, Table 2). Compared with an annual fishery, however, the 8-mo season resulted in a 5% decrease in the average weight of a shrimp in the catch (column 5, Table 2). The 6-mo season (closure during the breeding, ovigerous, and hatching periods) was only slightly less than the 8-mo season in yield and catch per unit effort, but it was better than the annual fishery. However, there was an 11%

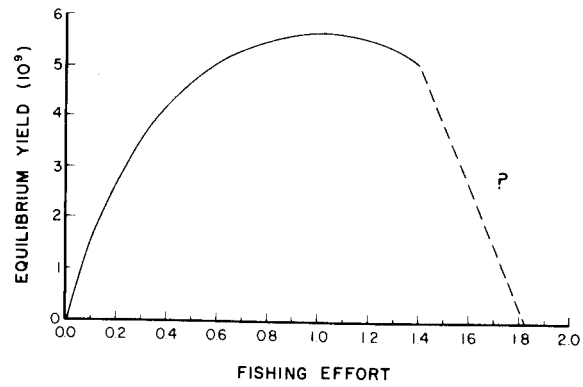

FIGURE 3.—Relationship between equilibrium yield and fishing effort for the simulated pandalid shrimp population. Dashed line represents nonequilibrium region.

TABLE 2.—Effect of season length, beginning subsequent to hatching, on maximum equilibrium yield and allied fishery parameters for the simulated pandalid shrimp population.

(1) Season length (months)	(2) Monthly fishing effort	(3) Season yield in weight	(4) Average monthly catch/effort	(5) Average individual weight	(6) Breeding success (percent)
12	1.0	5.60×10^9	0.467×10^9	3.7	85.5
10	1.2	5.68×10^9	0.474×10^9	3.6	82.0
8	1.5	5.70×10^9	0.475×10^9	3.5	76.1
6	2.0	5.67×10^9	0.472×10^9	3.3	71.3
4	3.0	5.63×10^9	0.469×10^9	3.1	71.3
2	6.0	5.57×10^9	0.464×10^9	2.9	71.3

decrease in average weight as compared to the annual fishery. The breeding success, defined as the fraction of available eggs which are fertilized, declined with the season length until a 6-mo season was reached.

An unknown factor not programmed into the simulation model, however, is the effect of trawling on the behavior of the shrimp during breeding or on the possibility of causing dislodgement of the egg clutches and a subsequent higher mortality rate. In view of these uncertainties, the adoption of a 6-mo season from hatching to the onset of breeding, as several states have, appears to be a biologically prudent approach for a natural population similar to the simulated population. The 6-mo season is only slightly lower in maximum equilibrium yield, catch per unit effort, and average size than the optimal 8-mo season, but is better than the annual fishery in the first two categories. The actual implementation of a 6-mo season on an annual fishery, however, would have to weigh socioeconomic factors because the maximum yield is obtained with twice the amount of fishing effort per month as compared with the annual season. If the fishery were only able, at the time of adopting the closed season, to exert a monthly effort of 1.0, the expected seasonal equilibrium yield is about 10-15% less than that for the annual fishery, but the expected equilibrium mean monthly catch per unit effort would increase 70-80%. The latter should provide a substantial increase in the economic standard of an average fisherman, provided that he has an alternative means of investment for the 6-mo closed season which would provide a sufficient return. The simulation model can be used also to evaluate the expected transitional states from an annual fishery to a seasonal closure fishery as well as the expected equilibrium results discussed here. A socioeconomically feasible strategy, then, may be determined given the current state of the fishery.

PROGRAM AVAILABILITY

A listing and card set-up documentation for program GXPOPS are available on request from the author.

ACKNOWLEDGMENTS

Douglas G. Chapman and Gerald J. Paulik of the University of Washington, Seattle, and Brian J. Rothschild of the National Marine Fisheries Service, La Jolla, Calif., read an earlier version of this manuscript and offered suggestions for improvement. I wish to express my gratitude for their time and helpful comments.

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CHARACTERIZATION OF THE OPTIMUM DATA ACQUISITION AND MANAGEMENT OF A SALMON FISHERY AS A STOCHASTIC DYNAMIC PROGRAM[1]

GARY E. LORD[2]

ABSTRACT

The optimum data acquisition and management of a typical Bristol Bay sockeye salmon fishery have been expressed as a problem in statistical decision theory. Optimality has been defined as that set of sequential decision rules that minimizes the Bayes risk over the duration of the run. Economic losses or costs are ascribed to acquisition of catch and escapement data in such a manner that an optimal data acquisition scheme can be defined in addition to defining the set of optimal management strategies.

The management and inshore harvesting of salmon stocks characteristically consist of several interrelated phases. Stock assessment and run profiling are of importance both to the management personnel and to segments of the industry in planning their respective operations. Prior knowledge of the run size and time profile is useful in the preliminary planning of a management strategy that will in some way permit the escapement of the desired number of spawners. Similarly, such information also serves the industry in planning the level of its anticipated activities (Mathews, 1967). The theoretical investigation described here was motivated by specific consideration of the data gathering and management schemes currently applied in the Bristol Bay sockeye salmon fisheries. However, the formulation is relatively abstract and of sufficient generality so that, properly interpreted, it may apply to a variety of fishery situations which are evolutionary or time varying in nature. Indeed, it is this dynamic aspect of the problem that is at once the crucial feature of the analysis and also the principal source of analytical and computational difficulty.

Rothschild and Balsiger (1971) treated the optimum management of the Kvichak fishery of Bristol Bay as a problem in linear programming in which the various entities comprising the run could be optimally allocated, subject to various constraints on escapement, sex ratios, etc., over the duration of the run. Optimality was chosen as that set of allocation rules which maximized the economic return, expressed as a linear objective function, subject to the satisfaction of a set of linear inequality constraints. This formulation and solution as a linear program are particularly powerful since the solution, easily obtained by standard techniques, is particularly rich in interpretive detail.

The formulation and solution as a linear program suffer from several disadvantages, as Rothschild and Balsiger noted in their paper. First, the solution is deterministic in that it assumes precise knowledge of the run size and its time profile. In actual practice, although there is considerable investment in stock assessment and run forecasting, the resulting estimates are subject to considerable variation. Second, not all of the constraints are "firm," i.e., inviolable. This applies especially to the escapement. Presumably a unique optimum escapement for each actual realization of the run exists, but it is not necessarily imperative that this escapement be attained. Instead it may be assumed that an escapement below the optimum is accompanied by some economic loss, suitably discounted, for the diminished future returns. Similarly, an excessive escapement will result in a loss due to the decreased catch and, if in the right-hand tail of a dome-shaped (Ricker

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Manuscript accepted April 1973.

type) spawner-return curve, there will be an additional loss due to decreased returns. Finally, the linear programming formulation is essentially static although Hillier and Lieberman (1967) discuss certain techniques that are applicable to a limited class of stochastic and dynamic allocation problems. However, the only such technique that would be readily applicable to the fishery management case is chance constrained programming in which the admissibility of "soft" constraints, i.e., constraints which may be violated with certain allowable probabilities, is permitted.

In the subsequent analysis an attempt is made to simulate directly the inherently stochastic and dynamic nature of the management of a typical salmon fishery. A brief discussion of the assumptions made as well as a comparison with the linear programming formulation of Rothschild and Balsiger will also be given. This comparison of methods should be considered to be somewhat subjective and reflects, to a certain extent, the author's own opinions and predilections. The interested reader may be able to arrive at more meaningful comparisons and conclusions after studying the respective analyses in more detail.

We will assume here gear of fixed selectivity with regard to sexes and year classes. This corresponds to the status quo with respect to Bristol Bay although Rothschild and Balsiger showed that an optimum allocation among the various entities comprising the run was economically advantageous, particularly in the case of altered sex ratios. The fixed selectivity assumption, which results in an allocation based only on total numbers of fish, is made principally in the interests of tractability although it is possible to generalize the loss functions and probability densities to include the various individual entities.

Hillier and Lieberman list and discuss the basic features which serve to characterize dynamic programming problems. The principal characteristics will be repeated here, paraphrased slightly, and it will be shown here and in the subsequent analysis that the salmon fishery management problem conforms quite naturally to the class of problems for which dynamic programming is applicable.

1) The problem can be divided into stages with a policy decision required at each stage. This is obviously the case in Bristol Bay where the stages consist of discrete fishing periods, for each of which a management decision must be made. Discreteness is not an essential feature, however, since continuous time allocation problems may also be treated by dynamic programming techniques.
2) Each stage has associated with it a (possibly infinite) number of states. The state of the system is somewhat difficult to characterize precisely. It will be sufficient to treat the state of the system, in this case the salmon fishery, at the start of any stage as reflecting the true state of nature, e.g., run size, time profile, migration patterns, etc., as well as the effects of all previous policy decisions through the preceding time period. Closely related is:
3) The effect of the policy decision at each stage is to transform the current state into a state associated with the next stage. We will generalize this slightly to include sequentially acquired data as an additional quantity serving to characterize the state of the system and the transformation from one state to the next. The remainder of the characterizing features enumerated by Hillier and Lieberman are related to the very fundamental "Principle of Optimality," the statement and discussion of which will will be deferred until the section on Discussion.

The close correspondence of the concepts of dynamic programming, and also the closely related sequential statistical decision theory, to the problem of salmon fishery management suggests that together they provide potentially powerful tools for the description and simulation of such processes. A caveat is appropriate here, however. In general there will be the loss of a considerable portion of the economic "fine structure" of the problem, particularly in comparison with the solution as a linear program. The solution of the linear programming primal

and its dual allows one to make inferences beyond simply the attainment of the optimum. This was emphasized adequately by Rothschild and Balsiger in their identification and discussion of the various shadow prices, etc. A more serious reservation concerns the very serious analytical and computational difficulties to be anticipated. It is a truism of dynamic programming that many more problems may be formulated than may be solved, and it is not at all certain at present whether the salmon fisheries problem falls into the soluble category. Thus, the present discussion will be confined to the presentation of the theory, which is self-contained. The very difficult problems of formulation of the loss functions and the selection of optimum decision rules will be the subject of subsequent investigations.

THEORY

It is helpful to think of the salmon run, its assessment, and its management as evolutionary processes in time. Prior to the start of fishing the management biologist has at his disposal certain prior information, such as preseason forecasts, on which to base his early management strategy. As the run proceeds, additional data are gathered so that, as his knowledge of the true state of nature increases, he may modify his strategy to conform more closely to the optimum strategy. This will now be developed more formally.

Assume that the entire run occurs over a total of m discrete nonoverlapping time intervals. If n_i is the number of fish entering the fishery on the ith day then the total run size, N_{tot}, is given by

$$N_{\text{tot}} = \sum_{i=1}^{m} n_i. \tag{1}$$

Define a parameter vector $\underset{\sim}{\theta}$, of arbitrary dimension, that is assumed to characterize all relevant details of the run. As a specific example, we could define $\underset{\sim}{\theta}$ of the m-dimensional vector $(n_1, n_2, \ldots n_m)$, i.e., the ith component of $\underset{\sim}{\theta}$ is the number of fish entering the fishery on the ith day. More generally, we can leave $\underset{\sim}{\theta}$ arbitrary and write $n_i = n_i(\underset{\sim}{\theta})$. For each known $\underset{\sim}{\theta}$ there exists some known set of optimum allocation rules $\eta_i(\underset{\sim}{\theta})(i = 1, \ldots m)$ where η_i is the optimum fraction of the fish to be allocated to the catch on the ith day. For example, the linear programming formulation of Rothschild and Balsiger provided a set of optimum allocation rules based on a fixed total run size and a two parameter time profile proposed by Royce (1965).

Let D be a finite set of decision rules and let δ_i, a member of D, be the decision adopted on the ith day. Typically the set D consists of such management decisions as fishery opening or closing, fishing area limitations, etc. For each δ_i there will be an actual allocation $\hat{\eta}_i$ where, in general, both η_i and $\hat{\eta}_i$ will be random variables. The former will depend on the true (unknown) state of nature, $\underset{\sim}{\theta}$, while the latter will also be a random function of $\underset{\sim}{\theta}$ as well as of the decision taken, δ_i. As the actual and optimum allocations differ, various economic losses will be assumed to accrue, and the average or expected loss will be these losses averaged over all possible outcomes. This will be developed more formally after considering the various loss functions.

We may postulate the existence of an overall loss function that reflects economic losses from all sources. For our purposes we will consider the loss as arising only from 1) the cost of data acquisition, 2) the catch, and 3) the escapement. Since the catch and the escapement are complementary quantities, their sum comprising the total run, we could consider either one individually as is done in a subsequent example using the Ricker (1958) spawner-return relation. However, an individual treatment of each permits the separate discussion of loss functions that are linear, additive, and separable, as for the catch, and those which are nonlinear and not additive, as will be postulated for the escapement.

First consider the cost of data acquisition. Generally, the sampling schemes to be used and the level of effort for each are selected prior to the run. There may be in-season variations, such as occasional stream surveys, etc. but the cost associated with these is much less than that allocated prior to the run. We denote the experimental design symbolically by ζ and, in line with the above argument, there is

associated with ζ some fixed cost $C(\zeta)$. The quanitity ζ, which is an abstract designation of the experimental design, will also appear as a conditioning quantity when we consider the various probability density functions associated with the sampled quantities, i.e., the distribution of the sample estimates will depend on, among other things, the manner in which the data are acquired.

Next is the loss associated with the catch. Consider the start of the kth time period where $1 \leq k \leq m$ but otherwise arbitrary. If the economic value of the catch is assumed to be linear and additive, we may write

$$L_X(k) = \sum_{i=1}^{k-1} v_i \left[\eta_i(\underset{\sim}{\theta}) - \hat{\eta}_i\right] n_i(\underset{\sim}{\theta}) \qquad (2)$$

as the loss through the (k - 1)st time period for the catch.[3] Here v_i is the unit value of the fish for the ith interval. Note that if $\hat{\eta}_i$ exceeds η_i, i.e., the actual catch exceeds the optimum catch, the loss function is negative and becomes a gain function. However, this apparent benefit must be offset by the loss associated with the corresponding decreased escapement. If this were not the case, then this would not be the correct optimum since any departure from the optimum must result in a nonnegative incremental loss.

Finally consider the loss function for the escapement. This function cannot be considered to be linear or additive since the average number of returns per unit of spawners escaping on any particular day will be a function primarily of the final value of the total escapement. This is a consequence of the fact that late spawners may interfere with the redds of the earlier arrivals and thus diminish the returns for this group. Also, excessive escapement may lead to increased competition for food among the fry to the general detriment of the population as a whole. Thus, to a first approximation, the loss function for the escapement depends only on the final values of the actual and optimum escapements. Symbolically this may be written as

$$L_E(m) = \phi(E, \hat{E}) \qquad (3)$$

where

$$E = \sum_{i=1}^{m} (1 - \eta_i)\, n_i(\underset{\sim}{\theta}) \qquad (4a)$$

is the optimum total escapement while

$$\hat{E} = \sum_{i=1}^{m} (1 - \hat{\eta}_i)\, n_i(\underset{\sim}{\theta}) \qquad (4b)$$

is the actual escapement and $\phi(\cdot,\cdot)$ denotes some suitable functional form. An even more general formulation is possible if the possibility is admitted that the magnitude and timing of the arrivals on the spawning beds are also significant. The loss function must still be expressed in terms of the entire run but the functional form would be of the type

$$L_E(m) = \phi'(E_1, E_2, \ldots E_m; \hat{E}_1, \hat{E}_2, \ldots \hat{E}_m) \qquad (3')$$

where E_i and $\hat{E}_i$ are, respectively, the optimum and actual escapements for the ith time period. However, the determination of the optimum total level of escapement, which is necessary to characterize $\phi(E, \hat{E})$, is a subject of current research and is by no means resolved at present. Thus, the characterization of a function of the generality of $\phi'(E_1, E_2, \ldots E_m; \hat{E}_1, E_2, \ldots \hat{E}_m)$ must await further biological data.

The Bayes risk is defined as the average or expected loss where the averaging is over all possible outcomes and an optimum strategy will be defined as that strategy that minimizes the Bayes risk.[4] An expression for the Bayes risk will now be constructed that is appropriate for the salmon management problem just out-

[3] If the capacity of the cannery becomes limiting, as may happen in cycle years, the loss function for the catch may be written in slightly more general form as

$$L_X(K) = \sum_{i=1}^{k-1} v_i \left\{\eta_i n_i(\theta) - \min\left[\hat{\eta}_i n_i(\theta), \mathrm{cap}(i)\right]\right\} \qquad (2')$$

where cap(i) denotes the cannery capacity for the ith time period. This relation implies that any actual catch that exceeds the cannery capacity will not decrease the corresponding loss. This function is no longer linear but it is still additive. Note also that no cost has been ascribed to the additional economically nonproductive fishing effort. Cannery capacity was one of the constraints imposed by Rothschild and Balsiger in their paper.

[4] The specification of the minimum Bayes risk as the criterion of optimality, while a reasonable one, is somewhat arbitrary. Other criteria are in common use, most notably the "Minimax," in which the optimum strategy is that which minimizes the maximum risk.

lined. Consider the start of the kth time period where $1 \leq k \leq m$ but otherwise arbitrary. The management biologist has at his disposal data observed through the $(k-1)$st period which will be designated by $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$. This is an abstract designation for data which may typically be in the form of catch reports, catch per unit effort data, tower counts, etc. By convention $\underset{\sim}{Y}_0$ represents the preseason information, such as the high-seas forecast, that is obtained prior to the start of the run. However, all future outcomes must be considered since the loss function for the escapement is formulated in terms of the final state of the system. The vector $\underset{\sim}{\theta}$, which characterizes both the run and the corresponding set of optimum allocation rules, is, from the biologists' point of view, an unknown parameter whose value he is attempting to infer. Generally $\underset{\sim}{\theta}$ may be considered to have some underlying prior distribution which may be inferred from historical data, etc. As additional data are gathered, the probability density of $\underset{\sim}{\theta}$ may be successively updated to reflect this additional information. Thus the probability density for $\underset{\sim}{\theta}$ at the beginning of the kth period may be written as

$$f_k(\underset{\sim}{\theta} \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta)$$

where the prior data, $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$, and the manner in which it is obtained, ζ, appear as conditioning quantities.

Now consider the distribution of the actual allocation $\hat{\eta}_i$. Generally $\hat{\eta}_i$ will be a random variable whose distribution will depend on the action taken, δ_i, and on the true state of nature, $\underset{\sim}{\theta}$. Thus the probability density of $\hat{\eta}_i$ may be written in conditional form as $g_i(\hat{\eta}_i \mid \delta_i, \underset{\sim}{\theta})$. This tacitly assumes that the allocation resulting from a decision taken during any particular time period is independent of the outcomes during any other time period which in turn implies that the individual fish is vulnerable during only a single time period. This condition is generally fairly well satisfied in most of Bristol Bay where the fishing districts are relatively small and the fish do not delay in their upstream migrations. Exceptions occur occasionally during extreme tides when the fish may enter and leave the fishery more than once before proceeding upstream. A similar exception would occur if a fishing district were of sufficient size that individual fish must necessarily spend more than a single time period in it. In these more general cases we must include all prior allocations as conditioning quanitities, i.e., the appropriate density would be of the form $g_i(\hat{\eta}_i \mid \hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_{i-1}, \delta_i, \underset{\sim}{\theta})$. An equivalent but more concise notation would be to condition the distribution of $\hat{\eta}_i$ by δ_i and by the state of the system at the start of the ith time period, S_i, i.e., $g_i(\hat{\eta}_i \mid \delta_i, S_i)$. That this is an equivalent conditioning follows from our previous definition of the state of the system as reflecting the true state of nature as well as the effects of all previous policy decisions. If we retain the assumption of independence of the allocations, the joint probability density of $(\hat{\eta}_i, \hat{\eta}_2, \ldots \hat{\eta}_m)$ may be written in factored form as

$$g(\hat{\eta}_i, \hat{\eta}_2, \ldots \hat{\eta}_m \mid \delta_1, \delta_2, \ldots \delta_m; \underset{\sim}{\theta}) = \prod_{i=1}^{m} g_i(\hat{\eta}_i \mid \delta_i, \underset{\sim}{\theta}). \tag{5}$$

It is now possible to construct the risk functions appropriate for the start of the kth time period where, as usual, k is arbitrary. The experimental cost, $C(\zeta)$, has been assumed fixed in advance in which case it is equal to its expected value. Thus the first term of the risk, $R_{1,k}(\zeta)$, is given simply by

$$R_{1,k}(\zeta) = C(\zeta) \tag{6}$$

for all k.

The risk function associated with the catch may be thought of as consisting of two parts. The first part is the risk corresponding to the loss already accrued through the kth time period for which the management decisions have already been made. The second is the risk over the remainder of the run for which the decisions $\delta_{k+1}, \delta_{k+2}, \ldots \delta_m$ remain to be made. From (2) and (5) we obtain

$$R_{2,k}(\delta_1, \delta_2, \ldots \delta_k \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) =$$

$$\sum_{i=1}^{k} v_i \int d\underset{\sim}{\theta}\, f_k(\underset{\sim}{\theta} \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta)$$

$$\int d\hat{\eta}_i\, (\eta_i(\underset{\sim}{\theta}) - \hat{\eta}_i)\, n_i(\underset{\sim}{\theta})\, g_i(\hat{\eta}_i \mid \delta_i, \underset{\sim}{\theta}) \tag{7}$$

for the risk through the kth time period. Although we are considering the start of the kth time period, $\underset{\sim}{Y}_{k-1}$ will have been acquired so that δ_k may be chosen on the basis of this and all previous observations. Similarly, the risk over the remainder of the run is given by

$$R_{3,k}(\delta_{k+1}, \delta_{k+2}, \ldots \delta_m \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) =$$

$$\sum_{i=k}^{m} \mathrm{v}_i \int d\underset{\sim}{\theta}\, \mathrm{f}_k(\underset{\sim}{\theta} \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta)$$

$$\int d\hat{\eta}_i\, (\eta_i(\underset{\sim}{\theta}) - \hat{\eta}_i)\, n_i(\underset{\sim}{\theta})\, \mathrm{g}_i(\hat{\eta}_i \mid \delta_i; \underset{\sim}{\theta}) \tag{8}$$

where, in an implicit sense, the decisions δ_{k+1}, $\delta_{k+2}, \ldots \delta_m$ will be conditional upon the prior decisions $\delta_1, \delta_2, \ldots \delta_k$ as well as upon the observations $\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}$. Equations (7) and (8) have a similar structure although in Equation (7) we are weighting past decisions by our present knowledge of the state of nature while in Equation (8) the future decisions must necessarily reflect only the information obtained through the (k-1)st time period.

The risk for the escapement is assumed to be nonseparable so that the entire run must be considered at once. The general expression for this portion of the risk is then given by

$$R_{4,k}(\delta_1, \delta_2, \ldots \delta_m \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) =$$

$$\int d\underset{\sim}{\theta}\, \mathrm{f}_k(\underset{\sim}{\theta} \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) \int d\hat{\eta}_1 \ldots$$

$$\int d\hat{\eta}_m\, \phi[E(\underset{\sim}{\theta}), \hat{E}(\hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_m)] \prod_{i=1}^{m} \mathrm{g}_i(\hat{\eta}_i \mid \delta_i; \underset{\sim}{\theta}). \tag{9}$$

The total Bayes risk is then the sum of the risks given by (6), (7), (8), and (9), i.e.,

$$R_k = \sum_{i=1}^{4} R_{i,k}. \tag{10}$$

These equations have been derived under very general conditions and assumptions with little effort towards characterizing any of the functions indicated. It is interesting to note, however, that loss functions of the same general form as those appearing in the integrands of (7), (8), and (9) may be obtained if we assume 1) a steady state spawner-return relation of the type proposed by Ricker (1958) and 2) the economic loss (or gain) is proportional to the catch. The steady state Ricker spawner-return relation is

$$\hat{N}_{\mathrm{tot}} = \theta_1 \hat{E} e^{-\theta_2 \hat{E}} \tag{11}$$

where the parameter vector $\underset{\sim}{\theta} = (\theta_1, \theta_2)$ describes the run and $\hat{N}_{\mathrm{tot}}$ and $\hat{E}$ denote the actual run size and the escapement respectively. The corresponding catch is given by

$$\hat{X} = \theta_1 \hat{E} e^{-\theta_2 \hat{E}} - \hat{E} \tag{12}$$

from which it follows that the optimum escapement, E, is given by the solution of

$$\frac{d\hat{X}}{d\hat{E}} = 0$$

or

$$\theta_1 (1 - \theta_2 E)\, e^{-\theta_2 E} = 1. \tag{13}$$

The appropriate loss function in terms of the catch is

$$L(X, \hat{X}) = \bar{\mathrm{v}}(X - \hat{X}) \tag{14}$$

where $\bar{\mathrm{v}}$ is the average unit value of the fish. The equivalent expression

$$L'(E, \hat{E}) = \bar{\mathrm{v}}\, [\theta_1 (E e^{-\theta_2 E} - \hat{E} e^{-\theta_2 \hat{E}}) - (E - \hat{E})] \tag{15}$$

in terms of the escapement is easily obtained by substituting (12) in (14). The term $\bar{\mathrm{v}}\theta_1 [\exp(-\theta_2 E) - \exp(-\theta_2 \hat{E})]$ is nonlinear while $\bar{\mathrm{v}}(E - \hat{E})$ is a linear and additive function of the daily escapements. The substitution of (15) into (9) would then result in an integral of the same general form as (9) and two additional integrals corresponding to (7) and (8).

As indicated earlier, the experimental design,

ζ, is usually fixed prior to the start of fishing and, except for minor variations, remains essentially unchanged during the run. We define the optimum experimental design, ζ^*, by

$$\min_{\zeta} R_0(\bar{\delta}_1, \bar{\delta}_2, \ldots \bar{\delta}_m; \zeta) = R_0(\bar{\delta}_1, \bar{\delta}_2, \ldots \bar{\delta}_m; \zeta^*) \tag{16}$$

where the overbars on the $\{\delta_i\}$ denote averaging overall allowable decision rules δ in the set D and the risks are determined prior to the taking of any observations. Similarly, the optimum decision rules $(\delta_1^*, \delta_2^*, \ldots \delta_m^*)$ are that set of decisions that minimizes the average risk over the duration of the run.

DISCUSSION

A mathematical description of a salmon fishery that includes both stochastic and dynamic elements has been formulated although the final result is relatively general and somewhat abstract. Indeed, the mathematics was formulated specifically to simulate the actual assessment and management of the typical Bristol Bay sockeye salmon fishery. The statistician or management biologist periodically acquires additional data, such as catch reports and test fishing results, from which he can make repeatedly more refined estimates of the true state of nature. Also, although perhaps quite unconsciously, he attempts to estimate the losses (or, if an optimist, the gains) associated with any course of action and the relative probability of occurrence of these losses. Then, based on all data obtained to date, including all past decisions and outcomes, he attempts to formulate a future strategy that will minimize his risk. The analysis of the preceding section attempted to express this sequence of events in a more formalized and quantitative manner.

The apparent fidelity of statistical decision theory to the real world suggests that it provides a very general theoretical tool for the description of such processes. However, the implementation of such a theory may give rise to some practical problems of considerable difficulty, some of which were discussed in the Introduction. In particular it was emphasized there that the ability to formulate a problem as a dynamic program or, almost equivalently, as a problem in sequential statistical decision theory, by no means assures that a solution may be obtained. In this section some additional general features of dynamic programming, as they apply to the fisheries management problem just formulated, will be further elaborated.

The set of optimum decision rules has been defined as that set that minimizes the Bayes risk over the duration of the run. From this it follows that the kth decision must be chosen optimally as a function of the set of prior observations $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$ and as a function of all prior decisions $(\delta_1, \delta_2, \ldots \delta_{k-1})$. In other words, δ must be chosen at each stage in an optimal manner taking into account all prior observations and decisions. At this point we continue Hillier and Lieberman's (1967) characterization of dynamic programming, the first three principles of which were presented in the Introduction. Their principle number four states that: Given the current state of the system, an optimal policy for the remaining stages is independent of the policies adopted in the previous stages. This is a paraphrase of the fundamental "Principle of Optimality" of Bellman (1957, p. 83) which states that: "An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision." The principle of optimality thus assures that the policy we have specified is indeed an optimal policy.

The contradiction, which is more apparent than real, will now be resolved between the principle of optimality just stated and our previous contention that the choice of an optimal decision δ_k depends not only on $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$ but also on the previous decisions $(\delta_1, \delta_2, \ldots \delta_{k-1})$. Recall that the state of the system at time k, say, S_k, is assumed to be uniquely determined by $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$, $(\delta_1, \delta_2, \ldots \delta_{k-1})$, and $\underset{\sim}{\theta}$, the true state of nature. The converse is not true, however, since a multiplicity of different decisions and observations may lead to the same S_k, i.e., there is generally no unique path to S_k. Thus, while it is perhaps more appropriate to state that the optimum δ_k is a function only of S_k, it should be borne

in mind that S_k has been uniquely determined by past decisions and observations so that, in an implicit sense, the $\{\delta_i\}(i = 1,...m)$ are not generally mutually independent.

Consider now a typical Bristol Bay salmon fishery. The usual allowable decision rules consist of either opening or closing the fishery. In addition the management biologists also have the option of allowing fishing over an increased or decreased area depending on whether the run is larger or smaller than normal. Thus, in the most general case, a total of four distinct strategies is available although it is unlikely that both increased and decreased fishing areas would be used during a single season.[5] In the usual case, then, a total of three distinct strategies is available each day from which it follows that a total of 3^m separate courses of action may be pursued during a fishing season m days long. Typically m is equal to about 20 days in Bristol Bay so that the total number of allowable strategies is of the order of 10^9. This is not a number to be taken lightly and is an example of what Bellman (1957, p. 6) refers to as "The Curse of Dimensionality."

The principle of optimality, which is particularly useful in multistage allocation processes, may be invoked in an effort to reduce this problem in many dimensions to a sequence of problems in one dimension. Assume that we are at the beginning of the mth time period where the state of the system is characterized by S_m where S_m reflects the observations $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1,...\underset{\sim}{Y}_{m-1})$ as well as past decisions $(\delta_1, \delta_2,... \delta_{m-1})$. Thus the only decision at our disposal is δ_m and presumably an optimal δ_m may be chosen as a function of S_m. Consider next the beginning of the $(m-1)$st time period for which the system is characterized by S_{m-1}. For every δ_{m-1} selected and executed the system is transformed, after the acquisition of the data $\underset{\sim}{Y}_{m-1}$, into the state S_m for which an optimal decision has already been obtained. Thus at this stage we need optimize only with respect to δ_{m-1}. In this manner we can proceed backward to the beginning of the first time period, characterized by an S_1 depending on Y_0 at which point an optimal δ_1 is selected.

This backward recursive scheme is typical of the method of attack on dynamic programming problems. For a concise but elegant example of this technique applied to a simulated, but numerical, fishery problem see Rothschild (1970). The particular example he used had discrete stages in time with a finite number of strategies available for each stage. The desired solution described the optimum sequence, or path, in time of visiting various fisheries, for a fixed total number of time periods, so that the total catch was maximized. While highly idealized, this problem constitutes a true dynamic program. However, it lacks the stochastic features that are an essential feature of the present discussion.

Verbally this method of solution appears to be most attractive since we have apparently overcome the problem of excessive dimensionality by the recursive consideration of a sequence of problems of lower dimension. This feature is emphasized in the previously cited example presented by Rothschild. However, in problems of larger scale, either in terms of the number of stages or the number of possible states per stage, a rather more subtle problem of dimensionality appears. This concerns the successive specifications of the states of the system $\{S_k\}$ $(k = 1,...m)$. We recall that S_k is characterized not only by $\underset{\sim}{\theta}$, the true state of nature, but all prior observations $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1,...\underset{\sim}{Y}_{k-1})$ and all prior decisions $(\delta_1, \delta_2,...\delta_{k-1})$. The observation vectors are necessarily multidimensional, each component of which represents a particular piece of data or the observation of a particular entity. To make matters worse, the dimension of the $\underset{\sim}{Y}_i$ will generally increase with i since new forms of data, such as catch reports, tower counts, catch per unit of effort, etc., will become successively available. Thus, the $\{\underset{\sim}{Y}_i\}(i = 0,...k - 1)$ required to specify S_k will bring with them their own dimensionality which will soon become overwhelming unless S_k can be described adequately by relatively few parameters. Obviously, aside from possible computer core limitations, the most useful algorithms are those that can accommodate the requisite dimensionality. In a more practical

[5] It is also possible to impose waiting periods for the entry of gear into selected fisheries but this will not be considered here.

sense, however, cognizance must be taken of dimensionality problems to avoid foundering in details, many of which may be irrelevant.

Possible alternative procedures to decrease the number of strategies to consider would be to: 1) combine various contiguous time periods into longer units and thus effectively decrease m and 2) reject those strategies that, based on the value of Y_0 available, have a sufficiently high a priori probability of being nonoptimal. The combining of time periods would be particularly appropriate near the beginning and end of the run when relatively few fish are entering the fishery and the consequences of nonoptional procedures are not so serious. Also, the necessity to consider increased or decreased fishing areas can often be resolved prior to the start of fishing by consideration of the preseason information contained in $\underset{\sim}{Y}_0$.

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THE LIFE HISTORY AND TROPHIC RELATIONSHIP OF THE NINESPINE STICKLEBACK, *PUNGITIUS PUNGITIUS*, IN THE APOSTLE ISLANDS AREA OF LAKE SUPERIOR[1]

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ABSTRACT

The ninespine stickleback is an important food of juvenile lake trout in the Apostle Islands area. It is the most numerous fish of the area and is distributed in deep waters during the winter and in shallow waters during the summer. Females grow faster than males, reaching an average total length of 80 mm at age 5. Males live to age 3 and attain an average length of 66 mm. Annulus formation on otoliths is complete by mid-July. Seasonal growth is more than half complete by early August; growth of mature females is delayed until after spawning.

Both sexes mature over a period of 3 yr. Spawning occurs from mid-June to late July. Males apparently do not live as long as females, possibly because of a post-spawning mortality. Egg number is a linear function of fish length, although this relationship is different for fish from two separate areas. Environmental differences between these areas, which may affect spawning time, possibly cause the differences in fecundity. Significant quantities of maturing eggs atrophy just prior to spawning, a phenomenon which changes the fecundity relationship.

Sticklebacks eat a variety of invertebrates, particularly the crustaceans *Mysis relicta* and *Pontoporeia affinis*. Food eaten by the stickleback and slimy sculpin is similar, but the adaptability of both species tends to eliminate serious competition. The lake trout is the only serious predator of stickleback.

Investigations were made by the Bureau of Commercial Fisheries (BCF) on the biology of the fishes of Lake Superior from the early 1960's. These studies have been primarily life history studies on economically valuable species such as the lake trout, *Salvelinus namaycush* (Walbaum), various coregonids, and the smelt, *Osmerus mordax* (Mitchill). Some of the more comprehensive of these include Bailey (1964), Dryer (1963), and Dryer and Beil (1964).

When it became apparent that these fish stocks were being rapidly modified by exotic species, particularly the sea lamprey, *Petromyzon marinus* L., additional emphasis was placed on ecological studies of noncommercial fishes whose life histories are interrelated with the exploited ones. One of these, the ninespine stickleback, occurs in BCF index trawl samples in greater numbers than any other. However, prior to the study presented in this paper, its ecological significance in these waters was largely unknown. This study was designed to investigate the life history of the ninespine stickleback in the Apostle Islands region of Lake Superior and determine the importance of its relationships to the economically important fish species of the area.

The ninespine stickleback is one of the most widely distributed northern fishes, occurring in freshwater, estuarine, and coastal saltwater environments (Bigelow and Schroeder, 1953). It is abundant in cool-water habitats similar to Lake Superior throughout the Northern Hemisphere. In middle western United States, it is found in all the Great Lakes except Lake Erie

[1] This work is a result of research sponsored in part by the Minnesota Agricultural Experimental Station, University of Minnesota, St. Paul, MN 55101.

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Manuscript accepted March 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

(Hubbs and Lagler, 1958). It has also been taken in inland lakes as far south as northern Indiana (Nelson, 1968a), and Moore and Braem (1965) found small numbers in some Lake Superior tributaries. It is a fish of cool, quiet water (Hubbs and Lagler, 1958), and it is generally abundant wherever it occurs in lakes or seas within its range.

METHODS AND MATERIALS

The data for the present study were collected in 1967-69 in cooperation with the BCF Great Lakes Biological Laboratory, Ann Arbor, Mich.[4]

Experimental sampling operations were conducted aboard the BCF research vessel *Siscowet* in conjunction with sampling by BCF in the Apostle Islands, Lake Superior. The main objectives of the BCF program were to enumerate juvenile lake trout, monitor spawning success, measure the impact of the lamprey on the trout population, and contribute research on the biology of other species in the lake.

One of the main objectives of the ninespine stickleback study was to define ecological relationships between the stickleback and other fish, particularly the lake trout. With this objective in mind, and within the limitations of the ongoing BCF program, sampling was essentially confined to seven stations within the Apostle Islands (Figure 1). Five of these stations (12, 24, 44, 75, and 86) were sampled regularly as juvenile trout index trawl stations and yielded data pertinent to questions of species interaction. Comparatively, they supported varying numbers of trout and sticklebacks, and historically they comprised the known lake trout nursery areas within the islands. At present, only stations 75 and 86 support good populations of juvenile trout. The other two stations, 2 and 3, support abundant midsummer stickleback populations and comprise shallow, inshore areas. These two stations were outside the regular BCF trout index sampling routine and required special sampling. Collections from these stations provided data for stickleback age and growth studies and supportive information about distribution and relative abundance.

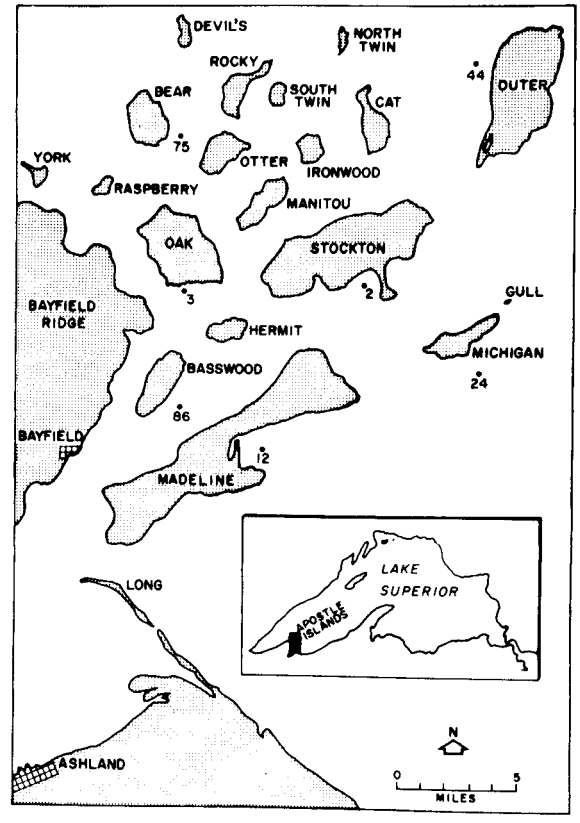

FIGURE 1.—Sampling stations in the Apostle Islands. Blacked out area in inset shows location of these islands in Lake Superior.

A small semi-balloon otter trawl with a 4.7-m headrope, 38.1-mm mesh body (stretched measure), and 12.7-mm mesh cod end was used from a 16-ft aluminum boat with a 40-horsepower outboard motor at stations 2 and 3. A large trawl of the same type (9.4-m headrope, 50.8-mm body, and 12.7-mm cod end) was used aboard the *Siscowet* for deepwater trawling. Adult lake trout were sampled with experimental gill nets ranging from 1.3- to 7.6-cm mesh (bar measure). Zooplankters and sticklebacks examined for stomach contents were collected with a sled-borne plankton net with a 1-m square mouth and 0.158-mm mesh, the bottom edge of which ran approximately 30 cm above the lake bottom. Temperature profiles

[4] Presently the Great Lakes Fishery Laboratory, U.S. Bureau of Sport Fisheries and Wildlife.

were obtained by bathythermograph at each station.

Trout index trawling aboard *Siscowet* was done for two 2-wk periods annually, one spring and one fall. A total of 286 tows, each 1 mile long, were conducted during the stickleback study from April 1967 through May 1970. Additional records from 322 index tows taken in all ice-free months dating back to April 1965 were also included in the study of distribution. A total of 46 ¼-mile tows were made from June through September, 1968 and 1969, with the small outboard trawl, and 18 tows were made with the sled at various times of the year at the index stations in 1968 and 1969. Trawl samples were separated by species, and the fish were counted. After lake trout were measured, fish samples were put in jars of appropriate size and preserved in 10% Formalin.[5] Samples from the plankton sled were flushed directly into jars and preserved in Formalin.

The main limitation of this sampling scheme was that the index trawl series was conducted at a limited number of stations representing trout nursery areas. It is possible that the biological communities and the resultant ecological interrelationships in these areas may not be representative of the entire Apostle Islands area. Also, since areas of sampling were limited and the efficiency of the index trawl was unknown, it was impossible to estimate absolute biomass of the stickleback population. Alternate methods of population estimation were unfeasible because of the immensity of the population and the area.

Additional methods are discussed in appropriate sections throughout the paper.

DESCRIPTION OF GROWTH

Sticklebacks used for age and growth studies were stratified by length, subsampled if catches were large, and frozen. Otoliths (sagittae) were removed, cleaned, dried in alcohol, cleared in creosote, and mounted on microscope slides in Canada balsam as described by Jones and Hynes (1950). The otoliths contained a series of transparent and opaque rings, and it was evident that the transparent zone was laid down at the beginning of the growing season in late June and early July. Therefore, the annulus was considered the outer edge of the opaque zone. Nomographs, based on the male and female body length-otolith length curves, respectively, were used to calculate body length at each annulus (Carlander and Smith, 1944).

Validation of the Otolith Method

Determination of age from otolith rings was made with little difficulty. In older fish the annulus on the outer margin was not as distinct as in young fish, but usually could be identified at the posterior portion of the otolith. After two independent age determinations of 808 pairs of otoliths, 37 pairs required reexamination because the first two were not in agreement.

Otoliths were analyzed from sticklebacks taken with experimental trawls in 1967 and 1968. The samples represented six year classes and five age-groups. The otoliths were from 372 fish taken at station 2 and 436 taken from station 3. Length-frequency distributions were estimated from 18,175 fish measured from 80 trawl samples.

The following evidence indicates that annuli on otoliths provide an accurate measure of stickleback age and growth:

1. Length distribution by age-group based on otolith readings and modes in length-frequency distribution of all measured fish were in close agreement; however, most distributions exhibited some degree of overlap (Figure 2 and 3). In the June sample (Figure 2), the distribution of age-group 0 fish truncated on the left-hand side because it had been discovered that all of these smaller fish were of 0-group.
2. Calculated lengths at the end of each year of life corresponded well between the various year classes (Tables 1 and 2).
3. There was a general increase in average body length with assigned age of the fish (Tables 3 and 4).
4. The average empirical length of aged fish collected in spring prior to annulus for-

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

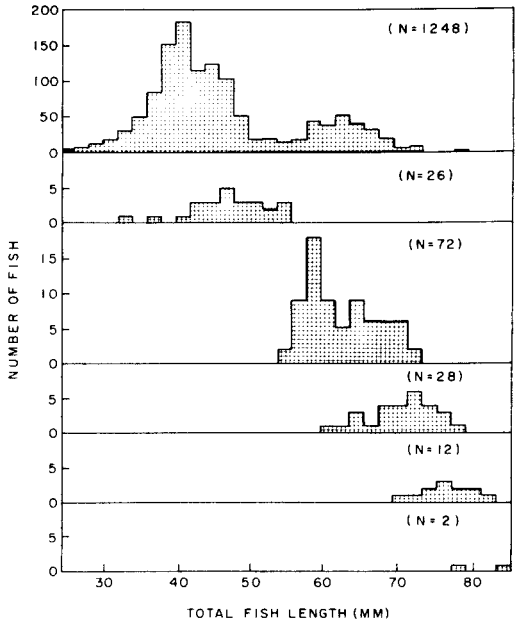

FIGURE 2.—Length-frequency distribution of sticklebacks (top graph) and length frequencies of age-groups 0 to IV based on otolith readings (lower graphs) of fish collected in June 1967. *N* equals number of fish.

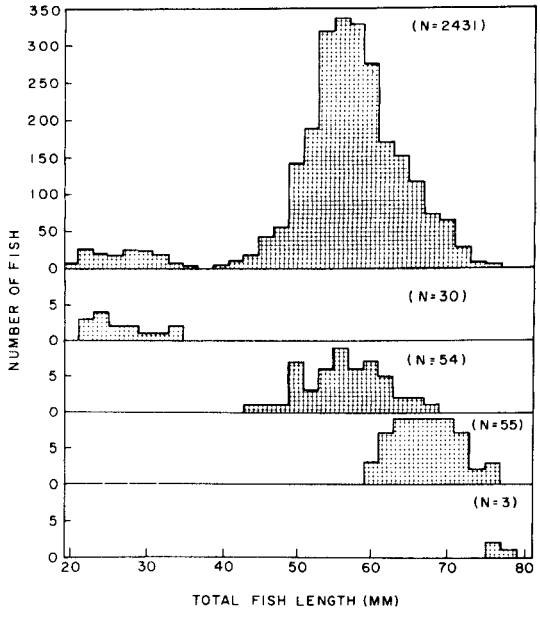

FIGURE 3.—Length-frequency distribution of sticklebacks (top graph) and length frequencies of age-groups 0 to III based on otolith readings (lower graphs) of fish collected in August 1967. *N* equals number of fish.

TABLE 1.—Average calculated total lengths in millimeters of female ninespine sticklebacks from stations 2 and 3 in the Apostle Islands.

Station	Year class	Number of fish	Years of life 1	2	3	4	5
3	1962	1	45.50	58.75	65.75	74.00	81.00
2	1963	16	46.25	58.25	66.25	73.50	
3	1963	19	48.75	61.53	68.56	76.62	79.00
2	1964	24	44.90	61.20	69.16		
3	1964	40	47.38	61.64	68.79	74.92	
2	1965	60	48.65	61.81	70.50		
3	1965	122	48.66	63.25	70.66		
2	1966	110	47.33	63.22			
3	1966	70	48.47	61.18			
2	1967	24	49.00				
3	1967	2	47.75				
[1]2		234	234	88	23	8	
[1]3		254	254	62	38	9	2
[2]2			47.22	61.87	68.63	73.50	
[2]3			47.75	61.27	68.44	75.18	80.00
Average empirical length of fish in spring prior to annulus formation			47.08	62.32	71.16	77.53	81.00

[1] Total number of fish.
[2] Grand average calculated length.

TABLE 2.—Average calculated total lengths in millimeters of male ninespine sticklebacks from stations 2 and 3 in the Apostle Islands.

Station	Year class	Number of fish	Years of life 1	2	3
3	1963	8	45.21	60.23	66.13
2	1964	8	44.25	59.25	65.50
3	1964	38	43.97	59.73	
2	1965	12	44.25	59.62	
3	1965	70	47.30	60.47	
2	1966	108	49.72	62.70	
3	1966	44	48.54	59.70	
2	1967	10	50.60		
3	1967	22	47.00		
[1]2		138	138	38	8
[1]3		182	182	50	2
[2]2			47.20	60.52	65.50
[2]3			46.40	60.03	66.13
Average empirical length of fish in spring prior to annulus formation			48.55	60.60	67.60

[1] Total number of fish.
[2] Grand average calculated length.

mation agreed closely with grand average back-calculated length of each assigned age-group (Tables 1 and 2). Empirical lengths slightly exceeded calculated lengths, indicating seasonal growth may already have begun.

TABLE 3.—Length frequency of the age-groups of female sticklebacks taken in July 1968 from the Apostle Islands.

Total length (mm)	Age-groups				
	I	II	III	IV	V
40-41	5	—	—	—	—
42-43	4	—	—	—	—
44-45	8	—	—	—	—
46-47	10	—	—	—	—
48-49	9	—	—	—	—
50-51	18	—	—	—	—
52-53	6	—	—	—	—
54-55	8	3	—	—	—
56-57	10	9	—	—	—
58-59	7	20	—	—	—
60-61	7	14	—	—	—
62-63	4	13	—	—	—
64-65	4	17	2	—	—
66-67	1	10	1	—	—
68-69	1	17	6	—	—
70-71	—	28	12	1	—
72-73	—	16	16	—	—
74-75	—	6	15	3	—
76-77	—	3	10	2	1
78-79	—	—	7	4	—
80-81	—	1	1	—	2
82-83	—	—	—	1	—
84-85	—	—	—	—	—
86-87	—	—	—	1	—
Average length	52.3	66.5	73.8	76.8	78.5
Number of fish	102	157	70	12	3

Growth in Length

The relationship between total fish length and otolith length was estimated from otoliths of 320 males and 488 females. Body lengths at each 1.0-mm interval of otolith length were averaged, and the mean total lengths were plotted against the otolith length. The relationships for fish from stations 2 and 3 were very nearly the same, but the relationship for males and females were empirically quite different (Figure 4). Second degree polynomial regressions were fitted to these data and the resulting equations were:

Males $Y = -25.864 + 2.146X - 0.011X^2$

Females $Y = -25.075 + 2.131X - 0.0010X^2$

where Y = total fish length (mm) and
X = projected anterior otolith radius (mm).

Coefficients of determination (r^2) values were 0.978 and 0.958 for male and female equations, respectively. An analysis of covariance showed the elevation was significantly different at the 0.01 level ($F_{1,78}$ = 48.32). Therefore, growth parameters were calculated separately for each sex. In Figure 4, the plots were extrapolated to intercept the body-length axis at 6 mm, the length of otolith formation of Alaskan threespine sticklebacks (Jones and Hynes, 1950).

Growth rates were determined for females for the 1962 through 1967 year classes (Table

TABLE 4.—Length frequency of the age-groups of male sticklebacks taken in July 1968 from the Apostle Islands.

Total length (mm)	Age-groups		
	I	II	III
46-47	5	—	—
48-49	1	—	—
50-51	4	—	—
52-53	2	—	—
54-55	11	—	—
56-57	12	—	—
58-59	11	—	—
60-61	7	5	—
62-63	13	5	—
64-65	7	8	1
66-67	4	18	—
68-69	1	8	1
70-71	—	4	4
72-73	—	2	1
74-75	—	4	2
Average length	51.8	66.7	69.4
Number of fish	78	54	9

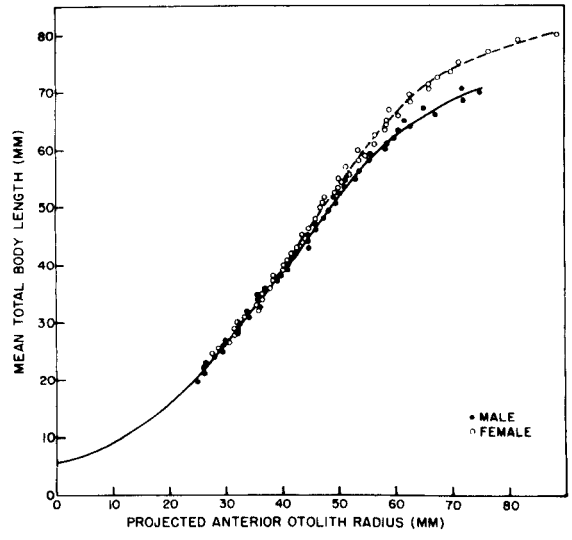

FIGURE 4.—Body length-otolith length relationship for Apostle Islands ninespine sticklebacks. Solid line, males; dashed line, females.

1) and for males for the 1963 through 1967 year classes (Table 2). Females averaged 47.5, 61.6, 68.5, 74.3, and 80.0 mm in total length at the first through fifth annuli, respectively. Age-groups I, II, and III in males averaged 46.7, 60.2, and 65.6 mm. There was little difference between growth rates of fish from stations 2 and 3. Females from station 2 were longer at the end of 2 of 5 yr of life, and males from station 2 were longer at the end of 2 of 3 yr of life. Females grew faster than males during the first year, being 0.02 and 1.35 mm longer at stations 2 and 3, respectively, at annulus I. These differences increased to almost 3 mm after 3 yr. Females reached age 5, males age 3.

Both sexes showed the greatest growth in length in their first year (Tables 5 and 6), when females attained about 60% and males about 70% of maximum size. The average annual increment calculated from the summation of annual increments was about 30% for both sexes during the second year and on the order of 10% per annum thereafter.

Annulus formation was evident in some sticklebacks as early as June in 1967, and all annulus formation was complete by the second week in July. Annulus formation occurred before spawning and started when surface water temperatures reached about 10°C in 1967 and 1968.

Percentage of annual growth completed at any date during the growing season was computed by comparing the length at capture on a given date in 1967, an average growth year as indicated by average annual increments, with the calculated length at annulus formation in 1968 (Table 7). Male growth was faster at the beginning of the growing season with about 50% of the annual growth being completed by late July. Early seasonal growth of females was slower than in males, and 50% of the annual growth was not complete until mid-August. Growth then declined and was complete or nearly complete in all fish by early December when fall turnover occurred. These calculations are consistent with length-frequency distributions of fish from stations 2 and 3 (Figures 5 and 6). These monthly distributions show that growth, as indicated by increasing modal length of the two apparent age-classes, had begun by July and continued into December.

Older fish had a tendency to grow slower in their first years of life than the younger fish (Tables 1 and 2). This growth pattern (Lee's phenomenon) has been reported for many fish

TABLE 5.—Grand average increment in total length of female ninespine sticklebacks from stations 2 and 3 expressed in millimeters.

Station	Year of life	1962	1963	1964	1965	1966	1967	Mean	Sums of means	Percentage of increment
2	1	—	46.25	44.90	48.65	47.33	49.00	47.22	47.22	—
3	1	45.50	48.75	47.38	48.66	48.47	47.75	47.75	47.75	—
2	2	—	—	12.00	16.30	13.16	15.89	14.33	61.55	30.3
3	2	—	13.25	12.78	14.26	14.59	12.71	13.51	61.26	28.2
2	3	—	—	—	8.00	7.96	8.69	8.21	69.76	13.3
3	3	—	—	7.00	7.03	7.15	7.41	7.14	68.40	11.6
2	4	—	—	—	—	7.25	—	7.25	77.01	10.3
3	4	—	—	—	8.25	8.06	6.13	7.48	75.88	10.9
3	5	—	—	—	—	7.00	2.38	4.69	80.57	6.1

TABLE 6.—Grand average increment in total length of male ninespine sticklebacks from stations 2 and 3 expressed in millimeters.

Station	Year of life	1963	1964	1965	1966	1967	Mean	Sums of means	Percentage of increment
2	1	—	44.25	44.25	49.72	50.60	47.20	47.20	—
3	1	45.21	43.97	47.30	48.54	47.00	46.40	46.40	—
2	2	—	—	15.00	15.37	12.98	14.45	61.65	30.6
3	2	—	15.02	15.76	13.17	11.18	13.78	60.18	29.6
2	3	—	—	—	6.25	—	6.25	67.90	10.1
3	3	—	—	5.90	—	—	5.90	66.08	9.8

TABLE 7.—Percent growth completed at various dates of the 1967 season for ninespine sticklebacks in the Apostle Islands.

Date	Male			Female				
	0	I	II	0	I	II	III	IV
July 22-27		48	75		28	5	37	75
August 8-19	62	69	98	64	54	27	60	
December 4	100	100	100	100	97	79	85	100

species (Lee, 1912). In the Lake Superior study, there appeared to be no significant disappearance of faster growing individuals from the length-frequency distributions (Figures 5 and 6). However, as will be shown below, there does appear to be a sex-specific mortality associated with spawning. Since faster growing males tend to spawn at an earlier age, slower growing males may be left in the population longer. This tendency does not explain the presence of "Lee's phenomenon" among females, where it is most prevalent. Figures 5 and 6 demonstrate that young-of-the-year fish were being sampled throughout the latter part of each season. Therefore, it is possible that biased sampling of precocious individuals in the younger age-groups creates the appearance that younger fish of both sexes are growing more rapidly than older fish did at the same age. To minimize these suspected biases in the growth-rate calculations, back calculations for each year class over successive collection years were averaged as unweighted means.

Growth was fairly stable from year to year (Tables 5 and 6) with the exception of 1964. No explanation for this poor growth year was discovered.

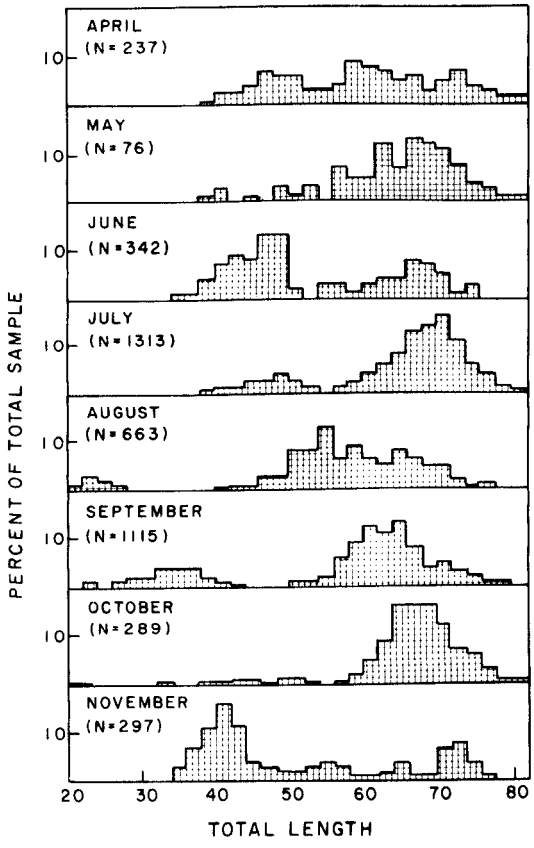

FIGURE 5.—Length-frequency histograms of station 2 sticklebacks expressed in millimeters. *N* equals number of fish in sample.

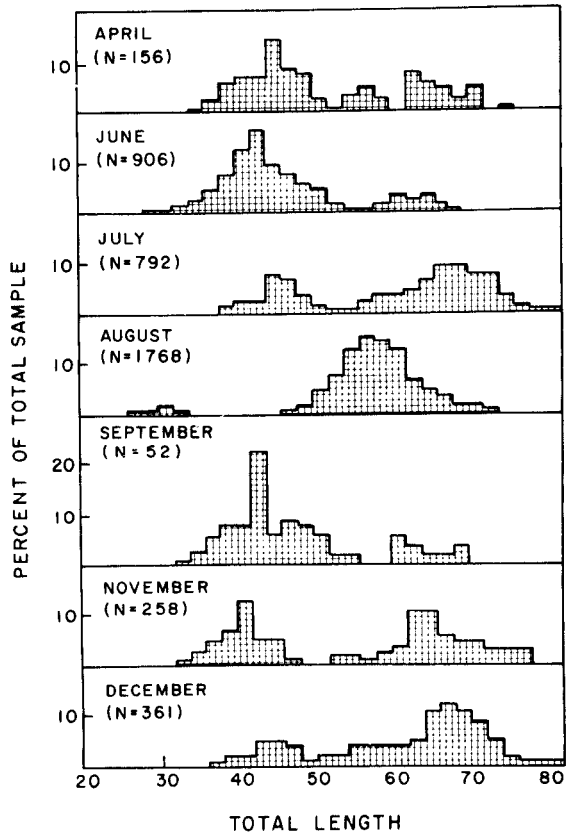

FIGURE 6.—Length-frequency histograms of station 3 sticklebacks expressed in millimeters. *N* equals number of fish in sample.

Ninespine sticklebacks from Lake Superior grow as large, or larger, than those reported in other areas. The most comprehensive growth calculations on the ninespine stickleback prior to this study was done by Jones and Hynes (1950) on a population in a small English stream. They found fish reached only 37 mm in 1 yr and 46 mm in 3 yr. The largest fish recorded was 55 mm. These fish were in direct competition with a population of threespine sticklebacks. Nelson (1968b) found the largest fish in a northern Indiana lake to be 67.3 mm. Bertin (1925) and Leiner (1934) both record European ninespine sticklebacks over 80 mm, but Blegvad (1917) found none over 50 mm in Danish brackish waters. McKenzie and Keenleyside (1970) report fish up to 75 mm in Lake Huron. The formula, TL = 1.14SL, was calculated from 300 Lake Superior fish and used to convert reported SL (standard length) to TL (total length) for these comparisons.

Walford (1946) proposed a transformation of growth data to be expressed as a straight line described by the equation:

$$L_{t+1} = L_\infty (1-K) + KL_t,$$

where L_{t+1} = body length at age $t+1$
L_t = body length at age t
L_∞ = ultimate length
K = slope.

The ultimate length is found graphically where the Walford line intersects a line drawn at 45° through the origin of the graph and is theoretically the greatest length a fish of the population will attain. The slope of the line, K, indicates the decrease in growth rate.

Walford lines were plotted for Apostle Islands sticklebacks from stations 2 and 3 (Figure 7). Means of stations 2 and 3 grand average calculated lengths at each annulus were used to combine station data for each sex.

Calculated values were:

Males	K	=	0.411
	L_∞	=	69.690
Females	K	=	0.672
	L_∞	=	87.660

The ultimate length for males is less than expected from what is known about male length frequency (Table 4). This is probably due to the small number of points used because of the short life span. More points can be included for the female relationship, and the ultimate length is reasonable.

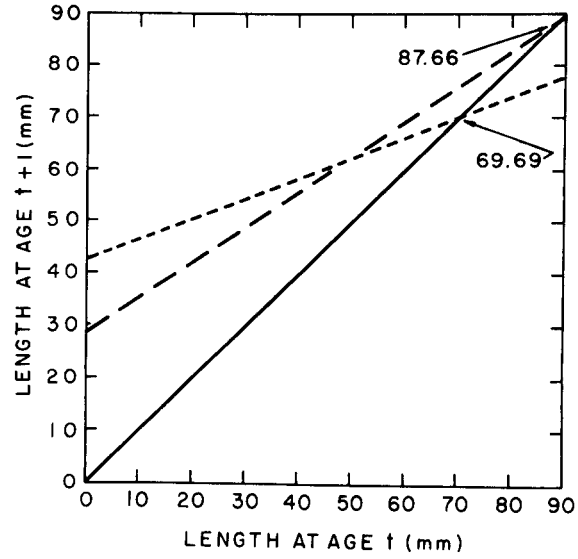

FIGURE 7.—Walford lines for Apostle Islands ninespine sticklebacks. Short dashed line, males; long dashed line, females.

Growth in Weight

Plots of weight against length were made for males and females by calculating average weights for fish at 1-mm intervals. Weights for females in the mature size range were less than male weights. The cause for this was the abrupt drop in weight of females which had just spawned, since the mature female gonad accounts for up to 10% of total fish weight. After females collected in late June and July were omitted from the length-weight plots, the lines for males and females appeared similar.

Analysis of covariance showed slope, and intercept differences were nonsignificant at the 0.05 level ($F_{1,745}$ = 2.71 and $F_{1,746}$ = 1.36, respectively), and the data were pooled to calculate a length-weight relationship. The resultant regression included 748 fish and was described by the formula:

$$\log W = -4.5681 + 3.2190 \log L$$

where $\log W$ = common log of the weight (0.1g) and $\log L$ = common log of the length (mm).

Growth in weight was calculated on the basis of weight at the time of each annulus formation (Table 8). The greatest increment in weight occurred in the second year of life for both sexes at both stations. After the second year, growth in weight declined rapidly, but the decline was more pronounced in males.

Instantaneous rates of growth in weight between consecutive ages varied from 0.804 to 0.223 for males and from 0.842 to 0.192 for females.

TABLE 8.—Calculated weight attained by Apostle Islands sticklebacks at the time of annulus formation.

Age-group	Male			Female		
	Total length (mm)	Calculated weight (g)	Percentage increment	Total length (mm)	Calculated weight (g)	Percentage increment
Station 2						
I	47.20	0.662	—	47.22	0.663	—
II	60.52	1.470	122.0	61.87	1.580	138.3
III	65.50	1.821	23.9	68.63	2.215	40.2
IV	—	—	—	73.50	2.751	24.2
Station 3						
I	46.60	0.627	—	47.75	0.687	—
II	60.03	1.401	123.4	61.27	1.494	117.4
III	66.13	1.955	39.5	68.44	2.185	46.2
IV	—	—	—	75.18	2.955	35.2
V	—	—	—	80.00	3.624	22.6

DISTRIBUTION

While some species of sticklebacks can be found in a marine environment far from shore, the ninespine stickleback is an inshore species (Bigelow and Schroeder, 1953). Hubbs and Lagler (1958) state that the species is abundant in the Isle Royale and Keewenaw Bay areas of Lake Superior. BCF operations found sticklebacks in Nipigon Bay, on the north shore of the lake. While sticklebacks were found throughout the Apostle Islands, it should not be concluded that these fish are similarly abundant on all Lake Superior shorelines. Anderson (1969) recovered only 0.1 stickleback per trawl tow in 90 tows in the Duluth area, sampling during all ice-free months. Degradation of water quality may well be the explanation for this; however, no historical records of stickleback abundance in the Duluth area are available to help justify this hypothesis.

Temperature profiles were secured concurrently with trawl tows. Sticklebacks were found in the warmer deep water in early spring, but were evenly distributed at all depths during spring turnover (Table 9). In midsummer they congregated on the warm shallow snoals where water temperatures reached as high as 20°C. When the fall turnover occurred in September, they were again fairly evenly distributed at all depths. By November the fish were beginning to congregate in the deeper water and were found there in great numbers during December. No data are available for midwinter, but it is assumed the deepwater habitat is used at this time since they were abundant there the following spring. Nelson (1968b) also noted sum-

TABLE 9.—Average numbers of sticklebacks caught per 30-min trawl tow each month at various depths during 1967-69.

[Numbers of tows are in parentheses.]

Depth (fathoms)	Apr.	May	June	July	Aug.	Sept.	Nov.	Dec.
3-9	0.0 (2)	2.7 (4)	12.8 (6)	615.7 (16)	641.5 (12)	75.4 (5)	0.3 (5)	
10-26	0.3 (15)	8.4 (11)	14.8 (45)	10.5 (17)	11.4 (16)	80.0 (42)	18.2 (15)	
27-50	58.4 (12)	11.7 (3)	32.7 (16)	0.1 (6)	0.0 (1)	147.1 (9)	114.7 (11)	267.3 (4)

mer inshore migrations of ninespine sticklebacks in Crooked Lake, Ind.

The shoal areas where sticklebacks concentrated in the summer were represented by stations 2 and 3 (Figure 1). Station 2 included a sandy beach, approximately 2 miles long, at Presque Isle Bay, Stockton Island, which gradually deepened and merged with the soft bottom muds of the deeper areas. In summer sticklebacks congregated in large numbers on the beach in ½ to 2 fathoms of water. The fish could easily be seen by eye and were evenly distributed over the bottom throughout the entire beach area. Station 3, along the south shore of Oak Island, was characterized by a sandy shelf about ¼ mile wide paralleling the shore which gradually deepened to 8 fathoms. The bottom then dropped steeply to 12 fathoms. This steep slope was covered with a dense growth of *Nitella* sp. The summer concentration of sticklebacks occurred in this vegetation. No fish could be seen over the sandy shelf, and no fish were caught unless the net was recovered with mats of *Nitella* sp. clinging to it.

Dryer (1966), Anderson and Smith (1971), and field observations by the senior author of this paper indicate that smelt, slimy sculpins, lake trout under 28-cm TL, and trout-perch, *Percopsis omiscomaycus* (Walbaum), had food habits similar to the stickleback and were apparently abundant enough to be potential competitors with the stickleback. Rank correlation coefficients (r_s) were obtained between the average number of sticklebacks caught per 1-mile trawl tow (CPE) and the CPE of these potential competitors in 100 trout index tows. The CPE's were ranked for each species, ties being given the mean rank, and r_s values were determined by the formula presented by Snedecor (1956). The 100 tows were randomly selected from all (322) trout index tows made at stations 86, 75, 44, 24, and 12 from 1965 to 1968. The significant relationships were those for juvenile smelt, trout-perch, and slimy sculpins (Table 10). Sticklebacks inhabited different areas than juvenile smelt and trout-perch, and sticklebacks and sculpins inhabited the same areas, at least during spring and fall. The results of the correlations do not preclude significant relationships at other times of the year or other places, nor do they consider possible effects of differences in availability to the gear. Further discussion of these correlations will be presented in the section on food habits.

TABLE 10.—Rank correlation coefficients (r_S) between stickleback CPE and CPE's of other species in 100 randomly selected index trawl tows in the Apostle Islands, 1965-68.

Species	r_S
Juvenile lake trout to 11 inches	−0.077
Smelt adults	+0.073
Smelt juveniles	−0.461**
Slimy sculpin	+0.568**
Trout-perch	−0.360**

**Significant at 0.01 level (98 degrees of freedom).

RELATIVE ABUNDANCE

Dryer (1966) reported that the ninespine stickleback was the most abundant species in 578 Apostle Islands experimental trawl tows from 1958 through 1963. The average CPE of stickleback during this period was 51.8. Smelt ranked second (CPE = 40.4), and slimy sculpin, *Cottus cognatus* Richardson, were third (CPE = 22.3). Lake trout CPE was 6.8.

Over the 1965-68 period, 322 trout index tows were made, and the relative rank of sticklebacks, smelt, and slimy sculpins was unchanged from the 1958-63 period (Table 11). The CPE's were 61.1, 50.3, and 17.7, respectively. The catch statistics of the two time periods show slight increases for sticklebacks, smelt, and lake trout. Further comparison is meaningless however, because sampling allocations between index stations used in the two time periods were not identical, and extreme between-tow variation was observed. Table 11 does not include data from stations 2 and 3 because they were not used by BCF as trout index trawl stations.

To sample the shallow inshore area of station 2, where sticklebacks congregated in midsummer, ¼ mile tows were made with the small outboard trawl. The wingspread opening of the trawl was determined by measuring the width of the trawl path on the bottom as indicated by ground-rope disturbance immediately after the

TABLE 11.—Average catch per 1-mile trawl tow (CPE) at various index stations in the Apostle Islands calculated from Bureau of Commercial Fisheries index trawling data, 1965 through 1968.

Species[1]	Station 86	75	24	12	44	Weighted mean
Number of tows	99	98	28	76	21	
Stickleback	42.13	93.22	53.52	60.01	4.69	61.11
Smelt	88.44	19.87	20.71	52.33	7.90	50.30
Lake trout	23.16	7.63	4.29	4.63	.76	10.71
Slimy sculpin	7.93	19.63	38.43	20.01	18.57	17.71
Fourhorn sculpin	.38	.72	.36	4.20	1.14	2.00
Spoonhead sculpin	.35	.47	.61	3.29	.14	1.06
Mottled sculpin	.04	.01	—	—	—	.01
Lake whitefish	.76	1.06	.14	.12	3.62	.81
Bloater	4.44	5.38	—	7.30	.33	4.63
Shortjaw cisco	.08	.06	—	.18	—	.08
Kiyi	.01	.01	—	—	—	<.01
Lake herring	.12	.05	—	.14	—	.08
Unidentified coregonid	5.80	.56	—	1.37	1.24	2.30
Round whitefish	1.00	—	13.93	—	13.33	2.03
Pygmy whitefish	.28	.71	.25	1.24	.86	.65
Alewife	.01	.04	—	—	—	.01
Trout-perch	3.08	1.02	.11	.17	7.28	1.69
Burbot	.17	1.03	.43	.45	.10	.50
Longnose sucker	.07	.14	—	—	—	.06
Johnny darter	.01	—	—	—	—	<.01

[1] Taken from: Bailey, R. M. (chairman). 1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc., Spec. Publ. 6, 149 p.

trawl was towed through the area. This allowed estimation of minimum density.

Catches with this trawl were highly variable even though visual sightings, during both day and night, indicated fish were quite evenly distributed. Light obviously influenced catch because no fish were caught during the daylight hours even though they could be seen. Moonlight intensity probably influenced the catch, as did wind direction and intensity, by adversely affecting the efficiency of the sampling operation. It is entirely possible these factors also influenced catches by *Siscowet* in deeper waters.

Summer nighttime trawl tows on the sandy beach, station 2, usually caught from 300 to 2,500 sticklebacks in ¼ mile (Table 12). These values correspond to minimum density estimates of 0.18 to 1.49 fish per square meter. Sticklebacks were the only species caught in the area during their summer concentration, but johnny darters, *Etheostoma nigrum* Rafinesque, pygmy whitefish, *Prosopium coulteri* (Eigenmann and Eigenmann), trout-perch, and smelt were found there in spring and fall.

TABLE 12.—Catches of sticklebacks in 1967 and 1968 on the sand beach of station 2 during the night using the 4.7-m otter trawl and outboard.

Month	Number of tows	Total sticklebacks	Average per tow
April	5	6	1.2
June	3	217	72.3
July	10	6,985	698.5
August	8	7,564	945.5
September	4	3,622	905.4
November	4	0	0.0

REPRODUCTION

Maturation

The gonads of 401 spring-collected fish from which otoliths were extracted were analyzed for maturity. In addition, 34 male and 72 female I annulus fish (determined from length-frequency histograms) were included in maturity studies.

Both male and female sticklebacks matured over 3 yr (Table 13). A greater percentage of males matured at age 1, with large size being a prerequisite for early maturity. By age 2, nearly all fish of each sex were sexually mature, but neither sex was 100% mature until the third year of life. Jones and Hynes (1950) found 99% of a sample of European ninespine sticklebacks mature with 2 yr.

TABLE 13.—Percent of Apostle Islands sticklebacks mature at each annulus with total number of fish in each group in parentheses.

	I's under 50 mm	I's 50 mm and over	II	III	IV	V
Male	34 (56)	56 (40)	93 (78)	100 (10)		
Female	5 (89)	35 (67)	97 (106)	100 (44)	100 (15)	100 (2)

Within the ovaries, several developmental groups of ova can be distinguished. The ovaries were classified into the following stages for maturity:

Immature (I)

Preserved in Formalin, the ova was translucent, spherical, and invisible to the naked eye. Ova of this group are present in the ovaries throughout the year. Ovaries in this stage are slender, elongate, white organs.

Intermediate (II)

The first yolk granules appear in this stage giving the ovary a pale yellowish tinge while making the ova visible without magnification.

Maturing (III)

The yolk granules appear as highly refractive, spherical bodies in the cytoplasm, and ova become opaque. The ovary becomes turgid and deep yellow in color, with ova readily visible but firmly embedded in the follicles. The size of ova in this stage varies widely.

Ripe (IV)

When the ova are about ready to be spawned, a single conspicuous golden oil globule appears in the yolk. The ova readily break from the follicles in which they were formed and flow freely from the oviduct when the sides of the fish are pressed. In Formalin-preserved fish, mature ova can readily be separated from ovarian tissue with a dissecting needle, a procedure which was almost impossible in Stage III fish. The fish is very rotund.

Partly spent (V)

Partly spent fish contained ripe ova but not the full complement. The ova are congregated in the anterior ends of the ovaries, with the posterior portion somewhat flaccid and lighter in color.

Spent (VI)

Ovaries were gradually resuming the appearance of those in the intermediate stage. Ova maturing for the next reproductive period are already visible to the naked eye. Following spawning, resorbing ova remnants were sometimes found.

Female fish were judged to be sexually mature when their ovaries contained ova in developmental Stage II or beyond. Male maturity was established by noting the presence of breeding color, an ink-black patch on the ventral surface as noted by McKenzie and Keenleyside (1970), remnants of which were detectable through the year after its original appearance.

Time of Spawning

The first spent females were observed on June 6 with no great increase in percentage frequency of occurrence until mid-July. By the end of July, all but one of 38 fish were spent, and that one was partly spent. It appears that the spawning season for these fish is approximately 8 wk long. Equally long spawning periods are reported by Nelson (1968b) and Bigelow and Schroeder (1953).

Spawning Habitat

The spawning act was not observed in the lake, therefore the exact location and spawning substrate cannot be identified. McKenzie and Keenleyside (1970) saw Lake Huron *Pungitius* spawning among rocks around the shore. No such activity was noted in superficial observation in the Apostle Islands. Ripe station 3 females and males displaying vivid reproductive coloration were found exclusively in the dense growth of *Nitella* sp. At station 2, ripe fish of both sexes were collected over highly organic

muds 12 to 24 fathoms deep, and Lake Superior *Pungitius* spawned successfully in this mud in the laboratory while no spawning resulted in rocky or sandy substrates (Griswold and Smith, 1972).

Fecundity and Egg Size

On 27 June 1969, stickleback samples at station 2 and 3 contained a large proportion of females which were in Stage IV of maturity. These fish were used in the analysis of fecundity. A total of 72 fish were examined from station 2 and 60 from station 3 (Table 14).

Several authors have found a high percentage of atresia in maturing eggs of a number of species. This may cause an overestimate of fecundity (Wagner and Cooper, 1963; Vladykov, 1956; Wydoskii and Cooper, 1966). To determine if appreciable atresia occurred in stickleback eggs, the number of eggs in the 132 ripe fish were compared to egg numbers in fish taken from the same stations about 3 wk prior to spawning (Table 15). Analysis of covariance (Snedecor, 1956) revealed egg numbers in the "green" fish were significantly greater (0.01 level) than those in corresponding size of ripe fish ($F_{1,29} = 7.67$). It appears atresia occurs in maturing ninespine stickleback eggs just prior to spawning. Eggs which appeared to be degenerating after some maturation were almost always present in maturing ovaries. The decrease in egg number at each length interval presented in Table 15 ranged from 24 to 39%. The amount of atresia was not dependent on fish size. Vladykov (1956) estimated atresia affected up to 60% of maturing eggs in natural brook trout populations. It is generally agreed that atresia is a physical reaction to the pressure caused by the growing ovary (Vladykov, 1956).

When means of ripe egg numbers at each millimeter body length interval were plotted for stations 2 and 3 ninespine sticklebacks, linear relationships were implied (Figure 8). Least squares equations which describe the lines were:

$$\text{Station 2} \quad Y = -79.75 + 2.37X$$
$$\text{Station 3} \quad Y = -67.81 + 2.12X$$

where Y = number of eggs and
X = length of fish in millimeters.

TABLE 14.—Average number of eggs counted from 132 ninespine sticklebacks of various lengths collected 27 June 1969.

	Station 2			Station 3		
Length (mm)	Mean number eggs	Mean fish weight (g)	Number of fish	Mean number eggs	Mean fish weight (g)	Number of fish
55	—	—	0	84.0	1.217	1
56	—	—	0	—	—	0
57	—	—	0	—	—	0
58	—	—	0	65.0	1.407	1
59	—	—	0	75.0	1.453	1
60	—	—	0	—	—	0
61	—	—	0	—	—	0
62	—	—	0	61.0	1.662	1
63	86.0	1.844	2	59.5	1.737	2
64	—	—	0	68.0	1.712	1
65	74.3	1.827	3	77.7	2.013	6
66	76.0	1.896	3	69.8	1.901	4
67	78.8	1.997	10	71.0	2.101	4
68	82.7	2.031	6	73.0	2.206	4
69	76.8	1.961	5	78.3	2.288	6
70	86.6	2.142	5	87.7	2.371	7
71	82.8	2.254	4	71.3	2.544	3
72	93.4	2.429	7	104.0	2.452	2
73	103.2	2.639	5	82.6	2.766	5
74	98.3	2.400	3	90.0	2.730	7
75	88.0	2.742	5	85.5	2.920	2
76	113.8	2.942	7	94.0	2.776	1
77	112.3	2.990	3	—	—	0
78	95.7	3.070	3	—	—	0
79	—	—	0	103.0	2.962	1
80	103.0	3.010	1	—	—	0
81	—	—	0	98.0	3.522	1

TABLE 15.—Comparison of mean number of eggs per female in fish taken in early June 1970 about 3 wk prior to spawning and fish which were in "running-ripe" condition.

Fish length (mm)	"Green" fish	"Running-ripe" fish
58	—	65.00
59	—	—
60	—	—
61	82.00	—
62	88.50	61.00
63	99.00	72.75
64	98.66	68.00
65	99.62	76.56
66	99.33	72.45
67	116.80	76.57
68	114.50	78.82
69	114.66	77.61
70	114.00	87.24
71	124.25	77.87
72	137.75	95.75
73	126.00	94.70
74	130.66	92.49
75	128.00	87.28
76	132.00	111.32
77	—	112.30
78	158.00	95.70
79	—	103.00
80	—	103.00
81	—	98.00
Total fish	58	132

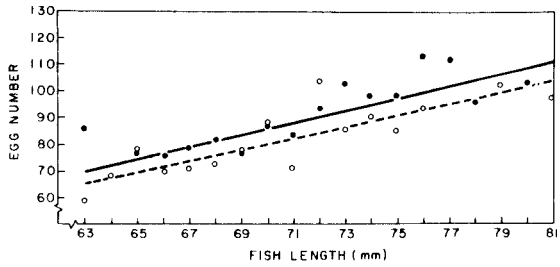

FIGURE 8.—Least squares regression lines indicating the relationship between fish length and number of eggs. Solid line and dots, station 2; dashed line and open circles, station 3.

Coefficient of determination (r^2) values were 0.71 and 0.72 for stations 2 and 3 respectively.

Differences in fecundity relationships between the two stations were implied and analysis of covariance revealed a significant difference (0.01 level) in elevation of the two regressions ($F_{1,28}$ = 19.0). With the presence of atresia, the most obvious theory for this difference would be a slight difference in time of spawning at the two stations. This is suggested by the slightly smaller mean weights of female fish from station 2 sticklebacks at the time of these ovary collections (Table 14). This could be interpreted to mean station 2 females had not matured as much as station 3 fish since female sticklebacks increase their weight by as much as 10% during the maturation period. Atresia would then have acted on the station 2 fish to reduce their fecundity. Any difference in spawning time is probably related to environmental differences between the stations, exemplified by the presence of rooted aquatics at station 3 and their apparent absence at station 2.

Measurements of egg size of six *P. pungitius*, 62-79 mm long, were made on eggs deposited in laboratory aquaria, since Vrat (1949) found stickleback eggs reached maximum size only on extrusion into the water. Eggs were left in the water about 15 min before they were removed and measured under a binocular microscope equipped with an optical micrometer. Egg size appeared to be rather constant with no relationship to size of fish. Egg diameter ranged from 1.53 to 1.98 mm ($\bar{x}$ = 1.76 mm).

Mean weight of ovaries containing ripe eggs was 10.2% and 9.8% of mean fish weight at stations 2 and 3, respectively. Since ovaries in immature fish are very small and some somatic growth had already taken place by spawning time, it is clear that gonad maturation requires a gain in weight of over 10% of the winter weight of the fish. However, early somatic growth in mature females is considerably less than in males (Table 7). It appears that most early annual weight gain in females goes into egg production and rapid somatic growth does not occur until after spawning.

Sex Ratio and Sex Specific Mortality

The sex ratio of sticklebacks was determined for various years of life and for various months because it was obvious from general observation that females predominated in the samples. All 808 fish from which otoliths were extracted were used in the sex ratio calculations. The ratios were:

Age-group	*Male:Female*	*Chi-square*
0	0.930:1	10.54 (7*df*)
I	.809:1	.68 (4*df*)
II	.339:1	22.19 (3*df*)**
III	.125:1	20.57 (3*df*)**
IV	all female	

The χ^2 values for age-groups II and older were significant at the 0.01 level, indicating the ratios were significantly different from 1 to 1.

The sex ratios by month of all fish 1+ and older beginning in April were:

Month	*Male:Female*
April	0.692:1
May	.714:1
June	.366:1
July	.197:1
August	.211:1
November	.137:1
December	.100:1

Monthly length-frequency histograms (Figures 5-6) indicate the presence of two distinct age-groups in most months, the older fish being strung out in an uneven pattern beyond the

second mode. However, the second mode disappeared in August as young-of-the-year began to appear in the catches. Since the 2-yr-old fish, which remained after August were predominantly female (Table 16), it appeared the die-off among old fish, as indicated by length-frequency diagrams, was more prevalent among males. The monthly sex ratios of the age-groups comprising most of the spawning population seemed to indicate that such mortality began to occur as early as June with a sharp drop in males in the catchable population through July. However, the die-off did not appear in the length-frequency diagrams until August. This discrepancy might be explained by a differential movement of males onto the spawning grounds in June to set up their territories and/or an increased awareness of the fishing gear by territorial males. Both these explanations could result in decreased male availability to the trawl during the spawning period. However, after the spawning period, males remained low in the catch throughout the rest of the year, indicating a high mortality among males which spawned.

These interpretations are strengthened by two other observations. Males which had spawned previously were identifiable at any time by vestiges of spawning colors on their ventral surface. Few of these individuals were seen in the collections. Also, in a laboratory experiment described by Griswold and Smith (1972), eight males brought off broods to the point where fry were actively swimming about in the aquaria. Seven of these males died within a month of spawning. There was no mortality observed among 10 females which spawned in the laboratory.

TABLE 16.—Ratio of male sticklebacks to females of different age-groups in various months. Annulus formation is complete after July.

Age	Apr.	May	June	July	Aug.	Nov.	Dec.	Mean[1]
0	0.5	1.2	0.7	—	2.0	0.9	0.5	0.9
1	.7	1.1	.2	0.3	.6	.9	1.6	.8
2	.3	.3	0	.1	.2	.4	.4	.3
3	0	0	0	.1	0	.1	.3	.1
4	—	—	0	0	—	—	0	0
Mean[2]	.4	.7	.3	.2	.7	.7	.7	

[1] Weighted for number of fish in each month.
[2] Weighted for number of fish in each age-group.

PARASITE INFECTION

The pleurocercoid stage of the cestode, *Schistocephalus pungitii* Dubinina (Pavlovskii, 1964), is the only parasite generally abundant among ninespine sticklebacks. The procercoid infects numerous species of copepods, and when these are eaten by sticklebacks, the procercoid burrows through the stomach wall to grow as a pleurocercoid in the body cavity. At this stage the parasite is species-specific as, so far as is known, it attacks only the ninespine stickleback. Two months are required for full growth of the pleurocercoid, at which time it may infect a number of fish-eating birds. No other stickleback parasites were noted in the study.

Rate of infection in Apostle Islands sticklebacks was low in 621 fish examined. Only 4 of 362 fish (1.10%) were infected prior to 1 August in all years of the study combined, and 13 of 259 fish (5.01%) were infected after 1 August. Summer and fall infection would intuitively be higher because of greater copepod abundance at that time. The largest pleurocercoid found was 22 mm long and weighed 0.225 g or 14% of the host's weight. Two fish had two pleurocercoids each which made up 18 and 14.5% of the fish's weight, respectively. These parasites were found in 7 male and 10 female sticklebacks. Fish infected at spawning time did not appear to be maturing.

FOOD HABITS OF THE STICKLEBACK AND ASSOCIATED SPECIES

Five papers mention the food of *P. pungitius*. Forbes (1883) found two specimens which contained equal amounts of diptera larvae and cladocerans. Blegvad (1917) found copepods and stickleback eggs predominant in 112 Danish fish. Hynes (1950) reported cladocera, amphipods, and chironomid larvae were the most important food items in fish from an English stream. Bigelow and Schroeder (1953) state that the stickleback feeds voraciously on fish eggs and fry and can be very destructive to other species in fresh water. Anderson and Smith (1971) report crustaceans make up more than 90% of the Lake Superior stickleback diet. In the present study, emphasis was placed on the food

habits of sticklebacks and several associated species with which they are most likely to compete or which may be involved in predator-prey relationships with sticklebacks.

In the stomach analyses, contents were removed from the upper esophagus to pyloric sphincter and measured by water displacement in 15-cm³ centrifuge tubes. The contents were then emptied into a gridded petri dish for indentification under a binocular microscope at 10× magnification. Organisms present in small numbers were counted, but larger numbers were estimated from counts in randomly selected squares of the dish. Percentage of each item in the total volume of each stomach was estimated. The data are reported as percentage frequency of occurrence and percentage of total volume for each food item in stomachs containing food.

Invertebrate Abundance

Invertebrates important in the stickleback diet were sampled with the mysis sled concurrently with sticklebacks used in food analysis; therefore, it is assumed that the gear sampled food organisms that were available to sticklebacks. One-mile tows were made with the sled and the invertebrate catch was preserved in 10% Formalin. Invertebrate samples were identified and enumerated on a gridded petri dish in the same manner as stomach contents.

The average number of organisms per 100 m of tow is shown in Table 17 for 18 tows on five dates. The data indicate the extreme abundance of *Pontoporeia affinis* adjacent to the bottom. Although copepods were also abundant, they were usually not as important in mass as either *Pontoporeia* or *Mysis*. Coregonid eggs and fry were found occasionally in fall plankton samples.

Food of the Stickleback

Food analyses of 421 stickleback stomachs in nine different months were made (Table 18).

Fish under 50 mm long fed primarily on *Pontoporeia* and copepods, which made up 79 and 13% of the total food volume, respectively. Cladocerans were of minor importance, and mysids were also present infrequently. Other organisms present in these smaller fish were chironomid and diptera larvae and a filamentous green alga.

Food of sticklebacks 50 mm and over were characterized by a variety of larger food items, suggesting that one factor limiting the diet of young fish is size of food items. *Pontoporeia* taken by the under 50-mm sticklebacks were small in size (4.0 mm average) compared with those found in adult stomachs (6.5 mm).

In these larger fish, *Pontoporeia* made up 61% of the total stomach volume, *Mysis* 21%, copepods 8%, and miscellaneous other items 10%. *Pontoporeia* was the major food item in all months but November. There is a suggestion from late fall and early spring samples that coregonid eggs may be an important food item in the winter. Except for these eggs, there is little to suggest that *P. pungitius* is significantly

TABLE 17.—Average number of invertebrates caught per 100 m in tows along bottom with mysis sled in the Apostle Islands.

[The percentage volume of each item found in stickleback stomachs is in parentheses.]

Organism	29 Apr. 1968	22 July 1968	13 Nov. 1968	29 Apr. 1969	27 June 1969
Number of tows	4	3	4	2	5
Amphipoda:					
Pontoporeia affinis	437,750 (88)	748,260 (61)	117,600 (33)	32,360 (84)	371,660 (69)
Mysidacea:					
Mysis relicta	120 (4)	6,110 (12)	34,280 (60)	1,370 (8)	320 (9)
Cladocera	3,170 (1)	1,040 (4)	280 (0)	30 (2)	2,610 (3)
Bosmina spp.	2,210	910	190	30	2,330
Daphnia spp.	920	120	90	0	90
Others	40	10	0	0	140
Fish eggs	0 (0)	0 (0)	0 (0)	0 (6)	0 (0)
Copepods	43,460 (7)	98,630 (23)	47,210 (0)	23,500 (0)	199,790 (16)
Diptera larvae	0 (0)	0 (0)	0 (6)	0 (0)	0 (3)
Mollusca					
Sphaeriidae	2 (0)	0 (0)	0 (0)	1 (0)	0 (0)
Other	0 (0)	0 (0)	0 (1)	0 (0)	0 (0)

TABLE 18.—Food of Apostle Islands sticklebacks expressed as percentage frequency of occurrence and (in parentheses) percentage of total volume for each food item.

Stickleback length	Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Under 50 mm	Number of Stomachs	0	0	13	18	4	0	5	14	0
	Number empty	0	0	2	1	0	0	0	0	0
	Crustaceans:									
	Pontoporeia affinis			62 (66)	100 (99)	100 (100)			93 (86)	
	Copepoda			15 (11)				100 (97)	7 (3)	
	Cladocera							20 (3)		
	Mysis relicta				6 (1)				7 (7)	
	Insects:									
	Chironomidae			8 (9)					14 (4)	
	Diptera									
	Algae			8 (9)						
50 mm and over	Number of stomachs	31	66	99	27	27	55	20	20	22
	Number empty	11	4	3	3	0	1	1	0	2
	Crustaceans:									
	Pontoporeia affinis	80 (75)	61 (49)	90 (75)	30 (24)	92 (92)	82 (62)	90 (80)	60 (30)	59 (45)
	Hyallela sp			1 (1)						
	Mysis relicta	5 (1)	56 (42)	30 (8)	11 (10)		44 (30)	25 (1)	70 (65)	36 (32)
	Copepoda	5 (2)	12 (3)	8 (13)	52 (38)	4 (2)	5 (1)	5 (12)		
	Cladocera	5 (2)		1 (1)	33 (9)	11 (6)	2 (1)	5 (2)		
	Insects:									
	Chironomidae			9 (1)	11 (5)		16 (3)			
	Other Diptera			2 (1)	7 (6)	4 (1)				
	Ephemeroptera		1 (1)							4 (3)
	Nemotoda						2 (1)			
	Coregonid eggs	5 (2)	12 (3)							27 (20)
	Unidentified	5 (15)	1 (2)	3 (2)	7 (7)		22 (3)	5 (5)	5 (5)	

destructive to fish eggs and fry in Lake Superior as Bigelow and Schroeder (1953) thought was generally the case. Neither eggs nor fry of any other kind were found in stickleback stomachs, although gravid females and young-of-the-year of smelt, trout-perch, slimy sculpins, and pygmy whitefish were taken in the same areas at about the same time as the stickleback stomach samples.

The percentage volume of total stomach contents for each day and for each food item taken in the mysis sled is given in Table 17. *Pontoporeia* was the most important food item except in the November sample. In that month, mysids were the most important food and were more abundant in plankton samples than at any other time. Copepods were most abundant in the June and July samples, and their relative contribution to stickleback diet was also highest in these months. In general, when mysids or copepods became relatively more abundant with respect to themselves or to other zooplankters in the plankton samples, they also become more important in the stickleback diet. This suggests that the stickleback shows no strong food preferences but is adaptable and eats what is most available.

Relation to Food Utilization of Other Forage Species

Juvenile smelt (less than 12.5 cm), trout-perch, and slimy sculpins were found to have diets similar to sticklebacks in Lake Superior (Anderson and Smith, 1971). Since all these species were common in the Apostle Islands, competitive relationships between them and the stickleback could exist. A rank correlation coefficient was used to measure the similarity of food composition between two samples and thus permit examination of interspecific and intraspecific feeding relationships.

Table 19 is an example of the computation as discussed by Snedecor (1956). In the case of

TABLE 19.—An example of the calculation of rank-correlation coefficients.

Food item category	10 stickleback rank	10 trout-perch rank	Difference d	d^2
Pontoporeia	1	1	0	0
Mysis	3	4	−1	1
Copepods	2	3	−1	1
Chironamidae	5	2	+3	9
Cladocera	4	5	−1	1

$n = 5 \qquad \Sigma d = 0 \qquad \Sigma d^2 = 12$

$$r_s = 1 - \frac{6(12)}{5(25-1)} = 1 - \frac{72}{120} = 0.40$$

a tie in importance of any two categories, the larger item was ranked first. An r_s value of +1.0 indicates that the various food categories were eaten in the same order of preference, and as r_s approaches −1.0, there is no agreement in order of occurrence.

To test the hypothesis that fish of the same species eat the same things in different areas, 10 randomly selected fish caught from one station within 3 days were compared. In interspecific tests, 10 fish of each species taken at the same station on the same day were used. Except for smelt, only adults were used in the tests because juveniles of other species were not completely available to the gear and not taken in large enough quantities to test.

Analyses of individual tests were not made; instead the results from several comparisons (N in Table 20) were combined and a test made using the combination of probabilities discussed by Snedecor (1956:216). The sum of the natural logarithms of the probabilities associated with each of several comparisons is multiplied by −2, and the resulting values have a chi-square distribution with two degrees of freedom for each comparison. Pearson (1924) presents a figure which allows graphical calculation of probabilities associated with r_s.

Intraspecific correlations were significant for all comparisons (Table 20). Indications are that food habits among individuals of the same species were almost identical within the Apostle Islands.

Significant interspecific correlations were found between sticklebacks and slimy sculpins in spring and summer and sticklebacks and

TABLE 20.—Food composition similarity measured by rank-correlation coefficients (r_S) between sticklebacks and other Apostle Islands species. (N equals the number of individual tests for each comparison, and n equals the number of food categories in each comparison.)

Comparison	N	n	Mean r_S	Chi-square
1. Between adult sticklebacks of stations 2 and 3	5	6	+0.94	36.89**
2. Between adult trout-perch from two stations	3	5	+.83	16.81*
3. Between juvenile smelt from two stations	3	4	+.85	16.98*
4. Between adult sculpins from two stations	5	6	+1.00	—
5. Between adult sticklebacks and other species within each catch:				
Spring:				
Trout-perch	7	5	+.70	30.89*
Smelt	10	4	+.40	34.29
Sculpins	10	6	+.89	62.02**
Summer:				
Trout-perch	4	5	+.43	13.94
Smelt	2	4	−.30	6.54
Sculpins	10	6	+.89	62.02**
Fall:				
Trout-perch	4	5	+.33	13.28
Smelt	4	4	+.40	13.72
Sculpins	5	6	+.37	16.87

* Significant at the 0.01 level.
** Significant at the 0.005 level.

trout-perch in spring. The significant rank correlation does not necessarily indicate the amount of competition for food, but merely the potential for such competition. For competition to occur, there must be a demand by more than one organism for the same food in excess of immediate supply. It can only be said that since the abundance of sticklebacks and slimy sculpins are positively correlated in the index catches and their food relationships are similar, the possibility of competition between the two species exists during some seasons. The actual existence of competition is highly questionable because of the apparent abundance of *Pontoporeia*, the number one food item, and the apparent adaptability of the stickleback in food utilization. The drop in correlation in the fall was due to greater use of chironomids by sculpins.

While the correlation with trout-perch also indicates potential competition for food, their abundance in the index trawl samples was negatively correlated and Dryer (1966) found trout-perch and sticklebacks to have different bathymetric distributions. While the trout-perch and sticklebacks utilized the same foods in spring, their secondary foods were different in summer and fall. Anderson and Smith (1971) found trout-perch fed on wider variety of food items than sticklebacks in the Apostle Islands. This combined evidence seems to indicate that competition between these two species is also unlikely.

Sticklebacks as Forage for Other Fish

Several fish species which occur in Lake Superior have been reported to feed on sticklebacks at various locations. These include lake trout; brown trout, *Salmo trutta* L.; rainbow trout, *Salmo gairdneri* Richardson; burbot, *Lota lota* (L.); and various sculpins. Of these, the lake trout was the only species which fed heavily on sticklebacks in the Apostle Islands.

Dryer, Erkkila, and Tetzloff (1965) related a change in diet in juvenile Lake Superior lake trout to their size. The diet, primarily a crustacean-insectivorous type in small trout, became piscivorous in larger fish.

In the present study, sticklebacks were found in 7.5% (33) of 436 lake trout less than 28 cm (11 in.) long (TL). Only 3.5% of the volume of stomachs from 142 fish under 25.4 cm (10 in.) was sticklebacks. In 294 trout from 25.4 to 28.0 cm, sticklebacks made up 32% of the volume of the diet.

Sticklebacks were a major part of the diet of lake trout from 28.0 to 38.0 cm (11.0 to 14.9 in.) (Figure 9). *P. pungitius* made up 39% of volume in the diet and were found in 42% of the 176 trout which contained food. Smelt was the second most abundant fish species in the diet of 28- to 38-cm trout. The food habits of trout remained about the same for all ice-free months (Anderson and Smith, 1971).

The major food of trout longer than 38 cm was smelt. Of 30 trout in this size range, 69% of the stomach contents were smelt remains. Sticklebacks were found in five of these fish and made up 17% of the volume. Nineteen adult sticklebacks and two sculpins were found in one 50-cm (19.7 in.) trout. Sticklebacks eaten by trout were all age-group I or older. No stickleback eggs or age-group 0 fish were found in over 4,500 trout stomachs sampled on the Lake Superior project.

The explanation of the absence of small sticklebacks in the trout diet is probably one of dis-

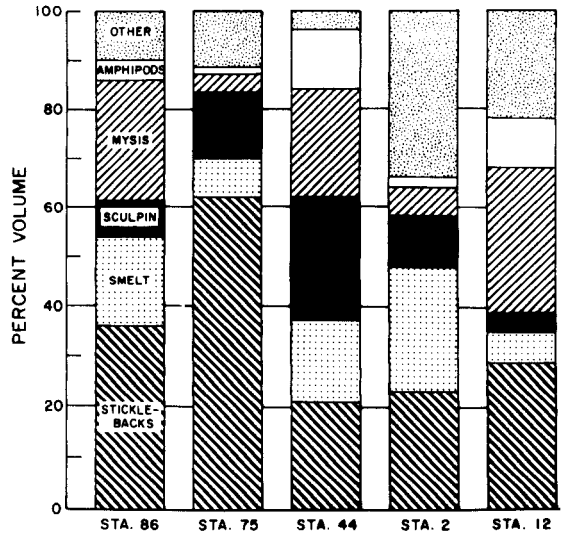

FIGURE 9.—Percent volume of various food items found in lake trout 28 cm and longer at various sampling stations in the Apostle Islands. Fish were taken in June and September during the two annual BCF index trawling cruises.

tribution. After hatching, the young sticklebacks congregate in the shallow sandy areas where they are unavailable to lake trout and most other species. By the time they leave the shallow water in late fall, they have grown to 45 mm or more. It is at this length that they begin to appear in trout stomachs the following spring.

Smaller trout cannot feed well on sticklebacks once the latter become available after a summer's growth, because of the protective spines. This inability explains the relative unimportance of sticklebacks in the diet of small trout. Similarly, Hoogland, Morris, and Tinbergen (1957) found young northern pike, *Esox lucius* L., rejected sticklebacks, first exhibiting a negative reaction to mechanical stimuli upon contact with the spines and then a visual avoidance. Upon reaching a certain size, the pike preferentially take sticklebacks (Frost, 1954). A discussion by Fortunatova (1959) supports this theory. The dietary shift to smelt by larger trout can be explained by assuming the optimum size of the prey increases as the trout grow larger.

Compared to all lake trout over 28 cm long taken from a number of trout index stations, fish from stations 75 and 86 ate a high percentage of sticklebacks (Table 21, Figure 9). At station 86, considered the best trout nursery area in the Apostle Islands, sticklebacks were the predominant food item even though juvenile smelt were more abundant in the index trawl samples (Table 9). At station 75, the second most important nursery area, sticklebacks were very abundant, and they made up more than 60% of the trout diet. Station 12 sticklebacks and smelt were about equal in the index catch, but sticklebacks were much more important in the trout diet. At station 44, the predominant forage fish in the trawl samples was sculpins, and these were dominant in trout stomachs. At this station, sticklebacks were comparatively rare in occurrence, but still made up 21% of the volume of the trout diet. It might be assumed from station 44 data that sculpins are an important item in the diet and that trout will substitute sculpins when sticklebacks and smelt are not readily available. However, the stations with high sculpin abundance relative to stickleback abundance do not support large numbers of trout. From these data, it appears that the availability of sticklebacks at the various stations is probably important in the selection of these areas by lake trout as

TABLE 21.—Percent frequency of occurrence and (in parentheses) percent total volume for each food item found in lake trout 28 cm and longer at various sampling stations in the Apostle Islands. Fish were taken in June and September during the two annual Bureau of Commercial Fisheries index trawling cruises.

Item	Station 86	Station 75	Station 44	Station 2	Station 12
Number of stomachs	77	45	24	51	33
Number empty	20	3	0	0	0
Crustaceans:					
Mysidacea	35 (25)	15 (4)	33 (22)	16 (6)	64 (29)
Amphipoda	18 (4)	8 (<1)	17 (12)	2 (<1)	36 (10)
Copepoda	—	1 (<1)	—	—	3 (<1)
Fish:					
Smelt	14 (18)	9 (8)	12 (16)	21 (25)	6 (6)
Stickleback	30 (36)	64 (62)	17 (21)	21 (23)	33 (29)
Sculpin	6 (7)	13 (13)	21 (25)	12 (10)	6 (4)
Unidentified	9 (8)	15 (11)	17 (3)	27 (36)	24 (19)
Fish eggs	—	—	—	1 (<1)	—
Insects:					
Chironomidae	6 (<1)	6 (<1)	2(<1)	—	3 (<1)
Coleoptera	1 (<1)	—	—	—	—
Trichoptera	1 (<1)	1 (<1)	—	—	—
Other	1 (<1)	7 (<1)	—	1 (<1)	6 (3)
Miscellaneous		1 (<1)	—	—	—

nursery areas, although other factors are also important because there are many areas where sticklebacks are abundant and trout are not. Conversely, no good trout nursery area are known where sticklebacks are not abundant.

The importance of the stickleback as a food item for the lake trout in the Apostle Islands appears to be substantial while the latter are between 28 and 38 cm long. No information is available, however, to indicate the amount of substitution which would occur if the sticklebacks were less available.

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ABUNDANCE AND SIZE OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, AND ASSOCIATED SPECIES IN LAKE ALEKNAGIK, ALASKA, IN RELATION TO THEIR ENVIRONMENT[1]

DONALD E. ROGERS[2]

ABSTRACT

Juvenile sockeye salmon, *Oncorhynchus nerka*, and associated fish in the littoral of Lake Aleknagik (Bristol Bay, Alaska) were sampled systematically from spring to midsummer (1962-72) with a beach seine. Apparent mortality rate and relative abundance were estimated from catches. Juvenile sockeye salmon and threespine stickleback comprised the majority of the population, and slimy sculpin, ninespine stickleback, and Arctic char fry the remainder. The annual abundance of juvenile sockeye salmon was related to the abundance of parent spawners. No correlation was evident among the annual estimates of abundance of the five species.

Age was determined from length-frequency distributions, and growth rates were calculated for sockeye salmon (age 0), Arctic char (age 0), and threespine stickleback (age I). The mean lengths of sockeye salmon fry and char fry on 20 June were positively correlated with water temperature, whereas the mean length of threespine stickleback (age I) on this date was inversely correlated with the average catch of sockeye salmon fry in the previous year. The mean lengths of all species on 20 July were inversely correlated with the mean catch of sockeye salmon fry. A limited capacity of the Lake littoral to sustain growth of individual fish was indicated.

The annual commercial catch of anadromous sockeye salmon, *Oncorhynchus nerka* Walbaum, from the Nushagak District of Bristol Bay declined from an average of about 5 million fish in the early 1900's to only about 1 million in recent years (Mathisen, 1971). Since the early 1950's, the Fisheries Research Institute has studied the freshwater life of the stock to understand the factors controlling the average abundance and annual variation in abundance of the adult run. We have assumed that a significant portion of the variation is related to the variation in abundance and growth of juveniles, especially fry (age 0), and have concentrated effort on the Wood River lake system because it has been the major producer among the river systems in the District (Figure 1).

The sockeye salmon fry inhabit different parts of each lake from spring to fall. From mid-May to mid-June, when the ice breaks up, to mid-July, they reside along the shore and in shallow bays; in mid-July they begin to move offshore; and from mid-August through September they occupy the pelagic areas (Burgner, 1962). Accordingly, the populations are sampled during early summer through beach seining and during August and September through townetting and echo sounding (Rogers, 1967). Beach seine sampling has been conducted throughout the District but has been concentrated in Lake Aleknagik. The catch and length statistics for sockeye salmon fry from an extensive effort in the lake in 1962 were analyzed by Pella (1968), and the catch statistics for five species of fish from 1964 through 1966 were examined by Waters (1969).

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Manuscript accepted March 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

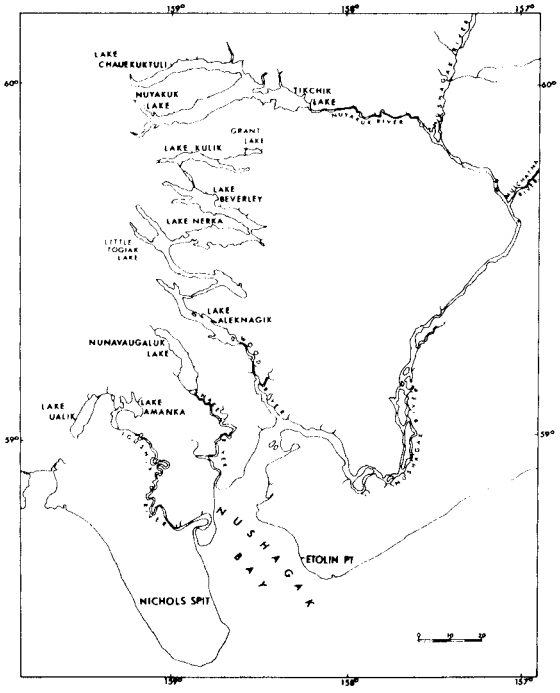

FIGURE 1.—The Wood River lake system and adjoining river systems in the Nushagak District, Bristol Bay, Alaska.

The primary objective in beach seine sampling has been to obtain periodic estimates of fish length in early summer. The secondary objectives have been (1) to estimate the annual relative abundance and growth of fish species associated with juvenile sockeye salmon to determine the effect, if any, that they may have on survival and growth of juvenile sockeye salmon and (2) to determine the relationships among relative abundance of sockeye salmon fry, abundance of parent spawners, and abundance of returning adult sockeye salmon. The data and statistical tests are detailed in Rogers (1972). The purpose of this report is to examine the relationships among annual estimates of the size and abundance of fish and the physical parameters of the environment during early summer.

MATERIALS AND METHODS

A detailed description of the gear and sampling procedures is given by Waters (1969). The seine used was 35 m in length and had a midsection of 6-mm mesh, 7.6 m long and 3.7 m deep. A 1.8-m bridle and a 17-m hauling rope were attached to each end of the net. The seine was set in a semicircle about 15 m from shore and hauled by hand, usually by two men. Catches consisting of less than 500 fish were preserved in 10% Formalin.[3] Larger catches were successively divided in half until approximately between 200 and 500 fish remained. These were preserved, and the fraction taken was recorded. For each haul the date, time, location, set direction, and surface water temperature were noted. Other physical parameters measured in connection with the beach seining were the date of ice breakup, lake level, and solar radiation.

In 1962, beach seine hauls were made at 24 stations on Lake Aleknagik in eight time periods between 20 June and 8 September. In 1963, nine of the stations were sampled on 24 July and 3 August. From 1964 through 1972, generally 10 stations (Figure 2) were sampled at five weekly intervals between 22 June and 23 July and once between 2 to 5 August. Seining was conducted at the 10 stations between 0930 and 1600 h, seldom during rough water conditions, i.e. when there were waves on shore. A description of the beach seine stations is given in Rogers (1972).

Between 1 and 7 days after collection, the fish were enumerated and measured to the nearest millimeter from tip of snout to end of middle ray of the tail. In 1962 only juvenile sockeye salmon and threespine stickleback, *Gasterosteus aculeatus* Linnaeus were measured, whereas in the remaining years fish of all species were measured. Also, only 50 sockeye salmon fry were measured in samples containing more than 75 sockeye salmon fry, and only 200 threespine stickleback were measured in samples containing over 250 of this species.

The length frequencies were plotted by species and lake area (Figure 2) and for areas combined. Partial age compositions were determined from the length frequencies, and mean lengths were calculated for those age groups

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

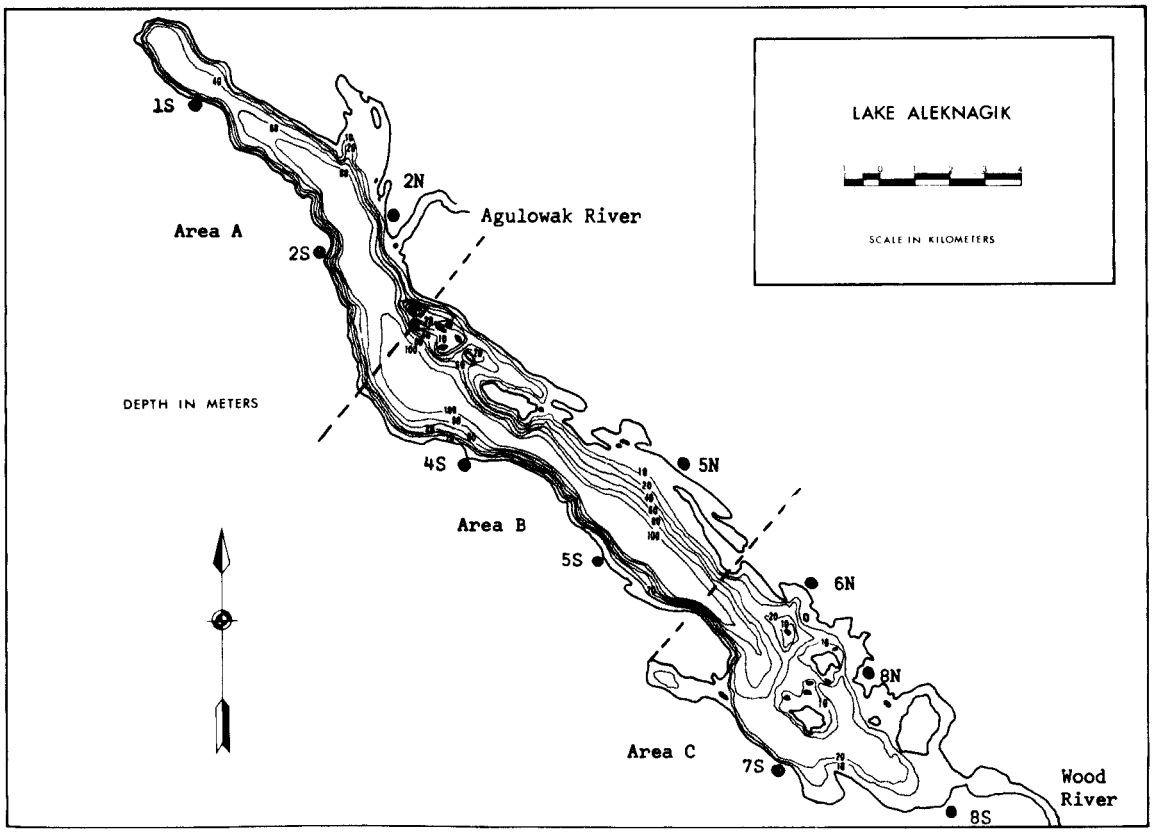

FIGURE 2.—Beach seine stations and lake sampling areas in Lake Aleknagik.

that were easily separated from the length frequencies. The mean lengths were converted to equivalent live lengths so as to adjust for the shrinkage due to preservation (Rogers, 1964). These were plotted by date and examined for determination of the most suitable growth model. A curvilinear relationship was indicated, and regressions of natural logarithm (ln) mean length on coded date (1 June = 1, 1 July = 31, etc.) were calculated through weighting the observations with geometric mean catch. A weighting procedure was used because (1) variance of the means tended to increase during the season as a result of the decline in catch (hence sample size) and (2) the accuracy of mean lengths from beach seine samples as estimates of mean length in the population tended to decrease in midsummer as the fish moved offshore. Annual growth rate and fish size in given periods were estimated from the regressions.

The beach seine catch data were analyzed through logarithmic transformation. An analysis of variance was conducted with the catches made in the first four periods of sampling (20 June-19 July) for the purpose of determining the significance of observed variation associated with location (station and lake area), date, and year. The last two periods (21 July-5 August) were excluded from the analysis since the catches of sockeye salmon fry in these periods were obviously lower than those in the other periods and age 0 fish of the longer lived species often appear at this time.

Mortality rate in a population is estimated commonly from changes in catch with time when catch per unit of effort can be reasonably assumed to be proportional at all times to true

TABLE 1.—Dates of ice breakup, surface water temperatures, and relative lake levels during beach seine sampling in Lake Aleknagik, 1962 through 1972.

Year	Date of ice breakup	Mean surface water temperature (°C)			Mean lake level (cm)		
		20-24 June	20 June-19 July	21 July-5 August	21-25 June	21 June-20 July	21 July-5 August
1962	1 June	9.0	11.8	12.0	157	137	89
1963	2 June	—	11.1	12.3	140	122	80
1964	15 June	7.7	9.4	11.6	150	139	82
1965	5 June	7.4	7.0	11.7	184	147	97
1966	6 June	7.6	8.5	12.8	157	148	112
1967	28 May	9.0	12.1	13.9	146	118	68
1968	31 May	10.8	13.3	14.9	102	84	50
1969	2 June	9.4	10.8	12.5	220	168	92
1970	23 May	7.8	9.8	11.2	154	134	109
1971	16 June	8.5	10.0	9.4	177	148	167
1972	8 June	4.3	7.5	12.0	191	171	108

population size. A frequent source of error is the variation in availability of the fish population to the sampling net. Beach seine catches of sockeye salmon fry and threespine stickleback decline seasonally as a result of movement offshore and mortality. Apparent mortality rates were estimated from linear regressions of ln mean catch on coded date.

The data were examined through stepwise multiple regression and linear correlation techniques for determination of significant relationships among the physical and biological parameters.

RESULTS

Climatological observations for the Wood River lake system are given in Rogers, Siler, and Croker (1970). The average date of ice breakup from 1951 to 1972 is 1 June, and the range in dates is from 14 May to 16 June. A summary of physical data collected in connection with the beach seine sampling in Lake Aleknagik is given in Table 1. Lake level usually rises rapidly after ice breakup until mid-June and declines through the summer. Inshore surface water temperatures rise gradually from ice breakup to late July and then level off. Water temperatures are lower on the average in the upper third of the lake (area A) than elsewhere. From 1962 to 1972 the average surface water temperatures during 20 June-19 July were 9.1°, 10.3°, and 10.7°C in areas A, B, and C, respectively.

Fish of 24 species have been collected in Lake Aleknagik, but only juvenile sockeye salmon and threespine stickleback have been greatly predominant in beach seine catches (Table 2). These two species are also the only ones that become pelagic in midsummer. Three other species appear in significant numbers in the catches: ninespine stickleback, *Pungitius pungitius* Linnaeus; slimy sculpin, *Cottus cognatus*

TABLE 2.—Sums of geometric mean beach seine catches of five fish species by lake area, Lake Aleknagik, 1962 through 1972.

	Area	Sockeye salmon		Threespine stickleback	Ninespine stickleback	Sculpin	Char fry	Sum
		Fry	Fingerling					
20 June-19 July								
	A	258	1	130	8	43	15	455
	B	265	2	303	11	25	2	608
	C	86	8	160	22	23	1	300
	Total	192	3	184	12	29	4	424
21 July-5 August								
	A	36	1	132	13	23	8	213
	B	20	2	75	7	8	3	115
	C	20	2	92	14	10	2	140
	Total	24	2	97	11	12	3	149

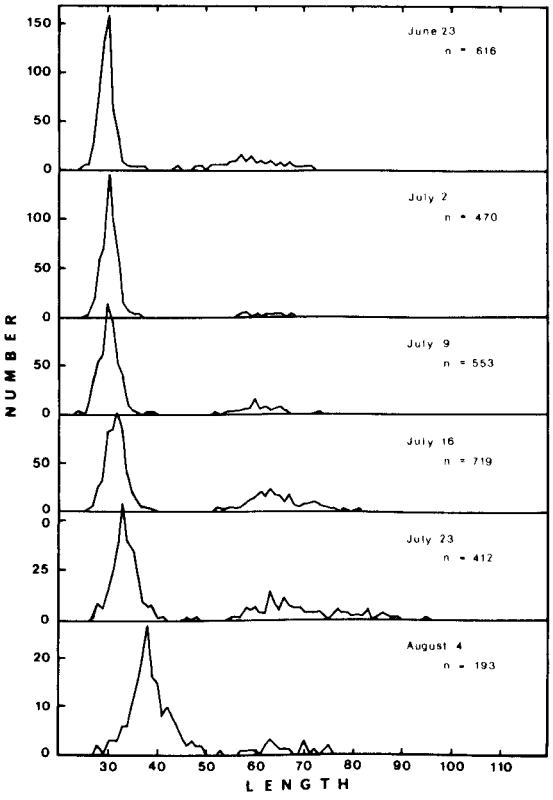

FIGURE 3.—Length-frequency distributions (mm) of sockeye salmon, 1966.

Richardson; and Arctic char fry, *Salvelinus alpinus* Linnaeus. Of primary value in the beach seine statistics are the annual estimates, since our main concern is with the source of the observed annual variation in adult sockeye salmon abundance. Geographical and temporal variations were examined and are discussed here to the extent necessary for procurement of valid annual estimates of abundance, growth and size.

Sockeye Salmon

Length-frequency distributions for juvenile sockeye salmon are shown in Figures 3 and 4 for a year in which growth was below average (1966) and a year in which growth was above average (1968). The length frequencies are based on number of fish measured and thus do not reflect variation in abundance among time periods and years. The apparent abundance of sockeye salmon fingerlings in comparison to fry is exaggerated since usually the entire sample of fingerlings, but often a subsample of fry, was measured.

Sockeye salmon fingerlings (primarily age I) ranged in length from approximately 45 to 118 mm. Many presumably originated in the upper lakes of the Wood River system and had been in Lake Aleknagik by early summer as smolts to migrate out of the lake system. Catches were significantly higher toward the lake outlet (area C) than elsewhere (Tables 3 and 4).

Sockeye salmon fry (age 0) ranged in length from approximately 25 to 60 mm. The length frequencies are symmetric and may be modeled

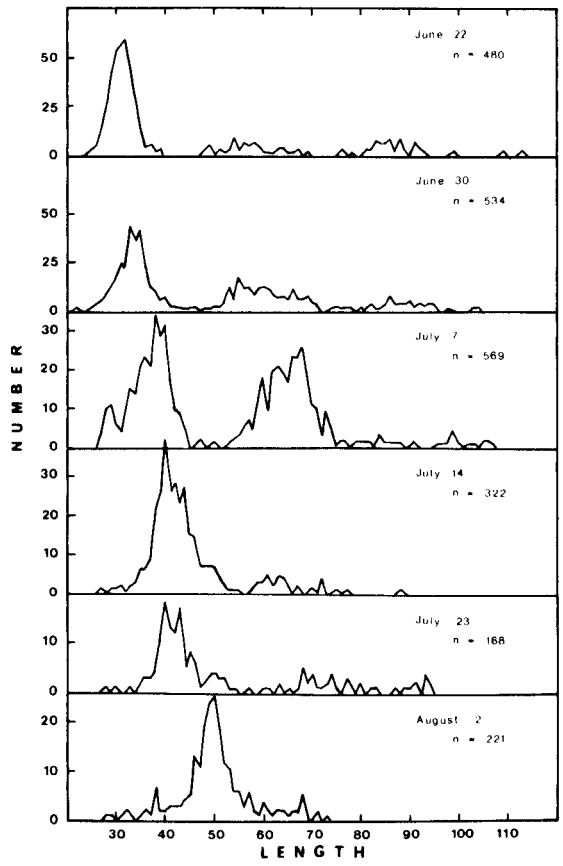

FIGURE 4.—Length-frequency distributions (mm) of sockeye salmon, 1968.

TABLE 3.—Geometric mean beach seine catches in Lake Aleknagik by area and year for the period 20 June-19 July 1962, 1964 through 1972.

Year	Area	*n*	Sockeye fry	Sockeye fingerling	Threespine stickleback	Ninespine stickleback	Sculpin	Char fry
1962	A	12	510.1	4.4	318.5	23.8	52.2	18.3
	B	12	384.8	0.2	301.5	6.2	28.1	4.1
	C	16	109.2	9.4	113.4	12.0	38.2	1.9
	Mean		277.8	3.1	221.7	12.1	38.3	5.6
1964	A	12	140.4	0.0	92.2	7.9	58.3	25.5
	B	12	294.3	0.9	497.2	22.3	52.3	2.1
	C	16	121.9	15.0	463.1	47.8	29.3	0.7
	Mean		171.4	2.1	276.9	20.3	44.7	4.2
1965	A	12	806.3	0.2	102.3	4.2	44.8	9.0
	B	12	1,137.0	1.6	593.8	10.7	25.5	0.9
	C	16	196.6	1.5	130.1	10.6	25.6	0.6
	Mean		564.9	1.0	199.2	7.8	30.8	2.1
1966	A	12	560.2	1.3	127.0	1.5	26.3	24.9
	B	12	446.3	3.0	705.8	5.9	13.3	4.0
	C	16	219.5	4.2	131.8	5.9	16.5	2.0
	Mean		380.0	2.6	227.8	3.7	17.9	6.3
1967	A	12	949.7	3.1	274.0	17.0	51.4	34.9
	B	12	273.7	13.0	737.1	21.6	10.8	3.0
	C	16	145.0	22.8	249.6	27.4	11.5	1.2
	Mean		335.3	10.1	369.4	21.6	18.6	5.8
1968	A	12	44.2	6.3	335.0	33.2	46.5	22.2
	B	12	17.0	4.2	151.8	12.0	17.9	2.4
	C	16	54.6	9.1	142.4	80.1	17.3	2.2
	Mean		34.5	6.3	193.5	31.7	24.3	5.3
1969	A	12	91.9	1.0	208.1	9.0	40.6	6.4
	B	12	106.9	1.9	309.2	15.6	15.8	0.3
	C	15	62.4	2.6	149.2	80.2	28.3	0.8
	Mean		84.9	1.8	212.5	22.4	26.3	1.6
1970	A	12	170.3	0.0	154.7	11.7	24.1	13.9
	B	12	100.9	1.0	95.0	9.6	30.5	2.0
	C	16	120.5	13.7	158.0	37.3	33.5	2.6
	Mean		127.5	2.1	132.4	16.1	29.1	4.4
1971	A	12	404.2	1.1	64.8	5.5	59.8	3.6
	B	12	792.1	4.0	333.8	11.8	35.6	1.3
	C	16	207.9	14.9	378.9	18.2	29.7	0.9
	Mean		405.3	4.5	201.6	10.6	39.8	1.7
1972	A	12	147.6	0.9	18.1	1.4	44.6	14.2
	B	12	721.1	2.5	94.4	4.1	47.4	2.7
	C	16	21.0	3.5	36.9	4.0	17.9	1.1
	Mean		130.7	2.1	39.8	2.8	33.6	3.5

by the normal distribution; however the variability in length in area C was more than in the other areas. This part of the lake tends to warm up earlier in the spring and has a lower abundance of fry. Mean lengths were calculated for 20 June and 20 July from the regression parameters in Table 5. These lengths represent the sizes of fish at the beginning and end of early summer, when sockeye salmon fry were abundant inshore. The fry were of similar length in the lake areas on 20 June, but had become larger in area C than in the others by 20 July (Table 6).

Sockeye salmon fry were more abundant in areas A and B than in area C, apparently because the major spawning ground, Agulowak River, is located here. They were more abundant at the stations adjacent to spawning grounds than at those stations located elsewhere. Most spawning occurs from early August to mid-September. The fry emerge from the gravel from late winter to early spring, and most are in the lake by early June.

Regressions in ln mean catch on coded date (23 June = 1, 1 July = 9, etc.) were calculated for the entire period of sampling (20 June-5 August) and for all periods except the first period (Table 7). The latter results appeared to have greater consistency than the former and indicated that fish were perhaps less available in early spring than later. Catches of sockeye salmon fry declined at a greater rate than

TABLE 4.—Geometric mean beach seine catches in Lake Aleknagik by area and year for the period 21 July-5 August, 1962 through 1972.

Year	Area	*n*	Sockeye fry	Sockeye fingerling	Threespine stickleback	Ninespine stickleback	Sculpin	Char fry
1962	A	6	12.9	2.1	64.8	5.4	26.0	9.2
	B	6	16.4	2.1	58.9	7.7	9.2	9.4
	C	8	3.2	0.0	17.2	2.4	4.5	1.6
	Mean		9.1	1.1	40.6	5.7	10.5	5.5
1963	A	6	0.3	0.4	16.5	4.9	26.7	11.9
	B	6	6.2	0.4	18.2	7.9	2.8	6.5
	C	8	6.5	1.6	40.8	1.2	4.2	7.8
	Mean		3.1	0.7	23.1	3.9	7.2	8.5
1964	A	6	25.3	0.9	395.8	26.6	20.5	21.2
	B	6	41.7	4.2	297.0	12.9	10.4	2.3
	C	8	11.2	0.3	64.6	12.9	9.7	3.4
	Mean		22.9	0.9	197.0	16.5	12.8	5.9
1965	A	3	3,476.8	4.0	756.5	13.5	16.1	15.7
	B	3	15.1	0.4	53.4	4.1	8.5	2.0
	C	4	9.0	0.0	187.8	13.2	11.0	3.2
	Mean		81.4	0.9	197.2	9.2	11.5	4.9
1966	A	6	7.4	0.3	101.4	5.6	9.7	2.1
	B	6	35.0	2.3	249.7	3.8	2.8	1.3
	C	8	26.7	6.1	175.2	7.5	15.2	0.5
	Mean		19.3	2.1	164.4	5.5	7.7	1.2
1967	A	9	127.2	9.9	337.6	15.4	20.0	14.7
	B	9	22.9	8.9	104.3	4.5	3.5	1.5
	C	12	62.2	10.5	100.5	33.3	9.3	0.4
	Mean		56.9	9.7	152.5	13.6	8.9	2.8
1968	A	6	6.1	0.4	167.7	47.5	20.5	0.7
	B	6	3.9	1.7	38.2	17.8	8.4	0.4
	C	8	7.6	1.2	81.0	99.0	14.2	0.0
	Mean		5.7	1.0	80.5	44.0	13.5	0.3
1969	A	6	28.0	0.6	370.4	36.8	39.6	10.2
	B	6	6.9	2.0	46.3	7.0	3.6	1.8
	C	8	26.9	0.7	111.7	46.8	7.9	1.1
	Mean		17.6	1.0	124.6	23.4	10.8	3.0
1970	A	6	46.7	0.0	166.7	16.4	7.0	8.3
	B	6	40.5	3.5	89.7	10.0	16.4	4.5
	C	8	62.3	1.0	221.3	37.4	13.8	3.0
	Mean		49.0	1.1	149.1	18.4	11.7	4.9
1971	A	6	102.3	0.0	43.3	8.6	57.4	4.0
	B	6	13.1	0.7	37.7	3.9	16.7	1.7
	C	8	126.8	6.4	198.3	12.3	11.1	2.0
	Mean		56.1	1.3	68.9	7.6	22.2	2.4
1972	A	6	87.1	11.0	39.9	5.1	53.3	9.0
	B	6	182.7	1.1	149.9	7.6	33.7	4.4
	C	8	25.8	11.2	62.2	7.7	26.0	2.2
	Mean		74.3	5.1	71.9	6.7	36.0	4.4

those of the other species caught by beach seining because this species moves offshore to the pelagic region in midsummer.

Threespine Stickleback

Threespine stickleback were of ages 0 to III and perhaps age IV. They ranged in length from 6 to 81 mm. In years of poor growth, the three major age groups had distinctive length frequencies (Figure 5), whereas in years of good growth, age groups II and III overlapped greatly in length distribution (Figure 6). When, also, ice broke up earlier and water temperatures were higher than average, age 0 fish appeared in the catches before mid-July; threespine stickleback spawn in June and July.

Age I threespine stickleback were usually easy to separate from other age groups from their length, especially within a given lake area. The mean lengths of age I threespine stickleback were greater in area C at both the beginning and end of early summer than in the two other areas (Table 6), but growth rates were similar among the three lake areas.

Threespine stickleback were more abundant along the north shore of the lake than the south. This shore is shallower and has more aquatic

TABLE 5.—Parameters from weighted exponential regression of ln, mean length (live equivalent) on coded date, for Lake Aleknagik beach seine sampling 16 June-5 August, 1962, 1964 through 1972.

		Area A		Area B		Area C		Combined	
Species	Year	[1]a	[2]b	a	b	a	b	a	b
Sockeye fry (Age 0)	1962	3.280	0.0070	3.271	0.0073	3.260	0.0094	3.273	0.0073
	1964	3.242	0.0068	3.293	0.0064	3.266	0.0066	3.291	0.0061
	1965	3.178	0.0087	3.353	0.0027	3.251	0.0051	3.234	0.0067
	1966	3.325	0.0033	3.308	0.0039	3.368	0.0026	3.324	0.0035
	1967	3.304	0.0044	3.229	0.0069	3.183	0.0095	3.267	0.0058
	1968	3.216	0.0097	3.291	0.0102	3.200	0.0122	3.194	0.0118
	1969	3.322	0.0059	3.213	0.0098	3.262	0.0095	3.255	0.0083
	1970	3.221	0.0093	3.236	0.0085	3.135	0.0125	3.192	0.0101
	1971	3.311	0.0040	3.369	0.0019	3.229	0.0069	3.298	0.0043
	1972	3.234	0.0062	3.288	0.0044	3.053	0.0103	3.225	0.0062
	Mean	3.263	0.0065	3.285	0.0062	3.221	0.0085	3.255	0.0070
Threespine stickleback (Age I)	1962	3.252	0.0055	3.218	0.0062	3.374	0.0040	3.269	0.0051
	1964	3.347	0.0033	3.360	0.0035	3.401	0.0029	3.392	0.0027
	1965	3.166	0.0059	3.305	0.0023	3.257	0.0048	3.256	0.0041
	1966	3.187	0.0044	3.232	0.0037	3.181	0.0053	3.215	0.0042
	1967	3.143	0.0059	3.238	0.0046	3.265	0.0057	3.262	0.0038
	1968	3.310	0.0050	3.259	0.0060	3.286	0.0075	3.302	0.0053
	1969	3.304	0.0050	3.448	0.0022	3.335	0.0056	3.399	0.0033
	1970	3.331	0.0053	3.274	0.0062	3.402	0.0050	3.344	0.0051
	1971	3.195	0.0061	3.436	0.0001	3.220	0.0064	3.268	0.0046
	1972	3.095	0.0081	3.209	0.0055	3.383	0.0024	3.216	0.0055
	Mean	3.233	0.0054	3.298	0.0040	3.310	0.0050	3.292	0.0044
Arctic char fry (Age 0)	1964	3.243	0.0049	3.291	0.0041	3.243	0.0050	3.247.	0.0048
	1965	3.238	0.0054	3.348	0.0013	3.312	0.0029	3.259	0.0047
	1966	3.324	0.0025	3.197	0.0057	3.235	0.0046	3.298	0.0032
	1967	3.216	0.0051	3.209	0.0055	3.260	0.0038	3.216	0.0051
	1968	3.332	0.0038	3.373	0.0042	3.075	0.0113	3.305	0.0048
	1969	3.206	0.0060	2.974	0.0105	3.267	0.0060	3.208	0.0061
	1970	3.266	0.0050	3.127	0.0093	3.231	0.0070	3.215	0.0066
	1971	3.270	0.0036	3.307	0.0031	3.270	0.0033	3.284	0.0033
	1972	3.187	0.0058	3.116	0.0085	3.154	0.0060	3.133	0.0074
	Mean	3.254	0.0047	3.216	0.0058	3.227	0.0055	3.241	0.0051

[1] Natural log of mean length on 31 May.
[2] Instantaneous growth rate in length.

vegetation and a larger area of mud bottom; therefore it provides a more suitable forage and spawning habitat. These fish were distributed in much the same pattern as sockeye salmon fry. The two species have common food and some common behavioral habits during the summer (Rogers, 1968). Age I and II fish usually became pelagic in midsummer, and age 0 and III fish tended to remain inshore by late summer.

Ninespine Stickleback

Ninespine stickleback were age 0 to II and perhaps age III. They ranged in length from 10 to 76 mm (Figure 7). The time of spawning and appearance of age 0 fish in the catches were similar to those of threespine stickleback, but growth was more rapid and ages I and II were not as distinctive from length frequencies.

The distribution of ninespine stickleback shows an even greater correlation with location of vegetation and mud bottom than that of threespine stickleback. At stations 2S and 4S where vegetation is sparse on the bottom, catches were always very low. Ninespine stickleback showed the lowest rate of decline in catches among the associated species (Table 7).

Slimy Sculpin

Sculpin ranged in age from 0 to perhaps V but were mostly age I from observations at Iliamna Lake of the Kvichak River system (Roger, 1971). They ranged in length from 8 to 91 mm (Figure 8). As with the sticklebacks,

TABLE 6.—Calculated mean lengths (live equivalent in mm) for 20 June and 20 July from weighted exponential regressions, 1962 through 1972.

Species	Year	20 June				20 July			
		Area A	Area B	Area C	Combined	Area A	Area B	Area C	Combined
Sockeye fry	1962	30.6	30.5	31.4	30.6	37.7	38.0	41.7	38.1
	1963[1]					39.6	45.5	44.0	44.9
	1964	29.3	30.6	29.9	30.3	35.9	37.0	36.4	36.4
	1965	27.4	30.2	28.6	29.0	35.5	32.7	33.2	35.5
	1966	29.7	29.5	30.6	29.8	32.8	33.2	33.0	33.0
	1967	29.7	29.0	29.2	29.5	34.0	35.7	38.8	35.1
	1968	30.2	32.9	31.3	30.8	40.5	44.7	45.2	43.9
	1969	31.2	30.2	31.6	30.6	37.3	40.6	41.9	39.2
	1970	30.2	30.1	29.6	29.8	39.9	38.9	43.1	40.4
	1971	29.7	30.2	29.0	29.5	33.5	32.0	35.6	33.5
	1972	28.7	29.3	26.0	28.5	34.6	33.4	35.4	34.3
	Mean[2]	29.7	30.3	29.7	29.3	36.2	36.6	38.4	36.9
	S.D.	1.05	1.07	1.68	0.75	2.63	4.05	4.33	3.45
Threespine stickleback (Age I)	1962	28.9	28.3	31.7	29.1	34.1	34.0	35.7	33.9
	1963[1]					36.7	39.3	38.4	36.9
	1964	30.3	30.9	31.8	31.4	33.4	34.3	34.7	34.0
	1965	26.7	28.5	28.6	28.1	31.9	30.5	33.0	31.8
	1966	26.4	27.3	26.8	27.0	30.2	30.5	31.4	30.6
	1967	26.1	27.9	29.4	28.2	31.1	32.1	34.8	31.5
	1968	30.3	29.4	31.1	30.2	35.2	35.2	39.0	35.4
	1969	30.1	32.8	31.4	32.0	34.9	35.1	37.1	35.3
	1970	31.1	29.9	33.2	31.4	36.4	36.0	38.6	36.6
	1971	27.6	31.1	28.4	28.8	33.0	31.2	34.4	33.1
	1972	25.9	27.6	30.9	27.8	33.0	32.6	33.1	32.8
	Mean[2]	28.3	29.4	30.3	29.4	33.3	33.2	35.2	33.5
	S.D.	2.01	1.79	1.96	1.74	1.92	2.04	2.46	1.91
Arctic char fry (Age 0)	1963[1]					35.8	36.1	32.1	35.3
	1964	28.2	29.2	28.3	28.3	32.7	33.1	33.0	32.7
	1965	28.4	29.2	29.1	28.6	33.5	30.3	31.7	32.9
	1966	29.2	27.4	27.9	28.9	31.5	32.6	32.0	31.8
	1967	27.6	27.7	28.1	27.6	32.2	32.7	31.6	32.3
	1968	30.2	31.7	27.1	30.0	33.8	36.0	38.0	34.7
	1969	27.8	24.2	29.6	27.9	33.3	33.1	35.4	33.6
	1970	29.0	27.4	29.1	28.4	33.6	36.2	35.9	34.6
	1971	28.2	29.0	28.1	28.5	31.4	31.8	31.0	31.5
	1972	27.2	26.7	26.4	26.6	32.3	34.5	31.6	33.2
	Mean[2]	28.4	28.1	28.2	28.3	32.7	33.4	33.4	33.0
	S.D.	0.92	2.08	1.01	0.93	0.91	1.91	2.47	1.12

[1] Means calculated from lengths on 24 July 1963 and growth rate in 1968.
[2] 1963 excluded.

spawning occurs primarily in June and July, and the entire lifespan is spent in Lake Aleknagik.

Sculpin were the most uniformly distributed of the fish commonly caught by beach seine, but they tended to be more abundant at stations where sockeye salmon spawning occurred (Stations 2N, 5S, 6N, and 7S) than at other stations. Roger (1971) discusses the role of sculpins as predators on sockeye salmon eggs in Lake Iliamna of the Kvichak River system.

Arctic Char Fry

Arctic char spawn in late fall. They are presumably in the lake by early June, although little is known of their reproduction and early life history in Lake Aleknagik. In early summer they are in the fry stage and range in length from 25 to 50 mm. The adults are major predators of juvenile sockeye salmon and threespine stickleback (Nelson, 1966).

Char fry averaged about 1 mm shorter than sockeye salmon fry on 20 June and about 4 mm shorter on 20 July. They did not differ significantly in average length among the lake areas on 20 June, but were smaller in area A than in the other areas on 20 July (Table 6).

Arctic char fry were the most unevenly distributed of the fish caught by beach seine and occurred infrequently in catches. They were more abundant in the upper region of the lake

TABLE 7.—Regression parameters for ln mean catch on coded date (23 June = 1), 1962, 1964 through 1972.

Year	Sockeye fry		Threespine stickleback Age I		Threespine stickleback Age II +		Ninespine stickleback[1]		Sculpin[1]		Char fry[2]	
	[3]a	[3]b	a	b	a	b	a	b	a	b	a	b
20 June-5 August												
1962	6.600	-0.1092	5.272	-0.0645	4.964	-0.0486	2.122	0.0009	4.188	-0.0472	2.294	0.0135
1964	5.924	-0.0786	5.364	-0.0191	4.844	-0.0175	3.176	-0.0105	4.353	-0.0526	3.022	0.0073
1965	6.104	-0.0239	4.173	0.0158	3.714	0.0344	2.226	-0.0057	3.748	-0.0286	1.582	0.0278
1966	7.040	-0.1012	4.548	-0.0157	4.766	0.0003	1.628	-0.0075	3.203	-0.0274	3.913	-0.0729
1967	6.392	-0.0605	5.397	-0.0454	5.169	-0.0116	2.904	-0.0102	3.250	-0.0305	3.159	-0.0055
1968	4.358	-0.0704	5.504	-0.0771	4.567	-0.0332	3.704	-0.0170	3.815	-0.0541	4.143	-0.1164
1969	4.933	-0.0507	5.106	-0.0131	3.750	-0.0024	3.365	-0.0094	3.582	-0.0311	1.695	0.0143
1970	5.679	-0.0580	3.786	0.0013	4.333	0.0057	2.894	0.0001	3.719	-0.0314	3.062	-0.0322
1971	6.722	-0.0686	4.578	-0.0208	4.633	-0.0081	2.121	0.0085	3.842	-0.0193	1.336	-0.0036
1972	5.081	-0.0275	2.687	-0.0106	3.041	0.0252	0.399	0.0456	3.343	0.0069	2.403	0.0042
Mean	5.383	-0.0649	4.642	-0.0249	4.378	-0.0056	2.454	-0.0005	3.704	-0.0353	2.661	-0.0164
30 June-5 August												
1962	7.226	-0.1299	6.007	-0.0888	5.407	-0.0632	2.721	-0.0182	4.351	-0.0524	4.206	-0.0475
1964	5.807	-0.0745	5.502	-0.0238	4.265	0.0023	3.325	-0.0156	4.248	-0.0491	3.148	0.0030
1965	7.635	-0.0783	5.050	-0.0159	4.310	0.0127	2.203	-0.0049	3.772	-0.0294	1.993	0.0138
1966	7.477	-0.1157	5.747	-0.0551	4.810	-0.0011	1.417	-0.0005	3.128	-0.0250	4.566	-0.0944
1967	6.365	-0.0597	6.666	-0.0848	6.266	-0.0458	3.705	-0.0352	3.739	-0.0457	3.837	-0.0267
1968	4.152	-0.0633	5.713	-0.0842	5.025	-0.0489	4.355	-0.0393	3.671	-0.0492	4.472	-0.1276
1969	5.187	-0.0589	5.774	-0.0346	4.254	-0.0187	3.644	-0.0184	3.781	-0.0376	1.333	-0.0260
1970	6.035	-0.0705	4.667	-0.0296	5.036	-0.0189	2.932	-0.0012	3.970	-0.0398	3.493	-0.0466
1971	7.163	-0.0834	5.338	-0.0463	5.308	-0.0306	2.655	-0.0093	4.061	-0.0265	2.143	-0.0304
1972	5.983	-0.0580	3.201	-0.0280	3.537	0.0085	0.832	0.0310	3.640	-0.0031	3.261	-0.0248
Mean	6.303	-0.0792	5.367	-0.0491	4.892	-0.0106	2.779	-0.0112	3.836	-0.0358	3.245	-0.0355

[1]Calculated from geometric mean catches except age 0.
[2]Calculated from geometric mean catches in lake area A only.
[3]The regression parameter a is the natural logarithm of the calculated catch on 22 June, and the parameter b is the instantaneous rate of decline in catch.

(area A) than in the middle section and the outlet with the exception of station 7S. They were never caught at station 8N. Their distribution in early summer probably reflected the distribution of parent spawners in the previous fall.

Catches of char fry tended to increase during the first four periods of sampling and then to decrease in the last two periods. They may not have been as available to the beach seine as early in the spring as sockeye salmon fry because of later emergence from the spawning grounds.

Annual Variation in Abundance

The geometric mean of the annual mean catches in each area during 20 June-19 July was considered the best estimate of the relative abundance in Lake Aleknagik during the period of the summer when sockeye salmon fry were concentrated inshore. On the average, juvenile sockeye salmon were the most abundant species in the littoral and also exhibited the greatest annual absolute as well as relative variation (coefficient of variation) over the years. Significant differences were detected in the mean catches by year for all species, but the relative annual variations in catches for the next two most abundant species (threespine stickleback and slimy sculpin) were low compared to that of juvenile sockeye salmon.

Linear correlation coefficients were calculated for the purpose of examining relationships among annual estimates of abundance, apparent mortality rates, and selected physical parameters. A total of 84 pairs of variables was examined for correlation and statistically significant correlations at the 5% level were found among 38 pairs. Obviously some caution is needed in the biological interpretation of these data. It is expected that 5% of the tests would reject the null hypothesis that they are independent. Some partial correlation coefficients were examined; however, none were found statistically significant. The notable results of the correlation analysis were: (1) significant positive correlations between water temperature and apparent mortality rate for threespine

stickleback (age I), ninespine stickleback, and sculpin (n = 10, r = 0.80, 0.84, and 0.76, respectively); (2) significant correlation between apparent mortality rates of ninespine stickleback and sculpin (r = 0.86); and (3) lack of significant correlations involving sockeye salmon fry. The correlations between water temperature and apparent mortality rate suggest that ninespine stickleback and sculpin populations (which do not become pelagic) experience higher mortality rates at higher water temperatures. The higher mortality may be the result of increased spawning rate and/or rate of predation. Since sockeye salmon fry constitute a major portion of the inshore fish community and exhibit greater annual variation in abundance than the rest,

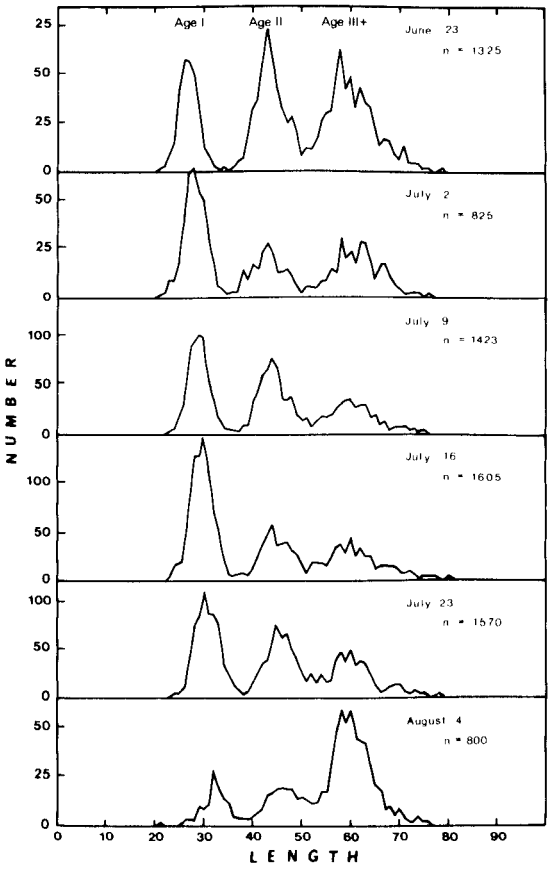

FIGURE 5.—Length-frequency distributions (mm) of threespine stickleback, 1966.

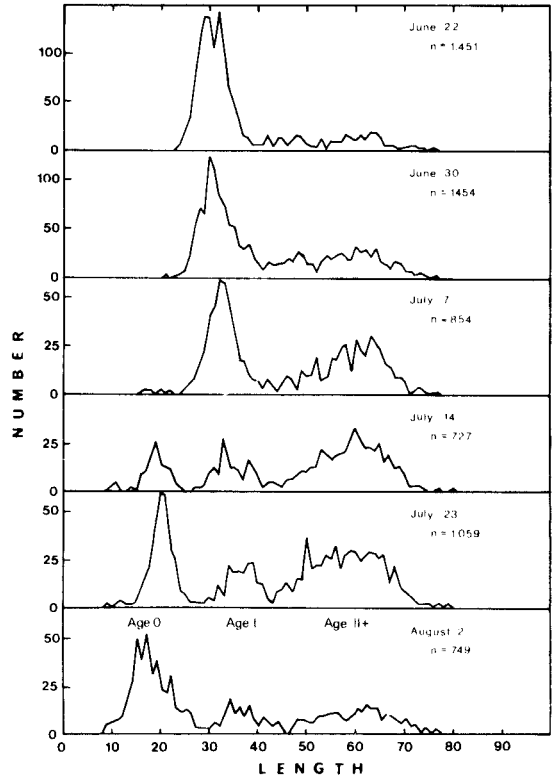

FIGURE 6.—Length-frequency distributions (mm) of threespine stickleback, 1968.

they would appear to have the greatest potential for affecting the abundance of fish of other species. The depressing effect of high abundance of sockeye salmon fry on the abundance of other species was suggested by Parr (1972), but such an effect may be observable only after a time lapse and would be detectable only with observations from a greater number of years. No significant correlation was detected between the catches of sockeye salmon fry and the catches of other species in the same year or in the following year.

A significant, although highly variable, relationship was apparent between the abundance of parent spawners and mean catch of sockeye salmon fry in Lake Aleknagik (r = 0.62, n = 11). A comparison of the density of sockeye salmon spawners with mean catch of sockeye salmon fry in the Nushagak District is given in Table 8. A positive relation between density of adult

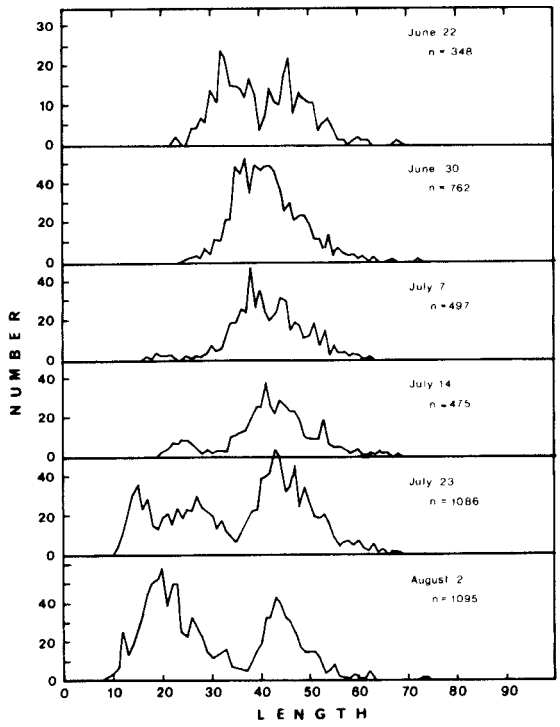

FIGURE 7.—Length-frequency distributions (mm) of nine-spine stickleback, 1968.

spawners and density of fry progeny among years and lakes is indicated. The relation between the abundance of fry and the abundance of returning adults is of primary interest because of the possible value in forecasting the magnitude of adult runs. More years of observations are necessary, however, before this relation can be adequately defined.

Annual Variation in Length

Estimates of the average size of the fish in Lake Aleknagik are more precise than estimates of abundance from catches. The annual relative variation in mean length is much less, moreover, than the relative variation in catch. For example, the coefficients of variation in annual mean catches and mean lengths (20 July) for sockeye salmon fry were 67 and 9%, respectively.

The annual estimates of mean length on 20 June and 20 July, which represent the sizes of the fish at the beginning and end of early summer, were examined for determination of the major factors regulating growth. Annual mean lengths of sockeye salmon fry, threespine stickleback (age I), and char fry on 20 June were not significantly correlated. A significant part of the annual variation in lengths of sockeye salmon fry and char fry at this time was explained by the surface water temperatures on 20-24 June (Figure 9). Water temperature on 20 June is largely a function of the date of ice breakup and amount of solar radiation. Thus the annual growth attained in the spring by sockeye salmon fry and char fry is primarily a function of climatological conditions. The mean length of age I threespine stickleback was most closely correlated, however, with the abundance of sockeye salmon fry in the previous year. The best rela-

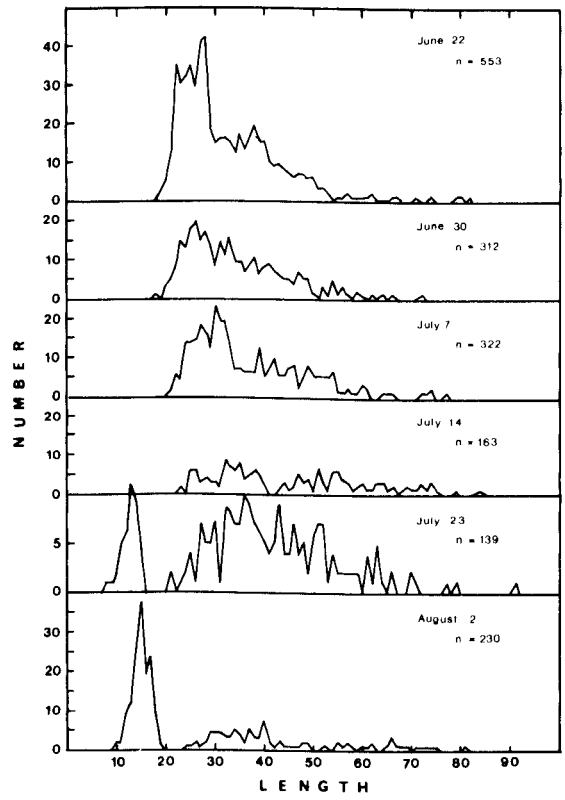

FIGURE 8.—Length-frequency distributions (mm) of slimy sculpin, 1968.

TABLE 8.—Densities of parent spawners and mean beach seine catches of sockeye salmon fry for years and lakes in which six or more seine hauls were made during 20 June-19 July for 1962 through 1972.

Lake	Year (i)	Sockeye salmon escapement in year i-1 (thousands)	Escapement density (number per km² of surface area)	Mean catch of sockeye salmon fry in year i	Adult sockeye salmon returns in years i+3-5 (thousands)
Tikchik lakes	1964	166	595	45	160
Igushik lakes	1965	129	1,743	163	640
Nunavaugaluk	1965	13	146	17	—
	1966	12	135	16	—
Kulik	1969	31	689	36	—
	1970	17	378	50	—
	1971	55	1,222	234	—
	1972	66	1,447	77	—
Beverley	1969	112	1,244	78	—
	1970	27	300	59	—
	1971	238	2,644	71	—
	1972	245	2,722	85	—
Aleknagik	1962	153	1,840	278	497
	1963	48	580	42	203
	1964	31	370	171	321
	1965	155	1,867	565	375
	1966	220	2,646	380	604
	1967	287	3,464	335	262
	1968	92	1,102	34	—
	1969	117	2,129	85	—
	1970	160	1,931	127	—
	1971	302	3,639	405	—
	1972	182	2,193	131	—

tionship was obtained by regressing the mean length on the logarithm of catch (Figure 10). Thus the mean length of threespine stickleback

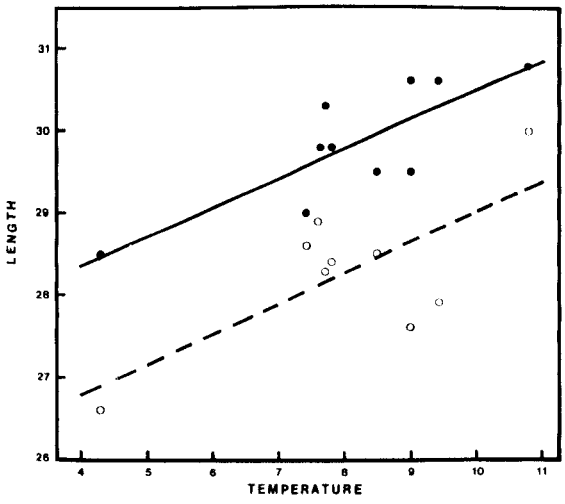

FIGURE 9.—Relationships between mean length (mm) on 20 June and mean surface water temperature from 20 to 24 June. Sockeye salmon fry (0): $Y = 26.93 + 0.36\ X$ ($r = 0.82$). Arctic char fry (0): $Y = 25.31 + 0.37\ X$ ($r = 0.71$).

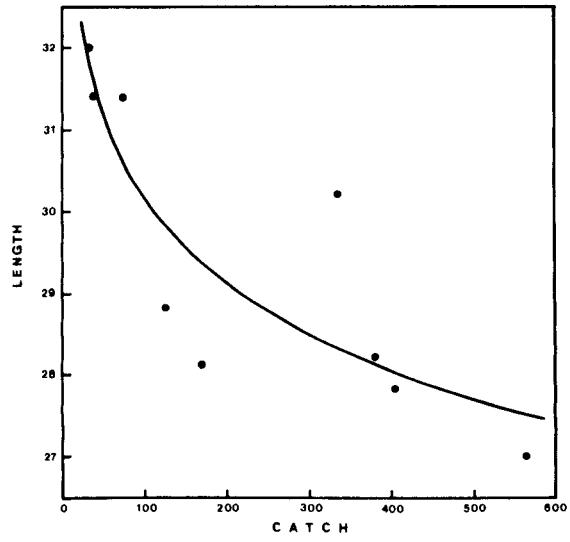

FIGURE 10.—Relationship between mean length (mm) of age I threespine stickleback on 20 June and mean catch of sockeye salmon fry in the previous year (20 June-19 July). $Y = 37.24 - 3.53 \log_{10} X$.

at age I is largely determined by the abundance of their main competitor when they were age 0.

The annual mean lengths on 20 July among

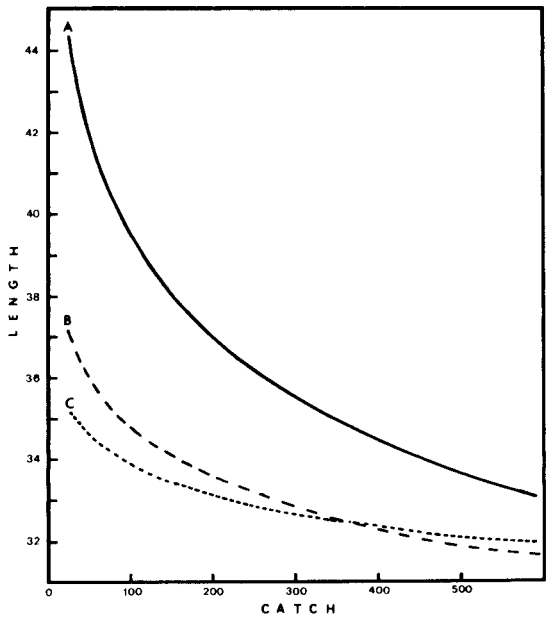

FIGURE 11.—Relationships between mean length on 20 July and mean catch of sockeye salmon fry from 20 June-19 July. A. Sockeye salmon fry: $Y = 56.82 - 8.62 \log_{10} X$ ($r = -0.86$). B. Age I threespine stickleback: $Y = 42.95 - 4.11 \log_{10} X$ ($r = -0.80$). C. Char fry: $Y = 38.93 - 2.56 \log_{10} X$ ($r = -0.85$).

the three species were significantly correlated but were most highly correlated between sockeye salmon fry and char fry ($r = 0.990$). Some correlation was evident between length and (1) date of ice breakup (small size — late date, large size — early date) and (2) average water temperature (small size — cold water, large size — warm water); however the highest correlations were between mean length and the mean catch of sockeye salmon fry. The last relationship appeared to be curvilinear, and regressions of mean length on logarithm of mean catch were significant at the 1% level (Figure 11).

Our main concern is with relationships involving sockeye salmon fry and threespine stickleback, as these are the most abundant species in the littoral. An increasing abundance of sockeye salmon fry results in a decreasing growth of these fish as well as of associated species in early summer. These data suggest a limiting capacity in the lake for growth of individual fish in the populations during the early summer but do not demonstrate a limiting capacity for the number of fish.

Annual variation in the relative abundance of other species did not appear to affect the growth of juvenile sockeye salmon; however, since growth of these species was density dependent (on juvenile sockeye salmon) and these species share a common food supply (primarily aquatic insects), there presumably was competition for food. If larger changes in the abundance of other species occurred in Lake Aleknagik, there would probably be corresponding changes in the growth of juvenile sockeye salmon. This question could best be examined by a comparison of growth and abundance among the lakes of the Wood River system.

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STOMACH CONTENTS OF PORPOISE, *STENELLA* SPP., AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, IN MIXED-SPECIES AGGREGATIONS

W. F. PERRIN,[1] R. R. WARNER,[2] C. H. FISCUS,[3] AND D. B. HOLTS[1]

ABSTRACT

Haul-by-haul analysis of stomach contents of spotted porpoise (*Stenella attenuata*), spinner porpoise (*S. longirostris*), and yellowfin tuna (*Thunnus albacares*) from six net hauls made on mixed-species aggregations in 1968 indicates that an ommastrephid squid (probably *Dosidicus gigas*) was the most important food item in terms of co-occurrences in the three species and in terms of the volume and number. The ommastrephid occurred in significant numbers and/or volume in each haul in all the species examined, albeit to a lesser degree in the spinner porpoise than in the other two species. Overlap of elements in the stomach contents was greatest between the tuna and the spotted porpoise. In addition to the ommastrephid, the small scombrid *Auxis* sp. and epipelagic exocoetids such as *Oxyporhamphus micropterus* were important to both. The portunid crab *Euphylax dovii* was very important in the tuna but absent in both species of porpoise. Onychoteuthid and enoploteuthid squids were important in some hauls in both species of porpoise but were all but absent from the tuna. Small mesopelagic fishes, mainly myctophids and gonostomatids, were important in the spinner porpoise, but not in the spotted porpoise or the tuna. Relative frequencies of empty stomachs and state of digestion of stomach contents indicated that the spinner porpoise does not feed at the same time as the spotted porpoise and tuna. In spite of overlap among the three species in nearly all of the food components, these results suggest that the tuna and spotted porpoise feed together largely on epipelagic prey, whereas the spinner porpoise for the most part feeds deeper and at different times of day; furthermore, only the tuna eats crustaceans.

Small pelagic delphinids (*Stenella attenuata*, *S. longirostris*, and *Delphinus delphis*) in the eastern tropical Pacific are commonly encountered with yellowfin tuna (*Thunnus albacares*) in large mixed-species aggregations. The association between the fish and the cetaceans is very tight (Perrin, 1969, 1970). Although the reason for the association is unknown, the possibility that it is food-based immediately suggests itself. Alverson (1963) examined the stomach contents of 2,846 yellowfin tuna from the eastern tropical Pacific and found the major components to be fish (46.9% of total volume) and crustaceans (45.4%). Cephalopods accounted for only 7.6% of the volume. He encountered a wide variety of food items and changes in species composition from area to area. He therefore concluded that yellowfin tuna are nonselective feeders, foraging on whatever pelagic or benthic organisms of suitable size are locally available. Fitch and Brownell (1968) reported on fish identified from otoliths taken from spotted porpoise, *Stenella graffmani* (= *attenuata*)[4] and spinner porpoise (*S. longirostris*) caught in

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Manuscript accepted May 1973
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

[4] The taxonomy of the spotted porpoises is confused. Recent morphological studies (Perrin, 1972) have shown that the spotted porpoise in the eastern Pacific is conspecific with the spotted porpoise that occurs around Hawaii. Accordingly, the name *S. attenuata* (Gray, 1846), which was applied by True (1906) to the Hawaiian form, is used here for the eastern Pacific form. This name has priority by date over *S. graffmani* (Lönnberg, 1934). This usage is provisional, pending the outcome of current studies comparing forms in the Atlantic and Pacific. *S. attenuata* may be a junior synonym of *S. frontalis* (Cuvier, 1829), which was described from the tropical North Atlantic.

TABLE 1.—Collection data for stomach contents examined from yellowfin tuna, spotted porpoise, and spinner porpoise from the eastern tropical Pacific.

Net haul	Date (1968)	Location (lat., long.)	Time of day (h)	Yellowfin tuna captured (t)	Estimated composition of porpoise school			Stomachs examined				
					Stenella attenuata (No.)	*Stenella longirostris* (No.)	*Thunnus albacares* (No.)	*S. attenuata*		*S. longirostris*		
								In field (No.)	In lab (No.)	In field (No.)	In lab (No.)
1	9 April	12°51'N, 93°18'W	1045	6	350	150			32		4
2	12 April	7°11'N, 90°32'W	1245	35	1,300	200	14		25	18	5
3	15 April	7°28'N, 91°15'W	1345	45	300		20	20			
4	16 April	7°30'N, 92°06'W	0800	60	1,500		21	24			
5	17 April	7°50'N, 92°32'W	1100	50	600		19	20			
6	18 April	7°58'N, 92°56'W	1130	35	350	50	5	19		19	
Total							79	83	57	37	9

association with tuna in the eastern tropical Pacific. On the basis of knowledge about the depth distributions of the species encountered, they concluded that the spotted porpoise had been feeding within 30 m of the surface and the spinner porpoise had been feeding to 250 m or more beneath the surface. Squid remains were present in some of the stomachs examined by Fitch and Brownell but were not included in their analysis.

In view of the nonselective feeding habits of the yellowfin tuna, analysis of comparative feeding habits of tuna and porpoise in mixed aggregations must be based on stomach contents collected from two or more of the species taken together in net hauls.

In this paper we report the results of the examination of stomach contents of 79 tuna, 140 spotted porpoise, and 46 spinner porpoise, taken in seine hauls on yellowfin tuna in 1968.

MATERIALS AND METHODS

The animals examined were captured in six net hauls by a tuna seiner (Table 1). The tuna were marked with numbered dart-type spaghetti tags and placed in the vessel's refrigerated fish holds. Stomachs were subsequently collected from the marked fish and preserved entire in 10% Formalin[5] when the catch was unloaded and prepared for processing ashore. Most of the porpoise stomachs were examined in the field and only selected items of the contents preserved in 10% Formalin for later identification (Table 1). The remainder of the stomachs were from animals frozen entire and later dissected ashore. Only the contents of the forestomach (oesophageal stomach) were examined.

The tuna taken during the cruise were nearly all about 1 m long. A random sample of 50 fish ranged from 846 to 1,164 mm fork length (average 1,079 mm).

The entire contents of stomachs opened in the laboratory were rough-sorted into fish, squid, and crustacean components. Each food item was identified to the lowest possible taxon,

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

and the volume was then measured. Whole undigested fish were identified by comparison of external characters with published keys or with identified museum specimens and species descriptions. Usually though, digestion had precluded such a procedure, so the remains were dissected and skeletal features were compared with a large series of radiographs of determined specimens from the collections of Scripps Institution of Oceanography, Fish otoliths extracted from the frozen porpoise stomachs allowed identification of completely and nearly completely digested fish. Because the tuna stomachs were initially preserved in unbuffered Formalin, it was not possible to use otoliths from those stomachs because diagnostic otolith features dissolve rapidly in an acidic solution. Some relatively intact squids (*Dosidicus gigas, Symplectoteuthis oualaniensis, Abraliopsis affinis,* and *Onykia* sp.) were found and identified in the stomach contents. Beaks from these specimens and from squids taken on the fishing grounds by dipnetting under lights at night were used to identify isolated beaks and beaks associated with otherwise unidentifiable fragments. Published and unpublished keys to cephalopod beaks and beaks from identified squids in the reference collection of the Marine Mammal Division, Northwest Fisheries Center, were also used in the identifications. Beaks from the ommastrephid squids were relatively easy to identify and separate from those of squids of other families. Although a few of the ommastrephids in the stomachs were identifiable to species, the data for the Ommastrephidae in the tables below are subdivided into only three categories: *ommastrephid A* (probably *Dosidicus gigas*), which includes positively identified *D. gigas* and those fragments (with associated beaks) and isolated beaks most probably belonging to that species on the basis of intrafamilial differences in size and darkening of the beaks; *ommastrephid B* (probably *Symplectoteuthis* sp.), which includes positively identified *S. oualaniensis* and those fragments and beaks most probably belonging to that species or another species of *Symplectoteuthis;* and *unidentified ommastrephid,* which includes those fragments and beaks identified only as from ommastrephids. The larger of the two counts of upper and lower beaks was interpreted as the minimum number of individuals represented. The only crustacean identified, *Euphylax dovii,* was present as readily identifiable nearly complete individuals or intact chelipeds. Because many of the porpoise stomachs contained both the remains (otoliths) of very small fish (myctophids, gonostomatids) and of squid, both of which eat small fish and squid, some of the fish and squid identified were almost certainly present only secondarily. The material was analyzed on a haul-by-haul basis, and the data for each haul are presented and discussed separately. Some effect of the nonselective feeding of tuna, the patchy distribution of prey items, may still be present, however. Since the material analyzed includes some stomachs that were full of relatively undigested food and some that contained only squid beaks and/or otoliths from well-digested meals, it is likely that more than one feeding may be represented in the data for some single-net hauls.

The presentation and analyses of the data are patterned after those in the paper by Pinkas, Oliphant, and Iverson (1971), in which both cephalopod beaks and otoliths were used to identify stomach contents of tunas. The analyses are in terms of volume (for the stomachs examined ashore only), numbers, and percent occurrence. Each of these methods distorts the picture in some way. In the numbers and percent occurrence analyses, unimportant small but numerous organisms may be disproportionately evident. The volume analyses are distorting because the various organisms are digested at different rates and because, as mentioned above, some of the contents were freshly ingested while others were only the remnants of well-digested meals. Otoliths and squid beaks tend to be retained in the gut. An ideal method would involve extrapolating an estimate of the original volume of each prey item and calculating caloric content, but these approaches were beyond the scope of the project. The above caveats notwithstanding, the data do yield considerable information on the relative feeding habits of the three species in mixed aggregations.

The stomachs are considered in three categories: full, with traces, and empty. Full stomachs are defined as those containing fleshy re-

TABLE 2.—Stomach contents of spotted and spinner porpoise taken in a single net haul in the eastern tropical Pacific: Haul 1.

	Spotted porpoise, *Stenella attenuata*, 32 stomachs (22 full, 7 with traces, 3 empty)						Spinner porpoise *S. longirostris*, 4 stomachs (all full)					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
Food item	ml	% of total	No.	% of total	No.	% (n = 29)	ml	% of total	total	% of total	No.	% (n = 4)
Total	7,619	100.0	6,101+	100.0	—	—	447	100.0	5,495	100.0	—	—
Fish	246	3.2	272+	4.5+	22	75.9	196	43.9	5,248	95.5	4	100.0
Exocoetidae	202	2.7	43	0.7	15	51.7	0	—	0	—	0	—
Oxyporhamphus micropterus	195	2.6	41	0.7	13	44.8	0	—	0	—	0	—
Exocoetus	7	<0.1	2	<0.1	2	6.9	0	—	0	—	0	—
Myctophidae	32	0.4	204	3.4	18	62.1	196 ml, not identified to species		3,868	70.4	4	100.0
Diogenichthys sp.	tr.	—	2	<0.1	2	6.9			3,374	61.4	4	100.0
Lampanyctus parvicauda	30	0.4	116	1.9	16	55.2			307	5.6	4	100.0
Lampanyctus idostigma	0	—	0	—	0	—			73	1.1	3	75.0
Benthosema panamense	0	—	0	—	0	—			24	0.4	4	100.0
Myctophum aurolaternatum	tr.	—	6	0.1	5	17.2			25	0.5	3	75.0
Hygophum sp.	0	—	0	—	0	—			5	0.1	4	100.0
Symbolophorus sp.	0	—	0	—	0	—			2	<0.1	1	25.0
Unid. myctophids	2	<0.1	80	1.3	13	44.8			58	1.1	3	75.0
Gonostomatidae:												
Vinciguerria sp.	tr.	—	1	<0.1	1	3.5			98	1.8	3	75.0
Bregmacerotidae:												
Bregmaceros sp.	tr.	—	2	<0.1	2	6.9			842	15.3	4	100.0
Melamphaidae	tr.	—	1	<0.1		3.5			424	7.7	2	50.0
Scopelogadus bispinosus	tr.	—	1	<0.1		3.5			413	7.5	2	50.0
Melamphaes sp.	0	—	0	—	0	—			11	0.2	1	25.0
Stromateidae	tr.	—	8	0.1	5	17.2			0	—	0	—
Cubiceps carinatus	tr.	—	3	<0.1	3	10.3			0	—	0	—
Cubiceps sp.	tr.	—	5	0.1	4	13.8			0	—	0	—
Bathylagidae:												
Bathylagus sp.	0	—	0	—	0	—			11	0.2	1	25.0
Scopelarchidae:												
Unid. scopelarchid	0	—	0	—	0	—			5	0.1	1	25.0
Unid. fish	12	0.2	13+	0.2+	10	34.5	0	—	0	—	0	—
Cephalopods	7,373	96.7	5,820	95.3	29	100.0	245	54.7	247	4.5	4	100.0
Onychoteuthidae:												
Onykia sp.	358	—	3,386	55.5	27	96.6	59	13.1	26	0.5	3	75.0
Ommastrephidae	157	—	1,569	25.8	29	100.0	47	10.4	68	1.2	3	75.0
Ommastrephid A (probably *Dosidicus gigas*)	127	—	1,108	18.2	29	100.0	47	10.4	45	0.8	3	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	17	—	216	3.5	27	93.1	0	—	0	—	0	—
Unid. ommastrephid	10	—	257	4.4	12	41.4	tr.	—	23	0.4	1	25.0

Enoploteuthidae: *Abraliopsis affinis*	3	—	672	11.0	29	100.0	69	15.3	151	2.7	4	100.0
Histioteuthidae: Unid. histioteuthid	tr.	—	1	0.1	1	3.5	0	—	0	—	0	—
Chiroteuthidae: Unid. chiroteuthid	tr.	—	3	0.1	1	3.5	0	—	2	0.1	1	25.0
Cranchiidae	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—
Unid. cranchiid	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—
Octopoteuthidae: *Octopoteuthis* sp.	tr.	—	1	<0.1	1	3.5	0	—	0	—	0	—
Unid. cephalopod fragments[1]	16,855	—	—	—	29	100.0	70	15.5	—	—	1	25.0
Unid. cephalopod beaks	3	—	174	2.9	18	62.1	0	—	0	—	0	—
Crustaceans	2	—	2	0.1	2	6.9	6	1.3	—	—	1	25.0
Unid. isopod	2	—	2	0.1	2	6.9	0	—	0	—	0	—
Unid. gammarid amphipods	0	—	0	—	0	—	6	1.3	—	—	1	25.0

[1] Includes bulk of fragments of specimens identified from beaks.

mains; stomachs with traces are those containing only squid beaks and fish otoliths and/or skeletal fragments. The volumetric analyses are based on the full stomachs only. The number and occurrence analyses are based on the full stomachs and those with traces. In addition to the material collected from simultaneous catches of two or more of the three predator species, fish otoliths were examined from another 5 spotted porpoise and 14 spinner porpoise captured with yellowfin tuna in various locations in the eastern tropical Pacific (Appendix Tables 1 and 2).

RESULTS

Haul 1

Only the two species of porpoise were sampled in Haul 1 (Table 2). The results for the species are sharply divergent. For the spotted porpoise, cephalopods predominated in volume, numbers, and occurrence. Onychoteuthid, ommastrephid, and enoploteuthid squids were the major food items. Fish made up an insignificant proportion of the volume and consisted primarily of the epipelagic *Oxyporhamphus micropterus*. In the four spinner porpoise examined, squid and fish were present in all the stomachs, each accounting for about half the total volume. The species composition of the squid component of spinner stomachs was different from that in the spotted porpoise mainly in that one of the unidentified ommastrephids (type B, probably *Symplectoteuthis* sp.) was completely absent, whereas it was present in 27 of the 29 spotted porpoise. Fish, primarily myctophids, predominated in numbers, the ratio of fish to squid being almost precisely the reverse of that for the spotted porpoise. Five myctophid species were present in all four stomachs. By far the commonest fish was *Diogenichthys* sp. (probably *laternatus*). A bregmacerotid, *Bregmaceros* sp., was also found in all four stomachs and was the next most common fish, followed closely by the melamphaid *Scopelogadus bispinosus* and the myctophid *Lampanyctus parvicauda*.

Haul 2

All three species were examined in Haul 2 (Table 3). The results for the spotted porpoise

TABLE 3.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 2.

Food item	Yellowfin tuna, *Thunnus albacares*, 14 stomachs (12 full, 1 with trace, 1 empty)						Spotted porpoise, *Stenella attenuata*, 25 stomachs (14 full, 8 with traces, 3 empty)						Spinner porpoise, *S. longirostris*, 23 stomachs (5 full, 3 with traces, 15 empty)					
	Volume		Number		Occurrence		Volume		Number		Occurrence		Volume		Number		Occurrence	
	ml	%	No.	% (n = 13)	No.	% (n = 13)	ml	%	No.	%	No.	% (n = 22)	ml (n = 2 full)	%	No.	%[1]	No.	%[1]
Total	1,591	100.0	177+	100.0	—	—	762	100.0	1,787	100.0	—	—	1	100.0	439	—	—	—
Fish	844	53.1	34+	19.2	12	92.3	140	18.4	154	8.6	10	45.5		1.8	420	100.0 95.7	2	100.0
Exocoetidae	525	33.0	26	14.7	10	76.9	25	3.3	127	7.1	7	31.8	0	—	0	—	0	—
Oxyporhamphus micropterus	425	26.7	21	11.9	10	76.9	25	3.3	90	5.0	4	18.2	0	—				
Cypselurus sp.	91	5.7	4	2.3	1	7.7	0	—	0	—	0	—	0	—				
Unid. exocoetid	9	0.6	1	0.6	1	7.7	tr.	—	36	2.0	5	22.7	0	—				
Scombridae:																		
Auxis sp.	137	8.6	1	0.6	1	7.7	110	14.4	1	0.1	1	4.6	0	—	0	—	0	—
Myctophidae	0	—	Contents preserved in Formalin; not examined for otoliths				tr.	—	17	1.0	6	27.3	tr.	—	321	73.1	2	100.0
Diogenichthys sp.							tr.	—	3	0.2	3	13.6			37	8.4	2	100.0
Lampanyctus parvicauda							tr.	—	1	0.1	1	4.6			1	0.2	1	50.0
Lampanyctus idostigma							0	—	0	—	0	—			7	1.6	2	100.0
Benthosema panamense							0	—	0	—	0	—			257	58.5	2	100.0
Myctophum aurolaternatum							0	—	0	—	0	—			2	0.5	1	50.0
Myctophum sp.							0	—	0	—	0	—			2	0.5	1	50.0
Symbolophorus sp.							tr.	—	1	0.1	1	4.6			3	0.7	2	100.0
Diaphus sp.							0	—	0	—	0	—			2	0.5	1	50.0
Unid. myctophids							tr.	—	12	0.7	4	18.2			10	2.3	2	100.0
Gonostomatidae:																		
Vinciguerria sp.							0	—	0	—	0				94	21.4	2	100.0
Bregmacerotidae:																		
Bregmaceros sp.							tr.	—	1	0.1	1	4.6			0	—	0	—
Melamphaidae:																		
Scopelogadus bispinosus							tr.	—	1	0.1	1	4.6			0	—	0	—
Stromateidae:																		
Unid. stromateoid							0	—	0	—	0	—			2	0.5	1	50.0
Paralepididae:																		
Unid. paralepidid							0	—	0	—	0	—			1	0.2	1	50.0
Unid. fish	182	11.4	7+	4.0	5	38.5	5	0.7	7	0.4	7	31.8			2	0.5	2	100.0
Cephalopods	363	22.8	131	74.0	13	100.0	622	81.6	1,633	91.4	22	100.0	54	98.2	19	4.3	6	75.0
Onychoteuthidae:																		
Onykia sp.	0	—	0	—	0	—	9	1.2	28	1.6	10	45.5	tr.	—	1	0.2	1	12.5

Ommastrephidae	105	6.6	89	50.3	11	84.6	114	15.0	1,476	82.6	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	103	6.5	74	41.8	10	76.9	74	9.7	1,220	68.3	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.	2	0.1	15	8.5	8	61.5	40	5.3	262	14.7	20	90.9	0	—	0	—	0	—
Unid. ommastrephid	0	—	0	—	0	—	tr.	—	6	0.3	1	4.6	0	—	0	—	0	—
Enoploteuthidae:																		
Abraliopsis affinis	0	—	0	—	0	—	1	0.1	109	6.1	16	72.7	tr.	—	1	0.2	1	12.5
Histioteuthidae:																		
Histioteuthis sp.	tr.	—	1	0.6	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—
Unid. octopod	0	—	0	—	0	—	tr.	—	1	0.1	1	4.6	0	—	0	—	0	—
Unid. cephalopod fragments[2]	258	16.2	—	—	5	38.5	498	65.4	—	—	11	50.0	0	—	—	—	0	—
Unid. cephalopod beaks	tr.	—	41	23.2	5	38.5	tr.	—	10	0.6	2	9.1	tr.	—	3	0.7	1	12.5
Crustaceans:																		
Portunidae:																		
Euphylax dovii	373	23.4	12	6.8	7	53.9	0	—	0	—	0	—	0	—	0	—	0	—
Unid. material	11	0.7	—	—	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—

[1] Only two stomachs were examined for otoliths; therefore the sample size for fish numbers and occurrence is two, while that for the cephalopods is eight.
[2] Includes bulk of fragments of specimens identified from beaks.

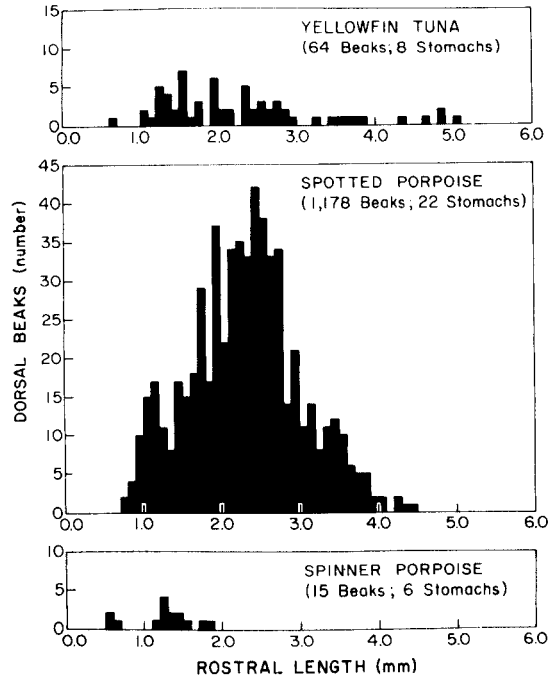

FIGURE 1.—Length frequency distributions of rostral lengths of beaks of ommastrephid squids (type A, probably *Dosidicus gigas*) from stomachs of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single-net haul (Haul 2) in the eastern tropical Pacific.

were much the same as for Haul 1, especially in that cephalopods strongly dominated in both volume and numbers. In this haul, however, ommastrephids rather than onychoteuthids predominated. Though scanty, the numerical results for the spinner were also similar to those for Haul 1. The relative squid volume was disproportionately large because the fish were represented only by otoliths. The contents of the tuna showed most overlap with those of the spotted porpoise. A scombrid, *Auxis* sp., was present in both. Cephalopods and epipelagic fish were important in both. This overlap, however, was overshadowed by some striking differences. The portunid crab *Euphylax dovii* occurred in half the tuna stomachs and accounted for a fourth of the total volume but was absent from the porpoise stomachs (both species). *Onykia* and enoploteuthid squids each occurred in about half the spotted porpoise stomachs but were absent in the tuna.

TABLE 4.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 3.

	Yellowfin tuna, *Thunnus albacares*, 20 stomachs (13 full, 3 with traces, 4 empty)						Spotted Porpoise, *Stenella attenuata*, 20 stomachs (none full, 19 with trace, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	837	100.0	112	100.0	16	100.0	75	100.0	—	100.0
Fish	379	45.3	12	10.7	6	37.5	0	—	0	—
Exocoetidae	20	2.4	3	2.7	3	18.8				
Exocoetus volitans	18	2.2	1	0.9	1	6.3				
Unid. exocoetid	2	0.2	2	1.8	2	12.5				
Scombridae:										
Auxis sp.	320	38.2	4	3.6	1	6.3				
Unid. fish	39	4.7	2	1.8	2	12.5				
Cephalopods	3	0.4	78	69.6	8	50.0	[1]75	100.0	19	100.0
Ommastrephidae	2	0.2	68	60.7	8	50.0	66	88.0	2	100.0
Ommastrephid A (probably *Dosidicus gigas*)	2	0.2	53	47.3	8	50.0	32	42.7	2	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	tr.	—	16	14.3	6	37.5	34	45.3	2	100.0
Enoploteuthidae:										
Abraliopsis affinis	0	—	0	—	0	—	9	12.0	2	100.0
Unid. Octopod	tr.	—	9	8.0	1	6.3	0	—	0	—
Unid. Cephalopod fragments	1	0.1	—	—	5	31.3	—	—	1	50.0
Unid. Cephalopod beaks	tr.	—	1	0.9	1	6.3	—	—	1	50.0
Crustaceans:										
Portunidae:										
Euphylax dovii	455	54.4	22	19.6	10	62.5	0	—	0	—

[1] Specimens were preserved from two stomachs only; therefore the sample size for the cephalopod taxa is two.

A striking difference between the data for tuna and spotted porpoise on one hand and the spinner porpoise on the other involved the relative number of empty stomachs encountered. Only 1 tuna stomach of 14 and 3 spotted porpoise stomachs of 25 were empty, whereas 15 spinner porpoise stomachs of 23 contained no food remains. The chance of this difference occurring by chance due to sampling error, based on chi-square analysis and assuming commonality of tuna and spotted porpoise, is less than 0.001, indicating that in the aggregation fewer spinner porpoise than spotted porpoise and tuna had been recently feeding or that the spinner porpoise had regurgitated their stomach contents during the fishing operation.

The spinner porpoise had eaten smaller squid than had the spotted porpoise and tuna. Clarke (1962) demonstrated that beak size within a species is closely correlated with total body weight. The sample of beaks of ommastrephid A (probably *Dosidicus gigas*) collected from the spinner porpoise clearly belong to a different size distribution than those taken from the spotted porpoise and the tuna (Figure 1), indicating that the spinner porpoise on the average had been feeding on smaller squid.

Haul 3

Only yellowfin tuna and spotted porpoise were examined in Haul 3 (Table 4). The porpoise stomachs were all nearly empty, containing only hard parts of squid. Except for the complete absence of fish in the porpoise stomachs, the results for the two species were similar

TABLE 5.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 4.

	Yellowfin tuna, *Thunnus albacares*, 21 stomachs (20 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 24 stomachs (23 full, 1 with traces)[1]					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	ml (n=3)	%	No.	%	No.	%
Total	1,411	100.0	139	100.0	20	100.0	653	100.0	—	—	—	—
Fish	108	7.5	10	7.2	5	25.0	2	0.3	6	—	5	21.7
Exocoetidae	54	3.8	4	2.8	4	20.0	1	0.2	4	—	4	17.4
Oxyporhamphus micropterus	24	1.7	2	1.4	2	10.0	—	—	1	—	1	4.4
Exocoetus monocirrhus	0	—	0	—	0	—	1	—	2	—	2	8.7
Exocoetus sp.	29	2.0	1	0.7	1	5.0	—	—	0	—	0	—
Unid. exocoetid	8	0.6	1	0.7	1	—	—	—	1	—	1	4.4
Scombridae:												
Unid. scombrid	0	—	0	—	0	—	—	—	1	—	1	4.4
Unid. fish	54	3.7	6	4.3	2	10.0	tr.		2	—	2	8.7
Cephalopods	633	43.9	77	55.4	0	—	652	99.9	85	—	23	100.0
Onychoteuthidae:												
Onykia sp.	0	—	0	—	0	—	tr.	—	4	—	1	4.4
Ommastrephidae	615	42.7	38	27.3	11	55.0	650	99.5	49	—	3	100.0
Ommastrephid A (probably *Dosidicus gigas*)	609	42.3	27	19.4	10	50.0	515	78.9	35	—	3	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	6	0.4	11	7.9	4	20.0	135	20.7	14	—	1	33.3
Enoploteuthidae:												
Abraliopsis affinis	0	—	0	—	0	—	tr.	—	31	—	3	100.0
Unid. octopod	tr.	—	1	0.7	1	5.0	0	—	0	—	0	—
Unid. cephalopod fragments	18	1.3	—	—	1	5.0	2	0.3	—	—		33.3
Unid. cephalopod beaks	tr.	—	2	1.4	2	10.0	tr.	—	1	—	1	33.3
Crustaceans:												
Portunidae:												
Euphylax dovii	700	48.6	37	26.6	14	70.0	0	—	0	—	0	—

[1] Complete contents were preserved and volumed for only three stomachs. All fish remains were preserved; therefore the sample size for fish number and occurrence is 23. For cephalopod taxa, the sample size is three.

to those in Haul 2. Overlap was greatest in the cephalopod component. The crab *Euphylax dovii* was dominant in the tuna and absent in the porpoise. The enoploteuthid squid *Abraliopsis affinis* was again present in the porpoise but absent from the tuna. Nearly all of the fish volume in the tuna was due to the presence of four frigate mackerel, *Auxis* sp., in one stomach.

Haul 4

Tuna and spotted porpoise were again sampled in Haul 4 (Table 5), and the same pattern emerged as in the previous hauls. Portunid crabs were important in the tuna but absent in the porpoise, and enoploteuthid squid were present in the porpoise but absent in the tuna. Except for *Abraliopsis*, the squid and fish components were very similar for the two species in this haul.

Haul 5

Both the tuna and the spotted porpoise in this haul were engorged with freshly ingested *Auxis* and squid (Table 6), and the makeup of the contents in both volume and number was remarkably similar. They had obviously fed on the same food at the same time. *Abraliopsis*

TABLE 6.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 5.

	Yellowfin tuna, *Thunnus albacares*, 19 stomachs (all full)						Spotted porpoise, *Stenella attenuata*, 20 stomachs (17 full, 2 with traces, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	17,411	100.0	222	100.0	19	100.0	194	100.0	19	100.0
Fish	13,019	74.8	110	49.6	19	100.0	[1]97	<50.0	16	84.2
Exocoetidae:										
Oxyporhamphus micropterus	197	1.1	8	3.6	6	31.6	1	<0.5	1	5.3
Exocoetus volitans	107	0.6	5	2.3	4	21.1	1	<0.5	1	5.3
Unid. exocoetid	29	0.2	1	0.5	1	5.3	0	—	0	—
Scombridae:	61	0.4	2	0.9	2	10.5	0	—	0	—
Auxis sp.	12,720	73.1	91	41.0	19	100.0	91	<46.9	15	79.0
Unid. fish	102	0.6	11	5.0	5	26.3	5	<2.6	5	26.3
Cephalopods	4,392	25.2	112	50.5			[2]>97	>50.0	18	94.7
Onychoteuthidae:										
Onykia	0	—	0	—	0	—	present		—	—
Ommastrephidae:										
Ommastrephid A (probably *Dosidicus gigas*)	4,389	25.2	88	39.6	15	79.0	present		—	—
Ommastrephid B. (probably *Symplectoteuthis* sp.)	tr.	—	10	4.5	4	21.1	present		—	—
Enoploteuthidae:										
Abraliopsis affinis	tr.	—	3	1.4	2	10.5	present		—	—
Unid. cephalopod fragments	3	<0.1	—	—	1	5.3	—		—	—
Unid. cephalopod beaks	tr.	—	11	5.0	5	26.3	—			

[1] Fish counted in 19 stomachs.
[2] Whole squid counted in 16 stomachs not saved ; only samples of beaks were saved for identification.

was present in the tuna (beaks from three individuals), the only occurrence in tuna in the six hauls. *Onykia*, however, was again present in the porpoise but not in the tuna.

Some of the frigate mackerel were sufficiently undigested to allow them to be measured. Thirty five ranged from 18 to 29 cm fork length (average 24 cm), and sizes did not differ in porpoise and tuna.

Haul 6

Nineteen stomachs of spinner porpoise were examined in this haul, and all were empty. The spotted porpoise contained freshly ingested *Auxis* and squid (Table 7), in about the same ratio as in Haul 5, but the tuna contained only small amounts of *Euphylax dovii*, along with well-digested fish and squid remains. The three species in this haul had fed on different food and/or at different times.

Summary of Results

Ommastrephid squid A (probably *Dosidicus gigas*) was the most important prey species in terms of co-occurrence in the tuna and both species of porpoise as an important food item (Table 8). The greatest overlap between species was in Haul 5, when *Auxis* and the ommastrephid were important in the tuna and the spotted porpoise. As regards specialization, *Diogenichthys* sp., *Benthosema panamense*, *Vinciguerria* sp., and *Bregmaceros* sp. were important only in the spinner porpoise, and *Euphylax dovii* was important only in the tuna. When spinner porpoise were sampled (three hauls), the rate of occurrence of empty stomachs and the state of

TABLE 7.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 6.

	Yellowfin tuna, *Thunnus albacares*, 5 stomachs (4 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 19 stomachs (12 full, 4 with traces, 3 empty)				Spinner porpoise, *S. longirostris*, 19 stomachs (all empty)
	Volume		Number		Occurrence		Number		Occurrence		
Food item	ml	%	No.	%	No.	%	No.	%	No.	%	
Total	217	100.0	>33	100.0	4	100.0	>113	100.0	16	100.0	
Fish	68	31.3	6	18.1	3	75.0	32	<28.3	9	56.3	
Exocoetidae:											
Oxyporhamphus micropterus	15	6.9	1	3.0	1	25.0	0	—	0	—	
Scombridae:											
Auxis sp.	0	—	—	—	0	—	32	<28.3	9	56.3	
Unidentified fish	53	24.4	5	<15.2	3	75.0	0	—	0	—	
Cephalopods	tr.	—	>8	>24.2	4	100.0	[1] >81	>71.7	16	100.0	
Ommastrephidae	tr.	—	5	<15.2	1	25.0			—	—	
Ommastrephid A (probably *Dosdicus gigas*)											
Unidentified cephalopod beaks	tr.	—	>3	>9.1	3	75.0			—	—	
Crustaceans:											
Portunidae:											
Euphylax dovii	149	68.7	5	<15.2	2	50.0	> 0	—	0	—	

[1] Whole squid counted in 12 full stomachs, not saved; beaks not counted or saved.

digestion of the stomach contents indicated that they had not fed at the same time as the tuna and/or the spotted porpoise.

DISCUSSION

Interpretation of the feeding habits of animals from their stomach contents is complicated by two factors. First, material from the stomachs of the primary prey may be mistaken as food items of the predator. This is especially true when, as in the present study, many stomachs contain squid, which are active piscivores in their own right. However, if we are concerned only with the general depth at which feeding takes place, it makes less difference whether the fish remains found in the gut are primary or secondary in origin. When two predators show consistent differences in the probable depth origin of their stomach contents, there are at least three alternative interpretations: the two predators feed at different depth ranges (gathering the material found directly or through some secondary predator), they feed at the same depths but at different times of the day, thus taking advantage of diurnal migration of some prey species, or they feed at the same depth with one only eating prey items that were recent predators at another depth. The first explanation seems most probable.

The other complicating factor is less easy to resolve. The depth distributions of many pelagic prey items are imperfectly known. This requires that much caution be exercised when interpreting food habits of predators from data based on rare or little-known prey.

Depth Distribution of Fish

Exocoetidae

Oxyporhamphus micropterus and species of both *Exocoetus* and *Cypselurus* are all constant inhabitants of epipelagic waters. Exocoetids were extremely common in the stomachs of tuna and *S. attenuata*. Only one exocoetid otolith was found in all 46 stomachs of *S. longirostris* examined.

Scombridae

The frigate mackerel, *Auxis* sp., is another common fish of surface waters and is of relatively large size. Its occurrence in specimen stomachs parallels that of the flyingfish, often being found in *S. attenuata* and yellowfin tuna

TABLE 8.—Summary of major identified stomach constituents of yellowfin tuna, spotted porpoise, and spinner porpoise taken from mixed-species aggregations in the eastern tropical Pacific. + = present, ● = important (≥ 10% of volume and/or numbers).

	Haul number														
	1		2			3		4		5		6			
Food item	Spotted	Spinner	Tuna	Spotted	Spinner	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Spinner	
FISHES:															
Oxyporhamphus micropterus	+		●	+				+	+	+	+	+			(all empty)
Auxis sp.			+	●		●				●	●		●		
Diogenichthys sp.	+	●	(Otoliths not collected)	+	+	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)		
Benthosema panamense		+			●										
Vinciguerria sp.	+	+			●										
Bregmaceros sp.	+	●		+											
SQUIDS:															
Onykis sp.	●	●		+	+										
Ommastrephid A (probably *Dosidicus gigus*)	●	●	●	●	●	●	●	●	●	●	●	●	(Squids not identified)		
Ommastrephid B (probably *Symplectoteuthis* sp.)	+		+	+		●	●	+	●	+	+				
Abraliopsis affinis	●	●		+	+		●			+	+				
CRAB:															
Euphylax dovii			●			●		●				●			

and completely absent as a food item of *S. longirostris*.

Myctophidae

At least 13 species of myctophids were identified from specimen stomachs. A majority of the genera found (*Diaphus*, *Diogenichthys*, *Ceratoscopelus*, *Hygophum*, *Myctophum*, *Symbolophorus*, *Benthosema*, and *Gonichthys*) are known to reach the surface at night during the course of vertical migrations, but most remain deep during the day. A second group consisting of *Lepidophanes*, *Lampanyctus*, *Lobianchia*, and *Triphoturus* are usually not caught in near-surface waters, even at night; their migrations probably do not take them as shallow as the first group. Myctophids were a consistent major food item of *S. longirostris* and occasionally were common in *S. attenuata*.

Gonostomatidae

Vinciguerria is a vertical migrator found below 200 m during the day, ranging up to surface waters at night. Three-fourths of the full stomachs of *S. longirostris* examined for otoliths contained gonostomatid remains. In the much larger sample of spotted porpoise stomachs, only two contained a few gonostomatid otoliths.

Stromateidae

Although some young stromateoids are often associated with floating objects, adults have large depth ranges. *Cubiceps carinatus* has been taken in a midwater trawl station in large numbers. Stromateoids appeared irregularly in the stomachs of both species of porpoise.

Melamphaidae

Melamphaes and *Scopelagadus* adults normally remain below 100 to 200 m) Ebeling, 1962; Ebeling and Weed, 1963). Melamphaid otoliths were found occasionally in large numbers in *S. longirostris* stomachs and rarely (cf. Appendix 1) in those of *S. attenuata*.

Bregmacerotidae

Although *Bregmaceros* is known to occur bathypelagically and is captured in midwater trawls, it also can be found at the surface at night (Fitch and Brownell, 1968). It occurred regularly in low frequencies in both species of porpoises; larger numbers were found in one associated group of four porpoise (*S. longirostris*).

Gempylidae, Trachipteridae

Species of both these families have been found both in surface waters and at depth. A trachipterid otolith was found in the gut of one *S. longirostris*. Gempylid remains were found in two spinner porpoise stomachs, and in one *S. attenuata* from the far-west sampling area (Appendix 1).

Paralepididae, Bathylagidae, Scopelosauridae, Evermannellidae, Opisthoproctidae

Adult members of these families are not normally found near the surface. Most museum specimens have been caught in midwater trawls. A few otoliths from species in these families were regularly found in the stomachs of *S. longirostris*. Two specimens of *S. attenuata* caught in the far-west sampling location (Appendix 1) also contained otoliths from these families, including the only records of scopelosaurids and opisthoproctids. Otoliths from many myctophids and melamphaids were also found in these specimens. The overall pattern closely parallels that seen for spinner porpoise normally (e.g., Appendix 2). This indicates that spotted porpoise are capable of shifting to a mesopelagic feeding pattern, although epipelagic feeding appears to be typical. The cause of the shift is unknown.

Shomura and Hida (1965) reported that the stomach of a Hawaiian spotted porpoise contained fish of the families Paralepididae, Alepisauridae, Gempylidae, Bramidae, and Myctophidae, as well as squids (the major component), nemertean worms, and crab larvae. The fish component was similar to that for the two westernmost specimens of eastern Pacific *S. attenuata* discussed above.

Depth Distributions of Squids

No discrete depth sampling of squids has been carried out in the area where the animals were collected. Some information, however, is available on the depth distributions of some of the families concerned from other areas.

Ommastrephidae

The most abundant squids found in the stomachs were probably *Dosidicus gigas* and *Symplectoteuthis* sp. Clarke (1966) reported that *D. gigas* and species of *Symplectoteuthis* migrate to the surface at night. *Dosidicus gigas* and *Symplectoteuthis oualaniensis* have been taken in the area by dip net at the surface under lights at night (unpublished data). In this area, the ommastrephids are the most abundant epipelagic squids.

Enoploteuthidae

The enoploteuthid squid *Abraliopsis affinis* occurred next in abundance to the ommastrephids. It is a mesopelagic species. Gibbs and Roper (1972) stated that enoploteuthids undergo diurnal vertical migrations. It appears that this species may move into or is resident within the diving ranges of the two species of porpoise,

but does not occur regularly in the possibly more epipelagic range of the tuna. Another possibility, of course, is that it is fed on selectively by the porpoise and not by the tuna.

Onychoteuthidae

Onykia sp. was not found in the stomachs of *Thunnus* and has not been taken by dip net at the surface in the area. However, it was found in the stomachs of the two species of porpoise and may be a mesopelagic species. Other members of the family, *Onychoteuthis* sp. for example, are regularly taken at or near the surface at night.

SUMMARY

While there is great overlap among the diets of the two porpoises and the tuna in mixed aggregations, there is evidence of specialization in prey items, time of day at which feeding occurs, and possibly in maximum feeding depth. Although the three species are intimately associated in tight mixed groups, they do not necessarily feed on the same items at the same time in the same place. If the association is food-based, however, the epipelagic ommastrephid squids seem to be the most probable candidates for a binding common factor in this region. The apparent trophic relationships among the three species can be crudely summarized in terms of taxa and depth distribution of the major prey items (Figure 2).

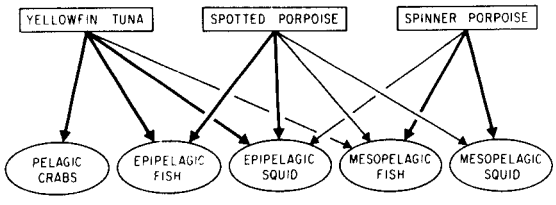

FIGURE 2.—Summary of apparent relative feeding habits of yellowfin tuna, spotted porpoise, and spinner porpoise in mixed aggregations in the eastern tropical Pacific, based on stomach-content data presented here and in Fitch and Brownell (1968) and Alverson (1963). Widths of lines crudely approximate relative importances of the major food categories.

ACKNOWLEDGMENTS

The senior author's wife, Gerlind, spent countless hours rough-sorting thousands of otoliths. John E. Fitch identified the otoliths, using his extensive reference collection to make direct comparisons in most cases. Clyde F. E. Roper provided much help in identifying squids. Richard H. Rosenblatt furnished information on fish-depth distribution. The captains and crews of the tuna seiners MV *Carol Virginia* (now *Carol S.*) and MV *Pacific Queen* made possible collections of the stomachs. Craig J. Orange collected the *Pacific Queen* specimens. The Inter-American Tropical Tuna Commission furnished measurements of a sample of the *Carol Virginia* tuna catch. Carl L. Hubbs and Richard H. Rosenblatt read the manuscript. We thank these persons and others who assisted us in the project.

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APPENDIX TABLE 1.—Fish identified from otoliths taken from stomachs of five spotted porpoise, *Stenella attenuata*, caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

	Locality			
	1	2	3	4
Fish	7°47'N 106°50'W 18 April 1969 (1 stomach)	7°-8°N 106°-107°W 27-28 April 1969 (1 stomach)	4°-7°N 86°-100°W June-July 1970 (1 stomach)	9°28'N 129°18'W 12 Aug. 1970 (2 stomachs)
	(minimum number of individuals)			
Exocoetidae:				
Cypselurus sp.			2	
Exocoetus sp.			1	9(2)
Oxyporhamphus sp.				2(2)
Unid. exocoetid(s)	2	3		
Myctophidae:				
Diaphus spp.				34(2)
Diogenichthys laternatus				62(2)
Hygophum spp.				4(2)
Lampanyctus spp.				340(2)
Lepidophanes sp.				12(2)
Myctophum spp.				6(2)
Symbolophorus sp.				26(2)
Unid. myctophids	6		1	76(2)
Melamphaidae:				
Melamphaes spp.				18(2)
Scopelogadus sp.				29(2)
Gonostomatidae:				
Unid. gonostomatid				4(1)
Stromateidae:				
Cubiceps carinatus				9(2)
Cubiceps sp.			1	
Unid. stromateoids				5(2)
Gempylidae:				
Unid. gempylid				3(1)
Paralepididae:				
Unid. paralepidid				3(2)
Bathylagidae:				
Bathylagus sp.				23(2)
Bregmacerotidae:				
Bregmaceros sp.				2(2)
Scopelosauridae:				
Scopelosaurus sp.				1
Opisthoproctidae:				
Dolichopteryx sp.				1
Evermannellidae:				
Evermannella sp.				2(1)
Total	8	3	5	671

APPENDIX TABLE 2.—Fish identified from stomachs of 14 spinner porpoise *Stenella longirostris*, caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

	Locality					
	1	2	3	4	5	6
Fish	7°-8°N 106°-107°W 26-27 Apr. 1969 (4 stomachs)	7°-8°N 107°W 28 Apr. 1969 (2 stomachs)	3°-10°N 110°-120°W June 1970 (1 stomach)	10°19'N 135°38'W 5 Aug. 1970 (1 stomach)	9°47'N 133°25'W 11 Aug. 1970 (5 stomachs)	9°10°N 128°-136°W Aug. 1970 (1 stomach)
Exocoetidae:						
Oxyporhamphus micropterus	1					
Myctophidae:						
Ceratoscopelus sp.	6(1)		1			1
Diaphus spp.	102(3)	3(2)	57	1	191(5)	58
Diogenichthys laternatus			624	5	3,347(5)	398
Diogenichthys sp.	8,732')3)	109(1)				
Hygophym spp.	100(1)	3(1)	4		60(5)	7
Lampanyctus parvicauda	8(3)	2(2)				
Lampanyctus idostigma	111(2)	10(1)				
Lampanyctus spp.			613	163	2,369(5)	899
Lepidophanes sp.			14		131(4)	15
Lobianchia dofleini			239		582(5)	236
Myctophum aurolaternatum	195(2)	1				
Myctophum spp.					10(3)	
Symbolophorus sp.	17(2)		12	1	38(5)	9
Benthosema panamense	68(2)	12(2)				
Gonichthys tenuiculum	79(2)					
Triphoturus sp.	3(1)					
Unid. myctophids	115(4)	29(1)			179(4)	8
Melamphaidae:						
Melamphaes spp.	6(1)	1	2		42(2)	
Scopelogadus bispinosus	1	2(1)		49		
Gonostomatidae:						
Vinciguerria sp.	32(2)	4(1)	50		55(5)	42
Unid. gonostomatids			2		52(2)	1
Stromateidae:						
Cubiceps carinatus	10(1)	1	1	6	2(2)	4
Cubiceps sp.					2(1)	
Unid. stromateoids	3(2)		3		3(2)	2
Gempylidae:						
Unid. gempylid				2	1	
Paralepididae:						
Unid. paralepidid			2			
Bathylagidae:						
Bathylagus sp.	22(1)		11		2(1)	5
Bregmacerotidae:						
Bregmaceros sp.	1		2		9(4)	1
Evermannellidae:						
Evermannella sp.	5(1)		1		2(2)	
Stomaitidae:						
Unid. stomiatoids	1		1			
Trachipteridae:						
Trachipterus fukuzakii	1					
Total	9,619	177	1,639	227	7,167	1,686

SEA GRASSES AT KHOR UMAIRA, PEOPLE'S DEMOCRATIC REPUBLIC OF YEMEN WITH REFERENCE TO THEIR ROLE IN THE DIET OF THE GREEN TURTLE, *CHELONIA MYDAS*

HAROLD F. HIRTH, LIONEL G. KLIKOFF, AND K. T. HARPER[1,2]

ABSTRACT

Studies were made on the sea grass pastures at Khor Umaira in the People's Democratic Republic of Yemen in July 1972. The standing crop in an equally mixed pasture of *Cymodocea serrulata* and *Syringodium isoetifolium* was greater than that in a pure stand of *C. serrulata*. The average caloric content of the leaves of five genera of sea grasses at Khor Umaira ranged between 4.54 and 4.66 kcal/g dry wt, ash free. These values are similar to those reported for sea grasses in the South Pacific and in the Caribbean. Our results show that the number of calories in the standing crop can be calculated from estimation of percent cover. The role of sea grasses in the management schemes of the green turtle, *Chelonia mydas*, is described.

Sea grass meadows are productive and important marine communities. Besides stabilizing the substrate sea grasses provide cover and are a source of food for a number of marine invertebrates and vertebrates. The leaves also support a variety of epiphytes and the grass debris serves as the energy base for detritus food chains. It is probable that in earlier days large numbers of manatees, dugongs, and green turtles grazed on these submarine pastures, but the sirenians and marine turtles have been so over-exploited that today many marine meadows are virtually ungrazed by any big vertebrate of economic importance to man. The green turtle, *Chelonia mydas*, has been proposed as a candidate for marine ranching by fencing them in underwater spermatophyte pastures (for review of management schemes see Hirth, 1971). The purposes of this paper are to describe some basic parameters of the sea grass pastures at Khor Umaira in the People's Democratic Republic of Yemen and to provide basic data aimed at answering the question, "What are the characteristics of good green turtle feeding pastures?" Khor Umaira has been mentioned as a possible site for a green turtle ranch (Food and Agriculture Organization, 1968).

THE SITE

Khor Umaira is the name of a bay (an arm of the Gulf of Aden) and village approximately 80 km west of Aden. The bay is almost completely landlocked by a long, narrow sandy spit that extends west-northwest along the coast. The bay itself is about 6.5 km long. Its width varies from about 550 m at the entrance to approximately 3.2 km in the middle. The depth of the water near the entrance is between 1 and 6 m, while the depth inside varies from 1 to 11 m.

Quantitative data were taken inside the bay where a few green turtles are always seen feeding. The grass pasture in the bay was adjudged similar to that off the nearby coast at comparable depths where large numbers of grazing turtles are caught in seines.

METHODS

Five adult female green turtles, all weighing over 91 kg, were caught on the Ras al Ara pastures (19 km west of Khor Umaira) on 22 July 1972. Their stomachs were full of leaves of sea grasses (chiefly *Syringodium* and *Cymodocea*) along with some stems and a few segments of

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[2] Most of the field work was done by the senior author during his tenure as Marine Turtle Consultant with the Food and Agriculture Organization of the United Nations.

Manuscript accepted May 1973.
FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

rhizomes (see Figure 1). Observations made in 1966-67 (Food and Agriculture Organization, 1968) also suggest that green turtles in the vicinity of Khor Umaira eat chiefly the leaves of sea grasses. The local name for all sea grasses is Zawee.

No turtles were observed grazing in the census plots at the time of collection, but substantial amounts of leaves had washed up on the shores of the bay.

The grasses were collected in the middle of what was considered good turtle pasturage on 28, 29, and 30 July 1972. This was during the peak of the Southwest Monsoon which in this area generally prevails from April through September. The collecting sites were approximately 500 to 600 m from the nearest shore. Thirty samples were taken in a homogeneous pasture of *Cymodocea serrulata* and 30 samples from a stand of *C. serrulata* and *Syringodium isoetifolium* adjudged to be equally mixed. The sample quadrats were 1/16 m^2. The 60 samples were taken at depths from 0.8 to 2.5 m with 70% of the samples from depths of 1.8 to 2.5 m. The sampling was done at or near low tide. Visibility, as measured with a white Secchi disc 20 cm in diameter, extended to the bottom. Pure stands of *Syringodium* were not seen in the bay but a more detailed census might reveal the presence of such stands.

The grasses were harvested at the ground surface and weighed. No attempt was made to separate epiphytic algae from the leaves. Wet weight was obtained after removing the external water by gentle blotting and dry weight was determined by drying to constant weight in an oven at 80°C. Cover was calculated by looking straight down on a 1/16 m^2 quadrat and estimating percent coverage to the nearest 10%. Caloric values were determined using a Parr semimicro bomb calorimeter[3] following the procedures of Lieth (1968). However, since some of the techniques with oxygen bomb combustion underestimate ash content (Paine, 1971; Reiners and Reiners, 1972) in a second series of combustions aliquots of the material were ashed at 500°C for 5 h in a muffle furnace for determination of ash content. All caloric determinations are means of three samples and each sample differed by less than 3%. Plant nomenclature and terminology follows den Hartog (1970). Regression procedures follow those given in Steel and Torrie (1960).

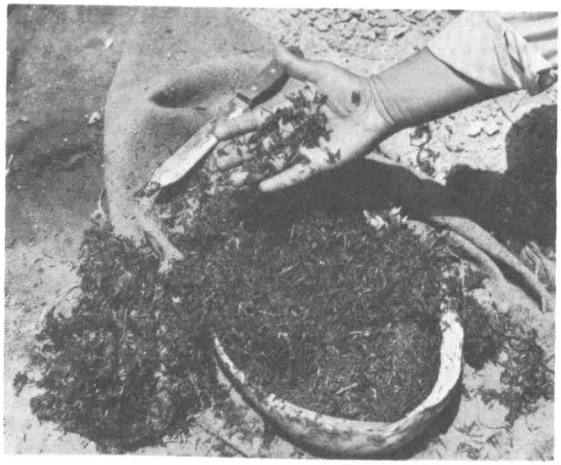

FIGURE 1.—The stomach contents of an adult, female green turtle caught on 22 July 1972 on the feeding pasture near Ras al Ara. The stomach was packed solidly with sea grasses.

RESULTS AND DISCUSSION

The dry weights of *C. serrulata* along with corresponding cover data are given in Figure 2. All of the leaf blades on the sample plots were less than 20 cm long, with shorter blades associated with shallow water. An average of 84.5% (range 79-90%) of the wet weight was water. As Figure 2 shows, one would expect to find a dry weight of 290 g/m^2 in a pasture of *Cymodocea* with 100% cover at Khor Umaira in July. The corresponding wet weight would register about 1,871 g/m^2. Gessner (1971) found that leaves of turtle grass, *Thalassia testudinum*, in a dense meadow off Venezuela registered 608 g/m^2 dry weight and 2,504 g/m^2 wet weight. The mean length of the leaves was 23 cm and the water depth was 60 cm. In two sample plots of *T. testudinum* off the Florida coast, Phillips (1960) recorded dry weight values of about 325 and 98 g/m^2. The lower biomass was associated with shallower water.

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

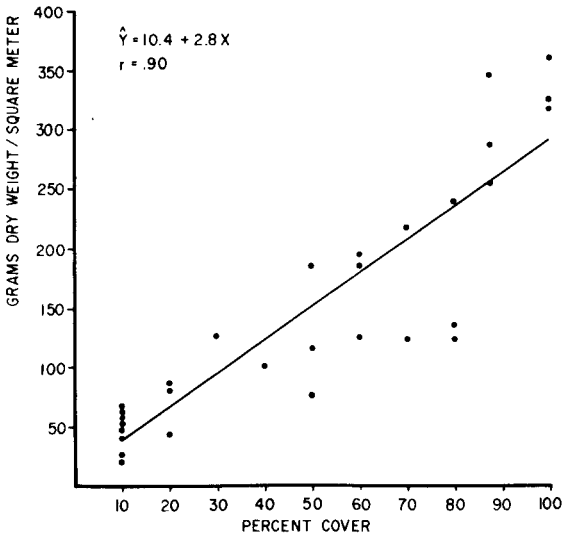

FIGURE 2.—Above-ground dry weight of *Cymodocea serrulata* regressed on field estimates of plant cover made at Khor Umaira.

The standing crop of an equally mixed pasture of *C. serrulata* and *S. isoetifolium* at Khor Umaira can be obtained from cover estimates in Figure 3. Leaf blades of both species here were less than 20 cm. On the average, water amounted to 88.7% of the wet weight of the leaves (range 83-91%).

In order to determine some chemical parameters associated with dense sea grass pasture, water samples were collected just above the leaves of an equally mixed stand of *C. serrulata* and *S. isoetifolium* with 100% cover at a depth of 1.75 m (at low tide) at 0915 h on 30 July 1972. The pH was determined using colorimetric standards and the other chemical parameters were obtained using standard methods for water analyses. The results are as follows: temperature 29.2°C; salinity 36.50‰; chlorinity 20.19‰; pH 8.2; free carbon dioxide 10 ppm; dissolved oxygen 5 ppm; total alkalinity 122 ppm, with 36 ppm as carbonate alkalinity and 86 ppm as bicarbonate alkalinity; magnesium chloride 4,000 ppm; and calcium chloride 999 ppm.

Substrate samples were taken at the same site and at the same time as the water samples. The substrate of this site consists largely of coarse fragments of shells. The bottom sample analyzed was a composite of five samples taken at a depth of 0-2.5 cm. The pH was obtained using a glass electrode, particle size was based on material passing a 2-mm sieve, and the other chemical parameters were determined using standard soil testing techniques. The results are as follows: pH 7.2; sand 97% ; silt 3% ; clay 0% ; phosphorus 0.027 mg/g substrate; calcium 73.5 mg/g substrate.

The regression lines in Figures 2 and 3 show that given equal cover, standing crop is greater in a mixed pasture of *Cymodocea* and *Syringodium* than in a homogeneous stand of *Cymodocea*. This may be due to the close packing of the terete leaves of *Syringodium* in the mixed pasture.

The caloric content of four genera of sea grasses collected in the bay at Khor Umaira and one genus *(Thalassodendron)* collected off the nearby coast at a depth of 4.5 m, are given in Table 1. The data show that the caloric content of the five genera are very similar.

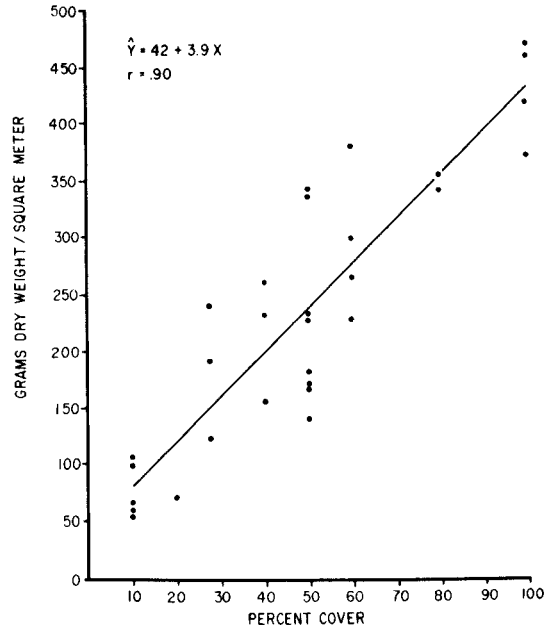

FIGURE 3.—Dry weight of a stand consisting of equal quantities of *Cymodocea serrulata* and *Syringodium isoetifolium* regressed on field estimates of plant cover. All data are from Khor Umaira and include only above-ground tissue.

For comparative purposes, the caloric content of five genera of sea grasses collected in various areas of the world and known to be eaten by green turtles there, are provided in Table 2. All of the samples from the South Pacific were burned according to the methods of Lieth (1968). It is likely that these values would be about 8% higher if independent ash determinations were made with a muffle furnace. Although green turtles were not actually seen feeding around Fulanga in the Lau Group of the Fiji Islands, leaves of *Halodule uninervis* collected in November 1970 around Fulanga registered 4.02 kcal/g dry wt, ash free when combusted by the Lieth (1968) method. *T. testudinum* around Grand Cayman Island is currently collected by a special underwater harvester and along with specially prepared food pellets is fed to captive green turtles in the turtle farm on Grand Cayman. Likewise, on some of the Tonga Islands, *Syringodium* and *Halodule* wrack washed up on the strand in large quantities after storms is fed to captive turtles kept in kraals. The findings reported in Tables 1 and 2 show that the caloric content of leaves of various kinds of sea grass are similar despite the fact the samples were collected at different times of the year and at widely scattered places. However, some interarea differences are evident in that the energy content of tissue of five genera from the Gulf of Aden (Table 1) averaged about 0.15 kcal/g dry wt, ash free, higher than the four genera from the South Pacific (Table 2) as measured by the Lieth method.

The caloric content of sea grasses reported in this paper are very similar to the value of 4.41 kcal/g dry wt, ash free reported for *Phyllospadix scouleri* by Paine and Vadas (1969). The caloric values are also similar to some of the benthic marine algae collected off the coast of the State of Washington where the modal values of green, red, and brown algae were respectively, 4.90, 4.75, and 4.45 kcal/g dry wt, ash free (Paine and Vadas, 1969). For 32 samples of aquatic monocotyledons, Cummins and Wuycheck (1971) give a mean of 4.77 kcal/g dry wt, ash free and for 359 samples of aquatic algae they list a mean of 4.63 kcal/g dry wt, ash free, but none of their samples were sea grasses.

The number of calories in the standing crop of sea grasses at Khor Umaira can be estimated by referring to the regression lines in Figures 2 and 3. For example, assuming that leaves of *C. serrulata* represent 3.01 kcal/g dry wt (Table 1) then a pasture with, say, 50% cover contains about 453 kcal/m^2 (Figure 2).

There are extensive sea grass pastures in some shallow coastal waters (for distribution see den Hartog, 1970) but before turtle ranching can become a reality, studies are needed on the energy provided by epiphytes and animal prey. It is likely that green turtles obtain some nutritional value from the epiphytic organisms on the sea grass leaves. Allen (1971) has provided detailed information on the energetics of epiphytic algae and bacteria in a lake ecosystem. Further, the digestive processes of green turtles ought to be examined in relation to the protein content of sea grasses and other food. Occasionally, it has been observed that

TABLE 1.—Caloric values of sea grasses (leaves only) at Khor Umaira. The plants were collected on 28, 29, and 30 July 1972.

Species	kcal/g dry wt	Ash %	kcal/g dry wt, ash free[1]
Halophila ovalis	3.07	33	4.58 (4.21)
Cymodocea serrulata	3.01	34	4.56 (4.19)
Halodule uninervis	3.09	32	4.54 (4.23)
Syringodium isoetifolium	3.12	33	4.66 (4.29)
Thalassodendron ciliatum	3.11	33	4.64 (4.27)

[1] Caloric values in parentheses were obtained using methods of Lieth (1968). The corresponding ash free caloric values are based on independent ash determinations; see text for explana-

TABLE 2.—Caloric values of sea grasses (leaves only).

Species	Local name	Locality	Date collected	kcal/g dry wt, ash free[1]
Halodule wrightii	Sigret	Masirah Isl., Arabian Sea	15 June 1972	4.54 (4.13)
Halophila ovalis	Sigret	Masirah Isl., Arabian Sea	15 June 1972	4.51 (4.10)
Thalassia testudinum	Turtle grass	Grand Cayman Isl., Caribbean Sea	24 May 1972	4.59 (4.24)
Halodule uninervis	Herbe á tortue	Noumea, New Caledonia	25 Nov. 1970	(4.07)
Cymodocea serrulata	Herbe á tortue	Noumea, New Caledonia	25 Nov. 1970	(4.09)
Halophila ovalis	Vutia	Suva, Fiji Isl.	10 Nov. 1970	(4.07)
Syringodium isoetifolium	Vutia	Suva, Fiji Isl.	10 Nov. 1970	(4.10)
Halodule uninervis	Limu	Nukualofa, Tonga Isl.	24 Oct. 1970	(4.07)
Syringodium isoetifolium	Limu	Nukualofa, Tonga Isl.	24 Oct. 1970	(4.11)

[1] Caloric values in parentheses were obtained using methods of Lieth (1968). The other three caloric values are based on independent ash determinations: see text for explanation.

adult green turtles have eaten invertebrates (viz. crustacea, snails, jellyfish, sponges). The importance of these animals to the nutrition of green turtles has yet to be determined. Studies on the effect of different intensities of turtle grazing on the sea grass community are also needed, especially if under high grazing pressure the entire plant is pulled up. In regards to the regrowth of sea grass, Phillips (1960) has demonstrated that *T. testudinum* off the Florida coast will regrow to normal height in about 3 mo after being cut to ground level. Taylor, Saloman and Prest (1973) have recently shown that *T. testudinum* suffered no damage when the leaves were harvested twice during a 6 mo growing season in Tampa Bay, Fla., and they postulated that in deeper or warmer waters where the growing season is protracted three or more cuttings per year may be possible.

ACKNOWLEDGMENTS

We gratefully acknowledge the following scientists for aid in identification of plants: John Parham (Agriculture Department, Suva), Maxwell Doty (University of Hawaii) and C. den Hartog (Rijksherbarium, Leiden). Robert Stone and Val Hinds helped Hirth collect plants in the South Pacific and Khazed Hariri provided logistic support in Aden. We are indebted to Stan Hollingworth for analyses of water samples under monsoon conditions at Khor Umaira. We thank Joseph Branham and David Gillespie for their helpful comments during the preparation of this paper.

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NOTES

FOSSIL TREE STUMPS FOUND IN SITU ON SUBMERGED RIDGE AT AMCHITKA ISLAND, ALASKA[1]

Two ancient tree stumps, in situ and partially embedded in bedrock, were found at a depth of 23 m off the Bering Sea coast of Amchitka Island in the western Aleutians. The stumps were found by the authors in October 1972 approximately 1.1 km north-northwest of Banjo Point (Figure 1) during underwater surveys of physical and biological damage associated with recent nuclear testing on Amchitka.

The two stumps were located at the base of a narrow ridge of bedrock which is over 100 m in length, rises abruptly from a generally level bedrock bottom at a depth of about 23 m, and is oriented approximately normal to the adjacent coastline. The height and thickness of the ridge range from about 4 to 8 m, and its clifflike faces are nearly vertical. This ridge is thought to be an abandoned erosional sea stack related to a brief stillstand of sea level during Pleistocene time at about 20 to 30 m below present sea level (L. M. Gard, U.S. Geological Survey, Denver, CO 80225, pers. comm.).

Each of the stumps is about 1 m high and seems to have a trunk diameter of about 30 to 40 cm. The one stump that was studied in detail is located in a slight recess at the base of the west face of the ridge (Figure 2). The base of the stump is at the level of the generally horizontal bedrock sea floor which extends westward from the ridge; at this place the ridge face is 8 m high. The stump itself is mostly surrounded by undisturbed bedrock (Figures 3, 4). With the exception of lower root extremities which extend outward several centimeters from the base of the cliff and disappear into the adjacent horizontal substrate, the stump is flush with or slightly recessed into the cliff face.

Directly above the stump in the roof of the rock recess is a vertical cylindrical hole about 20 cm in diameter and depth. The existence of a small diameter opening extending upward through the rock was indicated by a stream of fine air bubbles escaping from the cliff face about 4 m above the stump. The air was from the divers' exhalations that had become trapped in the hole above the stump. It appears that the stump had originally been totally encased in bedrock but was then partly exposed as the cliff face eroded away. The hole above the stump may once have contained a higher portion of the tree trunk, but the wood within the hole disintegrated, leaving the cavity in the rock.

Additional wood material was found in the immediate vicinity of the stump. On the horizontal bedrock sea floor within 2 to 5 m from the

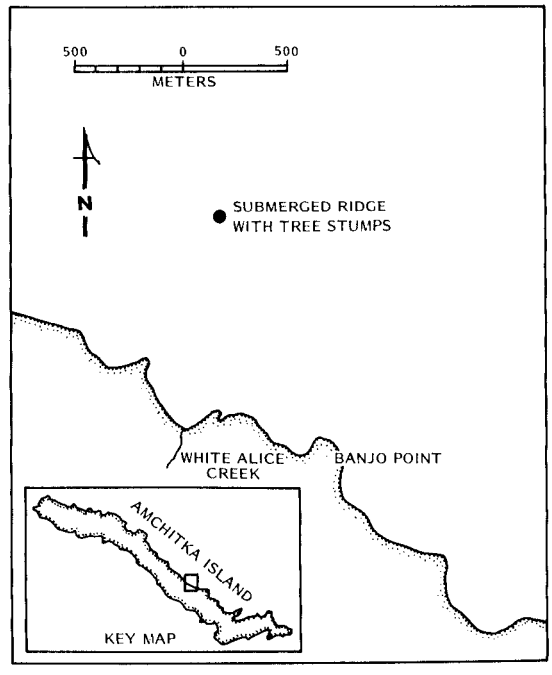

FIGURE 1.—Location of submerged ridge with in situ tree stumps in relation to the adjacent shoreline of Amchitka Island, Alaska.

[1] This work was supported by the U.S. Atomic Energy Commission as a part of its Amchitka Bioenvironmental Program.

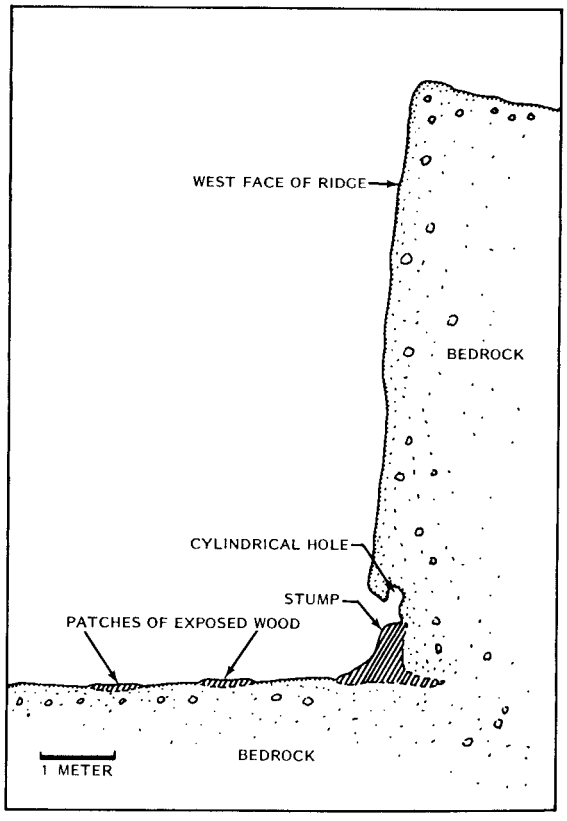

FIGURE 2.—Diagram showing approximate position of stump in relation to surrounding substrate features.

stump, several small areas of wood adhere tightly to or are partly encased in the bottom. The appearance and texture of this wood is similar to that of the stump, except that these small patches are worn down with upper surfaces flattened and generally conforming to the shape of the underlying bedrock. Although no direct connections were traced between these wood patches and the stump, their proximity and positions in relation to the stump suggest that they may be remnants of roots of the same tree. Probably buried in the substrate during the tree's life, the root remnants have now been exposed by the gradual eroding away of the rock in which they were encased.

Small samples of wood were collected from each stump. The wood is very dark brown in color and quite soft when wet but appears to be at least partially coalified. Pieces can easily be broken off or dug out with a knife. When dried, the wood becomes harder and more brittle and tends to distort and check. A sample of the wood was identified[2] as being from a coniferous tree, but further identification was not possible because the features necessary for generic identification had been removed by long-time hydrolysis.

A sample of the wood was submitted for radiocarbon dating. The indicated age of the wood exceeded 40,000 yr, the age limit of the C-14 technique of the laboratory[3] performing the analysis.

[2]Microscopic examination and identification was done by B. F. Kukachka, Center for Wood Anatomy Research, U. S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI 53705.

[3]Radiocarbon dating was done by Teledyne Isotopes, Westwood, NJ 07675.

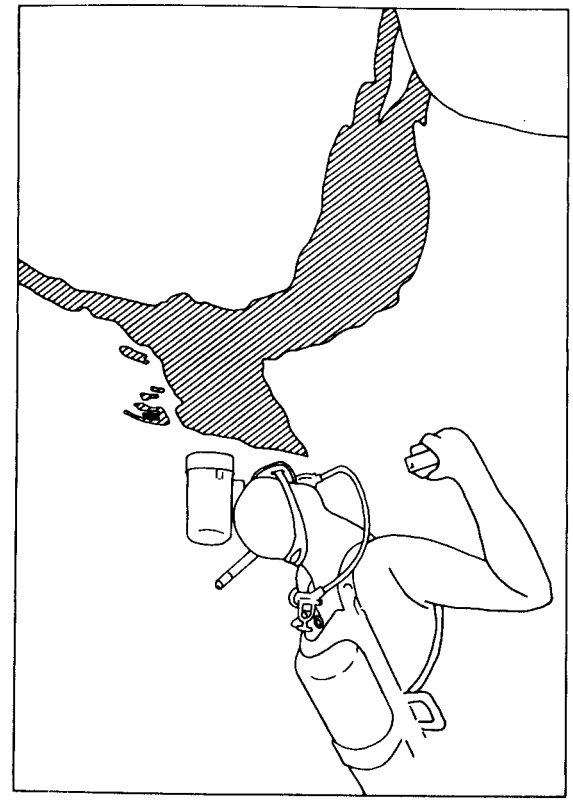

FIGURE 3.—Diagram indicating exposed wood (cross hatching) of the stump shown in the photograph of Figure 4.

FIGURE 4.—Outcrop of in situ stump at 23 m depth. Note texture of the volcanic mudflow deposit above the stump.

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The exposed parts of the stumps were partially encrusted with living organisms such as coralline algae, bryozoans, and sponges, but much of the exposed wood surface was barren of organisms. There was no visible evidence of any biological degradation of the wood, that is, no borer holes or indication of decay. The surfaces of the wood appeared to be shaped principally by mechanical weathering or erosion. Unlike new wood exposed in a marine environment, the wood of the stumps appears to have been immune to the usual attacks of wood-boring organisms. During the period of total encasement in the rock substrate, the wood probably underwent chemical changes that resulted in immunity to biodegradation.

As stated earlier and as shown in Figure 4, the substrate in direct contact with the stumps was undisturbed bedrock. Rock samples we obtained from fresh rockfalls along the cliff face containing the stumps were identified as coming from volcanic breccia of the Chitka Point Formation of the Miocene age (L. M. Gard, pers. comm.). The Chitka Point Formation is composed of subaerial lava flows, breccias, tuffs, and conglomerates derived from a volcano which must have been located on western Amchitka and eastern Rat Islands (Carr et al., 1971; L. M. Gard, pers. comm.). Potassium-argon dates obtained on lavas of the upper part of the Chitka Point Formation indicated an age of at least 12.4 ± 1.1 million yr (Carr et al., 1971).

Amchitka and all of the Aleutian Islands are now devoid of naturally occurring trees. Evidence that trees once grew on Amchitka does exist, however. During Miocene time, trees and other carbonaceous material were often incorporated into volcanic mudflows and debris flows of the Chitka Point Formation, as evident by the presence of this material in many of the outcrops of breccias, tuffs, and conglomerates along the Bering coast of Amchitka (Powers, Coats, and Nelson, 1960; L. M. Gard, pers. comm.).

The significance of the tree stumps reported in this paper derives from their in situ location 23 m below present sea level. Because of the offshore and submerged location of these stumps, they represent a time when the island was not only forested but larger and at least 23 m higher in relation to sea level.

Acknowledgments

L. M. Gard, Geologist, U.S. Geological Survey, assisted by supplying background information on the geologic history of Amchitka Island and by reviewing a draft of this manuscript for accuracy and aptness of interpretation. Theodore R. Merrell, Jr. assisted in the fieldwork and in the preparation of this report.

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ESTIMATION OF RATES OF TAG SHEDDING BY NORTHWEST ATLANTIC BLUEFIN TUNA[1]

A joint experiment was initiated by the Fisheries Research Board of Canada (FRBC), the National Marine Fisheries Service, and the Woods Hole Oceanographic Institution (WHOI) in 1971 under the leadership of F. Mather to estimate the rates of tag shedding by bluefin tuna. Five hundred and eighty bluefin tuna were double tagged with one of four types of dart tags off the east coast of the U.S. during the 1971 fishing season. Two types of darts, metal and plastic, were used and tags supplied by FRBC were slightly different from tags supplied by WHOI. Tags and tagging procedures

[1] Contribution No. 3010, Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

TABLE 1.—Tag releases and returns from east coast of U.S. bluefin tuna double tag study.

Agency and tag type	1971 Double tag releases	1971 First year returns			1972 Second year returns		
		n_{dd1}	n_{ds1}	t_1 (days)	n_{dd2}	n_{ds2}	t_2 (days)
FRBC							
Plastic dart	140	16	1	24.4	7	8	369.8
Metal dart	128	9	1	19.4	9	11	376.0
WHOI							
Plastic dart	150	4	0	7.2	20	9	349.9
Metal dart	162	4	1	18.6	10	9	371.1
Total							
Plastic dart	290	20	1	19.8	27	17	357.3
Metal dart	290	13	2	19.1	19	20	373.7
Total	580	33	3	19.5	46	37	364.7

were those described by the Food and Agriculture Organization (1972). The 1971 releases and returns in 1971 and 1972 are shown in Table 1 by tagging agency and dart type.

The notation and methodology in this study follows Bayliff and Mobrand (1972):

$$n_{ddk} = F\tau N_D \pi\rho^2 e^{-(F + X + 2L)t_k}$$

$$n_{dsk} = F\tau N_D \pi\rho (1 - \rho e^{-Lt_k}) e^{-(F + X + L)t_k}$$

where:

t_k = time at the middle of the kth period of length τ (k = 1, 2),

n_{ddk} = number of returns of double-tagged fish retaining both tags during the period centered at t_k,

n_{dsk} = number of returns of double-tagged fish retaining only one tag during the period entered at t_k,

N_D = number of fish released with double tags,

π = portion of tagged fish which remain alive after the Type-I (immediate) mortality has taken place,

ρ = portion of the tags which are retained after Type-I (immediate) shedding has taken place,

F = instantaneous rate of fishing mortality,

X = instantaneous rate of other mortality (other includes natural mortality, Type-II (long-term) tagging mortality and apparent mortality caused by migration from the fishery), and

L = instantaneous rate of shedding of tags.

Bayliff and Mobrand showed that

$$\ln \frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = -Lt_k + \ln\rho = Y_k$$

where Y_k is an estimate of the log of the proportion of tags retained up to time t_k.

Estimates of Y_k are shown in Table 2. Estimates of L and ρ are shown in Table 3. Although some differences among categories are indicated, a chi square test for differences in returns among categories was not significant at the 90% level of confidence. Thus the differences do not appear to be large enough to rule out the use of

TABLE 2.—Intermediate results in estimates of shedding rates from 1971 U.S. east coast bluefin double tag study.

Agency and tag type	Y_1	Y_2
FRBC		
Plastic dart	-0.03077	-0.45199
Metal dart	-0.05407	-0.47692
WHOI		
Plastic dart	0	-0.20294
Metal dart	-0.11778	-0.37156
Total		
Plastic dart	-0.02469	-0.27370
Metal dart	-0.07411	-0.42286
Total	-0.04445	-0.33802

TABLE 3.—Estimates of ρ and L from 1971 U.S. east coast bluefin double tagging study.

Agency and tag type	$\ln\rho$	L on daily basis	ρ	L (on annual basis)
FRBC				
Plastic dart	-0.00102	0.0012195	0.999	0.44512
Metal dart	-0.03106	0.0011858	0.969	0.43282
WHOI				
Plastic dart	0.00426	0.0005922	1.004	0.21615
Metal dart	-0.10439	0.0007199	0.901	0.26278
Total				
Plastic dart	-0.01008	0.0007378	0.990	0.26929
Metal dart	-0.05532	0.0009835	0.946	0.35898
Total	-0.02787	0.0008504	0.973	0.31041

the estimates obtained from the combined data. These estimates of $\rho = 0.973$ and $L = 0.31041$ are close to the estimates of Bayliff and Mobrand (1972) of $\rho = 0.913$ and $L = 0.278$ for yellowfin tuna in the eastern Pacific.

Acknowledgments

We thank Drs. W. H. Bayliff of the Inter-American Tropical Tuna Commission and W. W. Fox, Jr. of the Southwest Fisheries Center for reviewing an early version of the note, and Mr. D. C. Simmons of the Southeast Fisheries Center for providing his able assistance during the tagging work.

We also thank the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce for grant number GH-82, as well as A. Minis, Jr., P. A. B. Widener, the Charles W. Brown, Jr. Memorial Foundation, the Sport Fishing Institute, the U.S. Atlantic Tuna Tournament, Inc., the Associates of the Woods Hole Oceanographic Institution and several other individual sport fishermen and sport fishing organizations for their generous support which made the Woods Hole Oceanographic Institution's participation in this work possible.

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DISTRIBUTION AND ABUNDANCE OF THE SAND DOLLAR, *DENDRASTER EXCENTRICUS*, OFF THE COAST OF OREGON AND WASHINGTON

Dendraster excentricus is one of two known species of Clypeasteroid echinoids occurring along the Pacific coast of North America from British Columbia southward to Mexico. It lives on sandy bottoms from the low water zone to a depth of about 90 m[1] (Raup, 1956). Large beds of these animals have been reported in southern Puget Sound, Monterey Bay, Newport Bay, San Diego Bay, and El Estero de Punta Banda — just south of Ensenada, Mexico (Ricketts and Calvin, 1952). Merrill and Hobson (1970) made detailed observations on the behavior, distribution, and biotic relationships of *D. excentricus* along the Pacific coast of California and Baja California, Mexico. They remarked that relatively little was known about the populations of sand dollars along the exposed outer

[1] Richard J. Merrill, Department of Biological Sciences, University of California, believes this is too deep for *D. excentricus* and may refer to *D. laevis* (pers. comm.).

coast northward from Point Conception, Calif. The report presents new information on the distribution and abundance of sand dollars along the coast of Oregon and Washington.

Materials and Methods

The Seattle-based research vessel *John N. Cobb* of the National Marine Fisheries Service took large numbers of *D. excentricus* while dredging during two clam surveys along the Washington and Oregon coast in the summer of 1969. The dredge used during the surveys was an east coast type hydraulic clam dredge (Figure 1) which weighed approximately 1,021 kg (2,250 lb) and had a blade 91.4 cm (36 inches) wide with a maximum digging depth of 35.6 cm (14 inches). Each dredge haul was of 10 min duration, made from north to south, and covered an average distance of 0.56 km (0.3 nautical mile). The bottom area "swept" by each haul was approximately 508 m^2 (5,472 ft^2). Hauls were made only on sandy bottom areas believed to be free of rocks.

The first survey was conducted in June along the Washington coast between Cape Flattery and the Columbia River. Forty-six hauls were made: 9 at 9-11 m, 15 at 13-15 m, 8 at 16-18 m,

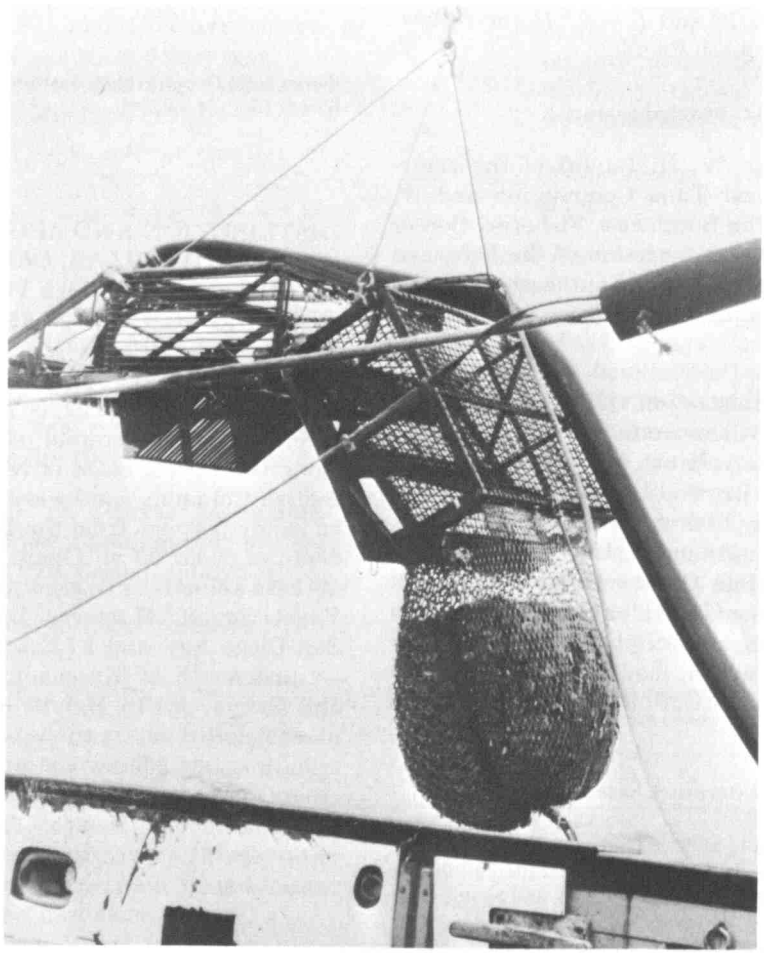

FIGURE 1.—A modified east coast type hydraulic clam dredge with a catch of over 1,000 lb of sand dollars being lifted board the RV *John N. Cobb*.

TABLE 1.—Average sand dollar catches off the Washington coast in kilograms per 10-min dredge haul and density (number of sand dollars) per square meter of bottom area. The catches are the total catch at each station, divided by the number of hauls shown in parentheses.

Sampling area (Lat)[1]	Catch, by sampling depth									
	9-11 m		13-15 m		16-18 m		24-27 m		29-37 m	
	Avg. catch (kg)	Avg. density (no./m^2)	Avg. catch (kg)	Avg. density (no./m^2)	Avg. catch (kg)	Avg. density (no./m^2)	Avg. catch (kg)	Avg. density (no./m^2)	Avg. catch (kg)	Avg. density (no./m^2)
46°23.0′N	—[2]	—	0 (6)	0.0	0 (2)	0.0	—	—	—	—
46°34.5′N	408 (3)	26.7	11 (1)	0.7	0 (1)	0.0	—	—	—	—
46°51.0′N	—	—	95 (2)	6.2	—	—	—	—	—	—
47°00.0′N	121 (1)	7.9	—	—	0 (1)	0.0	0 (1)	0.0	0 (1)	0.0
47°05.0′N	378 (2)	24.8	404 (3)	26.4	<1 (1)	0.0	—	—	—	—
47°34.0′N	<1 (3)	0.0	0 (3)	0.0	0 (3)	0.0	—	—	—	—
47°45.0′N	—	—	—	—	—	—	0 (5)	0.0	—	—
48°15.5′N	—	—	—	—	—	—	—	—	0 (7)	0.0
Total averages	234 (9)	15.3	94 (15)	6.2	<1 (8)	0.0	0 (6)	0.0	0 (8)	0.0

[1]Approximate midpoint of hauls.
[2]Dashes (—) indicate that no haul was made at the station.

TABLE 2.—Sand dollar catches off the Oregon coast in kilograms per 10-min dredge haul and density (number of sand dollars) per square meter, September 1969.

Sampling area		Catch, by sampling depth									
		9 m		14 m		18 m		23 m		27 m	
Lattitude[1]	Coastal landmark	Catch (kg)	Density (no./m²)	Catch (kg)	Density (no./m²)	Catch (kg)	Density (no./m²)	Catch (kg)	Density (no./m²)	Catch (kg)	Density (no./m²)
43°25.7′N	Coos Bay	1,814[3 4]	118.9	603	39.6	363	23.8	0	0.0	0	0.0
43°27.3′N	—	0	0.0	0	0.0	499	32.7	0	0.0	0	0.0
43°31.1′N	—	—[2]	—	—	0.0	0	0.0	0	0.0	0	0.0
43°34.9′N	Ten Mile Cr.	102[3]	6.7	454[3]	29.8	454	29.8	907	59.4	0	0.0
43°37.9′N	—	0	0.0	91	5.9	0	0.0	1,179	77.3	680	44.6
43°42.9′N	Umpqua River	1,134[3]	74.3	1,270	83.2	14	0.9	4	0.3	0	0.0
43°47.0′N	Tahkenitch C.	113[3 4]	7.4	1	0.1	0	0.0	544	35.7	499	37.2
43°51.0′N	Siltcoos R.	567[3]	37.2	45	3.0	567	37.2	23	1.5	23	1.5
43°55.0′N	—	0	0.0	2	0.1	0	0.0	0	0.0	0	0.0
43°59.1′N	Siuslaw R.	1[3]	0.1	0	0.0	0	0.0	0	0.0	0	0.0
44°03.1′N	Sutton Cr.	1,134[3 4]	74.3	0	0.0	0	0.0	0	0.0	0	0.0
44°07.3′N	Hecata Hd.	—	—	—	—	0	0.0	0	0.0	0	0.0
44°11.3′N	Rocky Knoll	23[3]	1.5	<1	0.0	0	0.0	0	0.0	0	0.0
44°15.4′N	Gwynn Knoll	113[3 4]	7.4	2[3]	0.1	0	0.0	0	0.0	0	0.0
44°19.4′N	Yachats R.	363[3 4]	23.8	0	0.0	<1	0.0	<1	0.0	0	0.0
44°23.7′N	Alsea Bay	4[3]	0.3	2	0.1	1	0.1	0	0.0	0	0.0
44°27.7′N	Seal Rocks	—	—	0	0.0	—	—	0	0.0	0	0.0
Total averages		384	25.1	154	10.1	118	7.8	156	10.2	71	4.9

[1] Approximate midpoint of hauls.
[2] Dashes (—) indicate that no haul was made at the station.
[3] Live specimens, all others were dead (empty tests).
[4] Catches which were sampled for width measurements.

6 at 24-27 m, and 8 at 29-37 m. The second survey was conducted in September between Coos Bay and Newport, Oreg. Eighty hauls were made: 14 at 9 m, 16 at 14 m, 16 at 18 m, 17 at 23 m, and 17 at 27 m. The areas sampled were uniformly spaced along the coast, approximately 7.4 km (4 nautical miles) apart.

Sand dollar catches were weighed using a dynamometer on the first several hauls of each of the surveys. Weights of catches were estimated on the remaining hauls according to the portion of the cod end and dredge that was filled. During the Washington survey, which was largely involved with development of dredging techniques, no data were collected on the proportion of live and dead specimens. On the Oregon survey the incidence of live specimens and "empty tests" (dead specimens) in each haul was recorded. Also width measurements were made on five samples of live specimens taken at a depth of 9 m. Sample sizes varied from 136 to 310 individuals.

Results

Washington. — Nearly all the *D. excentricus* were taken in the two shallowest depth intervals — 9-10 and 13-15 m (Table 1). No sand dollars occurred in hauls made at depths greater than 18 m. The largest single catch, 1,209 kg (2,666 lb), occurred in a depth of 15 m off Ocean City (lat. 47°05.0′N), and catches of up to 454 kg (1,000 lb) were taken in 9-11 m just south of the Willapa Bay entrance (lat. 46°34.5′N). The average density in each of the above two sampling areas was over 26 sand dollars per m².[2]

Oregon. — There was a consistent pattern in the incidence of live and dead (empty test) sand dollars with increasing depth in Oregon waters — only live animals were taken in the shallower water and only dead animals were taken in the deeper water (Table 2). The largest catch

[2] All estimates of numbers of sand dollars from weight of specimens based on an average weight per specimen of 30 gm (15.1 specimens per lb).

(1,814 kg, or an estimated 60,400 specimens) was at 9 m and occurred near Coos Bay. The 14-m depth was an area of transition between living and dead sand dollars. Catches made at 18, 23, and 27 m were composed entirely of dead animals. At these depths, the largest catches along the coast occurred between Ten Mile Creek and Siltcoos River.

Mean widths of the five samples of live specimens ranged from 76.4 to 85.9 mm; the overall mean was 80.1 mm. The catches from which these samples were taken are marked with a footnote in Table 2.

Discussion

Merrill and Hobson (1970) reported that two types of distribution patterns occur in sand dollar populations along the protected outer coast. In one type, the populations run parallel to shore as dense bands and maintain a characteristic pattern that is reformed when disrupted by occasional heavy seas. The outer margin of these populations is well-defined in 4-12 m of water and here the largest individuals and greatest densities occur. The other type of distribution is similar, except that it extends into deeper water, below about 10-15 m; individuals become progressively smaller with depth.

These distribution patterns are apparently similar off the exposed outer coasts of Oregon and Washington. My findings off Oregon and Washington indicate well-defined seaward limits, as essentially no live *D. excentricus* were taken by the dredge at depths below 15 m.

McCauley and Carey (1967) collected *D. excentricus* off Oregon in depths of 8 to 56 m. They found the mean widths of specimens to be 78.2 mm at 8 to 13m, 35.8 mm at 22 m, and less than 10 mm at 50 m. They concluded that mean widths show a decrease in size with depth, suggesting that animals may move shoreward with increase in size or that in some way depth may influence growth. They apparently sampled both the near-shore and deeper water types of distribution patterns.

Merrill and Hobson (1970) speculated that available food for *D. excentricus* off the protected outer coast is most abundant just seaward of the breaker line, where the water is about 10 m deep, and that beyond this depth available food decreases with depth. Our dredge catches of the species off Oregon and Washington support the hypothesis that optimum conditions for *D. excentricus* exist inside the 15-m depth interval.

It is difficult to explain why large numbers of dead sand dollars were found primarily in the deeper depths sampled during our surveys (18-27 m). Merrill and Hobson (1970) found that at Zuma Beach, Calif. (a protected outer coast area) much of the sand dollar population in shallow water is swept or carried seaward during heavy seas, but when the sea is calm individuals in the seaward part of the colony move shoreward. This seaward movement during heavy seas may be even more extensive in populations in exposed outer coast areas off Oregon and Washington where storms are often more frequent and severe. Empty tests would be even more subject to wave action and currents than live specimens. During heavy seas they may be swept seaward where they accumulate.

My findings support earlier observations that *D. excentricus* is widely distributed and, in addition, is abundant in many sandy bottom areas within a depth of 15 m off the coast of Oregon and Washington.

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